Historical review on individual autozooidal behaviour and feeding mechanisms in Bryozoa

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1. Introduction

During our studies on bryozoan autozooidal behaviour[1,2] we, following Winston, realized that 'the 19th [as well as 18th] century knowledge of individual (polypide) behaviour was never codified'.[3] This negligence in respect to the work of the old authors led to two main consequences. Firstly, the names of many brilliant naturalists, whose observations and detailed descriptions were, as a rule, perfect and whose results are the basement of modern knowledge, were either undeservedly forgotten or mentioned only in passing. Secondly, 'double work' was carried out since many of previously recorded phenomena and structures were newly redescribed, which is intimately connected with the problem of scientific priority. So, this paper was written with the aim to correct the situation in question at least partially. We present a historical survey on the development of views on individual autozooidal behaviour and feeding mechanisms in Bryozoa, with the emphasis on the priority in the recording of one or other type of activities and feeding/sensory structures.

2. Eighteenth century studies

The first description of bryozoan behaviour was given by Abraham Trembley,[4] who

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observed the phylactolaemate bryozoan *Lophophus*[5] in 1741. A brief summary of Trembley's notes was published first by Henry Baker,[6] who later made and published his own observations of phylactolaemates.[7] They both observed polypide protrusion and retraction, water currents carrying small animals into the lophophore, various movements of the lophophore and tentacles connected with both feeding and particle rejection (for instance, Trembley recorded tentacle flicks, lophophore expansion, accompanying the particle rejection, and particle transference along the oral grooves of lophophore), and defecation. Trembley[8] and later Baker attributed movements of water within and around the lophophore only to the perpetual swinging or 'vibrating motion' of the tentacles.[9] In contrast to Trembley, who believed that the tentacles did not touch the particles and bent inside the lophophore in order to create turbulent currents, Baker described particle capture by tentacles when these particles had escaped from the feeding current. Judging from the description, he was the first who recorded this kind of feeding by tentacular flicks when the previous mechanical contact between tentacle and particle was absent.[10] August Rösel von Rosenhof also worked on phylactolaemates and correctly remarked that during production of currents the tentacles were often motionless.[11] He supposed that the currents were produced by a stream issuing from the contracting mouth.

John Ellis was apparently the first to publish descriptions and drawings of living marine bryozoans, briefly mentioning that he saw their feeding and polypide excursions.[12] Leendert Bomme encountered cilia on the tentacles in freshwater as well as marine bryozoans and connected 'a strong whirlpool, sucking all nearby objects to the animal into its stomach' with the ciliary activity 'permanent movement from down upwards, across the tip, and downwards again'.[13] It should be noticed that Bomme was the first to record the travel of the ciliary movements over the tentacle tips in phylactolaemates. He criticized the inferences of Trembley,[14] but since Bomme's brief report was apparently little known at that time, some later investigators neglected it and followed Trembley's opinion (for example, Lazzaro Spallanzani).[15] Filippo Cavolini[16] was criticized by Lucien Joliet[17] for attributing the water currents to permanent tentacle movements, mainly because he did not recognize the tentacular cilia. However, precise examination of Cavolini's text shows that though he connected the lophophore with the origination of currents and often mentioned that 'tentacoli perpetuamente oscillano', he never wrote that their movements created these currents.[18] Cavolini gave the most detailed descriptions of marine bryozoan feeding in the 18th century, recording some behavioural reactions (pharyngeal rejection, single expansion of lophophore, bending of a single or 2-3 tentacles deep inside the lophophore, waving tentacular movements, bringing straight tentacles together) for the first time.

3. Nineteenth century studies

After Rösel von Rosenhof's book mentioned above,[19] several works on freshwater bryozoans with brief descriptions of their feeding behaviour were published during the next fifty years (summarized by William Sharpey[20] and George Allman[21]), and tentacular ciliature was redescribed by Johann Eichhorn.[22] Johann Steinbuch distinguished the cilia and their motion as the cause of water movements in *Plumatella repens* (Linnaeus) (as *Tubularia*), but, observing frequent retractions of polypides caused by an addition of extraneous particles, he inferred that the currents served chiefly, if not solely, for respiration.[23] Also, Steinbuch described and illustrated what seems to be water refiltration in the form of circular currents that had been already mentioned by Baker, who compared these currents with 'the turning of a mill-wheel'.[24]

