

Efficient Ornamentation in Ordovician Anthaspidellid Sponges

Author: Church, Stephen B.

Source: Paleontological Contributions, 2017(18) : 1-8

Published By: The Paleontological Institute at The University of Kansas

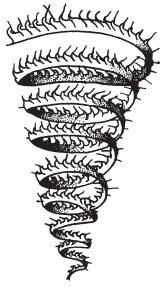
URL: <https://doi.org/10.17161/1808.24771>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



Paleontological Contributions

August 9, 2017

Number 18

EFFICIENT ORNAMENTATION IN ORDOVICIAN ANTHASPIDELLID SPONGES

Stephen B. Church

Department of Geological Sciences, Brigham Young University, Provo, Utah 84602-3300, churchsteve@hotmail.com

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 *Capsospongia* Rigby, 1986 together with *Fieldospongia* 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



Figure 1. *Archaeoscyphia minganensis*, BYU 20821 located in the Museum of Paleontology, Brigham Young University, Provo, Utah, shows transverse ridge-and-trough outer sponge wall ornamentation. Specimen collected by R. J. Elias from the Ordovician Shingle Formation, Egan Range, Nevada, $\times 1$.



Figure 2. *Rugocoelia eganensis*, BYU 20822 located in the Museum of Paleontology, Brigham Young University, Provo, Utah, shows a portion of the outer sponge wall with distinctive transverse ridge-and-trough ornamentation. Specimen collected by the author from the Ordovician Shingle Formation, Egan Range, Nevada, $\times 75$.

3, late Stage 5–early Paibian) *Rankenella* occupied reef-building settings on the North China Platform and in the Mela Formation of Iran (Hamdi, Rosanov, & Zhuravlev, 1995; Kruse & Zhuravlev, 2008; Kruse & Reitner, 2014; Lee, Woo, & Lee, 2016). Other anthaspidellids also began to occupy reef habitats in the Cambrian. The anthaspidellid sponge *Gallantinospongia* Okulitch & Bell, 1955 occupied paleoenvironments interpreted as moderate energy, open marine subtidal dendrolitic reef-mound settings during the Cambrian Furongian Series–early Paibian Stage in the western United States (Shapiro & Rigby, 2004). In the late Cambrian, Jiangshanian–Stage 10 of the Cambrian Furongian Series, the anthaspidellid sponge *Wilbernicyathus* Wilson, 1950 contributed up to 30 percent of reef volume in small patch reefs that occur in the Wilberns Formation of the central Texas Llano Uplift (Johns, Dattilo, & Spincer, 2007). 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 ornamentations 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 ornamentations, 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 gastral 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; *Anthaspidella* Ulrich & Everett in Miller, 1889; *Nevadocoelia* Bassler, 1927; *Rhopalocoelia* Raymond & Okulitch, 1940; and *Patellispongia* Bassler, 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 eganensis* Johns, 1994 as ridges and troughs with predictably consistent dimensions and noted such features to be genetic characters for *Rugocoelia* (Fig. 2).

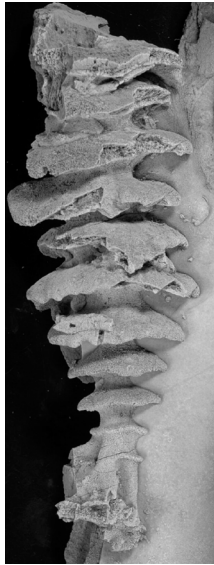


Figure 3. *Archaeoscyphia pulchra*, GSC117363 located in the National Type Collection of Invertebrate and Plant Fossils in Ottawa, Ontario, Canada, shows ornate, sponge outer-wall transverse ridge-and-trough features. Photograph courtesy of G.S. Nowlan, specimen is also figured in Rigby, Nowlan, & Rowlands (2002), $\times 0.5$

