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The organs of prey capture and digestion in the miniature predatory bivalve *Spheniopsis brasiliensis* (Anomalodesmata: Cuspidarioidea: Spheniopsidae) expose a novel life-history trait

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ABSTRACT

Spheniopsis brasiliensis, from depths of 17–148 m off the southern Atlantic coast of Brazil, is a predator of epipsammic micro-crustaceans which it sucks into the infra-septal chamber using a raptorial inhalant siphon and internally generated hydrostatic suction forces. Prey items, which include ostracods, are thought to be pushed into the funnel-shaped mouth using the foot. The stomach is capacious with a short style sac conjoined briefly with the mid gut and possessing a stubby crystalline style. Internal stomach architecture is simplified, with no identifiable sorting areas (unlike other cuspidarioids) and lined virtually completely by a gastric shield. The exoskeletal remains of digested prey are held in the posterior end of the stomach and not in a specialised waste storage pouch as in the con-familial *Grippina coronata*. The mid gut, hind gut and rectum are all extremely narrow and, thus, only the smallest of faeces can be accommodated and transmitted for anal discharge. *Spheniopsis brasiliensis*, like *G. coronata* is a self-fertilising simultaneous hermaphrodite with encapsulated lecithotrophic eggs brooded internally. Both taxa are thus ovovivaporous. It is also believed that both taxa are univoltine so that larvae and the exoskeletal prey remains are all released post mortem. Cuspidariids are generally regarded as dioecious but, recently, *Cardiomya costellata* has been shown to be a non-brooding simultaneous hermaphrodite. The distinguishing characters between cuspidariids and spheniopsids thus appear to be their differing reproductive strategies and life history traits.

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Introduction

The subclass Anomalodesmata Dall, 1889 comprises a richly diverse assemblage of exclusively marine bivalves, which vary in overall form related to the highly specialised niches they occupy and in the details of an unique variety of anatomies. The

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Anomalodesmata comprises some eight superfamilies (Runnegar 1974; Morton 1985, 2012), one of which, the Ceratomyoidea Arkell, 1929–1937, is extinct, although most putative families of the Palaeozoic Pholadomyoidea Gray, 1847 occur only as fossils (Runnegar 1974). The adaptive radiation expressed by the living representatives of the Anomalodesmata is spectacular but poorly appreciated because most extant taxa occur typically as solitary individuals in, as noted above, specialised niches. In the deep sea, the Anomalodesmata is represented by the numerous representatives of, remarkably, predatory bivalves often collectively referred to as the Septibranchia Pelseneer, 1888. The classification schemes erected for these latter bivalves have undergone many changes over the last 50 years and were last reviewed by Morton (2003, table 3). The septibranchs (a term now rarely used, however) are today thought to be represented by the fossil Orthonotoidea S.A. Miller, 1877 (Bieler et al. 2010) and three extant superfamilies: the Verticordioidea Stoliczka, 1870–1871 (Verticordiidae, Euciroidae [Dall, 1905 In Dall, 1890–1903] and Lyonsiellidae Dall, 1895), Poromyoidea Dall, 1886 (Poromyidae) and the Cuspidarioidea Dall, 1886 (Keen 1969; Bernard 1979; Bieler et al. 2010). Another family of deep-water predatory anomalodesmatans, the Parilimyidae Morton, 1982, is considered to have descended directly from a pholadomyoid ancestor, both possessing unusual taenioid muscles to assist in siphonal retraction (Morton 1982), although these are also possibly seen in *Lyonsiella fragilis* Allen and Turner, 1974 (Allen and Turner 1974, fig. 50d).

The predatory anomalodesmatan bivalves have received some attention that has largely focused on diversity (Knudsen 1967, 1970; Allen and Turner 1974; Bernard 1974; Allen and Morgan 1981) and anatomy, as follows. Yonge (1928) was perhaps the first to bring the septibranch bivalves *Cuspidaria* and *Poromya* to wider scientific attention although, earlier, Pelseneer (1888, 1911), Grobben (1893) and Ridewood (1903) had made comprehensive studies of numerous septibranchs, the latter author describing the structure of the septum in detail. The horizontal muscular septum is thought to have evolved from the typical bivalve ctenidium (Allen and Morgan 1981). Today, however, it is known that not all such predatory bivalves, including representatives of the Verticordiidae (Allen and Turner 1974) and Parilimyidae (Morton 1982), possess such a septum explaining why the term Septibranchia has largely disappeared from general use. Despite possessing a typical anomalodesmatan lamellibranch ctenidium, representatives of these two families, like their septate cuspidariid and poromyid colleagues, do, however, all possess an inhalant siphon modified for the capture of their prey, reduced labial palps and a stomach modified for the digestion of any captured food items (Morton 1982).

Allen and Turner (1974) examined the anatomy of the deep-water representatives of the Verticordiidae, and Allen and Morgan (1981) studied the Cuspidariidae and Poromyidae. In a series of studies, Morton (1981, 1982, 1984, 2003) undertook investigations of the anatomies of *Poromya granulata* (Nyst and Westendorp, 1839) (Poromyidae), *Parilimya fragilis* (Grieg, 1920) (Parilimyidae), *Lyonsiella formosa* (Jeffreys 1881) and *Bentholyonsia teramachii* (Habe, 1952) (Lyonsiellidae), also reviewing statocyst and siphon structure in representatives of the various families (Morton 1985, 1987). Nakazima (1967) studied the anatomy of *Halicardia nipponensis* Okutani, 1957 (Verticordiidae), while Oliveira and Sartori (2013) examined the arenophilic radial glands in the siphons of *Cuspidaria obesa* and a species of *Cardiomya*. Reid and Reid (1974)

examined aspects of the anatomy and behaviour of *Cuspidaria rostrata* (Spengler, 1793) and *C. obesa* (Lovén 1846) and Reid and Crosby (1980) subsequently undertook a study of how *Cardiomya planetica* (Dall, 1908) captured its prey. Purchon (1956) examined the stomach architecture of *Cuspidaria cuspidata* (Olivi, 1792 [as Dall et al. 1792]) and this was also examined in *Bathyneara demistriata* (Allen and Morgan 1981) by Tëmkin and Strong (2013). Reid (1978) has made the only physiological study of any carnivorous bivalve, again *C. planetica*, demonstrating the presence of proteolytic enzymes in the stomach to digest its prey.

The Cuspidarioidea was considered to comprise but one extant family – the Cuspidariidae – although the most recent classification by Carter et al. (2011) considered the superfamily to also include the (unstudied) Halonymphidae Scarlato and Starobogatov, 1983; Protocuspidariidae Scarlato and Starobogatov, 1983 and Spheniopsidae Gardner, 1928. Formerly, representatives of the Spheniopsidae were considered related to the Corbulidae Lamarck, 1818 (Gardner 1928; Keen 1969; Coan 1990; von Cosel 1995; Coan et al. 2000), the type species of *Spheniopsis* being the Oligocene fossil *Corbula scalaris* Braun, 1851. Marshall (2002), however, recognised their true affinity with the Cuspidarioidea, a view that was accepted by Mikkelsen and Bieler (2008). The reasons for such a discrepancy in taxonomic affinities lay within the fact that spheniopsid anatomy, other than that of the shell, was unknown. This, in turn, can be related to the fact that, without exception, spheniopsids are minute, adults typically being < 3 mm in shell length. The only anatomical study of a representative of the Spheniopsidae is that of *Grippina coronata* by Morton et al. (2015), who demonstrated that at least this species of the family is a predatory bivalve related to cuspidariids.

Simone and Cunha (2008), Oliveira and Absalão (2010) and Absalão and Oliveira (2011) have reviewed the species of Verticordiidae, Lyonsiellidae and Cuspidariidae, respectively, occurring in the deeper waters off Brazil. Machado and Passos (2015) described as new two spheniopsid species from waters off the coast of Brazil, *Spheniopsis brasiliensis* and *Grippina coronota*, and provided the first comprehensive descriptions of the species' shells. The latter taxon is characterised by a distinctively coronate prodissoconch Machado and Passos (2015, figs 3–4), whereas the former is not (fig. 2). Morton et al. (2015) exposed the significant fact that this cuspidarioid, contrary to the reports of other authors, for example Bernard (1974), is not dioecious but is a simultaneous, self-fertilising hermaphrodite. Most recently, Morton (2015a) showed that the cuspidariid *Cardiomya costellata* (Deshayes, 1833) is a non-brooding protandric consecutive hermaphrodite, the significance of which will become apparent. The study of the spheniopsid *G. coronata* also showed that this species, unlike other cuspidarioids, which discharge the skeletal remains of their prey in the typical bivalve way via an anus, did not do so and instead stored such material within an unique waste storage pouch. It was hypothesised by Morton et al. (2015) that these were lost from *G. coronata* post mortem, as were fertilised, internally brooded oocytes, which is not the case for any cuspidariid, including *C. costellata* (Morton 2015a). These studies thus exposed not just fundamental differences between the digestive and reproductive processes of cuspidariids and spheniopsids but also more significant differences in life-history traits.

This study was thus undertaken to examine the feeding and digestive anatomy of *S. brasiliensis* to determine: (1) whether the features identified for *G. coronata* were matched

by its generic cousin *Spheniopsis*; (2) whether the life-history trait exhibited by *S. brasiliensis* matches that of *G. coronata*; (3) thereby uncovering the species' lifestyle; and, finally, (4) identify biological features that separate the Spheniopsidae from the Cuspidariidae.