As is evident from the old published descriptions and illustrations, living marine as well as freshwater bryozoans were often observed by investigators in the XIX century (Thompson,[25] de Blainville,[26] Gervais,[27] Nordmann,[28] Hassall,[29] Van Beneden,[30] Reid,[31] Hancock,[32] Leidy[33-37] Gosse,[38] Busk,[39] Huxley,[40] Hincks,[41] Müller,[42] Smitt,[43, 44] Reichert,[45] Claparède,[46] Repiachoff,[47,48] Ehlers,[49] Joliet,[50] Vigelius,[51] Ostroumoff,[52] Pergens,[53] Prouho).[54] Following Bomme,[55] many observers thought that effective strokes of lateral cilia were directed upwards along one side of a tentacle and downwards along the other (Grant,[56] Lister,[57] Dalyell,[58] Allman,[59] Hincks).[60] Based on this opinion, some authors concluded that there were ascending and descending water currents along consistent tentacle surfaces (for instance, John Fleming,[61, 62] and George Johnston).[63, 64] In contrast, Alpheus Hyatt was sure that cilia were 'constantly vibrating towards the centre of the crown', observing apparently their beating across the tentacle.[65] Similar statements were made by Heinrich Nitsche[66] and Karl Kraepelin[67] (see also below). Asajiro Oka apparently observed refiltering currents and thought that the cilia of the outer (abfrontal) tentacle surface generated the ascending current and those on the oral (frontal) surface produced the descending current.[68] The last four authors all worked with phylactolaemates.

Some investigators did not find the tentacular cilia, apparently due to the imperfection of microscopes. Noteworthy, Barthelemy Dumortier, who published one of the best anatomical descriptions of fresh-water bryozoans at that time, could not distinguish cilia on the tentacles in some cases (see also papers of François Raspail)[69, 70] and made supposed absence of cilia the principal character of his new genus *Lophopus*.[71]

Robert Grant summarized previous works and gave a more detailed and correct description of marine bryozoan feeding. He was apparently the first to describe single and group tentacle flicks as a result of particle impacts in gymnolaemates.[72] John Lister, who also worked with marine bryozoans, was the first to describe transport of particles along the frontal tentacle surface, their concentration in the pharynx before swallowing or rejection, and single and paired 'hairs' (setae) on the abfrontal tentacular surface. Lister's illustrations show that he also found the groups of rigid cilia on the tips of the tentacles. Moreover, he was one of the first researchers who worked with living cyclostomates.[73]

The most prominent investigation of this period on the feeding and behaviour of marine bryozoans was made by Arthur Farre.[74] He gave an excellent description of feeding in seven ctenostomate and cheilostomate species. He was one of the first to use particles of carmine in his experiments to detect feeding currents. Many structures and reactions were recorded and beautifully illustrated by him for the first time: obliquely-truncate lophophores, scanning activity, testing-position, different variants of polypide protrusion, retraction and tentacle movements (for instance, writhing, curling, flattening of the lophophore when tentacles are almost perpendicular to the introvert), cessation of ciliature beating, etc. Moreover, he was the first to use the word 'vortex' which became very popular later to describe water turbulence within and nearby the lophophore (Bomme,[75] for instance, had used the Dutch word 'voortbrengen' = whirlpool) and proposed the filtration mechanism of bryozoan feeding. After Trembley,[76] Baker[77, 78] and Bomme's[79] observations it was generally accepted that the feeding process included a directed water transference into the tentacle crown by ciliary activity as well as the activity of tentacles which 'assist the ciliary currents, by their varied movements, in obtaining food'.[80] Some observers believed that the tentacles 'catch' the food,[81] whereas others were convinced that they 'arrest [retain] the prey' to 'conduct it to the mouth'.[82] Despite the fact that Farre described various tentacle movements too, he thought they worked like 'a sieve, of a degree of fineness proportioned to the number of the arms and the consequent width of their intermediate spaces'.[83] According to his opinion, the size of filtered particles is regulated by the size of the mouth and the gaps between the tentacles. The former prohibits the swallowing of too large particles, and the latter, forming the sieve, lets small particles pass while retaining those of an intermediate size. Also Farre mentioned particle selection inside the pharynx resulting in swallowing or rejection.

John Dalyell gave very accurate and detailed descriptions of the behaviour in about 30 gymnolaemate and 4 phylactolaemate species.[84] He recorded many reactions, some of which were not described before. Following Arthur Hassall,[85] who pictured a bending of all the tentacles of the lophophore towards the mouth, Dalyell described and illustrated this reaction. In fresh-water bryozoans he recorded and described for the first time the pharyngeal rejection, concentration of particles in the pharynx before swallowing, and faster ciliature beat as a result of an increase of particle concentration. Dalyell compared feeding in bryozoans with that in sedentary polychaetes, thinking they both were capable of the 'absorption of muddy matter' and fed on 'small animals' only incidentally.[86] He was likely one of the first to perform experiments with bryozoans under light and low temperature influences.

