Palaeobiodiversity and Palaeoenvironments (2021) 101:725–740
https://doi.org/10.1007/s12549-020-00450-3

SENCKENBERG

ORIGINAL PAPER

Famennian crinoids and blastoids (Echinodermata) from Mongolia

J. A. Waters[1] · J. W. Waters[2] · P. Königshof[3] · S. K. Carmichael[1] · M. Ariuntogos[3,4]

Received: 29 May 2020 / Revised: 5 August 2020 / Accepted: 10 August 2020 / Published online: 2 October 2020

Abstract

Herein we report on the most abundant and diverse fauna of Palaeozoic crinoids and blastoids collected from Mongolia to date. The fauna is from the Late Devonian (Famennian) Samnuuruul Formation in western Mongolia. The fauna consists of two genera of blastoids and twelve genera of crinoids—four genera of camerates, three genera of flexibles, one disparid genus, and four genera of cladids. The crinoids and blastoids were living on an active island arc complex in the Central Asian Orogenic Belt (CAOB) in a high physical stress environment with frequent and often voluminous pyroclastic eruptions. The Mongolian fauna is similar to coeval faunas collected from the Hongguleleng Formation in western China and supports the hypothesis that the CAOB was a biodiversity hotspot for Famennian echinoderms and a precursor to the very successful echinoderm communities that dominated Mississippian shallow-marine ecosystems globally. Three new taxa are described. *Mongoliacrinus minjini*, new genus and species, is the oldest member of the Acrocrinidae, previously known from the Mississippian and Pennsylvanian and the first occurrence of the family outside North America. *Eutaxocrinus ariunai* and *Eutaxocrinus sersmaai* are new species of the flexible crinoid *Eutaxocrinus*, a genus with a widespread distribution during the Early and Middle Devonian, which survived into the Lower Mississippian. It is restricted to the CAOB in the Late Devonian.

Keywords Central Asian Orogenic Belt (CAOB) · Crinoid · Blastoid · Devonian · Palaeobiogeography · Biodiversity hotspot

Introduction

Reports of Palaeozoic echinoderm communities from Mongolia are sparse even though the country has a long and complex geologic history in the Central Asian Orogenic belt (CAOB). The earliest reports of crinoid faunas from Mongolia were all based on columnals—five Silurian species, 15 Carboniferous species, and one Permian species (Stukalina 1973, 1994, 1997; Tungalag 1998). Webster and Ariunchimeg (2004) reported the first discovery of cups and thecae from Mongolia, a Lower Devonian (Emsian) fauna from the Sine Jinst area of southern Mongolia. They recognized five taxa but were able to name only one (*Cyathocrinites*) because of poor preservation of the collected material. Although sporadic reports of stem taxa continue to be published (e.g., Rozhnov et al. 2009), reports of diverse, identifiable crinoid faunas based on thecae from Mongolia have not been forthcoming prior to this study.

Herein we report on a Late Devonian (Famennian) crinoid fauna from the Samnuuruul Formation in western Mongolia. The fauna consists of 12 genera of crinoids—four genera of camerates, three genera of flexibles, one disparid genus, and four genera of cladids. We also have identified two genera of blastoids, the first occurrence of the class in Mongolia. The fauna has taxonomic affinities with Famennian echinoderm communities from the Hongguleleng Formation in Xinjiang Autonomous Region, China (Lane et al. 1997; Waters et al. 2003; Webster and Waters 2009).

The CAOB is the world's largest Palaeozoic accretionary orogenic belt and likely evolved in a similar fashion to the modern western Pacific. Mongolia lies in the center of the CAOB with up to 44 different terranes, including cratonic, metamorphic, passive margin, island arc, forearc/backarc,

This is a contribution to a special series on *The Central Asian Orogenic Belt (CAOB) during Late Devonian: new insights from southern Mongolia.*

✉ J. A. Waters
watersja@appstate.edu

1 Department of Geological and Environmental Sciences, Appalachian State University, Boone, NC 28006, USA

2 Houston, Texas, USA

3 Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325 Frankfurt, Germany

4 Mongolian University of Science and Technology, Baga toiruu, Sukhbaatar District, Ulaanbaatar, Mongolia

accretionary complex, and ophiolitic terranes, ranging in age from the Proterozoic through the Phanerozoic (Badarch et al. 2002). Windley et al. (2007) favored an island archipelago model similar to modern Indonesia for the Palaeozoic island arc terranes in the CAOB including Mongolia (Fig. 1). The Devonian was a time of major Palaeozoic terrane accretion in the CAOB.

IGCP 596 and its successor, the Western Mongolia Working Group, have been conducting fieldwork in Mongolia with the goal of identifying Late Devonian extinction and anoxia events that were previously recognized in coeval CAOB terranes in western China. Fieldwork in 2012, 2014, and 2018 identified three sections in the Samnuuruul Formation, Baruunhuurai Terrane, and Olonbulag Subterrane (Fig. 2) for detailed study (Kido et al. 2013; Ariunchimeg et al. 2014; Suttner et al. 2019). The Samnuuruul Formation is approximately 450 m thick consisting of reddish brown conglomerates, thin limestone beds, greenish gray and gray fine- to medium-grained sandstone, and siltstone with a significant volcaniclastic component. Three field localities were examined in detail for biostratigraphy and microfacies analysis: Buduun Khargait gol (N 45° 17′ 6″; E 90° 57′ 31″, Hushoot Shiveetiin gol (N 45° 16′ 1″; E 90° 3′ 20″), and Shiveet Mountain (N 45° 5′ 2″; E 91° 34′ 13″). Historically, the Samnuuruul Formation has been assigned a Famennian (Late Devonian) age based on macrofossils. Suttner et al. (2019) reported conodonts at Hushoot Shiveetiin gol from the *Palmatolepis minuta minuta* to *Palmatolepis rhomboidea* zones (Spalletta et al. 2017) confirming a Famennian age for the formation.

Results

Sedimentology of the crinoid bearing beds

Although the detailed sedimentology and conodont biostratigraphy of Hushoot Shiveetiin gol will be published elsewhere (Ariuntogos et al. this issue), the majority of the echinoderms reported herein were collected from a narrow stratigraphic interval in the *P. rhomboidea* Zone indicating a Middle Famennian age (Fig. 3). Overall, sediments were deposited in a shallow-water sequence of thin-bedded bioclastic limestones and shales with a significant pyroclastic volcanic component. Regional tectonics and local sedimentology indicate the sequence was deposited in an active island arc setting. Low-diversity, high-abundance brachiopod assemblages throughout the *P. rhomboidea* Zone suggest pioneer marine communities were living in shallow-water, high-physical-stress environments. These brachiopod pavements formed thin limestone beds that extend laterally for tens to hundreds of meters. The limestones are overlain by greenish gray shales or by volcaniclastic sediments that are mostly unfossiliferous. The sequence repeats itself at decimeter scales suggesting disruptions to marine colonization were frequent.

One interval in the *P. rhomboidea* Zone has reduced volcaniclastic activity, microfacies suggesting slightly deeper water, and faunas indicating higher diversity. Pioneer brachiopod pavements were overlain by masses of bryozoans (mostly trepostomes with minor fenestrate). Additional elements of the fauna include rare small solitary rugose corals, small tabulate corals, phacopsid trilobites, and orthocone cephalopods. This interval seems to record a more diverse marine

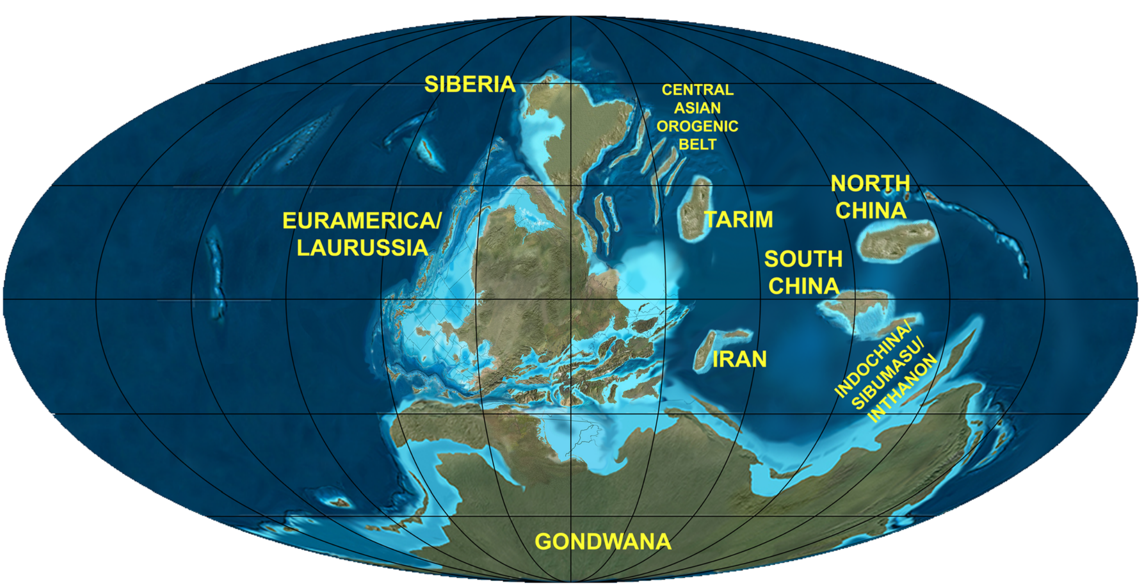

Fig. 1 Famennian paleogeographic reconstruction showing position of island arc in the Central Asian Orogenic belt. Base map from Blakey (2016) with changes in continental position and shape based on data in Hara et al. (2010), Metcalfe (2011), and Xiao et al. (2010)

