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Evolutionary anatomy of the muscular apparatus involved in the anchoring of Acanthocephala to the intestinal wall of their vertebrate hosts

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Abstract Different conceptions exist regarding structure, function, and evolution of the muscles that move the acanthocephalan presoma, including the proboscis, i.e., the usually hooked hold-fast anchoring these endoparasites to the intestinal wall of their vertebrate definitive hosts. In order to clarify the unresolved issues, we carried out a light microscopic analysis of series of semi-thin sections and whole mounts representing the three traditional acanthocephalan classes: Archiacanthocephala (*Macracanthorhynchus hirudinaceus*), Eoacanthocephala (*Paratenuisentis ambiguus*, *Tenuisentis niloticus*), and Palaeacanthocephala (*Acanthocephalus anguillae*, *Echinorhynchus truttae*, *Pomphorhynchus laevis*, *Corynosoma* sp.). Combining our data with published light, transmission electron, and scanning electron microscopic data, we demonstrate that receptacle protrusor and proboscis receptacle in Archi- and Eoacanthocephala are homologous to the outer and inner wall of the proboscis receptacle in Palaeacanthocephala. Besides the proboscis receptacle and a "surrounding muscle," the last common ancestor of Acanthocephala presumably possessed a proboscis retractor, receptacle retractor, neck retractor (continuous with lemnisci compressors), and retinacula. These muscles most probably evolved in the acanthocephalan stem line. Moreover, the last common ancestor of Acanthocephala presumably possessed only a single layer of muscular cords under the presomal tegument while the metasomal body wall had circular and longitudinal strands. Two lateral receptacle flexors (also lateral receptacle protrusors), an apical muscle plate (surrounding one or two apical sensory organs), a midventral longitudinal muscle, and the differentiation of longitudinal body wall musculature at the base of the proboscis probably emerged within Archiacanthocephala. All muscles have a common organization principle: a peripheral layer of contractile filaments encloses the cytoplasm.

Introduction

The mostly hooked proboscis of thorny-headed worms (Acanthocephala) is of central importance for anchoring of juveniles and adults to the intestinal wall of their vertebrate definitive hosts. Depending on the species and circumstances (heavy parasite burden, paratenic host infection), the proboscis can additionally be involved in penetration of the gut wall and invasion of the host's body cavity (e.g., Choi et al. 2010; Dezfuli et al. 2015). Furthermore, the proboscis plays an essential role in nutrition of the worms (Taraschewski 1989a; Taraschewski and Mackenstedt 1991a; Taraschewski 2000). Yet, despite this high relevance for acanthocephalan pathogenicity, there are considerable uncertainties regarding the composition and structure of the muscles that move the acanthocephalan proboscis. This is especially true for the (proboscis) receptacle (also vagina magno, Westrumb, 1821; Rüsselscheide, e.g., Hamann, 1891; proboscis sheath, e.g., Bhalerao, 1937; Petrochenko, 1956), a muscular sheath separating the body cavities of trunk (metasoma) and presoma, and the muscles

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associated with the proboscis receptacle. Thus, the proboscis receptacle of the archiacanthocephalan *Moniliformis moniliformis* is regarded as double-walled by some investigators (e.g., Schmidt 1972a; Taraschewski 2015; also Schmidt and Edmonds 1989) but according to the key of Amin (1987) should be single-walled. Moreover, according to Amin et al. (2013), Tubangui and Masilungan (1946), Petrochenko (1958), and Yamaguti (1954) misinterpreted the anterior portion of the proboscis receptacle in the archiacanthocephalan *Mediorhynchus gallinorum* as double-walled. Similarly, Amin and Dailey (1998) comment on the description of a double-walled receptacle in *Mediorhynchus papillosus* that Khokhlova (1966) "described, and illustrated (her fig. 7b), a double-walled proboscis receptacle (…), clearly mistaking the protrusal muscles for the outer sac."

The latter examples lead to discrepant conceptions regarding the muscular structures in close vicinity to the proboscis receptacle. Most authors concluded that contraction of the respective muscular strands (branches, cords, fibers) protrudes the receptacle's base and consequently considered them as receptacle protrusor(s) (Tables 1 and 2). Yet, other investigators referred to the respective strands in some eoacanthocephalan species as constituents of a so-called parareceptacle structure (PRS). The same investigators discussed alternative functions of the PRS including secretion and regulation of the hydrostatic pressure inside the presomal body cavity (Amin et al. 2002, 2016a, 2007). In a recent light microscopy (LM) investigation, Amin et al. (2016a) recognized that PRS and receptacle protrusor refer to homologous structures. However, the same authors categorically ruled out that the structure can contract at all in the eoacanthocephalans *Paratenuisentis ambiguus* and *Tenuisentis niloticus*. Amin et al. (2016a) further stated that the PRS in the latter two eoacanthocephalan species is confined to only one side of the receptacle. They additionally described a tubular posterior extension of the PRS that reaches beyond the receptacle's base into the body cavity of the trunk ("posterior limb" in Amin et al. 2016a). This contrasts with the observations made by Bullock and Samuel (1975) who reported for *P. ambiguus* "a prominent muscular sling around the proboscis receptacle 'which' encloses all of the receptacle except the extreme posterodorsal tip; muscle strands run diagonally from posteroventral to anterodorsal region of receptacle and attach to body wall just posterior to the insertion of the receptacle." Re-investigating the same species, Herlyn et al. (2001) confirmed a singular, though reticulate, receptacle protrusor without any posterior extension reaching beyond the receptacle's base.

In addition, discussions of the construction and fine structure of the subtegumental or body wall musculature are controversial. Thus, circular and longitudinal body wall musculature in the archiacanthocephalans *Macracanthorhynchus hirudinaceus*, *Macracanthorhynchus ingens*, and

Oligacanthorhynchus tortuosa reportedly consists of liquid-filled tubes that communicate through radial canals with lacunas inside the tegument (epidermis) (Miller and Dunagan 1976, 1977, 1978, 1985a). Combining specific preparation techniques involving the injection of dye and resin with subsequent inspection by the LM and scanning electron microscopy, Miller and Dunagan (1976, 1977) further described an extra system of tubes in close vicinity to the body wall musculature (rete system). However, to the best of our knowledge, neither interconnections between body wall musculature and lacunar system nor rete system have been confirmed by other investigators who used the transmission electron microscope (TEM) (e.g., Díaz Cosín, 1972; Nikishin, 2004). Moreover, the core of the subtegumental "tubes" was found to enclose cytoplasm (sarcoplasm) very rich in glycogen and interspersed with mitochondria, nuclei, and other organelles (e.g., fig. 30 in Díaz Cosín 1972; fig. 1 in Amin et al. 1993, fig. 23E in Taraschewski 2000; fig. 2C in Herlyn et al. 2001). Nonetheless, tubular body wall musculature and rete system descriptions entered diverse textbooks.

These examples illustrate the need for a comparative analysis of the muscles involved in movements of the anterior body section of Acanthocephala including the presoma and the proboscis. Thus, we screened the respective literature spanning more than 200 years and merged the data with new insights gathered from our analyses of several series of sections and whole mounts. Our species sample contained representatives of the major acanthocephalan taxa traditionally ranked as classes (e.g., Smales 2015), i.e., Palaeacanthocephala (*Acanthocephalus anguillae*, *Corynosoma* sp., *Echinorhynchus truttae*, *Pomphorhynchus laevis*), Eoacanthocephala (*P. ambiguus*), and Archiacanthocephala (*M. hirudinaceus*). Additionally, we re-analyzed museum deposits of *P. ambiguus* and *T. niloticus* that had previously been studied by Amin et al. (2016a). In doing so, we clarify the open questions on acanthocephalan anatomy. We further discuss the muscles' functions and conjointly present a parsimonious scenario of the evolutionary changes that presumably occurred in the stem line of thorny-headed worms and during acanthocephalan divergence.

Materials and methods

Altogether, 93 specimens representing seven acanthocephalan species (mostly both sexes; for species, see Table 3) were investigated with the light microscope. Sea lions (hosts of *Corynosoma* sp.) had been incidentally killed in commercial trawl fisheries in New Zealand waters; sampling from carcasses and subsequent analyses were covered by permission of the New Zealand Department of Conservation. All other definitive hosts were sacrificed by authorized personnel (for species, see Table 3).

Table 1 Terminology used for denoting the receptacle protrusor muscle in Archiacanthocephala

Reference	Taxon name[a]	Taxon synonym used in reference study	Synonymous muscle names
Zeder 1800	*Macracanthorhynchus hirudinaceus*	*Echinorhynchus gigas*	Musculi suspensorii that elevate the receptacle's base
Westrumb 1821	*Macracanthorhynchus hirudinaceus*	*Echinorhynchus gigas*	Protrusores
	Oncicola spirula	*Echinorhynchus spirula*	Protrusores
Leuckart 1876	*Macracanthorhynchus hirudinaceus*	*Echinorhynchus gigas*	Protrusor receptaculi
Pachinger 1884	*Macracanthorhynchus hirudinaceus*?	*Echinorhynchus haeruca*	Protrusor receptaculi
Hamann 1891	*Macracanthorhynchus hirudinaceus*	*Echinorhynchus gigas*	Protrusor (receptaculi) d + v; protrusores receptaculi
	Moniliformis moniliformis	*Echinorhynchus moniliformis*	Protrusores receptaculi
Kaiser 1893*	*Macracanthorhynchus hirudinaceus*	*Echinorhynchus gigas*	Protrusor receptaculi d + v
	Moniliformis moniliformis	*Echinorhynchus moniliformis*	Protrusor receptaculi d + v
Lühe 1904	*Macracanthorhynchus hirudinaceus*	*Echinorhynchus hirundinaceus*	Protrusores (referring to Zeder 1800)
Kilian 1932	*Oligacanthorhynchus microcephala*	*Hamaniella microcephala*	Protrusor(es) receptaculi (d + v)
Hyman 1951**	*Oligacanthorhynchus microcephala*	*Hamaniella microcephala*	d + v receptacle protrusors
Byrd, Kellog 1971	*Mediorhynchus grandis, M. papillosus, M. robustus*	*Mediorhynchus bakeri* (synonym of *M. papillosus*)	Paraproboscideal sac represented by bands of muscles
Schmidt 1972a	*Oncicola* sp.		(primary) d + v protrusors
Dunagan, Miller 1974	*Macracanthorhynchus hirudinaceus*		d + v receptacle protrusors
Wanson, Nickol 1975	*Oncicola spirula*	*Prosthenorchis elegans*	Receptacle protrusor(s/muscles)
	Moniliformis moniliformis	*Moniliformis dubius*	Receptacle protrusor(s/muscles)
Dunagan, Miller 1976	*Moniliformis moniliformis*		Receptacle protrusor muscles
Schmidt 1977	*Mediorhynchus robustus*		Protrusor muscle (sheath); d + v protrusor muscle(s)
Miller, Dunagan 1985b***	*Macracanthorhynchus hirudinaceus*		d + v receptacle protrusor muscle
Gee 1987	*Moniliformis moniliformis*		Receptacle protrusor muscles (outer wall of receptacle)
Taraschewski et al. 1989	*Moniliformis moniliformis*		Receptacle protrusor muscle(s)
Amin, Dailey 1998	*Mediorhynchus papillosus*		d + v protrusor (protrusal) muscles
Herlyn 2002; present study	*Macracanthorhynchus hirudinaceus*		Receptacle protrusor
Richardson et al. 2014	*Oligacanthorhynchus microcephala*	*Oligacanthorhynchus microcephalus*	d + v protruser muscles
Recommended term	Archiacanthocephala in general		Receptacle protrusor (po)

