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Retrospective Forthrightness Scientific Farewell—Daphnia Is Not a Filter Feeder: Innovative Review

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Abstract

Cinematographic video tape slow-motion analysis confirmed that in Daphnia, food particle retention occurs through assembling, not sieving. Particle abstraction is achieved by assembling and packing rather than by sieving. A straining action which requires energy, poses an ecological disadvantage. The achievement of internal fluid flow sieving through a mesh may be therefore a physiological disadvantageous trait. Sieving action of internal current could create flow irregularities and turbulence. Filtration induces laminar flow interference, resulting in a stirring effect. The two trunk limbs dangle freely within a chamber space where food particles are gathered. The food particles assembling and packing mechanism within the feeding process improves energy savings and animal resilience by locomotion improving vulnerability.

Keywords

Daphnia, Feeding Mechanism, Sieving, Assembling

1. The Reviewed Concept

The result of precise reevaluation of slow motion and frame-by-frame projection of the cinematographic video justified a misleading confirmation of previous interpretation we suggested [1]-[4]. Renovated interpretation of the feeding mechanism of *Daphnia* operated by P3 and P4 trunk limbs is presented here. The assembling and non-filter mechanism-definition as indicated here is the outcome of newly evaluated information reconsideration. The conceptual definition transition of the feeding mechanism in *Daphnia* from sieving to assembling was evidently confirmed by slow-motion and solid photos. During a long history of indirect eco-physiological research of freshwater filter-feeding Cladocera, the definition of "sieving mechanism" was accepted and implemented despite the absence of direct evidence. The conclusion given in this paper included literature review aimed at bridging the gap between indirect and direct observational evidence solely on the feeding process of *Daphnia*. Among the many researchers who studied the role of freshwater Cladocera within the ecosystem, M. Gliwicz was one who particularly stood out. As a diligent scientist of freshwater ecosystems, Gliwicz investigated feeding habits of Cladocera and Fish, though he accepted a-priori the sieving mechanism of Daphnia as utilized by the "so-called" filter-feeder Cladocera. The feeding mechanism of *Daphnia* is extracting algae from the feeding current, assembling and handling the particles to position them in front of the mandibles. For more than 100 years, the paradigm was that the flow of water passes through the setae and setulae bristle (STB) of P3 and P4 while the suspended particles get caught on the fine mesh formed by the setae, forming in this way a Dead-End filter.

The experimental facility and evaluation Method background which initiated the reconsideration and change of conclusion are given in previous documentations [1] [2].

2. Filtration (Sieving) Definition: Historical Background

The function of the feeding mechanism in Daphnia is extracting food particles a suspension, assembling, handling and moving them towards the mandibles. For more than 100 years, the paradigm was that the suspension flow passes through the setulae bristles of P3 and P4 while the suspended particles get caught on the fine mesh formed by the setae, forming in this way a Dead-End filter. However, the analyses of high-speed video [1] [2] using tracer dyes (Indian Ink) to track the suspension flow path could not verify the validity of this paradigm. P3 and P4 trunk limbs are the creators of the in-out suspension flow circulation that beside food particles supply also function as supporters of gas (DO) exchange for respiration [5], Filtration activity, food particles capture and motility disturb optimal flow velocity through the mesh achieving sufficient circulation rate for simultaneous effective respiration and food particles assembling [6]. Daphnia spp. features four pairs of appendages that are covered by the carapace. These appendages move at around 10 Hz and generate an in-out-current system to extract particles for food. Throughout the long history of limnological research, P3 and P4 appendages in *Daphnia* were reported as filters although direct observation of water flows through the seta and setulae bristle spaces was never documented [7]-[15]. P3 and P4 were defined as the only trunk limbs that are directly involved in the feeding process through filtering action [16]-[23], whilst other limbs accompanied supporters were documented [16]. The definition of filter feeding mechanism in *Daphnia* was stated distinctly for P3 and P4 which are responsible for filtration, and *Daphnia* is therefore a filter feeder [16]-[23]. By definition, filtration can be practiced if a particle-bearing current is drawn or pressed through a "filter" [21]-[23]. Low Reynolds number (viscous flow) regimes prevail, a boundary layer around the setulae bristles of the filter which may exceed their inter-setular bristle distances and little or no flow takes place between these setulae bristles [24]-[26]. Although the filtering (straining) function definition was widely accepted, the functional attribution of sieving that requires solid confirmation, was not documented. The definition of P3 and P4 as filters is, therefore, an unintentional blunder or circumstantial evidence. The research of feeding mechanism of *Daphnia* initiated at early previous century and due to lack of another suitable appropriate option, promptly "sieving" type was awarded [1]-[4] [16]-[23] [27]-[39]. The studies were focused on the anatomical structure and the most plausible ecological outcomes was filtration mechanism.

