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# Geographic bias in the fossil record: tests using Chinese early Paleozoic echinoderms

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## Abstract

The greater diversity of fossils known from North America and Europe, plus the correlation between outcrop area and paleobiodiversity, introduce a potential bias in the fossil record. We develop tests to detect actual bias using recent discoveries of Chinese early Paleozoic fossil echinoderms and the idea that geographic bias can exist only if poorly known parts of the globe contain novel fossils yet unknown to science. Fossil echinoderms had complex skeletons requiring rapid burial, so proportionately more novel forms may be undiscovered. Echinoderm diversity was high in the early Paleozoic, and this time interval includes several Chinese fossil Lagerstätten that enhance the chances of discovering novelties. Chinese fossil echinoderms are categorized as "genuine novelties" or "more of the same." We use taxonomic, phylogenetic, and morphological approaches because some novel echinoderms are undescribed and cannot be used in a taxonomic assessment alone. Results suggest that the known Chinese early Paleozoic echinoderm fauna is predominantly more of the same. Nevertheless, historic discovery curves show that knowledge of Chinese fossil echinoderms is increasing rapidly, so they are still poorly known. If significantly novel echinoderms are rare, as recent discoveries elsewhere suggest, then Chinese fossil echinoderms need further exploration to discover the rarities. Our preliminary results need confirmation. A potential explanation of our results is that modern continents include sedimentary rocks deposited in different provinces during the early Paleozoic, so each may well provide an adequate sample on which to build global diversity curves.

## Non-technical Summary

Historically more fossils have been described from the scientifically better explored parts of the globe, North America and Western Europe, than from other continents. If fossils from other continents were as well known, our current perception of the history of life might change, but only if fossils still to be discovered differ significantly from those already known. If the new fossils were the same as the old fossils, there could be no bias. We test this idea using new fossils recently described from China that were previously unknown to Western scientists. We use fossil echinoderms because they require special conditions to be preserved, and hence more fundamentally new forms might remain unknown. We use the early Paleozoic because high-level fossil echinoderm taxonomic diversity was maximal then and because the Chinese early Paleozoic contains several faunas that satisfy the special conditions echinoderms require to be preserved. So there is a greater chance of discovering new types. Our results show that most Chinese fossil echinoderms resemble forms already known from elsewhere, and thus, there is little evidence of bias. One possible explanation is that modern continents include sedimentary rocks deposited in different provinces during the early Paleozoic, so each may well provide an adequate sample on which to build global fossil diversity curves. Nevertheless, the rate at which new Chinese fossil echinoderms are being discovered is increasing rapidly, suggesting that the Chinese fossil record is still poorly known. Many new Chinese fossils remain to be found.

## Introduction

Raup (1976a) documented Phanerozoic species diversity using data from the Zoological Record and showed that about 70% of the fossil species were described from Europe, North America, and the USSR (as it then was). In a companion paper, Raup (1976b) demonstrated a correlation, significant at the 1% level, between species diversity and estimated area of outcrop or rock volume throughout the Phanerozoic. Raup concluded that despite the raw numbers of species, there was no compelling evidence for an increase in biodiversity from the Cambrian to the Recent. Combined, Raup's papers suggested that were the fossil record equally well known in all parts of the globe, a different pattern of evolution through the Phanerozoic might be revealed. This can be called the geographic bias hypothesis. Subsequent research has concentrated on further documentation of the correlation between outcrop area and biodiversity and methods to

compensate for the correlation (Sepkoski, 1976; Allison and Briggs, 1993; Alroy et al., 2001; Smith, 2001, 2007; Crampton et al., 2003; Smith and McGowan, 2005, 2007; Tarver et al., 2007; McGowan and Smith, 2008; Vilhena and Smith, 2013; Na et al., 2023). Despite this effort, the geographic bias hypothesis remains more a theoretical concept than a reality. No one has demonstrated that bias exists, but the possibility that it does cannot be dismissed.

The hypothesis of potential geographical bias may be tested using real examples of recent discoveries as well as by theoretical modeling. From a Western perspective, knowledge of Chinese early fossil echinoderms has recently grown significantly and may be used to test the geographical bias hypothesis. The fundamental question is whether newly discovered Chinese early Paleozoic echinoderms are more of the same forms we already know or whether the Chinese fossil record contains previously unknown types of echinoderms. If the Chinese fossil record is predominantly more of the same, very little bias can exist between a fossil record with and one without any Chinese fossils. Alternatively, if the Chinese fossil record contains many types of fossils previously unknown to science, we will be forced to revise our views of the history of life on Earth significantly.

The preceding question can be investigated taxonomically, phylogenetically, and morphologically. A taxonomic approach uses the hierarchy of taxa to evaluate the degree of novelty. Clearly, provided they are correctly identified, species described previously from other parts of the world and subsequently discovered in Chinese rocks have no novelty value whatsoever. A genuinely new species that can be attributed to a previously known genus has less significance than one representing a new order or class of echinoderms. Although there is no generally accepted echinoderm tree of life, a new genus that fits into an accepted lineage is going to be less novel than one whose phylogenetic position is obscure or truly novel. First occurrences of higher-level taxa are more important in evolution than last occurrences. Extending the known range of a well-established lineage into younger rocks would have far less significance than discovering examples that were significantly older than those previously known. So documenting older first occurrences among Chinese early Paleozoic echinoderms is important.

Morphologically, a fundamentally new feature such as a fully developed holomeric stem in pelmatozoan echinoderms will be most significant, but new combinations of morphological features, such as the co-occurrence of spiral ambulacra, a distinct cup, and well-developed stem in *Helicocystis* Smith and Zamora, 2013, would also be seen as a significant morphological novelty.

Finally, the composition of the whole fauna may present novelties or confirm similarities. North American mid-Cambrian echinoderm faunas are dominated by gogiid blastozoans of the family Eocrinidae Jaekel, 1918 (Sprinkle, 1973). So far, Chinese mid-Cambrian echinoderm faunas are dominated by similar forms (*Sinoeocrinus* Zhao et al., 1994; *Guizhoueocrinus* Zhao et al., 2007; *Globoeocrinus* Zhao et al., 2008; *Wudingeocrinus* Luo et al., 2008; *Kunmingeocrinus* Y.L. Zhao et al., 2022) although their taxonomic treatment has been different. North American eocrinids are still largely referred to the single genus *Gogia* Walcott, 1917, whereas Chinese eocrinid genera are mostly monotypic. Nevertheless, the morphological disparity of North American species within the genus *Gogia* is similar to if not greater than that of Chinese examples of the entire family Eocrinidae. Thus, morphological comparisons can be used as a check against different taxonomic practices. The dominance of eocrinids in the mid-Cambrian also suggests the Chinese and non-Chinese fossil records are similar.

Finally, we test the reliability of our preliminary results by using a discovery curve to assess the current state of knowledge of the Chinese echinoderm fossil record. Nevertheless, the principal aim of this paper is to outline approaches to testing for real geographic bias using actual examples. These tests can be applied repeatedly as our knowledge of the global fossil record improves. Equally, they can be applied to other taxonomic groups.

## Geological setting

Sources of the Chinese early Paleozoic echinoderms are shown in Figure 1. The exceptionally well-preserved Cambrian echinoderms in China are reported mainly from eight significant faunas of the South China Block, and only a few eocrinoids occurred on the margin of the North China Platform. Five of the Cambrian Series 2 biotas are Burgess Shale-like faunas, including the famous Chengjiang and Guanshan biotas located in eastern Yunnan Province (Shu et al., 2004; Hu et al., 2007; Y.L. Zhao et al., 2022), the Balang Fauna located in Guizhou Province (Zhao et al., 2007), the Huayuan biota in Hunan Province (Zeng et al., 2026), and the Jingshan fossil assemblage in central Hubei Province (Liu et al., 2010). Three of the later Cambrian biotas are also Burgess Shale-like, including the Kaili Biota from eastern Guizhou Province (Zhao et al., 2010), the Fulu biota from the southeastern corner of Yunnan Province (Peng et al., 2020), and the Guole biota located in Guangxi Province (Zhu et al., 2016). The Ordovician and Silurian echinoderms in China are mainly from the South China Block, Sibumasu of southwest Yunnan province, and Tarim Block of northwest Xinjiang (Reed, 1917; Sun, 1936; Regional Geological Team of Xinjiang Geological Bureau et al., 1981; Chen and Yao, 1993). The Ordovician echinoderms of the South China Block were reported from Guizhou, Hubei, and Hunan provinces (Sun, 1936; Li, 1993; Liu et al., 2024), while the Silurian echinoderms of the South China Block were reported from Guizhou, Hubei, and Sichuan provinces (Xu, 1962; Mu and Lin, 1987; Mao et al., 2017).

