New occurrences of *Sphenothallus* in the lower Cambrian of South China: Implications for its affinities and taphonomic mineralization of shelly fossils

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ABSTRACT

Sphenothallus, a tubular fossil that occurs in Paleozoic strata around the world, may be related to cnidarians or ‘worms,’ but its affinities remain controversial due to preservational variations among localities. Here, to test hypotheses regarding *Sphenothallus* taphonomy and affinities, we investigate the preservation of new fossils from the lower Cambrian Shuijingtuo Formation at Heziao and Jijiapo (Hubei Province) and the equivalent Niutitang Formation at Siduping (Hunan Province) in South China. Morphology and allometry suggest that the fossils represent a single species, and their biostratigraphy and authigenic mineralization indicate that they underwent similar pre-burial and early diagenetic processes, particularly transport and focused degradation via microbial sulfate reduction. However, the compositions and microstructures of the tests vary among localities. The Heziao tests consist of lamellar phosphatic material covered interiorly and exteriorly by layers of carbonaceous material. In contrast, the Siduping tests consist of non-lamellar phosphatic material associated with carbonaceous material, and the Jijiapo tests consist entirely of carbonaceous material. Based on these observations and experimental taphonomic data—which show that hydrochloric acid treatment of Heziao samples produces fossils that

compositionally and microstructurally resemble the Jijiapo specimens—we propose that the new tests constitute a taphonomic continuum between shelly and carbonaceous preservation. This taphonomic model suggests that the preservation of shells as carbonaceous fossils results from kerogenization of the organic matrixes and subsequent or concomitant demineralization of the biomineralized microstructures of the shells. Hence, variations in *Sphenothallus* composition and microstructure among localities may reflect varying extents of test demineralization, and the carbonaceous layers in Heziao specimens may have formed via demineralization of the tests' exterior and interior phosphatic lamellae. Our reconstruction based on this model indicates that pristine *Sphenothallus* tests consist of exteriorly sculptured and interiorly unsculptured organophosphatic lamellae. Thus, *Sphenothallus* microstructurally resembles and may be related to conulariids, and potentially, cnidarians.

Keywords: biomineralization, Cambrian Explosion, carbonaceous fossils, small shelly fossils, taphonomy

1. Introduction

The record of the problematic tubular fossil *Sphenothallus* spans from the lower Cambrian (Li et al., 2004; Peng et al., 2005) to the upper Paleozoic (Mason and Yochelson, 1985) with occurrences in North America (Bodenbender et al., 1989; Bolton, 1994; Hall et al., 1847; Mason and Yochelson, 1985; Neal and Hannibal, 2000; Pashin and Etensohn, 1987, 1992; van Iten et al., 1992; van Iten et al., 2002; Wei-Haas et al., 2011), South America (Clarke, 1913), Africa (van Iten et al., 2013), Europe (Fatka et al., 2012; Fauchald et al., 1986; Schmidt and Teichmüller, 1956; Stewart et al., 2014; Vinn and Kirsimäe, 201X), and Asia (Balinski and Sun,

2015; Choi, 1990; Li et al., 2004; van Iken et al., 2013; Wang et al., 2003; Zhu et al., 2000). Hall et al. (1847) originally described *Sphenothallus* as a plant, but in the past century, discussion of the taxon has focused on potential affinities with cnidarians (Peng et al., 2005; van Iken et al., 1992; van Iken et al., 2013) and various types of worms (Mason and Yochelson, 1985; Wilson, 1967). Nonetheless, despite the broad temporal and spatial distributions of the genus, the affinities of *Sphenothallus* remain controversial, in part, due to preservational variations among localities (Wei-Haas et al., 2011).

In general, the tubular *Sphenothallus* test consists of a pair of oppositely-situated longitudinal thickenings, which branch near the apex, extend up to its aperture, and are connected by two thinner transverse walls (Peng et al., 2005). The longitudinal thickenings and transverse walls are sometimes covered by low-relief transverse ribs (Bolton, 1994; Muscente and Xiao, 2015; Peng et al., 2005; van Iken et al., 1992; Zhu et al., 2000) or wrinkles (Choi, 1990), which are not always preserved (Fatka et al., 2012; Li et al., 2004; Mason and Yochelson, 1985; Stewart et al., 2014; Vinn and Kirsimäe, 201X). At some localities, tests are preserved as carbonaceous fossils (Bodenbender et al., 1989; Neal and Hannibal, 2000; Wei-Haas et al., 2011), but at others, they are phosphatic shells (Li et al., 2004; Muscente and Xiao, 2015; van Iken et al., 1992; Vinn and Kirsimäe, 201X). Electron microscopy and energy-dispersive X-ray spectroscopy indicate the apices and longitudinal thickenings of the phosphatic tests are sometimes comprised of submicron-thick laminations (van Iken et al., 1992; Wang et al., 2003), which may be associated with carbonaceous material (Li et al., 2004; Muscente and Xiao, 2015). The carbonaceous material sometimes occurs as micrometer-thick, coherent layers covering the interior and exterior surfaces of phosphatic tests (Muscente and Xiao, 2015). However, the origin and significance of these carbonaceous layers has not been thoroughly investigated, and in other

specimens, the phosphatic lamellae do not occur with carbonaceous material, vary in thickness between 10 and 170 μm , and lack sharp lamellar boundaries (Vinn and Kirsimäe, 201X). Hence, *Sphenothallus* tests may have originally been phosphatic (Mason and Yochelson, 1985; van Iten et al., 1992), organophosphatic (Li et al., 2004; Wang et al., 2003), or organic (Bodenbender et al., 1989). If they were originally organic, phosphatic specimens may be secondarily phosphatized, like co-occurring shelly fossils (Li et al., 2004). Regardless, the original composition and microstructure of the *Sphenothallus* test remains unclear.

Other notable variations in *Sphenothallus* preservation among localities relate to its basal attachment structures and non-biomineralized tissues. Some fossils are preserved with conical hold-fasts (Bodenbender et al., 1989; Feldmann et al., 1986; Mason and Yochelson, 1985; van Iten et al., 1992; Wang et al., 2003) that are sometimes phosphatic (van Iten et al., 1992) and other times carbonaceous (Bodenbender et al., 1989). In addition, *Sphenothallus* fossils from the Devonian Hunsrück Slate conserve putative non-biomineralized tissues, which suggest that the organism possessed a symmetrical feeding apparatus with paired tentacles (Fauchald et al., 1986). However, these tissues have not been reported from other localities. Overall, due to these variations in *Sphenothallus* soft tissue and test preservation, assessments of the taxon's affinities have thus far been inconclusive.

In this paper, we report new occurrences of *Sphenothallus* fossils from the lower Cambrian Shuijingtuo Formation at Heziao and Jijiapo in Hubei Province and from the equivalent Niutitang Formation at Siduping in Hunan Province of South China, and describe their preservation in order to test hypotheses regarding the taphonomy and phylogenetic affinities of the genus. Specifically, our investigation examines the biostratinomy, mineralization, test compositions, and skeletal microstructures of the new *Sphenothallus* fossils. In addition, we

compare the specimens from the three localities in terms of allometric growth curves, and present the results of a simple experiment, simulating taphonomic demineralization processes that may influence *Sphenothallus* preservation. Using the results of these analyses, we propose a taphonomic model for the preservation of *Sphenothallus* in the lower Cambrian of South China, interpret the origin of the carbonaceous layers covering the interior and exterior surfaces of some phosphatic specimens, and discuss the possible phylogenetic affinities of the genus.

2. Material and Geological Background

Sphenothallus fossils were discovered in black shales of the lower Cambrian (Stage 3) Shuijingtuo Formation at Heziao and Jijiapoin Hubei Province of South China (Fig. 1A–B). The Shuijingtuo Formation was deposited on the Yangtze Platform, which was part of a southeast-facing passive continental margin that formed following the break-up of the Rodinia supercontinent in the late Neoproterozoic (Wang and Li, 2003). During the Terreneuvian, carbonates were deposited on the shallow platform, shales were deposited in the basin, and interbedded carbonates and shales were deposited in transitional facies (Jiang et al., 2012). Subsequently, during the Cambrian Stage 3, widespread black shales were deposited, including the Shuijingtuo and middle-upper Niutitang formations (Peng and Babcock, 2001; Steiner et al., 2001). The Shuijingtuo Formation (~60 m in thickness) overlies the poorly-exposed Yanjiahe Formation (carbonate, phosphorite, chert, and shale) and underlies the Shipai Formation (shale and siltstone with minor limestone, Fig 1C). In general, it consists of three members. Member I is black shale containing meter-sized carbonate concretions. Overlying it, member II—which contains the *Sphenothallus* fossils reported in this study—is a carbonaceous black shale interbedded with thin limestone. Member III is a bioclastic carbonaceous limestone containing

possible animal embryos (Broce et al., 2014). Eodiscoid trilobites—such as *Tsunyiidiscus* (Fig. 2E–F), which first appears 6 m above the base of the Shuijingtuo Formation and is followed by *Sinodiscus* and *Hupeiidiscus* (Ishikawa et al., 2014; Wang et al., 1987)—are characteristic of the Nangaoan (Qiongzhusian) stage (Peng and Babcock, 2001), which has been correlated to Cambrian Stage 3 (514–521 Ma) (Peng et al., 2012). Therefore, the *Sphenothallus* fossils described herein are most likely Cambrian Stage 3.

The Heziao section (30° 30.722' N, 111° 08.947' E) outcrops along road cuts west of the town of Changyang (Fig. 1B). Poor exposure of the Shuijingtuo Formation prevented precise measurement of the sequence, but we estimate the formation's thickness between 50 and 80 m. At the locality (Fig. 2A–B), the Shuijingtuo Formation contains pyritized sponge spicules (Fig. 2C) and *Sphenothallus* at multiple levels. *Sphenothallus* typically occurs within the thick beds of the outcrop, which is made up predominantly of more finely-laminated black shales. The *Sphenothallus* specimens analyzed herein comes from a single interval (~10 cm thick, Fig. 2B), which includes whole tests—ones with relatively intact apexes, apertures, and thickenings—and fragmentary material (e.g. broken thickenings).

