Morphology of ctenostome bryozoans: 1. *Arachnidium fibrosum*

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Abstract
The morphology of ctenostome bryozoans remains little investigated with only few species having been subject to more detailed studies. From all the seven main different superfamilies, only few representatives have been studied. The superfamily Arachnidioida has particularly been neglected concerning detailed morphological and histological details. So far, not a single analysis specifically studied a representative of the family Arachnidiidae. *Arachnidium*-like forms have, however, often been regarded as potential cheilostome ancestors, the most successful group of bryozoans to date. The lack of any morphological data on this family called for a detailed investigation of one of its representatives. Hence, we analysed the general morphology and histology of *Arachnidium fibrosum*. Most striking morphological features previously unrecognized are a cardiac constrictor, previously almost unknown in the family, a single pair of apertural muscles consisting of proximal parieto-diaphragmatic and distal parieto-vestibular muscles, six pairs of duplicature bands, a lophophoral anus and retractor muscles attaching to the foregut. Although comparative data are limited, there seem to be two distinct different clades of arachnidid ctenostomes that are characterized by their aperture and details of gut morphology. Further analysis of additional arachnidioidian species are required to confirm this.

Keywords
Arachnidioida, cardiac constrictor, Gymnolaemata, gymnolaemate evolution

1 | INTRODUCTION

Bryozoans are a phylum of mostly colonial, sessile suspension feeders. Over 6,000 recent species are currently recognized. Colonies are composed of iterative, clonal modules termed zooids. The latter consist of a body wall, the cystid, that can be reinforced by chitinous, gelatinous or calcareous modifications, and the polypide, which essentially comprises the soft-tissue parts. The latter includes the ciliated tentacle crown or lophophore, the digestive tract and some other associated tissues (Mukai, Terakado, & Reed, 1997; Schwaha, 2020a).

Bryozoans are classified into two main clades, Phylactolaemata and Myolaemata (Schwaha, Ostrovsky, & Wanninger, 2020). The latter comprise Stenolaemata, which present the sister group of the Gymnolaemata. Gymnolaemates are the largest group of bryozoans that are separated into the small, uncalcified taxon of ctenostomes and the large and most dominant and calcified Cheilostomata (Taylor & Waeschenbach, 2015). Ctenostome bryozoans are paraphyletic and comprise about ~350 species that are mainly characterized as gymnolaemates without mineralized (calcified) cuticle. The colonies show a high variation in zooidal form and colony composition, which ranges, for example, from dense encrusters, erect stolonal ones, solitary or even endolithic forms (Schwaha, 2020b).

Ctenostome bryozoans lack any published modern phylogenetic analysis and all previous classifications and reconstructions are mostly based on colony growth forms and other externally distinguishable characters (see Jebram, 1973, 1986; Todd, 2000). A few characters of soft tissue morphology such as gut morphology or tentacle amount have been previously used for systematic and phylogenetic inferences.
The value of soft tissue morphological characters was recently evaluated and estimated to be significant for such research purposes (Schwaha et al., 2020). This study is the first of a series of studies emphasizing on soft tissue morphology of ctenostome bryozoans to start with the species *Arachnidium fibrosum*.

Traditional ctenostome systematics uses seven main superfamilies. One of them, Arachnidioidea, comprises taxa of heterogenous colony and zooidal morphologies (Schwaha, 2020b). Several members are commonly characterized by cystid appendages capable of anastomosing (Jebram, 1973). Two of its families are solitary, one is boring, and two are colonial, that is, Nolellidae and Arachnidiidae (Schwaha, 2020b). The latter is a little investigated family with few genera that, like the entire superfamily, requires thorough revision. The origin of cheilostomes, however, is often deduced from arachnidioidean-like ctenostome ancestors (Taylor, 1990), but morphological data on recent members of the Arachnidiidae is completely missing with the exception of some general information on colony structure. Therefore, we conducted the first morphological analysis of the arachnidid *Arachnidium fibrosum* from European waters. *Arachnidium fibrosum* forms flat encrusting colonies with distinct cystid appendages. The present work is the beginning of a series of studies dealing with the morphology of ctenostome bryozoans.

## 2 | MATERIALS AND METHODS

Samples of *Arachnidium fibrosum* Hincks, 1880 were collected on October eighth 2010 from barnacles on a Pacific Oyster (*Magallana gigas*) along the eastern Jetty of the harbour of Zeebrugge, North Sea coast of Belgium.

