

BIOLOGY, MORPHOLOGY,
AND SYSTEMATICS OF HYDROBIONTS

Somatic Musculature of Rotifers *Asplanchna girodi* Guerne, 1888 and *Trichotria pocillum* (Müller, 1776) (Rotifera, Pseudotrocha, Ploima): Comparative Aspect

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Abstract—Comparative study of somatic musculature in illoricate rotifer *Asplanchna girodi* Guerne, 1888 and loricate *Trichotria pocillum* (Müller, 1776) has been carried out by the method of phalloidin fluorescence and confocal laser scanning microscopy. Similar layering of muscles is revealed, while significant differences are observed in other aspects. Postcoronal transverse muscle of *A. girodi* and the dorsal portion of the anterior circular muscle of *T. pocillum* serve as attachment sites for the retractor muscles. All retractors are formed by smooth muscles or striated muscles, except the lateral retractors of *A. girodi*, which are formed by the most powerful oblique muscles. In *A. girodi* there are three pairs of retractors, ten longitudinal muscles, and five circular muscles, with a thick muscular plexus connecting them. In *T. pocillum* there are four pairs of retractors, five transverse muscles, strong foot retractors, and an arched structure of the head region (new for rotifers). Eight pairs of dorsoventral muscles, as identified in *T. pocillum*, are completely absent in *A. girodi*.

Keywords: Rotifera, *Asplanchna girodi*, *Trichotria pocillum*, musculature, phalloidin labeling

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INTRODUCTION

Rotifers are microscopic pseudocoelomic animals; only several tens of species reach a length of 1–2 mm, with the remaining being considerably smaller. On average, their length is $\leq 1-0.5$ mm. Approximately ~2000 species are known [22]. The systematic position of rotifers remains uncertain so far. Taxonomists more frequently accept the division of the group according to the structure of reproductive system into Monogononta and Digononta [28]. For Rotifera and Acanthocephala, the name Syndermata is suggested, which stresses their synapomorphy, namely a unique sincitial epidermis with a plate lying in the cytoplasm [7]. Later refinements were introduced and Acanthocephala and Rotifera with two subgroups: Bdelloidea and Monogomonta entered the group Syndermata [8, 29]. However, phylogenetic relationships within Syndermata have not been resolved until now. In the last study of Fontaneto and Jondelius [10], <1000 sequences of COI were studied and clades *Acanthocephala*, *Bdelloidea*, *Monogomonta*, and *Seisonidea* were supported. The interrelations of these groups remained unclear, except for the distinct distinguishing of sister relations between Acanthocephala and Bdelloidea.

In the systematics of rotifers, morphological traits play a large role as before. In connection with this, the

study of musculature received great attention. In the book of Riemann [18], all available evidence on the structure of musculature of rotifers obtained by classical histological methods was collected and generalized. Modern methods of phalloidin fluorescence in combination with confocal microscopy (CLSM) [26] was first used on illoricate *Philodina* sp. [13] and on loricate *Euchlanis dilatata* Ehrenberg and *Brachiomus quadridentatus* Hermann [15]. These studies stimulated the appearance of a series of papers on the structure of musculature of rotifers of different systematic positions [1–4, 11, 12, 14, 16, 17, 20, 21, 23–25, 30, 31]. The great diversity of forms of rotifers promotes continuation of such studies. Among studied forms, loricate forms dominate, exceeding the number of illoricate forms by a factor of 2. Such an unequal ratio served as a stimulus for performing a comparative study. A brief description of skin musculature of *Trichotria pocillum* was published earlier [1]; however, one should add a description of several new morphological elements required for a comparison of sites of somatic musculatures of illoricate and loricate rotifers from the group Monogononta, Ploima.

The purpose of this work was to study architectonics of location of the main elements of muscular system and perform their comparative analysis with refer-

ence to illoricate and loricate rotifers. Similar studies were not performed earlier.

