Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 125(3): 679-688. **November 2019**

PALEOECOLOGY AND FUNCTIONAL MORPHOLOGY OF THE PERMIAN LYTTONIID BRACHIOPOD *PIRGULIA*

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To cite this article: Stadtmauer D. & Butts S. (2019) - Paleoecology and functional morphology of the Permian lyttoniid brachiopod *Pirgulia*. *Riv. It. Paleontol. Strat.*, 125(3): 679-688.

Keywords: Semi-infaunal; brachidium; conical ventral valve; active filtration; pseudopunctae.

Abstract. The lyttoniid brachiopods of the Permian exhibit a unique valve morphology: a branched lobate structure takes the place of the dorsal valve. In one group of lyttoniids, the genus *Pirgulia*, the ventral valve wraps around to form a cone that fully encloses the lobate structure. This has consequences for the dynamics of water flow and mode of life possible for these heteromorphic brachiopods. Here, we describe the skeletal microstructure and morphology of *Pirgulia* collected from the Upper Permian Sosio Limestone megablocks of Sicily and housed at the Yale Peabody Museum. We reconstruct the paleoecology of *Pirgulia*, characterizing it as semi-infaunal in soft sediment. By analogy to *Richthofenia*, the conical ventral valve and flapping dorsal valve functional morphology could have resisted fouling and assisted feeding in this environment. By comparison with the functional morphology of *Pirgulia* with other lyttoniids and richthofenids, we propose a revised mode of life for this genus, which involves adaptation to secondary soft-bottom substrates and support by sediment sticking. Despite constraints to the fundamental brachiopod body plan, modification of the valves in *Pirgulia* to achieve a conical morphology allowed it to inhabit a paleoecological niche distinct from that of other reef-building lyttoniids.

INTRODUCTION

The family Lyttoniidae is a group of productide brachiopods that were common during the Permian. Lyttoniids are remarkable for their aberrant morphology, with a branching lobate structure that serves as the dorsal valve, generally leaving much of the ventral valve inner surface exposed. Having gone extinct by the end of the Permian, they have no close modern relatives, nor are there many adequate analogues for their morphology among extant fauna (Rudwick & Cowen 1967). As such, much effort has been directed into reconstructing the functional morphology of these unique brachiopods.

Lyttoniid shell shapes vary from cup or scoop-shaped (*Leptodus, Oldhamina,* and *Poikilosakos*) to subconical (*Eolyttonia* and *Choanodus)* or fully conical (*Pirgulia*). Based on the presence of a cicatrix of attachment, most are thought to have cemented to hard substrates such as reefs, rocky bottoms, or clasts, including skeletal debris. Reconstructions for the angle of attachment range from completely vertical to completely horizontal. Scoop-shaped lyttoniid shells are often found attached to one another and based on the orientation of multiple-shell assemblages, these taxa have been reconstructed as cemented in a vertical orientation (Seilacher 2013) or at a semi-reclining angle resulting from deflected shell growth away from the cementation disc formed early in development (Stehli 1956).

The Yale Peabody Museum (YPM) holds a small collection of brachiopods, including lyttoniids, from the Upper Permian Sosio Limestone of Sicily, collected by G. Bonafede of Palermo

Received: April 11, 2019; accepted: August 21, 2019

and given to Charles Schuchert in 1936. They were collected from within the Sosio megablocks that crop out three km from the Palazzo Adriano ("Pietra de Salomone" megablock of Flügel et al. 1991; 37.660653°, 13.382482°, uncertainty = 1.3 km radius). The assemblage also includes ammonoids, fusulinides, crinoid fragments, sponges, corals, and other brachiopods (orthide, orthotetide, productide, rhynchonellide, spiriferide, spiriferinide, and terebratulide species). The lyttoniids had been previously catalogued as *Leptodus fasciculata* and *Leptodus princeps*. However, based on the conical wrapping of the ventral valve and similarity with those described by Verna et al. (2010) from Tunisia, we place these in the genus *Pirgulia* sp. (species undetermined). *Pirgulia* also occurs in the Lower Permian of Thailand (Yanagida 1967) and the Upper Permian (Guadalupian) of Tunisia (Verna et al 2010, which also contains a comprehensive taxonomic history of the genus).

Lyttoniid brachiopods have a unique morphology characterized by a lobate dorsal valve with rib-like processes, resembling a ptycholophe support, which correspond with ridges, or septa, in the ventral valve. *Pirgulia* is morphologically like other lyttoniids in being inequivalve with a lobate dorsal valve. Whereas most lyttoniids have two valves parallel or subparallel to the commissural plane, *Pirgulia* has lateral margins which wrap around the dorsal valve and converge dorsally to form a conical ventral valve, like the trail of some productides (*Proboscidella*, Muir-Wood & Cooper 1960). It bears morphological similarity, and therefore possibly functional similarity, to richthofenioids in its conical shell, although it differs in the orientation of the dorsal valve relative to the ventral valve (parallel in lyttonioids and perpendicular in richthofenioids). The goal of this study was to use various techniques to examine the functional morphology of the modified valves to infer the lifestyle of the *Pirgulia*. Serial sections were used to examine shell structure and internal morphology and to infer the relationship to substrate and feeding methods.

