

Geometric morphometric analysis of *Protoconites minor* from the Cambrian (Terreneuvian) Yanjiahe Formation in Three Gorges, South China

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ABSTRACT

The Ediacaran to Cambrian transition is a critical interval of time during which major evolutionary changes occurred. Recently, abundant *Protoconites minor* have been recovered from the silty shales of the lower Cambrian Yanjiahe Formation (Terreneuvian, Fortunian – Stage 2) in the Three Gorges area of South China. These fossils represent an important ecological diversification of macroscopic organisms at the onset of the Cambrian. *Protoconites minor* is a probable cnidarian-grade organism preserved by carbon compression. Herein, geometric morphometric analyses are applied to crack out specimens of *P. minor* to reveal any cryptic morphological details that may have implications for their morphological diversity, ontogenetic processes, and taxonomic identification. These statistical analyses reveal a strong relationship between size and shape, which indicates that the overall shape of *P. minor* was mainly controlled by allometric growth. The smaller specimens are generally wider at the anterior and more commonly have straight-sides. Larger individuals tend to be narrower at the anterior, with bending more common. Our analyses demonstrate that there are transitional forms between larger, strongly bent specimens and smaller, straight specimens, suggesting that the assemblage likely consists of a single species.

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INTRODUCTION

During the late Ediacaran to middle Cambrian (635 to 505 Ma), fundamental biological, climatic, tectonic, and geochemical changes occurred (Zhu et al., 2003, 2007; Meert and Lieberman, 2004, 2008). The abrupt appearance of most major animal phyla in the early Cambrian is known as the Cambrian Radiation. Key early Cambrian fossils include ichnofauna, small shelly fossils (SSF), and exquisitely preserved soft-bodied fossils found in numerous, globally distributed lagerstätten, which are critical for understanding the diversity present in Cambrian ecosystems (Conway Morris et al., 1987; McCall, 2006; Li et al., 2007; Steiner et al., 2007; Shu, 2008, Shu et al., 2014; Zhang et al., 2014).

Limitations of the fossil record mean that the deep origins of animal phyla remain cryptic, primarily because early ancestors were often small and/or soft-bodied, with reduced preservation potential. Therefore, it has been suggested that the roots of animal evolution extend back into the Precambrian (Wray et al., 1996; Bromham et al., 1998; Aris-Brosou and Yang, 2003; Peterson et al., 2004, 2008; Blair, 2009; Zhang et al., 2014; Zhu et al., 2017; Cai et al., 2019). Linking the evolutionary relationships of the fossil communities of the late Precambrian with the small shelly fossils and soft-bodied taxa of the early Cambrian is a fundamental challenge. It is rare for small shelly fossils to be pre-

served in the same deposits as soft-bodied macrofossils (Guo et al., 2017). However, the early Cambrian Yanjiahe Biota bridges this gap as it includes macroscopic metazoans, macroalgae, small shelly fossils, spheroidal fossils (putative embryos), acritarchs, and cyanobacteria (Guo et al., 2008, 2009, 2010a, b, 2012, 2014, 2017, 2020a, b, c; Topper et al., 2019). Importantly, some key macrofossils exhibit characters of a transitional biota from Ediacaran to Cambrian, such as some types of macroalgae (Guo et al., 2010a) and the cnidarian-grade *Protoconites* (Guo et al., 2009).

Guo et al. (2009) reported *Protoconites* sp. from the lower Cambrian Yanjiahe Formation (Fm.) in the Three Gorges area, Hubei Province, South China. Chang et al. (2018a) redescribed similar specimens from the same interval in the Yanjiahe Fm., Shuijingtuo Fm., and Shipai Fm., and reasigned *Protoconites* (the Yanjiahe Fm.) to *Cambrohytium* cf. *major*. However, *Protoconites* specimens lack key features such as the tentacle-like structures and the transverse annulations seen in *Cambrohytium* (Xiao et al., 2002), hence the specimens herein are referred to *Protoconites*.

Protoconites minor are smooth, expanding tubes (5–50 mm long), with a pointed apex that expands to a squared-off termination or aperture. Although *P. minor* lacks tentacle-like structures and transverse annulations as in *Cambrohytium* (or *Archotuba conoidalis*, Hou et al., 1999) and similar

genera such as *Lantianella* and *Piyuania*, overall size and morphological similarities may implicate a close phylogenetic relationship between these taxa (Conway Morris and Robinson, 1988; Chen et al., 1996; Chen and Zhou, 1997; Hou et al., 1999, 2004; Xiao et al., 2002; Chen, 2004; Ponomarenko, 2005; Zhang and Hua, 2005; Guo et al., 2009, 2017; Yuan et al., 2011, 2016; Wan et al., 2016).

The biological affinities of many Precambrian and Cambrian conical fossils have been extensively debated (Conway Morris and Robinson, 1988; Chen et al., 1994; Xiao et al., 2002; Ponomarenko, 2005; Guo et al., 2009, 2017; Yuan et al., 2011, 2016; Wan et al., 2016; Chang et al., 2018a). Hyoliths for example, have been traditionally grouped with molluscs, but new data regarding soft morphology has resulted in their controversial reinterpretation as lophophorates (Moysiuk et al., 2017; Sun et al., 2018). Although they are broadly morphologically similar to some hyoliths, *Protoconites minor* lacks a mineralized skeleton (Xiao et al., 2002). *Protoconites minor* are enigmatic fossils, with interpretations ranging from cnidarians to algae (Xiao et al., 2002). They have a long stratigraphic range, from the Ediacaran [upper Doushantuo Fm. black shales at Miaohu, Yichang city, Hubei Province (Chen et al., 1994; Ding et al., 1996; Chen et al., 2002; Xiao et al., 2002; Yuan et al., 2002) and at Taoying, Jiangkou county, Guizhou Province (Zhao et al., 2004; Wang et al., 2005, 2011)] to the lower Cambrian [Yanjiahe Fm., Hubei Province (Guo et al. 2008, 2009; Chang et al., 2018a)].

Xiao et al. (2002) suggested that *Protoconites minor* could be a juvenile form of *Baculiphyca tae-niata* (clavate forms with rhizoidal holdfasts from the Ediacaran Miaohu Biota). This seems unlikely, however, as *P. minor* exhibits a larger divergent angle and lacks a rhizoidal holdfast. *P. minor* also bears close similarities to the Cambrian *Cambrorhytium* in size, shape, and style of preservation (Conway Morris and Robinson, 1988; Chen et al., 1996; Chen and Zhou, 1997), but lacks faint tentacle-like structures and transverse annulations. *Cambrorhytium major* has been interpreted as a possible scyphozoan cnidarian (Conway Morris and Robinson, 1988), comparable to the sheaths that enclose budding polyps in coronate scyphozoans such as modern *Stephanoscyphus* (Werner, 1966).

As *Protoconites minor* fossils exhibit high morphological diversity, total species presence remains uncertain. In general, smaller specimens

are generally wider at the anterior part, with straight sides, and larger specimens are relatively narrower at the anterior, and often exhibit some degree of lateral bending. Specimens with the wide apertures were interpreted as a different species to those with narrow apertures, such as *Cambrorhytium* (*C. major*, *C. cf. C. major*, *C. fragilis*, *C. minor* and *C. gracilis*) (Conway Morris and Robinson, 1988; Ponomarenko, 2005; Zhang and Hua, 2005; Chang et al., 2018a) and *Sphenothallus* (*S. taijiangensis*, *S. songlinensis*, and *S. kozaki*) (Zhu et al., 2000; Peng et al., 2005; Chang et al., 2018a). Alternatively, these morphological differences may be due to intraspecific variation.

Abundant *Protoconites minor* from the lower Cambrian Yanjiahe Fm. provide an excellent opportunity to test this using geometric morphometrics. The development of geometric morphometrics in the last two and a half decades was a “quantification revolution” for the analysis of shape (Adams et al., 2004; Chen et al., 2016). The method has been demonstrated as a very powerful tool for the study of diversity and evolution of life (e.g., Cooney et al., 2017). Sliding semilandmarks-based geometric morphometrics have a similar function to elliptical Fourier analyses when analyzing the shapes of outlines. However, the sliding semilandmark approach is more effective in circumstances where emphasis must be placed on particular segments, which can be easily achieved by using more points. Herein, we apply a combination of landmark and semilandmark-based geometric morphometric analyses to *P. minor* in order to explore their morphological space, and reveal any taxonomical information associated with morphology, and to determine whether overall shape change is associated with changes in size.

