RESEARCH ARTICLE

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 Arachnidioidea 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 arachnidiid ctenostomes that are characterized by their aperture and details of gut morphology. Further analysis of additional arachnidioidean species are required to confirm this.

KEYWORDS

Arachnidioidea, 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

(e.g., Braem, 1939, Braem, 1951). 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 deducted 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 arachnidiid *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,
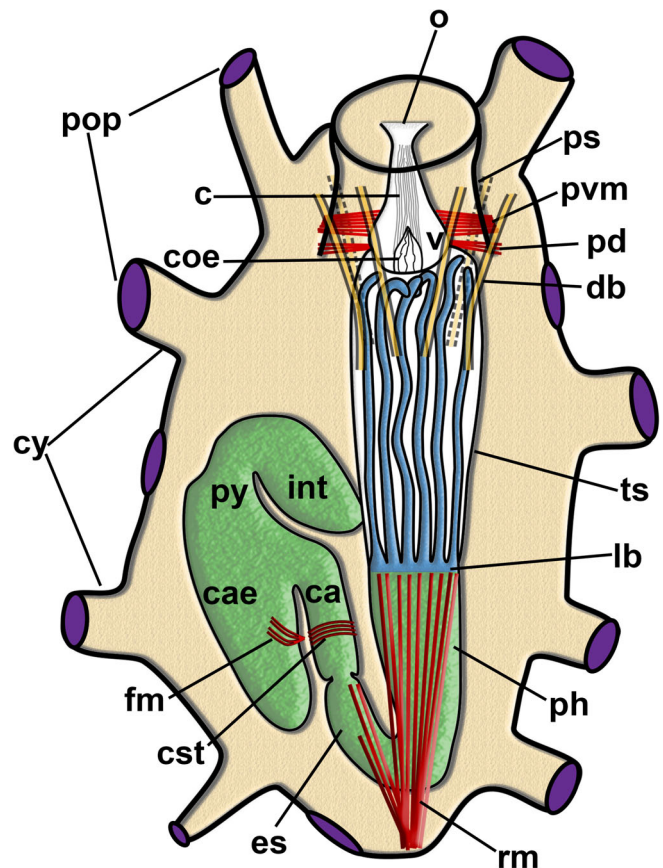
FIGURE 2 *Arachnidium fibrosum*, schematic drawing of a single zooid. c, collar; ca, cardia; cae, caecum; coe, collar epithelium; cst, cardiac constrictor; cy, cystid appendage; es, esophagus; fm, funicular muscle; int, intestine; lb, lophophoral base; o, orifice; pd, parieto-diaphragmatic muscle; ph, pharynx; pop, pore plate; ps, peristome; pvm, parieto-vestibular muscle; py, pylorus; rm, retractor muscle; ts, tentacle sheath; v, vestibulum

