

## Publication

### A complete three-dimensional reconstruction of the myoanatomy of Loricifera : comparative morphology of an adult and a Higgins larva stage

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**INTRODUCTION:** Loricifera is a group of small, marine animals, with undetermined phylogenetic relationships within Ecdysozoa (molting protostome animals). Despite their well-known external morphology, data on the internal anatomy of loriciferans are still incomplete. Aiming to increase the knowledge of this enigmatic phylum, we reconstruct for the first time the three-dimensional myoanatomy of loriciferans. Adult *Nanalaricus* sp. and the Higgins larva of *Armorlaricus elegans* were investigated with cytochemical labeling techniques and CLSM. We discuss our findings with reference to other loriciferan species and recently established phylogenies. **RESULTS:** The somatic musculature of both adult and larval stages is very complex and includes several muscles arranged in three orientations: circular, transverse and longitudinal. In adult *Nanalaricus* sp., the introvert is characterized by a net-like muscular arrangement, which is composed of five thin circular fibers crossed by several (up to 30) thin longitudinal fibers with bifurcated anterior ends. Two sets of muscles surround the pre-pharyngeal armature: 6 buccal tube retractors arranged 3 x 2 in a conical shaped structure, and 8 mouth cone retractors. Additionally, a thick, circular muscle marks the neck region and a putative anal sphincter is the posteriormost myoanatomical feature. In the Higgins larva of *A. elegans*, two circular muscles are distinguished anteriorly in the introvert: a dorsal semicircular fiber and a thin ring muscle. The posteriormost region of the body is characterized by an anal sphincter and a triangular muscle. **CONCLUSIONS:** Based on the currently available knowledge, the myoanatomical bodyplan of adult loriciferans includes: (i) 8 mouth cone retractors, (ii) a pharynx bulb composed of transversal fibers arranged radially, (iii) circular muscles of the head and neck, (iv) internal muscles of the spinoscalids, (v) longitudinal muscles spanning all body regions, and (vi) transverse (circular) muscles in the abdomen. Concerning the Higgins larva, the muscle subsets assigned to its myoanatomical ground pattern are the (i) longitudinal retractors of the mouth cone, introvert, and abdomen, (ii) abdominal transverse muscles, and (iii) a pharynx bulb composed of transverse, radial fibers. In a comparison with phyla traditionally regarded as phylogenetically close, our data show that the overall myoanatomy of Loricifera is more similar to Kinorhyncha and Nematomorpha than to Priapulida. However, the head musculature of all these groups is very similar, which supports homology of their introverts and head morphology.

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