

A new species of the primitive stromatoporoid *Cystostroma* from the Ordovician of East Asia

Juwan Jeon¹, Qijian Li^{2,3}, Jae-Ryong Oh^{4,5}, Suk-Joo Choh⁶, and Dong-Jin Lee^{1*}

¹Department of Earth and Environmental Sciences, Andong National University, Andong 36729, Republic of Korea

²CAS Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Nanjing 210008, China

³Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China

⁴Division of Polar Earth-System Sciences, Korea Polar Research Institute, Incheon 21990, Republic of Korea

⁵Polar Science, University of Science and Technology, Daejeon 34113, Republic of Korea

⁶Department of Earth and Environmental Sciences, Korea University, Seoul 02841, Republic of Korea

ABSTRACT: A new species of the most primitive rosenellid stromatoporoid *Cystostroma*, *C. primordia* sp. nov. is reported from the Hunhuayuan Formation (Lower Ordovician, Floian) of Guizhou Province in the South China Block and the Duwibong Formation (Middle Ordovician, Darriwilian) of the Taebaeksan Basin in mid-eastern Korea (North China Block). This species is the first representative of the genus found in both the North and South China blocks. *Cystostroma primordia* sp. nov. is characterized by the absence of denticles and distinctively smaller cyst plates (height 0.04–0.20 mm, length 0.09–0.39 mm) than any other known species of *Cystostroma*. The presence of *C. primordia* sp. nov. in Lower to Middle Ordovician strata of western Gondwana challenges the long-held view of the late Middle Ordovician emergence of Paleozoic stromatoporoids. The simple internal morphological features of this new species and its occurrence in the Lower Ordovician of South China strongly indicate that an Early Ordovician *Cystostroma*-type precursor from western Gondwana is located near the base of the stromatoporoid stock. This occurrence greatly preceded the late Middle Ordovician (late Darriwilian) stromatoporoid diversification in circum-equatorial regions worldwide.

Key words: *Cystostroma primordia* sp. nov., Ordovician, Floian, Darriwilian, China, Korea

Manuscript received January 10, 2018; Manuscript accepted July 20, 2018

1. INTRODUCTION

Paleozoic stromatoporoids have long been considered to have emerged during the late Middle Ordovician (Webby, 2015a). Five of seven families in the Order Labechiida appeared nearly contemporaneously during the Darriwilian throughout the low-paleolatitude regions of Laurentia, Siberia and Gondwana (Webby, 2004, 2015a, 2015c; Nestor and Webby, 2013; Stock et al., 2015). This rather sudden and almost simultaneous widespread Darriwilian appearance of diverse early stromatoporoids (Nestor and Webby, 2013; Stock et al., 2015; Webby, 2015a, 2015c) has been explained by two different hypotheses: the conventional view states that the early stromatoporoids arose from one or two basic skeletonized rosenellids such as *Cystostroma* or

Pseudostylodictyon (Galloway, 1957; Webby, 2015a), whereas the alternative hypothesis suggests that stromatoporoids rose from ‘a simple, non-calcifying sponge root stock’ that acquired the ability to secrete a mineralized skeleton during the Darriwilian (Nestor and Webby, 2013; Webby, 2015a).

The order Labechiida, representing the earliest unequivocal stromatoporoids (Webby, 2015a; Webby et al., 2015), is characterized by regularly repeating internal structures such as cysts with variable sizes and features (Webby, 2015c). Among labechiids, the family Rosenellidae is distinguished by the presence of simple intraskeletal components of cyst plates and denticles, which are commonly regarded as primitive features of stromatoporoids (Webby, 2015c). Because of the presence of upwardly convex cyst plates, which are regarded as a typical trait of the most primitive stromatoporoids (Stearn, 2015), *Cystostroma* and *Pseudostylodictyon* from the Middle Ordovician Chazy Limestone of Vermont, U.S.A. (Galloway, 1957) have long been assumed to be representatives of the most primitive stock of stromatoporoids (Webby, 2015c). The recent discovery of *Cystostroma* in the Lower Ordovician (lower Floian) of southwest China (Li et al., 2017),

*Corresponding author:

Dong-Jin Lee

Department of Earth and Environmental Sciences, Andong National University, Andong 36729, Republic of Korea

Tel: +82-54-820-5471, E-mail: djlee@anu.ac.kr

©The Association of Korean Geoscience Societies and Springer 2019

however, indicates that stromatoporoids emerged much earlier than previously known, and confirms that this genus is positioned near the root of all clades of Ordovician stromatoporoids.

This study complements previous work on *Cystostroma* from the Lower Ordovician Hunghuayuan Formation, Zhangzhai, Guizhou Province, China (Li et al., 2017) and the Middle Ordovician Duwibong Formation, Taebaek, Korea (Oh et al., 2015). We define a new species, *C. primordia* sp. nov., based on the size and shape of the convex cyst plates and their imbrication pattern (Appendix Table A1).

2. GEOLOGICAL SETTING AND METHODS

The Taebaeksan Basin, which is located at the eastern end of the North China (Sino-Korean) Block (Fig. 1a), is comprised of the Precambrian metamorphic basement (the Yeongnam Massif), Cambro-Ordovician mixed clastic-carbonate Joseon Supergroup, and Carboniferous–Lower Triassic clastic sediments of the Pyeongan Supergroup (Chough, 2013). The Joseon Supergroup in Taebaek area is referred to the Taebaek Group (Choi and Chough, 2005).

The Duwibong Formation is the topmost lithostratigraphic unit of the Taebaek Group, and consists of shallow subtidal

deposits including massive wackestone to grainstone, calcareous shale, and intercalated thin layers of limestone conglomerates (Fig. 1b; Hyeong and Lee, 1992; Lee et al., 2001; Choi et al., 2004; Choi and Chough, 2005; Kwon et al., 2006). Based on the presence of the *Plectodina onychodonta* and *Aurilobodus serratus* conodont assemblage zones and actinoceroid cephalopods, the formation is estimated to be Llanvirnian to early Llandeilian (mid to late Darriwilian) in age (Lee and Lee, 1986; Lee and Lee, 1990; Yun, 2000).

The Korean *Cystostroma* specimens were collected from the upper part of the Duwibong Formation in the Manhangjae and Sorotgol sections (Fig. 1b). These stromatoporoids occur as stromatolite-like columnar, bulbous, and domical as well as oncoid-like concentric forms (Fig. 2; Hong et al., 2018). In contrast, the Chinese *Cystostroma* specimens were recovered from lithistid sponge-*Calathium* reefs in the upper Hunghuayuan Formation at the Zhangzhai section (Fig. 1c; Li et al., 2017). The 82-m-thick formation mainly consists of gray skeletal wackestone to grainstone, peloidal packstone to grainstone, and numerous reefs of various compositions (Li et al., 2014). The Hunghuayuan Formation is constrained to the uppermost Tremadocian to lower Floian based on the presence of the *Triangulodus bifidus*, *Serratognathus diversus*, and *Prioniodus honghuayanensis* conodont biozones