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

PALEOECOLOGICAL SETTINGS INTERPRETED FROM SEDIMENTOLOGICAL OCCURRENCE

Genus/Species	Near shore to open marine small sponge reef/thrombo- litic buildups within bioclastic limestones	Outer edge and uppermost slope of carbonate platform with occasional hexactine spicules	Carbonates associated with cool, deep water (?) conodonts
	<u>Higher Energy</u>	<u>Moderate Energy</u>	<u>Lower Energy</u>
<i>Archaeoscyphia minghamensis</i>	X	X	
<i>Archaeoscyphia nana</i>	X	X	
<i>Archaeoscyphia bassleri</i>	X		
<i>Archaeoscyphia eganensis</i>	X		
<i>Archaeoscyphia pannosa</i>	X		
<i>Archaeoscyphia pulchra</i>	X	X	X
<i>Archaeoscyphia rossi</i>	X		
<i>Archaeoscyphia undulata</i>	X		
<i>Anthaspidella annulata</i>		X	
<i>Rugocoelia eganensis</i>	X		
<i>Jianghanian yichangensis</i>	X		
<i>Patellispongia brosiusae</i>	X		
<i>Nevadocoelia wistae</i>		X	
<i>Nevadocoelia grandis</i>		X	
<i>Rhopalocoelia sanxiaensis</i>	X		

Table 1. Sedimentary facies-based interpretation of paleoecological settings for ornamented anthaspidellid sponges. Data compiled from Beresi & Rigby (1993); Johns (1994); Bingli, Rigby, & others (1997); Rigby & Desrochers (1995); Rigby & Webby (1988); and Rigby, Nowlan, & Rowlands (2002).

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).

UTILITY OF ORNAMENTED SPONGE FEATURES

Dimensions of the ridges and troughs developed in individual annulated anthaspidellids can be graphically depicted as parameter boxes where width and height parameters of each box encompass the range of measured trough dimensions for mid-to-upper areas of each sponge plotted (Fig. 4). The utility of adding ridged outer-wall surfaces to an anthaspidellid sponge's bluff body design for hydrodynamic benefits of enhanced current capture i.e., vorticity entrainment (Vogel, 1994) in high-energy settings has yet to be evaluated in fluid mechanics laboratory studies. However, Vogel (1994) determined that drag-induced fluid vortex generation is to be expected in troughs wherever high-energy currents flow across regularly occurring ridges and troughs or corrugated surfaces. Inhibited feeding in turbulent flows affecting morphology of modern sponges, as reported by Bell, Barnes, and Turner (2002), may have also fostered the development

