

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

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

Introduction

Phosphatic or phosphatized small skeletal fossils are generally dominant components among early Cambrian faunal assemblages. These fossils, including spicules, tubes, plates, cap-shaped shells, and disarticulated sclerites, are usually millimetric in size and are collectively described as ‘small shelly fossils (SSFs)’ (Matthews and Missarzhevsky, 1975). Although the taxonomic affinities of many disarticulated sclerites remain unresolved, the discovery of extraordinarily well-preserved, articulated, multiplated, soft-bodied specimens in Burgess Shale-type Lagerstätten can provide significant insights into the functional morphology and phylogenetic position of SSF taxa. Perhaps the most influential examples are the descriptions of *Microdictyon sinicum* Chen, Hou, and Lu, 1989 from the Chengjiang Biota (Chen et al., 1995), *Halkieria evangelista* Conway Morris and Peel, 1995 from North Greenland (Conway Morris and Peel, 1990, 1995; Vinther and Nielsen, 2005), and *Wiwaxia corrugata* (Matthew, 1899) from the Burgess Shale (Conway Morris, 1985; Smith, 2014).

Minute net-like phosphatic plates were first reported by Matthews and Missarzhevsky (1975) from the *Strenuella* Limestone of Comley, England, and were described as problematic SSFs. The generic name, *Microdictyon* Bengtson, Matthews, and Missarzhevsky, 1981 in Missarzhevsky and Mambetov, 1981, was formally introduced on the basis of isolated reticulated sclerites from the lower Cambrian of Malyi

Karatau, South Kazakhstan. To date, isolated *Microdictyon* plates have been reported from South Australia (Bengtson et al., 1986, 1990; Gravestock et al., 2001; Topper et al., 2009, 2011), South China (Hao and Shu, 1987; Shu and Chen, 1989; Tong, 1989; Li and Zhu, 2001; Zhang and Aldridge, 2007; Yang et al., 2015), Kazakhstan (Missarzhevsky and Mambetov, 1981; Bengtson et al., 1986; Dzik, 2003), Uzbekistan (Bengtson et al., 1986), Mongolia (Esakova and Zhegallo, 1996), Siberia (Bengtson et al., 1986; Missarzhevsky, 1989; Demidenko, 2006; Varlamov et al., 2008; Kouchinsky et al., 2011, 2015), Turkey (Sarmiento et al., 2001), England (Shropshire, Avalonia; Matthews and Missarzhevsky, 1975; Bengtson et al., 1986; Hinz, 1987), Baltica (Bengtson et al., 1986), Northeast Greenland (Laurentia; Skovsted, 2006), Canada (British Columbia, Laurentia; Bengtson et al., 1986), United States (New York, California, Nevada, Utah, Laurentia; Bengtson et al., 1986; eastern Massachusetts, Avalonia; Landing, 1988), and Mexico (Laurentia; McMenamin, 1984; McMenamin and McMenamin, 1990). Although *Microdictyon* had a near cosmopolitan distribution in the lower and middle Cambrian, the large majority of species have been established exclusively on the basis of disarticulated sclerites; *Microdictyon sinicum* from the Chengjiang Biota (Chen et al., 1995; Hou and Bergström, 1995) and *Microdictyon* sp. from the Kaili Biota (Zhao et al., 1999, 2002, 2005) remain the only well-known articulated species.

These delicate specimens from the Chengjiang Lagerstätte show that *Microdictyon* is an elongated caterpillar-like animal

possessing paired uniramous lobopod limbs with nine pairs of reticulated plates positioned along both sides of the sub-cylindrical trunk (Chen et al., 1989, 1995; Ramsköld and Hou, 1991; Bergström and Hou, 2001; Hou et al., 2004). These soft-bodied specimens indicate that *Microdictyon* is quite similar to other fossils with uniramous lobopods, including *Aysheaia* Walcott, 1911 (Whittington, 1978), *Hallucigenia* Walcott, 1911 (Conway Morris, 1977), *Xenusion* Pompeckj, 1927 (Dzik and Krumbiegel, 1989), *Luolishania* Hou and Chen, 1989, *Onychodictyon* Hou, Ramsköld, and Bergström, 1991, and *Cardiodictyon* Hou, Ramsköld, and Bergström, 1991. In general, these fossils are assigned to Lobopodia (Hou and Bergström, 1995; Ramsköld and Chen, 1998), and comparisons of soft-part anatomy show great similarity to extant onychophorans (Ramsköld and Hou, 1991; Ramsköld and Chen, 1998; Smith and Ortega-Hernández, 2014). Some lobopodians with mosaic features of both lobopods and arthropods, such as *Miraluolishania haikouensis* Liu et al., 2004, *Jianshanopodia decora* Liu et al., 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.

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

In the Shangwan section, the Xinji Formation disconformably overlies the Luoquan Formation (Ediacaran),

which is composed predominantly of conglomerates, gravel-bearing siltstones, and shales (for stratigraphic column, see fig. 1 in Li et al., 2014). The Xinji Formation is approximately 20 m thick and can be subdivided into two parts. The 11 m thick lower part of the formation consists mainly of sandy phosphoric limestones, shales, and siltstones. The ~0.8 m thick basal bed consists mainly of phosphoric sandy limestones and contains abundant small shelly fossils. One isolated plate of *Microdictyon* described herein was collected from this bed. The upper part of the Xinji Formation consists mostly of calcareous sandstones and dolomitic limestones with trilobites, but scarce small shelly fossils. The Xinji Formation is conformably overlain by the Zhushadong Formation (Li et al., 2014).