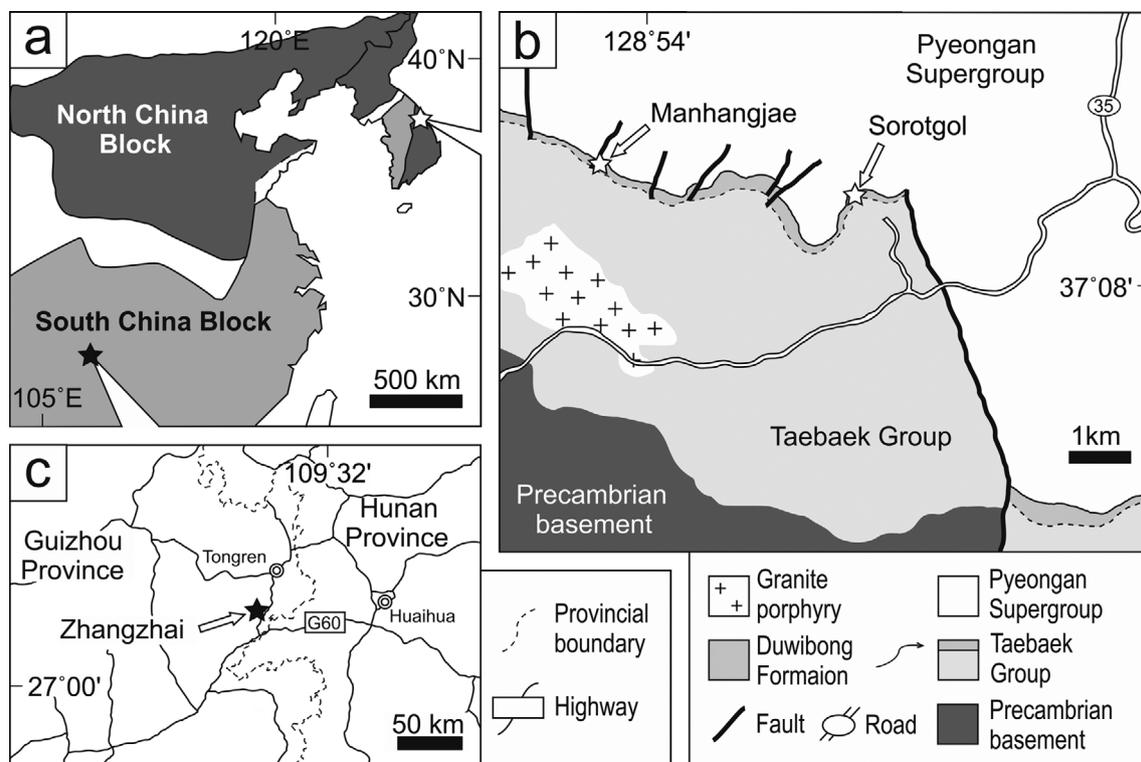


Fig. 1. (a) Simplified tectonic map of eastern Asia, showing the locations of the Taebaeksan Basin, Korea (white star) and Guizhou Province, China (black star), modified after Chough (2013). (b) Geological map and locations of the Sorotgol and Manhangjae sections (white stars), modified after Hong et al. (2018). (c) Location of the Zhangzhai section, near the border between Guizhou and Hunan provinces (black star), after Li et al. (2017).

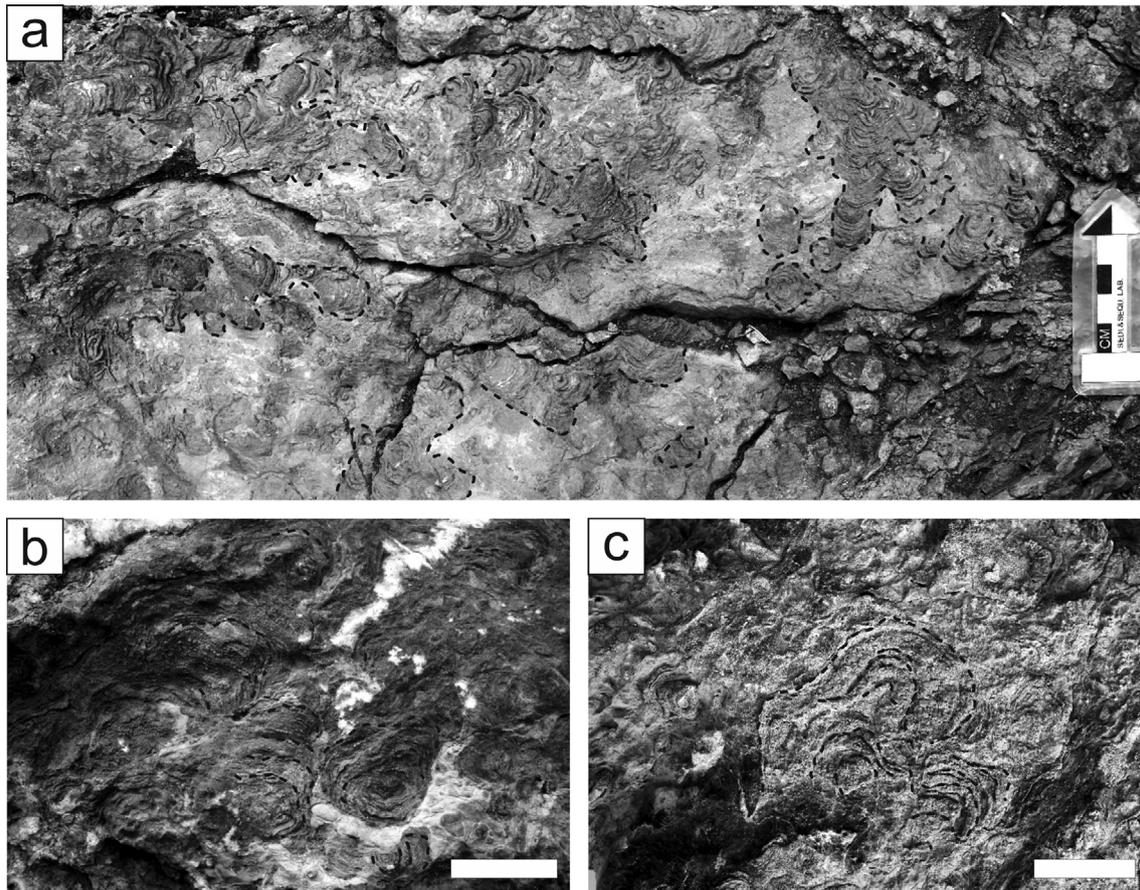


Fig. 2. Field photographs of a stromatoporoid-bryozoan skeletal reef in the Sorotgol section. (a) Outcrop photograph showing columnar to bulbous growth patterns. (b) Stromatolite-like structure composed of stromatoporoids and other organisms. (c) Domical growth pattern recorded by changes in growth direction. The dashed lines in each figure indicate the encrusting layers visible on the well-weathered surface. Scale bars in Figures 2b and c = 1 cm

(Zhen et al., 2009). The *Cystostroma*-bearing reefs in the upper part of the formation are early Floian in age (Zhen et al., 2009; Li et al., 2017).

