

THE EARLY CAMBRIAN PROBLEMATIC FOSSIL *VOLBORTHELLA*: NEW INSIGHTS FROM THE BASIN AND RANGE

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ABSTRACT

Volborthella tenuis is an enigmatic Lower Cambrian fossil, represented by small agglutinated cones with a central lumen. In the southwestern Great Basin, *Volborthella* occurs both as isolated specimens and in great abundance as mm- to dm-thick fossil concentrations; the latter are not just winnowed lag deposits, but likely represent locally high influxes of bioclastic debris. In the White-Inyo, Death Valley, and Mojave regions, *Volborthella* occurs in pretrilobitic strata and represents one of the earliest attempts at skeletal construction. We present a preliminary assessment of the mode of construction of *Volborthella* based on field observations, electron microscopic analyses, X-ray analyses, and microfocus computed tomographic analyses of fossils from this region. We assess the stratigraphic and paleoenvironmental distribution and mode of skeletal construction of *Volborthella*, and present and discuss hypotheses regarding its high-level taxonomic affinity and relationship to other Lower Cambrian fossils such as *Salterella*.

INTRODUCTION

The Neoproterozoic-Cambrian transition not only heralds the diversification of metazoans and the advent of new ecological interactions, but marks the onset of biomineralization. Although lightly calcified organisms are known from the Neoproterozoic (Grant, 1990; Grotzinger et al., 2000; Hofmann and Mountjoy, 2001), the radiation of organisms with mineralized skeletons is primarily a Cambrian event. Neoproterozoic-Cambrian strata of southwestern North America contain a number of taxa that highlight the radiation of biomineralized taxa, both below the base of the Cambrian (see summaries in Hagadorn

and Fedo, 2000; Hagadorn and Waggoner, 2000), and throughout the Lower Cambrian (e.g. Durham and Caster, 1963; Diehl, 1979; Signor and McMenamin, 1988; Hunt, 1990). Some of these mineralized taxa belong to known metazoan clades; others may represent independent “evolutionary experiments” in building skeletons by a combination of facultative and active mechanisms.

Volborthella tenuis is an agglutinated cone-shaped fossil found in Early Cambrian strata of North America, Greenland, Spitsbergen, and northeastern Europe. Its shape, unusual mode of skeletal construction, and lack of articulation make it a taxonomic and functional morphologic enigma. Its systematic position has been the subject of some debate: it was long thought to be an early cephalopod (e.g. Karpinsky, 1903; Gürich, 1934), but its agglutinated, aseptate structure is completely unlike any cephalopod. It has commonly been reconstructed as the tube of a worm-like animal, or possibly the test of an agglutinated protist (e.g. Lipps and Sylvester, 1968; Glaessner, 1976). Most recently, it has been hypothesized to be the spicules of a larger, armored bilaterian animal (Signor and Ryan, 1993; Donovan et al., 1994). Its occurrence in pre-trilobitic strata makes it relevant to understanding the proliferation of biomineralization within the Metazoa. The purpose of this paper is to 1) evaluate *Volborthella*'s temporal, paleoenvironmental, and geographic occurrence in the Great Basin; 2) present new observations about its construction; and 3) use these data to examine several hypotheses about its evolutionary relationships to other taxa.

GEOLOGIC CONTEXT

In the southwestern Basin and Range province, Neoproterozoic-Lower Cambrian strata

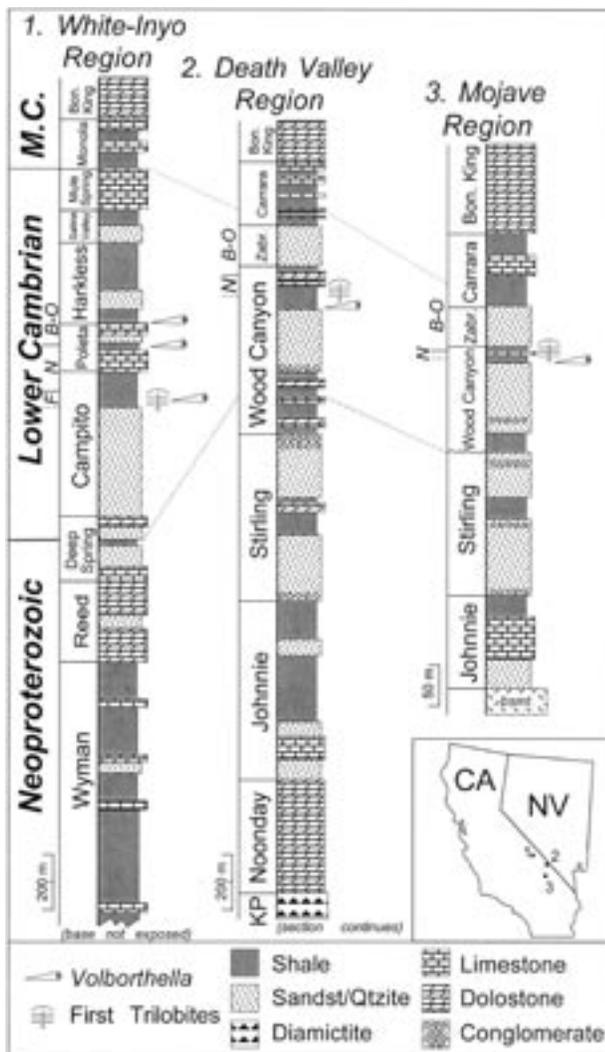


Figure 1. Locality map and stratigraphic context for occurrences of *Volborthella* in the Great Basin. Basal occurrences of biomineralized trilobite debris are indicated, as well as the known range of the *Bonnia-Olenellus* (B-O), *Nevadella* (N), and *Fallotaspis* (F) zones. Modified from Hagadorn et al., 2000; included are trilobite biostratigraphic data from Palmer and Hollingsworth (2002).

are exposed in three regions (Mojave, Death Valley, White-Inyo) which broadly represent interfingering successions of cratonal-to-offshore depositional environments (Nelson, 1978). *Volborthella* occurs in all three of these successions (Fig. 1). In the Mojave region, *Volborthella* is abundant in both the northern (Licari and Licari, 1987) and southern (Diehl, 1979; Hunt, 1990) Salt Spring Hills, in the upper member of the Wood Canyon Formation (hereafter umWCF). We have examined samples from both the northern and the southern Salt Spring

Hills, ~19 m above the top of the middle member of the Wood Canyon Formation (mmWCF), and ~85 m below the most basal of the regionally extensive echinoderm debris beds of the umWCF. All samples are from below the lowest known local occurrence of trilobite fragments (Hunt, 1990; Palmer and Hollingsworth, 2002). In the Death Valley region, Langille (1974) reported *Volborthella* from the mmWCF in the southern Nopah Range; however, we have not been able to confirm the presence of *Volborthella* in this interval. At this locality, Diehl (1979) reported volborthellids from 9 meters above the contact between the middle and upper members of the Wood Canyon Formation, and our field research has confirmed this observation. We hypothesize that Langille's occurrences were in what would now be defined as the umWCF. Death Valley region occurrences of *Volborthella* are ~120 m below the prominent echinoderm concentrations in the umWCF, and are well below the lowest occurrence of fallotaspid trilobites (Diehl, 1979; Hunt, 1990; Palmer and Hollingsworth, 2002).

