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Catching the particles: role of ciliary bands in filter-feeding marine invertebrates

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ABSTRACT: Claus Nielsen (1938–2024) was an outstanding zoologist and world-wide recognised as an expert of especially ectoprocts (bryozoans) and entoprocts. Here, we describe the ciliary mechanisms of catching particles in these two groups based on our studies made together with Claus Nielsen. Our interdisciplinary collaboration was based on studies of anatomical structures, microscope-video observations and fluid-mechanical calculations. We first give an outline of downstream particle catch-up retention in entoprocts, and next, we describe particle upstream retention in bryozoans (ectoprocts).
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KEY WORDS: particle catch-up, entoprocts, bryozoans, ectoprocts, upstream retention, Claus Nielsen.

Захват пищевых частиц: роль ресничных шнуров в питании морских беспозвоночных-фильтраторов

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РЕЗЮМЕ: Клаус Нильсен (1938–2024) был, по-настоящему, выдающимся зоологом с широчайшим кругозором во всех областях зоологической науки, но с особым вниманием к внутрипорошицевым и мшанкам. В этой статье мы описываем ресничный механизм захвата пищевых частиц, который имеет место у представителей этих двух групп: внутрипорошицевыхи мшанок, на основе тех данных, которые были получены вместе с Клаусом Нильсеном. Наше междисциплинарное сотрудничество включало как изучение анатомии внутрипорошицевых и мшанок, так и микроскопические видеонаблюдения и механистические калькуляции. Мы приводим описание механизма “down-stream” фильтрации у внутрипорошицевых и “up stream” механизма фильтрации у мшанок.
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Devoted to memory of Claus Nielsen.

КЛЮЧЕВЫЕ СЛОВА: захват пищевых частиц, внутрипорошицевые, мшанки, “up stream” механизма фильтрации, Клаус Нильсен.

Preface

It clearly appears from the obituaries by Telford *et al.* (2024), Hay-Schmidt & Hoeg (2024), and Heinze & Technau (2024) that Claus Nielsen (1938–2024) was an outstanding zoologist with a world-wide recognition as an expert of marine invertebrates, especially within systematics of ectoprocts (bryozoans) and entoprocts. With an evolutionary angle of approach (Nielsen, 2012), he also studied embryology and swimming larvae of benthic invertebrates, their morphology and ciliary systems using SEM and TEM in an exquisite manner producing high-quality pictures. We have had a very fruitful collaboration with Claus Nielsen within especially ecto- and entoprocts, with special emphasis on ciliary particle-capture mechanisms as it appears from the present account.

Introduction

According to Jørgensen *et al.* (1984) two types of metazoan feeding by means of ciliary bands can be distinguished: In one type, suspended food particles are captured behind the water transporting band of cilia (ciliary downstream retention) as in for example sabellid polychaetes. In the other type, particles are captured in front of the water pumping band (ciliary upstream retention) as in for example bivalves. However, observed particle retention efficiencies and the capture mechanisms remained unaccountable, and Jørgensen *et al.* (1984) hypothesized that capture of particles was dependent on an unknown fluid mechanical principle where viscous forces are acting upon the particles in the zone of contact between two perpendicular ciliary currents. However, the capture mechanisms turned out to be more mechanistic. Thus, subsequent studies on ciliary upstream retention in mussels showed that beating lateral cilia pump water in between the gill filaments while particle capture is accomplished by the action of laterofrontal cirri transferring particles from the main water current to the frontal gill filament currents driven by frontal cilia, see review by Riisgård *et al*. (2015).

Inspired by the hypothesized fluid-mechanical capture of particles presented by Jørgensen *et al.* (1984), downstream collecting was subsequently studied in adults of the polychaete *Sabella penicillus* by Riisgård & Ivarsson (1990) and Mayer (1994, 2000). Here, the water was observed to be driven by the beating of compound latero-frontal cilia and particles were observed to be retained downstream in a surface current produced by the frontal cilia on the pinnules. But it remained unknown how a single band of compound cilia could both produce a water current and capture particles. However, in the late 1990-ies we explored the downstream retention in entoprocts and upstream retention in ectoprocts (bryozoans) in close cooperation with Claus Nielsen who was a world leading expert within these two animal groups. Our interdisciplinary collaboration was based on studies of anatomical structures, microscope-video observations and fluid-mechanical calculations.