George Allman observed feeding in about 20 species of phylactolaemates, and summarized much research on this topic in his monograph.[87] In *Fredericella sultana* (Blumenbach) he also illustrated the bending together only of tips of the tentacles for the first time.[88]

Heinrich Nitsche encountered frontal cilia in sections of the tentacles of the freshwater bryozoan *Plumatella fungosa* (Pallas) (as *Alcyonella*).[89] He made his own observations on living colonies and was able to distinguish ciliary beating along the frontal surface of the tentacles.[90] In his opinion, the entire lateral ciliature performed an ascending-descending movement (see above), but like Hyatt[91] and Kraepelin,[92] Nitsche thought that the cilia beat across the longitudinal axis of the tentacle. He first mentioned phase differences in the beating of the cilia, meaning a metachronal wave, and he found long rigid cilia both on frontal and abfrontal sides of the tentacles in the phylactolaemate bryozoan studied.[93] Samuel Silbermann summarized the existing data on presumed sensory structures in bryozoans. He described and illustrated paired and non-paired setae on the outer (abfrontal) side of tentacles in *Alcyonidium mytili* Dalyell.[94] He also encountered the fusiform cells with stiff cilia between ciliated cells on the inner side of the tentacle, but it is difficult to judge from his description and illustrations[95] whether or not these were the latero-frontal cells later described by Geneviève Lutaud[96] in cheilostomates (see below). In phylactolaemates similar fusiform 'sensory' cells with a hairy terminal process were described later by Adolf Gerwerzhagen[97] in *Cristatella mucedo* Cuvier and by Paul Brien[98] in *C. mucedo* and *Plumatella fungosa*. Gewerzhagen reported that the cells found were irregularly distributed in bunches in the epithelial layer of the tentacle, whereas Brien believed that they are located on either side of a group of frontal cells with motile cilia, or even among them.[99, 100]

Alpheus Hyatt described feeding in the fresh-water bryozoan *Fredericella sultana*.[101] He was the first to report 'cagemaking',[102] bending of tentacles to place a particle directly to the mouth, and rejection of the particles away by tentacles. Hyatt stressed that tentacles are not only feeding, but also sensory organs. Thomas Hincks summarized the existing data on bryozoan behaviour, and also made many of his own observations.[103] He described, in particular, some different lophophore shapes and tried to apply them to the current classification. Louis Calvet, using sections, found frontal cilia on the tentacles of some gymnolaemates. He believed that lateral cilia beat from outside towards the centre of the lophophore and back, across the tentacle and simultaneously from the top to its base. According to him, this beating created a turbulent water current towards the mouth and 'préhension' of particles, and the polypide then retracted, swallowing them.[104] Similar phenomenon was first described by Baker,[105] but Calvet thought that each swallowing was accompanied by retraction.[106] Calvet was also the first to mention repeated expansions and contractions of lophophore with straight tentacles, resembling pulsation.

4. Twentieth century studies

In the first half of the twentieth century, the most important investigations of marine bryozoan feeding and behaviour were made by Folke Borg. In 1923 he published a preliminary report of his research on bryozoan ciliary feeding,[107] and then gave a detailed analysis of the processes, with the description of many reactions.[108] Borg was the first to ascertain an oblique beating of the lateral cilia in respect to longitudinal tentacle axis, with effective strokes towards the outside. He compared the activity of these cilia, which differ in phase, with the movement of an undulating membrane and thought that such undulation passes through the tentacle tips, as well as from one tentacle base to another. Borg correctly described the directions of water currents inside the lophophore and assigned an important role to the change of tentacle position and cilia beat direction as a reason for hydrodynamical changes inside and around the lophophore connected with feeding and particle rejection. In his opinion, the strongest current 'arises in the medial line of the tentacular crown in a direction straight downwards towards the mouth'[109] and 'mostly only those [particles which are contained in the current] in or near the medial line ... reach the mouth'.[110] The particles are then ingested through action of the stomodaeum musculature that 'acts as a suction pump',[111, 112] assisted by the pharyngeal ciliature.[113] Borg recorded reversal, cessation, and deceleration of ciliary beating. Also he noted that the frontal cilia of tentacles played a subordinate role in the feeding process. Frontal cilia, beating from above downwards, rarely caused a slow transference of particles along the frontal surface towards the mouth. The mechanism of ciliary feeding described is enhanced by tentacular activities such as bending of individual tentacles directing particles towards the central current and lophophore contractions. Borg stressed that bryozoans perceived the nature of suspended particles and avoided ingesting inedible ones. In contrast, no food preferences were noted and particles were swallowed without apparent selection in experiments of Erich Ries.[114, 115] For the first time Borg recorded a single lophophore contraction looking like a 'clap', brief series of tentacular pulsating movements during a rejection of particles, and bringing together only tips of the tentacles (accompanying a particle rejection in some cases).[116]