In the White-Inyo region, *Volborthella* occurs sporadically in several units. *Volborthella* is known from both the Andrews Mountain and Montenegro members of the Campito Formation in the Westgard Pass area (described as *Campitius* by Firby and Durham, 1974, but later synonymized with *Volborthella*; see Yochelson, 1977; Signor et al. 1985; Rozanov, 1992), from the middle member of the overlying Poleta Formation in the Poleta folds (this report), and from ~3 m above the base of the overlying Harkless Formation, near Waucoba Spring (Lipps and Sylvester, 1968) and near the group campgrounds in the Westgard Pass area (Signor and Ryan, 1993). In the Campito Formation, *Volborthella* occurs in the upper half of the Andrews Mountain Member, in the same beds as the lowest known occurrence of *Fallotaspis* (Firby and Durham, 1974) or just below *Fallotaspis* (Signor and Ryan, 1993). The younger occurrences in the Poleta and the Harkless Formations occur within the *Bonnia-Olenellus* zone (Nelson, 1976). *Salterella*, a morphologically similar and potentially related fossil, also occurs in the White-Inyo and Mojave regions — in the Harkless, Saline Valley, and possibly the Poleta Formation (see summary in Fritz and Yochelson, 1987). *Salterella* is thought to be restricted to the *Bonnia-Olenellus* Zone, and has not been noted within the underlying *Nevadella* or *Fallotaspis* zones.

In all three regions, *Volborthella* occurs in stratigraphic proximity to archaeocyathid bioherms, and is bounded by strata containing putative anemone resting traces (i.e., ornate *Bergaueria*) and other shallow subtidal trace and body fossils (see reviews in Alpert, 1976, 1977; Cooper and Stevens, 1991; Hagadorn et al., 2000). *Volborthella* in the Death Valley and Mojave regions occurs just above intertidal facies dominated by polygonally cracked, highly oxidized mudstones (particularly in the Salt Spring Hills and Nopah Ranges) and braided fluvial deposits of the mmWCF (Fedo and Cooper, 1990). Some *Volborthella*-bearing beds in the umWCF contain *Planolites* and treptichnid burrows on their bases, and strata intercalated within *Volborthella*-rich horizons of the umWCF do not exhibit evidence for subaerial exposure. Together, this evidence suggests that Great Basin *Volborthella* occurrences were deposited in rather shallow subtidal settings above storm wave base. These observations do not mean that the *Volborthella*-producer inhabited the environment of deposition, however, because widespread abrasion and breakage of *Volborthella* suggests that at least some degree of postmortem reworking occurred.

MATERIALS AND METHODS

For this study, *Volborthella* samples were collected from two localities in the upper Wood Canyon Formation, and from one locality in the Poleta Formation. Numerous fossil concentrations in the umWCF were sampled *in situ* from exposures in the southern Salt Spring Hills (Sheep Creek Spring 7.5" quadrangle; NE 1/4 NE 1/4 Section 31, T. 18 N, R. 7 E) and northern Salt Spring Hills (Saddle Peak Hills 7.5" quadrangle; ~700 m NE of Amargosa Spring in unsurveyed portion of T. 18 N, R. 7 E). Both localities are in northern San Bernardino County, California (see Troxel, 1967 for a general locality description). *Volborthella* was also observed in the Nopah Range (Tecopa Pass, CA 7.5" quadrangle; NE 1/4 Section 11, T. 20 N, R. 8 E) in Inyo County, California; these specimens have not yet been analyzed. Samples from the Poleta Formation were collected from talus weathering from the middle member, at exposures in the northern portion of the Poleta folds (Deep Springs Lake, 7.5" quadrangle; NE 1/4 NE 1/4 Section 25, T. 7 S., R. 35 E.) in Inyo County, California.

Samples from the Salt Spring Hills include a number of large slabs with bedding-plane surfaces completely covered by *Volborthella*. A 3 cm x 5 cm portion of one of these bedding-plane slabs was digitized, specimens of *Volborthella* were counted, and their horizontal orientations were measured using the program NIH Image 1.62. Oriana 1.0 was utilized to analyze and plot the data.

Slabs containing *Volborthella*, from both the Salt Spring Hills and the Poleta folds were cut, polished, and examined using standard thin-section petrography, backscattered scanning electron microscopy (BSEM), energy-dispersive X-ray spectroscopy (EDS), and EDS element mapping. EDS was carried out using an X-ray detector equipped with a beryllium window, which makes it possible to detect elements as light as boron. X-ray spectra of individual mineral grains, in both *Volborthella* specimens and the surrounding matrix, were compared with reference spectra in order to identify the minerals; the distribution of key elements was also mapped in selected polished sections. (See Reed, 1996 for protocols and reference spectra). Using backscattered electrons to form an SEM image provides additional information on the composition of a sample: regions with lower atomic weight appear darker on a backscattered SEM image. Because each mineral appears as a different shade of gray, this makes it possible to correlate specific grayscale values with specific mineral composition, and to use the distribution of grayscale values to determine the area taken up by any given mineral in cross-section. This in turn provides an estimate of the percentage by volume occupied by any given mineral. We used NIH Image 1.62 to measure the areas of each image occupied by various grayscale ranges.

Because *Volborthella* specimens are difficult to remove from the matrix without destroying the fossils, X-radiographic microfocus computed tomography (microCT) was used to visualize the three-dimensional morphology of fossils from the southern Salt Spring Hills. Samples with relatively unabraded *Volborthella* specimens oriented parallel to bed surfaces were selected for analyses. Bed surfaces were then polished to reveal longitudinal cross-sections through *Volborthella* fossils. Individual fossils and surrounding matrix were cut from these slabs to a size of approximately 16 mm³ and mounted on a lexan stub for microCT analysis. Although this approach only yielded information about

one-half of each *Volborthella*, it ensured that we would know the location, orientation and taphonomic condition of the fossils within each sample. Samples were analyzed using a Skyscan 1072 microtomograph. Samples were placed behind a 0.5 mm thick Al filter, and were exposed for 2.5 seconds per 0.45 degree rotation using a cone-shaped x-ray source operating at 80 kV/100 mA. Attenuation values which corresponded to the fossil skeleton were selected using a threshold value approach, and isosurface models were reconstructed using ANT visualization software (available from Skyscan Instruments, Belgium).

Specimens figured in this contribution will be curated in the Los Angeles County Museum of Natural History once studies are completed.

RESULTS

General morphology

No differences in morphology were observed between the Salt Spring Hills and Poleta *Volborthella*, or between samples from these localities and previously published descriptions of *Volborthella*. Fossils from both localities consist of subrounded to subangular detrital grains arranged in concentric curved layers; these layers are convex towards the narrow aperture (Figs. 2-7). Some Salt Spring Hills specimens exhibit an apparent outer rim of material that is lithologically distinct from the matrix; this is most evident in obliquely sectioned specimens (Fig. 7). These rims are composed of iron-enriched clay minerals, distinct from the silica-rich matrix. Not all Salt Spring Hills specimens exhibit this feature, and we did not observe it in the sample from the Poleta Formation (although the Poleta Formation sample was much smaller than the Salt Spring Hills sample). MicroCT-based volume renderings of Salt Spring Hills samples reveal morphologies that are consistent with the morphology inferred from thin sections (Fig. 8).

