

## Two Strategies of Acanthocephalan Interrelations with Paratenic Hosts

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**Abstract**—Data available on the peculiarities of the tegument structure and encapsulation of the acanthocephalans *Corynosoma strumosum* (Palaeacanthocephala, Polymorphidae) and *Sphaerostris picae* (Palaeacanthocephala, Centrorhynchidae) in paratenic hosts are summarized. Corynosomes are shown to have a capsule structure varying from fibroblastic to leukocytal depending on the species of the paratenic host (sea fish). The characteristic thick glycocalyx layer may or may not develop on the tegument surface of corynosomes surrounded by the leukocytal capsule in the hosts of different species. The acanthocephalan *S. picae* in a paratenic host (lizard) is also surrounded by a leukocytal capsule; however, no characteristic glycocalyx layer is formed on its tegument surface. Such a glycocalyx supposedly represents a protective reaction of the parasite to cellular encapsulation, but in the case of its absence the protective mechanism remains unclear. Based on these results, a hypothesis about two strategies of interrelations between acanthocephalans and paratenic hosts is advanced. According to the first strategy, the acanthocephalan (*C. strumosum* in the fish of the majority of the species studied), regardless of the structure of the capsule formed around it, is covered with a thick layer of glycocalyx, while the cells of the inner part of the capsule are destroyed. When invading paratenic hosts of other species (*C. strumosum* in flatfishes, as well as in experimentally infested aquarium fish and lizards, *S. picae* in lizards), the second strategy is realized: the acanthocephalan is surrounded by a leukocytal capsule; however, a thick layer of glycocalyx on its surface is not formed and the capsule's cells are not destroyed.

**Keywords:** Acanthocephala, interrelations with paratenic hosts, capsule, glycocalyx, *Corynosoma strumosum*, *Sphaerostris picae*

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### INTRODUCTION

Acanthocephalans are characterized by a complex life cycle with the obligatory inclusion of intermediate (crustacean or insect) and final (vertebrate) hosts into it. In the intestines of the former, the acanthor larva is released from the egg (embryonic) shells and penetrates into the cavity of its body, where it undergoes metamorphosis and develops into a cystacanth: an invasion stage for the next host. The varying degree of specificity of hosts of different categories is well known: if the adult form of a particular species of acanthocephalan can parasitize in a number of vertebrate species, sometimes very distant taxonomically, only one invertebrate species can usually act as an intermediate host. This difference, according to some authors, is due to the peculiarities of development of acanthocephalans in different hosts: they undergo intensive organogenesis in the intermediate acanthocephalans, reaching the stage of cystacanth, which requires a fairly strict “list” of conditions and factors, but at the final stage, only growth and physiological

maturation are accomplished. Since the cystacanth is a fully or almost fully developed juvenile form (Khokhlova, 1986; Sharpilo et al., 1998), the requirements for habitat conditions may be less stringent.

Many species of acanthocephalans (representatives of seven out of the eight existing orders; Sharpilo et al., 1996), however, include another host—paratenic (reservoir)—in their life cycle, which, unlike the intermediate and final hosts, is not obligatory. Previously, this host was considered only as a link that provides or facilitates the transfer of invasion from the intermediate to the final host, but over time, as data accumulated, this simplified view began to change. Analysis and synthesis of these facts led to a new understanding of paratenical parasitism, which was refined and enriched in the well-known and thus far unique monograph by Sharpilo and Salamatin (2005). The most fundamental conclusions of this work are the recognition, firstly, of the possibility of the development of the parasite in a paratenic host, and secondly, the possible specific nature of the relationships of

these organisms. As applied to acanthocephalans, their nonstop development at all phases of the life cycle, including in the paratenic host, is very clearly demonstrated by the example of *Centrorhynchus milvus*. The morphometric indicators of the tegument of this acanthocephalan significantly increase from the cystacanth in the intermediate host to the young worm in the paratenic host and further to the mature parasite in the final host (Marchand and Grita-Timoulali, 1992). Unfortunately, this study is the only one so far, but there is no reason to regard its results as exceptional.

