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ORIGINAL ARTICLE

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The musculature of the praesoma in *Macracanthorhynchus hirudinaceus* (Acanthocephala, Archiacanthocephala): re-examination and phylogenetic significance

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Abstract The endoparasitic Archiacanthocephala (Acanthocephala) consist of the Aporhynchida, Moniliformida, Gigantorhynchida and Oligacanthocephala. In the present study the organisation of the praesoma in *Macracanthorhynchus hirudinaceus* (Archiacanthocephala, Oligacanthorhynchida) was investigated by light microscopy based on series of semithin sections (5 µm) with special emphasis on the musculature. The study was carried out to substantiate the ground pattern of the Acanthocephala and to elucidate the phylogenetic relationships within the Archiacanthocephala. A comparison of the presented morphology in *M. hirudinaceus* with literature data leads to the assumption that the muscle plate and the midventral longitudinal muscle evolutionarily originated from the circular musculature of the praesoma and the receptacle, respectively. Whereas the midventral longitudinal muscle probably represents an autapomorphy of the taxon Oligacanthorhynchida, a muscle plate can be regarded as an autapomorphy of a monophylum consisting of the Moniliformida, Gigantorhynchida and Oligacanthorhynchida. Moreover, the outer wall in species with a double-walled receptacle probably corresponds to the receptacle protrusor or receptacle constrictor in species with a single-walled receptacle, and thus not only a receptacle but also an additional surrounding muscle can be assumed for the ground pattern of the Acanthocephala. For a better comparability the discussion includes a tabular survey of the synonyms used in the literature.

Introduction

Depending on the classification used, up to four taxa are distinguished within the Acanthocephala, i.e. the Palaeacanthocephala, Eoacanthocephala, Polyacanthocephala and Archiacanthocephala. The latter comprises the Aporhynchida, Moniliformida, Gigantorhynchida and Oligacanthorhynchida (Amin 1982, 1987). Whereas it is widely accepted that the Acanthocephala belong to the Syndermata Ahlrichs, 1995, the phylogeny within the taxon, especially within the Archiacanthocephala, is still far from being resolved (with respect to phylogenetic analyses based on morphological data see e.g. Herlyn 2000 and Monks 2001).

The present study was carried out to substantiate the ground pattern of the Acanthocephala, and to contribute to our knowledge of the phylogenetic relationships within the Archiacanthocephala. In particular it deals with the musculature of the praesoma in the Oligacanthorhynchida species *Macracanthorhynchus hirudinaceus* (Pallas, 1781). Although Meyer (1933) already investigated the praesoma of this species by light microscopy, his description was not unambiguous, especially with respect to the subepidermal musculature. Moreover, previous studies on the Palaeacanthocephala species *Acanthocephalus anguillae* (Müller, 1780) and the Eoacanthocephala species *Paratenuisentis ambiguus* (Van Cleave, 1921) (see Herlyn and Ehlers 2001; Herlyn et al. 2001) suggest that several functional entities described by Dunagan and Miller (1974) in *M. hirudinaceus* belong to greater morphological units. Both, the ambiguities in previous descriptions as well as the suggestions based on findings in other Acanthocephala species induced the present light microscopic re-examination of the praesoma in *M. hirudinaceus*.

Materials and methods

Four frozen adults of *M. hirudinaceus* were provided by Professor Dr. Taraschewski (University of Karlsruhe, Germany). Subsequently, the specimens were defrosted, fixed in 4% formalin and postfixed in Bouin for 3 days (room temperature). Thereafter, they were dehydrated in a graded ethanol series and embedded in Paraplast (Roth) with butanol and methyl benzoate for intermedia (room temperature). Series of cross- and longitudinal semithin sections (5 µm) were cut with steel knives on a Reichert Jung microtome, stained with aniline blue, orange G and nuclear red (Romeis 1989), and examined under an Axiophot (Zeiss) light

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Table 1 Nomenclature of the musculature (in alphabetical order)