MATERIAL AND METHODS

Two forms from the group Monogononta of the superorder Pseudotrocha were selected as study objects. The first was predatory illoricate rotifer *Asplanchna girodi* Guerne, 1888, representative of the fam. Asplanchnidae from order Ploima, plankton inhabitant. It has no foot; its glenoid body with a length of 500–700 μm is separated into head and trunk. Circumrotating apparatus with a great apical field and a simple ciliated band. Mastyx great, of incudate type. According to the type of movement, this is a swimming rotifer [5]. The material included small rotifers with a length of $\leq 500 \mu\text{m}$.

The second object was loricate rotifer *Trichotria pocillum* (Müller, 1776) from the fam. Trichotriidae order Ploima. The lorica of this rotifer consists of three independent parts which cover head, trunk, and foot individually. Head is protected by several cervical plates. The integral lorica of the trunk is flattened dorsoventrally. In the base of the two-segmental foot there are two spurs strongly varying by length. The second shorter segment of the foot ends in a pair of long toes with an unpaired spine between them. Mastax is of malleat type. This rotifer inhabits the coastal zone of freshwater water bodies and belongs to swimming–crawling forms [5]. The length of the trunk lorica of rotifer is 110–150 μm , the length of fingers 80–120 μm , and the length of toes 50–75 μm .

Material was collected in ponds of Yaroslavl oblast at the base of the Institute for Inland Waters, Russian Academy of Sciences (RAS) (Borok settlement) in summer 2012–2013 and fixed by Stefanini solution (2% paraformaldehyde with a 15% picric acid at 0.1 M Na-phosphate buffer, pH 7.6). To escape retraction of the head and foot into trunk to a state of “barrel” [27], rotifers were kept in a 2% solution of sulphate of magnesium; however, this did not always help. Rotifers were fixed for 1 h, then placed into eppendorphs and kept for several weeks in a fixative at a temperature of 4°C. After that, rotifers were washed off from 4 h to 2 days in 0.01M PBS (pH 7.4) with 20% saccharose to strengthen soft tissues. Directly before staining, material was washed 3 times for 5 min in 0.01M PBS (pH 7.4) with 0.25 Triton X-100 (PBS-T). Then the animals were stained by phalloidin, labeled TRITC (phalloidin-TRITC, Sigma, 1 : 200), for 2h at room temperature in darkness [26]. After rinsing in PBS, material was placed under cover glasses in the solution of glycerol with PBS (2 : 1) and scanned in Leica TCS SP5 confocal microscope. The series of optic sections were used to obtain projections of maximum intensity and three-dimensional reconstructions.

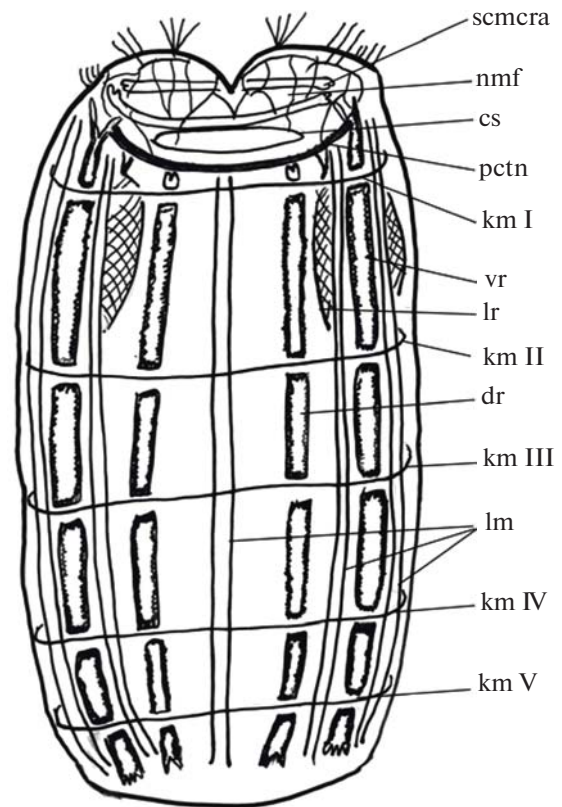


Fig. 1. Scheme of structure of musculature of *Asplanchna girodi*: (vp) ventral retractor, (dr) dorsal retractor, (km 1–km V) circular muscles, (lr) lateral retractor, (lm) longitudinal muscles, (scmcra) semicircular muscle of circumrotating apparatus, (pctn) postcoronary transverse muscle, (cs) corona sphincter, and (nmf) network of muscular fibers.