See also table 5.5 in Miller and Dunagan (1985b) and table 1 of Herlyn (2002)

d + v, dorsal and ventral or dorsalis and ventralis; *?*, uncertain species; (), abbreviation and alternative terminology

[a] Taxon names according to Yamaguti (1963) and Amin (2013). *Kaiser's description of *M. moniliformis* refers to the findings of Westrumb (1821). **Hyman (1951) refers to Kilian (1932). ***Miller and Dunagan (1985b) refer to Kaiser (1893), Rauther (1930), and Dunagan and Miller (1974)

Table 2 Terminology used for denoting the receptacle protrusor muscle in Palae- and Eoacanthocephala

Reference	Higher-level taxon (class)	Taxon name[a]	Taxon synonym used in reference study	Synonymous muscle names
Datta 1947	Eoacanthocephala	*Raosentis podderi*		Protractor muscle(s)
Van Cleave, Bullock 1950		*Neoechinorhynchus emydis*		Muscular sling of receptacle
Bullock, Samuel 1975		*Paratenuisentis ambiguus*		Muscular sling around the receptacle
Herlyn et al. 2001		*Paratenuisentis ambiguus*		Receptacle protrusor
Amin 2005; Amin et al. 2002, 2007, 2011, 2013, 2014		*Neoechinorhynchus* (5 species) *Acanthogyrus* (2 species)		Parareceptacle structure (PRS)
Gupta et al. 2015		*Pallisentis punctati*		Protractor muscle(s)
Amin et al. 2016a		*Paratenuisentis ambiguus, Tenuisentis niloticus*		Parareceptacle structure (PRS)
Recommended term		Eoacanthocephala in general		Receptacle protrusor (po)
Zeder 1800	Palaeacanthocephala	*Acanthocephalus lucii*	*Echinorhynchus lucii*	Musculi suspensorii
		Pomphorhynchus laevis	*Echinorhynchus nodulosus*	Musculi suspensorii
Kaiser 1893*		*Corynosoma strumosum*	*Echinorhynchus gibbosus*	Protrusores receptaculi
Nickol 1972**		*Fessisentis fessus*		Outer wall of (proboscis) receptacle
Herlyn, Ehlers 2001		*Acanthocephalus anguillae*		Receptacle constrictor
Recommended term		Palaeacanthocephala in general		Outer wall of proboscis receptacle (ow)

[a] Taxon names according to Yamaguti (1963) and Amin (2013). See also table 5.5 in Miller and Dunagan (1985b) and table 1 of Herlyn (2002). *Kaiser (1893) refers to von Siebold; yet, we could not clarify which of von Siebold's studies is meant. **Only one of the many studies using outer wall of proboscis receptacle. (), abbreviations and alternative terminology

For the present study, altogether 33 worms were extracted from the intestinal tract of naturally infected definitive hosts. Acanthocephalans were immobilized by cooling at 4 °C and brought to the laboratory in physiological saline solution. After fixation with Bouin's fluid for a minimum of 3 days (room temperature), worms were dehydrated in graded ethanol, transferred to butanol and methyl benzoate, and embedded in Paraplast (Roth). Complete series of semi-thin sections of ~5 μm were then stained applying a modified Azan protocol (Azan after Geidies) (Mulisch and Welsch 2015). Semi-thin sections of ~0.5 μm of one additional *P. ambiguus* specimen

were dyed with methylene blue after fixation in 5% glutaraldehyde buffered with 0.1 M sodium cacodylate, pH 7.4, at 4 °C for 24 h, post-fixation in 2% OsO₄ in the same buffer, dehydration in graded ethanol, transfer to propylene oxide, and embedding in araldite. Ten complete *P. ambiguus* specimens (both sexes) were mounted using Canada balsam (whole mounts in Table 3). Sixty other whole mounts of *P. ambiguus* and *T. niloticus* (both sexes) were made available by the US National Parasite Collection (USNPC) at the Smithsonian Institution, Washington, DC, USA. Sections and whole mounts were examined by a Primovert light microscope (Zeiss). The taxonomic

Table 3 Summary of the species and specimens investigated

Taxon name[a]	Preparation; number of specimens	Collection year; definite host; locality
Acanthocephalus anguillae (Palaeacanthocephala)	Semi-thin sections (~5 μm); 1 male, 3 females	1998; barbel, *Barbus barbus*; River Weser at Gimte near Göttingen, Germany
Corynosoma sp. (Palaeacanthocephala)	Semi-thin sections (~5 μm); 2 females	1996; New Zealand sea lion, *Phocarctos hookeri*; Southern New Zealand
Echinorhynchus truttae (Palaeacanthocephala)	Semi-thin sections (~5 μm); 1 male, 1 female	1998; brown trout, *Salmo trutta*; grayling, *Thymallus thymallus*; River Leine at Göttingen, Germany
Pomphorhynchus laevis (Palaeacanthocephala)	Semi-thin sections (~5 μm); 2 juveniles	1998; barbel, *Barbus barbus*; River Weser at Gimte near Göttingen, Germany
Paratenuisentis ambiguus (Eoacanthocephala)	Semi-thin sections (~5 μm); 3 males, 5 females	1997; European eel, *Anguilla anguilla*; River Weser at Gimte near Göttingen, Germany
Paratenuisentis ambiguus (Eoacanthocephala)	Semi-thin sections (~0.5 μm), 1 specimen	1987; European eel; *Anguilla anguilla*; River Weser, Germany
Paratenuisentis ambiguus (Eoacanthocephala)	Whole mounts; 2 males, 8 females	1997; European eel, *Anguilla anguilla*; River Weser at Gimte near Göttingen, Germany
Paratenuisentis ambiguus (Eoacanthocephala)	Whole mounts; 48 individuals of both sexes including all USNPC deposits analyzed by Amin et al. (2016a), besides additional ones; whole mounts	USNPC nos. 006471, 038594-038597, 072905-072907, 100026; see catalog for details
Tenuisentis niloticus (Eoacanthocephala)	Whole mounts; 12 individuals of both sexes including all USNPC deposits analyzed by Amin et al. (2016a), besides additional ones; whole mounts	USNPC nos. SH222-6-48-59; see catalog for details
Macracanthocephalus hirudinaceus (Archiacanthocephala)	Semi-thin sections (~5 μm); 1 male, 3 females	Domestic pig, *Sus scrofa*; slaughterhouse

[a] Taxon names according to Yamaguti (1963) and Amin (2013)

nomenclature used follows Yamaguti (1963) and Amin (2013) and the references used therein.

Results and discussion

Receptacle protrusor of Eo- and Archiacanthocephala: a syncytial muscle enclosing the proboscis receptacle

Westrumb (1821) was probably the first investigator who suggested a protrusal function for the mesh of muscular strands closely associated with the receptacle (Table 1). In his description of the archiacanthocephalans *Oncicola* (*Echinorhynchus*) *spirula* and *M. hirudinaceus*, he noticed: "The large sheath (= proboscis receptacle) is provided with a muscular apparatus, (that functions) betimes for protrusion and then for retraction of the proboscis, and these muscles I therefore name protrusors and retractors" (translated from Latin). Fifty-five years later, Leuckart (1876) described a protrusor receptaculi for *M. hirudinaceus*, thereby referring to the respective strands surrounding the receptacle. Since then, many authors used receptacle protrusor(s) and related terms for

denoting the muscular strands in archiacanthocephalan species belonging to Moniliformida, Gigantorhynchida, and Oligacanthorhynchida (Table 1), a tradition that we herein follow (po in Fig. 1c, f). The respective muscle is not restricted to archiacanthocephalans and also occurs in eoacanthocephalans including *P. ambiguus* (po in Figs. 1b, e and 2a, b; see also Amin et al. 2016a), *Raosentis podderi*, *Pallisentis punctati*, and several species of *Neoechinorhynchus* and *Acanthogyrus* (Table 2), not to mention ample evidence from micrographs and drawings showing the muscle without extra labeling (e.g., fig. 3 in Taraschewski 1989b; fig. 12 in Amin and Heckmann 1992; fig. 5B in Gendron and Marcogliese 2016). After all, palaeacanthocephalans have the muscle too, although it is mostly designated as the outer wall of a double-walled proboscis receptacle in this taxon (ow in Figs. 1a, d and 2c–f; Table 2; for homologization, see next Section).

