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The Feeding Mechanism of Daphnia is not Sieving

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Abstract

During a historical period of more than 100 years, the function of the P3 and P4 thoracic appendages in Daphnia was defined as filtering. The role of P3 and P4 flapping was indicated as the creator of internal water circulation aimed at gas exchange (respiration) and feeding mechanism. Precise examination of in vivo cinematographic film (high-speed camera, 250 frames per second) by a slow-motion and magnified projection of solid photos of tethered Daphnia confirmed that no water flows through the intra-settular micropore spaces of the P3 and P4 trunk limbs while fluttering was indicated. Therefore, Daphnia's feeding mechanism is suggested to achieve particle abstraction not by P3 and P4 waived sieving. Straining action requires extra metabolic energy investment, and saving it is an advantage. P3 and P4 appendages in Daphnia are not filters. These trunk limbs are compartments of internal water circulation and respiration cycle mechanisms in Daphnia. Food particle abstraction is not done by sieving, resulting in a saving of metabolic energy. Paddle or "flexible solid walls" functioned likeness of P3 and P4 indicates an optimization during evolution progress as physiological advantages are therefore justified. Evolutionary progressive development promotes resiliency and not ecological weakness. Solid walls function of P3 and P4 support ecological resiliency.

Keywords: "Daphnia" "Trunk Limbs" "Feeding" "Sieving" "Flexible Solid Walls"

1. Introduction

The study of evolution initiated discoveries of natural occurrence of evolutionary blunders which is dissimilar to the process of blunders evolution. The attribute of the sieving mechanism to the P3 and P4 trunk limbs is a blunder. Over one hundred years the observed ultrafine sifter structure of P3 and P4 was deciphered logically as a sieving or filtering apparatus. Thousands of handsome experienced well-known scientists published a vast number of zooplankton studies where filtration was confidently a counterpart key factor unique in the Daphnia's feeding mechanism apparatus. Nevertheless, "Experience is simply the name we give our mistakes" (Oscar Wilde). The thought of the absence of clear, solid direct observation documented indication confirmed water transfer through the micropores of P3 and P4 from one to the other side of the "structured wall" induced the present study. Actually, Wilde intended that blunder was compatible after having been done. The disadvantage of scientific blunders that attribute sieving ability to P3 and P4 is the decline of awareness of curiosity towards discovering the mechanism of particle abstraction. Solid documentation about the feeding mechanism of Daphnia included the P3 and P4 structure and the process of suspended particle abstraction. Although microscopical observations confirmed food particle accumulation on the internal surface of P3 and P4 evidence of sieving was never confirmed. Not even one scientific documented study about the feeding of Daphnia where the definition of filtering is not considered. Moreover, the lack of information about water transfer through P3 and P4 from one side to the other induced exaggeration of confidence that it exists, although never directly observed. Therefore, the definition of P3 and P4 as "filters" is probably a blunder. On the other hand, as other inevitable blunders, they enhanced scientific advances [1].

Limnological research for more than 100 years has indicated that the function of P3 and P4 trunk limbs of Daphnia are presented as filters and sieving mechanisms responsible for particle abstraction. A dual-purpose role of P3 and P4 was suggested: internal water circulation (inflow-outflow) aimed at the enhancement of gas exchange (respiration) and feeding mechanism. The feeding mechanism is a suspended particle abstraction inside the spaces between P3 and P4. It has been studied by an indirect conceptual methodology: The limbs are perforate structured, and particles are abstracted from the surrounding media, collected and transferred into the intestine filtering is therefore concluded. Nevertheless, the recent renovation of cinematographic technology justified the rejection of the filtering action. The mechanism of food particle abstraction in Daphnia was earlier disputed between

“sieving” and “not only sieving”. This paper represents the renovation of the widely accepted concept of filtering function attributed to P3 and P4 limbs. Sieving action is unlikely and P3 and P4 are probably not filters.