LOCALITY AND STRATIGRAPHY

All *Protoconites minor* utilized in this study were collected from four measured stratigraphic sections (the Dingjiaping, Gunziao, Yangjiachong, and Muyang sections) through the Yanjiahe Fm. in the Three Gorges area, South China (Figure 1.1–4). The Yanjiahe Fm. crops out mainly around the southern and western flanks of the Huangling Anticline, as well as the core of the Changyang Anticline, (Figure 1.1–2). The succession is particularly well-developed and well-exposed around the Yanjiahe Village (Sandouping Town) and the Dingjiaping Village (Changyang County) in the Yichang area (Figure 1.3–4).

The Yanjiahe Fm. rests unconformably on the underlying dolomitic Baimatuo Member of the

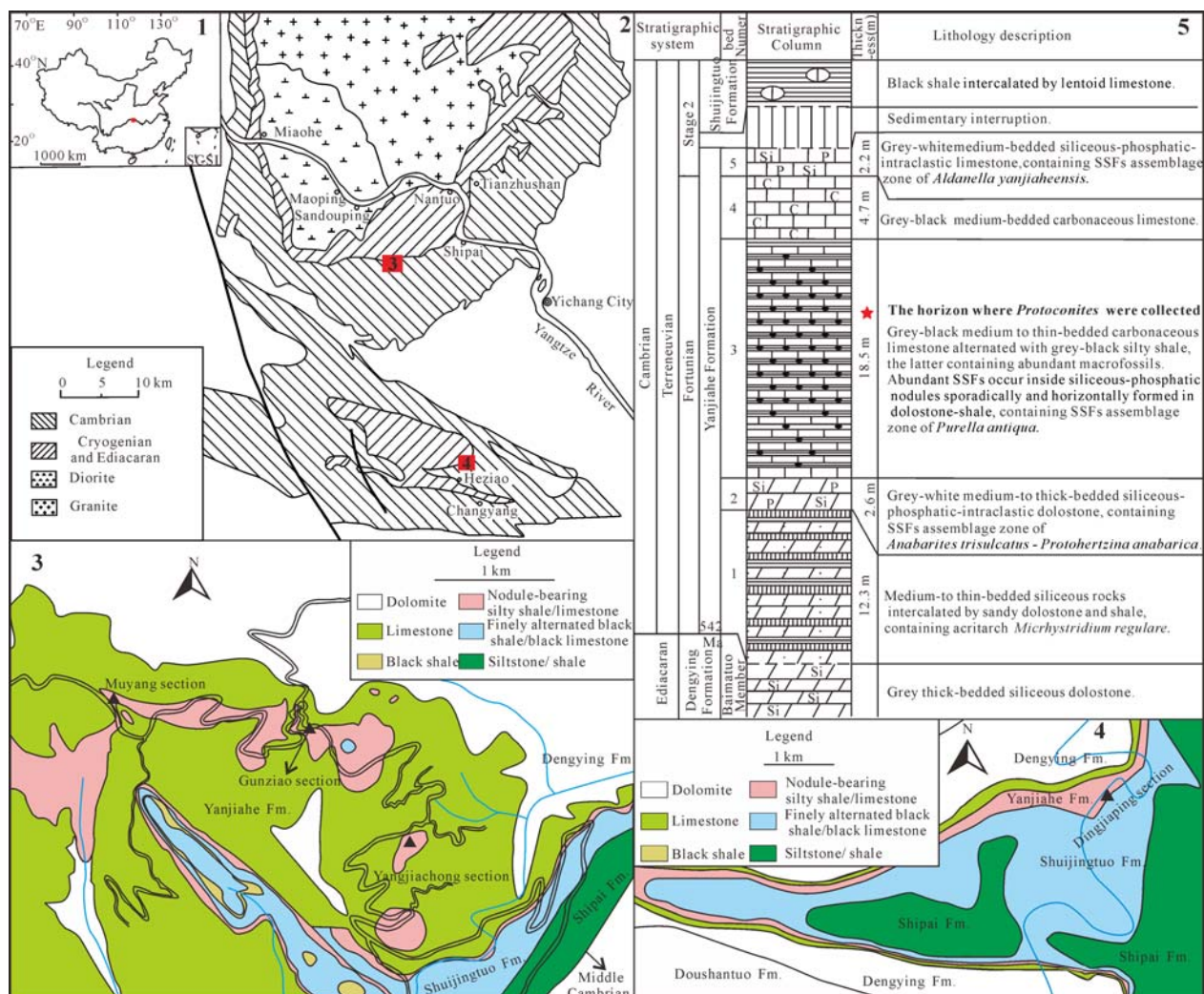


FIGURE 1. Locality and stratigraphy of the Cambrian (Terreneuvian) Yanjiahe Formation in Yichang, Hubei Province, China. **1.** Sketch map of the People’s Republic of China, showing the position of the collecting locality in Hubei Province; **2.** Simplified geological sketch map of the Three Gorges area, Hubei Province, South China, showing the outcrops of Cambrian strata. Red boxes around **3** (Yanjiahe area) and **4** (Dingjiaping area) denote areas that are enlarged for additional detail; **3.** Detailed geological sketch map of the Yanjiahe area, showing the outcrops of the Yanjiahe Formation; **4.** Detailed geological sketch map of the Dingjiaping area, showing the outcrops of the Yanjiahe Formation. (In **3** and **4** map: White = Ediacaran Dengying Formation; Pink and light green = Cambrian Yanjiahe Formation; Yellow and light blue = the Cambrian Shuijingtuo Formation; Green = Cambrian Shipai Formation; Black triangles indicate locations of measured stratigraphic sections) **5.** Stratigraphic sequence of Lower Cambrian strata in the Gunziao section, Three Gorge area, indicating the horizons where fossils were collected.

Dengying Fm. (Ediacaran). The Yanjiahe Fm. is subdivided on the basis of lithology into five beds (Figure 1.5). In the Gunziao section, Bed 1 is about 12.3 m thick and consists of siliciclastics intercalated with sandy dolostone and shale. Bed 1 contains the *Asteridium–Heliosphaeridium–Comasphaeridium* acritarch assemblage zone (Yao et al., 2005; Dong et al., 2009; Ahn and Zhu, 2017) and probable sponge spicules (Chang et al., 2017). Bed 2 is 2.6 m thick and consists of sili-

ceous–phosphatic intraclastic dolostones bearing shelly fossils from the *Anabarites trisulcatus–Protohertzina anabarica* Assemblage Zone (Guo et al., 2014), in addition to the tubular taxon *Megathrix longus* (Shang et al., 2016). Bed 3 is about 18.5 m thick and consists of grey-black limestone interbedded with silty shale. The silty shale contains macrofossils such as algae and enigmatic metazoans (*Yanjiahellia* and *Protoconites minor* studied herein) (Guo et al., 2008, 2009, 2010a, 2012; Topper et al.,

2019). Abundant shelly fossils (*Purella antiqua* Zone) (Guo et al., 2014) and the possible earliest radiolarian (Chang et al., 2018b) occur in siliceous-phosphatic nodules in Bed 3. Bed 4 is 4.7 m thick and consists of non-fossiliferous carbonaceous limestone. Bed 5 is about 2.2 m thick and consists of siliceous-phosphatic, intraclastic limestone containing fossils assigned to the *Aldanella yanjiaheensis* Assemblage Zone (= *A. attleborensis* Assemblage Zone, corresponding to the *Watsonella crosbyi* assemblage (Terreneuvian, Stage 2), Guo et al., 2014, 2020c).

Ahn and Zhu (2017) suggest that the Yanjiahe Fm. records the biogeochemical history of the South China platform throughout approximately the first 15 Ma of the Cambrian Period. There is a disconformity between the Yanjiahe Fm. and the overlying Shuijingtuo Fm., representing a relatively minor time-gap (Chen, 1984; Ding et al., 1992; Guo et al., 2008, 2009). The U-Pb age from zircons at the base of the Shuijingtuo Fm. in the Three Gorges area give an age of 526.4 ± 5.4 Ma (Okada et al., 2014).

MATERIAL AND METHODS

All 1048 specimens (see Appendix, supplementary Table S1) of *Protoconites minor* utilised for this study occur as carbonised films preserved on bedding surfaces (Figure 2). Obviously broken or extensively damaged specimens have been excluded from the analysis. Collection number “CH” indicates fossils from the Dingjiaping section. “Y” indicates fossils from the Yangjiachong section. Digital images were taken with a light camera (Canon EOS70D) under both natural light and with an external light source in Chang’an University, Xi’an, China. Specimens are housed in the collections at the School of Earth Science and Resources, Chang’an University.

