

The earliest evolutionary link of metazoan bioconstruction: Laminar stromatoporoid–bryozoan reefs from the Middle Ordovician of Korea

Jongsun Hong^a, Jae-Ryong Oh^{b,c}, Jeong-Hyun Lee^d, Suk-Joo Choh^{e,*}, Dong-Jin Lee^f

^a Department of Geology, Kangwon National University, Chuncheon 24341, Republic of Korea

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

^c Polar Science, University of Science and Technology, Daejeon 34113, Republic of Korea

^d Department of Geology and Earth Environmental Sciences, Chungnam National University, Daejeon 34134, Republic of Korea

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

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

ARTICLE INFO

Keywords:

Skeletal reef
Globular framework
Darriwilian
Reef evolution
GOBE

ABSTRACT

Sub-metre-scale patch reefs composed primarily of stromatoporoids and bryozoans are reported from the Duwibong Formation (upper Middle Ordovician), Taebaeksan Basin, Korea, in the eastern margin of the Sino-Korean Block. The reef framework is constructed of alternating thin laminae of the primitive labechiid stromatoporoid *Cystostroma*, the bryozoan *Nicholsonella*, subordinate *Solenopora* and minor siliceous sponges. Alternating laminae of stromatoporoids and bryozoans are largely responsible for the formation of a globular framework composed of columnar, branching, bulbous to irregular masses. *Solenopora* sporadically occurring as tiny patches or thin laminae attached to the stromatoporoid–bryozoan framework is considered to be subordinate encrusters. Siliceous sponges occur within the stromatoporoid–bryozoan framework and within the growth framework and bored cavities, interpreted as subordinate encrusters and cryptic dwellers. The compact globular framework of the Duwibong stromatoporoid–bryozoan consortium represents a new type of Ordovician skeletal bioconstruction, but with a certain structural similarity to Lower Ordovician bryozoan reefs in the South China Block. Together with coeval labechiid reefs occurring near the current study area, the Duwibong reefs suggest that incursion of the primitive stromatoporoids into the earliest bryozoan reefs resulted in the dominance of reef-building stromatoporoids in peri-Gondwana in contrast to coeval reefs in Laurentia, which commonly contain tabulate corals.

1. Introduction

Bryozoans were one of the earliest skeletal reef builders to form reefs alone without the aid of microbes (Cuffey et al., 2013). They can produce plastic colony forms to adapt various environmental conditions, e.g., erect, branching, fenestrate and lobate forms as well as sheet-like skeletons up to 1 m across (Hageman et al., 1997; Amini et al., 2004; Taylor and Ernst, 2004; Taylor, 2005; Moissette et al., 2010), and commonly settle on hard to firm substrates or stabilised sediments (Taylor and Ernst, 2004). Globular colonies of encrusting bryozoans can occasionally form free-rolling nodules called bryoliths; they also form reef frameworks where corals are absent in present day (Cuffey, 2006).

The fossil record of bryozoans goes back to the earliest Ordovician (Tremadocian), when they suddenly appeared with a mineralised

skeleton, prior to the advent of other principal reef elements of early skeletal reefs such as corals and stromatoporoids (Taylor and Ernst, 2004; Webby, 2004a; Ma et al., 2015). In the Early to Middle Ordovician, they were an integral part of the earliest skeletal reefs characterised by the superposition of laminar bryozoans or other metazoans (Webby, 2002; Taylor and Ernst, 2004; Adachi et al., 2011, 2012, 2013; Cuffey et al., 2013). The successive appearance of tabulate corals, *Solenopora* and labechiid stromatoporoids by the Middle Ordovician paved the way for the construction of diverse skeletal reefs, and eventually led to the major turnover from microbial- to skeletal-dominated reefs in the Middle to Late Ordovician (Webby, 2002). As larger, robust metazoans diversified during the Middle and Late Ordovician, the contribution of bryozoans to skeletal reefs diminished, and they were largely overshadowed by corals and stromatoporoids until the Late Devonian, when bryozoans once again were common components

* Corresponding author.

E-mail addresses: jhong@kangwon.ac.kr (J. Hong), gilli@kopri.re.kr (J.-R. Oh), jeonghyunlee@cnu.ac.kr (J.-H. Lee), sjchoh@korea.ac.kr (S.-J. Choh), djlee@andong.ac.kr (D.-J. Lee).

<https://doi.org/10.1016/j.palaeo.2017.12.018>

Received 9 October 2017; Received in revised form 16 December 2017; Accepted 16 December 2017

Available online 20 December 2017

0031-0182/ © 2017 Elsevier B.V. All rights reserved.

in Mississippian mud mounds (Copper, 2002; Webb, 2002; Webby, 2002; Cuffey, 2006).

The current study reports a new type of early skeletal reef from the upper Middle Ordovician of Korea, primarily formed by the trepostome bryozoan *Nicholsonella* in concert with the primitive labechiid stromatoporoid *Cystostroma*. The globular structures of a *Cystostroma*–*Nicholsonella* consortium are superficially analogous to those of the compact crust mounds dominated by the trepostome bryozoan *Nekhorosheviella* in the upper Tremadocian of Hubei Province, China (Adachi et al., 2012; Cuffey et al., 2013) and skeletal reefs built by various sheet-like metazoans in the upper Darriwilian of New York, USA (Pitcher, 1964; Cuffey et al., 2000; Kröger et al., 2017). Taken together with recently reported upper Middle Ordovician stromatoporoid-dominated reefs from Yeongwol, Korea (Hong et al., 2017; Park et al., 2017), composition and formation processes of these early skeletal reefs from the Sino-Korean Block reveal the impact of the unfolding Ordovician radiation on the oldest type of skeletal reef ecosystem, and its implications for the earliest pathway of skeletal reef evolution during the Early and Middle Ordovician.

2. Geologic setting and methods

Lower Palaeozoic strata are widely distributed in the Sino-Korean Block, occurring over > 1500 km from the Taebaeksan and Pyeongnam basins of the Korean Peninsula in the east to the Ordos Basin of north-central China in the west (Meng et al., 1997; Chough, 2013; Fig. 1A). The Taebaek Group at the eastern margin of the Sino-Korean Block represents mixed siliciclastic–carbonate successions deposited from Cambrian Epoch 2 to the Middle Ordovician (Kwon et al., 2006). The skeletal reefs investigated in this study are from the Duwibong Formation, the uppermost unit of the Taebaek Group. The formation, which is 40–80 m thick, is composed of oolitic and fossiliferous limestone with intercalated dolostone and shale, interpreted to have been deposited in a shallow subtidal carbonate ramp environment (Hyeong and Lee, 1992; Lee et al., 2001; Kwon et al., 2006). The unit has been estimated to be late Middle Ordovician (mid to late Darriwilian) in age based on the occurrence of the *Plectodina onychodonta* and *Aurilobodus serratus* conodont biozones (Lee and Lee, 1986, 1990).

The reef described in this study is located at the Sorotgol section, as part of a 7-m-thick exposure of the upper Duwibong Formation occurring along the road-cut section (Oh et al., 2015; Fig. 1). The reef constituents were analysed from polished slabs and several sets of large-format (5.2 × 7.6 cm) thin sections covering the slabs. The “white card technique” (Delgado, 1977; Zenger, 1979; Folk, 1987) was employed to differentiate the original microstructures of the constituents. The two-dimensional distributions of reef-building components within the frameworks were calculated using JMicrovision software (Table 1).