Materials and methods

The material containing living specimens of *Spheniopsis brasiliensis* was obtained from bottom samples collected by a box corer through the activities of the 'Habitats Project – Campos Basin Environmental Heterogeneity', in 2009 under the sponsorship of PETROBRAS SA. The samples were taken from the mouth of the Paraíba do Sul River, and the shelf and continental slope of the Campos Basin off the southeastern coast of the Brazilian states of Rio de Janeiro and Espírito Santo. The material was fixed in 4% buffered formalin, and sorted specimens then preserved in 70% ethanol. Only two individuals of *S. brasiliensis* with internal tissues were obtained, one of them being dehydrated in an ascending series of ethanol and critical-point dried for examination by scanning electron microscopy. The other was prepared for histological analysis by decalcification in an acid solution and was then embedded in methyl methacrylate (Historesin®) in order to obtain serial transverse sections 5 µm thick. Type specimens of *S. brasiliensis* are deposited at the Museum of Zoology 'Prof. Adão José Cardoso' of the State University of Campinas (ZUEC), the Museum of Zoology of the University of São Paulo (MZUSP) and the National Museum of Rio de Janeiro (MNRJ), Brazil (Machado and Passos 2015). Histological slides and septal membrane (SEM) stubs (internal tissues) are deposited at the Museum of Zoology of the State University of Campinas (ZUEC) with the accession numbers ZUEC-BIV 6486 and 6192, respectively.

Results

The shell

The shell of *S. brasiliensis* was described by Machado and Passos (2015) and is unlike that of *G. coronata* in being slightly elongate posteriorly, thus reminiscent of the outline of some cuspidariid shells, for example *Luzonia chilensis* (Dall, 1890–1903), *Luzonia simplex* Allen and Morgan, 1981, *Rhinoclama abrupta* (Allen and Morgan 1981), *Plectodon lepidus* Marshall, 2002 and species of Poromyidae such as *Dermatomya buttoni* Dall, 1916 comb. nov. to *Poromya trosti* Strong and Hertlein, 1937 (Coan and Valentich-Scott 2012, plate 321; Allen and Morgan 1981, figs 42 and 50 and Bernard 1974, plate 23[1–2], respectively). *Spheniopsis brasiliensis* does not, moreover, have the coronate prodissoconch of *G. coronata* (Machado and Passos 2015), which, however, it matches in approximate adult shell length (< 2.6 mm). Similarly, it has a shallow pallial sinus (illustrated in Figure 2, PS) indicating that the siphons are short in both taxa, and thereby also suggesting that the two feed upon similar prey items, notably epipsammic microcrustaceans (Morton et al. 2015, fig. 23).

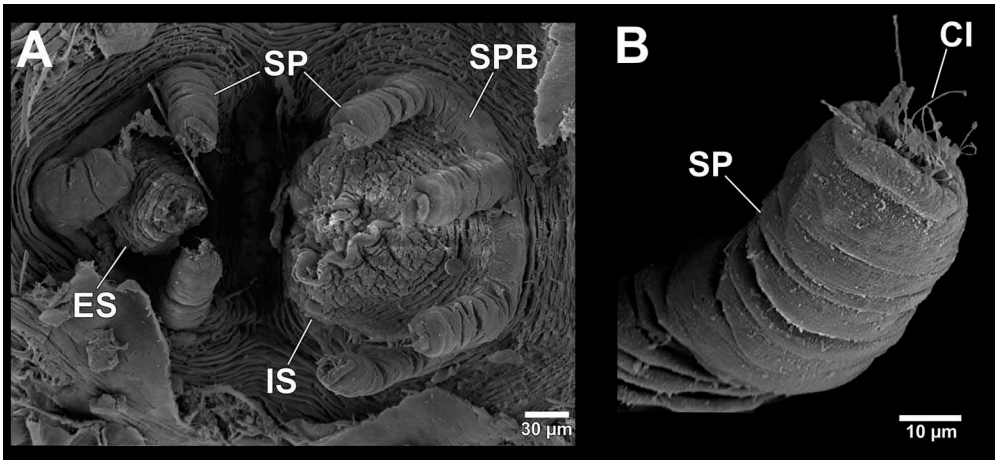

Figure 1. *Spheniopsis brasiliensis*. SEM views of the siphonal apparatus. (A) Posterior view of the exhalant and inhalant siphons, with three and four siphonal papillae, respectively. (B) Higher magnification view of a single siphonal papilla with a terminal array of sensory cilia. CI, Cilia; ES, exhalant siphon; IS, Inhalant siphon; SP, sensory papilla; SPB, base of sensory papillae.

The siphons

Allen and Morgan (1981) suggested that the siphonal apparatus was largely consistent in terms of structure for the wide range of cuspidariid species they examined. That is, the siphons were encompassed by seven siphonal papillae (or tentacles): four lateral and ventro-lateral to the inhalant and three dorsal and dorso-lateral to the exhalant. Morton et al. (2015) showed that the same generalisation applied to the spheniopsid *G. coronata*. Figure 1A is a posterior view of the exhalant and inhalant siphons of *S. brasiliensis* and shows that the same generalisation also applies to this species with three exhalant and four inhalant siphonal papillae, respectively. Figure 1B is a higher magnification view of a single siphonal papilla of *S. brasiliensis* showing the terminal array of cilia that each of the seven possesses, as with *G. coronata*.

The pallial sinus of *S. brasiliensis*, despite the posterior elongation of the shell, is shallow as in *G. coronata*. This suggests that the siphons of *S. brasiliensis* are relatively short, again as in *G. coronata* (Morton et al. 2015, fig. 5A), and thus that the method of prey capture is at least similar. As in *G. coronata* too, un-illustrated sections of the siphons of *S. brasiliensis* show that they are separate and formed by fusion of the inner folds and the inner surfaces of the middle mantle folds and are, thus, of Type B (Yonge 1948, 1957).

The organs of the mantle cavity

The organs of the mantle cavity and visceral mass of *S. brasiliensis* are illustrated in Figure 2. Oocytes are fertilised internally with encapsulated ova also being brooded within the gonadial follicles. This is alluded to here only to explain that these oocytes have been largely removed in this illustration to expose the course of the intestine. Similarly, in Figure 2, the septum (SE) is illustrated only as a dashed line. Figure 3 is a

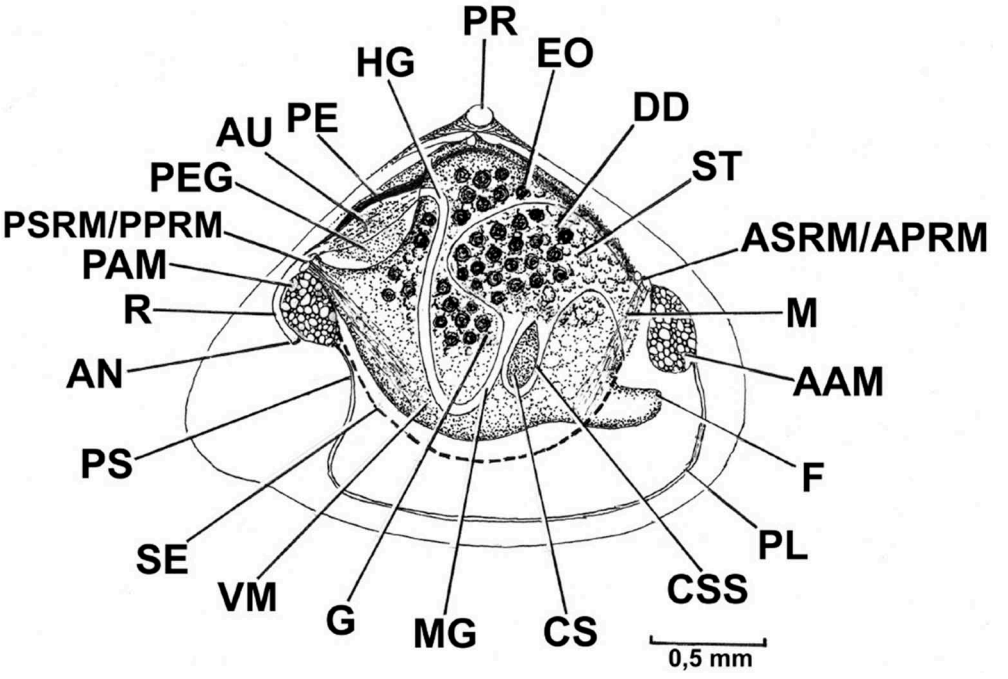

Figure 2. *Spheniopsis brasiliensis*. The organs of the mantle cavity and visceral mass, as seen from the right side after removal of the right shell valve and mantle lobe. AAM, anterior adductor muscle; AN, anus; APRM, anterior pedal retractor muscle; ASRM, anterior septal retractor muscle; AU, auricle; CS, crystalline style; CSS, crystalline style sac; DD, digestive diverticulae; EO, encapsulated oocyte; F, foot; G, gonad; HG, hind gut; M, mouth; MG, mid gut; PAM, posterior adductor muscle; PE, pericardium; PEG, pericardial gland; PL, pallial line; PPRM, posterior pedal retractor muscle; PR, prodissoconch; PS, pallial sinus; PSRM, posterior septal retractor muscle; SE, Septum; ST, stomach.

ventral view of the septum, foot and mouth of *S. brasiliensis*. The muscular septum (SE) is narrow posteriorly and anteriorly, and has an overall length of ~1 mm and a maximum width of ~750 µm. Around the foot (F), left and right halves of the septum are united by a thin SEM. The tip of the foot (F(T)) extends anteriorly towards the mouth (M). Ventrally, the densely ciliated foot, with an overall length (when contracted) of ~300 µm, has a groove that is probably the remnant of a juvenile byssal groove (BG) if, as in many bivalves, such a structure is used for byssal thread production to assist in the establishment of the juvenile in its chosen habitat. The tip of the foot is less densely ciliated and Morton (1981) suggested for *Poromya granulata* that this structure, in addition to being responsible for burrowing, probably also serves to push captured prey items into the mouth and, possibly, seal the opening after such an item is ingested to facilitate digestion. It is likely that the same functions apply to the foot of *S. brasiliensis*.