Samples were fixed in a 2% glutaraldehyde in 0.1 mol l\(^{-1}\) sodium cacodylate buffer for several days at room temperature. Afterwards,
samples were transferred into the same buffer solution and documented with a stereomicroscope. Postfixation was then carried out within 1% osmium tetroxide in distilled water. Afterwards samples were dehydrated with acidified dimethoxypropane. Before infiltration into Agar LVR (Low Viscosity Resin) (Agar Scientific, Stansted, Essex, UK), samples were rinsed in pure acetone to remove excess methanol from dehydration. Resin blocks were cured at 60°C overnight. Cured blocks were sectioned at a thickness of 1 μm with a Leica Ultramicrotome UC6 (Leica Microsystems, Wetzlar, Germany). Serially sectioned specimens were analysed and documented with a Nikon NiU light microscope equipped with a Nikon Ri2 microscope camera. Image stacks were imported into Amira 6.4, aligned and semi-manually segmented with a brush (see Ruthensteiner, 2008). Images of the surface reconstructions were taken with the Amira software.

3 | RESULTS

Arachnidium fibrosum forms dense encrusting colonies that are generally difficult to spot at first glance, because the colony is covered by coarse sediment or detritus attached to the cuticle (Figure 1). Also, numerous filiform cystid appendages extend irregularly to the lateral and frontal sides of each zooid, which additionally camouflage the colony. These appendages are non-kenozooidal, lacking pore complexes at their proximal attachment site, and can extend from various parts of the zooid including the peristome. The peristome is usually rather short, forming just a slight apertural papilla (Figure 2), but can also be longer, which appears to occur in colonies growing on thin, elongated substrates rather than broad, flat ones.

Individual zooids have multiple, commonly up to 10–11, connections to other zooids. These seem to be irregularly present on zooids and may be pedunculate or not (Figure 2). They originate from budding of zooids, or are mere cystid anastomoses between zooids. Pore plates separate the cuticular layers of adjacent zooids. The cuticle or ectocyst in A. fibrosum is generally rather thin (Figures 3a,b and 4) and underlain by a thin epidermal layer of the endocyst. Interzooidal septa in the pore plates show different staining properties in sections indicating a different composition and/or mechanical properties (Figure 4). Centrally, each septum is perforated by a cellular pore complex with a single, small pore. A complex of two to four special cells passes and plugs each pore. The proximal and distal enlarged part of these cells is surrounded on each side by a series of limiting cells that
work that reaches up to half the length of the vestibular wall. Bransous without any distinct thickenings and form an irregular net-
the collar folds, extend distally (Figure 3). These appear simple, mem-
and 6a,c). From this collar epithelium numerous acellular thin linings,
with several radial folds that protrude in distal direction (Figures 2, 3,
diaphragm, the vestibular wall is plicate forming the collar epithelium
sections, circular muscle fibres are distinguishable (Figure 3b). At the
parieto-vestibular muscles, vestibular wall musculature is present; in
inclusions (Figure 3). Distal of that area, at the insertion site of the
the epithelium is thicker and prominent, often with distinct vesicular
seem to show a regular pattern. Proximally, towards the diaphragm,
limiting cells. clc, coelomocytes; cp, communication pore; cw, cystid
wall; fuc, funicular cord; izes, interzooidal septum; li, limiting cell; ph,
pharynx; rm, retractor muscle; spe, special cell

FIGURE 4  Arachnidium fibrosum, longitudinal histological sections of interzooidal pore complexes. (a) Section close to a proximal pore plate showing the special cells passing through the interzooidal pore. (b) Pore plate showing coelomocytes in close association. (c) Pore plate with associated funicular cord. (d) Pore complex with special and limiting cells. clc, coelomocytes; cp, communication pore; cw, cystid wall; fuc, funicular cord; izes, interzooidal septum; li, limiting cell; ph, pharynx; rm, retractor muscle; spe, special cell

border the zooidal body cavity (Figure 4a,b,d). In some instances, dis-
tinct cellular cords, funicular cords emanate from the pore complex
(Figure 4c) towards the polypide, predominantly the caecum. From
the latter, several funicular cords may be present in a zooid
(Figure 5c–e). Based on the current study, a specific pattern on the
distribution of these cords has not become evident. They appear more
distally located in the zooid and only few show connections to the
pore plates.