The Jijiapo section (30° 45.142' N, 111° 02.004' E) outcrops south of Sandouping on the southern side of the Huangling anticline in the Yangtze Gorges area (Fig. 1B). Whole tests and fragmentary specimens of *Sphenothallus* occur throughout a poorly-exposed outcrop (<1 m thick) of thinly-bedded, dark brown silty-shale of Member II. The fossiliferous horizon is about 20 m above the base of the Shuijingtuo Formation and about 15 m above Member I with larger carbonate concretions. The eodiscoid trilobite *Tsunyiidiscus* (Fig. 1E–F) co-occurs with *Sphenothallus* at the Jijiapo section.

Floats of black shale pieces containing *Sphenothallus* were also recovered from the Siduping section (28° 55.023' N, 110° 26.946' E) in Hunan Province (Fig. 1A). The black shale pieces most likely come from the lower Cambrian Niutitang Formation, which is the major black shale unit in the Siduping area (Wang et al., 2012b). In general, the Niutitang Formation overlies the terminal Ediacaran Liuchapo Formation (bedded cherts and siliceous shales) (Jiang et al., 2012), which may contain the Precambrian-Cambrian boundary (Wang et al., 2012c), and is stratigraphically equivalent to the Shuijingtuo Formation in Hubei Province (Steiner et al., 2005; Wang et al., 2012c). In addition to *Sphenothallus*, the black shale pieces also contain conspicuous sponge spicules (Fig. 2D), which occur as bioclastic thin lenses in the Niutitang Formation (Wang et al., 2012a).

3. Methods and Fossil Preparation

3.1. Biostratigraphy

At the outcrop and in the lab, shale pieces containing *Sphenothallus* specimens were examined for conical holdfasts and for sedimentary structures informative about the depositional environments of the fossils. Qualitative notes were made regarding the relative densities of specimens on the shale pieces from the three sections and the relative abundances of whole and fragmentary specimens at each locality. In addition, a large (25 × 15 × 5 cm) stratigraphically oriented slab with abundant specimens was collected from Heziao. In the lab, the beds in this slab were separated, and the number, spacing, and spatial orientations of whole *Sphenothallus* specimens on each bedding surface was assessed.

3.2. Electron Microscopy and Elemental Analyses

All specimens illustrated in this study are repositied in the Virginia Tech Department of Geosciences. *Sphenothallus* specimens were initially photographed using standard reflected light techniques. Selected specimens were examined using two scanning electron microscopy (SEM) systems: (1) a Hitachi TM3000 tabletop thermionic (tungsten filament source) SEM with polepiece backscattered electron (BSE) solid-state detector (SSD) and Bruker XFlash compact energy-dispersive X-ray spectroscopy (EDS) detector housed in the Virginia Tech (VT) Department of Geosciences and (2) a FEI Quanta 600F low vacuum environmental SEM with a field emission gun electron source, polepiece BSE SSD, and BSE and secondary electron Everhart-Thornley detector (ETD) housed in the VT Institute of Critical Technology and Applied Science Nanoscale Characterization and Fabrication Laboratory. Whereas the SSD on the FEI Quanta 600F ESEM is a two-array detector, the SSD on the Hitachi TM3000 SEM is comprised of four arrays and capable of directional BSE detection (analogous to ‘illumination’) along two perpendicular axes without sample stage rotation (see Muscente and Xiao (2015) for additional technical details on this equipment).

Shale pieces containing *Sphenothallus* specimens were trimmed to dimensions no more than $6 \times 6 \times 2$ cm so that they fit inside the chambers of both SEM systems. As this study made use of low vacuum systems—in which the specimen chambers are held at pressures ($\sim 10^{-2}$ torr) allowing for the ionization and electrical conduction of surface charge by gases—conductive coating was not deposited on the specimens prior to imaging, except for one specimen from Jijiapo (indicated in figure caption), which was coated with a 20 nm conductive gold-palladium layer to reduce surface charging during imaging at high ($>25,000\times$) magnifications. To minimize charging during electron imaging, all shale pieces were wrapped in copper foil tape with only the fossils exposed, and mounted so that the foil was in contact with the sample stage, thereby

grounding surface electrical charge (Orr et al., 2002). High-resolution composite BSE images of specimens larger than the imaging area at the lowest magnification level (horizontal field width ~4 mm) were assembled from multiple high-magnification images acquired under identical operating conditions (focus setting, brightness, contrast, dwell time, probe spot diameter, working distance, and accelerating voltages, V_A) using the Hitachi TM3000 SEM.

SEM images were acquired using various imaging modes at V_A of 2–30 keV, working distances of 8–12 mm, and dwell times between 10–30 ms. For each image, the electron imaging mode and operating conditions were selected in order to optimize the visibility of certain specimen properties, such as compositional heterogeneity, surficial topography, and subsurficial mass-thickness variations (see Muscente and Xiao, 2015, for a review on mechanisms of contrast formation in electron imaging). To acquire images with optimal compositional (atomic number, or Z) contrast, specimens were imaged using the SSD(+) imaging mode, in which images are formed via digital addition of BSE signals detected by the individual SSD arrays (Muscente and Xiao, 2015, fig. 3). Conversely, for images with optimal topographic contrast, specimens were imaged using the ETD(+) imaging mode—in which images are formed using secondary electrons detected by the ETD with a positively-biased faraday cage—and the SSD(–) imaging mode, in which images are formed via digital subtraction of BSE signals collected by the individual SSD arrays (Muscente and Xiao, 2015, fig. 3). In addition, directional detection BSE images—based on BSE signals detected by individual SSD arrays—were also acquired. In these images, ‘shadows’ typically appear opposite the direction of BSE detection (the direction of ‘illumination’). The shadows result from topographic variations on the sample surface affecting BSE emission and detection. For this reason, directional detection BSE images generally represent intermediates between SSD(+) and SSD(–) images in terms of topographic and

compositional contrast (Muscente and Xiao, 2015). For each directional detection BSE image in this report, we designate the direction of BSE detection in terms of the perceived illumination. For instance, images acquired using SSD array(s) located on the rear side of the specimen are designated ‘bottom-illuminated shadow’ or SSD(BIS) images, and images acquired using SSD arrays located on the front side of the specimen are designated as ‘top-illuminated shadow’ or SSD(TIS) images (Muscente and Xiao, 2015, fig. 3).

In order to analyze variations in the relative masses and thicknesses of materials in the subsurfaces of *Sphenothallus* tests—specifically the uppermost few microns of the specimens—we imaged some fossils using the SSD(+) imaging mode at successively higher beam energies (e.g., 5, 6, 7 keV, etc.) in order to acquire ‘beam energy image series’ (see Muscente and Xiao, 2015, for a technical background on the acquisition and interpretation of beam energy image series). In general, variations in the masses and thickness of materials in the subsurface of a sample can be inferred from a beam energy image series via consideration of “mass-thickness contrast.” Mass-thickness contrast forms because, at a given point in an electron beam raster scan, the BSE signal intensity (essentially, the number of beam electrons backscattered from the sample) depends on the masses and thicknesses of materials within the volume of the sample interacting with the electron beam (see Muscente and Xiao, 2015, fig. 1f). Because BSE emission depth increases with V_A , mass-thickness contrast also depends upon electron beam energy. Because changes in mass-thickness contrast with V_A typically follow predictable patterns, which are evident in beam energy image series, observations of changes in image contrast through beam energy image series can be conceptualized to reconstruct the subsurficial microstructures of samples (see Muscente and Xiao, 2015, fig. 12). For this report, all operating conditions were constant through acquisition of each beam energy image series.

The EDS elemental maps in this study were collected using the Hitachi TM3000 SEM at a V_A of 15 keV and a working distance of 12 mm for 400–600 s live time with ~8000 counts/s. Given the operating conditions, the tungsten filament electron source, and the count rate, the dead time should be within an acceptable range (~10–40% live time) for elemental analysis. Elemental peaks were identified using the Quantax 70 Microanalysis Software by Bruker.

3.3. Taphonomic Experiment

A simple experiment was conducted to simulate taphonomic demineralization of *Sphenothallus* tests. First, a small shale piece measuring $1 \times 0.5 \times 0.25$ cm from Heziao containing a *Sphenothallus* test fragment was selected. The test fragment was photographed, and its preservation, composition, and microstructure were analyzed using SEM and EDS. Then, the shale piece was treated with several hydrochloric acid (HCl) solutions. A 10% HCl solution was added, several drops at a time, on the surface of the *Sphenothallus* test fragment. After several minutes, when the bubbling slowed, the shale piece was placed in a 32% HCl solution, which was warmed to a gentle boil, and allowed to react for 3 h. The shale piece was removed from the HCl solution, and washed with purified water. After several rounds of washing, the shale piece was placed in purified water, which was warmed to a gentle boil, and allowed to react for 1 h. Then, the shale piece was removed from the purified water and dried. Lastly, the *Sphenothallus* test fragment was photographed, and its preservation, composition, and microstructure were again analyzed using SEM and EDS.

3.4. Allometric Growth Analysis

Whole specimens (n=436) were sampled from the Heziao, Jijiapo, and Siduping sections for allometric growth analysis. Some of the sampled fossils include part-counterpart pairs. The fossils were photographed with scale bars via digital macrophotography under a variety of light and shadow regimes. The most representative photograph of each specimen was selected for data acquisition. Using ImageJ, digital measurements were collected from the four most-consistently available characters (Figs. 3A–B): aperture diameter (mm), apex diameter (mm), longitudinal thickening diameter (mm), and longitudinal thickening length (mm). Measurements of longitudinal thickening diameter were acquired from the best-preserved parts of the tests. In specimens with curved longitudinal thickenings, each longitudinal thickening length value was assessed as the sum of a series of relatively straight segments (Fig. 3C). To account for variability in fossil preservation, specimen exposure, and data acquisition, multiple measurements were collected for each character. For instance, four measurements of thickening diameter were taken from each specimen (two from each thickening), and the mean value was tabulated. Lastly, for each specimen, the preservational state of the transverse walls (absent, 0; present, 1) was also recorded. Whenever possible, both the part and counterpart of each fossil were examined for evidence of transverse walls.