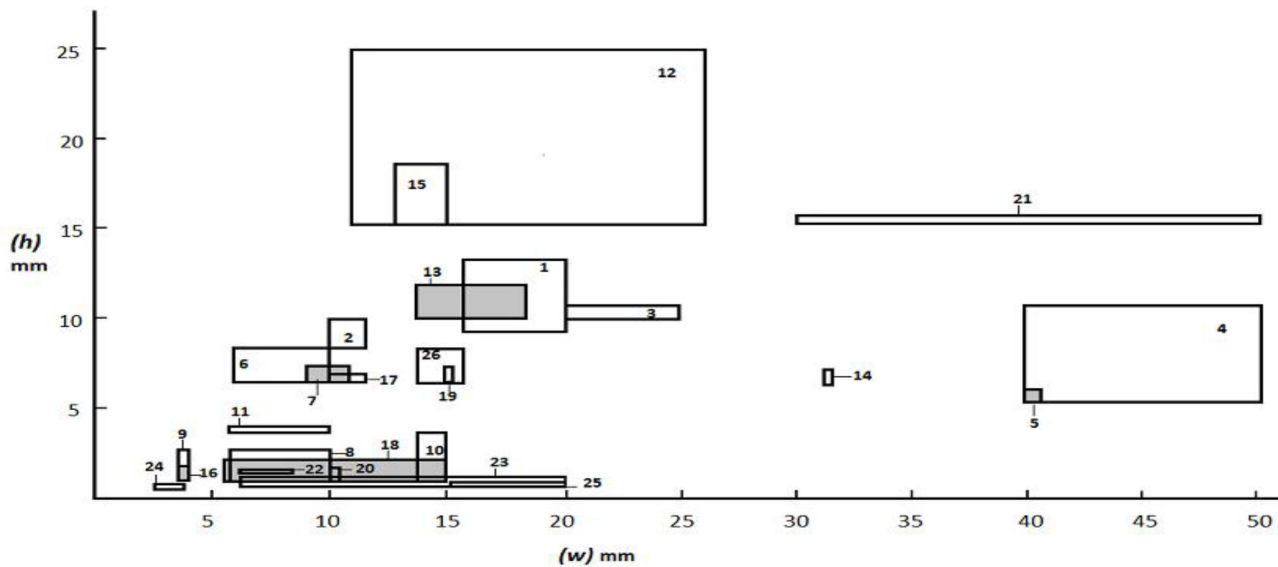


Figure 4. Measured outer wall ridge-and-trough width and height dimensions for individual anthaspidellid sponges depicted as parameter boxes. Range of trough heights (h) are plotted on the y-axis. Range of trough widths (w) are plotted along the x-axis: 1, *Archaeoscyphia manganensis* (Beresi & Rigby, 1993); 2, *Archaeoscyphia manganensis* (Bingli, Rigby, & Zhongde, 2003); 3, *A. manganensis* (Rigby & Webby, 1988); 4, *A. manganensis* (Bingli, Rigby, & others, 1997); 5, *A. manganensis* (Rigby & Desrochers, 1995); 6, *Archaeoscyphia nana* Beresi & Rigby, 1993 (Bingli, Rigby, & others, 1997); 7, *Anthaspidella annulata* Beresi & Rigby, 1993; 8, *Archaeoscyphia bassleri* Johns, 1994; 9, *Archaeoscyphia eganensis* Johns, 1994; 10, *Archaeoscyphia mazourkensis* Greife & Langenheim, 1963 (Johns, 1994); 11, *Archaeoscyphia pannosa* Johns, 1994; 12, *Archaeoscyphia pulchra* (Johns, 1994); 13, *A. pulchra* (Bingli, Rigby, & others, 1997); 14, *A. pulchra* (Rigby & Desrochers, 1995); 15, *A. pulchra* (Rigby, Nolan, & Rowlands, 2002); 16, *Archaeoscyphia rossi* Johns, 1994; 17, *Archaeoscyphia* sp. 1 Greife & Langenheim, 1963 (Johns, 1994); 18, *Rugocoelia eganensis* Johns, 1994; 19, *Jianghania yichangensis* Bingli, Rigby, & others, 1997; 20, *Archaeoscyphia undulata* Rigby & Desrochers, 1995; 21, *Archaeoscyphia boltoni* Rigby & Nitecki, 1973; 22, *Patellispongia brosiusae* Johns, 1994; 23, *Nevadocoelia grandis* Bassler, 1927 (Johns, 1994); 24, *Nevadocoelia wistae* Bassler, 1927 (Johns, 1994); 25, *Rhopalocoelia sanxiaensis* Bingli, Rigby, & others, 1997; 26, *A. manganensis*, BYU 20821, specimen shown in figure 1.

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,

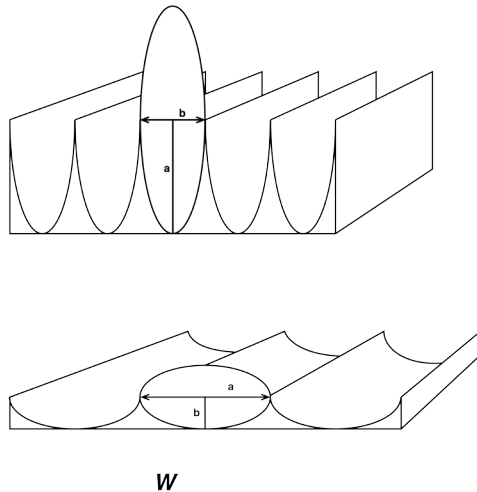


Figure 5. Diagram of theoretical sponge outer wall ridge-and-trough features, which represent individual trough cross sections as one-half the perimeter of an ellipsoid.

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

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, (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.

or factors such as ridge-crest widths or erosively modified surfaces. 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.