Terminology (abbreviations in brackets)	Semantic derivations	Synonyms
Cytoplasmic cone of the muscle plate (*cc*)	–	"Apical sensory cone" (Dunagan and Bozzola 1992)
Lateral receptacle flexor (*lrf*)	Derived from the term "lateral receptacle *protrusor*" Hyman (1951) used in an illustration of *Oligacanthorhynchus microcephala*; with respect to the probable flexing function, and for a clearer distinction from the "receptacle *protrusor*" termed "lateral receptacle *flexor*" in the present study	Protrusor receptaculi lateralis (Kaiser 1893; Kilian 1932), ventrolateraler rinnenförmiger Muskel (Meyer 1933), lateral protrusors (Schmidt 1972), receptacle protrusor muscle (Wanson and Nickol 1975)
Circular and longitudinal musculature of the praesoma (*pc*, *pl*)	Derived from the "circular and longitudinal muscle layer of the proboscis" Nickol and Holloway (1968) described in *Corynosoma hamanni* (Linstow, 1892); note: the longitudinal subtegumental muscle layer of the proboscis described in several Palaeacanthocephala and Eoacanthocephala species probably refers to the outer tube of the complex proboscis retractor (see Taraschewski 2000: Fig. 62A; Herlyn and Ehlers 2001; Herlyn et al. 2001)	Rüsselmuskulatur (Hamann 1891), Sarkolemmaring der Rüsselscheide (Kaiser 1893), erstes Muskelsegment der Körperwand (Meyer 1933)
Circular and longitudinal musculature of the trunk (*tc*, *tl*)	Derived from the circular and longitudinal body wall musculature (of the trunk) described by Hammond (1967) in *Acanthocephalus ranae* (Schrank, 1788)	Ringmuskelschicht und Längsmuskelschicht des Rumpfes (Meyer 1933), circular muscle layer (of the proboscis) (Hyman 1951), subtegumental musculature (of the metasoma) (Taraschewski 2000)
Medulla (*me*)	Anterior non-contractile part of the receptacle; derived from Dunagan and Miller (1974), who described a "medullary fluid" in its inside in *Macracanthorhynchus hirudinaceus*	Markraum der Rüsselscheide (Kaiser 1893), Markbeutel des Receptaculi proboscidis (Kilian 1932), Receptaculum-Plasma (Meyer 1933), cytoplasmic part of the proboscis receptacle wall (Taraschewski 2000)
Midventral longitudinal muscle (*ml*)	Adopted from Hyman (1951) who used the term in an illustration of *O. microcephala*	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 1972), ventral receptacle muscle of proboscis receptacle (Wanson and Nickol 1975)
Muscle plate (*mp*)	Derived from Haffner (1943) who described a "Muskelplatte" in *Oligacanthorhynchus thumbi*	Ringmuskelplatte (Kaiser 1893), muskulöse Platte (Kilian 1932)
Muscle sac (*ms*)	Posterior contractile part of the receptacle; term that comprises the probable homologous tissues inner wall (e.g. Taraschewski 2000) in species with a double-walled receptacle and receptacle wall muscle (Dunagan and Miller 1974) in species with a single-walled receptacle	Innere Rüsselscheidenwandung (Hamann 1891), innere Rüsselscheide (Kaiser 1893), Receptaculum-Muskelschicht (Meyer 1933), muscular wall (Schmidt 1972), receptacle wall (Hyman 1951, Wanson and Nickol 1975)
Pad syncytium (*b*, *d*, *p*)	Derived from the German term "Polsterring" used by Kilian (1932) for the anterior branches of this syncytium in *O. microcephala*	–
Proboscis retractor (*re*)	Adopted from Hyman (1951) who used the term in an illustration of *Acanthocephalus*; in the present definition the term comprises "proboscis retractor (part 1, 2)", "dorsal cone invertor" and "ventral cone invertor" described by Dunagan and Miller (1974) in *M. hirudinaceus*	Retraktor des Rüssels (Hamann 1891), Retractor proboscidis (Kaiser 1893; Kilian 1932), Invaginatormuskel (Meyer 1933), primary retractor muscles (Schmidt 1972), invertor muscle (Nickol and Holloway 1968), proboscis invertor (Wanson and Nickol 1975)
Receptacle protrusor (*po*)	Derived from Dunagan and Miller (1974) who described a dorsal and a ventral "receptacle protrusor" in *M. hirudinaceus*, termed "proboscis constrictor" when its contractile filaments are circularly orientated (see Fig. 4 in the present study)	Äußere Rüsselscheidenwandung (Hamann 1891), Protrusor receptaculi dorsalis (et) Protrusor receptaculi ventralis (Kaiser 1893; Kilian 1932), dorsal and ventral receptacle protrusors (Hyman 1951), primary dorsal and ventral protrusors (Schmidt 1972), äußere Rüsselscheide (Kaiser 1893), Receptaculumprotraktor (Herlyn 2000)