Ernst Marcus made many observations on marine as well as freshwater bryozoans,[117-121] but his main aim was experimental work with changes of temperature, salinity and mechanical stimuli,[122] and he did not study their feeding behaviour specifically. Marcus believed that the frontal cilia were immovable and stiff in at least one ctenostomate, *Farrella repens* (Farre).[123] Chandler Brooks was probably the first to describe scanning behaviour in Phylactolaemata.[124]

Daphne Atkins compared the tentacle ciliary activity and the water currents created in Entoprocta and marine Ectoprocta.[125] She was the first to use the term 'metachronal wave' in describing the beating of the lateral cilia, and studied the operation of the ventral rejection tract in the ctenostomate *Flustrellidra hispida* (Fabricius) first described by Henry Proucho.[126] In *Pherusella tubulosa* (Ellis and Solander) (as *Pherusa*),[127, 128] Atkins also divided the reactions connected with feeding behaviour into three groups that serve to: (1) increase the number of food particles, (2) prevent unwanted particles from reaching the mouth, (3) reject useless particles which have already reached the region of the mouth. Following Borg,[129] she suggested an important role of the frontal cilia situated at the base of tentacles in forming and directing water currents to the mouth.

In spite of two centuries of intensive observations, Carl Cori gave credit to the frontal cilia in creating the main water current.[130] He thought that their beat was across the tentacle whereas lateral cilia were motionless or beat incidentally. This conclusion was strange because Cori saw the ascending-descending lateral ciliary movements, and described and illustrated them in some ctenostomates, comparing them with clock-wise ciliary movements in Kamptozoa and Phoronis.[131] Using his own observations on the ctenostomate *Zoobotryon verticillatum* (Delle Chiaje) (as *Z. pellucidum*) and the data of Heinz Graupner, who investigated the anatomy of gymnolaemate tentacles,[132] Cori suggested that the immobile lateral cilia formed a filter, closing narrow intertentacular gaps between the bases of all tentacles.[133] Sucking action of the frontal cilia resulted in water transference through the filter where suspended particles were retained, and, becoming associated with the mucus strands, conveyed to the pharynx. Like Lister,[134] Cori illustrated the stiff apical tentacle setae in *Z. verticillatum* without mentioning them in the text.[135] He also recorded the pushing away of particles by tips of tentacles for the first time.

Lars Silén investigated the functioning of the digestive tract of gymnolaemates in detail.[136] According to him the delivery of captured particles to the mouth proper is mainly performed by ciliary beating in the area around the mouth, stomodaeum and neighbouring part of the pharynx. Periodical contractions of the mouth may assist this transfer and take place independently from pharyngeal dilations and contractions resulting in food suction and swallowing.[137,138] Later Silén described some zooidal behavioural reactions involving tentacles and entire polypides, and serving oviposition [139] and sperm release [140] (see also papers of Marcus,[141] Bullivant,[142] Cook,[143] Gordon,[144] Ström,[145] Chimonides and Cook,[146] Dyrynda and King,[147] summarized in the paper of Shunatova and Ostrovsky).[148]

Despite numerous studies there was no clear concept of a bryozoan feeding mechanism. Dividing suspension feeders into groups Bernhard Werner marked out ‘filterers’ and ‘whirlers’ in his paper.[149] In the latter group, cilia generate a current and water with suspended particles is transferred along the collecting surface where the particles are retained. Bryozoans were considered to belong to a group of ‘non-filtering suspension feeders’. In good agreement with Cori’s suggestion,[150] Carl Jørgensen speculated that mucus played an important role in particle retention.[151] In contrast, John Bullivant suggested that in all lophophorates a sharp deflection of water current passing through the lophophore causes particles to be thrown towards the mouth in a way which he compared with impingement separation used in industrial processes, and claimed that mucus plays no part in the feeding of marine bryozoans.[152, 153] He also supposed that laterofrontal cilia found by Lutaud[154] on the tentacles of the cheilostomate *Pentapora foliacea* (Ellis and Solander) (as *Hippodiplosia*)[155, 156] may either detect suspended particles in the water and initiate polypide retraction, tentacle flicking or reversal of lateral cilia, with the aim of rejection, or act as a sieve which retain the particles. Bullivant found and measured the laterofrontal cilia in the cyclostomate *Disporella separata* Osburn for the first time and used the term ‘laeoplectic’ to describe metachronal waves formed during lateral cilia beating.[157, 158, 159] Following Bomme[160] and Marcus,[161] he noted that metachronal waves transmitted over the tips of tentacles in phylactolaemates, but he doubted that this took place in marine bryozoans. In *Plumatella repens*, Bullivant recorded the abfrontal cilia and described particle rejection along the frontal ciliary tract on the tentacles. He also confirmed[162] observations of Günther Becker who described the rejection of particles by ciliature reversal of all of the tentacles in marine bryozoans.[163]

