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Response to Comment on “Small Bilaterian Fossils from 40 to 55 Million Years Before the Cambrian”

The comment of Bengtson and Budd (1) is predicated on a preconception that any structures in sectioned Doushantuo microfossils that are claimed to represent cellular features in the original animal must instead be diagenetic artifacts. This preconception is demonstrably false. There are many examples of cellular structures in sections through other Doushantuo microfossils (Fig. 1, A to D, and F) preserved in phosphorite, as are the *Vernanimalcula* sections (2). Indeed, a scanning electron microscopy (SEM) image (Fig. 1E) displays a very similar cleavage form, as does the section in Fig. 1D. Both large and small blastomeres are demonstrated in both images. In the sections, the locations of at least two essentially definitive cellular features of the original embryonic cells, viz, their boundaries [(that is, cell walls) (Fig. 1, A to D and F)] and their nuclei (Fig. 1A) can easily be seen. Thus, it is counterfactual to deny preservation of structural morphology at the cellular level in this kind of material.

Turning now to *Vernanimalcula*, Bengtson and Budd claim that the putative cellular structures [table 1 in (2)] are merely cracks in the fossil because they extend across to adjacent layers. This argument is false. The features in question here are the regularly spaced crosswise seams visible in many of the morphological layers of the holotype fossil, because these are in the positions expected of cell boundaries. Perhaps the image used by Bengtson and Budd was of insufficient resolution to reveal the details adequately; here, we offer another view (Fig. 1G), taken with polarized light under crossed nicols. There are indeed some true cracks that traverse the holotype fossil at the plane of focus shown. However, a careful count of all the crosswise partitions or seams tracing from the mesodermal to adjacent ectodermal or endodermal layers shows that only 17 out of 83 could possibly be accounted for as cracks using the criterion of Bengtson and Budd, that the seam is not confined to a single morphological layer. The large majority of the crosswise seams are indeed best taken as the remains of cell boundaries, although this is not a point we made in (2). Furthermore, Fig. 1G shows another prominent and revealing feature that directly affects this argument: Virtually every one of

the cuboidal areas delimited by the periodic seams has a greenish spot of birefringence within it, usually toward the middle. The proposition that the seams are diagenetic cracks provides no explanation whatsoever for the striking periodicity of these spots. However, the proposition that the seams delimit the remains of cells provides an excellent explanation for their periodicity: The greenish spots could represent a systematic compositional feature caused during phosphatization by the remains of coagulated constituents of each cell, cell by cell, or they could be the result of mineral accumulation on what were the cell nuclei. Note that in what is easily recognizable as a whitish

diagenetic deposit at the posterior end of the fossil there are also some greenish spots of birefringence, but they are much coarser, no two are the same, and they display no order or periodicity.

Images of the holotype specimen at a deeper plane of focus (Fig. 2) add two new items of information. First, and most important for the arguments raised by Bengtson and Budd, the “supposed cracks” do not even exist at this level, whereas the putative remains of the cell boundaries are now visible in even more regions of the specimen, and indeed can now be seen to be a feature of every morphological element of the specimen. The “cracks” that so impressed Bengtson and Budd are evidently just surface fractures on the section, of no consequence in any respect. Second, and most important from a scientific point of view, is that a new bilateral feature is revealed at this plane of focus, not visible at the plane shown in Fig. 1G. This is a structure bridging the walls of the coelom on both sides. As we pointed out in (2), the fossil section is close to what was

