

Body musculature of *Beauchampiella eudactylota* (Gosse, 1886) (Rotifera: Euchlanidae) with additional new data on its trophi and overall morphology

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Keywords:

confocal laser scanning microscopy, musculature, Rotifera, scanning electron microscopy, trophi

Accepted for publication:

15 June 2008

Abstract

Riemann, O., Wilts, E.F., Ahlrichs, W.H. and Kieneke, A. 2009. Body musculature of *Beauchampiella eudactylota* (Gosse 1886) (Rotifera: Euchlanidae) with additional new data on its trophi and overall morphology. — *Acta Zoologica* 90: 265–274

This study presents the results of confocal laser scanning microscopy and fluorescence-labelled phalloidin used to visualize the system of body musculature in *Beauchampiella eudactylota*. Moreover, the poorly known trophi of *B. eudactylota* are described based on scanning electron microscopy. In total, four paired longitudinal muscles (musculi longitudinales I–IV) and three circular muscles (musculi circulares I–III) were identified. Among these are the musculus longitudinalis ventralis, the musculus longitudinalis dorsalis and the musculus circumpedalis as documented in previous studies for other rotifer species. Compared to other species, *B. eudactylota* is characterized by the low number of lateral longitudinal muscles and the absence of some longitudinal muscles (musculi longitudinales capitum) and circular muscles (corona sphincter, musculus pars coronalis). Moreover, scanning electron microscopic data on the trophi of *B. eudactylota* reveal a number of striking similarities to the trophi in some species of Epiphanidae. This suggests that either (1) these similarities represent plesiomorphic characters present both in Epiphanidae and *B. eudactylota* or (2) they are synapomorphic features of *B. eudactylota* and some species of Epiphanidae, which would question the monophyly of Euchlanidae.

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Introduction

Morphological investigations of rotifers have in recent years been given a fresh impulse by the application of epifluorescence and confocal laser scanning microscopy (CLSM) to the study of phalloidin-labelled rotifer body musculature (Hochberg and Litvaitis 2000; Kotikova *et al.* 2001; Sørensen *et al.* 2003; Santo *et al.* 2005; Sørensen 2005a,b; Hochberg and Gurbuz 2007; Riemann *et al.* 2008). These studies have provided new insight into the system of body musculature in rotifers and complement the results of histological studies that were carried out in the first half of the 20th century and that were based on serial sections and traditional light microscopy (for a summary of these results,

see Remane 1929–33; Hyman 1951). In an attempt to provide a more systematic framework for the study of rotifer body musculature and, moreover, to address questions relating to the evolutionary development of its principal components, Riemann *et al.* (2008) have hypothesized a set of features for the ground pattern of body musculature in the large rotifer subtaxon Ploima. However, their conclusions rest on a limited taxon sampling representing only a small fraction of rotiferan subtaxa. To test their conclusions, additional data on other, uninvestigated taxa are needed.

Euchlanidae comprises a taxon of monogonont rotifers with currently 32 valid species (Segers 2007). Most of them occur periphytically in the littoral zone of freshwater habitats (Koste 1978) but there are also some species recorded from

brackish and marine environments (see Fontaneto *et al.* 2006 for details). Within Euchlanidae, *Beauchampiella eudactylota* deviates morphologically from all other members of this taxon. First, unlike all other members of Euchlanidae, *B. eudactylota* does not possess a stiff lorica with lateral epidermal infoldings (sulci), but rather a soft and flexible trunk integument. Second, the foot of *B. eudactylota* is characterized by the presence of very long foot segments that are remarkable for their strong internal musculature (see Koste 1978; Koste and Shiel 1989). Moreover, the toes of *B. eudactylota* are conspicuously long – in some specimens exceeding the length of the trunk – a fact never observed in other members of Euchlanidae. The toes can be moved in a jerky fashion brought about by rapid contraction of the strong muscle strands running through the foot segments. Taken together, these morphological features suggest an isolated position of *B. eudactylota* within Euchlanidae, which makes an assessment of its phylogenetic affinities difficult. Unfortunately, however, very little information on *B. eudactylota* can be obtained from the literature (Remane 1929–33; Wulfert 1940; De Beauchamp 1965; Kutikova 1970; Koste 1978; Koste and Shiel 1989). In particular, its trophi – although of crucial importance for rotifer taxonomy and phylogeny (see, for example, Markevich and Kutikova 1989; De Smet 1997; Sanoamuang 2002; Sørensen 2002; De Smet 2005) – are very little known. To remedy this situation, we give the first detailed description of the trophi based on scanning electron microscopy (SEM) and provide additional information on the overall morphology of *B. eudactylota*.

Thus, the aims of this study are twofold: (1) reconstruction of the system of body musculature of *B. eudactylota* and (2) provision of new data including SEM observations of the trophi of this poorly known but systematically relevant species.

Materials and Methods

Specimens of *B. eudactylota* (Gosse 1886) were obtained from the periphyton of a small pond near Leer, north-west Germany at the end of November 2007 (water temperature approximately 5 °C, pH 7.3, N 53°15'30", E 7°31'12"). Individual specimens were selected from the raw sample under a stereomicroscope and transferred onto microscopic slides for closer microscopic inspection. Light microscopic images were obtained on a Leica DMLB compound microscope using either bright-field illumination or differential interference contrast (DIC) and a digital camera for documentation (Olympus colour view I). Trophi preparations for SEM were made following the protocol given by Kleinow *et al.* (1990). The solution needed to dissolve the tissues surrounding the trophi was obtained by first preparing a stock solution (5.2 g sodium dodecyl sulphate + 0.24 g NH₄HCO₃ in 100 mL distilled water). Before applying this solution to the specimen, 0.1 g dithiothreitol (DTT) was added to 5 mL of the stock solution and vigorously stirred.