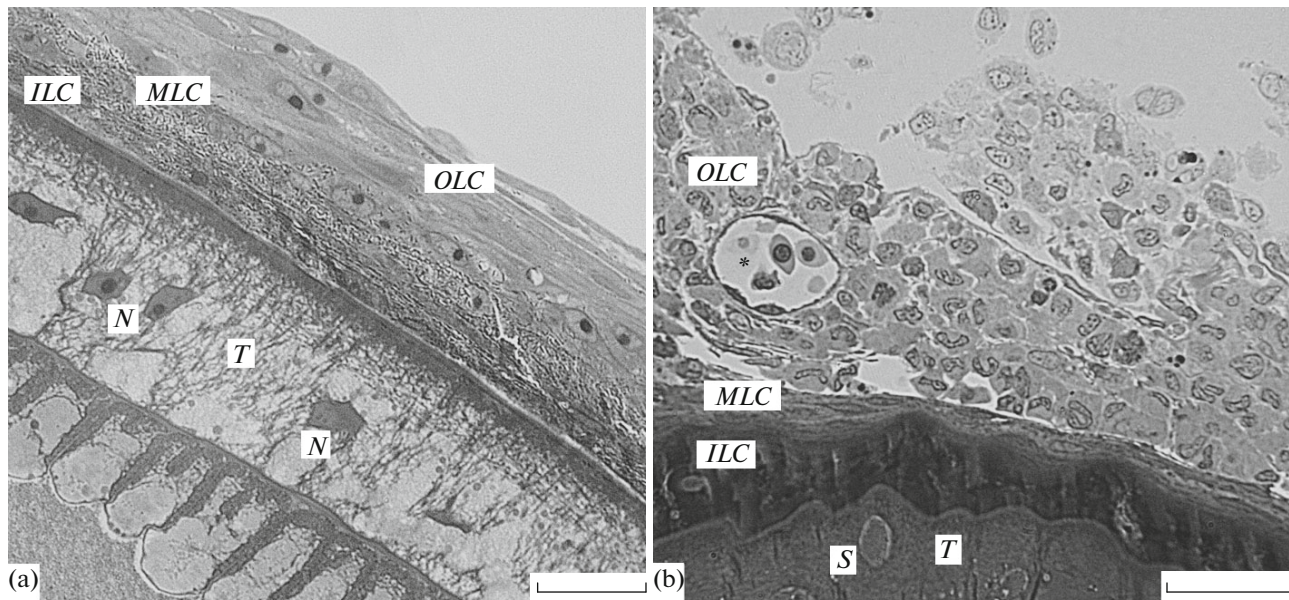
If we recognize the fact of development of acanthocephalans in paratenic hosts, it is natural to assume that the structural and physiological characteristics of the host organism must influence this process. But since these features are significantly different in representatives of different taxonomic groups, the process of development of an acanthocephalan in a particular paratenic host may vary to some extent; in other words, the relationships of organisms in such host–parasitic systems acquire specific features. Arguing about this, V.P. Sharpilo and R.V. Salamatin, in their monograph, cite the opinion of Shul'ts and Davtyan (1954): "... the host–parasitic specificity in reservoir (paratenical) parasitism is very little manifested...", which, according to the authors, may explain the very wide, in many cases, range of paratenic hosts. However, it is not so much the assessment of the degree of specificity that is important, but the recognition of the very fact of its existence. At the same time, the possible correspondence of any morphological features characterizing a particular parasite and one or another of its paratenic hosts with the level of specificity of the relationships of these animals has not been systematically studied until recently, especially using electron microscopy.

In this report, we analyze some results of a study of the relationships of acanthocephalans *Corynosoma strumosum* (Rudolphi, 1802) Lühe, 1904 and *Sphaerirostris picae* (Rudolphi, 1819) Golvan, 1956 with paratenic hosts, performed using light and electron microscopy. The acanthocephalan *C. strumosum*, which lives in warm-blooded animals (aquatic mammals and fish-eating birds), uses many species of marine fish that can reach significant numbers as paratenic hosts (Vitomskova, 2003; Atrashkevich, 2008). The second acanthocephalan parasitizes in the magpie (*Pica pica*), and its natural paratenic host is the sand lizard (*Lacerta agilis*) (Sharpilo, 1976). The research task was to study and compare, firstly, the structure of the surface part of the tegument of the acanthocephalans that inhabit, in cases of corynosomes, paratenic hosts of different species, and, secondly, the nature of the response of these hosts, which leads to encapsulation of parasites, that is, the structure of the capsules themselves. The acanthocephalans of the two species were investigated both from natural invasions and from animals infected in the experiments. The initial results of these studies were pub-

lished in part earlier (Nikishin and Skorobrechova, 2007; Skorobrechova, 2014; Skorobrechova and Nikishin, 2012, 2014, 2017; Skorobrechova and Nikishin, 2011, 2016; Skorobrechova et al., 2012), so in this paper, we summarize them with the substantiation of the hypothesis about the strategies of relationships of acanthocephalans and their paratenic hosts.

Although the encapsulation of acanthocephalans in paratenic hosts is well known, there are few works devoted to its study and no common opinion on its structure and composition has existed until recently (for a review of the literature, see Nikishin and Skorobrechova, 2015). In particular, in different cases, capsules were described consisting either of fibroblasts and collagen fibers (Bogitsh, 1961) or of the tissues of the organ on which the acanthocephalans were located (Ward, 1940) or of collagen fibers with the inclusion of numerous inflammatory cells, including adipocytes (Amin et al., 1996) and/or hyaline envelope (Amin et al., 1995). The inconsistency of this information was probably due to the lack of research using electron microscopy. Starting from 2007, similar studies have been carried out at the Institute of Biological Problems of the North, Far East Branch, Russian Academy of Sciences, mainly using the example of *Corynosoma strumosum*. A comparative analysis of the capsule surrounding this parasite in the natural (nine species of marine fish) and experimental (aquarium fish, lizard, frog, and grass snake) paratenic hosts showed that its cellular composition depends on the species affiliation of the latter. At the same time, taking into account that the encapsulation process takes a certain period of time, it can be assumed that there are differences in the structure of capsules of various ages.

