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Crypto-helical body plan in partially disarticulated gogiids from the Cambrian of South China

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Abstract

All living echinoderms have a pentaradial symmetry that is unique within the Bilateria. However, the Cambrian origin of echinoderm radial/pentaradiate symmetry is a long-standing problem. During the Cambrian (542–488 Ma), gogiids were the most common stalked echinoderm characterized by an “irregularly” plated body. Based on recently discovered material from the Balang Formation (Cambrian Series 2), eastern Guizhou, China, three unusual, partially disarticulated specimens of *Guizhoueocrinus* have clear evidence for a helical body plan. This helical plating is only evident in partially disarticulated specimens, thus a crypto-helical body construction is present. Crypto-helical construction in a gogiid raises the possibility of a phylogenetic connection among helicoplacoids, gogiids, and *Helicocystis*. The crypto-helical body construction may be an important evolutionary innovation among pre-radiate echinoderms.

Keywords: Cambrian explosion; Macroevolution; Echinodermata; *Guizhoueocrinus yui*; Taphonomy

1. Introduction

During ontogeny, echinoderms undergo dramatic physiological changes that involve a transformation of the body plan from bilateral symmetry in larvae to radial/pentaradiate symmetry in adults. However, the origin of radial/pentaradiate symmetry in adult echinoderms is a subject that has been intensely debated (e.g., Smith, 2008; Zamora et al., 2012). Thus, re-examination of key extinct taxa may provide additional evidence to address this issue. Echinoderms first appeared in the fossil record during the Cambrian, but the origination of modern taxa began during the Ordovician Radiation (Guensburg and Sprinkle, 2000). Among the Cambrian taxa, gogiids (generally considered eocrinoids) are widespread (Zamora et al., 2009), and the group is collectively long ranging (Sprinkle, 1973, 1992). Gogiids, in general, have three morphological attributes common among echinoderms: brachioles for feeding, a main body chamber for internal organs, and a holdfast for attachment to the substratum (Fig. 1). Despite their abundance, the origin of gogiids remains unclear (Sumrall and Brochu, 2008, pp. 166–167). Based on the fossil record, two main groups of erect echinoderms, Helicoplacoidea Durham and Caster, 1963, and Imbricata Sprinkle, 1973, occurred before the earliest gogiids. Several workers (e.g., Sprinkle, 1973; Mooi, 2001; Zamora and Smith, 2012) suggested that the Imbricata, including *Lepidocystis*, is the immediate sister group to the remainder of stalked echinoderms, but others disagree (Sumrall and Wray, 2007). In addition, the phylogenetic relationship between Helicoplacoidea and other echinoderms is unresolved (see Sprinkle and Wilbur, 2005). Incorporation of developmental/genetic data (Bottjer et al., 2006; Mooi and David, 2008; Smith, 2008) may provide a new perspective to assess the early echinoderm evolution. Zamora and Smith (2012) provided the latest study on the early evolution of stalked echinoderms, but it

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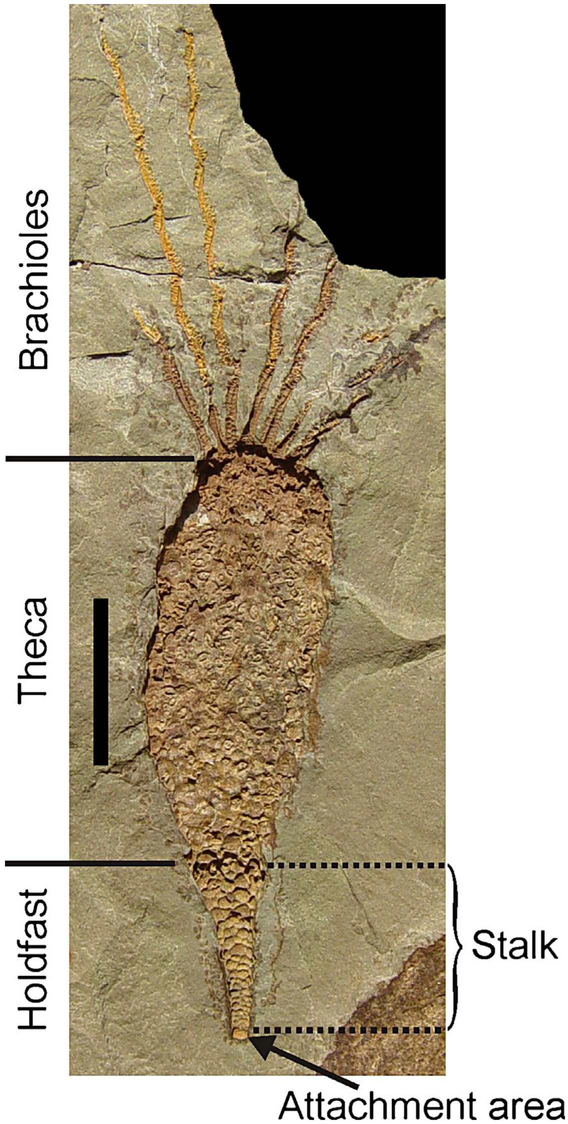