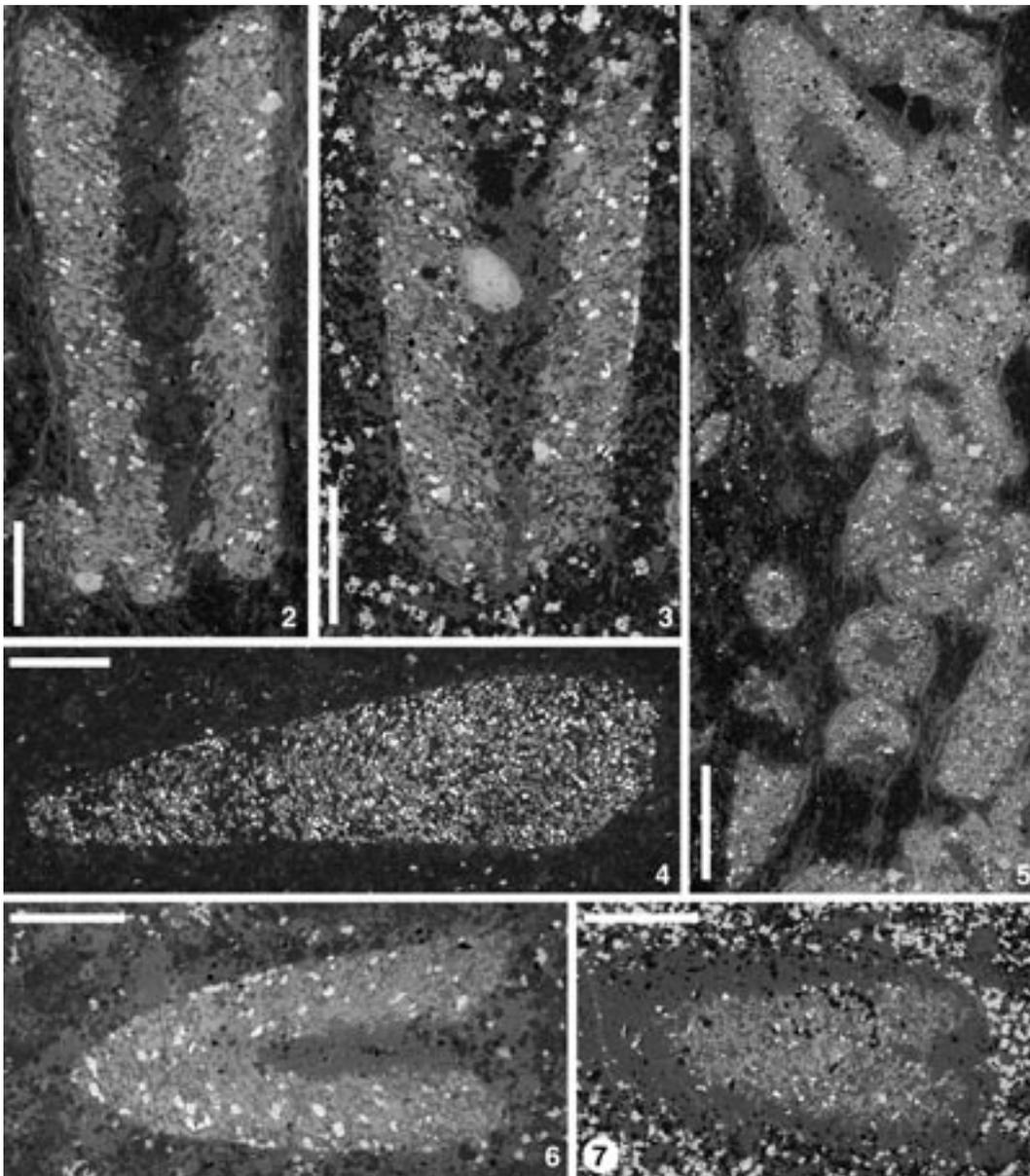
Specimens from the Campito, Poleta, Harkless, and umWCF do not exhibit significant curvature, which is a typical feature of *Salterella* (and *Lidaconus*, which is probably related; see Signor and Ryan, 1993) from this region. Most of the *Volborthella* specimens examined from the Campito, Poleta and umWCF have longitudinal margins that are quite straight, suggesting little

post-depositional bending of specimens occurred. Similarly, the angles of inclination of nested layers varies little between specimens, suggesting minimal lengthwise compression of specimens. However, at least 10% of the *Volborthella* individuals from the umWCF exhibit plastic deformation (without fractures) along their short axis (Fig. 4). At least 10% of specimens from the umWCF also appear to have been cleaved along their longitudinal axis. Together, these observations suggest that *Volborthella* from these deposits may have had markedly greater structural integrity along their long axis than across their short axis.

Taphonomy and sedimentology

In the Poleta Formation, *Volborthella* occurs as isolated specimens and in clusters of fewer than 10 individuals—all of which are oriented parallel to bed surfaces in tan- to buff-colored thinly bedded siltstones and shales. *Volborthella* specimens exposed on bed surfaces within the Harkless Formation exhibit a similar mode of preservation (Signor and Ryan, 1993). Campito Formation *Volborthella* specimens include isolated specimens oriented parallel to shaly bed surfaces, as well as thin concentrations of quasi-randomly oriented specimens (Firby and Durham, 1974) akin to the mm-thick pavements or stringers observed in the umWCF.

In the umWCF, *Volborthella* occurs in prolific abundance within an ~ 3 m thick interval characterized by interbedded fine- to very-fine grained sandstones, siltstones, and shales. Complete, fragmented, and disaggregated *Volborthella* are the dominant clastic grains in this interval. Fossils may occur as isolated specimens suspended within cm- to dm-thick planar-bedded siltstones (Fig. 12) and very fine-grained sandstones, and as isolated specimens on bed surfaces of mm- to cm-thick shales. More commonly, fossils occur as dense accumulations forming ~1-2 mm-thick pavements (Figs. 9, 11), mm- to cm-thick packstone stringers, and dm-thick laterally extensive packstone beds (Fig. 10). Packstone is not used *sensu strictu* herein; packstones in this unit have granular biogenic clasts arranged in a self-supporting framework, but do not have a calcareous matrix as do most packstones in carbonate-dominated environments. Fossils in thicker beds can be both matrix and clast supported (Figs. 4, 10, 12). Fossils make up the



Figures 2 through 7. Figure 2: Polished section through a Volborthella specimen, imaged using backscattered electron microscopy (BSEM). Specimen is from the southern Salt Spring Hills. Scale bar = 500 μm . Figure 3. Polished section through a Volborthella specimen, imaged using BSEM. Specimen is from the southern Salt Spring Hills. Scale bar = 500 μm . Figure 4. Polished section through a Volborthella bed, imaged using BSEM, showing numerous Volborthella and fragments in a variety of angles. Note specimens distorted by compaction. Top of bed is to the right. Sample is from the southern Salt Spring Hills. Scale bar = 1 mm. Figure 5. Polished section through a Volborthella specimen, imaged using backscattered electron microscopy (BSEM). Section does not pass through the internal lumen and is similar to specimens in Lipps and Sylvester (1968; fig. 7). Specimen is from the Poleta Formation. Scale bar = 500 μm . Figure 6. Polished section imaged using backscattered electron microscopy (BSEM), showing Volborthella sectioned tangentially, roughly parallel to the long axis. Note resemblance to the previously proposed Volborthella reconstruction shown in Figure 17. Specimen is from the southern Salt Spring Hills. Scale bar = 500 μm . Figure 7. Polished section imaged using backscattered electron microscopy (BSEM), showing Volborthella sectioned nearly tangential to the outer surface. Note rim consisting of Fe-rich clays separating agglutinated portion from the matrix. In this specimen, the matrix is rich in detrital iron oxides (bright angular grains). Specimen is from the southern Salt Spring Hills. Scale bar = 500 μm .

