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# *SPHENOTHALLUS*-LIKE FOSSILS FROM THE MARTINSBURG FORMATION (UPPER ORDOVICIAN), TENNESSEE, USA

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ABSTRACT—Tubular fossils, up to 2 mm in diameter and 60 mm in length, occur rarely in the upper Martinsburg Formation (Upper Ordovician), northeastern Tennessee Appalachians, U.S.A. The fossils are unbranched, straight or slightly bent, occasionally twisted and wrinkled, and not significantly tapered. Orientation of the fossils within shallow-marine tempestites suggests that they represent remains of organisms that were broken, transported, and deposited by storm waves and currents. The fossils are morphologically similar to many of the previously identified species belonging to the genus *Sphenothallus*, a relatively rare tube-dwelling Paleozoic marine invertebrate. Owing to the limited evidence for distal widening of the tubes, lack of holdfasts, and carbonaceous rather than phosphatic composition, the affinity of these fossils remains uncertain, and we refer to them as *Sphenothallus*-like.

## INTRODUCTION

IN THIS study we document the occurrence and characteristics of some rare and enigmatic fossils from Upper Ordovician strata at the Thorn Hill locality in the Valley and Ridge Province of the Tennessee Appalachians (Fig. 1). The fossils are centimeter-scale carbonaceous tubular forms from storm-dominated shallow-marine strata of the upper Martinsburg Formation (Sandbian to early Katian; formerly Sherman Stage of the Caradoc; Keith, 1993), below the contact with the overlying peritidal Juniata Formation (Fig. 2), which has well-developed coastal paleosols with animal and possible plant-root trace fossils (Driese and Foreman, 1991; Driese and Mora, 2001). We examined the fossils from the Martinsburg through petrographic, palynologic, and geochemical analyses, and explored their possible affinities as: 1) non-vascular terrestrial plants; or 2) the marine invertebrate *Sphenothallus*.

Recent analysis of Ordovician and Silurian organic matter from the Appalachians of Pennsylvania, Virginia, and West Virginia suggested the presence of extensive land floras predating the generally accepted timing of vascular plant emergence (Tomescu et al., 2009). An earlier study of the fossils from the Martinsburg Formation in Tennessee noted the similarity of these carbonaceous tubular forms to unbranched sporophytes of early non-vascular land plants (McKinstry et al., 2001). Therefore, we compare the Martinsburg fossils to some of the oldest documented megascopic non-vascular plant remains and present the results of palynological analysis and organic geochemistry of the fossil remains to address the question of their possible terrestrial affinity.

The Martinsburg fossils also are morphologically similar to species belonging to the genus *Sphenothallus* Hall, 1847, a taxon that has been identified from low-energy, fine-grained marine strata of Cambrian to Permian age (Mason and Yochelson, 1985; Van Iten et al., 1992, 2002; Neal and Hannibal, 2000; Yi et al., 2003). Although *Sphenothallus* was first interpreted as part of an ancient land plant (Hall, 1847), subsequent workers classified *Sphenothallus* as a tube-dwelling marine invertebrate, but its precise phylogenetic affinity continues to be debated (Yi et al., 2003). Mason and Yochelson (1985) suggested an annelid affinity and described *Sphenothallus* as a "worm tube." Feldmann et al. (1986) supported this classification, and Fauchald et al. (1986) used radiographs to document proposed soft-parts of the *Sphenothallus* "wormlike" organism but noted that the lack of evidence for segmentation prevents a firm association between *Sphenothallus* and annelids. Other cited invertebrate affinities for *Sphenothallus* include conulariids, thecate hydrozoans, and scyphozoan cnidarians (Ruedemann, 1896; Mason and Yochelson, 1985; Fauchald et al., 1986; Van Iten et al., 1992, 1996, 2002; Peng et al., 2005). Several authors also have classified *Sphenothallus* as incertae sedis above the genus level (Neal and Hannibal, 2000; Choi, 1990; Li et al., 2004).