BIOLOGY AND GROWTH OF THE LOBATE STRUCTURE AND LOPHOPHORE

Due to the strong similarity with the outline of the dorsal valve, virtually all reconstructions propose that the lobate structure supported a ptycholophous lophophore (Williams 1953; Stehli 1956; Rudwick & Cowen 1967). The dorsal valve structure consists of two submedian primary lobes that branch out periodically into secondary lobes that are equally spaced from one another (Rudwick & Cowen 1967). A submarginal groove present on the ventral side of the lobate structure, termed a flange by Watson (1917) or vallum by Cooper and Grant (1974: 385), has been proposed as the point where the lophophore would have attached (Stehli 1956). In this orientation, cilia occupying the gaps between lobes could have filtered water passing or pushed through. The large number of lobes to this theoretical lophophore at adult size would outnumber known extant examples, but is otherwise like modern ptycholophes (Williams 1953).

On the other hand, the homology of the lobate structure with standard brachiopod anatomy is controversial. The interpretation that is perhaps most parsimonious, and most consistent with the structure's function, is that it is a modified dorsal valve. Under this interpretation, abnormal structure of the valve may be explained by proposing a derived method by which the dorsal valve could have been deposited to achieve this shape. Based on the study of ontogenetic series of lyttoniids and apparent teratologies, Rudwick (1968) devised an ontogenetic growth model where the dorsal valve develops by controlled accretion and periodic branching. Patterns of growth lines suggest that the lobes of the dorsal valve grew independently by accretion on the distal edges, increasing in length but not in width, and expanded over ontogeny by addition of secondary lobes but not by enlargement (Rudwick & Cowen 1967; Rudwick 1968). That is, juvenile lyttoniids had fewer lobes of approximately the adult size rather than small multilobed structures (Rudwick & Cowen 1967).

However, an alternative interpretation of the lyttoniid lobate dorsal valve is that it is actually an internal skeleton-like structure of spicular calcite homologous to a brachidium (lophophore support), extending from a reduced true dorsal valve that articulates posteriorly at the hinge (Termier & Termier 1949). Williams (1953) proposed that the lobate dorsal valve structure was entirely encased in mantle tissue, with cirri extending from a ptycholophous lophophore mirroring the lobes. Observation of the microstructure of the dorsal valve in thin section revealed an internal pseudopunctate secondary layer and no primary layer, except in the posterior region in the false interarea. This triangular structure at the posterior was identified by Williams (1953) as a vestigial remnant of the true dorsal valve, based on the restriction of the putative primary layer to this area, and the presence of remnants of a cardinal process and denticular sockets. While the lyttoniids appear to be functionally bivalved, that interpretation makes them anatomically univalved.

A similar case has been reported in *Falafer*, a small cooperinid brachiopod that is preserved with a corresponding calcified ptycolophous brachidium. Grant (1972) used *Falafer* to argue by analogy that the lyttoniid lobate structure is also a brachidium. Secondary lateral lobes that support a ptycholophe could have evolved from a form with two primary lobes that supported a schizolophe (Williams 1953; Grant 1972), thereby paralleling the development of a ptycholophe from a simpler schizolophe (Rudwick 1962).

METHODS

All specimens used for this study are housed in the Yale Peabody Museum (New Haven, CT, USA). Specimens studied are *Pirgulia* from Sosio, Italy (locality described above). Comparative material included the lyttoniids *Leptodus* and *Collemataria* and the richthofeniid *Richthofenia* from the Permian of West Texas, from the Guadalupian (Word Fm.) and Leonardian (Bone Spring Fm.) and *Oldhamina* from the Salt Range of Pakistan. Specimens from the Permian of West Texas are silicified. All comparative material was free from matrix, so microfossil and lithological analyses were not possible. All material is available for study. Macrophotography was performed with a Canon EOS 60D camera with a 60 mm EF-S macro lens. Z-stacking was performed using the Cognisys StackShot rail on a Kaiser copy stand with incandescent light and stacked using Helicon Focus version 6.7.1 Pro.

Computerized Tomography (CT)

Two specimens (YPM IP 238672 and YPM IP 238678) from the Sosio Limestone, Palermo, Italy, were CT scanned (Harvard University, Cambridge, MA). Due to the similarity in mineral composition of the shell and the infill matrix, the visual contrast was insufficient to reveal the microstructure and disposition of the two valves.

Serial Sectioning

Standard unpolished serial sections were prepared both parallel (YPM IP 238672 and YPM IP 238678) and perpendicular (YPM IP 238677) to plane of symmetry by Vancouver GeoTech Labs, Richmond, British Columbia, Canada. Serial thin sections were viewed using a Leica M205 C Fusion Optics Stereo Microscope with a Leica DMC4500 camera using Leica Application Suite X Version 3.0.7.19082.

Abbreviations

YPM, Yale Peabody Museum; Fm., formation.

RESULTS

Ventral valve morphology

The ventral valve of *Pirgulia* forms a rugate cone which completely encloses and obscures the dorsal valve from the exterior (Fig. 1A). The dorsal