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, 1965 in Lu et al., 1965, *Estaingia* (*Hsuaspis*) *houchiuensis* Chang, 1963 in Hsiang, 1963, and *Redlichia* cf. *R. nanjiangensis* Zhang and Lin (Zhang and Zhu, 1979; Zhang et al., 1979; Miao, 2014). Judging from the trilobite assemblage, the Xinji Formation was correlated with the *Drepanuloides* Zone of the middle Tsanglangpuan stage (Cambrian Stage 4) on the Yangtze Platform (Zhang and Zhu, 1979; Zhang et al., 1979; Yu et al., 1984; He and Pei, 1985; Miao, 2014). The *Estaingia* trilobite assemblage can also be compared with the *Pararaia janeae* Zone of South Australia (Paterson and Brock, 2007; Miao, 2014). In addition, numerous small shelly fossils were discovered from the Xinji Formation, such as cancelloriid sclerites, sponge spicules, hyoliths, *Pojetaia runnegari* Jell, 1980, *Mackinnonia rostrate* Zhou and Xiao, 1984, *Stenothecca drepanoida* He and Pei, 1984 in He et al., 1984, *Pelagiella madianensis* Zhou and Xiao, 1984, *Cupithecya holocyclata* Bengston, 1990 in Bengston et al., 1990, *C. costellata* Xiao and Zhou, 1984, *Yochelcionella chinensis* Pei, 1985, *Cambroclavus absonus* Conway Morris, 1990 in Bengston et al., 1990, and *Apistocconcha* cf. *A. apheles* Conway Morris, 1990 in Bengston et al., 1990, and so on. (He et al., 1984; Yu et al., 1984; Pei, 1985; Feng et al., 1994; Li et al., 2014; Pan et al., 2015; Li et al., 2016; Skovsted et al., 2016). Most of these fossils have been reported from the Parara

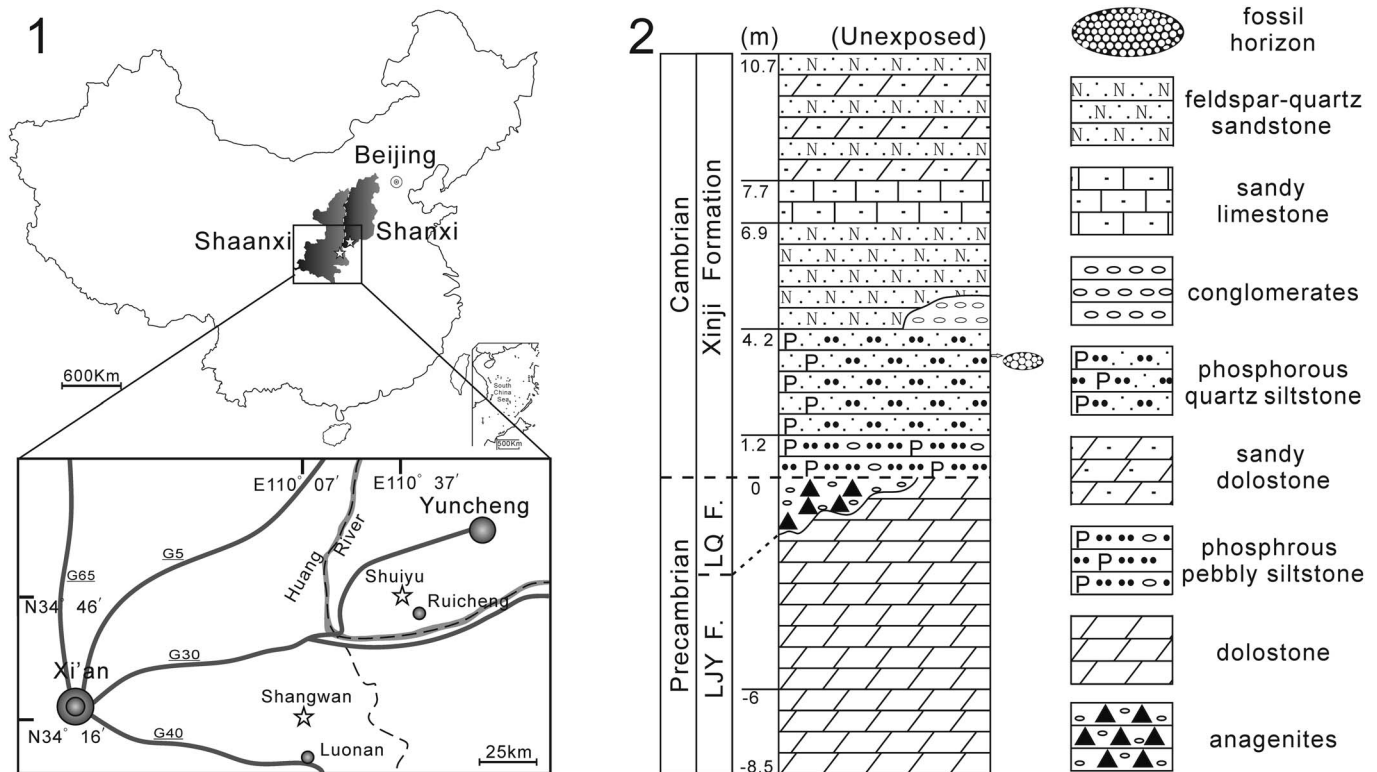


Figure 1. Locality map of sampled sections and the lithostratigraphic column of Shuiyu section. (1) Locality map showing the positions of Shuiyu section and Shangwan section; (2) lithostratigraphic column of the Xinji Formation at Shuiyu section, Ruicheng County, Shanxi Province. LQ F. = Luoquan Formation;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