In general, the early Paleozoic echinoderms in China occur mainly in the South China Block, Sibumasu, and the North China Block. These occurrences and abundant fossils have greatly expanded the paleogeographic distributions of echinoderms.

## Materials and methods

We use the fossil record of complete or nearly complete echinoderms from the early Paleozoic. Echinoderms possess complex skeletons that fall apart soon after death. Preservation of articulated echinoderms requires rapid burial soon after (or at) death (Donovan, 1991, and references therein). Thus, the echinoderm fossil record is likely to be less well known than those of major taxa with simpler skeletons, such as gastropods. We concentrate on the early Paleozoic because Konservat Lagerstätten are more common, and known high-level taxonomic diversity of echinoderms reached a peak during that stratigraphic interval. Thus, the possibility of discovering additional novel high-level taxa in a relatively unexplored part of the globe might be increased.

*Data gathering.* We use records from bibliographic databases on the occurrence of early Paleozoic echinoderms to compare known biodiversity in North America and Europe with that of the rest of the world and China in particular. Records from Bassler and Moodey (1943) are used unfiltered to establish the extent of the geographic bias in knowledge of the fossil record by the mid-twentieth century. This establishes a baseline for comparisons with modern knowledge.

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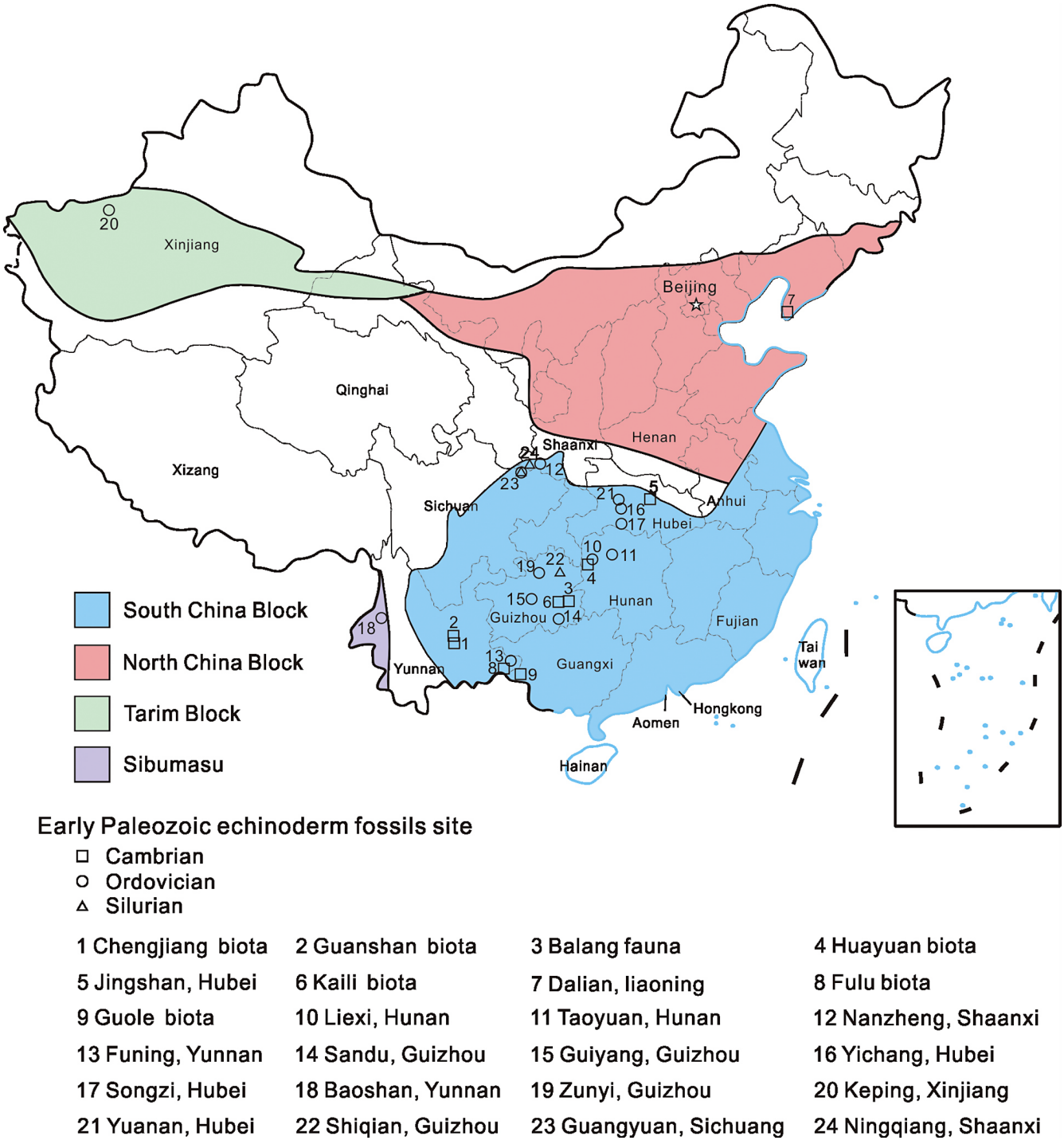



**Figure 1.** Map of modern China showing tectonic blocks and distribution of significant lower Paleozoic echinoderm fossil sites. Note the concentration in the South China Block.

From a Western perspective, the past several decades have significantly increased our knowledge of Chinese early echinoderms, including occurrences in several Lagerstätten. Thus, we have a real example on which to test the geographic bias hypothesis. For specific tests, we use Webster's (2014) index of crinoid crowns and parts of crowns and Webster and Webster's (2019) supplement; the supplementary table of all Cambrian echinoderms in Rahman and Zamora (2024); the paleobiology and geobiology databases; and our own compilations of early Paleozoic pelmatozoans post Bassler and Moodey (1943). We have then sought out the original publications to evaluate taxonomic interpretations. Thus, the records we use are based on original publications in which illustrations enable us to assess the identity of the echinoderms. Rarely, we have also used unpublished sources in which the authors have seen photographs of the specimens or personal communications from a trusted source. We have used all these sources to compile a spreadsheet of Chinese early Paleozoic echinoderms that is as reliable as possible. The publications on which our spreadsheet is founded have then been

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used to assess the relative novelty of recently described and illustrated Chinese echinoderms. The results are presented in tables that distinguish any source without publicly available illustrations.

Our tests are based on the fundamental assumption that geographic bias can affect our interpretation of the history of life on Earth only if currently undiscovered fossils differ fundamentally from those we already know. We then analyze the spreadsheet for degree of novelty among recently discovered Chinese early Paleozoic echinoderms. Our spreadsheet involves single occurrences, but multiple occurrences of the same taxon test the hypothesis of geographic bias equally well. Thus, where we know a fossil has been recorded from different Chinese provinces, this fact has also been recorded.

Taxonomically, species previously described from elsewhere in the world and recently reported from China have no novelty value at all. A new Chinese species is assigned a low novelty value, whereas a new class is assigned the highest value. These categories could be assigned numerical values and an average novelty score calculated. We have not done so because our results do not seem to justify it yet. In addition, we feel this approach needs to be applied to other major taxa before an agreed scoring system could be developed. Nevertheless, we have chosen the family level as a significant boundary. Any new Chinese fossil that can be assigned to a known family is considered as "more of the same"; those assigned to a new family or higher-level taxon are regarded as novel. In a few cases, significantly novel fossil echinoderms have been illustrated but not yet formally described. Using phylogenetic and morphological assessment allows us to include these discoveries.