3. Results

3.1. Duwibong stromatoporoid–bryozoan reefs

The Duwibong reefs, which are about 80 cm wide and 30 cm high, are composed of compactly stacked hemispherical laminae of stromatoporoids, bryozoans, minor *Solenopora* and siliceous sponges (Figs. 1B, 2). The reef-bearing bed overlies bioclastic packstone to grainstone with fragments of ramose bryozoans, siliceous sponges, brachiopods, gastropods and cephalopods, and is laterally surrounded and overlain by partly dolomitised bioturbated mudstone to wackestone (Fig. 1C).

3.1.1. Reef constituents

The stromatoporoids are characterised by laminar to crescentic structures with smooth outlines, and are up to 8 cm wide and < 3 cm high. Their internal structures are generally poorly preserved, and can only be recognised by means of the white-card technique. Faint micritic ghosts of stacked convex-upward cysts without denticles are present,

which may be assignable to the stromatoporoid *Cystostroma* (Oh et al., 2015; Fig. 2A, B). The stromatoporoids constitute about one-third (34%) of the Duwibong reef in cross section (Table 1). Bryozoans are laminar to crescentic, or minor slender ramose forms < 3 cm in size, comprising up to one-sixth (16%) of the Duwibong reef in cross section (Table 1). Their isolated zooecia enclosed by a granular wall structure and zooecial tubes with complete, straight diaphragms are characteristic of *Nicholsonella* (Fig. 2C, D; Bassler, 1953). Subordinate *Solenopora* is composed of bundles of tubes within small domal or lamina-shaped outlines (Fig. 2E), comprising about 4% of the reef. Another component is unidentified siliceous sponges with irregular spicule networks and indistinct outer boundaries (Fig. 3A–D), which make up about 0.1% of the reef. In cross section, up to 42% of reef constituents with poor preservation of internal fabric are classified as uncertain type (Table 1), though some of these uncertain elements are similar to the basal zooecial tubes of bryozoans (Fig. 3E) or are very thin layers with smooth surfaces resembling those of the stromatoporoids (Fig. 3F). It is, therefore, concluded that these uncertain elements probably represent poorly preserved bryozoans and stromatoporoids.

3.1.2. Reef structure

The sub-metre-scale domal reefs of the Duwibong Formation consist of columnar to branching structures a few centimetres wide and up to 10 cm high, with subordinate larger irregular structures up to 20 cm across and high (Figs. 4, 5). The frameworks are separated by burrowed wackestone a few millimetres to several centimetres wide and often show smooth and sporadic ragged margins, although sharp margins truncating these frameworks are also rarely found. The growth directions of the structures vary, but many are sub-vertical to horizontal with minor downward-growing examples (Figs. 4, 5). They consist of several globular units up to 3 cm high, within which the growth directions of the components are consistent (Fig. 5). Each globular unit is made of a characteristic millimetre-scale laminated framework consisting of ramose bryozoans and minor irregular siliceous sponges at the base of the unit, overlain by succeeding encrustations of laminar to crescentic stromatoporoids and bryozoans with minor *Solenopora* and siliceous sponges (Figs. 3D–F, 5). These units are attached to the tops or sides of the other units. The growth directions of them are commonly variable by about 10° to 20°, though up to 60° difference between the attached units is also present, forming columnar or branching structures overall (Fig. 5). These structures are occasionally enclosed by successive larger reef elements, resulting in the formation of accreted irregular masses (Fig. 4). Rare elongate cavities, up to a few centimetres long, occur between the stromatoporoid and bryozoan laminae. These cavities contain patches of sponge spicule networks pendant from the ceiling, with the rest of the space filled with lime mud (Fig. 3B). Similar spicule networks also occur rarely inside cylindrical borings < 1 mm in diameter that penetrate the laminated stromatoporoid–bryozoan skeletal laminae (Fig. 3C, D).

3.2. Interpretation

The sub-metre-scale Duwibong patch reefs are constructed of stacked hemispherical encrusting laminae (Fig. 5). The reefs appear to have initiated by attachment of stromatoporoids and bryozoans to scattered ramose bryozoans and other grainy sediments where these reef elements follow the underlying bioclasts in shape. Subsequent numerous encrustations of stromatoporoids, bryozoans, intermittent attachments of subordinate *Solenopora* and rare siliceous sponges formed the globular units. Upward, inclined attachments and aggregations of these units led to the formation of centimetre- to decimetre-scale columnar or extended bulbous to digitate forms. In some cases, several structures are further bounded by laminar reef elements, creating larger irregularly shaped frameworks (Fig. 4). The micritic sediments surrounding these skeletal frameworks (Figs. 4, 5) and smooth outline of the frameworks indicate that their growth was in a