Single specimens of *B. eudactylota* were placed into a droplet of the dissolving solution until the tissues had completely dissolved and only the trophi remained. Subsequently, the trophi were carefully washed with distilled water and left to dry on a round coverslip attached to an SEM stub. For SEM of complete specimens, individual animals were narcotized in water enriched with CO₂ and fixed with picric acid/formaldehyde at 240 mOsm (see Melone and Ricci 1995 for details). Following fixation, specimens were dehydrated in an increasing ethanol series and critical point dried. Before SEM, both trophi preparations and complete specimens were coated with gold. SEM was carried out on a Zeiss DSM 940 scanning electron microscope.

For CLSM preparations, specimens of *B. eudactylota* were anaesthetized in a 0.25% solution of bupivacaine (Bucain®). Fixation for 1 h was carried out with freshly prepared 4% formaldehyde buffered in 0.1 M phosphate-buffered saline (PBS). After rinsing in 0.1 M PBS, specimens were made permeable by incubation in a 0.1% solution of Triton X-100 buffered in 0.1 M PBS overnight. For staining, 2 µL of 38 µM methanolic Tetramethyl Rhodamine Iso-Thiocyanate (TRITC) phalloidin solution were added to 100 µL of 0.1% Triton X-100 buffered in 0.1 M PBS. Specimens were stained for 3 h. After staining, individual specimens were embedded in Cityfluor® and observed under a Leica TCS SP 5 confocal laser scanning microscope.

The positions and extensions of internal and external features of *B. eudactylota* are referred to as percentage body units (U). This is a commonly applied practice in species descriptions of the phylum Gastrotricha (see, e.g., Priyalakshmi *et al.* 2007). The total body length from the frontal edge of the rotatory organ (cilia not considered) to the caudal tip of the toes is treated as 100 units. For our description of the relative positions of the individual mastax jaw elements (trophi), we use terms introduced previously (see Riemann and Ahlrichs 2008; Riemann *et al.* in press). Both manubria and unci (together termed malleus) and rami and fulcrum (together termed incus) attach to one another. We treat these points of attachment as a point of reference for the terms 'distal' and 'proximal', i.e. the rami *proximally* attach to the fulcrum and *distally* expand away from the fulcrum. The fulcrum *proximally* attaches to the rami and its *distal* tip projects in the opposite direction. The manubria *proximally* attach to the unci; their *distal* sections project away from the unci. The unci *proximally* attach to the manubrial clava and *distally*, their teeth point medially. For labelling of the openings of both ramus subbasal chamber and ramus basal chamber, we propose the usage of new terminology. The terms *subbasifenestra* and *basifenestra* used by Markevich (1989) and Sørensen (2002) are replaced in this study by the terms *ramus foramen subbasalis* for the opening of the ramus subbasal chamber and *ramus foramen basalis* for the opening of the ramus basal chamber. This terminological modification is suggested to accommodate the fact that the openings in both ramus chambers are not covered by a membrane as the term

fenestra suggests (see Werner 1970 for details). Rather, they are places where cell material inside the ramus chambers communicates with epithelial cells outside (see Riemann and Ahlrichs 2008) and therefore they are not covered by a cuticular membrane. The elements of body musculature are labelled in accordance with Riemann *et al.* (2008). Longitudinal muscles are numbered consecutively from ventral to dorsal with individual names given to muscles whose homology across different rotifer species is very probable. Numbering of circular muscles proceeds from frontal to caudal. For taxonomy and nomenclature, we follow the most recent checklist of valid species names provided by Segers (2007).

Results

General body organization

The whole body of *B. eudactylota* (total length of about 600 μm) is separated into the four distinct sections head, trunk, foot and toes (Fig. 1). The borders between the four body sections are situated approximately at U10, U45 and U58 (Fig. 1). The head (U0 to U10) is cylindrical and, seen from dorsal view, has a convex frontal margin (Fig. 1). In lateral view, the frontal margin of the head is slightly tilted towards the ventral side (Fig. 1B). The rotatory organ forms two conspicuous tufts of longer cilia on either side of the head. The head has a width of approximately 50 μm and a height of approximately 40 μm (Fig. 2C,E). The trunk section (U10 to U45) is more or less ovoid in shape (Figs 1 and 2A). The most caudal section of the trunk, approximately at U45, is set off by a transverse fold in the integument (Figs 1 and 2A). In total, the trunk is about 225 μm long, 140 μm high and 175 μm wide. The foot section (U45 to U58, Fig. 2H) is about 85 μm long and composed of two segments (border situated at U52). The frontal foot segment is shorter and compact (40 μm long, around 25–35 μm in height) and the caudal one longer and thinner (45 μm long, 20 μm in height). The two foot segments are flexibly attached to one

another and, in their resting position, are kept at an angle of approximately 45° to each other (Fig. 2H). Internally, they are equipped with strong, cross-striated musculature running longitudinally along the length of the foot well into the frontal section of the toes (Figs 2H and 5D–F). The paired toes (Figs 1 and 2A,B) are very long and slender (U58 to U100). They are flexibly attached to the foot and can actively be spread laterally and lifted dorsally in a jerky fashion. The base of each toe is only little wider than the average diameter (5 μm) and each toe terminates in an acute tip (Fig. 2B). Seen from dorsal view, both toes are slightly curved laterally (Fig. 2B) and in lateral view, they are slightly curved dorsally (Fig. 1B).

Digestive tract

The gastric tract of *B. eudactylota* consists of the mouth opening, the bulbous mastax, a narrow and elongate oesophagus opening into the stomach and the intestine (Fig. 1). The hyaline intestine opens into the anus situated at the dorsal side of the most caudal section of the trunk (Fig. 1). The mouth opening is positioned subterminally at the caudal margin of the rotatory organ. The bulbous mastax is situated in the ventral half of the head and extends only slightly into the trunk section, approximately up to U12. In dorsal view, the caudal part of the mastax has a trilobate shape (Fig. 2E). The elongate and very slender oesophagus (2–3 μm in diameter, Fig. 2C) is dorsally attached to the mastax at U10, extends caudo-dorsally over a length of approximately 30 μm and abruptly opens into the voluminous stomach situated in the central trunk section between U15 and U25 (Figs 1 and 2A). The oesophagus has two small but conspicuous, possibly glandular, swellings frontal to the junction of oesophagus and stomach (Fig. 2C). The stomach consists of distinctly recognizable stomach cells and has a maximum diameter of 50 μm . A pair of dorsally projecting gastric glands attach to the frontal wall of the stomach at U18. Distally, each gastric gland branches into two club-shaped appendages (Figs 1A and 2C). The stomach is continued by the hyaline, internally ciliated intestine (U25 to U45) that stretches over a distance of nearly 100 μm and continuously tapers towards the anus (Fig. 1A).