FIGURE 1 *Arachnidium fibrosum*. (a) Overview on a colony attached to barnacles. (b) Single zooid. ap, aperture; fca, filiform cystid appendages
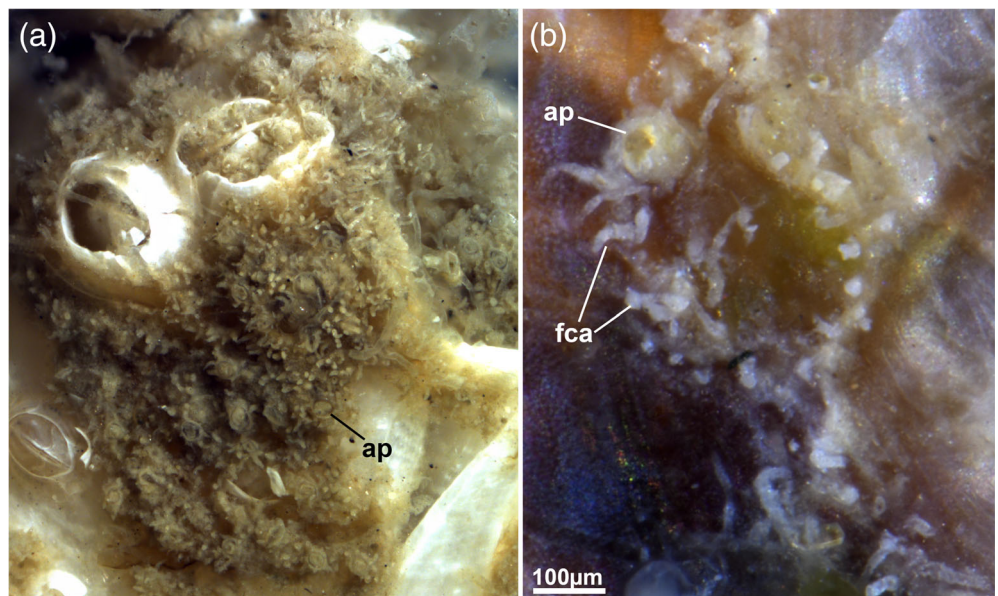
samples were transferred into the same buffer solution and documented with a stereomicroscope. Postfixation was then carried out within 1% osmium tetroxide in distilled water. Afterwards samples were dehydrated with acidified dimethoxypropane. Before infiltration into Agar LVR (Low Viscosity Resin) (Agar Scientific, Stansted, Essex, UK), samples were rinsed in pure acetone to remove excess methanol from dehydration. Resin blocks were cured at 60° 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
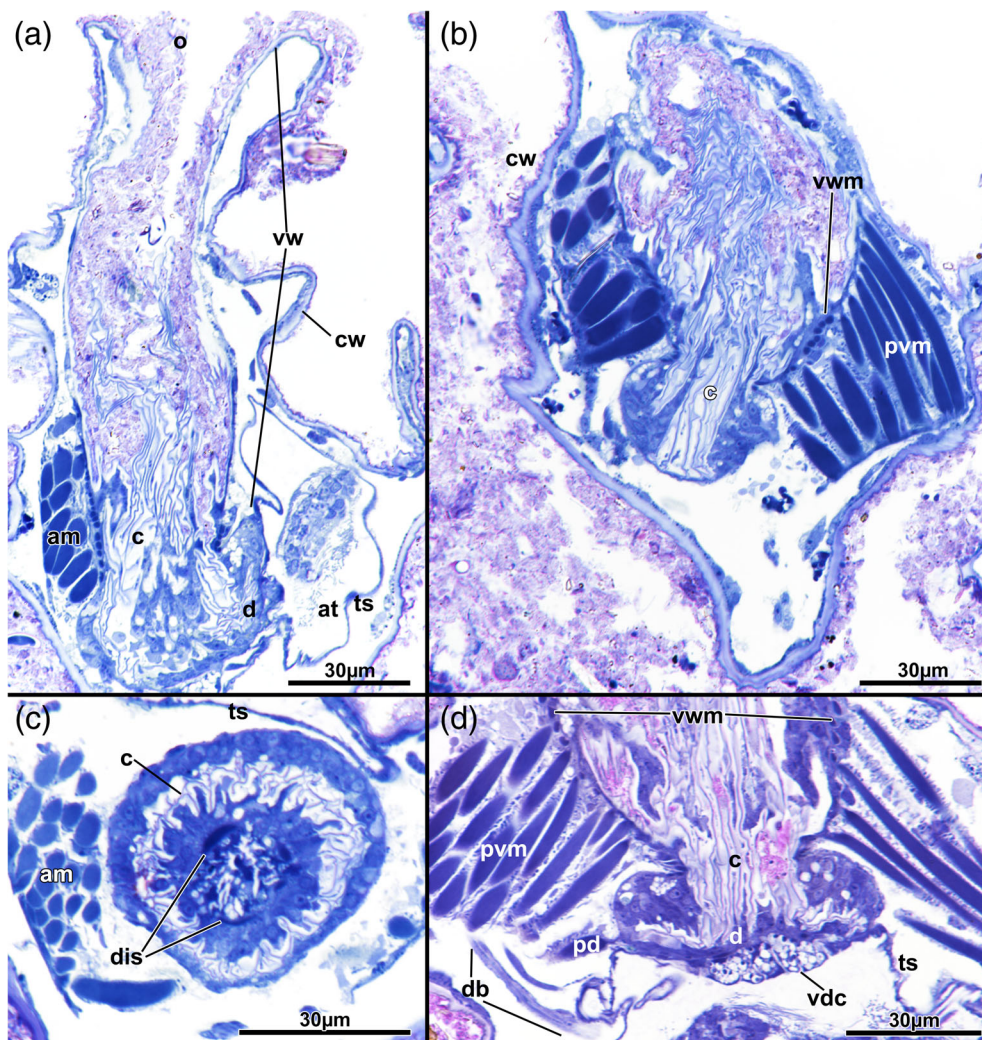