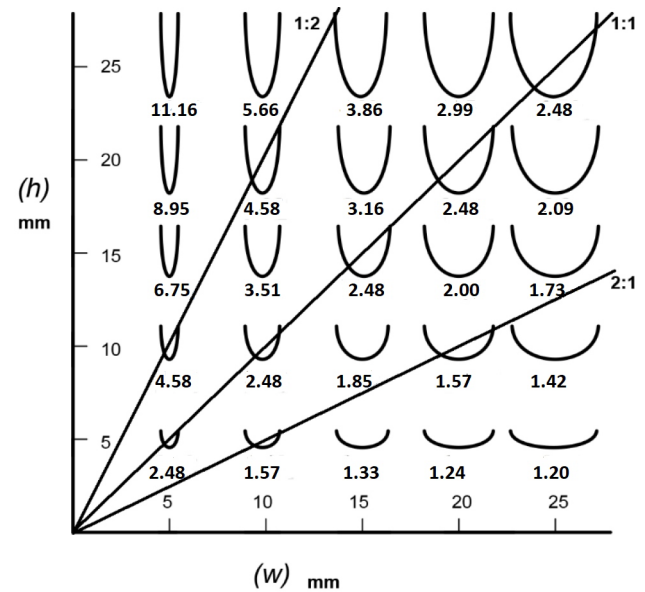


Figure 7. Morphospace diagram depicting a limited range of theoretical sponge outer-wall trough shapes. Trough height (h) dimensions are plotted on the y-axis. Trough width (w) dimensions are plotted along the x-axis. Calculated multiples using the formula in Figure 6 of increased sponge wall ridge-and-trough surface area compared to a planar sponge wall surface area of 300 mm² are noted under each associated trough shape. Trough width-to-height ratio slope lines of 2:1, 1:1, and 1:2 are plotted on the diagram.

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 paleoenvironments 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).”