The distal orifice on the frontal side leads into the vestibular wall
(in retracted zooids) (Figures 2 and 3). The latter is elongated and
folded in retracted zooids. Its cuticle is thin similar to the remaining
body wall (Figure 3a,b). Thus, the folds in retracted zooids do not
seem to show a regular pattern. Proximally, towards the diaphragm,
the epithelium is thicker and prominent, often with distinct vesicular
inclusions (Figure 3). Distal of that area, at the insertion site of the
parieto-vestibular muscles, vestibular wall musculature is present; in
sections, circular muscle fibres are distinguishable (Figure 3b). At the
diaphragm, the vestibular wall is plicate forming the collar epithelium
with several radial folds that protrude in distal direction (Figures 2, 3,
and 6a,c). From this collar epithelium numerous acellular thin linings,
the collar folds, extend distally (Figure 3). These appear simple, mem-
branous without any distinct thickenings and form an irregular net-
work that reaches up to half the length of the vestibular wall.

Medially the diaphragmatic sphincter is situated (Figure 3c) and
separates the distal cavity bordered by the vestibular wall, the
vestibulum, from the proximal one, the atrium, lined by the tentacle
sheath. At the proximal border of the diaphragm, the tentacle sheath
has prominent vacuolated cells, whereas the remaining epithelial lining
is thin and inconspicuous (Figure 3d).

Six duplicature bands are present in the apertural area. These
extend from the vestibular area of the tentacle sheath distally towards
the body wall. They are thin and thin longitudinal muscles are present
in each band (Figures 5b,c and 6a,b). More prominent and thicker are
the muscle fibers of the remaining apertural muscles. These consist of
a single, lateral pair with a series of bundles inserting proximally at the
diaphragm, the parieto-diaphragmatic muscles, and distally at the ves-
tibular wall, the parieto-vestibular muscles (Figures 2, 3, 5b,c, and 6).

The lophophore comprises about 13 tentacles. A cerebral gan-
glion lies at the lophophoral base in the area of the mouth opening.
The foregut commences with a pharynx comprising a short ciliated
area at the mouth opening followed by a larger non-ciliated part char-
acterized by its vacuolated cells and its myoepithelial nature
(Figures 5d and 7a,b). Adjoining the pharynx is the esophagus, which
has a thin epithelium without any distinct cellular inclusions. It leads
to the cardiac valve, which separates the foregut from the midgut
(Figures 5c–e and 7a,b). The tubular cardia is short and possesses a
prominent cardiac constrictor that consists of numerous smooth mus-
cle fibres (Figures 2, 7a,b, and 8a). The caecum is voluminous and
shows highest heterogeneity concerning its cells and inclusions
(Figure 7c). Medially, on the caecum a short bundle of funicular mus-
cles attaches the caecum to the basal body wall (Figures 2, 5c–e,
and 8b). A short pylorus is characterized by dense ciliation (Figures 2, 5d,e,
and 8b) and continues into the hindgut, represented by the intestine,
which has a thin epithelium and various contents of undigestible sub-
stances (Figures 2, 5, and 7c). The anus is lophophoral and terminates
in the tentacle sheath in close proximity to the lophophoral base
(Figure 7c). A prominent retractor muscle originates from the proximal
zooidal side and attaches to the lophophoral base and foregut. A few
fibres also extend down to the esophagus, almost to the cardia
(Figure 5b,c).

4  | DISCUSSION

4.1  | Arachnidioidea and previously described morphological features

Morphology of ctenostomes in general remains little investigated. Few
distinct families are recognized among archnidioideans: Arachnidiiidae,
Nolelliiidae and Immergentiiidae. Aethozooids and monobryozooids have
also previously been associated to this clade (Schwaha, 2020b). Mor-
phological data on Arachnidiiidae is limited to few observations in spe-
cies descriptions and general colony morphology (e.g., Harmer, 1915;
d’Hondt, 1978; Gordon, 1986, see also Hayward, 1985). Little information
is available for zooidal morphology such as Crytoparachnidium
argilla (Banta, 1967). The general morphology of Arachnidium fibrosum
was best described by Marcus (1938) who reported 1–9 attached cystid appendages, a short peristome and rounded aperture, a pair of apertural muscles attaching to the area of the diaphragm, and 12–16 tentacles. These features generally fit to the current investigation, although there are numerous important morphological details that were missed (see below).

Originally the superfamily Arachnidioidea sensu Jebram (1973) was intended for species capable of forming cystid anastomoses, but numerous genera and species that lack this feature are currently included (Jebram, 1986). Although, Jebram persisted on this definition and opposed the inclusion of any superficially similar species into the superfamily by other authors, he never revised his systematic categorization and offered little solution to the species involved (Jebram, 1986). In fact, only few species form cystid anastomoses, for example, such as Arachnidium fibrosum, the similar Cryptoarachnidium argilla (Banta, 1967), or several species of nolellids (Jebram, 1973, 1986).