4. Results

4.1. Preservation of *Sphenothallus* at Heziao

The fossiliferous slab from Heziao consists of three beds, each between 3 and 5 cm thick (Fig. 4A). *Sphenothallus* fossils occur throughout the beds (Fig. 4C–F), but are generally positioned parallel to sub-parallel relative to the bedding plane. The specimens are distributed randomly on the bedding surfaces, but their apexes are generally oriented in a bimodal pattern

(Fig. 4B) and they exhibit notable diversity in size and morphology (Fig. 5, Table 1). Although some specimens possess transverse walls (Fig. 5A–F) and transverse ribs (Fig. 5B,G), these features are missing in many specimens (Table 1).

Combined SEM and EDS analyses show that the *Sphenothallus* fossils at Heziao consist of lamellar phosphatic (Fig. 6A–C,F,G,J–N) and carbonaceous materials (Fig. 6D,E,O–T), which are encrusted by various minerals, including barite, pyrite, and gypsum (Fig. 6D,E,H,I,O–Z; 7A–C,H–M). Lamellae of the phosphatic material are visible in both in SSD(+) and ETD(+) images, and consist of nanocrystals (Fig. 6F,G; also see fig. 9E of Muscente and Xiao, 2015). Barite is generally restricted to *Sphenothallus* fossils (Figs. 6D,O–T, 7B, H–M), occurring as micrometer-sized crystals in thick encrusting structures (Fig. 7C). Pyrite occurs as euhedral crystals (Muscente and Xiao, 2015, fig. 8G) and as framboids (Fig. 6H,I, U–Z) on the *Sphenothallus* tests and throughout the shales. The framboids are generally most abundant in the matrix of the shales near *Sphenothallus* fossils (Fig. 6H). Unlike barite and pyrite, gypsum covers entire bedding surfaces, molding *Sphenothallus* specimens in some places (Muscente and Xiao, 2015, fig. 8E).

A typical longitudinal thickening at Heziao consists of lamellar phosphatic material covered interiorly and exteriorly by micrometer-thick nanoporous carbonaceous layers (Figs. 6G, 8, 9; also figs. 7–9 of Muscente and Xiao, 2015), encrusted by gypsum (Muscente and Xiao, 2015, fig. 8E) and framboidal pyrite (Fig. 6I,U–Z) in some places. The phosphatic and exterior carbonaceous layers contain subsurficial granular structures, which are apparent in beam energy SSD(+) image series (see fig. 9 of Muscente and Xiao, 2015). Nonetheless, the *Sphenothallus* tests at Heziao exhibit several examples of inter-specimen microstructural variation. First, the micrometer-thick interior carbonaceous layer (Fig. 8) is not present in all specimens (Figs. 6I,U–Z, 9J,U–Y). Second, although the exterior carbonaceous layer covers sculptured phosphatic

lamellae constituting the transverse ribs in some specimens (Muscente and Xiao, 2015, fig. 9Q–Z), it seems to cover smooth phosphatic lamellae in other specimens (Fig. 9A–F). In these specimens, transverse ribs are visible in SSD(–) (Fig. 9E) and in SSD(+) images acquired at beam energies >15 keV (Fig. 9D), but not in SSD(+) images acquired at lower V_A (Fig. 9C). Lastly, among various specimens, the range of the exterior carbonaceous layer thickness is 2 (Fig. 9F, P–T) to 6 μm (Fig. 9J,U–Y), and the range of the phosphatic layer thickness is 4 (Fig. 9J,U–Y) to 20 μm (see fig. 8E,F of Muscente and Xiao, 2015), suggesting the relative thicknesses of the carbonaceous and phosphatic layers vary among specimens.

In addition to these examples of inter-specimen variation, SSD(+) beam energy image series indicate that the thickness of the exterior carbonaceous layer also varies across the surfaces of some individual specimens. In general, in BSE images of these specimens, mass-thickness contrast depends upon V_A and the thickness of the exterior carbonaceous layer. At low beam energies ($V_A \leq 5$ keV), mass-thickness contrast among raster scan points on the exterior carbonaceous layer is low (Fig. 9H) because all BSEs originate in the exterior carbonaceous layer. However, through beam energy SSD(+) image series, the contrast increases among some raster scan points on the exterior carbonaceous layer (Fig. 9I). This contrast most likely corresponds to thickness variation in the exterior carbonaceous layer because, at higher beam energies (e.g. $V_A = 15$ keV, Fig. 9I), the BSEs also originate in the underlying phosphatic material and BSE signal intensity is inversely-related to exterior carbon-layer thickness (see fig. 11B of Muscente and Xiao, 2015, for Monte Carlo simulations of BSE emission in HeZiao tests).

Combined BSE imaging and EDS elemental mapping shows that the compositions and microstructures of transverse walls also vary among *Sphenothallus* specimens at HeZiao. In some specimens, the transverse walls—which may be encrusted by secondary minerals such as barite

(Fig. 7B,C,H–M)—are preserved as carbonaceous material without underlying phosphatic layers (Figs. 6D,O–T, 7A). In other specimens, the transverse walls are preserved as phosphatic material covered by the exterior carbonaceous layer (Fig. 7D–G, N–Y). The phosphatic transverse walls sometime conserve transverse ribs (Figs. 5B, 7E–G), but the ribs are not conserved in all phosphatic transverse walls (Figs. 5C, 7D) and have not yet been observed on transverse walls preserved as carbonaceous material (Figs. 5A,F, 6D, 7A).

4.2. Preservation of *Sphenothallus* at Jijiapo

Shales containing *Sphenothallus* fossils at Jijiapo are generally friable and <1.5 cm in bed thickness. The fossils are typically positioned parallel to the bedding plane, and exhibit diversity in size and morphology (Fig. 10, Table 1). Most specimens possess transverse walls (Figs. 10A,C,E and 11A) and some are covered by transverse ribs (Fig. 12A,C), but these features are missing in many specimens (Table 1). BSE imaging and EDS elemental mapping indicates that longitudinal thickenings and transverse walls of *Sphenothallus* tests at Jijiapo are preserved as carbonaceous structures (Fig. 10I,J), which can be traced to unexposed part of the tests (Fig. 10N) and are encrusted by barite, iron oxides, and more rarely, pyrite (Fig. 10). Barite occurs sporadically in the shale, but iron oxides are common throughout the matrix. Barite on the *Sphenothallus* fossils is typically bladed or tabular in morphology (Fig. 10K), but in some places, consists of large (>5 μm diameter) euhedral crystals (Fig. 10L). Similarly, iron oxides and pyrite on *Sphenothallus* primarily occur as micrometer-thick layers encrusting the carbonaceous material (Fig. 10A–F,I,J,O–Z). However, iron oxides also occur as framboids in shale matrix surrounding carbonaceous material (Fig. 10M). In general, the carbonaceous material comprising the fossils is 10 to 20 μm thick (Fig. 10N), has a cracked texture (Figs. 10J,N,11C), and is

characterized by nanometer-sized holes (Fig. 11D), suggesting it is a porous material, similar to nanoporous organic matter comprising other carbonaceous fossils (Muscente et al., 2015; Pang et al., 2013; Schiffbauer et al., 2007; Schiffbauer and Xiao, 2009).

Although no transverse ribs have been observed on transverse walls at Jijiapo, some specimens conserve transverse ribs on their longitudinal thickenings (Fig. 12A–D). The transverse ribs are evident in SSD(TIS) (Fig. 12G), SSD(BIS) (Fig. 12N), and SSD(–) (Fig. 12H,J) images, but not in the SSD(+) images (Fig. 12B,D,F). The transverse ribs are also evident in EDS elemental maps (Fig. 12K–M,O–R). Comparisons of directional detection BSE images (Fig. 12N) and EDS elemental maps (Fig. 12O–R) acquired with the active BSE and X-ray detectors oriented along the same axis show that the transverse ribs affect both BSE and X-ray detection. Specifically, in these BSE images and EDS elemental maps (Fig. 12N–R), shadows appear in the valleys of the transverse ribs, most likely because the peaks block the detection of BSEs and X-rays from the valleys. These observations suggest that the transverse ribs are principally preserved as topography rather than as compositional heterogeneity on the surfaces of the fossils. In addition, combined BSE imaging and EDS elemental mapping analyses indicates that the transverse ribs occur in both shale matrix and in the carbonaceous material (Fig. 12E–H), indicating that the transverse ribs are preserved as topography in the external molds of the tests and on the exterior surfaces of the carbonaceous material comprising the tests.

4.3. Preservation of *Sphenothallus* at Siduping

Sphenothallus fossils at Siduping occur sparsely in floats. The assemblage is dominated by fragmented and non-pristine specimens. Unbroken tests and tests with transverse walls are generally rare (Table 1), and none of the studied specimens conserve transverse ribs (Fig. 13A–

D), though the transverse walls of some specimens are covered by wrinkles (Fig. 14A–D). Combined BSE imaging and EDS elemental mapping indicates that the *Sphenothallus* tests consist of non-lamellar phosphatic material associated with relatively carbonaceous material (Fig. 15A–C, E–H). These materials occur in both the longitudinal thickenings (Figs. 13C–H, 15) and transverse walls (Figs. 13I–P, 14A–D) of the specimens. In some places, the carbonaceous material interiorly covers the phosphatic material (Fig. 15D, I–L), and elsewhere, the carbonaceous and phosphatic materials are encrusted—exteriorly (Fig. 12Q) and interiorly (Fig. 13R)—by gypsum and pyrite (Fig. 13Q–Z). Whereas the pyrite occurs as micrometer-thick structures made up of euhedral crystals on the *Sphenothallus* tests (Fig. 13Q–S) and as framboids in the shale matrix surrounding the fossils (Fig. 13T), the gypsum primary occurs as nanometer-sized needle- (Fig. 13Q, T) and petal-shaped crystals (Fig. 13S). In rare specimens, the carbonaceous materials are also encrusted by bladed, tabular barite crystals (Fig. 14E–L).