Suprageneric assignments and terminology of the internal and external morphologies of stromatoporoids follow those of Webby (2015b; 2015c), based on the architecture of the calcified skeleton. All specimens were prepared as thin sections to investigate internal structures. To clearly visualize specimens that have been affected by diagenesis, we routinely used the ‘white card technique’ (Delgado, 1977; Zenger, 1979; Folk, 1987). Although this method successfully revealed the internal structures of some Duwibong specimens that were partly obscured by diagenesis (Oh et al., 2015), it did not make noticeable improvement to the Hunghuayuan specimens. The Duwibong type specimens are deposited in the Geological Collections, Natural Heritage Center (NHCG 10925–10927) of the Cultural Heritage Administration in Daejeon, Korea; the Hunghuayuan specimens (NIGP 168416) are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

3. SYSTEMATIC PALEONTOLOGY

Phylum Porifera Grant, 1836

Class Stromatoporoidea Nicholson and Murie, 1878

Order Labechiida Kühn, 1927

Family Rosenellidae Yavorsky in Khalfina and Yavorsky, 1973

Genus *Cystostroma* Galloway and St. Jean, in Galloway, 1957

1961 *Cystostroma* Galloway and St. Jean, p. 11

1969 *Cystostroma* Galloway and St. Jean; Webby, p. 644

1985 *Cystostroma* Galloway and St. Jean; Webby, Wyatt and Burrett, p. 162

1988 *Cystostroma* Galloway and St. Jean; Bolton, p. 23

1991 *Cystostroma* Galloway and St. Jean; Webby, p. 212

2015 *Cystostroma* Oh, Choh and Lee, p. 26

2017 *Cystostroma* sp. Li, Li and Kiessling, p. 142

Type species: *Cystostroma vermontense* Galloway and St. Jean, 1957 in Galloway, 1957 from the Middle Ordovician Crown Point Formation, Lake Champlain area of New York and Vermont, U.S.A.

Diagnosis: Skeleton mainly consisting of comparatively small-sized, upwardly convex cyst plates that form imbricated patterns, with or without denticles (Modified after Webby, 2015c, p. 714).

Remarks: *Cystostroma* belongs to one of the oldest stromatoporoid families, the Rosenellidae, which is characterized by possession of the primitive feature of simple cyst plates with or without denticles. Two Ordovician rosenellid genera, *Rosenella* Nicholson, 1886 and *Pseudostylodictyon* Ozaki, 1938, occur across various low-paleolatitude regions, including Sibumasu (Malaysia), North China, and Laurentia. Another rosenellid genus, *Priscastroma* Khromykh, 1999, is only known from the Darriwilian succession

of Siberia (Stock et al., 2015). Compared with *Cystostroma*, *Rosenella* has larger and flatter cyst plates, whereas *Pseudostylodictyon* has long and low cyst plates resembling laminae. In its possession of chevron-shaped cyst plates, *Priscastroma* is different from other genera in the Family Rosenellidae.

Cystostroma primordia sp. nov.

Figures 3 and 4

Etymology: Latin, *primordia*, from *primordium*, “first beginning, elementary stage, origin” referring to the fact that it is the earliest

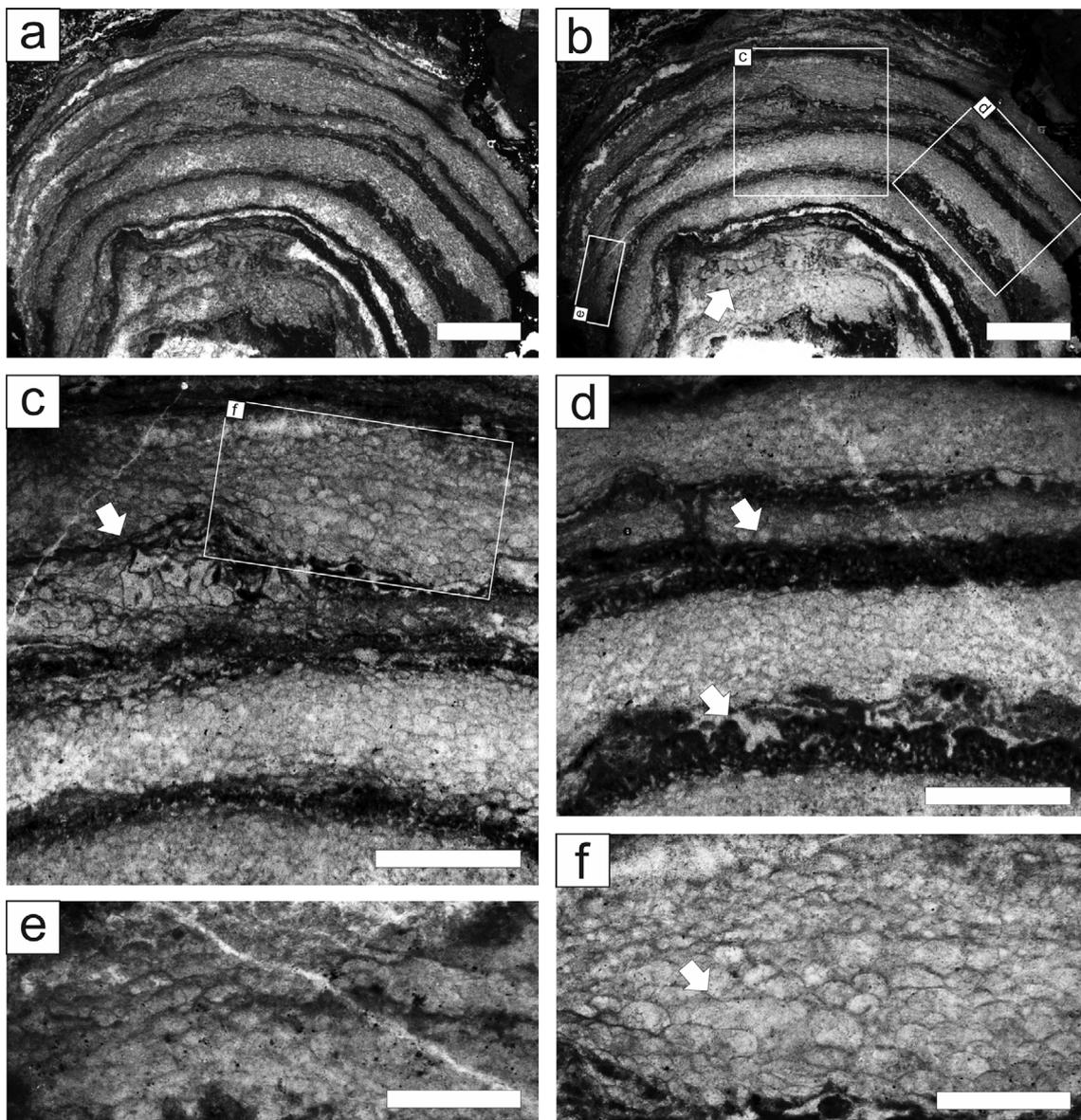


Fig. 3. (a) Plane-polarized transmitted light photomicrograph of a domical *Cystostroma primordia* sp. nov. showing well-developed latilaminae. Specimens from the Duwibong Formation, Sorotgol section. (b) Same area as (a) taken with “white card technique”. Scales in Figures 3a and b = 2 mm. (c–e) Enlargement of the areas marked by white rectangles in Figure 3b. (c) Well-developed and preserved latilaminae banding structure with an interlayered bryozoan (white arrow). (d) Particularly well-defined latilaminae interrupted by *Solenopora* (white arrows). Scales in Figures 3c and d = 1 mm. (e) Convex to irregularly shaped cyst plates of *C. primordia* sp. nov. (f) Enlargement of the area indicated by the white rectangle in Figure 3c, showing a remarkably wide cyst plate (white arrow). Scales in Figures 3e and f = 0.5 mm.

