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# DIVERSITY AND FUNCTIONS OF LORICAE IN CILIATES (CILIOPHORA)*)

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The article focused on morphological peculiarities, chemical composition and function of the loricae in ciliates. Pseudochitinous (tectinous), hyaline and mucopolysaccharide loricae differ by chemical composition. There are also composite (pseudochitinous + mucopolysaccharide) and agglutinated loricae. The morphological features and associated protective properties of loricae and semi-loricae of sessile ciliates are also discussed. The increase in floatability of cells has been reported in literature as the main function of mucopolysaccharide and hyaline loricae in planktonic ciliates. It is the authors' opinion that the main function of the lorica is to prevent the contact of extrusomes or other capturing organelles of unicellular predators or parasites from the cellular membrane of ciliates. It is also assumed that another important function of the semi-loricae and loricae in sessile ciliates is to protect joints between their stalk and zooid from hydrodynamic loads.

**Keywords:** ciliate, lorica, pseudochitin, hyaline, predator, parasite, extrusome, hydrodynamic load

The various loricae (also named in literature as tests, envelops, cases and shells) are widely occur among different ciliate taxa [14], whereas in such groups as Tintinnida Kofoid et Campbell, 1929 and Folliculinidae Dons, 1914 all representatives have a lorica and their structure characterizes these taxa [14].

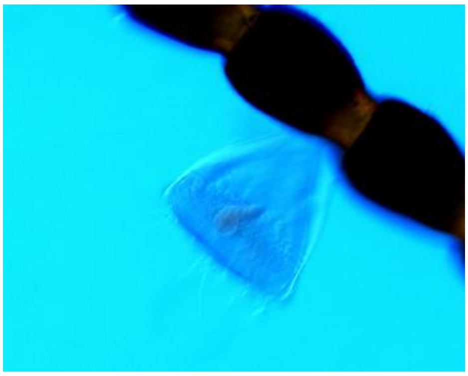

**Fig. 1.** Suctorian ciliate *Periacineta striata* Dovgal, 1993 with pseudochitinous lorica on aquatic beetle antenna (found in a bog near village Malaya Ugol'ka, Ukraine) (orig.)

**Рис. 1.** Суктория *Periacineta striata* Dovgal, 1993 с псевдохитиновой раковиной на антенне водного жука (обнаружена в болоте у с. Малая Уголька, Украина) (ориг.)

The loricae of some suctorian (Fig. 1), peritrich and folliculinid ciliates are composed by a protein-polysaccharide complex named pseudochitin (or tectin), and the hyaline loricae with different proteins are common in tintinnid ciliates [1] (Fig. 2) though earlier xanthoprotein and pseudochitin have been mentioned

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**Fig. 2.** Tintinnid ciliate *Amphorellopsis acuta* Schmidt, 1902 with hyaline lorica (found in Sevastopol Bay of the Black Sea) (orig.)

**Рис. 2.** Тинтиннида *Amphorellopsis acuta* Schmidt, 1902 с гиалиновой раковиной (обнаружена в Севастопольской бухте, Чёрное море) (ориг.)

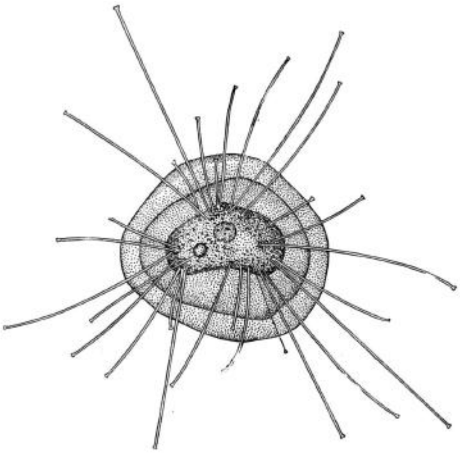

**Fig. 3.** Suctorian ciliate *Mucophrya pelagica* Gajewskaja, 1933 with mucopolysaccharide lorica (after [9])

**Рис. 3.** Сукторияя *Mucophrya pelagica* Gajewskaja, 1933 с мукополисахаридной раковиной (по [9])

among major lorica materials in the group [1, 13]. Finally, mucopolysaccharide (mucous) loricae are presented in some suctorian (Fig. 3), peritrich (*Ophrydium* sp.), stichotrich (*Stichotriha* sp.) and colpodean (*Maryna* sp.) ciliates [14].

