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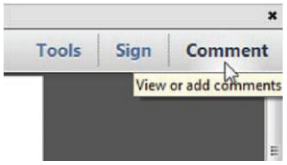

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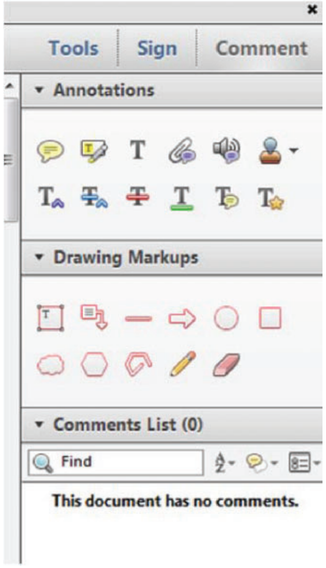

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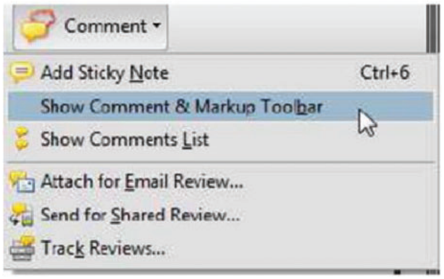

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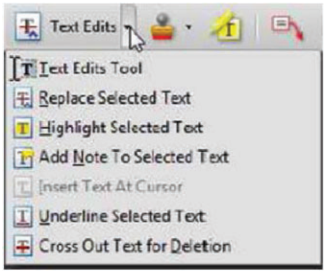

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The protobranch *Aequiyoldia eightsii* (Jay, 1839) (Nuculanida: Sareptidae) reveals uncommon siphonal anatomy among bivalves

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ABSTRACT

Siphons represent a remarkable example of evolutionary convergence in different bivalve lineages. In Protobranchia, the siphons, when present, are used exclusively to channel the water currents used for respiration, waste removal and gamete release. Their emergence is thought to be associated with the taxonomic and morphological diversification within the Nuculanida. While siphons have been extensively studied in other bivalve groups, particularly the Heterodonta, gaps remain in the knowledge of protobranch siphons, especially on their morphology, including the musculature and innervation, and their functioning. The few data on Protobranchia siphons are restricted to some Nuculanoidea, and information is still missing for other nuculanid lineages, such as the Sareptoidea. The present study provides a description of the siphonal morphology of *Aequiyoldia eightsii*, a sareptid bivalve. Histological data were obtained to investigate their organization and infer their functioning. All traits observed were compared with those of heterodont siphons. In *A. eightsii*, the siphons are fused with each other and distinguished by their reduced longitudinal musculature in bundles that do not form layers, by the presence of a blood lacunal system that fills most of the wall of the siphon and by the innervation that is likely diffuse. This suggests that the siphons are hydrostatic organs with a hydraulic mechanism whose expansion occurs when the lacunar system is filled with blood. Our results provide the first morphological and functional details of a protobranch siphon and thus contribute to knowledge on the comparative anatomy of Bivalvia.

INTRODUCTION

In most bivalve lineages, siphons are tubular organs formed by fusion and posterior extension of the marginal mantle folds, serving for the passage of incurrent and excurrent water (Carter *et al.*, 2012). Siphons represent a remarkable example of evolutionary convergence, with independent acquisitions in different bivalve lineages (Stanley, 1968; Audino, Serb & Marian, 2020). In Heterodonta, the siphons are widely variable in form and function, being generally used to capture food particles along with the incurrent water (Stanley, 1968). In contrast, siphons in Protobranchia, when present, are not involved in food-gathering. For example, different lineages of the order Nuculanida (Nuculanoidea + Sareptoidea) have siphons that exclusively channel the water currents used for respiration, waste removal and gamete release (Yonge, 1939).