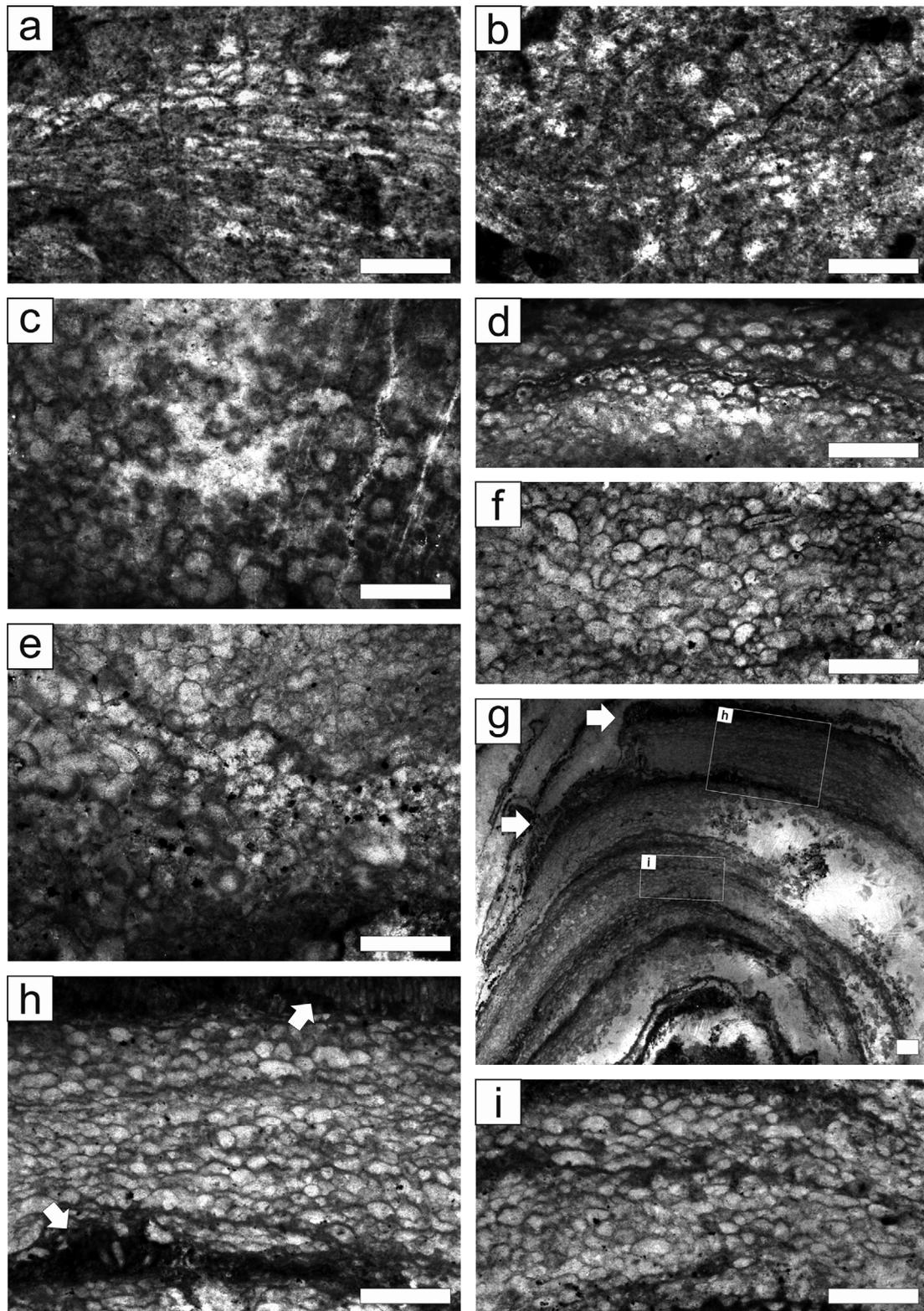


Fig. 4. (a and b) Vertical section of *Cystostroma primordia* sp. nov. under plane-polarized transmitted light showing convex cyst plates. Specimens from the Hunghuayuan Formation, Zhangzhai section (NIGP 168416). (c–i) Thin section photographs of *C. primordia* sp. nov. from the Duwibong Formation obtained using the ‘white card technique’. (c) Transverse section of holotype NHCG 10925 from the Sorotgol section. (d) Vertical section of holotype NHCG 10925. (e) Transverse and oblique section of paratype NHCG 10926 from the Sorotgol section. (f) Vertical section of paratype NHCG 10926 from the Sorotgol section. (g) Vertical section of paratype NHCG 10927 from the Manhangjae section showing multiple-layered laminar stromatoporoids alternating with layers of *Solenopora* (white arrows). (h and i) Enlargements of the area indicated by the white rectangles in Figure 4g. White arrows point to layers of *Solenopora* that were subsequently encrusted by a stromatoporoid. All scales in photomicrographs = 0.5 mm.

stromatoporoid with diagnostic characters of the smallest cyst size and simplest internal structure.

Types: Holotype: NHCG 10925 (one thin section; Figs. 4c and d), Sorotgol, Duwibong Formation (Middle Ordovician, Darriwilian), Taebaek, Korea (Fig. 1). Paratypes: NHCG 10926 (one thin section; Figs. 4e and f), Sorotgol; NHCG 10927 (one thin section; Figs. 4g–i), Manhangjae, Duwibong Formation (Middle Ordovician, Darriwilian), Taebaek, Korea (Fig. 1; Sorotgol section: 37°08'46.59"N, 128°56'35.82"E; Manhangjae section: 37°09'2.96"N, 128°53'57.22"E).

Material and occurrence: Two *Cystostroma* specimens (NIGP 168416) from the upper Hunghuayuan Formation (Early Ordovician, Floian), Zhangzhai section, Guizhou Province, China, occur within the intraskeletal crypts of a lithistid sponge-*Calathium* reef (Li et al., 2017). Nineteen specimens including the holotype (NHCG 10925) and a paratype (NHCG 10926), and forty five specimens including a paratype (NHCG 10927) were collected from the uppermost Duwibong Formation (Middle Ordovician, Darriwilian) at the Sorotgol and Manhangjae sections, Taebaeksan Basin, Korea, respectively (Fig. 1). *Cystostroma primordia* sp. nov. occurs as one of the main reef framework builders (about one-third of the reefs by volume) of decimeter-scale patch reefs co-constructed by alternating thin laminae of the bryozoan *Nicholsonella* and the alga *Solenopora* in the uppermost Duwibong Formation in the Sorotgol section (Oh et al., 2015; Hong et al., 2018). Together with bryozoans and *Solenopora*, *C. primordia* sp. nov. also forms spheroidal to ellipsoidal oncoïd-like structures

less than 30 mm high and up to 80 mm wide (Figs. 2 and 4g; see fig. 2a in Oh et al., 2015). Their internal structures (e.g., convex-upward cysts) are generally poorly preserved, and can usually be identified by means of the ‘white card technique’ (Figs. 3 and 4; see figs. 3c and d in Oh et al., 2015).