Dennis Gordon investigated tentacular ciliature in the gymnolaemate *Cryptosula pallasiana* (Moll) and found that laterofrontal cilia performed occasional flicking movements.[164] He also described abfrontal cilia of two types that alternate with each other - short tufts of several immobile cilia and solitary cilia, and found the 'tuft of cilia at the tentacle tip'.[165]

Bullivant's hypothesis was met with enthusiasm by some researchers, and John Ryland called bryozoans 'impingement feeders'.[166] Thomas Gilmour proposed a more detailed explanation of lophophorate feeding on the basis of the hypothesis in question and some theoretical generalizations.[167, 168] He considered the process as 'simultaneous acceptance of food particles and rejection of inedible wastes probably' depending 'on the impingement or inertial impaction of heavy, potentially inedible particles on rejectory surfaces and the filtration or direct interception of light, potentially edible particles by cilia' on the lophophore.[169] In his opinion light particles are either thrown directly to the mouth with the incoming current or, if they move with a deflecting component of the current, are caught by the oral area cilia in gymnolaemates. Heavy particles are collected on the frontal surfaces by impingement and conveyed by the reversal of their cilia beating towards the tentacle tips. Following Bullivant,[170] Gilmour described the particle rejection along the frontal surface of the tentacles in the fresh-water bryozoan *Plumatella* sp., and also found this type of rejection in *Membranipora* sp. Gilmour also described the laterofrontal cilia on the tentacles of both gymnolaemate and phylactolaemate species (see above), but he supposed they work as sensory organs only.

The impingement model of lophophorate feeding was strongly criticized by Richard Strathmann,[171, 172, 173] who argued that the velocities and the particle sizes and densities are too low for feeding by inertial impaction to operate.[174, 175, 176] Instead, Strathmann speculated that suspended particles are captured by a combination of local reversal of the lateral cilia, which produces a local reversal of the water current, and inward flicking of the tentacles. The reversed current transfers the particles to the frontal side of the tentacle and helps to retain and transport them along the frontal surface towards the mouth (so-called up-stream collecting system according to terminology of Claus Nielsen and Jørgen Rostgaard).[177, 178] It was suggested that this reversal must be induced by particles contacting either the lateral cilia themselves or the laterofrontal cilia. The latter may act as a sieve at the same time. This mechanism was first proposed for echinoderm larvae[179] and then extrapolated to lophophorates,[180, 181] and Michael Hart presented a possible physiological explanation for its existence.[182] In the ctenostomate *Flustrellidra hispida*, Strathmann used high speed cinefilms to observe local alterations of metachrony of ciliary bands in places where the particles arrived. Though local reversal of the effective ciliary stroke could not be directly observed, these alterations were suggested to be the consequences of the reversals.[183] Strathmann did not report the transport of particles by frontal cilia in bryozoans, only that the transport along the frontal tentacle surface is aided by the reversal of the lateral cilia. He doubted that frontal cilia could transport the particles 'since only a few [of them] would be moving a particle against the action of many lateral cilia'.[184] Strathmann also was the first to measure the length of the lateral cilia in *F. hispida*,[185] to record frontal transport of particles by means of jumps and to investigate in detail flicking activity, which sometimes accompanied the proximal particle transport along the flicking tentacle.[186]