Microscope-video observations of an entoproct (*Loxosoma pectinaricola*) showed that particles were accelerated with the water pumped by the compound lateral cilia and then caught up by the same compound cilia in their power strokes and pushed out of the main water current onto the frontal cilia (Riisgård *et al.*, 2000). This ‘catch-up principle’ (see Figs 1, 2) was also found to be in operation in ciliary filter-feeding polychaetes *Spirorbis tridentatus*, the cycliophore *Symbion pandora* (Riisgård *et al*., 2000), and in the polychaetes *Ditrupa arientina* and *Euchone papillosa* (Riisgård *et al*., 2002).

In another collaboration with Claus Nielsen, one of us (HUR) studied the tentacle structure and ciliary upstream retention in *Crisia eburnea* and other cyclostomatous bryozoans (Nielsen, Riisgård, 1998). We found that the bryozoan tentacle crown is a highly specialized pump- and filter system, where the particle capture mechanism is based on a close and sophisticated interaction between a sensory cilia-filter and a ciliary band, which drives a downwards flow of water towards the mouth (Nielsen, Riisgård, 1998; Larsen, Riisgård, 2002; Riisgård, Larsen, 2010).

Here, we describe the ciliary downstream and upstream retention based on our studies made together with Claus Nielsen, supplemented with a brief review of the more recent literature to evaluate the impact of our research collaboration. We have divided our contribution into two parts.

