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THE ENIGMATIC CAMBRIAN FOSSIL *VOLBORTHELLA* AND ITS OCCURRENCE IN CALIFORNIA

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ABSTRACT—*Volborthella* Schmidt is a minute, tubular, agglutinated, and conical fossil that is composed either of oriented heavy mineral grains or quartz and other mineral grains. It is found abundantly in Lower Cambrian strata in northern Europe and is reported for the first time from western North America. The fossil has been referred to the Cephalopoda, Pteropoda, Tunicata, Protozoa, or to an unknown group of organisms. In its selectivity and orientation of the mineral grains, tubular form, and absence of shelly material, *Volborthella* is similar to certain agglutinated foraminifera or polychaete worm tubes but certainly not to mollusks or tunicates. *Volborthella* is not assigned to a particular group but is regarded as possibly a small polychaete tube or a wormlike animal of unknown affinities.

Volborthella Schmidt is a peculiar, predominately Lower Cambrian fossil that was originally described as a minute cephalopod (Schmidt, 1888). Its relationships have since been the subject of much controversy, principally between those who believed it to be a cephalopod [Karpinsky (1904), Grabau (1929), Grabau & Shimer (1910), Schindewolf (1928, 1934)] and those who did not [Spath (1933), Gürich (1934), Miller (1943), Flower (1954), Donovan (1964)]. The fossils resemble internal casts of tiny orthoconic cephalopods or pteropods, certain agglutinated foraminifera, and some worm tubes. Its occurrence in Lower Cambrian strata on at least two continents is important in reconstructing the phylogeny of whatever group to which it belongs, for it is among the oldest-known organisms that have hard parts.

Of importance then are structures that were found by Sylvester in thin sections of a Lower Cambrian siltstone from the Inyo Mountains, California, and that are here assigned to the genus *Volborthella*. The Lower Cambrian sequence from which this material comes has already yielded an unique assemblage of organisms, including the peculiar echinoderms of the class Heliocoplacoidea [Durham & Caster (1963), Durham (1967)], *Rusophycus* Hall and (?)*Pteridinium* Gürich (Cloud & Nelson, 1966), the "mollusc" *Wyattia* Taylor (Taylor, 1966), as well as several Lower Cambrian trilobite genera.

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All illustrated specimens are in the collections of the University of California, Los Angeles (UCLA).

SYSTEMATIC PALEONTOLOGY

Family VOLBORTHELLIDAE Kiaer, 1916
Genus VOLBORTHELLA Schmidt, 1888

Description.—The test consists of an agglutinated, straight to conical tube that has a narrow central cavity. One end of the tube may be closed and rounded. Internal differentiation between the closed end and the remainder of the tube is not observed. Walls are composed of heavy mineral or quartz grains of about the same size without any apparent cementing groundmass. The grains are oriented in particular directions and commonly form cones sloping toward the apical end of the tube. The terminal opening is a small circle or elipse that is surrounded by a slight ridge on the broad end of the conical tube.

Type species.—*Volborthella tenuis* Schmidt, 1888; by monotypy.

VOLBORTHELLA TENUIS Schmidt
Pl. 43, figs. 1–9

Volborthella tenuis SCHMIDT, 1888, p. 25, Pl. 3, figs. 27–31.

Volborthella conica SCHINDEWOLF, 1934, p. 175, Pl. 18, figs. 4,5,21, Pl. 19, figs. 1–7.

Description.—The specimens from California are unattached, undivided, elongate tubes, most of which are incomplete, that are composed of agglutinated heavy mineral grains. Our specimens measure as much as 2.07 mm in length and .30 to .82 mm in width. They are most commonly parallel-sided or tapering, although some are slightly curved. One end of some tubes is closed and rounded. The walls are composed of loosely-packed zircon, magnetite, and pyrite grains; a few tourmaline grains are noted. The organism was selective for it used only the available heavy minerals and ignored quartz and other grains of the same size. No cementing groundmass, inner lining, or shelly material is evident. In general, the long axes of the grains are oriented tangentially to the external surface and may be parallel to the cross section of the tube or pointed toward the apical end, thus forming sloping rows of grains. Some rows may be made entirely or partially of dark mineral grains. At the closed end, the long axes may follow the curvature of the tube. The grains are arranged in layers, generally three or four of decreasing diameter, so that the diameter of the internal cavity is normally less than one-tenth that of the tube. This cavity may vary in width in a single individual but is generally a very narrow restricted passage. The closed end of the tube may be of slightly greater external diameter, but the size of the internal cavity does not vary from the rest of the tube.

