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What biology can we learn from nucleus-like intracellular inclusions in Proterozoic cells?

XIAO Shuhai^{1,*}, PANG Ke², James D. Schiffbauer³ and YUAN Xunlai²

¹ Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA.

² State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

³ Department of Geological Sciences, University of Missouri, Columbia, MO 65211, USA.

The rise of eukaryotes is an important milestone in evolution (Maynard Smith and Szathmáry, 1997) and paves the road for the evolution of sex, multicellularity, and eventually animals. The recognition of early eukaryote fossils, however, has been highly complicated. Certain molecular fossils (e.g., steranes) and cell wall ultrastructures have been proposed as diagnostic features specific to eukaryotes, but they are complicated by issues related to contamination and convergent evolution (Brocks et al., 1999; Javaux et al., 2004; Knoll et al., 2006; Sherman et al., 2007; Rasmussen et al., 2008; Moczyłowska and Willman, 2009).

The smoking gun for eukaryotic life would undoubtedly lie in fossilized nuclei, if their biological origin could be ascertained. Indeed, nucleus-like intracellular inclusions (ICIs) are known to be present in silicified coccoidal cells from early Neoproterozoic Bitter Springs Formation (Schopf, 1968; Schopf and Blacic, 1971), in phosphatized and silicified cells from the Ediacaran Doushantuo Formation (Hagadorn et al., 2006; Hultgren et al., 2011), and numerous organic-walled acritarchs from Proterozoic shales (Schiffbauer and Xiao, 2009). However, these structures have not been thoroughly characterized, and their origins have been a matter of debate (Knoll and Barghoorn, 1975; Schopf and Oehler, 1976; Golubic and Barghoorn, 1977; Hultgren et al., 2011; Schiffbauer et al., 2012; Xiao et al., 2012). In this study, we integrate microCT, microstructural, and microchemical analyses of ICIs preserved three-dimensionally in Doushantuo cherts and phosphorites, as well as compressed ICIs from the Paleoproterozoic Ruyang Group, to understand the morphological diversity, taphonomic history, and biological significance of these ICIs. Our data show that ICIs can have diverse origins: some of them may be biologically contracted protoplasts (to prepare for

encystment), others are likely taphonomically collapsed protoplasts (due to degradation), still others may be related to late diagenetic mineralization, but none can be unambiguously identified as fossilized nuclei. Thus, from these examples, the biology we can learn from ICIs is limited to degradation and encystment, still useful information about the physiology of early eukaryotes.

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* Corresponding author. E-mail:

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