Regardless of the affinity of *Sphenothallus*, this gregarious, opportunistic generalist is considered to be a sessile benthic organism that attached to the substrate by a basal holdfast (Van Iten et al., 1996) and inhabited environments ranging from hardgrounds to soft, muddy surfaces, including dysoxic benthic environments capable of supporting few other invertebrates (Neal and Hannibal, 2000). *Sphenothallus* may have also attached to other organisms such as brachiopods, conulariids, or other sphenothallids (Neal and Hannibal, 2000). Commonly observed and characteristic paired longitudinal thickenings are thought to have provided upright support for the *Sphenothallus* tubes (Mason and Yochelson, 1985; Choi, 1990; Van Iten et al., 1992), which typically taper to circular basal holdfasts with varying degrees of distal widening (Van Iten et al., 2002; Peng et al., 2005). Previous researchers described the composition of *Sphenothallus* remains as phosphatic (Mason and Yochelson, 1985; Van Iten et al., 1992, 2002; Peng et al., 2005), chitinous or organic (Bodenbender et al., 1989), or both phosphatic and organic (Fauchland et al., 1986; Yi et al., 2003; Li et al., 2004; Nakagaki and Xiao, 2008). Our comparison of the Late Ordovician carbonaceous tubular forms from the Martinsburg Formation to the documented examples of *Sphenothallus* aims at better characterizing this fossil genus and providing new information for the reconstruction of early Paleozoic environments at the critical interface between marine and terrestrial ecosystems.

## GEOLOGIC SETTING

The Thorn Hill section on Clinch Mountain in Tennessee, commonly referred to as a "classic" stratigraphic section of Paleozoic strata in the southern Appalachians (Walker and Byerly, 1985), begins with the Cambrian Rome Formation and terminates in the Carboniferous (Lower Mississippian) Grainger Formation. The Upper Ordovician Martinsburg

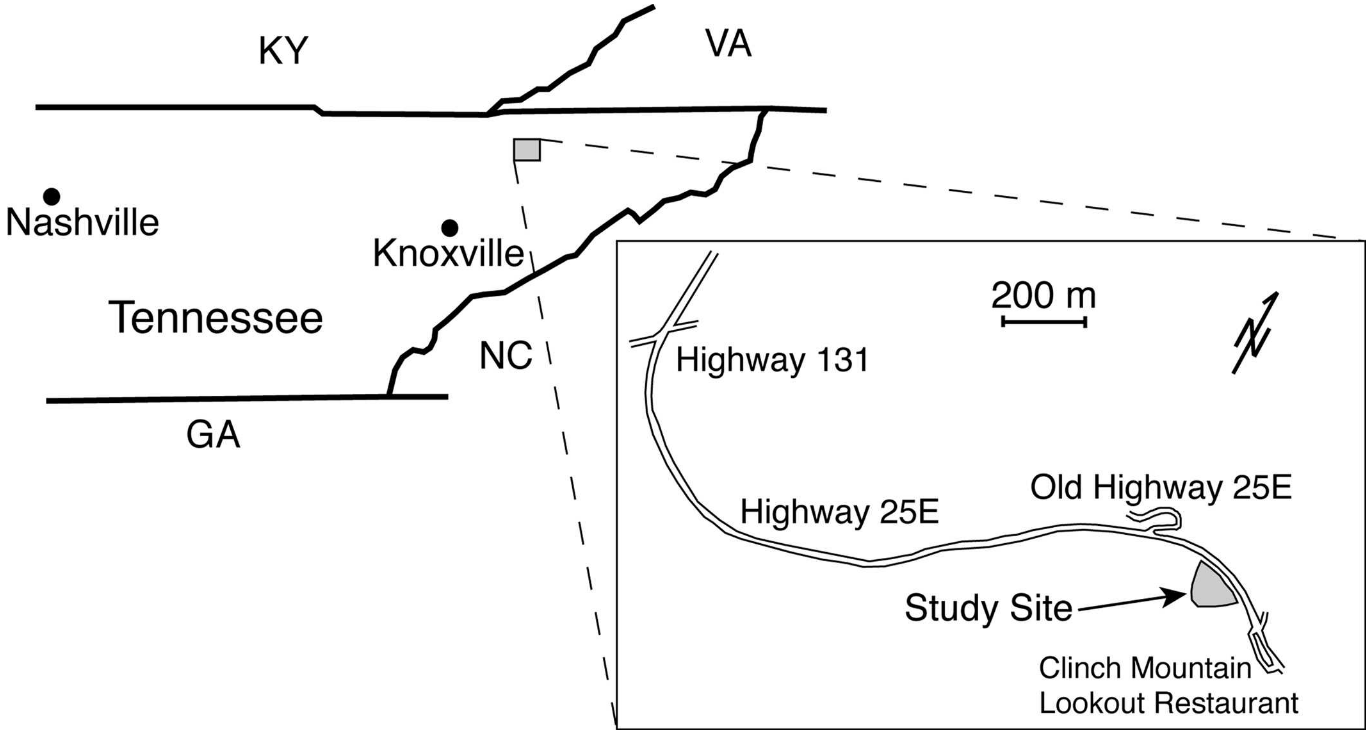


FIGURE 1—Location of the study site (N 36°21′, W 83°24′) in upper Martinsburg Formation, Thorn Hill locality along U.S. Highway 25E crossing Clinch Mountain in Grainger County, Valley and Ridge Province, northeast Tennessee Appalachians, U.S.A. (modified in part from Walker and Diehl, 1985).

