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Research Article

Assembling and Dewatering of Food Particles in Daphnia

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Abstract

The acceptance of P3 and P4 thoracic appendages in Daphnia as filters is a misleading. Thought, the particle abstraction is achieved not by sieving and assembling and packing definition is appropriate. Straining action require energy consumption which is an ecological disadvantage. The two trunk limbs are freely dangling within a chamber space where food particles are assembled. Such a mechanism of feeding process improve animal resiliency whilst avoiding ecological weakness. The assembled mechanism is closely related to size-fractionation of suspended particles mixed in microfluids.

Keywords: Daphnia, Feeding, P3 P4, Assemblers, Not Filters, Dewatering

Introduction

Throughout more than historical 100 years of limnological research, P3 and P4 appendages in Daphnia were considered as filters although direct observation of water flows in spaces between seta and setule was not documented. Definition of filter feeding mechanism in Daphnia was accepted and stated distinctly and was never modified [1-14]. By definition, filtration can be practised when particle-bearing current is drawn or pressed through a "filter" [4,5]. Under condition of low Reynolds number (viscous flow), the boundary layer around the setules may exceed their inter-setular distances and that little or no flow takes place between these setules [15]. Although filtering (straining) function definition was widely accepted, the functional attribution of sieving require solid directly observed to be confirmed which was not documented. The interpretation about Cladocera`s feeding mechanism was born from their anatomical structure. Nevertheless, it was criticized as misinterpretations of functional morphology and are completely erroneous [4,5]. Thought filtering mechanism maintained by water flow through a sieve and particles larger than the mesh size retained. On the contrary, assembled food particles transferred into the digestion truck of the Daphnia was observed in living animal and documented. This process resembled dewatering of algal and blood cells on micro-tubes known from commercial instrumentation. What is the activation principle involved in the feeding mechanism of Daphnia? Sieving, Assembling or Dewatering? Evaluation of slow motion and solid photos of cinematographic films was carried out [12-14] and sieving mechanism involvement within the feeding mechanism of Daphnia was negated. The slow-motion projection of the cinematographic film accompanied by solid photos are utilized to confirme assembling and rejecting filtration.

Material and Methods

A cinematographic study was carried out using a high-speed camera (Photo-Sonics 4C; 250 frames/second) operated through three dimensions (left-right, forward-backward, and up-down) fixed microscopical lenses [12,13]. The dorsal side of a tethered Daphnia magna (Straus, 1820) (3.7mm, length) was glued (Bostic Super-glue 4-Cyanoacrilate) onto the tip of a rigid plastic sieve inside a 50 ml glass container full of filtered (0.45μm filter paper) lake (Bodensee, Germany) water. The internal water flow within the space between the two transparent carapace valves was detected by a mini drop of Indian Ink, which was injected (superfine screw-thread injector) into the water media close to the animal intake location [12,13]. Analysis of the resulting film was carried out by a slow-motion projection, accompanied. by a time-motion analyzer, of a single frame-by-frame (10 millisecond intervals) and magnified solid photos. A visual indication of fluid penetration through P3 and P4, transported from the inner to the outer surface of these paddles, was carried out.

Results and Discussion

The ultra fine-structure of the trunk limbs consists of three components: 1) Setae; 2) Two rows of Setule located perpendicularly on each Setae;3) Two rows of ultrafine knobs (bosses) on both sides of each Setule (Figure1; Photos 1,2) [1,3,16,17].The interval between the Setule was measured as 0.6-0.7µm [18] whilst, the ultrafine structured knobs caused the free space in between the Setulae to be even narrower. This structure in Daphnia creates tiny micropores (0.6-0.7µm diameter) which was interpreted as a sieving apparatus [13], a straining organ that retains food particles.