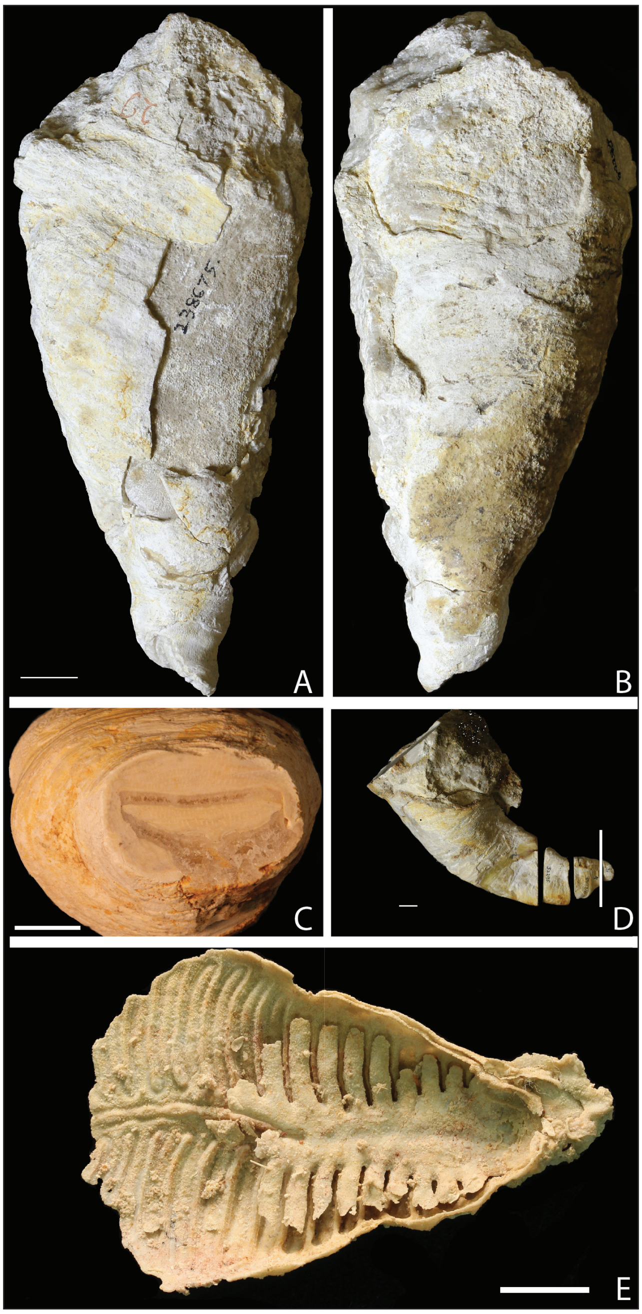

Fig. 1 - *Pirgulia* sp. from the Yale Peabody Museum Schuchert Collection A) YPM IP 238675, dorsal view, scale bar is 1 mm. B) YPM IP 238675, ventral view, showing partially exfoliated ventral valve bearing lobate structure, scale bar from 1A. C) cross section of YPM IPS 002295 with dorsal valve indicated with arrow, and D) specimen YPM IPS 002295 indicating the location of the cross section in Fig. 1C. E) YPM IP 036782, *Leptodus* sp., showing the morphology of a typical lyttoniid dorsal valve.
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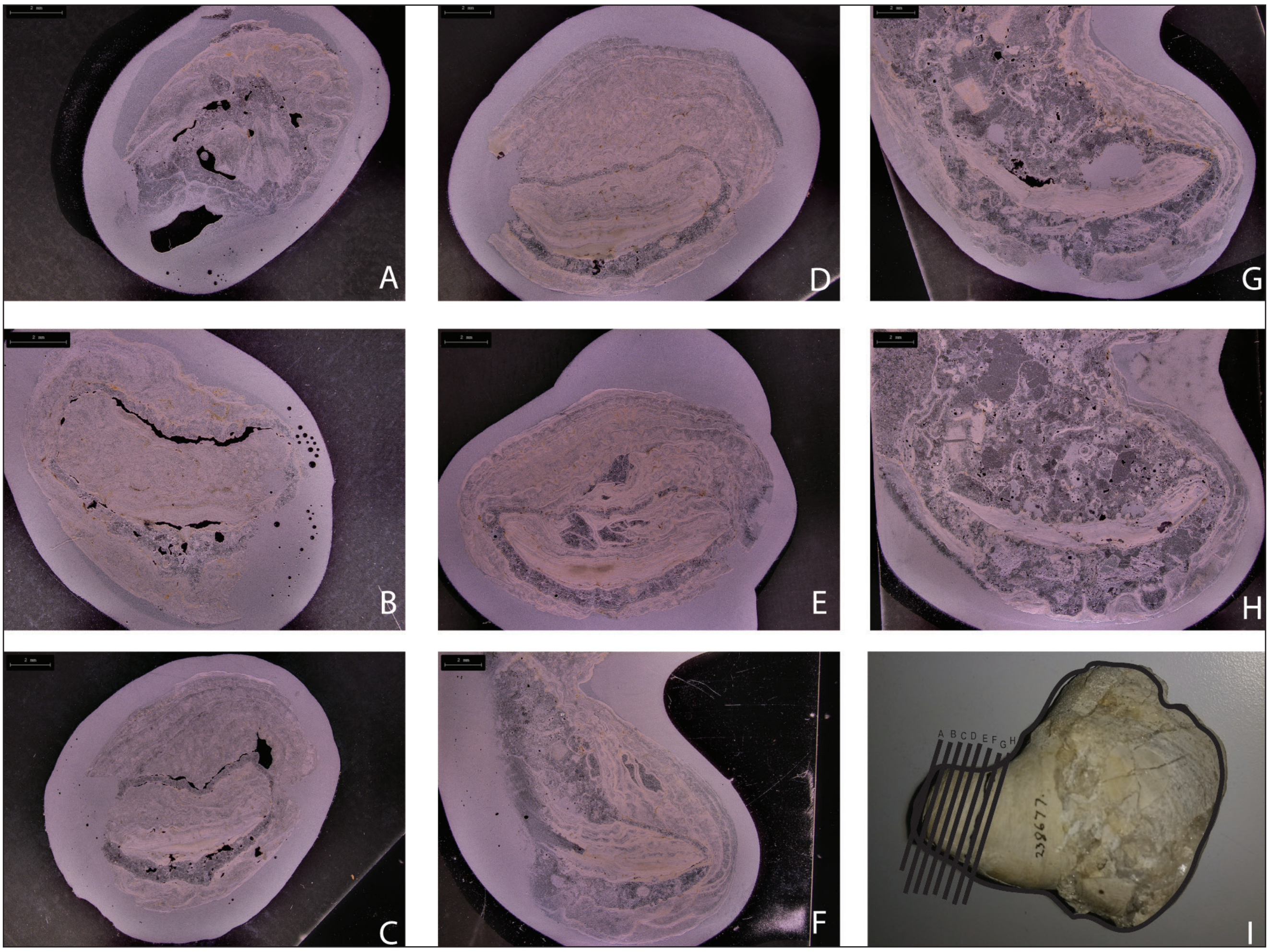