In the cases with natural paratenic hosts, all identified capsule variations were reduced to three main forms: fibroblastic, leukocytal, and intermediate (Skorobrechova and Nikishin, 2014). Fibroblastic capsules were found in pond (*Hypomesus olidus*) and Arctic rainbow (*Osmerus mordax dentex*) smelts and the saffron cod (*Eleginus gracilis*) (Nikishin and Skorobrechova, 2007; Skorobrechova and Nikishin, 2011) (Fig. 1a). They are formed almost exclusively from fibroblasts and their derivatives, i.e., collagen fibers, but in the case of the saffron cod, they also comprised single macrophages and granulocytes. In the intermediate capsules found in the white-spotted greenling (*Hexagrammos stelleri*), the number of leukocytes is noticeably higher, but the dominance of fibroblasts persists (Skorobrechova and Nikishin, 2014). Leukocytal capsules along with the cells of the fibroblastic series consist of quantitatively predominant macrophages and granulocytes, i.e., the cells of the inflammatory series. Such capsules are found around corynosomes from Steller's sculpin (*Myoxocephalus stelleri*), yellowfin sole (*Limanda aspera*), Pacific halibut (*Hippoglossus stenolepis*), eastern viviparous blenny (*Zoarces elongatus*), and, according to preliminary data, *Hadropareia middendorffii* (Skorobrechova



**Fig. 1.** (a) Fibroblastic and (b) leukocytic capsules surrounding the acanthocephalan *Corynosoma trumosum* on the mesentery of the intestine of (a) the Arctic rainbow smelt *Osmerus mordax dentex* and (b) Steller's sculpin *Myoxocephalus stelleri*. In both cases, the capsule is multilayered, and its inner layer (ILC) is formed by degenerating cells and their residues. However, in the first case, this layer is thin, and the whole capsule consists of fibroblasts and their derivatives (fibroblasts and collagen fibers); in the second case, this layer is massive, and leukocytes predominate in the capsule. MLC is the middle layer of the capsule, N are the tegument nuclei, OLC is the outer layer of the capsule, S is the base of the tegument spike, and T is the acanthocephalan tegument. An asterisk indicates a blood vessel in the thickness of the capsule. Semi-thin sections, coloring here and hereinafter: methylene blue–crystal violet. Scale 20  $\mu$ m.

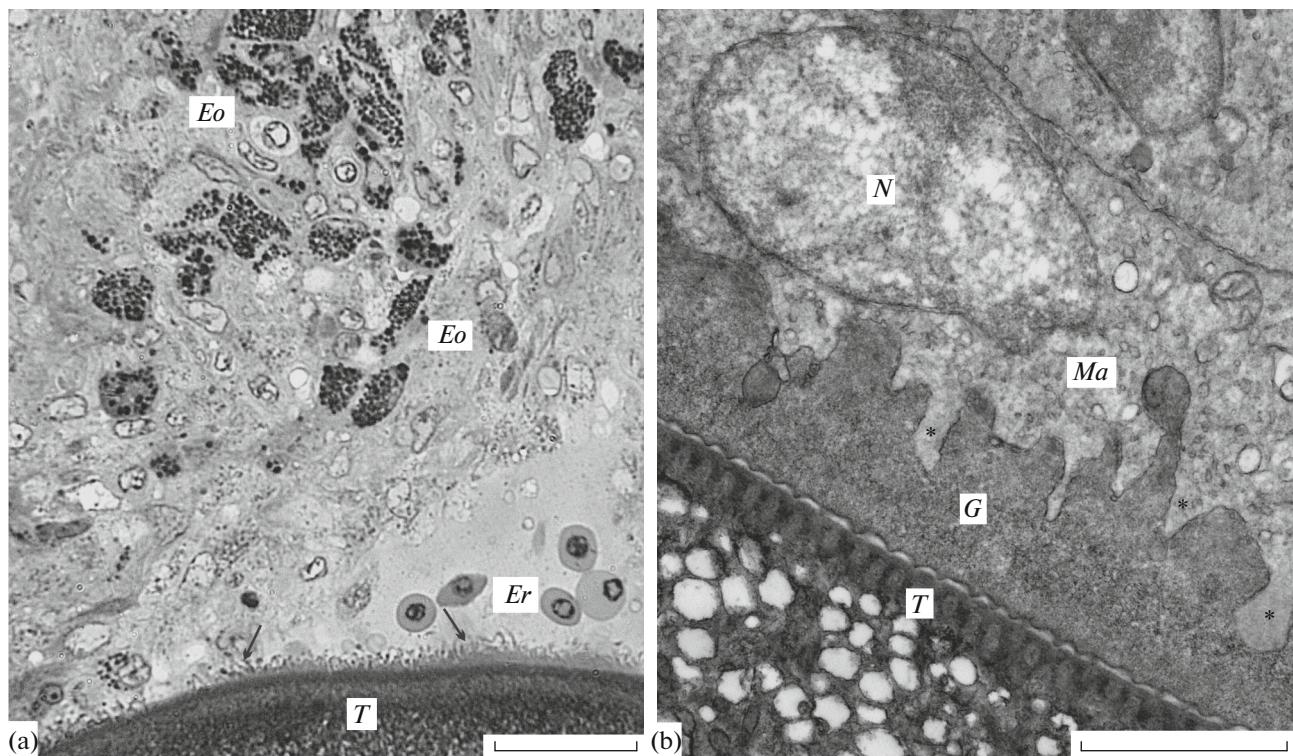
and Nikishin, 2011; Skorobrechova and Nikishin, 2014, 2017; Skorobrechova, 2014) (Figs. 1b, 2a, 3a). The presence and proportion of certain elements of the capsule in these hosts may vary somewhat, but its leukocytic character does not change. In most cases, the inner part of these capsules, as well as the aforementioned fibroblastic capsules, is formed by a layer of destroyed or degenerating cells, which indicates a pronounced conflicting nature of the relationship between organisms at the initial stage of paratenic host invasion regardless of the structure of the emerging capsule (Nikishin and Skorobrechova, 2015).