Allen and Morgan (1981) suggested that within the Cuspidarioidea, species of *Cuspidaria* (only) were characterised by a septum containing four pairs of septal pores. As in *G. coronata* too (Morton et al. 2015), the septum of *S. brasiliensis* is characterised by four pairs of septal pores (SEP(1) to SEP(4)), each of which has a diameter of only ~20 µm. Each of the pores is surrounded by a fringe of cilia, as too are the margins of the

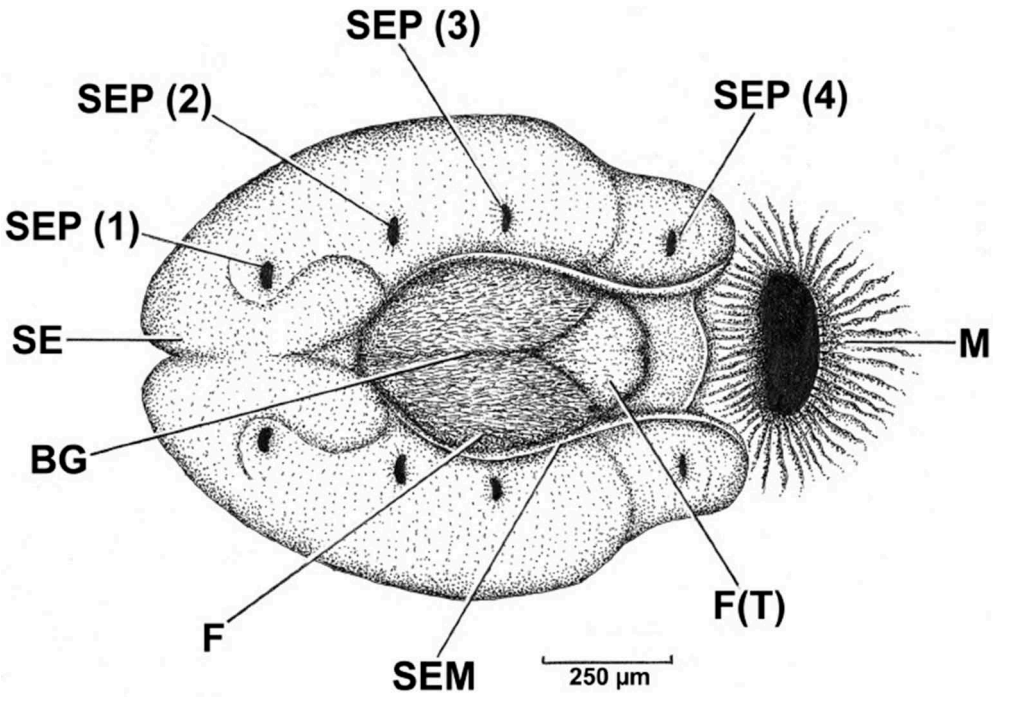

Figure 3. *Spheniopsis brasiliensis*. A ventral view of the septum, foot and mouth. BG, Byssal groove; F, foot; F(T), 'toe' of foot; M, mouth; SE, septum; SEM, margin of septal membrane; SEP(1),(2),(3),(4), septal pores.

septum, each of which has a continuous line of cilia starting from its posteriormost edge and ending near the mouth. A similar ciliary pattern was also demonstrated for *G. coronata* (Morton et al. 2015), and both are only apparent with the SEM. Anteriorly, the septum ends at the mouth (M). The mouth of *S. brasiliensis* (Figure 3, M) has a width of ~250 µm and is pleated around its entire circumference. It has a structure similar to that described for *Halicardia nipponensis* by Nakazima (1967). As in *G. coronata* (Morton et al. 2015, fig. 12), there are no labial palps, which in suspension feeding bivalves process particles of collected seston or detritus prior to ingestion (Stasek 1963). The anteriormost septal pores (SEP(4)) are situated close to the mouth, the remainder being aligned posteriorly and approximately equally along the length of the septum.

The visceral mass

The visceral mass (VM) of *S. brasiliensis* is located between approximately equal-sized anterior and posterior adductor muscles (Figure 2, AAM, PAM). These, in turn, are internally and dorsally demarcated by the anterior and posterior septal and pedal retractor muscles (ASRM/APRM, PSRM/PPRM), as in *G. coronata* (Morton et al. 2015). The visceral mass is almost globular and contains the intestine and the gonads (G). The intestine commences at the mouth (M), which is situated internal to the anterior adductor muscle (AAM) and between and below the points of insertion of the anterior

septal and pedal retractor muscles. This gives rise to a short oesophagus that opens into a capacious stomach (ST) and which is surrounded by the digestive diverticulae (DD). From the stomach's ventral border arises a short crystalline style sac (CSS) containing an equally small crystalline style (CS). The style sac is conjoined with the mid gut (MG) for a short distance, but these soon separate and the mid gut makes a simple loop in the visceral mass to become the hind gut (HG). This extends dorsally and then turns posteriorly to penetrate the ventricle of the heart, which is located inside the pericardium (PE). Within this are the left and right auricles of the heart whose walls are densely infiltrated by the pericardial gland (AU+PEG). The rectum then passes between the paired posterior septal and posterior pedal retractor muscles (PSRM/PPRM) to pass over the posterior adductor (PAM) and terminate in an anus (AN) on this muscle's posterior face.

As illustrated in Figure 2, the stomach of *S. brasiliensis* is capacious, occupying at least one-third of the volume of the visceral mass. A transverse section through the stomach in the region of the conjoined style sac and mid gut is illustrated in Figure 4. This section is approximately halfway along the length of the stomach and shows it to be lined by the gastric shield (GS) that is secreted by distinctive secretory cells (SC) beneath it. From the stomach's ventral border arises the conjoined crystalline style sac and mid gut (CSMG). The style sac (CSS) contains a small, simple-structured, crystalline style (CS). No sorting areas, seen for example in *G. coronata* (Morton et al. 2015) and in cuspidariids, for example *Cuspidaria cuspidata* (Purchon 1956), can be identified in this region of the stomach of *S. brasiliensis*. The stomach also contains small fragments of the remains of ingested prey items (FIPI).

Figure 5 shows transverse sections through the oesophagus, crystalline style sac, mid gut, hind gut and rectum of *S. brasiliensis*, all drawn to the same scale. The oesophagus (Figure 5A) is some 200 µm in diameter, with a deeply folded internal epithelium. This comprises elongate cells that are ciliated for the ventro-lateral two-thirds of the internal circumference. The oesophagus is surrounded by a thick coat of, possibly, collagen (CC). As described earlier, the crystalline style sac (Figure 5B) is about 250 µm in diameter and possesses a small (100 µm) crystalline style (CS). Morton (1969a) described the crystalline style sac of *Dreissena polymorpha* (Pallas, 1771) and showed how its epithelium was separated into four different epithelia. This is not the case in *S. brasiliensis* and the simplified style sac mainly comprises a uniform epithelium of ciliated cells some 20 µm in height, although ventrally it is more pleated.

In contrast to the above two elements of the intestine, the mid gut (Figure 5C) is extremely small, only about 60 µm in diameter, and comprises only about seven ciliated cells in transverse section. Similarly, the hind gut (Figure 5D) is of the same width and also comprises just a few ciliated cells. Finally, the rectum (Figure 5E) has a narrow lumen and also comprises a few ciliated cells.