Fig. 2 - Serial sections of *Pirgulia* sp., YPM IP 238677, showing the orientation of the dorsal valve relative to ventral valve, shell microstructure, infill matrix, and torsion of ventral valve. Approximate position of thin sections noted on specimen (prior to sectioning) in Fig. 2I.

extension of the ventral valve to create a conical shell shape matches reports in Sicilian lyttoniids (Rudwick & Cowen 1967). Specimens in which part of the ventral valve is exfoliated show the lobate pattern indicative of the septa (Fig. 1B). In cross section, the dorsal valve has a concave flexure and is nested in the ventral valve (Fig. 1C; Fig. 1D shows the location of the cross section). In serial sections of YPM IP 238677 (*Pirgulia* sp.), cut approximately perpendicular to the direction of growth (Fig. 2), it is possible to see the position of the dorsal valve relative to the ventral valve. The shell exhibits irregular torsion around the longitudinal axis, which suggests that the growth direction shifted throughout growth of the organism. We find no evidence of a cicatrix for attachment, even on specimens where the hinge is well-preserved, and no specimens are found cemented to other *Pirgulia* (although specimens were not observed in situ). The lack of an attachment surface (and lack of rhizoid spines, which can accompany the attachment surfaces), differentiates *Pirgulia* from the other lyttoniidines and the richthofenioids, their most morphologically similar relatives.

Dorsal valve morphology and apposition

Thin sections reveal lobes in the dorsal valve that are gently arched toward corresponding callused shell on the ventral valve, forming the septal apparatus. Although a disarticulated dorsal valve was not available in any of the *Pirgulia* specimens at YPM, it would likely have a similar disposition the dorsal valve in *Leptodus* (Fig. 1E), shown here with dorsal valve overlying a broad slightly flexed ventral valve. As viewed in thin section, the callused ridges of *Pirgulia* correspond to septa in the ventral valve which interdigitate with the lobes of the dorsal valve.

The gaps between the lobes of the dorsal valve are relatively consistent in size, as evidenced by imprints of the ventral valve septa on some exfoliated specimens. The two primary lobes are fused at the posterior end. The edges of the dorsal valve lobes are marked by a submarginal groove on the ventral side, which may have supported the lophophore (Stehli 1956). The fusion of the submarginal grooves of the two adjacent primary lobes in specimens where the primary lobes are close together forms a median incision (Rudwick 1968).

Shell structure

Pirgulia specimens were sectioned and examined directly by light microscopy, and thin sections were prepared to examine shell microstructure. The dorsal valve exhibits pseudopunctae (Fig. 1C), that give the surface a pustular texture made up of small rosettes (Williams et al. 2000: 310). Connected to the pseudopunctae appear to be taleolae, rods of calcite permeated by networks of organic material (Williams & Brunton 1993). More pseudopunctae appear to emerge from the dorsal side of the dorsal valve than from its ventral side. The layers accrete and form two convex primary lobes, the sides of which meet in the median of the ventral side of the valve to form the median incision. Primary shell is observed in the posterior region of the dorsal valve; the shell is otherwise secondary.

Discussion

Shell structure

One aim of studying the valve microstructure was to generate new evidence using different methods and taxa (the conical *Pirgulia*) to address the assertion made by Williams (1953) that the lack of a primary shell layer on the dorsal lobate structure implies that it was fully internalized. The laminar secondary shell layer that makes up the majority of both the ventral valve and the dorsal lobate structure was readily evident and resembled the texture from Williams' (1953) figures. Primary shell on the external surface of the ventral valve is expected to be thin, only around 10-100 μm (Williams 1997: 268). The fact that it was not confidently identified may have resulted from its failure to be preserved in the specimens studied, which is commonplace.