Geometric morphometric analyses required application of a combination of landmarks and sliding semilandmarks. Landmarks were used to cover static homologous anatomical loci that can be found unambiguously on every specimen (Zelditch et al., 2004), while sliding semilandmarks were used to cover curves where no homologous point can be precisely defined (Bookstein, 1997a, b; Gunz et al., 2005; Mitteroecker and Gunz, 2009; Gunz and Mitteroecker, 2013). In total, three Type II landmarks (Zelditch et al., 2004) and 34 sliding semilandmarks, were applied to each specimen using the software TpsDig2 v. 2.26 (Rohlf, 2010a; Figure 3.1-2). A sliders file was generated using the software TpsUtil v. 1.74 (Rohlf, 2011a).

Relative Warp (RW) analyses were carried out using the software TpsRelw v 1.74 (Rohlf, 2010b) using the Generalized Procrustes Analysis superimposition method (Figure 3.3; Zelditch et al., 2004; Gunz and Mitteroecker, 2013; Chen et al., 2016). The centroid is a measure of size that is mathematically independent of shape (Zelditch et al., 2004), and was calculated using the mean of all the landmarks’ coordinates automatically using TpsRelw v 1.74. Multivariable linear regression analyses were conducted using TpsRegr v 1.45 (Rohlf, 2011b). Data was also transferred to the Palaeontological Statistics Program (PAST) (Hammer et al., 2001) for simple linear regression.

Some specimens exhibit left or right curvature. As *Protoconites minor* was not mineralized, it is possible that extent of curvature is a taphonomic artefact. To control for bias associated with direction of curvature, we have reflected some of the images so all specimens curve in the same direction.

RESULTS

Size Spectra of *Protoconites minor* in the Yanjiahe Formation

The centroid size distribution for all specimens ($n=1048$) ranged from 5.24 mm to 50.8 mm. A Shapiro-Wilks test indicated a right-tailed, non-normal distribution (Figure 4.1; $W = 0.9885$, $p < 0.001$; Skewness = 0.2683; see supplementary Table S1). Specimens were then divided into those with obvious curvature and those without, and each group was analysed separately. The total distribution of the centroid size of “straight”-sided specimens ($n = 722$) ranges from 5.1 mm to 49.4 mm, and also shows a right-tailed non-normal distribution (Figure 4.2; Shapiro-Wilks test $W = 0.9905$, $p < 0.001$; Skewness = 0.2526; see supplementary Table S2).

Geometric Morphometric Analysis of Original Shape

To explore morphospace of *Protoconites minor*, we carried out Relative Warp (RW) analysis (Zelditch et al., 2004). In total, 1048 specimens were included in this analysis. Seventy relative warp (RW) scores were given by the analysis (see supplementary Table S1). RW 1 explains 38.79%, RW 2 explains 34.74%, and RW 3 explains 8.97% of the total variation. As shown in Figure 5.1, the average shape is straight-sided and triangular, located at the plot’s origin, and RW 1 mainly explains the direction of bending. Positive and negative RW 1 scores explain different directions and

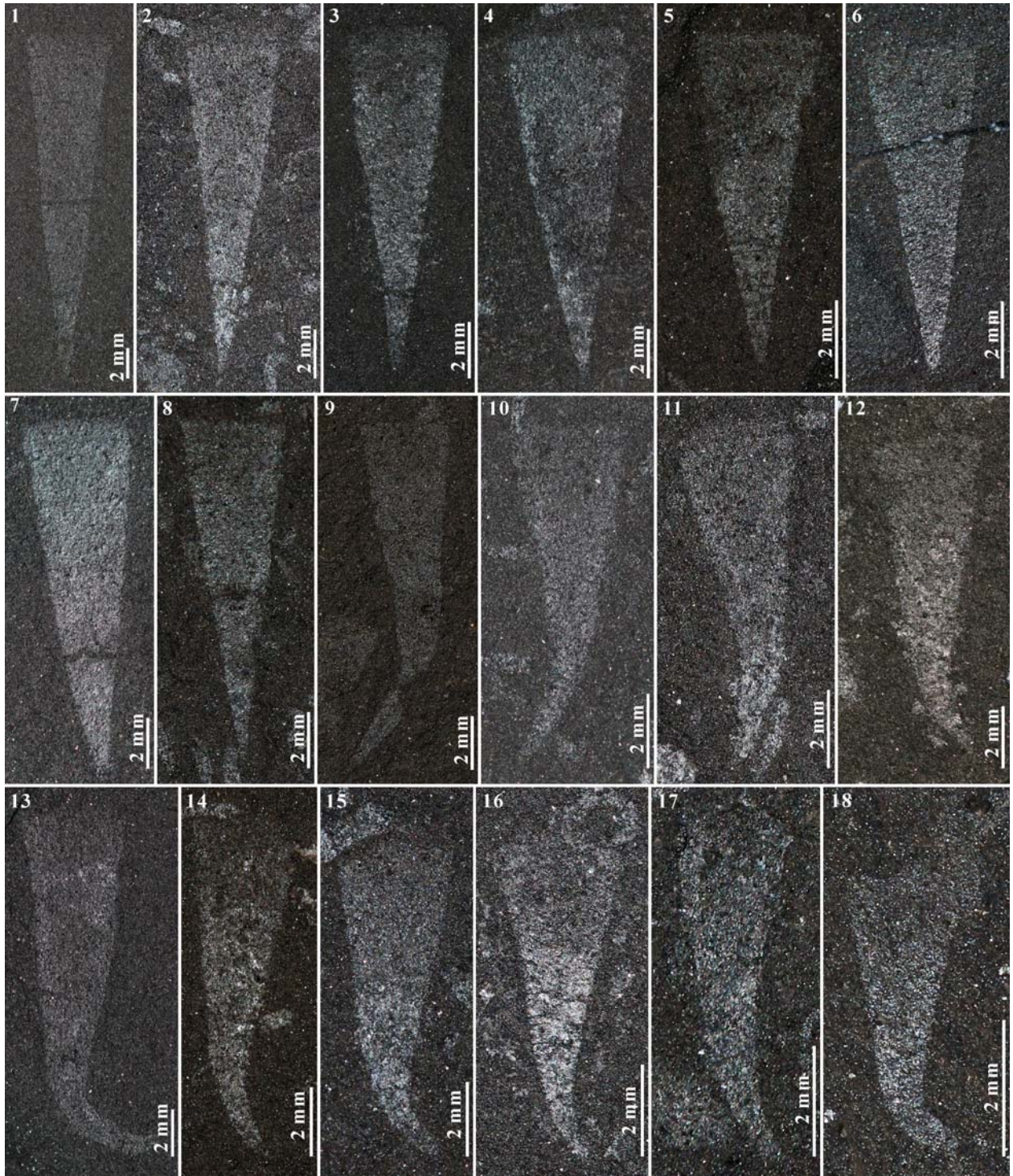


FIGURE 2. *Protoconites minor* from the Cambrian (Terreneuvian) Yanjiahe Formation in Yichang, Hubei, China. **1.** No. Y-24B (2); **2.** No. Y-41A (5)-1; **3.** No. Y-765A (3); **4.** No. Y-127B (1); **5.** No. Y-28 (2); **6.** No. CH-179A (3); **7.** No. Y-273A (1); **8.** No. Y-41A (14); **9.** No. Y-445 (2); **10.** No. Y-494 (2)-2; **11.** No. Y-40A (11); **12.** No. Y-1234 (3); **13.** No. Y-844A (2); **14.** No. Y-785 (2); **15.** No. Y-40B (9)-1; **16.** No. Y-880 (6); **17.** No. Y-596 (2)-1; **18.** No. Y-531 (3)-2. "CH" means the locality of the fossils from Dingjiaping section, "Y" means the locality of the fossils from Yangjiachong section.