Phylogenetically, some new genera have been described but not assigned to any higher taxon, except sometimes a class. Nevertheless, if they clearly fit into an already recognized lineage, they merely add detail. These are the equivalent of low-level taxa and assigned a low novelty value. The alternative would be a new fossil that either did not fit into any recognized lineage or perhaps linked two major lineages at an early stage of their differentiation. This would be assigned a high novelty value. Evidence that Chinese specimens are the oldest known examples of families or higher taxa is also considered important.

Finally, any new morphological feature or new combination of morphological features would rate a high novelty value, whereas repetition of combinations of well-known morphological features would be assigned a low score. We need all these approaches because a significant number of echinoderms have been reported but not formally described taxonomically. Applying only a taxonomic test would risk underestimating true novelty.

*Discovery curves.* Despite these new discoveries, the question remains as to how well known the Chinese early Paleozoic echinoderm fauna is. Bibliographies allow us to build historic discovery curves based on the dates of publication of new taxa. As used here, taxonomic discovery curves avoid the problems of taxonomic refinement and different taxonomic practices (lumpers versus splitters) by selecting the most up-to-date or accurate systematic classification and examining when within each taxon at each taxonomic level the first known example was described. Such discovery curves are all based on the same taxonomy. They can investigate growth of knowledge of stratigraphic or geographic distributions as well as numbers of taxa. If a better taxonomy is adopted, the same process will reassess growth of knowledge under the new taxonomy. Potentially, this approach could be adopted for a phylogeny; however, we are unaware of any such example.

Thus, our discovery curves enable recognition of the rate of growth of knowledge of the echinoderm fossil record, which in turn can be used to assess the completeness of our knowledge of that record (Paul,1980, fig. 3, p. 301, 1982, fig. 2, p. 129, 1998, p. 16 et seq.). We use as our starting point Bassler and Moodey's (1943) bibliography and index of Paleozoic pelmatozoans to establish the geographic bias in search effort (Table 1) as well as knowledge of Chinese early Paleozoic echinoderms by the mid twentieth century (Table 2). Then we have compiled separate files for current knowledge of Chinese Cambrian, Ordovician, and Silurian fossil echinoderms (Tables 3–5). These tables include the earliest date in which Chinese fossil echinoderms became known to science where this differs from the date of formal taxonomic description. From this, we construct a Chinese early Paleozoic echinoderm discovery curve. Finally, Webster's bibliography of echinoderms (Webster, 2014; Webster and Webster, 2019) allows us to estimate the change in effort involved in compiling the known Chinese fossil record over time. Comparison of the Chinese discovery curve with the global effort curve for crinoids enables us to assess how well known the Chinese early Paleozoic echinoderm fauna is.

**Table 1.** Number of entries for lower Paleozoic pelmatozoan echinoderms in Bassler and Moodey (1943)

| Bassler and Moody (1943) | North America | Europe | Rest of world | Total |
|---|---|---|---|---|
| Silurian | 527 | 315 | 8 | 850 |
| Ordovician | 412 | 341 | 27 | 780 |
| Cambrian | 9 | 22 | 0 | 31 |
| Totals | 948 | 678 | 35 | 1,661 |
| Percentage | 57.07 | 40.82 | 2.11 | |

## Results

Table 1 records the geographic bias in search effort by the mid twentieth century using all records in Bassler and Moodey (1943). Only 2.11% of 1,661 records came from areas outside North America and Europe. These included 28 records from Asia, six from Australia, and one from South America. Table 2 includes all the Chinese early Paleozoic echinoderms recorded by Bassler and Moodey (1943). There are nine identifiable genera and 24 records, all but two of which are Ordovician, and all can be referred to previously known families. The two Silurian genera are crinoids. Up to five species were previously described by Bather (1906) from Myanmar, but only two of them were illustrated by Reed (1917), so the status of the unillustrated taxa cannot be assessed. A sixth, "*Sphaeronites*" *shihtiensis* Reed, 1917, was later recorded from the Karakorums according to Bassler and Moodey (1943, p. 191) and from Thailand (Paul et al., 2019).

Tables 3–5 illustrate the current state (2026) of knowledge of Chinese early Paleozoic echinoderms. Taxonomically, the Chinese Cambrian (Table 3) includes 27 specific records, of which 13 are under open nomenclature or have been figured but not formally described. One species, *Turbanicystis inflatus* Parsley and Zhao, 2010, was assigned to a newly created family, the Turbanicystidae Parsley and Zhao, 2010, but it appears to us to be closely related to *Gogia* sensu lato. Seven taxa are unassigned to a family of which one, the eocrinoid with articulated spines on its thecal plates illustrated by Peng et al. (2020, fig. 4c), could potentially be referred to a new family. No other eocrinoid that we know of has spines on thecal plates although *Arthroacantha* Williams, 1883 is a Devonian

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**Table 2.** Lower Paleozoic echinoderms known from China by 1943

| Ordovician | | Original name | | | Modern identification | | |
|---|---|---|---|---|---|---|---|
| Class | Family | Genus | Species | Author | | Remarks | Date |
| Diploporita | Aristocystitidae | *Aristocystis* | *sinica* | (Sun, 1936) | Probably a sphaeronitid | Kweichou | |
| Diploporita | Aristocystitidae | *Sinocystis* | *loczyi* | Reed, 1917 | *Sinocystis loczyi* | Shih-tien | |
| Diploporita | Aristocystitidae | *Sinocystis* | *yunnanensis* | Reed, 1917 | *Sinocystis yunnanensis* probably valid | Shih-tien, | |
| Diploporita | Aristocystitidae | *Pyrocystis* | *orientalis* | (Reed, 1917) | Probably an aristocystitid | Shih-tien | |
| Diploporita | Aristocystitidae | *Eucystis* | cf. *E. raripunctata* | Reed, 1917 | Probably an aristocystitid | Shih-tien | |
| Diploporita | Sphaeronitidae | *Sphaeronis* | *lobiferus* | (Reed, 1917) | *Eucystis*? *lobiferus* | Shih-tien | |
| Diploporita | Sphaeronitidae | *Sphaeronis* | *shihtienensis* | (Reed, 1917) | A sphaeronitid but not *Sphaeronites* | Shih-tien | |
| Rhombifera | Caryocrinitidae | *Hemicosmites* | *jaekeli* | (Sun, 1936) | Almost certainly a caryocrinitid | Kweichou | |
| Rhombifera | Caryocrinitidae | *Caryocrinus* | sp. | (Reed, 1917) | *Caryocrinites* sp. | Shih-tien | |
| Rhombifera | Caryocrinitidae | *Caryocrinus* | cf. *C. turbo* | (Bather, 1906) | *Caryocrinites* cf. *turbo* | Pu-piao, | Reed, **1917** |
| Rhombifera | Caryocrinitidae | *Hemicosmites* | sp. | (Lóczy, 1899) | *Caryocrinites* sp. | Pu-piao | |
| Rhombifera | Cheirocrinidae | *Echinoencrinus* | sp. | (Reed, 1917) | *Cheirocystella sp.* | Pu-piao | |
| Rhombifera | Caryocystitidae | *Caryocystites* | *bicompressa* | (Reed, 1917) | *Heliocrinites bicompressa* | Shih-tien | |
| Rhombifera | Caryocystitidae | *Heliocrinus* | *fiscella* | (Bather, 1906) | *Lophotocystis fiscella* | Shih-tien, La-mêng | Reed, 1917 |
| Rhombifera | Caryocystitidae | *Heliocrinus* | *qualus* | (Bather, 1906) | *Lophotocystis qualus* | Shih-tien | Reed, 1917 |
| Rhombifera | Caryocystitidae | *Heliocrinus* | cf. *H. balticus* | (Reed, 1917) | *Heliocrinites* cf. *balticus* | Shih-tien | Reed, **1917** |
| Rhombifera | Caryocystitidae | *Heliocrinus* | *subovalis* | (Reed, 1917) | *Heliocrinites subovalis* | Shih-tien | |
| Rhombifera | Caryocystitidae | *Heliocrinus* | *kweichouensis* | (Sun, 1936) | *Heliocrinites kweichouensis* | Kweichou | |
| Rhombifera | Caryocystitidae | *Heliocrinus*? | sp. | (Reed, 1917) | *Heliocrinites* sp. | Pu-piao | |
| Rhombifera | Echinosphaeritidae | *Echinosphaera* | *asiatica* | (Reed, 1917) | *Echinosphaerites asiaticus* | Shih-tien | |
| Rhombifera | Echinosphaeritidae | *Echinosphaera* | *sinensis* | (Reed, 1917) | *Echinosphaerites sinensis* | Shih-tien | |
| Rhombifera | Echinosphaeritidae | *Echinosphaera* | cf. *E. aurantium* | (Reed, 1917) | *Echinosphaerites* sp. | Pu-piao | |
| Silurian | | | | | | | |
| Crinoidea | Scyphocrinitidae | *Camarocrinus* | *asiaticus* | (Reed, 1917) | *Scyphocrinites asiaticus* | Shih-tien, | Reed (**1917**) |
| Crinoidea | Scyphocrinitidae | Crinoidea? | Indet. | Yin and Lu, 1937 | *Carolicrinus siniaticus* Haude, 1992 | Yunnan | |
| Total | | | 24 | | 9 genera | | |