Some ciliates are provided with composite loricae, for instance suctorian ciliate *Metacineta baikalensis* (Jankowski, 1982) has pseudochitinous lorica with the aperture covered by mucopolysaccharide layer (Fig. 4) [11].

However, composite loricae, which have an organic base with agglutinated inorganic particles such as sand grains, diatom flaps, coccoliths, etc., are more distributed. In part, such loricae are present in several tintinnid ciliates (Fig. 5) [1, 13].

The great diversity of loricae has been reached in ciliates through different combinations of morphology and chemical compositions. The main function of loricae is usually monotonously interpret; most common is as mechanical defense [16] or protection from predators [2].

However, the so called semi-loricae cover only the antapical region of cell body or colony in sessile peritrich and suctorian ciliates [3, 21] (Fig. 6), and the function is difficult to explain from the point of view of protection from predators. It is German authors' opinion that the semi-lorica represents the microaquarium ("Kleinstaquarien") [16], which functions as a reservoir for water at a time when ciliate host (aquatic bug or beetle) migrate from one waterbody to another, being the protection from desiccation.

It is believed that both mucous and hyaline loricae of planktonic ciliates can increase the floatability of cells assisting ciliate swimming [13] especially in case of suctorian *Mucophrya pelagica* Gajewskaja, 1933 with absence of locomotor ciliature (see Fig. 3) [9].

Hence, the functions of loricae as a rule were indicated without special discussion of their realization. Thus, the purpose of this article is to make a more detailed analysis of the most important protective functions of the loricae in ciliates due to the peculiarities of their morphology.

**Protection against biotic factors.** Protection functions of ciliate loricae have been explained as a defense from multicellular predators such as calanoid copepods or invertebrate larvae [1].

However, for example, the tintinnid loricae were regularly found in calanoid copepod intestines [13, 26], and also the salpas are active eat of these ciliates [13], with the tintinnids being the food supply for euphausiids, planktonic crustacean larvae, chaetognathans [10, 18, 19], and fish larvae [24]. *Noctilluca scintillans* Kofoid et Swezy, 1921 feeds on tintinnids in accordance with literary [8, 20] and our data. It is believed that large loricae of tintinnids can serve as a protection only from specialized nannoplanktotrophic predators such as appendicularians [13].

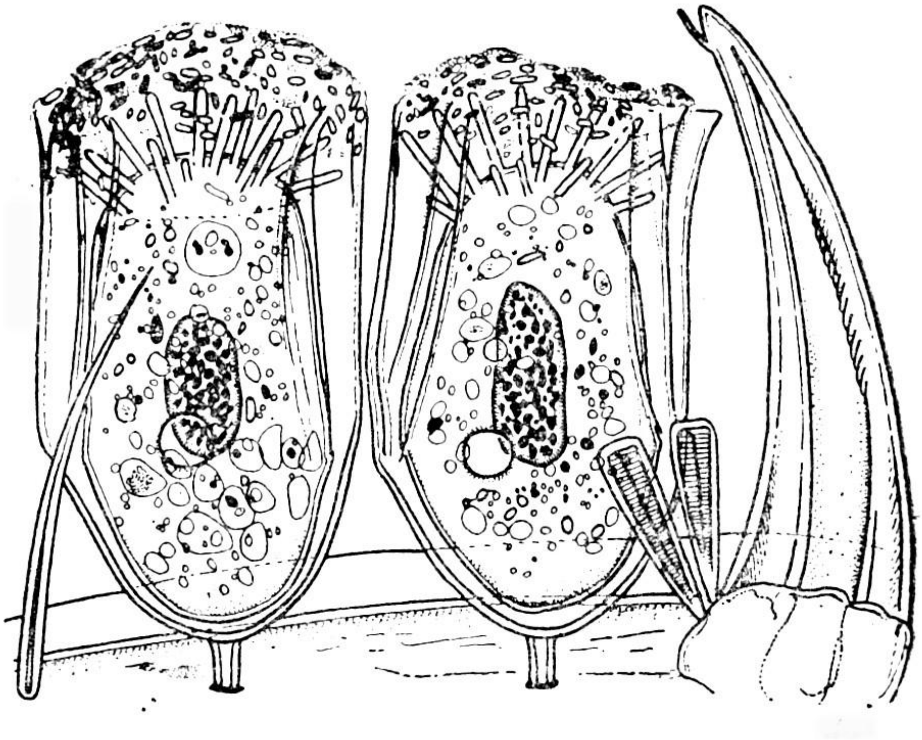

**Fig. 4.** Suctorian ciliate *Metacineta baikalensis* (Jankowski, 1982) with composite (pseudochitinous + mucopolysaccharide) lorica (after [11])