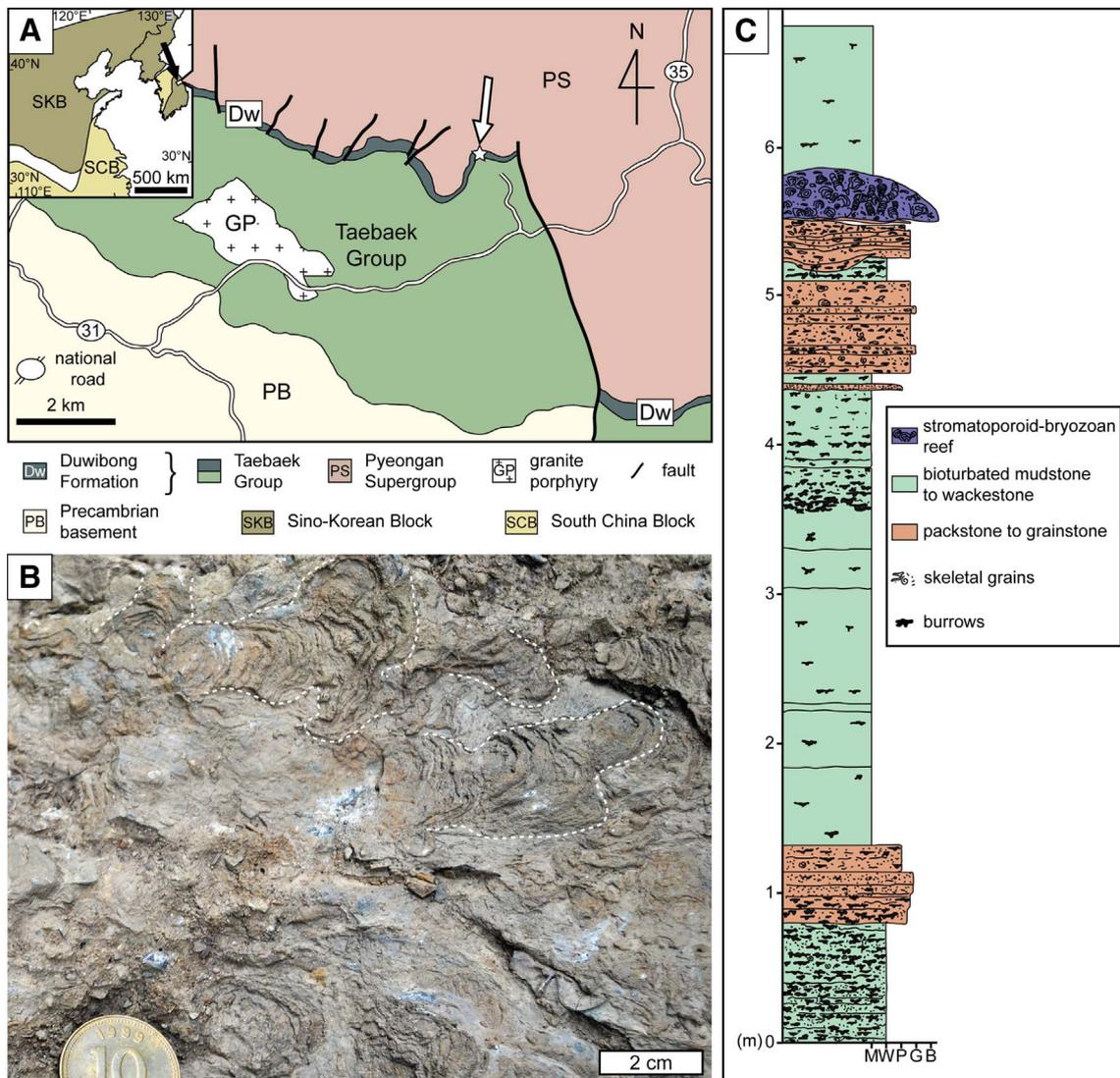


Fig. 1. A) Location of the study area (black arrow) in the Sino-Korean Block and simplified geologic map of the area (modified from Chough, 2013). The location of the reefs investigated in this study is marked by a white arrow. B) Cross-sectional outcrop photograph of a reef showing characteristic stacked encrusting layers (dashed lines) that are well exposed on the weathered surface. C) Stratigraphic section of the outcrop. The reef-bearing interval overlies bryozoan packstone to grainstone and is overlain by bioturbated mudstone to wackestone.

Table 1
Areal percentage of the component in the Duwibong reef frameworks.

Component	Areal percentage
Stromatoporoid	34.3
Bryozoan	16.1
<i>Solenopora</i>	3.9
Siliceous sponge	0.1
Dolomite	1.7
Internal sediment	1.5
Uncertain	42.4
Total	100.0

relatively low-energy environment (e.g., James and Wood, 2010). The presence of some erosive features and sideways-pointing frameworks (Figs. 1B, 4) might reflect the effect of occasional high-energy events such as storm currents.

Based on the frequency of occurrence and areal percentage of reef constituents, the stromatoporoid *Cystostroma* and the bryozoan *Nicholsonella* are the main reef framework-builders, and their upper surfaces were available for further attachments. They blanketed the underlying reef constituents as well as several columnar to branching

structures, and are thus considered to have functioned as encrusters and binders. Minor (< 5% of the framework) *Solenopora* and siliceous sponges also attached to the upper surfaces of the main reef constructors and are interpreted as encrusters. The rare siliceous sponges in borings and attached to the ceilings of cavities are interpreted as cryptic dwellers. In summary, the Duwibong skeletal reef framework can be characterised as a centimetre-scale skeletal framework, primarily formed by multiple encrustations of bryozoans and one of the earliest genera in stromatoporoids, containing primary cavities harbouring cryptic metazoans.

4. Discussion

The Cambrian radiation (Cambrian Explosion) and Ordovician radiation (Great Ordovician Biodiversification Event, or GOBE) resulted in the origin and diversification of early Palaeozoic sessile organisms, eventually leading to the rise of bioconstructions containing metazoans (Webby, 2002; Adachi et al., 2011, 2012; Kröger et al., 2017; Li et al., 2017). Lower Palaeozoic reefs witnessed a large-scale turnover from (i) Cambrian–lower Middle Ordovician microbial-dominated reefs with limited clusters of conical to branching skeletal organisms (archaeocyaths, siliceous sponges and calathiids) to (ii) upper Middle to Upper