The siphons in Protobranchia are formed by an extension of the posterior inner mantle folds (Yonge, 1948, 1982). In this group, Yonge (1939) associated the emergence of siphons with the displacement of the incurrent from an anterior to a posterior position in Nuculanida. Allen (1985) suggested the siphon as one factor that influenced the diversification of the order. Interestingly, siphonate Protobranchia (Nuculanida) currently comprises 648 species, in comparison with 293 species of other protobranchs lacking siphons (217 species in Nuculida and 76 species in Solemyida) (MolluscaBase, 2022). Some nuculanids (species of the genera *Pristigloma* Dall, 1900 and *Tindaria* Bellardi, 1875) lack siphons. However, it is uncertain if these lineages never had siphons or if they were secondarily lost. For example, the absence of siphons in *Pristigloma* may result from the extreme miniaturization that occurred in species of this genus (Sharma *et al.*, 2013).

The siphonal morphology of Heterodonta, mainly Imparidentia, has been extensively studied (e.g. Yonge, 1957; Duval, 1963; Amouroux, 1980; Fishelson, 2000). On the other hand, in Protobranchia, they have been little investigated and anatomical details are scarce. The siphons of Nuculanida are always fused, and the few data on them are restricted to this type of fusion. In *Neilonella sulculata* (A. Gould, 1852) and *Yoldiella lucida* (Lovén, 1846), the two regions of the incurrent siphon are not fused, and ciliary junctions are present between this and the excurrent siphon as well as in the ventral margin of the incurrent siphon (Stempell, 1898;

Yonge, 1939). In *Megayoldia montereyensis* (Dall, 1893), *Nuculana minuta* (O. F. Müller, 1776) and *Nuculana pernula* (O. F. Müller, 1779), a siphonal pallial septum, formed by tissue fusion, is present between the siphons, but the ventral margin of the incurrent siphon only shows ciliary junctions (Heath, 1937; Yonge, 1939). In *Lembulus pella* (Linnaeus, 1758), *Malletia pianii* (van Aartsen & Giannuzzi-Savelli, 1991) and *Yoldia limatula* (Say, 1831), the siphons are formed simply by tissue fusion (Yonge, 1939). Information on the siphonal characters of other Nuculanida is still missing. The only sareptid of which the siphons have been studied is *Aequiyoldia eightsii* (Jay, 1839) (Davenport, 1988), which is an abundant species in the Antarctic Peninsula and South Shetland Islands and is also reported from other places in the Antarctic continent, subantarctic islands and South Patagonia (Dell, 1990; Engl, 2012). While Davenport (1988) reported on the behaviour and aspects of the external morphology of this species, he did not provide any details of siphonal anatomy.

Many gaps still remain in our knowledge of the musculature, innervation and functioning of protobranch siphons. The lack of data prompts several questions. (1) Is the musculature organization of protobranch siphons similar to that observed in heterodonts? (2) How is the siphon innervated in protobranchs? (3) If bivalve siphons are functionally analogous, is this reflected in similar siphonal architecture? In order to expand knowledge on the siphons of Sareptidae and Protobranchia, the present study provides a detailed description of the siphons of *A. eightsii*. By using a histological approach, based on investigating the presence and organization of inner tissues, we here describe the anatomy of the siphons in *A. eightsii* and infer their functioning.

MATERIAL AND METHODS

Specimens of *Aequiyoldia eightsii* were obtained from bottom samples collected by van Veen grabs at depths of about 20–30 m in Admiralty Bay (58°21′W, 62°04′S), King George Island, South Shetlands, Antarctica, during the scientific activities of the Brazilian Antarctic Program (PROANTAR), from January to May 2001. Specimens ($n = 27$) were fixed for 24 h in Bouin's fluid (with acetic acid) and then preserved in 70% ethanol.

Siphonal morphology was studied by dissection of the ethanol-preserved individuals. Images were obtained by a camera coupled to a Zeiss SteREO Discovery V8 stereomicroscope. Detailed anatomy was investigated by histological sections. For this purpose, two siphons were isolated and progressively dehydrated in a graded ethanol series (70%, 80%, 95% and three successive rinses in 99% ethanol; 20 min each) prior to embedding in glycolmethacrylate resin (Leica Historesin Kit). We sectioned the distal portion of the siphon from one individual longitudinally and its proximal portion transversely. We also sectioned the siphon from a second individual transversely throughout. Histological sections (5–8 μm thick) were produced with a Leica RM2245 microtome and stained with toluidine blue for general histological investigation; we also used the two other staining techniques (Gomori trichrome and Mallory's trichrome) for investigating the musculature (Bancroft & Stevens, 1982). Sections were analysed and photographed with a camera coupled to a Leica DM4 B microscope. Dissected specimens were deposited in the zoological collection of the Museum of Biological Diversity of the University of Campinas (MDBio), São Paulo, Brazil, under the catalogue number ZUEC-BIV 8400, including the slides with histological sections (ZUEC-BIV 8401 and 8402). We follow the general terminology and definitions for bivalve anatomy used by Carter *et al.* (2012); the terminology used for the siphonal muscle layers of Heterodonta follows Vitonis *et al.* (2012).