**Рис. 4.** Суктория *Metacineta baikalensis* (Jankowski, 1982) с композитной (псевдохитиновой и мукополисахаридной) раковиной (по [11])

As for loricae of sessile ciliates, they also probably serve as a protection against scrape grazing animals like gastropods. Thus, it is unlikely that loricae are efficient enough as a defense from large predators.

However, the loricae of ciliates probably can serve as a protection against unicellular predators, the sizes of which are usually comparable with the sizes of the prey. For this reason, the ways of hunting in unicellular predators should be discussed.

For example, predator ciliate *Didinium nasutum* (Müller, 1786), prey organisms suitable for which are ciliates, flagellates, amoebae, and turbellarians [25], have feeding apparatus that consists of a cell protuberance (proboscis) furnished with two types of extrusomes – long trichocysts and short pexicysts (Fig. 7). The proboscis clamp solidly to the prey cell membrane by trichocysts whereas prey immobilizes through the action of toxin inherent in pexicysts [25], with the prey being ingested by the invagination of proboscis.

The tentacles are used by suctorian ciliates for prey capturing in the same manner as the conoid in katablepharid flagellates and peduncle (feeding tube) in phagotrophic dinoflagellates.

The suctorian tentacle tips are armed with extrusomes (haptocysts), whereas extrusomes (ejectosomes) in katablepharids are located at the cell forward end [7].

The centrohelid heliozoans capture their preys by axopodia, where the extrusomes (kinetocysts) are located, whereupon the preys move toward the heliozoan cell body and are phagocytized [17].

Thus, with all diverse ways of capturing and eating prey among unicellular predators, there is a common feature – the prey is captured and immobilized by extrusomes or other special organelles.

It should be mentioned that some unicellular ectoparasites (such as suctorians) also use the extrusomes for attaching to the host cell body.

In turn, the lorica of ectoparasitic ciliates, for example, suctorians from genera *Urnula* Claparede et Lachmann, 1859 (Fig. 8) [5] or *Pseudogemmides* Kormos, 1935 (Fig. 9) parasiting on other suctorians may serve as a protection from host extrusomes.

Accordingly, it can be assumed that the protective function of the loricae consists in the prevention of the contact of predator or parasite extrusomes or other capturing organelles with the ciliate cell membrane.

This raises the question of whether the fenestrated lorica of tintinnids of genus *Dictyocysta* Ehrenberg, 1854 (Fig. 10) can prevent the contact with predator extrusomes.

The fact is that ciliates when swimming rotate around the longitudinal axis of the body [22]. It is our point that the unicellular predators cannot synchronize their motion with prey rotation and correspondingly contact with the parts of prey cell membrane, which are unprotected by lorica. Thus, the perforated loricae also perform their function.

Probably the protection of the ciliate lorica aperture is more important, especially in sessile ciliates. For example, the ectoparasitic ciliates such as suctorian *Pseudogemmides globosa* Kormos, 1935 (see Fig. 9) attach to the host such as suctorian *Periacineta buckei* (Kent, 1881) cell body exactly in the aperture of their lorica.

Hence, the loricae of some peritrich ciliates (from genera *Pyxicola* Kent, 1882 and *Thuricola* Kent, 1881, and from the family Lagenophryidae Bütschli, 1889 [12, 15]) and tintinnids (of genus *Nolaclusilis* Snyder et Brownlee, 1991) are equipped with a lorica closing apparatus (Fig. 11). It is believed [1] that the closing apparatus might be a valuable protection against contact predators, which use feeding tubes (dinoflagellates) and pseudopodia (radiolaria). At the same time as it has been remarked above, some suctorian species have mucopolysaccharide loricae, without aperture.

