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**Occurrence of *Microdictyon* from the lower Cambrian Xinji
Formation along the southern margin of the North China
Platform**

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Microdictyon plates from the lower Cambrian of North China

Abstract.—Disarticulated net-like plates of the lobopod *Microdictyon* had a near
cosmopolitan distribution from the early to middle Cambrian, but are yet to be
documented from the North China Platform. Here we report isolated plates of

24 *Microdictyon* from the lower Cambrian Xinji Formation (Stage 4, Series 2) of the
25 North China Platform, extending the paleogeographic distribution of *Microdictyon* in
26 the early Cambrian. The plates of *Microdictyon* from the Xinji Formation are similar
27 to those of other species established on the basis of isolated plates, but do bear some
28 new characters, such as mushroom-shaped nodes with a single inclined platform-like
29 apex, and an upper surface that displays radial lines. However, the plates documented
30 here are left under open nomenclature due to an inadequate knowledge of intraspecific
31 and ontogenetic variation and low specimen numbers. Through comparison of the
32 node shapes of the isolated plates of different *Microdictyon* species, we consider that
33 low mushroom-shaped nodes could be a primitive and conservative character of
34 *Microdictyon*, while tall mushroom-shaped nodes may be derived character. Subtle
35 differences in shape and number of node apices may also represent intraspecific or
36 ontogenetic variation.

37

38 **Introduction**

39 Phosphatic or phosphatized small skeletal fossils are generally dominant components
40 among early Cambrian faunal assemblages. These fossils, including spicules, tubes,
41 plates, cap-shaped shells and disarticulated sclerites, are usually millimetric in size
42 and are collectively described as ‘small shelly fossils (SSFs)’ (Matthews and
43 Missarzhevsky, 1975). Although the taxonomic affinities of many disarticulated
44 sclerites remain unresolved, the discovery of extraordinary well-preserved, articulated,
45 multiplated, soft-bodied specimens in Burgess Shale-type Lagerstätten can provide

46 significant insights into the functional morphology and phylogenetic position of SSF
47 taxa. Perhaps the most influential examples are the descriptions of *Microdictyon*
48 *sinicum* Chen, Hou and Lu, 1989 from the Chengjiang Biota (Chen et al., 1995),
49 *Halkieria evangelista* Conway Morris and Peel, 1995 from North Greenland (Conway
50 Morris and Peel, 1990, 1995; Vinther and Nielsen, 2005), and *Wiwaxia corrugata*
51 (Matthew, 1899) from the Burgess Shale (Conway Morris, 1985; Smith, 2014).

52 Minute net-like phosphatic plates were first reported by Matthews and
53 Missarzhevsky (1975) from the *Strenuella* Limestone of Comley, England, and were
54 described as problematic SSFs. The generic name, *Microdictyon* Bengtson, Matthews
55 and Missarzhevsky, 1981, was formally introduced on the basis of isolated reticulated
56 sclerites from the lower Cambrian of Malyi Karatau, South Kazakhstan (in
57 Missarzhevsky and Mambetov, 1981). To date, isolated *Microdictyon* plates have been
58 reported from South Australia (Bengtson et al., 1986; Bengtson et al., 1990;
59 Gravestock et al., 2001; Topper et al., 2009, 2011), South China (Hao and Shu, 1987;
60 Shu and Chen, 1989; Tong, 1989; Li and Zhu, 2001; Zhang and Aldridge, 2007; Yang
61 et al., 2015), Kazakhstan (Missarzhevsky and Mambetov, 1981; Bengtson et al., 1986;
62 Dzik, 2003), Uzbekistan (Bengtson et al., 1986), Mongolia (Esakova and Zhegallo,
63 1996), Siberia (Bengtson et al., 1986; Missarzhevsky, 1989; Demidenko, 2006;
64 Varlamov et al., 2008; Kouchinsky et al., 2011, 2015), Turkey (Sarmiento et al., 2001),
65 England (Shropshire, Avalonia, Matthews and Missarzhevsky, 1975; Bengtson et al.,
66 1986; Hinz, 1987), Baltica (Bengtson et al., 1986), North-East Greenland (Laurentia,
67 Skovsted, 2006), Canada (British Columbia, Laurentia, Bengtson et al., 1986), United

68 States (New York, California, Nevada, Utah, Laurentia, Bengtson et al., 1986; eastern
69 Massachusetts, Avalonia, Landing, 1988) and Mexico (Laurentia, McMenamin, 1984;
70 McMenamin and McMenamin, 1990). Although, *Microdictyon* had a near
71 cosmopolitan distribution in the lower and middle Cambrian, the large majority of
72 species have been established exclusively on the basis of disarticulated sclerites and
73 *Microdictyon sinicum* from the Chengjiang Biota (Chen et al., 1995; Hou and
74 Bergström, 1995) and *Microdictyon* sp. from the Kaili Biota (Zhao et al., 1999, 2002,
75 2005) remain the only well-known articulated species.

76 These delicate specimens from the Chengjiang Lagerstätte show that
77 *Microdictyon* is an elongated caterpillar-like animal possessing paired uniramous
78 lobopod limbs with nine pairs of reticulated plates positioned along both sides of the
79 subcylindrical trunk (Chen et al., 1989, 1995; Ramsköld and Hou, 1991; Bergström
80 and Hou, 2001; Hou et al., 2004). These soft-bodied specimens indicate that
81 *Microdictyon* is quite similar to other fossils with uniramous lobopods, including
82 *Aysheaia* Walcott, 1911 (Whittington, 1978), *Hallucigenia* Walcott, 1911 (Conway
83 Morris, 1977), *Xenusion* Pompeckj, 1927 (Dzik and Krumbiegel, 1989), *Luolishania*
84 Hou and Chen, 1989 (Hou and Chen, 1989), *Onychodictyon* Hou, Ramsköld and
85 Bergström, 1991 and *Cardiodictyon* Hou, Ramsköld and Bergström, 1991 (Hou et al.,
86 1991). Generally, these fossils are assigned to Lobopodia (Hou and Bergström, 1995;
87 Ramsköld and Chen, 1998) and comparisons of soft-part anatomy show great
88 similarity to extant onychophorans (Ramsköld and Hou, 1991; Ramsköld and Chen,
89 1998; Smith and Ortega-Hernández, 2014). Some lobopodians with mosaic features of

both lobopods and arthropods, such as *Miraluolishania haikouensis* Liu and Shu, 2004, *Jianshanopodia decora* Liu and Shu, 2006 and *Diania* Liu et al., 2011, indicate that well preserved lobopodian fossils can potentially shed light on the origin of arthropods (Liu et al., 2004, 2006, 2011; Ma et al., 2009).

The high diversity and morphological disparity of disarticulated phosphatic lobopodian plates represent an excellent complement to soft-bodied Lagerstätte specimens. Despite their near cosmopolitan distribution in the Cambrian, *Microdictyon* plates had not been previously documented from the North China Platform. Here we report the first occurrence of *Microdictyon* plates from the Xinji Formation on the North China Platform, extending the paleogeographic distribution of this genus. The aim of this paper is to describe and illustrate the isolated plates from the North China Platform and to provide an overview of the paleogeographic and stratigraphic distribution of *Microdictyon* and taxonomic problems associated with these net-like sclerites.

Geological setting

Specimens of *Microdictyon* described herein were collected from the Xinji Formation at the Shuiyu section, Ruicheng County, Shanxi Province and at the Shangwan section, Luonan County, Shaanxi Province (Fig. 1.1), along the south margin of the North China Platform (Li et al., 2014).