Reactions to Strathmann's hypothesis were mixed. Some authors accepted it, but gave no direct evidence in support (Ryland,[187] Winston,[188, 189] LaBarbera,[190] McKinney and Jackson,[191] Hart,[192, 193]). John Ryland tried to reach a compromise between the hypothesis of Bullivant (see above) and that of Strathmann.[194] He wrote that 'heavier particles may, as Bullivant suggested, be projected towards the mouth; but mostly it seems that particles are retained ... by local reversal of the lateral cilia'.[195] Ryland also discussed the significance of the width of the intertentacular gap and the length of lateral cilia in relation to Strathmann's opinions on particle capture.[196, 196] According to Ryland's measurements of lophophores in different marine bryozoans, filtration should be fully effective in approximately the lower half of the tentacle crown since the lateral cilia should close the intertentacular gaps.[198, 199] This idea was thereafter questioned and modified. James Markham and John Ryland[200] and William Sanderson, John Thorpe and Andrew Clarke[201] found that the lateral cilia on the tentacles of *Flustrellidra hispida* and *Himantozoum antarcticum* (Calvet) correspondingly, 'exhibited a subterminal maximum length, decreasing proximally over more than half the tentacle and distally in about the last quarter'. Thus it was concluded that the actual closure of much of the intertentacular gap by the lateral cilia occurs along less than a quarter of the tentacle length or even lesser. The mechanism of local reversal would in principle be possible here as well, but it probably occurs in addition to other particle capture methods (see below). Filtration would be less effective in the upper part of the tentacle crown, where the distance between the tentacles is larger, but flicking might supplement the food collecting mechanism.

Michael Best and John Thorpe[202] denied the major role of local reversals in particle capture and transport towards the mouth.[203, 204] Working on clearance rates and velocities of feeding currents in some gymnolaemates, they observed a frontal transport of particles downward and assumed that it might be a result of local reversals.[205] At the same time Best and Thorpe came to the conclusion that the feeding process in the ctenostomate *Flustrellidra hispida* cannot be entirely explained by the local reversal-flicking hypothesis.[206] They calculated, for instance, that the rate with which the pharynx is normally filled and the quantity of swallowed food particles would imply several flicks and more than 1000 local ciliary reversals per second, which appears to be impossible. Following Borg[207] and Atkins,[208] Best and Thorpe supposed that long frontal cilia at the bases of the tentacles take an important part in bryozoan feeding. These cilia are used to direct the main feeding current towards the mouth, and 'the bulk of particles travel rapidly downwards in the current in the central area of the lophophore cone and proceed directly to the area above the mouth where they gather and are continuously ingested'.[209] Local reversals and particle transport by frontal cilia are considered to be possible supplementary mechanisms.[210,211] Best and Thorpe were the first to measure current velocities inside the lophophore.[212]

The most exhaustive research on individual as well as group behaviour and associated structures was made by Judith Winston, who investigated about 80 species of marine bryozoans.[213-216] She described and classified most of the feeding behavioural reactions known, recording many of them (collection of particles in a group inside the expanded lophophore near the mouth area, bending of all tentacle tips inside and outside the lophophore used for rejection at high particle concentrations, twisting activity, polypide retraction from under the particle, 'avoidance' retraction) for the first time. Winston also summarized the data on inferred sensory structures [217] and noted that the metachronal wave did not travel over the tentacle tips [218] (a fact which Bullivant doubted).[219] According to the prevailing reactions she distinguished 'filterers', 'tentacle feeders', 'scanners', 'cage-captors' and 'particle jugglers', and suggested that behavioural differences depend both on the physical and chemical characteristics of the food particles and behavioural characteristics of the various species.[220] She also investigated parameters of the lophophore and its shape, showed similar trends in its symmetry within three main taxa of marine bryozoans and discussed their siginificance in relation to zooidal activity, colony structure (zooid arrangement and growth form) and environment. Winston argued that the complexity of zooidal behaviour was correlated with the level of colonial integration. The most complex individual behaviour was mainly found in poorly integrated colonies, and the most complex forms of group behaviour were discovered in highly integrated ones. The variety of reactions also often depended on polypide size: larger polypides perform a greater range of reactions involving different movements of tentacles and the entire polypide, whereas in small ones ciliary activity was the most important component of feeding behaviour as it was shown in cyclostomates and ctenostomates. Winston stressed that during particle rejection polypides could 'utilize a combination of methods depending on the size and concentration of the particles'.[221]

Matthew Dick added to Winston's observations, recording for the first time in gymnolaemates an autocleaning of the colony surface by special activity of polypides in association with stiff abfrontal tentacular setae.[222] He described different types of rejection processes (particle flinging and partial retraction of polypide accompanying by pharyngeal rejection were described for the first time) and distinguished 'ejection' and 'rejection', and was the first to discuss the possible evolution of some behavioural reactions in bryozoans. Following Winston, who suggested that abfrontal ciliary structures 'could have some role in controlling polypide orientation relative to other polypides',[223] Dick speculated that 'long abfrontal cilia' perceive 'tactile stimulation from the tentacles of surrounding polypides' as well as 'vectors' of flow around the lophophore.[224]

Patricia Cook observed feeding behaviour of about 40 cheilostomates.[225] In some species she described different variants of a lophophore protrusion and retraction in details, noting the specific sensitivity relative to the external irritants. Cook pictured several tentacle crown shapes,[226] and described a temporary lophophore expansion with the tips of tentacles directed towards the colony surface for the first time. Since this reaction was "colony-wide", the author suggested that it might be a colonial rejection, accompanied by ciliary reversal and connected with cleaning, sperm release or other unknown functions.