Figure 6 is a transverse section through the visceral mass of *S. brasiliensis* towards the posterior end of the stomach. Here, the stomach is lined by the gastric shield (GS) completely. This is secreted by an underlying epithelium (SC) of densely granular cells, described earlier for *G. coronata* by Morton et al. (2015). In this location, however, the stomach is packed with the exoskeletal remains of ingested prey items (IPI) and FIPI. Here, the stomach is also surrounded laterally by six gonadial follicles (GF) most obviously comprising fertilised and encapsulated oocytes (EO). Mid ventrally in the visceral mass, there are terminal fibres of the anterior pedal retractor muscle (APRM) and a single digestive tubule (DT). A histological

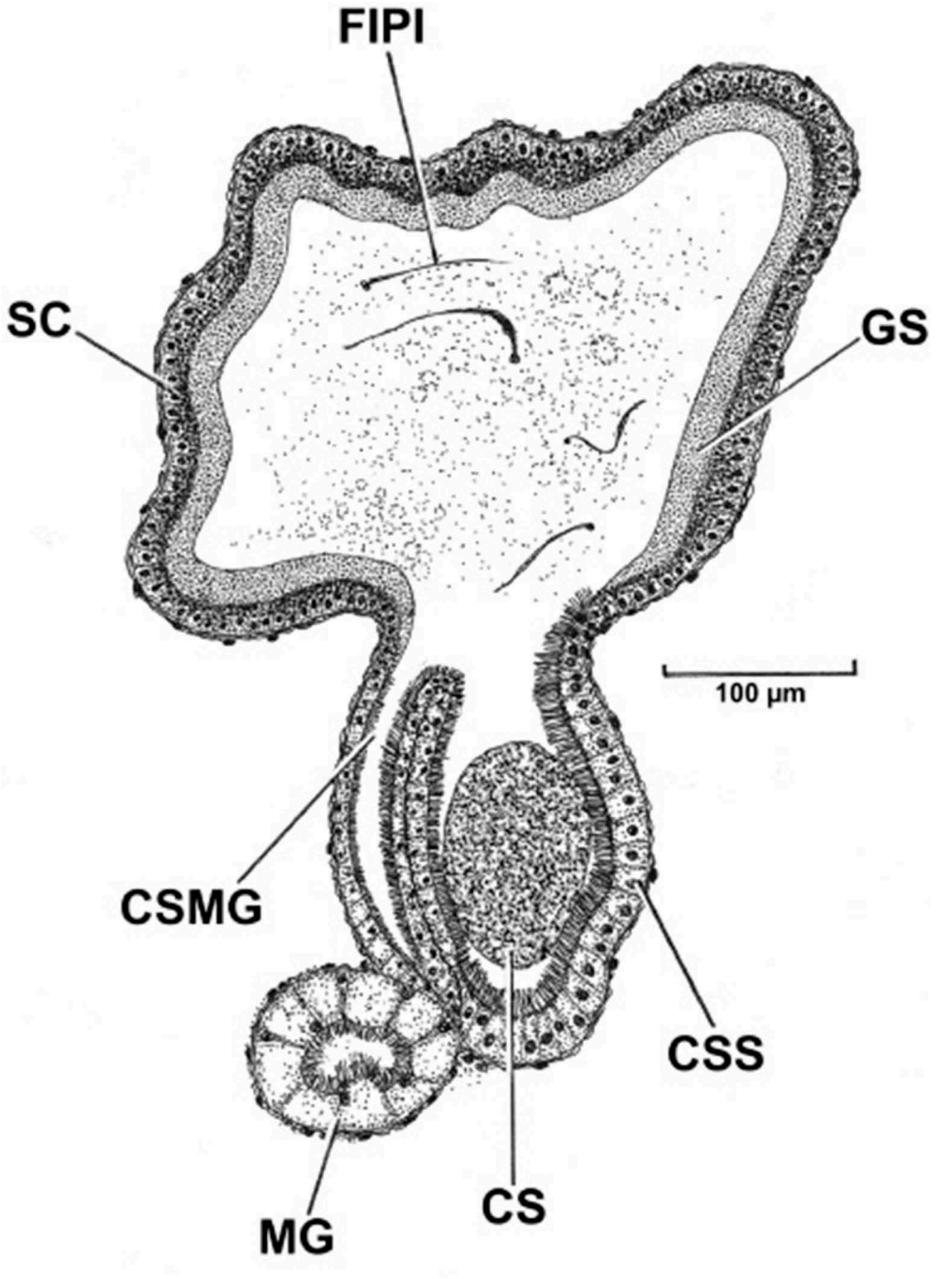

Figure 4. *Spheniopsis brasiliensis*. A transverse section through the stomach in the region of the conjoined style sac and mid gut. CS, Crystalline style; CSMG, conjoined style sac and mid gut; CSS, crystalline style sac; FIPI, fragments of ingested prey; GS, gastric shield; MG, mid gut; SC, secretory cells.

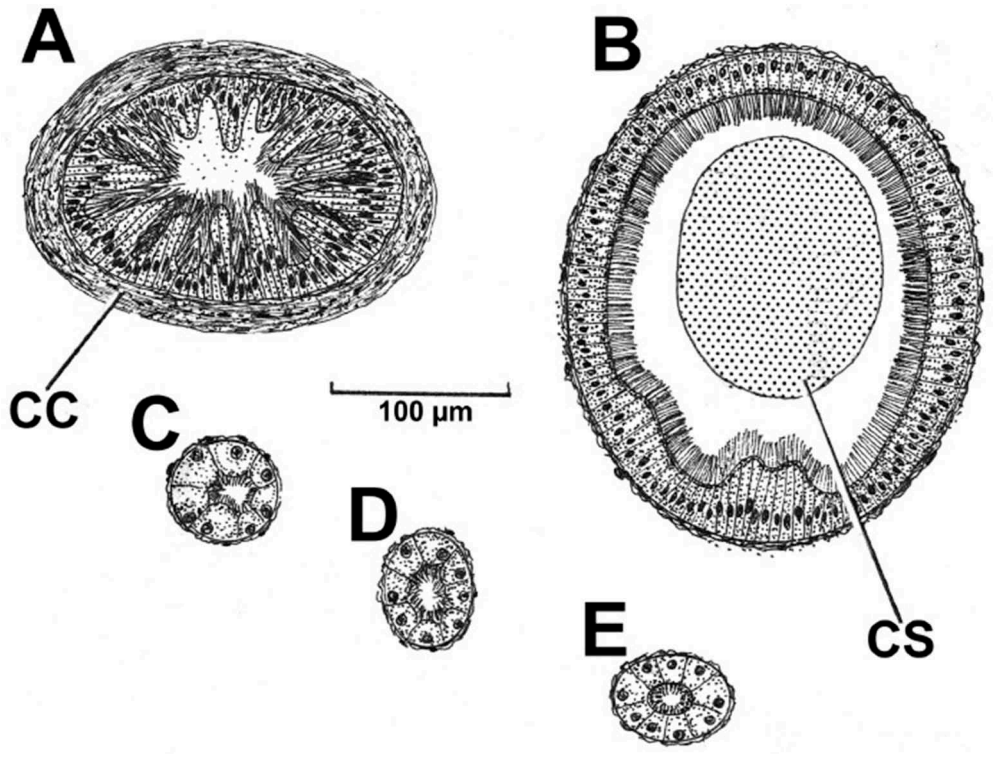

Figure 5. *Spheniopsis brasiliensis*. Transverse sections through the (A) oesophagous; (B) crystalline style sac; (C) mid gut; (D) hind gut; and (E) rectum, all drawn to the same scale. CC, Collagen coat; CS, crystalline style.

section through the visceral mass and IPI in the stomach of *S. brasiliensis* is illustrated in Figure 7A. Figure 7B and C illustrate the remains of captured and ingested ostracods while Figure 7D is the skeletal remains of an unknown prey item.

A transverse section through a single digestive tubule of *S. brasiliensis* (Figure 8) shows it to comprise digestive cells (DC) up to 50 µm in height that contain enormous numbers of vacuoles, each containing spheres of ingested material. Occasionally, there occur crypt cells (CRC) that were thought by Yonge (1926) to be responsible for the production of new digestive cells, although this has never been studied for any predatory bivalve. Large numbers of amoebocytes, occurring as they do throughout the intestine of *S. brasiliensis*, may also serve a role in removing unwanted particles from the gut and transporting them to the haemocoel for eventual abstraction by the pericardial glands.

The statocysts

Also situated in the visceral mass are the paired statocysts. All representatives of the Cuspidarioidea and the other septibranch families are lie-in-wait buried predators. Prey is caught in them all using the inhalant siphon. To achieve prey capture, it is vitally important that all such taxa are oriented correctly within the sediment. As a consequence, all studied species possess paired statocysts (Morton 1985). Figure 9 shows a transverse section

