

## A problematic animal fossil from the early Cambrian Hetang Formation, South China—A reply

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**Abstract.**—We recently reported *Cambrowania ovata* Tang and Xiao in Tang et al., 2019, from the early Cambrian Hetang Formation in South China and interpreted it as a problematic animal fossil, possibly related to either sponges or bivalved arthropods (Tang et al., 2019). Slater and Budd (2019) contested our taxonomic identification and phylogenetic interpretation; instead, they claimed that *Cambrowania ovata* is a large acritarch referable to morphotaxon *Leiosphaeridia* Eisenack, 1958, and thus is not an animal. Here we refute their criticisms, clarify the differences between *Cambrowania* and *Leiosphaeridia* and other acritarchs, and reiterate why an animal affinity for *Cambrowania* cannot be ruled out.

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The first difficulty with Slater and Budd's (2019) interpretation is that *Cambrowania* (~5 mm in diameter; Fig. 1.1) is at least an order of magnitude (three orders of magnitude in volume) larger than *Leiosphaeridia* (typically <200 µm in diameter; Fig. 1.2) (Jankauskas et al., 1989; Butterfield et al., 1994). Although rare leiospheres can reach as much as 1 mm in diameter (Slater and Budd, 2019), they are still significantly smaller than *Cambrowania*.

A second difficulty, related to the first, is that Slater and Budd (2019) speculated that *Cambrowania* represents unusually large *Leiosphaeridia* filled with cell aggregates. However, they presented no evidence for the existence of such cell aggregates in *Cambrowania*. In fact, our own observation using backscattered electron scanning electron microscopy revealed no trace of cell aggregates (Tang et al., 2019). Notably, this technique has previously been used to visualize cell aggregates in carbonaceous compression specimens such as *Chuarina* (Tang et al., 2017b).

A third difficulty with Slater and Budd's (2019) argument pertains to their suggestion that the biological structures we identified as crossbars and outgrowths in *Cambrowania* were instead taphonomic artifacts. In particular, Slater and Budd (2019) illustrated Cambrian *Leiosphaeridia* specimens with

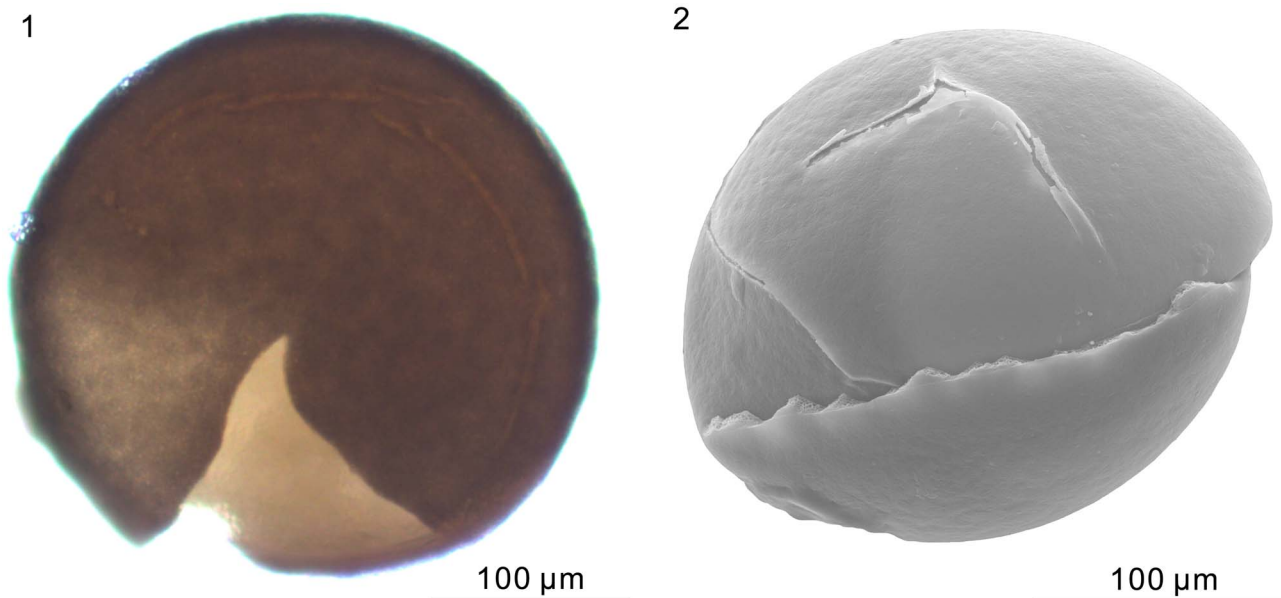
lanceolate folds to suggest that these might be the double crossbars and blades we found in *Cambrowania*. However, Slater and Budd's (2019) claimed similarity is superficial at best because compressed vesicles of *Leiosphaeridia* generally have concentric marginal folds in addition to lanceolate ones (Fig. 1.3). Indeed, concentric marginal folds have been documented extensively in the literature (Tang et al., 2013, 2015, 2017a; Slater and Willman, 2019). However, no *Cambrowania* specimens have concentric folds. An additional problem with Slater and Budd's (2019) suggestion that folds of *Leiosphaeridia* are the same as double crossbars of *Cambrowania* is that Slater and Budd (2019) compared transmitted light photographs of *Leiosphaeridia* with SEM images of *Cambrowania*, and such comparison can be misleading. This is because the former integrates light transparency through the entire thickness of the specimen, whereas the latter only illustrates surficial morphology. When a comparison is made using scanning electron microscopy, lanceolate surficial folds in *Leiosphaeridia* (Fig. 1.5) are clearly different from double crossbars in *Cambrowania* (Fig. 1.1). An additional difficulty with Slater and Budd's (2019) suggestion that the crossbars in *Cambrowania* are better interpreted as pyritized folds in carbonaceous vesicles of *Leiosphaeridia* is that the crossbars in *Cambrowania* are thin cylindrical structures (see figure 6 in Tang et al., 2019), whereas the folds of *Leiosphaeridia* are generally spindle-shaped and do not form cylinders. Yet another problem with Slater and Budd's (2019)