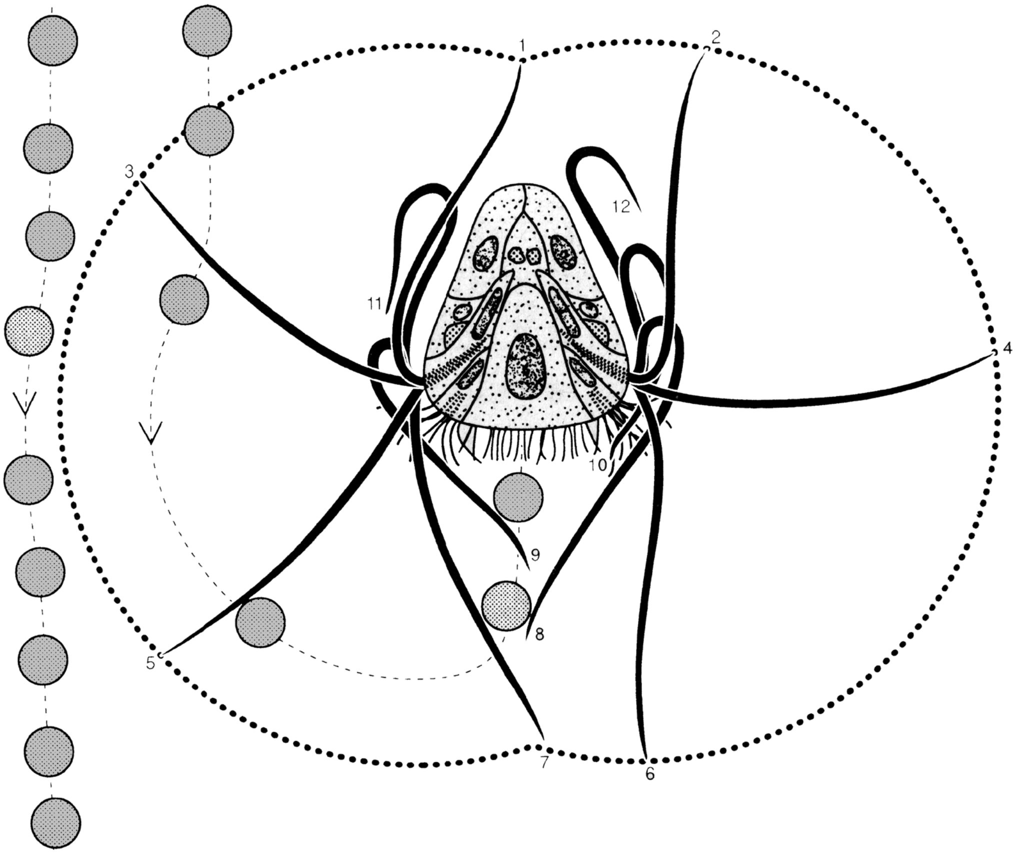

Fig. 1. Cross section of a *Loxosoma pectinaricola* tentacle showing how the compound lateral cilia catch up a particle, which becomes accelerated and transferred to the frontal side of the tentacle. The dotted line indicates the zone covered by the lateral cilia. Numbers give sequence of positions of beating compound lateral cilia: 1–7 — active stroke, 8–12 — recovery stroke. From Riisgård *et al*. (2000), with permission from Inter-Research Science Publisher.

The first part deals with downstream particle catch-up retention in entoprocts and other ciliary suspension feeders, the second part deals particle upstream retention in bryozoans (ectoprocts).

Downstream particle catch-up retention in entoprocts and other ciliary suspension feeders

The literature on ciliary downstream particle capture in suspension-feeding invertebrates has been reviewed by Riisgård & Larsen (2010), and therefore, only a brief description of the catch-up mechanism is given here, based on the entoproct *Loxosoma pectinaricola* studied by Riisgård *et al.* (2000). Parts of study was carried out at Kristineberg Marine Research Station, Sweden, where Claus Nielsen and HUR happened to be working at the same time. We had earlier worked together on upstream collecting in *Crisia eburnea* and other cyclostomatous bryozoans at the School of Biological Sciences, University of Wales (Nielsen, Riisgård, 1998). But now we wanted to study the particle-capture mechanism in the entoproct *L. pectinaricola*, which Claus Nielsen soon after obtained from the gills of the polychaete *Pectinaria belgica* dredged from a muddy bottom at 40 m depth in the nearby Gullmarsfjord.

Microscope video-observations of the paths and velocities of particles showed that suspended particles within reach of the tentacle crown of *Loxosoma pectinaricola* were accelerated with