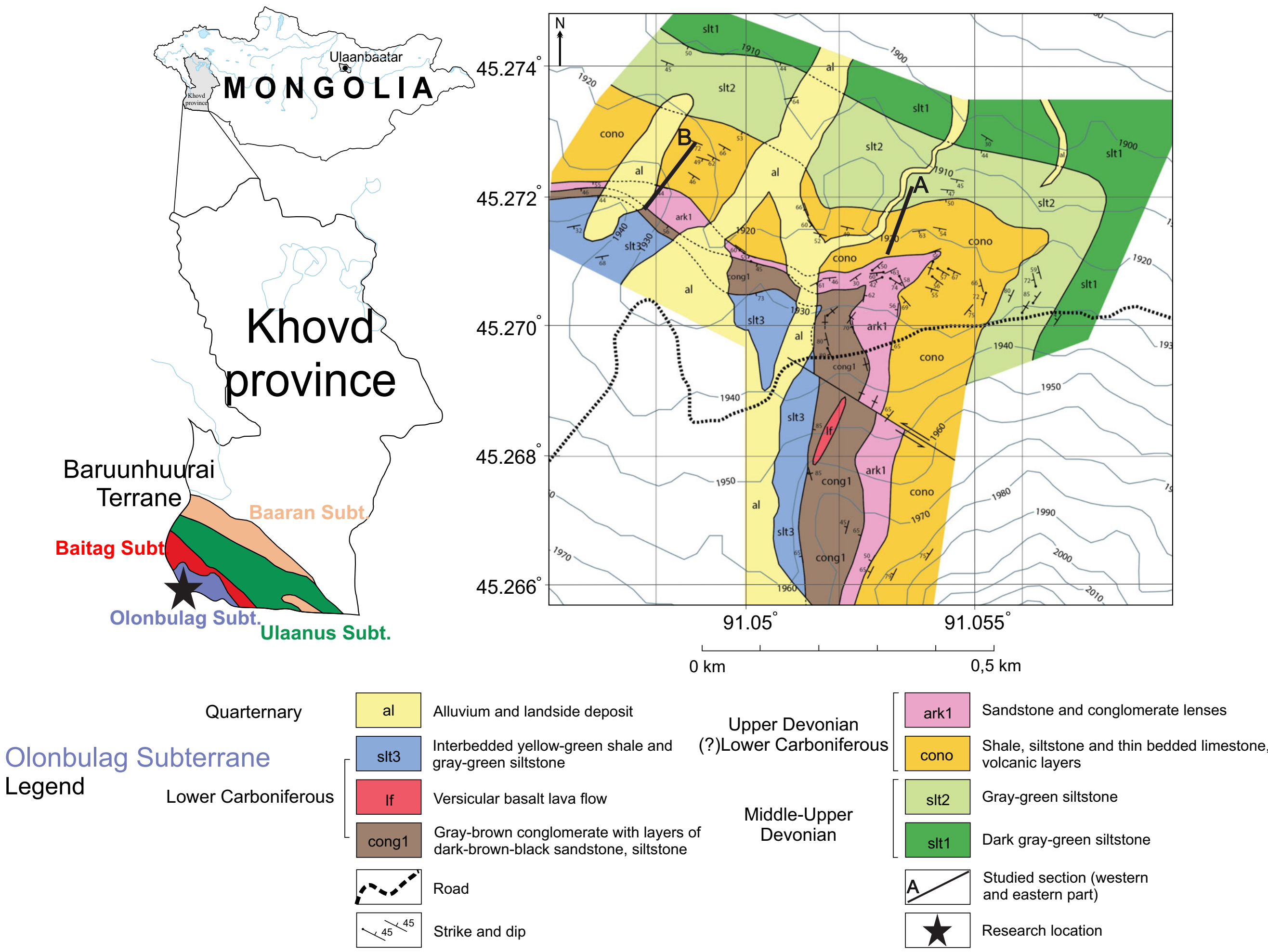

Fig. 2 Map of southwestern Mongolia showing the distribution of the geologic terranes and subterranes and the location of Hushoot Shiveetiin gol with inset geologic map of the locality

community living in environments with less physical stress in terms of water depth and siliciclastic input from pyroclastic volcanic activity.

The crinoids described herein were all collected from this interval of the section (Fig. 3) with a single exception. Specimens are preserved as thecae and crowns with arms (and occasionally proximal stems) attached indicating the assemblage is a biocenosis. Thin crinoidal limestones indicate accumulation of crinoid stem debris, but transportation seems minimal. Actual diversity is higher than reported herein. Tectonic cleavage has impacted our ability to recover many complete specimens. Thecae tend to be crushed making plate identification difficult. More or less complete sets of arms with the thecae sheared off occur but cannot be identified.

One specimen was collected from the Shiveet Mountain and is assigned a Famennian (undifferentiated) age based on the associated macrofauna. Famennian shales at this locality have undergone low-grade thermal alteration and the specimen is preserved as a mold in slaty shale. The description was made using a latex cast of the specimen.

Comparison of the Mongolian echinoderm faunas to coeval faunas

The Mongolian fauna is the second major Famennian echinoderm fauna to be described from the Central Asian Orogenic Belt. An echinoderm fauna from the Hongguleleng Formation in Xinjiang-Uyghur Autonomous Region, China, was first reported by Hou et al. (1993) and Lane et al. (1995). Lane et al. (1997), Waters et al. (2003), and Webster and Waters (2009) systematically described the fauna, tabulated the abundance and diversity of the taxa, and discussed the evolutionary and palaeobiogeographic implications of the fauna. Although smaller than the fauna described from the Hongguleleng Formation, the Mongolian fauna confirms many of the interpretations of the Hongguleleng fauna and corroborates the

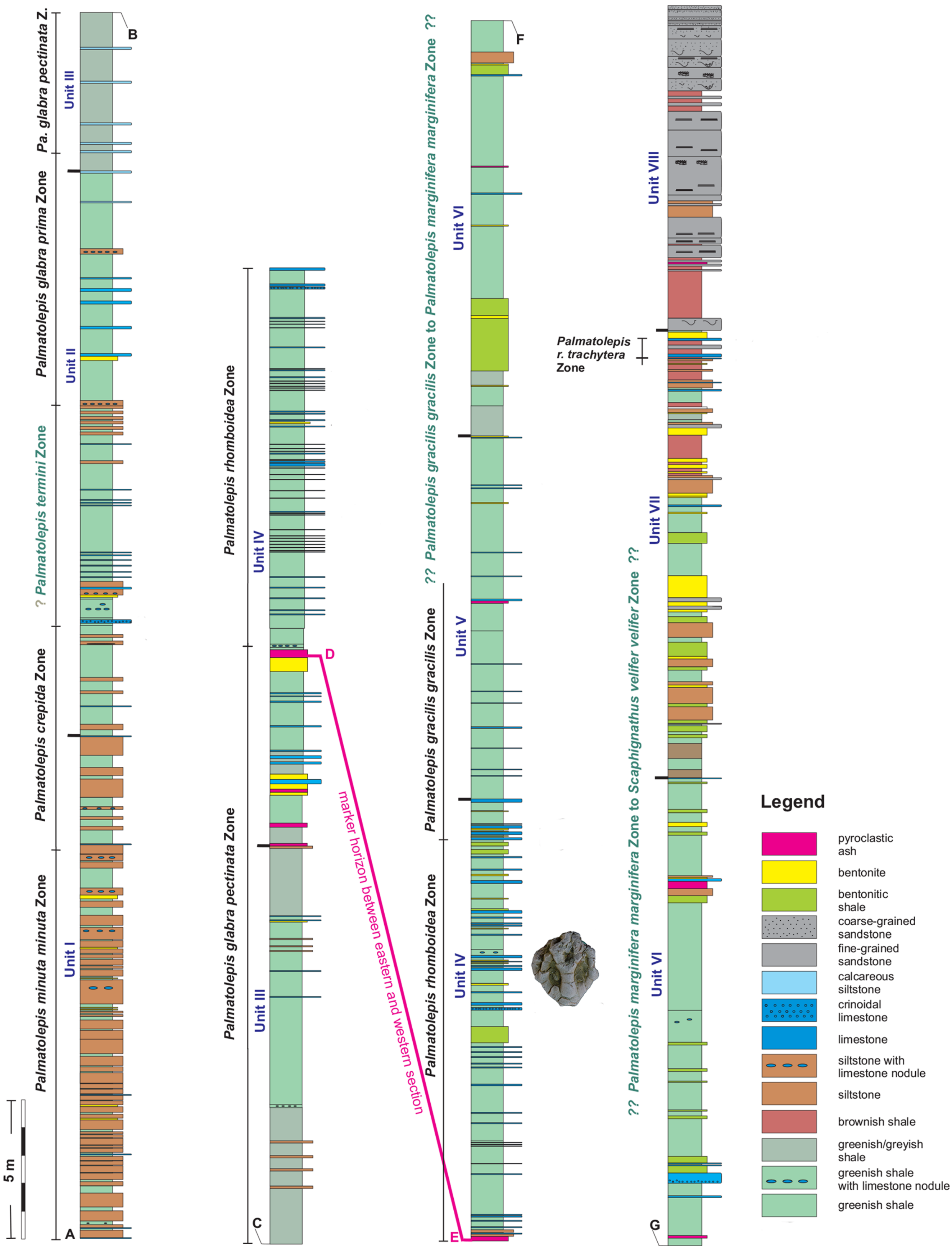

Fig. 3 Detailed lithologic map of Hushoot Shiveetiin gol showing crinoid interval in the *P. rhomboidea* Zone

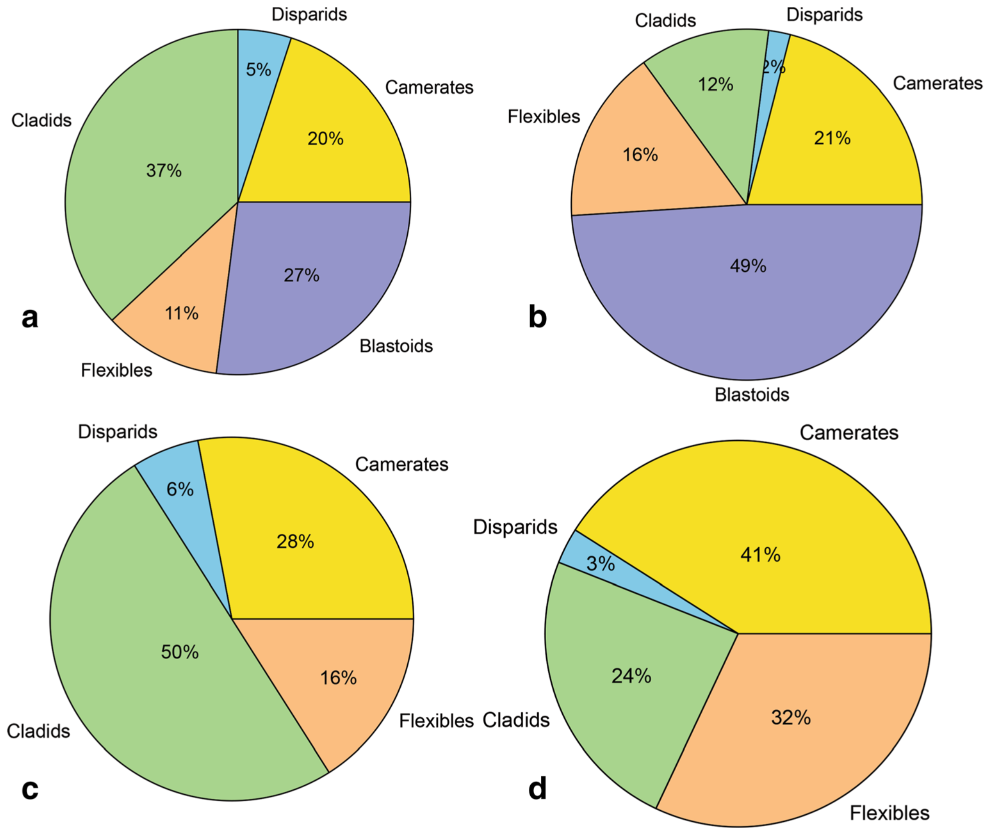

Fig. 4 Echinoderms in the Hongguleleng Formation. **a** Diversity of blastoids and crinoids. **b** Abundance of blastoids and crinoids. **c** Diversity of crinoids. **d** Abundance of crinoids

hypothesis that the CAOB was a biodiversity hotspot for the rebound of shallow-marine communities after the Frasnian/Famennian extinction event.