Ewan Hunter and Roger Hughes described an unusual variant of feeding in the cheilostomate *Celleporella hyalina* (Linnaeus) under high particle concentrations when 'food particles were drawn from below the lophophore into the feeding crown by a current generated by the lateral cilia'.[227] According to their observations 'particles continued to move upwards and out of the lophophore, unless ciliary reversal occurred, bringing particles down' to where finally they 'were drawn into the mouth on a current generated by cilia within the pharynx'. A similar feeding method was earlier described by Borg.[228] It is obvious from the texts that all of the authors postulate simultaneously changing ciliary movement on the tentacles, but not the local reversals proposed by Strathmann.[229, 230] Hunter and Hughes also recorded a retaining of particles inside the lophophore when the tentacles cramed them into the mouth.[231]

Hans Riisgård, Patricio Manrìques[232] and Claus Nielsen[233] reviewed a wide range of literature dealing mainly with physical aspects of particle capture by different suspension-feeders.[234-245] Using theoretical considerations and non-contradictory ideas from conflicting theories of bryozoan feeding mechanism (see above) as well as their own data they proposed that the laterofrontal cilia form a mechanical filter which 'strains the water while the central current, created by the special lophophore pump-design, and the action of flicking tentacles in co-operation clean the filter and transport the particles towards the mouth'.[246] The laterofrontal cilia are considered to be multifunctional sensors that trigger tentacle flicking and local reversal of lateral cilia and serve as a mechanical sieve. By this means three main components of particle capture in bryozoans are effected: the direct transfer of the particles within the middle part of the central current to the mouth, particle impacts to a tentacle resulting in a downward transport by frontal cilia, and tentacle flicks conveying particles into the central lophophore current and triggered by the particle impacts with laterofrontal cilia. Flicking is stated to prevail in catching the particles in comparison with frontal transport,[247] and the latter being impossible in at least some cyclostomates since frontal cilia are absent.[248, 249] This is why every particle, that collides with a tentacle, is captured by a single tentacle flick directing it into the central current in *Crisia eburnea* (Linnaeus). In all species investigated the frequency of flicking depends on concentration of particles. Riisgård and Manrìques did not observe the capture of particles by local reversals and disturbances in ciliary metachrony and doubted compatibility of their proposed mechanism with Strathmann's model, but did not deny it entirely.[250] They also noted that some results obtained by Best and Thorpe[251] and Sanderson and Thorpe[252] may be disputed because they had used too high concentrations of particles, tending to disturb normal feeding behaviour.[253]

Natalia Shunatova and Andrew Ostrovsky gave comparative descriptions of the behaviour in 40 species and subspecies of marine bryozoans.[254] Some of the activities (cleaning of the colony surface using ascending water current created by reversal of the lateral cilia; cleaning of the colony surface by the inclined polypide; bending of the tentacle tips inside the lophophore during polypide protrusion; particle capture by tentacle expansion; pulsation of polypides bringing tentacles together within a lower part of the crown; particle rejection by bringing straight tentacles together; particle rejection in clumps by a series of repeated retractions and protrusions of polypide) were recorded for the first time. Behavioural reactions described were classified using a morphological approach based on the structure (tentacular ciliature, tentacles and entire polypide) performing the reaction. Authors discussed both normal and so-called spontaneous reactions as well as differences and similarities in individual autozooidal behaviour and their probable causes. They also suggested that in some species polypides can detect particles at some distance and that polypide protrusion and retraction might be the basis of the origin of some other individual activities. In marine bryozoans individual autozooidal behaviour was 'considered to be a flexible and sensitive system of reactions in which the activities can be performed in different combinations and successions, and can be switched depending on the situation'.[255]