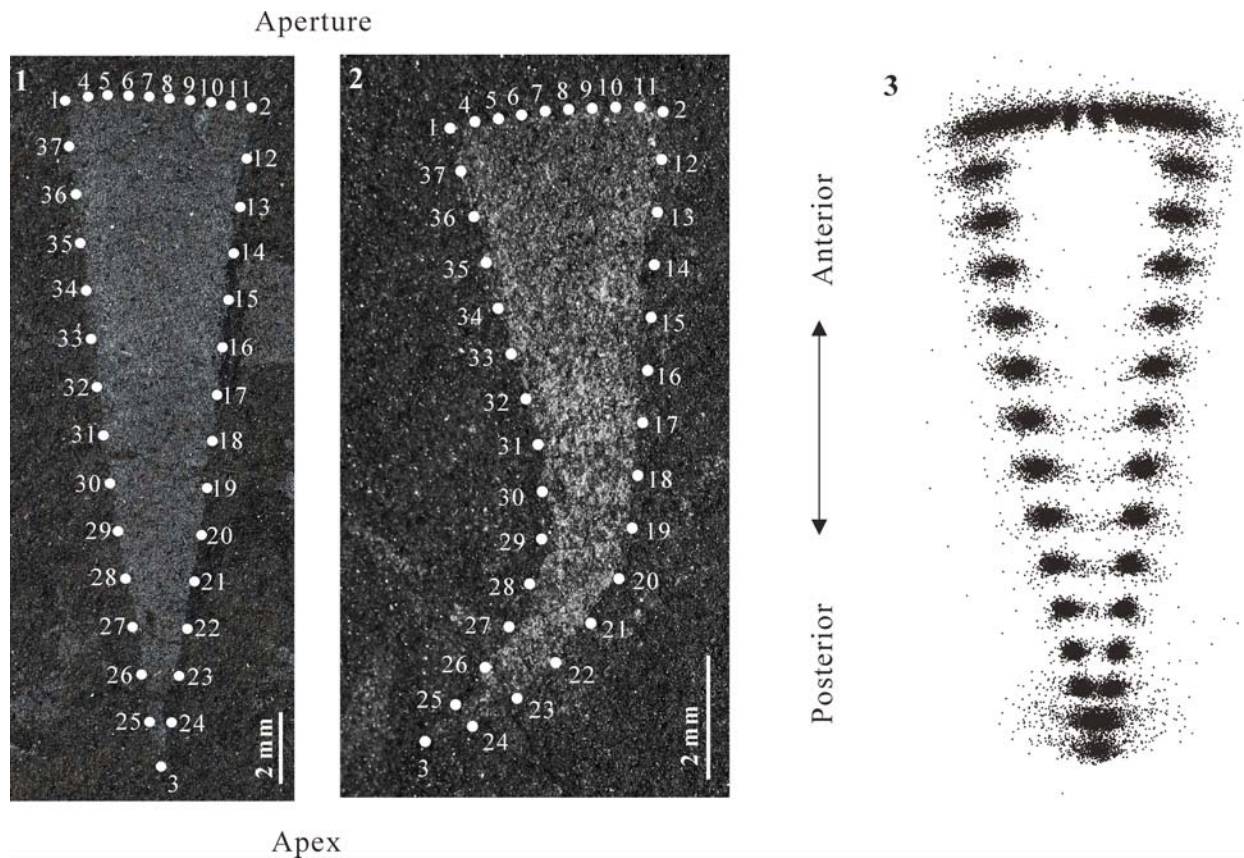


FIGURE 3. Definition of landmarks and semi-landmarks and the result of superimposition. **1.** and **2.** landmarks and semi-landmarks set on both straight and laterally bent specimens. Type II landmarks are 1, 2, and 3, and sliding semi-landmarks are 4–34 in **1.** and **2.**; **3.** consensus configuration after superimposition using Generalized Procrustes Analysis.

degree of bending (Figure 5.1). RW 2 mainly explains the relative width of the specimen. Specimens with a relatively wider anterior have positive RW 1 scores, while specimens which have an elongated slender shape, have negative RW 1 scores. RW 3 scores indicate variable twisting through the length of the specimens (Figure 5.2).

Specimens mainly cluster around the origin where the mean shape is straight.

Geometric Morphometric Analyses of Revised Data

Morphospace of overall specimens (n=1048). Because *Protoconites minor* is not mineralized, bending observed in many individuals is likely to be

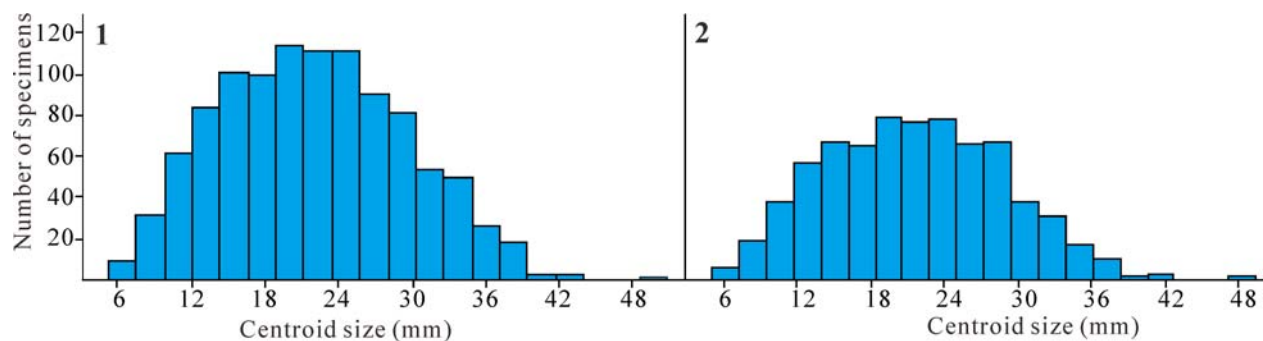


FIGURE 4. Histogram showing the size spectra of *Protoconites minor*. **1.** size distribution of all specimens analyzed in this study; **2.** size distribution without laterally bended specimens.

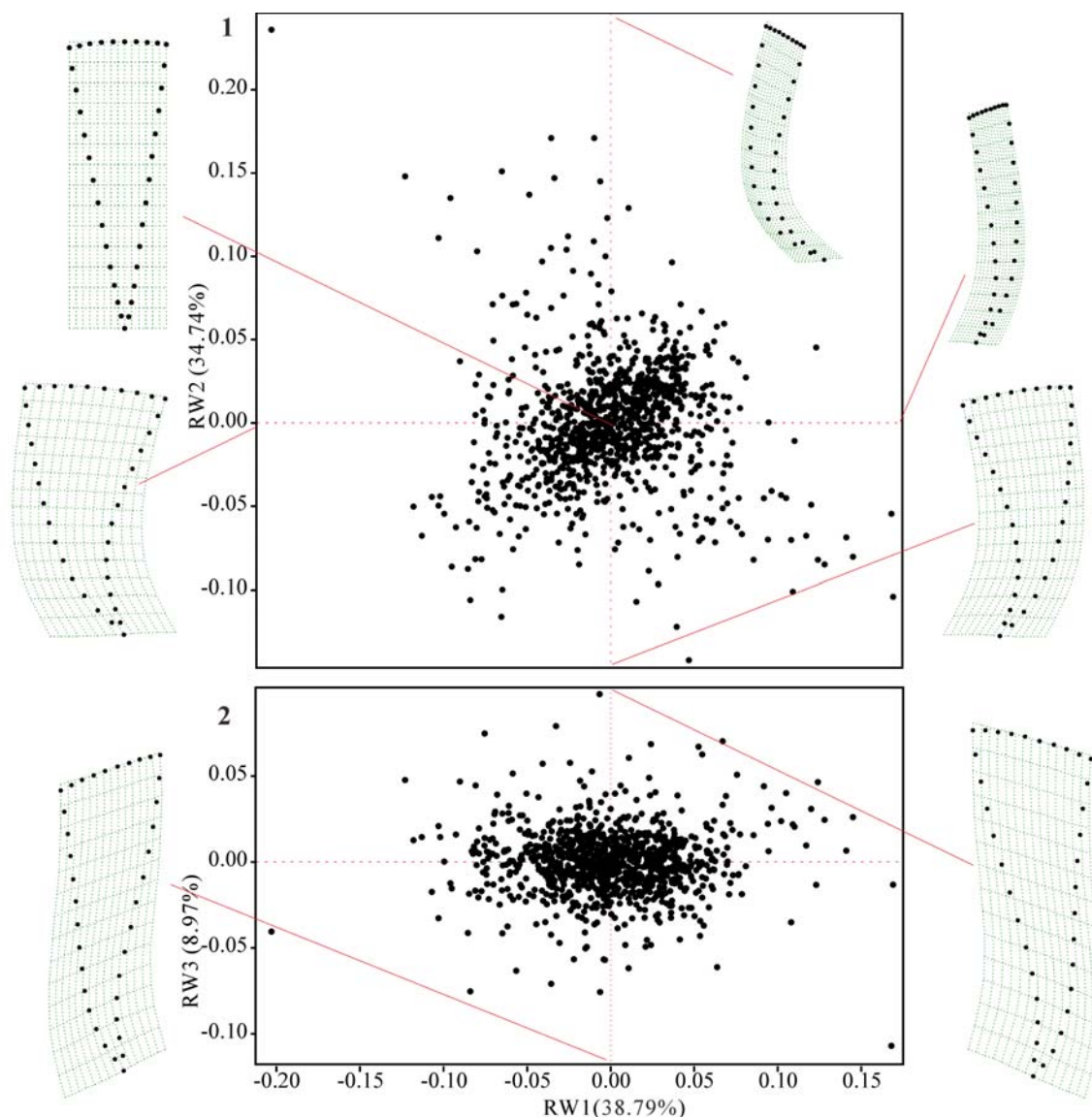


FIGURE 5. *Protoconites minor* morphospace generated by the Relative Warp (RW) analysis using un-mirrored specimens with indication of characteristic thin-plate splines. 1. plot for RW 1–2; 2. plot for RW 1–3. Thin-plate splines show the shapes of specimens in RW 1–2 and RW 1–3 planes, respectively.

taphonomic. To mitigate taphonomic bias, images of the bent specimens were mirrored so all that exhibited curvature did so in the same direction. In total 1048 specimens were included in this analysis and 70 relative scores are reported (see supplementary Table S3). The RW 1 explains 41.41% of the total shape variance (Figure 6.1), which mainly reflects the width of the aperture. RW 2 explains 31.82% of the total shape variance, reflecting both the width of aperture and the extent of lateral bending. Positive values of RW 2 indicates relatively narrow specimens and a slightly left side concave, while negative values of RW 2 suggests the specimen was wide and right side concave (Figure 6.1).