The recurrent usage of plural in the respective literature (e.g., Kaiser 1893; Kilian 1932; Hyman 1951; Schmidt 1972a; Dunagan and Miller 1974; Amin and Dailey 1998; Richardson et al. 2014) reflects the complex structure of the receptacle protrusor which, in archi- and eoacanthocephalans, is subdivided

into several branches (Tables 1 and 2). However, our complete series of sections (several specimens, both sexes) revealed that in *P. ambiguus*, the cords are interconnected by anastomoses, thus constituting a coherent syncytial muscle (po, red arrowhead in Fig. 2a). Obviously, this was already recognized by Bullock and

Samuel (1975) who reported for *P. ambiguus* a single muscular sling surrounding the receptacle, thereby again referring to serial sections. A singular receptacle protrusor was also observed in *Mediorhynchus robustus*, a representative of the archiacanthocephalan taxon (order) Gigantorhynchida (Schmidt
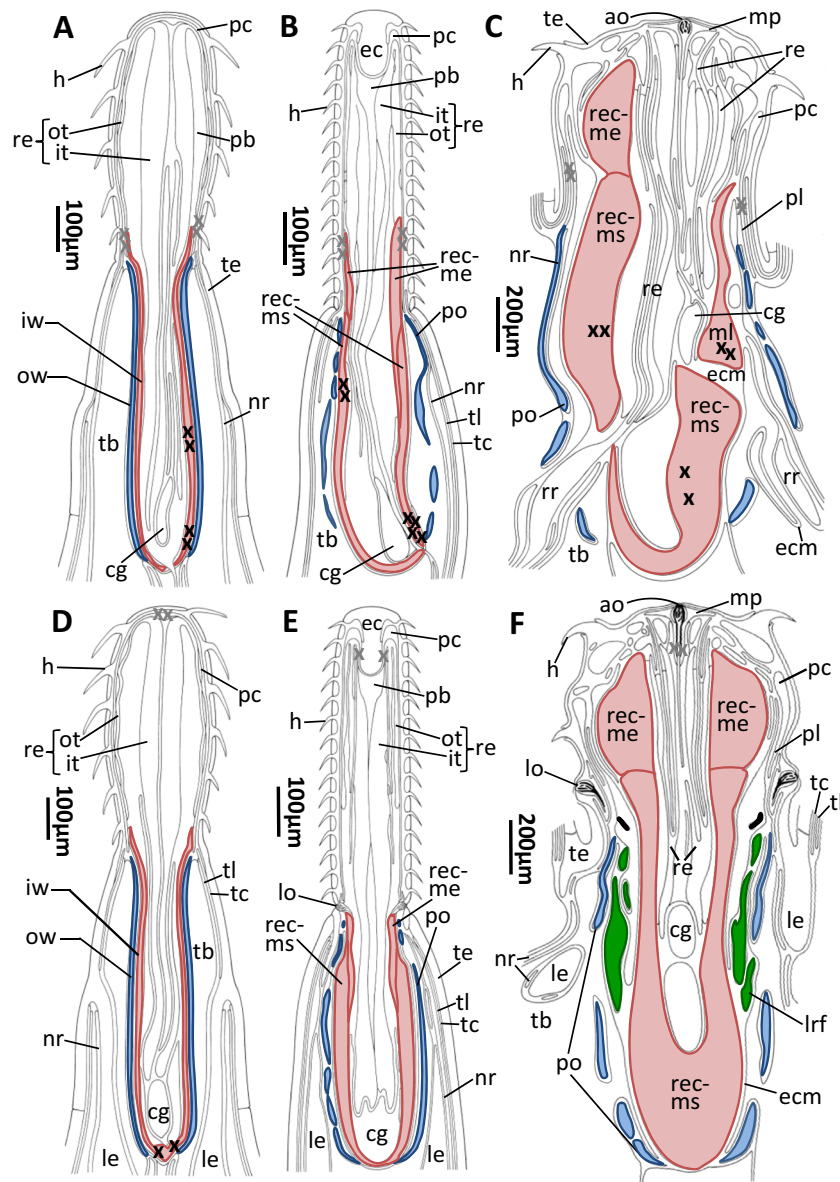

Fig. 1 The anterior body section of three species representing the major acanthocephalan taxa (classes). **a–c** Semi-schematic depiction of sagittal semi-thin sections (ca. 5 μm). **d–f** Sketches drawn from semi-thin horizontal sections. **a**, **d** *A. anguillae* (Palaeacanthocephala). **b**, **e** *P. ambiguus* (Eoacanthocephala). An epidermis cone (ec) at the proboscis apex seems to be apomorphic to a clade comprising Eo- and Polyacanthocephala. **c**, **f** *M. hirudinaceus* (Archiacanthocephala, Oligacanthorhynchida). Oligacanthorhynchida like *M. hirudinaceus* possess a midventral longitudinal muscle (ml) and a pair of lateral receptacle flexors (lrf). An anterior muscle plate (mp) surrounding one or two apical sensory organs (ao) could represent an evolutionary novelty of Moniliformida, Gigantorhynchida, and Oligacanthorhynchida. **b**, **c**, **e**, **f** In eo- and archiacanthocephalans, the receptacle has an anterior portion without (medulla, *rec-me*) and a posterior portion with contractile filaments (muscle sac, *rec-ms*). **a–f** The complement of muscles and their insertions and extensions reveals that outer (ow; *blue*) and inner wall of proboscis receptacle (iw; *reddish*) in palaeacanthocephalans and receptacle protrusor (po; *blue*) and proboscis receptacle (rec-ms, rec-me; *reddish*) in eo- and archiacanthocephalans are homologous structures. *cg* cerebral ganglion, *h* hook, *it* inner tube of proboscis retractor, *le* lemnisci, *lo* lateral sensory organ, *nr* neck retractor, *ot* outer tube of proboscis retractor, *pb* presomal body cavity, *pc* presomal circular body wall musculature, *pl* presomal longitudinal body wall musculature, *re* proboscis retractor, *rr* receptacle retractor, *tb* body cavity of the trunk, *tc* circular body wall musculature of the trunk, *te* tegument, *tl* longitudinal body wall musculature of the trunk, *X* position of nucleus. (Modified after Herlyn 2002)
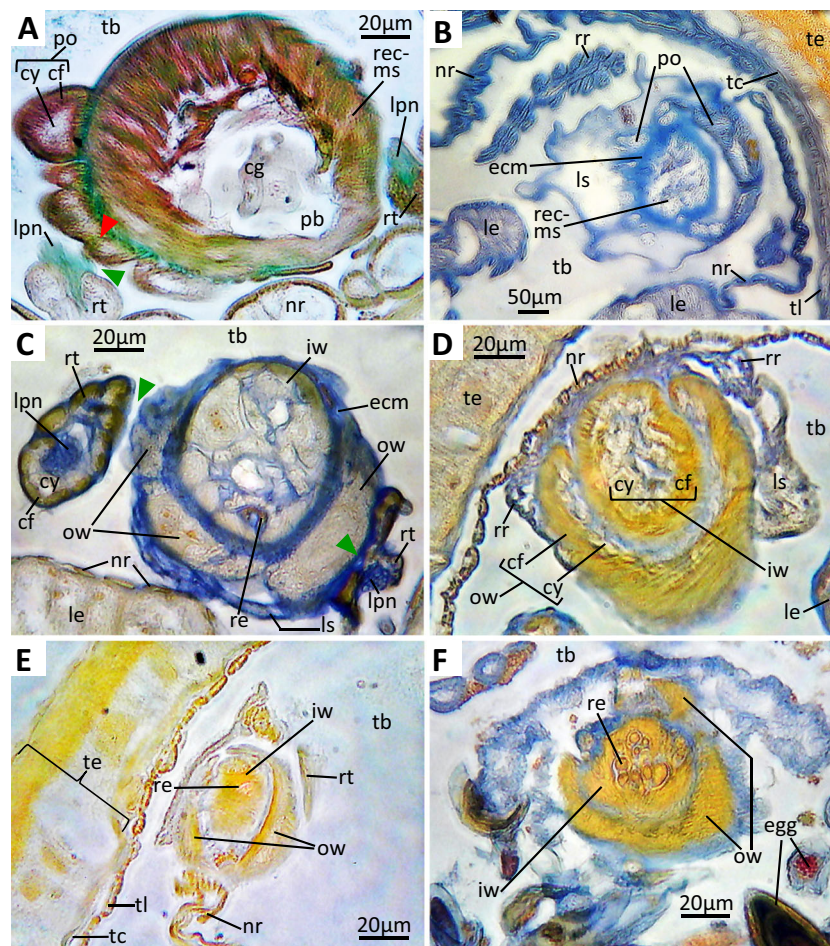
Fig. 2 LM micrographs of slightly oblique transverse sections (ca. 5 μm) through the receptacle's base of six acanthocephalan species. **a** *P. ambiguus*, male (Eoacanthocephala). The *red arrowhead* points to an anastomosis between two strands of the receptacle protrusor (po). **b** *M. hirudinaceus*, female (Archiacanthocephala, Oligacanthorhynchida). **c** *A. anguillae*, female (Palaeacanthocephala). **d** *E. truttae*, female (Palaeacanthocephala). **e** *P. laevis*, juvenile (Palaeacanthocephala). **f** *Corynosoma* sp., female (Palaeacanthocephala). **a–f** Consistent relative arrangements of the muscles support the homology of receptacle protrusor and proboscis receptacle (rec-ms) in eo- and archiacanthocephalans and outer (ow) and inner wall of proboscis receptacle (iw) in palaeacanthocephalans. **a, c** *Green arrowheads* highlight the discontinuity of retinacula (rt) and receptacle protrusor/ outer wall of proboscis receptacle. **a, b** The eo- and archiacanthocephalan receptacle protrusor seemingly encircles only part of the proboscis receptacle since the contralateral strands ended further anterior and thus are not in the section plane. **c–f** In palaeacanthocephalans, the outer wall of receptacle terminates before the inner wall of receptacle. **a, d** The muscles invariably consist of a peripheral layer of contractile filaments (cf) surrounding a cytoplasmic core (cy). *cg* cerebral ganglion, *le* lemnisc, *lpn* lateral posterior nerve, *ls* ligament sac, *nr* neck retractor, *re* proboscis retractor, *rr* receptacle retractor, *tc* circular musculature of the trunk body wall, *te* tegument, *tl* longitudinal musculature of the trunk body wall

1977). The existence of an extra pair of muscles, herein referred to as lateral receptacle flexors, further complicates the pattern in representatives of the archiacanthocephalan order Oligacanthorhynchida as exemplified by *M. hirudinaceus* (lrf, po in Figs. 1c, f and 3) and *Oligacanthorhynchus microcephala* (fig. 16 in Kilian 1932). Still, our semi-thin sections confirmed for *M. hirudinaceus* that the other longitudinal strands closely associated with the receptacle are interconnected by anastomoses (red arrowhead in Fig. 3a; see Section "Evolutionary novelties inside Archiacanthocephala" for more details). Thus, it is consequential to conclude a singular, though syncytial, receptacle protrusor muscle for eo- and archiacanthocephalans.