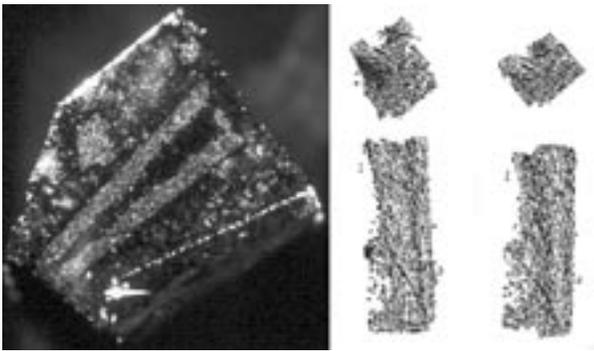


Figure 8. Polished rock chip containing a *Volborthella* exposed on the surface (left); viewed under reflected light. Four isosurface maps (right) of the same specimen produced by volume rendering of microCT data. Detrital grains and skeletal fragments next to the large specimen obscure some detail. Note the semicircular cross-section and the relatively large lumen. Specimen is approximately 2 mm wide and is from the southern Salt Spring Hills.

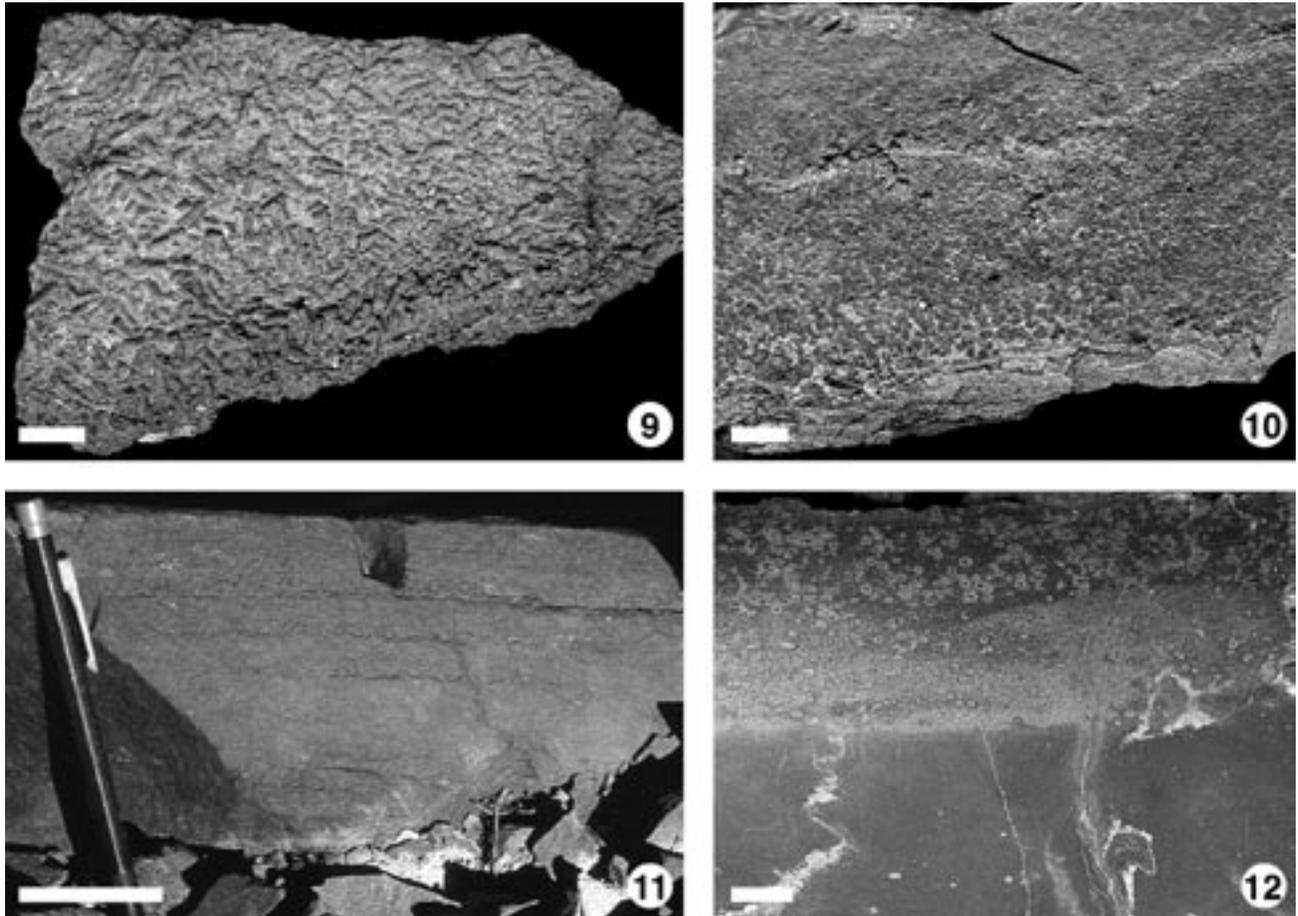
largest size fractions occurring at the tops of cm- to dm-thick upward-coarsening beds, as well as at the base and in the middle of fining-upward cm- to dm-thick beds. In both fining- and coarsening-upward beds, *Volborthella* and *Volborthella* fragments are the dominant sand-sized clastic component. Although beds thin and pinch out laterally, the thickest observed *Volborthella* packstone is ~32 cm thick and spans over three meters laterally along the outcrop face. Well-developed cross-bedding was not observed within *Volborthella*-dominated beds, and no dunes or ripples were noted where *Volborthella*-dominated bed surfaces were exposed. The *Volborthella*-dominated interval in the umWCF is bounded by shales and argillaceous fine-grained and medium-grained sandstones where quartz is the dominant sand-sized mineral grain.

More than half of the specimens from the Campito, Poleta, Harkless, and umWCF localities are abraded and/or have been shortened by breakage. These features suggest at least some degree of bioclastic reworking, and raises questions regarding where the *Volborthella* organisms were living. Clearly, fossils from thick packstones in the Salt Spring Hills, and in bedding plane accumulations from the Campito Formation (Firby 1972; Firby and Durham, 1974), may have been transported from elsewhere, and undergone at least minor reworking. However, in the Salt Spring