*Note:* Bold dates indicate no illustration of Chinese specimens exists. Last column refers to date first recorded from China.

crinoid with spines articulating on its cup plates. The Peng et al. (2020) specimen, although unnamed, is clearly a significantly novel Chinese Cambrian echinoderm. In addition, the new genus and species illustrated by Zamora et al. (2013, fig. 2B), here tentatively assigned to the Macrocystellidae, is a member of the lineage leading to dichoporite rhombiferans and closely related to *Jingxieocrinus.* All Chinese Cambrian echinoderms are endemic to China unless *Kailidiscus* is a junior synonym of *Walcottidiscus* Bassler, 1935.

The Chinese Ordovician (Table 4) includes 48 taxa in total, including those in Bassler and Moodey (1943). All but one, Cyclocystoid-like organism Fang et al., 2022, can be assigned to known families. The exception differs too much from true cyclocystoids (Kolata et al., 2023, 2025) to be included within that class. Three species were described previously from Myanmar by Bather (1906). Otherwise, these Chinese taxa appear to be endemic.

Finally, the Chinese Silurian (Table 5) includes 43 named species of crinoids, 12 of which were previously reported from elsewhere in the world. The scyphocrinitids were particularly cosmopolitan (Webster, 2014; Webster and Webster, 2019). All crinoid species are named, but two are of uncertain family. Several species have been reported from more than one Chinese province, which increases by 11 the total number of records from China.

In summary, the Chinese early Paleozoic echinoderm fauna includes a total of 118 specific taxa, of which 105 (88.98%) can be referred with reasonable confidence to known families. Fifteen (12.71%) are species first described from elsewhere in the world. The currently known fauna is predominantly more of the same. Alternatively, only three taxa, *Turbanicystis inflatus*, an unnamed spiny eocrinoid, and the cyclocystoid-like organisms from the Liexi fauna, are potentially significantly new in the sense that they have

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**Table 3.** Cambrian echinoderms known from China

| | Species | Family | Family date | Series | Stage | Craton | Date |
|---|---|---|---|---|---|---|---|
| Edrioasteroidea | *Cambroblastus guolensis* Zhu et al., 2014 | Astrocystitidae | Bassler, 1935 | Furongian | Jiangshanian | South China | 2013 |
| Edrioasteroidea | *Kailidiscus chinensis* Zhao et al., 2010 | Stromatocystitidae | Bassler, 1936 | Miaolingian | Wuliuan | South China | |
| Edrioasteroidea | *Sprinkleoglobus extenuatus* Y.L. Zhao et al., 2022 | Unassigned | | 2 | 3 | South China | |
| Eocrinoidea | *Balangicystis rotundus* Parsley and Zhao, 2006 | Lyracystidae | Sprinkle and Collins, 2006 | 2 | 4 | South China | |
| Eocrinoidea | Gen. and sp. indet. Peng et al., 2020, fig. 4b | Unassigned | | Miaolingian | Wuliuan | South China | |
| Eocrinoidea | Eocrinoidea indet B Huang, 2012 | Unassigned | | 2 | 4 | South China | |
| Eocrinoidea | *Globoeocrinus globulus* Zhao et al., 2008 | Eocrinidae | Jaekel, 1918 | Miaolingian | Wuliuan | North China | 2007 |
| Eocrinoidea | *Globoeocrinus zhaoyuanlongensis* Yang et al., 2015 | Eocrinidae | Jaekel, 1918 | 2 | 4 | South China | |
| Eocrinoidea | *Guizhoueocrinus yui* Zhao et al., 2007 | Eocrinidae | Jaekel, 1918 | 2 | 4 | South China | |
| Eocrinoidea | *Kunmingeocrinus cupuliformis* J. Zhao et al., 2022 | Eocrinidae | Jaekel, 1918 | 2 | 4 | South China | |
| Eocrinoidea | *Sinoeocrinus lui* Zhao et al., 1994 | Eocrinidae | Jaekel, 1918 | Miaolingian | Wuliuan | South China | |
| Eocrinoidea | *Sinoeocrinus* sp. Liu et al., 2010 | Eocrinidae | Jaekel, 1918 | 2 | 4 | South China | |
| Eocrinoidea | Spiny eocrinoid Peng et al., 2020, fig. 4c | New family? | | Miaolingian | Guzhangian | South China | |
| Eocrinoidea | *Turbanicystis inflatus* Parsley and Zhao, 2010 | Turbanicystidae | Parsley and Zhao, 2010 | Miaolingian | Wuliuan | South China | |
| Eocrinoidea | *Vyscystis spinosa* Wang et al., 2024 | Lepidocystidae | Durham, 1968 | 2 | 4 | North China | |
| Eocrinoidea | *Wudingeocrinus rarus* Hu et al., 2007 | Eocrinidae | Jaekel, 1918 | 2 | 4 | South China | 2006 |
| Rhombifera | Possible dibrachicystid Peng et al., 2020, fig. 4f | Dibrachicystidae | Fatka and Szabad, 2014 | Miaolingian | Wuliuan | South China | |
| Rhombifera | New genus and species Zamora et al., 2013 | Macrocystellidae? | Bather, 1899 | Furongian | Jiangshanian | South China | |
| Rhombifera | *Jingxieocrinus guoleensis* Chen and Han, 2014 | Ridersiidae | Jell et al., 1985 | Furongian | Jiangshanian | South China | 2013 |
| Soluta | Soluta indet. Zamora et al., 2013 | Unassigned | | Furongian | Jiangshanian | South China | |
| Stylophora | Basal mitrocystitid Peng et al., 2020, fig. 4d | Unassigned | | Miaolingian | Guzhangian | South China | |
| Stylophora | Lagynocystid Zamora et al., 2013 | Lagynocystidae | Jaekel, 1918 | Furongian | Jiangshanian | South China | **2013** |
| Stylophora | *Flabellicarpus* Peng et al., 2020, fig. 4a, e | Cothurnocystidae | | Miaolingian | Guzhangian | South China | |
| Stylophora | *Drepanocarpos*-like Zamora et al., 2013 | Hanusiidae | Cripps, 1991 | Furongian | Jiangshanian | South China | |
| Stylophora | *Phyllocystis* ? *jingxiensis* Han and Chen, 2008 | Current research | A cornute | Furongian | Jiangshanian | South China | |
| Stylophora* | *"Nanocarpus guoleensis* Chen and Han, 2013" | Mitrocystitidae | Ubaghs, 1968 | Furongian | | South China | |
| Total | 27 | | | | | | |

*Note:* Bold date indicates not illustrated. Date column indicates first record from China if earlier than formal description.
*This taxon is a basal mitrocystitid (Lefebvre and Ausich, 2021, p. 939–940).

been or could be assigned to new families unknown outside China. Even so, *Gogia guntheri* Sprinkle, 1973, from North America is very similar to *Turbanicystis inflatus* from China, and the spiny eocrinoid seems closely related to Eocrinidae. Only the cyclocystoid-like echinoderm (Fang et al., 2022, fig. 2f) appears to be a truly novel early Paleozoic echinoderm from China. The specimens differ too much from true cyclocystoids (Kolata et al., 2023, 2025) to be included within that class. The single photograph does not show enough detail to be sure what it is, but the preservation of apparently soft-tissue peripheral tentacles, but total lack of central plating, is difficult to interpret as a cyclocystoid. We suggest it might be a somasteroid, but it needs thorough description.