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**Figure 1.** Size and morphological differences between *Cambrowania* (1) and *Leiosphaeridia* (2–5). (1) Backscattered electron scanning electron microscopic photograph of *Cambrowania* from the early Cambrian Hetang Formation, preserved on bedding surface; HT-T8-9V-25, VPIGM-4729. (2–5) Acid-extracted specimens of *Leiosphaeridia* from the Tonian Gouhou Formation; (3) is a magnification of (2), showing concentric folds; 11-GH-10-SEM-3-19, VPIGM-4795; (4, 5) light microscopic and SEM photographs, respectively, of the same specimen, showing spindle-like lanceolate folds (arrowheads); 11-GH-10-SEM-5-17, VPIGM-4796; (1 and 2) are shown to the same scale (the 2 mm scale) to emphasize the size difference between typical *Cambrowania* and *Leiosphaeridia* specimens. The 100 µm scale applies to (3–5).



**Figure 2.** Resting eggs of extant brine shrimp showing a leiospheric vesicle wall and medial split structure. (1, 2) Transmitted light and scanning electron microscopy photographs, respectively; VPIGM-4797 and VPIGM-4798, respectively.

assertion about the equivalence of crossbars and folds is that the number and size of lanceolate folds on a *Leiosphaeridia* (or any other acritarch) vesicle are limited by the surface area of a sphere relative to that of a compressed disc. By contrast, the distribution of crossbars in *Cambrowania* is remarkably dense (compare Fig. 1.1 with Fig. 1.3, 1.4). A final problem related to Slater and Budd's (2019) claim that outgrowths in *Cambrowania* can be simply interpreted as pyritized folds, tears of the vesicle wall, or excystment structures is that none of these interpretations accounts for cylindrical crossbars that extend beyond well-preserved vesicle margins that show no evidence of tearing or excystment structures (e.g., figure 3.8 in Tang et al., 2019). At this time, of course, we cannot rule out that there could be some folds in some specimens of *Cambrowania*, but the totality of evidence suggests a lack of homology between the crossbars of *Cambrowania* and vesicle folds of *Leiosphaeridia*. Therefore, crossbars in *Cambrowania* appear to represent biological structures and not taphonomic artifacts.

Finally, and critically for the argument of Slater and Budd (2019), bona fide *Leiosphaeridia* fossils have previously been reported from the Hetang Formation (Zhang et al., 2013), but they are fundamentally distinct from *Cambrowania* in their size, morphology, and preservation. In particular, they are invariably <100 µm in diameter, within the standard size range of acritarchs, and much smaller than *Cambrowania*. Further, these fossils show both lanceolate and marginal concentric folds, and poorly preserved but coherent vesicle walls, as they should, but they do not have any structures resembling cylindrical rods seen in *Cambrowania*. Furthermore, one of the distinctive structures of *Cambrowania* is the prominent (either raised or depressed) terminal aperture present in some specimens (e.g., figure 3.1–3.5 in Tang et al., 2019), but this structure is not found in any of Zhang et al.'s (2013) specimens of *Leiosphaeridia* from the Hetang Formation.

Whether one would like to expand the diagnosis of *Leiosphaeridia* and force *Cambrowania ovata* into the genus *Leiosphaeridia* is a subjective matter, because *Leiosphaeridia* is a morphogenus after all. But we would like to point out that no existing *Leiosphaeridia* species can accommodate *Cambrowania ovata* because of the morphological differences discussed above, and that *Cambrowania ovata* is drastically different from *Leiosphaeridia baltica* Eisenack, 1958, which is the type species of *Leiosphaeridia* and only 84 µm in diameter.

Slater and Budd's (2019) phylogenetic comment re-emphasizes the challenges in determining the affinities of long-extinct taxa such as *Cambrowania*. As we acknowledged in the original publication (Tang et al., 2019), what we presented were two hypotheses that need additional testing. On the other hand, even if *Cambrowania ovata* would be taxonomically forced into *Leiosphaeridia*, this does not necessarily mean that “a metazoan affinity can be ruled out” (Slater and Budd, 2019). This is because *Leiosphaeridia* and leiospheric acritarchs in general are polyphyletic assemblages. Acritarchs, including both leiospheres and acanthomorphs, can be remarkably similar to the resting eggs of animals in their size, shape, ornament, medial split structure, and concentric marginal and lanceolate folds (van Waveren, 1992; van Waveren and Marcus, 1993). Consider, for example, the extant brine shrimp *Artemia*, which produces “leiospheric” resting eggs with smooth-walled vesicles and medial split structures (Fig. 2). One of the best ways to differentiate smooth-walled resting cysts of animals, algae, and protists is via comparison of ultrastructure (Cohen et al., 2009).

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