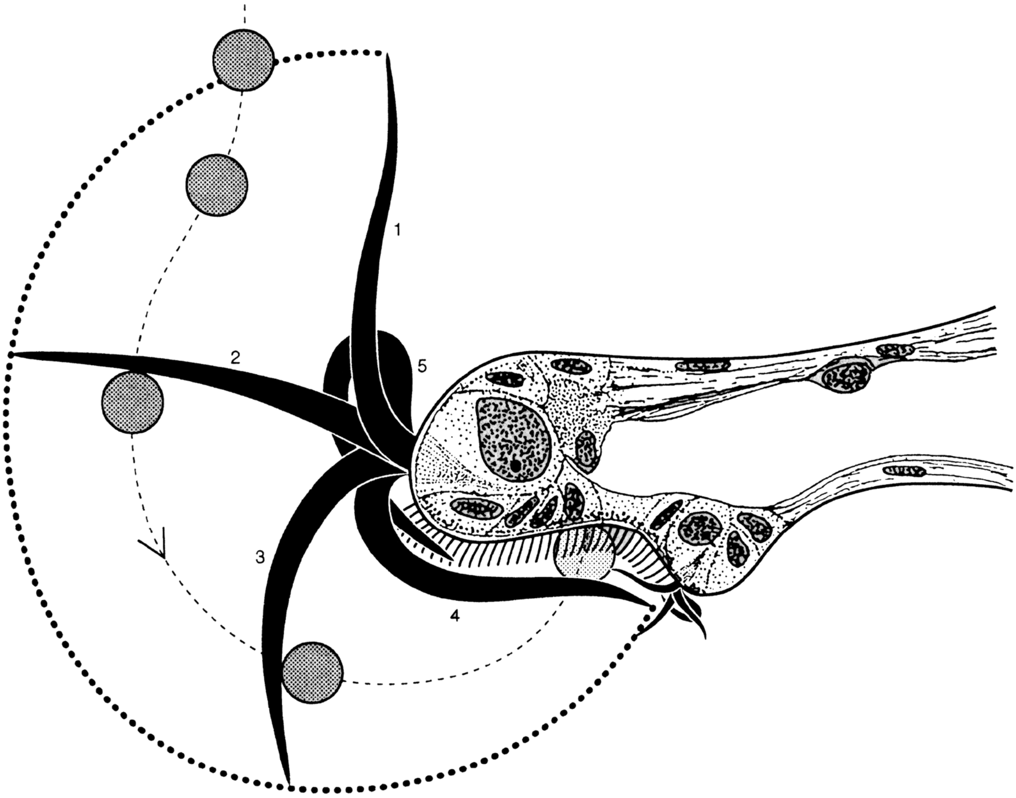

Fig. 2. Cross section of the velar edge of a gastropod showing the downstream-collecting ciliary system. The large compound cilia of the prototroch catch up with the particles in the water and push them into the adoral ciliary zone. Numbers give sequence of positions of beating compound lateral cilia: 1–4 — active stroke, 5 — recovery stroke. From Riisgård *et al.* (2000), with permission from Inter-Research Science Publisher.

the water that entered the region swept by the compound lateral cilia and then became caught up by these cilia in their power stroke (Figs 1, 2). Thus, in the power stroke the particle was pushed out of the water current which moved past the tentacle, and as the compound lateral cilia came to rest in their angular motion so did the particle and surrounding fluid. Subsequently, the frontal cilia carried the particle to the food groove and mouth. This downstream particle-capture mechanism was denoted the 'catch-up principle' (Riisgård *et al.*, 2000). The principle of particle catch-up as described for *L. pectinaricola* was subsequently found to apply also for the polychaete *Spirorbis tridentatus* and the cycliophore *Symbion pandora* (Riisgård *et al.*, 2000), in the polychaetes *Ditrupa arientina*, *Euchone papillosa* (Riisgård *et al.*, 2002), and *Fabricia stellaris* (Riisgård, Nielsen, 2006), but not in the polychaete *Sabellaria alveolata* where the tentacle crown is designed for passive filter feeding (Riisgård, Nielsen, 2006).

Based on fluid mechanical considerations and literature descriptions of structure and function of the ciliary bands of trochophore larvae of annelids, molluscs and rotifers it was concluded that the feeding mechanisms of these organisms are based on the catch-up principle (Riisgård *et al.*, 2000). Thus, the capture mechanism in all ciliary downstream collecting suspension-feeders is based on the same catch-up principle according to which compound cilia generate a flow with suspended particles that enter the ciliary region where the same cilia, during their power stroke, catch up with suspended particles and transfer them to a food grove, or a mouth cavity. In the particle-size retention spectrum, the lower size limit depends on the spacing between cilia that beat in phase, while the upper size limit depends on cilia length. The last phase of transfer may