Non-kenozooidal cystid appendages (filiform processes) such as found in Arachnidium fibrosum are present in the arachnididiids Arachnoideella barentsia (d’Hondt, 1983) and Cryptoarachnidium argilla (Banta, 1967), and the nolellids Nolella sawayal (Marcus, 1938), Nolella horrida (O’Donoghue & O’Donoghue, 1926) and Nolella spinifera (O’Donoghue, 1924). The relevance of these cystid characters, whether indicating possible close relationship remains unknown.

4.2 | Characters for systematic and phylogenetic inferences

Despite the apparent lack of data on other arachnidioideans, there are several important characters for systematic and evolutionary implications. One of them is an additional report of a cardiac constrictor in the family Arachnidiiidae, which so far was only described for
Cryptoarchnidium argilla (Banta, 1967). This specific circular musculature was previously commonly addressed as "cardiac sphincter" (see Schwaha, 2020b), but should be referred to as constrictor in the future, since it is not a sphincter permanently obstructing the gut passage, but a functional adaptation to crush food particles (Jebram, 1982). A distinct sphincter may only be addressable when a cardiac valve that normally hinders reflux of ingested particles during the retraction process would be missing (Schwaha et al., 2020). Evidence for such a reduction is currently not present. There appears to be only a slight notice of prominent circular musculature following an elongated esophagus in Arachnoidea evelinae (Marcus, 1937), but was subsequently not recognized or ignored (Jebram, 1973). Indications for a muscular proventriculus similar to the genus Hislophia were given for the freshwater species Arachnoidea raylankesteri (Annandale, 1911), which turned out to be erroneous. A gizzard- or proventriculus-like structure was also described for Nolella blakei (Rogick, 1949) (which perhaps is a closely tied to the genus Arachnidium). Strong muscular areas in form of a cardiac constrictor or even a gizzard are common among numerous ctenostome bryozoans (Jebram, 1973, 1986; Markham & Ryland, 1987; Schwaha, 2020a, 2020b; Schwaha et al., 2020; Schwaha, Wood, & Wanninger, 2011) and rare among cyclostomes and cheilostomes (Schwaha et al., 2020). The prominent gizzard armed with distinct teeth is easily recognizable and had been recognized early (see for example, Farre, 1837). Simpler cardiac constrictors are less conspicuous, but have importance as systematic character, for example, in victorellid ctenostomes (Braem, 1951; Jebram & Everitt, 1982; Jebram & Pisano, 1980a, 1980b). They are
quite abundant among ctenostomes (Schwaha, 2020a, 2020b; Schwaha & Wanninger, 2018). Its presence or absence, along with other zooidal characters, might prove helpful in the future for classifying arachnidioidean species in the future (see also below).

The collar is quite large in *Arachnidium fibrosum* and fills almost half of the entire vestibulum. A collar of similar proportion is present in *Cryptarachnidium argilla*, and was also depicted as general arachnidiid character (d’Hondt & Geraci, 1976), although most species descriptions lack...
proper descriptions of this structure. Several ctenostome species have a setigerous collar that is reinforced by longitudinal cuticular reinforcements that characteristically pleat and unfold the collar (McKinney & Dewel, 2002). In Arachnoidella argilla, and also Arachnoidella evelinae (Marcus, 1937). Detailed information on the presence, absence and extent of the collar among arachnidiids is more or less entirely missing. Detailed reports on the collar in nolellids are few, but also indicate a short, probably setigerous collar (e.g., Calvet, 1900; Rogick, 1949). Immengertid are also reported to have short setigerous collars (Soule & Soule, 1969).

Funicular strands in connection to interzooidal pore plates were previously considered common among ctenostomes, but were recently found to be rather uncommon (Schwaha et al., 2020). It is found predominantly in the stolonate Vesicularioidea, the Victorellidae and probably the Nolellidae. At least a proximal funiculus emanating from the caecum tip was considered reduced among arachnidioides (Jebram, 1973). The current study confirms a funicular muscle in Arachnoidium fibrosum extending from the caecum to the basal body wall. Funicular muscles are frequently unrecognized (Schwaha et al., 2020), which is not surprising given their short size and that in most cases it is not visible in live or fixed material without sectioning. Muscular funicular strands are common among bryozoans including ctenostomes (Schwaha & Wanninger, 2018) and one or two of these strands extending from the caecum to the lateral walls were presumed ancestral for gymnolemates (Schwaha et al., 2020). However, in addition to the funicular muscle, several non-muscular funicular cords were found in the current study. These seem to predominantly originate from the caecum and emanate to the distal body wall, with only few being in contact to pore plate complexes. This is the first histological confirmation of funicular cords in an arachnidiid ctenostome, whereas previous indications were only given by camera lucida drawings of Cryptoarachnoidium argilla (Jebram, 1986, see also Schwaha et al., 2020). The current study recognizes predominantly such cords in the distal area of the zooid, which also includes pore-associated cords that generally lack a counterpart on the adjacent zooid where a cord is not present. This resembles the condition often found in victorellid ctenostomes that, however, more commonly only show a proximal cord (Braem, 1951).

