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1 First report of lepidocystid echinoderm in the Cambrian of North China:
2 Evolutionary and Palaeobiogeographic implications

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17
18 Keywords: Blastozoa; Lepidocystidae; Palaeobiogeography; Evolution; North China; Cambrian

19
20 Abstract:

21 The diversification of the earliest echinoderms is "explosive" in both space and time. Lepidocystids are the most basal
22 blastozoans and their earliest known occurrences (Cambrian Series 2) provide crucial evidence on the dispersal of early
23 echinoderms. Here we report a new lepidocystid *Vyscystis? spinosa* sp. nov. based on well-preserved specimens from the
24 Cambrian (Series 2, Stage 4) Mantou Formation in North China. *Vyscystis? spinosa* sp. nov. is characterized by a long aboral
25 imbricate cup, flattened tessellate oral surface and coiled brachioles. The aboral cup is composed of imbricate plates with
26 nipple-shaped ornamentation. *Vyscystis? spinosa* sp. nov. documents the first occurrence of lepidocystids in North China
27 Block and thus contributes to increase the taxonomic diversity and global distribution of early blastozoans.
28 Palaeogeographical analysis indicates that there are biogeographic connections among North China, west Gondwana and
29 Laurentia in early Cambrian, and the palaeogeographic expansion in Cambrian eocrinoids precedes the taxonomic
30 diversification.

1. Introduction

Our knowledge of morphological disparity and ecological diversity in early echinoderms has significantly increased in recent years, revealing the importance of early blastozoans in the structuration of Cambrian ecosystems (e.g. Dornbos, 2006; Zamora et al., 2012; Smith et al., 2013; Deline et al., 2020). However, the initial diversification of blastozoans remains poorly known, as well as their phylogenetic relationships with other major echinoderm groups (e.g. "carpoids", crinoids, edrioasteroids), which are still unresolved and controversial (Nardin et al., 2009; Nardin et al., 2017; Rahman and Zamora, 2024). Lepidocystids, a small group of blastozoans, characterized by a strongly differentiated 'calyx' with both tessellate and imbricate plates, are widely acknowledged as the most basal blastozoans (e.g. Sprinkle, 1973; Paul & Smith, 1984; Zamora et al., 2013; Nardin et al., 2017; Nohejlová et al., 2019). They have been reported from western Gondwana and Laurentia, where they range from Cambrian Stage 3 to the Drumian (Sprinkle, 1973; Fatka & Kordule, 1990; Smith et al., 2013; Nardin et al., 2017; Nohejlová et al., 2019). This family includes three genera *Lepidocystis* Foerste, 1938, *Kinzercystis* Sprinkle, 1973, and *Vyscystis* Fatka & Kordule, 1990. Although new echinoderm materials were reported in recent years from China, no convincing lepidocystid remains have been documented (Parsley et al., 2006; Hu et al., 2007; Zhao et al., 2007; 2008; Huang et al., 2012). Recent studies demonstrate that North China is an important new area for studying Burgess Shale-type Lagerstätten (Sun et al., 2020a, 2020b). On the basis of continuous ongoing research, here we report *Vyscystis? spinosa* sp. nov. from the basal Mantou Formation (Cambrian Stage 4, Series 2) in Jiangsu Province, which is the first lepidocystid described from North China. This study aims to provide a detailed morphological description of this new taxon, to review the geographical distribution of early blastozoans in Cambrian and, finally to review our current knowledge on their early diversification.

2. Materials and methods

The studied outcrop is situated in a quarry close to the Xiaobeiwan (34°14'7.14"N, 117°6' 34.78"E) and Dananzhuang (34°27'41.02"N, 117°22' 33.98"E) villages, in the northern part of Jiangsu Province, North China (Fig. 1). The Cambrian succession is well exposed in the studied area. The Mantou Formation ranges from the middle Cambrian Stage 4 to the top of the Wuliuan. This lithostratigraphic unit is characterized by widely distributed siliciclastic deposits in the North China Block. In this study, the definition of the Mantou Formation follows Zhang et al. (1996), and thus corresponds to the Maozhuang, Xuzhou and Mantou formations.

All specimens of *Vyscystis? spinosa* sp. nov. were collected from purple mudstones in the lower part of the Mantou Formation together with numerous hyoliths and trilobites (e.g. *Redlichia murakamii*). This level occurs in the *Redlichia chinensis* trilobite Zone, corresponding to the Cambrian Stage 4 in the international global stratigraphic chart (Peng, 2009; Geyer, 2019). This new horizon is equivalent in age to the Balang Formation in South China and to the Kinzers Formation in

61 Laurentia, which both yielded an abundant and diverse echinoderm fossil record. In addition, it is slightly older than Kaili
62 Formation from South China, which yielded diverse echinoderm fossils too (Kaili Biota, ~508Ma).