Finally, two crinoids, *Eopetalocrinus sinensis* and *Muicrinus dawanensis*, appear to be the only known Ordovician examples of their respective families, the Petalocrinidae and Iocrinidae. In addition, Chinese Petalocrinidae seem to be more diverse both taxonomically and morphologically than those known from elsewhere in the world.

## Discussion

*Significance of our results.* At first sight, our results overwhelmingly suggest that the known Chinese early Paleozoic echinoderm fauna differs little from that already known from elsewhere in the world and therefore there is little evidence of geographic bias. This view is reinforced by the fact that six Silurian species have been reported from more than one province (Table 5). Treated as separate occurrences, these would add another 11 records to our database. In addition, the Geobiodiversity Database (https://geobiodiversity.com) records the genus *Petalocrinus* from six Chinese provinces and *Pisocrinus* from four. Furthermore, we have not identified even one significantly novel taxon at class level, such as the helicoplacoids or ctenocystoids. Nevertheless, our results should be regarded as preliminary for at least three reasons. First, they depend on how well known Chinese echinoderms are. Second, recently discovered new echinoderm classes are rare and not very diverse (see below);

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**Table 4.** Ordovician echinoderms known from China

| Class | Species | Family | Stage | Province | Date |
|---|---|---|---|---|---|
| Asteroidea | *Protopalaeaster*? *sinensis* Zhang and Han, 1991 | Hudsonasteridae Schuchert, 1914 | | Zhejiang | |
| Crinoidea | *Eopetalocrinus sinensis* Li, 1993 | Petalocrinidae Weller and Davidson, 1896 | Darriwilian | | |
| Crinoidea | *Muicrinus dawanensis* Lin et al., 2018 | Iocrinidae Moore and Laudon, 1943 | Floian–Dapingian | Hubei | |
| Crinoidea | *Pseudaristocystis yunnanensis* Sun, 1948 | Scyphocrinitidae Jaekel, 1918 | | Yunnan | |
| Unassigned | Cyclocystoid-like organism Fang et al., 2022 | | Floian | Hunan | |
| Rhombifera | *Caryocrinites jaekeli* (Sun, 1936) | Caryocrinitidae Bernard, 1895 | | Yunnan | |
| Rhombifera | *Caryocrinites ludianensis* Chen and Yao, 1993 | Caryocrinitidae Bernard, 1895 | | Yunnan | |
| Rhombifera | *Caryocrinites turbo* (Bather, 1906) | Caryocrinitidae Bernard, 1895 | | Yunnan | **1917** |
| Rhombifera | *Caryocrinites* sp. Lóczy, 1899 | Caryocrinitidae Bernard, 1895 | | Yunnan | |
| Rhombifera | *Caryocrinites* sp. Li et al., 2023, fig. 2e, f | Caryocrinitidae Bernard, 1895 | Floian | Guiyang | |
| Rhombifera | cf. *Fusicystis* sp. Lee and Zhang, 2022 | possibly Echinoencrinitidae Bather, 1899 | | Mongolia | **2022** |
| Rhombifera | Hemicosmitoid plates Paul et al., 2016 | Caryocrinitidae Bernard, 1895 | Floian | Guizhou | 2014 |
| Rhombifera | *Paracaryocrinites subglobosus* Chen and Yao, 1993 | Caryocrinitidae Bernard, 1895 | | Yunnan | |
| Rhombifera | *Polycosmites* sp. Paul et al., 2016 | Caryocrinitidae Bernard, 1895 | Floian | Guizhou | 2014 |
| Rhombifera | *Polycosmites* sp., Li et al., 2023 | Caryocrinitidae Bernard, 1895 | Floian | Guiyang | |
| Rhombifera | "*Cheirocrinus*" *penniger* Mao et al., 2021, non Eichwald | Cheirocrinidae Jaekel, 1899 | | | |
| Rhombifera | "*Cheirocrinus*" sp. Paul et al., 2016 | Cheirocrinidae Jaekel, 1899 | Floian | Guizhou | 2014 |
| Rhombifera | *Cheirocystella* sp. (Reed, 1917) | Cheirocrinidae Jaekel, 1899 | | Yunnan | |
| Rhombifera | *Cheirocystella* sp. (Xia et al., 1990) | Cheirocrinidae Jaekel, 1899 | | Hunan | |
| Rhombifera | *Cheirocystis liexiensis* Liu et al., 2024 | Cheirocrinidae Jaekel, 1899 | Floian | Hunan | 2022 |
| Rhombifera | *Macrocystella* sp. Li et al., 2023, fig. 4f | Macrocystellidae Bather, 1899 | | Guiyang | |
| Rhombifera | *Pleurocystites bassleri* Sun, 1948 | A glyptocystitoid, but not *Pleurocystites* | | Yunnan | |
| Diploporita | *Aristocystites sinicus* (Sun, 1936) | Aristocystitidae Neumayr, 1889? | Darriwilian | Yunnan | |
| Diploporita | *Pyrocystis orientalis* Reed, 1917 | Aristocystitidae Neumayr, 1889? | | Yunnan | |
| Diploporita | *Sinocystis loczyi* Reed, 1917 | Aristocystitidae Neumayr, 1889 | | Yunnan | |
| Diploporita | *Sinocystis yunnanensis* Reed, 1917 | Aristocystitidae Neumayr, 1889 | | Yunnan | |
| Diploporita | *Sinocystis shaanxiensis* Xia et al., 1990 | Aristocystitidae Neumayr, 1889 | | Hunan | |
| Diploporita | *Sinocystis* sp. Wang et al., 2022 | Aristocystitidae Neumayr, 1889 | Darriwilian | Yangtze | **2022** |
| Diploporita | *Eucystis*? *jenhochiaoensis* (Sun, 1948) | Sphaeronitidae Neumayr, 1889 | | Yunnan | |
| Diploporita | *Eucystis*? *lobiferus* Reed, 1917 | Sphaeronitidae Neumayr, 1889 | | Yunnan | |
| Diploporita | *Eucystis* cf. *E. raripunctata* Reed, 1917, non Angelin, 1878 | Aristocystitidae Neumayr, 1889 | | Yunnan | |
| Diploporita | *Eucystis* sp. unpublished | Sphaeronitidae Neumayr, 1889 | Katian | Yunnan | 2024 |
| Diploporita | *Haplosphaeronis*? *jenhochiaoensis* (Sun, 1948) | Sphaeronitidae Neumayr, 1889 | | Yunnan | |
| Diploporita | *Sphaeronis shihtienensis* Reed, 1917 | Sphaeronitidae Neumayr, 1889 | | Yunnan | |
| Rhombifera | *Caryocystites cylindratus* Chen and Yao, 1993 | Caryocystitidae Jaekel, 1918 | | Yunnan | |
| Rhombifera | *Heliocrinites* cf. *H. balticus* (Reed, 1917) | Caryocystitidae Jaekel, 1918 | | Yunnan | **1917** |
| Rhombifera | *Heliocrinites bicompressa* (Reed, 1917) | Caryocystitidae Jaekel, 1918 | | Yunnan | |
| Rhombifera | *Heliocrinites kweichouensis* (Sun, 1936) | Caryocystitidae Jaekel, 1918 | | Yunnan | |
| Rhombifera | *Heliocrinites subovalis* (Reed, 1917) | Caryocystitidae Jaekel, 1918 | | Yunnan | |
| Rhombifera | *Heliocrinites szetui* Sun, 1948 | Caryocystitidae Jaekel, 1918 | | Yunnan | |
| Rhombifera | *Lophotocystis fiscella* (Bather, 1906) | Caryocystitidae Jaekel, 1918 | | Yunnan | 1917 |
| Rhombifera | *Lophotocystis qualus* (Bather, 1906) | Caryocystitidae Jaekel, 1918 | | Yunnan | 1917 |