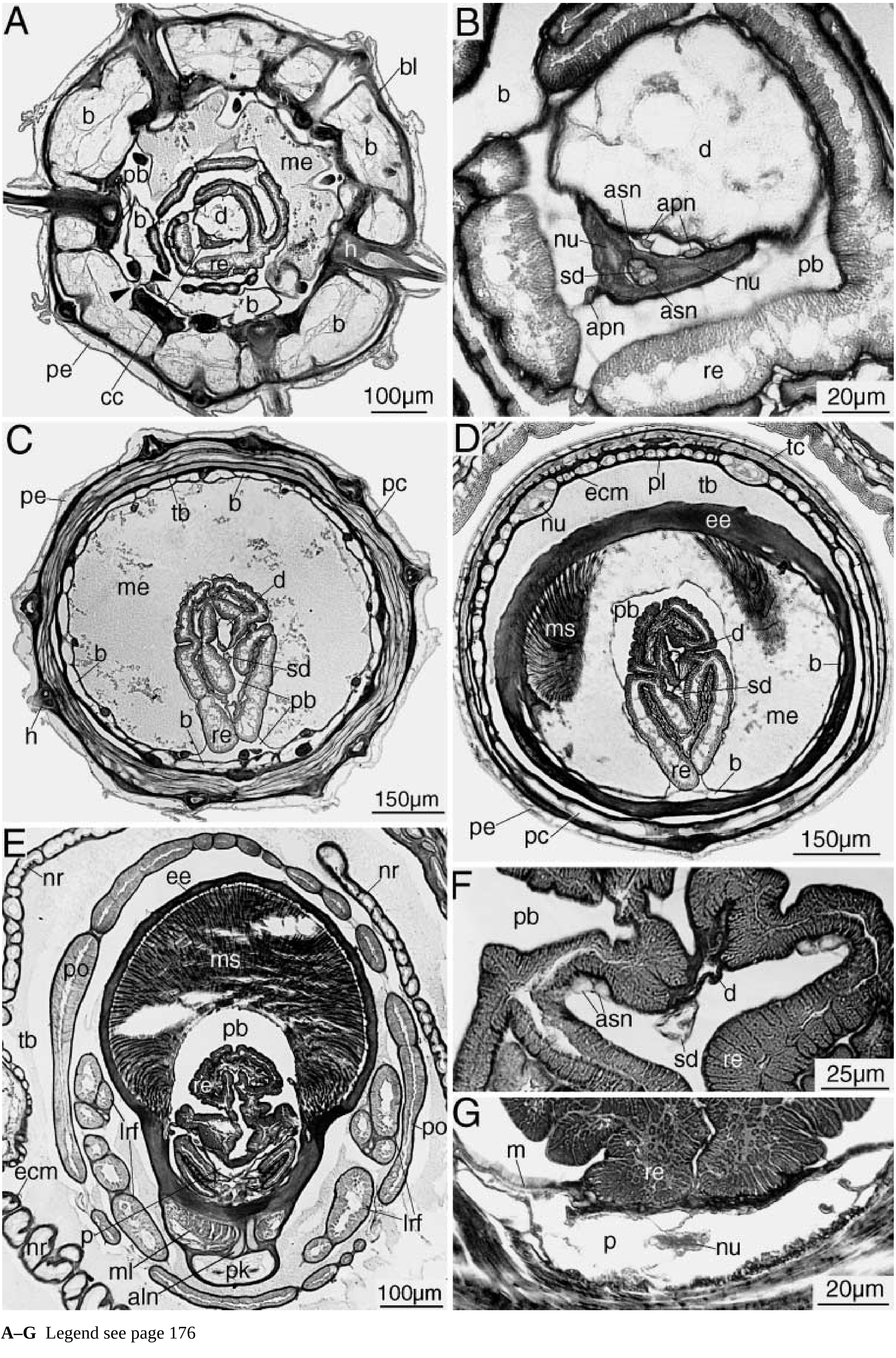


Fig. 1A–G Legend see page 176

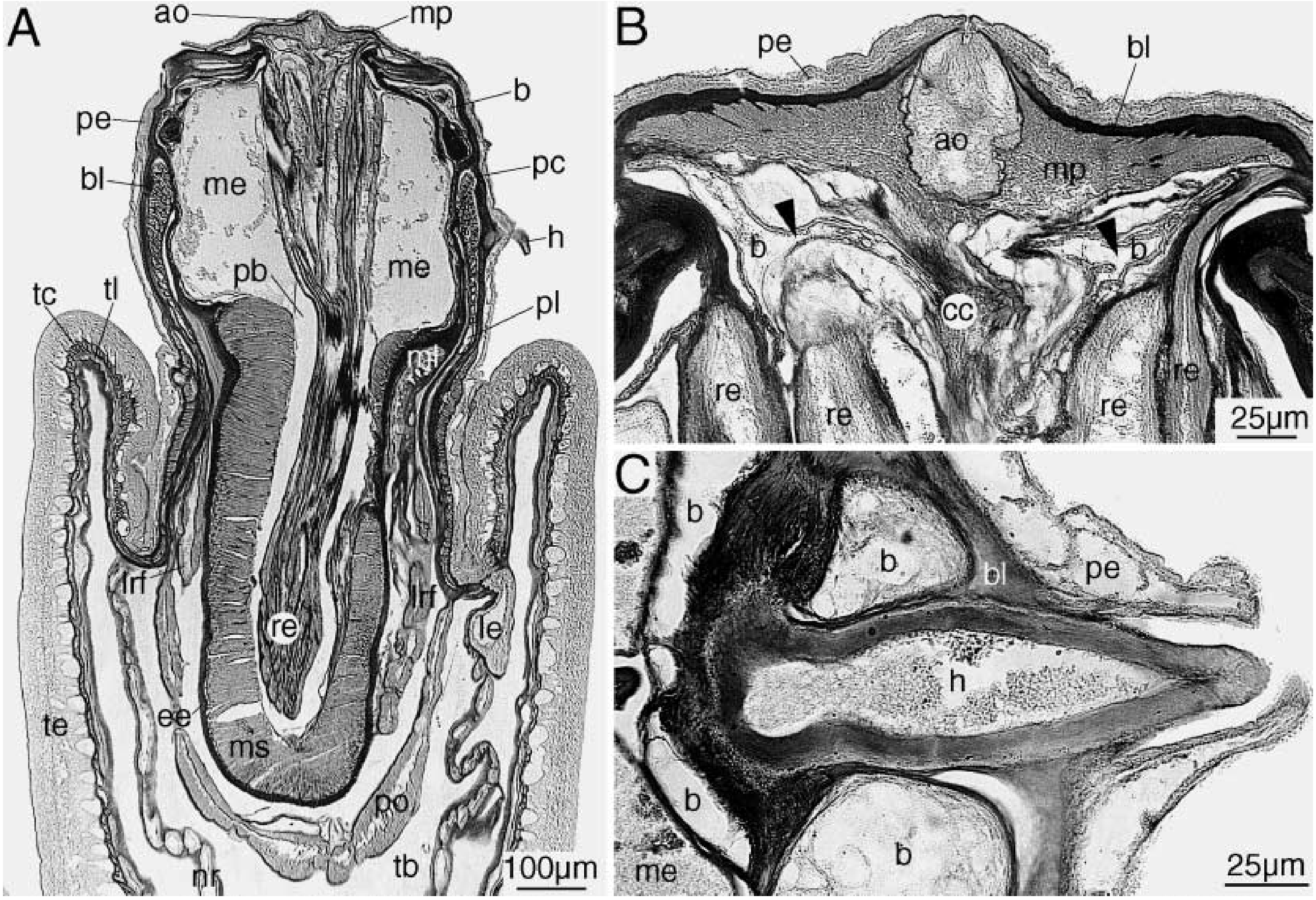


Fig. 2A–C *M. hirudinaceus*. Light micrographs of two longitudinal sections (**A**, **B**) and one cross-section (**C**) through the praesoma (5 µm). **A** Slightly oblique section giving an overview of the praesoma. **B** The muscle plate surrounds the apical sense organ. **C** The hooks of the anterior hook circles basally are embedded into the branches of the pad syncytium. *ao* Apical sense organ, *b* branch of the pad syncytium, *bl* basal lamina, *cc* cytoplasmic cone of the muscle plate, *ee* ecm envelope of the muscle sac, *h* hook, *le* lemniscus, *lrf* lateral receptacle flexor, *me* medulla, *ml* midventral longitudinal muscle, *mp* muscle plate, *ms* muscle sac, *nr* neck retractor, *pb* body cavity of the praesoma, *pc* circular musculature of the praesoma, *pe* epidermis of the praesoma, *pl* longitudinal musculature of the praesoma, *po* receptacle protrusor, *re* proboscis retractor, *tb* body cavity of the trunk, *tc* circular musculature of the trunk, *te* epidermis of the trunk, *tl* longitudinal musculature of the trunk. *Arrowheads* in **B** point to ramifications of the pad syncytium

◀ **Fig. 1A–G** *Macracanthorhynchus hirudinaceus*. Light micrographs of cross-sections (5 µm) through the praesoma; for the sectioning planes see Fig. 3. **A** Branches of the pad syncytium. **B** Enlargement of **A**; nerves accompany the cytoplasmic cone of the muscle plate. **C** The medulla widely fills the proboscis lumen. **D** Transition of the circular musculature of the praesoma into the longitudinal musculature of the praesoma. **E** Arrangement of the muscles around the muscle sac. **F** Enlargement of the ducts of pad syncytium and supporting