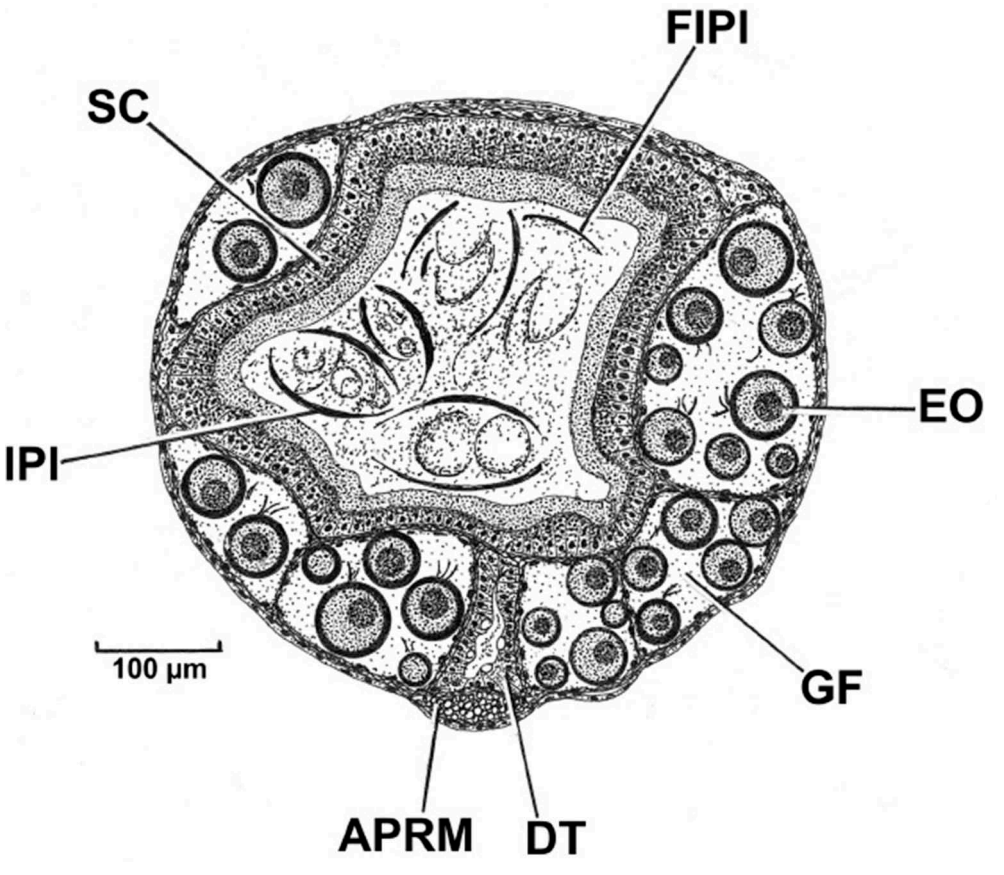

Figure 6. *Spheniopsis brasiliensis*. A transverse section through the visceral mass, towards the posterior end of the stomach and illustrating the disposition of the paired gonads. APRM, Anterior septal retractor muscles; DT, digestive tubule; EO, encapsulated oocyte; FIPI, fragment of ingested prey item; GF, gonadial follicle; IPI, ingested prey item; SC, secretory cells.

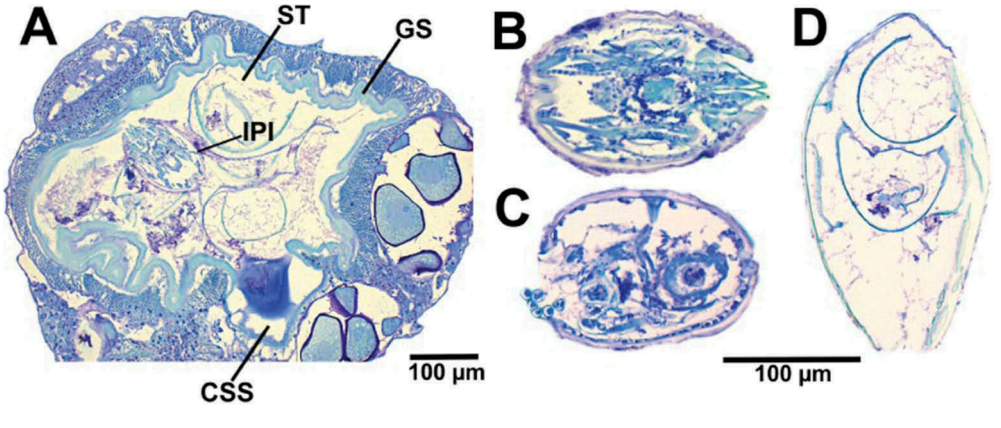

Figure 7. *Spheniopsis brasiliensis*. Histological sections through the visceral mass and ingested prey items. (A) A transverse section through the stomach with ingested prey items inside it. (B, C) The remains of captured and ingested ostracods. (D) The skeletal remains of an unknown prey item. CSS, Crystalline style sac; GS, gastric shield; IPI, ingested prey item; ST, stomach.

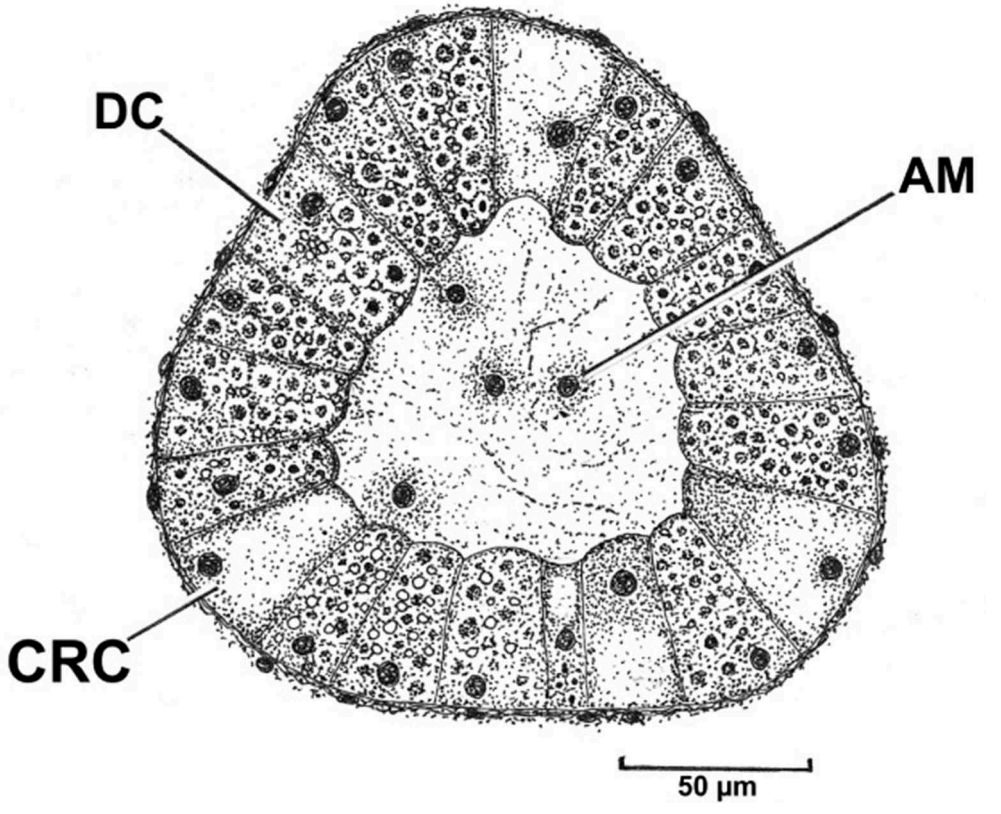

Figure 8. *Spheniopsis brasiliensis*. A transverse section through a single digestive tubule. AM, Amoebocyte; CRC, crypt cell; DC, digestive cell.

through the pedal ganglia and the statocysts of *S. brasiliensis*. The tiny (50 µm) paired pedal ganglia (PEGA) possess a pair of statocysts (STAT), ~30 µm in diameter, that are situated dorso-laterally to them. The statocyst capsules are formed, in transverse section, by ~6–8 vacuolated cells each having a single darkly staining statolith (STL) some 20 µm in diameter in the centre. Morton (1985) examined statocyst structure in numerous representatives of the Anomalodesmata, and those of *S. brasiliensis* are different from those of other species of the Cuspidariidae and the spheniopsid *G. coronata* in which, typically, the statocysts are separate from the pedal ganglia – that is, Type C. Those of *S. brasiliensis* are thus more similar to Type B_1 and were as illustrated for *Poromya granulata* (Nyst and Westendorp, 1839) and *Lyonsiella abyssicola* (G.O. Sars, 1872) among others by Morton (1985, fig. 3c and d). The statocysts of *S. brasiliensis* are, however, in the possession of a strangely complex statolith and vacuolated statocyst cells, also similar to those of *Cuspidaria suganumai* Nomura, 1940 (Morton 1985, fig. 3a) (Type C).

The pericardium, heart and rectum

The location of the pericardium and heart of *S. brasiliensis* is identified in Figure 2. Figure 10 is a transverse section through the heart. The PE is a capacious bag-like structure

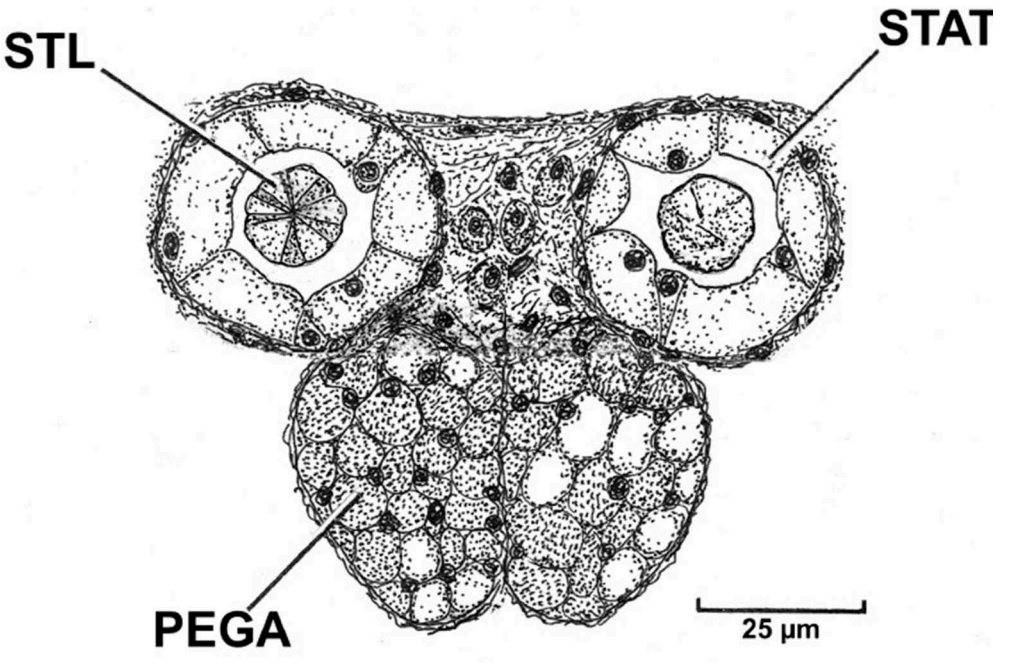

Figure 9. *Spheniopsis brasiliensis*. A transverse section through the pedal ganglia and the statocysts. PEGA, Pedal ganglia; STAT, statocyst; STL, statolith.