Discussion.—The California specimens are composed only of heavy mineral grains, whereas those from Europe are mainly of quartz but have some heavy mineral grains. In agglutinated foraminifera selectivity of building materials may vary according to geographic location and is not necessarily a distinguishing specific character (Loeblich & Tappan, 1964, p. *C*89). For this reason, and because the over-all shape and grain orientation of the specimens from both continents are the same, no specific distinction is made.

Within an assemblage, the fossils vary in shape from parallel-sided tubes to straight elongate cones. Illustrations of *Volborthella* assemblages from Europe [Karpinsky (1904, Fig. 1), Schindewolf (1934, Pl. 17), Gürich (1934, Pl. 12, fig. 1)] indicate similar variation in the European specimens. *Volborthella conica* is therefore considered an interspecific variation, as it was described from the same material as that containing *V. tenuis*.

Volborthella, when finally sectioned, was said to possess septa that were similar to those in cephalopods (Schindewolf, 1928, 1934). These so-called septa, as pointed out by Flower (1954, p. 42), are merely layers of dark mineral grains. The California specimens show that the "septa" are indeed layers of dark mineral grains, which are not always equally spaced or continuous (Pl. 43). The external transverse furrows on the tubes result from periodic growth and do not indicate internal septa.

The California material clearly demonstrates that *Volborthella* was an agglutinating organism that had the power to select and orient the grains that were used in the construction of its tube, as previously suggested by Gürich (1934). An internal cast would not be expected to contain only the minor heavy-mineral grains from the enclosing sediment oriented in parallel layers.

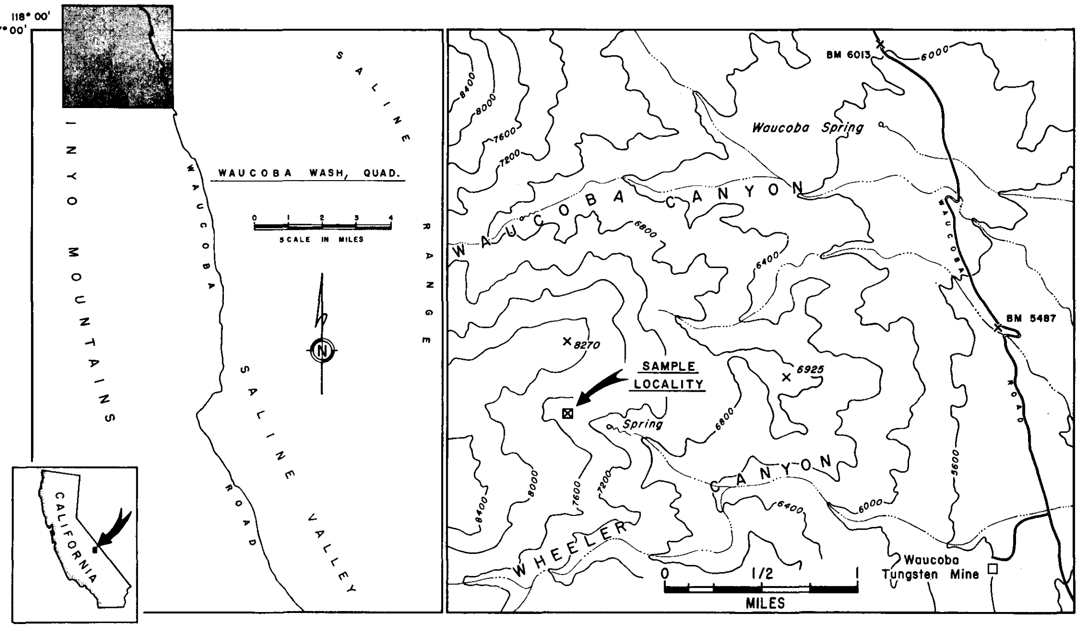
OCCURRENCE

Volborthella is now known from two continents. In Europe, this genus is abundant at its type locality in the Lower Cambrian Blue Clay of Estonia, as well as at other northern European localities. It is also reported from the Middle Cambrian of Bohemia (Prantl, 1948). In North America, specimens were reported from the Lower, and possibly the Middle, Cambrian of New Brunswick (Matthew, 1889), but this record is doubtful (Miller, 1932, p. 11). The fossils described herein were found in the Inyo Mountains of California in western North America.