Limestone (Stansbury Basin) and Mermerna Formation (Arrowie Basin) in South Australia (Bengtson et al., 1990; Gravestock et al., 2001; Topper et al., 2009; Betts et al., 2016, 2017). Judging from the trilobite and small shelly fossil assemblages, and similarities with South Australian assemblages, the Xinji Formation can be roughly correlated with Cambrian Series 2, Stage 4 (mid-late Botoman age in Siberian terminology).

Materials and methods

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

Samples collected from the Shuiyu section were processed by digestion in 6% acetic acid, and samples from the Shangwan section were processed by digestion in 10% acetic acid. The selected specimens were placed on stubs, gold coated, and photographed using the scanning electron microscopy facility (LEO 1530VP) at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.

Repository and institutional abbreviation.—All the illustrated specimens are housed and cataloged at storage facilities of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing.

Taxonomy of isolated eoconchariid plates

The Cambrian net-like isolated plates, including *Microdictyon*, are usually described under the family Eoconchariidae (Chen et al., 1995; Demidenko, 2006; Zhang and Aldridge, 2007; Topper et al., 2009), which consists of three genera: *Microdictyon* Bengtson, Matthews, and Missarzhevsky, 1981, in Missarzhevsky and Mambetov, 1981, *Quadratopora* Hao and Shu, 1987, and *Fusuconcharium* Hao and Shu, 1987. Isolated eoconchariid plates retrieved from acid residues are perforated, and each hole is surrounded by a series of nodes on the external surface. Different genera are predominantly recognized on the basis of plate shape, perforation size and arrangement, and node morphology. For example, *Microdictyon* exhibits hexagonally arranged holes with mushroom-shaped or spiky nodes; *Quadratopora* exhibits tetragonally arranged holes with sharply crested walls; *Fusuconcharium* exhibits a disorderly hexagonal hole arrangement with spine-like or rounded nodes (Zhang and Aldridge, 2007). Demidenko (2006) established the genus *Onychomicrodictyon* due to its plates combining features of *Microdictyon* (net-like perforated plates with five to seven mushroom-shaped nodes around one hole) and *Onychodictyon* Hou, Ramsköld, and Bergström, 1991 (strong spine-like process) and assigned it to Eoconchariidae. However, Steiner

et al. (2012) consider that hole size and the overall plate dimensions of *Onychomicrodictyon* together with one unnamed plate documented by Bengtson (1991) are identical with *Onychodictyon ferox* Hou, Ramsköld, and Bergström, 1991. Therefore, *Onychomicrodictyon* was considered to be a junior synonym of *Onychodictyon* (Steiner et al., 2012; Topper et al., 2013). Because of the anatomy of soft-bodied specimens, *Onychodictyon* was assigned to Onychodictyidae Hou and Bergström, 1995 (Hou and Bergström, 1995; Liu et al., 2008).

After the discovery of the soft-bodied *Microdictyon sinicum*, it has been well known that the trunk of this species has nine pairs of plates along sides of the caterpillar-like body. The plates show a regular net-like morphology with a hexagonal hole arrangement but vary distinctly in size and outline. Chen et al. (1995) delineated four morphotypes: elongate (the anterior pair), round (the second pair), ovoid (the third to eighth pairs), and rhomboidal (the posterior pair). *Microdictyon sinicum* demonstrates that the plate outline is variable along the trunk of a single animal, indicating that plate outline is not a reliable taxonomic character. The soft-bodied specimens were preserved in fine siliciclastic rocks, and unfortunately the details of node morphology and microstructure have been obscured by diagenetic processes, complicating detailed comparisons with isolated phosphatic plates retrieved from acid residues. Zhang and Aldridge (2007) have demonstrated that node microstructure is relatively consistent at species level according to a large collection of isolated plates from southern China. Zhang and Aldridge (2007) do report some morphological variation within species, and it remains to be seen whether the degree of variation represents intraspecific variation or warrants the erection of a separate species. Conjoined plates of *Microdictyon* and *Onychodictyon* that are interpreted as having preserved the molting process display identical ornamentation, indicating that plate ornamentation did not vary during ontogeny (Zhang and Aldridge, 2007; Topper et al., 2013). However, these specimens only represent a single molt stage, and the entire ontogenetic sequence of plate-bearing lobopodians remains unclear. With the information currently at our disposal, the description of *Microdictyon* plates must focus on the arrangement of holes and microstructure of the nodes, rather than on plate outline and size.