Formation at Thorn Hill is lithologically distinct from the typical Martinsburg Formation in the central Appalachians of Pennsylvania and northern Virginia, which is characterized by deep-water turbidites, even though these strata occupy approximately the same stratigraphic interval (Walker and Diehl, 1985). At Thorn Hill, the Martinsburg Formation is about 600 m thick and consists of a basal shale facies, a middle carbonate facies, and an upper mixed carbonate-siliciclastic facies (Diehl, 1982). The gradual upward progression of these facies reflects an initial deepening event followed by a shallowing-upward trend that culminates in peritidal deposits of the overlying uppermost Ordovician Juniata Formation (Walker and Diehl, 1985).

This study focuses on fossils from the upper mixed carbonate-siliciclastic facies of the Martinsburg, which consists of decimeter-scale successions composed of skeletal limestone overlain by siltstone and shale (Fig. 2.2). The skeletal component includes common brachiopods and bryozoans, and less abundant mollusks, crinoids, ostracodes, and trilobites. The fining-upward limestone beds commonly have horizontal and hummocky cross-laminations as well as sharp, undulatory erosional bases and coarse fossil lag deposits that grade upward into skeletal packstone capped by bioturbated shale. Consequently, these deposits have been interpreted as tempestites or storm deposits formed in a shallow-marine shelf environment (Walker and Diehl, 1985). The fossils described herein are preserved in siltstone deposits from the upper part of one of the tempestite beds, about 25 m below the contact with the Juniata Formation (Fig. 2).

## METHODS

Samples described reside in the Smith College Paleontological Collection, collection numbers 6512 to 6521. Select samples were examined using a scanning electron microscope (SEM), and elemental composition was determined through X-ray microanalysis using an Oxford Link ISIS electron dispersive spectroscopy (EDS) system. A sample of siltstone was analyzed for palynomorphs at the Paleobotany Laboratory of Boston College.

Following the removal of trace carbonates, carbon isotope composition ($\delta^{13}C$) and carbon and nitrogen content of the fossil remains were measured on a continuous-flow gas-ratio mass spectrometer (Finnigan Delta PlusXL) at the University of Arizona. Samples were combusted using an elemental analyzer (Costech) coupled to the mass spectrometer. Standardization was based on acetanalide for elemental concentration, and on NBS-22 and USGS-24 for $\delta^{13}C$. Precision was better than $\pm$ 0.06 for $\delta^{13}C$ ($1\sigma$), based on repeated internal standards.

## RESULTS

The fossils are black carbonaceous tubular forms up to 60 mm long and 0.5–2 mm wide, oriented parallel to bedding and commonly aligned subparallel to each other (Fig. 3.1). They are mostly straight or slightly bent and occasionally twisted and wrinkled (Figs. 3.2, 3.3) and do not branch. In cross section, the well-preserved tubes are elliptical (compressed) or circular (uncompressed). The tubes appear to have been hollow and are now filled with silty sediment, scattered organic material, pyrite, and calcite cement (Figs. 3.4, 3.5). Longitudinal thickenings located on opposite sides of the tube are occasionally present, producing two lateral ridges in hand samples and crescent-shaped thickenings in cross section (Fig. 3.4). The tubes primarily maintain a constant diameter, but a few examples of lateral widening were found (Fig. 3.6).

Many tubes exhibit a regular fracture pattern, with straight fractures oriented parallel to each other and at variable angles (from near perpendicular to as low as approximately 20°) to the axis of tube elongation (Fig. 3.7). Breakage along these and other irregular fractures produced all observed tube