The blastoid fauna from the Hongguleleng (12 genera) is the most diverse Famennian fauna and the second most diverse blastoid fauna of any age in the world. It contains the oldest occurrence of many blastoid families that are important components of Carboniferous echinoderm communities, particularly in North America and Europe, and suggests that the CAOB was the center of blastoid diversification after the Late Devonian mass extinction events. Blastoids are very abundant in the Hongguleleng constituting 49% of all the echinoderm specimens collected to date (Fig. 4b).

The crinoid fauna from the Hongguleleng is the largest Famennian crinoid fauna currently known from anywhere in the world. The fauna is more diverse and abundant than the faunas described by Whidborne (1898) and redescribed by Lane et al. (2001a) from the Late Devonian of England. The crinoid fauna is also more diverse than coeval faunas from Germany (Lane et al. 2001b), Colorado (Webster et al. 1999), and Australia (Jell and Jell 1999). The fauna from the Hongguleleng Formation fills a major gap in the history of crinoid phylogeny and suggests that the CAOB was a biodiversity hotspot for Famennian crinoids and was the precursor to the abundant and diverse Mississippian crinoid communities that dominated the carbonate factories globally.

One result of fieldwork by IGCP 596 and the Western Mongolian Working Group is the discovery of a large, diverse Famennian echinoderm fauna that is the largest Palaeozoic echinoderm fauna collected from Mongolia to date. This fauna allows us to test the hypothesis that the CAOB was a hotspot for Famennian echinoderm biodiversity and confirms many of the evolutionary and palaeobiogeographic implications of the Hongguleleng echinoderm fauna.

The Mongolian fauna has similarities to the Hongguleleng fauna, but also has some important differences. The Mongolian fauna is less abundant than the fauna from the Hongguleleng, perhaps because it was living in an environment with more frequent and more voluminous volcanic activity than the faunas of the Hongguleleng. In addition, the fauna is restricted to a single stratigraphic interval rather than several distinct intervals in the Hongguleleng. It also was collected in a significantly smaller outcrop belt caused by steeply dipping strata and more complex tectonic activity.

Blastoids are virtually missing from the Mongolian fauna, being represented by two partial specimens identifiable as *Houiblastus* and a diagnostic radial plate identified as *Junggaroblastus*. In contrast, the 12 genera of blastoids from the Hongguleleng represent 27% of the echinoderm diversity and 49% of the specimens collected (Fig. 4a, b). Although we do not have a hypothesis for the disparity in blastoid distribution between the two localities, we do not think it is the result of taphonomic bias. We can examine crinoid, rather than echinoderm, taxonomic diversity, and abundance (Fig. 6c, d) of the Hongguleleng and Mongolian faunas by removing blastoid abundance and diversity from the data. In the Hongguleleng crinoid fauna, cladids are the most diverse (50%) followed by camerates (28%), flexibles (16%), and disparids (6%). Camerates (41%) are the most abundant group of crinoids followed by flexibles (32%), cladids (24%), and disparids (3%). The disparity in ranking between crinoid diversity and crinoid abundance is likely attributable to the two most common genera *Chinacrinus*, a camerate, and *Eutaxocrinus*, a flexible, accounting for 56% of the specimens collected.

The Mongolian fauna consists of 12 genera of crinoids—four camerate genera, one disparid genus, four cladid genera, and three genera of flexibles identified from 70 specimens (Fig. 5a). With the exception of a single new genus, all genera found in the fauna were also found in the Hongguleleng. The disparid is known from two specimens, but the camerates (26%), flexibles (29%), and cladids (38%) are all significantly more abundant (Fig. 5b).

The most abundant crinoid in the Mongolian fauna is the flexible *Eutaxocrinus* as in the Hongguleleng fauna but in contrast the camerate *Chinacrinus* is known only from a single specimen. The most abundant camerates are actinocrinids, which are present in the Hongguleleng, but are rare. The Mongolian fauna does contain the first Famennian occurrence of the camerate family Acrocrinidae with the description of *Mongoliacrinus minjini*, new genus and species. The acrocrinids are characterized by a diagnostic thecal plating with numerous intercalaries separating the bipartite basals from the radials. Crowns are large and many have recumbent arms which are present in *Mongoliacrinus minjini*. Acrocrinids previously were only known from the Mississippian and Pennsylvanian. Cladids in the Mongolian fauna are very similar to those in the Hongguleleng with *Julieticrinus*, *Pachylocrinus*, and *?Parisocrinus* known from multiple specimens.

Abundance and diversity differences between the Hongguleleng and Mongolian faunas are not surprising given that they occurred on two separate island arc systems with different palaeoecological conditions and differing eruptive volcanic behaviors. Their similarities reinforce the concept that the CAOB was a biodiversity hotspot for Famennian echinoderms that later radiated globally rather than a relict Devonian fauna that survived the Frasnian/Famennian extinction in a geographically isolated area. The dominance of actinocrinids and platycrinids in the camerate faunas at both localities rather than families dominant in the Lower and Middle Devonian provides an indication of the "Mississippian" aspect of the faunas. Flexible faunas are dominated by *Eutaxocrinus*, a taxon well known from both the Devonian and Mississippian. However, the flexible faunas in both localities also contain genera, such as *Taxocrinus* and *Euonychocrinus*, only known from the Mississippian and Pennsylvanian outside the CAOB. Arm branching patterns and thecal morphology of the cladid genera common to both locations are characteristic of Mississippian cladids rather than Devonian genera (see discussion in Lane et al. 1997).

Systematic palaeontology

All specimens are housed in the Mongolian University of Science and Technology (MUST) research collections. In addition to the taxa identified below, 12 additional unidentified specimens are in the collection.

Class Blastoidea Say 1825
Order Fissiculata Jaekel 1918
Family Phaenoschismatidae Etheridge Jr. and Carpenter 1886

Junggaroblastus hoxtolgayensis
Fig. 7(5)

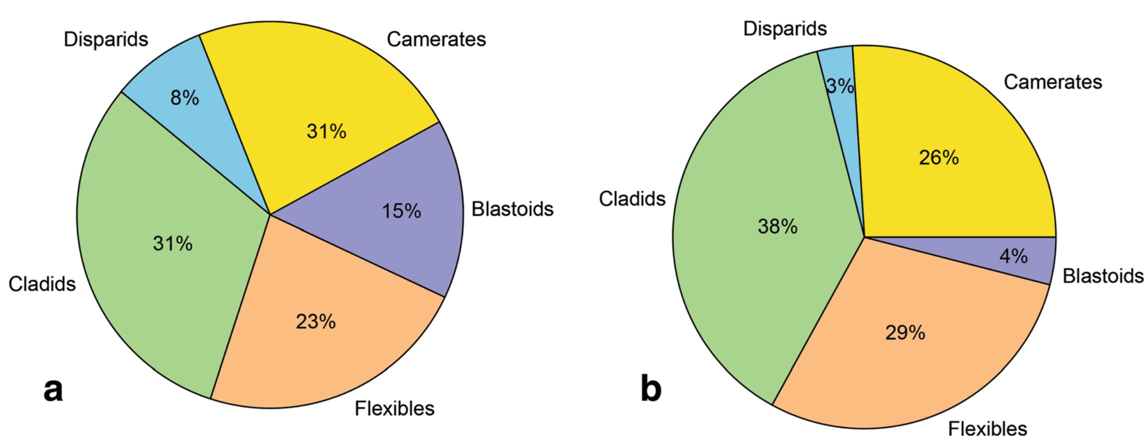

Fig. 5 Echinoderms from the Famennian of Mongolia. **a** Diversity of blastoids and crinoids. **b** Abundance of blastoids and crinoids

Specimens: One partial theca. MUST-RCSR-BLA-0001.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: A single radial (H = 7 mm; W = 4 mm) convex in lateral outline with distinct external ornamentation consisting of growth lines differentially raised into ridges. Ambulacral sinus prominent occupying 50% of radial height; angle of sinus 90°. Ambulacrum missing but aboralmost part of hydrospires preserved confirming fissiculate condition. Radiodeltoid suture is not visible in side view indicating deltoid crest not deltoid body.
Remarks: Although the Mongolian specimen is a single radial, it preserves enough characteristics to identify the specimen as a phaeonoschismatid. *Junggaroblastus* has a similar radial shape with very distinct growth lines and deltoid crests allowing us to identify the specimen as *Junggaroblastus hoxtolgayensis*.

Order Pentremitida Matsumoto 1929, emended Waters and Horowitz 1993
Family Orbitremitidae Fay 1964
Genus Houiblastus Lane et al. 1997

Houiblastus devonicus Lane et al. 1997
Figure 4.16 Fig. 7(4)

Specimens: Two partial thecae. MUST-RCSR-BLA-0002; 0003.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: The two specimens are partial thecae preserving radial plates and deltoids. Specimens are godoniform thecae 10 mm long and 5 mm wide. Radials long and relatively narrow contributing 95% of lateral outline. Radial body pierced by hydrospire tubelets along ambulacral sinus. Ambulacra not preserved, but radial sinus narrow indicating narrow ambulacra. Deltoids very small, barely visible in side view. Basals missing but sutures suggest protruding basalia. Spiracles not observed.
Remarks: Hydrospire tubelets in thecal plates are a diagnostic feature of the Orbitremitidae (Breimer and Joysey 1968a, 1968b) with a limited distribution in the blastoids. Among described Famennian blastoids, only two genera have thecal plates with hydrospire tubelets, *Houiblastus* and *Xinjiangoblastus*. *Xinjiangoblastus* has distinctive thecal ornamentation that is lacking in the Mongolian specimens. The two partial thecae have similar thecal shape and plate configurations to *Houiblastus* and are assigned to *Houiblastus devonicus*.