RESULTS

Asplanchna girodi. Muscular fibers containing F-actin were found in somatic musculature (Figs. 1, 2a–2i). Somatic musculature of *A. girodi* is represented by sphincter of the corona; a pair of semicircular muscles of the circumrotating apparatus; ten longitudinal and five to six circular muscles; dense plexus of muscular fibers in the head and over the entire trunk; transverse postcoronary muscle; and three pairs of retractors: ventral, dorsal, and lateral. In the region of the head there is a pair of semicircular muscles of the circumrotating apparatus. One of them lies on the ventral side and the other on the dorsal side; in lateral regions they converge, thus forming a ring. Each muscle consists of two similar in width fibers and reaches 3.2 μm (Figs. 1, 2a). In the center of the corona there is an elongated ellipsoid sphincter with a length of 66 and width of 21 μm ; the width of the head of this compressed at fixation specimen is 145 μm . The thickness of proper sphincter is 1.7 μm (Fig. 2b).

Ten longitudinal muscles pass through the entire trunk of the rotifer, two of which from each side follow

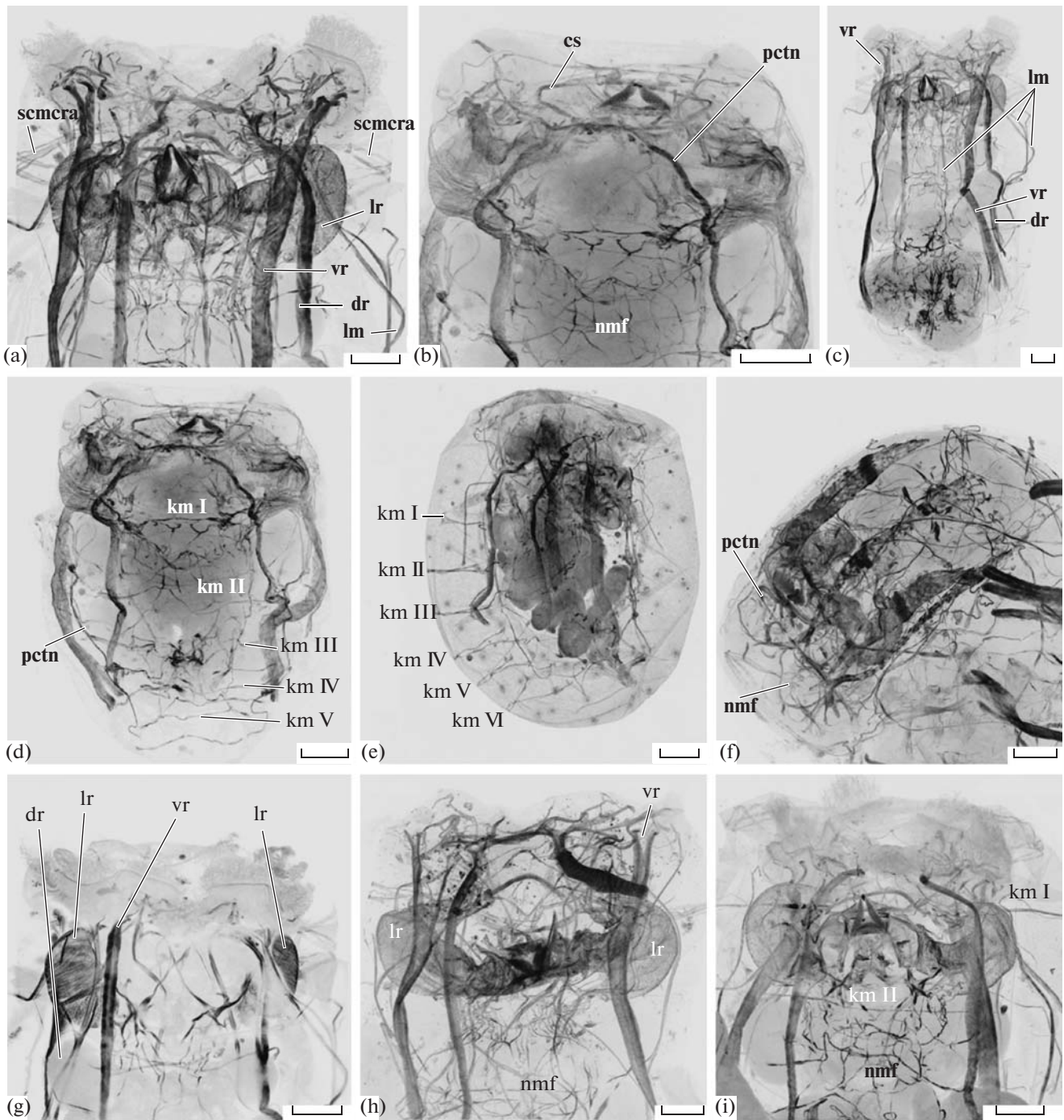


Fig. 2. *Asplanchna girodi*, phalloidin staining of musculature, projections of optic sections from confocal microscope: (a, b, h, i) anterior end of the body, (c, d, e) general view of body muscles, (f) posterior end of the body with an embryo, and (g) optical section at the level of lateral retractors. Scale 30 μm . The remaining designations are the same as in Fig. 1.

in lateral regions and the remaining six are in the center (Fig. 2c). Lateral longitudinal muscles are with thickness of 1–1.5 μm , central muscles reach 2.5 μm . The first circular muscle (km 1) lies at the level of proximal sites of lateral retractors and the second (km II) is behind them and mastax (Fig. 2d). All the

remaining circular muscles (km III–IV) are at a similar distance from each other, up to the posterior end (Figs. 2d, 2e).

At the upper boundary of the trunk there is a post-coronary transverse muscle with a thickness up to 6 μm (Figs. 2b, 2f). It passes in the central region

