Efficient Ornamentation in Ordovician Anthaspidellid Sponges

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ABSTRACT

Lithistid orchoclad sponges within the family Anthaspidellidae Ulrich in Miller, 1889 include several genera that added ornate features to their outer-wall surfaces during Early Ordovician sponge radiation. Ornamented anthaspidellid sponges commonly constructed annulated or irregularly to regularly spaced transverse ridge-and-trough features on their outer-wall surfaces without proportionately increasing the size of their internal wall or gastral surfaces. This efficient technique of modifying only the sponge's outer surface without enlarging its entire skeletal frame conserved the sponge's constructional energy while increasing outer-wall surface-to-fluid exposure for greater intake of nutrient bearing currents. Sponges with widely spaced ridge-and-trough ornament dimensions predominated in high-energy settings. Widely spaced ridges and troughs may have given the sponge hydrodynamic benefits in high wave force settings. Ornamented sponges with narrowly spaced ridge-and-trough dimensions are found in high energy paleoenvironments but also occupied moderate to low-energy settings, where their surface-to-fluid exposure per unit area exceeded that of sponges with widely spaced surface ornamentations.

Keywords: lithistid sponges, Ordovician radiation, morphological variation, theoretical morphology

INTRODUCTION

Early sponge communities found in lower and middle Cambrian strata are divided into two types of communities: siliciclastic deep shelf or basin spiculate communities and carbonate platform archaeocyath communities (Carrera & Botting, 2008). Isolated lithistid demosponge spicules from the spiculate sponge community were reported at the base of the Cambrian (Braun & others, 2007). Whole-fossil lithistid sponges appeared later in middle Cambrian to Early Ordovician shallow-water limestones. Adaptations developed by these lithistid sponges included cemented attachments and interlocking spicules in triangulated nets, which allowed lithistids to occupy shallow environments including reef settings. Anisotropic triangulated skeletal nets in Early Paleozoic lithistid orchoclad sponges from the family Anthaspidellidae Ulrich in Miller, 1889 were constructed from siliceous desma spicules known as dendroclones (Finks, 2003a; Finks & Rigby, 2004). The entire sponge body consisted of a rigid skeletal framework of triangulated spicule compartments resistant to compression, comprising the elongate tubular to conical shape assumed by most anthaspidellids. Anthaspidellids from the Cambrian Burgess Shale in British Columbia, Canada, and anthaspidellids from Sirius Passet, Greenland, appear to have first occurred and diversified in platform settings (Botting & Peel, 2016). Basal whole-body lithistids such as the thin-walled anthaspidellid Capsozonia Rigby, 1986 together with Fieldspongia Rigby, 1986 from the late middle Cambrian (Series 3, Drumian Stage) Burgess Shale in British Columbia, Canada (Rigby, 1986) imply an earlier record of similar sponges. These relatively thin-walled taxa may have originated in sheltered positions within platform environments before becoming robust enough to cope with full-wave exposure. As lithistid sponges developed structure robust enough to maintain rigidity in agitated waters, they began to invade reef environments in the middle to late Cambrian following the demise of archaeocyaths (Carrera & Botting, 2008). The oldest recognized anthaspidellid sponge, Rankenella Kruse, 1983, occurred in the early middle Cambrian (Series 2, Stage 4) Ranken Limestone of Australia where it is interpreted to have occupied habitats in an anaerobic, low-energy shelf area of limited circulation (Kruse, 1996). During the middle Cambrian (Series

These scattered Cambrian, Series 3–Furongian anthaspidellid reef buildups were precursors to the widespread lithistid buildups found in lower to middle Ordovician rocks where anthaspidellid sponges were important reef constituents (Toomey, 1970; Rigby, 1971; Church, 1974; Webby, 2002; Wang, Deng, & others, 2012; Hong, Choh, & Lee, 2015). The robust nature of anthaspidellid skeletal construction was advantageous for occupying widespread environments subject to mechanical disruption during the Ordovician radiation (Carrera & Rigby, 1999). Carrera and Rigby (2004) attributed development of environments suitable for sponge occupancy during the Early Ordovician to an abundance of hard substrates and microbial structures related to seawater chemistry changes and to incursion of nutrient-rich waters from deep basin or inner platform settings during the late Tremadocian transgression. The availability of high-energy shallow water ecological niches on Early Ordovician shelves in turn likely influenced the concurrent development of robust skeletal characteristics in lithistid sponges (Finks, 2003b). Anthaspidellid sponges persisted in shallow water environments until their replacement by other suspension feeders in shallow water ecological niches and the establishment of middle Paleozoic reef ecosystems dominated by tabulate and rugose corals, stromatoporoids, and other sponges. By middle to late Devonian, lithistid sponges had become more common in deeper water communities or in low-energy shallow settings (Wood, 1999; Copper, 2001).