FIGURE 3 *Arachnidium fibrosum*, histological sections with details of the apertural area. (a) Longitudinal section showing an elongated vestibular wall with the collar projecting into the vestibulum. (b) Detail of apertural muscles at the diaphragm. Oblique section. Note also circular vestibular wall muscles. (c) Cross section of the diaphragmatic sphincter at the collar epithelium. (d) Longitudinal section of the diaphragm showing proximal vacuolar cells at the diaphragm. am, apertural muscles; at, atrium; c, collar; cw, cystid wall; d, diaphragm; db, duplicature band; dis, diaphragmatic sphincter; o, orifice; pd, parieto-diaphragmatic muscle; pvm, parieto-vestibular muscle; ts, tentacle sheath; vdc, vacuolar diaphragmatic cells; vw, vestibular wall; vwm, vestibular wall muscles
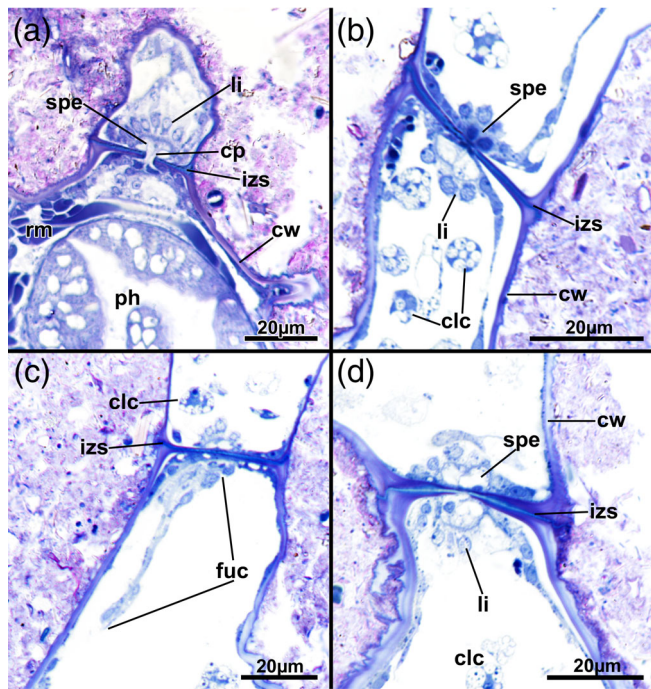
FIGURE 4 *Arachnidium fibrosum*, longitudinal histological sections of interzooidal pore complexes. (a) Section close to a proximal pore plate showing the special cells passing through the interzooidal pore. (b) Pore plate showing coelomcytes in close association. (c) Pore plate with associated funicular cord. (d) Pore complex with special and limiting cells. clc, coelomocytes; cp, communication pore; cw, cystid wall; fuc, funicular cord; izs, 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, distinct 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, membranous without any distinct thickenings and form an irregular network 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 vestibular wall, the parieto-vestibular muscles (Figures 2, 3, 5b,c, and 6).