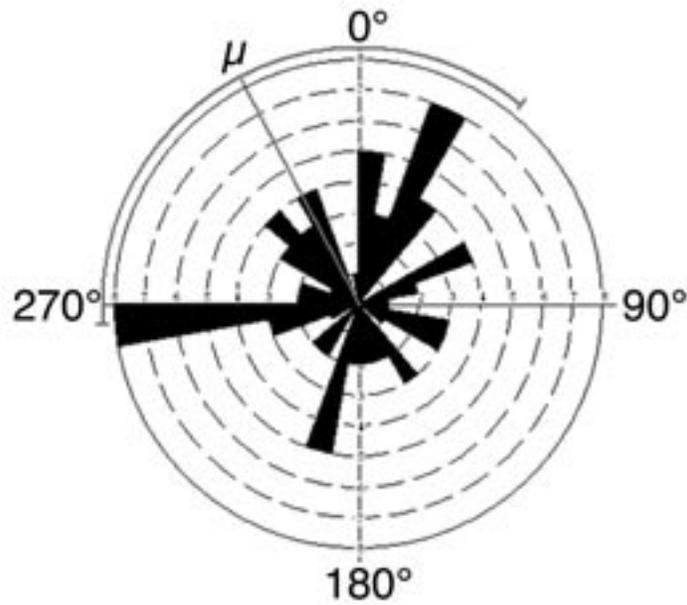
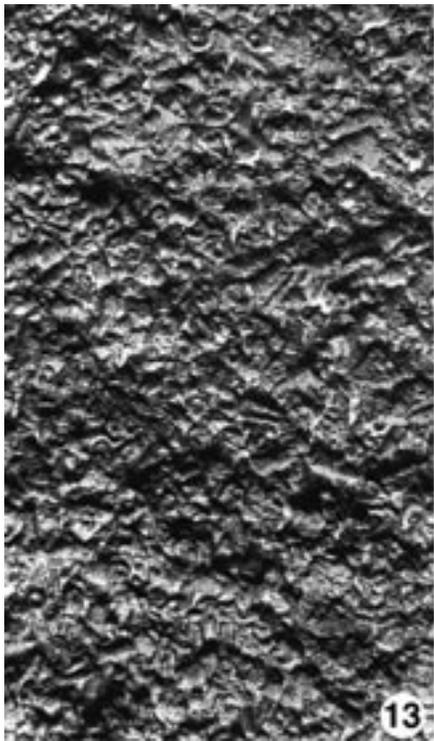
Hills, the wide variety of textural features and bedform geometries associated with the fossils suggests that *Volborthella* concentrations do not merely represent winnowing of available heavy detrital grains. Furthermore, *Volborthella* beds do not contain abundant medium to coarse quartz sand (elsewhere abundant in overlying/underlying beds at these localities), which further suggests that the beds were not winnowed. Rather, this sedimentologic context suggests that there was a localized influx of skeletal material which bypassed or diluted “background” input of coarser quartz clastics. Additional contextual information is needed to determine if this skeletal material was winnowed elsewhere and then transported to its present location, or if biogenic factors (such as a population explosion) could have mediated concentration of skeletal material in situ within these paleoenvironments. Although stratigraphic evidence from the Great Basin suggests that *Volborthella* in this region is widespread and distributed throughout the Lower Cambrian, the genus is usually confined to very narrow stratigraphic intervals within a given section — similar to patterns of distribution exhibited by modern opportunistic taxa.

Analysis of the orientation of *Volborthella* specimens on bed surfaces may inform hypotheses regarding how and to what degree fossils may have been reworked in these deposits. In a pilot study of the umWCF, we analyzed a well-preserved bedding-plane accumulation of *Volborthella*, containing 195 identifiable specimens (Fig. 13). Of these, 109 specimens were close enough to vertical orientation that their horizontal angle could not be measured; only the tip or open aperture were visible. The remaining 86 specimens were lying close enough to horizontal that their orientation could be measured. This sample did not show a significant directional orientation using the Rayleigh test of uniformity ($p = 0.24$), suggesting that hydrodynamic conditions during deposition were not such that elongate fossils were not preferentially oriented (Fig. 14). It may also be significant that the majority of specimens (55.9%) were not oriented horizontally at all; this is also not consistent with significant winnowing of the specimens. Additional samples from other localities need to be analyzed before the postmortem taphonomy of *Volborthella* occurrences can be understood.

In all four formations, *Volborthella* occurs



Figures 9-12: Figure 9: Photograph of bed surface pavement comprised of *Volborthella*, from the Southern Salt Spring Hills. Scale bar = 1 cm. Figure 10. Field photograph of the side of a dm-thick packstone comprised entirely of *Volborthella*. The upper bed surface is at the top of the image; clasts are well-sorted and grading is not apparent. Basal portion of bed exhibits loading into a thin very fine-grained quartz sand layer; the base of this layer is characterized by a variety of bed-parallel trace fossils. Slab is from ~20.1 m above the base of the umWCF in the northern Salt Spring Hills. Scale bar = 1 cm. Figure 11. Field photograph of the side of a dm-thick very fine to fine grained quartzite within the most fossiliferous interval, ~18.8 m above the base of the umWCF in the southern Salt Spring Hills. Several *Volborthella*-dominated layers are visibly weathering along the slab face, including i) two thin (~1-2 mm thick) pavements located to the right of the end of the pocket clip on the pencil; and ii) one ~2 cm thick layer at the top of the slab which is comprised entirely of volborthellids. Note that all three beds have relatively sharp planar bases. Scale bar = 1 cm. Figure 12. Polished slab of a bed adjacent to the slab illustrated in Figure 11, illustrating: i) isolated *Volborthella* suspended in unlaminated unbioturbated siltstone (several specimens occur between 1.5 and 4 cm to the right of the scale bar); ii) a roughly upward-coarsening 4 cm-thick bed comprised of fragmented *Volborthella*, relatively complete *Volborthella*, and silt-sized grains. Note that fossils are both matrix and clast supported; convex upward bedform at upper right may represent cross-bedding. Scale bar = 1 cm.



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Figures 13 and 14: Figure 13: Sample bed surface from southern Salt Spring Hills, with numerous *Volborthella* specimens weathered from the matrix. This sample was selected for orientation analysis. Note that the specimen has been sectioned lengthwise. Field of view is approximately 2 cm wide. Figure 14. Rose diagram illustrating the orientation of 86 *Volborthella* specimens which were oriented with their long axis parallel to bedding on the sample in Fig. 13. Gray line indicates the mean vector (μ), 332.3°; gray arc indicates 95% confidence intervals for the mean vector (265.66° - 38.94°). Rayleigh test of uniformity revealed no significant orientation ($p = 0.24$).

in strata which are bounded by rather intense bed-parallel bioturbation, and in the Poleta and Harkless occurrences, by significant vertically-oriented bioturbation. In contrast, bioturbation was minimal on *Volborthella*-bearing surfaces. For example, in the Poleta and Harkless samples, burrowing is not evident on individual slabs; the extent of burrowing in Campito examples is unknown, but shales from this interval do not typically exhibit significant vertically oriented burrowing activity. In the umWCF, there are non-bioclastic fine-grained sandstones ~2 m above and ~4 meters below the *Volborthella*-dominated interval; several of these beds have abundant 0.5-4 mm long/wide mud chips and heterogeneous assemblages of siliceous detrital grains. These beds exhibit well-preserved bed-parallel bioturbation and 1-3 cm deep vertically oriented bioturbation, but do not appear to contain *Volborthella*. Where *Volborthella* packstones and *Volborthella*-bearing very-fine-grained sandstones overlay siltstones and shales,

traces such as *Planolites* and *Treptichnus* occur on bases of slabs (e.g. Fig. 10). Conversely, burrows were not noted on the upper surfaces of *Volborthella*-bearing beds. Collectively, this evidence suggests that the activities of burrowing organisms were significantly reduced or halted during and shortly after deposition of *Volborthella* in these environments.

Mineralogy

Energy-dispersive X-ray spectroscopy (EDS) and backscattered scanning electron microscopy (BSEM) were used to identify a suite of grains from several *Volborthella* specimens. Although minerals cannot always be absolutely identified by EDS, comparisons of the spectra against the standards provided in Reed (1996) allowed us to obtain provisional identifications for all components of the *Volborthella* skeleton.