The California fossils are found in a black laminated siltstone of the lower part of the Harkless Formation that crops out in the bottom of the north fork of Wheeler Canyon (Text-fig. 1), approximately 2500 feet S. 60° W. from the northeast corner of sec. 19, T. 11 S., R. 37 E., Mount Diablo Base and Meridian. The locality [University of California, Los Angeles (UCLA) 5737] is 400 feet upstream from the only spring in the north fork and 10 feet stratigraphically above the top of a massive blue- to buff-colored limestone bed that marks the top of the Poleta Formation (Text-fig. 2).

The area in Wheeler Canyon has undergone low-grade thermal metamorphism which resulted from the emplacement of a granitic pluton 1000 feet west of the fossil locality. This metamorphism, of the albite–epidote hornfels facies (temperature $<300°C.$, pressure <3 kilobars), did not recrystallize quartz or zircon, but did alter chlorite and sericite to biotite and muscovite. Sedimentary laminations and worm burrows were not affected by the metamorphism. The resulting rock, from which the fossils were recovered, is a dark-grey, weakly laminated, sandy siltstone that is composed chiefly of angular and subangular quartz grains and ragged laths of muscovite and biotite. Accessory minerals include zircon, magnetite, and tourmaline in small quantities. The laminations result from the alternation of quartz- and mica-rich layers which probably represent relic sedimentary layering that survived the metamorphism. Stratigraphically equivalent and petrographically similar unmetamorphosed rocks elsewhere in the Inyo Mountains are also laminated and contain quartz having fine-grained mats of chlorite and sericite instead of biotite and muscovite.

The Harkless Formation, named by Nelson (1962), is within the Lower Cambrian Waucoban Series, the type locality of which is located



TEXT-FIG. *1*—Right, map of the northwestern part of the Waucoba Wash Quadrangle and southwestern part of the Waucoba Spring Quadrangle, Inyo County, California, showing the sample locality [University of California, Los Angeles (UCLA) 5737] from which specimens of *Volborthella tenuis* Schmidt were obtained. Left, Waucoba Wash Quadrangle showing area of the right map (gray pattern). Inset left, California showing the location of the Waucoba Wash Quadrangle (arrow).

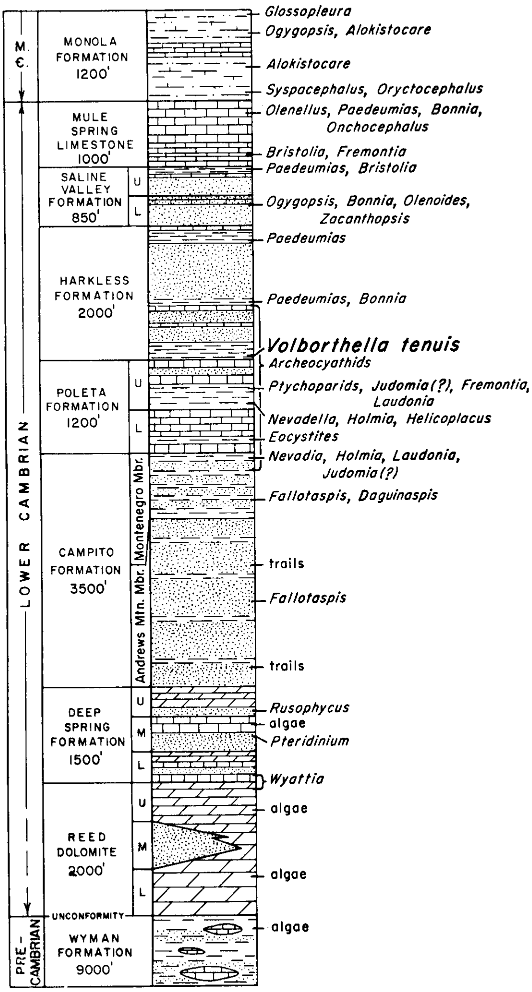
nearby at Waucoba Spring [Text-fig. 1; see Walcott (1912)]. The position of the base of the Cambrian in this area is questionable. Nelson (1962) first considered the base of the Cambrian to lie just below the lowest occurrence of trilobites (*Fallotaspis* Hupé) in the Campito Formation, although he noted that the underlying Deep Spring Formation and Reed Dolomite might be either of Cambrian or Precambrian age. Recently, Cloud & Nelson (1966) provisionally placed the boundary at the base of the Reed Dolomite, including in the Lower Cambrian both the Campito and Deep Spring Formations but questioning the inclusion therein of the entire Reed Dolomite. Middle Cambrian trilobite taxa (*Syspacephalus laevigatus* Rasetti and *Oryctocephalus* Walcott) are present in the Monola Formation (Nelson, 1965), some 3840 feet above the fossil locality. Thus, in this area *Volborthella tenuis* is found well within the Lower Cambrian and possibly lies as much as 8200 feet above the base of the Cambrian (Text-fig. 2).