through the entire body of the rotifer and serves as a connecting link combining the entire musculature of the trunk into a single unit. Bifurcated proximal ends of dorsal retractors come to the central site of this muscle, which indicates the presence of two longitudinal muscular fibers in them (Fig. 2a). These retractors with a width of 9 μm pass through the entire trunk up to the posterior end. Bifurcated sites of proximal ends of the strongest ventral retractors formed by four longitudinal muscles whose number is distinctly seen at the posterior end of the trunk at their distal site come to the lateral region of transverse muscle. The thickness of ventral retractors is up to 15 μm (Figs. 2, 2a, 2c). Between dorsal and ventral retractors there are lateral retractors that have an elongated shape with rounded proximal and narrowed distal ends. These retractors occupy the first one-third of the trunk. They are connected with the transverse postcoronary muscle by short roots. The wall of lateral retractor includes a dense plexus of diagonal oblique muscular fibers that are directed from right to left and back from left to right towards each other. As a whole, this structure looks like a cocoon with widened proximal and narrowed distal ends (Figs. 2a, 2g). The length of lateral retractor is 65 μm ; thickness at the middle site is 24 μm and near roots ≤ 3 μm . The length of these and all other retractors of *A. girodi* is determined by the degree of compression of the animal at fixation.

In the region of the head, an intensive branching of proximal processes of all muscular retractors forming a queer muscular network is observed. No less dense network of entangled muscular fibers is observed over the entire trunk of this rotifer (Figs. 2h, 2i).

***Trichotria pocillum*.** Muscular fibers containing F-actin were found in somatic musculature (Figs. 3, 4a–4d). Somatic musculature of *T. pocillum* consists of arched structure in the region of corona, several pairs of retractors: of the corona, medial, dorsal, lateral, ventral, trunk, four retractors of the first segment of the foot, two retractors of the second and a pair of longitudinal muscles of the toes of the foot, and one circular and five transverse muscles, as well as two pairs of oblique muscles of the trunk and eight pairs of dorsoventral muscles.

A unique arched structure was revealed in the region of the corona (Fig. 4a). It is formed by four longitudinal filaments connected by a flexuous transverse filament. A pair of thin muscular fibers passes through the arched structure from the base of the anterior dorsal tentacle; in the base of proper tentacle there are four muscles of an elongated or triangular shape with a length reaching 3 μm (Figs. 4b, 4c).