3. Why Sieving Is a Misleading Interpretation

The interpretations of the functional morphology [21]-[23] as sieving apparatus is erroneous. Filtering mechanism is maintained by water flow through a sieve and particles larger than the mesh size are retained. Despite of food particles lumps transformation into the digestion truck of the *Daphnia* were observed and documented in living animals the mechanism of their formation was not. This process resembled the dewatering action of algal and blood cells on micro-tubes known from commercial instrumentation. So far, what is the definition of a process involved in the feeding mechanism of *Daphnia*? Sieving, Assembling or Dewatering. Recognition of water fluency through the open space between the P3 and P4 components is based on a cinematographic study [1] [2] [4]. The Cinematographic video confirmed sucking effect created by upward movement P3 and P4 which suck water from the environment into the space between the two carapace valves into the space defined as "filtering chamber" [21]-[23]. The downward move of P3 and P4 squeeze the water continuous flow outward laterally directed underneath the carapace exit. The daphniid mechanism evolved by restricting particle abstraction to trunk limbs 3 and 4, while limbs 1 and 2 are not involved in the feeding process [21]-[23]. Several functional synonym definitions have been given to the P3 and P4 limbs: trunk limbs, comb, filter, sieve, sifters, strainers, thoracic appendages, solid walls, flexible walls, and paddles. *Daphnia* employs two internal alternate micro-flows carrying food particles, one of which is directed into the space between P3 and P4 [1] [2]. The conclusion that particles can be caught by filter plates bearing a filterary setulae bristles was concluded from documented solid still photos and resulted illustrations [3] [16] [21]-[23]. It is a circumstantial evidence since neither photo nor cinematographic film did not evidently confirm it. P3 and P4 are not network-structured, where every node is interconnected with every other node, forming a lattice-like pattern of connections. The setulae bristles are freely separated from each other. The documented functional anatomical structure of P3 and P4 [21]-[23]) is not appropriate for a filtering action. A sieving action includes a lattice mesh through which fluid flow and suspended particles are retained on its surface. Solid particles are removed by a filter medium that permits the fluid to pass through, while particles larger than the filter mesh size are retained. The setae of P3 and P4 are employed as flexible solid paddles that suck water inside and press it outside [1]-[4], while free setulae bristles are hovered inside the interlimb space defined as "filter chamber" [21]-[23]) which is full of fluid medium collecting suspended solid food particles. Several assumptions have been considered as mechanisms of particle attachment to the bristles, such as chemical, electric, and adhesion linkages. Consequently, particles are assembled by the setulae bristles, not by sieving. P3 and P4 are gleaners or gatherers that compile suspended particles, but not filters. The appropriate term for particle abstraction is therefore "assembling". The particles are not trapped or captured as a result of being larger than the mesh size, they are collected. Moreover, calculations based on capillarity dynamic rules enabled rejection of capillary force involvement in water migration processes within the *Daphnia*'s body. The Poiseuille capillarity equation is not applicable. Despite of the small pore size created between the setulae bristles in *Daphnia*'s trunk limbs, while considering the entire trunk limbs structure, the assumption that filtration occurs through sieving is therefore not applicable to *Daphnia* feeding upon algae.

4. The Fine Ultra Structure of P3 and P4

The ultra-structure of these limbs consists of three components: 1) Setae; 2) Two rows of Setulae bristles located perpendicularly on each Setae; 3) Two rows of ultrafine knobs (bosses) on both sides of each Setulae [17] [19] [21]-[23]. The space between the setulae bristle was measured as 0.6 - 0.7 µm whilst, the ultrafine structured knobs caused the free space between the setulae bristles to be even narrower. Consequently, if P3 and P4 are filters that collect particles by sieving, all particles larger than 0.6 - 0.7 µm are strained and abstracted, whilst selection is well known [3]. Filtration as feeding mechanism of aquatic organisms is precisely define of a system composed of two ultimate components: solid strainer and suspended particles within fluid solution. The innovative analysis of the cinematographic video, presented in this paper, does not confirm existence of straining activity. Nevertheless, food particles are accumulated and transferred towards the Daphnia mouth parts. It is therefore suggested that the particles are collected (and assembled) by sticking to the setulae bristle tips (**Figure 1**).