The lophophore comprises about 13 tentacles. A cerebral ganglion 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 characterized 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 muscle 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 muscles 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 substances (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: Arachnidiidae, Nolellildae and Immergentiidae. Aethozooids and monobryozooids have also previously been associated to this clade (Schwaha, 2020b). Morphological data on Arachnidiidae is limited to few observations in species 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 *Cryptoarachnidium argilla* (Banta, 1967). The general morphology of *Arachnidium fibrosum*
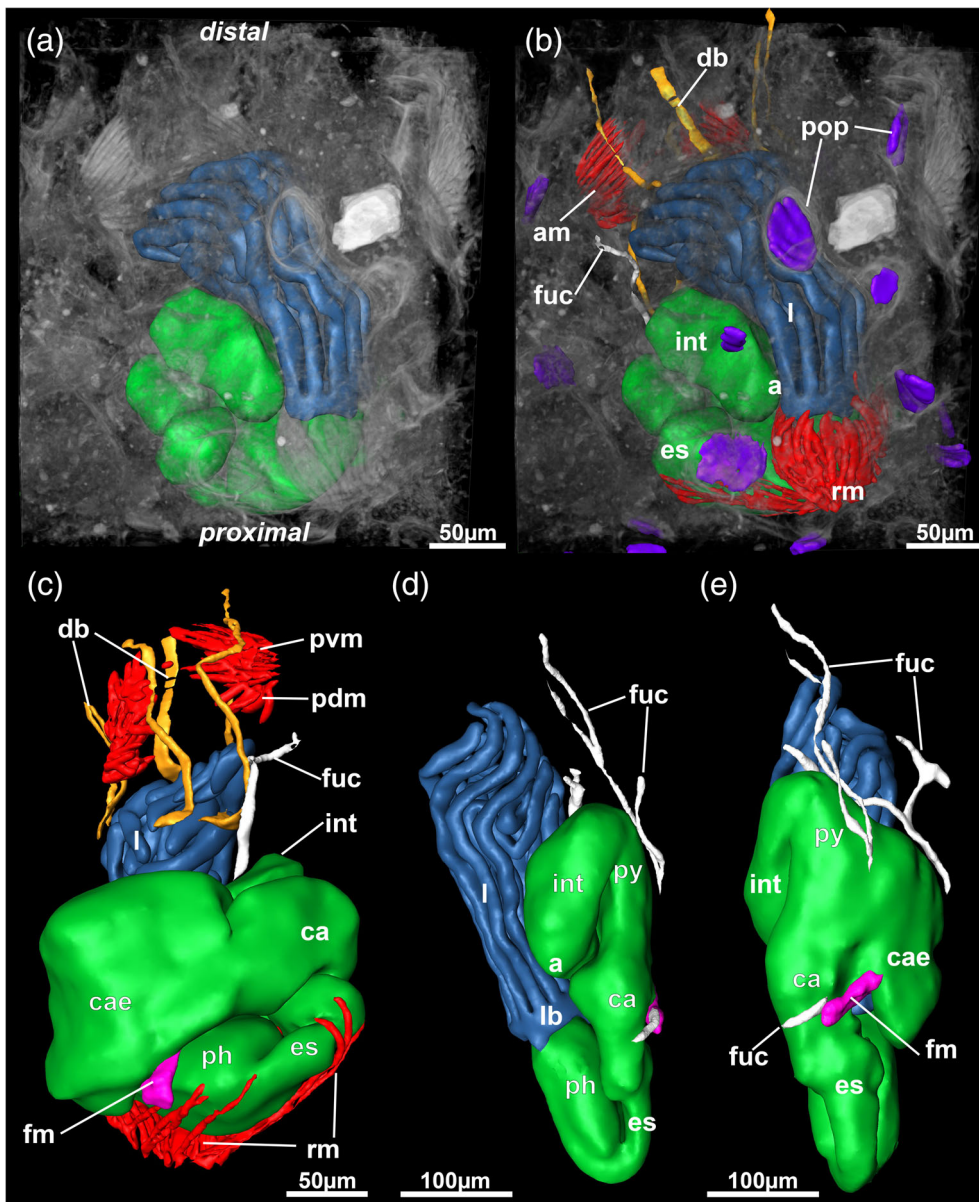
FIGURE 5 *Arachnidium fibrosum*, 3D-reconstruction of the polypide anatomy based on serial semithin sections, retracted zooids. (a,b) General overview of a polypide (lophophore in blue, gut in green) with surrounding dense tissues displayed as volume rendering. (a) Gut and lophophore. Note muscles and pore plates are distinguishable (compare to b). (b) Additional morphological features displayed. (c) Associated structures of the polypide: apertural and retractor muscles, duplicature bands and funicular cord and muscle. Note the retractor muscles with branches extending to the esophagus. (d,e) Different reconstructed zooid showing less contorted digestive tract and distal funicular cords and the caecal funicular muscle. a, anus; am, apertural muscles; ca, cardia; cae, caecum; db, duplicature band; es, esophagus; fm, funicular muscle; fuc, funicular cord; int, intestine; l, lophophore; lb, lophophoral base; pdm, parieto-diaphragmatic muscle; ph, pharynx; pop, pore plate; pvm, parieto-vestibular muscle; py, pylorus; rm, retractor muscle

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 fribrosum*, 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 arachnidiids *Arachnoidella barentsia* (d'Hondt, 1983) and *Cryptoarachnidium argilla* (Banta, 1967), and the nolellids *Nolella sawayai* (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 Arachnidiidae, which so far was only described for