Class Crinoidea Miller 1821
Subclass Camerata Wachsmuth and Springer 1885
Order Monobathrida Moore and Laudon 1943
Family Actinocrinitidae Austin and Austin Jr. 1842
Genus *Abactinocrinus* Laudon and Severson 1953

Abactinocrinus sp., aff *A. rossi(?)*
Fig. 7(1, 2)

Specimens: Two specimens MUST-RCSR-CRI-0001, 0002.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Remarks: *Abactinocrinus* is characterized by having strongly grouped arms, a lobate calyx, few fixed brachials, and a periproct opening directly through the tegmen.

Abactinocrinus is known from two species, the type species *Abactinocrinus rossei* Laudon and Severson (1953) from the Kinderhook (Mississippian) of North America and *Abactinocrinus devonicus* Waters et al. (2003) from the Famennian Hongguleleng Formation of Xinjiang Autonomous Region, China. Differences between the species include the following: shape of the cup (bowl-shaped versus straight-sided), smooth versus ornamented cup plates, and location of the periproct on the tegmen. Although each species is based on a single specimen, Brower (1967) noted the significance of the genus in the evolution of the Actinocrinidae. The figured specimen is not well preserved and is missing the basals, but it does compare well with the description of *Abactinocrinus rossei* in Laudon and Severson (1953) and has ornamented plates lacking in *Abactinocrinus devonicus*. The primary difference between the Mongolian specimen and *Abactinocrinus rossei* lies in the tegmen plates, with *Abactinocrinus rossei* having more numerous, small tegmen plates. We are reluctant to describe a third species based on only two poorly preserved specimens and questionably assign the specimen to *Abactinocrinus rossei*.

Genus *Actinocrinites*
Actinocrinites sp.
Fig. 7(13)

Specimens: Four specimens. MUST-RCSR-CRI-0003-0006.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Remarks: Specimens are assigned to *Actinocrinites* based on the presence of theca with grouped arms in each ray, hexagonal first primibrachial, two plates above a hexagonal primanal, and three plates in proximal interrays. Details of the tegmen and presence of an anal tube are unknown because of poor preservation of the thecae which are crushed. The specimens are similar to *Actinocrinites zhaoae* Waters et al. 2003 from the Hongguleleng Formation. Rhenberg et al. (2015) revised the generic concepts in the Actinocrinidae and removed *Actinocrinites zhaoae* from the Actinocrinidae declaring it *incertae sedis*. *Actinocrinites zhaoae* (Lane et al. 1997) was removed from *Uperocrinus* and reassigned to *Actinocrinites* based upon the hexagonal first primibrachials (Waters et al. 2003). *A. zhaoae* has three plates above the primanal which

eliminates it from the Actinocrinidae as currently defined. Although a crown with crushed calyx, one specimen from this fauna (MUST-RCSR-CRI-0003) shows a hexagonal primanal with two, rather than three, plates above. Lane et al. (1997) discussed the intermediate morphologic nature of the single specimen of *Actinocrinites zhaoae* which included characters defining four closely allied genera. Rhenberg et al. (2015) concluded that *Actinocrinites zhaoae* should be excluded from the Actinocrinidae until more specimens could be recovered to ascertain whether three plates above the primanal was the norm or an aberration. The presence of two plates above the primanal in the Mongolian fauna permits us to assign the specimens to *Actinocrinites*. We support the assertion by Rhenberg et al. (2015) that "there is a more extensive, but undocumented, evolutionary history for the Actinocrinitidae during the Devonian" and believe that specimens from the CAOB will play a significant role in that Famennian history.

Suborder Glyptocrinina Moore 1952
Superfamily Hexacrinitacea Wachsmuth and Springer 1885
Family Playcrinitidae Austin and Austin Jr. 1842
Genus Chinacrinus Lane et al. 1997

Chinacrinus xinjiangensis Lane et al. 1997
Fig. 7(3)

?Hapalocrinoid Hou et al. 1993[1994], p. 5, pl. 2, figs. 1, 2.
Platycrinoid Lane et al. 1995. pl. 2, figs. 1, 2.
Chinacrinus xinjiangensis Lane et al. 1997, p. 19, figs. 5.10–5.16, 6.1–6.8, 6.10, 6.12.

Chinacrinus xinjiangensis Waters et al. 2003. p. 938, Figure 12.10-12-12.

Diagnosis: A platycrinoid with two primibrachs in each ray, a stem that is circular in outline proximally, becoming elliptical some distance below the calyx, and recurved arms that are uniserial proximally, biserial distally, and completely hide the sides of the calyx where in place.
Specimens: MUST-RCSR-CRI-0007
Occurrence. Samnuuruul Formation, Middle Famennian *(P. rhomboidea* Zone), Hushoot Shiveetiin gol
Description: Specimen laterally crushed slightly. Calyx high bowl-shaped; basals 3, unequal, radials large, with narrow articular facets. Primibrachials 2. Arms missing above secundibrachials, Stem attachment circular.
Remarks: *Chinacrinus xinjiangensis* was the most abundant crinoid in the coeval Hongguleleng fauna in which it was first described. Only a single theca was present in the current study. Although the specimen is missing the characteristic recurved arms, the thecal morphology is sufficient to ascribe the specimen to *Chinacrinus xinjiangensis*.

Family Acrocrinidae Wachsmuth and Springer 1885
Subfamily Acrocrininae Wachsmuth and Springer 1885

Remarks: The defining characteristic of the Acrocrinidae is the presence of numerous intercalaries that separate the bipartite basals from the radials (Moore and Strimple 1969).

Genus *Mongoliacrinus* new genus

Type Species: *Mongoliacrinus minjini* by monotypy.
Etymology: The generic name *Mongoliacrinus* is named for the country of Mongolia.
Diagnosis: An acrocrinid with vase-shaped theca, small basals slightly visible in side view, relatively large tuburculate intercalaries, and radials slightly higher than wide. Radial articular facets about half radial width. Arms large, biserial, pinnulate and pendent.

Mongoliacrinus minjini.
Fig. 6(2) and 7(11)

Diagnosis: Same as diagnosis for genus.
Etymology: The species *Mongoliacrinus minjini* is named in honor of Chuluun Minjin, a pioneer in Mongolian geology.
Specimens: Holotype MUST-RCSR-CRI-0008.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: Large crown with crushed theca. Height 23.7 mm; maximum width at level of radials 20.8 mm. Minimum width at basals 3.0 mm. Crown pyramidal, calyx vase-shaped, arms pendent biserial pinnulate. Basals and radials separated by numerous relatively large polygonal intercalaries. Intercalary plates ornamented with tubercles. Basals two, small, but visible in side view. Flange for stem attachment partially preserved. Anal series not known. Approximately 12 rows of polygonal, predominantly pentagonal and hexagonal intercalaries separate basals from radials. Radials poorly preserved, radials slightly higher than wide. Articular facet about one half radial width. Primibrachials and secundibrachials not preserved. Arms large, biserial, recurved, unbranching as preserved. Arms pinnulate.
Remarks: The Acrocrinidae is a unique family of camerate crinoids having thecae with numerous intercalary plates separating the basals and radials. This is the first report of a Devonian acrocrinid. Previously described genera range in age from the Mississippian (Kinderhookian–Chesterian) to the Pennsylvanian (Moore and Strimple 1969). These genera were all restricted to North America. Moore and Strimple (1969) described ten genera of

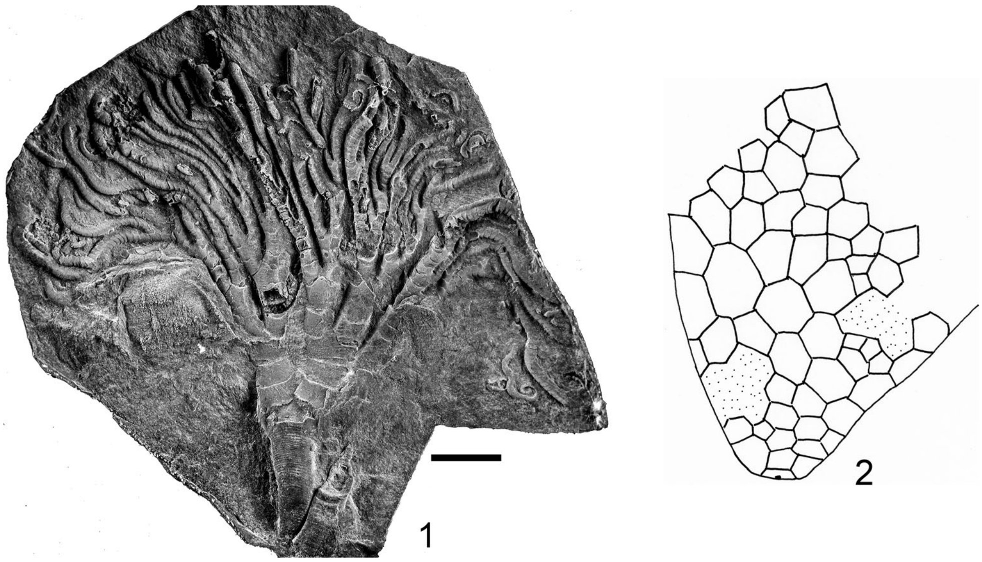

Fig. 6 (1) *Eutaxocrinus ariunai*. Specimen collected from Shiveet Mountain. Large crown with 2 secundibrachials, and long undulating arms coiled at the tips. Scale bar = 1 cm. (2) Plate diagram of *Mongoliacrinus minjini* new genus and species drawn from holotype (MUST-CRI-0008) showing polygonal intercalaries in theca. Compare to Fig. 7–11

acrocrinids divided into two subfamilies. *Mongoliacrinus* is assigned to the Acrocrininae based on thecal shape and the numerous rows of intercalaries.

Although the specimen described herein is crushed obscuring some morphological details, it clearly fits the acrocrinid thecal gestalt with the large vase-shaped theca with numerous intercalaries and large biserial pendent arms.