The Xinji Formation is regionally the lowermost Cambrian strata, disconformably

112 overlying Precambrian strata and consists of siliciclastic rocks intercalated with
113 carbonates, and is mainly distributed on the southwestern to southern margin of the
114 North China Platform (Liu et al., 1991; Liu et al., 1994). The thickness of the Xinji
115 Formation decreases from the south to the north, along the south margin of the North
116 China Platform and the lithology varies (Liu, 1986; Liu et al., 1991; Yan, 1993). Due
117 to its diverse and well-preserved small shelly fossils, the Xinji Formation has attracted
118 considerable attention (He et al., 1984; He and Pei, 1985; Feng et al., 1994; Pei and
119 Feng, 2005; Li et al., 2014; Pan et al., 2015; Li et al., 2016; Skovsted et al., 2016),
120 though isolated plates of *Microdictyon* were not recovered previously. Trilobites were
121 also reported from the Xinji Formation (Zhang and Zhu, 1979; Zhang et al., 1979).

122 In the Shangwan section, the Xinji Formation disconformably overlies the
123 Luoquan Formation (Ediacaran), which is composed predominantly of conglomerates,
124 gravel-bearing siltstones and shales (for stratigraphic column see figure 1 in Li et al.,
125 2014). The Xinji Formation is approximately 20 m thick and can be subdivided into
126 two parts. The 11 m thick lower part of the formation consists mainly of sandy
127 phosphoric limestones, shales and siltstones. The ca. 0.8-m-thick basal bed consists
128 mainly of phosphoric sandy limestones and contains abundant small shelly fossils.
129 One isolated plate of *Microdictyon* described herein was collected from this bed. The
130 upper part of the Xinji Formation consists mostly of calcareous sandstones and
131 dolomitic limestones with trilobites, but scarce small shelly fossils. The Xinji
132 Formation is conformably overlain by the Zhushadong Formation (Li et al., 2014).

133 In the Shuiyu section, the Xinji Formation disconformably overlies the

Precambrian strata, either the Luoquan Formation (Ediacaran, predominantly conglomerates) or the Longjiayuan Formation (Paleoproterozoic or Mesoproterozoic, gray dolostones) (Fig. 1.2). There is a karst surface between the Luoquan Formation and the Longjiayuan Formation. According to a local geological survey report, the Xinji Formation at Shuiyu section is about 39.8 m thick and can be subdivided into two parts: the lower part is dominated by gray-black phosphatic conglomerates, purple-red shale and phosphoric sandstone, and the upper part consists of red quartz sandstone intercalated with argillaceous dolostone (Bureau of Geology and Mineral Resources of Shanxi Province, 1989). Here, only the basal part (10.7 m) has been observed with the upper part of the section covered by vegetation. There are abundant trace fossils in the basal rocks, and the trace fossil assemblage belongs to a typical *Cruziana* ichnofacies (Miao and Zhu, 2014), indicating a subtidal environment for the basal Xinji Formation at the Shuiyu section. Several isolated plates of *Microdictyon* described herein were collected from a strongly weathered bed of calcic phosphoric quartz siltstone, 3.4 m above the base of the Xinji Formation (Fig. 1.2).

The Xinji Formation yields a small trilobite fauna, consisting of *Estaingia* (*Bergeroniellus*) *lonanensis* Hsiang, *Estaingia* (*Hsuaspis*) *houchiuensis* Chang, and *Redlichia* cf. *nanjiangensis* Zhang and Lin (Zhang and Zhu, 1979; Zhang et al., 1979; Miao, 2014). Based on the trilobite assemblage, the Xinji Formation was correlated with the *Drepanuloides* Biozone of the middle Tsanglangpuan stage (Cambrian Stage 4) on the Yangtze Platform (Zhang et al, 1979; Zhang and Zhu, 1979; Yu et al., 1984; He and Pei, 1985; Miao, 2014). The *Estaingia* trilobite assemblage can also be

156 compared with the *Pararaia janeae* trilobite Zone of South Australia (Paterson and
157 Brock, 2007; Miao, 2014). In addition, numerous small shelly fossils were discovered
158 from the Xinji Formation, such as cancelloriid sclerites, sponge spicules, hyoliths,
159 *Pojetaia runnegari*, *Mackinnonia rostrata*, *Stenotheca drepanoida*, *Pelagiella*
160 *madianensis*, *Cupithea holocyclata*, *C. costellata*, *Yochelcionella chinensis*,
161 *Cambroclavus absonus*, and *Apistoconcha* cf. *apheles*, etc. (He et al., 1984; Yu et al.,
162 1984; Pei, 1985; Feng et al., 1994; Li et al., 2014; Pan et al., 2015; Li et al., 2016;
163 Skovsted et al., 2016). Most of these fossils have been reported from the Parara
164 Limestone (Stansbury Basin) and Mernmerna Formation (Arrowie Basin) in South
165 Australia (Bengtson et al., 1990; Gravestock et al., 2001; Topper et al., 2009; Betts et
166 al., 2016, 2017). Based on the trilobite and small shelly fossil assemblages, and
167 similarities with South Australian assemblages the Xinji Formation can be roughly
168 correlated with Cambrian Series 2, Stage 4 (mid-late Botoman age in Siberian
169 terminology).

170

171 **Materials and methods**

172

173 One well preserved plate and four fragmented plates of *Microdictyon* were retrieved
174 from calcic phosphoric fine quartz sandstone samples, collected from a horizon 3.4 m
175 above the base of the Xinji Formation at the Shuiyu section, Ruicheng County, Shanxi
176 Province. Only one poorly preserved fragment of *Microdictyon* plate was retrieved
177 from phosphoric sandy limestone samples, collected from the base of the Xinji

178 Formation at the Shangwan section, Luonan County, Shaanxi Province.

179 Samples collected from the Shuiyu section were processed by digestion in 6%
180 acetic acid, and samples from the Shangwan section were processed by digestion in
181 10% acetic acid. The selected specimens were placed on stubs, gold coated and
182 photographed using the Scanning Electron Microscopy facility (LEO 1530VP) at the
183 Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences
184 (acronym NIGPAS), Nanjing.

185 ***Repositories and institutional abbreviations.***—All the illustrated specimens are
186 housed and cataloged at storage facilities of the NIGPAS, Nanjing.

187

188 **Taxonomy of isolated eoconchariid plates**

189

190 The Cambrian net-like isolated plates, including *Microdictyon*, are usually described
191 under the family Eoconchariidae (Chen et al., 1995; Demidenko, 2006; Zhang and
192 Aldridge, 2007; Topper et al., 2009), which consists of three genera: *Microdictyon*
193 Bengtson, Matthews and Missarzhevsky, 1981, *Quadratapora* Hao and Shu, 1987 and
194 *Fusuconcharium* Hao and Shu, 1987. Isolated eoconchariid plates retrieved from acid
195 residues are perforated and each hole is surrounded by a series of nodes on the
196 external surface. Different genera are predominantly recognized on the basis of plate
197 shape, perforation size and arrangement and node morphology. For example,
198 *Microdictyon* exhibits hexagonally arranged holes, with mushroom-shaped or spiky
199 nodes, *Quadratapora* exhibits tetragonally arranged holes with sharply crested walls,

200 *Fusuconcharium* exhibits a disorderly hexagonal hole arrangement with spine-like or
201 rounded nodes (Zhang and Aldridge, 2007). Demidenko (2006) established the genus
202 *Onychomicrodictyon* due to its plates combining features of *Microdictyon* (net-like
203 perforated plates with five to seven mushroom-shaped nodes around one hole) and
204 *Onychodictyon* Hou, Ramsköld, and Bergström, 1991 (strong spine-like process) and
205 assigned it to Eoconchariidae. However, Steiner et al. (2012) considers that hole size
206 and the overall plate dimensions of *Onychomicrodictyon* together with one unnamed
207 plate documented by Bengtson (1991) are identical with *Onychodictyon ferox* Hou et
208 al., 1991. Therefore, *Onychomicrodictyon* was considered to be a junior synonym of
209 *Onychodictyon* (Steiner et al., 2012; Topper et al., 2013). Based on the anatomy of
210 soft-bodied specimens, *Onychodictyon* was assigned to Onychodictyidae Hou and
211 Bergström, 1995 (Hou and Bergström, 1995; Liu et al., 2008).

