

# Comparative morphology of the somatic musculature in species of *Hexarthra* and *Polyarthra* (Rotifera, Monogononta): Its function in appendage movement and escape behavior

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## Abstract

Species of *Hexarthra* and *Polyarthra* are freshwater rotifers with well-known escape behaviors that result from interactions with planktonic predators. Both rotifers bear a suite of mobile appendages that function in evasive maneuvers and saltatory jumps through the water column, but the anatomical and functional bases of these actions are poorly understood. Here, we use a combination of phalloidin staining, confocal laser scanning microscopy, and video analysis to describe the morphology of the somatic muscles that supply the mobile appendages in order to understand how they function in escape behavior. Results show that species of *Hexarthra*, which bear six radially distributed limbs, possess a highly complex trunk musculature that supplies the inside of each limb with its own abductor and adductor muscles, i.e., a direct muscle supply. The singular dorsal and ventral limbs each receive a pair of large abductor and adductor muscles (four muscles total per limb), while the paired dorsolateral and ventrolateral limbs each receives three muscles (two abductors, one adductor per limb). Contraction of the abductor muscles creates a power stroke in the form of an anterior sweep of the limbs, which leads to a three-dimensional tumbling of the rotifer through the water column. Alternatively, species of *Polyarthra* possess 12 blade-like appendages that are arranged into four equal bundles; each bundle receives an indirect muscle supply that attaches to the shoulder of the paddles. A single longitudinal paddle muscle supplies each dorsolateral bundle, while a pair of longitudinal paddle muscles supplies each ventrolateral bundle. Contraction of these muscles, whether singly or in concert, functions to abduct the paddles in a power stroke, leading to rotation of the body and movement of the rotifer. The recovery stroke is hypothesized to be a multi-step process that begins with reorientation of the appendages prior to adduction, followed by contraction of various muscles to antagonize the paddle muscles. In total, these observations reveal novel complexities in the rotifer muscular system that aids our understanding of the biophysics of predator avoidance in appendage-bearing rotifers. © 2008 Elsevier GmbH. All rights reserved.

**Keywords:** Rotifer; Muscles; Confocal; Functional morphology

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## 1. Introduction

Ever since van Leeuwenhoek's description of rotifers in 1677, in which he described the rotifer head as "two little wheels" (Dobell 1958), the study of rotifer locomotion has

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focused on the activity of the corona (e.g., Epp and Lewis 1984; Charoy and Clément 1993; Santos-Medrano and Rico-Martinez 2001), a structure composed of one or two ciliated discs that sit atop the head. Metachronal waves pass through the coronal cilia, or trochal discs, and propel rotifers swiftly through the water column. The corona is a retractable structure under the direct control of longitudinal muscles that insert on the ciliary rootlets – these muscles also control the direction of locomotion (Clément 1977, 1987). In general, most rotifers travel through a helical swimming path, presumably due to viscosity (Purcell 1972) or as an efficient means to orient toward an external stimulus (Crenshaw 1996). Regardless, the helical trajectory results from a single muscle's unilateral control of most directional movement – rotifer's make mostly right-handed 45° turns during normal ciliary swimming (Clément 1987). However, muscles control more than the direction of movement in rotifers; muscles also control the rate of ciliary beat and hence, swimming speed (Clément 1987; Clément and Wurdak 1991), which generally does not exceed 0.3–0.5 mm/s during regular swimming (Santos-Medrano and Rico-Martinez 2001). Exceptions to these velocities are present, however, in a few planktonic species that can dramatically increase their speed of locomotion. For example, species of *Keratella* can rapidly increase the frequency of their ciliary beat and swim at 1.8 mm/s, thereby avoiding interference competitors (e.g., copepod, Williamson 1987) or predators (e.g., *Asplanchna*, Gilbert and Kirk 1988). The actual mechanism that leads to increased ciliary activity, e.g., muscle contraction or direct neural stimulation, is undetermined.

Rotifer locomotion need not be constrained by the coronal ciliature, however. Species of *Filinia*, *Hexarthra* and *Polyarthra* possess a suite of unusual appendages that appear to function in quick bouts of locomotion, or saltation, that may be independent of coronal activity. In species of *Filinia*, these appendages are elongate, flexible setae, and in *F. novaezealandiae*, receive an indirect muscle supply that controls setal abduction and adduction (Hochberg and Ablak Gurbuz 2007). These setal flexions occur during encounters with predators but do not always lead to rapid locomotion (Williamson 1987); hence, they are best considered defensive structures that inhibit predation rather than appendages used for locomotion (Hochberg and Ablak Gurbuz 2007). Still, in species of *Hexarthra* and *Polyarthra*, where the appendages are much shorter and less likely to prevent ingestion, their main function appears to be rapid locomotion (Gilbert and Williamson 1978; Williamson 1987; Kak and Rao 1998; Starkweather 2005). For example, species of *Hexarthra* possess six arms distributed radially around the body, and when moved in quick fore-to-aft cycles, lead to rapid “jumps” through the water column. Santo et al. (2005) investigated the musculature of *H. mira* and found that each arm receives its own muscular supply, which is quite different

from that observed for the other appendage-bearing species of *Filinia* or *Polyarthra*. As in *F. novaezealandiae*, species of *Polyarthra* possess appendages with an indirect muscle supply that only attaches to the shoulder region of the appendage (Allen 1968). In *P. vulgaris*, six muscles appear to control the movement of 12 paddle-like appendages – the appendages are distributed in two bilateral pairs of three overlapping paddles (Allen 1968). Movement of the paddles appears to be coordinated and leads to a “tumbling” of the rotifer through the water column and away from the predator (Gilbert 1985).

To date, few observations on the musculature of species of *Hexarthra* and *Polyarthra* have restricted our understanding of the functional morphology of escape locomotion in these rotifers, despite a series of 2D and 3D videographic analyses that analyzed some of their movement patterns (e.g., *Polyarthra*, Gilbert 1985, 1987). And while previous investigations using transmission electron microscopy (Allen 1968) and confocal laser scanning microscopy (Santo et al. 2005) have provided important details on general muscular organization, there is still a poor understanding of how these rotifers control the direction of their escape, and which muscles orchestrate the response. The purpose of the current investigation is to improve our understanding of escape locomotion in species of *Hexarthra* and *Polyarthra* through a detailed analysis of their musculature. Here, we use a combination of phalloidin staining, confocal laser scanning microscopy, and imaging software to visualize rotifer muscles in three dimensions, and together with video analysis of live specimens, attempt to correlate the patterns of escape locomotion with knowledge of their muscular anatomy.

## 2. Material and methods

### 2.1. Collection and identification

Specimens of *Hexarthra* cf. *mira* Hudson, 1871 and an unidentified species of *Hexarthra* were collected with a 64 µm plankton net from a pond at the Smithsonian Marine Station in Fort Pierce, FL, USA (N27°27.627', W80°18.682') in June and July 2005, 2006. Live rotifers were observed in a petri dish for interactions with other invertebrates. Several specimens were also observed alive on glass microscope slides and viewed with a Leica compound microscope. Several of these specimens were then anaesthetized in 1% MgCl<sub>2</sub> and photographed with a Nikon Coolpix digital camera. Animals were identified with brightfield optics using the taxonomic key of Jersabek et al. (2003). Specimens of *Polyarthra* cf. *vulgaris* Carlin, 1934 and *P. major* Burckhardt, 1900 were collected with a 64 µm plankton net at Mascopic pond in Tyngsboro, MA, USA (N42°40.703',

W71°24.032') from June to September 2006. Specimens were observed alive on glass slides and video recorded with a Leica compound microscope (20×) equipped with a Canon Powershot digital camera. Digital AVI video files were used to observe the behavior of *Polyarthra* and interpret the functions of muscles. Individual frames from these videos were imported in Adobe Photoshop CS and made into figures. The only adjustments made to these frames are from cropping, changes of brightness and contrast, and changes to grayscale. The original videos are available from the primary author by request.

## 2.2. Muscle staining and microscopy

Several rotifers (*Hexarthra*,  $n = 9$ ; *Polyarthra*,  $n = 11$ ) were anesthetized in 1% MgCl<sub>2</sub> for 20 min at the time of collection and fixed in 4% paraformaldehyde in 0.1 M Sorensen's phosphate buffer (PB) for 24 h at room temperature. Specimens were rinsed ( $3 \times 10$  m) in 0.1 M PB (pH 7.2) and transferred to Alexa Fluor 488 Phalloidin (Molecular Probes, Eugene, OR) in PB plus 0.2% Triton X-100 for 12 h at 4 °C. Specimens were next rinsed in PB, mounted in Fluoromount G (Electron Microscopy Sciences, Hatfield, PA) on glass slides, and refrigerated at 4 °C for at least 24 h before examination. Control specimens (fixed but unstained) were checked for autofluorescence, which was negligible.