Herein the RW 3 explains 11.35% of the total shape variance, and indicates degree of tortuosity (Figure 6.2).

Morphospace of “straight”-sided specimens (n=722). The RW 1 explains 64.14% of the total shape variance (Figure 7.1), followed by 13.11% of RW 2, 8.74% of RW 3, and 5.46% of RW 4. RW 1 explains mainly the relative width of the aperture of these specimens (see supplementary Table S2). RW 2 mainly shows the difference of tortuosity, with the positive and negative values indicating different directions of torsion. RW 3 mainly indicates the difference of the width of the central part of the specimens. Specimens with negative values have

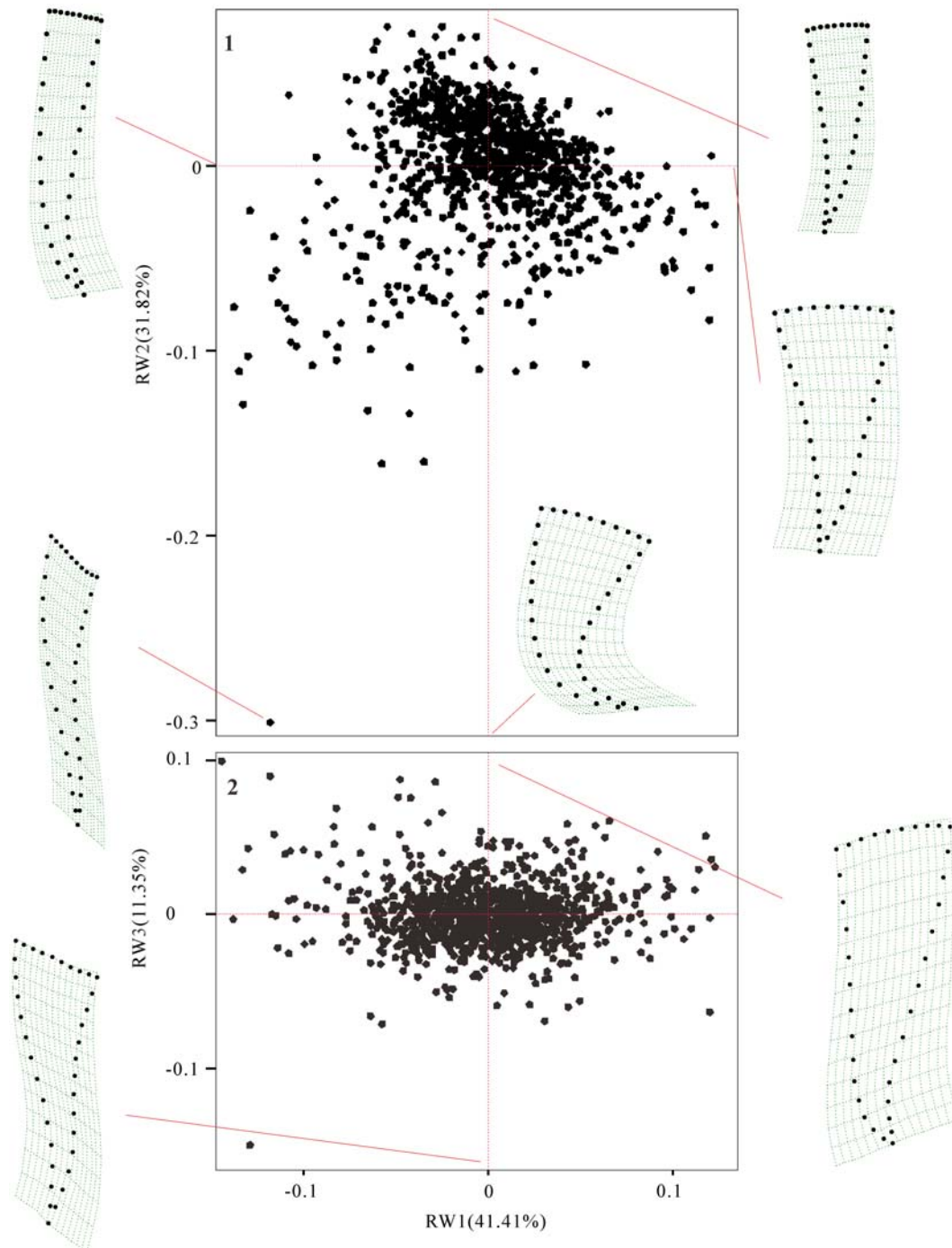


FIGURE 6. *Protoconites minor* morphospace generated by the Relative Warp (RW) analysis using mirrored specimens. **1.** plot for RW 1–2; **2.** plot for RW 1–3. All thin-plate splines correspond to points (indicated as a line) within the morphospace in RW 1–2 and RW 1–3 planes, respectively.

a narrow central part, while specimens with positive RW 3 values are expanded through the centre (Figure 7.2).

Morphospace of bent specimens (n=326). The RW 1 explains 42.06% of the total shape variance,

followed by 27.18% of RW 2, 13.80% of RW 3, and 6.24% of RW 4 (see supplementary Table S4). RW 1 reflects both the extent of lateral bending and tortuosity. RW 2 mainly shows the difference of the relative width of the aperture.

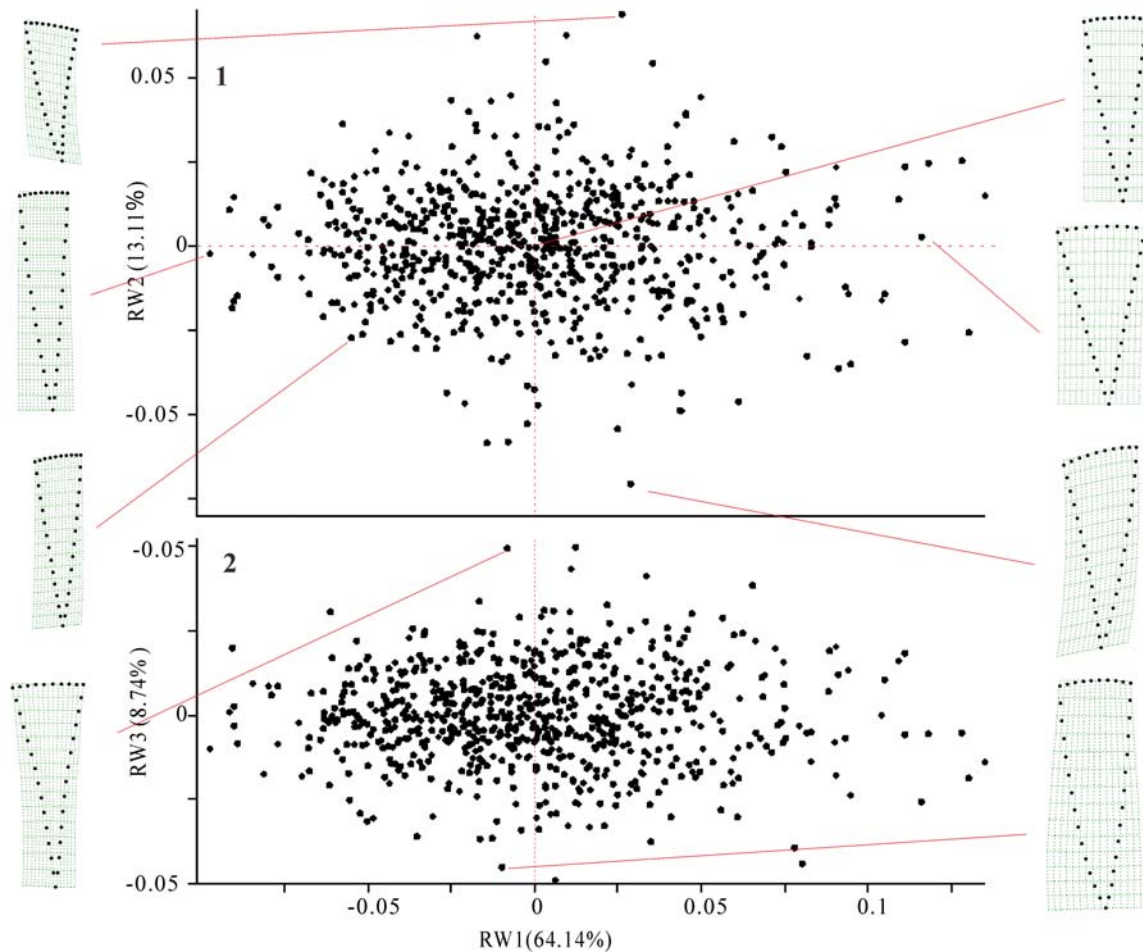


FIGURE 7. Morphospace of straight shell *Protoconites minor* generated by the Relative Warp (RW) analysis. **1.** plot for RW 1–2; **2.** plot for RW 1–3. All thin-plate splines correspond to the shapes of specimens in RW 1–2 and RW 1–3 planes, respectively.