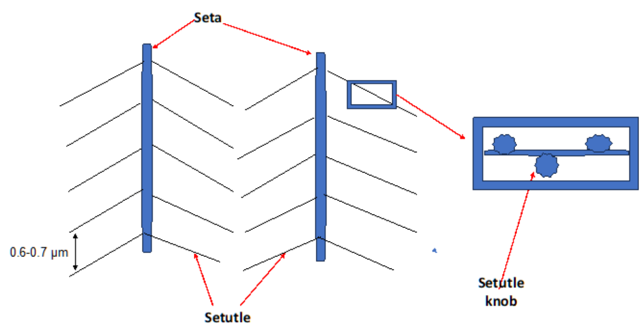
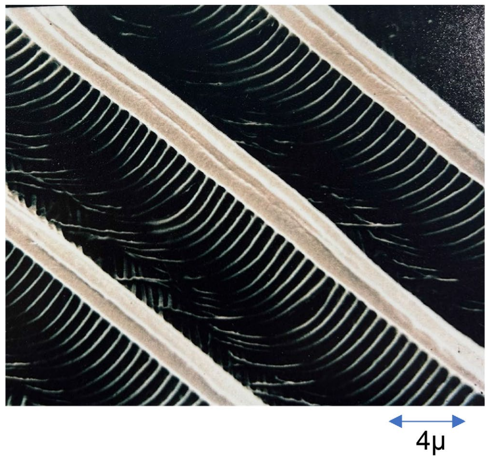


Figure 1. Schematic illustration of P3 and P4 trunk limbs: Setae, Settula and Setule knobs (Bosses) are indicated separately.



No.1 (upper): of the external surface of P3 setulae's bristle comb: the trunk limb is upward positioned drawing backward P3 comb expanding the "filter chamber" (see text) causing volume sucking inlet water flow, with suspended food particles. The water along the P3 internal surface whereas no water leaking (sieved) "solid wall" through the setula were detected (Photo: W. Geller). No. 2 (lower): External section surface view of the P3 comb, thick Seta and fine thin setulae bristles are shown.

Photo 1. Scanning electron microscope images (photos: W. Geller).

5. Particle and Mesh Sizes Interdependence

Historically, definition of "Mesh-Size" in Daphnia is refer to the distributional distance between adjacent seta and strictly considered as size selective tool which is correlated with ingested particles size but was denied by the Cinematographic Video. In fact, this correlation exist but not as a result of inter seta distances but through the size and density of the setulae. That is because, smaller "mesh size" include thinner, longer and denser BST (Bristle Setulae) which enhance efficiency of small particles retain.

Earlier experimental studies [3] documented results about the correlation between 7 plastic-beads particle (Polystiren Latex Plano GmbH, FRG) sizes (diameter) ranged between 0.109 and 5.0 µ and ingestion efficiency by *Daphnia*. The correlation coefficient calculation was based on premise of particle ingestion by sieving mechanism (**Photo 1**) hypothesis thought the size composition of the feeding media and the gut content of the animals are comparable. The scope of the present paper is assembling replacement of denied filtering mechanism of food particles ingestion by *Daphnia*. The contact area between the surface area of the particle and the setulae bristles determines its ingestion efficiency. It is suggested that efficiency of particle retention is its surface area: The higher is the area the more efficient is its retention. The reason for lower retainment efficiency of small particles is not the mesh size but their lower surface area. Consequently, comparative presentation of beads particles size expressed by diameter and surface area is given in **Table 1**.

Table 1. Calculated Volume (μ^3) and Surface area (μ^2) of Micronic plastic beads used in experimental study of particle size impact on ingestion efficiency by *Daphnia* (modified from [3].