Receptacle protrusor and proboscis receptacle in Eo- and Archiacanthocephala are homologous to the outer and inner wall of the proboscis receptacle in Palaeacanthocephala

The intimate contact of the receptacle protrusor and proboscis receptacle in palaeacanthocephalans led to the widespread view that in this taxon, the receptacle is double-walled, thus consisting of an outer and inner wall (ow, iw in Figs. 1a, d and 2c–f; also, e.g., Nickol 1972). A likewise close association of both muscles can give the impression that a double-walled receptacle also exists in the
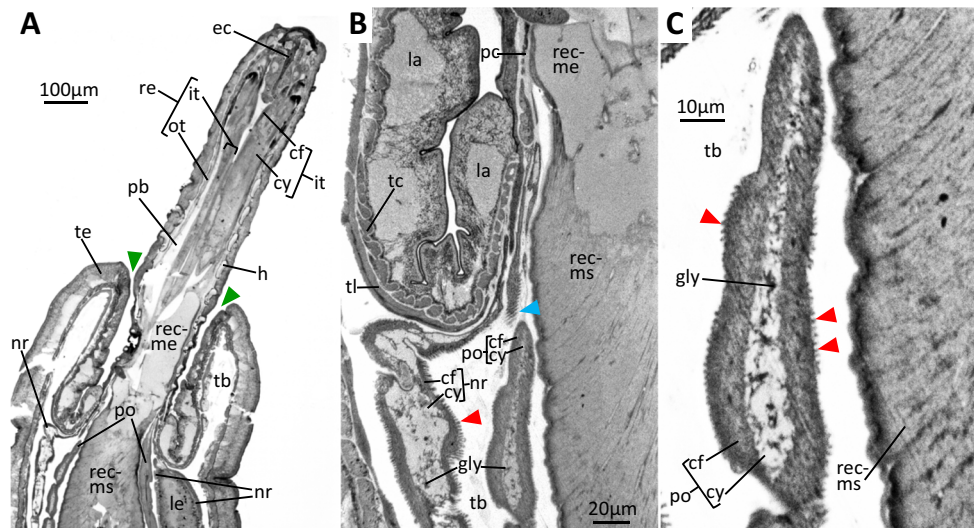
Fig. 3 LM micrographs of sections (ca. 5 μm) through the anterior body of females of *M. hirudinaceus* (Archiacanthocephala, Oligacanthorhynchida). **a** Slightly oblique parasagittal section showing that the proboscis receptacle is subdivided into an anterior medulla (rec-me) and a posterior muscle sac (rec-ms); the latter possesses a peripheral layer of contractile filaments (cf) lined at its inner surface by cytoplasm (cy). Receptacle protrusor (po), proboscis retractor (re), presomal circular and longitudinal body wall musculature (pc, pl), circular and longitudinal body wall musculature of the trunk (tc, tl), neck retractor (nr), lateral receptacle flexors (lrf), and midventral longitudinal muscle (ml) are additional muscles involved in movements of the anterior body section. The receptacle protrusor shows no limb-like posterior extension. The strands of the receptacle protrusor are interconnected by anastomoses (see *red arrowhead*). *Green arrowheads* highlight the circular furrow

resulting from partial invagination of the presoma and fore-trunk. The *yellow arrowhead* points to an anastomosis between two cords of the lateral receptacle flexor. In this section plane, the receptacle retractor (rr in **c**) is not visible and the receptacle protrusor seems to fully enclose the proboscis receptacle (but compare Fig. 2b). **b, c** Transverse sections (**b** further anterior, **c** further posterior) showing that the dorsal portion of the proboscis retractor penetrates the proboscis receptacle behind the ventral portion; the proboscis retractor is continuous with the receptacle retractor (rr) extending through the trunk (tb; see also Fig. 1c). For *yellow arrowhead*: see legend to (**a**). *cy* cytoplasm, *ecm* extracellular matrix, *h* hook, *la* lacuna of tegument, *le* lemnisc, *pb* presomal body cavity, *pk* perikaryon of so-called support cell (Stützzelle), *tc* circular musculature of the trunk, *te* tegument, *tl* longitudinal musculature of the trunk

moniliformid genera *Moniliformis* and *Promoniliformis*. In turn, a receptacle is commonly regarded single-walled or single-layered when the receptacle protrusor is not as firmly attached to the (inner wall of) receptacle, as is the case in eoacanthocephalans and in "non-moniliformid" archiacanthocephalans (po, rec-ms in Figs. 1b, c, e, f, 3, 4, and 5d; also, e.g., Van Cleave 1921; Harada 1931; Wanson and Nickol 1975; Amin 1987; Bolette 1997; Gudivada et al. 2010). Yet, when taking into account the entire complement of acanthocephalan muscles, their relative arrangement and extension, it becomes obvious that the outer wall of the proboscis receptacle is homologous to the receptacle protrusor, while the inner wall represents the proboscis

receptacle sensu stricto (Fig. 1). Zeder apparently recognized this homology across the different acanthocephalan taxa as early as 1800 and properly used a consistent terminology (musculi suspensorii) for denoting the respective strands in the archiacanthocephalan *M. hirudinaceus* and in the two palaeacanthocephalans *Acanthocephalus lucii* and *Pomphorhynchus laevis* (Tables 1 and 2). Likewise, Kaiser (1893) took notice of the respective muscular cords as constituents of the protrusores receptaculi in the archiacanthocephalans *M. hirudinaceus* and *M. moniliformis* and in the palaeacanthocephalan *Echinorhynchus gibbosus* which, according to Yamaguti (1963) and also Amin (2013), is a synonym of *Corynosoma strumosum* (Tables 1 and 2).

Fig. 4 LM micrographs of longitudinal sections (0.5 μm) through the presoma of *P. ambiguus* (Eoacanthocephala). **a** The cords of the receptacle protrusor (po) line up along both sides of the receptacle (rec). The receptacle has an anterior medulla (rec-me) and a posterior muscular portion (rec-ms). The proboscis retractor (re) consists of a subtegumental outer (ot) and an inner tube (it) shaped by anastomosing longitudinal cords; these merge at the proboscis apex, thereby enclosing an epidermis cone (ec, also apical organ). Only the cords constituting the inner tube penetrate the receptacle's base while the subtegumental strands terminate more anteriorly. *Green arrowheads* highlight the circular grove resulting from partial invagination of the presoma and fore-trunk. **b** Enlargement of (**a**) showing that the body wall musculature of the trunk consists of longitudinal (tl) and circular fibers (tc) while the presomal body wall musculature has exclusively circular fibers (pc). Staining and structure of the contractile layer are essentially the same across receptacle protrusor, muscular portion of the proboscis receptacle, and neck retractor (nr). The surface of neck retractor and receptacle protrusor is increased by furrows and ridges shaped by the plasmalemma (*red arrowheads* when cut transversally; *blue arrowhead* when cut horizontally). **c** Enlargement of (**a**) + (**b**) detailing the subdivision of a receptacle protrusor strand into a peripheral layer of contractile filaments (cf) and a central cytoplasmic core (cy) which contains organelles and glycogen particles (gly). Plasmalemma ridges cover wide parts of the surface (*red arrowheads*). *h* hook, *la* lacuna of tegument, *le* lemnisc, *pb* presomal body cavity, *tb* body cavity of the trunk, *te* tegument

The above considerations illustrate that proboscis receptacle and outer wall of proboscis receptacle are actually synonyms denoting homologous structures. This again implies that the last common ancestor of living Acanthocephala possessed a receptacle and a "receptacle surrounding muscle." However, it remains to be elucidated whether this receptacle surrounding muscle had the structure of a widely detached receptacle protrusor or more resembled an outer wall of a proboscis receptacle ensheathing the (inner wall of) proboscis receptacle. Among others, this limitation is due to the highly modified organization of acanthocephalans that hampers comparisons with their closest living phylogenetic relatives, i.e., Seisonidea and Bdelloidea (Wey-Fabrizius et al. 2014; Sielaff et al. 2016; also, e.g., Sørensen and Kristensen 2015). Either way, considering the extension and attachment sites of receptacle protrusor (po in Figs. 1b, c, e, f and 2-6) and outer wall of proboscis receptacle (ow in Figs. 1a, d and 2c–f) across the different acanthocephalan taxa, their contraction should consistently result in a relative forward-move of the receptacle's posterior pole. This conclusion is supported by several in vivo observations reported for more than 200 years (p. 116 in Zeder 1800; Kaiser 1893, p. 123; Hammond 1966, p. 208; Table 1). In terms of the relative forward-move, the usage of the long-established term "receptacle protrusor" for denoting the respective cords seems justified—at least with respect to single-walled eo- and archiacanthocephalans (Tables 1 and 2).

These conclusions are independent of the detailed muscular anatomy of Polyacanthocephala, i.e., the fourth taxon inside Acanthocephala that has been ranked as a class, besides Palae-, Eo-, and Archiacanthocephala (Amin 1987; Smales 2015). Thus, mt-sequence analyses suggest that Polyacanthocephala either are sister to (all other) Eoacanthocephala (García-Varela et al. 2002; Verweyen et al. 2011) or have a nested position within Eoacanthocephala (Gazi et al. 2016). A monophyletic origin of Poly- and Eoacanthocephala is further supported by the shared presence of an epidermis cone at the proboscis apex, frequently referred to as apical organ (ec in Figs. 1b, e and 4a; also, e.g., Taraschewski and Mackenstedt 1991a; Amin and Dezfuli 1995; Amin et al. 1996; Herlyn 2001; Smales et al. 2012). Given such phylogenetic affiliation, the muscular organization of Polyacanthocephala should not affect the proposed homology of receptacle protrusor and receptacle on the one hand and outer and inner wall of proboscis receptacle on the other. Similarly, the detailed phylogenetic position of Apororhynchida, i.e., the fourth archiacanthocephalan taxon ranked as an order (e.g., Smales 2015), should not affect the present conclusions.