Diagnosis: *Cystostroma* composed of distinctively small cyst plates (height 0.04–0.20 mm and length 0.09–0.39 mm) without denticles.

Description: Skeleton of laminar to domical shape, forming part of multiply stacked encrusting laminae composed of alternating stromatoporoids, bryozoans, and *Solenopora* (Figs. 3 and 4). Thickness of each latilamina 1.3–29 mm (mean = 9.0 mm, n = 100; Oh et al., 2015), composed of imbricated and upwardly convex cysts 0.04–0.20 mm high (mean = 0.11 mm, n = 200) and 0.09–0.39 mm long (mean = 0.18 mm, n = 200; Appendix Table A1). Cyst plates commonly composed of a dark layer with compact microstructure. Denticles and mamelons absent. In tangential section, cysts exhibit irregular and rounded outlines.

Remarks: The Hunghuayuan specimens occur in reefs constructed mainly by *Calathium* and lithistid sponges (see Li et al., 2017). The Duwibong specimens either form spheroidal to ellipsoidal coated grains less than 30 mm high and up to 80 mm wide (Fig. 4g; see Oh et al., 2015), or construct sub-meter-scale skeletal reefs with other encrusting organisms (Figs. 2 and 3a, b; see Hong et al., 2018). Despite their occurrence at a different locality, all internal morphological characteristics of the Hunghuayuan *Cystostroma*, including the range of height and length, imbricated

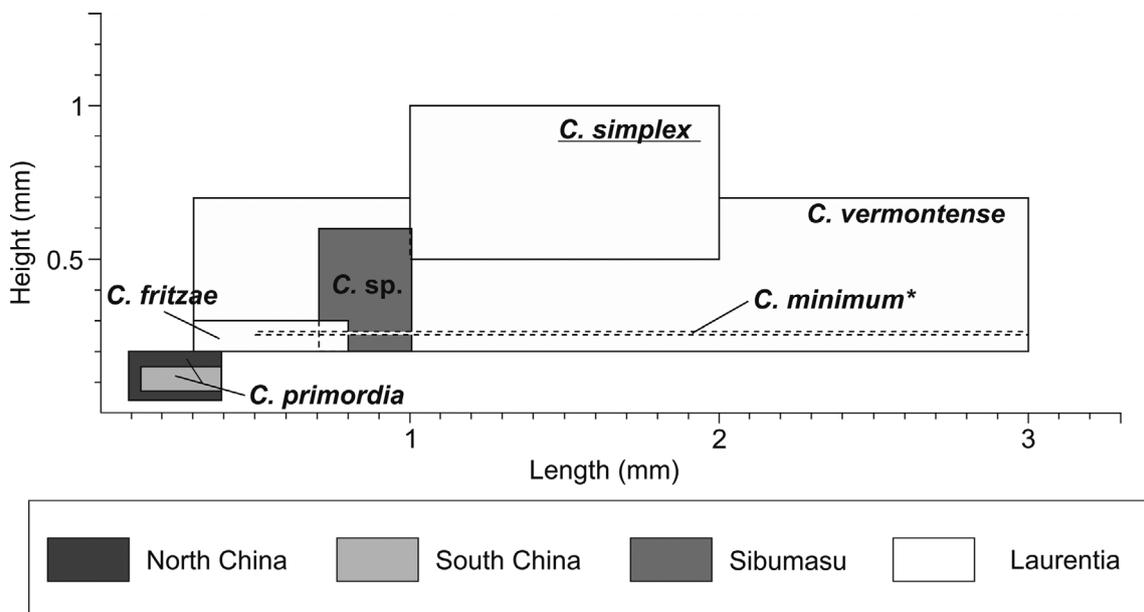


Fig. 5. Comparison of morphologic characters of Ordovician *Cystostroma* from various paleocontinents: North China (including Korea), South China, Sibumasu (present-day Malaysia), and Laurentia (North America). Data are based on Galloway (1957), Galloway and St. Jean (1961), Webby et al. (1985), Oh et al. (2015), and Li et al. (2017). The asterisk for *C. minimum* indicates that the height of cyst plates is only given as a mean value of 0.25 mm in Galloway and St. Jean (1961). The underlining of *C. simplex* indicates that the data only from the specimens with denticles were employed.

pattern of cysts, and absence of denticles, agree with those of the Duwibong specimens in every detail (Appendix Table A1; Figs. 4 and 5), and these specimens are therefore considered conspecific.

Cystostroma primordia sp. nov. is distinguished from other species of the genus by the small size of its cyst plates. Both the height and length of cysts in the species are much smaller than those of any known species of *Cystostroma* from the Middle Ordovician of North America and Malaysia. The height and length of cysts of *Cystostroma vermontense* Galloway and St. Jean, 1957 in Galloway, 1957, *C. simplex* Galloway and St. Jean, 1957 in Galloway, 1957, *C. minimum* (Parks, 1910), *C. fritzae* Galloway and St. Jean, 1961, and *Cystostroma* sp. from Malaysia (Webby et al., 1985) are compared with *C. primordia* sp. nov. (Fig. 5). Denticles are rare in Ordovician *Cystostroma*: five of six species of *Cystostroma* reported from Lower to Middle Ordovician strata do not have denticles (Fig. 5; Galloway, 1957; Galloway and St. Jean, 1961; Webby et al., 1985). Denticles are well developed in only one species, *C. simplex* from the Middle Ordovician succession of North America (Galloway, 1957).

4. DISCUSSIONS

4.1. Early Diversification of Stromatoporoids

Though some Ordovician rosenellid genera, including *Rosenella* and *Pseudostyloclyon*, have previously been reported from the North China Block (Yabe and Sugiyama, 1930; Ozaki, 1938), *Cystostroma* was not known from the Far East prior to the recent reports of Oh et al. (2015) and Li et al. (2017). The only other occurrence of *Cystostroma* in the region is a poorly preserved *Cystostroma?* sp. Webby, Wyatt and Burrett, 1985 from the Middle Ordovician Setul Limestone, Sibumasu (present-day Malaysia), which was located in Gondwana, near South China, during the Ordovician (Webby et al., 1985).

In contrast, four species of *Cystostroma* have been reported from the upper Middle Ordovician Chazy Group of New York and Vermont, U.S.A. (Galloway, 1957; Galloway and St. Jean, 1961). Galloway (1957) proposed *Cystostroma* and *Pseudostyloclyon* to be the earliest and the most primitive known true stocks of stromatoporoids, based on the development of cyst plates with denticles being the most primitive stromatoporoid traits. Galloway and St. Jean (1961) further suggested that the 'regular' laminar-like cyst plates of *Pseudostyloclyon* are even more primitive than the convex cyst plates of *Cystostroma*. Hence, the conventional idea that "a few simple (one or two basic) skeletonized morphologies of *Cystostroma*- or *Pseudostyloclyon*-type first evolved during the middle Darriwilian and then spread circum-equatorially over the next one to three million years, prior to the end of Middle Ordovician time" (see Webby, 2015a, p. 583) was

the prevailing view on the origin of stromatoporoids, until Nestor and Webby (2013) proposed an alternative hypothesis.

