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The oldest iocrinid crinoids from the Early/Middle Ordovician of China: Possible paleogeographic implications

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ABSTRACT

This study reports new crinoid material, which is identified as *Muicrinus dawanensis* new genus and new species from South China, representing the oldest known iocrinid in the world. These new fossils, which are characterized by bearing simple primibrachials and a helically coiled column, are from the lower-middle part of the Dawan Formation, which ranges from the upper Floian (Lower Ordovician) to the lower Dapingian (Middle Ordovician) (~470 Ma). A total of 11 related taxa with 80 characters were selected to conduct phylogenetic analyses. Our results indicated that South China specimens are closely related to ones that are endemic to Laurentia. Synapomorphies shared between species in those two cratons include elongate supraradial plates and isotomous arm branching. Furthermore, the phylogenetic closeness of endemic taxa that only occurred in two cratons leads us to suggest a geographic connection between those regions during deep time. Combining biogeographic evidence reported from Cambrian studies, this study supports the "missing-link" configuration of Rodinia during the breakup phase. Based on the crinoid global biodiversity pattern updated here, the potential for discovery of new Paleozoic crinoid faunas in China is very high.

1. Introduction

Stalked echinoderms are higher invertebrate animals that specialize in subdividing food resources above the sediment-water interface; thus, they played a key role for building a local benthic marine epifaunally tiered community during the Great Ordovician Biodiversity Event (GOBE) (Ausich and Bottjer, 1982). During the GOBE complexities of ocean circulation resulting from fragmentation of large continents triggered large-scale faunal migrations (Rozhnov, 2010). During this time, the morphologic disparity and biodiversity of the Echinodermata reached its highest peak (Guensburg and Sprinkle, 2001) due to rapid origination of new taxa adapting into empty ecologic niches created by changing environments (Deline and Ausich, 2011; Ausich and Deline, 2012). For example, the Bromide Formation of Oklahoma, USA contains the single most diverse echinoderm fauna in the world with more than 11,000 specimens collected, belonging to 13 classes and 61 genera (Sprinkle, 1982).

The oldest crinoids known are from the early Tremadocian (Guensburg and Sprinkle, 2003, 2009; Guensburg, 2010). During the Great Ordovician Biodiversification Event, crinoids underwent an adaptive radiation (Sprinkle and Guensburg, 2003, 2004; Peters and Ausich, 2008; Ausich and Deline, 2012) to form the Early Paleozoic Crinoid Evolutionary Fauna (CEF) (Baumiller, 1994; Ausich et al., 1994). The oldest crinoids are from Laurentia. By the late Tremadocian crinoids are also known from Gondwana (Ubaghs, 1969; Ausich et al., 2007), and the oldest crinoids on other paleocontinents are as follows: Avalonia, Floian; Baltica, Darriwilian; Siberia, Sandbian; South China Block, Dapingian. Fig. 1 depicts the Phanerozoic biodiversity of crinoids and illustrates the three CEFs.

Crinoids suffered a mass extinction at the onset of the glacial epoch responsible for Late Ordovician (Hirnantian) extinctions (Peters and Ausich, 2008), and recovery to pre-existing biodiversity level was reached by the close of the Llandovery (Peters and Ausich, 2008; Ausich and Deline, 2012). The Llandovery radiation initiated the Middle Paleozoic CEF that culminated in the "Age of Crinoids" during the lower Mississippian (Kammer and Ausich, 2006; Sallan et al., 2011). The primary extinction episode among crinoids during this interval was an end-Givetian extinction rather than the more widely recognized Frasnian-Famennian extinction (Baumiller, 1994). After crinoids from important Middle Paleozoic CEF clades became extinct at or near the close of the early Viséan, the Late Paleozoic CEF radiated with biodiversity peaks during the Serpukhovian and Artinskian (the lows between these

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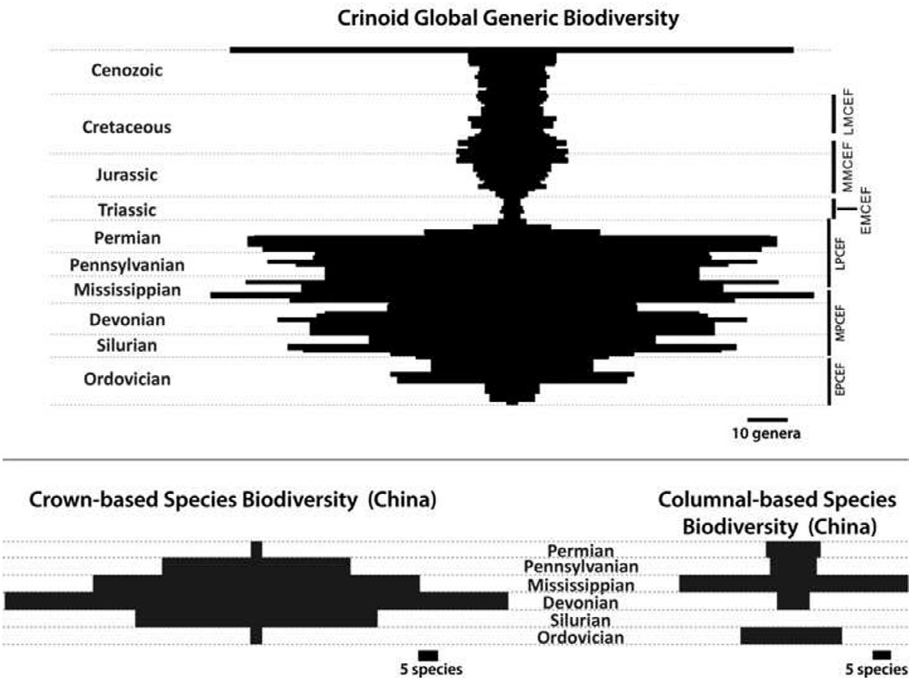