Pseudopunctae are evident under direct observation of sections by light microscopy (Fig. 3). The pseudopunctae appear to be the calcitic taleolae characteristic of the aberrant productides, and which are thought to have evolved independently in multiple strophomenate groups (Williams & Brunton 1993; Williams 1997: 305-309). Pseudopunctation is a trait in strophomenate brachiopod shells and therefore its presence is not surprising, but there is a possibility that the distribution of pseudopunctae may infer properties of the mantle-mediated shell deposition. One proposed function of pseudopunctae is as a holdfast for mantle tissue (Williams 1997: 310-311). This would imply that surfaces directly in contact with mantle would have more pseudopunctae penetrating the surface. Although both valves exhibit pseudopunctation throughout (Fig. 3A), pseudopunctae in contact with the surface of a valve are concentrated on the dorsal side of the dorsal valve (Fig. 3B-D) and the inner surface of the ventral valve (Fig. 3E-F). Curiously, this is different from what would be expected if the lobate structure is a normal valve, in which case mantle tissue would be expected on the ventral side but not the dorsal side. However, the apparent asymmetry in the distribution of pseudopunctae also does not fit perfectly with the theory by Williams (1953) of complete mantle tissue enclosure of the dorsal valve, as pseudopunctae would be expected to serve as holdfasts on the ventral side of the structure as well. It is possible that the presence of a lophophore on the ventral side of the lobate structure affects the growth of mantle tissue, or if cells in the submarginal groove are indeed involved in lophophore attachment, this may limit mantle growth. In the posterior shell, the dorsal and ventral valves appear similar in structure and we confirm the presence of taleolar pseudopunctae, consistent with the theory that at least the posterior dorsal structure is a normal brachiopod valve. However, more anterior sections also exhibited similar typical productide secondary layer microstructure, making it difficult to support theories that the rest of the lobate structure is a modified brachidium or internal calcified skeleton. Based on our findings in YPM specimens, we cannot reject the hypothesis that the lobate structure is merely a modified valve rather than a novel internal skeleton. Going forward, better resolution from sections at more locations along the antero-posterior axis will be helpful in testing this provocative theory more rigorously.

Musculature

Lyttoniids have very little in the way of identifiable sites of attachment for diductor muscles,

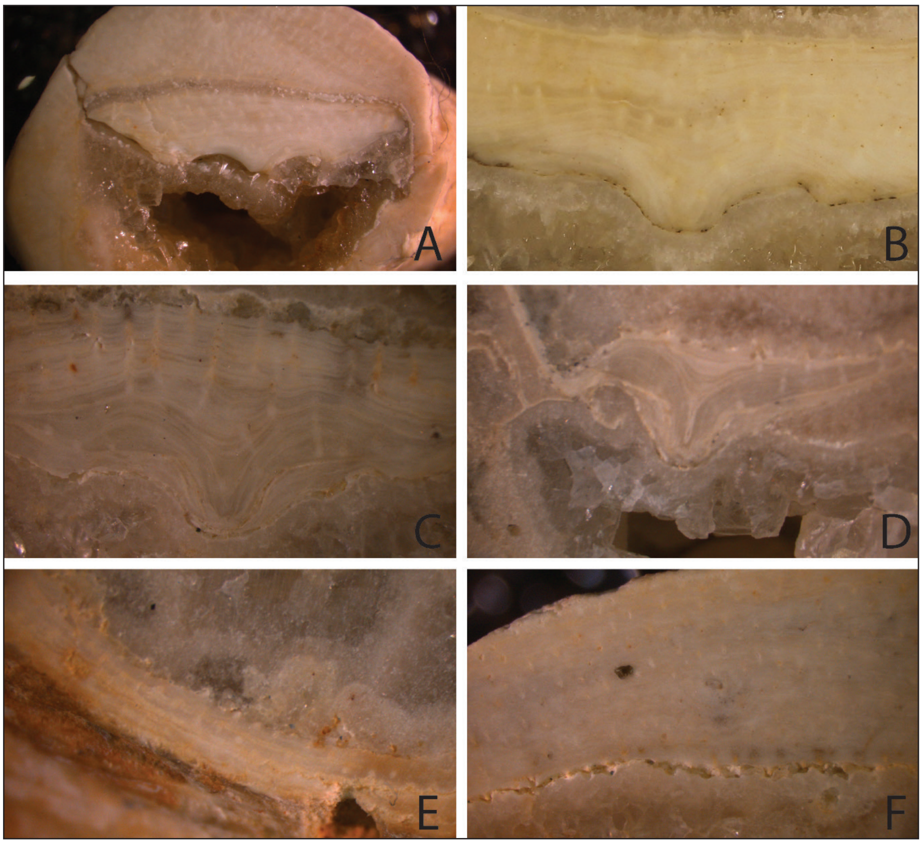

Fig. 3 - Pseudopunctae in *Pirgulia* sp., YPM IP S-2295, showing dorsal and ventral valve structure (A), dorsal valve (B-D), and ventral valve (E-F) from cut and polished specimens. Within these three groups, images are ordered from posterior to anterior slices. Dorsal side is upward in all images. Red arrows mark the places where pseudopunctae (calcitic taleolae) protrude from the surface of a valve. The dorsal valve exhibits growth lines and a median incision made up of the meeting of the two primary lobes (C-E). Scale, width of image is A) est. 6 mm (specimen fragment was prepared as serial longitudinal thin sections), B) 5 mm, C) 3.5 mm, D) 8 mm, E) 6.5 mm, and F) 6 mm.

which led Williams (1953) to suggest that lyttoniid musculature was atrophied and weak. Later work used phylogenetic inference and the potential identification of muscle scars on lyttoniids to support the presence of developed muscle (Stehli 1956; Rudwick & Cowen 1967). Stehli (1956) argued that reduced but still functional musculature was necessary due to the extreme shallowness of the shell that is characteristic of oldhaminids, because without active movement, their gape would have been insufficient for passive filtration. This formed the basis of the active "flapping valve" model for feeding by rhythmic movement of the dorsal valve (Fig. 4A) (Rudwick & Cowen 1967; Cowen 1975), for which the need for well-developed musculature and energetic cost were primary points of criticism (Grant 1972). If musculature was indeed developed, Stehli (1956) argued that its presence is incompatible with the dorsal valve being a mantle-enclosed structure, although Grant (1972) pointed out that muscles attaching posteriorly could have moved the lobate structure even if it was fully enclosed in tissue and not homologous to a true valve.