Mongoliacrinus can be distinguished from *Acrocrinus* based on the shape of the radials, lack of ornamentation on the intercalary plates and the upright arms. *Amphoracrocrinus* has a very different thecal shape and lacks ornamentation on the intercalary plates. *Platyacrocrinus* also has a distinctly different thecal shape and configuration of the radials. Arms are not known.

This occurrence of *Mongoliacrinus* represents the first occurrence of the family in the Devonian and the first occurrence outside North America.

Subclass Disparida Moore and Laudon 1943
Superfamily Allagecrinoidea Carpenter and Etheridge Jr. 1881
Family Anamesocrinidae Goldring 1923
Genus Anamesocrinus Goldring 1923

Anamesocrinus sp.

Specimens: MUST-RCSR-CRI-0009.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: Deeply weathered crown with partial stem, cup and arms preserved on slab. The details of the cup plating are difficult to discern because of weathering. Radials support multiple unbranching arms with long slender brachials.
Remarks: Although the specimen is poorly preserved, the presence of radials supporting multiple atomous arms is a distinctive feature of allagecrinids. Because *Anamesocrinus* is the only genus of the superfamily described from the Hongguleleng, we have assigned the specimen to *Anamesocrinus* sp.

Subclass Cladida Moore and Laudon 1943
Family Scytalocrinidae Moore and Laudon 1943
Genus Julieticrinus Waters et al. 2003

Julieticrinus romeo Waters et al. 2003
Fig. 7(12, 18)

Specimens: *Julieticrinus romeo* is known from eight specimens. MUST-RCSR-CRI-0010-0017.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: Waters et al. (2003) characterized *Julieticrinus romeo* as a scytalocrinoid with low cup and ten arms with conspicuous flanges on alternate sides of each secundibrachial. The flanges on brachials in adjoining rays form conspicuous ledges.
Remarks: Specimens from Hushoot Shiveetiin gol consist of thecae and diagnostic sets of arms missing the cup. Thecae have a low bowl-shaped cup, infrabasals visible in side view and three anal plates in the cup. Second primibrachials are axillary, large, with a prominent ledge projecting outward along distal part of plate. Sets of arms have secundibrachials with prominent spinose flanges on alternating sides of plates. Flanges meet similar flanges on neighboring secundibrachials forming a conspicuous ledge.

Family Pachylocrinidae Kirk 1942
Genus Pachylocrinus Wachsmuth and Springer 1880

Pachylocrinus subpentangularis Waters et al. 2003
Fig. 7(16, 17)

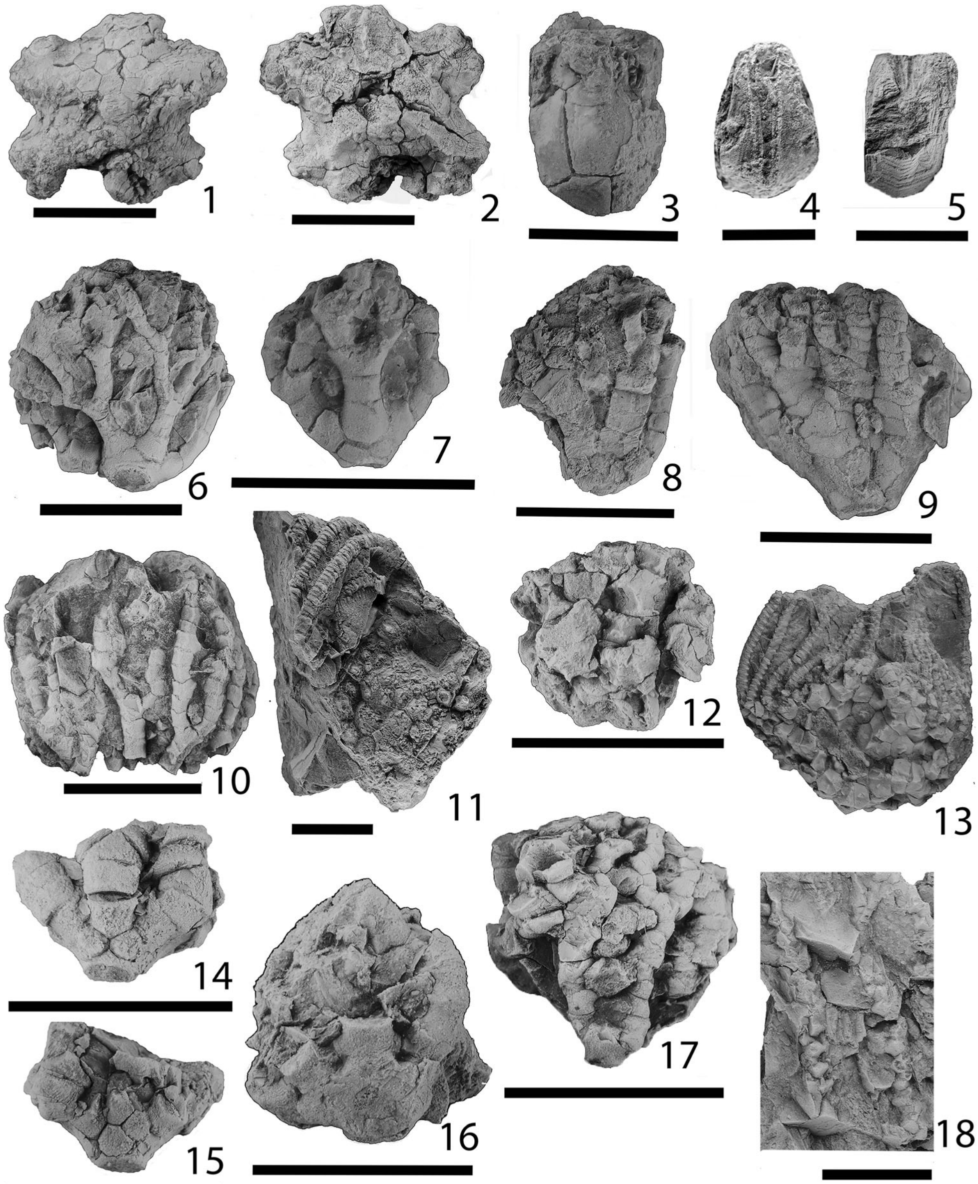

Fig. 7 Crinoids and blastoids from the Famennian of Mongolia. All specimens were collected from Hushoot Shiveetiin gol except as noted. Scale bars 1 cm for crinoids; 5 mm for blastoids. (1, 2) *Abactinocrinus rossi?* (MUST-CRI-0001) oral view showing tegmen (1) and aboral view showing thecal plating (2). Basals missing. Other thecal plates ornamented with diagnostic ridges. (3) *Chinacrinus xinjiangensis* (MUST-CRI-0007) side view of theca showing basals, radials, and arms with 2 primibrachials. (4) *Houiblastus devonicus*. MUST-RCSR-BLA-0001. Partial calyx with large radials and very small deltoids contributing > 5% lateral profile. Radial body pierced by hydrospire tubelets along ambulacral sinus. (5) *Junggaroblastus hoxtolgayensis*. MUST-RCSR-BLA-0002. Fissiculate radial ornamented with growth lines differentially raised into ridges. (6) *Eutaxocrinus sersmaai* (MUST-CRI-0028) Crown showing trapezoidal radials, brachials higher than wide producing slender arms, and no interbrachial plates. (7) A juvenile specimen of *Eutaxocrinus chinaensis* (MUST-CRI-0031). (8) *Grabeauicrinus* (MUST-CRI-0026). (9) *Taxocrinus anomalous* (MUST-CRI-0029). Three primibrachials (the third axillary) in some rays with two primibrachials in others. Arm branching isotomous. (10) *Euonychocrinus* (MUST-CRI-0030) set of arms with regularly spaced ramules. Brachials have prominent petaloid processes. (11) *Mongoliacrinus minjini* new genus and species (MUST-CRI-0008). Large crown with vase-shaped theca composed small bipartite basals separated from radials by rows of intercalary plates. Arms large, biserial, pinnulate, and pendent. (12, 18) *Julieticrinus romeo* partially disarticulated cup (MUST-CRI-0010) (12) with circular stem attachment, infrabasals visible, basals, and radials. Second primibrachials axillary, large, with a prominent ledge (18) (MUST-CRI-0011). Set of arms showing secundibrachials with prominent spinose flanges on alternating sides of plates. (13) *Actinocrinites* sp. (MUST-CRI-0003). Crown with crushed theca. Thecal plates ornamented with knobs and ridges. (14, 15) *Parisocrinus nodosus* (14) (MUST-CRI-0022). Cup wider than high, infrabasals visible in side view, large basals, radials equant, second primibrachial axillary (15) (MUST-CRI-0023). Cup showing three anal plates. (16, 17) *Pachylocrinus subpentangularis* (16) (MUST-CRI-0018). Partial distorted crown showing subpentangular stem attachment, infrabasals visible in side view, and radials ornamented with vermiform ridges. (17) (MUST-CRI-0019) view of opposite side of specimen showing arm branching

Specimens: *Pachylocrinus subpentangularis* is known from 4 specimens. MUST-RCSR-CRI-0018-0021.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: Waters et al. (2003) described *Pachylocrinus subpentangularis* as having a low, cone-shaped cup, infrabasal tips visible in side view of cup, three primibrachials pinched in at the waist and cuneate brachials.
Remarks: *Pachylocrinus subpentangularis* is known from thecal cups and crowns that show diagnostic features described by Waters et al. (2003). Cups are cone-shaped with radials showing vermiform ornamentation. Stem impression is subpentangular. Infrabasals visible in side view. Basals relatively large. Radials wider than high. Three anal plates in the cup. Third primibrachial axillary with higher brachial plates cuneate.

Family Euspirocrinidae Bather 1890
Genus Parisocrinus Wachsmuth and Springer 1880

?Parisocrinus nodosus Waters et al. 2003
Fig. 7(13, 14)

Specimens: *?Parisocrinus nodosus* is known from 4 specimens, MUST-RCSR-CRI-0022-0025.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: Small cup, wider than high, Infrabasals clearly visible in side view. Basals large, convex. Radials equant. Radial facet narrow, horseshoe-shaped, directly outward. Cup plates ornamented with fine nodose pattern. Anal plates not visible nor are arms above the primibrachial. Three proximal columnal plates are observed. Lumen round.
Remarks: Waters et al. (2003) described two new species of cladids *?Parisocrinus nodosus* and *?Parisocrinus conicus.* The specimens in the Mongolian fauna compare favorably with the descriptions of specimens from the Hongguleleng ascribed to *?Parisocrinus nodosus* although they are too incomplete to provide additional information on the veracity of the generic assignment.