We explained such significant differences in the structure of capsules surrounding corynosomes in paratenic hosts of different species by the varying degrees of mutual adaptation of these organisms, assuming that the number of inflammatory cells included in the capsule is directly proportional to the level of conflict of the acanthocephalan's relationship with the host (Skorobrechova and Nikishin, 2014). This assumption is not original, and for the first time it was expressed on the basis of the results of studying the encapsulation of the plerocercoids of some cestodes in the second intermediate hosts (freshwater fish) of different species (Pronina and Pronin, 1988). The authors associated the phenomenon of structural diversity of capsules with the degree of mutual adaptation of partners, i.e. with the taxonomic status of the host. According to Pronina and Pronin, a thicker cap-

sule, which is dominated by leukocytes, indicates a less balanced relationship between the parasite and the host than the fibroblastic capsule, which is relatively thinner. The thickness of the capsules studied by us also varied considerably; however, in our opinion, these variations were more dependent on the location of the capsule than on the degree of mutual adaptation. For example, for the corynosomes from the arctic rainbow and pond smelts, as well as from the yellowfin sole, the thickness of the capsules did not differ significantly, although in the first two species, the capsules were fibroblastic in terms of organization, whereas in the sole, they were leukocytic (Skorobrechova and Nikishin, 2011). At the same time, the available data indicate a noticeably smaller thickness of capsules found on other organs of the host compared to the capsules located on the mesentery (Skorobrechova, 2014). In addition, in many cases, the thickness of the capsule was not the same throughout its entire length: for example, in the capsules localized on the liver of the yellowfin sole, in the area facing the body cavity, it could be much thicker than in the areas making contact with the organ (Skorobrechova, 2014). Finally, the already mentioned dependence of the morphometric parameters of capsules on their age is quite possible.

Thus, in the case of corynosomes, the structure of the capsules surrounding them in paratenic hosts, as well as in the cases of cestode plerocercoids in the sec-





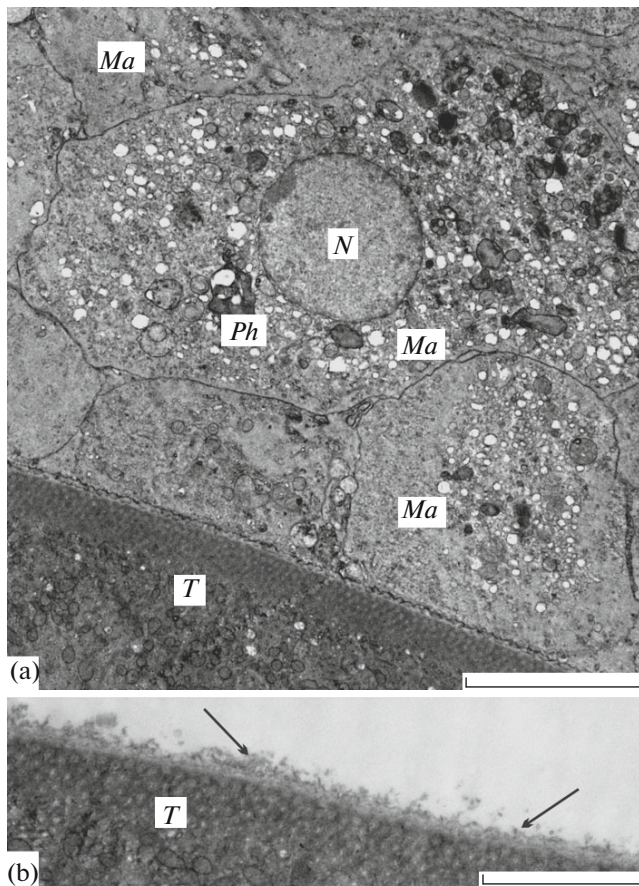
**Fig. 2.** An acanthocephalan *Corynosoma strumosum* on the mesentery of the intestines of the eastern viviparous blenny *Zoarces elongatus*. (a) Fragment of the acanthocephalan and the capsule surrounding it. The tegument (*T*) of the acanthocephalan is covered with a dark-colored layer of glycoalyx with villus-like outgrowths (arrows), near the outer boundary of which erythrocytes are located in “empty” spaces (*Er*). In the thickness of the capsule, numerous eosinophils (*Eo*) can be seen, which are easily identified by the large granules in their cytoplasm. (b) A macrophage (*Ma*) forms processes (shown by asterisks) that penetrate into the glycoalyx, reaching its middle. *G* is glycoalyx, and *N* is the nucleus of the macrophage. (a) Semi-thin section and (b) electron microscopy. Scale ( $\mu\text{m}$ ): (a) 20, (b) 2.

ond intermediate host, described by Pronina and Pronin (1988), may reflect the degree of balance between the parasite and the host, more precisely, the degree their mutual adaptation. In other words, the relationship between the paratenic host and the acanthocephalan, accompanied by the formation of leukocytic capsules, which are dominated by the cells of the inflammatory series (leukocytes and macrophages), can be viewed as more conflicting or, respectively, less balanced than the cases in which the capsules are formed mainly or exclusively from fibroblasts.