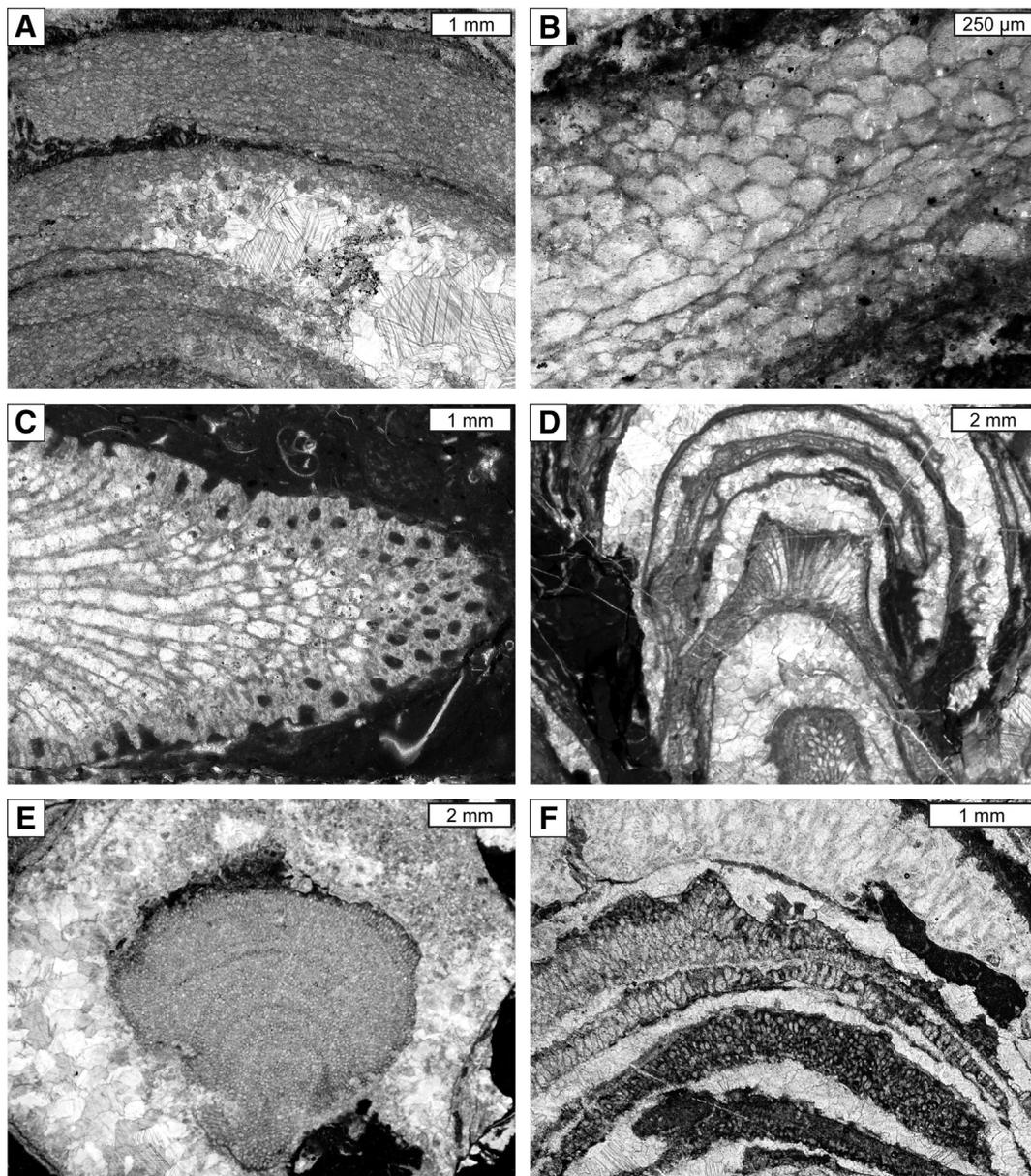


Fig. 2. Photomicrographs of reef constituents in the Duwibong reefs. A) Layered *Cystostroma* stromatoporoids with partially obscured internal microstructure replaced by neomorphic calcite. B) Longitudinal-cut photomicrograph of a stromatoporoid taken using the “white card technique”. The well-preserved convex-upward cyst plate is the diagnostic characteristic of *Cystostroma*. C) Photomicrograph of a ramose bryozoan *Nicholsonella*. Isolated zooecia surrounded by granular wall structure and straight diaphragms are well-developed. D) Bryozoan encrustations alternating with possible stromatoporoids with poorly preserved internal structures. E) *Solenopora* with barely visible cross-sectional partitions overgrown by poorly preserved stromatoporoids. F) Layers of uncertain tubular organisms with various tube dimensions that repeatedly encrust poorly preserved stromatoporoids. The limited longitudinal views of the organism inhibit its proper identification.

Ordovician skeletal-dominated reefs composed of laminar encrusting to robust skeletal organisms (bryozoans, corals, stromatoporoids and *Solenopora*; Rowland and Shapiro, 2002; Webby, 2002; Servais et al., 2010; Lee et al., 2015; Kröger et al., 2017). This major shift from microbial- to skeletal-dominated reefs occurred within a 20-Myr interval, from the first appearance of the oldest known skeletal reefs in the Lower Ordovician of South China (Adachi et al., 2011; Cuffey et al., 2013) to the upper Middle Ordovician when various skeletal reefs became dominant for the first time in the geologic record (Webby, 2002). Such diachronous transformation in reef composition across different regions associated with physiochemical and biological changes have been considered as a characteristic of the GOBE (Servais et al., 2010) (Fig. 6).

Bryozoans pioneered the skeletal reef framework revolution, as the first appearance of trepostome bryozoans resulted in the initiation of the oldest known skeletal reefs in the Lower Ordovician of the South

China Block (Xia et al., 2007; Adachi et al., 2011, 2012; Cuffey et al., 2013; Ma et al., 2015). These skeletal reefs were built by aggregated globular colonies (up to 2 cm across and 5 cm high) of the laminar bryozoans *Nekhorosheviella*, together with subordinate skeletons of lithistid sponges, calathiids and pelmatozoan holdfasts (Fig. 6). However, with the exception of bryozoan skeletal reefs and skeletal frameworks from South China, the record of early skeletal reefs is surprisingly sparse throughout the upper Lower to lower Middle Ordovician (Fig. 6). The propagation of bryozoans, coupled with the advent of tabulate corals in Laurentia, became a foundation for various skeletal reef frameworks built in concert with pre-existing and newly emerged reef-building skeletal organisms in the Chazyan (upper Darriwilian) of Laurentia (Pitcher, 1964; Kobluk, 1981; Desrochers and James, 1989; Cuffey et al., 2000, 2013; Webby, 2002). Such skeletal reef frameworks include centimetre- to decimetre-scale stacked colonies of the laminar

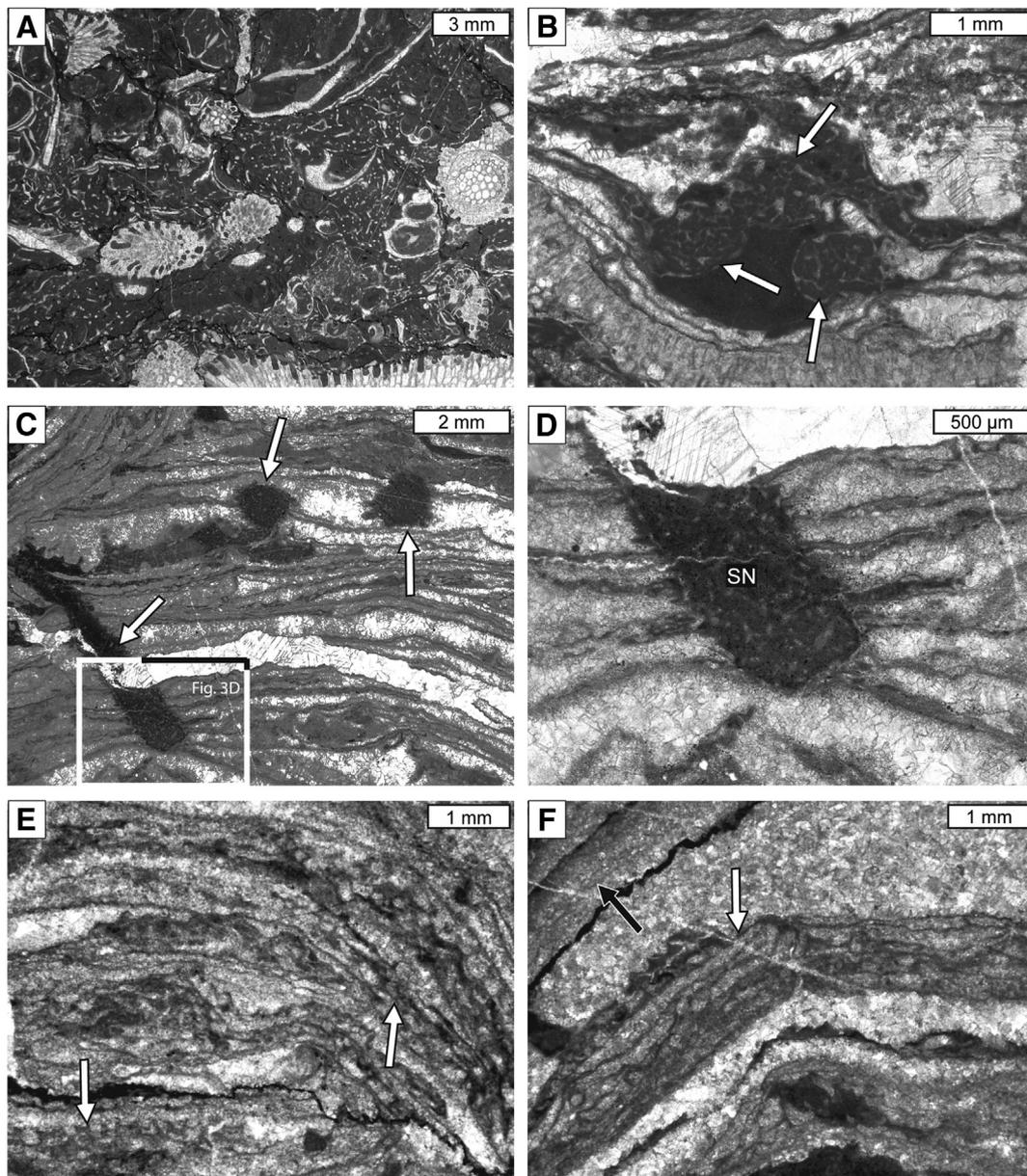


Fig. 3. Photomicrographs of siliceous sponges and components of uncertain affinities of the Duwibong reefs and their substrates. A) Siliceous sponges co-occurring with fragments of bryozoans, gastropods, brachiopods and mollusc shells in substrate of the boundstone. B) Spicule networks (arrows) with rounded outer boundaries attached to the roof of a cavity. C) Tubular borings (arrows) cut through poorly preserved stromatoporoid latilaminae. D) Enlarged view of the area indicated by the rectangle in Fig. 4C, showing spicule networks (SN) occurring inside a boring. E) Uncertain encrusting elements with poorly preserved microstructures. Arrows point to areas resembling the microstructure of bryozoans. F) Microstructure of an uncertain encruster (white arrow), similar to that of stromatoporoids (black arrow).