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

All specimens recovered from the Xinji Formation possess the typical hexagonal meshwork arrangement and mushroom-shaped nodes that characterize *Microdictyon*. The plates described herein show similarities to some formally established species but also bear some new characters. Due to the small sample set, and without detailed information regarding scleritome configuration and intraspecific and ontogenetic variation (see Topper et al., 2011), the authors here take a cautious approach and describe the *Microdictyon* specimens under open

nomenclature at species level. The morphological characteristics of the plates will be described in detail.

Systematic paleontology

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

Phylum Lobopodia Snodgrass, 1938

Class Xenusia Dzik and Krumbiegel, 1989

Order Archonychophora Hou and Bergström, 1995

Family Eoconchariidae Hao and Shu, 1987

Genus *Microdictyon* Bengtson, Matthews, and

Missarzhevsky, 1981 in Missarzhevsky and Mambetov, 1981

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

Other species.—*M. rhomboidale* Bengtson, Matthews, and Missarzhevsky, 1986; *M. robisoni* Bengtson, Matthews, and Missarzhevsky, 1986; *M. chinense* Hao and Shu, 1987; *M. sphaeroides* Hinz, 1987; *M. sinicum* Chen, Hou, and Lu, 1989; *M. depressum* Bengtson in Bengtson et al., 1990; *M. fuchengense* Li and Zhu, 2001; *M. jinshaense* Zhang and Aldridge, 2007.

Remarks.—The plates of *Microdictyon*, *Quadratopora*, and *Fusuconcharium* show similarity in meshwork arrangement, with each perforation surrounded by a number of protruding nodes. Genera are distinguished by the arrangement of holes and the microstructure of the nodes. *Microdictyon* plates exhibit a regular hexagonal meshwork that is distinct from *Quadratopora* plates, with a regular tetragonal meshwork, and *Fusuconcharium* plates, which display a slightly more irregular meshwork. Only *Microdictyon* is well known from soft-bodied preservation. The isolated plates of *Quadratopora* and *Fusuconcharium* have only been reported from the Shuijingtuo Formation in Zhenba, Shaanxi, South China (Hao and Shu, 1987), where they co-occur with *Microdictyon* (Zhang and Aldridge, 2007). In the Shuijingtuo Formation, the number of plates belonging to *Quadratopora* (63) and *Fusuconcharium* (28) is quite small in comparison to that of the documented plates of *Microdictyon* (577; data from Zhang and Aldridge, 2007), and it is possible that the plates of *Quadratopora* and *Fusuconcharium* are aberrant forms or representatives of other *Microdictyon* species. *Microdictyon rozanovi* Demidenko, 2006 was erected on the basis of two broken plates that display a characteristic extended edge (Demidenko, 2006). This lateral extension is somewhat similar to the edge of *M. rhomboidale*, but we consider this subtle variation of the plate edge as insufficient evidence to erect a new species and, on the basis of node morphology, we suggest that these specimens most 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