Wholemout specimens were examined on two microscopes: (1) a Zeiss Axioimager equipped with epifluorescence, digital AxioCam, and Axiovision software at the University of Massachusetts, Lowell; and (2) a Nikon Eclipse E800 confocal microscope equipped with a Biorad Radiance 2000 laser system at the Smithsonian Marine Station in Fort Pierce, Florida. For confocal microscopy, Lasersharp software (v. 4.0) was used to collect a series of 0.05–0.1 μm optical sections with maximum intensity projection along the  $z$ -axis. Confocal images were imported into Confocal Assistant (v. 4.02) and made into TIF files. Additional digital files were imported into Volocity v 4.0 (Improvision) to render 3-D images and create  $X$ – $Y$ – $Z$  rotations in TIF and AVI formats. No manipulations of the original images were made other than changes of color (false coloring or grayscale) or cropping. Video files are available from the primary author by request.

## 3. Results

### 3.1. *Hexarthra*

#### 3.1.1. General morphology

Species of *Hexarthra* are stout, somewhat conical in appearance, and 200–270 μm long (Fig. 1A and C). A

large, ciliated, coronal field (trochus) is present anteriorly and a smaller ring of cilia is present around the mouth, outside of the trochus (Fig. 1A and C). Six appendages are arranged radially around the body: one elongate ventral appendage (VA), two short ventrolateral appendages (VLA), two short dorsolateral appendages (DLA), and one stout dorsal appendage (DA) (Fig. 1A and C). Long setose bristles extend from the tip of each appendage.

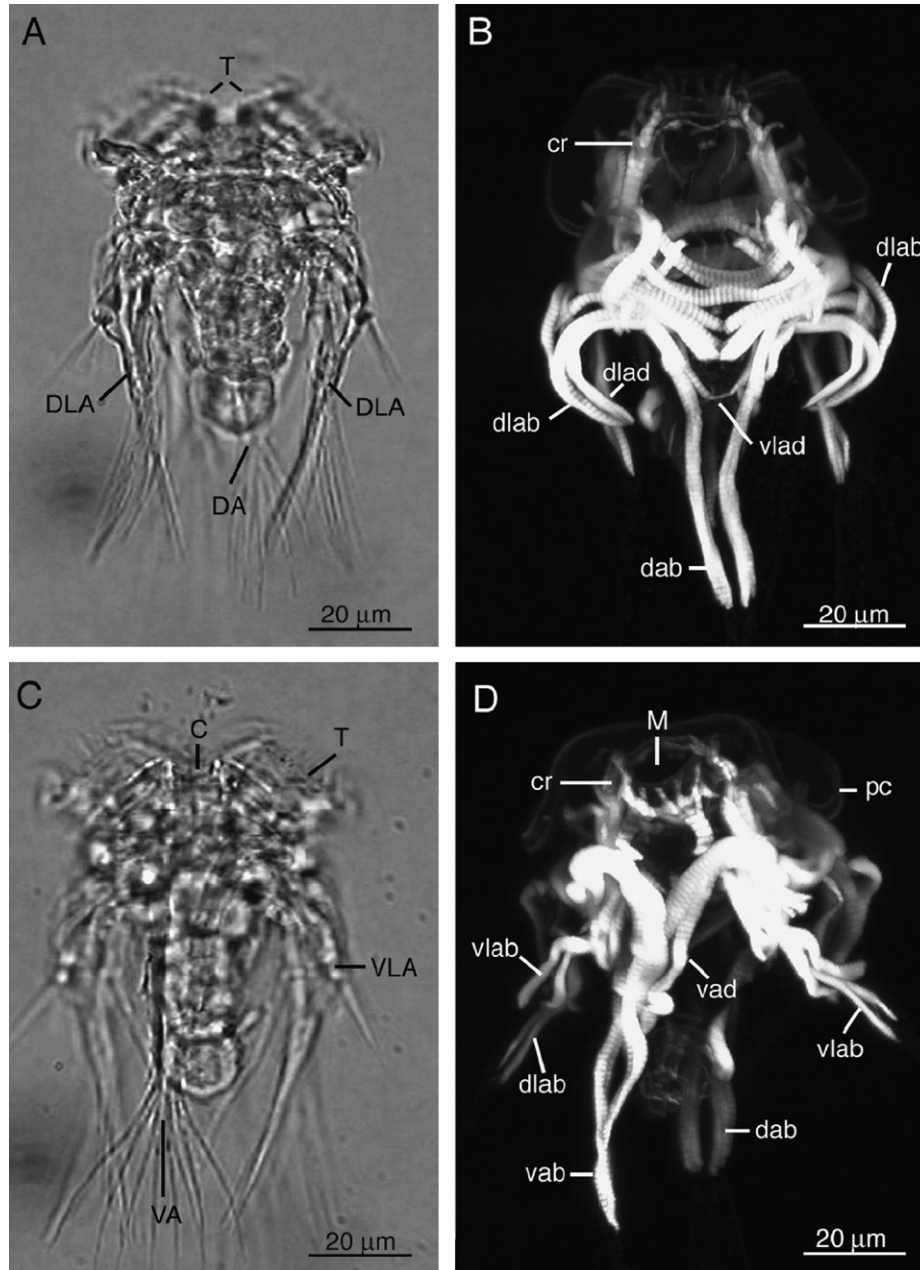
#### 3.1.2. Behavioral observations

Species of *Hexarthra* swim through the water in a helical fashion using their corona. Cycles of appendage abduction/adduction were not observed unless a rotifer encountered a potential predator (e.g., copepod). In an encounter, appendage movements appeared to be restricted to the ventro- and dorsolateral appendages, though occasional abductions of the dorsal appendage were also observed. These cycles of movement did not always lead to jumps through the water column, although they did always result in rotation of the body and orientation away from the potential predator. During specific encounters with the predatory rotifer, *Asplanchna brightwellii*, specimens of *Hexarthra* did abduct most or all of the six appendages and “tumble” haphazardly through the water column. Path analysis of individual trajectories was not assessed, but in most cases, the rotifers appeared to tumble in random directions. Several individuals were also placed on glass microscope slides to observe appendage movement; however, most specimens remained quiescent and did not engage in any locomotor activity.

#### 3.1.3. Musculature

The somatic musculature of species of *Hexarthra* sp. and *H. mira* is highly complex due to the presence of numerous interweaving muscle fibers that form intricate layers. Despite this complexity, both species appeared to have identical muscle patterns. All muscles are bilaterally arranged and dominated by longitudinal and transversely oriented fibers (Figs. 1–4). The only somatic circular muscle present in the body is the pars coronalis (pc), present as a single fiber that outlines the trochus (Figs. 1D, 2C, 3B, 4). Additional splanchnic circular fibers are present in the region of the mastax and the visceral region (not described).

Functionally, the somatic musculature can be divided into three sets: head/coronal retractors, appendage abductors and appendage adductors. There are approximately eight pairs of longitudinal muscles that insert in the region of the corona/head/neck and may function in coronal retraction or movement of the head (Figs. 1–4). A pair of short retractors extends from a region just below the ventral appendage and onto the mouth margin where they form digitate extensions (Fig. 1D,