Thus, mechanical protection against extrusomes or other capturing organelles of predating protists can be reasonably considered as one of the principal functions of the loricae in ciliates. However, it can hardly be performed by the semi-loricae of sessile ciliates such as peritrichs and suctorians. The function of the latter structures should probably be discussed from the point of view of protection from abiotic factors.

**Protection against abiotic factors.** Sessile ciliates are mainly represented by stalked zooid. The hydrodynamic loads can be considered as the main abiotic factors effecting sessile protists including ciliates [4, 6, 23].

The reduction of cell body shape to geometrical figures are usually used for comparative estimation of these loads. In particular, the stalk of ciliates can be considered as a cylinder, whereas the cell body (zooid) as a sphere [23].

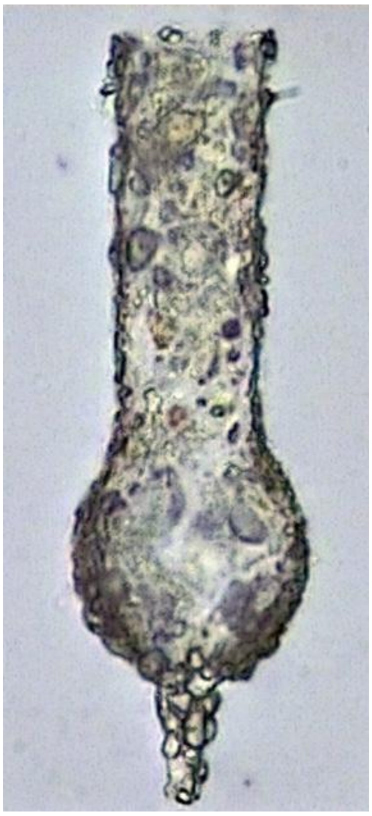

**Fig. 5.** Tintinnid ciliate *Tintinnopsis tocantinensis* Kofoid et Campbell, 1939 with agglutinated lorica (found in Sevastopol Bay of the Black Sea) (orig.)

**Рис. 5.** Тинтиннида *Tintinnopsis tocantinensis* Kofoid et Campbell, 1939 с агглютинированной раковиной (обнаружена в Севастопольской бухте, Чёрное море) (ориг.)