COMPARISONS OF VOLBORTHELLA

Introductory statement.—The fossils described above have similarities to tubes of some worms, tests of agglutinated foraminifera, or internal casts of certain mollusks. We know of no inorganic process that could select only heavy mineral grains from a sediment that was composed predominantly of quartz grains of the same size and assemble these into tubes in which the grains are oriented in particular directions.

Foraminifera.—The Lower Cambrian fossils resemble agglutinated foraminifera of the superfamily Ammodiscacea Reuss, and the families Astrorhizidae Brady and Saccamminidae Brady [see Loeblich & Tappan (1964)]. The selection and orientation of mineral grains and the small size of *Volborthella* are characters that are common to genera of these families. Foraminifera are even known to place dark mineral grains at particular places in their tests (Tappan, 1962, p. 148), as did *Volborthella*, although the pattern of the grains in the Cambrian form is not known in foraminifera. The narrow internal cavity of *Volborthella* is unlike most foraminifera, but some foraminiferal species do have narrow or labyrinthic cavities. In these forms, the protoplasm is not restricted solely to the cavity but may also extend between the grains and external to the test.

Rhizammina Brady, 1879: Members of this Recent genus possess a straight or branching test that has a thin wall of large grains set in a finely arenaceous groundmass. *Volborthella* differs in having thick walls that are composed of



TEXT-FIG. 2.—Stratigraphic column of Cambrian and Precambrian strata in the Inyo Mountains, California, showing the horizon of the *Volborthella tenuis* Schmidt occurrence, and its relation to other fossil occurrences and rock formations. The Cambrian–Precambrian boundary is considered by J. W. Durham to lie just below the lowest occurrence of the trilobite *Fallotaspis* in the Campito Formation (Nelson & Durham, 1966). From Nelson & Durham (1966), as modified from Nelson (1962, 1965).

heavy mineral grains of about the same size, and its tube is commonly conical.

Bathysiphon M. Sars *in* G. O. Sars, 1872: Species of this genus are known from the Ordovician (and possibly the Lower Cambrian, see below) to the Recent. They are commonly relatively large and have a wide internal cavity which may, however, be filled at one end by the organism with waste products. In general, the wall contains sand grains that are set in a fine matrix, generally calcareous or ferruginous. Some species are known to select only particular kinds of minerals or other material for test construction (Dick, 1928), as did *Volborthella*. The present form differs from *Bathysiphon* in its smaller size, conical to straight shape, narrow internal cavity, primarily closed end, and absence of a cementing agent between the grains.

Marsipella Norman, 1878: The test of this genus is cylindrical, commonly twisted or irregular, and open at both ends. It may also be highly selective in obtaining test-building materials, for example, using only sponge spicules that are aligned along the length of the test. It is reported from the Late Ordovician to the Recent. Our Cambrian fossils differ in being smoothly arenaceous, symmetrical in outline, and closed at one end.

Hyperammina Brady, 1878: This Lower Ordovician to Recent foraminiferan has a globular proloculus that is followed by a second straight chamber. *Volborthella* has only a single chamber closed at one end.

Jaculella Brady, 1879: This genus closely resembles the Lower Cambrian specimens in its tapering, tubular test, and coarsely arenaceous wall. It differs primarily in its rounded apertural opening, wider cavity, and much larger and sharply tapering test.

Botellina Carpenter, Jeffreys & Thomson, 1870: *Botellina* has a globular proloculus and a second undivided tubular chamber. The internal cavity is poorly defined and has grains protruding into it. The walls have little cement; the grains of the wall are held in place by an inner pseudochitinous lining. The genus is known only from the Recent. *Volborthella* is similar in having a constricted internal cavity but differs in the absence of a well-defined globular proloculus.