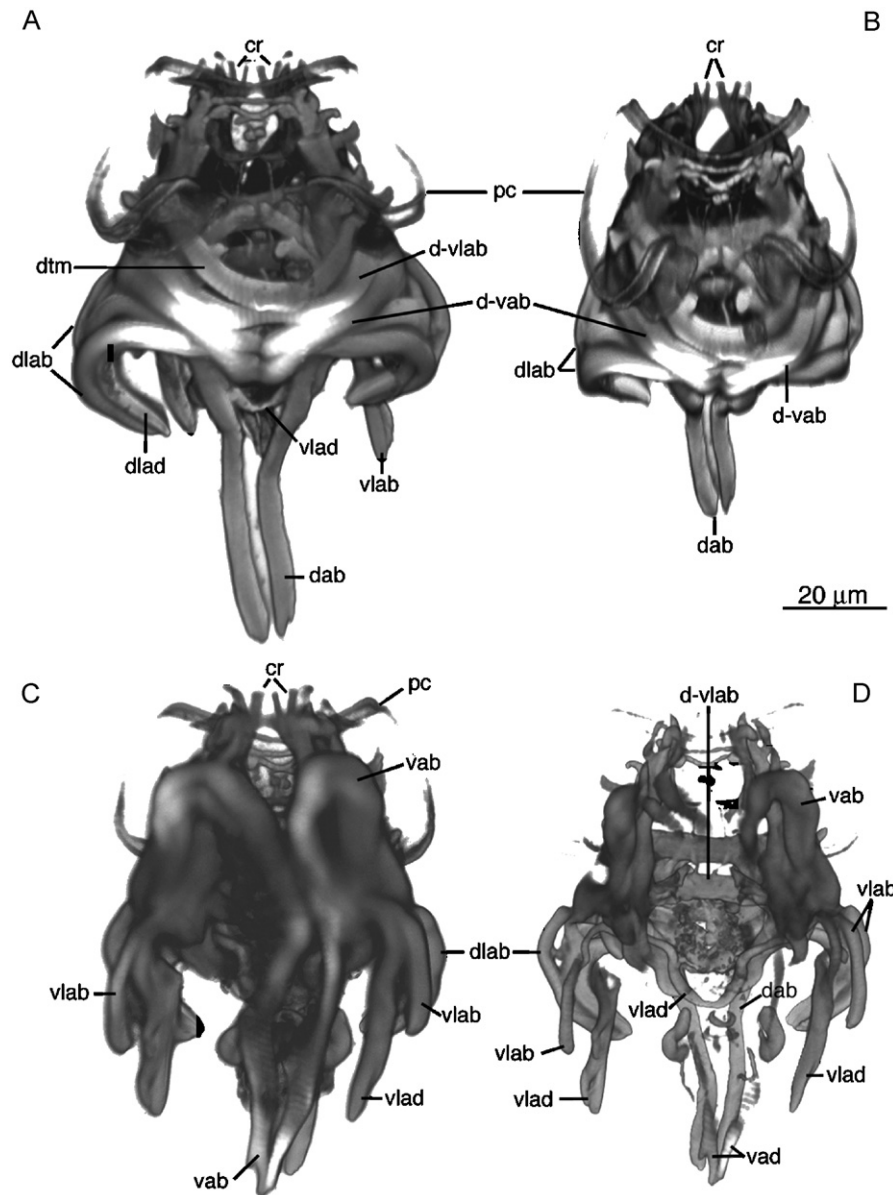


**Fig. 1.** General morphology and musculature of *Hexarthra* sp. Anterior is up: (A) dorsal view of rotifer with brightfield optics; (B) dorsal view of rotifer stained with phalloidin and viewed with CLSM; (C) ventral view of rotifer with brightfield optics and (D) ventral view of rotifer stained with phalloidin and viewed with CLSM. C, cingulum; cr, coronal retractor; DA, dorsal appendage; DLA, dorsolateral appendage; dab, dorsal abductor muscle; dlab, dorsolateral abductor muscle; dlad, dorsolateral adductor muscle; M, mouth; pc, pars coronalis; T, trochus; VA, ventral appendage; vab, ventral abductor muscle; vad, ventral adductor muscle; VLA, ventrolateral appendage; vlab, ventrolateral abductor muscle and vlad, ventrolateral adductor muscle.

2B, 3). At least two retractors originate in the mid-trunk region and insert close to the mouth. Three short retractor muscles with origins on the dorsolateral side of the body next to the dorsolateral appendages insert into the dorsal neck region. Lastly, a single, thick transverse muscle (dorsal transverse muscle, dtm) curves from the dorsal body wall and connects to an intricate series of muscles behind the mouth (Fig. 2A).

Muscles that function in appendage abduction and adduction are defined by their position within individual appendages, i.e., outer (abduction) versus inner (adduction) surface of the appendage. Some muscles have dorsal origins and ventral insertions within the trunk of the body; in these cases, the dorsal portion of the muscle is labeled differently to indicate its origin (e.g., see vab and d-vab in Fig. 4C; also below).

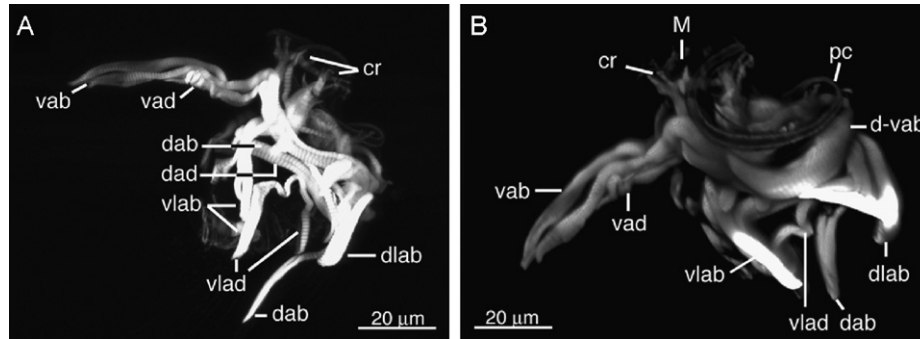




**Fig. 2.** Computer-rendered views of the musculature of *Hexarthra* sp.: (A) dorsal view, anterior is up; (B) frontal view, dorsal is down; (C) ventral view, anterior is up and (D) partial view of the dorsal muscles as seen from the ventral side (some optical sections of the dorsal muscles are removed), anterior is up. cr, coronal retractor; dab, dorsal abductor muscle; dlab, dorsolateral abductor muscle; dlad, dorsolateral adductor muscle; dtm, dorsal transverse muscle; d-vab, dorsal origin of the ventral abductor muscle; d-vlab, dorsal origin of the ventrolateral abductor muscle; pc, pars coronalis; vab, ventral abductor muscle; vad, ventral adductor muscle; vlab, ventrolateral abductor muscle and vlad, ventrolateral adductor muscle.

The largest pair of abductors/adductors in the body are those that control the singular ventral appendage. The ventral abductors (vab) are thick, paired muscles that originate at the midline of the dorsal body wall (d-vab; Figs. 1A, 2C, 3, 4). Their dorsal origin is defined by a branching of each abductor muscle (Figs. 1B, 2A, 4), which may indicate that each muscle consists of two anatomical and/or functional units (see below). Each ventral abductor muscle wraps around the dorsal body wall to the ventral side, where it arches anteriorly and inserts in the ventral appendage (Figs. 3, 4C). Both

abductors extend to the tip of the appendage. Immediately beneath each ventral abductor muscle, i.e., running along the inner edge of the appendage, is a ventral adductor muscle (vad; Figs. 2D, 3, 4C). The vad is a noticeably thinner muscle than the vab – its origin is also on the dorsal side of the body, but the precise location is difficult to determine. There are two options for the origin of the vad: (1) the ventral adductor muscle may branch from the ventral abductor muscle on the dorsal side (d-vab), thereby explaining the split appearance of the vab; or (2) the ventral adductor muscle may have its



**Fig. 3.** Lateral views of the musculature of *Hexarthra* sp.: (A) Z-projection of the musculature, dorsal is down and (B) computer-rendered view of the musculature, dorsal is to the right. cr, coronal retractor; dab, dorsal abductor muscle; dad, dorsal adductor muscle; dlab, dorsolateral abductor muscle; d-vab, dorsal origin of the ventral abductor muscle; M, mouth; pc, pars coronalis; vab, ventral abductor muscle; vad, ventral adductor muscle; vlab, ventrolateral abductor muscle and vlad, ventrolateral adductor muscle.

origin (o-vad; Fig. 4B) at the base of the dorsal appendage just beneath the dorsal adductor muscle (dad). If the first option is correct, then the muscle labeled o-vad (Fig. 4B) has an undetermined insertion point and function.

Abduction and adduction of both ventrolateral appendages appears to be controlled by only two (unpaired) muscles in the body. The larger of the two muscles is the abductor (vlab) and is positioned just anterior to the ventral abductor muscle on the dorsal side (d-vab, Figs. 1, 4A, C). The ventrolateral abductor (vlab) is somewhat u-shaped and bends around the sides of the body, eventually curving beneath the ventral adductor muscle (vad) and branching to form two short muscle arms (Figs. 1D, 2D, 3A, 4). Each muscle arm inserts partway into the ventrolateral appendage. The second muscle that controls ventrolateral appendage movement is the ventrolateral adductor muscle (vlad), a single, thin, u-shaped muscle that inserts close to the tip of both ventrolateral appendages (Figs. 2–4). The midpoint of this elongate muscle is on the dorsal side of the body and appears to loop just posterior of the d-vlab (Figs. 1B, 2A, 3, 4).