Fig. 5 LM micrographs of *P. ambiguus* (Eoacanthocephala). **a** Whole mount of a female. The receptacle medulla (rec-me) is fraught with glycogen particles (gly) appearing as dark granules. **b** Phase contrast image of the whole mount in (**a**). **c** Horizontal section (ca. 5 μm) of a male. Juxtaposition of obliquely sectioned cords of the receptacle protrusor gives the impression of cellular structures (*1–4*). **d** Phase contrast image of a transverse section through a female. **a**–**c** The strands of the receptacle protrusor (po) terminate at the receptacle's base; there is no posterior extension reaching beyond the receptacle's base. The strands of the receptacle protrusor line both sides of the muscle sac shaped by the proboscis receptacle (rec-ms); they are discontinuous with other structures (*green arrowheads*). **c**, **d** The strands of the receptacle protrusor have a peripheral layer of contractile filaments (cf) surrounding the cytoplasm (cy); they are interconnected by anastomoses (*red arrowheads*). Also, the muscle sac of the proboscis receptacle has a peripheral contractile layer encircling the cytoplasm. *cg* cerebral ganglion, *le* lemnisc, *pb* presomal body cavity, *tb* body cavity of the trunk, *te* tegument, *re* proboscis retractor
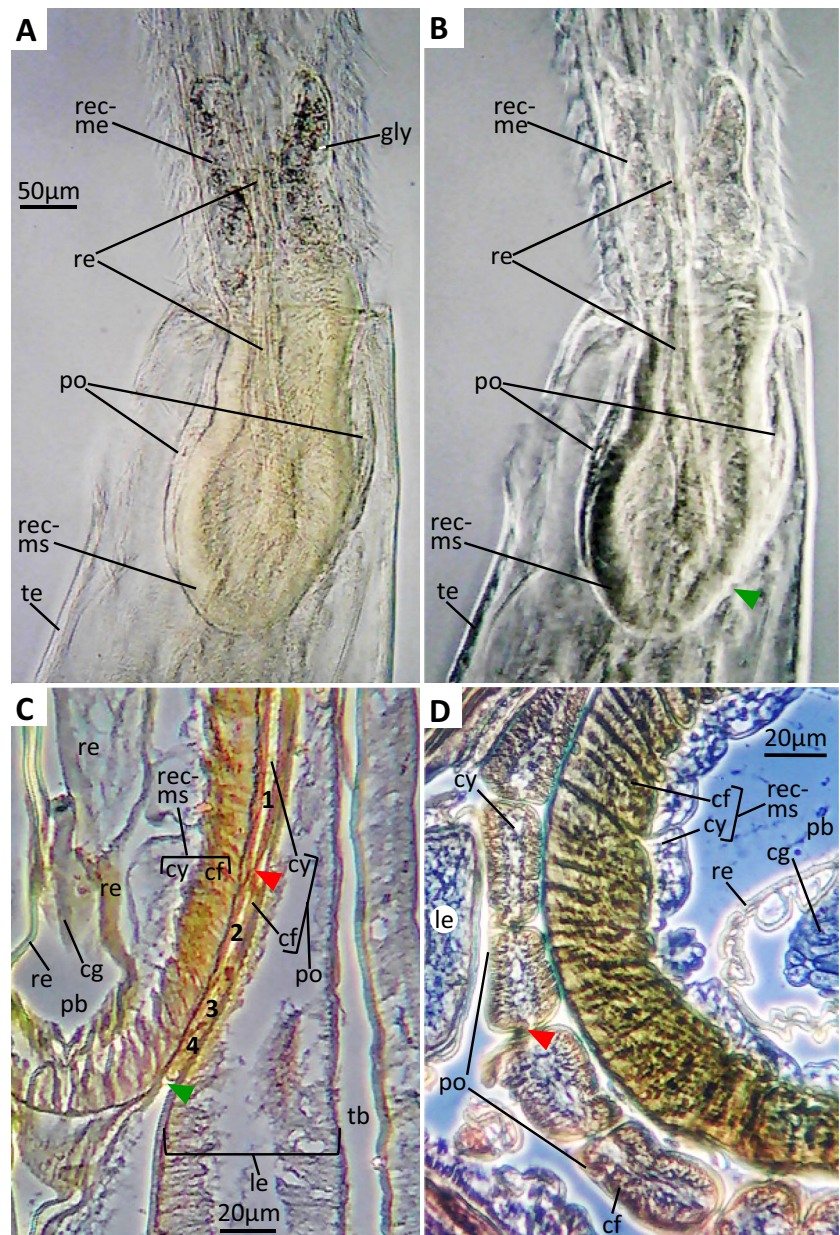
Proboscis retractor, receptacle and neck retractor, and body wall musculature add to the list of muscles involved in proboscis movements

The muscular apparatus moving the proboscis also includes the proboscis retractor (also retractor proboscides, Hamann 1891; retractores proboscides, Kaiser 1893). The muscle extends from the inner surface of the anterior proboscis pole in a posterior direction (re in Figs. 1, 4a, and 5a, b; also, e.g., Miller and Dunagan 1985b). In most species, the muscle shapes two concentric tubes, each consisting of anastomosing longitudinal cords that merge at the proboscis apex (ot and it in Figs. 1a, b, d, e and 4a; also, e.g., fig. 1C in Herlyn et al. 2001; fig. 2A in Herlyn and Ehlers 2001). Extending from the

proboscis apex, the subtegumental cords (outer tube) run in a posterior direction up to their termination in front of the receptacle. In contrast, the strands of the inner tube lack the close contact with the tegument and, instead, extend from the proboscis apex in a posterior direction through the entire presomal body cavity before they penetrate the receptacle at its posterior end (Fig. 1a, b, d, e). The muscle continues further posteriorly, now constituting the receptacle retractor(s) (retractores receptaculi, Hamann 1891; Kaiser 1893), through the body cavity of the trunk up to its attachment sites at the inner surface of the body wall. This is essentially the same in most acanthocephalan taxa including eoacanthocephalans such as *P. ambiguus* and *T. niloticus* (re in Figs. 4a, 5c, d, 6, and 7) and palaeacanthocephalans like *A. anguillae*, *E. truttae*,

P. laevis, and *Corynosoma* sp. (re in Fig. 2c, e, f; rr in Figs. 1c, 2b, d, 5b, 6b, d, and 7). Consequently, the last common ancestor of Acanthocephala most probably possessed a proboscis retractor with subtegumental (outer tube) and central longitudinal cords (inner tube). Secondary deviations from the general pattern in Archiacanthocephala are considered in the next Section (Fig. 1c, f).

The neck retractor [retractor(es) colli in, e.g., Kaiser 1893; Kilian 1932] may or may not be continuous with the longitudinal body wall musculature of the trunk, but it is certainly involved in proboscis movement. The muscle is another mesh-like syncytium composed of predominantly longitudinal muscle strands; it extends from the inner surface of the body wall through the body cavity of the trunk to its posterior attachment site, again at the body wall. The fibers of the neck retractor are frequently lined up along each other very tightly, thus giving a fan-like appearance (e.g., figs. 4g and 5a in Aznar et al. 2006). The neck retractor partially encircles the proboscis receptacle, the receptacle protrusor, and, when present, additional muscles that will be dealt with in the next section (nr in Figs. 1, 2b, d, e, 3a, c, and 4a, b; also, e.g., fig. 359A in Leuckart 1876; fig. 6 in plate 5 of Hamann 1891). Though