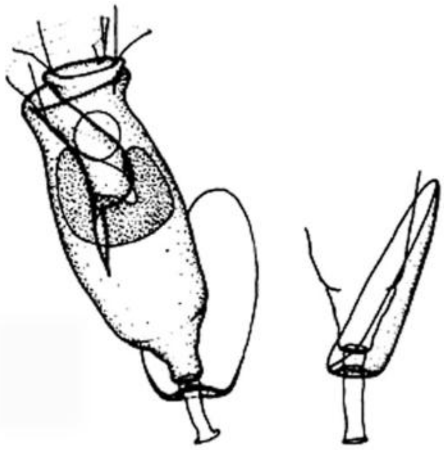

**Fig. 6.** Peritrich ciliate *Propyxidium tectiformis* (Scheubel, 1973) with pseudochitinous semi-lorica (after [21])

**Рис. 6.** Перитриха *Propyxidium tectiformis* (Scheubel, 1973) с псевдохитиновой полураковиной (по [21])

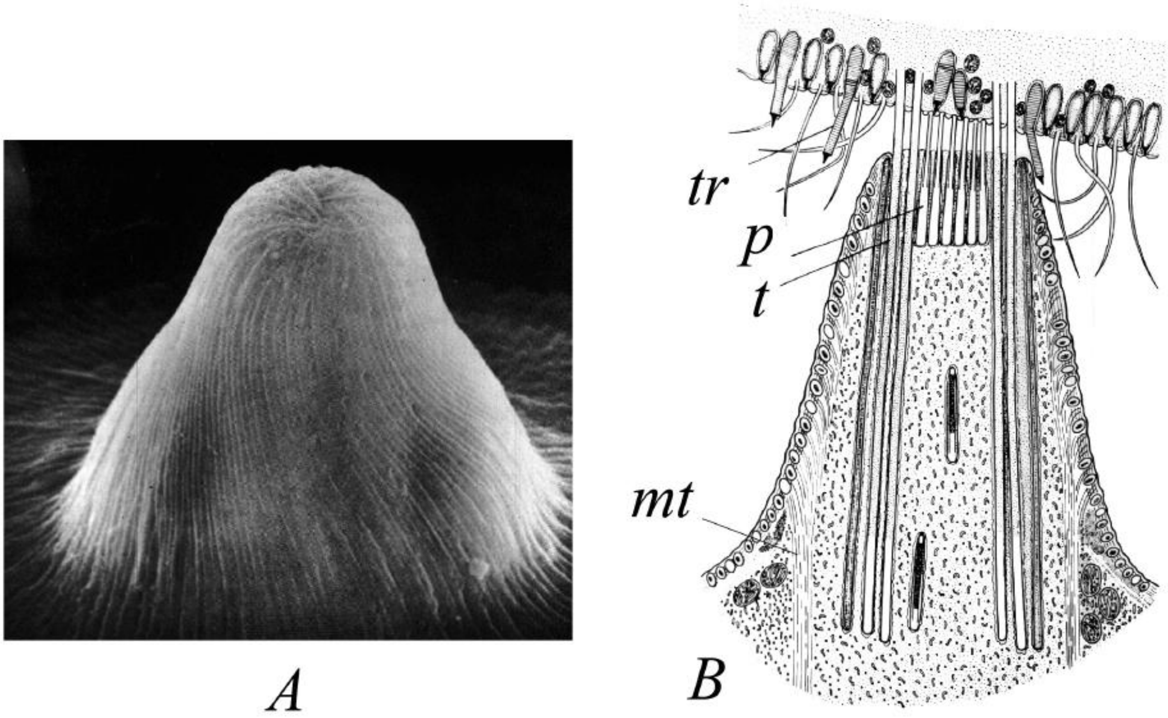

**Fig. 7.** *A* – general view (SEM) and *B* – schematic drawing of the proboscis structure of *Didiniun nasutum* Müller, 1786 (after [25]); *mt* – mictotubules, *t* – trichocysts, *p* – pexicysts, and *tr* – prey trichocysts

**Рис. 7.** *А* — общий вид (сканирующая электронная микроскопия) и *В* — схема строения хоботка *Didiniun nasutum* Müller, 1786 (по [25]); *mt* — микротрубочки, *t* — трихоцисты, *p* — пексицисты, *tr* — трихоцисты жертвы

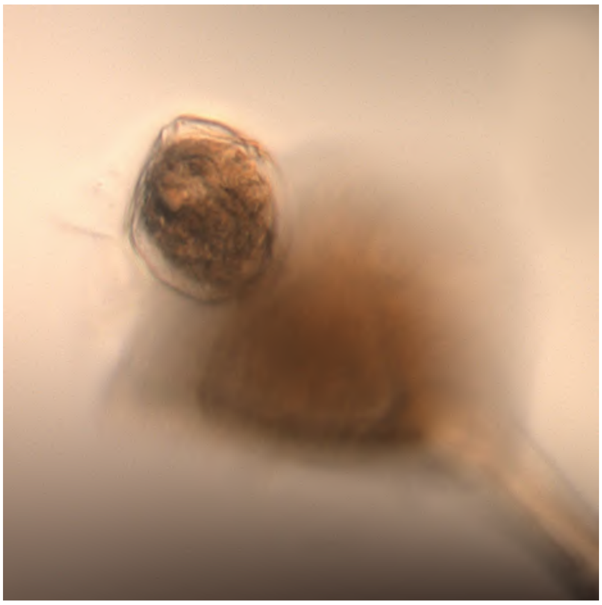

**Fig. 8.** Parasitic suctorian ciliate *Urnula turpissima* Kormos K., 1958 localized near lorica aperture of suctorian ciliate *Periacineta hydrochi* (Matthes, 1954) (after [5])

**Рис. 8.** Паразитическая сктория *Urnula turpissima* Kormos K., 1958 у устья раковины суктории *Periacineta hydrochi* (Matthes, 1954) (по [5])