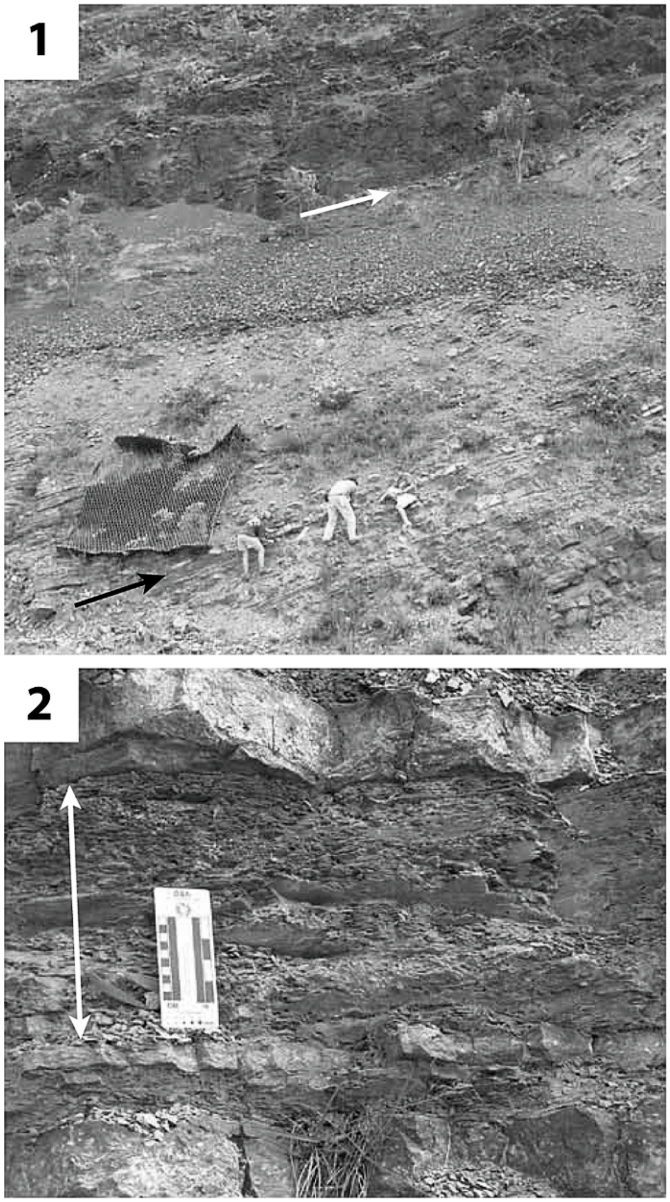


FIGURE 2—Outcrop photographs: *1,* the fossil-bearing horizon (black arrow) in the upper Martinsburg Formation, about 25 m below contact with the Juniata Formation (white arrow); *2,* characteristic stratification pattern of storm deposits (tempestites) in the upper Martinsburg. Thicker skeletal limestone layers are interbedded with thin-bedded to laminated siltstone and shale layers. Arrow indicates the fossil-bearing siltstone horizon in the upper part of a tempestite bed. Photoscale=16 cm.

terminations and no evidence for holdfasts or other forms of tube endings were found.

SEM analyses revealed a variable exterior surface texture, from bumpy (Fig. 4.1) to smooth (Fig. 4.2). The tube walls range in thickness from 3 to 80 μm and lack complex structure. The only apparent structure present is that of thin laminations, on a micrometer scale, parallel to the tube wall (Fig. 4.2).

EDS analyses (elemental maps and spectra) of the petrographic thin sections indicated organic composition of the examined fossil tubes and confirmed their infilling of silt-sized pyrite, quartz, and feldspar grains, similar to that of the matrix sediment (Fig. 4.3). Palynomorph analysis of the matrix revealed the presence of acritarchs and 2 or 3 species of chitinozoa (P.K. Strother, personal commun., 2006).

Carbon is the dominant element in most of the analyzed specimens (Fig. 5), and the $\delta^{13}C$ values of organic matter from the fossil tubes range from −29.30 to −28.71‰ VPDB with an average of −28.95‰ VPDB (Table 1). The C/N ratios of the fossil remains range from 13.46 to 19.12, clustering toward the upper limit of the range (Fig. 5).