(*Continued*)

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**Table 4.** (*Continued*)

| Class | Species | Family | Stage | Province | Date |
|---|---|---|---|---|---|
| Rhombifera | *Echinosphaerites asiaticus* (Reed, 1917) | Echinosphaeritidae Neumayr, 1889 | | Yunnan | |
| Rhombifera | *Echinosphaerites* cf. *E. aurantium* Reed, 1917, non Gyllenhaal, 1772 | Echinosphaeritidae Neumayr, 1889 | | Yunnan | |
| Rhombifera | *Echinosphaerites sinensis* (Reed, 1917) | Echinosphaeritidae Neumayr, 1889 | | Yunnan | |
| Rhombifera | *Echinosphaerites* sp. Wang et al., 2022 | Echinosphaeritidae Neumayr, 1889 | Darriwilian–Sandbian | Yangtze | **2022** |
| Ophiuroidea | Undescribed ophiuroids (B. Lefebvre, personal communication, 2026) | | Hirnantian | Guizhou | **2026** |
| Stylophora | Undescribed mitrates (B. Lefebvre, personal communication, 2026) | Anomalocystitidae Bassler, 1938 | Hirnantian | Guizhou | **2026** |
| Total | 48 | | | | |

*Note:* Bold date indicates no Chinese specimens were illustrated. "*Cheirocrinus*" is in quotes because the specimens can be attributed only to the family Cheirocrinidae, not the genus *Cheirocrinus*. Rhombifera listed before and after Diploporita represent dichoporite and fistuliporite Rhombifera, respectively.

if randomly discovered they are likely to be the last taxa discovered. Finally, application of the test to other fossil groups might produce different results. We next consider how well known the Chinese echinoderm fossil record is.

*Discovery curves.* Chinese fossil echinoderms are just as much subject to "the law of diminishing returns" as are fossils from anywhere else. Experience shows that when searching for fossils, the common ones are soon discovered, but it takes increasing effort to add new species to the list of fossils found. If significantly new types of fossils were rare, only after thorough searches could we become confident that they were truly absent because the common fossils would be found first. Equally, the common Chinese fossils are more likely to have been common elsewhere and therefore already known. As used here, discovery curves (Fig. 2) provide a means of assessing how complete our knowledge of the local fossil record is (Paul, 1982, p. 102). In this context, discovery curves plot increasing taxonomic knowledge against search effort. Common examples are plots of number of species against number of specimens, or against area searched, or against time spent searching, all collectively called "effort." So, if one plots the rate of discovery of taxa at various taxonomic levels, one can compare the shape of the resulting curve with a standard discovery curve (Fig. 2). The early part of the curve rises steeply and implies there is a lot more still to be discovered; the last part of the curve is nearly horizontal and implies that most of the fossil biota has been found. Paul (1980, fig. 67, p. 207, 1982, fig. 13, p. 103) compared global discovery curves for species, genera, and families of cystoids (Diploporita and Rhombifera) from 1772 to 1975. This showed that whereas both genuinely new species and genera were still being discovered at a rapid rate, the curve for families had flattened significantly since 1900 (Fig. 3). In 2026, the number of families is still 25, but genera have increased from 110 to 132. Raup (1972, p. 1067) discussed the theoretical basis for this relationship between lower- and higher-level taxa.

In this context, counting the number of families, genera, or species is not adequate. Some may be synonyms, others homonyms, and in the case of families and genera, many will result from refined taxonomy. For example, the first two blastozoans known to science were described under the generic name *Echinus* by Gyllenhaal (1772). Subsequently, one was recognized as the fistuliporite rhombiferan genus *Echinosphaerites* Wahlenberg, 1818 and the other as the diploporite *Sphaeronites* Hisinger, 1828. Each is now recognized as the type genus of its respective family, the Echinosphaeritidae Neumayr, 1889 and Sphaeronitidae Neumayr, 1889. The difficulties that changes in taxonomy introduce can be overcome by assigning all taxa to the best modern classification and then finding when the first species within any higher taxon was described. So, the first known fistuliporite and echinosphaeritid was *Echinosphaerites aurantium* (Gyllenhaal, 1772). The subclass Fistuliporita, family Echinosphaeritidae, and genus *Echinosphaerites* all date from 1772. Equally, the class Diploporita, family Sphaeronitidae, and genus *Sphaeronites* all date from 1772. Even this approach may not truly reflect when a taxon first became known to science. According to Regnéll (1945, p. 1) and Kesling (1968, p. S152), both *Echinosphaerites aurantium* and *Sphaeronites pomum* were mentioned by Linnaeus (1745) but were regarded as "crystal apples" and so thought to belong in the mineral kingdom. It could be argued that they were known to science from 1745. Kesling (1968, p. S152–S159) discussed numerous previous classifications of cystoids (a taxon no longer recognized), but whichever classification is chosen, *E. aurantium* and *S. pomum* date from 1772. Similarly, however many or few species one may assign to the two genera, *E. aurantium* and *S. pomum* were still the first species described. Taxonomic synonymies allow the date of publication to be established and thus for historic discovery curves to be constructed easily.

*Effort curves.* A related phenomenon is the effort involved in finding and describing fossils. This too can be analyzed historically, and typically such curves show an increase in effort through time. Webster (2014, appendix 1) provided a compilation of the number of publications dealing with Paleozoic crinoids annually from 1758 to 2012. Webster and Webster (2019) enable us to extend that to 2018 (Fig. 4). Although these will not all have been taxonomic papers, they give a sense of the growth in study of Paleozoic crinoids. Progress was very slow until the mid-nineteenth century then increased rapidly until the mid-twentieth century and even more rapidly since. The first period represents the era of gentleman scientists of independent means; the second represents the growth of practical state geological surveys and museums; the final part represents the increase in global wealth and geology departments in universities, all fueled by the dramatic increase of the global population. Nevertheless, if the rate of discovery declines despite the very significant recent increase in search effort, then we must be getting to know the fossil record quite well. Tarver et al. (2007, fig. 3, p. 180) present estimates for worker effort on trilobites (papers per year and number of authors per decade recorded in

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**Table 5.** Silurian echinoderms known from China