Duplicature bands as part of the apertural musculature are present in the ground pattern of bryozoans including all phylactolaemates and cheilostomes (Schwaha, 2020c; Schwaha et al., 2011). In the gymnolemate ground pattern a set of four apertural muscles including the bands are present (Schwaha et al., 2020). This includes most ctenostomes, but some taxa such as victorellids, vesicularioideans and few others have reduced them (Schwaha et al., 2011; Schwaha & Wanninger, 2018). Six bands were detected in Arachnoidium fibrosum, which for ctenostomes is an unusual number and recently reported in Pherusella sp. (Decker, Wanninger, & Schwaha, 2020). The significance of the number of duplicature bands is not entirely understood, but in the future might hold relevance as a systematic character perhaps even a suitable character for phylogenetic inferences. Unfortunately, there are no data on any other arachnidiid ctenostome. The closely related Nolellidae have four (Schwaha & Wanninger, 2018).

The remaining apertural muscles also show various arrangements among ctenostomes and range from a set of four in victorellids and vesicularioideans (e.g., Braem, 1951), hislopodi (Schwaha et al., 2011), aethozeoids (Schwaha, Edgcomb, Bernhard, & Todaro, 2019), nolellids (Calvet, 1900; Schwaha & Wanninger, 2018), and immengeritids (Silén, 1947; Soule & Soule, 1969) to rarely five in Pottsiella (Braem, 1940), or two in many alcyonioides (e.g., Schwaha, 2020c; Schwaha & Wanninger, 2018). The presence of two in Arachnoidium fibrosum is thus showing a closer similarity to flat encrusting forms such as alcyonioides rather than such with elongated peristomes such as victorellids or nolellids. Arachnidioid genera and species show a high variability of peristome sizes (Schwaha, 2020b), but the relation of many structures associated with the apertural area and peristome size remain little understood.

Reactor muscles were generally asserted to insert merely on the lophophoral base in gymnolemate bryozoans (cf. Mukai et al., 1997; Schwaha et al., 2020). However, Arachnoidium fibrosum has additional bundles to the foregut, including some to the esophagus. A wide insertion area of reactor muscles on the entire oral side of the gut was recently found in Aethozooides uraniae (Schwaha et al., 2019), and subsequent studies on ctenostome muscle systems also confirmed additional fibres inserting at the esophagus (Decker et al., 2020).

5 | CONCLUSION

The first of a series of studies on ctenostome bryozoans focused on Arachnoidium fibrosum. As confirmed in this study, soft body morphology holds a plethora of interesting characters that seem vital for understanding ctenostome biology and relationships. As substantiated by this study is a possible division of arachnidiid ctenostomes into those species with round or quadrangular aperture including a cardiac constrictor such Arachnoidium fibrosum, Arachnoidella evelinae and Cryptoarachnoidium argilla, vs. species with a pentagonal orifice as Arachnoidium lacourtii (d’Hondt & Faasse, 2006), Arachnoidea diondi (Franzén & Sandberg, 2001), Pararachnoidea rylansii (d’Hondt, 1978). At least in A. raylankesteni a muscular cardia is absent, whereas data for the other genera is missing. Possibly, the position of the anus (lophophoral vs. vestibular) might also be an additional character different in these taxa (see Schwaha, 2020c).

Concerning the aperture shape, round to quadrangular variations are also present in species assigned to the closely-related family Nolellidae (see d’Hondt, 1983), which also have a cardiac constrictor (Schwaha & Wanninger, 2018). Future research aims to study a larger variety of arachnidiid species morphologically, but also support current findings by molecular sequences, which are currently entirely missing for the family.

AUTHOR CONTRIBUTIONS

Thomas Schwaha: Conceptualization; investigation; methodology; visualization; writing-original draft. Hans De Blauwe: Conceptualization; data curation; methodology; resources; writing-review and editing.

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DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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