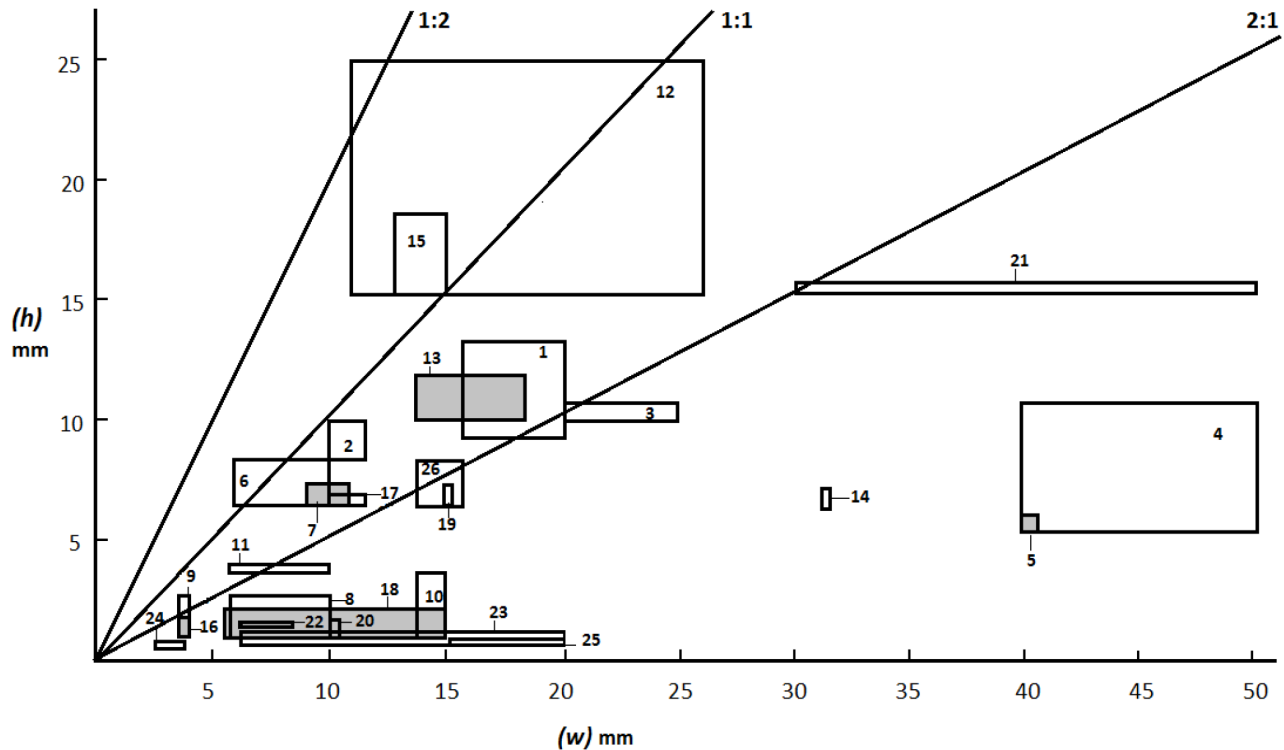


Figure 8. Measured sponge trough dimension parameter boxes from Figure 4 are overlain by theoretical sponge trough width-to-height ratio slope plots from Figure 7. Sponges categorized in Table 1 that plot below the 1:1 ratio slope line with $w > h$ occur predominately in high energy paleoenvironments, while those plotting above or near to the 1:1 ratio slope line with $w < h$ can also occur in moderate to lower energy settings.

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 gastral 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.

ACKNOWLEDGEMENTS

Brooks Britt and Rodney Scheetz provided access to Brigham Young University Museum of Paleontology paleontological collections. Joe Botting and an anonymous reviewer critically reviewed the manuscript and helped improve its quality.

REFERENCES

- Bassler, R. S. 1927. A new Early Ordovician sponge fauna. *Washington Academy of Sciences Journal* 17:390–394.
- Bassler, R. S. 1941. The Nevada Early Ordovician (Pogonip) sponge fauna. *Proceedings of the United States National Museum* 91(3126):91–102, 6 pl.
- Bell, J. J., & D. K. A. Barnes. 2000. The influence of bathymetry and flow regime on the morphology of sublittoral sponge populations at Lough Hyne MNR. *Journal of the Marine Biological Association of the United Kingdom* 80:707–718.
- Bell, J. J., D. K. A. Barnes, & J. R. Turner. 2002. The importance of micro and macro morphological variation in the adaptation of a sublittoral demosponge to current extremes. *Marine Biology* 140:75–81.
- Beresi, M. S., & J. K. Rigby. 1993. The Lower Ordovician sponges of the San Juan Formation, Argentina. *Brigham Young University Geology Studies* 39:1–64.
- Billings, E. 1859. Fossils of the calciferous sandrock, including some of the deposit of White Limestone at Mingan, supposed to belong to the formation. *Canadian Natural Geology, Natural History Society of Montreal. Proceedings* 4 (27):345–346.
- Bingli, Liu, J. K. Rigby, Jiang Yanwen, & Zhu Zhongde. 1997. Lower Ordovician lithistid sponges from the eastern Yangtze Gorge area, Hubei, China. *Journal of Paleontology* 71:194–207.
- Bingli, Liu, J. K. Rigby, & Zhu Zhongde. 2003. Middle Ordovician lithistid sponges from the Bachu-Kalpin area, Xinjiang, northwestern China. *Journal of Paleontology* 77(3):430–441.