cell. **G** Perikaryon of the pad syncytium. *aln* Anterior lateral nerve, *apn* apical proboscis nerve, *asn* anterior sensory nerve, *b* branch of the pad syncytium, *bl* basal lamina, *cc* cytoplasmic cone of the muscle plate, *d* duct of the pad syncytium, *ecm* extracellular matrix, *ee* ecm envelope of the muscle sac, *h* hook, *lrf* lateral receptacle flexor, *m* membrane of the perikaryon of the pad syncytium, *me* medulla, *ml* midventral longitudinal muscle, *ms* muscle sac, *nr* neck retractor, *nu* nucleus, *p* perikaryon of the pad syncytium, *pb* body cavity of the praesoma, *pc* circular musculature of the praesoma, *pe* epidermis of the praesoma, *pk* perikaryon of the sensory support cell, *pl* longitudinal musculature of the praesoma, *po* receptacle protrusor, *re* proboscis retractor, *sd* sensory support cell duct, *tb* body cavity of the trunk, *tc* circular musculature of the trunk. *Arrowheads* in **A** indicate connections between branches of the pad syncytium

microscope. The terminology of the neuronal structures (nerves, sense organs, sensory support cell) has been adopted from Dunagan and Miller (1983) and Miller and Dunagan (1985). Regarding the musculature, the nomenclature used in the present study is listed in Table 1 (for a comparison see also Miller and Dunagan 1985: Table 5.5).

Results

Subepidermal musculature, muscle plate and proboscis retractor

In *M. hirudinaceus* the subepidermal musculature of the praesoma can be subdivided into two sections. The anterior section consists of anastomosing circular muscle fibres and is here referred to as circular musculature of the praesoma. In contrast, the posterior section is composed of anastomosing longitudinal muscle fibres and consequently is termed here longitudinal musculature of