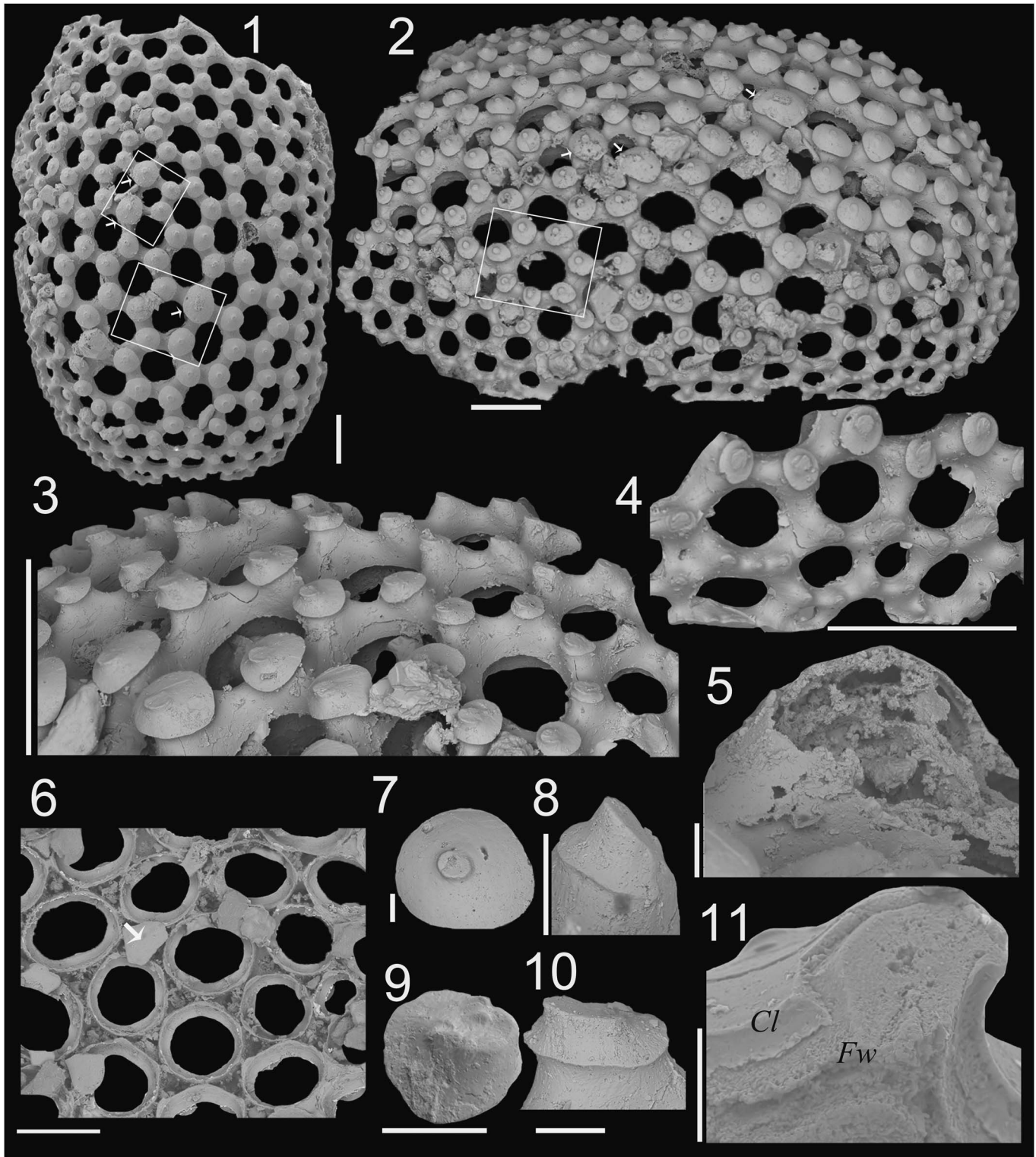
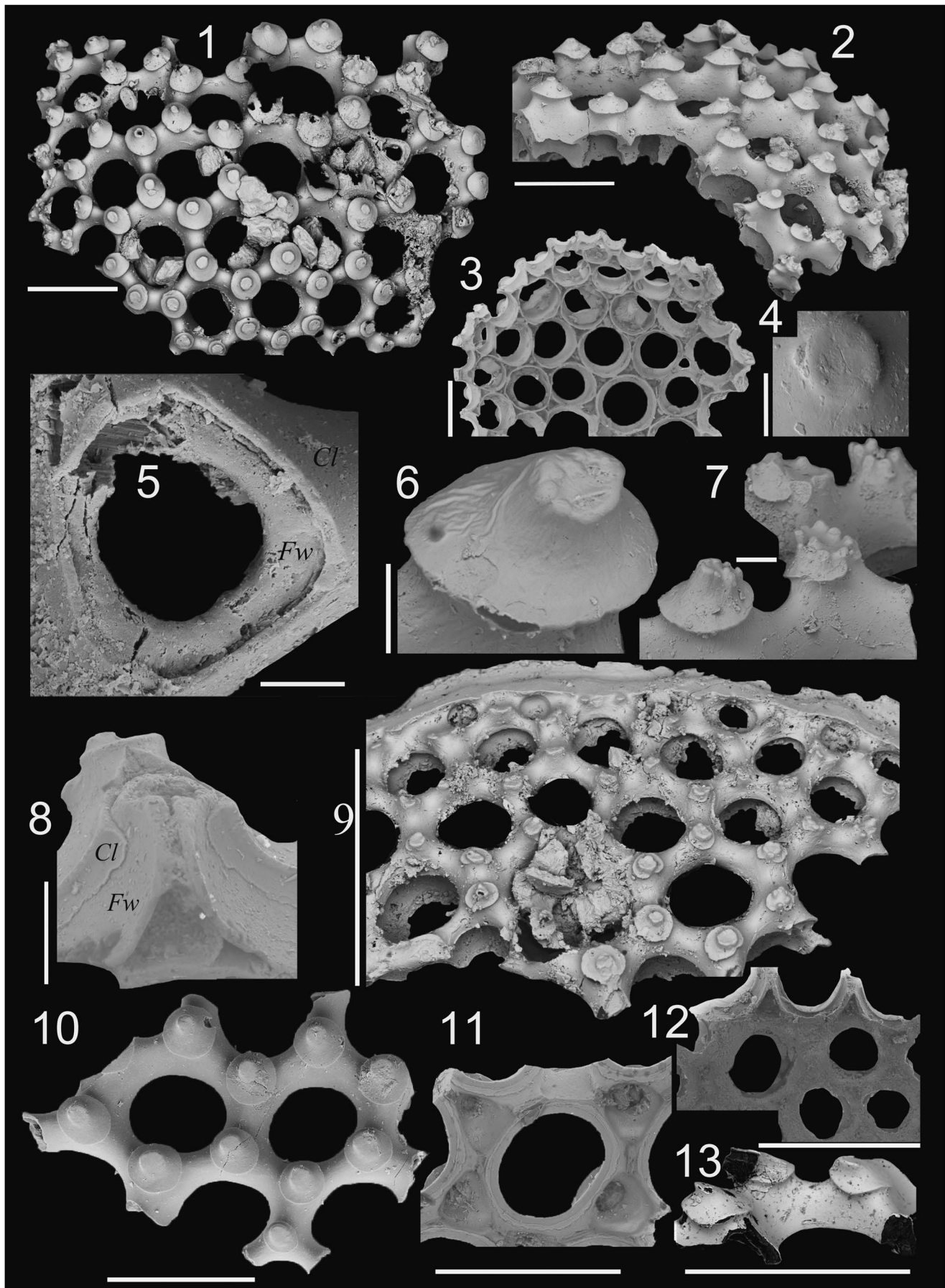


Figure 2. *Microdictyon* sp. from the Xinji Formation at Shuiyu section. (1–11) Plate S1, 166027; (1) plan external view; (2) oblique view; (3) magnification of the nodes at the margin of the plate; (4) magnification of the nodes to show the deformation of the nodes at the periphery of plate; (5) magnification 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. (1–4, 6) Scale bars = 200 μm ; (5, 7–11) scale bars = 20 μm . *Cl* = capping layer; *Fw* = framework.