Fig. 1. Crinoid biodiversity. A, Crinoid generic biodiversity (modified from Baumiller and Messing, 2007; Sallan et al., 2011; Ausich and Kammer, 2013; Gorzelak et al., 2016). B, Crown-based species biodiversity (China). C, Columnal-based species biodiversity (China). EPCEF, Early Paleozoic Crinoid Evolutionary Fauna; MPCEF, Middle Paleozoic Crinoid Evolutionary Fauna; LPCEF, Late Paleozoic Crinoid Evolutionary Fauna; EMCEF, Early Mesozoic Crinoid Evolutionary Fauna; MMCEF, Middle Mesozoic Crinoid Evolutionary Fauna; LMCEF, Late Mesozoic Crinoid Evolutionary Fauna.

peaks probably reflect, at least in part, sampling and monographic biases). After the early Permian, crinoid biodiversity declined steadily until the end-Permian mass extinction, which nearly resulted in complete extinction of the Crinoidea. It should also be noted that this pattern is based largely by data collected from the United States and Europe, thus largely from Avalonia, Baltica, northern Gondwana, and Laurentia.

Prior to 1993, the only Ordovician crinoids known from China were columnals, including fifteen named species and taxa left in open nomenclature (Table 1). However, whether all these taxa belong to the Crinoidea or to other Pelmatozoa is uncertain. In 1993, *Eopetalocrinus sinensis* Li, 1993 was described from the Dawan Formation (Hubei Province). *Eopetalocrinus* is the oldest member of the Petalocrinidae, which include very unusual crinoids with the arms comprised principally of one large triangular to cylindrical brachial plate (Mao et al., 2015, 2017). The Petalocrinidae underwent a later local radiation in China during the Llandovery, resulting in three additional Chinese petalocrinid genera; one of which, *Petalocrinus*, became cosmopolitan beginning during in the Llandovery. *Petalocrinus* persisted into the Llandovery(?) on Avalonia, Wenlock on Baltica, and into the Ludlow on Laurentia.

Table 1
Pelmatozoan columnal taxa described from China.

Taxa
Cyclocyclicus sp. in Mu and Wu (1975)
Ellipsoellipticus himalayensis (Mu and Wu, 1975)
Hexagonocyclicus banzhuangensis (Mu and Wu, 1974)
Hexagonocyclicus douyunensis (Mu and Wu, 1974)
Pentagonocyclicus spp. (Mu and Wu, 1975)
Pentagonocyclicus cylindricus (Mu and Lin, 1983)
Pentagonocyclicus jiawangensis (Mu and Lin, 1983)
Pentagonocyclicus ornatus (Mu and Lin, 1983)
Pentagonocyclicus uniformis (Mu and Lin, 1983) (non Stukalina, 1973)
Pentagonopentagonalis ex. gr. *fragilis* (Yeltyschewa, 1955)
Pentagonopentagonalis nyalamensis (Mu and Wu, 1975)
Pentagonopentagonalis ex. gr. *tridens* (Yeltyschewa, 1955)
Pentagonopentagonalis sp. nov. in Mu and Wu (1975)
Pentagonopentagonalis spp.

Our material represents the second crinoid known from the Dawan Formation; and similar to *Eopetalocrinus* (i.e., Mao et al., 2015, 2017), the new species reported here is the oldest known member of its family. The Iocrinidae became cosmopolitan perhaps as early as the late Dapingian and remained cosmopolitan through the Katian, with its last occurrence in the Llandovery of Laurentia. In addition, by reporting the second Dawan Formation crinoid with very well-preserved specimens along with many incomplete specimens of unknown taxa, it suggests that the unit has the potential for discovery of a more diverse fauna. This potential is evaluated qualitatively by comparing the global crinoid generic biodiversity (based on crowns) to the crown-based and columnal-based biodiversities of crinoids reported from China (Fig. 1). In contrast, the species biodiversity of crinoid crowns from present-day China, which is an amalgamation of paleocontinents (Waters et al., 2008; Zhang et al., 2014), is unimodal with a biodiversity peak during the Devonian (Fig. 1B). With a third fewer taxa, the Mississippian is the period in China with the second highest biodiversity. Neither the Ordovician nor the post-early Viséan radiations are recorded in the Chinese fossil record of crown-based taxa. On the other hand, many columnal-based taxa have been described from China (Webster and Webster, 2014) (Fig. 1C). Peak columnal taxonomic count was during the Mississippian, which is parallel to global biodiversity, but otherwise the column-based pattern parallels neither global biodiversity nor the described Chinese biodiversity based on crowns.

Currently, our knowledge of fossil crinoids from China is clearly a function of monographic biases. Of particular note are the following crown-based studies for Silurian faunas (Mu and Lin, 1987; Wang, 1995; Mao et al., 2015, 2017), for Devonian faunas (Chen, 1990; Chen and Yao, 1993; Hou et al., 1994; Lane et al., 1997; Waters et al., 2003; Webster, 2003; Waters and Webster, 2009), for Mississippian faunas (Chen, 1984; Chen and Yao, 1993; Webster, 2003; Webster et al., 2009a), and for Pennsylvanian faunas (Lane et al., 1996; Webster et al., 2009b, 2009c). Important studies of columnal taxa include (Dubatolova and Shao, 1959; Xu et al., 1962; Mu and Wu, 1974, 1975; Mu and Lin, 1983). The primary question is whether the monographic biases are artificial or whether they reflect more the likelihood of fossil crinoid collecting inherent in the Chinese rock record. We predict that the former is true and that a rich Paleozoic crinoid record is yet to be discovered in China.