63 The material of *Vyscystis? spinosa* sp. nov. includes 8 complete well-preserved individuals, 10 slightly disarticulated
64 specimens (only preserved with fractional imbricate aboral appendage) and massive amount (over 100) of disarticulated
65 specimens, mainly isolated plates. All of them are preserved as natural molds in mudstones. Therefore, few latex casts were
66 made to produce the original aspect of their morphology. Since most specimens are highly weathered, it was too risky and
67 thus not allowed to cast the most important specimens with preserved oral surface. To prevent damage to the fossil specimens,
68 we made a CT-scan of the best-preserved specimen instead. Studied material is housed in the Nanjing Institute of Geology
69 and Palaeontology, Chinese Academy of Sciences (NIGPAS). Photographs were taken using a Nikon D810 camera with a
70 Nikkor AF-S 105 mm lens. Composite images integrating fossil anatomy were produced by merging precisely aligned photos
71 in Adobe Photoshop 2020. Detailed anatomy of *Vyscystis? spinosa* sp. nov. was captured using a Carl Zeiss SteREO Discovery
72 V16 microscope linked to an AxioCam HR3 digital microscope CCD camera. The specimen NIGP176283 was subjected to
73 tomographic analysis using a Carl Zeiss Xradia 520 Versa X-ray tomographic microscope. Slice data were analyzed and
74 manipulated using VGStudioMax. All analysis was done at the State Key Laboratory of Palaeobiology and Stratigraphy,
75 NIGPAS.

76 3. Results

77 Systematic Palaeontology

78 Phylum **Echinodermata** Klein 1778

79 Subphylum **Blastozoa** Sprinkle, 1973

80 Family **Lepidocystidae** Durham, 1968

81 **Remarks.** Lepidocystid echinoderms were originally assigned to their own distinct class, Lepidocystoidea (Durham, 1968).
82 In Sprinkle's classification (1973), lepidocystids were considered as a new order (Imbricata) within the class Eocrinoidea.
83 Recent studies suggest that the class Eocrinoidea represents a paraphyletic assemblage of blastozoans and thus, can not be
84 considered as a valid taxon. Therefore, lepidocystids are here considered as a distinct family of early blastozoans (see Nardin
85 et al. 2017; Nohejlová et al. 2019). The diagnosis of the family was emended by Nardin et al. (2017). Currently three genera
86 have been assigned to the family Lepidocystidae: *Lepidocystis*, *Kinzercystis* (both from Cambrian Series 2 of Laurentia) and
87 *Vyscystis* (Miaolingian of European peri-Gondwana) (Ubaghs, 1968; Sprinkle, 1973; Paul and Smith, 1984; Smith, 1984;
88 Parsley and Zhao, 2006; Nardin et al., 2017; Nohejlová et al. 2019).

89
90 Genus *Vyscystis* Fatka & Kordule, 1990

91 **Type Species.** *Vyscystis ubaghsi* Fatka & Kordule, 1990. Jince Formation (Drumian, Miaolingian), Příbram-Jince
92 Basin (Czech Republic).

93 **Diagnosis.** (emended from Nohejlová et al. 2019). Cone-shaped aboral cup consisting of adorally overlapping imbricate
94 plates, without epispires. Flattened tessellate oral surface made of numerous adjacent polygonal plates, bearing epispires.
95 Curved ambulacra showing a 2-1-2 pattern, extending over oral surface toward lateral edge. Coiled brachioles mounted
96 unilaterally to ambulacral ray. Mouth close to centre of oral surface.

97 **Remarks.** Two species are assigned here to the genus *Vyscystis*: *V. ubaghsi* (Drumian, Czech Republic) and, tentatively,
98 *Vyscystis? spinosa* sp. nov. (Stage 4, China).

99 *Vyscystis? spinosa* sp. nov.

100 **Figs. 2-5**

101 **Zoobank** LSID: urn:lsid:zoobank.org:act:AA0DF88E-B37F-4D9F-8BA4-FFA3E258DB40

102 **Derivation name/ Etymology.** Species name from the Latin *spinosa*, reference to the presence of the nipple-shaped
103 ornamented plates.

104 **Diagnosis.** A species of *Vyscystis?* with nipple-shaped ornamentation on imbricate cup plates.

105 **Material.** Eight complete specimens, ten slightly disarticulated individuals and over 100 incomplete ones (preserved distal
106 parts of the aboral cup and isolated imbricate plates with diagnostic nipple-shaped ornamentation (umbo)).

107 **Holotype:** NIGP176281 (Fig. 2A, B)

108 **Paratypes:** NIGP176282 (Fig. 2C, D)

109 **Horizon and locality/Occurrence.** *Redlichia chinensis* Zone (Cambrian Series 2, Stage 4), lower Mantou Formation at
110 Dananzhuang section, Xuzhou city, Jiangsu Province, North China.

111 **Description.**

112 Large body wall composed of cone-shaped aboral cup closed by flattened oral surface bearing the ambulacral system.
113 Conical aboral cup made of imbricate adorally overlapping plates without epispires. Aboral cup relatively elongate (especially
114 in incomplete specimens without oral surface), about twice longer than wide, length of aboral cup varying from 14 mm to 32
115 mm, width varying from 4 mm to 10 mm. Body wall narrowing distally. Plates wide, often lenticular in shape, decreasing in
116 size aborally. Imbricate plates gradually increasing in size adorally by a factor of about 3, from about 0.6 mm in length (major
117 axis) and 0.5 mm in width (minor axis) (aboral extremity) to 1.8 mm in length (major axis) and 0.9 mm in width (minor axis)
118 (adorally) (Fig. 2C, D, Fig. 4, Fig. 5). Lenticular cup plates bearing a strong, central, nipple-shaped umbo (Fig. 2G). Nipple-
119 shaped umbos one or two times as long as the plates (Figs. 2-4). In some specimens, aboral cup ending with a discoidal
120 attachment zone made of small roundish plates (Fig. 5).