Family Decadocrinidae Bather 1890
Genus Grabauicrinus Waters et al. 2003

Grabauicrinus sp.
Fig. 7(8)

Specimens: *Grabauicrinus* sp. is known from one specimen—MUST-RCSR-CRI-0026.
Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.
Description: Partial crown with deeply weathered theca. Stem attachment circular. Crown cylindrical with bowl-shaped cup, infrabasals visible in side view, small basals, radials with plenary facets. Anal plates weathered, but appear to number three. Arms ten branching on third primibrachial.
Remarks: The specimen fits the description of *Grabauicrinus xinjiangensis* in Waters et al. (2003) with the exception of arm branching on the third rather than the second primibrachial. Because the specimen is weathered, we have assigned it to *Grabauicrinus* sp.

Subclass Flexibilia Zittel 1895
Order Taxocrinida Springer 1913
Superfamily Taxocrinoidea Angelin 1878
Family Taxocrinidae Angelin 1878
Genus Eutaxocrinus Springer 1906

Eutaxocrinus ariunai new species
Fig. 6(1)

Diagnosis: A species of *Eutaxocrinus* with large crown, 2 secundibrachials lacking petaloid processes and long gracile, undulating arms coiled at the tips.
Etymology: This species is named for Y. A. Ariunchimeg, Mongolian geologist, who has been invaluable during our fieldwork, and who collected the specimen while sliding down a steep talus slope with a broken arm.
Specimens: The holotype and only known specimen is MUST-RCSR-CRI-0027.
Occurrence: Samnuuruul Formation, Famennian, Shiveet Mountain Locality.
Description: Specimen flattened on shale plate, moldic. Description from latex cast. Crown large (height = 57.5 mm; width = 83 mm at level of secundibrachials). Triangular in outline. Cup relatively large, infrabasals slightly exposed at margins of proxistele. Basals wider than high (H = 4.0 mm; W = 3.0 mm), completely exposed. Radials and primibrachials lack petaloid processes. Primibrachials 2. Secundibrachials 2, tertibrachials 2–4 in all exposed rays. Tips of arms gracile, undulating, tightly coiled at tips in one to two coils. Interradial plates not observed.
Remarks: Lane et al. (1997) provided a chart showing the known distribution of species of *Eutaxocrinus*. All species were known from North America or Europe and ranged from the Silurian to the Mississippian. No species were known from the Famennian. Table 1 updates that chart with four Famennian species subsequently described from the CAOB and Iran. *Eutaxocrinus ariunai* differs from *E. basellus* and *risehensis* in having 2 rather than 3 secundibrachials. *E. chinaensis* and *E. boulongourensis* both have distally coiled arms, but the arms of these two species are robust. In addition, the arms of *E. boulongourensis* do

Table 1 Distribution of species of *Eutaxocrinus*, showing presence (+)/absence (−) of interradial plates, and number of secundibrachials (from Lane et al. (1997) with subsequent additions). *CAOB* Central Asian Orogenic Belt

Location	Age	Species	IBRR +, −	IIBRR
North America	Mississippian	*E. dero* Laudon 1933	+	3
North America	Mississippian	*E. fletcheri* Worthen 1882	+	2.3
North America	Mississippian	*E. montanensis* Springer 1920	+	2.3
North America	Mississippian	*E. pulvinatus* Laudon et al. 1952	–	3–5
CAOB	Famennian	*E. chinaensis* Lane et al. 1997	–	2–4
CAOB	Famennian	*E. boulongourensis* Lane et al. 1997	?	?
CAOB	Famennian	*E. basellus* Lane et al. 1997	–	3
CAOB	Famennian	*E. ariunai* this paper	–	2
CAOB	Famennian	*E. sersmaai* this paper	–	3
Iran	Famennian	*E. risehensis* Webster et al. 2007	–	3
North America	Late Frasnian	*E. alfredi* Goldring 1935	–	3–5
North America	Late Frasnian	*E.? amplus* Springer 1920	+	4
North America	Late Frasnian	*E.? pulcher* Springer 1920	–	4
North America	Late Frasnian	*E. tenuiramosus* Goldring 1935	–	3–5
North America	Late Frasnian	*E. elleri* Goldring 1935	–	3–5
North America	Early Frasnian	*E. alpha* Williams 1882	–	3–4
North America	Early Frasnian	*E. curtus* Williams 1882	–	3–4
North America	Early Frasnian	*E. dumosus* Goldring 1923	–	5–6
North America	Givetian	*E. gracilis* Meek and Worthen 1865	+	3
North America	Givetian	*E.? perplexus* Springer 1920	+	2–5
North America	Givetian	*E. whiteavesi* Springer 1920	–	3
Europe	Givetian	*E. widerneri* Kesling and Strimple 1971	–	3–4
Europe	Givetian	*E.? kergervensis* Le Menn 1985	?	?
Europe	Eifelian	*E. affinus* Müller 1856	+	4
Europe	Eifelian	*E. eifelensis* Springer 1920	–	3
Europe	Eifelian	*E. juglandiformis* Schultze 1867	–	4
Europe	Eifelian	*E. conferprognatus* Schmidt 1952	–	4
Europe	Emsian	*E. prognathus* Schmidt 1934	–	4
Europe	Emsian	*E.sincerus* Schmidt 1932	–	2–5
Europe	Emsian	*E. sturtzii* Follmann 1887	–	4
Europe	Emsian	*E. sturtzii spinifer* Schmidt 1934	–	4
Europe	Emsian	*E. rhenanus* Roemer 1851	–	4
Europe	Emsian	*E. fuchsi* Schmidt 1942	+	3–5
Europe	Emsian	*E. immersus* Dubatolova 1964	–	4
Europe	Emsian	*E. maureri* Schmidt 1942	+	4
Europe	Emsian	*E. patulus* Schmidt 1942	+	3–4
Europe	Emsian	*E. procerus* Schmidt 1942	–	4–5
Europe	Emsian	*E. sandbergeri* Schmidt 1942	+	3–4
Europe	Pragian	None known		
Europe	Lochkovian	None known		
Europe	Silurian	*E. maccoyanus* Salter 1873	–	3–4
Europe	Silurian	*E. oblongatus* Angelin 1878	–	3–4

not branch above the primibrachials and form 3 or 4 complete coils. Arm coiling in these two species thus differs from the slender, gracile, undulating arms of *Eutaxocrinus ariunai*.

Eutaxocrinus sersmaai new species
Fig. 7(6)

Diagnosis: A eutaxocrinid with trapezoidal radials, higher than wide producing slender arms down to primibrachials; two primibrachials lacking petaloid processes, three secundibrachials with petaloid processes; interbrachial plates lacking.

Etymology: The species is named for Sersmaa Gonchigdorj, Mongolian geologist, who has been invaluable during our fieldwork.

Specimens: The holotype and only known specimen is MUST-RCSR-CRI-0028.

Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.

Description: Crown small with maximum width at level of secundibrachials. Arms curve inward distally. Cup relatively large with infrabasals exposed at lateral margin of stem attachment. Basals small, wider than high. Radials trapezoidal shape with radial basal suture wider than suture between radial and first primibrachials. Radials touching except the CD interray where they are separated by high CD basal. Lateral margins of radials arcuate. Primibrachials two in each ray, narrower than radial, lacking petaloid processes. Secundibrachials 3 in each ray with prominent petaloid processes. Interbrachial plates not observed.

Remarks: The distinctive trapezoidal shape of the radials results in a narrower suture with the primibrachial. As a result, the arms are narrower than in other Famennian species of *Eutaxocrinus* producing a more open crown. Other species tend to have a more massive aspect to the crown. *Eutaxocrinus sersmaai* differs from *Eutaxocrinus ariunai* in having 3 secundibrachials rather than 2. Although the distal tips of the arms of *Eutaxocrinus sersmaai* are incurved, they differ from the undulating and coiling seen in the distal arms of *Eutaxocrinus ariunai*.

Eutaxocrinus chinaensis Lane et al. 1997
Fig. 7(7)

1993 [1994] *Eutaxocrinus* sp. Hou et al., pp. 6–7, pl. 21, figs. 9, 10, 12, 13.
1995 *Eutaxocrinus* sp. Lane et al., pl. l, figs. 9, 10, 12, 13.
1997 *Eutaxocrinus chinaensis* Lane, N. G., J. A. Waters and C. G. Maples, pp. 20–24. Figures Figs. 7.1–7.3, 7.6, 7.12–7.14, 8.1–8.5
2003 *Eutaxocrinus chinaensis* Waters et al., p. 938, Figures 9.6, 12.13.

Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.

Remarks: Twelve specimens (MUST-RCSR-CRI-0031-0042) including two juveniles are assigned to *Eutaxocrinus chinaensis* based on the robust triangular architecture of the crown.

Genus *Taxocrinus* Phillips in Morris, 1843

Taxocrinus anomalus Waters et al. 2003
Fig. 7(9)

Specimens: The only known specimen is stored in the Paleontological Institute Mongolia (MUST-RCSR-CRI-0029).

Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.

Description: Crown expanding upward to level of secundibrachials, then constricting in width distally. Cup low, broad, small, infrabasals completely covered by stem. Basals small, projecting beyond stem attachment, all approximately equal in size, CD basal not identified. Radials high, broad, in lateral contact all around cup, not separated by enlarged CD basal. Relative large hexagonal interradial plate presumed to be anal plate. Small polygonal interradial plates seen in two rays. Three primibrachials (the third axillary) in some rays. Other rays appear to have two primibrachials. All arm branching isotomous. Three secundibrachials in each half ray, the distal one axillary. Tertibrachials up to seven per quarterray. Stem unknown.

Remarks: The specimen is comparable to the figures and description of *Taxocrinus anomalus* in Waters et al. (2003), with the distinctive feature of five equally sized basals being a key character. The authors expressed concern that the configuration of the basals might be an aboration. The discovery of a second specimen from a different locality with the same configuration reduces that concern. The Mongolian specimen preserves an anal plate and polygonal interradial plates lacking in the specimen from the Hongguleleng Formation.

Family Synerocrinidae Jaekel 1918
Genus *Euonychocrinus* Strimple 1940

Euonychocrinus sp.
Fig. 7(9)

Specimens: The only known specimen is MUST-RCSR-CRI-0030.