212 After the discovery of the soft-bodied *Microdictyon sinicum*, it has been well
213 known that the trunk of this species has nine pairs of plates along sides of the
214 caterpillar-like body. The plates show a regular net-like morphology with a hexagonal
215 hole arrangement, but vary distinctly in size and outline. Chen et al. (1995) delineated
216 four morphotypes: elongate (the anterior pair), round (the second pair), ovoid (the 3rd
217 to 8th pairs) and rhomboidal (the posterior pair). *Microdictyon sinicum* demonstrates
218 that the plate outline is variable along the trunk of a single animal indicating that plate
219 outline is not a reliable taxonomic character. The soft-bodied specimens were
220 preserved in fine siliciclastic rocks and unfortunately the details of node morphology
221 and microstructure have been obscured by diagenetic processes, complicating detailed

222 comparisons with isolated phosphatic plates retrieved from acid residues. Zhang and
223 Aldridge (2007) have demonstrated that node microstructure is relatively consistent at
224 species level based on a large collection of isolated plates from southern China. Zhang
225 and Aldridge (2007) do report some morphological variation within species and it
226 remains to be seen whether the degree of variation represents intraspecific variation or
227 warrants the erection of a separate species. Conjoined plates of *Microdictyon* and
228 *Onychodictyon* that are interpreted as having preserved the moulting process, display
229 identical ornamentation indicating that plate ornamentation did not vary during
230 ontogeny (Zhang and Aldridge, 2007; Topper et al., 2013). However, these specimens
231 only represent a single moult stage and the entire ontogenetic sequence of
232 plate-bearing lobopodians remains unclear. With the current information that we have
233 at our disposal, the description of *Microdictyon* plates must focus on the arrangement
234 of holes and microstructure of the nodes, rather than plate outline and size.

235 To date, there are eight *Microdictyon* species that were erected on the morphology
236 of isolated plates (only *M. sinicum* was established on soft-bodied preservation). All
237 the soft-bodied fossils of *Microdictyon* recovered from the Chengjiang Biota at
238 different sections in eastern Yunnan belong to *Microdictyon sinicum*. Without
239 knowledge of the detailed plate morphology of *M. sinicum* it is entirely possible that
240 many of these species based solely on isolated plates may be plate morphotypes of *M.*
241 *sinicum*.

242 All specimens recovered from the Xinji Formation possess the typical hexagonal
243 meshwork arrangement and mushroom-shaped nodes that characterize *Microdictyon*.

244 The plates described herein show similarities to some formally established species but
245 also bear some new characters. Due to the small sample set, and without detailed
246 information regarding scleritome configuration and intraspecific and ontogenetic
247 variation (see Topper et al., 2011) the authors here, take a cautious approach and
248 describe the *Microdictyon* specimens under open nomenclature at species level. The
249 morphological characteristics of the plates will be described in detail.

250

251 **Systematic paleontology**

252 The terminology used to describe the *Microdictyon* plates follows that of Zhang and
253 Aldridge (2007).

254

255 Phylum Lobopodia Snodgrass, 1938

256 Class Xenusia Dzik and Krumbiegel, 1989

257 Order Archonychophora Hou and Bergström, 1995

258 Family Eoconchariidae Hao and Shu, 1987

259 Genus *Microdictyon* Bengtson, Matthews and Missarzhevsky, in Missarzhevsky and

260 Mambetov, 1981

261 **Type species.**—*Microdictyon effusum* Bengtson, Matthews and Missarzhevsky, 1981.

262 **Other species.**—*M. rhomboidale* Bengtson, Matthews and Missarzhevsky, 1986; *M.*

263 *robisoni* Bengtson, Matthews and Missarzhevsky, 1986; *M. chinense* Hao and Shu,

264 1987; *M. sphaeroides* Hinz, 1987; *M. sinicum* Chen, Hou and Lu, 1989; *M.*

265 *depressum* Bengtson in Bengtson et al. 1990; *M. fuchengense* Li and Zhu, 2001; *M.*

266 *jinshaense* Zhang and Aldridge, 2007.

267 **Remarks.**—The plates of *Microdictyon* Bengtson, Matthews and Missarzhevsky 1981,
268 *Quadratapora* Hao and Shu, 1987, *Fusuconcharium* Hao and Shu, 1987 show
269 similarity in meshwork arrangement with each perforation surrounded by a number of
270 protruding nodes. Genera are distinguished by the arrangement of holes and the
271 microstructure of the nodes. *Microdictyon* plates exhibit a regular hexagonal
272 meshwork that is distinct from *Quadratapora* plates with a regular tetragonal
273 meshwork and *Fusuconcharium* plates that display a slightly more irregular
274 meshwork. Only *Microdictyon* is well known from soft-bodied preservation. The
275 isolated plates of *Quadratapora* and *Fusuconcharium* have only been reported from
276 the Shuijingtuo Formation in Zhenba, Shaanxi, South China (Hao and Shu, 1987),
277 where they co-occur with *Microdictyon* (Zhang and Aldridge, 2007). In the
278 Shuijingtuo Formation, the number of plates belonging to *Quadratapora* (63) and
279 *Fusuconcharium* (28) is quite small in comparison to that of the documented plates of
280 *Microdictyon* (577, data from Zhang and Aldridge, 2007), and it is possible that the
281 plates of *Quadratapora* and *Fusuconcharium* are aberrant forms or representatives of
282 other *Microdictyon* species. *Microdictyon rozanovi* Demidenko, 2006 was erected
283 based on 2 broken plates that display a characteristic extended edge (Demidenko,
284 2006). This lateral extension is somewhat similar to the edge of *M. rhomboidale*, but
285 we consider this subtle variation of the plate edge as insufficient evidence to erect a
286 new species and based on node morphology we suggest that these specimens most
287 likely represent interspecific variants of *M. rhomboidale*. McMenamin (1984)

informally described a new species, *M. multicavus* from the lower Cambrian of Sonora, Mexico. However, due to the poor preservation of the specimens illustrated and the lack of a subsequent formal description we do not recognize the species as valid, pending further study.

Microdictyon sp.

Figures 2–4

Materials.—One nearly complete specimen and four small fragmented specimens (described as S1, S2, S3, S4 and S5 respectively) were collected from the Xinji Formation at the Shuiyu section. One poorly preserved specimen (S6) was collected from the Xinji Formation at the Shangwan section.