Alternatively, Seilacher (2013) reconciled the apparent absence or atrophy of diductor musculature with the need for active motion by proposing that the role of a diductor muscle was accomplished by a ligament between the dorsal and inner ventral valves. This ligament would have stored energy upon ventral valve closure for a quick reopening and made active filtration possible whereas slow (smooth) diductor muscles were limiting (Seilacher & Gishlick 2014: 214). The ligament, in this model, was proposed to be made of an extension of mantle tissue from the dorsal side of the dorsal valve, therefore linking it with the Williams (1953) model and providing a mechanism for active filtration with a tissue-enclosed valve. The observation that many *Leptodus* are preserved with shells in an open state and at a consistently small angle was given as support for this hypothesis (Seilacher and Gishlick 2014: 214); however, other fossil evidence for this theory is poor. Muscle presence and strength are considerations in assessing theories of active filter feeding, but were not observable based on the preservation of our specimens.

Paleoecology and functional morphology

The lifestyle of *Pirgulia* was inferred from morphology, microstructure, and by analogy to other organisms. Based on attachment scars, most lyttoniids are thought to have been attached by cementation to hard substrates such as reefs, rocky bottoms, or invertebrate skeletal debris (Stehli 1956; Seilacher 2013); the *Pirgulia* examined in this study exhibited no cicatrix, apical spines, or other signs of attachment. The absence of signs of a fixed sessile lifestyle, deviating from both the richthofenioids and from other lyttoniidines, led us to investigate types of secondary soft-bottom dwellers (Seilacher 2005) as a potential lifestyle for *Pirgulia*. Secondary soft-bottom dwellers lack functional pedicles/pedicle openings and have functional morphologies that point to resting, passive stabilization, or anchoring on soft substrates. Three modes of secondary soft-bottom lifestyles are recliners, passive implanters, and sediment stickers (Seilacher & Gishlick 2014). Thin sections of *Pirgulia* did not reveal any shell deflections, thickening or ballasting of the ventral valve (as in Seilacher 2005), nor keel (Seilacher et al. 2008) which would support a theory of secondary soft bottom reclining. Passive implanters also bear thickening of the shell in the umbonal region (Seilacher & Gishlick 2014: 206). Despite the aberrant morphology of *Pirgulia* not producing the typical umbonal region of a typical biconvex brachiopod, there is still no shell thickening in the area that would have been embedded in the sediment in the manner of a passive implanter. In *Pirgulia*, the shell is relatively uniform in thickness, externally rugate, and exhibits torsion throughout the growth of the organism. These characters are suggestive of an organism which inhabited low-energy environments characterized by deposition of mud or fine sediment, in which the organism grew upwards to keep up with sedimentation, a lifestyle facilitated by the presence of a conical shell ("sediment sticking" of Seilacher & Gishlick 2014: 187). The conical shells described by Seilacher and Gishlick (2014) are achieved by expansion of interarea and umbonal region (for example, on an othothetide), rather than a true conical shell, but the conical ventral valve is better adapted to this lifestyle, since there is less possibility of fouling via burial of the gape. Although apical attachment to the substrate may have occurred in the juvenile to support initial growth, the thinness of the *Pirgulia* ventral valve suggests that the surrounding sediment was likely the primary support system for the organism. Rudwick and Cowen (1967) suggested that the conical forms would have laid flat on top of substrate, but the potential for such an orientation to quickly bury an organism with this shape, and the irregular torsion of some *Pirgulia* specimens, suggest otherwise. The rugosity of the ventral valve would have provided additional purchase in accumulating sediments during growth. Torsion of the conical shell would have slightly reoriented the aperture relative to sedimentation, but those deflections were insufficient to preclude functioning of the dorsal valve.

For lyttoniids like *Leptodus*, reconstructions for the angle of attachment range from completely vertical to completely horizontal. Attachment to substrate in most lyttoniids is often established by root lamellae of the ventral valve and through cementation at the hinge or along the ventral valve. Seilacher (2013) reconstructed the scoop-shaped lyttoniids as building reefs of individuals that stick out of a hard substrate in subparallel arrays. Alternatively, Rudwick and Cowen (1967) agreed that vertical attachment to hard surfaces was feasible for juvenile *Lyttonia* "Form B" (mentioned as *Pirgulia* therein and reclassified as *Pirgulia* per Verna et al., 2010), but argued that due to their lack of spines, adults would have been secondarily free-lying. Interpretation of assemblages of multiple individuals and of different ontogenetic stages in situ, when preserved in life position, is one of the best methods for determining these different reconstructions.

Several functional explanations for the unique morphology of lyttoniids have been proposed. Rudwick (1961) first used the aberrant morphology of *Prorichthofenia* (now classified as *Richthofenia*) to exemplify the paradigm method for reconstructing function, in which he proposed a flapping valve functional morphology. Later, Rudwick and Cowen (1967) applied this method to the aberrant lyttoniids as well and suggested a similar flapping valve mechanism. Rudwick and Cowen (1967) proposed that the unique dorsal valve of lyttoniids aided in active filter feeding by rhythmic movement. The conical ventral valve divided the shell into two chambers. Flapping both passed water through the lophophore as it moved between the chambers and created negative and positive pressure moving current in and out of the aperture of the cone. One potential difficulty with this model is the tendency for recirculation of already filtered water within the end of the cone. Active filtration was supposedly necessary due to the shallow angle of opening (Stehli 1956; Rudwick & Cowen 1967; Seilacher & Gishlick 2014: 284).