4.4. Taphonomic Experimentation

Light microscopy, SEM, and EDS elemental mapping of the *Sphenothallus* test fragment (Fig. 16A) on the surface of a Hezia shale piece selected for taphonomic experimentation show that, prior to HCl treatment, the preservation, composition, and microstructure of the test fragment matched other Hezia fossils. Specifically, the analyses show that the test fragment had transverse ribs (Fig. 16A–D, F, G) and consisted of lamellar phosphatic material covered by an exterior carbonaceous layer, though SSD(+) images acquired at low beam energies ($V_A=5$ keV) indicate that exterior carbonaceous layer was missing in multiple areas on the surface of the test (Fig. 16B, C). No micrometer-thick interior carbonaceous layer, barite, or pyrite was observed on

the test fragment (Fig. 16E), and gypsum was localized to the matrix around the fossil (Fig. 16B).

The treatment of the shale piece with the 10% HCl solution resulted in the production of gases (probably CO₂), and the treatment with 32% HCl solution significantly increased the friability of the shale piece, possibly via the dissolution of carbonate cements. Due to this friability, a notable crack formed in the *Sphenothallus* fragment (Fig. 17A–C).

Light microscopy, SEM, and EDS elemental mapping of the test fragment after HCl treatment show that it consists entirely of carbonaceous material with no evidence of phosphatic material (Fig. 17A–C,H–M). Carbonaceous material fully replicates the test fragment, even occurring in places where, prior to HCl treatment, the lamellar phosphatic material was exposed without the overlying exterior carbonaceous layer (Fig. 16B). The carbonaceous material is encrusted, in some places, by gypsum crystals (Fig. 17E,F), which precipitated during the experiment (Fig. 16E). Evidently, as indicated by light microscopy (Fig. 17D) and SSD(–) images (Fig. 17G), HCL treatment weakened but did not completely obliterate the transverse ribs.

4.5. *Sphenothallus* Allometry

Sphenothallus tests from Heziao, Jijiapo, and Siduping exhibit similar character size ranges and allometric growth trends (Table 1, Fig. 18A). In general, R² values show allometric scaling accounts for most of the variations in measurements of *Sphenothallus* characters (Table 2). The aperture, apex, and thickening diameters of tests from all three collection localities scale negatively with the longitudinal thickening length, suggesting that the rate of aperture expansion decreased relative to the rate of test elongation during the lifespan of the *Sphenothallus* organism

(Fig. 18B). Most specimens sampled for quantitative analyses have longitudinal thickenings between 2 and 11 mm in length, but smaller and larger specimens also occur in the sample sets (Fig. 18A). The preservation state of the transverse walls (present/absent) does not notably vary with the length of the longitudinal thickenings (Fig. 18A). Specimens with transverse walls and longitudinal thickening <2 mm in length are scarce, but this observation may simply be a sampling or analytical bias, given the small sample size in this class of specimens.

5. Discussion

In general, the newly-discovered *Sphenothallus* fossils in the Shuijingtuo and Niutitang formations are short conical-tubular tests, possessing longitudinal thickenings (~1–14 mm in length) and transverse walls. Specimens from the Heziao and Jijiapo sections are covered by low-relief transverse ribs (~100–200/cm; Figs. 7F,G, 9E,G, 12E–H,J,N; Muscente and Xiao, 2015, fig. 10C), and specimens from Siduping are covered by wrinkles (Fig. 14A–D), which may represent transverse ribs. In all sections, the diameters of the tests' apertures, apices, and longitudinal thickenings scale negatively with longitudinal thickening length (Fig. 18B). Given these similarities, we hypothesize that the fossils from the three localities in this report may represent a single species. The fossils broadly resemble *Sphenothallus songlinensis*, which has a short conical-tubular test (up to 17.5 mm in length) with transverse ribs (24–45/cm) and occurs in the Niutitang Formation in Guizhou Province of South China (Peng et al., 2005), except that its transverse ribs are less densely packed. However, taxonomic and phylogenetic analyses of the newly-discovered tests are complicated by their compositional and microstructural differences.

5.1. *Sphenothallus* composition and microstructure

At Heziao, the tests typically consist of a lamellar phosphatic material covered exteriorly and more rarely interiorly by nanoporous carbonaceous layers. Although both the phosphatic and exterior carbonaceous layers contain granular ($<1\ \mu\text{m}$ in diameter) structures, the relative thicknesses of these layers seem to vary among specimens and only the phosphatic material consists of distinct nanocrystals. The nanocrystals in the Heziao phosphatic material broadly resembles crystallites ($<500\ \text{nm}$ in diameter) occurring in *Sphenothallus* fossils with homogenous microstructure from the Ordovician of Baltica (Vinn and Kirsimäe, 201X). The lamellar phosphatic material in some Heziao specimens consists of interior (unsculptured) lamellae with smooth surfaces and exterior (sculptured) lamellae with surface topography, constituting the low-relief transverse ribs of those specimens (Muscente and Xiao, 2015). However, the exterior phosphatic lamellae are unsculptured in some specimens (Fig. 9F), suggesting the sculptured lamellae were taphonomically degraded or physically abraded prior to SEM analysis. Regardless, when preserved, the transverse ribs are evident in SSD(–) and SSD(+) images acquired at higher (e.g. $\sim 15\ \text{keV}$) beam energies with the valleys of the transverse ribs appearing brighter than the peaks. The contrast between the valleys and peaks of the transverse ribs (the ‘peak-valley contrast’) in the SSD(+) images acquired at relatively high beam energies corroborates reconstructions of the Heziao specimens, which propose that the exterior carbonaceous layer is thicker on the peaks than in the valleys of the transverse ribs. This interpretation is based on the observation that, at higher beam energies, BSE signal intensity is lowest in thick parts of the exterior carbon layer (Muscente and Xiao, 2015).

Analyses of Heziao specimens corroborate observations in other studies, which suggest that the phosphatic lamellae in *Sphenothallus* tests may contain organic carbon. First, the lamellae of Heziao specimens are evident in both SSD(+) and ETD(+) images (Fig. 6F,G) most

likely as compositional and topographic contrast respectively, though differences in the packing density of apatite nanocrystals in the lamellae may also manifest in the contrast of the SSD(+) images (Schiffbauer et al., 2012). Compositional contrast in the lamellar microstructure may indicate that the phosphatic material consists of alternating phosphatic and organic lamellae, as suggested by SEM and TEM analyses of *Sphenothallus* specimens from the lower Cambrian Guojiaba and Xiannudong formations of China (Li et al., 2004). Such organic lamellae may have been replaced by diagenetic apatite in *Sphenothallus* fossils at other localities (Vinn and Kirsimäe, 201X). Second, EDS analyses of the Heziao tests and other phosphatic *Sphenothallus* specimens show notable carbon peaks in EDS spectra (Fauchald et al., 1986; Li et al., 2004; Muscente and Xiao, 2015; Wang et al., 2003). Although the carbon peaks detected in these analyses most likely correspond, in part, to carbonate substituting for phosphate in the apatite of the tests (van Iten et al., 1992; Vinn and Kirsimäe, 201X), Muscente and Xiao (2015) show that the carbon, phosphorus, calcium, and oxygen contents of the phosphatic material in the Heziao tests are $\sim 33.78 \pm 2.63$, 5.04 ± 1.03 , 12.05 ± 2.07 , and 47.32 ± 4.38 at% (atomic percent), respectively. Assuming the phosphatic material in the Heziao tests occurs as carbonate fluorapatite with the chemical formula $\text{Ca}_5[(\text{PO}_4)_3(\text{CO}_3)]_3\text{F}$, a simple stoichiometric calculation using these data shows that about 6.5% of the carbon signal comes from carbonate and the remaining 93.5% comes from organic carbon. Because these data are based on EDS analyses of unpolished and carbonaceous samples (Muscente and Xiao, 2015)—which may yield inaccurate data (Goldstein et al., 2003)—their interpretation warrants caution. Still, they suggest the phosphatic material in the Heziao tests contain a significant organic carbon, in addition to carbonate carbon (van Iten et al., 1992; Vinn and Kirsimäe, 201X). Lastly, the taphonomic experiment in this report shows that the Heziao tests are preserved as carbonaceous material following demineralization via HCl

treatment (Fig. 17). Given that the test fragment in the experiment did not possess an obvious micrometer-thick interior carbonaceous layer and that the carbonaceous material replicating the test fragment occurs in places where, prior to HCl treatment, the phosphatic material was exposed without the overlying exterior carbonaceous layer (Fig. 16), we surmise the carbonaceous material conserved through HCl treatment may have originally been organic matter in and/or between the phosphatic lamellae. Overall, these results may indicate the tests at Heziao are organophosphatic.

Unlike specimens at Heziao, *Sphenothallus* at Jijiapo are preserved entirely as nanoporous carbonaceous material (Fig. 11). The carbonaceous material does not contain granular structures, but sometimes conserves topography on its exterior surface constituting transverse ribs (Fig. 12E–R). Although the tests appear to be compressed, their transverse ribs are preserved as exterior molds in the shale matrix (Fig. 12E–H), and their carbonaceous material forms a three-dimensional structure extending to the unexposed part of the fossil (Fig. 10N), suggesting the tests were externally molded by shale matrix material rather than compressed into organic film. Compositionally and microstructurally, the *Sphenothallus* tests at Siduping seem to represent an intermediate between those at Heziao and Jijiapo, consisting of non-lamellar phosphatic material associated with carbonaceous material (Fig. 15). Unlike the Heziao fossils, transverse ribs, granular microstructures, and nanometer-sized crystallites are apparently not preserved or present in *Sphenothallus* tests at Siduping. Thus, the results of this report document notable differences in the compositions and microstructures of *Sphenothallus* tests among the three localities. In the following sections, we interpret data on the biostratinomy, authigenic mineralization, and taphonomic demineralization of the fossils in order to identify possible preservational processes affecting the compositions and microstructures of *Sphenothallus* tests.

Based on these interpretations, we propose a taphonomic model for *Sphenothallus*, and use the model to assess the phylogenetic affinities of the genus.