Nestor and Webby (2013) argued that the simple rosenellid-type morphology was insufficient to explain the rather sudden and nearly contemporaneous widespread Darriwilian appearance of diverse early stromatoporoid stocks. They suggested that initially a simple, non-calcifying sponge root stock that was present in warm shallow seas of most paleo-equatorial regions acquired the ability to secrete a mineralized skeleton, then subsequently underwent rapid diversification during the Darriwilian. However, in light of the recent report of an Early Ordovician *Cystostroma* from China (Li et al., 2017), it is suggested that the advent of a *Cystostroma*-type precursor in the Floian from western Gondwana eventually culminated in the nearly simultaneous appearance of diverse early stromatoporoids around circum-equatorial regions during the Darriwilian.

In Darriwilian, twelve labechiid genera (*Pseudostyloclyon*, *Cystostroma*, *Rosenella*, *Priscastroma*, *Labechia*, *Labechiella*, *Pachystylostroma*, *Aulacera*, *Ludictyon*, *Thamnobeatricea*, *Sinodictyon*, and *Lophiostroma*), belonging to five families, have been recorded from seven regions around the world (Nestor and Webby, 2013; Webby et al., 2015). All of these genera, with the exceptions of *Priscastroma* and *Pachystylostroma*, occur in the North China Block (Nestor and Webby, 2013; Stock et al., 2015; see table 1 in Jeon et al., 2017). This allows us to suggest that the advent of stromatoporoids took place much earlier than previously known, and rosenellids, especially *Cystostroma*, are ancestral to other Ordovician stromatoporoid lineages. Thus, the description of *Cystostroma* with primitive morphological features from the Lower to Middle Ordovician strata of East Asia provides an updated scenario of the Early Ordovician origin of Paleozoic stromatoporoids from a *Cystostroma*-type precursor in western Gondwana.

4.2. Transition from Cryptic Fauna to Reef Builders

Empirical data indicate that many ecological features established during the "Great Ordovician Biodiversification Event" became the basis for marine ecosystems for the rest of the Phanerozoic (Harper, 2006). Based on a thorough analysis of 18,621 marine animal genera from the Cambrian to the present day, a recent assessment of ecological modes confirmed that the most significant growth in functional diversity took place during the Ordovician (Knope et al., 2015). In Ordovician reefs, sheet-like metazoan builders such as bryozoans, stromatoporoid sponges, and tabulate corals showed an ecological shift from early representative forms growing on hard substrates to more complex intergrown metazoan-microbial consortia (Kröger et al., 2017). With this critical ecological shift, sheet-like metazoans blended

with calcimicrobes and were therefore able to create skeletal frameworks with distinct topographic relief (Kröger et al., 2017).

One of the best examples, *Pulchrilamina*, the earliest Ordovician stromatoporoid-like encruster, appeared in late Tremadocian–Floian reefs, much earlier than the diversification of indisputable stromatoporoids (Webby, 2002; Adachi et al., 2012). Pulchrilaminids have recently been interpreted as a separate, independent group of hypercalcified sponges rather than true stromatoporoids (Webby, 2015d), but pulchrilaminids had a life habit similar to that of some *Cystostroma*-type stromatoporoids. As a typical sheet-like metazoan builder, *Pulchrilamina* displayed a strong association with microbes during the Early Ordovician, as indicated by the common mutual encrustation of these stromatoporoids and calcimicrobes (Adachi et al., 2012). *Pulchrilamina* even constructed frameworks in some Early Ordovician reefs of Texas and southern Oklahoma (Toomey and Ham, 1967).

In contrast to *Pulchrilamina*, the earliest in situ stromatoporoids (*Cystostroma*) in South China appeared in crypts, yet formed a framework during the Darriwilian, lagging behind the first appearance of their respective skeletal ancestors. In South China, the size of *Cystostroma* specimens is limited to the millimeter-scale, and well-preserved specimens occur exclusively on the hard substrates provided by *Calathium* (Li et al., 2017). Accordingly, it is reasonable to assume that, as a small encruster in the Early Ordovician, *Cystostroma* was unable to overgrow microbial fabrics, and by the Middle Ordovician, *Cystostroma*-type stromatoporoids had developed the novel ability to colonize microbial fabrics, allowing them to build frameworks together with other encrusting metazoans. It is also worth noting that this transition from cryptic fauna to reef builders probably required no identifiable changes in their skeletons. This evolutionary transition of life habit is broadly consistent with the patterns observed in other sheet-like stromatoporoids as well as some reef-building bryozoans and tabulate corals, which led to the expansion of novel reef habitats in more complex substrates during the Ordovician (Kröger et al., 2017).

5. CONCLUSIONS

A new species of *Cystostroma*, *C. primordia* sp. nov., is recognized from the Lower Ordovician (Floian) Hunghuayuan Formation of Guizhou Province, southwest China and the Middle Ordovician (Darriwilian) Duwibong Formation of the Taebaeksan Basin, Korea. The new species is characterized by possession of distinctively smaller cyst plates (height 0.04–0.20 mm and length 0.09–0.39 mm) than any other previously described species of *Cystostroma* and the absence of denticles. The present study significantly modifies previous ideas on the advent of early stromatoporoids by providing direct evidence of the presence of

Cystostroma-type stromatoporoids possessing the most primitive and simplest skeletal components during the Early Ordovician. Initially, *C. primordia* sp. nov. was an encruster inhabiting cryptic spaces, then became a framework builder by Middle Ordovician time. Although further discoveries and detailed studies of early stromatoporoids are required to reveal the complete phylogenetic relationships and life strategy changes of early Paleozoic stromatoporoids, the greater diversity of stromatoporoids in Gondwana than in Laurentia suggests that Gondwana was the center for inception and diversification of the stromatoporoid root stock during the Early to Middle Ordovician.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Prof. Deyuan Dong of NIGPAS, who contributed significantly to the study of stromatoporoids of East Asia. This study was supported by grants from the National Research Foundation of Korea (2018R1A2A2A05018469) to SJC and (2018R1A2B2005578) to DJL, and from the National Natural Science Foundation of China (41521061 and XDB26000000) to QL. We deeply appreciate the constructive comments of two anonymous reviewers, which greatly improved the manuscript. We also thank K. Liang of NIGPAS and M. Lee of the Korea Polar Research Institute for their helpful comments on an earlier version of the manuscript.

REFERENCES

- Adachi, N., Liu, J.B., and Ezaki, Y., 2012, Early Ordovician stromatoporoid *Pulchrilamina spinosa* from South China: geobiological significance and implications for the Early development of skeletal-dominated reefs. *Paleontological Research*, 16, 59–69.
- Bolton, T.E., 1988, Stromatoporoidea from the Ordovician rocks of central and eastern Canada. *Geological Survey of Canada, Bulletin*, 379, 17–45.
- Choi, D.K. and Chough, S.K., 2005, The Cambrian–Ordovician stratigraphy of the Taebaeksan Basin, Korea: a review. *Geosciences Journal*, 9, 187–214.
- Choi, D.K., Chough, S.K., Kwon, Y.K., Lee, S.-B., Woo, J., Kang, I., Lee, H.S., Lee, S.M., Sohn, J.W., Shinn, Y.J. and Lee, D.-J., 2004, Taebaek Group (Cambrian–Ordovician) in the Seokgaegae section, Taebaeksan Basin: a refined lower Paleozoic stratigraphy in Korea. *Geosciences Journal*, 8, 125–151.
- Chough, S.K., 2013, *Geology and Sedimentology of the Korean Peninsula*. Elsevier, Amsterdam, 363 p.
- Delgado, F., 1977, Primary textures in dolostones and recrystallized limestones; a technique for their microscopic study. *Journal of Sedimentary Petrology*, 47, 1339–1341.
- Folk, R.L., 1987, Detection of organic matter in thin-sections of carbonate rocks using a white card. *Sedimentary Geology*, 54, 193–200.
- Galloway, J.J., 1957, Structure and classification of the Stromatoporoidea.