Irina Antipenko studied in detail feeding of four fresh-water bryozoans recording many activities for the first time.[256] For instance, testing-position was recorded for Phylactolaemata for the first time (in *Fredericella sultana*). She showed that, in contrast with marine bryozoans, frontal particle transport is one of the main feeding mechanisms (together with mechanical-filtering and tentacle flicking) in phylactolaemates. Small particles slide quickly whereas middle-sized ones usually move in jumps along the tentacle frontal surface toward the mouth. Instead, large particles are rejected being lifted by a reversal of frontal ciliature beat. When such a particle reaches a tentacle tip the rejecting tentacle sometimes sharply deflects outward shaking the particle off. If a particle is of 'intermediate' size, it often starts to travel down and up before it is either swallowed or rejected. Large particles can also be rejected by a brief reversal of lateral ciliature of all tentacles, expansion of lophophore, bending either of a single or several tentacles outside, sharp shaking of all of the tentacles. In *Cristatella mucedo* rejecting particles can be rolled from tentacle to tentacle towards the end of the lophophore 'arm'. The polypide can cross 'arms' in this species, and perform a 'clap' to catch more particles. Finally, Antipenko stressed the great similarity in autozooidal behaviour of *F. sultana* (possessing ring lophophore) and that of marine bryozoans.

Quantitative characteristics of feeding in marine bryozoans have been investigated since the works of John Bullivant[257] and N. Ravindranatha Menon[258] who measured clearance rates by calculating theoretical volumes of water cleared of particles per unit time, and Judith Dudley [Winston][259] and John Ryland[260] who studied dimensional parametres of the lophophore.[261-266] Best and Thorpe,[267, 268, 269] Sanderson *et al.*,[270] Sanderson and Thorpe[271] and Riisgård and Manrìques[272] made direct measurements of feeding current velocities for various marine Bryozoa. These studies indicate that velocities vary across the diameter of the lophophore and are the strongest axially.[273, 274] Velocities of feeding current may also vary considerably depending on a number of parameters including food type, food particle size and concentration and the extent to which the colony has been starved.[275, 276, 277] Both intraspecific and interspecific variations in lophophore behaviour and morphology were documented, although generally parameters of lophophore width, tentacle length and tentacle number correlate quite strongly.[278-283] It was supposed that interspecific (and intergeneric) differences in behaviour and morphology of the lophophore probably result in corresponding differences in diet,[284-292] and 'that bryozoans [with] … a substantial difference in the size of the lophophore and tentacle number … may be able to coexist by means of niche partitioning'.[293, 294] Phytoplankton (mainly, diatoms) is almost certainly the most important food source for shallow-water bryozoans, but various motile protists (like ciliates and flagelliates), small planktonic arthropods, detritus, bacterial suspensions and dissolved organic matter are considered to be potential food sources as well.[295-306] Seasonal and tidal changes in food composition and concentrations have been recorded [307-310] and intraspecific behavioural variability may be partially explained by these factors.[311] Feeding is also influenced by an increased temperature.[312-316]

Current regimes have been shown to influence feeding of marine bryozoans. Relationships between ambient flow velocity, particle sizes and feeding success in the colonies of different growth forms were intensively studied by Beth Okamura.[317-320] She found that the capture of particles of different sizes may be affected in different ways under various conditions of flow and suggested a possible switch in feeding behaviour from filtering to capturing by tentacles.[321] It has been also shown that bryozoan feeding was significantly affected by the interacting influences of the flow velocity and degree of association with neighbouring suspension-feeders, for instance, other bryozoans,[322, 323] and these conclusions conform with the results of previous work by Leo Buss[324] and Michael Best and John Thorpe[325,326] on feeding-current interactions among neighbouring colonies.[327, 328, 329] Feeding of some marine bryozoans was also investigated in laminar[330] and turbulent flow.[331] Both studies showed that feeding rates increase with increasing flow velocity. Unfortunately, phylactolaemates are almost non-studied in these respects.[332, 333]

5. Conclusions

In conclusion, we would like to stress that in spite of more than 250 years of research our knowledge of bryozoan feeding behaviour is still far from satisfactory, and implied feeding mechanisms are based more on hypotheses and suggestions than on facts. Structural uniformity of the bryozoan polypide and tentacles implies common feeding mechanisms. It is generally accepted that bryozoans probably use several mechanisms depending on polypide morphology and size within different taxa, and changes of environment.[334-340] Supposedly, the basic lophophore filter-feeding principle is added by tentacle flicking, frontal transport and, may be, local reversals. Some of these mechanisms can apparently be used simultaneously, but their importance for feeding is, probably, different. Further investigations are necessary to prove these speculations. Microscopical size and the impossibility to observe bryozoans in natural habitats are the main reasons of many existing problems and theoretical controversies. We hope that the complex approach of using sophisticated videoequipment, carefully planned and accomplished quantitative experiments and anatomical work [341, 342, 343] could improve this situation.

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