RESULTS

Siphonal morphology

The siphons of *Aequiyoldia eightsii* were pinkish when fixed. They were externally smooth, and the siphonal apertures were devoid of papillae and tentacles (Fig. 1A). Putative sensorial organs, such as tentacles, were restricted to the posterior region of the mantle lobe margins, being rounded, digitated and short (*c.* 1.5 mm long when contracted) (Fig. 1A).

The incurrent and excurrent siphons of *A. eightsii* were completely united through their extension, with the incurrent and excurrent channels separated by a siphonal pallial septum formed entirely by fused tissue (Fig. 1A, B). Both incurrent and excurrent siphons had the same length (*c.* 10 mm after fixation); however, the diameter of the incurrent siphon was about four times larger than the excurrent (Fig. 1A, B). The diameters of both siphons were not uniform along their length, increasing towards the base.

In transverse section, the siphons revealed a pair of blood vessels running below the outer siphonal epithelium, laterally, at both ends of the pallial siphonal septum, and a siphonal musculature formed mainly of circular and radial muscles (Fig. 1B). At the base of the siphons, the longitudinal fibres spread to form a fan-shaped retractor siphonal muscle (Fig. 1C). This muscle was attached to each valve, forming the pallial sinus (Fig. 1D), which measures about a quarter of the shell length (measured from between the end of the pallial line and the end of the sinus).

Histology

The outer epithelium was continuous in both siphons (Fig. 2A) and had a mean thickness of about 30–35 μm. The inner epithelium of the incurrent siphon was 25–30 μm thick, while in the excurrent siphon it was thinner, about 15–20 μm thick. Inner and outer epithelia were comprised of unstratified, cuboidal cells with centrally positioned nuclei (Fig. 2B). No connective tissue was differently stained by the different staining methods we applied.

The siphonal circular musculature was observed as an outer thicker layer (25–30 μm) close to the outer epithelium and an inner layer (10–15 μm thick) close to the inner epithelia of both siphons (Fig. 2B, C). Unlike these layers of circular fibres, the longitudinal musculature was composed of bundles placed immediately subjacent to the outer and inner circular muscle layers (Fig. 2B, C), the former being more developed than the latter. The radial musculature comprised regularly spaced fibres that were attached to and extended from both epithelia, crossing the circular muscle layers (Fig. 2B, C). Radial fibres were also present in the siphonal pallial septum, connecting the inner epithelia of the incurrent and excurrent siphons.

The circular and radial muscles defined irregularly shaped spaces (Fig. 2B), likely forming enlarged blood lacunae (*sensu* Carter *et al.*, 2012). In both siphons, these spaces were perpendicular to the siphonal channels, being compartmentalized by radial muscles. In addition, numerous haemocytes-containing cytoplasmic granules were observed within these spaces (Fig. 2D, E). Therefore, the siphons of *A. eightsii* are characterized by a remarkable blood lacunal system. The blood vessels (380–440 μm wide) were not delimited by an endothelium (Fig. 2A, C). It is noteworthy that nerve cords were not observed in the histological sections. Longitudinal sections showed that the excurrent siphon exhibited a flap at the tip formed by an expansion of the siphonal pallial septum, which partly obstructs the opening. This element was barely visible in fixed specimens (Fig. 2F).