Fig. 6 LM micrographs of two representative whole mounts of *P. ambiguus* (Eoacanthocephala) deposited at the Smithsonian Institution at Washington DC, USA. Structures are highlighted and labeled in the copies at the *right*, thus allowing for an unimpaired inspection of the micrographs at the *left*. **a**, **b** Female, USNPC no. 1339176, storage location 1130-19. **c**, **d** Female, USNPC no. 1368478, storage location 1131-3. **a**–**d** The strands of the receptacle protrusor (po) are recognizable on both sides of the muscle sac shaped by the receptacle (rec-ms). The strands of the receptacle protrusor terminate at the receptacle's base and do not extend further posteriorly. *te* tegument, *re* proboscis retractor
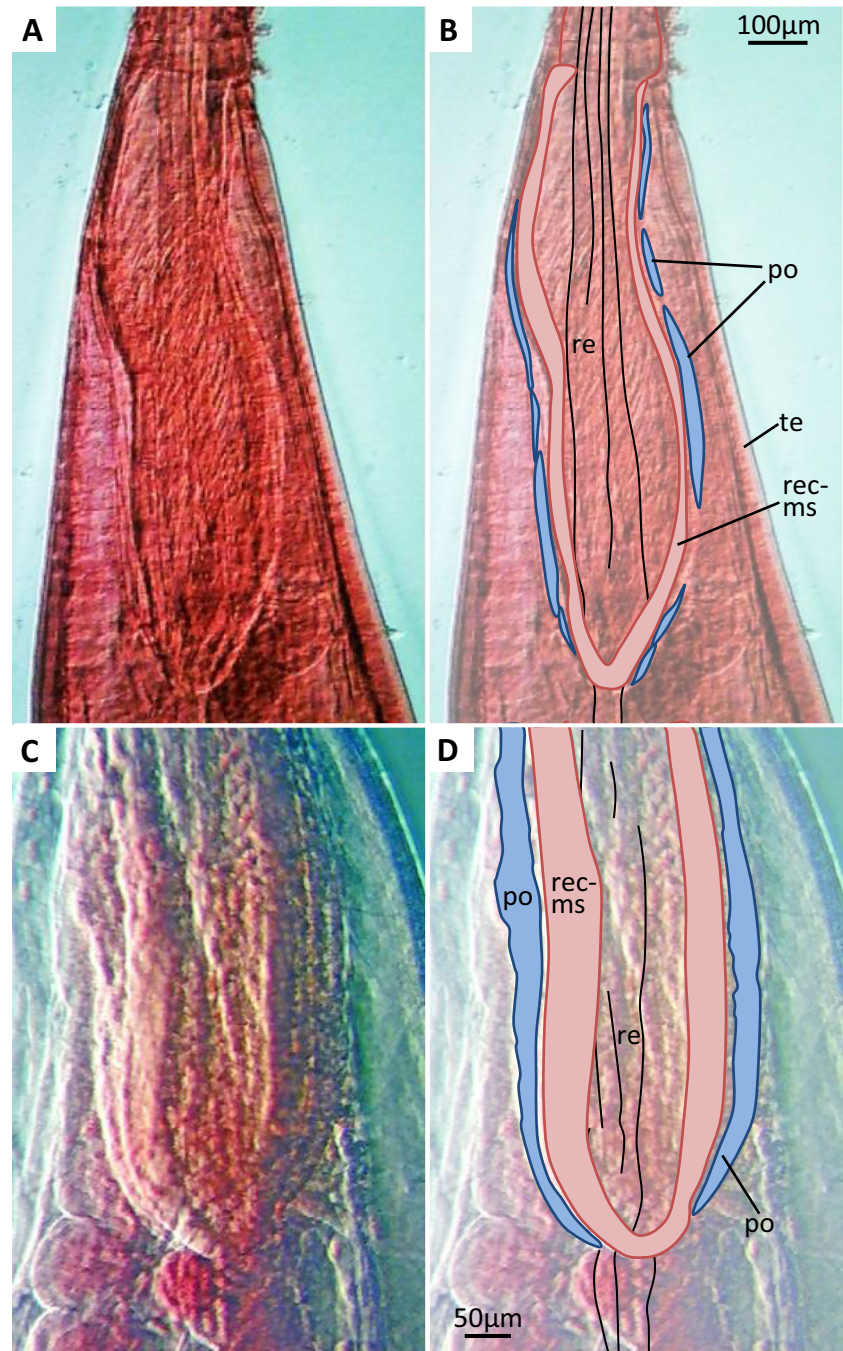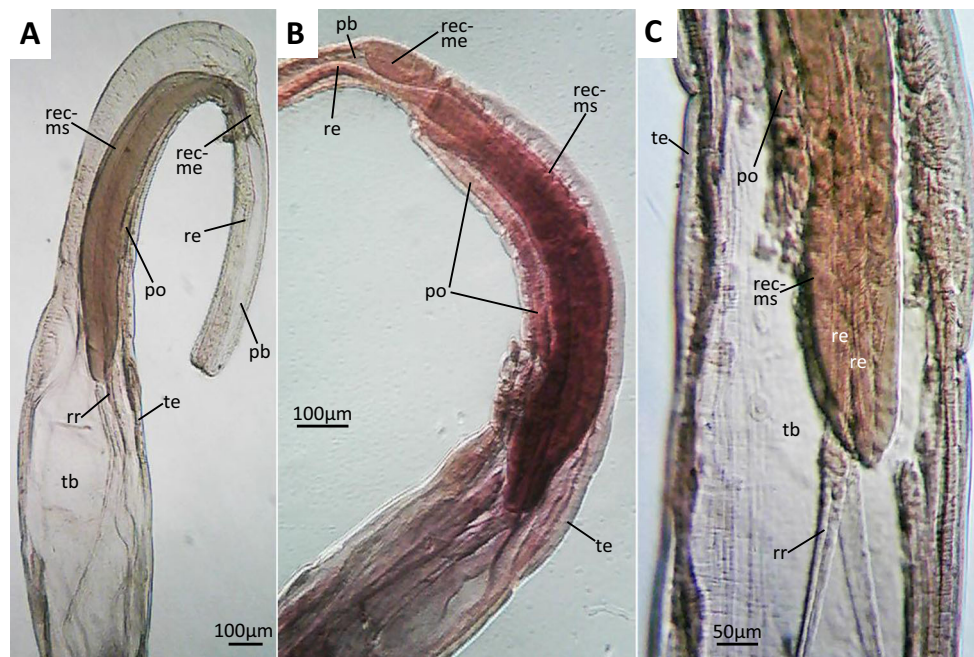
Fig. 7 LM micrographs of three representative whole mounts of *T. niloticus* (Eoacanthocephala) deposited at the Smithsonian Institution at Washington DC, USA. **a** Male, USNPC no. 1360498, storage location SH222-6-53. **b** Male, USNPC no. 1360498, storage location SH222-6-59. **c** Female, USNPC no. 1360498, storage location SH222-6-50. **a–c** The receptacle protrusor (po) is visible on only one side of the proboscis receptacle. The receptacle protrusor is discontinuous with the fibers of the receptacle retractor (rr). **a, b** The proboscis receptacle is subdivided into an anterior medullary portion (rec-me) and a posterior muscular portion (rec-ms). *pb* presomal body cavity, *tb* body cavity of the trunk, *te* tegument

clearly visible in cross-sections, the neck retractor is not always discernible in whole mounts (compare Figs. 6 and 7). Furthermore, some of the muscle's cords enclose the lemniscs (Figs. 2c, 3c, and 4a; fig. 5b in Aznar et al. 2006; also, e.g., Kaiser 1893; Kilian 1932; Herlyn 2002) which led to their alternative naming as lemnisc compressors or compressor(es) lemniscorum (Leuckart 1876; Kaiser 1893). In accordance with this nomenclature, compression of the neck retractor not only results in the withdrawal of the neck (nr and green arrowheads in Figs. 3a and 4a) but also shortens the lemniscs. This will squeeze lacunar fluid from the lemniscs into the presomal tegument which again contributes to proboscis protrusion (e.g., Kaiser 1893; Hammond 1966).

Presomal and trunk body wall musculature share the basic principle of anastomosing cords as described above for receptacle protrusor and other muscles. Both types of body wall musculature are separated from each other and, furthermore, differ in composition. The trunk body wall musculature reflects the widespread pattern of two concentrically arranged layers of cords whereby the circular musculature lies just beneath the tegument, thus enclosing the more central longitudinal cords (tc and tl in Figs. 2b, e and 3a, c; also, e.g., fig. 1 of Plate XI in Hamann 1891; fig. 2a, b in Das 1952; text-fig. 2 in Hammond 1966). In contrast, the presomal body wall musculature is mostly confined to circular cords (pc in Fig. 1a, b, d, e; see also, e.g., figs. 3 and 4 of Plate I in Baltzer 1880; fig. 12 of Plate XI in Hamann 1891; text-fig. 4 in Hammond 1966;

compare fig. 1 in Amin et al. 1993). This feature and the existence of proboscis receptacle/inner wall of the proboscis receptacle, receptacle protrusor/outer wall of proboscis receptacle, and neck retractor(s) probably represent evolutionary novelties of Acanthocephala as a whole (Table 4).

Evolutionary novelties inside Archiacanthocephala

The differentiation of longitudinal fibers in the presomal body wall musculature, besides the existence of circular strands, is most likely a secondary condition that emerged inside Archiacanthocephala. As exemplified by *M. hirudinaceus*, the condition apparently evolved in close association with a reorganization of the proboscis retractor which now is confined to the central cords (inner tube) (pc, pl in Figs. 1c, f and 3a; see also, e.g., fig. 16 in Kilian 1932; Leuckart 1876, p. 752; see also Baltzer 1880, p. 12).

M. hirudinaceus is further distinguished from the remainder species sampled, by having a binucleate muscle plate at the proboscis apex, a term derived from German "Muskelplatte" (also Ringmuskelplatte, muskulöse Platte; see Kaiser 1893; Kilian 1932; von Haffner 1943, 1950). The structure contains circular myofilaments and presumably is a derivative of the presomal circular body wall musculature (Herlyn 2002). Yet, the muscle is not specific to *M. hirudinaceus* and has been documented for several oligacanthorhynchid, moniliformid, and gigantorhynchid

Table 4 Muscles of anterior body section that presumably evolved in the stem line of Acanthocephala

Recommended terminology	Synonyms (references in main text)
Neck retractor (nr)	Retractores colli; compressor(es) lemniscorum or Lemniskenmantel when referring to cords enclosing the lemniscs
(Proboscis) receptacle (rec) when referring to Eo- and Archiacanthocephala; homologous to the inner wall of (proboscis) receptacle (iw) in Palaeacanthocephala	Vagina magno, Receptaculum, Rüsselscheide, proboscis sheath
Proboscis retractor (re), continuous with receptacle retractor (rr)	Retractor proboscides, retractores proboscides; retractores receptaculi, retractor colli
"Receptacle surrounding muscle": either as receptacle protrusor (po; as in Eo- and Archiacanthocephala) or as outer wall of (proboscis) receptacle (ow; as in Palaeacanthocephala)	For an exhaustive list of synonyms, see present Tables 1 and 2
Retinacula (rt; two of them)	

Circular (tc) and longitudinal (tl) body wall musculature of the trunk should be evolutionary older. See also table 5.5 in Miller and Dunagan (1985b) and table 1 of Herlyn (2002). (), abbreviations and alternative terminology

species where it encloses either an unpaired or a paired apical sensory or sense organ, depending on the taxon (ao, mp in Fig. 1c, f; see, also, e.g., fig. 11 of Plate X in Kaiser 1893; fig. 22 in Kilian 1932; figs. 2 and 8 in von Haffner 1943; figs. 8, 9, 10, and 11 in Gee 1987; fig. 2B in Herlyn 2002; compare fig. 313 in Meyer 1933). Even though little is known about the internal organization of Apororhynchida, they certainly have a very aberrant morphology (e.g., figs. 178 and 179 in Meyer 1933) and we are not aware of any report of a muscle plate in representatives of this group (e.g., Okulewicz and Maruszewski 1980). Additionally, taking into account the lack of complementary structure in Palae- and Eoacanthocephala (Fig. 1a, b, d, e; also, e.g., fig. 3 in Herlyn 2001; fig. 1 of Plate V, fig. 10 of Plate VII, and fig. 38 of Plate VIII in Hamann 1891), the muscle plate could have evolved in the common stem line of Moniliformida, Gigantorhynchida, and Oligacanthorhynchida (Table 5).

In Oligacanthorhynchida and Gigantorhynchida, the receptacle extends in a posterior direction beyond the position of the cerebral ganglion. This extension is obviously linked to a relative forward-relocation of the cerebral ganglion and the sites where the cords of the proboscis retractor penetrate the receptacle (rec-ms, re, rr in Figs. 1c and 3b, c; see also, e.g., fig. 1 in Bhalerao 1937; fig. 1 in von Haffner 1943; fig. 3 in Das 1952; fig. 620 in Yamaguti 1963; fig. 3 in Schmidt 1972b; fig. 11 in Schmidt 1977). Leaving aside the special organization of Apororhynchida (e.g., Okulewicz and Maruszewski 1980), the predominant alternative character state is shown by moniliformids like *M. moniliformis* (syn. *Moniliformis dubius*; fig. 144a, g in Petrochenko 1958; also Amin 1987) and by palae- and eoacanthocephalans such as *A. anguillae* and *P. ambiguus*. In the respective species, the proboscis retractor penetrates the rear pole of the proboscis receptacle (re, iw, rec-ms in Figs. 1a, b, d, e and 2c, e, f; fig. 6 in Amin et al. 2016b). Thus, the feature "posterior extension of the receptacle/forward-relocation of the cerebral ganglion" could

point to a monophyletic origin of Gigantorhynchida and Oligacanthorhynchida.