In contrast to the flapping valve model, in which filter feeding occurs as water passes between the dorsal valve lobes as it opens and closes, Williams (1953: 284) and Grant (1972) proposed that filter feeding in the scooplike or subconical lyttoniids was achieved simply by water passing through troughs formed by the septal apparatus of the ventral valve. In this passive filtration model, water entered the distal ends of the ventral valve secondary troughs, passed by lophophore cilia protruding from the lobes, and left via the two primary troughs of the median incision. This more closely approximates the function of a normal ptycholophe, and differs from Rudwick and Cowen's model (1967), where active closure of the dorsal valve pushes water through the narrow gaps between the lobes and food is filtered by cilia reaching between the lobes (Fig. 4B). To support this model, Williams (1953: 284) suggested that the septal apparatus on the ventral valve served to prop up the dorsal valve from below to ensure a steady flow of water through the troughs. However, we find instead that the septal ridges commonly fall between, rather than directly under, the dorsal valve lobes (e.g. Fig. 1E), resulting in a tighter closure that may have precluded the flow of water in this manner.

It has also been suggested that the lyttoniids housed photosymbionts, analogous the modern giant clam *Tridacna* supporting photosynthetic Zooxanthellae (Cowen 1970). The theoretical necessities of photosymbiosis can be analyzed through comparison with a model paradigm (sensu Rudwick 1961), but such a trait generally leaves little trace in the fossil record. However, photosymbiosis and active filtration are not necessarily exclusive, for example, the mixotrophic lifestyle of *Gigantoproductus,* determined through biogeochemical signatures of symbionts (Angiolini et al. 2019).

Our findings for *Pirgulia* valve morphology are consistent with the flapping valve functional morphology proposed for richthofenioids (Rudwick 1961) and modified for lyttoniids (Rudwick and Cowen 1967). The flapping valve behavior is most effective when the ventral valve completely encloses the dorsal valve, because water is pushed through the lobes on both adduction and diduction. The dynamics of water flow to the lophophore via flapping are potentially complicated by the fact that *Pirgulia* exhibits complete ventral valve enclosure, and has the conical form of a richthofeniid com-

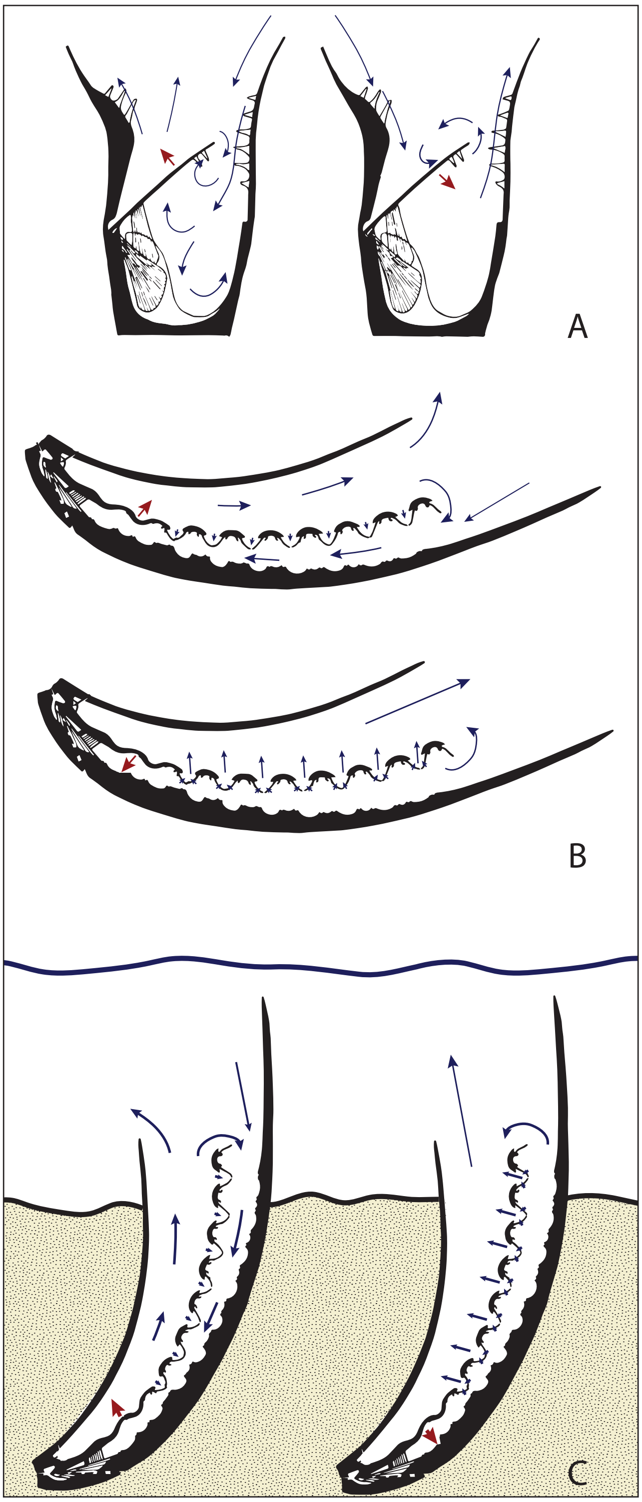

Fig. 4 - Water flow models in lyttoniid and richthofeniid morphologies A) *Sicularia* (*Richthofenia sicula*) with inflow phase with dorsal valve opening (top) and filtering phase with dorsal valve closing bottom. Modified from Fig. 17 of Rudwick and Cowen (1967). B) Water flow model for with inflow phase with dorsal valve opening (top) and filtering phase with dorsal valve closing (bottom). Modified from Fig. 23 from Rudwick and Cowen (1967) C) Re-interpretation of flow regime of reclining semi-infaunal *Pirgulia* based on this analysis of functional morphology. Blue arrows indicate direction of water flow (smaller blue arrows indicate flow near the lophophore), red arrows indicate direction of valve movement.

bined with the dorsal valve orientation of a lyttoniid. However, this morphology also makes active contraction of the dorsal valve even more valuable not only for feeding but also as a way to remove sediment (Fig. 4C).