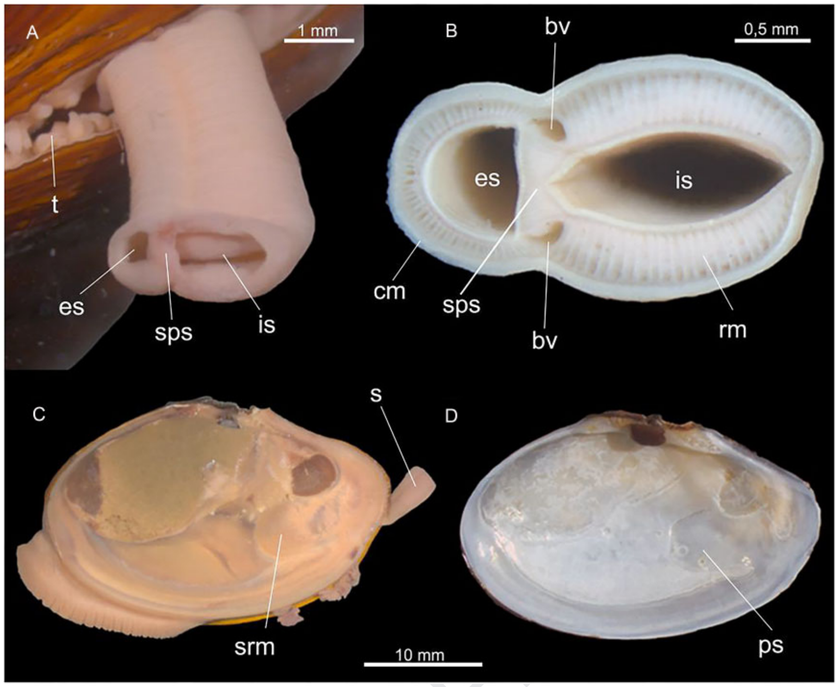

Figure 1. Siphonal morphology of fixed specimens of *Aequiyoldia eightsii*. **A.** Siphons. **B.** Cross-section of siphons. **C.** View from the left side of a specimen, with the valve removed. **D.** Internal view of the right valve. Abbreviations: bv, blood vessel; cm, circular muscle; es, excurrent siphon; is, incurrent siphon; ps, pallial sinus; rm, radial muscle; sps, siphonal pallial septum; srm, siphonal retractor muscle; t, tentacles.

DISCUSSION

Our results for *Aequiyoldia eightsii* expand the knowledge of the siphons of Protobranchia, especially for the Sareptidae, a group for which detailed anatomical information is particularly scarce. The siphonal morphology of the investigated species revealed unusual morphological conditions, such as the longitudinal musculature reduced to bundles (not organized in layers), a blood lacunal system that filled almost the entire siphonal wall, and likely diffuse innervation. Based on the observed anatomical features, the expansion of the siphons of *A. eightsii* occurs when the blood lacunar system is filled with blood.

Comparative siphonal anatomy among bivalves

The siphons of Nuculanoidea are classified as type A, that is, they are formed by only the inner marginal mantle folds (Yonge, 1957), such as in some Galeommatoidea and all Tellinoidea. In *A. eightsii*, the siphons are long, fused with each other along their length, without ciliary junctions, lacking tentacles or papillae, and very similar to the siphons of other nuculanids, such as *Lembulus pella*, *Malletia pianii* and *Yoldia limatula* (Yonge, 1939). In general, type A siphons are roughly similar in appearance, being widely regarded as smooth organs without papillae, tentacles or eyes at the tips of the siphons. The siphons of galeommatids, such as *Kellia laperousii* (Deshayes, 1839) (Yonge, 1952), also follow this pattern. In contrast, the siphons of all Tellinoidea are also classified as type A, although exhibiting papillae and tentacles in many species (e.g. Narchi & Domaneschi, 1993; Passos & Domaneschi, 2004).

Nerve cords were not observed in the histological sections of the siphons of *A. eightsii*. In this case, the siphonal innervation is likely diffuse (Fig. 3A). Conversely, a different condition is observed in Heterodonta species, where they are easily distinguished (Fig. 3B–D), innervating the tentacles and papillae located in the aperture and on the outer epithelium, respectively (Duval, 1963). Interestingly, tentacles and papillae were lacking in the siphons of *A. eightsii*, in which nerve cords were not observed.