bryozoans *Batostoma* and *Ceramopora*, which constituted the bulk of skeletal reefs, and were sometimes intergrown with lithistid sponges and pelmatozoans (Pitcher, 1964; Pratt, 1989; Kröger et al., 2017; Fig. 6). These laminar bryozoans often occurred in conjunction with new reef-builders such as the laminar to low domal tabulate coral *Billingsaria*, the subordinate encrusting *Solenopora*, hemispherical to irregular bundles of the tabulate coral *Eofletcheria*, and the ramose to fenestrate bryozoans *Batostoma*, *Nicholsonella*, *Stictopora* and *Phylloporina* (Pitcher, 1964; Desrochers and James, 1989). Bryozoan-bearing bioconstructions were persistent until the early Sandbian, in that ramose and encrusting forms contributed to the formation of coral-stromatoporoid-algal reefs, bryozoan-dominated reefs and mud mounds (e.g., Read, 1982; Ruppel and Walker, 1982; Cuffey and Cuffey, 1995; Hender and Dix, 2008), and subsequently became less prominent (Webby, 2002). Sheet-like bryozoans as one of main reef-builders were also reported from sub-metre- to decametre-sized reefs and mounds in

the Katian to Hirnantian successions of eastern Canada (Kobluk, 1981) and northern Estonia (Kröger et al., 2017).

The earliest indisputable stromatoporoids are labechiids, and principally heralded the biggest boom of skeletal reefs in the geological record (Copper, 2002; Webby, 2002). The oldest known labechiid is preserved in the Lower Ordovician lithistid sponge-*Calathium* reefs of South China, in that *Cystostroma* was a minor cryptic element within the internal cavities of *Calathium* (Li et al., 2017). The subsequent diversification of early labechiid stromatoporoids and their incorporation into reef frameworks took place in both the Sino-Korean Block and Laurentia during the Darriwilian (Webby, 2015). These early labechiid stromatoporoids (*Pseudostyloclyctyon*, *Labechia*, *Pachystylostroma* and *Cystostroma*) were subordinate encrusters in various Chazyan skeletal reefs, forming stacked laminar labechiid skeletons 0.15–1 m across with *Billingsaria*, lithistid sponges, *Solenopora*, *Batostoma*, and calcimicrobes *Rothpletzella* and *Girvanella* (Pitcher, 1964; Kapp, 1975; Kapp and

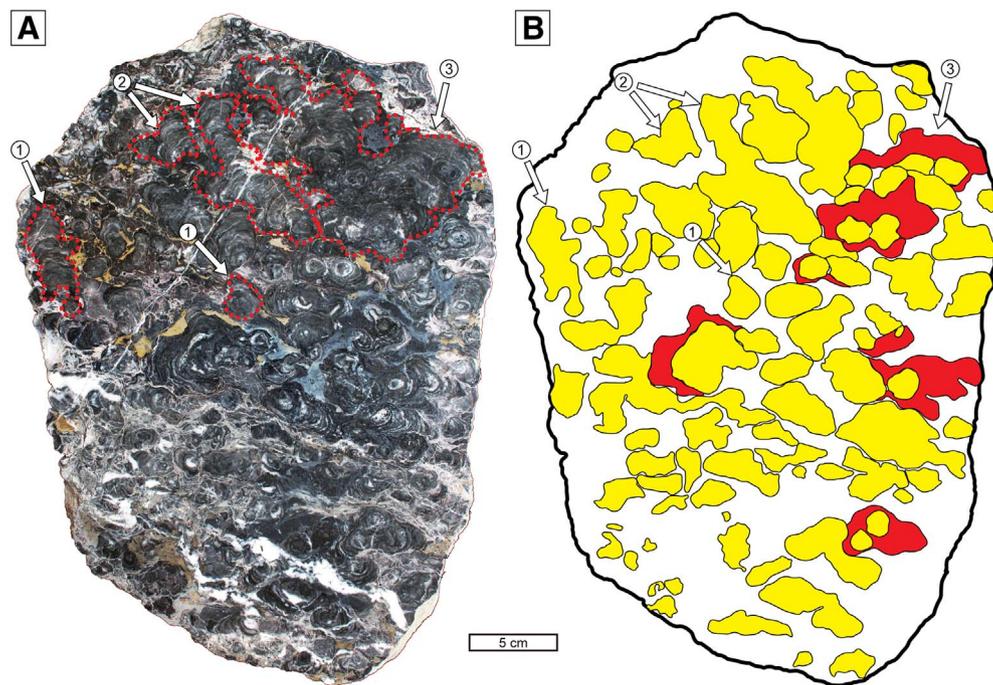


Fig. 4. A) Photograph and B) interpretive tracing of a polished slab of a reef. Various shaped globular to columnar (arrow 1), branching (arrow 2) to irregular or massive (arrow 3) frameworks are present. Note the prevalence of discrete globular, columnar and branching frameworks (yellow area), and several reef elements (red area) that interconnect and form larger irregular frameworks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Stearn, 1975; Desrochers and James, 1989; Webby, 2002; Kröger et al., 2017; Fig. 6). In the Sino-Korean Block, decimetre-scale labechiid skeletal reefs, composed primarily of laminar *Labechia* (~80% of the reef) up to 15 cm across with minor bryozoans, were recently reported from the upper Darriwilian Yeongheung Formation of Korea (Hong et al., 2017; Fig. 6).

The centimetre-scale laminar framework of the Duwibong reefs is a new type of early skeletal reef framework in terms of both reef-building components and shape. The framework superficially resembles that of

the Lower Ordovician bryozoan reefs in the common occurrence of bryozoans and their globular structures, but was primarily built by the primitive stromatoporoid *Cystostroma* (Khromych, 2010; Oh et al., 2015; Li et al., 2017) and the bryozoan *Nicholsonella*. In this regard, the Duwibong *Cystostroma*–*Nicholsonella* skeletal laminar reef reflects the advent of stromatoporoids into one of the oldest metazoan reef frameworks primarily built by bryozoans. This occurrence also signals the advent of skeletal reefs built by the more structured labechiid *Labechia*, as demonstrated by some of the oldest known labechiid-dominated