While many lithistid orchoclad sponges maintained a relatively smooth outer-wall surface, several anthaspidellid sponges added ornaments to their external form as they occupied high-energy shelfal habitats during the Ordovician radiation. Low-amplitude gently undulating walls first appeared in the thin-walled anthaspidellid *Capsospongia* from the late middle Cambrian (Series 3, Drumian Stage) Burgess Shale in British Columbia, Canada (Rigby, 1986). During lithistid orchoclad sponge expansion in the Ordovician, anthaspidellids constructed additional ornaments, including nodular surfaces, vertically ribbed surfaces, and most commonly, annulated irregular to regular transverse ridge-and-trough surfaces (Bassler, 1941; Johns, 1994; Finks & Rigby, 2004). Anthaspidellid sponges from at least seven genera added annulated surface modifications to their outer skeleton walls while retaining relatively smooth gastrical surfaces. Annulated or transverse ridge-and-trough surfaces are prominent in the genus *Archaeoscyphia* Hinde, 1889, which is perhaps the most widely distributed and easily recognized anthaspidellid sponge in the Ordovician, represented here by *Archaeoscyphia minganensis* Billings, 1859 (Fig. 1), but also occur in *Rugocoelia* Johns, 1994; *Jiangshania* Bingli & others, 1997; *Anthuspidella* Ulrich & Everett in Miller, 1889; *Nevadocoelia* Basoller, 1927; *Rhopalocoelia* Raymond & Okulitch, 1940; and *Patellispongia* Basoller, 1927. Annulated sponge outer walls range from weakly ridged to distinctly or strongly ridged surfaces. Johns (1994) described exterior dermal features in the distinctly annulated *Rugocoelia* minganensis Johns, 1994 as ridges and troughs with predictably consistent dimensions and noted such features to be genetic characters for *Rugocoelia* (Fig. 2).
The annulated sponge *Anthaspidella annulata* Beresi & Rigby, 1993 has inconsistent ridges or annulations 6–8 mm apart in the lower or early growth stage of the sponge increasing to regularly-spaced ridge-and-trough features 9–11 mm apart and 6–7 mm high in the upper portion of the sponge. The ornately annulated *Archaeoscyphia pulchra* (Bassler, 1927) (Fig. 3) has lowermost annulations that are relatively minor (2–3 mm high and wide), which widen and increase in amplitude towards the uppermost part of the skeleton where they extend up to 25 mm laterally from the sponge (Johns, 1994; Rigby, Nowlan, & Rowlands, 2002).

**METHOD OF STUDY**

Ornamented features of anthaspidellid sponges from seven genera were studied using dimensions of ornamentations reported in the literature and measured specimens located in the Brigham Young University Paleontological Museum. The possible utility of ornamented outer walls to anthaspidellid sponges was evaluated through a simple mathematical analysis to determine their increased surface exposure to nutrient-bearing currents relative to a defined planar surface area. Morphological variation of sponge surface ornamentations related to facies-based interpretation of paleoenvironments were analyzed and categorized using a theoretical morphospace analysis.

**HABITAT-RELATED MORPHOLOGY IN ORNAMENTED SPONGES**

The capacity for morphological variation in individual sponges as well as in sponge communities has been recognized in modern sponges where body shape has been found to vary according to magnitude of prevailing local currents (Palumbi, 1986; Kaandorp, 1999; Bell & Barnes, 2000). The modern demosponge *Cliona celata* Grant, 1826 was observed to develop six distinct morphological types that varied in relation to environmental factors (Bell, Barnes, & Turner, 2002). Ridged forms were developed where flow conditions were most turbulent. Bell, Barnes, and Turner (2002) considered both sponge morphology and size to be affected by inhibited feeding in turbulent flow and the increased probability of being hit or damaged by material being carried in suspension. Sponges were observed to be larger in low-energy sites where conditions were more stable over time with reduced probability of mortality or damage from destructive wave force and material in suspension. Bell, Barnes, and Turner (2002, p. 75) concluded that although sponge gross morphology was not static in modern sponges, “phenotypic variation can only occur within a genetically predetermined framework.” The effect of increasing wave force on the modern intertidal demosponge *Halichondria panicea* Pallas, 1766 was studied by Palumbi (1986) where the sponge was widely distributed along a wave force gradient, being absent only from areas of the highest wave action. His study found that tissue density, strength, and spicule content increased with increasing wave force. Sponges in high wave force habitats had 45 percent higher spicule density. In addition, total spicule surface area and total spicule volume per unit tissue volume were higher in sponges from high wave force habitats. High wave force sponges had fewer large pores and more numerous small pores than sponges in low-energy sites, increasing tissue strength by distributing tensile loads over a greater tissue area. Smaller ostia required that elements of the water transport system within sponges from high-energy environments be smaller resulting in higher resistance to water flow in their internal piping. Although these robust sponges were relatively resistant from wave-induced damage, they probably had increased water pumping costs suggesting that “engineering principles governing acclimation of sponges to high wave force environments appear to carry an associated energetic cost (Palumbi, 1986, p. 213).”