Character distribution, including the number of nuclei, further suggests that a smaller ventral portion split from the remaining proboscis receptacle inside Archiacanthocephala, possibly in the stem lineage of Oligacanthorhynchida (Fig. 1). Most authors retain the term (proboscis) receptacle for the major portion, while the smaller ventral portion is alternatively named by different investigators: Leuckart (1876, pp. 760–761) described the muscle as a flat longitudinal structure beneath the receptacle that complements the wall enclosing the presomal body cavity. Other investigators designated this muscle as Innerer Deckmuskel des Receptaculums (Kaiser 1893), ventraler Belagmuskel (Kilian 1932), vorderer und hinterer (ventraler) Rinnenmuskel (Meyer 1933), midventral receptacle muscle (Hyman 1951), primary ventral protrusors and longitudinal band (Schmidt, 1972a), midventral longitudinal receptacle muscle (Dunagan and Miller 1974), and ventral longitudinal muscle of proboscis receptacle (Wanson and Nickol 1975). Following Herlyn (2002), we refer to the respective muscle as midventral longitudinal muscle (ml in Fig. 3a, b; Table 5).

Oligacanthorhynchids are once more specific by possession of lateral groups of longitudinal muscle cords extending from the neck region to the receptacle's base (lrf in Fig. 3; see also Pl in fig. 11 of Plate X in Kaiser 1893; Prl in fig. 16 of Kilian 1932). Other investigators regarded the respective muscle cords in different oligacanthorhynchids and gigantorhynchids as protrusores receptaculi lateralis (Kaiser 1893; Kilian 1932), lateral protrusors (Hyman 1951; Schmidt 1972a), lateral receptacle protrusors (Dunagan and Miller 1974), receptacle protrusor muscles (Wanson and Nickol 1975), lateral protrusor muscles (Schmidt 1977), lateral receptacle protrusor muscle(s) (Miller and Dunagan 1985b), lateral protruser muscles (Richardson et al. 2014), and ventrolateraler rinnenförmiger Muskel (Meyer 1933).

Table 5 Muscular differentiations that probably emerged within Archiacanthocephala

Recommended terminology	Synonyms (references in main text)
Lateral receptacle flexor (lrf, two of them)	Protrusores receptaculi lateralis, lateral protrusors, lateral receptacle protrusors, receptacle protrusor muscles, lateral (receptacle) protrusor muscle(s), and lateral protruser muscles;ventrolateraler rinnenförmiger Muskel
Midventral longitudinal muscle (ml)	Innerer Deckmuskel des Receptaculums, ventraler Belagmuskel, vorderer und hinterer (ventraler) Rinnenmuskel, midventral receptacle muscle, primary ventral protrusors and longitudinal band, midventral longitudinal receptacle muscle, and ventral longitudinal muscle of proboscis receptacle
Muscle plate (mp)	Muskelplatte, Ringmuskelplatte, muskulöse Platte

See also table 5.5 in Miller and Dunagan (1985b) and table 1 of Herlyn (2002). (), abbreviations and alternative terminology

However, we found the cords of each lateral group, in *M. hirudinaceus*, being interconnected among each other by anastomoses (yellow arrowheads in Fig. 2a, b) albeit being discontinuous with their contralateral counterparts and other muscles (see also Herlyn 2002). Considering that contraction of only one of these muscles should result in a sideward flexion of the presoma relative to the trunk, we herein name these muscles lateral receptacle flexors (lrf in Figs. 1c, f and 3; Table 5). It is further worth noting that we observed a single nucleus per lateral receptacle flexor (Herlyn 2002), which distinguishes these muscles from the majority of syncytial structures discussed herein. Whether or not the lateral receptacle flexors are always separate units, their strands run centrally of the (other strands of the) receptacle protrusor alongside the proboscis receptacle as exemplified by *M. hirudinaceus* and *O. microcephala* (lrf, po, rec-ms in Fig. 3; see also, e.g., fig. 8 of Plate I in Kaiser 1893; fig. 16 in Kilian 1932; fig. 5.2a in Miller and Dunagan 1985b). In contrast, the homonymic structures of gigantorhynchids line up with the other protrusal cords, thus giving the impression of a continuous mesh-like cylinder concentrically surrounding the proboscis receptacle (e.g., figs. 1–3, 8, and 11 in Schmidt 1977). Accordingly, the oligacanthorhynchid condition could represent the derived state.

Acanthocephalan muscles: peripheral contractile filaments and central cytoplasm

As mentioned in the "Introduction" section, the strands of the (metasomal) body wall musculature in the archiacanthocephalans *O. tortuosa*, *M. hirudinaceus*, and *M. ingens* have been described as fluid-filled tubes communicating with the lacunar system of the tegument through radial canals (Miller and Dunagan 1977; see also Miller and Dunagan 1976, 1978, 1985a). However, we are not aware of any micrograph of a semi- or ultra-thin section of the metasomal or presomal body wall showing radial canals between body wall musculature and the tegumental lacunar

system. Moreover, the strands of the body wall musculature are not hollow, although they frequently look alike in LM micrographs (e.g., tl in Fig. 3c). Rather, the strands embody a peripheral layer of contractile filaments (myofilaments) covering the cytoplasm (sarcoplasm, cytoplasmic core). The pattern has been clarified by TEM analyses (e.g., fig. 2C, D, and F in Herlyn et al. 2001; see also Amin et al. 1993; Díaz Cosín 1972; Taraschewski 2000; Nikishin 2004) and also is recognizable by LM examination of suitable semi-thin sections (tc, tl in Fig. 2b, e; tc, tl, la in Figs. 3a and 4b). Thus, radial connections and tube-like appearance are most likely preparation artifacts. This seems indeed possible considering that the respective observations were made after quite a robust treatment of "living" worms which involved their inversion, injection of dye or resin, manual pressure, and disintegration of the tissue by potassium hydroxide (Miller and Dunagan 1976, 1977, 1978, 1985a).

Similar to the body wall musculature, the cords of proboscis retractor, neck retractor, and receptacle protrusor frequently appear hollow in histological preparations (e.g., Fig. 3; also Wanson and Nickol 1975, p. 76). However, this is again a consequence of a preparation-related removal of the cytoplasmic core. In all these muscles, the contractile layer widely or fully surrounds the cytoplasm, thus reflecting a circomyarian or coelomyarian organization (cf, cy in Figs. 2a, 4, and 5c, d; also, e.g., VRP and DRP in fig. 4 of Dunagan and Miller 1974; cp, ot in fig. 4 of Taraschewski and Mackenstedt 1991b; for muscular terminology, see, e.g., fig. 5.5 in Schmidt-Rhaesa 2007). The cytoplasmic core contains organelles such as nuclei and mitochondria and can further be fraught with glycogen particles as energy storage (gly in Fig. 4b, c). Receptacle protrusor and neck retractor additionally have a folded plasmalemma whereby the ridges look like villi when cut transversally (red arrowheads in Fig. 4b, c). However, the longitudinal extension of the ridges becomes apparent when the respective cords are horizontally sectioned (light-blue arrowhead in Fig. 4b). It is obvious that the folding increases the surface of the respective muscle

cords suggesting raised exchange rates with the content of the metasomal body cavity.

The basic principle of peripheral contractile filaments and central cytoplasm is principally shared by outer and inner wall of proboscis receptacle and proboscis receptacle (sensu stricto) (e.g., iw in Fig. 2d, rec-ms in Figs. 3a and 5c, d; also, e.g., M in fig. 4 of Dunagan and Miller 1974). The same is true for retinacula (see next Section), lateral receptacle flexors, and the muscle plate. In particular, the eo- and archiacanthocephalan proboscis receptacle can have a very thin cytoplasmic lining when compared to the strong contractile layer. However, this "deficit" is apparently compensated for by an additional cytoplasmic portion in front of contractile portion in eo- and archiacanthocephalans. The respective portion has been alternatively named Markraum, Markbeutel (Kaiser 1893; Kilian 1932), cytoplasmic part, or cytoplasmic finger (fig. 23A in Taraschewski 2000; fig. 14C in Taraschewski 2012). Relating to Dunagan and Miller (1974) who referred to its content as proboscis or medullary fluid, we herein distinguish an anterior medulla (rec-me in Figs. 1b, c, e, f, 3a, 4a, b, 5a, b, and 7a, b) from a posterior muscle sac in the respective taxa (rec-ms in Figs. 1b, c, e, f, 2a, b, 3, 4a, b, 5, 6, and 7; also Herlyn 2002). The medulla may have a hydrostatic function but is certainly important for the muscle's metabolism as indicated by densely packed glycogen particles (rec-me, gly in Fig. 5a, see also, e.g., Taraschewski and Mackenstedt 1991a; Taraschewski 2000; Herlyn et al. 2001; Nikishin 2004).

In summary, all the aforementioned muscles share a basic organization principle: a layer of peripheral contractile filaments encloses the cytoplasm. Still, this organization principle seems not to be evolutionarily new to Acanthocephala and rather evolved in the stem line of a more comprehensive taxon. Hence, muscle cords with a peripheral contractile layer also occur in the probable acanthocephalan sister group, Seisonidea (see, e.g., m in fig. 76A in Ahlrichs 1995; for phylogeny, see Ahlrichs 1997; Herlyn et al. 2003; Wey-Fabrizius et al. 2014; Sielaff et al. 2016). And the same is true for at least some muscles in representatives of the other two taxa traditionally ranked as classes within Rotifera, i.e., Monogononta (see, e.g., M in fig. a of Plate V in Clement 1987, M in fig. a of Plate II, and fig. 2a in Clement and Amsellem 1989) and Bdelloidea (see, e.g., fig. c of Plate VII in Clement and Amsellem 1989). Thus, the last common ancestor of Acanthocephala and traditional rotiferan taxa (Syndermata; Rotifera sensu lato) might already have possessed mainly circomyarian, partly coelomyarian, muscles.