121 Flattened oral surface circular in outline, composed of numerous polygonal adjacent plates. Tessellate plates bearing small
122 epispires (Fig. 3A, B, Fig. 4D). Tessellate portion reduced, about one eighth of the length of imbricate one. Ambulacral system
123 confined to the oral surface, but precise pattern difficult to assess because of insufficient preservation. Anal pyramid,
124 hydropore and gonopore unknown. Ambulacra probably with 2-1-2 pattern. Peristome in the central part of the oral surface.

125 Coiled brachioles originating at the border of peristomial area, being mounted on two large ambulacral flooring plates (Fig.
126 4B). Brachioles biserial composed of polygonal plates. Maximum number of preserved brachioles: eight. A minimal estimate
127 of the maximum length of brachiole: about 9.6 mm (Figs. 2A, 3C, D). Brachioles composed of numerous alternating biserial
128 flooring plates (Fp), bearing food groove on adoral surface. Food groove covered by two sets of opposite, staggered cover
129 plates (Cp), about 100 μm in length. Flooring plates pentagonal and unornamented, alternating in a biserial pattern (Fig. 3B-
130 E).

131 **Remarks.** The Chinese echinoderm *Vyscystis? spinosa* possesses distinctive features of the family Lepidocystidae, such as a
132 cone-shaped aboral cup made of imbricate plates and a well-defined oral surface consisting of epispire-bearing, tessellate
133 elements. *Vyscystis? spinosa* exhibits distinct features compared to other lepidocystids (*Lepidocystis* and *Kinzercystis*).
134 *Vyscystis? spinosa* resembles *Kinzercystis* and *Lepidocystis* in the location of the ambulacral flooring plates (embedded in
135 the oral disc), the morphology of the tessellate region, the morphology and the plating of the stalk-like appendage. It differs
136 from *Lepidocystis* and *Kinzercystis* in the presence of coiled brachioles, absence of a well-developed stem and flattened oral
137 surface (Sprinkle 1973). Detailed comparison of *Vyscystis* with the two other genera of lepidocystids was done recently (see
138 Nohejlová et al. 2019). The herein described lepidocystid is morphologically closer to the Czech genus *Vyscystis*, with which
139 it shares the possession of coiled brachioles. However, the latter feature (coiled brachioles) represents a widely distributed
140 character within early blastozoans (e.g. it occurs also in the gogiids *Gogia spiralis* and *Globoeocrinus globulus*). Moreover,
141 some diagnostic features of the genus *Vyscystis* (e.g. detailed composition of the oral surface) could not be observed in the
142 studied Chinese material, because they are not well-preserved enough. Consequently, the new lepidocystid from North China
143 is only tentatively and provisionally assigned to *Vyscystis (Vyscystis? spinosa)*, pending the discovery of more complete and/or
144 better preserved material. Morphological differences between *V. ubaghsi* and the Chinese specimens suggest that the latter
145 probably belongs to a distinct species *Vyscystis? spinosa*. For example, the aboral cup of *Vyscystis ubaghsi* is wider than in
146 *Vyscystis? spinosa*, where it is markedly narrowing distally (in some specimens the aboral end of the cup is tapering to the
147 tip). The main other difference concerns the morphology of imbricate plates: in *V. ubaghsi* they are smooth, squamose and
148 subulate, whereas in *Vyscystis? spinosa* they are lenticular in shape and nipple-shaped ornamentation.

149 In tiny individuals (TH about 5 mm, e.g. NIGP201714), imbricate plates from the aboral cup already possess well-
150 developed nipple-shaped ornamentation, which expands on almost half of the plate (Fig. 4C, Fig. 5D). In larger specimens
151 (TH about 14 mm, e.g. specimen NIGP20171), the relative proportion of the ornamentation is more reduced (e.g. in
152 NIGP176281; Fig. 2A). The relative strength of the nipple-shaped ornamentation thus seems to be connected with the
153 ontogenetic development. A similar pattern has already been documented in other blastozoans (e.g. Allaire et al., 2017,

154 Makhoulf et al., 2017). In *Vyscystis? spinosa*, nipple-shaped ornamentation is particularly obvious in smaller (probably
155 juvenile) specimens but strongly reduced to almost absent in the largest specimens (probably adult ones). Thus suggests that
156 ornamentation gradually disappears during the ontogenetic development. Meanwhile, albeit most specimens of *Vyscystis*
157 *ubaghsi* are relatively large (TH about 10 mm, e.g. Fig. 2C in Nohejlová et al. 2019, fossil number: L28664) and with smooth
158 plates. No trace of nipple-shaped ornamentation had been observed from any small plates from the base part of the imperforate
159 extension, we think this is not the result of lacking small (juvenile) ones or simply by heterochronic processes. The general
160 body outlines of *Vyscystis? spinosa* sp. nov. resemble those of yet undescribed gogiid eocrinoids from Liaoning, which also
161 occur in the Mantou Formation (Huang et al., 2012). Although most of these eocrinoids occur as isolated plates, complete
162 specimens from Liaoning are smaller (less than 20 mm) than *Vyscystis? spinosa* and they are possessing a theca, composed
163 of tessellate, epispire-bearing polygonal plates. However, the precise taxonomic identification of this eocrinoid species is
164 beyond the scope of this paper.