2. Methods

A cinematographic study was carried out using a high-speed camera (Photo-Sonics 4C; 250 frames/second) operated through fixed microscopical lenses [2] [3]. The dorsal side of a tethered *Daphnia magna* (Straus, 1820) (3.7 mm, 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 (0.45 μm filter paper) lake (Bodensee, Germany) water [2]. 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 into the water media close to the animal intake site [2] [3]. 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. The visual indication for fluid penetration through P3 and P4, or transportation from the inner to the outer surface of these paddles, was carefully carried out. In the vast capacity of documentation, the following synonym titles are given to *Daphnia*'s P3 and P4 organs: Trunk limbs, Combs, Filter, Sievers, Sifters, Strainers, Thoracic appendages, Solid walls, Flexible walls, and paddles.

3. Results and Discussion

3.1. Historical background

Throughout the long history of limnological studies, P3 and P4 appendages in *Daphnia* were hypothetically reported as filters although direct observation of water penetration through the intra-settular spaces of P3 and P4 was not reported. A breakthrough of this historical research in Limnology is reported here: Food particle abstraction by *Daphnia* (and probably other non-predator Cladocera) is not a result of the sieving mechanism. An attempt to modify the traditional concept of the sieving mechanism in *Daphnia* is presented. Therefore, the consideration of P3 and P4 appendages as “flexible solid paddle (walls)” [4] is not incorrect. These appendages are two components within the complex mechanism that activate two alternate internal micro-water currents in *Daphnia* supporting gas exchange (respiration) and food particle abstraction [2] [3] but not by sieving.

The definition of filtering (sieving, straining) execution by the anatomic structure described for P3 and P4 thoracic appendages in nonpredator freshwater Cladocera organisms (emphasized *Daphnia* spp.) was widely accepted. The definition of a term for the function of P3 and P4 as a filter (sieve) was born as a reasonable outcome of their newly discovered structure. It makes sense as an interpretation of an indirect observational investigation but was not confirmed by a directly indicated observation.

The functional interpretation of a comb-like structure of *Daphnia* comprised of flexible long and short seta in a row induced the definition of a filter organ by the scientific community. The terminological implication of bird feather structure to P3 and P4 structure indicates the Rachis, Barb and Barbules organ parts similarity. This structure creates tiny micropores (0.6-0.7 μm diameter) which researchers have attributed to sieving capability [3]. During the long history of zooplankton feeding mechanism research, this structural type was considered a sieving organ that supports food particles within the feeding or grazing mechanism. The surface area (Korinek and Machacek 1980; Korinek et al. 1980), the diameter of the intra-settular micropore in relation to abstracted particle size and density [5], of P3 and P4 and their suitability to ecological conditions were widely documented. Thienmann and Naumann established (1921) the relationship between the physicochemical properties of lakes and their biological productivity, (Seetypenlehre). It was accompanied by freshwater zoology research definition of feeding habits of Cladocera as filtration (quote): “The water is driven out towards the caudal edge, and in so doing it must pass through a filter chamber formed by delicate feathered hairs on the edge of the Podobranchs” ([6-11] . Further wide acceptance of this definition was formulated as: ”Herbivorous planktonic Cladocera obtain food by filtration” [12-18] [26]. Nevertheless, this definition is misleading because no evidence was reported for water transfer through the P3 and P4 limbs from one to the other side resulting in particles retained. If water does not migrate through the setae, particle accumulation on the internal surface of P3 and P4, which was precisely confirmed, is driven not by sieving but probably by other factors, such as solid capture, physical, chemical or static electricity.

The research on the feeding mechanism of non-predator Cladocera (mostly *Daphnia*) was intensively expanded in two directions: 1) the ecological significance aimed at metabolic properties and ecological consequences and 2) the settular structure features and the physicochemical properties of P3 and P4. The research about the function of P3 and P4 reflected and mostly induced by their settular image which strictly resembles a strainer (Filter, Sieve, Sifter, Colander). Research attentions were therefore dedicated to the morphological,

mechanical and later chemical properties of both the trunk limbs and the food particles and their interactions. These studies considered only one option of operational management - filtration [2] [3-5] [13] [19-25]. Although a conclusion of “not only by sieving” was suggested with regard to the function of P3 and P4 and was documented [18] [26], the major importance was granted speculatively to sieving.