In the Salt Spring Hills specimens, a

magnesium aluminosilicate clay with significant iron, potassium, oxygen, and titanium makes up the fine-grained material between the grains of the test; its spectrum is closest to that of biotite. Five types of mineral grains were found to make up the wall of *Volborthella*: (1) silicon and oxygen-rich grains with only traces of other elements, presumably quartz grains; (2) silicon and zirconium-rich grains with minor oxygen and only traces of other elements, presumably zircons; (3) iron- and titanium-rich grains, presumably ilmenite or a related TiFe oxide; (4) iron-rich grains with oxygen and minor silicon, sometimes amorphous but also occurring in cubical shapes, presumably iron oxides that may be pseudomorphs of pyrite; and (5) rare grains enriched in cerium, lanthanum, neodymium, and thorium, presumably monazite. The lumens of *Volborthella* from the Salt Spring Hills are almost always filled primarily with clays, and silicon dioxide grains are rare in the lumen, whereas the surrounding matrix is predominantly made up of fine silicon dioxide with varying amounts of iron oxide grains. (See Fig. 15 for a typical analysis)

The *Volborthella* specimens from the Poleta Formation have a similar composition to the Salt Spring Hills specimens, including titanium-rich grains, zircons, and silicon dioxide grains. However, the Poleta specimens contain virtually no iron oxide grains. Many of the titanium-rich grains contain oxygen but almost no iron; these are presumably titanium oxides such as rutile, anatase, or brookite. However, some titanium-rich grains have iron-rich rinds, presumably ilmenite, surrounding iron-poor cores. X-ray mapping confirms that there are no iron-rich grains in the *Volborthella* specimens that do not also contain titanium. Rare grains contain phosphorus and yttrium, along with traces of samarium, gadolinium, and ytterbium; these are tentatively identified as xenotime (YPO₄).

Following up on these analyses of individual grains, backscattered SEM was used to quantitatively estimate the percentages of each mineral in a number of cross-sectional profiles of *Volborthella* fossils (Fig. 16). The material in the lumen and the surrounding matrix was deleted from each image before the estimates were made. Because each mineral appears as a different shade of gray, it is possible to correlate specific grayscale values with specific mineral composition, and to use the distribution of grayscale values to determine the area represented by any given

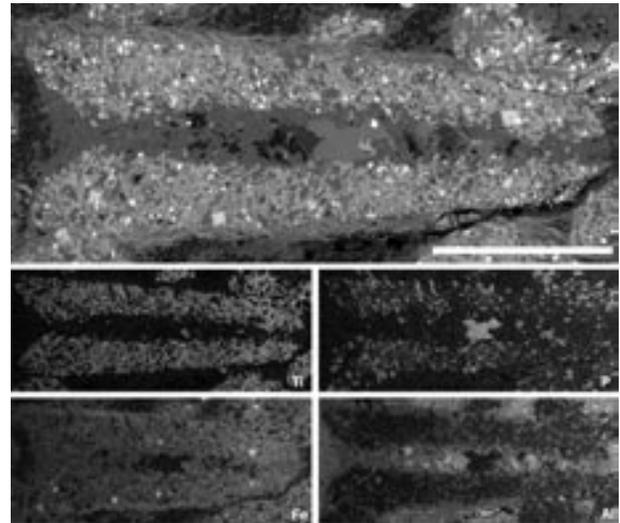


Figure 15. Backscattered electron micrograph of a near-complete *Volborthella* specimen from the southern Salt Spring Hills. Elemental maps below show distribution of four major elements, mapped using energy dispersive X-ray spectroscopy (EDS); light regions on the maps correspond to titanium (Ti, indicating ilmenite), phosphorus (P, indicating zircons), iron (Fe, indicating both ilmenite and iron oxides), and aluminum (Al, indicating clays). Scale bar = 1 mm.

mineral in cross-section. This in turn provides an estimate of the percentage by volume occupied by any given mineral. Some error is associated with measurements of the cross-sectional areas. The precise boundary between a specimen and the matrix is not always obvious; some grains that are part of a specimen may have been excluded, and some matrix material may have been included. The plane of sectioning may also have had an effect; since grains were laid down in layers, a plane that intersects a grain-rich layer will have a different composition from a plane that intersects a clay-rich layer. Furthermore, it was not always possible to adjust the grayscale in such a way as to maximize the differences among all mineral types. Some images did not exhibit a grayscale differentiation between zircons and iron pseudomorphs, for example. However, these values serve as at least rough estimates of the composition of *Volborthella*.

Quantitative analyses of *Volborthella* specimens from the Salt Spring Hills (n=12, except as noted) indicate that an average of 50.6% (42.3%-62.9%) of the cross-sectional area is clay minerals, whereas an average of 38.4% (22.4%-47.5%) is

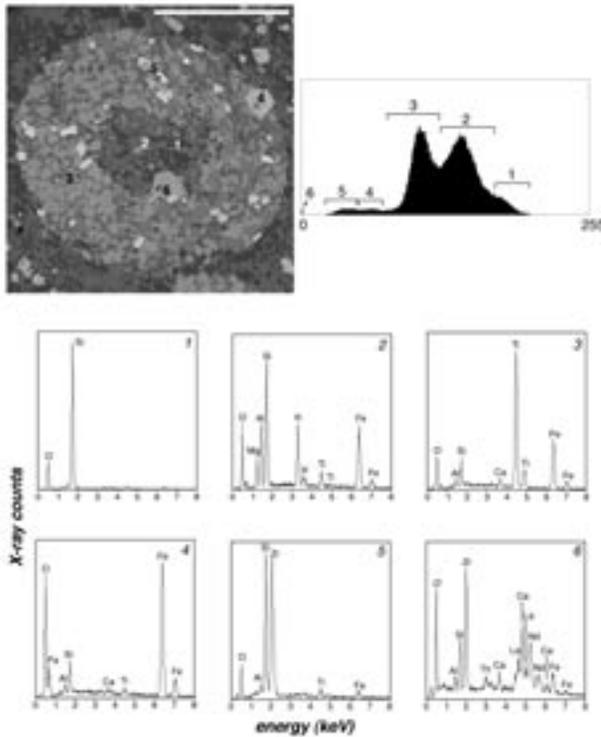


Figure 16. Backscattered electron micrograph of a *Volborthella* specimen from the southern Salt Spring Hills, showing six sample points at which X-ray analyses were taken. Note that each measured grain shows a different level of brightness. The graph of grayscale values for the *Volborthella* specimen (with the surrounding matrix removed) shows different grayscale values which were found to correspond to different grain types. Below: X-ray spectra at the six points shown in the micrograph, showing composition of each grain type: (1) silicon dioxide; (2) clay; (3) ilmenite; (4) iron oxide; (5) zircon; (6) monazite. Scale bar = 1 mm.

ilmenite. Silicon dioxide is uncommon, averaging 5.5% (2.4%-8.6%) of the sectional area. Zircons and iron oxides collectively make up an average of 5.5% (4.0%-7.5%) as well. Where they can be distinguished, iron oxides comprise an average of 2.1% (1.7%-2.5%; n=4) and zircons comprise 3.1% (2.8%-3.8%; n=4). Monazites make up no more than 0.13% of the cross-sectional area. The matrix contains clays, silicon dioxide grains and variable amounts of detrital iron-rich grains, but rarely contains titanium minerals or monazite. Fine silicon dioxide grains are abundant in the matrix (averaging 64.1%; n=9); the remainder of the

matrix is comprised of clays (average 29.2%) and iron-rich grains (average 6.6%).