## DISCUSSION

Orientation of the fossils within the tempestite bed suggests that they represent remains of organisms that were broken, transported, and deposited by storm waves and currents. The coastal environments represented by the overlying Juniata Formation may have served as a source for terrestrial input, including plant remains, into the adjacent shallow-marine environment characteristic of the upper Martinsburg Formation. Therefore, the Martinsburg fossils were compared to *Eohostimella*, which is one of the oldest documented plant megafossils of uncertain origin (Edwards and Wellman, 2001; but see also Strother and Lenk, 1983). *Eohostimella* was first described in situ from coarse siltstones interbedded with sandstones containing marine invertebrate fossils from the Silurian (Llandovery) Frenchville Formation in Maine, U.S.A. (Schopf et al., 1966). Similar to the Martinsburg specimens, *Eohostimella* consists of tubular axes 1 to 2 mm in diameter, with a persistent carbonized outer cortical layer, internal sediment filling, and no trace of vascular tissue. The *Eohostimella* axes have erect habit and were also found parallel to bedding. Unlike the Martinsburg fossils, *Eohostimella* exhibits dermal outer surfaces roughened by irregularly arranged minute spinulate appendages and commonly dichotomous branching (Schopf et al., 1966). These differences, plus the lack of conclusive evidence for any spore-bearing organs and the very simple structure of the tube walls, refute a terrestrial origin for the Martinsburg fossils.

Also inconsistent with a terrestrial plant affinity are the results of the palynomorph analysis of the Martinsburg matrix material, which indicate that the terrestrial input comprised a negligible fraction of the sediment. Geochemical analyses of the fossil remains further support this conclusion. The carbon/nitrogen ratios of the Martinsburg fossils (13.46 to 19.12) do not resemble modern terrestrial plant materials, which have C/N ratios greater than 20 (Gröcke, 1998). These ratios are characteristic of benthic marine primary producers, which have variable C/N ratios with a median of 18.3 (Atkinson and Smith, 1983). The average $\delta^{13}C$ values (−28.95‰ VPDB) are lower than previously analyzed *Sphenothallus* remains (−21.68‰ to −18.65‰ VPDB; Yi et al., 2003) and values characteristic of marine invertebrates (approximately −20‰ VPDB; Dickens et al., 1995). A recent carbon isotope analysis of early Paleozoic fossil and sedimentary organic matter indicates that marine carbon tends to be isotopically lighter than the coeval terrestrial material (Tomescu et al., 2009). Significant overlap between the isotopic ranges of organic matter may exist (Tomescu et al., 2009), and diagenetic modifications may result in shifts towards more negative values. Thus, even though the $\delta^{13}C$ and the C/N values cannot conclusively indicate affinity for the fossil remains, they suggest a marine invertebrate rather than terrestrial plant origin for the fossils and provide information for further comparisons and possible future diagenetic and biomarker studies.

The Martinsburg fossils compare closely with some of the previously described examples of *Sphenothallus* from lower