Linear Regression Analyses

Linear regression of overall specimens (n=1048). To reveal if shape is related to ontogenetic allometry, we conducted multivariable linear regression analysis between the overall shape variance (generalized least squares aligned by tps-Relw v. 1.65) and the log10-transformed centroid size of 1048 specimens using the software Tps-Regr v 1.45. This indicates a strong relationship between size and shape (Generalized Goodall F-test: $F = 235.856$, $p < 0.001$; Wilks' Lambda test: $\lambda = 0.437$, $p < 0.001$; see supplementary Table S3 for 1000 permutation test). A linear regression analysis using the method of ordinary least-squares was also carried out between RW 1 and centroid size with the software PAST (Hammer et al., 2001) to visualize the relationship between shape and size (Figure 8). This indicates a significant relationship between shape and RW 1 (mainly specimen width)

($r^2 = 0.340$; $p < 0.001$; see supplementary Table S3). Small, specimens are generally wider at the anterior part, and commonly have straight sides. Larger specimens are relatively narrower at the anterior. In addition, more of the larger specimens exhibit lateral bending.

Linear regression of “straight”-sided specimens (n=722). Multivariable linear regression analysis between the overall shape (Generalized least squares aligned by TpsRelw v. 1.65) variance and the log10-transformed centroid size of these 722 specimens was conducted by the software TpsRegr v 1.45. The analysis suggests an even stronger relationship between shape and size than the analysis including bent specimens (Generalized Goodall F-test: $F = 333.808$, $p < 0.001$; Wilks' Lambda test: $\lambda = 0.391$, $p < 0.001$; see supplementary Table S2 for 1000 permutation test). We also conducted a simple linear regression analysis between RW 1 and centroid size by the software

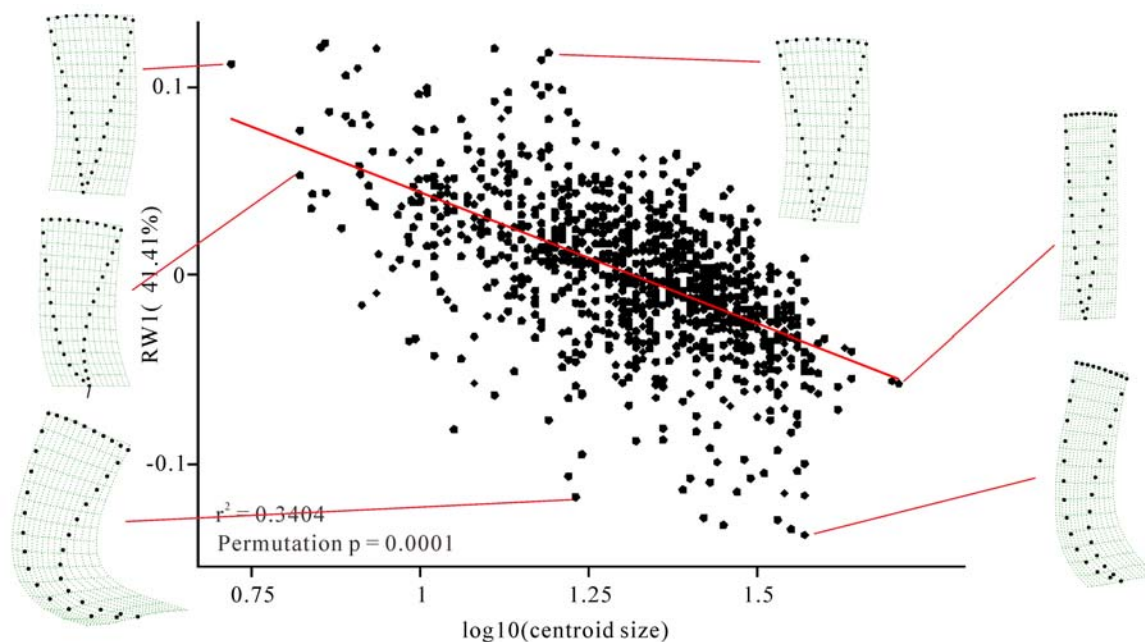


FIGURE 8. The ordinary least-squares linear regression of the shape of mirrored *Protoconites minor* with \log_{10} -transformed centroid size. Characteristic specimens are shown in thin-plate splines corresponding to the shapes of specimens in RW 1–2 plane.

PAST (Hammer et al., 2001). The analysis indicates a significant relationship between centroid size and RW 1 ($r^2 = 0.486$; $p < 0.001$; see supplementary Table S2; Figure 9). Small specimens have positive RW 1 scores, which normally indicate a wider aperture. While large shells have negative RW 1 scores, indicating a relatively narrow anterior.

Linear regression of bent specimens (n=326). Multivariable linear regression analysis between the overall shape variance and the \log_{10} -transformed centroid size of these 326 specimens was conducted using the software TpsRegr v1.45. The analysis suggests a poor relationship between shape and size (Generalized Goodall F-test: $F = 44.823$, $p < 0.001$; see supplementary Table S4 for 1000 permutation test). A simple linear regression analysis between RW 1 and centroid size by the software PAST (Hammer et al., 2001). The analysis indicates no obvious relationship between centroid size and RW 1 ($r^2 = 0.0071$; $p < 0.13$; see supplementary Table S4).

DISCUSSION

Size Spectra

The body size of an animal is a key trait impacting prey capturing, longevity, reproductive success, food acquisition, and consumption (Hone

and Benton, 2005; Bell, 2014), as well as metabolic rate (Gillooly et al., 2001). Centroid size is mathematically independent of shape and thus can be used as a proxy for true size. Numerous studies have reported positively-skewed distributions, which suggest that size spectra are a result of hydrodynamic transportation or sorting (Knouft and Page, 2003; Clauset and Erwin, 2008; O’Gorman and Hone, 2012; Chen et al., 2016). The specimens analyzed here have a wide centroid size distribution, ranging from 5.24 mm to 50.8 mm and have a right-tailed non-normal distribution. This indicates that the size distribution of *Protoconites minor* in the Yanjiahe Fm. is not due to transportation or sorting.

Morphospace of Overall Specimens and Implications for Taxonomy

Different species often cluster in separate regions in morphological space (e.g., Matthews and Stynder, 2011; Cruz et al., 2012). Similarly, the results of relative warp analyses can also be applied to discriminate different species, (e.g., Cruz et al., 2012; Karahan et al., 2014). RW1 of the original data (unmirrored images) with 1048 specimens (Figure 5) is related to the width of the specimen and the direction of bending, suggesting that the main shape variation of *Protoconites minor* is the relative width of the anterior aperture and the