5.2. Biostratinomy

Several lines of evidence suggest that the fossils at Heziao, Jijiapo, and Sidupingmay have been transported prior to burial. First, the absence of conical holdfasts indicates that the *Sphenothallus* fossils at the three sections were transported after death. Second, the abundance of fragmentary specimens along with relatively unbroken tests is also consistent with pre-burial transport. Lastly, the bimodal orientation of unbroken *Sphenothallus* tests at Heziao(Fig. 4B) may represent evidence of pre-burial transport. Although some bimodal orientations of fossils maybe the result of oscillatory processes(Muscente and Allmon, 2013), the bimodal orientation of *Sphenothallus* tests at Heziaomay alternatively be the result of pre-burial transport in directional flows, possibly turbidity currents. Flume studies using clay models of hyolith tests indicate that, although cones preferentially orient their apertures against the direction of flow in slow (~10 cm/sec) currents, they become oriented in various hydrodynamically-favorable positions in moderate (10–25 cm/sec) currents and tumble and roll in fast (>25 cm/sec) currents (Marek et al., 1997). The observation that cones exhibit multiple hydrodynamically-favorable positions in currents may account for bimodal distributions of tentaculitids(Wendt, 1995) and *Turritella*(Toots, 1965). Although reconstructing paleocurrents using fossil orientations is challenging, and bimodal distributions may sometimes result from wave action (Nagle, 1967), the directional flow interpretation is most consistent with the inferred depositional environment of the Shuijingtuo Formation, which was deposited below fair weather wave base during maximum transgression on the Yangtze Platform (Peng and Babcock, 2001).

5.3. Authigenic mineralization and weathering

The results of combined SEM and EDS analyses suggest that *Sphenothallus* tests served as sources of hydrogen sulfide and/or as nuclei for pyrite precipitation during diagenesis of the host sediments. Pyrite—including framboidal (Fig. 6I,U–Z) and encrusting (Figs. 10F,U–Z,13Q–S,U–Z) forms—coats *Sphenothallus* tests at Heziao, Jijiapo, and Siduping, and also occurs in shale matrix near *Sphenothallus* tests at Heziao (Fig. 6H) and Siduping (Fig. 13T). In addition, iron oxides occurring throughout the shale matrix (Fig. 10M) and encrusting *Sphenothallus* tests (Fig. 10A–D,I,J,O–T) at Jijiapo may derive from oxidative weathering of pyrite. Iron oxide pseudomorphs of pyrite commonly occur on pyritized fossils (Cai et al., 2012; Forchielli et al., 2012; Gabbott et al., 2004). Overall, the occurrence of pyrite and its pseudomorphs with the *Sphenothallus* fossils suggests that the tests experienced focused microbial sulfate reduction at all three localities (Muscente et al., 2014; Xiao et al., 2010).

Although *Sphenothallus* tests from all three localities in this report are encrusted by barite (Figs. 7B,C,H–M, 10A,B,I,J,O–T, 14A,B,E–L), reports of shelly fossils encrusted and/or associated with barite are generally rare (Kouchinsky and Bengtson, 2002; Wilby et al., 1996; Zabini et al., 2012). Nonetheless, in modern environments, sedimentary barite typically forms via biogenic, hydrothermal, cold seep, and diagenetic pathways (Griffith and Paytan, 2012; Raiswell et al., 2002), and barite formed via these pathways can be distinguished, to a degree, in terms of its crystal size and morphology (Griffith and Paytan, 2012; Paytan et al., 2002). Biogenic barite—which is produced by planktonic organisms or is formed in microenvironments near decaying organic matter—typically occurs as ellipsoidal crystals <5 µm in diameter (Paytan et al., 2002). In contrast, barite formed via hydrothermal and diagenetic processes typically

occurs as bladed tabular crystals ($>20\text{ }\mu\text{m}$ in diameter), which form rosettes and diamond-shaped clusters (Paytan et al., 2002). The barite encrusting *Sphenothallus* tests in this report (Figs. 7C, 9K,L, 14F) most closely resembles hydrothermal and diagenetic barite crystals. Although petrological and geochemical analyses provide some evidence for early Cambrian hydrothermal venting in Hunan and Guizhou provinces of South China (Chen et al., 2009; Steiner et al., 2001), the Shuijingtuo Formation in Hubei Province—a source of the barite-encrusted *Sphenothallus* tests in this report—does not show any evidence of hydrothermal or volcanic influence. Therefore, the barite may be diagenetic in origin. If so, it may have precipitated on *Sphenothallus* tests buried near the anoxic-oxic boundary. In modern sediments, biogenic barite sourced from planktonic organisms dissolves and accumulates in anoxic and sulfate-depleted pore waters within sediments. Barite may then precipitate at the redox boundary where sulfate-rich fluids mix with barium-rich and sulfate-poor pore fluids from below the microbial sulfate reduction zone (Bolze et al., 1974; Brumsack and Gieskes, 1983; Griffith and Paytan, 2012; Paytan et al., 2002). This scenario is consistent with the co-occurrence of barite and framboidal pyrite (Fig. 10M), indicating sulfate-reducing conditions, and the proposed origins of sedimentary barite in the lower Cambrian of North China (Zhou et al., 2015). Alternatively, late diagenetic changes in fluid pressures and temperatures may have induced barite precipitation by creating conditions of low barite solubility (Hanor, 2000) or by inducing mixing of Ba- and SO_4 -rich fluids (Hein et al., 2007). These hypotheses require testing with additional (e.g. isotopic) data.

Unlike the pyrite and barite, gypsum associated with the *Sphenothallus* fossils at Heziao (Fig. 6D,O–T) and Siduping (Fig. 13B, J,Q–Z) likely precipitated during recent weathering. The Shuijingtuo and Niutitang formations were deposited below fair-weather wave base (Peng and Babcock, 2001), rather than in shallow-water, evaporative environments where gypsum typically

precipitates (Murray, 1964). In addition, gypsum in the Heziao section occurs exclusively between beds of shales or along fractures, covering entire bedding surfaces and filling cracks and pores. At Siduping, gypsum crystals cover all exposed surfaces but do not occur in the interiors of float pieces. Gypsum minerals with these characteristics in black shales are typically interpreted as weathering products (Martens, 1925), as chemical weathering of black shales causes carbonate dissolution and pyrite oxidation that can drive calcium sulfate precipitation (Ritsema and Groenenberg, 1993). The Shuijingtuo/Niutitang black shales at Heziao and Siduping contain carbonate minerals and pyrite, which is most abundant near *Sphenothallus* tests (Figs. 6H,I,U–Z, 13Q–Z). In addition, the weathering of phosphatic tests of *Sphenothallus* releases calcium and supports precipitation of gypsum, which in some cases, molds *Sphenothallus* fossils (Muscente and Xiao, 2015, fig. 8E,N–S).

5.4. Taphonomic Experiment and Secondary Demineralization

The processes involved in the preservation of shells as carbonaceous fossils have not been thoroughly investigated. In particular, the sources of the carbonaceous materials comprising the fossils remain controversial. Although the carbonaceous materials have variably been interpreted as the remains of individual coherent layers—such as periostraca—in or on the shells (Butterfield and Harvey, 2012; Harvey et al., 2012), it has recently been hypothesized that carbonaceous materials may actually represent the organic matrixes of the shells (Martí Mus, 2014). If so, the preservation of shells as carbonaceous fossils likely involves two sequential (or possibly concomitant) processes: (1) the formation of aliphatic compounds that are stable over geological timescales via *in situ* diagenetic polymerization (‘kerogenization’) of compounds in the shells’ organic matrixes and (2) the loss of the biomineralized microstructures of the shells

(Briggs et al., 1999; Gupta and Briggs, 2011; Martí Mus, 2014; Stankiewicz et al., 2000). In essence, the second process results in demineralization of the shells' microstructures, so that only insoluble carbonaceous materials remain in the fossils. Carbonaceous preservation is likely favored if demineralization occurs after kerogenization, as soluble and highly reactive organic matrixes are readily degraded under a variety of conditions (Glover and Kidwell, 1993). In this context, the taphonomic experiment in this report provides an analog to understand the effects of demineralization on *Sphenothallus* composition, morphology, and microstructure, as HCl treatment of Heziao fossils simulates demineralization in shells containing kerogenized carbonaceous materials. Overall, results show that some shells conserve carbonaceous material through demineralization, though their morphology is weakened and their microstructure is lost.

5.5. Taphonomic Model

We propose a taphonomic model that incorporates both pre-burial and post-burial (diagenetic and weathering) processes to account for the various test morphologies, compositions, and microstructures of *Sphenothallus* fossils from Heziao, Jijiapo, and Siduping (Fig. 19). For this model, we assume the *Sphenothallus* fossils from the three sections represent a single species—as suggested by their similar morphologies and allometric growth patterns—and were originally organophosphatic tests, as suggested by the preservation of apatite nanocrystals and organic matter in the Heziao fossils. The fossils at Heziao do not occur with sedimentary phosphorite (Muscente et al., 2014), and contain no evidence of secondary phosphatization (Muscente et al., 2015; Schiffbauer et al., 2012; Xiao and Schiffbauer, 2009).

The amount of time between the death of the organisms and the burial of their tests, as well as the placement and duration of the tests within various microbial zones in the sediment

column(Schiffbauer et al., 2014), likely affected the preservation of the fossils in several key ways. First, a protracted post-mortem stay on sediment surfaces or in the aerobic zone within sediments likely favored the degradation of the organisms' non-biomineralized tissues, such as their putative tentacles (Fauchald et al., 1986). In general, the preservation of non-biomineralized tissues occurs when rates of authigenic mineralization (e.g. pyritization) exceed those of soft tissue degradation (Briggs, 2003). For this reason, soft tissue preservation is favored in the anaerobic zones within sediments, in which biogeochemical processes create geochemical conditions conducive to authigenic mineralization (Muscente et al., 2014; Schiffbauer et al., 2014), and typically requires the burial of an organism before or soon after death. Although the fossils in this report contain evidence of non-pervasive pyritization, they were not buried soon after death, so their non-biomineralized tissues may have been degraded prior to authigenic mineralization. Second, a protracted interval between the death and burial of *Sphenothallus* likely favored the fragmentation of its tests due to physical and biotic processes (Best and Kidwell, 2000a) and the accumulation of test fragments, which occur at Heziao, Jijiapo, and Siduping. Lastly, the time between death and burial may have also allowed for physical and chemical alteration of *Sphenothallus* test surfaces. Actualistic studies show that physical and chemical processes commonly alter shell surfaces in modern environments (Best and Kidwell, 2000a, b; Cutler, 1995; Powell et al., 2011). Physical abrasion—resulting from shell-sediment and shell-shell collisions during specimen transport—results in exfoliation, flaking, and pitting of shell surface layers (Cutler, 1995). Activities of colonizing algae, fungi, and microbes can also modify shell surfaces (Best and Kidwell, 2000a, b). Such processes may account for the absence and poor preservation of transverse ribs in some *Sphenothallus* specimens, as these processes

may have driven pre-burial deterioration of the exterior lamellae constituting the tests' low-relief transverse ribs (Muscente and Xiao, 2015).