Brachysiphon Chapman, 1906: The Permian genus *Hyperamminita* Crespin, 1958, was considered a synonym of the Recent *Brachysiphon* by Loeblich & Tappan (1964, p. *C*196). Although differences in morphology exist between these two genera that could be considered sufficient for generic distinction, both can be separated from *Volborthella* by certain common features. These features include their wide internal cavity, nonselectivity in the type of test-building material, nonuniformity of grain size, and a constricted apertural opening. In *Hyperamminita* the grains of the wall are firmly cemented (Crespin, 1958). *Volborthella* has none of these characters.

Other Cambrian or older objects referred to Foraminiferida: Many objects obtained from Cambrian or older rocks have been assigned to the foraminifera, but most of these have been reallocated to other animal or plant groups or are inorganic. Certain of these fossils displaying similarities to *Volborthella* are discussed below.

The Reitlingerellida Vologdin, 1958, consisting of variously coiled tubes of a constant diameter, were described from Lower Cambrian and Ordovician strata of Russia [Reytlinger (1948), Vologdin (1958)]. They are now regarded as algae or as organisms whose affinities are unknown and are no longer placed in the order Foraminiferida (Loeblich & Tappan, 1964, p. *C*787). These fossils differ from *Volborthella* in the coiled, narrow-walled nonagglutinated tubes.

Pflug (1965) described agglutinated objects from the Precambrian Belt Series of North America; these are now considered to be inorganic (Glaessner, 1966) or may perhaps represent blue-green algal tubes. In the same paper (Pflug, 1965), fossils reportedly from Upper Cambrian rocks of Europe were illustrated and described as foraminifera. These fossils are remarkably well organized, having alternating chambers constructed of radially arranged calcium prisms. In this respect, they differ markedly from the agglutinated tubes of *Volborthella*.

Playsolenites antiquissimus Eichwald, known from the same north European Lower Cambrian strata as *Volborthella*, was described as an annelid worm (Eichwald, 1860, p. 678) and later considered to be a cystoid (Schmidt, 1881, p. 12–13; 1888, p. 25–26). It was referred to the foraminiferal genus *Bathysiphon* by Glaessner (1963). Eichwald's brief description and illustrations are inadequate for determining the relationships of this organism. He noted that the fossils were siliceous, irregularly flattened, ranging from cylindrical to entirely flat, and had a definite internal cavity that contained an organism with a cylindrical body. Schmidt (1888, p. 25–26, Pl. 2, figs. 32, 33) showed long, hollow cylinders, striated with transverse grooves and furrows, and made of crystalline calcareous material. The transverse furrows produced a constricted or divided appearance in the tubes (Timofeev, 1955, p. 52). The tubes, according to Timofeev, measure 1.75 mm. wide and 15 mm. long; this is relatively long for *Bathysiphon*, although some modern species of this genus attain that size. *Platysolenites antiquissimus* may indeed belong to *Bathysiphon*, but further study is necessary for positive identification. Nevertheless, the information given by Eichwald, Schmidt, and Timofeev clearly indicates that this fossil is different from *Volborthella*. The California specimens are not nearly as large, they do not have a large central cavity, and they may be conical in shape. The "siliceous" or "crystalline calcareous" tubes of *Platysolenites* implies that they are not coarsely agglutinated, as in *Volborthella*.

In addition to *Bathysiphon*, whose recorded Cambrian occurrence is based on Glaessner's (1963) statement (Helen Tappan, personal communication), only one other object from the Cambrian was placed in the order Foraminiferida in the *Treatise on Invertebrate Paleontology* (Loeblich & Tappan, 1964). This was the genus *Chitinodendron* Eisenack, 1937, which was considered to be an allogromiid. This genus has branching organic-walled tubes and terminal saclike chambers. Its resemblance to *Volborthella*, allogromiids, or to other foraminifera is not close, and its inclusion in the order is considered questionable.

Worms.—Certain annelid worms of the order Polychaeta build tubes of sand grains, some species even selecting particular kinds of grains. These worms, for the most part, belong in a group of 28 families classed as Sedentaria (see Hartman, 1959). Hartman (1959, p. 6) accepted 355 of the 676 described genera and 2166 of the 4608 described species of Sedentaria, mostly living taxa. The number of known fossil forms is much smaller (Howell *in* Hass and others, 1962). The tubes built of sand grains are generally much larger in size than *Volborthella* and have a wide central cavity compared with the tube thickness.