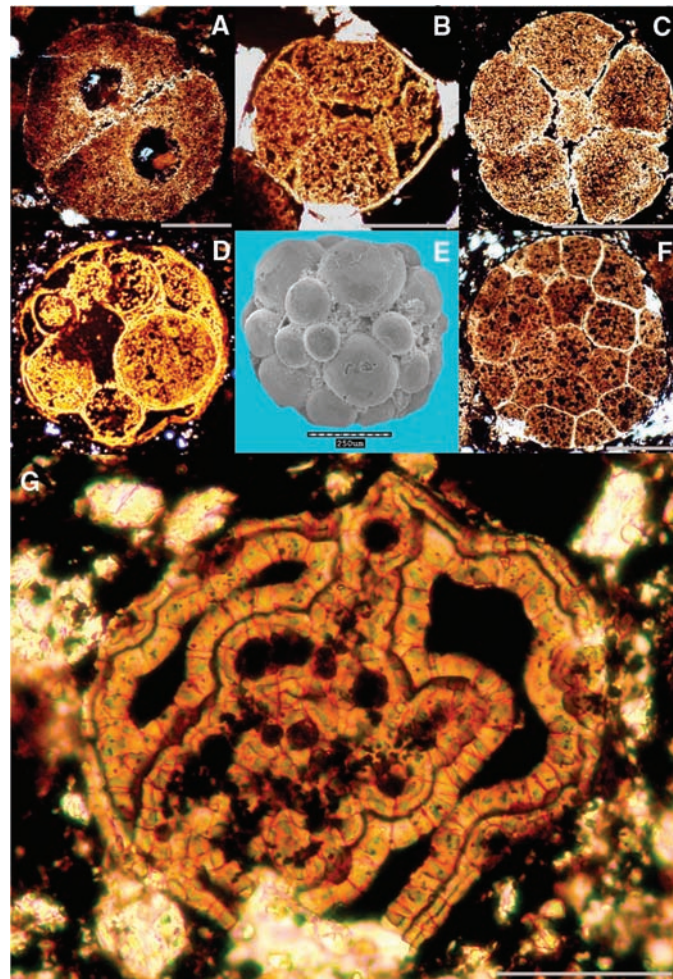
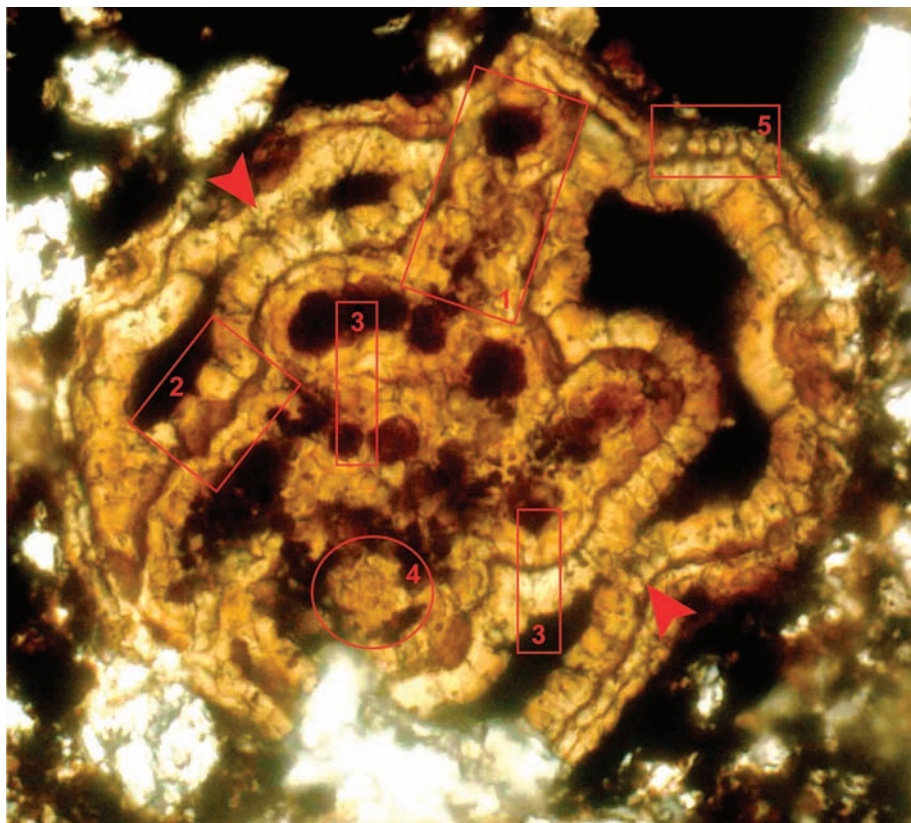


Fig. 1. Images of Doushantuo microfossils showing evidence for cellular preservation. Scale bars represent 200 μm unless otherwise indicated; (D) is similar in scale to (E); for (G), the scale bar represents 40 μm . (A) Thin section micrograph of early cleavage embryo showing preservation of nuclear domain. (B) Thin section micrograph of early cleavage embryo. (C) Thin section micrograph of mid-cleavage embryo. (D) Thin section micrograph of mid-cleavage embryo displaying cells of different size. (E) SEM image of embryo similar to (D). (F) Thin section micrograph of late cleavage embryo. (G) Holotype of *Vernanimalcula* under polarized light with crossed nicols.