165 4. Discussion

166 4.1 Taphonomic features

167 Fossil echinoderms were found in the fine-grained sediments from the basal Mantou Formation, mostly oriented parallel to
168 the bedding plane. Mudstones often contain thin parallel-laminated silty layers and structureless homogeneous clay after
169 reworking process (Fig. 6A, B). In both localities (Xiaobeiwang and Dananzhaung villages), disarticulated echinoderm
170 fragments are preserved in aggregations with several complete specimens co-occurring with trilobites, brachiopods and
171 hyoliths.

172 It is noted that fossil assemblages from basal Mantou Formation were preserved in a proximal environment of tidal-flat
173 environment (Lee and Chough, 2020). The softground surfaces are developed on a thick purple mudstone interval in both two
174 localities. The surfaces suggest a stabilized substrate including typical soft-substrate epifauna (e.g. echinoderms, hyoliths,
175 brachiopods and trilobites) with few traces and vertical burrows. Furthermore, fossils from Xiaobeiwang and Dananzhuang
176 villages exhibit different preservation features. Echinoderm fossils from Xiaobeiwang village are mostly preserved as isolated
177 luminous yellowish ossicles and few complete specimens with fan-shaped brachioles (in feeding posture). In same interval,
178 specimens of trilobites and hyoliths were found unoriented with high abundance (Fig. 6C). As a result, we suggest that the
179 Xiaobeiwang locality shows a mixture of freshly killed (dead) fully articulated individuals and already decayed and
180 disarticulated specimens, and most fossils from this locality are autochthonous. In Dananzhuang locality, near-complete
181 echinoderm specimens were collected with argillaceous concretions containing hyoliths and brachiopods (Fig. 6D, E). On the
182 surface, abundant isolated brachiopod shells, hyoliths preserved as casts and moulds in a directional alignment are observed.
183 Additionally, specimen sizes (e.g. diameter of brachiopod shells, body length of hyoliths) are tightly clustered in the

184 concretions. These evidences support that these specimens underwent a quick burial event, suddenly smothered by an obrution
185 deposit (Fig. 6E). The dorsal shields of trilobites are mainly preserved as exoskeletons. The ornament of the brachiopods and
186 hyoliths preserved in concretions as moulds is ambiguous in all specimens. Soft part preservation haven't been found.
187 Sediments infill tubular fossils like hyoliths (Fig. 7J). The preservation type of fossils at two localities are mainly through
188 biomineralization in accordance with most fossil assemblages in South China (e.g. Balang Biota, Kaili Biota). Echinoderm
189 specimens in Balang Biota and Kaili Biota were frequently preserved completely as mould aggregations (Zhao et al., 2007;
190 Zhao et al., 2008; Parsley et al., 2012; Zhao et al., 2015). Electronic scanning analysis conducted on these fossils has revealed
191 the enrichment of iron in fossil specimens from the Balang Biota and the Kaili Biota. Particularly, echinoderm specimens
192 (most are gogiids) shows high concentrations of iron oxides on the body parts, which indicate extensive weathering effect
193 (Lin, 2007).

194 *Vyscystis? spinosa* from the Mantou Formation also shares similarities with gogiid echinoderms from the Balang Biota and
195 the Kaili Biota in disarticulation sequence. Lin et al. (2008) established a disarticulation sequence beginning with the
196 detachment and disarticulation of brachioles, disarticulation of theca and ending with the disarticulation of holdfast. In
197 *Vyscystis? spinosa*, we could observed similar disarticulation sequence, characterized by an ordered disarticulation process
198 from the top part (brachioles) to the bottom part (the aboral extension) of the specimens (Fig. 2A, C, D; Fig. 3C; Fig. 4A, B,
199 F, G). In addition, Lin et al. (2015) documnted partially articulated *Guizhoueocrinus yui* with postmortem elongation from
200 the Balang Biota, and Lin suggested that “the gogiid specimens displaying a crypto-helical construction could only be
201 preserved in a very narrow taphonomic window”. What's more, few Kaili specimens were preserved with stereomic
202 microstructure which occurs on the external surfaces of thecal plates in two gogiid species. However, no convincible evidence
203 of such preservation type has been observed in *Vyscystis? spinosa*. We suggest that this could be explained by collection bias
204 and retain the possibility of the occurence of these partially disarticulated specimens.