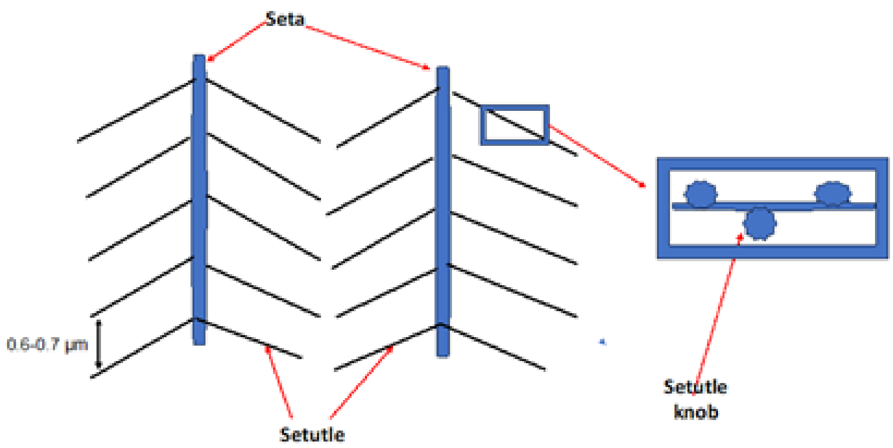

Figure 1: Schematic illustration of P3 and P4 trunk limbs: Setae, Settula and Setule knobs (Bosses) [16,17] are indicated.

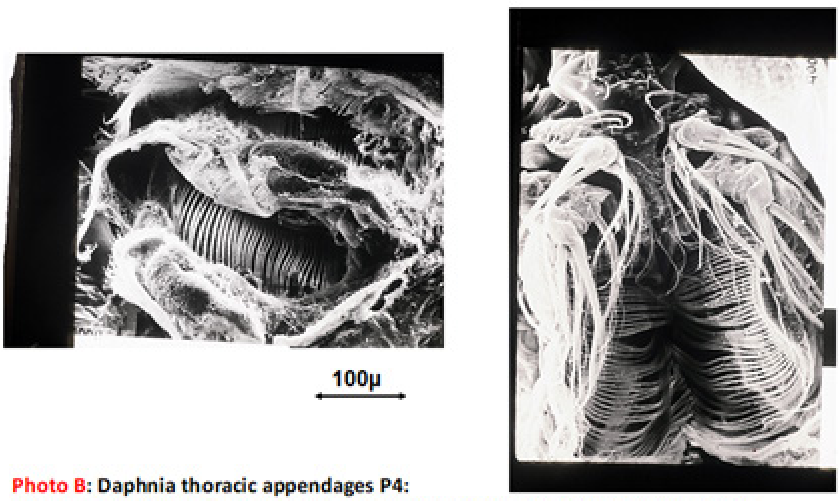

Photo B: Daphnia thoracic appendages P4:
Left: external view ; Right: front external vew two p4 apendages on both sides;
scanning electron microscope
(Photo: W. Geller)

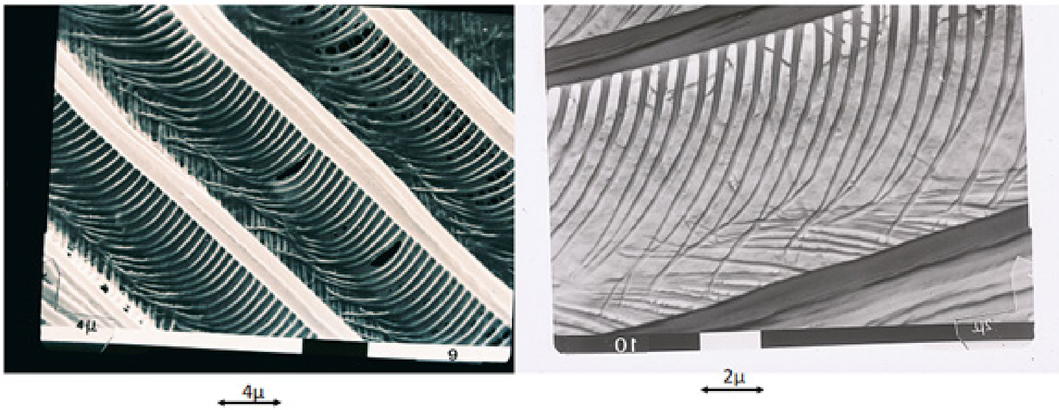

Photo A: Daphnia thoracic appendage P4 external view, scanning electron microscope (Photo: W. Geller)