Description.—Plate S1 is ovoid and strongly convex, measuring 2030 μm in length, 1372 μm in maximum width, with a measured ratio of length and width at 1.48 (Fig. 2.1, 2.2). The holes are circular to ovoid in shape. The diameter (21.6 μm to 189 μm with the average of 115.35 μm) of the holes decreases toward the periphery of the plate (Fig. 2.1, 2.2, 2.4). Typically, each hole is surrounded by six hexagonally arranged nodes protruding from the junction of the walls. There is slight variation with one hole surrounded by four nodes and 13 other holes are respectively surrounded by five and seven nodes in plate S1 (square in Fig. 2.1, 2.2). In most cases, each node connects three walls, however a few nodes can be observed connecting four walls in plate S1 (arrows in Fig. 2.1, 2.2, 2.6). Most of the nodes are low and mushroom-shaped, with an ovate to subtriangular outline. The length of the nodes

310 ranges from 29.24 μm to 160.94 μm with the average of 77.26 μm and decreases
311 toward the periphery of the plate. The majority of nodes show a single acentric low
312 apex that protrudes from the surface. The apices roughly point in a single direction
313 (Figs. 2.2, 2.3, 3.1, 3.10). It is noteworthy that many apices have a distinct circular or
314 subcircular rim that forms a slightly concave platform at an oblique angle with the
315 surface of the mushroom-shaped nodes (Fig. 2.3, 2.7–2.10). The apex of the node in
316 plate S3 is quite distinct with a relatively planar surface (Fig. 4.1, 4.2, 4.4, 4.5). The
317 diameter of the apices ranges from 10.00 μm to 33.29 μm with the average of 21.52
318 μm . Towards the periphery of the plate, the mushroom-shaped nodes of plate S1 and
319 S5 deform, giving the appearance of a single sharp tubercle with an indistinct rim
320 (Figs. 2.2–2.4, 3.9) and some apices of nodes of plate S2 separate into multiple little
321 tips (Fig. 3.1, 3.2, 3.7). The multiple tips only cover half of the apex of one node in
322 plate S2 (Fig. 3.6). The upper surface of the nodes in plate S3 bear radial lines that
323 originate from the apex and extend outwards to the rim of the node (Fig. 4.4–4.6);
324 possibly extending into the base of the nodes (Fig. 4.5). The mushroom-shaped nodes
325 are hollow and sealed by one capping layer (Figs. 2.5, 3.8, 4.8, 4.9). On the inner
326 surface, each hole has a cylindrical tubular wall with a basal opening (Figs. 2.6, 3.3).
327 The peripheral girdle has a slightly inclined outer edge and an upright inner edge (Fig.
328 3.9). The plate microstructure consists of one basal framework layer (*Fw*) and one
329 upper capping layer (*Cl*) attaching on the framework (Figs. 2.11, 3.5, 3.8, 4.8, 4.9).
330 One poorly preserved fragment retrieved from the Shangwan section shows that holes
331 are surrounded by regularly hexagonally arranged mushroom-shaped nodes (Fig. 4.7).

Remarks.—The isolated plates of *Microdictyon* from the North China Platform show similar characteristics to previously reported isolated plates of *Microdictyon*. The ovoid, strongly convex plate and low mushroom-shaped nodes are quite similar to the type species, *M. effusum* (Bengtson et al., 1986), but the single oblique platform-like or relatively protruding planar apices of the plates from North China contrast with the single spiny apices of *M. effusum*. Multi-tip apices have been described in *Microdictyon chinense* and *M. jinshaense* (Zhang and Aldridge, 2007; Topper et al., 2009), but this represents a rather pervasive character over the entire plate, rather than the rare peripheral occurrences observed in the North Chinese material. The spiny nodes of the plates from North China occur in many species of *Microdictyon*, such as *Microdictyon chinense*, *Microdictyon* cf. *effusum*, *Microdictyon jinshaense* (Zhang and Aldridge, 2007) and *Microdictyon* cf. *depressum* (Skovsted, 2006). But the plates described herein can be easily distinguished from the plates of these species by the combination of characters listed above. The outline and arrangement and microstructure of the nodes on the North China *Microdictyon* plates also show some similarities to the plates of *M. depressum* (Bengtson et al., 1990), but the plates of *M. depressum* are quite flat and their single-tip apices are low. Topper et al. (2011) reported 6 types of plates from the Ajax Limestone in South Australia. Like the specimens documented herein, some of them also bear multi-tip apices, but the shape and combination of the tips are obviously different. Both assemblages are relatively small (herein: 5 specimens, Topper et al., 2009: 6 specimens), impeding a detailed comparison. The radial line on the surface of the nodes is here reported for the first

time on *Microdictyon* plates.

Discussion

Stratigraphical range and distribution of Microdictyon.—*Microdictyon* has a cosmopolitan geographic distribution from the Cambrian uppermost Stage 2 to uppermost Stage 5 (Figs. 5, 6). Complete soft-bodied specimens however have only been discovered from South China. *Microdictyon* is here documented from the lower Cambrian Xinji Formation of the North China Platform for the first time, extending the paleogeographic range of the genus in the late early Cambrian (Stage 4). The earliest occurrence of *Microdictyon* is from the lower *Micrina etheridgei* Zone (below the *Abadiella huoi* trilobite zone) of the Ajax Limestone in section AJX-M from South Australia (Topper et al., 2011; Betts et al., 2016), which may represent the uppermost Cambrian Stage 2. Bengtson et al. (1986) also reported *Microdictyon? tenuiporatum* revised as *Quadratopora tenuiporatum* by Zhang and Aldridge (2007) from the Tommotian Stage (pretrilobite stratum). In Stage 3, *Microdictyon* is reported from the *Abadiella huoi* zone in Australia (Bengtson et al., 1990; Topper et al., 2011) that correlates with the oldest trilobite zone, *Parabadiella* Zone in South China (Betts et al. 2016, 2017). This may be approximately coeval to the *Eofallotaspis* Zone in Morocco and the *Profallotaspis jakutensis* Zone in Siberia, as suggested by Yuan et al. (2011). The genus then rapidly dispersed to many paleocontinents, with the majority of described species documented from the *Eoredlichia-Wutingaspis* Zone in South China

(Chen et al., 1995; Li and Zhu, 2001; Zhang and Aldridge, 2007), the lower *Nevadella* Zone in Laurentia (British Columbia/Canada, New York, California, Nevada, Utah/United States, Mexico, Bengtson et al., 1986; McMenamin, 1984), the *Callavia* zone in Avalonia (Avalonian part of eastern Massachusetts/United States, Bengtson et al., 1986; Landing, 1988; Shropshire/England, Hinz, 1987), and the upper *Delgadella anabara* Zone to the *Judomia* Zone in Siberia (Kouchinsky et al., 2015). Some isolated plates of *Microdictyon* are also reported in the uppermost strata of Stage 3, in localities such as Kazakhstan (Bengtson et al., 1986; Dzik, 2003), Uzbekistan (Bengtson et al., 1986), Siberia (Bengtson et al., 1986; Varlamov, 2008) and Mongolia (Esakova and Zhegallo, 1996). In Stage 4, *Microdictyon* has been documented from the *Pararaia bunyeroensis* Zone in Australia (Topper et al., 2009), the *Lermontovia grandis* zone of Siberia (Demidenko, 2006), the *Bonnia-Olenellus* zone in North-East Greenland (Skovsted, 2006), the *Elliptocephala asaphoides* assemblage in USA (Laurentia part of eastern New York, Bengtson et al., 1986), the *Strenuella* Limestone and *Protolenus* Limestone in Shropshire (England/Avalonia, Bengtson et al., 1986; Hinz, 1987), and North China (herein). There is a sharp decrease in distribution and diversity of *Microdictyon* in this period, with only *M. sphaeroides*, *M. depressum*, and *M. jinshaense* reported from Stage 3. In stage 5, *Microdictyon* is reported from the *Oryctocephalus indicus* zone in South China (Zhao et al., 1999, 2002, 2005), the *Kuonamkites* zone in Siberia (Kouchinsky et al., 2011), the *Acadoparadoxides murensis* zone in Turkey (Sarmiento et al., 2001; stratigraphy revised by Dean, 2005), and the *Ptychagnostus gibbus* zone (uppermost Stage 5) in North America and

398 Baltica (Bengtson et al., 1986). Species reported include *M. robisoni* (new
399 occurrence), *M. sphaeroides* and a few undetermined species.