All four pairs of retractors diverge from the postcoronary circular muscle; only ventral and lateral retractors diverge from its thin ventral site. The strongest dorsal and the longest medial retractors come up to the dorsal side of the postcoronary muscle. Nearer the posterior end of the body, two pairs of thin oblique

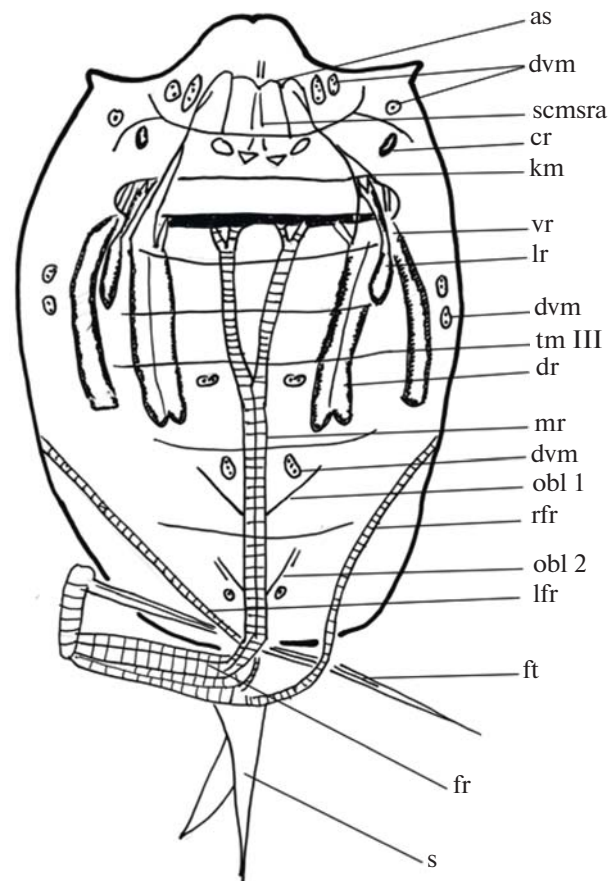


Fig. 3. Scheme of structure of musculature of *Trichotria pocillum*: (as) arched structure, (dvm) dorsoventral muscles, (obl 1, obl 2) oblique muscles, (lfr) left foot retractor, (mr) medial retractor, (dtm) dorsal tentacle muscles, (ft) foot toe, (tm III) third transverse muscle, (rfr) right foot retractor, (cr) corona retractor, (fr) foot retractor, and (s) spine. The remaining designations are the same as in Fig. 1.

muscles diverge forward at an angle of 45° from the medial retractor. The first pair is the upper pair of muscles (obl 1) (Figs. 3, 4a–4c); the second pair is the lower pair (obl 2). The second pair is two times shorter than the first; it originates near foot base and its proximal site consists of two parallel fibers (Figs. 4a, 4c, 4d). Medial retractor and foot retractor look like oblique muscles.

Five thin transverse muscles pass through the entire body, originating below the level of postcoronary circular muscle and going to the posterior end of the body; the muscles are located actually at a similar distance from each other (Figs. 3, 4b).

One pair of circular and a second pair of elongated dorsoventral muscles with diameters of 5–7 μm were revealed at the level of the arched structure. The third pair lies lower and more laterally. The fourth and fifth pairs of dorsoventral muscles are located in lateral regions at the boundary of distal sites of lateral retractor.