Mastax hard parts (trophi)

The system of trophi (Figs 3 and 4) is organized in a strictly bilaterally symmetrical way. The unpaired fulcrum seen from lateral view is approximately 5 μm long and obliquely attaches to the rami (Figs 3E and 4E). Distally, the fulcrum slightly widens and forms a bunchy structure (Fig. 3E, arrowhead, 4D,E). In dorsal view (Fig. 4C), the fulcrum is narrow and expands distally. The paired rami taken together appear almost rhombic when viewed from a caudo-dorsal direction (Fig. 3A). At their dorso-distal tips, fan-shaped cuticular material, probably portions of indistinct epipharyngeal

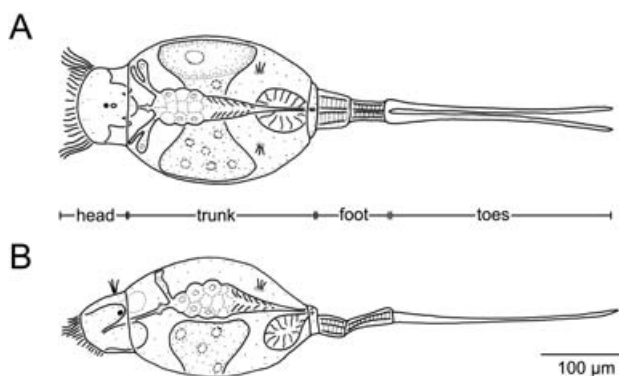


Fig. 1—General body organization of *Beauchampiella eudactylota*. —A. Specimen from dorsal side. —B. Specimen in lateral view.

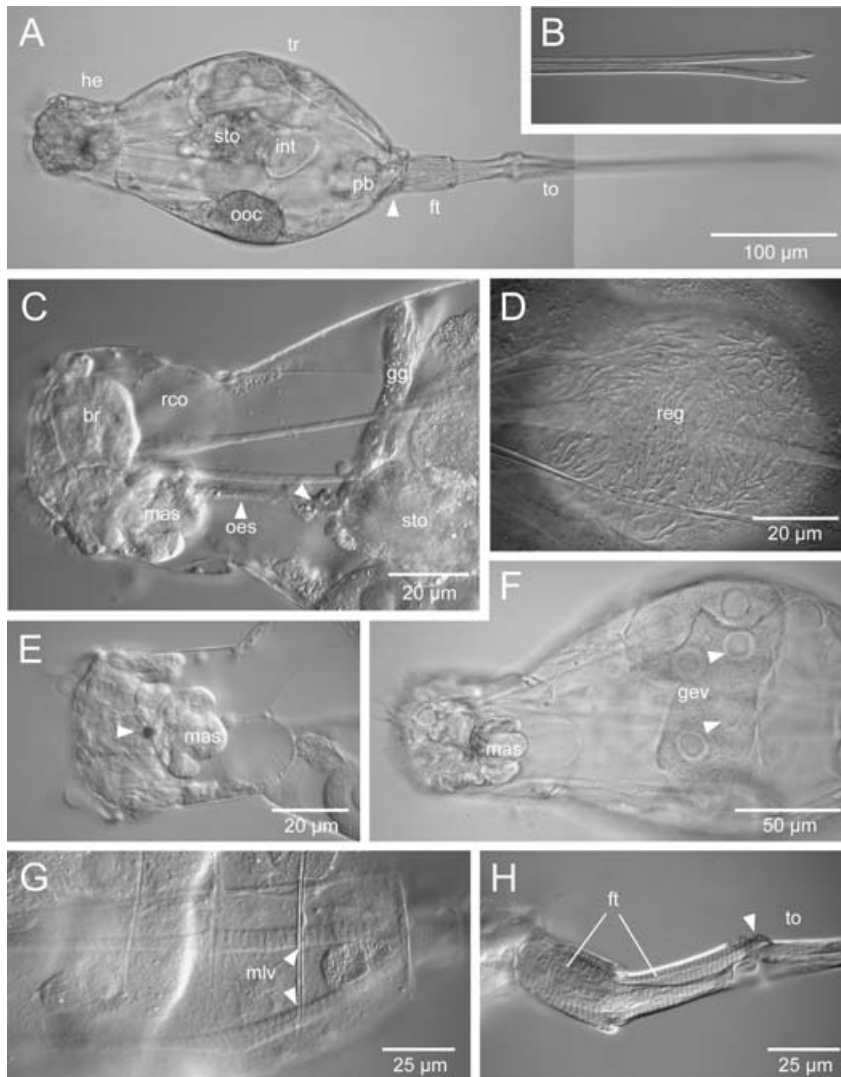
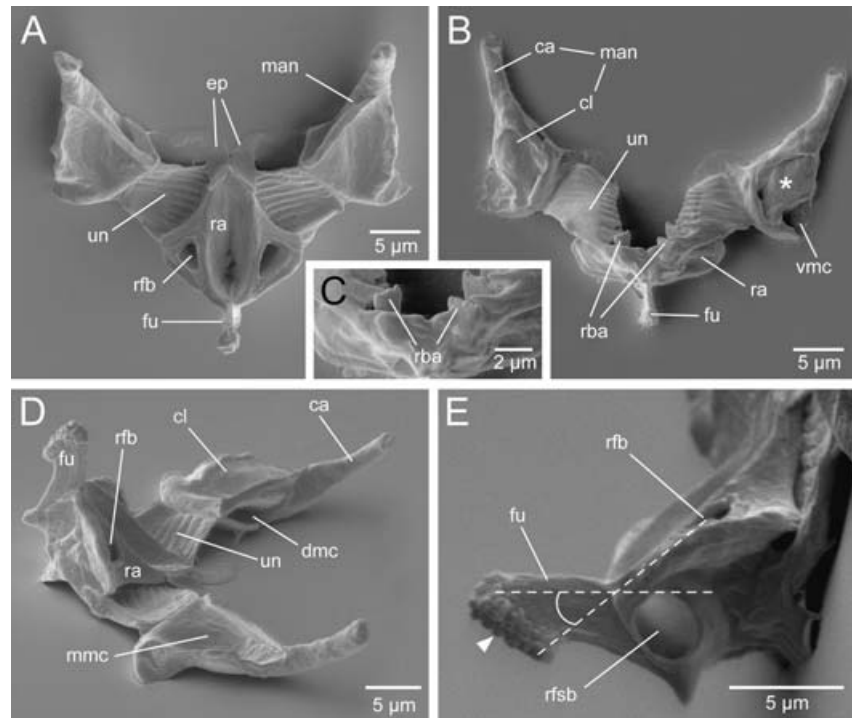