containing the heart. This comprises a central, again capacious, ventricle (V) and lateral auricles (AU). Within the ventricle is the rectum (R), which is suspended within the cavity by suspensory membranes (SM), unseen in any other bivalve. The rectum here is filled with amoebocytes (AM). The auricles are similarly capacious and their ventral margins are infiltrated by elements of the pericardial gland (PG). The bivalve pericardial gland is a poorly known bivalve structure that has only been researched anatomically by White (1942) and experimentally in *Dreissena polymorpha* (Pallas, 1771) by Morton (1969b, fig. 3Y), although it was identified for *Cuspidaria cuspidata* by Grobben (1893). It was shown for *D. polymorpha* that ingested particles of colloidal graphite were passed through the intestine and taken by amoebocytes into the blood. They were then abstracted from the blood by the pericardial glands and thereby excreted via the kidneys. This study of *S. brasiliensis* shows that the pericardial gland also seems to be abstracting waste material from the blood, each gland cell containing vacuoles of fine particles.

Figure 11 is a more detailed view of a transverse section through the rectum of *S. brasiliensis*. It shows that the rectum comprises an epithelium of ciliated cells (CI) and minute fragments of prey just a few (1–2) microns in size. In the rectum's lumen are also numerous amoebocytes, which may, it is believed, be abstracting the finest remains of ingested and valuable food fragments.

The reproductive system

The disposition of the paired left and right gonads in the visceral mass of *S. brasiliensis* is illustrated in Figure 7. Each gonad is divided into a number of follicles (GF). Figure 12 is a

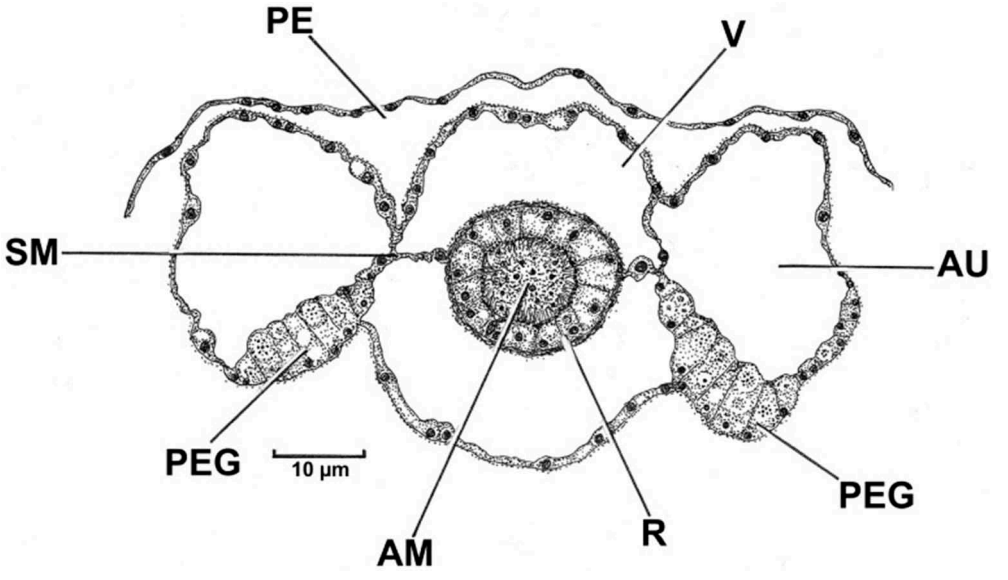

Figure 10. *Spheniopsis brasiliensis*. A transverse section through the heart. AM, Amoebocyte; AU, auricle; PE, pericardium; PEG, pericardial gland; R, rectum; SM, suspensory membrane; V, ventricle.

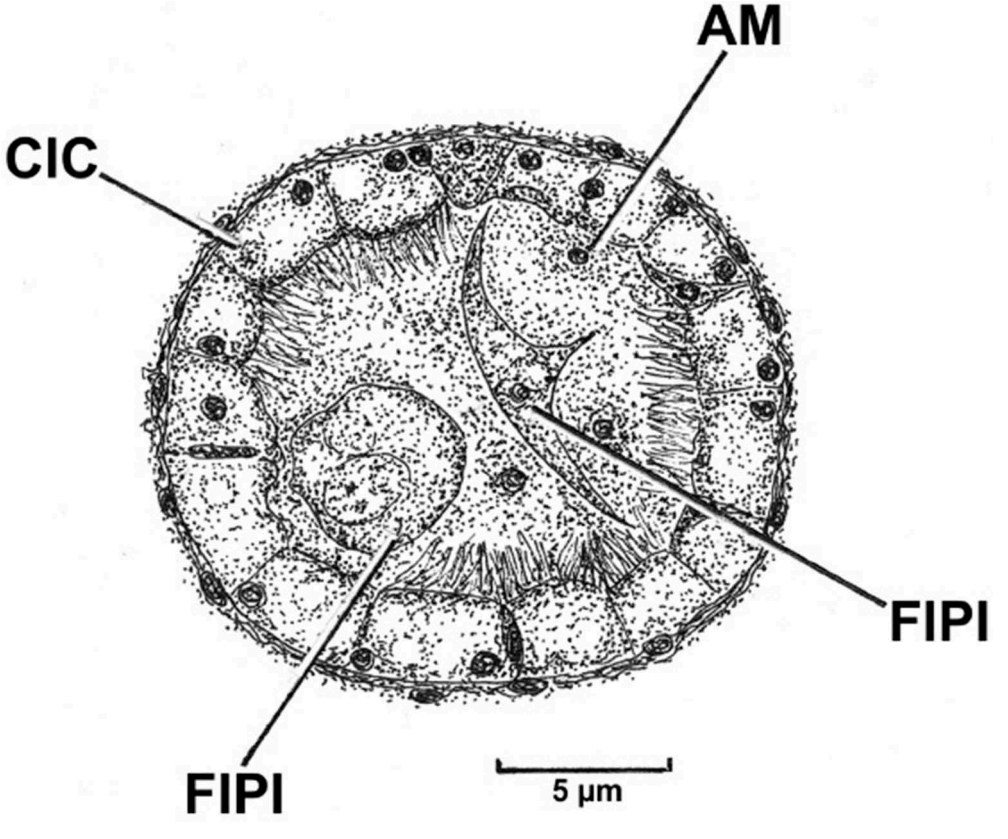

Figure 11. *Spheniopsis brasiliensis*. A transverse section through the rectum, showing minute fragments of ingested and digested prey items. AM, Amoebocyte; CIC, ciliated cell; FIPI, fragment of ingested prey item.