Circular, longitudinal and radial muscles were present in the siphons of *A. eightsii*, with the circular musculature organized in layers, similar to the siphons of Heterodonta, which have been described in more detail by Ansell (1961), Duval (1963) and Vitonis *et al.* (2012); these descriptions are used here for the comparisons made in the schematic drawings in Figure 3B–D. In Heterodonta, the longitudinal muscles were also organized in multiple layers, and a bunch of dense longitudinal muscles formed most of the siphonal wall (Fig. 3B–D). For example, the median longitudinal layer is the main component of the siphons of Imparidentia (Duval, 1963). However, in *A. eightsii*, longitudinal muscles are reduced to bundles and not organized in layers, indicating a more simplified longitudinal musculature for the siphons of Sareptidae (Fig. 3A).

In between the muscular fibres of the siphons of *A. eightsii*, there were spaces forming a blood lacunal system, which differs in size and form from other ‘haemocoelic spaces’ (*sensu* Ansell, 1961; Duval, 1963; Vitonis *et al.*, 2012) observed in the siphons of other bivalve species (Fig. 3B–D). In *A. eightsii*, the blood lacunal system is large (occupying three-fourths or more of the siphon wall) and delimited by circular muscle layers. In some groups of Heterodonta, such as Myoidea, Tellinoidea and Veneroidea, the haemocoelic spaces are smaller (less than a quarter of the siphonal wall) and usually located between the outer median longitudinal layer, median circular layer and inner median longitudinal layer (e.g. Yonge, 1949; Chapman & Newell, 1956; Duval, 1963; Vitonis *et al.*, 2012). Based on histological data, the siphonal radial muscles observed in *A. eightsii* and other bivalves are responsible for defining the blood lacunal system and the haemocoel spaces as compartments perpendicular to the siphonal channels.

In *A. eightsii*, two large blood vessels transport the blood. Blood vessels are also found in the united siphons of *Mya arenaria* Linnaeus, 1758, where they are smaller (290 µm wide) and represented by four vessels: one dorsal (subdivided), one ventral (subdivided)