Alteration of *Sphenothallus* test surfaces may have also occurred within sediments following burial. Shells in modern organic-rich, muddy sediments show notable signs of alteration (Best and Kidwell, 2000a), including exfoliation and terracing of surfaces (Cutler, 1995). In such modern environments, shell surface alteration results from microbial attack on the organic matrixes comprising shells (Glover and Kidwell, 1993) and from the concomitant acidification of sediment pore waters under the influence of aerobic respiration and microbial sulfate reduction (Walter and Burton, 1990). Such processes may have affected *Sphenothallus* test surfaces during early diagenesis of the Shuijingtuo and Niutitang formations. The observation that the tests experienced focused microbial sulfate reduction suggests that their organic matrixes may have been a source of organic matter for microbial sulfate reduction, which could have produced hydrogen sulfide, driven pyrite precipitation, and acidified pore waters (Muscente et al., 2014) and thereby promoted deterioration of the fossils' transverse ribs. If so, the surfaces of *Sphenothallus* tests may have concomitantly been dissolved and pyritized, and a relationship may exist between the extent of pyritization and preservation of transverse ribs in the fossils. Nonetheless, after prolonged burial of the *Sphenothallus* fossils, further alteration of the test surfaces may have been limited by transformation of organic matrixes into relatively insoluble and recalcitrant aliphatic compounds via kerogenization (Stankiewicz et al., 2000).

Although the fossils at Heziao, Jijiapo, and Siduping may have followed similar taphonomic pathways up to kerogenization, their paths may have diverged during a demineralization process (Fig. 19). The extent of demineralization plausibly depends upon the microstructures of the shells and the chemistry (e.g. pH and saturation levels) of the surrounding

fluids involved in the reaction, which is most likely favored at the surfaces of shells, where biomineral interfacial surface area is greatest and fluid mixing may limit re-mineralization. These inferences suggest that demineralization proceeded at the exterior and interior surfaces of the *Sphenothallus* tests, and may have ceased in response to changing reaction parameters. If so, the newly-discovered *Sphenothallus* fossils may constitute a taphonomic continuum. According to the model, the fossils at Jijiapo underwent complete demineralization, and consequently, retain carbonaceous material in place of their mineralized test. However, at the other localities, demineralization did not proceed to completion, and tests conserve characters compositionally and microstructurally intermediate between shelly and carbonaceous fossils. Whereas demineralization proceeded nearly to completion in the Siduping fossils, which retain carbonaceous and phosphorus-rich (generally carbonaceous) materials in place of phosphatic tests (Fig. 15), the process was restricted to the surfaces of the Heziao tests and consequently left micrometer-thick carbonaceous layers in place of exterior and interior lamellae (Figs. 6F, 8D; fig. 8 of Muscente and Xiao, 2015).

Variations among *Sphenothallus* specimens at Heziao may correspond to different reaction parameters during demineralization of the tests. For instance, variations in the relative thicknesses of the phosphatic and carbonaceous layers among specimens (Figs. 6F, 8D, 9F,J) may correspond to different extents of demineralization. In addition, the absence of micrometer-thick interior carbonaceous layers in some specimens (Fig. 6I, 9J) may indicate that the interior surfaces of those fossils were protected or non-conducive to demineralization. Lastly, variations in the thicknesses of exterior carbonaceous layers within some individual specimens (Fig. 9H,I) may reflect heterogeneity in reaction parameters during demineralization. Overall, these

observations suggest that demineralization proceeded to varying extents among Heziao specimens as well as among *Sphenothallus* specimens from the three localities.

The results of this study provide data to test several key predictions of the taphonomic model regarding demineralization. Notably, the taphonomic experiment in this report demonstrates that, beginning with a test comprised predominantly of lamellar organophosphatic material, a simple HCl treatment can replicate the demineralization process inferred to have occurred in preservation of *Sphenothallus* tests as carbonaceous fossils. The results indicate that, although the demineralization process alters fossil composition and microstructure, it does not significantly affect fossil morphology, as the experimental test fragment retains its overall shape and, to a lesser degree, transverse ribs through complete dissolution of its phosphatic material. Moreover, the morphological, compositional, and microstructural similarities between the experimental test fragment after HCl treatment (Fig. 17) and the fossils from Jijiapo (Figs. 11, 12) corroborate the prediction that the Jijiapo tests underwent complete demineralization.

Observations of beam energy SSD(+) image series of Heziao *Sphenothallus* tests may corroborate another prediction of the taphonomic model. Assuming that the phosphatic lamellae in *Sphenothallus* are relatively thick in the transverse ribs—as they are in the transverse ribs and internal carina of conulariids (Van Iten, 1992; van Iten et al., 1992)—the taphonomic models predicts that, if the exterior lamellae constituting the transverse ribs have been demineralized, the exterior carbonaceous layer in *Sphenothallus* should be thicker on the peaks than in the valleys of its transverse ribs, even if no sculptured lamellae are conserved (Fig. 19). Beam energy SSD(+) images series corroborate this prediction (Fig. 9C–E, G–I; also see Muscente and Xiao, 2015, figs. 10 and 12A–D, for additional description).

The taphonomic model does not constrain the timing of demineralization *after* kerogenization in post-burial history, instead predicting that demineralization may potentially occur during diagenesis or recent weathering, if fluids surrounding shells favor biomineral dissolution. In addition, the model predicts that, if demineralization occurs before sediment cementation, it may create space and allow for the collapse and compaction of the carbonaceous material comprising the fossil. If so, the magnitude of carbonaceous material compaction depends upon both the extent and timing of demineralization relative to sediment cementation, and shells that undergo demineralization prior to sediment cementation may experience greater compaction than shells that undergo demineralization during weathering. In the latter case, the fossils may be preserved as carbonaceous structures molded by sediments and exhibiting no diagenetic compaction. Observations of fossils from rocks of various lithologies, facies, and diagenetic and weathering histories provide some evidence for these predictions. Although carbonaceous in composition, *Sphenothallus* tests at Jijiapo conserve notable topographic relief (Figs. 10G,H,N, 12A–H), indicating they did not undergo much diagenetic compaction. In addition, the iron oxide framboids (interpreted as pseudomorphs of pyrite) associated with the fossils (Fig. 10M) indicate that the shales experienced significant oxidative weathering, suggesting that the Jijiapo tests underwent demineralization during weathering. Forchielli et al. (2012) similarly attributed the carbonaceous preservation of linguliform brachiopods in early Cambrian shales of South China to the dissolution of apatite during weathering. Hence, demineralization via weathering may be a common pathway for the preservation of organophosphatic shells as carbonaceous fossils. Of course, shells preserved as carbonaceous compressions with negligible topographic relief are also common, particularly in the Cambrian (Butterfield and Harvey, 2012; Butterfield and Nicholas, 1996; Harvey, 2010; Harvey and

Butterfield, 2011; Harvey et al., 2012; Martí Mus, 2014). The miniscule topographic relief observed in these carbonaceous compressions suggests that those shells underwent demineralization during diagenesis (Martí Mus, 2014).

Overall, these observations suggest that the taphonomic model in this report illuminates the taphonomy of shells preserved as carbonaceous fossils. The taphonomic model may also account for the preservation of carbonaceous layers covering the interior and exterior surfaces of some shelly fossils (Zabini et al., 2012), though additional work is necessary to determine if these layers are original tissues or taphonomic artifacts of incomplete shell demineralization.

5.6. *Sphenothallus Reconstruction and Affinities*

The taphonomic model implies that the most pristine *Sphenothallus* fossils in this report—the fossils with the highest fidelity morphological, compositional, and microstructural preservation—occur at Heziao. Nonetheless, the model suggests several characters in these fossils may be taphonomic features, and therefore, may not be reliable for phylogenetic analyses. For instance, the taphonomic model suggests the carbonaceous layers may have formed via demineralization of exterior and interior phosphatic lamellae. If so, they may not be the remains of individual coherent layers, like periostraca of mollusks or brachiopods, which may indicate phylogenetic affinities. The granular structures in the exterior carbonaceous layer and phosphatic material in the Heziao specimens (Muscente and Xiao, 2015) may have also formed via this taphonomic process. We hypothesize that the granular structures in the exterior carbonaceous layer may be remnants of phosphatic material remaining after demineralization of surrounding lamellae. The granular structures in the phosphatic layer may similarly be regions of high-density or high-Z that remain following partial demineralization of the phosphatic material.

Alternatively, the granular structures in the phosphatic layer may be diagenetic apatite crystals that are larger than surrounding nanocrystals. Regardless, the uncertainties regarding the origins of these features suggest they should not be used for phylogenetic analysis.