Fig. 2—Internal organization of *Beauchampiella eudactylota*. Light micrographs. —**A**. View of complete specimen seen from dorsal side. Arrowhead indicates most caudal section of the trunk slightly set off from the main part of the trunk. —**B**. Detail of distal end of toes. —**C**. Head and frontal section of trunk seen from lateral. Arrowhead points out glandular swellings of oesophagus. —**D**. Surface structure of resting egg. —**E**. Head and mastax seen from dorsal view. Note large pigmented cerebral eyespot. —**F**. Head and trunk with germovitellarium. Arrowheads point out nuclei of vitellarium. —**G**. Detail of trunk showing musculi longitudinales ventrales. —**H**. Foot in lateral view. Note the two foot segments and internal musculature. Arrowhead indicates insertion of toes. br, brain; ft, foot; gev, germovitellarium; gg, gastric glands; he, head; int, intestine; mas, mastax; mlv, musculi longitudinales ventrales; oes, oesophagus; ooc, oocyte; pb, protonephridial bladder; reg, resting egg; rco, retrocerebral organ; sto, stomach; to, toes; tr, trunk.

elements, is attached (Figs 3A and 4A,C,E). Both the ramus subbasal and the ramus basal chamber display distinct openings with the rounded ramus foramen subbasalis pointing caudo-laterally (Figs 3E and 4D,E) and the more triangular ramus foramen basalis pointing caudo-dorsally (Figs 3A,D,E and 4A,C,E). Seen in lateral view (Figs 3D,E and 4E), the rami are roughly triangular. The longitudinal axis of the fulcrum and the edge connecting the proximal section of the rami and their most dorsal tip form an angle of approximately 45° (Figs 3E and 4E). The median space between the rami forms a fairly deep, dorso-ventrally elongate convex bowl (Fig. 3A). The inner margin of the rami is constituted by a weakly developed molar surface whose blunt projections interdigitate with the teeth of the unci (Figs 3B and 4B). Elements of a subuncus are absent. In the ventro-distal section of the rami, paired shovel-shaped basal apophyses are situated (Figs 3C and 4B). The paired unci each consist of 10 unci teeth that continuously decrease in

length from the most ventral to the most dorsal tooth (Figs 3A,B and 4A,B). For the greater part of their length, the unci teeth are interconnected by cuticular material and only their bluntly triangular tips (about 1.5 to 2 µm) are distinct projections (Figs 3B and 4B). The manubria attach to the unci over a length of approximately 6 µm (Fig. 3A,B). They are divided into a widened clava (approximately 10 µm in length and 8 µm in width) and a narrow cauda of about 8 µm in length (Figs 3A,B,D and 4F,G). The three chambers that form the manubrium are not very clearly distinguishable (Figs 3A,B and 4F,G). While the median chamber constitutes the largest part of the clava and also forms the distally elongate cauda, the manubrial chambers positioned dorsal and ventral to the median chamber are smaller and restricted to the clava (Figs 3A,B,D and 4F,G). Both the dorsal (Fig. 3D) and the ventral manubrial chamber (Fig. 3B) represent small cuticular pockets with lamellar walls and distinct openings. The dorsal manubrial chamber opens to the surroundings

Fig. 3—Mastax hard parts (trophi). Scanning electron microscopic (SEM) images. —**A**. Trophi in dorso-caudal view. —**B**. Trophi seen from ventral side. Asterisk (*) indicates opening of median manubrial chamber. —**C**. Detail of B, ventral view of ramus basal apophyses. —**D**. Trophi seen in lateral view. —**E**. Detail of fulcrum and ramus in lateral view. Note bunched structure of distal end of fulcrum. Angle of fulcrum and ramus axis indicated by dotted lines (see Discussion). ca, cauda; cl, clava; dmc, dorsal manubrial chamber; ep, epipharynx; fu, fulcrum; man, manubrium; mmc, median manubrial chamber; ra, ramus; rba, ramus basal apophyses; rfb, ramus foramen basalis; rfsb, ramus foramen subbasalis; un, uncus; vmc, ventral manubrial chamber.



dorso-laterally (Figs 3D and 4F), the ventral manubrial chamber ventro-laterally (Figs 3B and 4F). The elongate median chamber displays a large round, laterally projecting opening in the clava region (Figs 3B and 4F).

Nervous system and sensory structures

The brain of *B. eudactylota* is positioned in the frontal section of the head dorsal to the mastax (Figs 1B and 2C). Caudal to the brain, there is a round and very hyaline retrocerebral organ (Fig. 2C). At the caudal end of the brain, an unpaired, strongly pigmented red cerebral eyespot (Fig. 2E) is positioned at approximately U5. Approximately at the beginning of the caudal section of the head, there is an unpaired dorsal antenna in the dorsal head integument (Fig. 1B). Paired lateral antennae (at U35) are positioned dorso-laterally in the integument of the caudal third of the trunk section (Fig. 1).