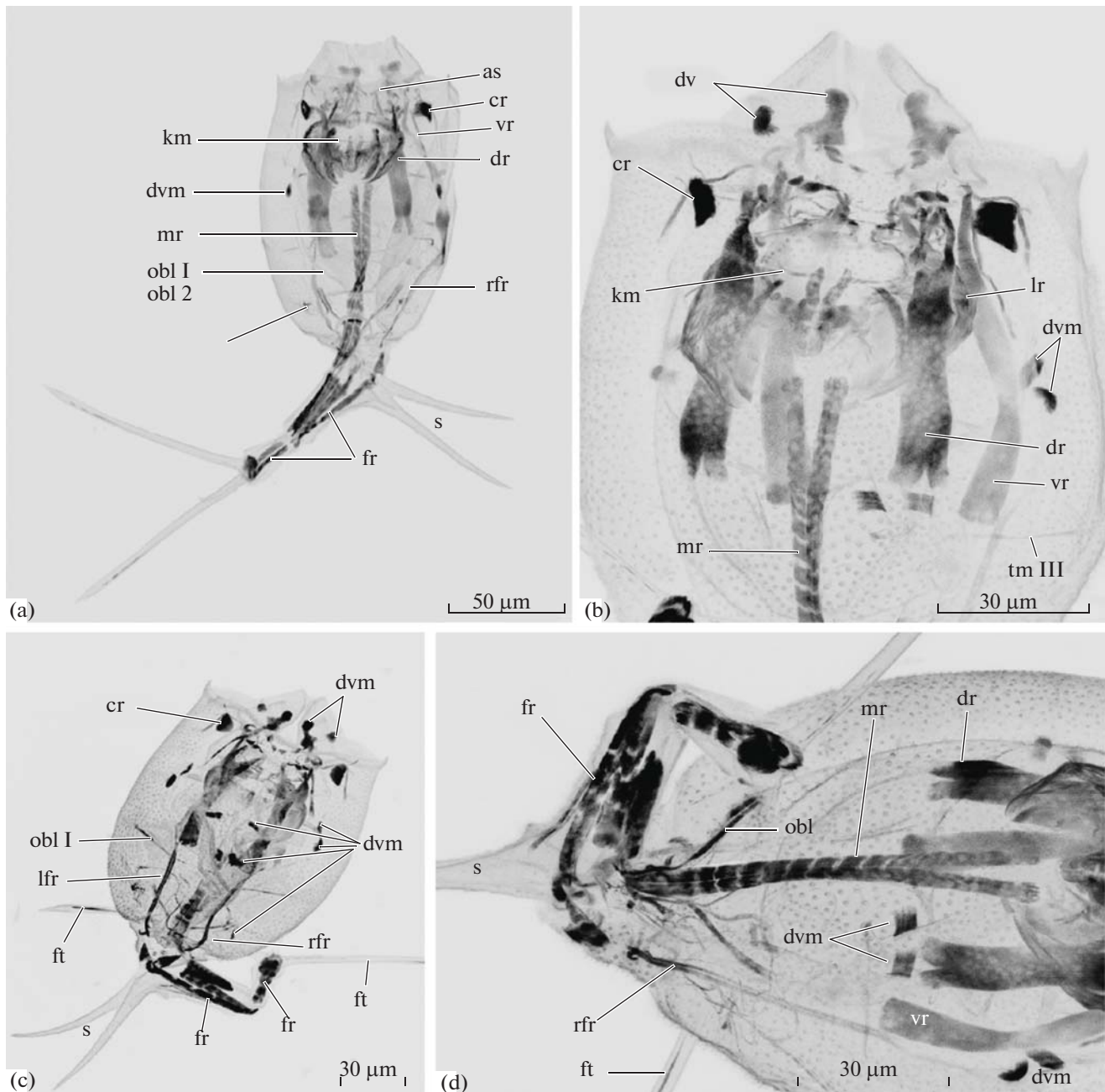


Fig. 4. *Trichotria pocillum*, phalloidin staining of musculature, projections of optical sections from confocal microscope: (a, c) general view of body muscles, (b) anterior end of the body, and (d) posterior end of the body. The remaining designations are the same as in Figs. 1 and 3.

tors. The sixth pair lies on each side of the site of bifurcation of medial retractors, and two last ones (seventh and eighth) were found along the medial retractor above the first oblique (obl 1) and under the second oblique (obl 2) muscles of the trunk, respectively (Figs. 3, 4a–4d).

The musculature of two-segmental foot demonstrates a complex structure. In the first segment there are four retractors, two of which are a continuation of

a medial retractor consisting of two supposedly oblique muscular bundles (Figs. 4a, 4c, 4e). The second pair is formed by the right and left foot retractors, also oblique muscles that originate from the lateral sites of the body wall, beginning in its posterior one-third. The right retractor follows directly to the foot and the left retractor bends under the distal site of medial retractor and only then passes into the first segment of the foot. One pair of retractors remains in the

second segment of the foot. Long toes of the foot have one thin muscular fiber each.