Parareceptacle structure and receptacle protrusor: partial lack of confirmation and potential polymorphism

In none of the *P. ambiguus* specimens prepared by us, the receptacle protrusor was restricted to one side of the receptacle. Longitudinal sections and whole mounts give the impression that the receptacle protrusor is a paired structure lined up along both sides of the muscular portion of the receptacle, which we herein refer to as muscle sac (po in Figs. 4a, 5a, b, and 6). However, in its anterior section, the receptacle protrusor also has a dorsal and ventral portion (po in Fig. 1b, e), thus fully enclosing the proboscis receptacle (po in Fig. 1F of Herlyn et al. 2001). Posteriorly, the cords dissociate and eventually constitute two lateral groups that leave median parts of the receptacle surface uncovered (po in Figs. 1b and 2a; also po in fig. 1G of Herlyn et al. 2001). This organization was also noticed by Bullock and Samuel (1975) and has a noteworthy consequence: the muscle may occasionally appear one-sided just because the "other" side is not in the section or optical plane. It is also worth mentioning that, from our point of view, a one-sided PRS/receptacle protrusor cannot be concluded from LM investigation of the *P. ambiguus* whole mounts that we received from the USNPC. Notably, our sample comprised all USNPC specimens that were investigated by Amin et al. (2016a). Still, the muscle may be one-sided in some *P. ambiguus* specimens and, in *T. niloticus*, the restriction of the receptacle protrusor to a single (ventral) side might even be the rule rather than the exception (po in Fig. 7; compare Amin et al. 2016a).

Slightly oblique cross-sections along with longitudinal sections and whole mounts revealed that the cords of the receptacle protrusor terminate posteriorly at the receptacle's base in *P. ambiguus*. The muscle does not extend into the body cavity of the trunk, neither in our own preparations of *P. ambiguus* (po in Figs. 2a and 5a–c) nor in the re-investigated museum deposits of the same species (po in Fig. 6). Thus, we cannot confirm the existence of a previously reported posterior limb for the specimens investigated by us (po in Fig. 1b, e). A posterior limb was also absent in re-investigated museum material of *T. niloticus* (po in Fig. 7) and in own preparations of *M. hirudinaceus* (Figs. 1c, f, 2b, and 3a). Furthermore, the palaeacanthocephalan counterpart of the receptacle protrusor, the outer wall of proboscis receptacle (see above Section "Receptacle (...) Palaeacanthocephala"), does not extend into the metasomal body cavity beyond the posterior end of the inner wall of the proboscis receptacle; this is exemplified by slightly oblique transverse sections prepared from *A. anguillae*, *E. truttae*, *P. laevis*, and *Corynosoma* sp. specimens (ow in Figs. 1a, d and 2c–f).

Retinacula (e.g., Hamann 1891; Kaiser 1893) may in some preparations look like posterior extensions of the receptacle protrusor (compare fig. 3 in Amin et al. 2007 and fig. 1G in Herlyn et al. 2001). These muscles are paired structures occurring in Palae-, Eo-, and Archiacanthocephala that extend from the posterolateral margin of the proboscis receptacle (inner wall of receptacle) to their further posteriorly located subtegumental attachment sites, thereby stretching through the metasomal body cavity. Each retinaculum first joins and

further posteriorly encloses the ipsilateral nerve projecting from the cerebral ganglion to the body wall of the trunk (lateral posterior nerve) (rt and lpn in Fig. 2a, c, also, e.g., Kilian 1932). The strands constituting the retinacula are much smaller in diameter than those of the cords of the eo- and archiacanthocephalan receptacle protrusor. Moreover, according to our observations, retinacula and receptacle protrusor are discontinuous (rt, po, and green arrowheads in Fig. 2a, c; also fig. 1G in Herlyn et al. 2001) which coincides with their distinct functions: while contraction of the receptacle protrusor (and outer wall of proboscis receptacle) contributes to the eversion of the proboscis (Section "Receptacle (…) Palaeacanthocephala" and "Conclusions"), contraction of the retinacula folds the lateral posterior nerves when proboscis and proboscis receptacle are withdrawn and the distance between the nerves' origin (cerebral ganglion) and their projection sites (body wall) is shortened (e.g., Hammond 1966). Besides the retinacula, the receptacle retractor can occasionally have the appearance of a posterior extension of the receptacle protrusor (rr in Figs. 5b, c and 7). Finally, though the strands of the receptacle protrusor generally have a longitudinal orientation, they additionally make a diagonal shift alongside the receptacle; when these strands are cut transversely (numbers in Fig. 5c; also, e.g., figs. 5, 10 in Byrd and Kellog 1971; fig. 11 in Schmidt 1977), they are remindful of the "cellular structures" reported for the parareceptacle structure (Amin et al. 2002; also figs. 22, 37 in Amin et al. 2011).

Conclusions

As detailed above, eo- and archiacanthocephalan receptacle protrusor and palaeacanthocephalan outer wall of the proboscis receptacle are homologous structures (Tables 1 and 2). The same holds true for the proboscis receptacle in eo- and archiacanthocephalans and the inner wall of the proboscis receptacle in palaeacanthocephalans (Fig. 1). Consequently, the last common ancestor of Acanthocephala probably possessed a "receptacle surrounding muscle" (receptacle protrusor/outer wall of proboscis receptacle), besides a proboscis receptacle/inner wall of the proboscis receptacle. Disregarding the unclear structure of the ancestral receptacle surrounding muscle, it is very likely that proboscis retractor (with central and subtegumental cords), receptacle retractor, neck retractor, and retinacula collectively add up to the muscles which moved the anterior body section of the acanthocephalan stem species. All these muscles presumably evolved in the acanthocephalan stem line (Table 4). Another evolutionary novelty of acanthocephalans could be the existence of only a single layer of musculature under the presomal tegument while the possession of circular and longitudinal muscle layers under the metasomal tegument should be evolutionarily older.

Joint contraction of receptacle protrusor/outer wall of the receptacle and proboscis receptacle/inner wall of the proboscis receptacle increases the hydrostatic pressure inside the presomal body cavity which leads to proboscis eversion (Hammond 1966). Joint contraction of the presomal circular musculature could constrict the proboscis during eversion, thus facilitating the introgression into host tissue. Rotation of the everting proboscis along the body axis in species with spirally arranged receptacle protrusor strands (outer wall of receptacle) will further aid in the process of anchoring (e.g., text-fig. 1 in Hammond 1966; figs. 3, 8 in Taraschewski et al. 1989; fig. 6.1A in Smales 2015; also, e.g., Schmidt and Edmonds 1989). Proboscis eversion alternates with withdrawal by the joint action of the proboscis retractor and receptacle retractor until the worm is anchored (Hammond 1966). The different movements and positions implicate a variation of the distance between origin and projection sites of the lateral posterior nerves which is apparently compensated for by contraction and relaxation of the retinacula (Hammond 1966).

Quite obviously, the anchoring and depending on the species and circumstances (mass infection, paratenic host infection) also the perforation of the intestinal wall is usually aided by the action of hooks (e.g., Brázová et al. 2014). Secretions might also play a role in this process (Taraschewski 1989a, 2000; Taraschewski and Mackenstedt 1991a; but see Dezfuli et al. 2015). Once anchored, the neck retractor partially withdraws the evaginated proboscis along with part of the foretrunk wall. During this process, some fibers of the neck retractor compress the lemniscs so that lacunar fluid is squeezed into the presomal tegument, thus stabilizing the eversion of the proboscis (Kilian 1932; Hammond 1966). The resulting resting position implicates a furrow which is concentric with the longitudinal body axis (green arrowheads in Figs. 3a and 4a; also, e.g., fig. 3 in Taraschewski 1989b; figs. 18A, 46, 57 in Taraschewski 2000; figs. 1, 14 in Dezfuli et al. 2002). In situ preparations frequently show an additional invagination at the proboscis apex which is involved in the collection of lipids and other remnants of the damaged host tissue (fig. 1 in Taraschewski 1989a; fig. 18B in Taraschewski 2000; fig. 5.4 in Taraschewski 2015). Consequently, the presoma does not only serve as a holdfast of the adult worm but also is relevant for nutrition of these endoparasites of vertebrates.

While the aforementioned structures and their function stand for the last common ancestor of all living acanthocephalans, the muscular anatomy underwent considerable reorganization inside Archiacanthocephala (Fig. 1c, f; Table 5): a muscle plate enclosing one or two apical sensory organs represents a derived state that most likely evolved in the common stem line of Moniliformida, Gigantorhynchida, and Oligacanthocephala. The midventral longitudinal muscle presumably arose by bipartition of the proboscis receptacle, potentially in the stem line of Oligacanthorhynchida. The same is true for the pair of lateral receptacle flexors (lateral receptacle

protrusors) which according to our observations are the only cellular muscles in the anterior body section of Acanthocephala. Although more data are needed, it seems possible that the differentiation of presomal longitudinal body wall musculature within Archiacanthocephala compensates for the evolutionary loss of subtegumental strands of the proboscis retractor (outer tube). It is tempting to speculate that the evolutionary novelties within Archiacanthocephala reflect the enormous increase of body size that apparently occurred in this clade. Thus, adult worms reach and reportedly even exceed 20 cm in some moniliformid, gigantorhynchid, and oligacanthocephalan species while palae- and eoacanthocephalans are usually much smaller (e.g., Petrochenko 1956, 1958).

Within Eoacanthocephala, the receptacle protrusor possibly underwent a reduction in the number of cords up to a state reported for the PRS. If true, the character has not been fixed—at least not in *P. ambiguus*. Moreover, we found no support for a posterior extension of the cords of the receptacle protrusor (parareceptacle structure) beyond the receptacle's base, neither in our preparations nor in re-investigated museum deposits of *P. ambiguus* and *T. niloticus*. Also, we did not observe any evidence for a glandular or pumping function of the structure as occasionally discussed for the PRS. Instead, our data and that of other investigators demonstrate that the structure (receptacle protrusor/PRS) is a muscle whose cords extend from the neck region to the receptacle's base. The established name receptacle protrusor reflects that contraction of the muscle protrudes the posterior end of the proboscis receptacle (Tables 1 and 2).

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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