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.



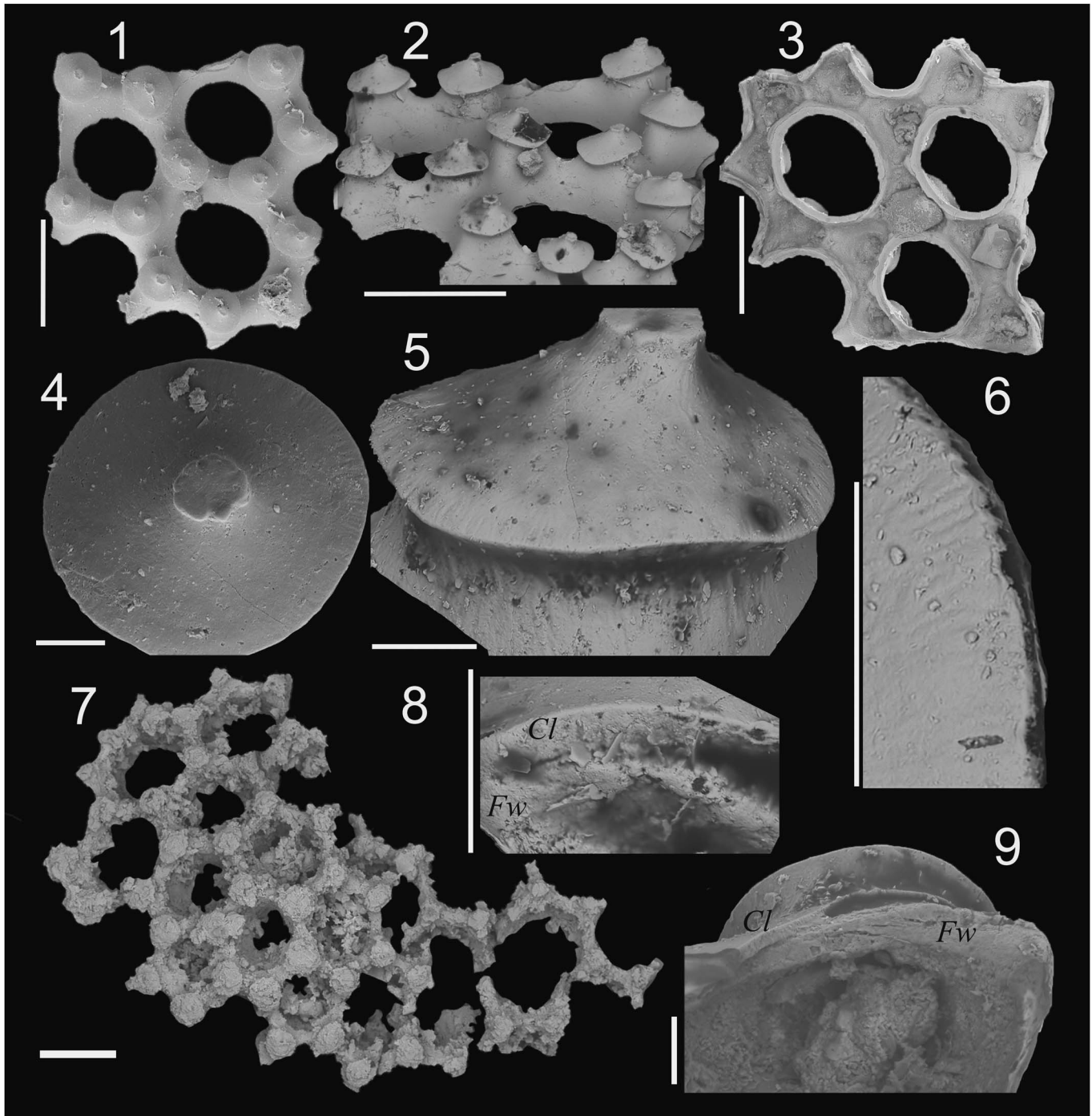


Figure 4. *Microdictyon* sp. from the Xinji Formation. (1–6, 8, 9) Plate S3, 166029, collected at Shuiyu section; (1) plan external view of the fragment; (2) oblique external view of the fragment; (3) internal view; (4) plan view of a node; (5) lateral view of a node; (6) magnification of the periphery 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. (4–6, 8, 9) Scale bars = 20 μ m; (1–3, 7) scale bars = 200 μ m. *Cl* = capping layer; *Fw* = framework.