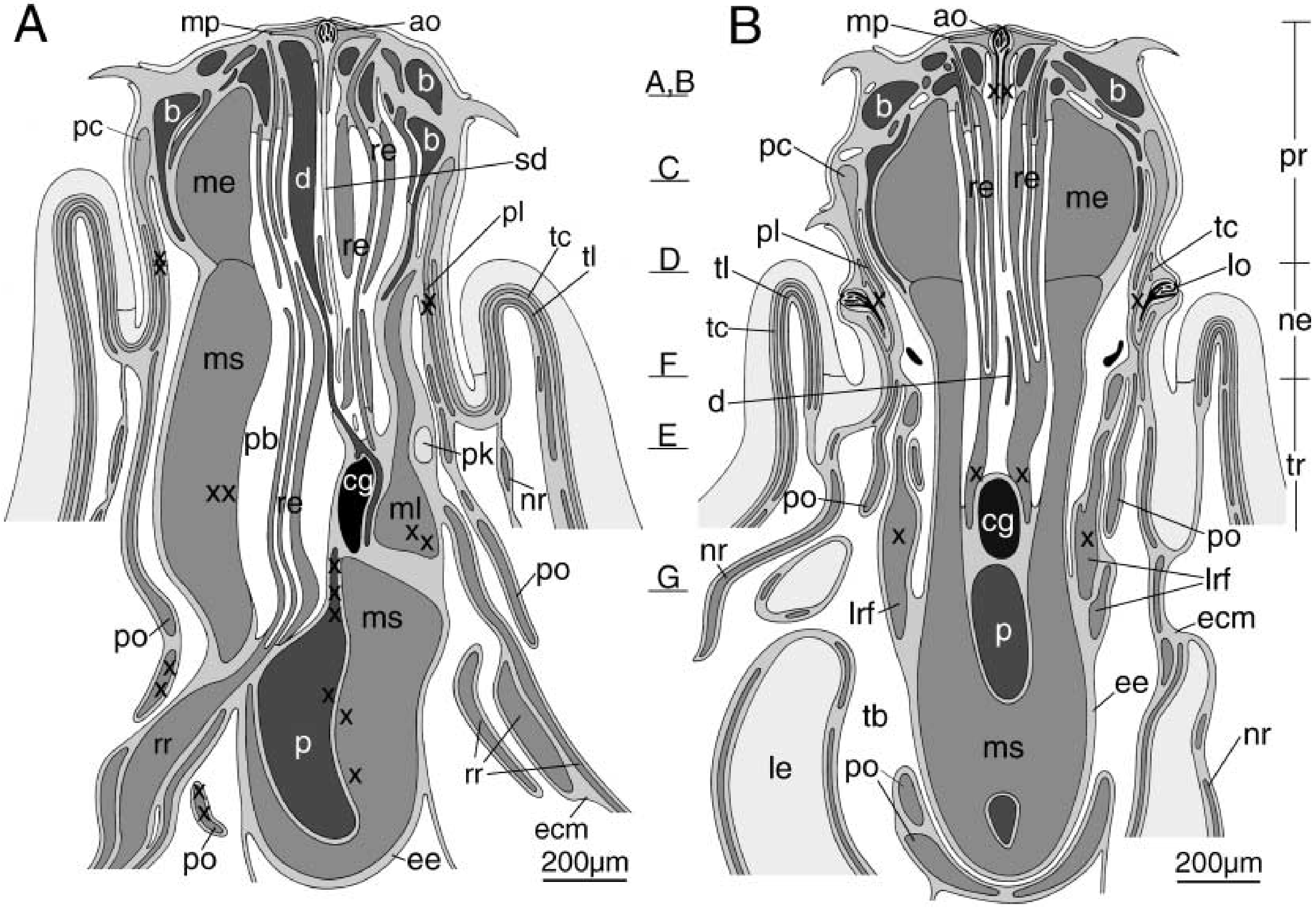


Fig. 3A, B *M. hirudinaceus*. Semi-schematic drawings of a longitudinal (**A**) and a horizontal section (**B**) reconstructed on the basis of series of cross-sections (5 µm); every *x* corresponds to a nucleus. *ao* Apical sense organ, *b* branch of the pad syncytium, *cg* cerebral ganglion, *d* duct of the pad syncytium, *ecm* extracellular matrix, *ee* ecm envelope of the muscle sac, *le* lemniscus, *lo* lateral sense organ, *lrf* lateral receptacle flexor, *me* medulla, *ml* midventral longitudinal muscle, *mp* muscle plate, *ms* muscle sac, *ne* neck, *nr* neck retractor, *p* perikaryon of the pad syncytium, *pb* body cavity of the praesoma, *pc* circular musculature of the praesoma, *pl* longitudinal musculature of the praesoma, *pk* perikaryon of the sensory support cell, *po* receptacle protrusor, *pr* proboscis, *re* proboscis retractor, *rr* receptacle retractor, *sd* sensory support cell duct, *tb* body cavity of the trunk, *tc* circular musculature of the trunk, *tl* longitudinal musculature of the trunk, *tr* trunk. *Lines lettered with A–G* indicate the sectioning planes of the micrographs in Fig. 1

the praesoma (Figs. 2A, 3; Table 1). Anteriorly, the circular musculature of the praesoma measures up to 50 µm in diameter. Posteriorly, it decreases to about 20 µm in diameter (Fig. 1C, D). At the level of the proboscis–neck transition it merges rectangularly with the longitudinal musculature of the praesoma that houses the four nuclei of this bipartite syncytium (Figs. 1D, 3A).

In addition to the longitudinal musculature of the praesoma the circular musculature of the trunk contributes to the formation of the neck body wall (Fig. 3). Its muscle fibres are located peripherally to the longitudinal musculature of the praesoma (Fig. 1D). Within the praesoma the circular musculature of the trunk exhibits two nuclei, one beneath each lateral sense organ (Fig. 3B). In contrast to this, the longitudinal musculature of the trunk does not extend into the praesoma (Fig. 3; Table 1).

In the proboscis apex a muscular differentiation, here referred to as muscle plate, of about 270 µm diameter surrounds the apical sense organ (Figs. 2A, B, 3; Table 1). Posteriorly, the muscle plate prolongs into a binucleate cytoplasmic cone that appears crescent-shaped to triangular in cross-sections. Centrally, the muscle plate and its cytoplasmic cone form a hole which allows the anterior sensory nerves and a duct of the sensory support cell to pass towards the apical sense organ (Fig. 1A, B). Overall, the muscle plate measures almost 205 µm in longitudinal extension.

Beneath the outer rim of the muscle plate, the proboscis retractor inserts at the apical proboscis body wall (Figs. 2B, 3; Table 1). The muscle fibres of the proboscis retractor are interconnected by anastomoses, thus forming a morphological coherent syncytium (Fig. 1B, F). Anterior to the cerebral ganglion the proboscis retractor ramifies into a dorsal and a ventral branch that both penetrate the receptacle separately and give way to the receptacle retractor. Within the praesoma the proboscis retractor bears two nuclei (Fig. 3B).