Commercial instrumentation of cultured algal harvesting [19] represent dissimilar concept to the Daphnia feeding mechanism. The cultured microalgal biomass is assembled on a permeable barrier and dewatering by liquid removal through the membrane [19]. On the contrary, the P3 and P4 assemblers of food particles are not a permeable barrier. These trunk limbs are dangled freely within the suspension mixture and food particles are captured. Algal properties such as cell size and auto-flocculation are significantly involved in the dewatering process. A permeable membrane divider which retains the solids and allows the liquid to pass through is not the case of Daphnia feeding mechanism. In case of algal harvest through membrane collector, screening and pore size, control the system efficiency. The solid particles that are larger than the screen pore size are retained, while the liquid passes through the screen [19]. Thought, in Daphnia the entire spectrum of particle size are collected even smaller then the setule space, Assembling efficiency is particle density and size because it is not straining but collecting. It is like a draw of a rake: assembling efficiency of larger and denser is higher then that of smaller and diluted particles.

The space between P3 and P4 trunk limbs (syn. trunk limbs, combs, filters, sievers, sifters, strainers, thoracic appendages, solid walls, flexible walls, and paddles) was defined as " filter chamber" [4,5]. The daphniid feeding mechanism was evolved by restricting particle abstraction to trunk limbs 3 and 4, whilst limbs 1 and 2 are not involved in the feeding process [4,5]. Daphnia employ two internal alternate micro-flows carrying food particles of which one is directed through the space between P3 and P4 and the other flow underneath the carapace [12]. These two currents comprised of the same mixture of fluid contain suspended particles. The assumption of particles cany (attached) by filter plates bearing filtratory setule was raised [4,5]. It is considered as circumstantial evidence unless a confirmation by cinematographic filmed documentation is presented. The structure of P3 and P4 is not a network where every node is inter connected with every other node, forming a lattice like a mesh pattern. The seta are separated from each other and the branched setule are totally free and singly isolated all along from the basis to tip end. The documented anatomical structure of P3 and P4 [4,5] by itself is not sufficient to be defined as operative filtration achieving. The physical definition of filtration include fluid mixed with suspended particles flow through the lattice mesh while particles retained on its surface. It is likely that individual free dangeling setule bristles within the chamber space while particles are adhered to them. Filtration definition is appropriate when solid particle are removed by a filter mediator that permit the fluid to pass through but solid particles larger than the filter mesh size retained. The seta of P3 and P4 are employed as flexible solid paddles which suck water inside and pressured injecting them outside. Meanwhile, free flexible bristled setule are hovering inside the interlimb space the so-termed, "filter chamber" [4,5] full of fluid medium collecting suspended solid food particles. When P3 and P4 limbs are flapping forward the mixture of water and particles is expelled posteriorly. Whilst, when P3 and P4 are flapping backward this mixture is sucked into the chamber. There is a short flash time (milli-seconds) when the solid particles and the bristles are contacted to maintain an attachment. It is not clear how the particles are adhered or attached to the bristled setule and efficiently disconnected to be further transported towards the midgut. Several assumptions were considered as mechanism of particles attachment such as chemical, electric and adhesion linkage. Particles are assembled by the bristled setule not by sieving. The P3 and P4 trunk limbs are gleaners or gatherers which compile suspended particles, but they are not filters. Better suitable physical term definition of the particle abstraction is therefore assembling. The definition dispute between filter and assembler is not a semantic issue. Sieving (filtering) and assembling are physically dissimilar. The particles are not trapped or captured as the result of being larger than the mesh-size, they are collected. It is like a rake shoveling where the setule are symbolizing the rake which compile suspended particles from flowing fluid while passing through the "extensive filter Chamber" [4,5].

The trunk limbs activate the rhythmic mixture of water and particles cycle by driving it into the "filter chamber" and forwarded to the interlimb spaces and expelled posteriorly. Slow-motion projection of the cinematographic film and solid photos confirmed that no water is leaking through the seta. Microscopical observations confirmed solid particle (algal cells) attached to the setule but fluid flow in between the setule spaces was not confirmed.