Integration of the taphonomic model with observations of the *Sphenothallus* tests from Heziaoyields a new longitudinal cross-sectional reconstruction of the problematic fossil (Fig. 20), which omits the unreliable features possibly produced by taphonomic processes. In this reconstruction, the test of *Sphenothallus* consists of exterior sculptured phosphatic lamellae and interior unsculptured phosphatic lamellae. The exterior sculptured phosphatic lamellae constitute the transverse ribs. Organic carbonaceous materials located in and/or between the phosphatic lamellae comprise the organic matrix of the test. In general, this reconstruction corroborates phylogenetic analyses that propose placement of *Sphenothallus* among conulariids (Muscente and Xiao, 2015; van Iten et al., 1992; van Iten et al., 2013), affirming that the tests of both groups consist of outer phosphatic layers with transverse ribs and inner phosphatic layers with smooth phosphatic lamellae (Muscente and Xiao, 2015; van Iten et al., 1992). Additionally, tests in both groups are composed of carbonate-rich apatite, and possess evidence of internal cross walls (schotts) and clonal branching (Van Iten, 1991, 1992; van Iten et al., 1992). However, notable differences exist between *Sphenothallus* and conulariid fossils in terms of test microstructure and composition. First, various conulariid genera occurring in the Cambrian-Pennsylvanian interval are preserved with microscopic circular pores, canals, and crater-like pits (2 to 12 μm in diameter) in their phosphatic lamellae (Van Iten et al., 2006; Van Iten et al., 2005), which have not been reported in *Sphenothallus*. Second, X-ray diffraction data suggest that lattice parameters of the apatite minerals in *Sphenothallus* are different than those of the apatite minerals in conulariid fossils (Vinn and Kirsimäe, 201X). Lastly, whereas conulariid tests are phosphatic

(Van Iten, 1992), electron microscopy and EDS analyses suggest that *Sphenothallus* tests are organophosphatic in composition and that their phosphatic lamellae are associated with organic carbonaceous material (Li et al., 2004; Muscente and Xiao, 2015; Wang et al., 2003). Nonetheless, these differences between *Sphenothallus* and conulariid fossils may reflect modifications of their tests due to ecological, taphonomic, and diagenetic processes. The circular pores, canals, and pits observed in conulariids but not *Sphenothallus* may be microscopic borings (Van Iten et al., 2005) or bioclastrations (Van Iten et al., 2006) rather than original anatomical features (Van Iten et al., 2005). Similarly, the different lattice parameters may reflect, to a degree, diagenetic recrystallization, and organic material may be absent in conulariid fossils due to replacement by diagenetic apatite (Vinn and Kirsimäe, 201X) or taphonomic or diagenetic degradation. Thus, the observations do not disprove a close phylogenetic relationship between *Sphenothallus* and conulariids. Overall, the lamellar microstructures, clonal growth habits, and schotts of *Sphenothallus* and conulariids may indicate that both groups are related to cnidarians (Li et al., 2004; Muscente and Xiao, 2015; van Iten et al., 1992; Vinn and Kirsimäe, 201X; Wang et al., 2003).

6. Conclusions

In summary, we have described the preservation of newly-discovered *Sphenothallus* fossils from the lower Cambrian Shuijingtuo and equivalent Niutitang formations of South China. Our results show that the tests from the Heziao, Jijiapo, and Siduping localities may represent a single species, and generally experienced similar pre-burial and early diagenetic taphonomic processes. The tests were transported, fragmented, and likely abraded prior to burial, and once buried within sediments, acted as focal sites of microbial sulfate reduction and as nuclei

for the precipitation of barite and pyrite. However, these taphonomic processes do not account for the different compositions and microstructures of the tests, which variably consist of phosphatic and carbonaceous materials. Instead, we propose that the preservation of *Sphenothallus* involved two sequential or concomitant processes: kerogenization and demineralization. This taphonomic model suggests that the different compositions and microstructures of *Sphenothallus* fossils in the lower Cambrian of South China correspond to varying extents of test demineralization during diagenesis and weathering, and that the carbonaceous layers covering the interior and exterior surfaces of the phosphatic tests at Heziao—which were interpreted as possible original anatomical characters (Muscente and Xiao, 2015)—may have formed via taphonomic demineralization of phosphatic lamellae and should not be used for phylogenetic analysis. Overall, the newly-discovered *Sphenothallus* fossils with the highest preservational fidelity microstructurally resemble and thus may be related to conulariids, and potentially, cnidarians. Given these insights into the taphonomy and affinities of *Sphenothallus*, this study represents a valuable contribution to the study of shelly fossils during the Cambrian radiation of animals, when mineralized skeletons exhibit unique mineralogical and morphological diversity (Bengtson and Conway Morris, 1992; Knoll, 2003; Kouchinsky et al., 2012). The taphonomic model proposed in this study also illuminates the diversity of shells preserved as carbonaceous fossils, which are widespread in Cambrian rocks (Butterfield and Harvey, 2012; Butterfield and Nicholas, 1996; Forchielli et al., 2012; Harvey, 2010; Harvey and Butterfield, 2011; Harvey et al., 2012; Martí Mus, 2014).

Acknowledgements

The research was supported by the Clay Mineral Society, Geological Society of America, National Science Foundation, Sigma Xi Scientific Research Society, and Virginia Tech Department of Geosciences. Analyses were conducted at the VT-ICTAS-NCFL with technical assistance from A. Giordani, S. McCartney, and Chris Winkler. We thank Jesse Broce, Drew Hawkins, Mike Meyer, Michael Nakagaki, Ken O'Donnell, and Qing Tang for assistance in *Sphenothallus* collection. We additionally thank H. Van Iten and O. Vinn for critical comments that greatly improved the quality of this report.

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Fig. 1. Maps of fossil localities and stratigraphic column of Shuijingtuo Formation. (A) Tectonic map showing the Yangtze, Cathaysia, North China, and Tarim blocks in China. White star indicates area magnified in (B) with Heziao and Jijiapo fossil localities. The Siduping (SDP) locality is marked by arrow. (B) Geological map showing fossil localities marked by black triangles and labeled as HZA (Heziao) and JJP (Jijiapo). (C) Generalized stratigraphic column of the Shuijingtuo Formation in Hubei Province. Arrow indicates estimated position of beds containing abundant *Sphenothallus* specimens at Heziao. Abbreviations: SHP, Shipai Formation; Terre, Terreneuvian; YJH, Yanjiahe Formation.

Fig. 2. Outcrops of *Sphenothallus* horizons and co-occurring sponge and trilobite fossils. (A–B) Field photographs of the Shuijingtuo Formation at the Heziao section. Rock hammer near arrow in (A) is 35 cm in length. Interval containing abundant *Sphenothallus* specimens indicated by arrow in (A) and bracketed by the dashed lines in (B). All Heziao fossils, including the fossiliferous slab (Fig. 4), were collected from this interval. (C–D) Photographs of sponge

spicules co-occurring with *Sphenothallus* in the Shuijingtuo Formation at Heziao (C) and in the Niutitang Formation at Siduping (D). (E–F) Photographs and corresponding drawings of a cephalon and pygidium of the eodiscoid trilobite *Tsunyiidiscus* co-occurring with *Sphenothallus* in the Shuijingtuo Formation at Jijiapo.

Fig. 3. Morphological characters measured for quantitative analysis. (A) Schematic drawing and (B) photograph of a *Sphenothallus* specimen with morphological characters labelled. (C) Photograph of a *Sphenothallus* specimen with curve longitudinal thickenings, and the segments (marked by the numbers) used to calculate the lengths of the left (1+2) and right (3+4+5) thickenings.

Fig. 4. Biostratinomic analysis of a fossiliferous slab containing abundant *Sphenothallus* specimens, collected from the Shuijingtuo Formation at Heziao (see Fig. 2B). (A) Schematic drawing of the slab, showing individual beds. Values in the black boxes indicate the numbers of relatively complete specimens observed on the exposed bedding surfaces. (B) Rose diagram showing the preferential orientation of *Sphenothallus* specimens exposed on the surfaces indicated in (A). Enclosed values are the numbers of specimens and outside values are percentages of specimens with their apices oriented in each direction. Key enclosed by box. An arbitrary vector was chosen as the zero degree direction and applied consistently in all bedding surfaces. (C–F) Schematic drawings showing the orientation, density, and relative spacing of *Sphenothallus* specimens on bedding surfaces indicated in (A).

Fig. 5. Photographs of *Sphenothallus* fossils from the Shuijingtuo Formation at Heziao, showing variable sizes, longitudinal thickenings (A–I), transverse walls (A–F), transverse ribs on longitudinal thickenings (B,G), and transverse ribs on transverse walls (B).

Fig. 6. Microstructures and elemental and mineralogical compositions of *Sphenothallus* specimens from the Shuijingtuo Formation at Heziao. (A) Composite SSD(+) image of specimen in Fig. 5D. (B) Photograph and (C) composite SSD(+) image of *Sphenothallus* specimen. (D, E) Composite SSD(+) images of specimens in Fig. 5A and 5G, respectively. (F) SSD(+) and (G) ETD(+) images of naturally-exposed cross section through *Sphenothallus* test, indicated by arrow in (C), showing lamellar phosphatic material. (H–I) Magnified SSD(+) images of boxes in (E), showing framboidal pyrite encrusting *Sphenothallus* test (white arrow) and located in matrix near specimen (black arrow). (J–N, O–T) EDS elemental maps of boxed areas in (A) and (D), respectively. (U–Z) EDS elemental maps of (I). Abbreviations: Cm, carbonaceous material; ECL, exterior carbonaceous layer; ICL, interior carbonaceous layer; PL, lamellar phosphatic layer.

Fig. 7. Microstructures and elemental and mineralogical compositions of transverse walls in *Sphenothallus* specimens from the Shuijingtuo Formation at Heziao. (A, B) Composite SSD(+) images of specimens in Fig. 5F and 5E, respectively. (C) Magnified image of arrowed area in (B), showing barite crystals encrusting *Sphenothallus* test. (D, E) Composite SSD(+) images of specimens in Fig. 5C and 5B, respectively. (F) Magnified photograph of boxed area in Fig. 5B, showing phosphatic transverse walls with transverse ribs (arrows). (G) SSD(TIS) image of boxed area in (E), showing phosphatic transverse wall with transverse ribs (arrows). (H–M)

1134 EDS elemental maps of specimen in (B). (N–S) EDS elemental maps of boxed area in (D). (T–Y)
 1135 EDS elemental maps of (G). Abbreviations: Cm, carbonaceous material; ECL, exterior
 1136 carbonaceous layer.

1137

1138 **Fig. 8.** Interior carbonaceous layer in *Sphenothallus* specimen from the Shuijingtuo Formation at
 1139 Heziao. (A) Photography and (B) SSD(+) image of specimen. (C, D) Magnified SSD(+) images
 1140 of boxes in (B) and (C), respectively, showing interior carbonaceous layer (ICL), lamellar
 1141 phosphatic layer (PL), and exterior carbonaceous layer (ECL). (E–J) EDS elemental maps of (C).