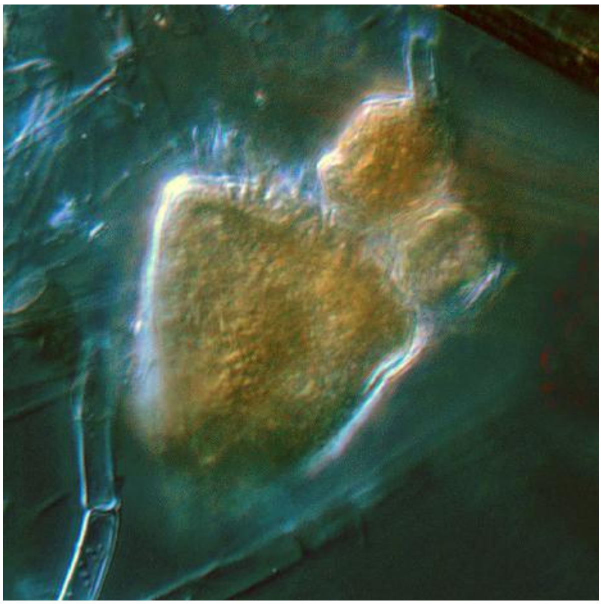

**Fig. 9.** Two individuals of parasitic suctorian ciliate *Pseudogemmides globosa* Kormos, 1935 localized in lorica aperture of suctorian ciliate *Periacineta buckei* (Kent, 1881) (found in Prypyat’ River, Ukraine) (orig.)

**Рис. 9.** Две особи паразитической суктории *Pseudogemmides globosa* Kormos, 1935 в устье раковины суктории *Periacineta buckei* (Kent, 1881) (обнаружены в р. Припять, Украина) (ориг.)

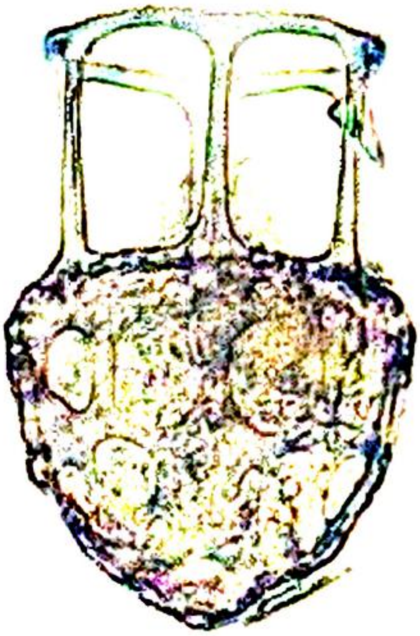

**Fig. 10.** Tintinnid ciliate *Dictyocysta lepida* Ehrenberg, 1854 with perforated hyaline lorica (found near Oman coast of the Aravian Sea) (orig.)

**Рис. 10.** Тинтиннида *Dictyocysta lepida* Ehrenberg, 1854 с перфорированной гиалиновой раковиной (обнаружена у побережья Омана, Аравийское море) (ориг.)

The forces, which increase with height of body above the substrate, are significant ones for stalked sessile ciliates.

As illustrated in [23], the force over the cylinder of length *l* and radius *a* perpendicular to the substrate (i. e. stalk) is:

$$F = 4\pi\mu \left(\frac{dU}{dy}\right) \int\limits_0^l \frac{y\,dy}{2 - \ln \mathrm{Re}}\,,$$

where *y* is the distance from the substratum surface;

$U$ is bulk flow velocity;

$\mu$ is the coefficient of dynamic viscosity;

Re is the Reinolds number.

At the same time for the sphere (zooid) of radius *r* touching the substratum the force would be:

$$F = 10.2\pi\mu r^2 \left(\frac{dU}{dy}\right)_0 \qquad [23].$$

In addition, the turning moment *T* affects the sphere, which would be:

$$T = 4\pi\mu r^3 \frac{dU}{dy} \qquad [23].$$

Thus, the magnitude of the load affecting the stalk does not depend on stalk radius (since the latter is constant). At the same time, loads proportional to the square and the cube of the stalk radius, accordingly affect the zooid.

Taking into account that $r > a$, the hydrodynamic load rises steeply in the zone of joints between stalk and zooid of sessile ciliate.