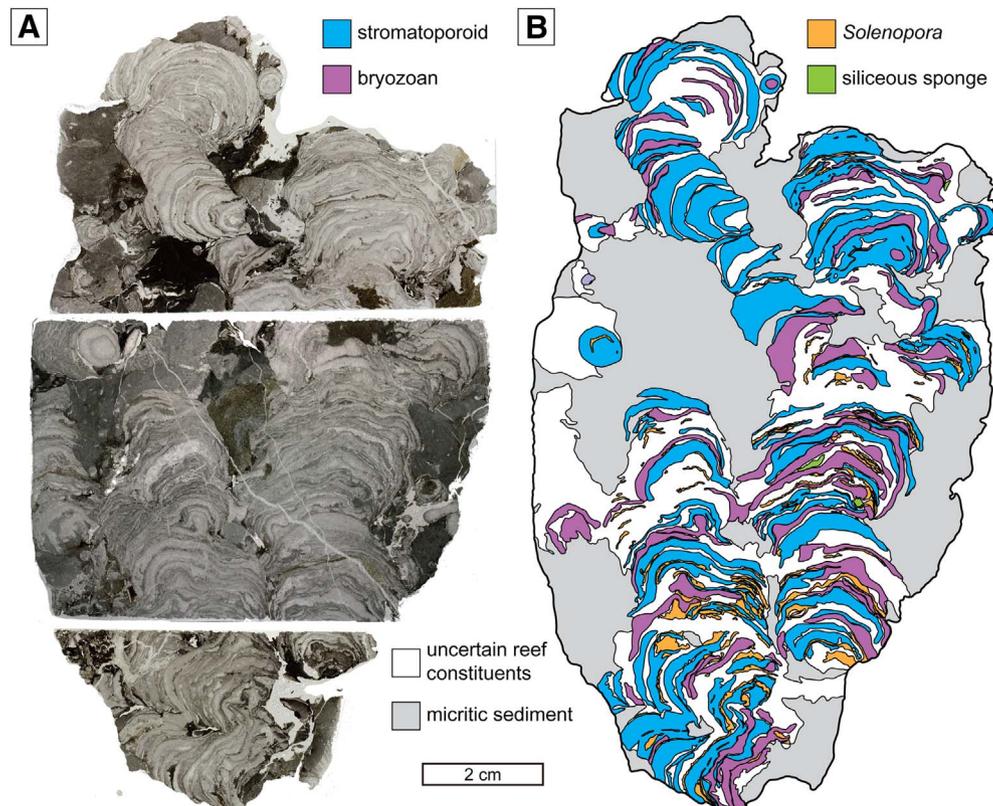


Fig. 5. A) Thin sections of the columnar to extended bulbous reef frameworks used for constituent analysis (Table 1). B) Tracing of the reef frameworks made up of laminar reef elements such as stromatoporoids and bryozoans, enclosed by micritic sediments.

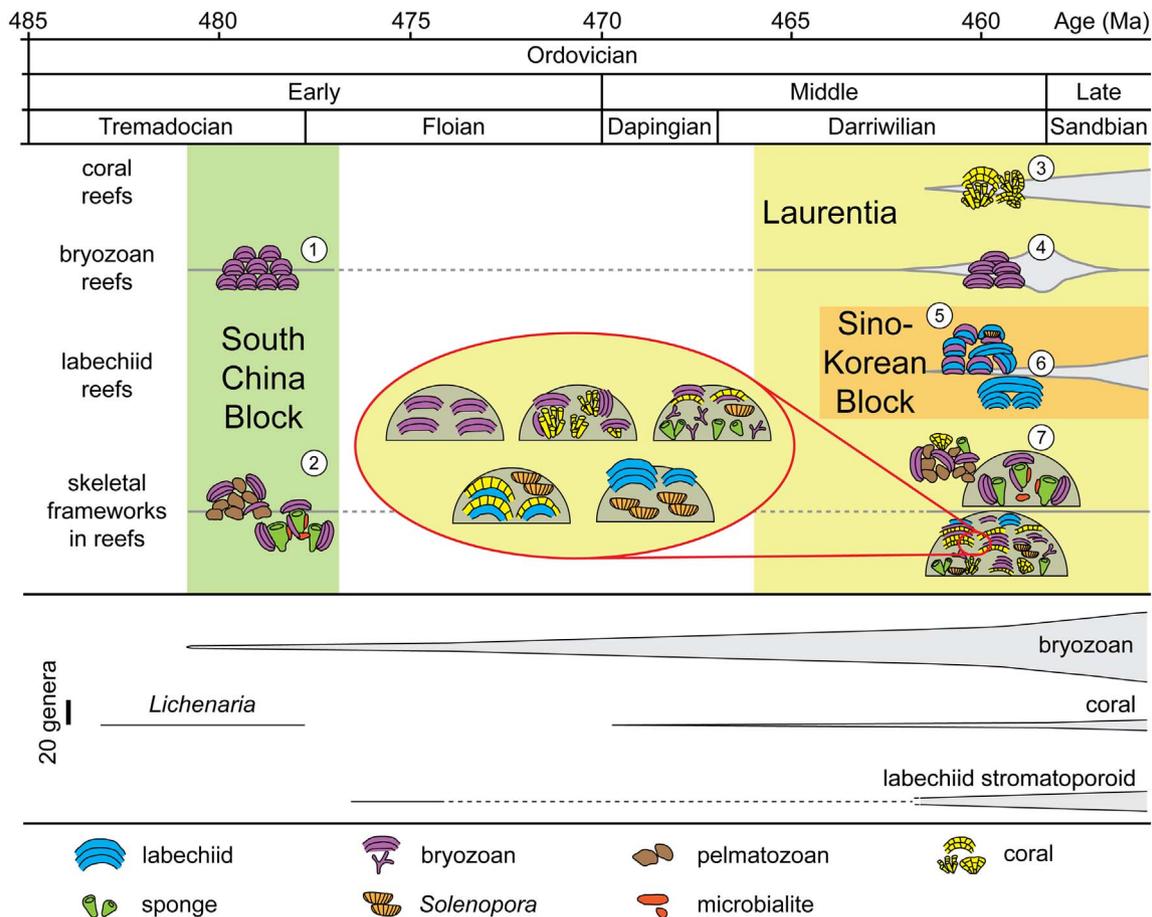


Fig. 6. Spatio-temporal patterns of Lower to Middle Ordovician skeletal reefs and diversity of reef-building metazoans. The Duwibong labechiid–bryozoan reefs (5) have a similar framework structure to Lower to Middle Ordovician laminar bryozoan skeletal reefs (1, 2 and 4). Note the distinctive reef composition of Sino-Korean reefs (5 and 6) compared with coeval Laurentian reefs (3, 4 and 7) and changes in relative abundance of reef frameworks indicated by grey spindles. 1: bryozoan skeletal reefs (Cuffey et al., 2013); 2: bryozoan–pelmatozoan and bryozoan–lithistid sponge reefs (Adachi et al., 2012, 2013); 3: coral reefs (Desrochers and James, 1989); 4: bryozoan reefs (Pitcher, 1964; Kobluk, 1981; Cuffey et al., 2000); 5: labechiid–bryozoan skeletal reefs (this study); 6: labechiid reefs (Hong et al., 2017); 7: pelmatozoan–bryozoan–coral reefs and bryozoan–lithistid sponge frameworks, and bryozoan, coral, *Solenopora*, lithistid sponge and labechiid frameworks of reefs (Pitcher, 1964; Desrochers and James, 1989; Pratt, 1989; Kröger et al., 2017). The diversity of bryozoans, corals, and stromatoporoids is after Taylor and Ernst (2004), Webby (2004b), Webby et al. (2004), Adachi et al. (2011), Nestor and Webby (2013) and Li et al. (2017).

reefs in the Yeongheung Formation of Korea (Hong et al., 2017). In terms of reef constituents and frame structure, the Duwibong reef is broadly similar to coeval Laurentian reefs, in which bryozoans, labechiid stromatoporoids, *Solenopora* and siliceous sponges are contributors to frameworks. However, the stromatoporoid–bryozoan framework in this study is fundamentally different from the Laurentian skeletal frameworks, notably in terms of the dominance of stromatoporoids and lack of tabulate corals (cf. Pitcher, 1964; Desrochers and James, 1989; Webby, 2002).