The pretentious denial of historical milestone definition which existed during a long history of limnological research is a bold action. Although there is a history of more than 100 years of limnological research and a vast number of publications about the feeding mechanism of nonpredator Cladocera organisms, direct microscopic observation of the function of P3 and P4 has evidently never been reported. Numerous publications based on an indirect interpretation were documented. Moreover, a group of scientists even indicated P3 and P4 limbs as “not solid paddle walls” [4], which consequently confirms the conclusion of being filters. The present study confirms that no water penetration through the setae of P3 and P4 occurs. Conclusively, P3 and P4 are flexible solid paddle walls that are not filters.

3.2. Why Evolvement of Filtering Action was Unsuccessful

Previous studies [2] [3] [5] documented two alternate microcurrents within the body space between two carapace valves. One flows beneath the carapace and the body's soft tissues, and the second splits between P3 and P4. The water mass in the 2nd microflow is in contact with the internal surfaces of P3 and P4. Water penetration through the setae of P3 and P4 and transferred to the other side of the appendage justify the filtration definition, but it was not confirmed, therefore, the sieving conclusion is speculative. Particles straining out of a fluid matter require liquid mass transfer from one (inner) to the other (exterior) side of the filter. This is likely not the case and water loaded with particle suspension flows just along and intact with the inner space of the appendages. It was therefore concluded that feeding is not a result of filtering action and grazing is not maintained by sieving. Grazing is the result of particle abstraction by the P3 and P4 limbs, which probably exist by mechanisms other than sieving. Particles are adhered onto the inner side of the P3 and P4 trunk limbs, being abstracted from the water mass was not done by sieving, and probably other factors are involved. The terminology of filtration action such as filtration rate, or filter feeding, should therefore be replaced by different definitions, probably as chasing, abstraction, accumulation, etc.

The contact between suspended particles within the water and P3 and P4 internal surfaces initiate adhesive interactions suggested to be either physical (surface-tension), chemical

(chemical bounds) or static electricity-driven forces. The maintenance of filtration through the setae intra-settular micropores (0.7-0.6 μ diameter) [2] [3] [5], demands energy which increases with increasing water viscosity and Reynolds number reduction. Water transfer (filtration) through the micropores of P3 and P4 requires extra energy investment which is probably beyond the organism's capabilities (Vogel 1988). If feeding particles were abstracted by sieving, the ecological distribution of Cladocera might be limited to water properties with low viscosity which enable efficient water migration through the micropore. If the feeding mechanism of Cladocera is not maintained by sieving, feeding and sieving through fine mesh size filters are independent. If the feeding mechanism is maintained by sieving the impact of water quality (viscosity) is critically efficient. The sieving operation requires energy investment, which might slow down the rate of beat stroke and water flow velocity. Consequently, reduction of the frequency of the entire appendage system and consequently the swimming speed and floatation capability, of the animal and gas exchange (respiration). The reduction in swimming speed and floatation capability and therefore enhancement of vulnerability to predators is also predicted. The evolutionary shift from sieving to other particle-adhering factors evolved an ecological advantage. The evolutionary elimination of the sieving and management function of P3 and P4 as "solid paddle walls" is an advantage [27]. In other words, the non-existent sieving mechanism in non-predator Cladocera organisms is an environmental benefit. The ecological advantage of the reduced vulnerability by the maintenance of two alternate internal microcurrents was previously documented [2] [3] [5].

The volumes of the two diverging microcurrents within the body of the Daphnia in between the two carapace valves are alternatively coordinated and not equally split: the lateral lumps divergence includes 65% of the total water inflow whilst 35%-in the internal branch lumps [2]. Both lumps flow through body compartments such as thoracic appendages and, the internal surface of chitinous carapace valves. The water lumps are conveyed (dragged, pushed, or both) inside these internal body open spaces where fluid resistance force is acting opposite to the motion of water. This existing force is between the water and the solid internal surface of the trunk limbs. This drag force is dependent on the micro-water current velocity as defined by Reynold Number. Surface Friction force decreases fluid velocity in relation to adjacent solid objects such as P3, and P4.