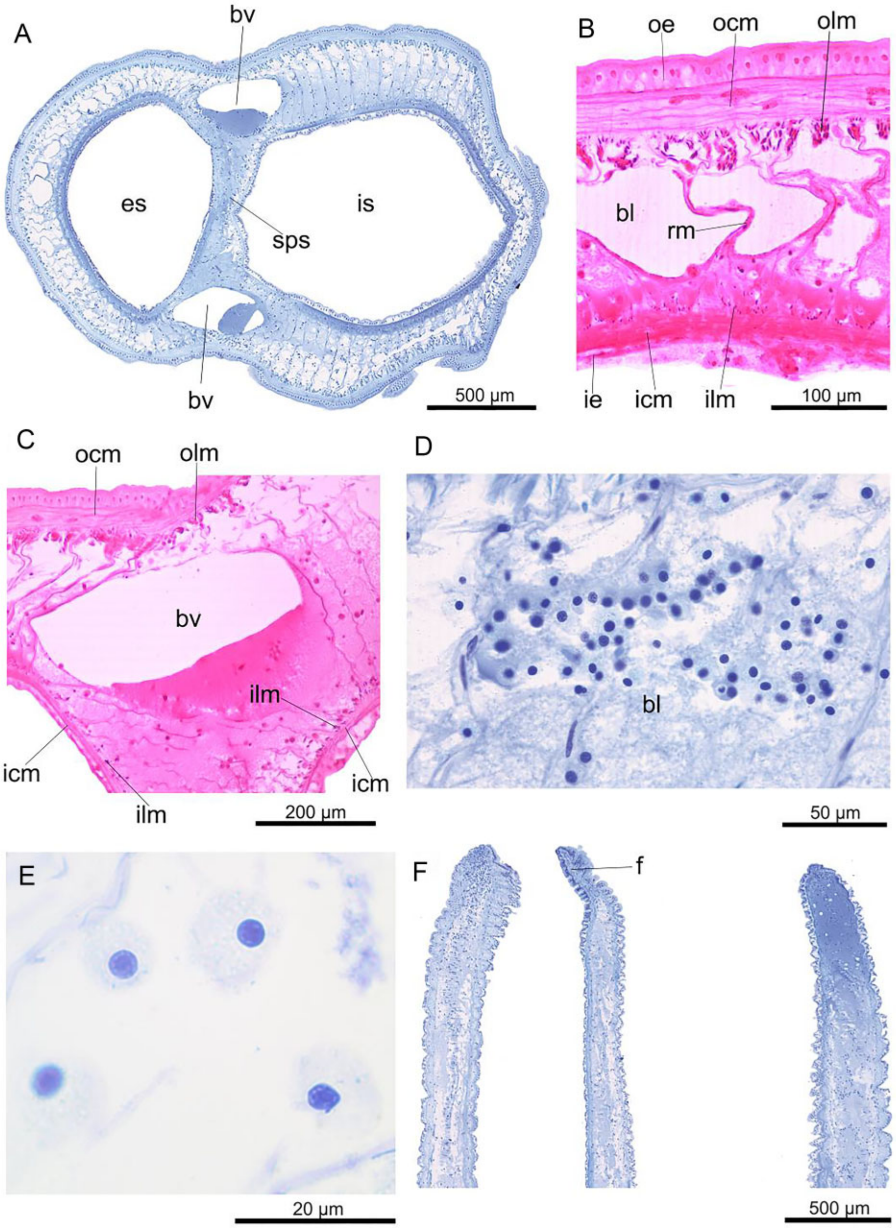

Figure 2. Histological sections of *Aequiyoldia eightsii*. **A.** General view of a transverse section of both siphons, stained with toluidine blue (TB). **B.** Pattern of tissue organization pattern of the siphons, stained with Gomori trichrome (GT). **C.** Detailed view of a blood vessel (GT). **D.** Haemocytes in blood lacuna (TB). **E.** Granulocytes (TB). **F.** Longitudinal section of the distal part of the siphons (TB). Abbreviations: bl, blood lacuna; bv, blood vessel; es, excurrent siphon; f, flap; icm, inner circular muscle; ie, inner epithelium; ilm, inner longitudinal muscle; is, incurrent siphon; oe, outer epithelium; ocm, outer circular muscle; olm, outer longitudinal muscle; rm, radial muscle; sps, siphonal pallial septum.

and two lateral (Chapman & Newell, 1956). The blood vessels of other species of Heterodonta have also been described by Duval (1963). Duval (1963) suggested that four blood vessels are present in species in which the siphons are large, united and relatively thick, as observed in some species of Mactridae, Myidae, Pholadidae and Veneridae. In contrast, species with separate siphons have two blood vessels in each siphon (Duval, 1963). Our results reveal that the united siphons of *A. eightsii*, with two blood vessels, clearly deviate from the anatomical pattern observed in the united siphons of Heterodonta. Therefore, the siphonal anatomy of this sareptid species represents an unusual condition among bivalves and indicates that distinct patterns of siphonal architecture have evolved in this class.

Functional morphology of the siphons of A. eightsii

The siphons of bivalves are hydrostatic organs with a hydraulic mechanism; that is, their function is based on fluid displacement from one location to another to cause shape changes or exert force elsewhere (Kier, 2012). For example, in *Scrobicularia plana* (da Costa, 1778) (Semelidae), the extension of the separated siphons is promoted by the intrinsic musculature of the siphonal walls in combination with the haemolymph contained by the walls, with the volume of the haemolymph being fixed during all stages of the extension (Chapman & Newell, 1956). In *M. arenaria* (Myidae), the extension of the united siphons is also aided by the water forced into them from the mantle cavity after contraction of the adductor muscles (Chapman & Newell, 1956). Despite the variation in