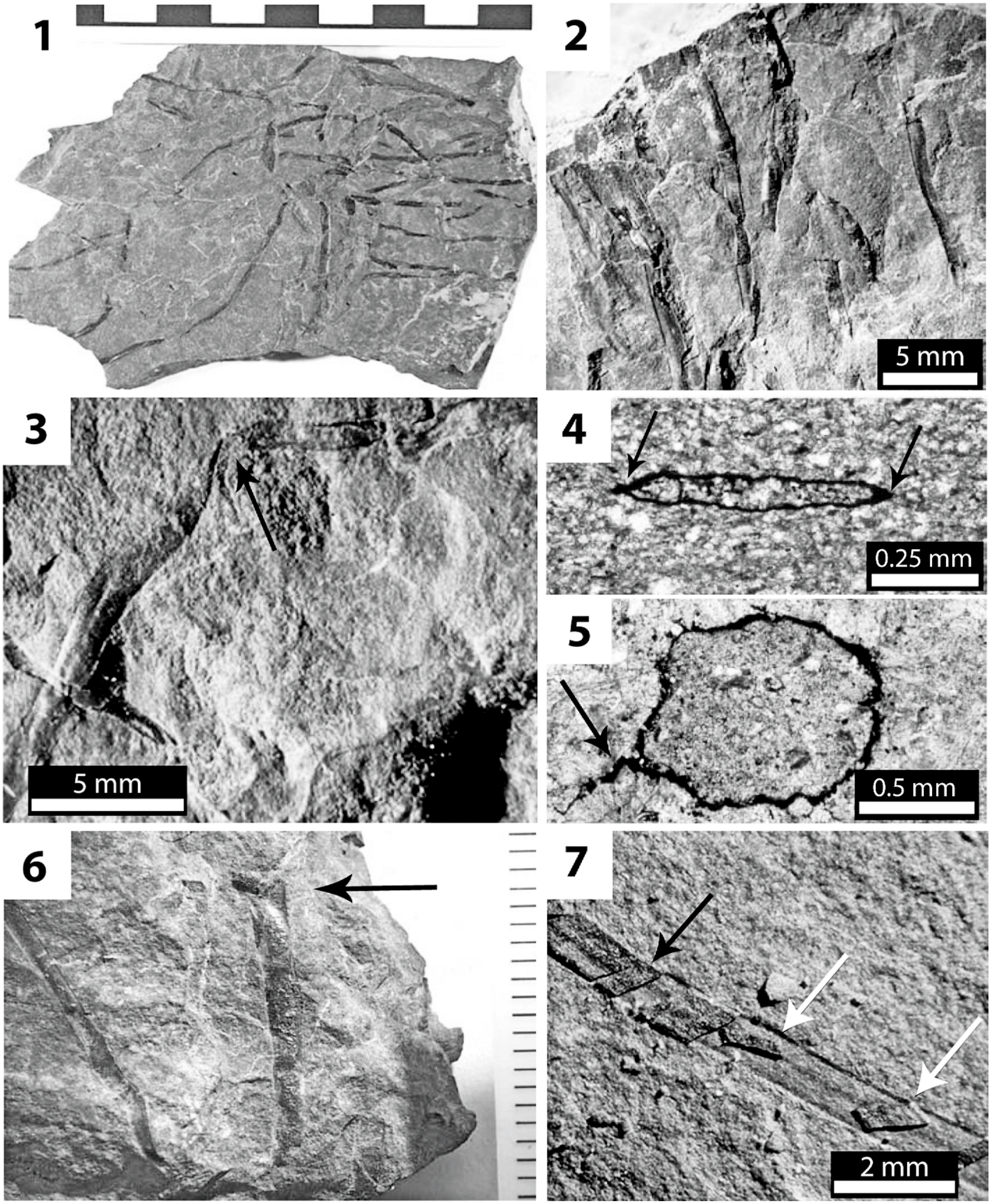


FIGURE 3—Martinsburg Formation fossils: *1,* siltstone bedding plane displaying characteristic shape and orientation of the fossils, scale in cm; *2,* close-up of bedding plane with several carbonaceous tubular specimens, slightly bent, occasionally twisted, and oriented sub-parallel to each other; *3,* example of a twisted tube (arrow); *4,* thin-section photomicrograph of siltstone with compressed cross-section of a tubular fragment displaying crescent-shaped longitudinal thickenings (arrows); *5,* thin-section photomicrograph with nearly circular tube in cross-section, filled with sediment and organic matter; tube is flattened on one side (arrow), yet displays no evidence of lateral thickenings; *6,* tube showing diameter expansion at distal end (arrow), scale in mm; *7,* tube with regular fractures parallel to one another and at an angle to tube long axis. Black arrow indicates fractures at high angle to tube elongation; white arrows indicate displaced segments of the carbonaceous tube.