Receptacle and proximate muscles

The receptacle consists of an anterior cytoplasmic part, here referred to as medulla, and a posterior, mainly contractile, part that projects into the trunk, here, for simplicity, designated as muscle sac (Figs. 2A, 3; Table 1). The cytoplasmic medulla widely fills the lumen of the proboscis except for a central canal that allows the proboscis retractor to pass (Figs. 1C, D, 2A). At the posterior end of the proboscis the medulla merges with the contractile muscle sac (Fig. 1D). The narrow non-contractile inner lining of the muscle sac houses the four nuclei of the receptacle, one dorsal pair and one ventral pair (Fig. 3A). Ventrally, the muscle sac leaves a longitudinal gap that contains the midventral longitudinal muscle (Figs. 2A, 3A). In principal, the midventral longitudinal muscle represents a simple longitudinal muscle fibre with a strongly folded peripheral layer of contractile filaments. It continuously extends from the proboscis–neck transition to its posterior insertion ventral to the cerebral ganglion, interrupted only by two neuronal fibres of the anterior lateral nerve (Fig. 1E). The two nuclei of the midventral longitudinal muscle are located near its posterior end within the cytoplasmic core (Fig. 3A).

The receptacle protrusor and the pairwise arranged lateral receptacle flexors surround the muscle sac of the receptacle (Figs. 1E, 2A, 3; Table 1). As in the proboscis retractor, the receptacle protrusor and the lateral receptacle flexors consist of interconnected circomyar muscle fibres. Whereas the lateral receptacle flexors are cellular formations, the receptacle protrusor represents a syncytial structure with two pairs of nuclei (Fig. 3).

Pad syncytium

The posterior one-third of the receptacle surrounds the perikaryon of a structure which in this paper will be called pad syncytium (Table 1). The perikaryon contains four nuclei and measures 560 µm in length and 200 µm in diameter (Figs. 1G, 3). Anteriorly, a duct of about 20 µm in height stretches from the perikaryon, turns dorsally and penetrates the proboscis retractor. Towards the proboscis apex the duct constantly broadens (Figs. 1, 3). Proximal to the muscle plate it enters the subepidermal extracellular matrix and ramifies into branches of different sizes that basally enclose the hooks of the anterior three hook circles. Posteriorly, the decreasing branches envelope the medulla (Figs. 1A, 2C, 3).

Discussion

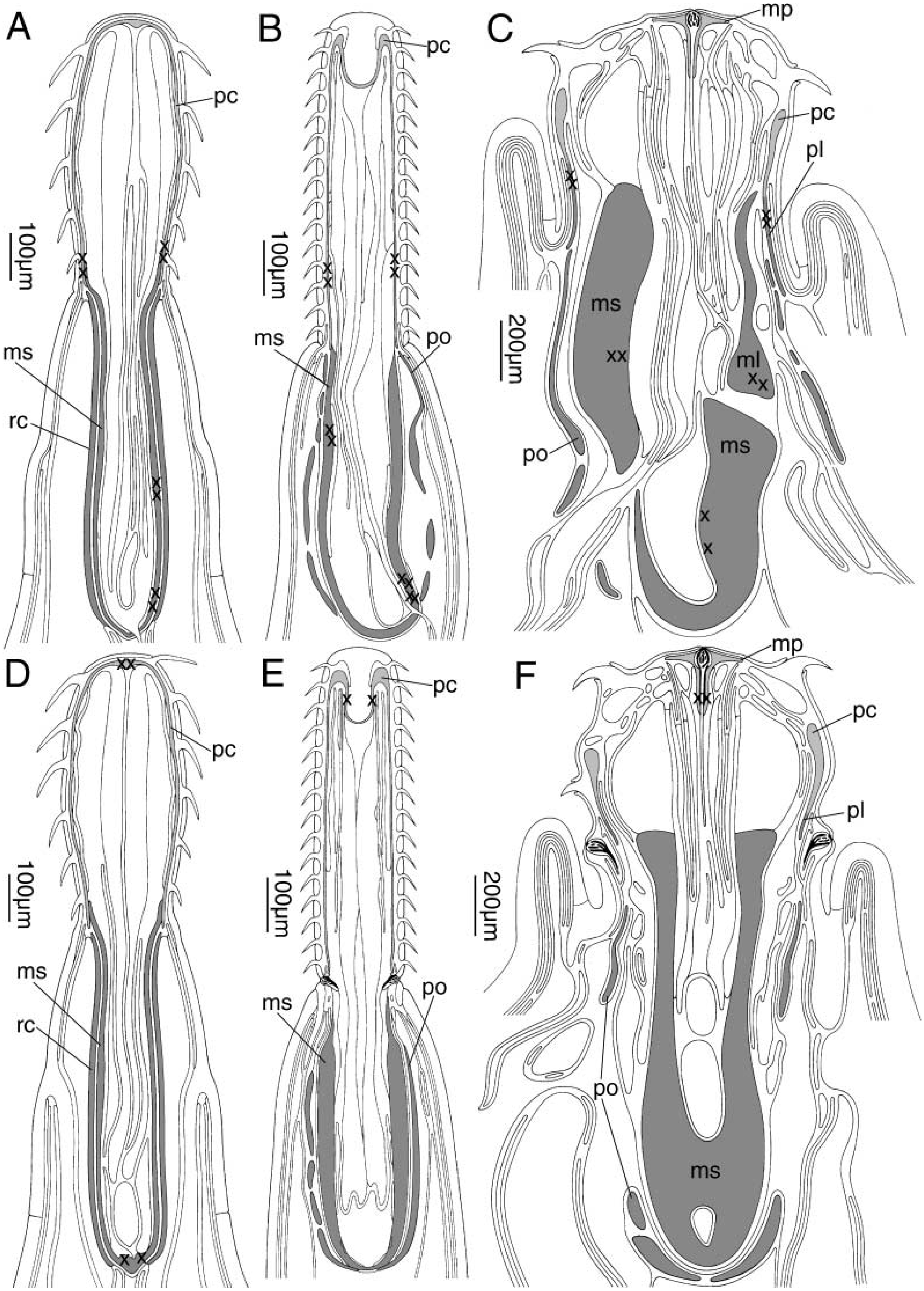
The presented findings confirm the suggestion that several structures described by Dunagan and Miller (1974) in *M. hirudinaceus* belong to greater morphological entities, a phenomenon that Van Cleave and Bullock (1950) discussed already for the musculature of the praesoma in *Neoechinorhynchus emydis* (Leidy, 1851). Moreover, for some structures no or at least no English terms have been established so far. Both necessitate a nomenclature that partly differs from the terminology used in the literature. To warrant the comparability of the nomenclature used in the present study with the descriptions in the literature, Table 1 has been added (see also Miller and Dunagan 1985: Table 5.5).