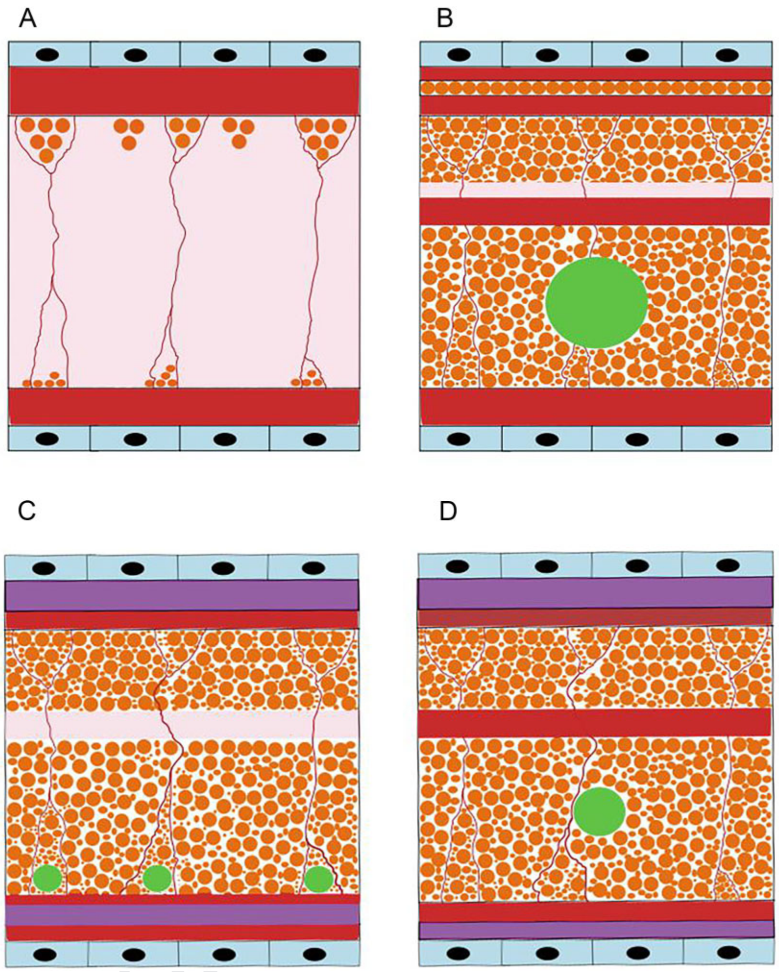

Figure 3. Comparative diagram of the tissue organization in the siphons of *Aequiyoldia eightsii* and some heterodont species. **A.** *Aequiyoldia eightsii*. **B.** *Eurytellina lineata* (W. Turton, 1819), based on Vitonis *et al.* (2012). **C.** *Zirfaea crispata* (Linnaeus, 1758), based on Duval (1963). **D.** *Chamelea striatula* (da Costa, 1778), based on Ansell (1961). Colours: blue, epithelium; green, nerve cord; light pink, blood lacuna (in *A. eightsii*) and 'haemocoel' (in others); orange, longitudinal musculature; purple, connective tissue; red, circular and radial musculature.

mechanisms of siphonal extension, a hydraulic mechanism is a common explanation for siphonal functioning in bivalves.

The siphonal architecture of *A. eightsii*, including the musculature, blood lacunal system and large blood vessels, indicates that the siphons are also hydrostatic organs with a hydraulic mechanism. The simplified longitudinal musculature suggests that the siphons cannot move freely or bend. Consequently, the blood lacunar system must play a major role in regulating the hydrostatic pressure of the siphons. We hypothesize that the siphonal expansion of *A. eightsii* occurs when the blood lacunal system is filled with blood transported by the paired vessels, which inflates the siphons and causes their extension. Future studies with living specimens of *A. eightsii* should provide additional data to understand siphonal performance and hydrostatic function in this species.

In conclusion, our study has provided the first details on the anatomy of a protobranch siphon, thus contributing to the knowledge of the comparative anatomy of Bivalvia. Overall, the siphons of *A. eightsii* have uncommon siphonal anatomy, including the absence of neural cords, a reduced longitudinal musculature and the presence of a broad blood lacunal system that fills most of the siphon wall. These are unique traits that have not been documented for any other bivalves so far. In addition, the siphons of *A. eightsii* are inferred to be hydrostatic organs that function with a hydraulic mechanism, similar to the siphons of heterodonts. Thus, the morphological disparity between protobranch and heterodont siphons illustrates how different siphonal architectures can perform similar functions. Further comparative studies with siphonate species of nuculanids are needed to determine whether the features found here represent an anatomical pattern in siphonate protobranchs. Q6

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