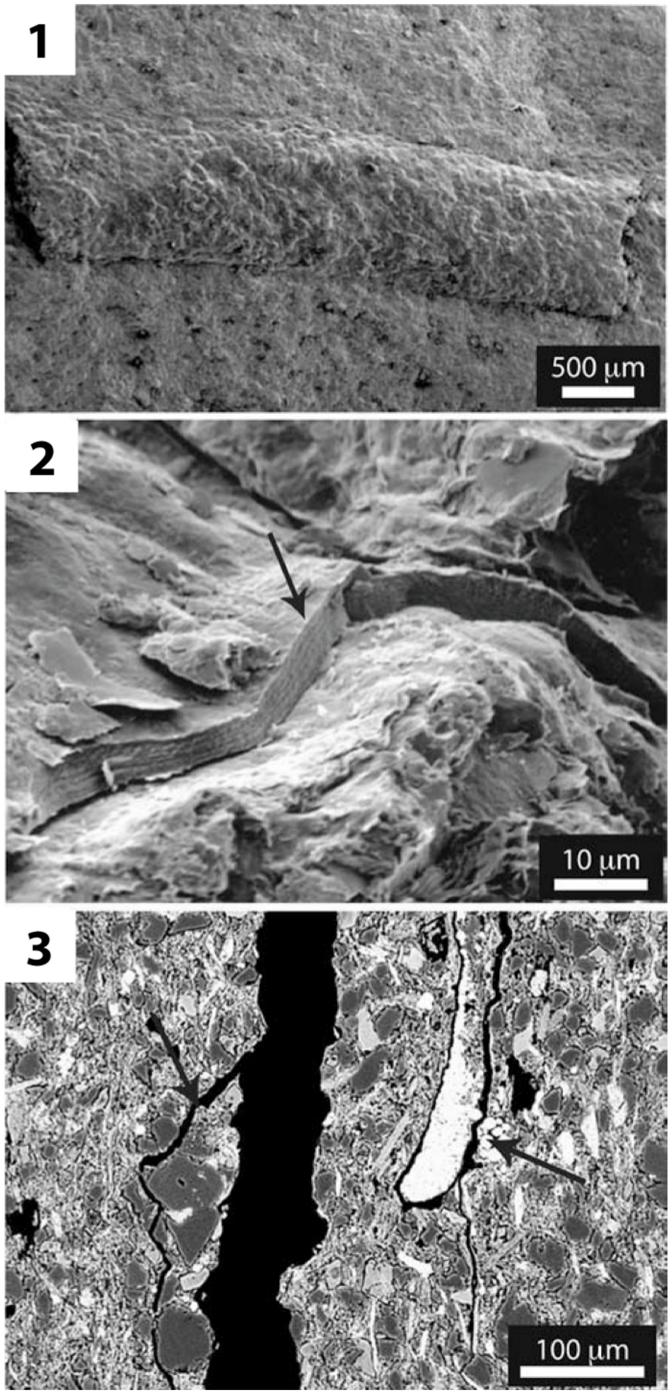


FIGURE 4—SEM images of Martinsburg fossils: *1,* tube exterior showing irregular, bumpy outer surface; *2,* fragmented wall of specimen displaying fine laminations oriented parallel to the wall surface (arrow); *3,* back-scattered electron image of two tubes (arrows) aside an open fracture in the center of the image. Tube to right of the fracture is infilled mainly with pyrite and tube at left contains quartz grains and other sediment and cement similar to surrounding matrix.

Paleozoic marine deposits. Mason and Yochelson (1985) suggested that when the organisms were alive, *Sphenothallus* tubes were flexible. This characteristic is evident in the Martinsburg fossils by common sharp bending, twisting, and wrinkling of the tubes. The bumpy texture of the tube exterior appears to be an impression of the surrounding matrix, suggesting that the tube was originally composed of very thin

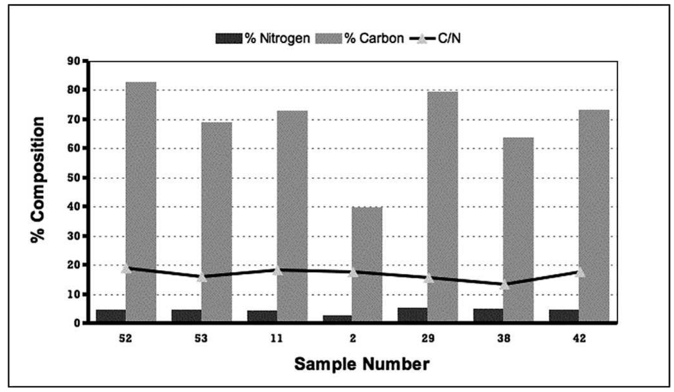


FIGURE 5—Percent composition of carbon and nitrogen and carbon/nitrogen (C/N) ratio for seven samples of the Martinsburg fossils. Black line indicates the C/N ratio at same scale as the percent composition.

and flexible material. Although not diagnostic of the genus, the lack of complicated structure and the presence of micrometer laminations in the walls of the Martinsburg fossils are common to many lower Paleozoic specimens of *Sphenothallus* (Van Iten et al., 1992, 2002; Li et al., 2004; Peng et al., 2005). The small size and limited lateral widening of the Martinsburg specimens are additionally comparable to many other lower Paleozoic examples, but also to Late Devonian and Carboniferous *Sphenothallus bicarinatus* Girty, 1911, a species that has a distinctly smaller size and narrower tubes than the characteristic larger conical tubes of many middle to upper Paleozoic species such as *Sphenothallus carbonarious* M'Coy, 1844 (Mason and Yochelson, 1985), and *Sphenothallus ruedemanni* Kobayashi, 1934 (Choi, 1990). The Martinsburg tubes, however, show limited evidence for paired longitudinal thickenings common to most middle to upper Paleozoic *Sphenothallus* species (Feldmann et al., 1986; Neal and Hannibal, 2000; Yi et al., 2003). In the Martinsburg fossils this feature is primarily associated with tubes that are flattened or elliptical in cross-section, indicating that the thickenings may be compression features. Although the thickenings are not always present in early Paleozoic species assigned to this genus, some of the Burgess Shale *Sphenothallus* specimens, which are circular in cross-section and lack distinct thickenings proximally, distally become elliptical with distinct thickenings (Van Iten et al., 2002). This suggests that the Martinsburg *Sphenothallus*-like fossils may represent various fragmented parts (proximal and distal) of the original tubes. Furthermore, this fragmentation may account for the lack of holdfasts recovered from the Martinsburg Formation, which limits conclusions that may be drawn about the life mode of these *Sphenothallus*-like organisms.