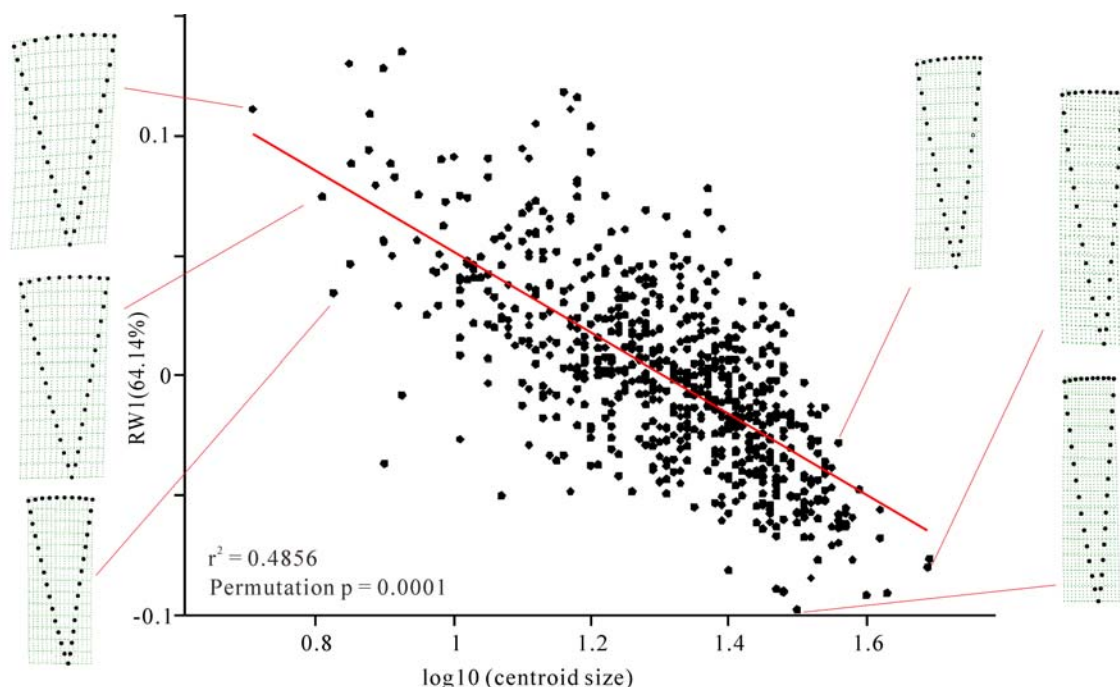


FIGURE 9. The ordinary least-squares linear regression of the shape of straight-shelled *Protoconites minor* with \log_{10} -transformed centroid size. Characteristic specimens are shown in thin-plate splines corresponding to the shapes of specimens in RW 1–2 plane.

whether they bend to the left or right. Specimens are distributed in the RW1-RW2 morphospace with the highest density around the plot's origin, indicating that most specimens are straight-sided (Figure 5). There are transitional forms between straight-sided and laterally bent specimens, with no obvious clustering observed in morphospace indicating that both straight and laterally bent specimens are probably the same species.

Relative warp analysis using mirrored images (1048 specimens), in which all fossils curve to the same side, also has the highest density around the plot's origin within the RW1-RW2 of the morphospace. There are transitional forms between strongly bent specimens and straight specimens, and no obvious clustering in morphospace. Very strongly bent specimens are rare. This indicates that most specimens are more or less straight sided, and our analyses demonstrate that both straight-sided and laterally bent specimens are the same morphospecies.

Morphospace of Straight-sided Specimens

The analysis of only straight-sided specimens gives RW1 (64.14%) scores that are strongly related to the width of the upper part of the shell (Figure 7), indicating that the morphological variation of specimen is mostly controlled by the relative

width of the anterior. Within morphological space, most specimens are clustered around the plots' origin, with decreasing density away from the origin. As discussed above, the distribution of straight-sided specimens within morphospace does not support the suggestion that there are multiple species within the assemblage.

Allometry and Its Implications for Taxonomy

Allometry is the study of the statistical links between shape and overall size of organisms (Mosimann, 1970; Klingenberg, 1998), and ontogenetic allometry examines the relationship between size and shape during the growth of an organism (e.g., Adams et al., 2013; Shi and MacLeod, 2016; Chen et al., 2016).

This is the first study to statistically explore allometry in the Cambrian *Protoconites minor*. The linear regressions indicate a strong relationship between size and shape for the total assemblage. Shape is strongly controlled by size, with small specimens having a relatively wide aperture, while large specimens have a relatively narrow aperture. Meanwhile, most strongly bent specimens are large, and almost no smaller specimens showed strong lateral bending. However, multivariable linear regression analysis between the overall shape of the 326 laterally bent specimens and the \log_{10} -

transformed centroid size suggests a poor relationship between shape and size (see supplementary Table S4). This suggests that the bending was not developed during their ontogenetic development, and that larger individuals are more prone to bending during either pre- or postmortem taphonomic phases (Figure 8). In the “straight”-sided specimens, the linear regression indicates a very strong relationship between shape and size (Figure 9). In these specimens the relative anterior width became narrower throughout ontogeny (Figure 10), indicating that the main way for these organisms to increase their size is aggradation on the margin of anterior aperture, as there is no aggradation or growth on other areas.

Our analyses indicate that the morphology of *Protoconites minor* was mainly controlled by ontogenetic allometry. It was believed that wide anterior and narrow anterior shelled fossils may represent different species, such as *Cambrorhytium* (*C. major*, *C. cf. C. major*, *C. fragilis*, *C. minor*, and *C. gracilis*; Conway Morris and Robison, 1988; Ponomarenko, 2005; Zhang and Hua, 2005; Chang et al., 2018a) and *Sphenothallus* (*S. taijiangensis*, *S. songlinensis*, and *S. kozaki*; Zhu et al., 2000; Peng et al., 2005; Chang et al., 2018a). However, both the relative warp analysis and the linear regression analysis suggest that shape variation on *Protoconites* specimens belong to the same species, and different relative widths at the aperture represent different ontogenetic stages.

CONCLUSIONS

This study demonstrates the power of geometric morphometric techniques for teasing out cryptic morphological aspects of problematic organisms. These studies can clarify aspects of growth, development and taxonomy not readily ascertained by traditional methods. This is the first geometric morphometric study of the early Cambrian taxon *Protoconites minor* from South China. *P. minor* from the Yanjiahe Fm. in the Three Gorges area are abundant, allowing for robust analyses of their overall shape. Morphometric analyses show that these specimens have undergone minimal transportation, mitigating any sorting or sampling bias. As *P. minor* were unmineralised, probably conical organisms, the direction and degree of bending seen in these fossils is likely to have been influenced by taphonomic factors. Relative Warp (RW) analyses indicate that the primary influence in shape variation is the relative width of the anterior aperture.

Our analyses show that the variation in the morphology of *Protoconites minor* is mainly controlled by ontogenetic allometry. Both the relative warp analyses and the linear regression analyses indicate that these specimens all belong to the same species: *P. minor*, and that different apertural widths represent different growth stages. The smaller specimens tend to have wider apertures relative to their length, while the larger specimens have narrow apertures relative to their length. Consequently, the variation on shape is not considered here to be a useful diagnostic character at either the generic or the specific rank.

SYSTEMATIC PALAEOLOGY

?Phylum Cnidaria Verrill, 1865

Class, Order and Family uncertain

Genus *Protoconites* Chen, Xiao, and Yuan, 1994

Type species. *Protoconites minor* Chen, Xiao, and Yuan, 1994; from Miaohu Biota, Three Gorges area, South China.

Protoconites minor Chen, Xiao, and Yuan, 1994
Figure 2.1–18; Figure 10.1–27

- 1994 *Protoconites minor* Chen, Xiao, and Yuan, p. 397, pl. IV, figures 10–11
- 1996 *Protoconites minor*; Ding et al., pl. 33, figure 9
- 2002 *Protoconites minor*; Chen et al., pl. 4, figure 6
- 2002 *Protoconites minor*; Xiao et al., p.368, figures 7.9–7.11, 7.14–7.15
- 2002 *Protoconites minor*; Yuan et al., p.65, figure 77
- 2004 *Protoconites cf. minor*; Zhao et al., figure 2(e)
- 2005 *Protoconites*; Wang et al., figure 4.2
- 2008 *Protoconites minor*; Guo et al., figure 5.(a)–(c)
- 2009 *Protoconites* sp.; Guo et al., figure 3.(a)–(e)
- 2011 *Protoconites minor*; Wang et al., figure 4.J–K
- 2017 *Protoconites* sp.; Guo et al., figures 1.1–1.2, 3.2
- 2018a *Cambrorhytium cf. C. major*; Chang et al., figure 3.M

Types. Holotype (HBM-496) and paratype (HBM-506) were designated by Chen et al. (1994) and repositied in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

Material. More than 1048 specimens from the Terreneuvian Yanjiahe Fm., in Three Gorges (mainly derived from the Dingjiaping, Gunziao, Yangjiachong, and Muyang sections). All specimens are repositied in Chang’an University.