Fig. 2. A deep focal plane image of the holotype specimen of *Vernanimalcula*. Box 1 highlights the pharynx lumen that in this image is clearly continuous between the stomach at the posterior end of the passage and the mouth at the anterior. Box 2 shows a particular view of the juxtaposition of the inner colelomic mesodermal layer and the endoderm. The cuboidal cell-like units of the two layers have clearly different thickness and periodicity. This is typical of biological tissues that perform different functions. The boxes marked 3 are two areas that contain major visible "cracks" in Fig. 1G, but as can be seen here, these "cracks" do not extend to this deeper focal plane. The oval 4 surrounds a clump of globular structures, each of which bears a darker round shadow in the center. The bounded globular structures could be cells, and the darker shadows nuclei. Box 5 highlights a new feature not visible in Fig. 1G: The external layer is also made of repetitive, cell-like units. Note that the dark boundaries between these cell-like units do not invade the inside thick layer surrounding the coelom. The two red arrowheads show a new bilaterally arranged feature not seen before, a structure that crosses the coelom on each side of *Vernanimalcula*. Orientation and dimension are as in Fig. 1.



the ventral surface of the animal; hence, these structures may represent inward bilateral ridges in the floor of the coelomic cavities.

Bengtson and Budd claim that the bilaterally situated pits we noted on the external surface of the fossil are spheroid fans, a common diagenetic form that they illustrate. To make this assertion, however, they assign that identity to indentations on a specimen that we never claimed were surface pits. Perhaps these indentations are spheroid fans; it is irrelevant to the pits in question. Once again, the notion that these features are diagenetic fails to explain the presence within them of distinctively small, regular bounded elements [figure 2A in (2)], some of which include the greenish spots discussed above (Fig. 1G).

The main point is that the multiple specimens of *Vernanimalcula* show consistent, bilateral morphology. Bengtson and Budd (1) imply that we examined 50,000 miscellaneous specimens and picked out these 10 because they had an apparent morphology we were seeking. In fact, as we explained (2), the 50,000 microfossils we alluded to were all defined by the presence of recognizable forms, mostly of eggs and embryos. Only the specimens of *Vernanimalcula* have its consistent and particular morphological features. The argument of Bengtson and Budd (1) regarding diagenesis is nullified by its own implicit assumption that diagenetic processes would accidentally

produce 10 bilaterally symmetrical fossils of similar size and form.

Bengtson and Budd provide images of encrustation within a fossil brachiopod as examples of diagenetic artifacts that are supposed to resemble *Vernanimalcula*. This example is irrelevant, however; it is clearly an error to use deposits on a template of unquestioned biological origin as a model for forms that are supposed to display no biological features. It is impossible to see what they think is similar to *Vernanimalcula* in the morphology of the encrusted brachiopod. Furthermore, it is not obvious that their example even represents what they think it does: The branching structure in the brachiopod could well be the fossilized remains of a fungal organism.

Taphonomy and diagenesis must of course be considered in the analysis of any novel fossil form, but the considerations of Bengtson and Budd provide no answers. They cannot explain the reproducible features, the symmetric morphology, or the internal structural periodicity of the *Vernanimalcula* fossils. Just as it would be a mistake to ignore taphonomy and diagenesis altogether, refusing to look beyond them precludes further exploration and insights into early animal evolution. We confidently predict that many additional specimens of *Vernanimalcula* will be found before long and that they will provide an enhanced view of its anatomy and three-dimensional structure. Discovery of this and other new forms

will depend on study of further tens of thousands of specimens.

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