Fig. 1. *Guizhoueocrinus yui* (ZJ-15-5-10) from the Balang Formation (Cambrian Series 2: Duyunian Stage) near Kaili City, Guizhou, China, illustrating key morphologic features (see also Lin et al., 2008 for terminology). Scale bar: 10 mm.

challenges the monophyly of the Order Gogiida (see Parsley and Zhao, 2006, 2012; Zhao et al., 2008). In particular, it places *Lyracystis* farther away from gogiids, such as *Gogia* and *Sinoeocrinus*, than previously thought (Sprinkle and Collins, 2006; Sprinkle et al., 2011).

The discovery of key, new fossil specimens, such as the gogiids described here, can significantly impact our understanding. During the course of studying the taphonomy of the Cambrian echinoderms from eastern Guizhou, China (Lin et al., 2008), a few specimens (Fig. 2; Lin et al., 2008, figs. 6j, 7a, b) of *Guizhoueocrinus yui* Zhao, Parsley and Peng, 2007, were found with evidence of previously unknown features. Six additional specimens have been discovered since. Together, these unusual fossils allow us to propose a new hypothesis for the construction of gogiids that may have implications for phylogenetic relationships between them and other coeval echinoderms.

2. Geological setting

The new *Guizhoueocrinus yui* material was recovered from a shale interval of the Balang Formation (Cambrian Series 2: Duyunian Stage) near Kaili City, Guizhou, China. The precise thickness of the unit is yet to be determined, but temporal correlation of the fauna is well constrained based on the concurrence of an important index trilobite *Redlichina* (*Pteroredlichia*) *murakamii* (Peng et al., 2005). The Balang echinoderm fauna is known from several localities with at least one thousand gogiid specimens deposited in local museums (Zhao et al., 2007; Parsley, 2009). The studied area is rich in tectonic history (Bureau of Geology and Mineral Resources of Guizhou Province, 1987), and a few arthropod specimens are noted with distinctive, post-burial features in the Kaili Biota, which occurs in a younger deposit nearby (i.e., Lin, 2006, figs. 3c, d, 4). However, in a given locality, the Balang echinoderm preservation ranges from fully articulated to isolated plates (Lin et al., 2008), and no tectonic distortion is known on robust thecal plates. Thus, tectonic modification is minimal on the hand-sample size scale.

3. Materials

Gogiids are relatively common at several known productive localities in the Balang Formation and the younger Kaili Formation (Lin et al., 2008). Two other important species, *Sinoeocrinus lui* (e.g., Parsley and Zhao, 2006) and *Globoeocrinus globulus* (e.g., Zhao et al., 2008), are reported from the younger Kaili fauna. No specimens from the Kaili fauna are known that exhibit the partial state of disarticulation discussed herein. After five years of searching and examining more than 300 specimens from Balang, nine specimens (i.e., Lin et al., 2008, figs. 6j, 7a, b; and this study) of *G. yui* are known with an unusual mode of preservation. Among the nine unusual specimens, three are known from both part and counterpart (Fig. 2). Based on the greenish-gray appearance of the matrix, the best-preserved specimen (Fig. 2E, F) is relatively fresh and not deeply weathered. According to Lin et al. (2008), the yellow stains associated with echinoderm plates consist of iron oxides, and the brown-colored plates along the edge of the rock may contain manganese oxides due to processes related to groundwater.

The best specimen is well-preserved, and fine features, such as brachiolar plates (Fig. 2G, H), immature stalk plates (miniature plates below the theca-holdfast boundary; Fig. 2K, L), and thecal plates (Fig. 2G–L), are identifiable in submillimeter-scale on latex molds. In a discussion of gogiid morphology, Parsley (2012) identified the theca/stalk boundary on the basis of the presence/absence of suture pores in adults. However, in partially disarticulated specimens, it is impractical to recognize this transition due to shifting of plates. Alternatively, the theca/holdfast boundary is marked by the presence/absence of stellate plates (presumably the sutures are formed in between these plates) in this study. Morphologies and contrast enhancement methods applied to the whole images are defined and described in Lin et al. (2008). The illustrated specimens are deposited in the Paleontological Museum at the Guizhou University, Guiyang, China (with KW- and ZJ-specimen number prefixes). New specimens