It has to be considered that suspended particles within the fluid enhance internal friction, and therefore reducing surface friction force is critical.

It is suggested that P3 and P4 creation of partial or complete sieving action has the potential for fluid flow to undergo irregular disturbances or even mixing turbulent flow. Whereas, without sieving interference creating a laminar flow where fluid moves in smooth layers is possible. It is not impossible that sieving might have an impact that causes the stirring effect. From the evolutionary point of view, the following topic is curious: Why settular structure was developed and not a solid surface wall (paddle) for intermittent flapping limbs? A tentative definition might be that the settular structure of fluttering limbs saves energy.

In previous studies, [2] [3] [5] [25] we estimated a water flow speed of 127 mS (milliseconds) along 36.25 μm route (L) through either P3 or P4 which is 36.25mm per second. It is a high speed which is associated with low Reynold Number (Re) which is a characteristic feature of Laminar flow. Moreover, if viscous forces (resistance to flow) within the water flow along the P3 and P4 are dominant, the flow is laminar and Re is low. High Re indicates turbulent flow and erratic velocity profile. Diminishment of flow velocity and prolongation of flow route (L) factors might cause erratic turbulent flow and higher Re. These are the factors that enhance the impact of sieving maintenance which enhances the investment of metabolic energy. Laminar flow enables optimization of the micro-water currents management. The result of sieving interference is flow velocity reduction, prolongation of flow route, erratic turbulent flow and Re elevation. Paddle likeness as “flexible solid walls” which optimized evolutionary advantages is therefore justified.

The appropriate perceptive concept of the internal space between P3 and P4 and the settular intervals (spaces) as one operational internal system comprised of two different diameters of water flow spaces: 1) The distance between P3 and P4, diameter dimensioned in mm; 2) the intra-settular spaces (0.6-0.7 μm diameter) defined as thin micropore capillaries. The operational mechanism of the trunk limbs is a rhythmic pulsated stroke beat that transfers water lumps towards internal channels alternatively. The rate of the flow was calculated as 1.02 ml/hour [3]. A coordination is required between the two microcurrents of which one is channeled between the trunk limbs and the second underneath the carapace along its internal surface. If the water lumps in between the limbs are filtered, the microcurrent will be slow in disturbing the perfectly coordinated system. The flow velocity through the large diameter passages is high and requires lower energy investment than the predicted velocity through the intra-settular thinner diameter if filtration is actioned accompanied by extra Δp operative demands. Sieving operation demands pressing water from the large diameter space through the capillaries between the intra-settular spaces. Water transfer from a wide diameter

cylindrical space where the flow velocity is higher to a much smaller diameter free space passage (or short capillary micropores) maintaining slower velocity accompanied by demands for extra energy investment. This kind of water transfer is not possible without extra energy investment. The similarity of fluid mechanics rules implication in vascular Angiosperm plants [28] to *Daphnia*'s properties is considered. Upward water transfer in Angiosperm plants occurs through vessel elements (cells), 1-4 mm in length each with partition with open punctures in between the elements. The elements are structured one on each other forming long pipes for water transportation. The proximal (top) and the distal (bottom) end partitions of the vessel are perforated by bordered pits and not punctures. The flow velocity through the bordered pits slows down the fluid velocity because the passage of open space through the punctures is wider than that through the bordered pits [28]. The measure of water conductivity through pipes and its implication to water transportation in Angiosperm plants was widely studied [28-31]. Fluid velocity increases from the wall to the central part of the flow. In plants, the wider the Trachea (water transport vessel parts) the higher the fluid velocity in the central part of the vessel. The implication to *Daphnia* indicates similarly, where the flow velocity in the middle space between P3 and P4 is higher than in the margins scratching P3 and P4 reducing available Δp energy required for pressing water pass through the intra-settular spaces. Nevertheless, a significant dissimilarity exists between upward water transportation in plant vessels and water transmission as alternate pulsed micro-currents in *Daphnia*. The functional dissimilarity between plants and *Daphnia* does not deny optional physical rules supported evaluation. The functional concept of internal water mass migration in Angiosperm vascular plants and in *Daphnia* are differently anatomically organized but deserve similarity in the usage of physical rules of which Cavitation– micro gas bubbles production occurs. For the maintenance of filtration, it is probably not impossible that fluid alternate exchange between high and low pressures may induce cavitation. Therefore, evolution processes probably "replaced" filtration (as suggested) with a different appropriate mechanism for food particle subtraction or simpler, no capillarity type of water movement exists in *Daphnia*.