Reproductive organs

Parthenogenetic females of *B. eudactylota* have a massive, ribbon-shaped germo-vitellarium situated in the ventral part of the trunk section (U15 to U35). It contains large nuclei (approximately 10 µm in diameter) and envelopes the other organs (i.e. the stomach) in a bowl-shaped manner (Figs 1A and 2F). Some of our specimens, probably fertilized mictic females, bore large, ovoid resting eggs (approximately 60 µm across) that are covered with numerous hairy projections (Fig. 2D).

Excretory system

There are paired protonephridia with distinct terminal organs whose exact number and position, however, were not determined. The protonephridia open into a contractile protonephridial bladder in the caudal section of the trunk (U30 to U40). The protonephridial bladder is positioned ventral to the intestine and opens, together with the anus, in a dorsal cloaca (Figs 1B and 2A).

Body musculature

The system of body musculature of *B. eudactylota* comprises paired, bilaterally symmetrical longitudinal and circular muscle strands. The circular muscles are external to the longitudinal muscles. In total, we have detected four paired longitudinal muscles and three circular muscles. All longitudinal muscles show a conspicuous pattern of cross-striation. Cross-striation, however, was not observed in the circular muscles. The fine musculature surrounding the gastric tract (see Fig. 5C) is not described in detail.

Longitudinal muscles

The **musculi longitudoventrales (musculi longitudoventrales I, U5–U50, Figs 5A–D,F and 6)** are the most ventral pair of longitudinal muscles and span the whole length of the trunk, enter the foot and terminate caudally at the junction of the first and second foot segment. Frontally,

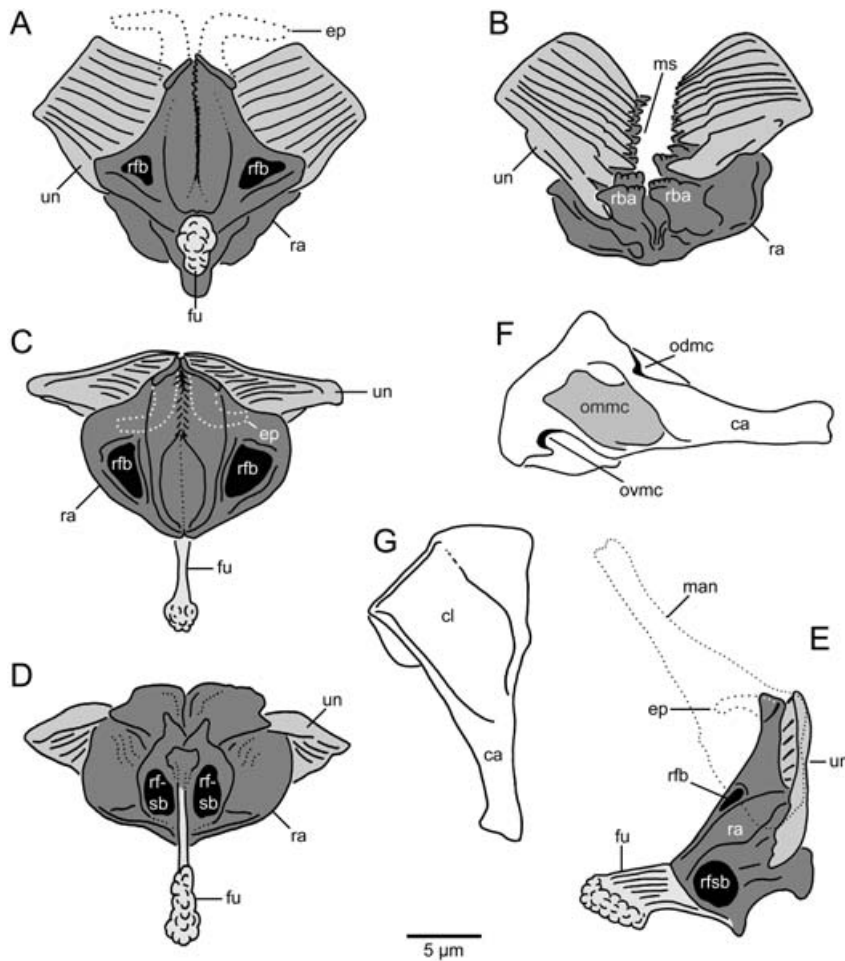


Fig. 4—Diagrammatic drawings of mastax hard parts (trophi). Individual trophi delimited by different grey scales. Note that for clarity, in A–D manubria are not depicted. All drawings are reconstructions based on SEM images obtained in standardized views from each perspective. Dotted lines in A, C and E delimit epipharynx. —**A.** Caudal view. —**B.** Fronto-ventral view. —**C.** Dorsal view. —**D.** Ventral view. —**E.** Lateral view. —**F.** Manubrium, view of side that projects laterally —**G.** Manubrium, view of side that projects medially. ca, cauda; cl, clava; ep, epipharynx; fu, fulcrum; man, manubrium; ms, molar surface; odbc, opening of dorsal manubrial chamber; ommc, opening of median manubrial chamber; ovmc, opening of ventral manubrial chamber; ra, ramus; rba, ramus basal apophysis; rfb, ramus foramen basal; rfsb, ramus foramen subbasalis; un, unci.