Therefore, the Duwibong *Cystostroma*–*Nicholsonella* reefs in the upper Middle Ordovician of the Sino-Korean Platform would have showcased the incorporation of stromatoporoids into bryozoan-dominated reefs and their impact on the evolutionary path of early skeletal reefs in which corals were not yet reached in this region and not involved in reef frameworks. The contribution of bryozoans to early skeletal reefs was suggested to have been declined during the Late Ordovician with the arrival of sturdy reef-building corals and possibly stromatoporoids, based on Laurentian examples (Cuffey, 2006). As described in the current study and for the coeval Yeongheung reefs (Hong et al., 2017), the emergence of stromatoporoids as the principal reef builders and the eventual minor occurrence of bryozoans within the stromatoporoid frameworks illuminate early evolution of skeletal reefs, when bryozoans began to lose their dominance in the development of skeletal reefs with the advent of stromatoporoids in early skeletal reefs. It has become more apparent in recent years that

although our current understanding of the evolutionary pattern of Ordovician skeletal reefs remains patchy (Fig. 6), regional variation on diversification of reef-building metazoans and types of skeletal bioconstructions would have resulted in dissimilar evolutionary paths of the earliest skeletal reefs in time and space during the Great Ordovician Biodiversification Event.

5. Conclusions

Upper Middle Ordovician skeletal-dominated patch reefs are reported from the Duwibong Formation of the Taebaeksan Basin, Sino-Korean Block. These reefs are composed mainly of labechiid stromatoporoids (*Cystostroma*) and bryozoans (*Nicholsonella*) with subordinate *Solenopora* and siliceous sponges. Stacking-up of laminar to low domal stromatoporoids and bryozoans primarily formed columnar, branching, amalgamated bulbous and irregular masses that eventually formed globular reef frameworks. The framework shape and common presence of bryozoans in the Duwibong reefs are analogous to Lower Ordovician bryozoan reefs in the South China Block, suggesting a persistent development of earliest skeletal bioconstructions in the Sino-Korean Block. This early skeletal reef transition from bryozoan- to stromatoporoid-dominated consortia was different in Laurentian skeletal reefs, in which tabulate corals were incorporated and were the major reef-builders during the late Middle to Late Ordovician. These findings reveal regional variations in early skeletal reef evolution and additional

findings of early skeletal reefs made from upper Lower to lower Middle Ordovician strata of South China, Siberia and Laurentia would enable us to resolve the puzzle of the early skeletal reef revolution.

Acknowledgments

This study was supported by grants from the National Research Foundation of Korea to JH (2017R1C1B1007344), JHL (2016R1C1B1012104), SJC (2015R1A2A2A01007063) and DJL (2013R1A2A2A01067612). We deeply appreciated the editor T. Algeo and two anonymous reviewers for their constructive comments on an early version of the manuscript. We also thank M. Lee of Korea Polar Research Institute and N.G. Kim and J.W. Jeon of Andong National University for assistance in the field and for the preparation of slabs and thin sections.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <https://doi.org/10.1016/j.palaeo.2017.12.018>. These data include the Google map of the most important areas described in this article.