Apparently, in all Acanthocephala species the receptacle is surrounded by an additional muscle (termed receptacle protrusor, receptacle constrictor or outer wall) (see, for example, Kilian 1932; Nickol and Holloway 1968: Fig. 9; Wanson and Nickol 1975; Fig. 4 in the present study). Thus, the distinction between the character states double-walled receptacle and single-walled receptacle (see Amin 1982, 1987; Monks 2001) probably refers to homologous tissues, a conclusion that, however, is doubted by other authors (for example, Schmidt 1972). From the assumed homology it follows that not only a receptacle but also an additional muscle that surrounds the receptacle, more exactly the muscle sac of the receptacle, belong to the ground pattern of the Acanthocephala. For the time being, however, it remains unresolved whether this “surrounding muscle” was differentiated as a receptacle constrictor (with circular contractile filaments) or as a receptacle protrusor (with more or less longitudinally orientated contractile fibres) in the stem species of the Acanthocephala.

As it could be shown the morphology of the subepidermal musculature of the praesoma in *M. hirudinaceus* is not so complex as previously has been reported: in contrast to Meyer's (1933) description the circular musculature of the praesoma (“erstes Muskelsegment der Körperwand” in his terminology) does not fuse with the circular musculature of the trunk (“Ringmuskelschicht des Rumpfes”). Instead, the subepidermal musculature of the praesoma is entirely separated from that of the trunk and consequently a lateral cross-texture (“laterale Kreuztextur”) as postulated by Meyer (1933) does not exist in *M. hirudinaceus*.

Regarding the number and position of the nuclei of subepidermal musculature and muscle plate, remarkable congruencies are to be found between *M. hirudinaceus* on the one hand and *P. ambiguus* (Eoacanthocephala) and *A. anguillae* (Palaeacanthocephala) on the other hand. Constantly, there are three pairs of nuclei with fairly similar positions (Fig. 4), one ventral pair, one dorsal

Fig. 4 The praesomata of *Acanthocephalus anguillae*, a representative with a so-called double-walled receptacle (**A**, **D**), and of *Paratenuisentis ambiguus* (**B**, **E**) and *M. hirudinaceus* (**C**, **F**), both representatives with a so-called single-walled receptacle. Semi-schematic drawings of longitudinal (**A–C**) and horizontal sections (**D–F**) reconstructed on the basis of series of cross-sections (5 µm). Probable homologous tissues are highlighted with *grey*, every *x* corresponds to a nucleus. *ms* Muscle sac (= inner wall or receptacle wall muscle), *ml* midventral longitudinal muscle, *mp* muscle plate, *pc* circular musculature of the praesoma, *pl* longitudinal musculature of the praesoma, *po* receptacle protrusor, *rc* receptacle constrictor (= outer wall). [**A**, **D** and **B**, **E** modified after Herlyn and Ehlers (2001) and Herlyn et al. (2001), respectively] ▶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pair and one apical pair, the latter being located within an apical cytoplasmic swelling in *A. anguillae*, lateral to the epidermis cone in *P. ambiguus* and within the cytoplasmic cone of the muscle plate in *M. hirudinaceus* (see also Herlyn 2001). These anterior two nuclei can also be seen in a drawing of the epidermis cone in the Eoacanthocephala species *N. emydis* (Van Cleave and Bullock 1950: Fig. 4 *pn*). Apart from this, Meyer [1933: Fig. 313, *ApSP(2 K)*] and Gee (1987: Figs. 9, 10) confirm the binucleate character of the muscle plate in *M. hirudinaceus*. Furthermore, a binucleate muscle plate is known from the Oligacanthorhynchida species *Oligacanthorhynchus microcephala* (Rudolphi, 1819) and *Oligacanthorhynchus thumbi* Haffner, 1939, from the Gigantorhynchida species *Gigantorhynchus echinodiscus* (Diesing, 1851) and from the Moniliformida species *Moniliformis moniliformis* (Bremser, 1811) (see Kilian 1932: Fig. 22; Haffner 1943: Figs. 2, 8; Gee 1987: Fig. 8). Provided that the nuclei are homologous, the binucleate muscle plate of the Oligacanthorhynchida, Gigantorhynchida and Moniliformida corresponds to the anterior section of the circular musculature of the praesoma in species such as *N. emydis*, *P. ambiguus* and *A. anguillae*. Since a muscle plate seems to be absent outside the Moniliformida, Gigantorhynchida and Oligacanthorhynchida the character probably represents an autapomorphy of a monophylum comprising these three Archiacanthocephala taxa. This in turn suggests that six nuclei can be assumed for the circular musculature of the praesoma in the ground pattern of the Acanthocephala, a pattern that is to be found in species such as *P. ambiguus* and *A. anguillae* (Fig. 4).