205 4.2 Evolutionary implications

206 Lepidocystids form a well-defined clade, which is the sister-group of all other more derived blastozoans (Nohejlová et al.,
207 2019). Within early blastozoans, the details of aboral plating (imbricate vs. tessellate) is of great importance in illustrating
208 their evolutionary trend. Nardin et al. (2017) discussed the progressive replacement of imbricate aboral appendages by
209 tessellate parts within early blastozoans. As a typical calyx-bearing lepidocystid, *Vyscystis? spinosa* confirms this evolutionary
210 process by presenting a relatively large imbricate aboral cup. Furthermore, based on the work of Nohejlová et al. (2019), the
211 PBS (Peristomial Border Systems) type A2 of *Vyscystis ubaghsi* is convergent with the PBS of some primitive edrioasteroids
212 and more derived eocrinoids and rhombiferans (Kammer et al., 2013). However, the accurate plating pattern of the oral surface
213 could not be reconstructed in *Vyscystis? spinosa*. The presence of nipple-shaped plate ornamentations in aboral extension is
214 lacking in other lepidocystids (e.g. *Kinzercystis*, *Lepidocystis*), but still can be found (though more reduced) on the plates

forming the holdfast of some gogiids (e.g. *Gogia palmeri*, *G. radiata*, *G. spiralis*). In gogiids, since the holdfast is composed of variously sized plates, it is difficult to describe the ornamentation on each plate. However, larger stem plates bear a “knob” ornamentation in the center part, which indicates a stable evolutionary character in early blastozoans. These plates are morphologically equivalent to those forming the aboral cup of *Vyscystis*.

Early blastozoan eocrinoids exhibit morphological disparity in holdfasts (Zamora et al., 2017). Unlike most other eocrinoids (e.g. gogiids, trachelocrinids), *Vyscystis? spinosa* does not possess any differentiated aboral appendage (stalk or stem). Similarly to other known lepidocystids, the perforate extraxial body part in *Vyscystis? spinosa* is restricted to a relatively narrow tessellate oral surface, whereas its imperforate extraxial part forms the imbricate, aboral cup-shaped part of the body. Besides, compared to a holomeric column or a multi-plated stem, the irregular plating pattern of the aboral cup of *Vyscystis* also represent a plesiomorphic plate arrangement in blastozoans.

4.3 Spatial and temporal distribution of basal blastozoans in Cambrian

In the analysis below, "eocrinoids" is used as an informal term to designate felbabkacystid, gogiid, lepidocystid, lichenoid and trachelocrinid blastozoans. All together, they form a paraphyletic assemblage of basal blastozoans, which gave rise to most taxa generally assigned to "diploporitans", paracrinoids, and "rhombiferans" (Sprinkle, 1973; Paul, 1988; Nardin et al., 2009; Zamora & Smith, 2012; Zamora et al., 2013; Sheffield and Sumrall, 2019; Limbeck et al., 2024), and possibly also, to the various classes of "carpoids" (Haugh & Bell, 1980; Sumrall, 1997; Parsley 1999; David et al., 2000; Nardin et al., 2009; but see Jefferies, 1990; Smith, 2005; Zamora & Rahman, 2014). *Yanjiahella* (Yanjiahe Formation, Fortunian), *Dianchicystis* and *Vetulocystis* (Yu'anshan Formation, Cambrian Stage 3) have been reported as ancestral echinoderms (Shu et al., 2004; Topper et al., 2019). However, these three taxa exhibit no echinoderm characters (e.g. water vascular system, stereom), and their echinoderm affinities are more than doubtful (Based on the single figure provided in Smith et al. (2013, Fig. 4k), it is not clear whether this yet undescribed Moroccan lepidocystid belongs to *Vyscystis* or not. Very little of its morphology is actually visible. Smith, 2004; Swalla & Smith, 2008; Clausen et al., 2010; Zamora et al., 2020). As a result, they have been excluded from this analysis.

Cambrian eocrinoids have been globally distributed with recorded occurrences in Laurentia (Durham, 1978; Sumrall & Zamora, 2015; Sprinkle, 1973; Sprinkle & Collins, 2006; Ubaghs & Robison, 1985; Sprinkle & Collins, 2006; Sumrall et al. 1997; Ulrich 1929; Sprinkle, 1973; Zamora et al., 2015), Gondwana (Ubaghs & Vizcaino, 1990; Zamora et al. 2009; Zamora, 2010; Smith et al., 2013; Barrande 1887; Ubaghs, 1953; Parsley & Prokop, 2004; Prokop & Fatka, 1985; Barrande, 1887; Fatka & Kordule, 1984; Fatka & Kordule, 1991; Nohejlová and Fatka, 2016; Nardin et al., 2017; Fatka & Kordule, 1990; Nohejlová et al., 2019), South China (Liu et al., 2010; Hu et al., 2007; Hu & Luo, 2008; Zhao et al., 2007, 2008, 2015; Parsley & Zhao, 2006, 2010; Peng et al., 2020), North China (Huang, 2012), Baltica (Zamora et al., 2013) and Siberia (Yakovlev, 1956). Until the present time 61 eocrinoid species have been reported and studied in the Cambrian period (Zamora et al.,