Studies have also shown that differences are observed not only in the morphology of the capsules surrounding corynosomes in different species of paratenic hosts, but also in the structure of the tegument of these acanthocephalans, and they are most pronounced in the organization of their surface. In the majority of natural paratenic hosts, corynosomes, encapsulated with both fibroblastic and leukocytic capsules, form on the surface of the tegument a thick (up to 2  $\mu\text{m}$  and more) layer of glycoalyx. Morphologically and morphometrically, this glycoalyx is similar to that formed on the surface of cystacanths in intermediate hosts (Skorobrechova and Nikishin, 2014; Nikishin and Skorobrechova, 2015; Nikishin,

2018) (Fig. 2b). Exceptions are the corynosomes from flatfish, which, according to our data, did not form such a powerful layer of glycoalyx, and its thickness was only a few tenths of a micrometer (Skorobrechova and Nikishin, 2011; Skorobrechova and Nikishin, 2017) (Fig. 3b). Recall that, in the studied flatfishes of both species, corynosomes are enclosed in leukocytic capsules. Among other acanthocephalan species that parasitize in paratenic hosts, glycoalyx, no less developed than in corynosomes from most species of fish and erroneously called cysts by the authors, is noted on the surface of the acanthocephalan *Centrorhynchus milvus* from the toad *Bufo regularis* (Marchand and Grita-Timoulali, 1992). Other acanthocephalans have not been investigated in this respect, and, unfortunately, there is no description of the structure of the capsule in this paper. The thick layer of glycoalyx on the surface of corynosomes forms quickly, and during experimental infection of *Hadropareia middendorffii* it is detected already on the third day (Skorobrechova, 2014). It is assumed that the material necessary for the formation of glycoalyx can be released in the form of small vesicles through the “canals” of the cross-stripped tegument layer (Skorobrechova and Nikishin, 2017), similar to the process described in the cysticer-





**Fig. 3.** Acanthocephalan *Corynosoma strumosum* on the mesentery of the intestine of the Pacific halibut *Hippoglossus stenolepis*. (a) Fragment of the tegument of an acanthocephalan with a capsule surrounding it. The capsule contains macrophages (*Ma*) with numerous vesicles and small phagosomes (*Ph*) in the cytoplasm. The macrophages are closely adjacent to the acanthocephalan, and the glycocalyx on its surface is not defined. (b) Fragment of the tegument of an acanthocephalan with a “typical” thin layer of glycocalyx (arrow) on its surface. *N* is the nucleus of the macrophage, and *T* is the tegument. Electron microscopy. Scale ( $\mu\text{m}$ ): (a) 5, (b) 2.

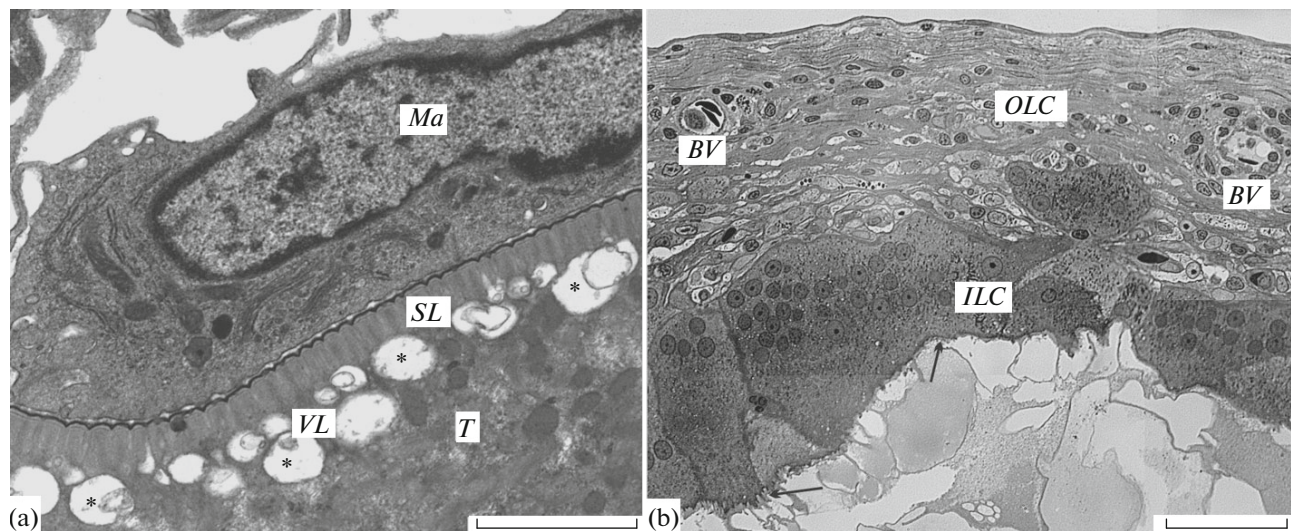
coids of the cestodes from the suborder Hymenolepidata (Nikishin, 2017), the cyst surface of which also has a similar thick layer of glycocalyx.