The paired dorsolateral appendages are each controlled by three independent muscles (Figs. 1B, 2B, 3, 4). Two short abductor muscles (dlab) originate close to the dorsal midline of the trunk and extend laterally into each appendage. Both muscles appear to coalesce into a single muscle that parallels the outside contour of the appendage and insert at approximately two-thirds of appendage length (Fig. 4A). A third muscle, the dorsolateral adductor muscle (dlad), originates between the two abductors on the dorsal side, parallels the inside surface of the appendage, and inserts close to the appendage tip.

The single dorsal appendage receives a pair of thick, dorsal abductor muscles (dad) that insert at the appendage tip (Figs. 1B, 2B, 4A). These abductors appear to originate close to the ventral midline of the

body (Fig. 4C). It is undetermined if these muscles represent separate abductors or if they form one continuous u-shaped muscle similar to the d-vab/d-vlab. The dorsal adductor muscle is a much smaller muscle that only inserts close to the shoulder of the dorsal appendage (Fig. 4C). Like its counterpart, this muscle has its origin near the ventral body midline.

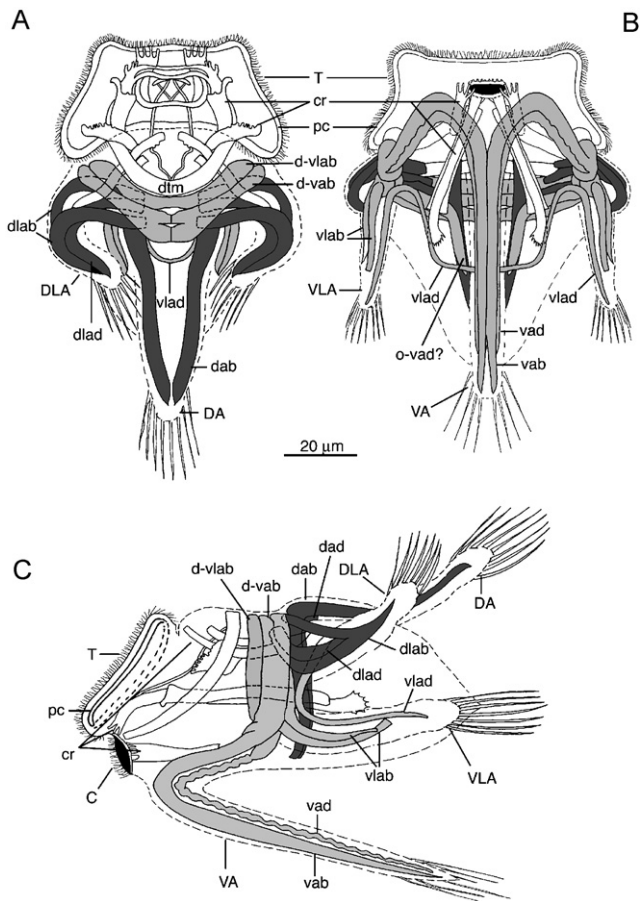
## 3.2. Polyarthra

### 3.2.1. General morphology

Both *Polyarthra* cf. *vulgaris* and *P. major* were approximately 150–230  $\mu\text{m}$  in length, possessed a single median eye (EY) and a pair of antennae (DA) within the corona (Fig. 7). Each species possessed a total of 12 blade-shaped appendages distributed in two pairs: one pair of three paddle-like appendages is present on the dorsolateral surface (DP, Fig. 6A) and a second pair is present on the ventrolateral surface (VP, Fig. 6B). Individual appendages are serrated and overlapping, with shoulder hinges (SPH) distributed in a somewhat diagonal orientation (Fig. 5G). A dorsal shelf (DS) extends between the dorsolateral bundles of paddles (Fig. 5I, 7A). The anatomy of *P. vulgaris* is reviewed by Allen (1968).

### 3.2.2. Behavioral observations

Locomotion in *P. vulgaris* has been covered extensively by Gilbert (1985), so our observations here only elaborate on specific movements of the appendages. It is important to indicate that observations of appendage movement were made while rotifers were mounted under coverslips on glass slides. The compression of the coverslip did appear to affect appendage movement, i.e., appendages occasionally stuck to the coverslip, and the resulting movements of the body were strictly two-dimensional. Nevertheless, our observations indicate that individuals could control movement in all four sets



**Fig. 4.** Diagrams of the somatic musculature of *Hexarthra* spp. based on observations of nine specimens (*Hexarthra* sp. and *H. mira*). The outline of the body is dashed. The viscerocloacal musculature is not shown: (A) dorsal view, anterior is up; (B) ventral view, anterior is up and (C) lateral view, anterior to the left, ventral is down. C, cingulum; cr, coronal retractor; DA, dorsal appendage; dab, dorsal abductor muscle; dad, dorsal adductor muscle; DLA, dorsolateral appendage; dlab, dorsolateral abductor muscle; dlad, dorsolateral adductor muscle; dtm, dorsal transverse muscle; d-vab, dorsal origin of the ventral abductor muscle; d-vlab, dorsal origin of the ventrolateral abductor muscle; o-vad, origin of the ventral adductor muscle; pc, pars coronalis; T, trochus; VA, ventral appendage; vab, ventral abductor muscle; vad, ventral adductor muscle; VLA, ventrolateral appendage; vlab, ventrolateral abductor muscle and vlad, ventrolateral adductor muscle.

of appendages simultaneously, two sets of similar appendages simultaneously (e.g., both dorsolateral pairs), or a single set of appendages at a time (e.g., left-side ventrolateral). For example, a quick cycle (~0.3 s) of abduction/adduction of the left-side ventrolateral appendages caused a ca. 90° counterclockwise rotation of the entire body (Fig. 5A–C). In several instances, abduction appeared to occur faster than adduction, though this might be the result of appendages rubbing against the coverslip. In fact, the

adduction of individual appendages was often slow enough to capture digitally (see Figs. 5D–F, 6C), whereas appendage abduction could not be captured in a single frame. As seen in Fig. 5D–F, appendage adduction did not always lead to movement of the rotifer, i.e., animal remains relatively stationary.

The rapidity of the abduction/adduction cycle made it difficult to confirm the position of the corona during appendage movement, i.e., abduction leads to rotation of the body and blurred images of the corona. However, limited observations indicate that the corona was always partially or fully withdrawn prior to the recovery stroke (Fig. 6C). Whether or not coronal withdrawal was simultaneous with abduction, or occurred sequentially, just prior to adduction, remains unknown. Nevertheless, the corona was extended fully during the recovery stroke.

### 3.2.3. Musculature

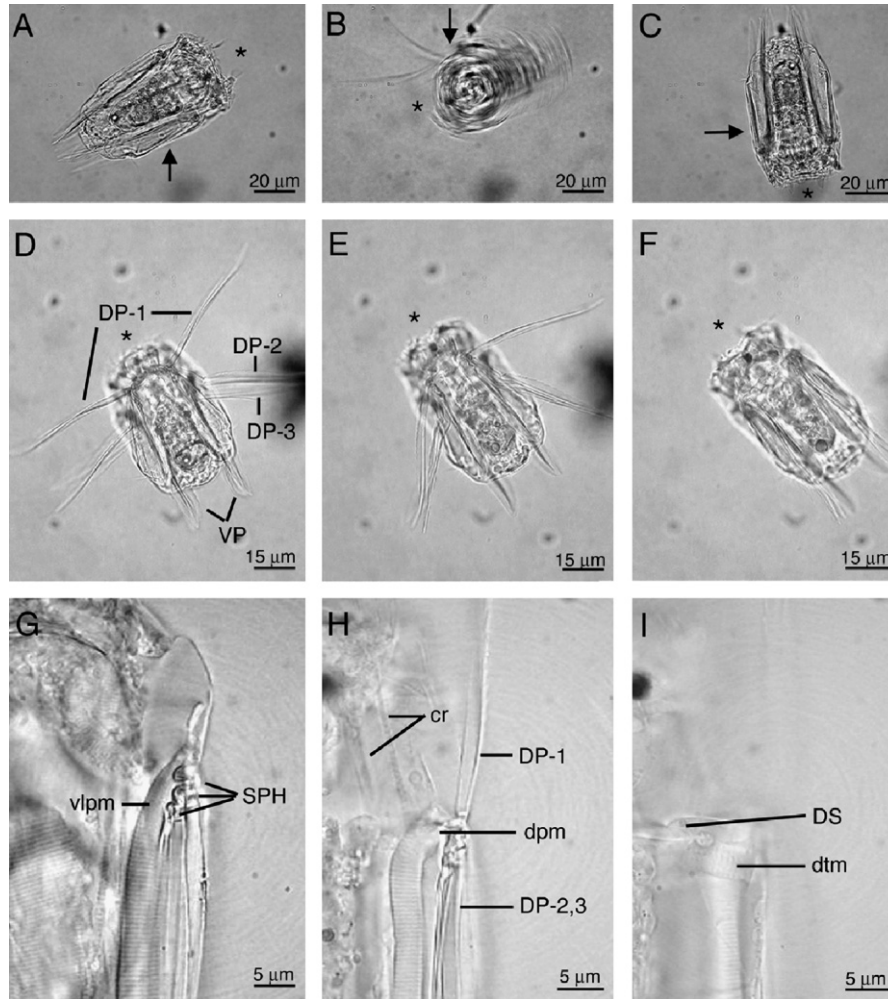
A description of the somatic musculature of *P. vulgaris* is covered by Allen (1968) using light microscopy and transmission electron microscopy. Here, we provide additional details of the somatic musculature to confirm these earlier observations (Figs. 7–9). There are no obvious differences in the organization of the somatic musculature among specimens observed in this study.