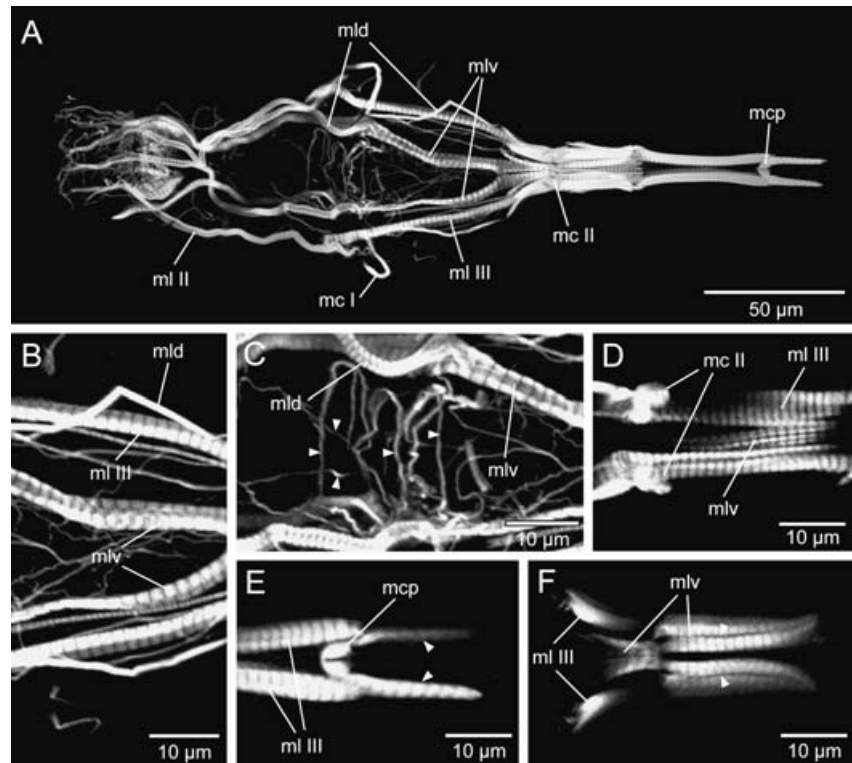
both muscles of this pair branch off into numerous fine filaments. In the first foot segment, the musculi longitudinales ventrales increase in width and are each constructed of two filament bundles separated by a narrow gap. Continuing dorsally, the musculi longitudinales ventrales are followed by two pairs of lateral longitudinal muscles. The **paired musculus longitudinalis II** (U5–U30, Figs 5A and 6) consists of two muscle strands that originate in the head and continue into the trunk, where they terminate just frontal to the musculus circularis I (see below). Frontally, the **musculi longitudinales II** produce filamentous offshoots. More dorsally, the musculi longitudinales II are followed by the paired **musculus longitudinalis III** (U30–U55, Figs 5A,B,D–F and 6A,B). The two muscles of this pair begin in the trunk section slightly frontal to where the musculi longitudinales II end and continue through both foot segments up to the musculus circumpedalis (see below). In the most dorsal position in the specimen, there are the **musculi longitudinales dorsales (musculi longitudinales IV, U5–U45, Figs 5A–C and 6)**. They originate in the head section and continue through the trunk up to the musculus

circumpedalis (see below). Each of the two muscles of this pair is interrupted in the trunk section by a narrow gap.

Circular muscles

In total, we have detected three circular muscles. All of them are incomplete muscular rings composed of muscular subunits. The **musculus circularis I** (at U30, Figs 5A and 6) is positioned roughly in the middle of the trunk section and is constituted by two slender muscular belts that are interrupted by a wide ventral and dorsal cleft. The **musculus circularis II** (at around U45, Figs 5A,D and 6) is situated at the very caudal end of the trunk and is similarly interrupted by ventral and dorsal gaps. It can be seen to tightly envelop the longitudinal muscle strands entering the first foot segment. At the junction of foot and toes, the **musculus circumpedalis (musculus circularis III, at around U55, Figs 5A,E and 6)** is situated. Its fluorescence signal is ambiguous: Rather than being composed of two subunits divided by ventral and dorsal gaps, it appears to be a massive muscular layer medially divided by a narrow gap.

Fig. 5—Body musculature of *Beauchampiella eudactylota*. Fluorescent phalloidin-staining of f-actin filaments, confocal laser scanning microscopy (CLSM). —**A–C**. Maximum projections, —**D–F**. single images. —**A**. View of complete specimen. —**B**. Detail of **A** in caudal trunk region, note cross-striation of longitudinal musculature. —**C**. Musculature surrounding gastric tract (arrowheads). —**D**. Detail of frontal foot segment and internal musculature. —**E**. Detail of caudal foot segment and base of toes. Note musculature inside toes indicated by arrowheads. —**F**. Detail of frontal foot segment and musculi longitudinales ventrales. Arrowheads indicate narrow gaps between the two parts of musculi longitudinales ventrales. mc I, musculus circularis I; mc II, musculus circularis II; mcp, musculus circumpedalis; ml II, musculus longitudinalis II; ml III, musculus longitudinalis III; mld, musculus longitudinalis dorsalis; mlv, musculus longitudinalis ventralis.



Discussion

Body musculature in Monogononta

Our investigation confirms the presence of several elements of body musculature recorded from other rotifer species. To start with, *B. eudactylota* with many other species investigated to date shares the presence of uninterrupted ventral musculi longitudinales ventrales *sensu* Riemann *et al.* (2008) (also detected in *Philodina* sp., see Hochberg and Litvaitis 2000; *Notholca acuminata*, see Sørensen *et al.* 2003; *Notommata glyphura*, *Brachionus urceolaris*, *Floscularia ringens*, see Santo *et al.* 2005; *Proales daphnicola*, *Proales fallaciosa*, *Proales reinhardti*, see Sørensen 2005a; *Dicranophorus forcipatus*, *Enicentrum mucronatum*, see Riemann *et al.* 2008). This observation provides another piece of evidence suggesting that paired musculi longitudinales ventrales were already present in the stem species of Ploima and, probably, also in the stem species of Rotifera (comprising Monogononta, Bdelloida, Seison and Acanthocephala, see Sørensen and Giribet 2006) as a whole.