Occurrence: Samnuuruul Formation, Middle Famennian (*P. rhomboidea* Zone), Hushoot Shiveetiin gol.

Remarks: The specimen is a more or less complete set of arms with the theca and primibrachials missing. The specimen is assigned to *Euonychocrinus* based on the presence of regularly spaced ramules on the arms, which are composed of brachials with prominent petaloid processes.

Conclusions

The crinoid fauna described from Hushoot Shiveetiin gol is the largest and most diverse Palaeozoic crinoid fauna from Mongolia. The two genera of blastoids are the first reports of the class from Mongolia although they are based on partial thecae. The crinoids and blastoids were living on an active island arc complex in the CAOB in a high physical stress environment with frequent and often voluminous pyroclastic eruptions.

Crinoids and blastoids suffered a major extinction event at the Givetian/Frasnian boundary before diversifying globally into the "Age of Crinoids" during the Mississippian (Kammer and Ausich 2006). Globally, information is lacking on Late Devonian echinoderm faunas compared to Middle Devonian and Early Mississippian faunas, so any new Famennian echinoderm fauna is significant.

Waters and Webster (2009) reviewed Famennian echinoderm palaeoecology, community structure, and palaeobiogeography. Famennian echinoderm faunas are rare in eastern North America and Europe reflecting a tectonically derived sedimentological megabias. The most abundant and diverse Famennian echinoderm fauna currently known is from the Hongguleleng Formation located in the CAOB as discussed earlier in the paper. Patterns of biogeographic distribution, morphologic evolution and the stratigraphic distribution of echinoderms from the Hongguleleng indicate that it was a Famennian biodiversity hotspot. The Mongolian echinoderm fauna is similar to the Hongguleleng fauna and supports the hypothesis that the CAOB was a biodiversity hotspot for Famennian echinoderms and a precursor to the very successful echinoderm communities that dominated Mississippian shallow-marine ecosystems globally.

The CAOB in general and Mongolia in particular remain prime areas for future discoveries of Palaeozoic echinoderm communities given the large expanse of outcrop area, the complex palaeogeographic and palaeoecological relationships of the terranes in the CAOB and the paucity of detailed stratigraphic and palaeontological examination to date.

Acknowledgments We thank the entire Mongolian team for their tremendous support in preparing the expedition and facilitating our time in the field under difficult circumstances. O. Pascall and A. Dombrowski were instrumental in preparing the structural map of the locality and measuring the stratigraphic section. J. A. Waters and S. K. Carmichael received support from National Geographic (CP-113R-17) and Appalachian State University. P. Königshof received funding from Deutsche Forschungsgemeinschaft (DFG-KO-1622/19-1). M. Ariuntogos received funding from the German Academic Exchange Service (DAAD, Research Grant—Doctoral Programe in Germany, September 1, 2018–September 1, 2021; 57381412). This paper is a contribution to IGCP Project 652 (Reading geologic time in Paleozoic rocks: the need for an integrated stratigraphy [2017–2021]). The manuscript was significantly improved by reviews by J. E. Bauer and an anonymous reviewer.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Angelin, N. P. (1878). *Iconographia crinoideorum in stratis Sueciae Siluricis fossilium* (pp. 1–62). Stockholm: Samson and Wallin.

Ariunchimeg, Ya., Bayasgalan, A., Waters, J.A., Kido, E., Suttner, T.J., Sersmaa, G., Undariya, J., & Otgonbaatar, D. (2014). IGCP 596 IGCP 580 Field Workshop Guidebook. 8–18th August 2014, Ulaanbaatar, Mongolia. *Paleontological Center, Mongolian Academy of Sciences*, pp. 1–55.

Ariuntogos, M., Königshof, P., Hartenfels, S., Jansen, U., Nazik, A., Carmichael, S.K., Waters, J.A., Sermaa, G., Cronier, C., Ariunchimeg, YA., Pascall, O., Dombrowski, A. (in press). The Hushoot Shiveetiin gol section (Baruunhuurai Terrane): sedimentology and facies from a Late Devonian island arc setting. *Palaeobiodiversity and Palaeoenvironments*, (this issue).

Austin, T., & Austin, T. Jr. (1842). XVIII-Proposed arrangement of the Echinodermata, particularly as regards the Crinoidea, and a subdivision of the Adelostella (Echinidae). *Annuals and Magazine of Natural History*, *series l*, *10/63*, 291–294.

Badarch, G., Cunningham, W. D., & Windley, B. F. (2002). A new terrane subdivision for Mongolia: implications for the Phanerozoic crustal growth of Central Asia. *Journal of Asian Earth Sciences, 21*, 87–104.

Bather, F.A. (1890). The classification of the Inadunata Fistulata (cont.). *Annals and Magazine of Natural History*, *6/5*, 485–486.

Blakey, R. (2016). Devonian - 380 Ma, global paleogeography and tectonics in deep time series. Deep Time Maps™ Paleogeography.

Breimer, A., & Joysey, K. A. (1968a). Anatomical studies of *Orbitremites* and *Ellipticoblastus* (Blastoidea) I. *Proceedings of the Koninklijke Nederlandsche Akademie van Wetenschappen- Amsterdam, B 71*, 175–190.

Breimer, A., & Joysey, K.A. (1968b). Anatomical studies of *Orbitremites* and *Ellipticoblastus* (Blastoidea) II. *Proceedings of the Koninklijke Nederlandsche Akademie van Wetenschappen- Amsterdam*, *B 71*, 191–202.

Brower, J. C. (1967). The actinocrinid genera, Abactinocrinus, Aacocrinus and Blairocrinus. *Journal of Paleontology, 41*, 675–705.

Carpenter, P.H., & Etheridge, R., Jr. (1881). Contributions to the study of the British Paleozoic crinoids - no. I. On *Allagecrinus*, the representative of the Carboniferous limestone series: *Annuals & Magazine Natural History*, *5/7*, 281–298.

Dubatolova, Y.A. (1964). Morskikhliliy devona Kuzbassa. *Akademie Nauk SSSR, Sibirsk Otdel Institut Geologii i Geofiziki, Trudy*, pp. 1–152 Eichwald.

Etheridge, R., Jr., & Carpenter, P.H. (1886). Catalogue of the Blastoidea in the Geological Department of the British Museum (Natural History), with an account of the morphology and systematic position of the group, and a revision of the genera and species. British Museum, London, pp. 1–322.

Fay, R. O. (1964). An outline classification of the Blastoidea. *Oklahoma Geology Notes, 24*, 81–90.

Follmann, O. (1887). Unterdevonische Crinoiden. *Verhandlungen des naturhistorischen Vereins der preußischen Rheinlande und Westfalen*, *5/4*, 113–138.

Goldring, W. (1923). The Devonian crinoids of the state of New York. *New York State Museum Memoir, 16*, 1–670.

Goldring, W. (1935). Some upper Devonian crinoids from New York. *Annals of the Carnegie Museum, 24*(164), 337–349.

Hara, H., Kurihara, T., Kuroda, J., Adachi, Y., Kurita, H., Wakita, K., Hisada, K., Charusiri, P., Charoentitirat, T., & Chaodumrong, P. (2010). Geological and geochemical aspects of a Devonian siliceous succession in northern Thailand: implications for the opening of the Paleo-Tethys. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *297/ 2*, 452–464.

Hou, H. F., Lane, N. G., Waters, J. A., & Maples, C. G. (1993 [1994]). Discovery of a new Famennian echinoderm fauna from the Hongguleleng formation of Xinjiang, with redefinition of the formation. *Stratigraphy and Paleontology of China, 2*, 1–18.

Jaekel, O. M. J. (1918). Phylogenie und System der Pelmatozoen. *Paläontologische Zeitschrift, 3*, 1–128.

Jell, P. A., & Jell, J. S. (1999). Crinoids, a Blastoid and a Cyclocystoid from the Upper Devonian Reef Complex of the Canning Basin, Western Australia. *Memoirs of the Queensland Museum, 43*, 201–236.

Kammer, T. W., & Ausich, W. I. (2006). The "Age of Crinoids", a Mississippian biodiversity spike coincident with widespread carbonate ramps. *PALAIOS, 21*, 238–248.

Kido, E., Suttner, T. J., Waters, J. A., Ariunchimeg, Y., Sersmaa, G., Atwood, J. W., & Webster, G. D. (2013). Devonian deposits of the Baruunhuurai Terrane, western Mongolia (IGCP 596 Field Workshop). *Episodes, 36*, 242–254.

Kesling, R. V., & Strimple, H. L. (1971). *Eutaxocrinus wideneri*, a new flexible crinoid from the Middle Devonian Silica Formation of northwestern Ohio. *University of Michigan, Contributions of the Museum of Paleontology, 23*, 291–303.

Kirk, E. (1942). *Rhopocrinus*, a new fossil inadunate crinoid genus. *United States National Museum Proceedings, 92*, 151–155.

Lane, N. G., Waters, J. A., & Maples, C. G. (1997). Echinoderm faunas of the Hongguleleng formation, Late Devonian (Famennian), Xinjiang-Uygur Autonomous Region, China. *Paleontological Society Memoir, 47*, 1–43.

Lane, N. G., Maples, C. G., & Waters, J. A. (2001a). Revision of Late Devonian (Famennian) and some Early Carboniferous (Tournaisian) crinoids and blastoids from the type Devonian area of North Devon. *Palaeontology, 44*, 1043–1080.

Lane, N. G., Maples, C. G., & Waters, J. A. (2001b). Revision of Strunian crinoids and blastoids from Germany. *Paläontologische Zeitschrift, 75*, 233–252.

Lane, N.G., Maples, C.G., Waters, J.A., & Marcus, S.A. (1995). Paleozoic echinoderms from China. *Mid-American Paleontological Society (M.A.P.S.) Digest*, *18*, 84–97.

Laudon, L. R. (1933). The stratigraphy and paleontology of the Gilmore City Formation of lowa. *Iowa University Studies in Natural History, 15*, 1–74.

Laudon, L. R., Parks, J. M., & Spreng, A. C. (1952). Mississippian crinoid fauna from the Banff Formation, Sunwapta Pass, Alberta. *Journal of Paleontology, 27*, 505–536.

Laudon, L. R., & Severson, J. L. (1953). New crinoid fauna: Mississippian Lodgepole Formation, Montana. *Journal of Paleontology, 27*, 505–536.