If the acanthocephalan is covered with a thick layer of glycocalyx and surrounded by a leukocytal capsule, the macrophages often form cytoplasmic processes that penetrate the glycocalyx (Fig. 2b), which may appear partially or even completely destroyed in these areas (Skorobrekova and Nikishin, 2014). These facts suggest that glycocalyx counteracts the host’s cellular response to invasion. In order to study the relationship between the acanthocephalans and unnatural paratenic hosts and, in particular, to test this assumption, the aquarium African jewelfish (*Hemichromis bimaculatus*) (Skorobrekova and Nikishin, 2012), sand lizards (Skorobrekova et al., 2012), common

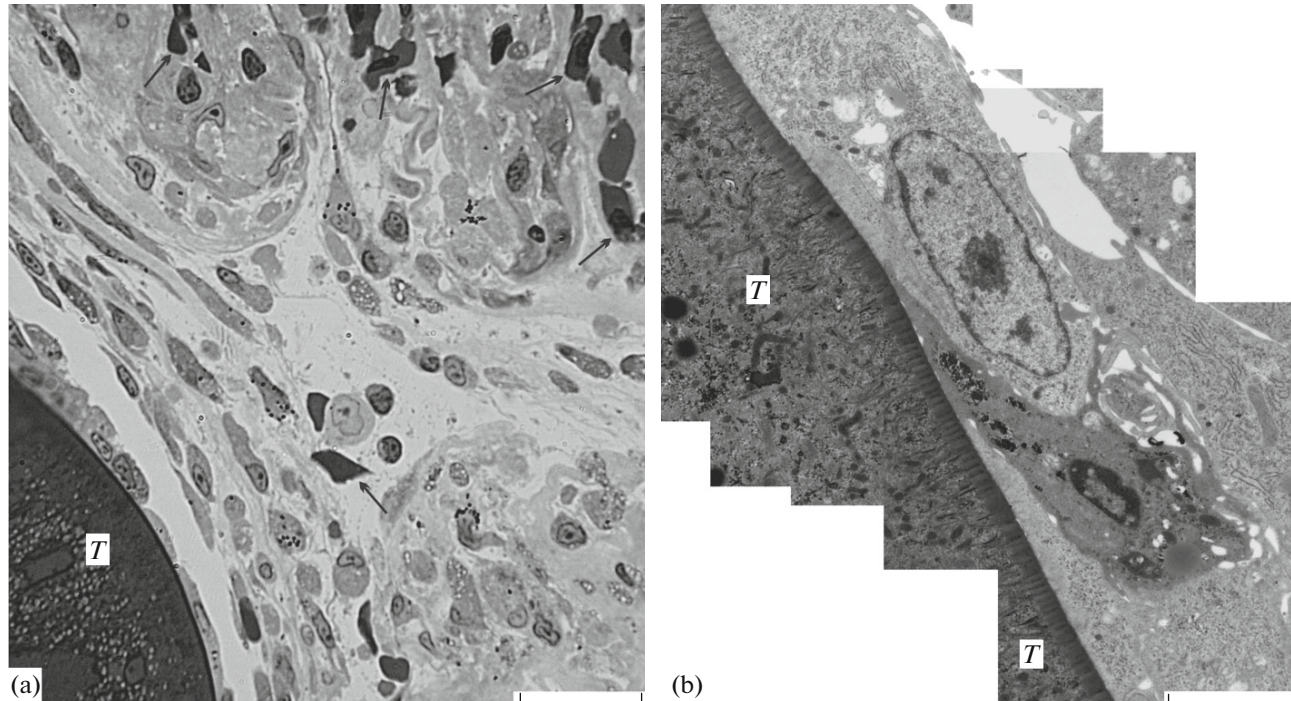
frogs (*Rana temporaria*), and grass snakes (*Natrix natrix*) (Skorobrekova, 2014) were infected with corynosomes. In the case of the reptiles and amphibians, the acanthocephalans remained viable for at least a few weeks and were encapsulated with leukocytal capsules, the inner part of which was formed by giant multinuclear macrophages; a thick layer of glycocalyx did not develop on their surface (Figs. 4a, 4b). We consider the formation of giant macrophages and the absence of the characteristic glycocalyx as an indicator of an acute conflicting relationship, so it is not surprising that after a few weeks only dead acanthocephalans were detected in the infected lizards (the experiment with them was the longest) (Fig. 4b). In the case of the jewelfish, the results were not so clear. Some of the acanthocephalans were surrounded by a leukocytal capsule and had a clearly depressed appearance, while others maintained a “normal” appearance, and fibroblasts prevailed among the cells encapsulating them. In both cases, a thick layer of glycocalyx was not observed on the surface of the acanthocephalans, but they remained alive for at least a month (the duration of the experiment). However, when interpreting the results of this experiment, one should take into account the small size of the fish compared to the corynosomes and, as a result, the clearly limited protective potencies of the host. Nevertheless, it can be stated with certainty that in all cases of experimental infection of unnatural paratenic hosts with *Corynosoma strumosum*, regardless of their taxonomic position, no thick layer of glycocalyx formed on its surface.