Similarly, like many other rotifer species, *B. eudactylota* possesses dorso-laterally positioned musculi longitudinales dorsales *sensu* Riemann *et al.* (2008) (also present in *Philodina* sp., see Hochberg and Litvaitis 2000; *Notholca acuminata*, see Sørensen *et al.* 2003; *Notommata glyphura*, *Brachionus urceolaris*, *Floscularia ringens*, see Santo *et al.* 2005; *Proales fallaciosa*, *Proales reinhardti*, *Proales daphnicola*, see Sørensen 2005a;

Dicranophorus forcipatus, *Enicentrum mucronatum*, see Riemann *et al.* 2008). This observation corroborates our previous assumption that the musculi longitudinales dorsales are a ground pattern feature of Ploima and probably also of Rotifera. Unlike in, for example, *Dicranophorus forcipatus* (see Riemann *et al.* 2008) and *Notholca acuminata* (see Sørensen *et al.* 2003), the musculi longitudinales dorsales in *B. eudactylota* are not continuous in their course from the head to the caudal end of the trunk, but divide into a frontal and a caudal section interrupted by a narrow gap. Such breaking up of longitudinal muscles into frontal and caudal portions, however, is not uncommon in rotifers and has been known for a long time (see Hyman 1951).

The presence of the musculus circumpedalis in *B. eudactylota* is shared by other ploimid rotifer species (for example in *Euchlanis dilatata unisetata*, *Brachionus quadridentatus*, see Kotikova *et al.* 2001; *Proales reinhardti*, see Sørensen 2005a; *Dicranophorus forcipatus*, *Enicentrum mucronatum*, see Riemann *et al.* 2008). This observation confirms assumptions of the musculus circumpedalis being a component of the system of body musculature in the ground pattern of Ploima. The presence of such a muscle in the ground pattern of Rotifera, however, remains ambiguous at present (compare Riemann *et al.* 2008).

Compared to other ploimid rotifer species, *B. eudactylota* is conspicuous for the absence of a number of both longitudinal and circular muscle strands. First, we could not confirm the presence of paired musculi longitudinales capitum (*sensu*

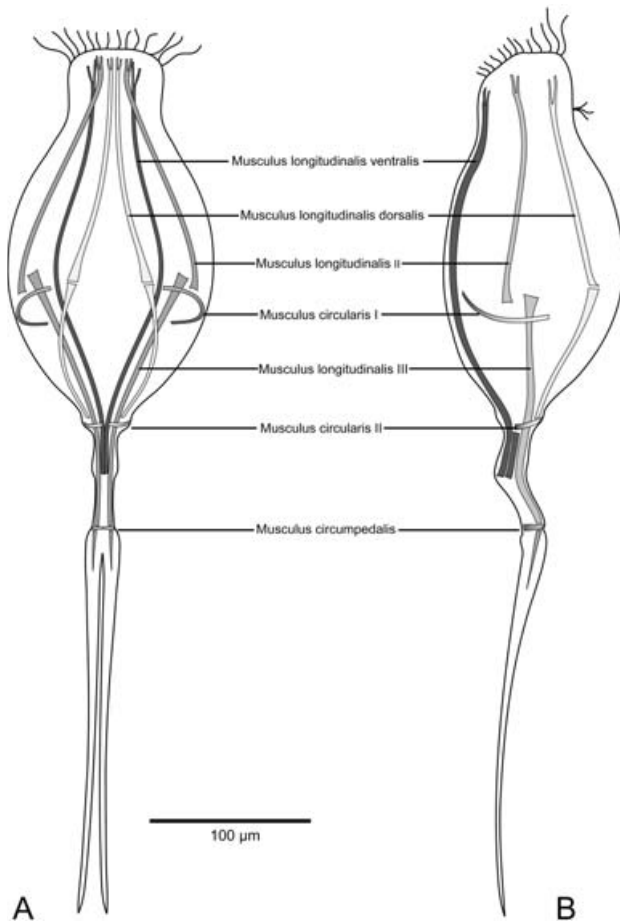


Fig. 6—Body musculature of *Beauchampiella eudactylota*, semidiagrammatic. —**A.** Dorsal view. —**B.** lateral view.

Riemann *et al.* 2008) as reported for other species of Ploima (*Epiphanes senta*, see Martini 1912; *Proales daphnicola*, *Proales fallaciosa*, *Proales reinhardti*, see Sørensen 2005a; *Dicranophorus forcipatus*, *Enicentrum mucronatum*, see Riemann *et al.* 2008 and, maybe equivalent, in *Notholca acuminata*, see Sørensen *et al.* 2003). Likewise, the number of lateral longitudinal muscles (*sensu* Hyman 1951) is limited in *B. eudactylota* compared to, for example, *Dicranophorus forcipatus* and *Enicentrum mucronatum* (see Riemann *et al.* 2008). Moreover, we observed neither a distinct pars coronalis (documented in *Epiphanes senta*, see Martini 1912; *Rhinoglena frontalis*, *Brachionus pala*, *Euchlanis pellucida*, see Stoßberg 1932; *Notholca acuminata*, see Sørensen *et al.* 2003; *Proales daphnicola*, *Proales fallaciosa*, *Proales reinhardti*, see Sørensen 2005a; *Enicentrum mucronatum*, see Riemann *et al.* 2008) nor did we find a corona sphincter (as in *Epiphanes senta*, see Martini 1912; *Brachionus pala*, *Rhinoglena frontalis*, see Stoßberg 1932; *Brachionus quadridentatus*, see Kotikova *et al.* 2001; *Notholca acuminata*, see Sørensen *et al.* 2003; *Floscularia ringens*, see Santo *et al.* 2005b; *Proales daphnicola*, *Proales*

reinhardti, see Sørensen 2005a). Fine filaments at the frontal edge of the head are present, but in our opinion there is no evidence for a distinct musculus pars coronalis.