The functional definition of P3 and P4 in Daphnia, as a filters was recognized as a reasonable outcome of their structure whilst direct observed sieving action was not documented [1-11]. The response of Daphnia to food limitation condition as P3 and P4 surface area size were reported and consequently indicated as an improvement of food biomass sieving pickup collection [7,8,20,21] although sieving action was not confirmed. Such a morphological change might be also interpreted as enhancement of water circulation demands possibly supported by larger paddle`s surface. If P3 and P4 are filters which collect particles by sieving, all particles larger than 0.6-0.7μm should be, possibly, strained and abstracted whilst selection is well known [18]. If particles gathering is not drive by sieving it is probably done by other factors, suggested as, physical adhesion, chemical or static electricity attachment. The indication of "not only by sieving" was raised [15,22]. A functional structure of P3 and P4 as "not solid paddle walls", [9] was consequently speculated as filtration. Fluid flow through the seta in-between the setule was not confirmed. A misleading interpretation of filtration was defined as the mechanism of food particles abstraction in Daphnia [4,5], where small and large non-selected particles are retained. The assembled operated mechanism of P3 and P4 is closely related to size-fractionation of suspended particles mixed in microfluids. The result of the study of the flow-driven features was a model of Deterministic Lateral Displacement (DLD) is aimed at Microfluidic Systems conditions and size-separation of suspended particles. The particles move along a principal direction in the micro tube until a locked-to-zigzag transition takes place when the driving force reaches a critical angle [23-26]. Filtering is not involved in the process of particles assembling and abstraction exist without sieving. The ability to separate specific targets (suspended particle) in a micro fluid is essential for selective food items abstraction where a myriad of different particles are presented as size mixture is moving between P3 and P4 in Daphnia [27-29].

The existence of filtration through micropores diameter of 0.7-.0.6μm or less, [13,16,18], require investment of energy. Moreover, increase of water viscosity and Re decline is accompanied by enhancement of energetical investment. Sieving action has the potential for fluid flow to undergo irregular disturbances or even creating of turbulent flow. A smooth laminar flow which is optimal for undisturbed microflow system whilst sieving cause a stirring effect. Evaluated solid photos taken from the cinematographic film, [12-14] estimated time span of 127 milliseconds (mS) for fluid lump to pass a distance of 36.25μm of which estimation of flow velocity is 0.285μm per 1mS associated with Laminar Flow type and low Re. Flow velocity retardation probably affected by sieving might cause erratic turbulent flow and Re. increase. Laminar flow enables optimization of the micro-water currents management. The operational mechanism by the trunk limbs is a rhythmic pulsated stroke beat [12,13] that transfer water lumps through the "filter chamber" [4,5] from the proximal to the distal body part. Coordination is maintained between two microcurrents whereas filtering might cause system disturbances. Sieving activity as fluid flow through a mesh might be also an ecological disadvantage property. Evolutionary progressive development promotes resiliency and diminish ecological weakness. The development of P3 and P4 functional usage has evolved towards resiliency opposing fragility. The functional operation of P3 and P4 as "flexible solid walls" followed by food particles assembling improve animal resiliency. The definition of "solid flexible walls" [9] of P3 and P4 appendages is right but "strainer" is inappropriate. The food particle abstraction process start by particles assemblages, than packing (dewatering) for transportation. The P3 and P4 are functioned as pumping-injecting apparatus but not as filters [28]. Dispersed food particles are adhered onto setule and packages are formed. Created particle packages are transferred through the mouth to be grounded by pair of mandibles and forwarded into the midgut. The rate of packages delivery from the "filter chamber" [4,5] towards the mouth and through the mandible into the midgut depend on their biomass accumulation rate. The higher the particles density and size are, the higher is the packages delivered rate (Figure 1).

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Competing Interests

The authors have no conflict of interest that may affect this article.

Data availability

All the data generated and/or analyzed during performing this current study are available upon request. There is no restriction on the availability of materials and data from the corresponding author on request.

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Contributions

M. Gophen, K. Kolhage and *W. Geller* cooperated in the design and constructing the Cinematographic system and the execution of the experiments.

Ethics Declarations

Competing interests

The authors declare no competing interests.

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