- Botting, J. P., & J. S. Peel. 2016. Early Cambrian sponges of the Sirius Passet Biota, North Greenland. *Papers in Palaeontology*. doi:10.1002/spp2.1048.
- Braun, A., J. Chen, D. Waloszek, & A. Maas. 2007. Siliceous microfossils and biosiliceous sedimentation in the lowermost Cambrian of China. *Geological Society, London, Special Publications* 286(1):423–424.
- Carrera, M. G., & J. P. Botting. 2008. Evolutionary history of Cambrian spiculate sponges: implications for the Cambrian evolutionary fauna. *Palaos* 23:124–138. doi:10.2210/palo.2006.p06-09r.
- Carrera, M. G., & J. K. Rigby. 1999. Biogeography of Ordovician sponges. *Journal of Paleontology* 73:26–37.
- Carrera, M. G., & J. K. Rigby. 2004. Sponges. In B. D. Webby, M. L. Droser, F. Paris, I. G. Percival, eds., *The Great Ordovician Biodiversification Event*. Columbia University Press. New York. p. 102–110.
- Church, S. B. 1974. Lower Ordovician patch reefs in western Utah. *Brigham Young University Geology Studies* 21(3):41–62.
- Copper, Paul. 2001. Evolution, radiations, and extinctions in Proterozoic to mid-Paleozoic reefs. In G. D. Stanley, Jr., ed., *The history and sedimentology of ancient reef systems*. Kluwer Academic/Plenum. New York. p. 89–119.
- Finks, R. M. 2003. Functional morphology and adaptation. In R. L. Kaesler, ed., *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera vol. 2. The Geological Society of America & University of Kansas. Boulder & Lawrence*. p. 211–222.
- Finks, R. M. 2003a. Paleozoic demosponges: morphology and phylogeny. In R. L. Kaesler, ed., *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera. vol. 2. The Geological Society of America & University of Kansas. Boulder & Lawrence*. p. 63–80.
- Finks, R. M. 2003b. Evolution and ecological history of sponges during Paleozoic times. In R. L. Kaesler, ed., *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera. vol. 2. The Geological Society of America & University of Kansas. Boulder & Lawrence*. p. 261–274.
- Finks, R. M., & J. K. Rigby. 2004. Paleozoic demosponges. In R. L. Kaesler, ed., *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera vol. 3. The Geological Society of America & University of Kansas. Boulder & Lawrence*. p. 9–173.
- Grant, R. E. 1826. Notice of a new zoophyte (*Cliona celata* Gr.) from the Firth of Forth. *Edinburgh New Philosophical Journal* 1:78–81.
- Greife, J. L., & R. L. Langenheim. 1963. Sponges and brachiopods from the Middle Ordovician and Upper Ordovician conodont biostratigraphy of carbonate facies in Nevada and southeast California and comparison with some Appalachian sections. *Brigham Young University Geology Studies* 26(3):7–43.
- Hamdi, B., A. Y. Rosanov, & A. Y. Zhuravlev. 1995. Latest Middle Cambrian metazoan reef from northern Iran. *Geological Magazine* 132:367–373.
- Hinde, G. J. 1889. On *Archaeocyathus* Billings, and on other genera, allied to or associated with it, from the Cambrian strata of North America, Spain, Sardinia, and Scotland. *Quarterly Journal of the Geological Association of London* 45:125–148.
- Hong, Jongsun, S. J. Cho, & D. J. Lee. 2015. Untangling intricate microbial–sponge frameworks: The contributions of sponges to Early Ordovician reefs. *Sedimentary Geology* 318:75–84. Elsevier. doi:10.1016/j.sedgeo.2015.01.003.
- Johns, R. A. 1994. Ordovician lithistid sponges of the Great Basin. Nevada Bureau of Mines and Geology. NBMG Open-file Report 94-1. 140 p.
- Johns, R. A., B. F. Dattilo, & B. Spincer. 2007. Neotype and rediscovery of the Upper Cambrian anthaspidellid sponge, *Wilberniccyathus donegani* Wilson, 1950. *Journal of Paleontology* 81:435–444.
- Kaandorp, J. A. 1999. Morphological analysis of growth forms of branching marine sessile organisms along environmental gradients. *Marine Biology* 134:295–306.
- Kruse, P. D. 1983. Middle Cambrian '*Archaeocyathus*' from the Georgina Basin is an anthaspidellid sponge. *Alcheringa* 7:49–58.