1142

1143 **Fig. 9.** Exterior carbonaceous layer in *Sphenothallus* specimens from the Shuijingtuo Formation
 1144 at Heziao. (A) Photograph and (B) composite SSD(+) image of a *Sphenothallus* longitudinal
 1145 thickening. (C, D) SSD(+) and (E) SSD(–) images of box in (B). (F) SSD(+) image of box in
 1146 (D). (G) SSD(–) and (H, I) SSD(+) images of box in Fig. 6E. (J) SSD(+) image of box in (I) with
 1147 ECL, UPL, and matrix delineated by lines. (K–O, P–T, U–Y) EDS elemental maps of (C), (F),
 1148 and (J), respectively. Arrows in (E) and (G) indicate transverse ribs. Abbreviations: ECL,
 1149 exterior carbonaceous layer; ICL, interior carbonaceous layer; UPL, unsculptured lamellar
 1150 phosphatic layer.

1151

1152 **Fig. 10.** Microstructures and elemental and mineralogical composition of *Sphenothallus*
 1153 specimens from the Shuijingtuo Formation at Jijiapo. (A, C, E, G) Photographs and (B, E, F, H)
 1154 corresponding composite SSD(+) image of specimens. (I) Magnified photograph of box in (A).
 1155 (J) Magnified SSD(TIS) image of box in (B). (K) Magnified SSD(+) image of tabular barite,
 1156 indicated by arrow in (B). (L) Magnified SSD(+) image of euhedral barite crystals, indicated by

arrows in (B) and (J). (M) SSD(+) image of barite, framboidal iron oxides (possibly pseudomorphs of pyrite), and carbonaceous material in sedimentary matrix located out of the view on the left side of specimen in (C, D). (N) Magnified SSD(+) image of box in (H), showing cracked carbonaceous material extending to the right where the specimen is unexposed. (O–T) EDS elemental maps of (J). (U–Z) EDS elemental maps of box in (F). Abbreviations: Cm, carbonaceous material; Fe(oxide), iron oxide mineral.

Fig. 11. Nanometer-sized pores on surface of carbonaceous material comprising *Sphenothallus* fossils from the Shuijingtuo Formation at Jijiapo. Specimen coated with ~20 nm thick gold-palladium layer. (A) Photograph and (B) composite SSD(+) image of specimen. (C) Magnified SSD(+) image of box in (B), showing carbonaceous material. (D) Magnified ETD(+) image of box indicated by arrow in (C), showing pores. (E–H) EDS elemental maps of (C).

Fig. 12. Transverse ribs of *Sphenothallus* specimens from the Shuijingtuo Formation at Jijiapo. (A, C) Photographs and (B, D) and composite SSD(+) images of specimens. (E) Photograph, (F) SSD(+), (G) SSD(TIS), and (H) SSD(–) images of box in (D). (I) Photograph, (J) SSD(–) image, and (K–M) elemental maps of box in (D). (N) SSD(BIS) and (O–R) EDS elemental maps of box in (J). EDS detector in (K–M) and (O–R) located to rear of specimen (i.e. toward the relative bottom of the figure).

Fig. 13. Microstructures and elemental and mineralogical compositions of *Sphenothallus* specimens from the Niutitang Formation at Siduping. (A) Photograph and (B) composite SSD(+) image of specimen. (C) SSD(+) and (D) SSD(–) images of box in (B). (E–H) EDS elemental

1180 maps of (C, D). (I) Photograph and (J) composite SSD(+) image of specimen. (K–P) EDS
 1181 elemental maps of box in (J). (Q, R) SSD(+) images of boxes in (J), showing pyrite encrusting
 1182 interior and exterior surfaces of *Sphenothallus* specimen. Needle-like crystals in (Q) are gypsum.
 1183 (S) SSD(+) image of box in (B), showing thick structures made of euhedral pyrite crystals and
 1184 petal-shape gypsum crystals. (T) SSD(+) image of area indicated by arrow in (J), showing
 1185 framboidal pyrite and needle-shaped gypsum crystals. (U–Z) EDS elemental maps of (Q).

1186
 1187 **Fig. 14.** Wrinkles and barite on transverse wall in *Sphenothallus* specimen from the Niutitang
 1188 Formation at Siduping. (A) Photograph and (B) composite SSD(+) image of specimen. (C)
 1189 Magnified SSD(+) and (D) SSD(–) images of box in (B), showing wrinkles (arrows). (E, F)
 1190 Magnified SSD(+) images of boxes in (B) and (E), respectively, showing bladed barite crystals.
 1191 (G–L) EDS elemental maps of (F).

1192
 1193 **Fig. 15.** Carbonaceous and phosphatic layers in *Sphenothallus* specimens from the Niutitang
 1194 Formation at Siduping. (A) Photograph and (B) composite SSD(+) image of longitudinal
 1195 thickening. (C, D) SSD(+) images of boxes in (B), showing non-lamellar phosphatic material
 1196 (Pm) and carbonaceous material (Cm). (E–H, I–L) EDS elementals maps of (C) and (D),
 1197 respectively.

1198
 1199 **Fig. 16.** SEM images and EDS elemental maps of test fragment from Heziao before taphonomic
 1200 experiment. (A) Photograph and (B, C) SSD(+) images of test fragment. Arrows in (B) indicate
 1201 areas of test fragment where lamellar phosphatic material is exposed without overlying exterior
 1202 carbonaceous layer. (D) Magnified photograph of box in (A). (E) Magnified SSD(+) image of

1203 area indicated by arrows in (B, C), showing lamellar phosphatic layer (PL) and exterior
1204 carbonaceous layer (ECL). (F) Magnified SSD(+) and (G) SSD(–) images of boxes in (B, C).
1205 Arrows in (D, G) indicate transverse ribs. (H–M, N–S) EDS elemental maps of (B, C) and (F,
1206 G), respectively.

1207

1208 **Fig. 17.** SEM images and EDS elemental maps of test fragment from Heziao after taphonomic
1209 experiment. (A) Photograph and (B, C) SSD(+) images of test fragment. Arrows in (B, C)
1210 indicate areas of test fragment where lamellar phosphatic material was exposed without
1211 overlying exterior carbonaceous layer prior to demineralization experiment. (D) Magnified
1212 photograph of box in (A). (E) Magnified SSD(+) image of area indicated by arrows in (B, C),
1213 showing gypsum crystals encrusting and carbonaceous material (Cm) replicating the fossil. (F)
1214 Magnified SSD(+) and (G) SSD(–) images of boxes in (B, C). Arrows in (D, G) indicate
1215 transverse ribs. (H–M, N–S) EDS elemental maps of (B, C) and (F, G), respectively.

1216

1217 **Fig. 18.** Results of quantitative morphological analysis. (A) Histogram showing cumulative
1218 number of specimens from the three fossil localities versus mean longitudinal thickening length.
1219 Chart below histogram shows the relative proportion of specimens in each class preserved with
1220 and without transverse walls. (B) Simple regressions of aperture diameter, mean thickening
1221 diameter, and apex diameter against mean longitudinal thickening length. The allometric
1222 trendlines, equations, and R^2 values are shown.

1223

1224 **Fig. 19.** Generalized taphonomic model for *Sphenothallus*, based on the results of this
1225 investigation and a review of the literature. Although decay of non-biomineralizing tissues,

1226 transport, fragmentation, and pre-burial surface alteration—as well as authigenic mineralization,
 1227 post-burial surface alteration, kerogenization, and demineralization—are illustrated as sequential
 1228 processes, they may variably be concomitant. Model does not illustrate diagenetic
 1229 recrystallization of *Sphenothallus* phosphatic material, the pathways involved with preservation
 1230 of *Sphenothallus* holdfasts, or the processes involved in the precipitation of barite and gypsum.
 1231

1232 **Fig. 20.** Reconstruction of *Sphenothallus* test longitudinal section based on results and
 1233 taphonomic model in this report and observations by Muscente and Xiao (2015). Dashed lines
 1234 indicate morphological characters that were not preserved in *Sphenothallus* fossils at the new
 1235 localities in South China. Depictions of these characters are based on descriptions in the
 1236 literature (Bodenbender et al., 1989; Fauchald et al., 1986; van Iken et al., 1992). Overall, this
 1237 reconstruction assumes that the carbonaceous layers in the Heziao specimens formed via
 1238 demineralization of inner and outer phosphatic lamellae, thus representing taphonomic (not
 1239 anatomical) features. Illustration modified from fig. 12 of Muscente and Xiao (2015).

Table 1. Results of quantitative morphological analysis. The numbers outside and inside the parentheses are the means values and ranges, respectively.

Locality	No. of specimens sampled	Thickening length range (mm)	Aperture diameter range (mm)	Thickening diameter range (mm)	Apex diameter range (mm)	No. of specimens (walls present)	No. of specimens (walls absent)	Proportion of specimens (walls present)	Proportion of specimens (walls absent)
Heziao	211	13.50 (1.17–14.67)	3.17 (1.00–4.17)	0.56 (0.24–0.80)	0.93 (0.50–1.43)	141	70	0.67	0.33
Jijiapo	207	13.49 (1.46–14.95)	3.19 (1.14–4.33)	0.49 (0.31–0.80)	0.82 (0.56–1.38)	126	81	0.61	0.39
Siduping	18	12.36 (2.01–14.37)	3.22 (1.06–4.28)	0.37 (0.28–0.66)	0.77 (0.50–1.27)	2	17	0.12	0.88

Table 2. R^2 values in simple regression analyses of morphological characters, assuming each relationship is a power function (e.g., $y = kx^a$).

Character	Longitudinal thickening Length	Longitudinal thickening diameter	Aperture diameter	Apex diameter
Longitudinal thickening Length	1			
Longitudinal thickening diameter	0.76	1		
Aperture diameter	0.81	0.77	1	
Apex diameter	0.66	0.10	0.67	1

Figure 2

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Figure 12

Figure 13

Figure 14

Figure 15

Figure 16

Figure 17

Figure 18

A

B

Figure 19

Figure 20

Graphical Abstract

***Sphenothallus* fossils preservational continuum**

New taphonomic model

New *Sphenothallus* Reconstruction