Description.—Plate S1 is ovoid and strongly convex, measuring 2,030 mm in length and 1,372 mm in maximum width, with a measured ratio of length to width at 1.48 (Fig. 2.1, 2.2). The holes are circular to ovoid in shape. The diameter (21.6 μ m to

189 μ m with the average of 115.35 μ m) 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

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. (1–3, 9–13) Scale bars = 200 μ m; (4–8) scale bars = 20 μ m. *Cl* = capping layer; *Fw* = framework.

variation, with one hole surrounded by four nodes and 13 other holes 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 ranges from 29.24 to 160.94 μm with the average of 77.26 μm and decreases toward the periphery of the plate. The majority of nodes show a single acentric low apex that protrudes from the surface. The apices roughly point in a single direction (Figs. 2.2, 2.3, 3.1, 3.10). It is noteworthy that many apices have a distinct circular or subcircular rim that forms a slightly concave platform at an oblique angle with the surface of the mushroom-shaped nodes (Fig. 2.3, 2.7–2.10). The apex of the node in plate S3 is quite distinct, with a relatively planar surface (Fig. 4.1, 4.2, 4.4, 4.5). The diameter of the apices ranges from 10.00 to 33.29 μm with the average of 21.52 μm . Toward the periphery of the plate, the mushroom-shaped nodes of plates S1 and S5 deform, giving the appearance of a single sharp tubercle with an indistinct rim (Figs. 2.2–2.4, 3.9), and some apices of nodes of plate S2 separate into multiple little tips (Fig. 3.1, 3.2, 3.7). The multiple tips only cover half of the apex of one node in plate S2 (Fig. 3.6). The upper surfaces of the nodes in plate S3 bear radial lines that originate from the apex and extend outward to the rim of the node (Fig. 4.4–4.6), possibly extending into the base of the nodes (Fig. 4.5). The mushroom-shaped nodes are hollow and sealed by one capping layer (Figs. 2.5, 3.8, 4.8, 4.9). On the inner surface, each hole has a cylindrical tubular wall with a basal opening (Figs. 2.6, 3.3). The peripheral girdle has a slightly inclined outer edge and an upright inner edge (Fig. 3.9). The plate microstructure consists of one basal framework layer (*Fw*) and one upper capping layer (*Cl*) attaching on the framework (Figs. 2.11, 3.5, 3.8, 4.8, 4.9). One poorly preserved fragment retrieved from the Shangwan section shows that holes 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 China material. The spiny nodes of the plates from North China occur in many species of *Microdictyon*, such as *Microdictyon chinense*, *Microdictyon* cf. *M. effusum*, *Microdictyon jinshaense* (Zhang and Aldridge, 2007), and *Microdictyon* cf. *M. depressum* (Skovsted, 2006). But the plates described herein can be easily distinguished from the plates of these species by the combination of characters listed in the preceding. 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: five specimens; Topper et al., 2009: six 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* 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 *Quadratapora 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 *Eofal-lotaspis* Zone in Morocco and the *Profal-lotaspis 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 et al., 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 Northeast Greenland (Skovsted, 2006), the *Elliptocephala asaphoides* assemblage in the United States (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

Chrono-stratigraphy			North China	Australia	South China	Kazakhstan	Uzbekistan	Mongolia	Siberia	Turkey	Avalonia		Baltica	Laurentia					
Period	Series	Stage									Shropshire	E. Mas.		Greenland	Canada	USA	Mexico		
Cambrian	Series 3	Stage 5	• <i>Microdictyon</i> sp.																
		Stage 4		• <i>M. jinshanensis</i> • <i>M. depressum</i> • <i>Microdictyon</i> sp.	• <i>M. aff. rhomboidale</i> • <i>M. jinshanensis</i> • <i>M. fuchengensis</i> • <i>M. cf. effusum</i> • <i>M. chinensis</i> • <i>M. sinicum</i> • <i>Microdictyon</i> sp.	• <i>M. effusum</i>	• <i>M. rhomboidale</i>	• <i>Microdictyon</i> sp.	• <i>Microdictyon</i> sp. • <i>M. cf. rhomboidale</i> • <i>M. rhomboidale</i> • <i>M. effusum</i> • <i>M. cf. rhomboidale</i> • <i>M. roborisoni</i> • <i>M. sphaeroides</i>	• <i>Microdictyon</i> sp.	• <i>M. cf. effusum</i> • <i>M. sphaeroides</i>		• <i>Microdictyon</i> sp.						
	Stage 3										• <i>Microdictyon</i> sp.	• <i>M. effusum</i>	• <i>M. cf. depressum</i>	• <i>M. cf. rhomboidale</i>	• <i>M. cf. rhomboidale</i> • <i>Microdictyon</i> sp. • <i>Microdictyon</i> sp. • <i>M. roborisoni</i>				
	Stage 2																		
	Terreneuvian	Stage 2																	

Figure 5. Stratigraphic occurrences of *Microdictyon* species documented from different paleocontinents ranging from Cambrian Stage 2 to Stage 5. E. Mas. = eastern Massachusetts.