DISCUSSION

Phyllotoxins connected with fluorescent stain bind F-actin of muscular cells, marking thus the largest and small muscular fibers [19]. In the somatic musculature of *Asplanchna girodi* and *Trichotria pocillum*, there is a similar layering of its elements: external circular muscles, with longitudinal muscles lying under them, and submerged stronger retractors formed by two to four longitudinal fibers is observed. At this, the similarity of the studied muscular patterns ends.

There are enough published sources on the morphology of musculature of rotifers; illoricate and loricate forms were studied. Many authors restrict themselves to a description of morphological specific features of the species studied by them [17, 18, 23]; less frequently, the main tendencies for the emergence of new structures are formulated or attempts are made to explain their function [9, 11, 16].

Loricata and illoricate rotifers demonstrate a considerable diversity of all elements of musculature. Among illoricate rotifers of the fam. Asplanchnidae, the muscular system of two species—*Asplanchna girodi* and *Asplanchnopus multiceps* (Schrank)—was studied [16]. Both species have a circumrotating apparatus of *Asplanchna* type, but in the first it includes an apical field surrounded by a circumapical ciliated band; in the second, a discontinuous circumapical band with long cilia and two lateral papillae is located. In the head region of *Asplanchna girodi* at dorsal and ventral sides there are two semicircular muscles that approach each other in lateral regions and form a ring. In each muscle, two fibers with a thickness of $>3 \mu\text{m}$ were recorded. A more complex structure of the circumrotating apparatus of *Asplanchnopus multiceps* leads to the emergence of semicircular muscles of similar location; however, each muscle here includes already 6 to 10 cross-striated muscular bundles ($3\text{--}16 \mu\text{m}$), over the entire length of which anastomoses are seen. The circumrotating apparatus of Asplanchnidae serves mainly for the swimming of these predatory rotifers, but to some degree it is capable of supplying nanoplaston particles that are elements of the diet.

Circular muscles have different configuration: they can be thin, bearing one fiber, like in *Asplanchna girodi*, *Asplanchnopus multiceps* [16], in colonial *Sinamtherina socialis* (Linnaeus) [12], loricate *Euchlanis dilatata*, and *Brachiomus quadridentatus* [15], as well as strong, consisting of several fibers, which is typical for the dorsal part of the circular muscle of *Trichotria pocillum* [1] or for the closed circular muscle of *Lecane luna* [3]. Incomplete circular muscles also occur. As a rule, they are not closed at the ventral side. The most brilliant example is illoricate rotifer *Philodina* sp., which has up to 14–16 strong circular mus-

cles that by power are ahead of retractors [13]. Researchers who described these unclosed circular muscles explain their functions by the need of exercising inchworm's mode of locomotion [13]. Another example of incomplete circular muscles is demonstrated by illoricate swimming–crawling rotifer *Dicranophorus forcipatus* (Müller) [20], in which seven incomplete circular muscles of different configurations and one complete pedal muscle were revealed.

As for longitudinal muscles, a different amount of them was described. Unfortunately, several researchers do not differentiate longitudinal muscles as passing along the body, but submerged deeper retractors, as is seen from a description of musculature of two species from the fam. Dicranophoridae and Euchlaridae [20, 21], in which nine and four pairs of longitudinal muscles were observed, respectively.

It is more difficult to unravel their complex configuration. The location of retractors is directly related to the body shape of rotifers. In rotifers whose body is extended in length, all retractors pass along the longitudinal axis of the body, differing in number and power [1–3, 15, 16]. In two rotifers belonging to different suborders, but having similar circular body shapes, all retractors attach themselves to the transverse postcoronary muscle and pass at an angle of 45° downwards and laterally. These are *Testudinella patina* (Hermann), (Gnesiotrocha, Flusculariaceae) [4], and *Lecane luna* (Pseudatrocha, Lecanidae) [3].