These results, it would seem, unequivocally emphasize the role of glycocalyx in protection against the cellular response of the paratenic host organism and imply the necessity of forming a massive layer for the parasite’s survival. However, the latter assumption is contradicted by two facts. First, as mentioned above, in flatfish, which, among others, are natural paratenic hosts, a thick layer of glycocalyx does not form on the surface of corynosomes, and the parasites, although they are contained in a leukocytal capsule, nevertheless retain their viability for an indefinite period and can accumulate in large quantities. The second fact is associated with the parasitizing of the *Sphaerirostris picae* acanthocephalan in the natural paratenic host, the sand lizard *L. agilis*, in which this parasite is neither in natural conditions nor experimentally covered by a thick layer of glycocalyx, although it is also surrounded by a leukocytal capsule (Figs. 5a, 5b), including, especially in its interior, giant multinuclear macrophages (Skorobrekova and Nikishin, 2016). Despite the obviously acute conflict relationship of organisms and the absence of a massive layer of glycocalyx on the surface of the acanthocephalans, the parasites in both these cases remain quite viable for an indefinitely long period, especially in flatfish, in which the intensity of invasion can be very high (Vitomszkova, 2003). In both these cases, the parasite is probably protected from the host’s cellular



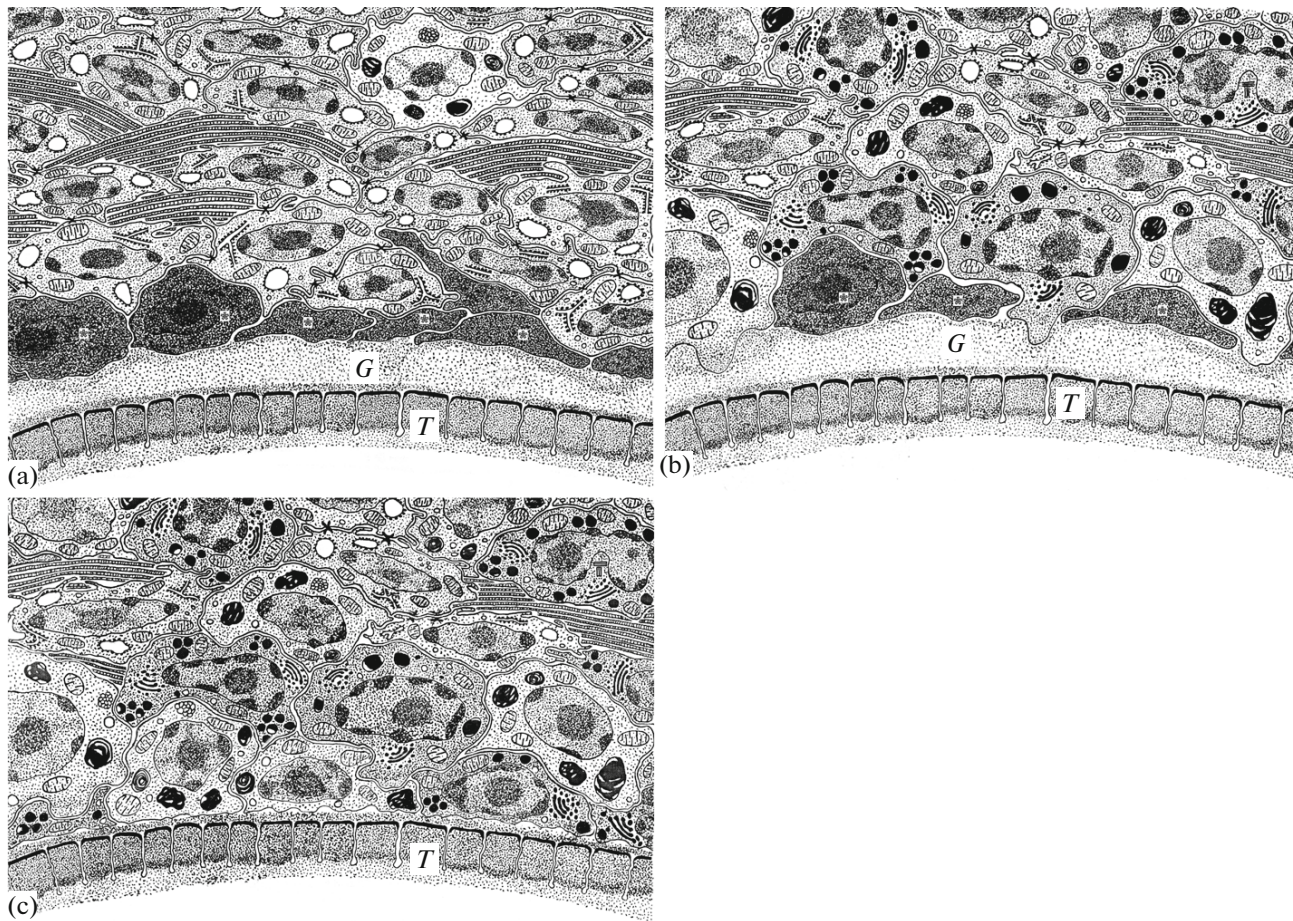


**Fig. 4.** An acanthocephalan *Corynosoma strumosum* on the intestine of the sand lizard *Lacerta agilis* (experimental invasion). (a) Two days after the infection. On the surface of the tegument (*T*) of the acanthocephalan, there is no thick layer of glycocalyx, and the submerged parts of the “channels” of its transverse striated layer (*SL*), forming the vesicular layer (*VL*), are extended (\*). The macrophage (*Ma*) of the host is adjacent to the surface of the acanthocephalan. (b) Ninety days after the infection. The acanthocephalan is degenerated. The capsule is bilayer, and the cells forming it are tightly arranged with minimal intercellular spaces. The inner layer of the capsule (*ILC*) consists of large multinuclear cells, from which numerous thin processes (arrows) depart, which probably penetrated into the “channels” of the cross-striated layer of the acanthocephalan tegument. As part of the outer layer of the capsule (*OLC*), cells of different types are identified, and blood vessels (*BV*) are observed. The surface part of this layer is formed by densely located fibroblasts and their processes. (a) Electron microscopy, (b) a semi-thin section. Scale ( $\mu\text{m}$ ): (a) 2, (b) 40.