We infer that the conical shape of *Pirgulia* is derived with respect to other lyttoniids like *Leptodus* and *Poikilosakos* that were open scoops. The fully conical ventral valve is not widespread among productides, occurring in *Pirgulia* and *Richthofenia*, although several subconical or cup-shaped forms exist, as well as innovations like apron trails. That said, there may be a general trend within lyttoniids towards wrapping around of the ventral valve, as subconical morphology appears to have evolved multiple times in both the Lyttoniinae (e.g. *Eolyttonia, Keyserlingia,* and *Loxophragmus*) as well as in their sister clade the Poikilosakinae (*Pseudoleptodus* and *Choanodus*) (Williams et al. 2000: 635-637). Wrapping around of the ventral valve may have functioned as a protective dorsal covering within this clade of uniquely exposed brachiopods. It also could have adjusted the circulation of water within the valve to enable the flapping valve as a feeding mechanism. If *Pirgulia* indeed lived stuck in soft sediment, the combination of lophophore-driven water flushing and dorsal valve flapping with the conical ventral valve morphology would have played an important role in preventing fouling and could have been used to flush sediment from the corpus. Understanding the morphological evolution of the highly modified lineage *Pirgulia* helps contextualize wider lyttoniid evolution and convergent patterns in other biomineralizing species.

***Pirgulia* in context of lyttoniid evolution**

A substantial difference between the morphology of the scoop-shaped (*Leptodus*; Rudwick & Cowen 1967) and conical (*Pirgulia*; Williams et al. 2000: 634-635) morphologies is the complete enclosure of the dorsal valve by the ventral valve. Of the specimens in this study, all of the conical forms identified were collected from the Sosio megablocks of Sicily, but others have reported both scoop-shaped and conical forms in multiple localities including West Texas (Williams et al. 2000: 634-635); thus, both forms were widespread and coexisted.

Potential adaptive hypotheses for the evolution of conical ventral valve morphology from planar-convex “scoops” or vice versa are numerous. Polarity of this trait between *Leptodus* and *Pirgulia* is not absolute, but the conical morphology is not widespread among lyttoniids, occurring only in *Pirgulia,* with *Pseudoleptodus*, *Chaoella*, and *Choanodus* having subconical ventral valves that wrap around partially (Williams et al. 2000: 635-637). *Poikilosakos*, the oldest known lyttoniid, is also a small and scoop-shaped form. If the conical shell is indeed derived, it may have arisen for protection from predation, as a secondary reacquisition of protective dorsal covering after this feature was lost from the ancestral brachiopod body plan by modification of the dorsal valve into the lobate structure. Notably, if the superposition of valves in *Leptodus* leaves exposed mantle tissue on the ventral valve (as in Williams 1953), the conical ventral valve resolves this issue. In the flapping valve model of Rudwick and Cowen (1967), the conical extension of the ventral valve functions to create a semi-closed chamber wall for the dorsal valve to push water against to direct flow between the lobes. There was presumably a benefit to losing this protective function in the first place, such as better access to current for filter feeding or even access to light to host photosymbiotic organisms (Cowen 1970). The conical and scoop-shaped lyttoniids may therefore represent different niches or modes of life possible with this modified dorsal valve morphology, and there need not be a single reconstruction for mode of life for all lyttoniids.

The heteromorphic morphology of the lobate dorsal valves of lyttoniid brachiopods has been a topic of debate and speculation for more than 100 years (e.g. Watson 1917). Numerous theories for their functional morphology exist (summarized in Williams et al. 2000: 619-630), and the purpose of this study was to study the Yale specimens through the lens of these theories in order to test their plausibility. Initial microstructural analysis of the dorsal and ventral lyttoniid valve structures has identified pseudopunctate lamellar secondary shell layers in both dorsal and ventral valves and shown structural similarity of the lobate structure to the ventral valve. On the other hand, the presence of pseudopunctae emerging on the dorsal side of this structure suggest that it may have had mantle tissue on this side, unlike a normal valve. Ongoing analysis of these and other microstructural data should allow for the reassessment of the hypothesis by Williams (1953) of the lobate structure being an internal skeleton and the dorsal valve being reduced to a posterior support. The conical shell is conducive to flow of water and prevention of fouling via lophophore-mediated flow and flapping of valves, although whether that was accomplished by the action of muscles or a functioning ligament is still unclear. By comparing the functional morphology of *Pirgulia* (aberrant amongst the aberrant brachiopods) with other lyttonioids and richthofenioids, we are able to provide a revised mode of life for members of this genus which involves adaptation to secondary soft-bottom substrates and support by sediment sticking. This peculiar group of brachiopods has the potential to become a study case in fundamental evolutionary issues such as homology and the processes by which drastic morphological innovation can occur.

Acknowledgments: This research was conducted initially as an independent term project (by D.S.) for the Yale College course Invertebrate Paleontology, which benefited from constructive comments from Professor Derek E. G. Briggs, Department of Geology and Geophysics and Yale Peabody Museum, Yale University. The authors appreciate thoughtful reviews from Lucia Angiolini, David A.T. Harper, and Francisco Sour-Tovar.

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