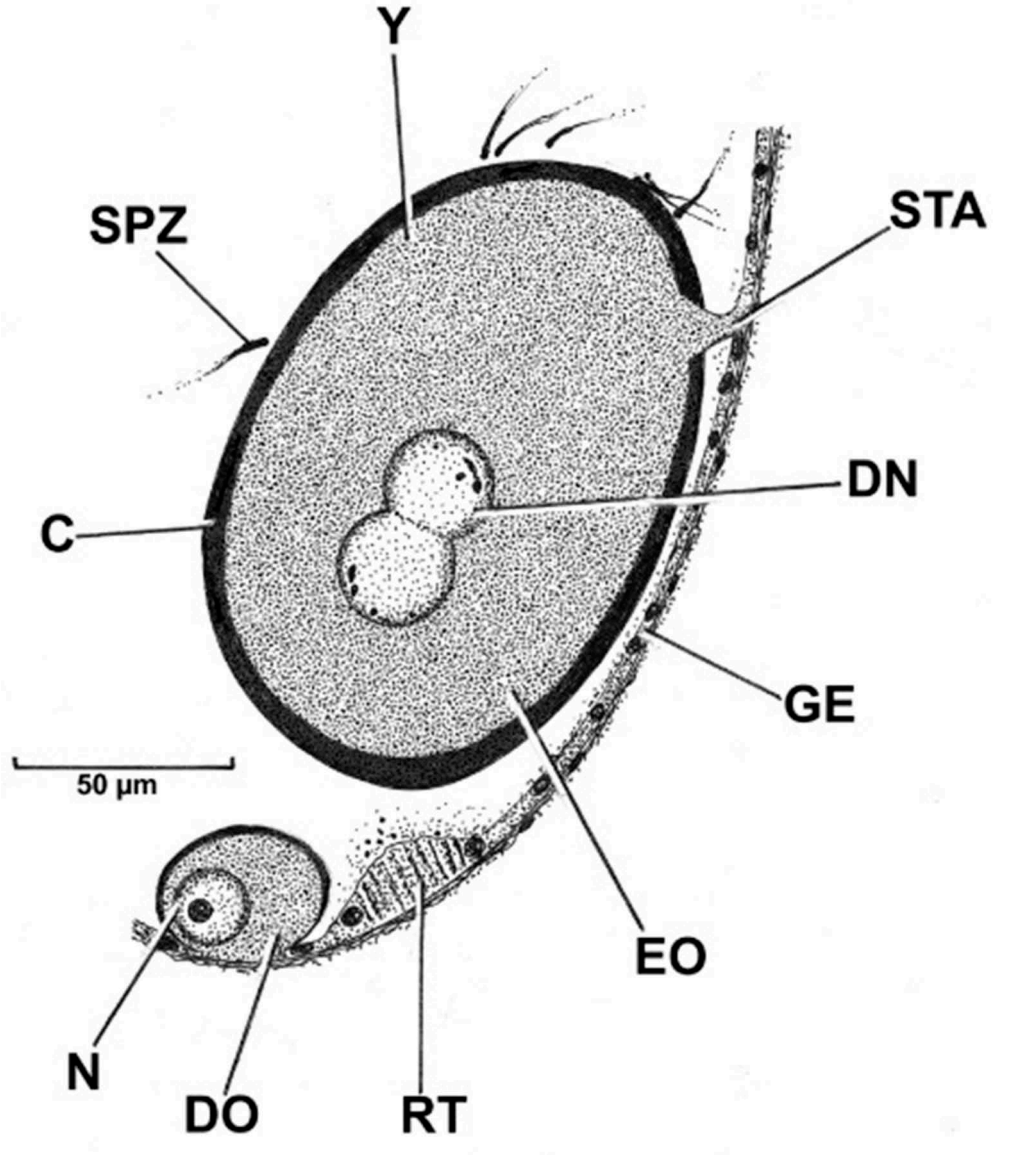

Figure 12. *Spheniopsis brasiliensis*. A section through a portion of a gonadial follicle. C, Cuticle; DN, dividing nucleus; DO, developing oocyte; EO, encapsulated oocyte; GE, germinal epithelium; N, nucleus; RT, regressing testes; STA, stalk; SPZ, spermatozoan; Y, yolk.

section through a portion of a gonadial follicle of *S. brasiliensis*. The gonadial epithelium of the follicles is thin except where developing oocytes (DO) occur, each with a distinctive nucleus (N). There are also patches of mesodermal elements that constitute the testes, which in this individual are apparently in regression (RT). This view is supported by the fact that no un-encapsulated oocytes were identified as being budded off from the germinal epithelium, and few spermatozoa could be identified. Within the follicles of *S. brasiliensis* are encapsulated and, therefore, fertilised oocytes (EO) at various

stages of maturity, including the one illustrated that is still attached to the germinal epithelium by a narrow stalk (STA). Mature oocytes measure up to ~60 µm in diameter and are enclosed in a capsule (C), which also encloses a large yolk reserve (Y). In the mature oocyte illustrated, the nucleus is seen to be dividing (DN), with what are probably chromosomal elements visible. Also within the follicles are a few spermatozoa (SPZ), which have elongate acrosomal heads. The spermatozoa of *Cuspidaria latesulcata* (Tenison-Woods 1878), also with long acrosomal heads, were described by Healeys et al. (2008).

Clearly, the described structure of the gonads of the sectioned individual of *S. brasiliensis* shows that it was fully mature, with no evidence of un-encapsulated oocytes being produced nor any spermatocytes or spermatids in evidence. A few spermatozoa were, however, still present in the follicles but, because all oocytes present were encapsulated, these were in excess of necessity. No oviducts or seminal ducts connecting the paired gonads to the supra-septal chamber have been identified. Similarly, no fertilised oocytes have been identified within the supra-septal chamber, and nor have they been identified for *G. coronata* (Morton et al. 2015).

Discussion

Interest in the Spheniopsidae initially focused on their relationships to other bivalve groups. Initially considered to be related to the Corbiculidae (Gardner 1928), they were placed subsequently in the Cuspidarioidea by Marshall (2002). The anatomical studies of Machado and Passos (2015) and Morton et al. (2015) confirmed this view of affinity and showed that representatives of *Grippina* were amongst the smallest of all deeper water predatory bivalves. The present study also confirms this for *S. brasiliensis*. Morton et al. (2015) clearly identified a cuspidarioid affinity for *G. coronata* but with a sufficiently different suite of characters, such as a non-rostrate shell, a prodissoconch shaped like a crown and a waste storage pouch to the stomach, to warrant inclusion in a separate family – the Spheniopsidae. This investigation of *S. brasiliensis*, however, blurs this distinction because the species has been shown to possess a somewhat rostrate shell and a non-coronate prodissoconch, and there is no waste storage pouch. Similarly, in terms of the hinge plate and shell characters, *S. brasiliensis* is also similar to some species of the genus *Rhinoclama* Dall and E.A. Smith, 1886 (in Dall, 1886) (Cuspidariidae) such as *Rhinoclama abrupta* (Allen and Morgan 1981), *R. notabilis* (Jeffreys 1876), *R. halimera* (Dall, 1886), *R. brevirostris* Powell, 1937, *R. raoulensis* Powell, 1958 and *R. brooki* Marshall, 2002 that also have two teeth in the right valve and an edentulous left valve, plus an overlap between the antero- and postero-dorsal margins of right and left valves as illustrated by Allen and Morgan (1981, figs 42 and 47), Marshall (2002, fig. 13), and Machado and Passos (2015, figs 1D, 2D and F). *Grippina coronata* also has similar shell characters (Machado and Passos 2015). Furthermore, anatomical characters such as the presence of a septum pierced by four pairs of pores, an absence of lateral septal attachments, and siphons with seven sensory papillae (called tentacles by Allen and Morgan 1981 for *Rhinoclama notabilis*) are also shared with other species of *Rhinoclama* (Allen and Morgan 1981, figs 45 and 48) and *G. coronata* (Morton et al. 2015). Such similarities might suggest the removal of *Rhinoclama* from the Cuspidariidae and re-allocation in the Spheniopsidae. On the basis of present knowledge, however, and until

more detailed studies are made of the anatomies of a wider range of cuspidarioids, including species of *Rhinoclama*, such familial affinities must remain speculative.

Notwithstanding, in terms of its reproductive strategy and life-history traits, *S. brasiliensis* is clearly distinct from (the studied) species of *Cuspidaria* and its allies and is closely related to *G. coronata*. This is of taxonomic importance because *Spheniopsis* is the type genus of the Spheniopsidae (Walchner 1851; Gardner 1928; Coan 1990).

Prey capture and digestion

As with the previous study of *G. coronata* (Morton et al. 2015), this study of *S. brasiliensis* identifies it as a predator, mostly of epipsammic micro-crustaceans, notably ostracods. That is, it possesses an inhalant siphon with apically ciliate siphonal papillae/tentacles that are used as mechanoreceptors of vicinal movement. Such behaviour has been elegantly described for the Cuspidariidae by Reid (1978), Reid and Crosby (1980) and Reid and Reid (1974). *Spheniopsis brasiliensis* also possesses a muscular pumping septum with pairs of septal pores. These features too are characteristic of other cuspidarioids (Allen and Morgan 1981), thereby reinforcing alliance with this superfamily.

Like *Halicardia nipponensis* (Verticordiidae) (Nakazima 1967), *S. brasiliensis* possesses no labial palps, a wide funnel-shaped mouth and a foot that is probably used to push inhaled prey from the infra-septal chamber into it and, thereby, also into the wide oesophagus. The stomach is comparatively large (in relation to the rest of the visceral mass) and is used for the processing and digestion of the species' micro-crustacean prey. The cuspidariid stomach was described by Purchon (1956) and Tëmkin and Strong (2013) and that of *G. coronata* was described by Morton et al. (2015). These stomachs all show a remarkable consistency of internal architecture. In this, however, *G. coronata* varies in the possession of a waste storage pouch for the retention until death of the exoskeletal remains of its prey, thereby distinguishing it from the anatomically investigated Cuspidariidae. Conversely, however, *S. brasiliensis* does not possess a waste storage pouch. Instead, it stores the exoskeletal remains of its prey in the posterior end of its capacious stomach. Also, however, the stomach of *S. brasiliensis* seems to lack the sorting areas found in the stomachs of *G. coronata* and the cuspidariids studied hitherto.

This anatomical comparison between *S. brasiliensis* with *G. coronata* is summarised in Table 1. This shows that the two taxa are closely allied such that they are clearly representatives of the same family – the Spheniopsidae. As such, therefore, and as compared with representatives of the Cuspidariidae (Morton 2015a, table 1; Morton et al. 2015, table 1), they are distinct from but allied to this family and, aptly, therefore, both are located in the same superfamily – the Cusopidarioidea. This study of *S. brasiliensis* (and that of *G. coronata*) also exposes a few additional aspects of spheniopsid digestive biology.

Firstly, as with *G. coronata* (Morton et al. 2015), the intestine of *S. brasiliensis* is extremely narrow, with each component possessing a minute cilia-fringed lumen. It is clear that in neither species can significant fragments of exoskeleton be transported through it save for, as shown herein, the minutest of pieces. Instead, it appears that largely non-skeletal waste is transported in this way for discharge at the anus. Secondly, this study suggests that amoebocytes are used as a means to scavenge even this

Table 1. A morphological and life-history comparison between *Spheniopsis brasiliensis* and *Grippina coronata* (After Machado and Passos 2015; Morton et al. 2015; this study).