Specimens from the Poleta Formation (n=4) average 22.7% silicon dioxide, 36.1% clays, 14.6% titanium oxides, 15.5% ilmenite, 9.0% zircons, and 0.21% xenotime, as measured by cross-sectional area. The matrix (n=6) contains on average 68.0% silicon dioxide, 31.0% clays, and 1.0% zircons, virtually identical to the matrix from the Salt Spring Hills.

DISCUSSION

Stratigraphy

Rozanov (1992) stated that *Volborthella* was restricted to the “*Fallotaspis*” trilobite zone throughout its range. Signor and Ryan (1993) suggested that *Volborthella* was biostratigraphically useful, as its lowest occurrence often marked the first occurrence of the oldest trilobites in this region, again in the “*Fallotaspis*” zone. However, in the Great Basin, *Volborthella* has a longer range: in the White-Inyo region it extends from the Andrews Mountain Member of the Campito Formation through the Poleta Formation and into the Harkless Formation, a range that overlaps with both the Montezuman and Dyeran Stages of Palmer (1998) and which corresponds to the Atdabanian and Botomian Stages in Siberia. In the Death Valley region, *Volborthella* occurs in the umWCF, which extends its range at least through most of the Montezuman Stage and well into pretrilobitic strata of the Begadean Stage (equivalent to the Tommotian of Siberia; Palmer, 1998).

If *Salterella* and *Volborthella* are synonymous or closely related (Yochelson 1977, 1983), then the range of *Volborthella*-like organisms can be extended further, into slightly younger strata in the White-Inyo, Death Valley and Caborca regions (see summary in Fritz and Yochelson, 1987). Regardless of this synonymy, *Volborthella* clearly originates in the pretrilobitic Lower Cambrian, and extends through much of the trilobite-bearing Lower Cambrian. It may be significant that several other agglutinated forms span the same time interval, notably *Platysolenites* (McIlroy et al., 2001) and *Onuphionella* (Hagadorn and Waggoner, 2000; Signor and McMenamin, 1988). Thus, *Volborthella* evolved its mode of skeletal construction before tissue-mediated

metazoan biomineralization became widespread, and it persisted while this change was occurring. *Volborthella* and its relatives may have died out afterwards, or modified their skeletal-construction approaches so that they are unrecognizable in other parts of the fossil record.

Composition

The Salt Spring Hills specimens contain ilmenite, silicon dioxide, iron oxides, zircons, and monazite, whereas the Poleta Formation specimens contain silicon dioxide, titanium oxides, ilmenite, zircons, and xenotime. These compositions are similar to those of *Volborthella* from other localities, but there is both qualitative and quantitative variation in composition. *Volborthella* specimens from the lower Harkless Formation of the White-Inyo Mountains consist of zircon, magnetite, and pyrite grains with minor tourmaline (Lipps and Sylvester, 1968). Specimens from Germany consist of quartz, zircons, pyroxenes, magnetite, ilmenite, pyrite, and phosphorites (Gürich, 1934). Rozanov (1992) reported that Russian *Volborthella* consisted primarily of silicon dioxide polymorphs (quartz, cristobalite and tridymite), although it is possible that this represents secondary silicification. “*Campitius*” from the Campito Formation of the White-Inyo Mountains, which is probably synonymous with *Volborthella* (Yochelson, 1977; Signor et al., 1985; Rozanov, 1992; but see Donovan et al., 1994), consists of ilmenite and quartz along with “a very small amount of unidentified material” (Firby and Durham, 1974, p. 1112). There are components that are common to four or five of these *Volborthella* samples, such as silicon dioxide and ilmenite, but apparently there are no grain types that are universally present in *Volborthella*. Although there is less quantitative data available on *Volborthella* composition, proportional composition also differs between localities; for example, silicon dioxide is much less common in *Volborthella* from the Salt Spring Hills (5.5%) than in *Volborthella* from the Poleta Formation (22.7%). It is possible that these differences are taxonomically significant, indicating different species of *Volborthella*; however, we have not observed any significant morphological differences between our samples, other than grain composition, that would support this hypothesis. We find no reason to exclude any of our samples from *V. tenuis*.

Lipps and Sylvester (1968) argued that *Volborthella* selected heavy mineral grains; if this is the case, we should see variation in *Volborthella* composition from different localities and horizons, depending on which mineral grains were locally available. Our findings support the hypothesis that *Volborthella* selected heavier mineral grains from the surrounding sediment. In all cases, grains primarily consist of sub-rounded to sub-angular or oblate detrital minerals of a similar size class. Given the range in grain sizes and types in the adjacent, underlying, and overlying matrix, organisms were clearly selecting grains based on size, shape, and composition. Since the external wall surfaces are not serrated or irregular in texture, as would be expected if grains were placed in random orientations and flattened within individual laminae, the size and arrangement of the grains suggests that the *Volborthella*-maker was not only selecting grains but was able to arrange them in a preferred orientation.

It may be possible in the future to work out the provenance of Cambrian sediments using specific grain types in *Volborthella* as tracers. *Volborthella* presumably selected heavy grains, and thus are enriched in heavy minerals that could be traced back to source rocks. Composition might also be useful in constraining the ecology of *Volborthella*. For example, *Volborthella* from the Salt Spring Hills made use of cubical iron minerals that are probably pseudomorphs of pyrite, whereas the Poleta *Volborthella* did not. If these grains were still pyrite when they were incorporated, it could imply that *Volborthella* could tolerate both aerobic and dysaerobic conditions. At present, this hypothesis is highly speculative, as other explanations for the presence of pyrite pseudomorphs are possible, but it should be further tested.

Volborthella and *Salterella*

Volborthella has often been compared with *Salterella*, an Early Cambrian conical fossil with a calcareous wall. Lipps and Sylvester (1968) disclaimed an affinity between *Volborthella* and *Salterella*, on the grounds that the first was agglutinated and the latter was mineralized. However, Yochelson (1977, 1981) reported that *Salterella* incorporated exogenous mineral grains into the shell, in layers “sandwiched” between sheets of calcium carbonate. *Salterella* specimens

from the Scottish Highlands (Yochelson, 1983) intergrade between mineralized “*Salterella*-type” specimens and agglutinated “*Volborthella*-type” specimens, and Yochelson (1983) used these fossils to formally synonymize *Salterella* and *Volborthella*. Although we have not used this synonymy, we agree that the two genera are likely to be closely related. In fact, several specimens of *Volborthella* have traces of an outer clay envelope, enriched in iron compared to the surroundings (Fig. 7). We suspect that this envelope represents the diagenetic remains of an external wall or envelope surrounding the agglutinated grains of *Volborthella*, in the same way that the calcareous wall surrounds *Salterella*. Some specimens of *Volborthella* appear to lack this wall; this could be explained by post-mortem wear, dissolution or diagenesis. We cannot be sure of the wall’s original composition; it may have been calcareous, but the presence of specimens that have been compressed without fracturing suggests that it was not likely to be strongly mineralized. We tentatively hypothesize that it represents a tough organic envelope, which could serve as a substrate for mineralization in related species, or perhaps in the same species under different environmental conditions. Karpinsky (1903) made similar observations, suggesting that *Volborthella* had a conchiolin-like envelope which was later removed during burial diagenesis. Thus our work indirectly supports the hypothesis of a close link between *Volborthella* and *Salterella*.