TABLE *1*—Carbon isotope analysis results. $\delta^{13}C$ values and mean value expressed in ‰ VPDB for 10 Martinsburg fossil samples.

| Sample | $\delta^{13}C$ value (‰ VPDB) |
|---|---|
| 11 | −28.71 |
| 38 | −29.16 |
| 2 | −29.12 |
| 29 | −29.02 |
| 41 | −28.95 |
| 42 | −29.30 |
| 52 | −28.89 |
| 53 | −29.07 |
| MIXED | −28.93 |
| 22+23 | −28.81 |
| Average: | −28.95±0.17 |

One difference between the Martinsburg fossils and other species belonging to *Sphenothallus* is their organic rather than phosphatic composition. The paucity of phosphorous within the analyzed fossil tubes was indicated on our EDS elemental maps and spectra, and carbon proved to be the dominant element in most of the analyzed samples (Fig. 5). If these tubular fossils were originally at least partially phosphatic then only severe leaching could account for their present-day composition. Leaching of calcium phosphate from weathered *Sphenothallus* tubes from Cambrian deposits in China was reported by Nakagaki and Xiao (2008). It is possible that similar processes operated during diagenesis of the Martinsburg strata, but since phosphatic composition is by most researchers considered critical for positive identification of specimens as belonging to *Sphenothallus* then the organic composition of the Martinsburg fossils precludes us from referring to them as sphenothallids.

One additional characteristic of these fossils is the pattern of parallel fractures perpendicular or at an angle to the elongation axis of the tubes. Transverse ridges and striae were also observed in some Cambrian examples from China (Peng et al., 2005), and interpreted as exfoliation of multilamellal tube tests (Zhu et al., 2000). Bolton (1994) described Late Ordovician *Sphenothallus* specimens from Ontario with similar fine transverse striations interpreted as weathered "cut-ends" of the laminae, rather than the result of a regular fracturing pattern. The fractures observed in the Martinsburg specimens may be the result of post-mortem compression and post-depositional deformation. The regularity of breaks, however, seems to indicate an underlying structural weakness within the tube walls, which could be related to their lamellar structure. Fracturing along these areas of weakness may reflect taphonomical changes of the tubes during transport by high-energy storm waves and currents, and their subsequent deposition and compression within rather coarse-grained shallow-shelf siltstone deposits. This is in contrast to the majority of previously documented *Sphenothallus* specimens, which were found in dark shales and lime mudstones of low-energy restricted basins and shelf slope facies (Van Iten et al., 2002), and can account for some of the observed morphological differences of the Martinsburg fossils.

Although the carbonaceous tubular fossils preserved in the tempestites of the upper Martinsburg Formation in Tennessee have features that suggest they represent fragments of *Sphenothallus*, the affinity of the Martinsburg fossils remains uncertain. However, the characteristics of *Sphenothallus* previously have not been well defined, and some *Sphenothallus* remains may have been misidentified, necessitating careful re-evaluation and documentation of this genus. Documentation of the occurrence of these Late Ordovician *Sphenothallus*-like forms, geochemistry of their remains, and palynology of the host sediment contributes new information towards better understanding of the potentially widespread but still enigmatic Paleozoic genus *Sphenothallus*.

## CONCLUSIONS

Fragmented carbonaceous tubular fossils, up to 2 mm in diameter and 60 mm in length, are preserved in storm deposits (tempestites) in a shallow marine shelf facies of the upper Martinsburg Formation (Upper Ordovician) from the northeastern Tennessee Appalachians. The predominance of other marine fossils and palynomorphs, lack of evidence for reproductive structures, and low C/N ratios are inconsistent with a terrestrial plant affinity for these fossils. The flexible, finely lamellar tubes of the Martinsburg fossils are morphologically similar to many of the previously identified forms of marine invertebrate *Sphenothallus*. Nonetheless, no holdfast structures were recovered and the Martinsburg specimens are of organic rather than phosphatic composition and display only limited evidence for distal widening of the tubes and paired lateral thickenings common to most species of *Sphenothallus*. This precluded us to identify these fossils with certainty as sphenothallids and instead we refer to them as *Sphenothallus*-like.

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