Description. Smooth conical compressions about 5–50 mm long, with a pointed apex that expands to a squared-off termination (with the aperture). Tubes 0.2–0.4 mm in diameter at apex and up to 1–7 mm at aperture. Angle of divergence 13–25

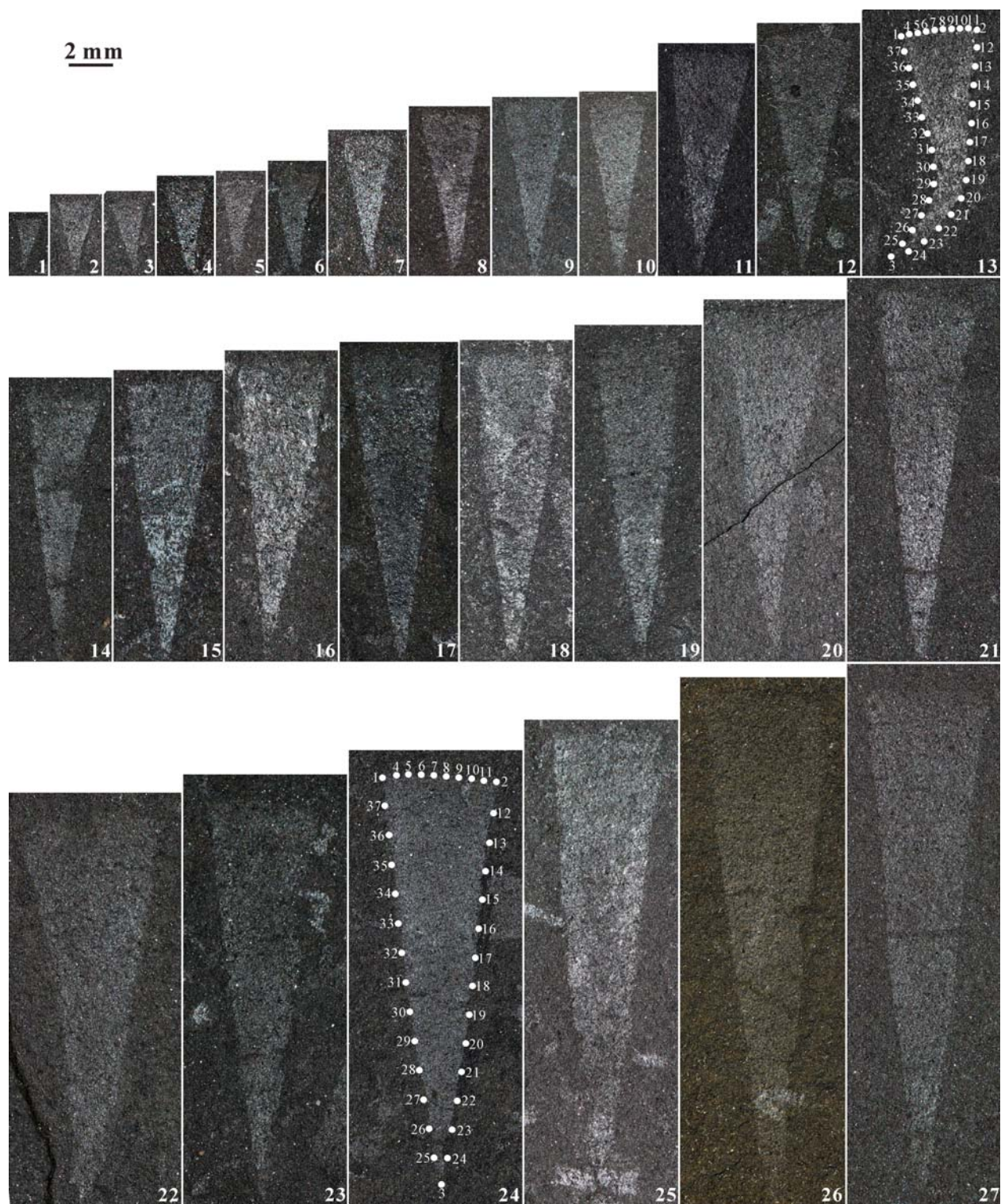


FIGURE 10. *Protoconites minor* from the Cambrian (Terreneuvian) Yanjiahe Formation showing morphological variance during the ontogeny. Size of these specimens increases from right to left and from top to bottom. **1.** No. Y-596 (2)-**2;** No. Y-735A (20)-**2;** **3.** No. Y-800A (19)-**2;** **4.** No. Y-469B (5); **5.** No. Y-581 (2); **6.** No. Y-134 (10); **7.** No. Y-523; **8.** No. Y-1236 (2); **9.** No. Y-29; **10.** No. Y-617A (4)-**3;** **11.** No. Y-558A (17); **12.** No. Y-141A (19)-**1;** **13.** No. Y-558A (33); **14.** No. Y-617A (2); **15.** No. Y-546A (2); **16.** No. Y-732A (20); **17.** No. Y-142A (8)-**1;** **18.** No. Y-816A (4); **19.** No. Y-1230A (45); **20.** No. Y-425A (2); **21.** No. Y-561A (5); **22.** No. Y-567 (2); **23.** No. Y-732A (32)-**1;** **24.** No. Y-173A (4); **25.** No. Y-1227A (10); **26.** No. Y-51A (2); **27.** No. Y-24B (2). “Y” means the locality of the fossils from Yangjiachong section.

degrees. Straight or bent at the posterior part. No preserved holdfast or tentacle-like structures; no annulations or transverse markings. During the early ontogenetic stage, they are relatively wide at the aperture. Growth is primarily by aggradation on the margin of anterior aperture. Smallest specimens show no lateral bending, however, with the increasing of size, specimens are often preserved with lateral bending.

Discussion. *Protoconites* bears some similarities with *Cambrorhytium*, a tubular form that is found in Stages 3–Wuliuan in Canada (Stephen Fm.), Utah (Marjum Fm.), South China (Shuijingtuo Fm. and Shipai Fm.) and Siberia (Sinsk Fm.) (Conway Morris and Robison, 1988; Ponomarenko, 2005; Zhang and Hua, 2005; Chang et al., 2018a). However, *Cambrorhytium* is much larger (30–50 mm long) than *Protoconites*. *Cambrorhytium major* is also characterized by faint tentacle-like structures and transverse annulations. In their original diagnosis, Chen et al. (1994) noted annulations on *Protoconites minor*, but careful re-examination by Xiao et al. (2002) revealed no such features. *Archotuba conoidalis* (Hou et al., 1999) from the lower Cambrian Chengjiang Biota also shares a broadly similar overall shape with *Protoconites*, but like *Cambrorhytium* is much larger and bears transverse annulations not seen in *Protoconites*. *Lantianella* and *Piyuania*, similar tubular genera from the Ediacaran Lantian Biota in South China (Yuan et al., 2011, 2016; Wan et al., 2016), also have tentacle-like structures, transverse annulations and internal structures which distinguish them from *P. minor*. *Protoconites* also bears similarities to *Sphenothallus* from Cambrian Stages 3–Wuliuan in South China (Shuijingtuo Fm., Niutitang Fm., Shipai Fm., and Kaili Fm.) (Zhu et al., 2000; Peng et al., 2005; Muscente and Xiao, 2015; Chang et al.,

2018a). However, *Protoconites* can be easily distinguished from *Sphenothallus* by lacking a pair of robust, longitudinal thickenings and transverse ribs. While *P. minor* lacks tentacle-like structures, transverse annulations and internal structures seen in *Cambrorhytium*, *Archotuba conoidalis*, *Lantianella*, and *Piyuania*, broad morphological similarities may implicate a close phylogenetic relationship between these taxa.

Occurrence. The holotype and Ediacaran specimens are derived from the upper Doushantuo Fm. black shales at Miaohu, Yinchang city, Hubei Province (Chen et al., 1994; Ding et al., 1996; Chen et al., 2002; Xiao et al., 2002; Yuan et al., 2002) and Taoying, Jiangkou county, Guizhou Province (Zhao et al., 2004; Wang et al., 2005, 2011). The material described herein is derived from the middle Yanjiahe Fm. silty shale (Bed 3, Terreneuvian, Fortunian), Yichang area, Hubei Province.

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APPENDICES

The following data files associated with this study are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.7wm37pvr8>.

Supplementary Table S1. Centroid size and RW scores of overall specimens (1048 specimens, un-mirrored). Supplied in zipped file at <https://palaeo-electronica.org/content/2020/3177-fossil-plants-from-tennessee>.

Supplementary Table S2. Centroid size and RW scores of straight shelled specimens (722 specimens, laterally bended specimens excluded). Supplied in zipped file at <https://palaeo-electronica.org/content/2020/3177-fossil-plants-from-tennessee>.

Supplementary Table S3. Centroid size and RW scores of overall specimens (1048 specimens, partly mirrored). Supplied in zipped file at <https://palaeo-electronica.org/content/2020/3177-fossil-plants-from-tennessee>.

Supplementary Table S4. Centroid size and RW scores of bent specimens (326 bent specimens, partly mirrored). Supplied in zipped file at <https://palaeo-electronica.org/content/2020/3177-fossil-plants-from-tennessee>.