- Kruse, P. D. 1996. Update on the northern Australian Cambrian sponges *Rankenella*, *Jawonya*, and *Wagima*. *Alcheringa* 20:161–178.
- Kruse, P. D., & J. R. Reitner. 2014. Northern Australian microbial-metazoan reefs after the mid-Cambrian mass extinction. *Memoirs of the Association of Australasian Palaeontologists* 45:31–53.
- Kruse, P. D., & A. Y. Zhuravlev. 2008. Middle-Late Cambrian *Rankenella-Girvanella* reefs of the Mila Formation, northern Iran. *Canadian Journal of Earth Sciences* 45:619–639.
- Lee, J. H., Jusun Woo, & D. J. Lee. 2016. The earliest reef-building anthaspidellid sponge *Rankenella zhangxianensis* n. sp. From the Zhangxia Formation (Cambrian Series 3), Shandong Province, China. *Journal of Paleontology* 90(1):1–9. doi:10.1017/jpa.2015.53.
- McGhee, G. R., Jr. 1999. *Theoretical Morphology: the Concept and Its Applications*. Columbia University Press. New York. 316 p.
- Miller, S. A. 1889. Class Porifera. In *North American Geology and Paleontology*. Published by the author. Cincinnati. p. 152–167.
- Okulitch, V. J., & W. G. Bell. 1955. *Gallantinospongia*, a new siliceous sponge from the Upper Cambrian of Wyoming. *Journal of Paleontology* 29:460–461.
- Pallas, P. S. 1766. *Elenchus Zoophytorum sistens generum adumbrationes generales et specierum cognitarum succinctas descriptiones cum selectis auctorum synonymis*. Haegae Comitum, P van Cleef. The Hague. 451 p.
- Palumbi, S. R. 1986. How body plans limit acclimation: responses of a demosponge to wave force. *Ecology* 67:208–214.
- Raymond, P. E., & V. J. Okulitch. 1940. Some Chazyan sponges. *Bulletin of the Museum of Comparative Zoology at Harvard College* 86:197–214.
- Rigby, J. K. 1971. Sponges of the Ordovician Cat Head Member, Lake Winnipeg, Manitoba. In D. C. McGregor, F. H. Cramer, R. H. Flower, & J. K. Rigby, eds., *Contributions to Canadian Paleontology, Fossils of the Ordovician Red River Formation (Cat Head Member), Manitoba*. Geological Survey of Canada Bulletin. p. 35–78.
- Rigby, J. K. 1986. Sponges of the Burgess Shale (Middle Cambrian) British Columbia. *Palaeontographica Canadiana* 2:105 p.
- Rigby, J. K., & Andre Desrochers. 1995. Lower and Middle Ordovician Lithistid demosponges from the Mingan Islands, Gulf of St. Lawrence, Quebec, Canada. *Journal of Paleontology Memoir* 41:35 p.
- Rigby, J. K., & M. H. Nitecki. 1973. New *Archaeoscyphia* (Porifera) from the Ordovician of Anticosti Island, Quebec. *Fieldiana Geology* 33(1):1–10.
- Rigby, J. K., G. S. Nowlan, & P. A. Rowlands. 2002. A new occurrence of *Archaeoscyphia pulchra* (Bassler) from the Ordovician of western Canada. *Canadian Journal of Earth Science* 39:1065–1069.
- Rigby, J. K., & B. D. Webby. 1988. Lower Ordovician sponges from the Malongulli Formation of central New South Wales, Australia. *Palaeontographica Americana* 56:147 p.
- Shapiro, R. S., & J. K. Rigby. 2004. First occurrence of an in situ anthaspidellid sponge in a dendrolite mound (upper Cambrian; Great Basin, USA). *Journal of Paleontology* 78:645–650.
- Shimeta, A. J., & P. A. Jumars. 1991. Physical mechanisms and rates of particle capture by suspension feeders. *Oceanic Marine Biology Annual Review* 29:191–257.
- Toomey, D. F. 1970. An unhurried look at a Lower Ordovician mound horizon, Southern Franklin Mountains, west Texas. *Journal of Sedimentary Petrology* 40:318–334.
- Vogel, Steven. 1994. *Life in Moving Fluids* (second edition). Princeton University Press. New Jersey. 467 p.
- Wang J. P., X. J. Deng, Guan Wang, & Yue Li. 2012. Types and biotic successions of Ordovician reefs in China. *Chinese Science Bulletin* 57(10):1160–1168. doi:10.1007/s11434-011-4936-7.
- Webby, B. D. 2002. Patterns of Ordovician reef development. In Wolfgang Kiessling, Erik Flügel, & Jan Glonka, eds., *Phanerozoic reef patterns*. Society for Sedimentary Geology (SEPM) Special Publication 72:129–179.
- Wilson, J. L. 1950. An Upper Cambrian pleospongoid from Texas. *Journal of Paleontology* 24:591–593.
- Wood, Rachel. 1999. *Reef Evolution*. Oxford University Press. New York. 414 p.