Characters	*Spheniopsis brasiliensis*	*Grippina coronata*
The shell		
Length and shape	Up to 2.6 mm, subtrigonal, posteriorly somewhat rostrate	Up to 1.8 mm, ovate-trigonal, posteriorly truncate (arostrate)
Umbones	Slightly prosogyrate	Prominent, orthogyrate
Prodissoconch I	Small, circular and smooth	Large, pronounced with two central elevations
Prodissoconch II	Not visible	Not visible
Micropits in the outer surface	Present, randomly distributed, absent in the prodissoconch	Present, randomly distributed, absent in the prodissoconch
Hinge teeth	Right valve with two diverging teeth; left valve edentulous	Right valve with two diverging teeth; left valve edentulous
Ligament	Amphidetic, located on resilifers	Amphidetic, located on resilifers
Lithodesma	Present	Present
Internal anatomy		
Foot	Short, stubby, pedal/byssal groove present	Short, stubby, pedal/byssal groove present
Byssus	Possibly present in the post-larval	Possibly present in the post-larval
Siphons	Separate (Type B)	Separate (Type B)
Siphonal papillae/tentacles	Seven: four around the inhalant, three around the exhalant	Seven: four around the inhalant, three around the exhalant
Byssus		
Ciliated sensory papillae	Present	Present
Arenophilic glands	Absent	Absent
Mantle fusions	Type B	Type B
Musculature	Isomyarian	Isomyarian
Septal retractor muscles	Present	Present
Septal pores	Four pairs	Four pairs
Pedal musculature	Present but reduced	Present but reduced
Labial palps	Absent	Absent
Stomach type	Type II	Type II
Waste storage pouch	Absent	Present
Intestine	Short	Short
Style sac and mid gut	Conjoined	Conjoined
Rectum	Penetrates ventricle of heart	Penetrates ventricle of heart
Suspensory rectal membranes in the rectum	Present	Absent
Statocysts	Type C	Type C
Life history trait		
Recorded depth range	17 to 148 m	21 to 53 m
Life habit of	Sedentary predator	Sedentary predator
Food habit	Carnivorous	Carnivorous
Prey	Micro-crustaceans, possibly ostracods	Harpacticoid copepods, possibly ostracods
Sexuality	Simultaneous hermaphrodite	Simultaneous hermaphrodite
Fertilisation	Internal, self-fertilising	Internal, self-fertilising
Development	Direct	Direct
Brooding	Internally	Internally
Larval release mechanism	Post mortem	Post mortem

material, Figures 10 and 11 showing these wandering cells within the rectum. Similarly and thirdly, any such scavenged waste material must find its way to the blood and eventually, therefore, the heart and, as suggested by White (1942) and experimentally determined by Morton (1969b), the pericardial gland. The function of this gland, sometimes referred to as Keber's organ, has never been resolved satisfactorily but it was thought by White (1942) and Morton (1969b) to filter the blood. That is, any material removed from the blood by the glands would be released into the pericardial fluids and these, containing the unwanted material, would eventually find their way to the kidneys

via the reno-pericardial apertures and thereby be excreted from the kidneys at the left and right renal apertures. It is, however, a sad reflection upon the researches of the deep-water predatory bivalves that the only paper that discusses any aspect of their physiology was by Reid (1978).

Finally, this study suggests that there is a continuum in terms of the types of prey captured by the rostrate species of the Cuspidariidae, the partly rostrate *S. brasiliensis* and the arostrate *G. coronata*, as follows. Figure 13 illustrates prey capture by (A) *G. coronata*, (B) *S. brasiliensis* and (C) *Cuspidaria rostrata*, all drawn to the same scale and with possible prey items also identified. Morton et al. (2015) showed that *G. coronata* fed principally on harpacticoid copepods and ostracods. This study of *S. brasiliensis* shows how a major component of the diet includes ostracods (Figure 8B and C). Although Reid and Reid (1974) did not identify any natural prey items of *C. rostrata*, they illustrated this species capturing a cumacean (Figure 1), and Bernard (1974, table on p. 13) also identified crustaceans and a cumacean from the diet of species of *Cuspidaria*. It thus seems possible that cuspidarioids select prey in relation to (1), its swimming or crawling habit and (2) the length of the rostrum and contained inhalant siphon. The arrows also show how development of the rostrum has allowed deeper residence in the sediments, perhaps for their own protection from surface-roving predators.

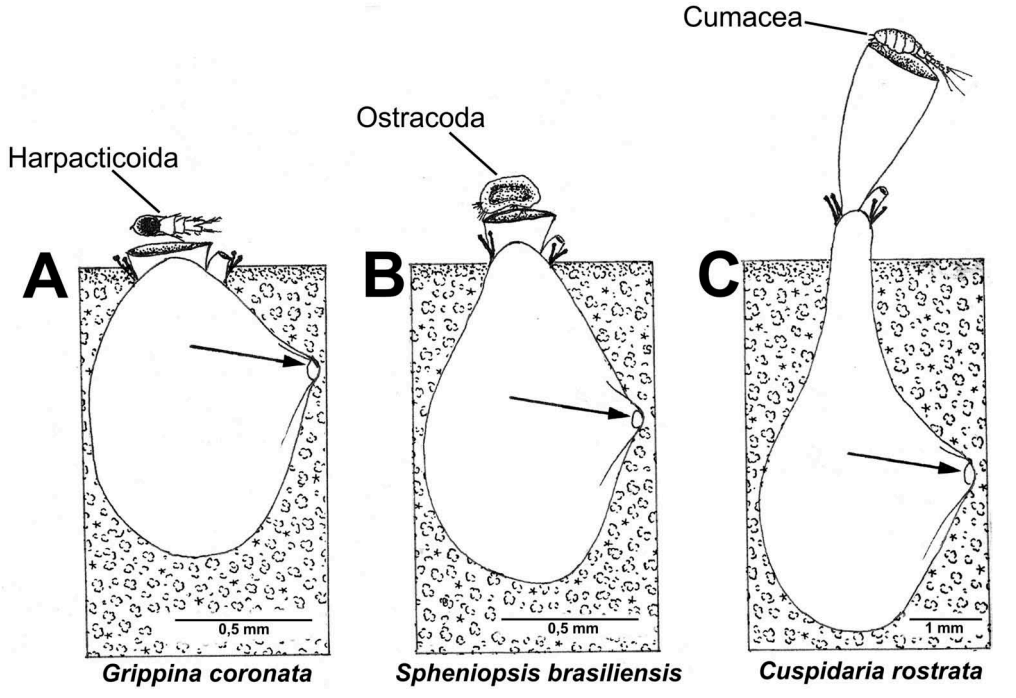

Figure 13. Illustrations of prey capture by (A) *Grippina coronata*; (B) *Spheniopsis brasiliensis*; and (C) *Cuspidaria rostrata*, all drawn to approximately the same scale. (A redrawn partly after Morton et al. (2015, fig. 24 C) and C redrawn partly after Reid and Reid (1974, fig. 1). Possible prey items are also identified. The arrows show how evolution of the rostrum has allowed deeper residence of the sediments presumably for enhanced protection.

Life-history trait

At < 3 mm in shell length, it seems likely that *S. brasiliensis* does not live for long. The same conclusion was reached for the yet smaller (< 1.8 mm shell length) *G. coronata* by Morton et al. (2015). Recent studies by Morton (2012, 2015b) on two other deeper water and similarly miniature (3 mm) bivalves, that is *Nucula pusilla* Angas, 1877 (Protobranchia) and *Neolepton salmoneum* (Carpenter 1857) (Neoleptonidae), respectively, showed that these also brooded fertilised oocytes, seemingly putting all energy into reproduction and parental care rather than into growth and longevity. Small species of shallow-water (26–75 m depth) cyamids, such as *Cyamiocardium domaneschii* Passos and Machado, 2014 (< 3 mm), also provide a good example of parental investment in their offspring by incubating their eggs until the juvenile stage (Passos and Machado 2014). The reproductive strategies and life-history traits described for the minute *G. coronata* and *S. brasiliensis* are also similar to those of the deep-water species of *Microgloma* (Protobranchia: Pristoglomidae) described by Sanders and Allen (1973) and, for which, at any one time, only two mature oocytes occur in left and right ovarian follicles. These authors attributed this reduction in egg numbers to the small size of these protobranchs such that, as a consequence, they are unable to produce large numbers of planktotrophic larvae. This is a situation which, it seems, may characterise other small (millimetre scale) deep-water bivalves including, as herein demonstrated, species of the Spheniopsidae – albeit with interfamilial diversity reflecting their differing phylogenetic origins.

The life-history trait expressed by *G. coronata* and *S. brasiliensis* (summarised in Table 1) with the release of fertilised and encapsulated oocytes and, it is believed, the digested exoskeletal remains of their prey resulting from parental death, however, introduces an even more dramatic life-history trait into the suite of such characters being slowly developed for the deeper-living Bivalvia. Such post-mortem semelparity and univoltism in these two tiny predatory spheniopsids constitute a digestive and reproductive life-history trait hitherto unseen in the Bivalvia, and which is apparently unique to them. Their cuspidariid cousins apparently possess an altogether simpler suite of traits, although the detailed anatomies of many of these species, particularly with regard to their reproductive strategies, remain unstudied.

Disclosure statement

No potential conflict of interest was reported by the authors.

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