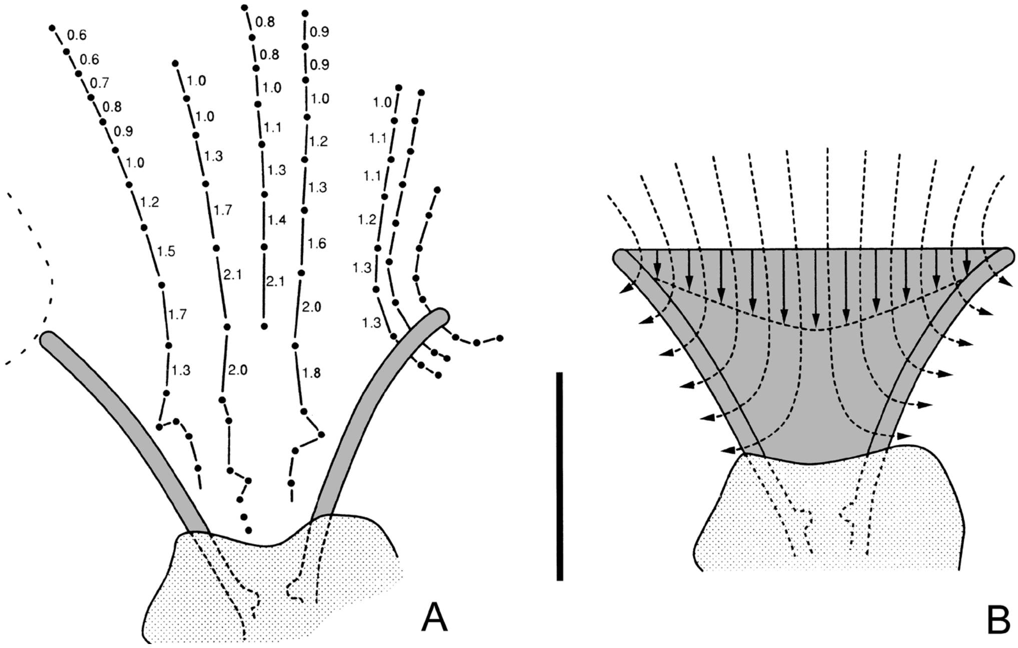

Fig. 3. Flow pattern in the region of the tentacle crown of the cyclostomate bryozoan *Crisia eburnea*. A — numbers give velocities (mm s^{-1}) of particles along flow lines, based on a time interval of 0.02 s between subsequent video frames; B — sketch of flow pattern (dotted lines) and velocity distribution of particles (arrows) in the entrance region where the maximum velocities of the incoming particles occur. Scale bar 100 µm. From Nielsen & Riisgård (1998), with permission from Inter-Research Science Publisher.

involve interaction with other cilia systems that prevent intercepted particles from escaping. In his well-received and accredited book on animal evolution Claus Nielsen subsequently suggested that the ciliary catch-up principle should be considered as a character in the classification of protostomes (Nielsen, 2012).

Among examples of studies by other authors related to the topic, here we mention Mayer (2001) who studied particle capture in *Sabella penicillus* by experiments and by numerical modelling. It was observed that most of the particles that approach pinnules are captured, even though the interpinnule channel is too wide (about 80 µm) for the two bands of 20 µm long compound latero-frontal cilia to fully cover the flow area during their effective stroke. This apparent paradox was explained by the computational model presented, which showed how cilia driven currents cause particle transfer towards tentacles.

Motivated by the "catch-up" mechanism for downstream particle capture, Ding & Katso (2015) proposed a computational discrete model system for particle capture by bands of synchronously and asynchronously beating cilia. In the capture strategies studied, the same cilia generate feeding currents and intercept, hence 'catch' particles when the particles are on the downstream side of the cilia, but only when cilia are at random phase, or in a metachronal wave. It was suggested that the findings may have "important implications on the design and use of biomimetic cilia" in for example micro-fluid sorting of particles.

Upstream particle retention in bryozoans (ectoprocts)

The tentacle structures and ciliary particle capture mechanisms in bryozoans have been studied thoroughly over many years (e.g. Riisgård, Manríquez, 1997; Nielsen, Riisgård, 1998) and reviewed by Larsen & Riisgård (2002). The lateral ciliary bands of the bryozoan tentacles produce feeding currents directed down into the tentacle crown (lophophore) and out between the tentacles (Figs 3, 4). The design of the