2013). The stratigraphic scaling of the phylogenetic hypothesis supports the concept of a rapid diversification of eocrinoids in the Cambrian period (Guensburg and Sprinkle, 1992; Smith et al., 2013). Their fossil record starts in the early Cambrian (Series 2, Stage 3) with numerous occurrences of isolated plates, but few articulated specimens assigned to gogiids (e.g. *Alanisicystis andalusiae*; Ubaghs & Vizcaïno, 1990) and yet undescribed doubtful lepidocystids (Smith et al., 2013) (Fig. 7, 8). Stage 4 is characterized by a marked increase in diversity for gogiids (e.g. *Gogia ojenai*, *Guizhoueocrinus yui*, *Kunmingeocrinus cupuliformis*, *Protogloboeocrinus yini*, *Wudingecrinus rarus*; see e.g. Sprinkle, 1973; Hu et al., 2007; Zhao et al., 2007, 2015, 2021) and lepidocystids (*Kinzercystis durhami*, *Lepidocystis wanneri*, *Vyscystis ubaghsi*; Sprinkle, 1973; Fatka & Kordule, 1990). The diversity of eocrinoids peaked during the Wuliuan, with particularly diverse and palaeobiogeographically widespread gogiids (e.g. *Balangicystis rotundus*, *Gogia gondi*, *G. prolifica*, *G. parsleyi*, *Sinoeocrinus lui*; Sprinkle, 1973; Ubaghs, 1987; Zhao et al., 1994; Parsley & Zhao, 2006; Zamora et al., 2009), along with yet undescribed lepidocystids (Smith et al., 2013) and lichenoids (Zamora 2010; Smith et al., 2013). Several groups of eocrinoids coexisted during the Drumian: gogiids (e.g. *Akadocrinus jani*, *Gogia spiralis*, *Marjumicystis mettae*; Sprinkle, 1973; Ubaghs & Robison, 1985; Nohejlová & Fatka, 2016), felbabkacystids (*Felbabkacystis luckae*; Nardin et al., 2017), lepidocystids (*Vyscystis ubaghsi*; Fatka & Kordule, 1990; Nohejlová et al., 2019), and lichenoids (*Lichenoides priscus*; Ubaghs, 1953). However, most of them (felbabkacystids, lepidocystids and lichenoids) have their youngest occurrences during this time interval and gogiids show a significant decrease in diversity in the Drumian. From the Guzhangian to Stage 10, the total diversity of eocrinoids shows a continuous decrease (e.g. *Nolichuckia casteri*, *Pareocrinus Ijubzovi*, *Tatonkacystis codyensis*, *Trachelocrinus resseri*; Yakovlev, 1956; Sprinkle, 1973; Sumrall et al., 1997).

In summary, the diversity of Cambrian eocrinoids exhibits a rising and then declining trajectory with a peak in the Wuliuan. It should be noted, however, that the post-Wuliuan decrease in diversity is at least partly the consequence of a taxonomic bias: all early blastozoans acquiring apomorphies of well-defined groups (or clades) are no longer considered as "eocrinoids": for example, dibrachicystids are assigned to glyptocystitid rhombiferans (see Zamora & Smith, 2012; Fatka & Szabad, 2014). The post-Wuliuan decrease in eocrinoid diversity can thus be interpreted as a gradual, more or less continuous faunal turnover, with the progressive replacement of plesiomorphic morphologies (felbabkacystids, gogiids, lepidocystids and lichenoids) by more advanced ones (e.g. glyptocystitids, trachelocrinids). This transition was extremely smooth and long time ranging: some Cambrian-like taxa persisted at least until Early Ordovician (see Lefebvre et al., 2016) and conversely, some typical 'Ordovician' taxa (e.g. glyptocystitids) originated as early as the middle Cambrian (Zamora & Smith, 2012). This corresponds more or less to the replacement of Sepkoski's Cambrian Evolution Fauna by the Palaeozoic Evolutionary Fauna. It is very likely that some environmental changes (e.g. the major development of hardgrounds at low latitudes in the late Cambrian) triggered this transition (see Guensburg & Sprinkle, 2000; Rozhnov 2019).

With all the limitations related to taphonomic (eocrinoids are "type 1 echinoderms" *sensu* Brett et al., 1997), historical and sampling biases, some general palaeobiogeographic trends can be documented for the diversification of Cambrian eocrinoids (Fig. 9). After the first appearance of gogiids and lepidocystids in peri-Gondwanan areas in Cambrian Stage 3, eocrinoids

were present in most palaeocontinents during Stage 4, with apparently the exception of Siberia, where their earliest record is dated from the Miaolingian (*Pareocrinus ljubzovi*, Siligir Formation). Abundant occurrences of eocrinoids are known from most palaeocontinents in the Miaolingian. Meanwhile, North China block exhibits a lack of fossil record after Stage 4, but it still has a high potentiality for yielding eocrinoid fossils. As a result, West Gondwana, Laurentia, and to a lesser extent, South China, turn out to be the main contributing palaeocontinents yielding remains of early blastozoans (Fig. 9; Zamora et al., 2013).

Vyscystis? spinosa is the first lepidocystid described from North China, adding important information to palaeogeographical distribution of basal blastozoans. Together with other recent reports of characteristic fossils of Laurentia in Wuliuan shales, West Gondwana and in the North China Block from the Mantou Formation in Shandong Province (e.g. Sun et al., 2020b), these findings provide more evidences that North China Block has potential biogeographic connections with both West Gondwana and Laurentia. Since the exploration of North China Block started, findings achieved prosperity in recent years. North China is an important new area for studying early echinoderms and their evolution.