- Bulletins of American Paleontology, 37, 345–480.
- Galloway, J.J. and St. Jean, J., 1961, Ordovician Stromatoporoidea of North America. *Bulletins of American Paleontology*, 43, 5–119.
- Grant, R.E., 1836, Animal kingdom. In: Todd, R.B. (ed.), *The Cyclopaedia of Anatomy and Physiology*, Vol. 1. Sherwood, Gilbert and Piper, London, p. 107–118.
- Harper, D.A.T., 2006, The Ordovician biodiversification: setting an agenda for marine life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232, 148–166.
- Hong, J., Oh, J.-R., Lee, J.-H., Choh, S.-J., and Lee, D.-J., 2018, The earliest evolutionary link of metazoan bioconstruction: laminar stromatoporoid-bryozoan reefs from the Middle Ordovician of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 492, 126–133.
- Hyeong, K.-S. and Lee, Y.I., 1992, Depositional facies of oolitic grainstones in the Ordovician Duwibong Formation, Korea. *Journal of Geological Society of Korea*, 28, 227–238.
- Jeon, J., Park, J., Choh, S.-J., and Lee, D.-J., 2017, Early labechiid stromatoporoids of the Yeongheung Formation (Middle Ordovician), Yeongwol Group, mideastern Korean Peninsula: Part II. Systematic paleontology and paleogeographic implications. *Geosciences Journal*, 21, 331–340.
- Khalifina, V.K. and Yavorsky, V.I., 1973, Klaifikatsiya stromatoporoidey [Classification of stromatoporoids]. *Paleontologičeskij Žurnal*, 1973, 19–34.
- Khromykh, V.G., 1999, Novyi rod drevneishikh stromatoporoidey [New genus of the earliest stromatoporoids]. *Doklady Akademii Nauk*, 364, 801–803.
- Knöpe, M.L., Heim, N.A., Frishkoff, L.O., and Payne, J.L., 2015, Limited role of functional differentiation in early diversification of animals. *Nature Communications*, 6, 1–6.
- Kröger, B., Desrochers, A., and Ernst, A., 2017, The reengineering of reef habitats during the Great Ordovician Biodiversification Event. *Palaios*, 32, 584–599.
- Kühn, O., 1927, Zur Systematik und Nomenklatur der Stromatoporen. *Zentralblatt Mineralogie, Geologie und Paläontologie, Abteilungen B*, 546–551.
- Kwon, Y.K., Chough, S.K., Choi, D.K., and Lee, D.J., 2006, Sequence stratigraphy of the Taebaek Group (Cambrian–Ordovician), mid-east Korea. *Sedimentary Geology*, 192, 19–55.
- Lee, K. and Lee, H.-Y., 1990, Conodont biostratigraphy of the Upper Choseon Supergroup in Jangseong–Dongjeom area, Gangweon-do. *Journal of the Paleontological Society of Korea*, 6, 188–210.
- Lee, Y.I., Hyeong, K., and Yoo, C.M., 2001, Cyclic sedimentation across a Middle Ordovician carbonate ramp (Duwibong Formation), Korea. *Facies*, 44, 61–74.
- Lee, Y.N. and Lee, H.-Y., 1986, Conodont biostratigraphy of the Jigunsan Shale and Duwibong Limestone in the Nokjeon–Sangdong area, Yeongweol-gun, Kangweondo. *Journal of the Paleontological Society of Korea*, 2, 114–136.
- Li, Q., Li, Y., and Kiessling, W., 2014, Early Ordovician sponge-*Calathium*-microbial reefs on the Yangtze Platform margin of the South China Block. *GFF*, 136, 157–161.
- Li, Q., Li, Y., and Kiessling, W., 2017, The oldest labechiid stromatoporoids from intraskeletal crypts in lithistid sponge-*Calathium* reefs. *Lethaia*, 50, 140–148.
- Nestor, H. and Webby, B.D., 2013, Biogeography of the Ordovician and Silurian Stromatoporoidea. In: Harper, D.A.T. and Servais, T. (eds.), *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoir, 38, p. 67–79.
- Nicholson, H.A., 1886, A monograph of the British Stromatoporoids, Part 1. Palaeontographical Society, London, 39, 1–130.
- Nicholson, H.A. and Murie, J., 1878, On the minute structure of *Stromatopora* and its allies. *Zoology Journal of the Linnean Society*, 14, 187–246.
- Oh, J.-R., Choh, S.-J., and Lee, D.-J., 2015, First report of *Cystostroma* (Stromatoporoidea; Ordovician) from Sino-Korean Craton. *Geosciences Journal*, 19, 25–31.
- Ozaki, K.E., 1938, On some stromatoporoids from the Ordovician limestone of Shantung and South Manchuria. *Journal of the Shanghai Science Institute*, 2, 205–223.
- Parks, W.A., 1910, Ordovician stromatoporoids. University of Toronto Studies, Geological Series, 7, 1–52.
- Stearn, C.W., 2015, Internal morphology of the Paleozoic Stromatoporoidea. In: Selden, P.A. (ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, Vol. 4–5*. The University of Kansas, Paleontological Institute, Lawrence, p. 487–520.
- Stock, C.W., Nestor, H., and Webby, B.D., 2015, Paleobiogeography of the Paleozoic Stromatoporoidea. In: Selden, P.A. (ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, Vol. 4–5*. The University of Kansas, Paleontological Institute, Lawrence, p. 653–689.
- Toomey, D.F. and Ham, W.E., 1967, *Pulchrilamina*, a new mound-building organism from Lower Ordovician rocks of West Texas and southern Oklahoma. *Journal of Paleontology*, 41, 981–987.
- Webby, B.D., 1969, Ordovician stromatoporoids from New South Wales. *Palaeontology*, 12, 637–662.
- Webby, B.D., 1991, Ordovician stromatoporoids from Tasmania. *Alcheringa*, 15, 191–227.
- Webby, B.D., 2002, Patterns of Ordovician reef development. In: Kiessling, W., Flügel, E., and Golonka, J. (eds.), *Phanerozoic Reef Patterns*. SEPM (Society for Sedimentary Geology) Special Publication, 72, p. 129–179.
- Webby, B.D., 2004, Stromatoporoids. In: Webby, B.D., Paris, F., Droser, M.L., and Percival, I.G. (eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, p. 112–118.
- Webby, B.D., 2015a, Early evolution of the Paleozoic Stromatoporoidea. Selden, P.A. (ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, Vol. 4–5*. The University of Kansas, Paleontological Institute, Lawrence, p. 575–592.
- Webby, B.D., 2015b, Glossary of terms applied to the hypercalcified Porifera. Selden, P.A. (ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, Vol. 4–5*. The University of Kansas, Paleontological Institute, Lawrence, p. 397–416.
- Webby, B.D., 2015c, Labechiida. In: Selden, P.A. (ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, Vol. 4–5*. The University of Kansas, Paleontological Institute, Lawrence, p. 709–754.
- Webby, B.D., 2015d, Class Uncertain, order Pulchrilaminida: systematic descriptions. In: Selden, P.A. (ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, Vol. 4–5*. The University of Kansas, Paleontological Institute, Lawrence, p. 837–844.