FIGURE 6 *Arachnidium fibrosum*, 3D-reconstruction of the apertural area of a retracted zooid. (a) View from apertural side showing lateral apertural muscles and six duplicature bands. (b) Lateral view showing location of apertural muscles and orifice. (c) Lateral view of the dome shaped, ridged collar epithelium. am, apertural muscles; coe, collar epithelium; d, diaphragm; db, duplicature band; fca, filiform cystid appendages; o, orifice; pd, parieto-diaphragmatic muscle; pvm, parieto-vestibular muscle; v, vestibulum
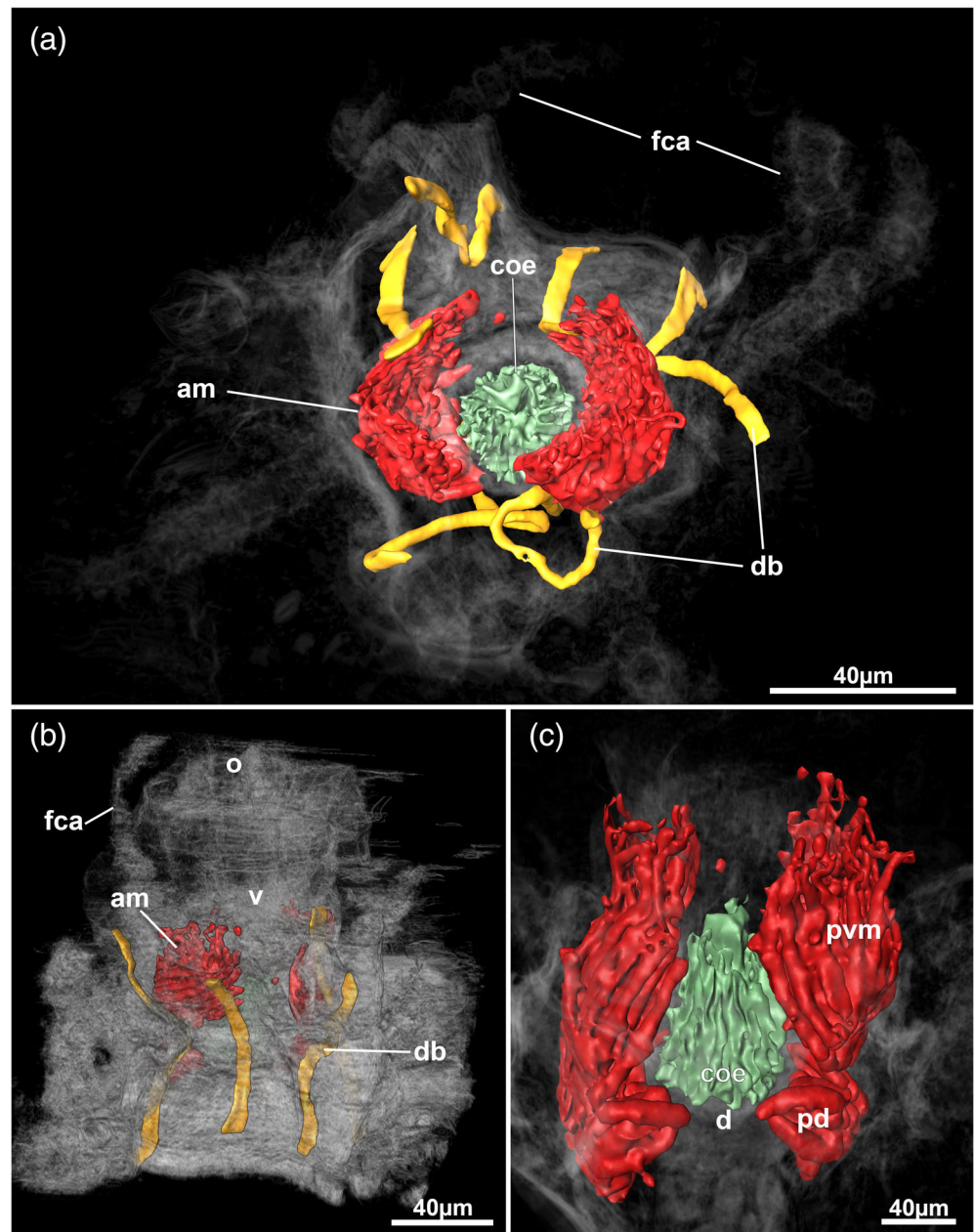
Cryptoarchnidium argilla (Banta, 1967). This specific circular musculature was previously commonly addressed as "cardiac sphincter" (see Schwaha, 2020b), but should be referred to as constrictor in the future, since it is not a sphincter permanently obstructing the gut passage, but a functional adaptation 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 *Arachnoidella evelinae* (Marcus, 1937), but was