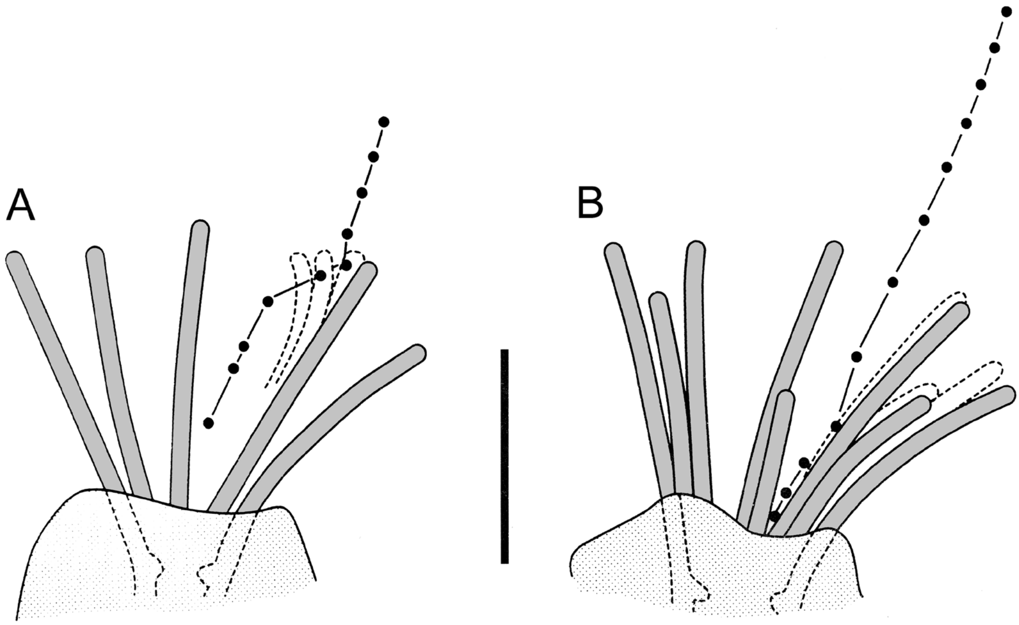

Fig. 4. Sketches of tentacle flicking in *Crisia ebunea* based on video-microscope pictures. A — illustration of individual flicking caused by a single particle capture on the distal part of a tentacle. The particle is trapped by the laterofrontal ciliary filter, and this provokes immediately a single individual tentacle flick which brings the particle into the central current and thus downwards in the direction of the mouth; B — a particle entering the tentacle crown close to the central current is trapped on the frontal side of the proximal part of a tentacle, and this triggers collective flicking of 3 or 4 of the nearest tentacles. Scale bar 100 µm. From Nielsen & Riisgård (1998), with permission from Inter-Research Science Publisher.

lophophore ensures a strong core-current directed straight towards the mouth. A row of sensory stiff laterofrontal cilia (Nielsen, Riisgård, 1998) is positioned upstream of this water-pumping band (Fig. 5). Particles in the currents are retained by the laterofrontal ciliary filter and subsequently either transferred to the frontal surface of the tentacles to be transported towards the mouth by means of the frontal cilia, or the particles are transferred to the core-current by means of inward tentacle flicks triggered by the drag force of the water current on the captured particles (Larsen, Riisgård, 2002).

Among examples of studies by other authors related to the topic, we will mention Pratt (2004) and Strathmann (2006). Most recent bryozoan species form encrusting sheets, and these colonies have densely packed feeding zooids. Pratt (2004) tested whether tight packing of feeding zooids affects food capture and found that ingestion rate increased when zooids were closest together, probably because this reduces refiltration. Qualitatively, this agrees with the calculated recirculation flow generated by an isolated zooid (Larsen, Riisgård, 2002, Fig. 10 therein). Particle capture has also been studied in cyphonautes larvae of a bryozoan, *Membranipora membranacea* (Strathmann, 2006) which revealed that adult and larval bryozoans use both ciliary sieving by laterofrontal cilia and a local induced change of beat of lateral cilia in the capture of particles. In addition, they use occasional laterofrontal cilia flicks to bring particles back into the inhalant chamber.

Epilogue (by HUR)

During my collaboration with Claus Nielsen, I learned to appreciate his enthusiasm and humour (Figs 6, 7). He was a meticulous perfectionist with his work, but he could also be spontaneous as it appears from the following closing story.

In 2005, the feeding mechanism of the polychaete *Sabellaria alveolata* was described by Dubois *et al.* (2005) who concluded that it is a suspension feeder that uses a ciliary system