Fluid velocity through pipes is positively correlated with hydraulic conductivity and Hydraulic conductivity is related to the pipe radius to the fourth power. A minor change in the pipe radius creates a big difference in the fluid volume passing through the pipe and enhances resistance to flow. For example, diameter reduction from 40 to 80 μm reduced flow through volume by 93% and relative conductivity declined 16 times [28-31]. Taking these principles into account, there is a thought-provoking doubt about the filtration functioning of P3 and P4

in Daphnia. Moreover, scanning electron-microscopical images confirmed the existence of the app. 40-60 intra-settular 0.6-0.7 μm thickness passages which enhance the Δp required pressure (energy) for press water flows in-between the intra-settular spaces [2] [3] [5] [25]. In vascular Angiosperms, plants lignified cells (trachea) create long-tapered vessels. A similar function of the tracheary vessels is water transmission and in Daphnia where high and low-pressure exchange spaces are involved in the water transportation process, therefore rules of fluid mechanics are relevant for both systems.

3.3. Why capillarity was not evolved in Daphnia?

Capillarity of the lateral microflow water through the micropores of P3 and P4 might confirm the existence of a sieving mechanism within the feeding process of Daphnia but was not evidently supported. Capillarity action within the porous spaces of the P3 and P4 structure is created when forces of adhesion between water molecules and the micropore walls, cohesion force of water molecules among themselves, and surface tension within a slid static system which is not the case. The double alternate micro-currents of the sub-carapace and lateral dynamically comprised moveable components. The system maintains the pulsated pushing of water lumps when each full (upward and downward) stroke continues at 127 mS which is a frequency of 7.87 beats per second [2] [3] [5]. Consequently, the flexible and moveable micropore in a stable system causes deformation of the length, diameter and shape of the pores, and therefore water transfer by capillarity with the pulsation of 7.78 per second is unlikely. Conclusively, water transfer through the P3 and P4

“flexible walls” require energy investment. The avoidance of such an investment of metabolic energy is therefore considered an evolutionary advantage. Moreover, capillary flow rate is linearly dependent on surface energy and inversely linearly on viscosity which might cause flow fluency disturbances. Capillarity action occurs as a result of stuck water molecules to each other (cohesion) and water molecules stronger stick to external material (adhesion). The release of the capillary water from the micropore into the free space on the other side of the “flexible wall” requires energy (ΔP). Metabolic energy balance consideration in Daphnia therefore justifies the indication of no water transfer through P3 and P4, i. e. no sieving.

The relationships between pressure, fluidic pressure and flow rate were widely documented (among others) [28-31]. Fluidic resistance is proportional to the length of the device, which is the plant tracheary vessels wide (mm) interspace between P3 and P4 and the super narrow (0.6-0.7 μm) intra-settular micropore intervals. In Daphnia.

The Hagen and Poiseuille equation under stationary describes the laminar flow in a pipe [28-31]:

$$\Delta p = \frac{8\mu L}{\pi R^4} Q; \text{ or: } \Delta p = \frac{8\mu L Q}{\pi R^4}$$

Where:

Δp = Pressure difference between the two pipe ends

Viscosity = μ ;

volumetric flow rate = Q ;

pipe length = L ;

pipe radius = R ;

$$\pi = 3.14$$

Demanded pressure (Δp) that is required to exit water mass trapped within the wide (R) interspace between P3 and P4 is much lower than the pressure (Δp) required to press water into the narrow (R) intra-settular spaces.