The somatic musculature of *Polyarthra* consists of numerous longitudinal muscles, few transverse muscles, and a single circular muscle. The single circular muscle is the pars coronalis, a thin circular fiber that underlies the corona, and on the ventral side, dips down towards the mouth (Figs. 7B, 8B–D, 9). The contour of the pars coronalis is highly variable and appears to be dependent on the state of contraction of the rotifer.

As described by Allen (1968), there are six longitudinal muscles (“paddle muscles”) in proximity to the paddle-like appendages (Fig. 7). Dorsally, there is a pair of broad, sheet-like, longitudinal paddle muscles (dpm) that originate in the posterior part of the trunk and insert in the shoulder region just above the paddles (Figs. 7B, 8A, 9A). The insertion point has a characteristic inverted v-shape (Fig. 8B). A longitudinal groove at the center of each paddle muscle extends along its length from the muscle’s origin to its insertion (Figs. 7B, 8A). The external, paddle-like appendages of the dorsolateral series are oriented in the center of this groove (see Fig. 5H). The posterior origin of each muscle is slightly serrated and appears to form multiple contact points with the posterolateral body wall (Fig. 7B).

There are two transverse muscles in the dorsal body region. A single transverse muscle (dtm) extends between the dorsal paddle muscles (dpm) at their anterior point of insertion (Figs. 5I, 7B, 8C, 9A). This muscle runs along the DS that connects the dorsolateral



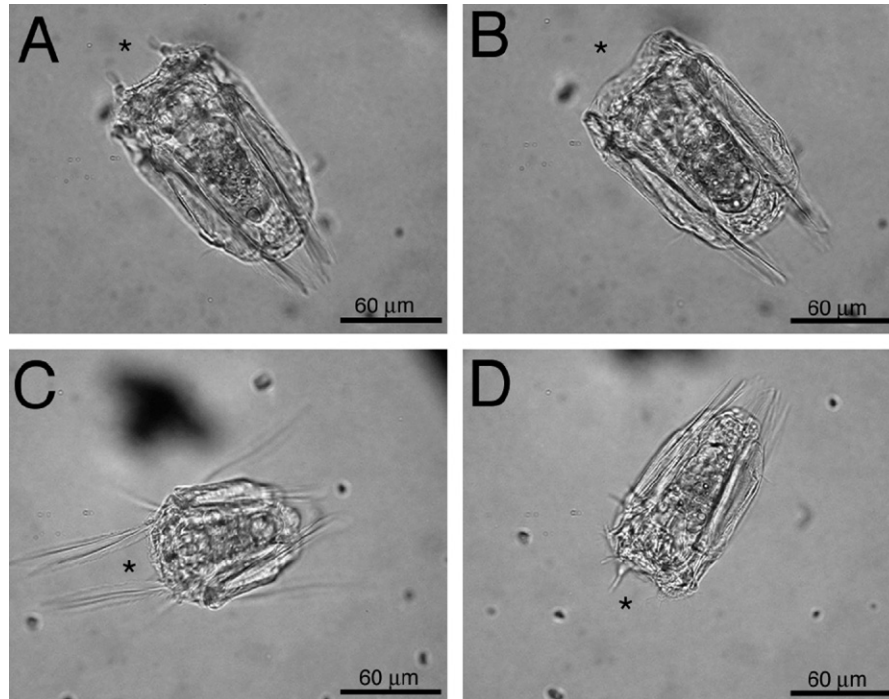


**Fig. 5.** Individual frame grabs from digital videos of *Polyarthra* sp. on a microscope slide. Asterisk (\*) indicates anterior end of rotifer: (A–C) sequential frames showing abduction of the dorsolateral appendages (arrow) leading to a counterclockwise rotation of the rotifer in less than 0.3 s; (D–F) adduction of the dorsolateral appendages. These frames are sequential but not continuous (intervening frames were removed); (G–I) optical sections through the shoulder region, anterior is upwards; (G) ventral view showing the connection of the ventral appendages with the body wall; (H) dorsal view revealing a single abducted paddle prior to the recovery stroke and (I) dorsal view showing the dorsal shelf (DS). cr, coronal retractors; DP-1, first (top) paddle of the dorsolateral bundle; DP-2, second paddle of the dorsolateral bundle; DP-3, third paddle of the dorsolateral bundle; dpm, dorsal longitudinal paddle muscle; dtm, dorsal transverse muscle; SPH, shoulder hinges of the ventrolateral paddles; VP, ventral paddles and vlpm, ventrolateral paddle muscle.

pairs of appendages (Fig. 5I). The contour of this muscle changes with the state of contraction of the animal. Several short, thin, longitudinal muscles are closely associated with the dtm and extend toward the corona or toward the viscerocloacal musculature (Figs. 7B, 8C). A single transverse muscle (posterior transverse muscle, ptm) is present in the posterior body region close to the point of origin of the dorsal paddle muscles (Figs. 7D, 8A, 9). This muscle extends between both muscles, but it is undetermined if the muscle is physically connected to them or to the body wall. Some longitudinal muscles of the viscerocloacal region extend toward the center of the ptm and may connect with it (see Fig. 9).

Ventrally, there are two pairs of sheet-like longitudinal paddle muscles that flank the appendages. The ventral paddle muscles (vpm) are located along the ventral body wall. In between the vpm is a series of short longitudinal muscles that presumably make up some (or all) of the mastax musculature (mm, Figs. 7D, E, 8D, 9B). A single pair of transverse muscles (vtm) extends from the mm toward the vpm (Fig. 8B, D). It is undetermined if these transverse muscles are connected directly to the mastax muscles or instead to the body wall. Lateral to the vpm is a second pair of sheet-like muscles, the ventrolateral paddle muscles (vlpm). Both the vpm and vlpm are in proximity to each other and





**Fig. 6.** Individual frames grabs from digital videos of *Polyarthra* sp. Frames reveal the shape of the body during different states of muscle contraction. Asterisk (\*) indicates the anterior end of the rotifer: (A–B) sequential images of *Polyarthra* sp. before and during retraction of the corona. Note an increase in body width in the second frame. (C–D) Sequential frames showing *Polyarthra* during partial abduction of the dorsolateral appendages, and after complete adduction. Note the drastic change in body shape.