Le Menn, J. (1985). Les crinoides du Devonien inferieur et moyen du massif Armoricain. *Memoires de la Societe Geologique et Mineralogique de Bretagne, 30*, 1–268.

Matsumoto, H. (1929). Outline of a classification of Echinodermata. *The Science Reports of the Tohoku Imperial University*, *Sendai*, *Japan*, *series 2 (Geology) 13*, 27–33.

Meek, F.B., & Worthen, A.H. (1865). Descriptions of new species of Crinoidea, etc. from the Carboniferous rocks of Illinois and some of the adjoining states. *Proceedings of the Academy of Natural Sciences*, *Philadelphia*, *Series I/17*, 143–155.

Metcalfe, I. (2011). Tectonic framework and Phanerozoic evolution of Sundaland. *Gondwana Research*, *19/ 1*, 3–21.

Miller, J. S. (1821). *A natural history of the Crinoidea or lily-shaped animals, with observations on the genera Asteria, Euryale, Comatula, and Marsupites* (pp. 1–150). Bristol, England: Bryan and Co..

Moore, R. C. (1952). Evolution rates among crinoids. *Journal of Paleontology, 26*, 338–352.

Moore, R.C., & Laudon, L.R. (1943). Evolution and classification of Paleozoic crinoids. *Geological Society of America*, *Special Paper 46*, 1–153.

Moore, R. C., & Strimple, H. L. (1969). Explosive evolutionary differentiation of unique group of Mississippian - Pennsylvanian crinoids (Acrocrinidae). *The University of Kansas Paleontological Contributions. Paper, 39*, 1–43.

Müller, J. (1856). Über neue Crinoidean aus dem Eifeler Kalk. *Kaiserliche Akademie der Wissenschaften Berlin, Monatsberichte 1*, 353–356.

Phillips, J. (1843). Genus *Taxocrinus*, In J. Morris (ed.), A catalogue of British fossils, comprising all the genera and species hitherto described; with reference to their geological distribution and to the localities in which they have been found. John Van Voorst. London, p. 59.

Rhenberg, E. C., Ausich, W. I., & Kammer, T. W. (2015). Generic concepts in the Actinocrinidae Austin and Austin, 1842 (class Crinoidea) and evaluation of generic assignments of species. *Journal of Paleontology, 89*, 1–19.

Roemer, C. F. (1851). Beiträge zur Kenntnis der fossilen Fauna des devonischen Gebirges am Rhein. *Verhandlungen des naturhistorischen Vereins der preußischen Rheinlande und Westfalen, 8*, 357–376.

Rozhnov, S.V., Minjin, Ch., & Kushlina, V.B. (2009). The first record of echinoderms in the Ordovician of Mongolia: biogeographical significance, In Abstracts of Meeting of Project IGCP 503 Early Palaeozoic Biogeography and Palaeogeography (Copenhagen, 2009).

Salter, J. W. (1873). *A catalogue of the collection of Cambrian and Silurian fossils contained in the Geological Museum of the University of Cambridge* (pp. 1–204). Cambridge: University Press.

Say, T. (1825). On two genera and several species of Crinoidea. *Journal of the Academy of Natural Sciences of Philadelphia*, *series l 4*, 289–296. [Reprinted in Bulletins of American Paleontology 1, 347–354].

Schmidt, W. E. (1932). Crinoideen und Blastoideen aus dem jüngsten Unterdevon Spaniens. *Palaeontographica, 76*, 1–34.

Schmidt, W. E. (1934). Die Crinoideen des Rheinischen Devons. Teil I, Die Crinoideen des Hunsrückschiefers. *Abhandlungen der Preußischen Geologischen Landesanstalt N.F.*, *163*, 1–149.

Schmidt, W. E. (1942). Die Crinoideen des Rheinischen Devons. Teil II. A. Nachtrag zu: Die Crinoideen des Hunsrückschiefers. B. Die Crinoideen des Unterdevons bis zur Cultrijugatus-Zone (mit Ausschluss des Hunsrückschiefers). *Abhandlungen der Preußischen Geologischen Landesanstalt N.F.*, *182*, 1–253.

Schmidt, W. E. (1952). Crinoides y Blastoideos del Devonica inferior de Asturias. *Publicatione Alemana, Geologie España, 6*, 119–182.

Schultze, L. (1867). Monographie der Echinodermen des Eifeler Kalkes. *Denkschrift der Mathematisch Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, 26(2)*, 113–230.

Spalletta, C., Perri, M. C., Over, D. J., & Corradini, C. (2017). Famennian (Upper Devonian) conodont zonation: revised global standard. *Bulletin of Geosciences, 91*, 31–57.

Springer, F. (1906). Discovery of the disk of *Onychocrinus*, and further remarks on the Crinoidea Flexibilia. *Journal of Geology, 14*, 467–523.

Springer, F. (1913). Crinoidea 2, In K. A. von Zittel (ed.), (C.R. Eastman, transl. and ed.). Textbook of Paleontology. Macmillan and Co., Ltd., London, pp. 173–243.

Springer, F. (1920). The Crinoidea Flexibilia. *Smithsonian Institution, Publication, 2501*, 1–486.

Strimple, H.L. (1940). 940a, four new crinoid species from the Wewoka formation and two from the Ochelata group. *Bulletin of America Paleontology, 25*, p.92.

Stukalina, G. A. (1973). Pozdnepaleozoiskie Morskie Lilii Zabaikalya i Mongolii [Late Pale- ozoic crinoids of Transbaikal and Mongolia]. In A. G. Pormnov, & A. I. Suzukov, (Eds.), Stratigrafiyi i

Paleontologiya Osadochnkh Geologicheskik kh Formapii Zabaikalya [Stratigraphy and Paleontology of the Sedimentary Geological Formations of Transbaikal]. *Geograficheskoe Obshchestvo SSSR. Zapiski Zabaikalskogo Filiala, 94*, 16–55.

Stukalina, G. A. (1994). Kharakteristike Siluriiskikh krinoidei Mongolii [characteristics of Silurian crinoids of Mongolia]. *Paleontologicheskii Zhurnal, 4*, 55–63 (English translation in Paleontological Journal, 1995, 28:73–82).

Stukalina, G. A. (1997). Novie Kamennougolnie morskie lilii Mongolii [new carboniferous crinoids from Mongolia]. *Paleontologicheskii Zhurnal*, *6*, 39–43 (English translation in Paleontological Journal 31, 605–608).

Suttner, T.J., Kido, E., Ariunchimeg, YA., Sersmaa, G., Waters, J.A., Carmichael, S.K., Batchelor, C.J., Ariuntogos, M., Hŭskovág, A., Slavík, L., Valenzuela-Ŕıos, J.I., Liao, J.-C., & Gatovsky, Y.A. (2019). Conodonts from Late Devonian island arc settings (Baruunhuurai Terrane, western Mongolia). *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*. 1–22. https://doi.org/10.1016/j.palaeo.2019.03.

Tungalag, F. (1998). Carboniferous crinoids of Bayankhongaor area. *Mongolian Geoscientist, 8*, 2–3.

Von Zittel, K. A. (1895). Grundzüge der Paläontologie (Paläozoologie), 1st edition. R. *Oldenbourg, München, Berlin, 1895*, 1–971.

Wachsmuth, C., & Springer, F. (1880). Revision of the Palaeocrinoidea, part l. The families lchthyocrinidae and Cyathocrinidae. *Academy of Natural Sciences, Philadelphia, Proceedings for, 1879*, 226–378.

Wachsmuth, C., & Springer, F. (1885). Revision of the Palaeocrinoidea, part 3, sec. I. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions. *Academy of Natural Sciences, Philadelphia, Proceedings for, 1884*, 223–364.

Waters, J. A., & Horowitz, A. S. (1993). Ordinal level evolution in the Blastoidea. *Lethaia, 26*, 207–213.

Waters, J. A., Maples, C. G., Lane, N. G., Marcus, Liao, S. Z., Liu, L., Hou, H. F., & Wang, J. X. (2003). A quadrupling of Famennian pelmatozoan diversity: New Late Devonian blastoids and crinoids from Northwest China. *Journal of Paleontology, 77*, 922–948.

Waters, J. A., & Webster, G. D. (2009). A re-evaluation of Famennian echinoderm diversity:implications for patterns of extinction and rebound in the Late Devonian. In P. Königshof, (ed.). Devonian Change: Case Studies in Palaeogeography and Palaeoecology. *The Geological Society of London. Special Publications*, *314*, 149–161.

Webster, G. D., & Ariunchimeg, Y. (2004). The northern most Emsian crinoids known, a Devonian fauna from the Chuluun Formation, Shine Jinst area, Southern Mongolia. *Geobios, 37*, 481–487.

Webster, G. D., Maples, C. G., & Yazdi, M. (2007). Late Devonian and Early Mississippian echinoderms from central and northern Iran. *Journal of Paleontology, 81*, 1101–1113.

Webster, G. D., & Waters, J. A. (2009). Late Devonian echinoderms from the Hongguleleng Formation of Northwestern China. In P. Königshof (ed.). Devonian Change: case studies in Palaeogeography and Palaeoecology. *The Geological Society, London*, *Special Publications, 314*, 263–287.

Webster, G. D., Hafley, D. J., Blake, D. B., & Glass, A. (1999). Crinoids and stelleroids (Echinodermata) from the broken rib member, dyer formation (Late Devonian, Famennian) of the White River Plateau, Colorado. *Journal of Paleontology, 73*, 461–486.

Whidborne, G. F. (1898). A monograph of the Devonian fauna of the south of England, volume 3, the fauna of the Marwood and Pilton beds. *Palaeontological Society of London, pp.*, 1–236.

Williams, H. S. (1882). New crinoids from the rocks of the Chemung period of New York State. *Academy Natural Sciences*, *Philadelphia*, *Proceedings* 17–34.

Windley, B. F., Alexeiev, D., Xiao, W. J., Kröner, A., & Badarch, G. (2007). Tectonic models for accretion of the Central Asian Orogenic Belt. *Journal of the Geological Society (London), 164*, 31–47.

Worthen A.H. (1882). Descriptions of fifty-four new species of crinoids from the Lower Carboniferous limestones and coal measures of Illinois and Iowa. *Illinois State Museum Natural History*, *Bulletin l*, 1–38.

Xiao, W., Huang, B., Han, C., Sun, S., & Li, J. (2010). A review of the western part of the Altaids: a key to understanding the architecture of accretionary orogens. *Gondwana Research*, *18/2*, 253–273.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.