The robust, dense, interlocking-spicule skeletal morphology of ornamented Ordovician anthaspidellid sponges in this study equipped them for high-energy habitats, but may have also increased associated internal water pumping energy costs as in modern wave-resistant demosponges. Paleoenvironments interpreted from sedimentary facies associated with the occurrences of these sponges are shown in Table 1. Ornamented sponges were found in moderate to high-energy paleoenvironmental settings with the majority occurring in high-energy environments as compiled from interpreted paleoecological settings reported in the literature.

Ordovician anthaspidellid sponge morphology varied in settings where sponge outer-wall, ridge-and-trough spacing and amplitude were influenced by energy levels of prevailing currents. High-energy flows appeared to foster development of widely spaced, width greater than height (w>h), ridge-and-trough surfaces in anthaspidellid sponges, such as *R. eganensis*, which occurs in shallow water carbonate reef facies indicative of high-energy conditions often as broken plates incorporated within or cemented to outer surfaces of reefs (Johns, 1994). Widely-spaced, low-amplitude ridge-and-trough outer-wall features developed in the ectosomal layer of *R. eganensis* exhibit a well-developed, thickened or dense dermal spicule layer in ridge crests that is only poorly developed in the troughs. This dense armoring of exposed ridges would have provided protection from erosion in high-energy currents and was noted by Johns (1994, p. 19) to be “differential development rather than differential preservation.”

The large anthaspidellid *A. pulchra* is comprised of a robust, interlocking-spicule skeletal construction equipped for high-energy
habitats but with laterally extensive, width less than height (w<h), ridge-and-trough ornamentations. Johns (1994) reported *A. pulchra* from paleoenvironments interpreted as open marine settings along the uppermost slope or outer shelf of a carbonate platform in Nevada. In another study, *A. pulchra* was interpreted to have migrated into potentially lower energy settings in western Canada indicated by its association with conodonts “representative of the North Atlantic Faunal Realm, suggestive of cool and possibly deep water (Rigby, Nowlan, & Rowlands, 2002, p. 1065).” The small anthaspidellid *Archaeoscyphia nana* Beresi & Rigby, 1993 with laterally extensive ridge-and-trough ornamentations of w<h occurs in a hexactine spicule-bearing, dark limestone member of the early Ordovician San Juan Formation of Argentina (Beresi & Rigby, 1993), which may indicate habitats in potentially moderate energy settings. *A. nana* has been placed in synonymy with *A. pulchra* (Rigby, Nowlan, & Rowlands, 2002). In moderate to lower energy conditions, the laterally extensive, ridge-and-trough outer-wall ornamentations of *A. pulchra* and *A. nana* would have maximized sponge surface exposure to the water column. Outgrowths or lateral extensions of sponge bodies occupying quiet waters have been recognized as a functional advantage to sponges for nutrient intake from surface exposure to as large of a volume of water as possible (Finks, 2003).
of ridge-and-trough geometries in anthaspidellids to slow high fluid velocities through vorticity entrainment and current capture. The effects of fluid flow, with associated vortex generation, are of interest in studies of other modern benthic suspension feeders. In a review of pertinent literature, Shimeta and Jumars (1991) discussed several possible advantages of fluid vortex formation to suspension feeders. Velocity reduction of fluids and retention efficiency potentially enhance concentration of nutrients within vortices or eddies for organism intake. Entrainment of nutrients and high residence time within the vortex may also allow repeated passes of nutrients past pores. Vortex generation and probable reduced current velocity in high-energy settings could have aided the ornamented sponge’s active suspension-feeding mechanism or ciliary pump to function with reduced metabolic expenditure, helping to offset the higher energy pumping costs experienced by dense skeletal sponges engineered for high wave force environments as reported by Palumbi (1986).