400 The FAD of *Microdictyon* has been included in discussions as a potential marker
401 for defining the global Stage 3 basal boundary (Peng et al., 2012), however the
402 uncertainties regarding plate taxonomy and the sporadic appearance of *Microdictyon*
403 specimens in Stage 2 in South Australia (Topper et al., 2011; Betts et al., 2016)
404 hampers the biostratigraphic application of *Microdictyon* at the species level. There
405 are morphological similarities between the species documented from China and
406 Australia, for example nodes with multiple-tip apices only occur in the plates of *M.*
407 *chinense* and *M. jinshaense* from South China (Zhang and Aldridge, 2007) and *M.*
408 *jinshaense* from South Australia (Topper et al., 2009, 2011) and the plates illustrated
409 herein. This could indicate that North China had a close paleogeographic position
410 with South Australia and South China in the early Cambrian. The early occurrence
411 (Stage 2), wide distribution and long stratigraphic range of *Microdictyon* suggests that
412 the genus may have been a pioneering member of Cambrian communities displaying a
413 strong adaptability to a variety of environments during the Cambrian explosion.

414
415 *Morphological variation of the nodes of the isolated Microdictyon plates.*—It is
416 obvious that some characters of the nodes of *Microdictyon* plates can occur in
417 different *Microdictyon* species. For instance, the short spiny nodes over the entire
418 external surface of some medium-sized plates (possibly representing an intermediate
419 ontogenetic growth stage) of *Microdictyon chinense* (Zhang and Aldridge, 2007) are

also observed at the margin of the plates of several other species, such as *Microdictyon* cf. *effusum*, *Microdictyon jinshaense* (Zhang and Aldridge, 2007), *Microdictyon* cf. *depressum* (Skovsted, 2006), and the plates herein. Thus the short spiny node, which occurs in particular positions on plates or potentially in selective ontogenetic stages of some species, may be an intraspecific or ontogenetic variable character. The mushroom-shaped nodes are also quite common among isolated *Microdictyon* plates. Low mushroom-shaped nodes occur in nearly all the species of *Microdictyon*, but tall mushroom-shaped nodes only occur in the plates of *M. robisoni* (see Kouchinsky et al., 2011). Based on the later occurrence (Cambrian, Stage 5) of *M. robisoni* with the tall mushroom shaped nodes, this character might be considered as a derived feature and low mushroom-shaped nodes may be an primitive and conservative character. As discussed, the character of the node apices is critical to distinguishing species of *Microdictyon* when presented with only isolated plates, however a cautious approach has been advocated (Zhang and Aldridge, 2007; Topper et al., 2009, 2011). As noted above, the nodes with single-tip apices and multiple-tip apices can coexist in a single plate (Fig. 3.1, 3.2, 3.7) and possibly represents intraspecific or ontogenetic variation. Comparing with other types of single-tip apices documented in the literature, the oblique platform-shaped apices of the nodes figured herein are quite distinct, but bear subtle similarities to the apices of the tall mushroom-shaped nodes of *M. robisoni* from Siberia described by Kouchinsky et al. (2011, figs. 28, 29). The apices of *M. robisoni* from Siberia however, also typically bear several flattened tubercles that are not observed in the specimens herein. Due to

the small sample set it is not known whether the single oblique platform-shaped apices is a stable character of *Microdictyon* plates from North China and the significance of this character for the taxonomy of the isolated *Microdictyon* plates is uncertain. The radial surface lines described herein on one specimen (Fig. 4.5, 4.6), may represent an aberrant form similar to the strong spine of *Microdictyon* cf. *effusum* and *Microdictyon jinshaense* (Zhang and Aldridge, 2007) or it may simply be a preservational artefact.

Conclusion

Microdictyon plates are reported for the first time from the lower Cambrian Xinji Formation (Stage 4, Series 2) of the North China Platform, extending the Cambrian paleogeographic range of *Microdictyon*. The plates described herein are characterized by low mushroom-shaped nodes and single oblique platform-like apex. Some morphological variations do exist with nodes in some plates characterized by multiple apices and the upper surface of the nodes on another plate bears radial lines that extend from the apex to the rim of the node. These radial lines are a new nodular microstructure and may represent a case of intraspecific variation, or a preservational artefact. Due to uncertainties regarding intraspecific and ontogenetic variation and the small sample size, the specimens herein have been left in open nomenclature. *Microdictyon* species described from isolated plates have in the past been established on the combination of several characters. However studies dealing with the

464 taxonomy of isolated plates should comprehensively analyze whether the
465 morphological variability observed in the assemblage could represent intraspecific or
466 ontogenetic variation. Much of this can only be done when examining large data sets.
467 It appears possible that low mushroom-shaped nodes may represent a primitive
468 character of the genus while the tall mushroom-shaped nodes may be a more derived
469 character. It is likely that the minor morphological variations observed in this small
470 assemblage represent intraspecific or ontogenetic variation, however in the absence
471 of additional material this remains unresolved.

472

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481

482 **References**

- 483 Bengtson, S., 1991, Oddballs from the Cambrian start to get even: *Nature*, v. 351, p.
484 184–185.
- 485 Bengtson, S., Matthews, S.C., and Missarzhevsky, V.V., 1986, The Cambrian netlike

- 486 fossil *Microdictyon*: in Hoffman, A. and Nitecki, M.H., eds., Problematic Fossil
487 Taxa: Oxford, Oxford University Press, p. 97–115.
- 488 Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A., and Runnegar, B.N., 1990,
489 Early Cambrian fossils from South Australia: Memoirs of the Association of
490 Australasian Palaeontologists, v. 9, p. 332–335.
- 491 Bergström, J., and Hou, X., 2001, Cambrian Onychopora or Xenusians: Zoologischer
492 Anzeiger, v. 240, p. 237–245.
- 493 Betts, M.J., Paterson, J.R., Jago, J.B., Jacquet, S.M., Skovsted, C.B., Topper, T.P.,
494 and Brock, G.A., 2016, A new lower Cambrian shelly fossil biostratigraphy for
495 South Australia: Gondwana Research, v. 36, p. 163–195.
- 496 Betts, M.J., Paterson, J.R., Jago, J.B., Jacquet, S.M., Skovsted, C.B., Topper, T.P.,
497 and Brock, G.A., 2017, Global correlation of the early Cambrian of South
498 Australia: Shelly fauna of the *Dailyatia odyseii* Zone: Gondwana Research, v.
499 46, p. 240–279.
- 500 Bureau of Geology and Mineral Resources of Shanxi Province, 1989, Regional
501 Geology of Shanxi Province: Beijing, Geological Publishing House, p. 116–120.
502 (In Chinese)
- 503 Chen, J., Hou, X., and Lu, H., 1989, Early Cambrian netted scale-bearing wormlike
504 sea animal: Acta Palaeontologica Sinica, v. 28, p. 1–16. (In Chinese)
- 505 Chen J., Zhou, G., and Ramsköld, L., 1995, The Cambrian lobopodian *Microdictyon*
506 sinicum: Bulletin of the National Museum of Natural Science, v. 5, p. 1–93.
- 507 Conway Morris, S., 1977, A new metazoan from the Cambrian Burgess Shale of