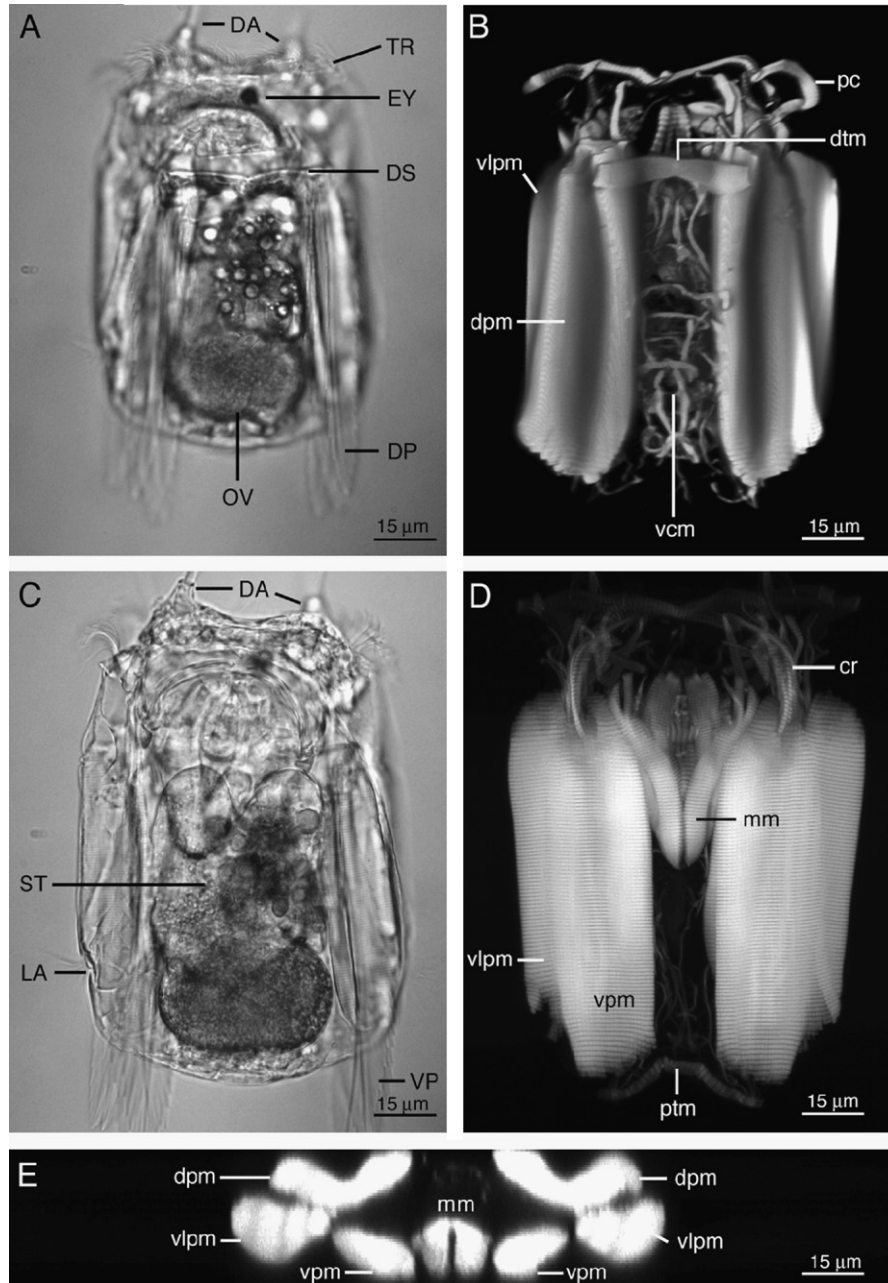
overlap slightly, giving them the appearance of a singular, flat muscle similar in width to the dpm. A cross section reveals that both muscles are separate (Fig. 7D). Both the vpm and vlpm insert at the shoulder region of the ventral appendages, but their insertion points are serrated and unlike the insertion of the dpm. The longitudinal groove that is apparent in Fig. 8B represents the separation between the vpm and vlpm, unlike the groove in the dpm that is a function of a groove in the individual muscle. Both the vpm and vlpm extend to the posterior body region where each forms a serrated point of attachment to the body wall (Fig. 7D).

The sheet-like paddle muscles are so broad in species of *Polyarthra* that they mask a series of additional longitudinal muscles that flank the digestive system and presumably control retraction of the corona (cr, Figs. 6D, 7, 8). There are at least six pairs of thin longitudinal muscles in the region of the corona: one pair inserts in the antennae (dar; Fig. 9), two pairs insert in the corona and extend the length of the animal, and three pairs insert in the corona and extend to approximately mid-trunk level. Many of these muscles are directly associated with or in proximity to the viscerocloacal muscles (vcm). The vcm consists of a series of thin, circular muscles around the digestive tract and additional muscles in various other orientations (see Fig. 9).

In addition, there are several smaller muscles in the region of the mastax (Figs. 7D, 8D, 9B).

#### 4. Discussion

The microscopic size of rotifers makes them highly susceptible to predatory zooplankton, yet their extraordinary abundance in freshwater lakes and ponds is testament to more than just their reproductive powers. Many rotifers have evolved a suite of developmental and behavioral responses to minimize predation (see Gilbert and Waage 1967; Stemberger and Gilbert 1987; Gilbert and Kirk 1988; Gilbert 2001), while others possess specialized morphologies to prevent ingestion and aid in escape (Williamson 1987; Kak and Rao 1998). The escape responses of rotifers are noteworthy because of the rapid change in acceleration they can achieve and the means by which they do it. For example, species of *Keratella* can dramatically increase the beat frequency of their coronal cilia to attain a 3.6-fold increase in escape speed (Gilbert and Kirk 1988). Other rotifers may also have this ability, e.g., species of *Filinia* can move rapidly away from predators through a presumed combination of coronal activity and movement of their elongate setae (Hochberg and Ablak Gurbuz 2007). Species of

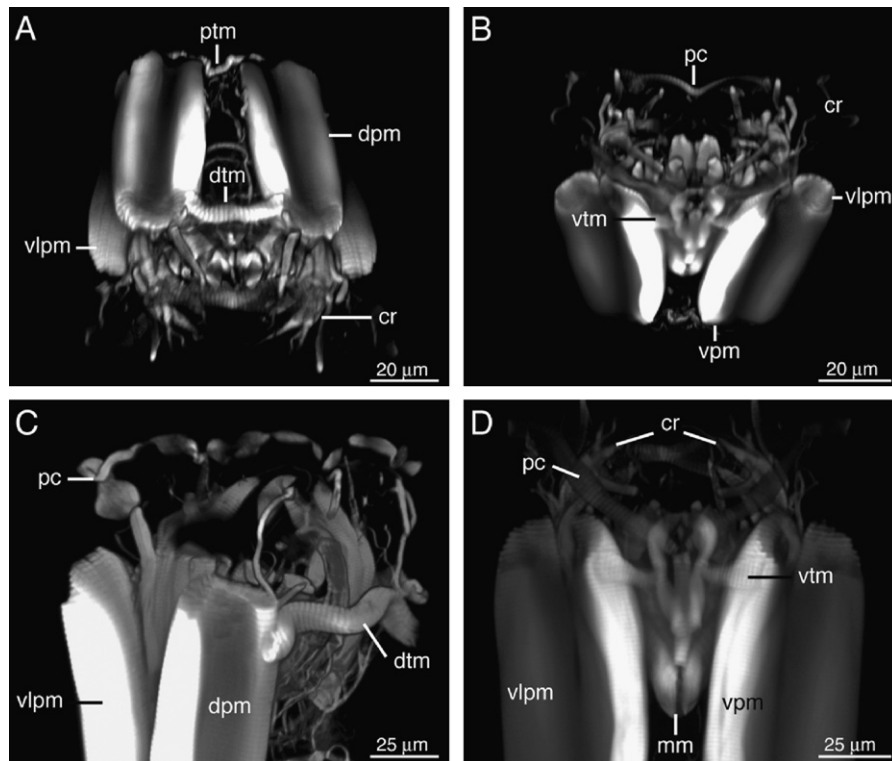


**Fig. 7.** General morphology and musculature of *Polyarthra* sp.: (A) dorsal view with brightfield optics, anterior is up; (B) computer-rendered view of the dorsal musculature, anterior is up; (C) ventral view with brightfield optics, anterior is up; (D) Z-projection of the musculature in ventral view, anterior is up and (E) computer-rendered cross section of the musculature at approximately 50% body length. cr, coronal retractor; DA, dorsal antennae; DS, dorsal shelf; DP, dorsal bundle of paddles; dpm, dorsal paddle muscle; dtm, dorsal transverse muscle; EY, eyespot; LA, lateral antenna; mm, mastax muscles; OV, ova; pc, pars coronalis; ptm, posterior transverse muscle; ST, stomach; TR, trochus; vcm, viscero-cloacal muscles; VP, ventral bundle of paddles; vpm, ventral paddle muscle and vlp, ventrolateral paddle muscle.

*Hexarthra* and *Polyarthra*, however, rely solely on the movement of their appendages to jump through the water column and escape predators.