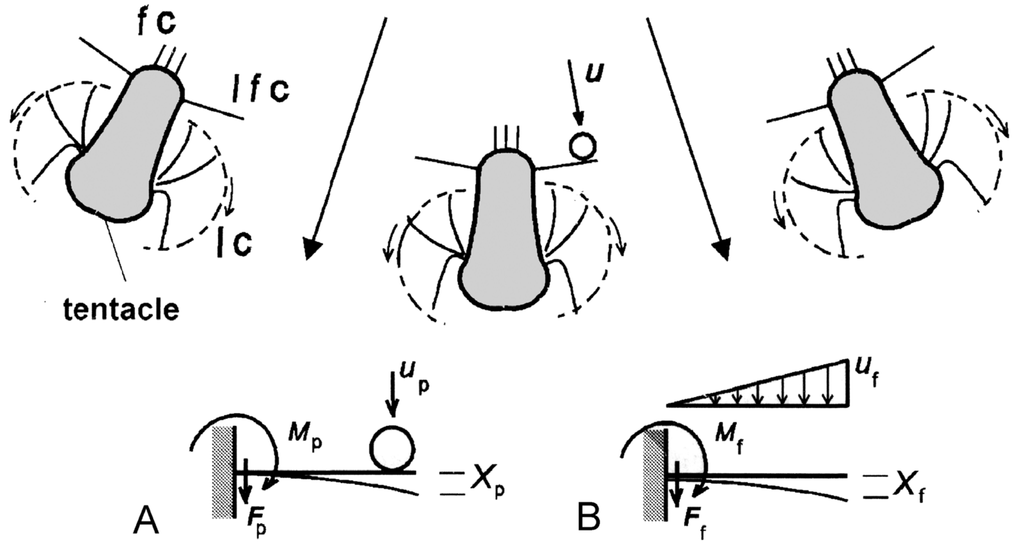

Fig. 5. Water pumping and ciliary sieving in bryozoans. (Upper) Cross section of three tentacles of a bryozoan tentacle crown (lophophore) with frontal cilia (fc), water pumping lateral cilia (lc), stiff laterofrontal cilia (lfc) acting as a mechanical sieve, and a stopped particle subject to downward water velocity *u*. (Lower) Laterofrontal cilium subject to load from (A) drag on particle (p) and (B) 'background' drag on cilium from water velocity (f), increasing linearly from root to tip, both giving rise to force *F*, bending moment *M* at point of fixation to tentacle, and deflection of cilium tip *X*. The stiff lfc are sensory (Nielsen, Riisgård, 1998) and the bending caused by a particle retained by the ciliary filter triggers a tentacle flicking. From Larsen & Riisgård (2002), with permission from ELSEVIER.

Fig. 6. During my (HUR) sabbatical stay at the School of Biological Sciences, University of Wales, Bangor, in 1997, Claus Nielsen came to work together with me on bryozoans. A — the photo shows Claus collecting macroalgae with bryozoans in the nearby Menai Strait where the difference between low and high tide is about 8 m giving excellent conditions for plenty species of bryozoans. Claus' enthusiasm was infectious and in all the rush he forgot his rubber boots, instead — as it appears from the photo — he just rapidly covered his shoes with two plastic bags! B — soon after in the laboratory in Bangor, Claus narcotized the collected bryozoans dissected the tentacle crowns out for subsequent scanning electron microscopy home in his laboratory at the Zoological Museum, University of Copenhagen, Denmark. Photo: HUR.