Diameter (μ)	Volume (μ^3)	Surface area (μ^2)
0.109	0.7×10^{-3}	0.038
0.176	2.9×10^{-3}	0.101
0.284	12×10^{-3}	0.251
0.357	24×10^{-3}	0.402
0.500	66×10^{-3}	0.791
1.010	0.533	3.178
5.000	65.6	78.5

Results given in **Table 1** indicate distinct sharp increase of bead's size, volume and surface area between 0.5 and 1.010 μ of bead's diameter and Ingestion efficiency was enhanced respectively [3]. The sieving mechanism concept indicates this stage of ingestion efficiency improvement as size dependent whilst the assembling concept respect the surface area as the critical factor. The assembling efficiency of large particles, having larger surface area, including attached bacteria are considered [24] [25]. The critical factor is not the surface area in relation to the particle volume which is higher as the volume is smaller. The crucial factor is the particle absolute surface area. The longer the diameter is, the larger the particle volume is, as well as its surface area. The feeding mechanism, particles assembling, is controlled by the efficiency of surface-to surface encounter between Setulae bristles tips and the particle surface.

Water flow through setulae bristles was speculated but not evidently confirmed by the "Filter Feeding" paradigm supporters. Therefore, an alternative option of particle gathering driven not by sieving but by other force factors, such as physical adhesion, chemical or static electricity. Moreover, the conclusion of "not only by sieving" was already suggested earlier [26]. Assembling is a concise alternative definition, to sieving, for the Daphnia's feeding mechanism. Filtration refer to fluid flow through sieve network and suspended particles retrain whilst assembling refer to suspension flow through space where setulae bristles are distributed and particles are encountered and adhered onto their surface. Physico-chemical processes are probably involved [24] [26]. Electric charge residing on a surface is a process which can lead to a surface charge. Adsorption of cations (positive) and anions (negative) which are interact with the particle surface create particle adsorption onto the surface of the rod shaped setulae bristle tips. Dissociation of chemical substances is also a mechanism of surface charge [24] [26].

The functional structure of P3 and P4 limbs as "not solid paddle walls" [27] was consequently defined as filtering speculation. The concluded statement presented here define food particle abstraction by *Daphnia* is not a sieving mechanism, particles are assembled but not strained. P3 and P4 are operators of the alternate internal micro-water currents supporting gas exchange (respiration), food particle accessibility for abstraction [1] [2]. and locomotion, but not enabling particle sieving.

Filtration through micropores diameter of 0.7 - 0.6 μm or less [2] [3] [16] [40]-[42] require investment of energy. An increase in water viscosity and Reynolds Number (Re) might be accompanied by an enhancement of energetic investment. Sieving by P3 and P4 has the potential for fluid flow to undergo irregular disturbances or even create turbulent flow. Whereas, without interferences caused by sieving, a laminar flow is smoothly granted as an undisturbed microflow system, while sieving causes a stirring effect. In previous studies [1]-[4], we estimated a water flow velocity of 127 mS (milliseconds) along a 36.25 μm path (L) (the distance between P3 and P4), which is 0.285 μm during 1 mS. It is a rather high velocity that is associated with a low Re, which is a characteristic feature of Laminar flow. When viscous forces (resistance to flow) [43] within the water flow along the P3 and P4 are enhanced, the flow is laminar and Re is low. Flow velocity reduction impacted by sieving causes erratic turbulent flow and higher Re [43]. Laminar flow enables optimization of the micro-water currents. The operational mechanism of the trunk limbs is a rhythmic pulsated stroke beat that transfers water lumps through the "filter chamber" [21]-[23] from the proximal to the distal body part. Coordination is maintained between the two microcurrents, whereas filtering might cause system disturbances. A combination of carapace open-close movements and internal up and downwards movements of the trunk limbs regulates the intake ("inhale")-outflow ("exhale") of the internal suspended algal cells' microcurrents. The gap between the carapace valves opens when the animal "inhales" algal particles from the surrounding water. Backward movement of the carapace valves towards gape closing "exhale" algal suspension of which the assembled (consumed) particles are absent. These cycled alternate operational activities are perfectly coordinated and should not be interrupted to ensure smooth regulation while sieving, as this can cause disturbance.