Pectinaria Lamarck, 1818: This genus builds straight conical tubes of sand grains. Another genus, *Amphictene* Savigny, 1820, constructs a similar tube, except it is slightly curved. The internal cavity of both genera is very wide in comparison with the thickness of the tube wall. These genera are also larger than *Volborthella*.

Phragmatopoma Mörch, 1863: Species of this genus live together in massive colonies that consist of numerous sand tubes. The organism selects tabular sand grains or shell fragments and orients them in conical layers that slope toward the closed end, much as the grains of *Volborthella* are oriented. The spaces between the tubes are filled by sand that was carried there by currents and waves. In this genus also, the internal cavity of the tubes is much wider than the walls, and most tubes are larger than those of *Volborthella*.

Terebellites Howell, 1943: *Terebellites franklini* Howell, described from a single specimen as an annelid tube, resembles *Volborthella*. The holotype of *T. franklini* is partially embedded in rock matrix and has only one end exposed. It is described as a small tube built of sand grains and has relatively thick walls, as in *Volborthella*. It is slightly larger than most specimens of *Volborthella* and appears to have an expanded rim around the terminal opening. *Terebellites* is reported to range from Early to Middle Cambrian (Howell, 1943, p. 237).

Mollusks.—*Volborthella* has variously been represented as the internal casts of primitive cephalopods, pteropods, or a separate order of unknown affinities. These speculations were based on its orthoconic shape and external transverse furrows, which were thought to be indications of septa. An external calcareous shell has never been found with the casts, even in sediments that contained other shelled organisms. Because of its radial symmetry, agglutinated tubular construction, and the selection and orientation of mineral grains, *Volborthella* can be excluded from the mollusks.

Volborthella has commonly been grouped with *Salterella* Billings [Kobayashi (1937), Teichert *in* Teichert and others (1964, p. *K*486)] and *Vologdinella* Balashov (Teichert *in* Teichert and others, 1964, p. *K*487) as doubtful nautiloids. *Vologdinella* is poorly known and needs additional description before it is fully understood. *Salterella* possesses a calcareous, septate shell, and is probably a mollusk of unknown affinities (Teichert *in* Teichert and others, 1964, p. *K*486). As *Volborthella* is an agglutinated form, it is distinct from *Salterella*.

Tunicates.—Gürich (1934) compared *Volborthella* to ascidians. These animals have a tough external test that is composed of a substance similar to cellulose, in which sand grains may become embedded. *Psammaplidium* Herdman, 1886, for example, incorporates sand and shells in its test as it grows larger (Herdman, 1886). No selection or orientation of the incorporated material, however, is apparent. The test contains a relatively large internal cavity which houses the remainder of the animal. *Volborthella* differs from tunicates in the narrow internal cavity and the selection and orientation of the sand grains of its tube.

CONCLUSIONS

The agglutinated, conical tubes of *Volborthella* are unlike any known mollusk or tunicate but resemble some polychaete tubes or arenaceous foraminiferal tests. The small size and narrow internal cavity is unusual for worm tubes, although the shape and grain orientation are common to such tubes. No foraminifera are known that have the shape of *Volborthella*, and, additionally, the restricted cavity and peculiar orientation of sand grains are uncommon in this order. For these reasons, *Volborthella* is not assigned definitely to either of these groups. It may, in fact, represent an extinct group that is unlike any known organism, as suggested by Teichert (*in* Teichert and others, 1964, p. *K*485). We conclude that *Volborthella* was most likely a worm-like animal, possibly a small polychaete, and that it is not related to any group of tunicates or mollusks, particularly cephalopods.

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(*Explanation of Plate 43 appears on the following page*)

EXPLANATION OF PLATE 43

All figures are photomicrographs of thin sections of specimens from the lower part of the Harkless Formation, Lower Cambrian (Waucoban Series) in the north fork of Wheeler Canyon, Inyo Mountains, California [University of California, Los Angeles (UCLA) locality 5737].

All specimens are hypotypes.

FIGS. *1–9*—*Volborthella tenuis* Schmidt. *1*. Transverse section showing the arrangement and orientation of the heavy mineral grains, chiefly zircon (UCLA 45954), *2,3,4*, Longitudinal sections (UCLA 45957,45960, 45965). *5*, Thin section (UCLA 45966) showing a transverse section, a longitudinal section, and a fragment. *6,7,8*, Oblique sections (UCLA 45961,54958,45959). *9*, Section through the closed end of a tube (UCLA 45962).