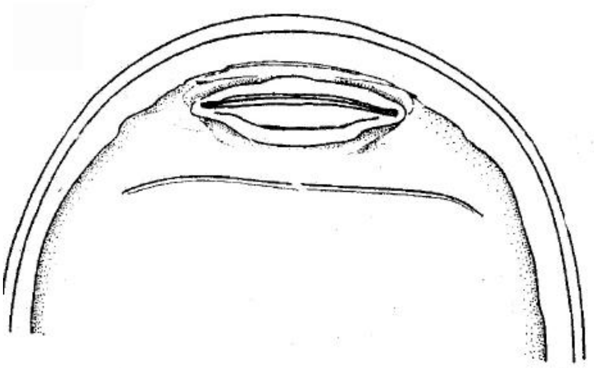

**Fig. 11.** Closing apparatus (loricastome) of lorica aperture in peritrich ciliate *Lagenophrys leniusculus* (Jankowski, 1986) (after [12])

**Рис. 11.** Замыкающий аппарат устья раковины перитрихи *Lagenophrys leniusculus* (Jankowski, 1986) (по [12])

It must be recognized that the above-mentioned equations are valid in case of laminar flow and in stationary conditions when the flow parameters do not vary with time. However, the water flow rate near surface in flowing water is permanently irregular in natural conditions [6], which causes peak loads that in turn can lead to the interruption of ciliate zooid from the stalk.

Thus, the strength of the connection between the stalk and the cellular body becomes important when ciliate inhabit at substrate in flowing water. The strength is most often provided by forming the allometric widening of the stalk upper part [3, 6].

As a result, on the one hand the contact area between stalk and cell body significantly increases. On the other hand, the character of the force affecting on the widened part of the stalk corresponds to the load on the sphere; that is, higher load falls on the structure consisting of extremely durable material, armored with microfilaments [3, 6].

Probably, the protection is even more effective when the zone of connection of the stalk and cell body of the ciliate is covered by a cup-like extension, i. e. when there is a semi-lorica.

It is our point that the mechanic defense of stalk-cell body zone from hydrodynamic loads is essential function of semi-lorica in sessile stalked ciliates [3, 6].

It is possible that intensification of the function followed the order when the semi-lorica to cover large and large part of ciliate cell body. At one time, the semi-lorica begins to perform the additional function of protection from predators and parasites. The intensification of the latter function in turn leads to the formation of a lorica completely covering the cell body of the ciliates [3, 6].

**Conclusions.** As suggested in the literature [13], the function of both mucous and hyaline loricae of planktonic ciliates can increase the floatability of cells and assist to swimming of ciliates.

The hypothesis about the function of a semi-lorica as microaquarium, which protect against desiccation [16], requires further testing because it is not confirmed by observations or experiments.

It is our opinion that, irrespective of morphology and material, the ciliate lorica is a barrier preventing the contact of extrusomes or other capturing organelles of unicellular predators or parasites from the cell membrane of ciliate pray or hosts.

Protection of the joint zone between the stalk and cell body from hydrodynamic loads is the initial function of the pseudochitinous semi-loricae and loricae of the sessile ciliates.

It should be mentioned that between representatives of Ciliophora there is a great variety of other ways to protect against predators, parasites and physical loads. Among them, the formation of various adhesive organelles [6], alternative ways to strengthen the joint zone between stalk and zooid (for example, the endostyle in chonotrichs), the formation of the cuticle (in chonotrichs), the selection of protected localizations on the substrate, etc., may be listed [4, 6].

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# РАЗНООБРАЗИЕ И ФУНКЦИИ РАКОВИН ИНФУЗОРИЙ (CILIOPHORA)*)

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В статье обсуждаются особенности морфологии и химического состава, а также функции раковин инфузорий. По химическому составу различаются псевдохитиновые (тектиновые), гиалиновые и мукополисахаридные раковины. Также существуют композитные (состоящие из псевдохитина и мукополисахаридов) и агглютинированные раковины. Обсуждаются морфологические особенности и связанные с ними защитные свойства раковин и полураковин сидячих инфузорий. В качестве основной функции мукополисахаридной и гиалиновой раковин планктонных инфузорий ранее было указано повышение плавучести клеток. По мнению авторов, основной функцией раковины является препятствие контакта экструсом или иных органелл захвата одноклеточных хищников или паразитов с клеточной мембраной инфузорий. Кроме того, функцией псевдохитиновой полураковины и раковины сидячих инфузорий является защита зоны соединения стебелька и клеточного тела от гидродинамических нагрузок.

**Ключевые слова:** инфузория, раковина, псевдохитин, гиалин, хищник, паразит, экструсома, гидродинамическая нагрузка

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