The scarcity of rotifers that bear mobile appendages is perhaps surprising considering their effectiveness at avoiding predation or competitive inference. For exam-

ple, Gilbert (1987) found that 97% of individuals of *Polyarthra remata* caught in the inhalant current of *Daphnia* could escape. Similarly, species of *Polyarthra* and *Filinia terminalis* use their appendages, albeit differently, to escape predation by the predatory rotifer *Asplanchna intermedia* (Iyer and Rao 1996) and the



**Fig. 8.** Computer-rendered views of the musculature of *Polyarthra* sp.: (A) dorso-anterior view; (B) ventro-anterior view; (C) dorsolateral view of the anterior end and (D) ventral view of the anterior end. cr, corona retractor; dpm, dorsal paddle muscle; dtm, dorsal transverse muscle; mm, mastax muscles; pc, pars coronalis; ptm posterior transverse muscle; vlpm, ventrolateral paddle muscle; vpm, ventral paddle muscle and vtm, ventral transverse muscle.

copepod *Diaptomus* (Williamson 1987); *Polyarthra* uses its appendages to “jump” away from the predator, while *F. terminalis* uses its setae to prevent ingestion. Species of *Hexarthra* are also highly evasive and can readily avoid large cladocerans by saltation (Kak and Rao 1998). In most cases, escape movements by these evasive rotifers leads not only to a quick separation of prey from predator, but also to a change in direction that makes the prey less vulnerable to a secondary attack.

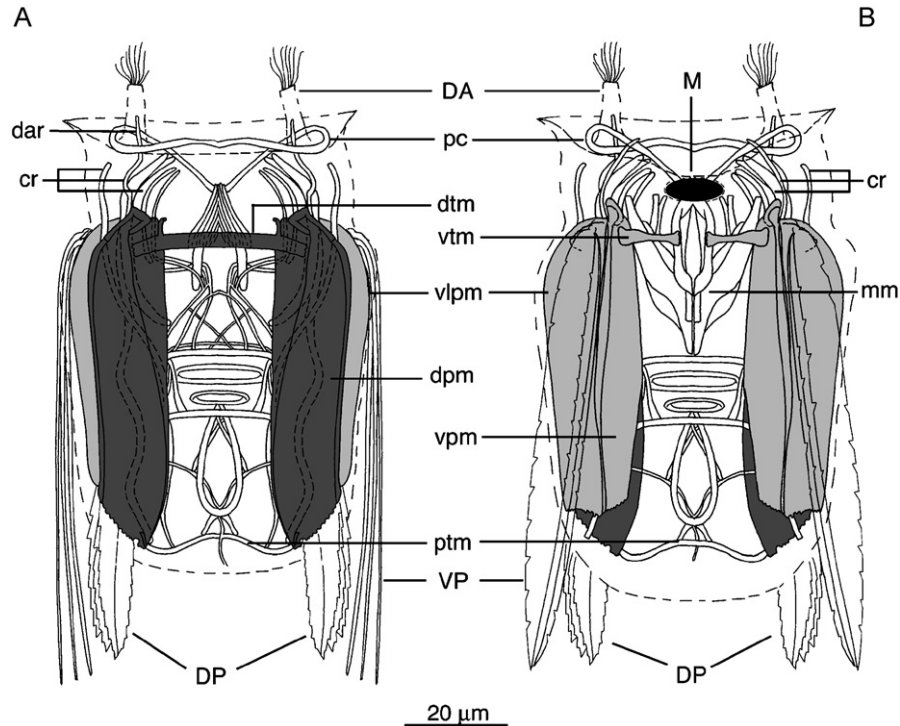
#### 4.1. Control of appendage movement

As noted in previous studies (Allen 1968; Santo et al. 2005), species of *Polyarthra* and *Hexarthra* deviate dramatically in the structure of their muscular systems relative to other planktonic rotifers. Allen (1968) noted that *P. vulgaris* lacked the typical circular muscles characteristic of other planktonic forms, and Santo et al. (2005) found that the musculature of *H. mira* is exceedingly complex and unlike that of any other rotifer. It appears evident from these studies and the current investigation that the organization of the rotifer muscular system covaries more with the presence of mobile appendages than any other feature including general body shape, ecology, and/or phylogeny. For

example, epiphytic species of *Proales* (Sørensen 2005a), colonial, planktonic species of *Conochiloides* (Hyman 1951), and sessile species of *Floscularia* (Fontaneto et al. 2003; Santo et al. 2005) show more similarities in general muscle organization to each other than do either species of *Polyarthra* and *Hexarthra*, which are relatively similar in size and shape (excluding the appendages). In fact, the evolution of mobile appendages appears to account for much of the variability in muscle organization that occurs in all rotifers with appendages, including species of *Filinia*, which may not use their appendages for locomotion (at least, not entirely; see Hochberg and Ablak Gurbuz 2007).

The appendages of species of *Filinia*, *Hexarthra* and *Polyarthra* are drastically different in morphology, position and quantity, so perhaps it should not be surprising that the muscles that control their movements are also quite different. For example, in *F. novaezealandiae*, the bilateral pair of elongate setae appears to be under the control of transverse muscles that insert close to the setal shoulder, i.e., the appendages have an indirect muscle supply (Hochberg and Ablak Gurbuz 2007). A single transverse muscle controls setal abduction, and a different transverse muscle controls setal adduction, leading to coordinated movements of the bilateral appendages. An analogous condition exists in





**Fig. 9.** Diagrams of the musculature of *Polyarthra* spp. based on observations of nine specimens (*Polyarthra* sp. and *P. vulgaris*). The outline of the body is dashed, anterior is up: (A) dorsal view and (B) ventral view. cr, coronal retractor; DA, dorsal antennae; dar, dorsal antenna retractor; DP, dorsal bundle of paddles; dpm, dorsal paddle muscle; dtm, dorsal transverse muscle; M, mouth; mm, mastax muscles; pc, pars coronalis; ptm posterior transverse muscle; VP, ventral bundle of paddles; vpm, ventral paddle muscle; vlpm, ventrolateral paddle muscle and vtm, ventral transverse muscle.

species of *Polyarthra*, where an indirect muscle supply controls appendage movement. However, there are two notable differences from *Filinia*: (1) saltation in *Polyarthra* is not unidirectional, but instead follows multiple, short paths depending on the orientation of the body as the result of out-of-sync appendage abduction (see Gilbert 1985); and (2) in species of *Polyarthra*, the muscles are much larger and appear to be more directly associated with appendage movement than do those in species of *Filinia*.

In species of *Polyarthra*, three pairs of longitudinal paddle muscles control the movement of a total of 12 appendages (see Allen 1968). The appendages are arranged into four bundles of three paddles each, distributed in two bilateral pairs on the dorsal and ventral sides of the body. Each set of dorsal appendages is abducted by a single longitudinal paddle muscle, while each set of ventral appendages is abducted by two longitudinal paddle muscles. Contraction of the longitudinal muscles presumably pulls down on the shoulder region (“attachment hooks” of Allen 1968) of each bundle of appendages, and since the appendages are “stacked” one above the other, their movement in an anterior arc is dictated by their position in the stack (see Gilbert 1985). For example, video analysis reveals that

the most anterior appendage (e.g., DP-1) always abducts prior to the appendages beneath it (DP-2, DP-3) (see also Gilbert 1985). Video analysis further reveals that the entire body shortens during the power stroke, the corona undergoes partial withdrawal, and the contour of the posterior body wall changes, i.e., when the paddle muscles contract, they pull on their posterior origin, creating a distortion in the posterior body wall (see Fig. 6C). This distortion does not occur during the contraction of the coronal/head retractors alone (see Fig. 6B), suggesting that the paddle muscles are indeed the source of the power stroke. Allen (1968) hypothesizes that transverse muscle II (dtm; Fig. 9A) enhances abduction and adds strength to the power stroke. However, this seems unlikely given the size of the paddle muscles relative to the dtm. Alternatively, the position of the dtm (and vtm) suggests that their contraction might function to “pinch” the shoulders inward, thereby changing the position of the shoulder hinge and ultimately the orientation of the appendages. A change in orientation would be especially important during the recovery stroke so as to avoid an identical thrust in both directions, which would cancel out any forward movement. This change in orientation further explains why, in slide-mounted specimens, the appen-



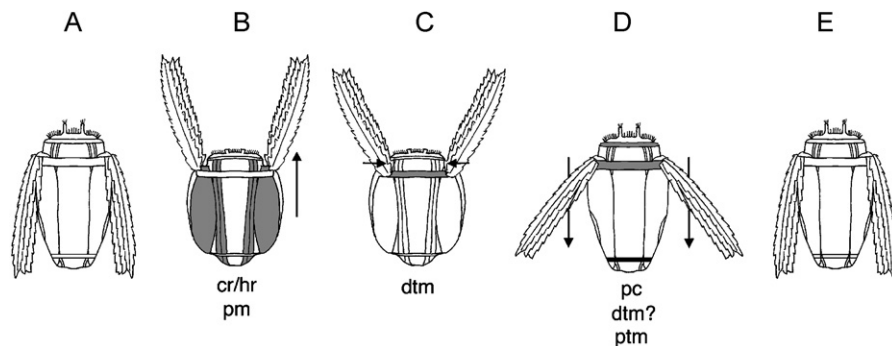
pages “stick” to the coverslip during the recovery stroke but not during the initial power stroke.