**Fig. 5.** An acanthocephalan *Sphaerirostris picae* on the mesentery of the intestine of the sand lizard *Lacerta agilis*, enclosed in a leukocytal capsule. (a) Light microscopy, semi-thin section. (b) Electron microscopy. The capsule has no inner layer of destroyed cells. The cells of the capsule are in contact with the tegument (*T*) of the acanthocephalan, on the surface of which there is no characteristic thick layer of glycocalyx; the “channels” of the tegument transverse-striated layer are not extended. Noteworthy is the abundance of erythrocytes (arrows) in the capsule. (a) Semi-thin section, (b) electron microscopy. Scale ( $\mu\text{m}$ ): (a) 20, (b) 3.





**Fig. 6.** Scheme of the organization of the surface of the tegument of the acanthocephalans and the capsules surrounding them with different strategies of their relationship with paratenic hosts. (a, b) When implementing the first strategy, the acanthocephalan on the surface of the tegument (*T*) forms a thick layer of glycocalyx (*G*); the host, depending on its species, surrounds the parasite with a (a) fibroblastic or (b) leukocytic capsule, the cells of which that are in contact with the glycocalyx are destroyed (shown by asterisks). (c) When implementing the second strategy, the acanthocephalan is surrounded by a leukocytic capsule, but a thick layer of glycocalyx is not formed on the surface of its tegument, and the cells of the inner part of the capsule are not destroyed. (Relative dimensions are not met.)

reaction by mechanisms other than by the formation of a powerful layer of glycocalyx.

Thus, the available data allow us to state the presence of two forms of relationships between the thorny-headed worms *Corynosoma strumosum* and their paratenic hosts at the organismal level. Depending on the host species, these forms differ markedly (Fig. 6). The first form of corynosome getting into the corresponding paratenic host forms a powerful layer of glycocalyx within just a few days, protecting it from the host's cellular response. As a result, host cells that have migrated to the parasite at the initial stage of encapsulation are destroyed and their residues form the inner layer of the forming capsule. However, depending on the host species, a fibroblastic (in relatively more balanced systems, according to the terminology of Pronina and Pronin (1988), with the participation of hosts of the same species) or a leukocyte (in relatively less balanced systems with the participation

of hosts of other species) capsule can form around the parasite. This form of interrelations takes place in the cases of corynosome invasion of most of the natural paratenic hosts studied by us with the exception of flatfish (Figs. 6a, 6b).

In the case of invasion of other paratenic hosts, both natural (flatfish) and unnatural (amphibians, reptiles), by corynosomes, the second form of relationship is realized. In these cases, a massive layer of glycocalyx is not formed on the surface of the parasite, but the acanthocephalan is necessarily surrounded by a leukocytic capsule, which does not contain an inner layer of residues of destroyed cells (Fig. 6c). An exception to this, which is, in our opinion, of little consequence, is the aquarium fish *Hemichromis bimaculatus*, in which corynosomes can be surrounded either with a leukocytic capsule or a capsule close to fibroblastic, and the appearance of acanthocephalans can be, respectively, either oppressed or "normal," but in

both cases a thick layer of glycocalyx is also not formed on the surface of the parasites. The same form of relationship develops between the *Sphaerostris picae* acanthocephalan and its natural paratenic host, the sand lizard. It can be assumed that in all these cases the acanthocephalan is protected from the host's cellular response not by forming a thick layer of glycocalyx, but by using other mechanisms.

In their work, Parker et al. suggested that "... paratenity should be recognised as one component of a set of growth strategies, rather than as a "transport" event or "ecological bridge"..." thereby bringing paratenic hosts closer to the intermediate ones to a certain extent (Parker et al., 2009). Of course, such a rapprochement is very conditional and the fundamental difference between the paratenic and second intermediate hosts, consisting in the randomness of the first and the obligatory nature of the second, persists in all cases. We believe, however, that such a complication of the view on paratenical parasitism is fully justified. Moreover, taking into account the aforementioned and morphologically pronounced significant differences in the relationship of the acanthocephalans with natural paratenic hosts of different species, both the described forms of these relationships can be viewed as different growth or life cycle strategies, the implementation of which depends on the species of these hosts. In other words, paratenic parasitism as a phenomenon is not one, but a complex of (in our case, at least two) strategies, not necessarily, but quite possibly, implemented during the life cycles of different species of acanthocephalans and in different paratenic hosts. In further research, the authors intend to confirm or refute this hypothesis, and, in the case of its validity, explore the possibility of its application to other cases of tissue parasitism.

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#### COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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