Consequent conclusion from flow dynamics rules derived from Stoke's Law domain: Water flows with a speed of ~1 mm/s around structures < 1 mm in size are laminar—the particles flow in ordered layers (laminar) without eddies or turbulence [43]. Analysis of the cinematographic video resulted flow velocity of 285 μm per second which is in agreement with Stokes definition of laminar flow type. A conclusive statement was documented [36] as follows: "With respect to fluid dynamics rules, our study provides no reason to reject the hypothesis that *Daphnia* collects food by sieving water through its thoracic limbs" [36]. Despite of sieving mechanism orientation of their study, the micro-structure of the filter and exact location of sieving implementation is not indicated. Therefore, sieving conclusion is doubtful. Brendelberger *et al.* [36] and many others had draw conclusions from microscopical still images of the anatomical structure of P3 and P4 suggesting that the logical and most reasonable conclusion is, that they are strainers and filtration action is caried out. Moreover, P3 and P4 are therefore not solid walls for water circulation activity, but, strainers, and filtration paradigm was consequently claimed [36].

A unique consideration that analyzed *Daphnia*'s feeding mechanism is the issue of the impact of drag force (friction) created between suspension feeding fluid and the animal limbs [43]. Three optional models were investigated: slender body, gap and parallel-cylinder. The comparative consideration aimed at selection of the appropriate model ultimately require distinct information about the micro-structure of the *Daphnia*'s filter. As of recent light-microscopy studies did not confirm the existence of net-work system on the inner side of the "comb" inside the "filter chamber" [21]-[23]. Network system includes particular units attached one to each other and free spaces in between. The evaluation of SEM photos might be misleading because significant modifications occur during the preparation process. There is no firmly established evidence to confirm the solid contact between the Bristle-Setulae (BST) of P3 and P4 on both sides of the "filter chamber" and disconnected alternately to create a temporary network for each limb beat. The present study considers free tips of the BST swing freely within the "filter chamber" space maintaining assemble of suspended particles. Therefore, the paradigm of suspended particles retention from a flowing along current through moveable BST network structure [21]-[23] [36] is unacceptable categorized as a legitimate disagreement.

A tentative supportive confirmation of the sieving mechanism [43] was studied experimentally through the impact of drag force on micro-currents. Nevertheless none of the experimental models is precisely correspond to reality [43]: 1): "Slender body shape", probably scarcely short filamentous algal colonies or rod-shape bacilli whilst amorphic detritus particles are not slender morphological phytoplanktonic algae shapes are; 2): "Gap", empty space between solid items, whilst network was not documented; 3): "Cylinder", whereas the intra BST intervals are round shape spaces. Although the three models' study [43] are not perfectly match reality, considering the range of 1 - 10 mm of water column is sufficient for potential overcome drag force resistance to continue smoothly undisturbed laminar flow to achieve sieving mechanism. Consequent conclusion by [43] and sieving mechanism is denied here not because of no friction disturbances impact but due to the absence of network. Conclusively there is an apparent practical reason to define P3 and P4 trunk limbs as assemblers and not filters with water passing through the inter limbs space ("Filter Chamber") and flexible free setulae bristles are freely swinging there. As long as the existence of solid network is not confirmed, the Cinematographic Video analysis confirmed the deny of sieving mechanism and therefor the validation of assembling function of the setulae bristles is confirmed.