The distinguishing feature of somatic musculature of loricate rotifers are dorsoventral muscles. At their sections they usually have an extended or circular shape with a thickness of 4 to 7 μm . The number of such muscles fluctuates from two to eight pairs at different locations. At an extended body shape, as in *Trichotria pocillum*, eight pairs of dorsoventral muscles are located in lateral regions of the trunk, in the region of corona, and in the foot base. In *Platyias patulus* (Müller), two pairs of these muscles lie laterally at the boundary of the corona and trunk [16]; in *Euchlanis dilatata* and *Mytilina ventralis* (Ehrenberg) [3, 4, 16], on the contrary, the same two pairs of dorsoventral muscles are located already in the posterior part of the trunk at the foot level. The circular body shape of *Testudinella parina* led to the formation of 17 dorsoventral muscles, the largest part of which lies laterally in the region of the corona and the upper part of the trunk, two lower pairs are along the gut sides, and only an unpaired muscle is in the base of the anterior dorsal tentacle [4]. Of five pairs of dorsoventral muscles of *Lecane luna* [3], two pairs are confined to corona retractors and three muscles lie along body sides at an equal distance from each other. Dorsoventral muscles connect ventral and dorsal lorica plates. Sorensen [25], considering the musculature of *Notolca acuminata* (Ehrenberg) (Ploima, Brachionidae) that he studied, suggested that incomplete circular muscles can change into dorsoventral ones. The location of these

muscles is also affected by the foot structure, number of retractors in it, and the sites of their divergence.

Differences in the amount and location of muscular retractors of feet were found. For instance, in *Brachionus diversicornis* (Daday), *Platyias quadricornis* [2], and *Brachionus calyciflorus* Pallas [18] (all from the fam. Brachionidae), whose musculature was studied by different methods, the presence of two pairs of foot retractors at the common plan of structure of their musculature was revealed. In these species, external ventral foot retractors attach themselves to lateral sites of the body wall in the mastax region; then, upon approaching each other, they follow to the foot base and enter it. The second pair of thinner dorsal retractors also passes within the foot. In this family, feet, as a rule, are wormlike, retractile, or segmental. The changed pattern is observed in other fam. Trichotriidae (also from the Ploima group) in *Trichotria pocillum*. The strong two-segmental foot with two spurs near the base has the same two retractors, the ventral pair of which originates in the same way as in Brachionidae described above, but one of its branches goes directly to the foot and the second branch bends under the distal site of medial retractor and only then passes to the first segment of the foot. The second pair of foot retractors is formed by a continuation of distal sites of medial retractor. In the second foot segment, only one pair of retractors remains.

According to the structure, skeletal muscles of the studied rotifers can be smooth, more frequently cross-striated and more rarely oblique. According to the results of electron-microscopic studies, oblique muscles have characteristics of rapid muscles [9] and probably can be adaptations for predation. Proceeding from these assumptions, one can consider the smallest lateral retractors of *Asplanchna girodi* rapid and, moreover, the rotifer possessing them actually a true predator.

According to the system of G.I. Markevich [6], devised from the results of a morphofunctional study of the corona and mastax as determining structures of rotifers, *A. girodi* was assigned to the order Saltiramida and *Trichotria pocillum* to the order *Transversiramida*; both orders belong to the group Monogononta, Ploima. The described models of somatic musculature of rotifers do not give a clue as to the unraveling evolutionary relations between the studied species, the amount of which became 20. Until now it has not been obvious which characters of muscular system have phylogenetic importance and which are determined by sizes, body shape, degree of flattening, or the type of movement. The limits of variations of the structure of musculature among closely related species are also not clear.

CONCLUSIONS

A comparative study of somatic musculature of the illoricate rotifer *Asplanchna girodi* and loricate *Trichotria pocillum* revealed similar layering of elements of

their musculature. Main differences were recorded in the amount and location of elements forming these layers, namely circular, longitudinal muscles, and retractors. In *Asplanchna girodi*, three pairs of retractors were revealed; one more pair was recorded in *Trichotria pocillum*. These retractors are formed by smooth, cross-striated, and oblique muscles. The distinguishing feature of loricate *T. pocillum* is the presence of eight pairs of dorsoventral muscles, which are completely absent in *Asplanchna girodi*.

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