4.4 Paleoeecology

The associated fauna found in the same levels as the lepidocystid *Vyscystis? spinosa* (redlichiid trilobite fragments and hyoliths) is indicative of a shallow, well-oxygenated marine environment (Huang et al., 2012). In comparison, *V. ubaghsi* lived in relatively deep and quiet environment (Fatka and Mergl, 2009; Fatka and Szabad, 2014).

Herein, two different preservation types of the fossils were recognized from different layers: (1) isolated plates of lepidocystid *Vyscystis? spinosa*, redlichiid trilobite fragments and hyoliths, which indicates a long, time-averaging in situ disarticulation; (2) complete specimens of *Vyscystis?*, trilobites and hyoliths, which may indicate a in situ/short distanced transportation burial event. The distal end of the aboral cup is observed in some specimens, and that is regularly tapering to a distal tip. The absence of a well-developed attachment disc in fossil specimens of *Vyscystis? spinosa* questions the possibility of an epibenthic life style, attached onto the hard substrate. As a result, unlike *Globoeocrinus*, *Kinzercystis*, *Marjumicystis* and *V. ubaghsi*, which all possessed the ability to attach to relatively large exoskeletal parts of arthropods, *Vyscystis? spinosa* possibly shared the same anchoring strategy as some Cambrian long stemmed eocrinoids (e.g. *Guizhoueocrinus*, *Sinoeocrinus*) (Zamora et al., 2017; Nohejlová et al., 2019). Since these individuals have no anchoring structures at their distal extremity and were probably partly buried (aborally), we speculate that that the nipple-shaped ornamentation might also simply helped as an anchoring device, in particular, for the juvenile small individuals. Besides, coiled brahioles also expand the food gathering space and promote the chance to grasp food particles or small organisms from the water column. In all, it can be inferred that diverse ecological strategies of blastozoans possibly had already appeared in early Cambrian. And this view further echoes the idea that “The dominant Cambrian ecospace pattern in blastozoan echinoderms, in contrast, is one of progressive partitioning of persisting life habits instead of evolving fundamentally new ones” (Novack-Gottshall et al., 2022).

Nipple-shaped ornamentation is a very unusual morphological character in *Vyscystis? spinosa*. In some blastozoans (e.g. *Calix sedgwicki*), protuberances were restricted to the aboral extremity of the body and probably helped anchoring the organism to the substrate (Chauvel, 1941). The strong thecal ornamentation (protuberances, spikes) observed in some other blastozoans (e.g. *Lepidocalix pulcher*, *Rhopalocystis havliceki*) was probably inefficient for anchoring purposes, but possibly represents an adaptation against predation onto the soft parts housed in respiratory structures (diplopores, epispires; Makhlof et al., 2017). According to Bicknell et al. (2021), redlichiid trilobites possessed effective durophagous abilities and are well-adapted to masticate hard preys. The nipple-shaped ornamentation in *Vyscystis? spinosa* thus possibly represents an adaptation to the predation pressure from bottom-level animals like trilobites. The progressive reduction of the strength of this ornamentation during the ontogeny suggests that predation pressure was possibly higher in juvenile specimens.

In summary, *Vyscystis* provides more information to understand the ecological structure of Cambrian marine ecosystem. By filling a niche as primary consumers, this taxon contributed to the biogeochemical cycling, functioning, and long-term stability of the Palaeozoic seas. Furthermore, investigations into the life habits and environmental preferences of *Vyscystis* and other echinoderms continue to contribute to the understanding of evolutionary and ecological processes that operated in marine systems.

5. Conclusion

Vyscystis? spinosa represents a possible new occurrence of the genus *Vyscystis*, which was originally described from the Barrandian area of the Czech Republic. *Vyscystis? spinosa* is the first lepidocystid reported from the North China block. It is described here based on abundant, well-preserved specimens from the Cambrian Series 2, Stage 4 Mantou Formation in Jiangsu Province, North China. Czech material of the *Vyscystis ubaghsi* is younger, as it was described from the Jince Formation - Miaolingian (Drumian). This new finding also expands the taxonomic diversity and palaeogeographical distribution of early blastozoans during the Cambrian. Early blastozoans ("eocrinoids") had a global distribution during the Cambrian. *Vyscystis? spinosa* provides crucial information about the diversity of early blastozoans. A comprehensive palaeogeographic analysis also convinces that the palaeogeographic expansion in Cambrian eocrinoids precede the taxonomic diversification.

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343

344 **Accessibility of supplemental data**

345 CT data available from the Geobiodiversity Database: <https://doi.org/10.12091/fossil-ontology.20240201>.

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676 **Figure captions**

677 Fig.1 Geographic position of the fossil locality and stratigraphic column. (A) Map showing major tectonic boundaries of the
678 North China Plate (NCP) and studying area. TP: Tarim Plate, SCP: South China Plate; (B) Distribution of Cambrian outcrops
679 in study area, fossil localities are indicated in red stars (A, B, after Chough et al., 2010); (C) Synthetic stratigraphic column
680 of the Mantou Formation with the occurrence of the echinoderm species. Modified from Fang (1991).