subsequently not recognized or ignored (Jebram, 1973). Indications for a muscular proventriculus similar to the genus *Hislopia* 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
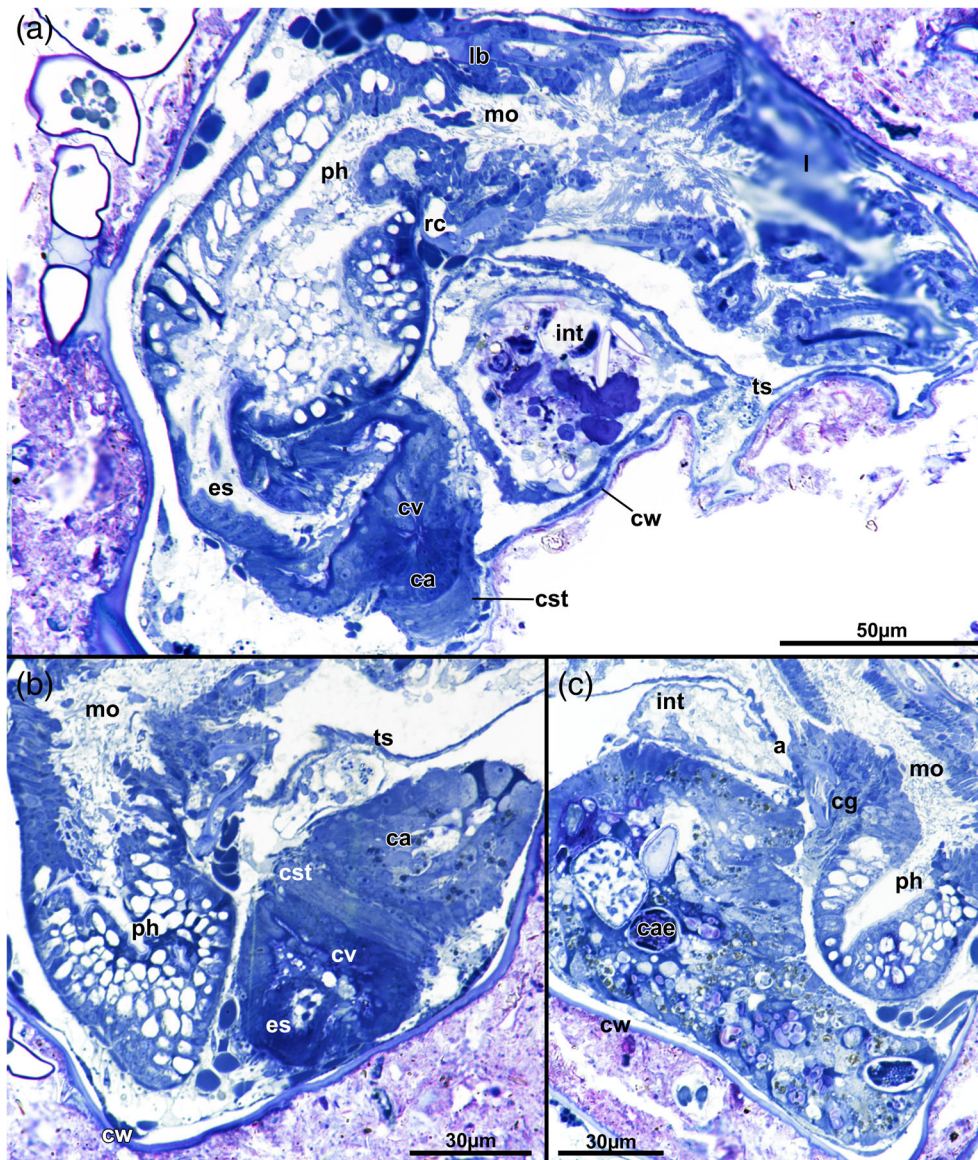
FIGURE 7 *Arachnidium fibrosum*, histological sections, overview of the digestive tract. (a) Longitudinal section of the foregut showing vacuolar cells of the pharynx, the less conspicuous esophagus and the circular muscle of the cardiac constrictor. (b) Longitudinal section of the transition from foregut (esophagus) to midgut (cardia) showing the cardiac constrictor. (c) Caecum morphology and thin epithelium of the intestine including lophophoral anus. a, anus; ca, cardia; cae, caecum; cg, cerebral ganglion; cst, cardiac constrictor; cv, cardiac valve; cw, cystid wall; es, esophagus; int, intestine; l, lophophore; lb, lophophoral base; mo, mouth opening; ph, pharynx; rc, ring canal; ts, tentacle sheath
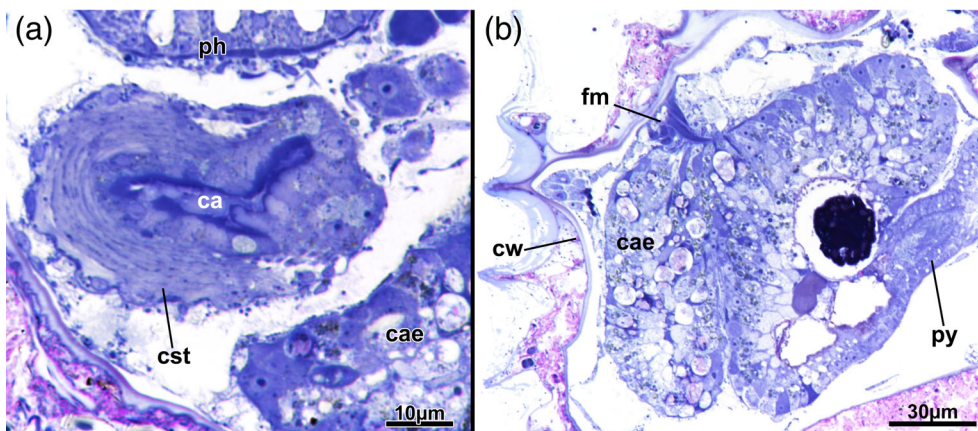