What remains difficult to understand is how appendage adduction (the recovery stroke) is initiated in *Polyarthra*. Our observations indicate that the corona is withdrawn while the rotifer’s appendages are abducted, and only reextends as the appendages move through their recovery stroke. The rapidity of the recovery stroke suggests that it results from more than just a relaxation of the paddle muscles and the corona/head retractors. In fact, Allen (1968) hypothesized that the elasticity of the body wall and the contraction of circular muscle I (pars coronalis; Fig. 9) also aid in adduction. Our video analysis cannot confirm or deny this hypothesis, but the size of the pars coronalis alone appears insufficient to create the antagonistic pressure necessary to counteract the force of the large paddle muscles, let alone the corona/head retractors. Instead, we hypothesize that the following series of events occurs to initiate a complete recovery stroke (see Fig. 10): (1) relaxation of the longitudinal paddle muscles (vpm, vlpm, dpm) and corona/head retractors (cr, hr); (2) contraction of the transverse muscles (dtm, vtm) to change the orientation of the paddles prior to adduction; (3) simultaneous contraction of the pars coronalis and ptm against the pressure of the body cavity to reextend the corona and (4) allow the elasticity of the bodywall to recover the resting position of the paddles (see Fig. 10). This series of events would occur almost simultaneously and therefore be difficult to capture digitally. However, a future effort to immobilize species of *Polyarthra* while allowing the appendages to move freely (in three dimensions) would help to clarify if the paddles in fact change orientation between power and recovery strokes.

While species of *Polyarthra* and *Filinia* are reliant on an indirect muscle supply to control their paddles and setae, respectively, species of *Hexarthra* have muscles that directly supply their limb-like appendages. Santo

et al. (2005) confirmed that the muscle supply to these limbs is direct and often complex, with layers of interweaving fibers often supplying a single limb. As verified in this study, each of the six appendages does indeed receive its own muscular supply, but the proximity of the muscles to one another and their entangled orientation within the trunk, makes a study of their functional roles difficult at best. In the simplest case, all appendages are supplied with both abductor and adductor muscles that can be distinguished by their position within the limb, i.e., muscles that are closest to the exterior surface of the limb are abductors, while muscles that are closest to the internal surface are adductors. Beginning with the largest limb, the ventral appendage, one pair of abductors and adductors supply the limb. The ventral abductors (vab) are much thicker muscles with an obvious origin on the dorsal body wall, whereas the origin of the adductors remains obscure. Contraction of the large abductors creates the power stroke to rotate the body around its longitudinal axis. Curiously, the abductors are separate muscles, and unless electrically coupled, would require two neural stimuli to initiate full contraction and movement of the single appendage. Clément and Amsellem (1989) verified that many rotifer somatic muscles are indeed coupled by gap junctions, thereby coordinating multiple muscles to act as a single motor unit.

Species of *Hexarthra* also possess two pairs of lateral appendages: one pair in a ventrolateral position and one pair in a dorsolateral position. These appendages are generally smaller than the singular ventral or dorsal appendage, but like them, are equipped with setose bristles that may function to increase resistance during a power stroke. Movement of these appendages appears to cause a “wobbling” of the body as it jumps through the water column. Interestingly, the muscular supply to these appendages is quite different from each other. The paired dorsolateral appendages are controlled by a



**Fig. 10.** Diagram of the somatic muscles that are hypothesized to control appendage movement in *Polyarthra* sp.: (A–E) a hypothetical sequence of dorsal appendage abduction (power stroke) and adduction (recovery stroke) from left to right. Arrows point in the direction of appendage movement. Only a single pair of appendages is shown in their final positions for clarity. Contracted muscles are shaded and listed in abbreviations below each diagram. cr/hr, coronal/head retractors; dtm, dorsal transverse muscle; pc, pars coronalis; pm, longitudinal paddle muscle and ptm, posterior transverse muscle.

bilateral suite of three, short, transversely oriented muscles that originate on the dorsal body wall; two abductor muscles coalesce prior to insertion in each appendage, while the adductor muscle remains separate and extends further into each appendage. Contraction of the abductors or adductors would presumably “pull” against the dorsal body wall and cause movement of the limb. Alternatively, the paired ventrolateral appendages are controlled by only two muscles (in total). The single, ventrolateral abductor is a thick muscle that curves around the dorsal body wall and branches as it reaches each of the ventrolateral limbs. The ventrolateral adductor muscle is also singular, but is much thinner and loops down into the posterior trunk prior to supplying the limbs. If these interpretations are correct, that both ventrolateral limbs are controlled by the same muscles, then slow-motion video analysis should reveal that their movements (power stroke and recovery stroke) are always coordinated. Unfortunately, the size of the limbs made analysis of their individual movements difficult to follow.

The demands of escape and evasion in planktonic rotifers do not necessitate the evolution of mobile appendages, as evidenced by the fact that so few species possess such appendages. Still, a series of observations and experiments over the past two decades have shown that appendage-bearing species can evade potential predators much more effectively than species without appendages (e.g., Kak and Rao 1998; Walton 1988; Williamson 1987; Iyer and Rao 1996; Hampton and Starkweather 1998). These species generally rely on saltation that in many cases, not only distances the prey from the predator, but also removes the prey from the predator’s “line of sight” through haphazard rotations of the prey’s body and its corresponding movement in erratic directions. While such movements are highly effective at preventing direct ingestion by predators (e.g., *Asplanchna*) or interference competitors (e.g., *Daphnia*), their effectiveness is limited against other animals (e.g., *Branchinecta mackini*, Starkweather 2005). Future studies on the dynamics of rotifer evasion with a detailed analysis of small-scale movements would help clarify the limits of their mobility and susceptibility to such predators. Gilbert (1987) also cautions that one species’ escape response should not be generalized to all members of the genus since there may be differences in escape velocities, path trajectories, etc. that dictate an animal’s vulnerability. These differences would likely be the result of external anatomical differences in the quantity and/or arrangement of appendage bristles (e.g., *Hexarthra* limbs) or the different shapes of appendages (e.g., *Polyarthra* paddles). These seemingly minor differences that have taxonomic significance are also undoubtedly important in a world of low Reynolds numbers where a change in the surface of a limb may dramatically effect its propulsive action (see review by

Vogel 1996). Future studies that seek to understand the escape behaviors of rotifers should take these differences into account.

## 4.2. Conclusions

Abundant information on the rotifer muscular system is beginning to accumulate with the application of fluorescent stains and fluorescence microscopy, leading to a better understanding of both rotifer locomotion and a reconstruction of the rotifer ground pattern. To date, species across both major clades, Bdelloidea and Monogononta, have been examined in detail (Hochberg and Litvaitis 2000; Kotikova et al. 2001, 2004, 2006; Sørensen et al. 2003; Santo et al. 2005; Sørensen 2005a,b; Hochberg and Ablak Gurbuz 2007), and confirmed many of the earlier observations on the rotifer muscular system (e.g., Remane 1929–1933). The accumulated observations indicate that rotifer muscles are organized into a standard series of antagonistic layers, with outer circular fibers encompassing a suite of longitudinal muscles. Both of these muscle systems work against the pressure of the body cavity to change the shape of the body, extend the corona and coordinate movements during locomotion. While this basic arrangement is present in most rotifers, many have diverged from this ground pattern during their evolutionary history. Moreover, evidence from a range of studies (e.g., current study; Santo et al. 2005; Hochberg and Ablak Gurbuz 2007) shows that the evolution of mobile appendages has drastically altered the topology of rotifer muscles to such a degree that statements about their homology remain difficult. To remedy this, a larger number of species within these genera require examination. Moreover, closely related species that exhibit the presumed plesiomorphic condition for the clade, i.e., species without appendages, or species that hatch from mictic eggs and lack appendages (e.g., *aptera* forms of *Polyarthra*), might provide insight into the evolution of particular muscle groups. Future knowledge of phylogenetic relationships within Rotifera, particularly Flosculariacea (containing *Hexarthra*) and Synchaetidae (containing *Polyarthra*), should provide evidence for testing hypotheses about the evolution of these appendage-bearing rotifers.

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