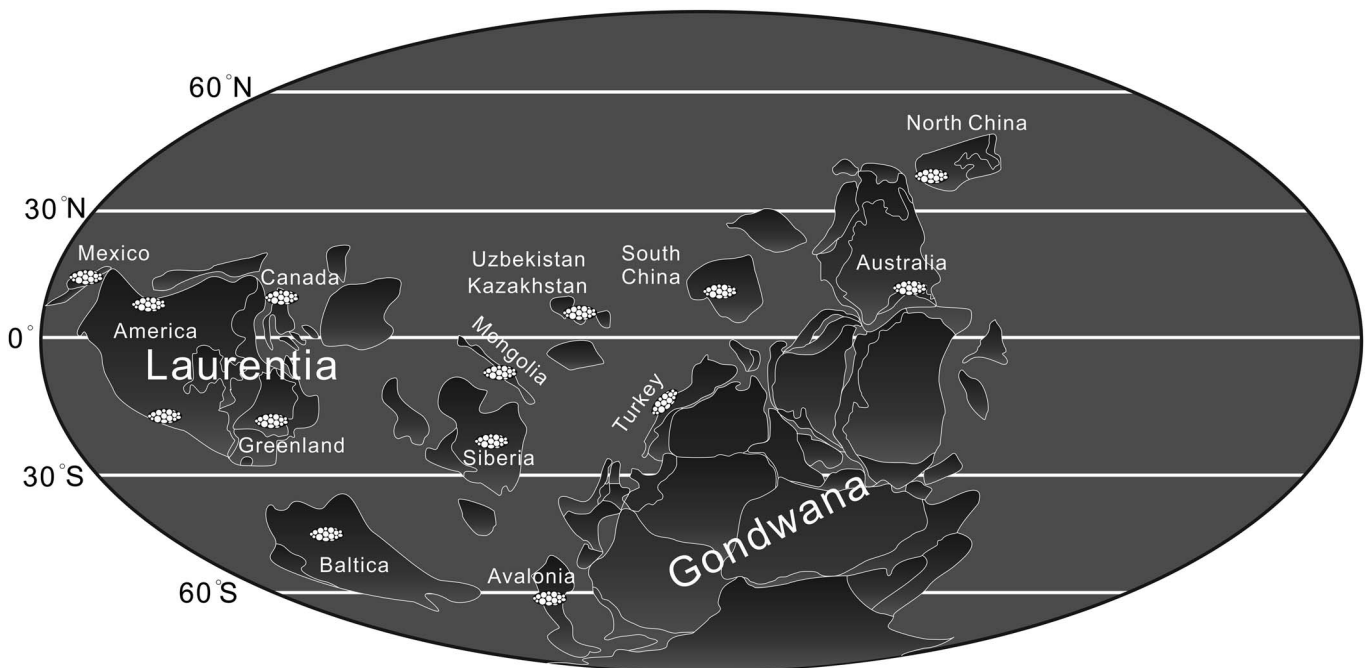


Figure 6. Paleogeographical distribution of *Microdictyon* from Cambrian Stage 2 to Stage 5 (paleogeographic map modified from Yang et al., 2015).

of *Microdictyon* in this period, with only *M. sphaeroides*, *M. depressum*, and *M. jinshanensis* 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* Biozone in Siberia (Kouchinsky et al., 2011), the *Acadoparadoxides mureroensis* Zone in Turkey (Sarmiento et al., 2001; stratigraphy revised by Dean, 2005), and the *Ptychagnostus gibbus* Zone (uppermost Stage 5) in North America and Baltica (Bengtson et al., 1986). Species reported include *M.*

roborisoni (new occurrence), *M. sphaeroides*, and a few undetermined species.

The first appearance datum (FAD) of *Microdictyon* has been included in discussions as a potential marker for defining the global Stage 3 basal boundary (Peng et al., 2012); however, the uncertainties regarding plate taxonomy and the sporadic appearance of *Microdictyon* specimens in Stage 2 in South Australia (Topper et al., 2011; Betts et al., 2016) hamper the biostratigraphic application of *Microdictyon* at the species level.

There are morphological similarities between the species documented from China and Australia; for example, nodes with multiple-tip apices only occur in the plates of *M. chinense* and *M. jinshaense* from South China (Zhang and Aldridge, 2007) and *M. jinshaense* from South Australia (Topper et al., 2009, 2011) and the plates illustrated herein. This could indicate that North China had a close paleogeographic position with South Australia and South China in the early Cambrian. The early occurrence (Stage 2), wide distribution, and long stratigraphic range of *Microdictyon* suggest that the genus may have been a pioneering member of Cambrian communities displaying a strong adaptability to a variety of environments during the Cambrian explosion.

Morphological variation of the nodes of the isolated Microdictyon plates.—It is obvious that some characters of the nodes of *Microdictyon* plates can occur in different *Microdictyon* species. For example, the short spiny nodes over the entire external surface of some medium-sized plates (possibly representing an intermediate 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. *M. effusum*, *Microdictyon jinshaense* (Zhang and Aldridge, 2007), *Microdictyon* cf. *M. 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). Because of the later occurrence (Cambrian, Stage 5) of *M. robisoni* with the tall mushroom-shaped nodes, this character might be considered a derived feature, and low mushroom-shaped nodes may be a 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 in the preceding, nodes with single-tip apices and multiple-tip apices can coexist in a single plate (Fig. 3.1, 3.2, 3.7) and possibly represent 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 are 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. *M. 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 a 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 taxonomy of isolated plates should comprehensively analyze whether the morphological variability observed in the assemblage could represent intraspecific or ontogenetic variation. Much of this can only be done when examining large data sets. It appears possible that low mushroom-shaped nodes may represent a primitive character of the genus while the tall mushroom-shaped nodes may be a more derived character. It is likely that the minor morphological variations observed in this small assemblage represent intraspecific or ontogenetic variation; however, in the absence of additional material, this remains unresolved.

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