681
682 Fig. 2 Photographs of *Vyscystis? spinosa* sp. nov. (Mantou Formation, North China). (A) Holotype in general view. (B)
683 Enlarged view of (A), dotted line partitioning the tessellate and imbricate parts of the body wall, NIGP176281. (C)-(G)
684 Paratype of *Vyscystis? spinosa* sp. nov., NIGP176282. (C)-(D) are two counterparts of the same specimen, (C) presents
685 external surface view, (D) presents the internal surface view. (E)-(F) is the detailed view of the upper box and the lower box
686 in (C), respectively. (G) Enlarged view of isolated ossicle with typical lenticular shape. Abbreviations: ar, axial region; per:
687 perforate extra-axial region; ier, impeforate extra-axial region; ip, imbricate plates; cs, central “spike”; isp, isolated plate; rr,
688 raised rim.

689
690 Fig. 3 *Vyscystis? spinosa* sp. nov (A) Specimen showing the oral surface, NIGP176283. (B) a virtual mold using μ CT
691 reconstruction of (A). (C) Slightly disarticulated specimen with coiled brachioles, NIGP176285. (D) Specimen with oral
692 surface, brachioles and aboral cup, NIGP176284 (E) Drawing of the specimen NIGP176284 showing morphological details..
693 Abbreviations: br, brachiole; ep, epispire; tp, tessellate plate; fp, floor plate; cp, cover plate; np, nipple-shaped imbricate plate,
694 sdbr, slightly disarticulated brachiole.

695
696 Fig. 4 External surface of the specimens *Vyscystis? spinosa* sp. nov showing the imbricate parts of the body wall. (A) General
697 view, NIGP176286. (B) Two individuals showing clustering preservation, NIGP176287. (C) Imbricate plating of the calyx
698 with the nipple-shaped ornamentation, NIGP176288. (D) latex cast of specimen, NIGP176289, (E) linear sketch of specimen
699 NIGP176289 (D), showing attachment zone. (F)-(G) Long aboral cup with imbricate plating, noted that aboral part has
700 relatively smaller imbricate plates, NIGP176290, NIGP176291. (H) linear sketch of specimen NIGP201710 (G), exhibiting
701 conical aboral extension of the calyx. Abbreviations; br, brachiola, cy, calyx; i1, individual 1; i2, individual 2; np, nipple-
702 shaped ornamentation; ep, epispire; isp, isolated plate.

703
704 Fig. 5 Photographs of latex casts whitened with ammonium chloride of *Vyscystis? spinosa* sp. nov (Mantou Formation, China).
705 (A)-(B), External view of NIGP201708 and NIGP201709 showing the cone-shaped body wall and multiple lenticular-shaped
706 imbricate plates. (C) External view showing the gradual transition from the large plates to tiny plates of the body wall and the
707 long aboral extension with imbricate plating without ornamentation, NIGP201710. (D) NIGP201711, general view of a small
708 specimen with nipple-shaped ornamentation of imbricate plates. Scale bar equal 2 mm.

709

710 Fig. 6 Polished slabs (A-B) and fossils preservation features (C-E) from the basal Mantou Formation in Xiaobeiwan and
711 Dananzhuang villages. (A) Polished slabs from the basal Mantou Formation in Xiaobeiwan village. (B) Polished slabs from
712 the basal Mantou Formation in Dananzhuang village. (C) Fossils performed a directional alignment from the basal Mantou
713 Formation in Xiaobeiwan village. (D)-(E) Abundant fossils preserved in concretion, sample from the basal Mantou
714 Formation in Dananzhuang village. All scale bars equal 1 cm.

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717 Fig. 7 3D scatter plot of metrics used in this study. Size of the cube represents species-level taxonomic diversity. Abbreviations:
718 WG, west Gondwana; La, Laurentia; SC, South China; NC, North China; Si, Siberia; Lep: Lepidocystidae, Fel:
719 Felbabkacystidae, Eoc: Eocrinidae, Lic: Lichenoidae, DB: Derived blastozoa.

720

721 Fig.8 Time distribution of early blastozoan echinoderms from Cambrian Series 2 to Miaolingian. Time range of Cambrian
722 blastozoan echinoderms based on articulated specimens found in global scale. Representatives of each group are made in
723 lineal sketches modified from Nardin et al., 2016. Phylogenetic tree modified from Nardin et al., 2017. Abbreviations: Lep:
724 Lepidocystidae, Fel: Felbabkacystidae, Eoc: Eocrinidae, Lic: Lichenoidae, DB: Derived blastozoa.

725

726 Fig.9 Palaeogeographic distribution of early blastozoan echinoderms. Size of the dot represents the diversity of each group.
727 Fossil sketches represent different groups of early blastozoan echinoderms. Symbols in different colors represent fossils in
728 different time-property: Orange, Cambrian Series 2; Purple, after Miaolingian. Earth palaeogeography in Cambrian Stage 3
729 modified from Zhao et al., 2021. Numbers in the right of the symbols represent the taxonomic diversity of each group at
730 species level.