Change in natural conditions consequently implies an increase of Δp [28-31]. Elevation of Δp occurs when commonly water viscosity (μ) increases; extra Δp is required due to longer L when pressed into the intra-settular spaces; the lower R of the intra-settular spaces makes Δp significantly higher. The function of P3 and P4 trunk limbs in *Daphnia* (and probably in other non-predator Cladocera) is cycling internal water flows. Nevertheless, their waving is not dysfunctional but logically aimed at internal water cycling whilst straining is not maintained.

Conclusively, the functional operation of P3 and P4 in *Daphnia* as filters is denied, the appendages act as solid flexible walls which transfer water mass as micro-currents within the body of *Daphnia*. Energy directing (Δp) to operate filtration through the intra-settular spaces will interfere with the entire system of water transmission.

3.4. Evolutionary advantage of the absence of sieving function

Evolutionary development is commonly aimed at the optimization of ecological adaptabilities. The advanced progress trend of ecological adaptability improvement of P3 and P4 function is presented as flexible solid walls. Evolutionary proceeding of implementing improvement is therefore towards flexible solid walls whilst the sieving function is a disadvantage property. Evolutionary progressive development promotes resiliency and not ecological weakness. Flexible solid walls function of P3 and P4 therefore supports improvement of ecological

resiliency. Evolutionary development or functional ecology improvement was evolved towards progressive adaptation of P3 and P4 through minimizing metabolic energy investment to achieve the highest efficiency of food particle abstraction. Therefore elimination of sieving function from P3 and P4 usage in Daphnia is compatible. The development of the P3 and P4 functional usage evolved towards resiliency and not fragility. If these trunk limbs function as “flexible solid walls” without a sieving role, the extra energy investment is saved. Such an improvement in energy balance enhances the channeling of energy to other animal necessities. P3 and P4 sieving functions might deteriorate escapeability and enhance vulnerability and refuge necessity, whilst eliminated sieving functions improve animal resiliency.

3.5. Only dead fish go with the flow (M. Muggeridge)

A tentative “beyond the pale” approach to the non-sieving feeding mechanism of Daphnia is supported by studies carried out in Vascular Plants. The combination of the physical rules of fluid mechanics and the energy balance of Daphnia for the consideration of not sieving in Cladocera was not thoroughly considered earlier. Energy balance and the evaluation of living expenses are critical for the analysis of the P3 and P4 functional roles. Herewith an assumptive usage of fluid mechanics rules is implied to confirm that P3 and P4 are not filters. Conclusively, the abstraction of water-transported particles by Daphnia is not executed by sieving. The definition of “solid flexible walls” [4] of P3 and P4 appendages is an appropriate definition and the strainer is wrong.

Scientific blunders are not only inevitable but also critical for scientific progress. It is predicted that the definition of the sieving trait of P3 and P4 as a blunder would be probably a stimulator for further investigation. The impact of a new scientific definition within the community can be probably approximated by the intensity of objections by those who have a lot to lose [1]. I have dedicated a significant part of my career to protecting the “filtering” or “not solid walls” definitions and have not easily changed my mind. Nevertheless, due to the essence of science, new evidence justify the change presented in this paper. It is known that the more scientists are obliged to a certain idea the more difficult the change is.

4. Conclusion

1: Cinematographic analysis in Daphnia confirmed no liquid transfer through P3 and P4 trunk limbs while in action.

2: P3 and P4 trunk limbs create a flexible “wall” but not filters.

3: The feeding mechanism of Daphnia and probably other herbivore Cladocera is not sieving.

4: The P3 and P4 complex settular structure optimize appropriate internal water flows and undisturbed backward stroke.

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6. Conflict of Intertests:

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

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