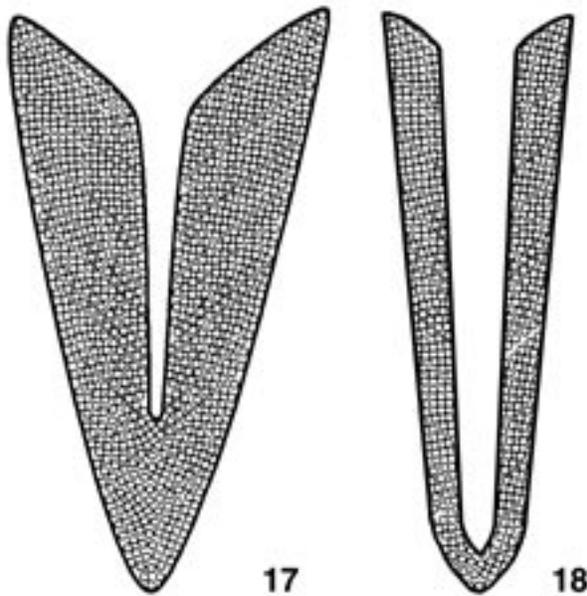
Affinities of *Volborthella*

Could *Volborthella* represent a failed evolutionary experiment in biomineralization? This is possible; it may be that *Volborthella* is not closely related to any extant organisms, a proposal formalized by Yochelson (1977) in his creation of the extinct Phylum Agmata for *Volborthella* and *Salterella*. However, as Bengtson (1986) noted, a phylum is a statement of taxonomic ignorance: if we could be sure that two phyla were related, we would either merge them into one, or at least create a supraphyletic grouping to hold both. Although *Volborthella* may not fit into any extant metazoan crown group, it is nonetheless useful to consider a range of living organisms as analogues and potential relatives of *Volborthella*.

It seems highly unlikely that *Volborthella* was planktonic or nektonic. Non-reworked

specimens are commonly found perpendicular to bedding, which would not be expected if the organisms were falling onto the sediment from the water column. Furthermore, the apparent selection of dense mineral grains by the organism suggests that *Volborthella* spent much time in or near the sediment. The dense composition and relatively thick walls would not be expected in organisms that float or swim. Seilacher (1999) hypothesized that *Volborthella* was a sessile “mat sticker”, presumably a suspension feeder, growing upwards with the conch mostly buried in microbially-stabilized laminated sediments. The large number of *Volborthella* specimens that are preserved perpendicular or oblique to bedding in at least some of our samples is consistent with this hypothesis. However, wrinkle structures such as elephant skin and “Kinneyia ripples” have not been found associated with *Volborthella* (Hagadorn and Bottjer, 1999). Another possibility is that *Volborthella* was mobile on or within the sediment, analogous to pectinariid polychaete worms and to many extant agglutinated foraminiferans. Small *Planolites*-like trace fossils are present on the lower surfaces of beds containing *Volborthella*; burrowing organisms of the same size as *Volborthella* were present at the right place and time. However, there is no direct evidence, such as association of a *Volborthella* specimen with a trace fossil, that conclusively shows that *Volborthella* represents an independently motile organism.

Traditionally, *Volborthella* has been compared to members of two extant taxa: polychaete annelids and foraminiferans with agglutinated tests. Members of both of these taxa are capable of selecting and arranging particular grain types. We could not detect consistent pores in the test, which would imply that *Volborthella* is not a crown-group foraminiferan; however, it is possible that the pores lay between grains and have been filled in by clay minerals. Glaessner (1976) has argued that tubicolous polychaetes often arrange the grains of their tubes in the same pattern as *Volborthella*. However, an argument against this hypothesis (although perhaps not a fatal one) is the fact that the grains in *Volborthella* form a very smooth outer wall surface, lying flush along the outside, but do not form a small inner wall surface. Specimens that have been sectioned nearly parallel to the long axis (e.g. Figs. 2, 3, 15) often show a rough internal margin. This margin is not what would be expected if *Volborthella* was made by



Figures 17 and 18: Figure 17: Reconstruction of *Volborthella* according to Signor and Ryan (1993). Figure 18: Our alternative reconstruction of *Volborthella*, based on cross-sectional and microCT analyses. Our reconstruction of the narrow apex is conjectural, as the apex is broken or abraded in most specimens.

a motile worm-like animal which lived inside the lumen. It is possible that the inner lumen was lined with a smooth organic or mineralized lining, as was the case in *Salterella*; there is no clear evidence of an internal lining in our sample of *Volborthella*, but examination of more well-preserved specimens might clarify the matter.

On the basis of a single specimen from the lower Harkless Formation in the White Mountains, Signor and Ryan (1993; see also Donovan et al. 1994) argued that *Volborthella* is a sclerite of a larger wormlike animal. In support of this hypothesis, they argued that the central canal of *Volborthella* is extremely narrow, and the concave space at the aperture is extremely shallow (Fig. 17). Thus it seemed unlikely that the shell was the conch of an individual animal; there would have been little space for the living organism, especially for an organism that presumably had to exert itself in picking up suitable grains and thus was relatively metabolically active. Glaessner (1976), in contrast, pointed out that extant sabellariid polychaetes have long narrow “tails”; a polychaete worm with such a shape might be able to fit inside a *Volborthella*-like tube. However, our results call into question the

premises of both arguments: specimens from the Poleta and Wood Canyon Formations (e.g. Figs. 6, 15), as well as specimens in the Harkless Formation (e.g., figs 3, 4, 7 of Lipps and Sylvester, 1968) exhibit a wider central canal and thinner walls than the reconstructions in both Glaessner (1976) and Signor and Ryan (1993). MicroCT analyses confirm this conclusion: isosurface maps of fossils (Fig. 12) illustrate that the walls are roughly half as thick as the diameter of the central canal (see reconstruction in Fig. 18). We hypothesize that the thick walls and narrow lumen illustrated in previous reconstructions are artifacts of oblique sectioning. Sections through *Volborthella* that resemble Signor and Ryan’s reconstruction appear shorter than longitudinal sections and were probably sectioned obliquely (e.g. Fig. 11). This does not disprove the hypothesis that *Volborthella* was a sclerite, but it removes an objection to the hypothesis that *Volborthella* was an individual test.

We have not yet found any specimens similar to the “articulated specimen” described by Signor and Ryan (1993), even in regions where little reworking has occurred and where there are hundreds of clusters consisting of 5-20 individuals on bed surfaces. Thus, we suspect that the lone specimen figured by Signor and Ryan (1993) could be a fortuitous arrangement, akin to “*Campitius*” (Firby and Durham, 1974; Glaessner, 1976; Yochelson, 1977; Signor et al., 1985). Even if *Volborthella* is a sclerite, it may not be a bilaterian sclerite. A number of sea anemones bear papillae on the column, which are often sites for the attachment of agglutinated particles held together by an organic matrix. In a few anemone species, the papillae secrete multilaminar septate cones made up of thick layers of a chitin-like substance; these structures are known as tenacula (Fautin and Mariscal, 2002). We do not believe that we can further support this hypothesis at this time, but include it here to illustrate the point that a wide range of taxonomic assignments are consistent with the available data on *Volborthella*.

CONCLUSIONS

Volborthella remains an enigmatic fossil. However, its wide stratigraphic range within the Early Cambrian and its unusual mode of skeletal construction suggest that it may be important in evaluating the mechanism(s) by which

organisms began to construct skeletons during the Neoproterozoic-Cambrian transition.

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