| Subclass | Species | Family | Series/Stage | Province | Date |
|---|---|---|---|---|---|
| Camerata | *Camarocrinus* cf. *C. subornatus* (Waagen and Jahn, 1899) | Scyphocrinitidae Jaekel, 1918 | Pridolian | Yunnan | |
| | *Carolicrinus shidianensis* Chen and Yao, 1993 | Scyphocrinitidae Jaekel, 1918 | Pridolian | Yunnan | |
| | *Carolicrinus siniaticus* Haude, 1992 | Scyphocrinitidae Jaekel, 1918 | Pridolian | Yunnan | **1937** |
| | *Marhoumacrinus pyburnensis* Springer, 1917 | Scyphocrinitidae Jaekel, 1918 | Telychian | Yunnan | |
| | *Neoarchaeocrinus shiquianmensis* Wang, 1995 | Rhodocrinitidae Roemer, 1855 | Llandovery | Guizhou | |
| | *Scyphocrinites duanjiapoensis* Chen and Yao, 1990 | Scyphocrinitidae Jaekel, 1918 | Telychian | Yunnan | |
| | *Scyphocrinites elegans* Zenker, 1833 | Scyphocrinitidae Jaekel, 1918 | Telychian | Yunnan | |
| | *Scyphocrinites mutabilis* Springer, 1917 | Scyphocrinitidae Jaekel, 1918 | Telychian | Yunnan | |
| | *Scyphocrinites stellatus* (Hall, 1879) | Scyphocrinitidae Jaekel, 1918 | Telychian | Yunnan | |
| Cladida | *Caelocrinus stellifer* Xu, 1962 | Euspirocrinidae Ulrich, 1925 | Wenlock | Szuchuan | |
| | *Dazhucrinus guizhouensis* Mu and Wu, 1974 | Uncertain | Wenlock | Kweichou | |
| | *Dazhucrinus shanxiensis* Mu and Wu, 1974 | Uncertain | Wenlock | Shensi | |
| | *Petalocrinus chiai* Mu, 1949 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Kweichou, Wuchuan, Guizhou, Shihchien | |
| | *Petalocrinus eximius* Mu and Wu, 1974 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Kweichou, Guizhou | |
| | *Petalocrinus guizhouensis* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Petalocrinus inferior* Bather, 1898 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Kweichou, Guizhou, Sichuan, Hubei | 1949 |
| | *Petalocrinus inflatus* Mu, 1949 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Kweichou, Guizhou | |
| | *Petalocrinus involucrus* Mu and Wu, 1974 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Kweichou, Guizhou, Sichuan | |
| | *Petalocrinus latus* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Petalocrinus magnus* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Petalocrinus sinensis* Mu and Wu, 1974 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Hupei, Guizhou, Sichuan | |
| | *Petalocrinus stenopetalus* Mao et al., 2017 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Petalocrinus tenuis* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Petalocrinus validus* Mu and Wu, 1974 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Kweichou | |
| | *Sinopetalocrinus involutus* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Sinopetalocrinus robustus* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Sinopetalocrinus shiquianensis* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus abnormis* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus circularis* Mao et al., 2017 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus dextrosus* Mao et al., 2017 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus longus* Mu and Wu, 1974 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus multiramus* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus pauciramus* Mu and Lin, 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus typicus* Mu and Wu, 1974 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| | *Spirocrinus uniformis* Mu and Lin 1987 | Petalocrinidae Weller and Davidson, 1896 | Aeronian | Guizhou | |
| Disparida | *Parapisocrinus ollula* (Angelin, 1878) | Pisocrinidae Angelin, 1878 | Telychian | | 1996 |
| | *Parapisocrinus pateriformis* (Wang, 1996) | Pisocrinidae Angelin, 1878 | Telychian | | |
| | *Parapisocrinus sphaericus* (Rowley, 1904) | Pisocrinidae Angelin, 1878 | Telychian | | 1996 |
| | *Pisocrinus bohemicus* Bouška, 1956 | Pisocrinidae Angelin, 1878 | Telychian | | 1996 |
| | *Pisocrinus brevis* Wang, 1996 | Pisocrinidae Angelin, 1878 | Telychian | | |

(*Continued*)

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**Table 5.** (*Continued*)

| Subclass | Species | Family | Series/Stage | Province | Date |
|---|---|---|---|---|---|
| | *Pisocrinus kosovensis* Bouška, 1956 | Pisocrinidae Angelin, 1878 | Telychian | | 1996 |
| | *Pisocrinus pilula* de Koninck, 1858 | Pisocrinidae Angelin, 1878 | Telychian | | 1996 |
| | *Pisocrinus pilula yin*i Mu, 1954 | Pisocrinidae Angelin, 1878 | Wenlock | Szechuan | 1954 |
| Total | 43 | | | | |

*Note:* They are all crinoids. Bold date = no illustration of Chinese examples.

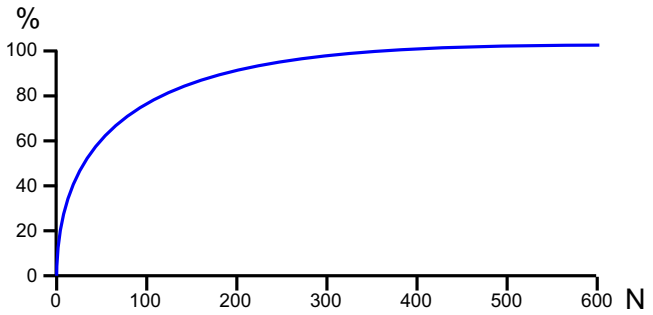



**Figure 2.** Generalized discovery curve. N = number of specimens; % = percentage of total biota known. In this case, even at 100 specimens, > 20% of the biota would be unknown but there would be no point in collecting beyond 600 as all the species would have been found. Redrawn from Paul (1982, fig. 2).

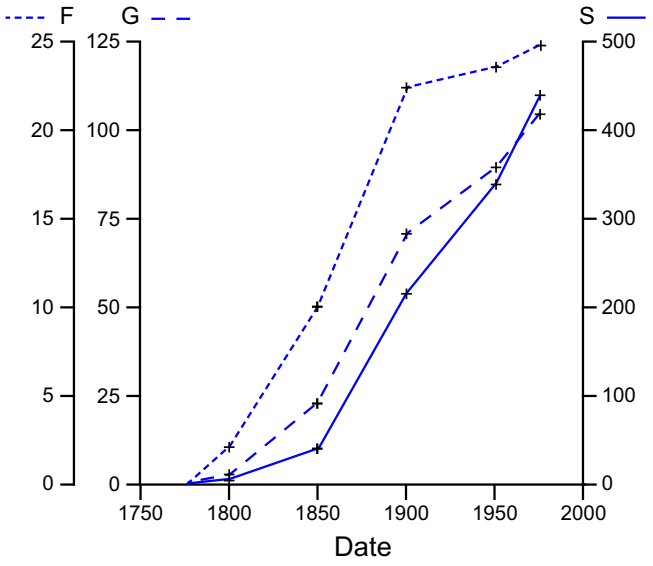



**Figure 3.** Historic discovery curves for F = families (leftmost scale), G = genera (left scale), S = species (right scale) of Rhombifera and Diploporita from 1772 to 1975. Note that most of the families were known by 1900, but both genera and species were still increasing rapidly after 1950. Redrawn from Paul (1982, fig. 13, p. 103).

the ISI Web of Science, https://clarivate.com), showing a dramatic increase after World War II. Tarver et al. (2007, fig. 4, p. 180) also illustrate discovery curves for trilobite families and genera plotted against this worker effort. The generic curve is linear and almost entirely reflects effort, whereas the familial curve flattens out about halfway through the plot, despite the increase in effort. It would seem the trilobite fossil record is quite well known, at least at family level.

An historic discovery curve of Chinese early Paleozoic echinoderms (Fig. 5) may be compared with global cystoid discovery

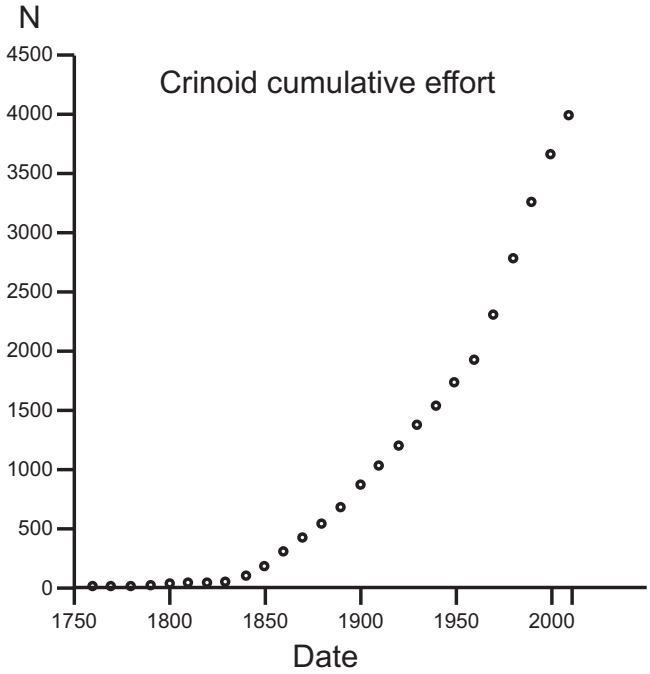



**Figure 4.** Cumulative number of publications (N) on Paleozoic crinoids from 1758 to 2018. Data from Webster (2014, appendix 1; Webster and Webster, 2019, supplement 1). Note the slow start followed by an exponential increase, especially since 1850.

(Fig. 3) and global Paleozoic crinoid effort (Fig. 4) curves. Clearly, the Chinese discovery curve is concave-up and more like the global crinoid effort curve (Fig. 4) but only to the early part of the global cystoid species discovery curve (Fig. 3). At present, it would be wise to conclude that although there is very little evidence for geographic bias in the fossil record using the Chinese early Paleozoic echinoderm discovery curve, it is early still, and the situation may change in the future.