- 508 British Columbia: Palaeontology, v. 20, p. 623–640.
- 509 Conway Morris, S., 1985, The Middle Cambrian metazoan *Wiwaxia corrugata*
510 (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia,
511 Canada: Philosophical Transactions of the Royal Society of London, Series B,
512 Biological Sciences, v. 307, p. 507–582.
- 513 Conway Morris, S., and Peel, J.S., 1990, Articulated halkieriids from the Lower
514 Cambrian of north Greenland: Nature, v. 345, p. 802–805.
- 515 Conway Morris, S., and Peel, J.S., 1995, Articulated halkieriids from the Lower
516 Cambrian of North Greenland and their role in early protostome evolution:
517 Philosophical Transactions of the Royal Society of London B, v. 347, p. 305–
518 358.
- 519 Dean, W.T., 2005, Trilobites from de Çal tepe formation (Cambrian) near seydeşehir,
520 central taurides, Southwestern Turkey: Turkish Journal of Earthences, v. 14(1), p.
521 1–71.
- 522 Demidenko, Y.E., 2006, New Cambrian lobopods and chaetognaths of the Siberian
523 Platform: Paleontological Journal, v. 40(3), p. 234–243.
- 524 Dzik, J., 2003, Early Cambrian lobopodian sclerites and associated fossils from
525 Kazakhstan: Palaeontology, v. 46, p. 93–112.
- 526 Dzik, J., and Krumbiegel, G., 1989, The oldest ‘onychophoran’ *Xenusion*: a link
527 connecting phyla? : Lethaia, v. 22, p. 169–181.
- 528 Esakova, N.V, and Zhegallo, E.A, 1996, Biostratigraphy and fauna of the lower
529 Cambrian of Mongolia: Sovmestnaya Rossiisko-Mongolskaya

- 530 Paleontologicheskaya Ekspeditsiya Trudy, v. 46, p. 1–214. (In Russian)
- 531 Feng, W., Qian, Y., and Rong, Z., 1994, Study of monoplacophora and gastropoda
532 form lower Cambrian Xinji Formation in Yexian, Henan: Acta
533 Micropalaeontologica Sinica, v. 11(1), p. 1–19. (In Chinese)
- 534 Gravestock, D.I., Alexander, E.M., Jago, J.B., Rozanov, A.Y., Zhuravlev, A.Y., et al.,
535 2001, The Cambrian biostratigraphy of the Stansbury Basin, South Australia:
536 Moscow, Transactions of the Palaeontological Institute, v. 282, p. 1–344.
- 537 Hao, Y., and Shu, D., 1987, The oldest known well preserved Pheodaria (Radiolaria)
538 from Southern Shaanxi: Geoscience, v. 1(3–4), p. 301–310. (In Chinese)
- 539 He, T., and Pei, F., 1985, The discovery of bivalves from the lower Cambrian Xinji
540 Formation in Fangcheng County, Henan Province: Journal of Chengdu College
541 of Geology, v. 1, p. 61–68. (In Chinese)
- 542 He, T., Pei, F., and Fu, G., 1984, Small shelly fossils from the lower Cambrian Xinji
543 Formation in Fangcheng County, Henan Province: Acta Palaeontologica Sinica,
544 v. 23(3), p. 350–357. (In Chinese)
- 545 Hinz, I., 1987, The Lower Cambrian microfauna of Comley and Rushton, Shropshire,
546 England: Palaeontographica Abteilung A, p. 41–100.
- 547 Hou, X., and Bergström, J., 1995, Cambrian lobopodians—ancestors of extant
548 onychophorans? : Zoological Journal of the Linnean Society, v. 114, p. 3–19.
- 549 Hou, X., and Chen, J., 1989, Early Cambrian arthropod-annelid intermediate sea
550 animal, *Luolishania* gen. nov. from Chengjiang, Yunnan: Acta Palaeontologica
551 Sinica, v. 28(2), p. 207–213. (In Chinese)

- 552 Hou, X., Ramsköld, L., and Bergström, J., 1991, Composition and preservation of the
553 Chengjiang fauna—a Lower Cambrian soft-bodied biota: *Zoologica Scripta*, v. 20,
554 p. 395–411.
- 555 Hou, X., Aldridge, R.J., Bergström, J., Siveter, D.J., and Feng, X., 2004, The
556 Cambrian Fossils of Chengjiang, China: the flowering of early animal life: Oxford,
557 Blackwell Publishing, p. 1–233.
- 558 Kouchinsky, A., Bengtson, S., Clausen, S., Gubanov, A., Malinky, J.M., and Peel, J.S.,
559 2011, A Middle Cambrian fauna of skeletal fossils from the Kuonamka Formation,
560 northern Siberia: *Alcheringa*, v.35, p. 123–189.
- 561 Kouchinsky, A., Bengtson, S., Clausen, S., and Vendrasco, M.J., 2015, A lower
562 Cambrian fauna of skeletal fossils from the Emyaksin Formation, northern Siberia:
563 *Acta Palaeontologica Polonica*, v. 60 (2), p. 421–512.
- 564 Landing, E., 1988, Lower Cambrian of eastern Massachusetts: stratigraphy and small
565 shelly fossils: *Journal of Paleontology*, v. 62, p. 661–695.
- 566 Li, G., and Zhu, M., 2001, Discrete sclerites of *Microdictyon* (Lower Cambrian) from
567 the Fucheng section, Nanzheng, South Shaanxi: *Acta Palaeontologica Sinica*, v. 40,
568 p. 227–235.
- 569 Li, G., Zhang, Z., Hua, H., and Yang, H., 2014, Occurrence of the enigmatic bivalved
570 fossil *Apistoconcha* in the lower Cambrian of southeast Shaanxi, North China
571 platform: *Journal of Paleontology*, v. 88(2), p. 1–8.
- 572 Li, L., Zhang, X., Yun, H., and Li, G., 2016, New occurrence of *Cambroclavus*
573 *absonus* from the lowermost Cambrian of North China and its stratigraphical

- 574 importance: *Alcheringa*, v. 40(1), p. 45–52.
- 575 Liu, J., Shu, D., Han, J., and Zhang, Z., 2004, A rare lobopod with well-preserved
576 eyes from the Chengjiang Lagerstätte and its implications for origin of arthropods:
577 *Chinese Science Bulletin*, v. 49, p. 1063–1071.
- 578 Liu, J., Shu, D., Han, J., Zhang, Z., and Zhang, X., 2006, A large xenusiid lobopod
579 with complex appendages from Chengjiang Lagerstätte (Lower Cambrian, China):
580 *Acta Palaeontologica Polonica*, v. 51, p. 215–222.
- 581 Liu, J., Shu, D., Han, J., Zhang, Z., and Zhang, X., 2008, The lobopod *Onychodictyon*
582 from the lower Cambrian Chengjiang Lagerstätte revisited: *Acta Palaeontologica*
583 *Polonica*, v. 53(2), p. 285–292.
- 584 Liu, J., Steiner, M., Dunlop, J.A., Keupp, H., Shu, D., Ou, Q., Han, J., Zhang, Z., and
585 Zhang, X., 2011, An armoured cambrian lobopodian from China with
586 arthropod-like appendages: *Nature*, 470, 526–30.
- 587 Liu, Q., Ma, L., Zhu, Y., Jin, R., Dai, W., Chen, Y., Fan, X., Zhang, T., and Zhang, Z.,
588 1994, Lithofacies palaeogeography and gypsum deposits of the lower Cambrian of
589 North China platform: Beijing, Geologic Publishing House, p. 1–144. (In Chinese)
- 590 Liu, Y., 1986, The lower Cambrian Xinji Formation in Hennan Province: *Henan*
591 *Geology*, v. 4(4), p. 28–35. (In Chinese)
- 592 Liu, Y., Wang J., Zhang, H., and Du, F., 1991, The Cambrian and Ordovician Systems
593 of Henan Province: Beijing, Geological Publishing House, p. 1–225. (In
594 Chinese)
- 595 Ma, X., Hou, X., and Bergström, J., 2009, Morphology of *Luolishania longicruris*