FIGURE 8 *Arachnidium fibrosum*, histological sections, details of digestive tract anatomy. (a) Cardiac constrictor. (b) Funicular muscle extending form the caecum to the body wall. ca, cardia; cae, caecum; cst, cardiac constrictor; cw, cystid wall; fm, funicular muscle; ph, pharynx; py, pylorus

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 *Cryptoarachnidium 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 *A. fibrosum* it is not setigerous in contrast to *C. 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). Immergentiids 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 arachnidioideans (Jebram, 1973). The current study confirms a funicular muscle in *Arachnidium 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 gymnolaemates (Schwaha et al., 2020). However, in addition to the funicular muscle, several nonmuscular 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 *Cryptoarachnidium 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 gymnolaemate 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 *Arachnidium 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 arachniid 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), hislopiids (Schwaha et al., 2011), aethozooids (Schwaha, Edgcomb, Bernhard, & Todaro, 2019), nolellids (Calvet, 1900; Schwaha & Wanninger, 2018), and immergentiids (Silén, 1947; Soule & Soule, 1969) to rarely five in *Pottsiella* (Braem, 1940), or two in many alcyonidioideans (e.g., Schwaha, 2020c; Schwaha & Wanninger, 2018). The presence of two in *Arachnidium fibrosum* is thus showing a closer similarity to flat encrusting forms such as alcyonidioideans rather than such with elongated peristomes such as victorellids or nolellids. Arachnidioidean 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.

Retractor muscles were generally asserted to insert merely on the lophophoral base in gymnolaemate bryozoans (cf. Mukai et al., 1997; Schwaha et al., 2020). However, *Arachnidium fibrosum* has additional bundles to the foregut, including some to the esophagus. A wide insertion area of retractor 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 *Arachnidium 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 *Arachnidium fibrosum*, *Arachnoidella evelinae* and *Cryptoarachnidium argilla*, vs. species with a pentagonal orifice as *Arachnidium lacourti* (d'Hondt & Faasse, 2006), *Arachnoidea dhondti* (Franzén & Sandberg, 2001), *Parachnoidea rylandi* (d'Hondt, 1978). At least in *A. raylankesteri* 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.

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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