Finally, we use class-level taxa as the ultimate example of significant new discoveries. Paleozoic echinoderms are well known for having several classes that are very distinct morphologically but very small (low biodiversity) and relatively rare. If yet unknown Chinese new classes of echinoderms were similarly rare, statistically they would be the last to be discovered. It is premature to take our results at face value.

## Other tests

We chose to use a real example to illustrate a potential test of the geographic bias hypothesis. Other approaches are equally valid. It is not necessary to wait until another area of the globe yields significant numbers of new echinoderms or other fossils. One might, for

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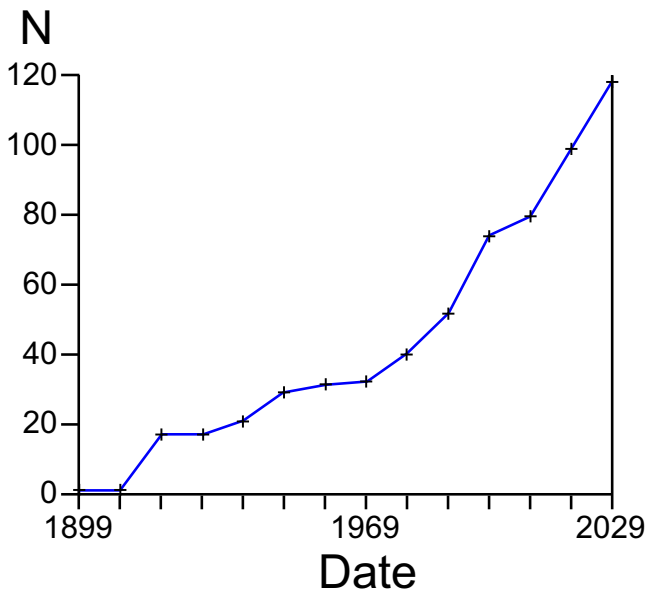



**Figure 5.** Cumulative rate of discovery of Chinese lower Paleozoic echinoderm species. Note the curve starts at the very end of the nineteenth century and resembles an effort curve rather than a discovery curve. There are many more Chinese lower Paleozoic echinoderms still to be found. N = number of species; Date = time of first description.

**Table 6.** Currently known geographic occurrence of a random sample of 294 Paleozoic crinoid genera

| Province | Crinoid genera | % | Exclusive to | % |
|---|---|---|---|---|
| North America | 200 | 68.03 | 131 | 44.56 |
| Europe | 120 | 40.82 | 51 | 17.35 |
| Elsewhere | 75 | 25.51 | 32 | 10.88 |
| Total | 294 | | | |
| 1 province | 190 | 64.63 | | |
| 2 provinces | 59 | 20.07 | | |
| 3+ provinces | 21 | 7.14 | | |

*Note:* Data from Webster and Webster (2019). See text for further explanation.

example, degrade our existing knowledge by deleting the North American or European fossil record and comparing the resulting loss of information. To test this, we used a randomly chosen subsample of Webster and Webster's (2019) crinoid data (all generic names beginning with A, B, and C). We assigned their occurrences to North America, Europe, and 'Elsewhere' (Table 6). As expected, most of the genera (68%) occur in North America, many (41%) in Europe, and the smallest proportion (25.5%) in the rest of the world. Nearly two-thirds (65%) occur in only one province, 20% in two provinces, and 7% in three or more provinces. If the North American fauna were unknown, just under half of the crinoid genera in the sample (44.56%) would be unknown. Loss of the European fauna would reduce known crinoid genera by 17.35%, and if the record were confined to just North America and Europe, only 10.88% of crinoid genera would be unknown. Another, perhaps more significant, effect of loss of the North American fauna would be that all Tremadocian (lowest Ordovician) crinoid genera would be unknown except for *Aethocrinus* Ubaghs, 1969, which is known from southern France and Morocco (Lefebvre et al., 2016), and an undescribed genus from the USA and France.

Webster and Webster (2019) list eight named Tremadocian crinoid genera, attributed to subclasses Aethocrinea, Disparida, Cladida, Camerata, and Hybocrinida, plus the order Protocrinoida, which is not assigned to a subclass. Thus, Tremadocian crinoids were already very diverse. All but one of the new genera were assigned to new families. Western North America appears to have been the cradle of the Crinoidea.

Another approach might be to consider where in the world recent new class-level discoveries have been made. For example, since the mid-twentieth century, *Camptostroma* Ruedemann, 1933, *Helicoplacus* Durham and Caster, 1963, *Ctenocystis* Robison and Sprinkle, 1969, and *Helicocystis* Smith and Zamora, 2013 have been discovered or reinterpreted as echinoderms. All are significant new "class-level" discoveries only one of which, *Helicocystis*, came from outside North America. They also illustrate the previously mentioned point about rarity. *Camptostroma* and *Helicocystis* are still known from a single species. Helicoplacoids comprise three monotypic genera (Wilbur, 2006). Only ctenocystoids are moderately diverse. Currently, seven genera and about 16 species are recognized although some taxa are still under open nomenclature. In addition, ctenocystoids have since been recorded from Europe (Fatka and Kordule, 1985), Australia (Jell et al., 1985), and Africa (Smith et al., 2013), but the other taxa are still confined to the continent from which they were originally described.

## Possible explanations

If novelty is an essential quality for geographic bias to exist, then bias is more likely to occur during periods of high endemicity in shallow continental seas. Despite deliberately choosing taxa and a stratigraphical interval that might be expected to increase the chances of discovering novelties, our results suggest the Chinese early Paleozoic echinoderm fauna is largely more of the same. One possible explanation of our results, especially in relation to early Paleozoic fossils, is plate tectonics. The parts of the global landmass that currently make up Europe and China, for example, were not always in the same geographic position; nor were they homogeneous regions. Waters et al. (2008, fig.16.1) divided modern China into at least seven named regions, one of which was labeled "composite" and all of which presumably had separate geologic histories. What is now China was part of at least three distinct provinces, just as early Paleozoic rocks in Europe include parts of North America, Baltica, Avalonia, and Gondwanaland. It seems likely that the better-explored parts of the world may well have sampled an adequate set of both latitudinal environments and longitudinally wide basins to provide a reasonable sample of early Paleozoic life, thus overcoming the effects of endemism.

By coincidence, the first paper published by one of us (Paul, 1965) apparently recorded an enormous increase in paleogeographic range of comarocystitid paracrinoids, a small taxon of early echinoderms with very distinctive thecal plates. Previously, all comarocystitids had been found in rocks then thought to be of Middle Ordovician age from the Midwest of North America. The new specimens came from the Upper Ordovician of Girvan, Scotland. At the time, this appeared to be an increase in geographic range of several thousand kilometers, but that was before plate tectonics had been proposed, let alone accepted. Now, we know that all of Scotland north of the Southern Uplands was part of North America in the Ordovician. In addition, the American occurrences are now regarded as of early Late Ordovician age, so the increase in

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stratigraphic range has also been reduced. The tiny island of Britain contains early Paleozoic rocks from at least two major provinces. How much more diverse were the early Paleozoic faunas of Western Europe or North America?

## Conclusion

The disproportionate number of fossils found in the scientifically better-explored parts of the globe (North America and Europe) may introduce a bias in the known fossil record. Recent increases in knowledge of the Chinese early Paleozoic echinoderm fauna have been used in a preliminary test of the geographic bias hypothesis. The basic approach designates newly discovered Chinese echinoderms as genuine novelties or more of the same. This test can be applied taxonomically, phylogenetically, or morphologically. Our preliminary results suggest that the Chinese early Paleozoic echinoderm fauna is predominantly more of the same. A potential explanation of our results is that areas such as Europe and China are composed of several different early Paleozoic provinces, and each alone may provide an adequate sample on which to build global diversity curves. This suggestion will be tested by future discoveries. Nevertheless, historic discovery curves show that the rate of new Chinese fossil echinoderm discoveries is rising sharply and therefore that the Chinese early Paleozoic echinoderm fauna is still relatively poorly known.

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