The intuitive benefits of increased surface exposure to nutrient-bearing currents for ornamented anthaspidellids can be determined by comparing the amount of surface-to-fluid contact they attained relative to sponges with smooth or planar surfaces. Increased sponge surface-to-fluid exposure can be quantified by evaluating an idealized surface area of sponge wall. An area of sponge wall arbitrarily defined here for comparison purposes has a length of 10 mm and width of 30 mm. This defined outer perimeter unit area of sponge wall is held constant, and theoretical ridge-and-trough dimensions postulated within the defined area are allowed to vary for analysis. Increased surface area relative to a planar surface resulting from added ridge-and-trough features is determined by first calculating the surface area for one idealized trough width (w). An individual trough surface area is calculated by applying a simplified half-ellipsoid perimeter formula to the cross section of the trough (Fig. 5). The surface area calculated for one trough is then multiplied by the total number of troughs with equal dimensions that can fit within the defined unit boundary. The complete equation used for determining total ornamented sponge surface area (A) exposed in the defined unit area is shown in Figure 6. In this equation, (α) is the major radius of a trough-fitting ellipsoid, and (β) is the minor radius of the ellipsoid normal to (α), with (W) being the ridge crest to ridge crest width of a sponge trough. The constants (10 mm) and (30 mm) are outer perimeter dimensions of the defined unit area of 300 mm². With an aim towards simplicity, this approach gives the area (A) in square millimeters for increased sponge surface-to-fluid exposure resulting from various magnitudes of ridge-and-trough dimensions. The simplified equation is useful for general comparative purposes but does not take into account increasing surface error as ellipsoid eccentricity increases, dimension variance among individual troughs,
Increased surface area multiples derived from the above equation for ornamented sponge ridged surfaces compared to the defined planar sponge surface unit area of 300 mm² are listed numerically under each associated trough dimension in a theoretical trough shape diagram (Fig. 7). Plotted trough width-to-height dimension ratio lines on the theoretical trough diagram confirm the intuitive notion that increased height relative to width of individual ridge-and-trough features effectively increases sponge surface exposure to the water column without increasing the overall vertical height profile of the entire sponge. As shown in Figure 7, when a trough width-to-height ratio is 2:1 the increased surface area in the defined area is 1.57 times greater than the planar surface. A trough width-to-height ratio of 1:1 gives a surface area that is 2.48 times greater than a planar surface and a trough width-to-height ratio of 1:2 gives a surface area that is 4.58 times greater than a planar or smooth surface.

Figure 6. Mathematical formula for determining increased ornamented sponge surface exposed relative to a planar surface in a defined unit area of idealized sponge outer wall. In this equation, \( A \) is the total ornamented sponge outer-wall surface exposed in the defined unit area, \( \alpha \) is the major radius of a trough-fitting ellipsoid, and \( \beta \) is the minor radius of the ellipsoid normal to \( \alpha \), with \( W \) being the ridge crest to ridge crest width of a sponge trough. The constants (10 mm) and (30 mm) are outer perimeter dimensions of the defined unit area of 300 mm².

\[
A = \pi \sqrt{\frac{\alpha^2 + \beta^2}{2}} \times 10\text{mm} \times 30\text{mm}/W
\]

Sponge trough dimension parameter boxes from Figure 4 overlain by the theoretical trough width-to-height ratio plots of 1:2, 1:1, and 2:1 from Figure 7 show that the majority of anthaspidellid sponges in this study constructed ridge-and-trough ornamentations that fall below the trough width-to-height ratio line of 1:1 where trough dimensions have \( w > h \) (Fig. 8). Sponges with trough dimensions of \( w > h \) include sponges such as \( R. eganensis \), which is found in palaeoenvironments interpreted as high-energy shelfal habitats (Johns, 1994). This observation is consistent with the conclusion of Carrera and Rigby (1999) that Ordovician anthaspidellids predominately occur in shallow-shelf, high-energy conditions. The limited sample of anthaspidellid sponge trough dimensions that plot above or near the 1:1 width-to-height ratio line in Figure 8 with \( w < h \) or \( w = h \) ridge-and-trough dimensions as found in \( A. pulchra \), \( A. nana \), and \( A. minganensis \) are indicative of sponges that can be associated with paleoenvironments that are potentially moderate or lower energy settings as well as high-energy settings. The minimally populated area of the graph that lies above the theoretical trough width-to-height ratio plot of 1:2 represents an area in which ornamented sponges are as yet undescribed or undiscovered in nature or, most likely represents an area of theoretical “morphologies that function poorly in natural environments (McGee, 1999, p. 12).”
CONCLUSIONS

Constructional energy was conserved by ornamented Ordovician anthaspidellid sponges that increased their surface-to-fluid exposure for greater nutrient intake by adding ridge-and-trough geometries to outer-wall surfaces without constructing additional gas- tral surface area. Annulated anthaspidellid sponge ridge-and-trough constructional strategy also potentially slowed high fluid velocity through hydrodynamic vortex formation and altered dimensions of sponge outer-wall features in response to the magnitude of prevailing currents. High-energy current flow settings were predominately occupied by sponges having ridge-and-trough structures with w\(>h\) trough dimensions. Ornamented sponges with w\(<h\) trough dimensions or dimensions approaching w\(=h\) are found in high-energy paleoenvironments but also occupied moderate to low-energy settings, where their surface-to-fluid exposure per unit area exceeded that of sponges with widely spaced surface ornamentations.

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REFERENCES