The contractile ability of the muscle plate assumed on the basis of light microscope studies (Kaiser 1893; Kilian 1932; Haffner 1943) meanwhile has been corroborated by TEM studies that show a peripheral layer of contractile filaments (Dunagan and Bozzola 1989: Figs. 3, 6 *za*). It is probable that the contraction of the muscle plate causes an elevation of the apical sensory organ(s) (in some taxa the proboscis apex bears two apical sensory organs), as it can be seen in several SEM micrographs of the proboscis tip (see, for example, Zhao et al. 1990: Fig. 3).

Similarly, the midventral longitudinal muscle can be derived from the ventral part of the receptacle. In accordance with the present findings in *M. hirudinaceus*, Kilian (1932) found one pair of nuclei within the midventral longitudinal muscle and two pairs within the receptacle of *O. microcephala*. On the other hand, in Acanthocephala species without a midventral longitudinal muscle such as *N. emydis*, *A. anguillae* and *P. ambiguus*, the receptacle in general houses three pairs of nuclei (Van Cleave and Bullock 1950; Fig. 4A, B, D in the present study). Apart from *M. hirudinaceus* and *O. microcephala*, a midventral longitudinal muscle is known exceptionally in other representatives of the Oligacanthorhynchida such as *O. thumbi* (Haffner 1943: Fig. 4), *Oligacanthorhynchus taenioides* (Diesing,1851) (Meyer 1933: Fig. 207), *Pachysentis ehrenbergi* Meyer, 1931, *Pachysentis canicola* Meyer, 1931, *Pachysentis procumbens* Meyer, 1931 (Meyer 1933: Figs. 257a, 260, 262) and *Prosthenorchis elegans* (Diesing, 1851) (Wanson and Nickol 1975: Fig. 11). Again, the number and position of the nuclei leads to the possible evolutionary origin of one of the tissues: probably the binucleate midventral longitudinal muscle of the Oligacanthorhynchida corresponds to the ventral part of the receptacle in Acanthocephala species without a midventral longitudinal muscle (Fig. 4). The absence of a midventral longitudinal muscle outside the Oligacanthorhynchida suggests that the character represents an autapomorphy of the taxon, an assumption that implicates six receptacle nuclei in the ground pattern of the Acanthocephala.

As far as I know, there is only one reference relating to a pad syncytium in species other than *M. hirudinaceus*. Kilian (1932) described [“Polsterring der Rüsselhakenwurzeln”, “reticuläre(s) (...) Protoplasma” the anterior branches as well as the perikaryon of a homologous structure in *O. microcephala*]. In so far, the present data are restricted to two representatives of the Oligacanthorhynchida. However, the data are too insufficient to draw any phylogenetic conclusions. Regarding the function, a contractile ability seems probable at least for the anterior branches of the pad syncytium since TEM micrographs of *M. hirudinaceus* (Taraschewski 2000: Fig. 40A) reveal a thin layer of contractile filaments in their periphery. On the other hand, the bloated appearance of the branches points to a possible function as pads that compensate the deflections of the anterior hooks (see Fig. 2C in the present study).

In conclusion:

1. In *M. hirudinaceus* the circular musculature of the praesoma rectangularly merges with the longitudinal musculature of the praesoma. In so far, the subepidermal musculature of the praesoma represents a bipartite syncytium. Although the circular musculature of the trunk extends into the neck the two syncytia do not fuse.
2. The character states “single-walled receptacle” and “double-walled receptacle” refer to homologous tissues (receptacle and “surrounding muscle”). In so far, not only a receptacle but also a “surrounding muscle” belong to the ground pattern of the Acanthocephala. Yet, it remains unresolved how this “surrounding muscle” was differentiated in the stem species of the Acanthocephala (proboscis protractor vs proboscis constrictor).
3. A binucleate muscle plate can be assumed as an autapomorphy of a monophylum comprising the Oligacanthorhynchida, Gigantorhynchida and Moniliformida. Probably, the muscle plate has its evolutionary origin in the anterior section of the circular musculature of the praesoma. In the stem species of the Acanthocephala, the circular musculature of the praesoma probably housed six nuclei.

4. Presumably, the binucleate ventral longitudinal receptacle muscle represents an autapomorphy of the Oligacanthorhynchida. The midventral longitudinal muscle probably originated evolutionarily from the ventral part of the receptacle for which in the ground pattern of the Acanthocephala altogether six nuclei can be assumed.
5. Hitherto, a pad syncytium is known only from representatives of the Oligacanthorhynchida (*M. hirudinaceus*, *O. microcephala*). However, it appears premature to draw any phylogenetic conclusions from the restricted data.

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