- Webby, B.D., Stearn, C.W., and Nestor, H., 2015, Biostratigraphy of the Paleozoic Stromatoporoidea. In: Selden, P.A. (ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, Vol. 4–5. The University of Kansas, Paleontological Institute, Lawrence, p. 613–630.
- Webby, B.D., Wyatt, D., and Burrett, C., 1985, Ordovician stromatoporoids from the Langkawi Islands, Malaysia. *Alcheringa*, 9, 159–166.
- Yabe, H. and Sugiyama, T., 1930, On some Ordovician stromatoporoids from South Manchuria, North China and Chosen (Corea), with notes on two new European forms. *Tōhoku Imperial University, Science Report Series 2 (Geology)*, 14, 47–62.
- Yun, C.-S., 2000, Actinoceroid cephalopods from the Duwibong Formation (Middle Ordovician), Taebaek–Yeongwol area, Korea. *Journal of the Paleontological Society of Korea*, 16, 67–92.
- Zenger, D.H., 1979, Primary textures in dolostones and recrystallized limestone; a technique for their microscopic study; discussion. *Journal of Sedimentary Petrology*, 49, 677–678.
- Zhen, Y.Y., Percival, I.G., Liu, J., and Zhang, Y., 2009, Conodont fauna and biostratigraphy of the Honghuayuan Formation (Early Ordovician) of Guizhou, South China. *Alcheringa*, 33, 257–295.
- Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

APPENDIX

Table A1. Raw data matrix of cyst height and length of *Cystostroma primordia* sp. nov. from the Duwibong Formation in the Sorotgol and Manghangjae sections, Korea, and the Hunghuayuan Formation, mid-eastern Guizhou, China

Specimen		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Mean	Min.	Max.	SD
Holotype-NHCG10925	height	0.16	0.1	0.1	0.11	0.12	0.12	0.09	0.14	0.08	0.11	0.13	0.13	0.15	0.15	0.12	0.14	0.1	0.12	0.12	0.1	0.12	0.16	0.2	0.16	0.14	0.13	0.08	0.2	0.03
	length	0.25	0.18	0.13	0.21	0.39	0.12	0.18	0.22	0.16	0.14	0.31	0.26	0.23	0.32	0.14	0.3	0.18	0.21	0.22	0.17	0.18	0.3	0.35	0.18	0.18	0.22	0.12	0.39	0.07
Paratype-NHCG10926	height	0.16	0.18	0.2	0.13	0.1	0.15	0.13	0.13	0.1	0.08	0.08	0.11	0.09	0.14	0.11	0.09	0.07	0.09	0.08	0.09	0.14	0.1	0.15	0.12	0.09	0.12	0.07	0.2	0.03
	length	0.25	0.22	0.24	0.11	0.11	0.14	0.11	0.17	0.14	0.13	0.13	0.16	0.11	0.11	0.19	0.13	0.12	0.13	0.17	0.11	0.14	0.19	0.17	0.18	0.15	0.15	0.11	0.25	0.04
Paratype-NHCG10927	height	0.12	0.1	0.09	0.1	0.09	0.14	0.07	0.05	0.1	0.09	0.09	0.1	0.07	0.07	0.08	0.05	0.09	0.07	0.06	0.1	0.08	0.04	0.05	0.05	0.06	0.08	0.04	0.14	0.02
	length	0.2	0.16	0.11	0.13	0.12	0.13	0.13	0.09	0.14	0.23	0.1	0.14	0.16	0.15	0.24	0.11	0.16	0.13	0.17	0.16	0.15	0.12	0.12	0.22	0.2	0.15	0.09	0.24	0.04
SR-1	height	0.12	0.08	0.14	0.09	0.07	0.15	0.1	0.09	0.11	0.06	0.06	0.1	0.08	0.09	0.07	0.09	0.1	0.1	0.05	0.07	0.09	0.11	0.12	0.08	0.08	0.09	0.05	0.15	0.02
	length	0.17	0.1	0.17	0.14	0.15	0.21	0.15	0.16	0.22	0.11	0.11	0.13	0.14	0.16	0.1	0.17	0.21	0.17	0.1	0.1	0.18	0.24	0.21	0.15	0.13	0.16	0.1	0.24	0.04
SR-2	height	0.07	0.12	0.1	0.08	0.09	0.12	0.09	0.12	0.12	0.1	0.07	0.09	0.1	0.1	0.11	0.12	0.11	0.2	0.12	0.15	0.19	0.18	0.12	0.12	0.1	0.12	0.07	0.2	0.03
	length	0.13	0.16	0.18	0.17	0.16	0.14	0.16	0.17	0.13	0.17	0.13	0.1	0.13	0.12	0.19	0.21	0.13	0.21	0.17	0.22	0.29	0.22	0.24	0.15	0.17	0.17	0.1	0.29	0.04
SR-3	height	0.11	0.08	0.1	0.11	0.07	0.08	0.09	0.14	0.16	0.13	0.12	0.17	0.12	0.13	0.14	0.15	0.1	0.17	0.11	0.1	0.07	0.11	0.11	0.11	0.15	0.12	0.07	0.17	0.03
	length	0.12	0.13	0.19	0.2	0.1	0.15	0.14	0.26	0.2	0.18	0.15	0.26	0.16	0.14	0.16	0.2	0.15	0.21	0.18	0.15	0.12	0.14	0.12	0.17	0.21	0.17	0.1	0.26	0.04
SR-4	height	0.07	0.1	0.08	0.05	0.04	0.08	0.09	0.11	0.11	0.09	0.12	0.08	0.08	0.11	0.08	0.06	0.13	0.08	0.12	0.09	0.14	0.12	0.1	0.13	0.1	0.09	0.04	0.14	0.02
	length	0.12	0.21	0.18	0.1	0.12	0.13	0.16	0.2	0.14	0.16	0.24	0.17	0.11	0.15	0.15	0.13	0.26	0.11	0.22	0.2	0.31	0.23	0.19	0.23	0.17	0.18	0.1	0.31	0.05
NIGP168416	height	0.08	0.09	0.08	0.08	0.13	0.11	0.11	0.13	0.15	0.08	0.09	0.08	0.08	0.07	0.1	0.08	0.07	0.08	0.14	0.1	0.07	0.1	0.11	0.11	0.13	0.1	0.07	0.15	0.02
	length	0.26	0.2	0.2	0.15	0.31	0.18	0.21	0.3	0.22	0.2	0.32	0.17	0.19	0.13	0.23	0.19	0.28	0.17	0.23	0.39	0.2	0.2	0.24	0.19	0.2	0.22	0.13	0.39	0.06

SR, specimen from the Duwibong Formation at the Sorotgol section; NIGP 168416, specimen from the Hunghuayuan Formation at the Zhangzhai section; min., minimum; max., maximum; SD, standard deviation.