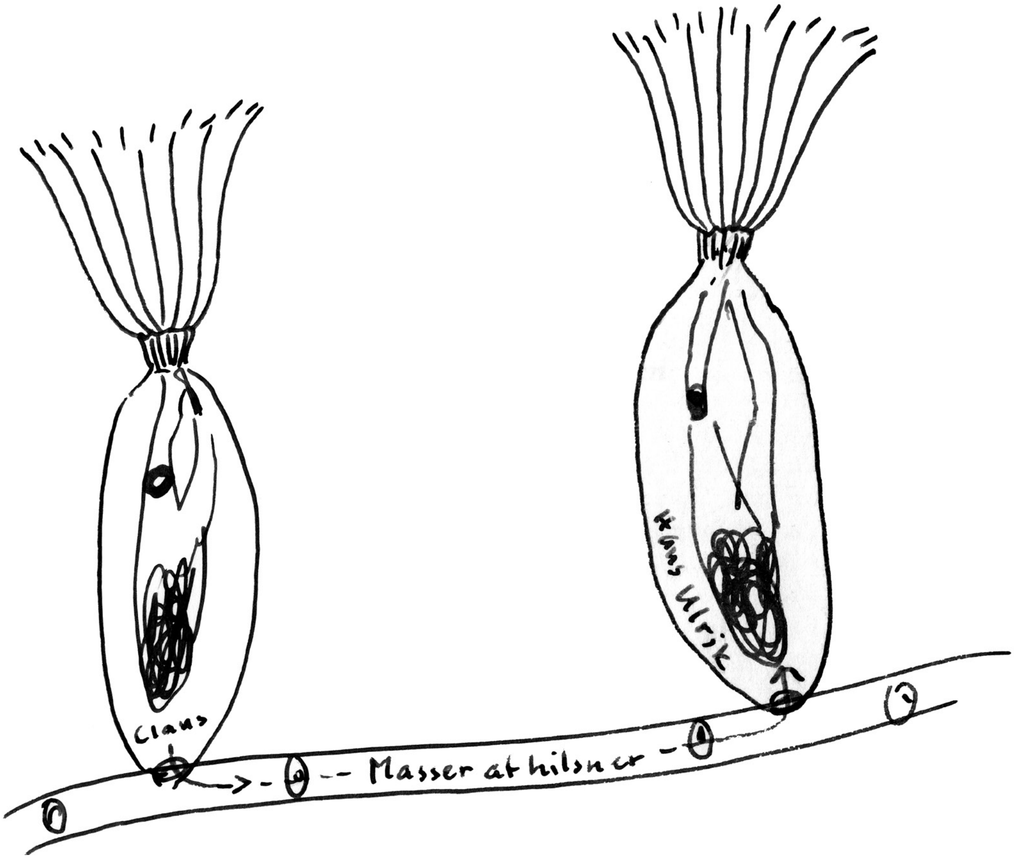

Fig. 7. Claus Nielsen was very good at making high-quality drawings and sketches for his publications (see e.g. Figs 1, 2). When I (HUR) bought the first edition of his renowned book "Animal evolution: interrelationships of the living phyla" in Bangor in 1997 I asked Claus during his visit to sign it. Within two minutes I got the book back with this drawing. Experts on bryozoans can easily see that it is two *Bowerbankia* individuals connected by a stolon carrying greetings from the left individual (Claus) to the right (Hans Ulrik). His fine, gentle and dry sense of humour was well-known and irresistible.

working alternately as a downstream- and an upstream-collecting system. But Claus Nielsen and I did not find the documentation convincing, and we decided to re-investigate the feeding mechanism. Therefore, Claus spontaneously telephoned his friends at the Station Biologique, Roscoff, France, where he often worked, and ordered blocks of tubes of *S. alveolata*. Soon after to my surprise, a post-service car one morning delivered a big box with worm-tube blocks to my laboratory at the Marine Biological Research Centre, Kerteminde, Denmark, where Claus and I soon after made video-microscope observations. The videos along with SEM and TEM of the ciliated epithelia clearly showed that *S. alveolata*'s tentacle crown is designed only for passive suspension feeding (Riisgård, Nielsen, 2006). However, the blocks from Roscoff also contained associated specimens of the polychaete *Fabricia stellaris*, which we showed has a ciliary feeding system based on the particle catch-up principle (Riisgård, Nielsen, 2006, fig. 14 and video clip #3 therein). During our cooperation in Kerteminde, we also used the opportunity to study particle capture in the tentacle crown of the bryozoan *Electra pilosa* using a new inverted microscope equipped with a high-speed camera. This resulted in some good video-observations of the particle capture, which however, we never published. Therefore, it seems appropriate to publish the video clips along with this closing story (Supplementary videos).

Supplementary videos

Video-microscope observations of particle capture in the tentacle crown of the bryozoan *Electra pilosa* were made by means of an inverted microscope (Leica DM IRB) equipped with a high-speed digital camera (CMOS camera MC13xx, recording 280 frames s^{-1}) connected to a computer. The bryozoan was placed in an observation chamber on the inverted microscope and particles (6 µm diameter algal cells, *Rhodomonas salina*) were added to the water in the observation chamber. The recordings were made during the study by Riisgård & Nielsen (2006), but never published.

Video clip #1 shows a particle capture and its downward transport in the tentacle crown of *Electra pilosa*. A particle which enters the outer region of the water-pumping tentacle crown, is stopped by stiff laterofrontal cilia on the distal part of a tentacle. This triggers the tentacle to flick, which brings the particle back into the central core flow and further down towards the mouth. However, it is captured again deeper down in the tentacle crown, but this does not trigger a noticeable tentacle flick, rather a quick displacement, possibly by cilia action, which brings the particle back into the central current to be eventually sucked into the mouth

Video clip #2 shows the capture of a particle by a tentacle in *Electra pilosa*. The particle enters the tentacle crown but is stopped by contact with a tentacle and this triggers the tentacle to flick so that the particle is pushed back into the downward central current and brought towards the mouth.

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