Given the presence of the musculus longitudinales capitum, lateral longitudinal muscles, a corona sphincter and a musculus pars coronalis in the above taxa occupying different positions within Monogononta (compare with Sørensen and Giribet 2006), it appears more plausible to assume that these elements of body musculature were lost secondarily in *B. eudactylota* than that their absence represents a plesiomorphic state. However, compared to what we know about body musculature in other rotifer species, *B. eudactylota* is remarkable for its strongly developed foot musculature. Although certainly different in structural detail, it is only equalled in degree of development by the foot musculature in species of the genus *Scaridium* Ehrenberg, 1830 (see Segers 1995). With species of the genus *Scaridium*, *B. eudactylota* has in common the presence of long toes and the ability to rapidly move the toes in a jerky manner resulting in skipping movements of the whole animal (see Koste and Shiel 1989). Possibly, these skipping movements represent a defence mechanism against predators functionally equivalent to movements in species of the genus *Filimia* brought about by long movable appendages (Hochberg and Gurbuz 2007). Although strikingly similar in species of the genus *Scaridium* and *B. eudactylota*, the evolution of strong musculature in the foot in conjunction with a skipping movement brought about by rapid spreading and lifting of the toes probably evolved independently in the two taxa and thus represents an impressive case of parallelism (Segers 1995).

The evolution of a strongly muscular foot accompanied by an overall reduction of body musculature (see above) may be seen as an adaptation to the microenvironment inhabited by *B. eudactylota*. Our personal observations and literature sources (Koste 1978; Koste and Shiel 1989) reveal this species to be an inhabitant of the periphyton. More specifically, we found *B. eudactylota* to slowly move about in the free water body among the loose meshwork of filamentous green algae. Apart from occasional skipping movements, its overall movement, if undisturbed, was a remarkably even and slow drifting through the water propelled along by the beating of the coronal cilia. This mode of movement contrasts markedly with the lifestyle of many benthic–periphytic rotifers investigated so far whose body musculature is comparatively more complex. Such rotifers move along substrates and engage in frequent, rapid changes of direction brought about by muscular action rather than swimming in the free water column (for example *Proales daphnicola*, *Proales fallaciosa*, *Proales reinhardti*, see Sørensen 2005a; *Dicranophorus forcipatus*, *Enicentrum mucronatum*, see Riemann *et al.* 2008).

The mastax hard parts of Euchlanidae

A comparison of the trophi in *B. eudactylota* to those of other species of Euchlanidae is hampered by the fact that very few

SEM investigations of euchlanid trophi exist and that drawings based on light microscopic techniques are only to a certain extent comparable to SEM pictures. Sørensen (2002) provides SEM pictures of the trophi of *Euchlanis contorta* and *Euchlanis incisa* that show different structural details from those of *B. eudactylota* in several features. First, the number of uncus teeth (five to six in both species of the genus *Euchlanis*, 10 in *B. eudactylota*) differs considerably. As far as we can tell from light microscopic observations given in the literature, this difference apparently also holds true for other species of *Euchlanis* and *B. eudactylota* (see Koste 1978 and references given therein). Among Euchlanidae, only *Dipleuchlanis propatula* (seven to 10 uncus teeth, Koste 1978) is comparable to *B. eudactylota* in this respect. Second, the lateral sides of the rami of *B. eudactylota* seen in ventral view are evenly rounded, whereas in *Euchlanis contorta* they show a blunt, triangular projection, possibly an alula. Available data on other species of *Euchlanis* (see Koste 1978) seem to confirm this slight, but possibly significant difference.

Surveying available data on other monogonont rotifer trophi, especially those of some members of the taxon Epiphanidae, reveals a couple of structural similarities to the trophi of *B. eudactylota*. The trophi of *Mikrocodides chlaena* (Gosse 1886) in ventral view are remarkably similar to those of *B. eudactylota* both in terms of the number of uncus teeth and shape of the rami. The same holds true for *Cyrtonia tuba* (Ehrenberg 1834) (<http://users.unimi.it/melone/trophi/index.html>, rotifer trophi web page hosted by University of Milan, preparation of *Mikrocodides chlaena* by M. V. Sørensen and of *Cyrtonia tuba* by D. Fontaneto and G. Melone; for *Mikrocodides chlaena*, see also Sørensen 2006). The manubria of both these species, especially the pocket-shape of their openings, are strikingly similar to those of *B. eudactylota* as well. Moreover, a distinct epipharynx, as in *B. eudactylota* attached to the dorso-distal tips of the rami, is also present in *M. chlaena*.

It is difficult to tell, of course, whether these structural similarities do indeed hint at closer phylogenetic relationships between *B. eudactylota* and some taxa of Epiphanidae (i.e. if the similarities discussed represent synapomorphic characters) than between *B. eudactylota* and the rest of the Euchlanidae. However, our observations raise two possibilities. First, the trophi of *B. eudactylota* are characterized by many plesiomorphic features realized in several outgroup taxa – among them many Epiphanidae – as well. Such a scenario would suggest that the lack of a stiffened lorica in *B. eudactylota* is probably primary and that the specific lorica of Euchlanidae evolved in the stem lineage of only a subtaxon of Euchlanidae comprising the genera *Euchlanis* Ehrenberg 1832, *Diplois* Gosse 1886, *Dipleuchlanis* De Beauchamp 1910 and *Tripleuchlanis* Myers 1930. Moreover, the limited number of uncus teeth in species of the genus *Euchlanis* compared to *B. eudactylota* could be seen as a derived reduction. Alternatively, there is no closer phylogenetic relationship

between *B. eudactylota* and the rest of Euchlanidae, which would render Euchlanidae not monophyletic and move *B. eudactylota* closer to other rotiferan subtaxa such as, for example, Epiphanidae. Clearly, these tentative conclusions are little more than working hypotheses. A more satisfactory systematic placement of *B. eudactylota* can only be attempted in the framework of cladistic analyses that include as many informative characters as possible and a sufficiently large number of more closely and more distantly related outgroup taxa. For such an analysis to be successful, however, more detailed investigations of organ systems such as the mastax hard parts or body musculature in Euchlanidae and possible outgroups are needed.

Acknowledgements

We gratefully acknowledge support for this study provided by DFG (Deutsche Forschungsgemeinschaft) and Evangelisches Studienwerk Villigst. Valuable comments on this manuscript given by M. V. Sørensen and an anonymous reviewer are greatly appreciated.

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