6. Synopsis

The role definition of the trunk limbs, P3 and P4 in *Daphnia*, as filters, which function as sieve organ was not earlier thoroughly argued nor disputed. The research of the structure of those trunk limbs since early 1920's obviously granted them a definition of filters which is in contradiction with the "Solid walls" terminology adopted by other scientists. The establishment of the long-term and worldwide acceptance of the sieving concept of *Daphnia*'s filter feeding mechanism was not criticized scientifically. Contrary to that, the filter feeding mechanism of *Daphnia* was widely confirmed and supported by interpretation induced by the anatomical structure observation [21]-[23]. Significant progress of the research was accomplished by cinematographic method presented by several scientists afterwards in which the "solid wall deny" conclusion was replaced by filtration (sieving) paradigm. The disputed response to the query: *Daphnia*'s feeding mechanism is sieving or assembling might promote research and knowledge with potential implications on eco-limnological conditions. Nevertheless, the impact of renovated view on the feeding mechanism of *Daphnia* is predicted to be intensively objected. The more scientists are obliged to the sieving mechanism, the more difficulties are in the confirmation of changes. The objective of the present paper is to highlight innovative paradigm of *Daphnia*'s feeding mechanism model. Reconsideration of primary interpretation initiated the change of functional definition of P3 and P4 from sieving to assembling might be a stimulator for further improvements of a research blunder. Correlation between mesh-size and particle-size retention was evidently accepted as the result of dimension analyses. Nevertheless, it is an indirect conclusion because water-flow through the mesh was not confirmed despite clear evidence of water-flow along internal sides of the comb (mesh) being documented. The reconsidered indication does not deny similarity between setulae intervals and particle dimensions. The bigger the particle is, the higher the efficiency of its capture or assembly is. This is due to enhanced encounter opportunities between the free-tilted fine setula bristles and particles surfaces area. Fine mesh size was reported in *D. Magna*, *D. cucullata*, *D. longispina*, *Sida spp*, *Holopedium spp. and Diaphanosoma spp*. The feeding mechanism operated by those crustaceans is probably assembling as well. Finer size (mesh) and density of the bristles improve the efficiency of adhesive touch between particles and the bristles and therefore assembling capacity. The feeding mechanism of fine and coarse mesh-size daphnids is similar: assembling method. The consumption of fine and coarse particles by *Daphnia* is carried out by the same type of mechanism, which is not sieving. Evidence of water transfer, from the inner to the outer side, to the trunk limb comb (paddle) was not confirmed. Consequently, further analytical assessment is required for the comparative functional indication of small and large structured-mesh sizes. Suggested interpretation besides the previous use of assembling efficiency is due to the rate of the paddle beats. The size, and density of the bristles, as well as the food particles have an impact on demands of energetic investment and consequently beating rate of the trunk limbs. The functional definition of P3 and P4 in *Daphnia*, as filters, was recognized as a reasonable outcome of their structure. Actually, it is substantial evidence because a direct observation was not documented [17]-[23] [28]-[44]. The response of *Daphnia* to food limitation, as morphological changes of the size of P3 and P4 surface area were reported and consequently indicated as an improvement of food biomass pickup collecting [6] [29] [30] [45] but distinct sieving action was not confirmed. Such a morphological change might also indicate an enhancement of water exchange supported by a larger paddle's surface. Sieving activity, as fluid flow through a mesh, is an ecologically disadvantageous property. Sieving requires investment of additional energy resulted by pressure drop [46]. Evolutionary progressive development promotes resiliency and diminishes ecological weakness. The solid walls function of P3 and P4 supports the improvement of ecological resiliency. The development of P3 and P4 functional usage has evolved toward resiliency and not fragility. The functional operation of P3 and P4 as "flexible solid walls," followed by food particles assembling, improves animal resiliency. The definition of "solid flexible walls" [16] [36] of P3 and P4 appendages is probably correct, but "strainer" is inaccurate. Studies conducted on dead animals and Scanning Electron Microscopy (SEM) [3] [16] [36] were based solely on solid photos of P3, P4, and other trunk limbs with or without attached algal cells. Functional operative involvement was obviously concluded. Nonetheless, the descriptive interpretation process of interception from feeding current, collection and channeling of particles into the food groove, compaction (packing), and transport was not documented [16]. The food particle abstraction process requires dewatering for further digestion. Because low Re (viscous flow) regimes prevail, the boundary layer around the setulae bristles within the "filter chamber" [21]-[23] may exceed their inter-setulae distances, resulting in little or no flow between these setulae bristles [25]. The P3 and P4 function as water pumps [25] and food particle assembling but not as filters is more plausible [47] [48]. Assembled food particles are collected, not by sieving, but by assembled packing together. Created particle packages are pushed through the mouth to be ground by a pair of mandibles and forwarded into the midgut. The rate of package delivery from the "filter chamber" [21]-[23] toward the mouth and through the mandible into the midgut depends on particle density and size: the higher the density and the particle size, the higher is the rate of package delivery. The absence of evidence does not prove the absence of the phenomenon. It is not possible to directly observe water flows with suitable optical resolution passing the ultrafine structure of *Daphnia* setulae-filters [49]. The filter feeding mechanism was undoubtedly justified scientific conclusion. Nevertheless, further evaluation of Cinematographic Videos probably confirmed that it was an unintentional scientific blunder conclusion. Scientific research conclusion is valid if facing criticism is justify, if not, it might be considered as a conclusive blunder [50].

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Data Availability

All the data generated and/or analyzed during performing of 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 of the Cinematographic system and the execution of the experiments.

Conflicts of Interest

The author has no conflict of interest that may affect this article.

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