- 596 (Lower Cambrian, Chengjiang Lagerstätte, SW China) and the phylogenetic
597 relationships within lobopodians: *Arthropod Structure and Development*, v. 38, p.
598 271–291.
- 599 Matthew, G.F., 1899, Studies on Cambrian faunas: *Transactions of the Royal Society*
600 of Canada, v. 5, p. 39–66.
- 601 Matthews, S., and Missarzhevsky, V., 1975, Small shelly fossils of late Precambrian
602 and early Cambrian age: a review of recent work: *Journal of the Geological*
603 *Society*, v. 131, p. 289–304.
- 604 McMenamin, M.A.S., 1984, Paleontology and stratigraphy of lower Cambrian and
605 Upper Proterozoic sediments, Caborca region, northwestern Sonora, Mexico [Ph.
606 D. thesis]: University of California, Santa Barbara, USA.
- 607 McMenamin, M.A.S., and McMenamin, D.L.S., 1990, The Emergence of
608 Animals—the Cambrian Breakthrough: New York, Columbia University Press, p.
609 1–217.
- 610 Miao, L., 2014, Biostratigraphy of the basal Cambrian Xinji Formation and the
611 Houjiashan Formation from the Southern North China Platform [Master thesis]:
612 University of Chinese Academy of Sciences, 127 p. (In Chinese)
- 613 Miao, L., and Zhu, M., 2014, Trace fossils from the basal Cambrian Xinji Formation
614 in Southern North China Platform and its chronological significance: *Acta*
615 *Palaeontologica Sinica*, v. 53(3), p. 274–289. (In Chinese)
- 616 Missarzhevsky, V.V., 1989, Oldest skeletal fossils and stratigraphy of Precambrian
617 and Cambrian boundary beds: *Trudy Akademii Nauk SSSR*, v. 443, p. 1–236. (In

- 618 Russian)
- 619 Missarzhevsky, V.V., and Mambetov, A.M., 1981, The stratigraphy and fauna of the
- 620 Cambrian–Precambrian boundary beds of the Lesser Karatau Range: Moscow,
- 621 Trudy Geologicheskogo Instituta Akademia Nauk SSSR, v. 326, p. 1–92. (In
- 622 Russian)
- 623 Pan, B., Miao, L., Yang, H., and Li, G., 2015, Enigmatic tubular fossil *Cupithec* from
- 624 the lower Cambrian Xinji Formation of Luonan, Shaanxi Province: Acta
- 625 Micropalaeontologica Sinica, v. 32, p. 384–395. (In Chinese)
- 626 Paterson, J.R., and Brock, G.A., 2007, Early Cambrian trilobites from Angorichina,
- 627 Flinders Ranges, South Australia, with a new assemblage from the *Pararaia*
- 628 *bunyerensis* Zone: Journal of Paleontology, v. 81, p. 116–142.
- 629 Pei, F., 1985, First discovery of *Yochelcionella* from the lower Cambrian in China and
- 630 its significance: Acta Micropalaeontologica Sinica, v. 2(4), p. 395–400. (In
- 631 Chinese)
- 632 Pei, F., and Feng, W., 2005, Discovery of the molluscan fauna from the lower
- 633 Cambrian Xinji Formation of Zhuyang, Linbao of Henan^①: Journal of
- 634 Stratigraphy, v. 29, p. 458–461. (In Chinese)
- 635 Peng, S., Babcock, L.E., and Cooper, R.A., 2012, The Cambrian Period, in Gradstein,
- 636 F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M., eds., The Geologic Time Scale:
- 637 Amsterdam, Elsevier, p. 446.
- 638 Ramsköld, L., and Chen, J., 1998, Cambrian lobopodians: morphology and phylogeny,
- 639 in Edgecombe, G.D. ed., Arthropod fossils and phylogeny: New York, Columbia

- University Press, p. 107–150.
- Ramsköld, L., and Hou, X., 1991, New Early Cambrian animal and onychophoran affinities of enigmatic metazoans: *Nature*, v. 351, p. 225–228.
- Sarmiento, G.N., Fernández-Remolar, D., and Göncüoglu, M.C., 2001, Cambrian small shelly fossils from the Cal Tepe Formation, Taurus Mountains, Turkey: *Coloquios de Paleontologia*, v. 52, p. 117–134.
- Shu D., and Chen, L., 1989, Discovery of Early Cambrian Radiolaria and its significance: *Science in China Series B-Chemistry*, v. 32(8), p. 986–994.
- Skovsted, C.B., 2006, Small shelly fauna from the late Early Cambrian Bastion and Ella Island Formations, North-East Greenland: *Journal of Paleontology*, v. 80, p. 1087–1112.
- Skovsted, C.B., Pan, B., Topper, T.P., Betts, M.J., Li, G., and Brock, G.A., 2016, The operculum and mode of life of the lower Cambrian hyolith *Cupitheca* from South Australia and North China: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 443, p. 123–130.
- Smith, M.R., 2014, Ontogeny, morphology and taxonomy of the soft-bodied Cambrian ‘mollusc’ *Wiwaxia*: *Palaeontology*, v. 57, p. 215–229.
- Smith, M.R., and Ortega-Hernández, J., 2014, *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda: *Nature*, v. 514, p. 363–366.
- Snodgrass, R.E., 1938, Evolution of the Annelida, Onychophora, and Arthropoda: *Smithsonian Miscellaneous Collections*, v. 97 (6), p. 1–159.
- Steiner, M., Hu, S., Liu, J., and Keupp, H., 2012, A new species of *Hallucigenia* from

- the Cambrian Stage 4 Wulongqing formation of Yunnan (South China) and the structure of sclerites in lobopodians: *Bulletin of Geosciences*, v. 87 (1), 107–124.
- Tong, H., 1989, A preliminary study on the *Microdictyon* from the Lower Cambrian of Zhenba, South Shaanxi: *Acta Micropalaeontologica Sinica*, v. 6, p. 97–101.
- Topper, T.P., Brock, G.A., Skovsted, C.B., and Paterson, J.R., 2009, Shelly fossils from the lower Cambrian *Pararaia bunyeroensis* Zone, Flinders Ranges, South Australia: *Memoirs of the Association of Australasian Palaeontologists*, v. 37, p. 199–246.
- Topper, T.P., Brock, G.A., Skovsted, C.B., and Paterson, J.R., 2011. *Microdictyon* plates from the lower Cambrian Ajax Limestone of South Australia: Implications for species taxonomy and diversity: *Alcheringa*, v. 35(3), p. 427–443.
- Topper, T.P., Skovsted, C.B., Peel, J.S., and Harper, D.A.T., 2013, Moulting in the lobopodian *Onychodictyon* from the lower Cambrian of Greenland: *Lethaia*, v. 46(4), p. 490–495.
- Varlamov, A.I., Rozanov, A.Y., Khomentovsky, V.V., Shabanov, Y.Y., Abaimova, G.P., et al., 2008, The Cambrian System of the Siberian Platform, Part 1, The Lena-Aldan Region: Moscow–Novosibirsk PIN RAS, p. 232.
- Whittington, H.B., 1978, The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia: *Philosophical Transactions of the Royal Society of London B*, v. 284, p. 165–197.
- Yan, G., Zhang, E., and Wang, D., 1993, Evolution of North China-Type Cambrian sedimentary environments and trace fossils assemblage in Henan Province:

- 684 Sedimentary Facies and Palaeogeography, v. 13(3), p. 18–32. (In Chinese)
- 685 Yang, B., Steiner, M., and Keupp, H., 2015, Early Cambrian palaeobiogeography of
686 the Zhenba–Fangxian Block (South China): Independent terrane or part of the
687 Yangtze Platform?: *Gondwana Research*, v. 28(4), p. 1543–1565.
- 688 Yu, W., Xu, J., and Yi, K., 1984, Discovery of molluscan fauna from lower Cambrian
689 Xinji Formation of Luonan, Shannxi: *Journal of Stratigraphy*, v. 8(3), p. 234. (In
690 Chinese)
- 691 Zhang, W., and Zhu, Z., 1979, Notes on some trilobites from lower Cambrian
692 Houjiashan Formation in southern and southwestern parts of North China: *Acta*
693 *Palaeontologica Sinica*, v. 18(6), p. 513–29. (In Chinese)
- 694 Zhang, W., Zhu, Z., Yuan, K., Lin, H., Qian, Y., Wu, H., and Yuan, J., 1979, The
695 boundary of the Cambrian-upper Precambrian in the southern and southwestern
696 parts of North China: *Acta Stratigraphica Sinica*, v. 3(1), p. 51–56. (In Chinese)
- 697 Zhang, X., and Aldridge, R.J., 2007, Development and diversification of trunk plates
698 of the Lower Cambrian lobopodians: *Palaeontology*, v. 50, p. 401–415.
- 699 Zhao, Y., Yuan, J., Zhu, M., Yang, R., Guo, Q., Qian, Y., Huang, Y., and Pan, Y., 1999,
700 A progress report on research on the early Middle Cambrian Kaili Biota, Guizhou,
701 PRC: *Acta Palaeontologica Sinica*, v. 38 (Supplement), p. 1–14. (In Chinese)
- 702 Zhao, Y., Yuan, J., Zhu, M., Yang, R., Guo, Q., Peng, J., and Yang X., 2002, Progress
703 and significance in research on the early Middle Cambrian Kaili biota, Guizhou
704 Province, China: *Progress in Natural Science*, v. 12 (9), p. 649654.
- 705 Zhao, Y., Zhu, M., Babcock, L.E., Yuan, J., Parsley, R. L., Peng, J., and Wang, Y.,

2005, Kaili Biota: a taphonomic window on diversification of metazoans from the basal Middle Cambrian: Guizhou, China: Acta Geologica Sinica (English Edition), v. 79 (6), p. 751–765.

Figure 1. Locality map of sampled sections and the lithostratigraphic column of Shuiyu section. **(1)** Locality map showing the positions of Shuiyu section and Shangwan section; **(2)** Lithostratigraphic column of the Xinji Formation at Shuiyu section, Ruicheng County, Shanxi Province. Abbreviations: LQ F., Luoquan Formation; LJY F., Longjiayuan Formation.

Figure 2. *Microdictyon* sp. from the Xinji Formation at Shuiyu section. **(1–11)** plate S1, 166027; **(1)** plan external view; **(2)** oblique view; **(3)** magnification of the nodes at the margin of the plate; **(4)** magnification of the nodes to show the deformation of the nodes at the periphery of plate; **(5)** magnification of the hollow node; **(6)** internal view of the central region of the plate; **(7–10)** magnification of the nodes showing apex details; **(11)** magnification of the broken wall to show the microstructure of the plate. Scale bars are 200 μm **(1–4, 6)**; 20 μm **(5, 7–11)**. Abbreviations: *Cl*, capping layer; *Fw*, framework.

Figure 3. *Microdictyon* sp. from the Xinji Formation at Shuiyu section. **(1–8)** plate S2,

166028; (1) plan external view; (2) oblique view; (3) internal view; (4) magnification
of the apex of a node; (5) magnification of the broken base of a node; (6–7) oblique
view of the nodes with multiple tip apices; (8) oblique internal view of a broken node;
(9, 12) plate S5, 166031; (9) plan external view; (12) internal view; (10, 11, 13) plate
S4, 166030; (10) external view; (11) internal view; (13) lateral view of the nodes.
Scale bars are 200 μm (1–3, 9–13); 20 μm (4–8). Abbreviations: *Cl*, capping layer; *Fw*,
framework.

Figure 4. *Microdictyon* sp. from the Xinji Formation. (1–6, 8, 9) plate S3, 166029,
collected at Shuiyu section; (1) plan external view of the fragment; (2) oblique
external view of the fragment; (3) internal view; (4) plan view of a node; (5) lateral
view of a node; (6) magnification of the periphery of a node; (8) lateral view of a
broken wall; (9) interval view of node; (7) plate S6, 166032, collected at Shangwan
section, plan external view. Scale bars are 20 μm (4–6, 8, 9); 200 μm (1–3, 7).
Abbreviations: *Cl*, capping layer; *Fw*, framework.

Figure 5. Stratigraphic occurrences of *Microdictyon* species documented from
different palaeocontinents ranging from Cambrian Stage 2 to Stage 5. Abbreviations:
E. Mas., Eastern Massachusetts.

Figure 6. Palaeogeographical distribution of *Microdictyon* from Cambrian Stage 2 to
Stage 5 (palaeogeographic map modified from Yang et al., 2015).

Locality map of sampled sections and the lithostratigraphic column of Shuiyu section. (1) Locality map showing the positions of Shuiyu section and Shangwan section; (2) Lithostratigraphic column of the Xinji Formation at Shuiyu section, Ruicheng County, Shanxi Province. Abbreviations: LQ F., Luoquan Formation; LJY F., Longjiayuan Formation.

101x57mm (600 x 600 DPI)

Figure 2. *Microdictyon* sp. from the Xinji Formation at Shuiyu section. (1–11) plate S1, 166027; (1) plan external view; (2) oblique view; (3) magnification of the nodes at the margin of the plate; (4) magnification of the nodes to show the deformation of the nodes at the periphery of plate; (5) magnification of the hollow node; (6) internal view of the central region of the plate; (7–10) magnification of the nodes showing apex details; (11) magnification of the broken wall to show the microstructure of the plate. Scale bars are 200 μ m (1–4, 6); 20 μ m (5, 7–11). Abbreviations: Cl, capping layer; Fw, framework.

180x201mm (300 x 300 DPI)

Figure 3. *Microdictyon* sp. from the Xinji Formation at Shuiyu section. (1–8) plate S2, 166028; (1) plan external view; (2) oblique view; (3) internal view; (4) magnification of the apex of a node; (5) magnification of the broken base of a node; (6–7) oblique view of the nodes with multiple tip apices; (8) oblique internal view of a broken node; (9, 12) plate S5, 166031; (9) plan external view; (12) internal view; (10, 11, 13) plate S4, 166030; (10) external view; (11) internal view; (13) lateral view of the nodes. Scale bars are 200 μm (1–3, 9–13); 20 μm (4–8). Abbreviations: Cl, capping layer; Fw, framework.

180x252mm (300 x 300 DPI)

Figure 4. *Microdictyon* sp. from the Xinji Formation. (1–6, 8, 9) plate S3, 166029, collected at Shuiyu section; (1) plan external view of the fragment; (2) oblique external view of the fragment; (3) internal view; (4) plan view of a node; (5) lateral view of a node; (6) magnification of the periphery of a node; (8) lateral view of a broken wall; (9) interval view of node; (7) plate S6, 166032, collected at Shangwan section, plan external view. Scale bars are 20 μm (4–6, 8, 9); 200 μm (1–3, 7). Abbreviations: Cl, capping layer; Fw, framework.

180x191mm (300 x 300 DPI)

Terrestrial Stage	Cambrian				Chrono-stratigraphy	Period
	Series 2		Series 3			
	Stage 2	Stage 3	Stage 4	Stage 5		
					North China	
					Australia	
					South China	
					Kazakhstan	
					Uzbekistan	
					Mongolia	
					Siberia	
					Turkey	
					Avalonia	
					Shropshire	
					E. Mas.	
					Baltica	
					Laurentia	
					Greenland	
					Canada	
					USA	
					Mexico	

Figure 5. Stratigraphic occurrences of *Microdictyon* species documented from different palaeocontinents ranging from Cambrian Stage 2 to Stage 5. Abbreviations: E. Mas., Eastern Massachusetts.

86x41mm (600 x 600 DPI)

Figure 6. Palaeogeographical distribution of *Microdictyon* from Cambrian Stage 2 to Stage 5 (palaeogeographic map modified from Yang et al., 2015).

87x43mm (600 x 600 DPI)

Review Only