References

- Adachi, N., Ezaki, Y., Liu, J., 2011. Early Ordovician shift in reef construction from microbial to metazoan reefs. *Palaios* 26, 106–114.
- Adachi, N., Ezaki, Y., Liu, J., 2012. The oldest bryozoan reefs: a unique Early Ordovician skeletal framework construction. *Lethaia* 45, 14–23.
- Adachi, N., Liu, J., Ezaki, Y., 2013. Early Ordovician reefs in South China (Chenjiasha section, Hubei Province): deciphering the early evolution of skeletal-dominated reefs. *Facies* 59, 451–466.
- Amini, Z.Z., Adabi, M.H., Burrett, C.F., Quilty, P.G., 2004. Bryozoan distribution and growth form associations as a tool in environmental interpretation, Tasmania, Australia. *Sediment. Geol.* 167, 1–15.
- Bassler, R.S., 1953. Treatise on Invertebrate Paleontology: Part G, Bryozoa. Geological Society of America and University of Kansas Press, Lawrence, Kansas, pp. 1–253.
- Chough, S.K., 2013. Geology and Sedimentology of the Korean Peninsula. Elsevier, Amsterdam, pp. 363.
- Copper, P., 2002. Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*. SEPM Special Publication No. 72, Tulsa, Oklahoma, pp. 181–238.
- Cuffey, R.J., 2006. Bryozoan-built reef mounds—the overview from integrating recent studies with previous investigations. *Courier Forschungsinstitut Senckenberg* 257, 35–47.
- Cuffey, C.J., Cuffey, R.J., 1995. The Chickasaw bryozoan reef in the Middle Ordovician of south-central Oklahoma. In: Cooper, J.D., Droser, M.L., Finney, S.C. (Eds.), *Ordovician Odyssey*. Pacific Section SEPM, Fullerton, California, pp. 435–438.
- Cuffey, R.J., Cawley, J.C., Lane, J.A., Bernarsky-Remington, S.M., Ansari, S.L., McClain, M.D., Ross-Phillips, T.L., Savill, A.C., 2000. Bryozoan reefs and bryozoan-rich limestones in the Ordovician of Virginia. In: *Proceedings 9th International Coral Reef Symposium*. 1. pp. 23–27.
- Cuffey, R.J., Chuantao, X., Zhu, Z., Spjeldnaes, N., Hu, Z.-X., 2013. The world's oldest-known bryozoan reefs: Late Tremadocian, mid-Early Ordovician; Yichang, central China. In: Ernst, A., Schafer, P., Scholz, J. (Eds.), *Bryozoan Studies 2010*. Springer, Berlin, pp. 13–27.
- Delgado, F., 1977. Primary textures in dolostones and recrystallized limestone: a technique for their microscopic study. *J. Sediment. Petrol.* 47, 1339–1341.
- Desrochers, A., James, N.P., 1989. Middle Ordovician (Chazyan) bioherms and biostromes of the Mingan Island, Quebec. In: Geldsetzer, H.H.J., James, N.P., Tebbult, G.E. (Eds.), *Reefs, Canada and Adjacent Area*. Canadian Society of Petroleum Geologists Memoir 13, Calgary, Alberta, pp. 183–191.
- Folk, R.L., 1987. Detection of organic matter in thin-sections of carbonate rocks using a white card. *Sediment. Geol.* 54, 193–200.
- Hageman, S.J., Bone, Y., McGowan, B., 1997. Bryozoan colonial growth-forms as paleoenvironmental indicators: evaluation of methodology. *Palaios* 12, 405–419.
- Hender, K.L.B., Dix, G.R., 2008. Facies development of a Late Ordovician mixed carbonate-siliciclastic ramp proximal to the developing Taconic orogeny: Lourdes Formation, Newfoundland, Canada. *Facies* 54, 121–149.
- Hong, J., Choh, S.-J., Park, J., Lee, D.-J., 2017. Construction of the earliest stromatoporeid framework: labechiid reefs from the Middle Ordovician of Korea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 470, 54–62.
- Hyeong, K., Lee, Y.I., 1992. Depositional facies of oolitic grainstone in the Ordovician Duwibong Formation, Korea. *J. Geol. Soc. Korea* 28, 227–238.
- James, N.P., Wood, R., 2010. Reefs. In: James, N.P., Dalrymple, R.W. (Eds.), *Facies Models 4*. St. John's: Geological Association of Canada, pp. 421–447.
- Kapp, U.S., 1975. Paleogeology of Middle Ordovician stromatoporeid mounds in Vermont. *Lethaia* 8, 195–207.
- Kapp, U.S., Stearn, C.W., 1975. Stromatoporeids of the Chazy group (Middle Ordovician), Lake Champlain, Vermont and New York. *J. Paleontol.* 49, 163–186.
- Khromych, V.G., 2010. Evolution of stromatoporoidea in the Ordovician–Silurian epicontinental basin of the Siberian platform and Taimyr. *Russ. Geol. Geophys.* 51, 684–693.
- Kobluk, D.R., 1981. Cavity-dwelling biota in Middle Ordovician (Chazy) bryozoan mounds from Quebec. *Can. J. Earth Sci.* 18, 42–54.
- Kröger, B., Desrochers, A., Ernst, A., 2017. The reengineering of reef habitats during the Great Ordovician Biodiversification Event. *Palaios* 32, 584–599.
- Kwon, Y.K., Chough, S.K., Choi, D.K., Lee, D.J., 2006. Sequence stratigraphy of the Taebaek group (Cambrian–Ordovician), mid-east Korea. *Sediment. Geol.* 192, 19–55.
- Lee, Y.N., Lee, H.Y., 1986. Conodont biostratigraphy of the Jingunsan Shale and Duwibong Limestone in the Nokjeon-Sangdong area, Yeongweol-gun, Kangweondo. *J. Paleontol. Soc. Korea* 2, 114–136.
- Lee, K.W., Lee, H.Y., 1990. Conodont biostratigraphy of the Upper Choson Supergroup in Jangseong-Dongjeom area, Gangweon-do. *J. Paleontol. Soc. Korea* 6, 188–210.
- Lee, Y.I., Hyeong, K., Yoo, C.M., 2001. Cyclic sedimentation across a Middle Ordovician carbonate ramp (Duwibong Formation), Korea. *Facies* 44, 61–74.
- Lee, J.-H., Chen, J., Chough, S.K., 2015. The middle-late Cambrian reef transition and related geological events: a review and new view. *Earth Sci. Rev.* 145, 66–84.
- Li, Q., Li, Y., Kiessling, W., 2017. The oldest labechiid stromatoporeids from intraskeletal crypts in lithistid sponge-*Calathium* reefs. *Lethaia* 50, 140–148.
- Ma, J., Taylor, P.D., Xia, F., Zhan, R., 2015. The oldest known bryozoan: *Prophyllodictya* (Cryptostromata) from the lower Tremadocian (Lower Ordovician) of Liujiachang, south-western Hubei, central China. *Palaeontology* 58, 925–934.
- Meng, X., Ge, M., Tucker, M.E., 1997. Sequence stratigraphy, sea-level changes and depositional systems in the Cambro-Ordovician of the North China carbonate platform. *Sediment. Geol.* 114, 189–222.
- Moissette, P., Cornee, J., Koskeridou, E., 2010. Pleistocene rolling stones or large bryozoan nodules in a mixed siliciclastic-carbonate environment (Rhodes, Greece). *Palaios* 25, 24–39.
- Nestor, H., Webby, B.D., 2013. Biogeography of the Ordovician and Silurian stromatoporoidea. In: Harper, D.A.T., Servais, T. (Eds.), *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, pp. 67–79.
- Oh, J.-R., Choh, S.-J., Lee, D.-J., 2015. First report of *Cystostroma* (Stromatoporoidea; Ordovician) from Sino-Korean Craton. *Geosci. J.* 19, 25–31.
- Park, J., Hong, J., Lee, J.-H., Choh, S.-J., Lee, D.-J., 2017. Early labechiid stromatoporeids of the Yeongheung Formation (Middle Ordovician), Yeongwol Group, mid-eastern Korean Peninsula: Part I. Environmental distribution. *Geosci. J.* 21, 317–329.
- Pitcher, M., 1964. Evolution of Chazyan (Ordovician) reefs of eastern United States and Canada. *Bull. Can. Petrol. Geol.* 12, 632–691.
- Pratt, B.R., 1989. Small early Middle Ordovician patch reefs, Laval Formation (Chazy group), Caughnawaga, Montreal area, Quebec. In: Geldsetzer, H.H.J., James, N.P., Tebbult, G.E. (Eds.), *Reefs, Canada and Adjacent Area*. Canadian Society of Petroleum Geologists Memoir 13, Calgary, Alberta, pp. 218–223.
- Read, J.F., 1982. Geometry, facies, and development of Middle Ordovician carbonate buildups, Virginia Appalachians. *Am. Assoc. Pet. Geol. Bull.* 66, 189–209.
- Rowland, S.M., Shapiro, R.S., 2002. Reef patterns and environmental influences in the Cambrian and earliest Ordovician. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*. SEPM Special Publication No. 72, Tulsa, Oklahoma, pp. 95–128.
- Ruppel, S.C., Walker, K.R., 1982. Sedimentology and distinction of carbonate buildups: Middle Ordovician, East Tennessee. *J. Sediment. Petrol.* 52, 1055–1071.
- Servais, T., Owen, A.W., Harper, D.A.T., Kröger, B., Munnecke, A., 2010. The Great Ordovician Biodiversification Event (GOBE) of the palaeoecological dimension. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 294, 99–119.
- Taylor, P.D., 2005. Bryozoans and palaeoenvironmental interpretation. *J. Paleontol. Soc. India* 50, 1–11.
- Taylor, P.D., Ernst, A., 2004. Bryozoans. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 147–156.
- Webb, G.E., 2002. Latest Devonian and Early Carboniferous reefs: depressed reef building after the middle Paleozoic collapse. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*. SEPM No. 72, Tulsa, Oklahoma, pp. 271–338.
- Webby, B.D., 2002. Patterns of Ordovician reef development. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*. SEPM Special Publication No. 72, Tulsa, Oklahoma, pp. 129–180.
- Webby, B.D., 2004a. Introduction. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 1–37.
- Webby, B.D., 2004b. Stromatoporeids. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 112–118.
- Webby, B.D., 2015. Early evolution of the Paleozoic stromatoporoidea. In: Selden, P.A. (Ed.), *Treatise on Invertebrate Paleontology, Part E (Revised), Hypercalcified Porifera*. vol. 5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 575–592.
- Webby, B.D., Elias, R.J., Young, G.A., Neuman, B.E.E., Kaljo, D., 2004. Corals. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 124–146.
- Xia, F.-S., Zhang, S.-G., Wang, Z.-Z., 2007. The oldest bryozoans: new evidence from the late Tremadocian (Early Ordovician) of east Yangtze Gorges in China. *J. Paleontol.* 81, 1301–1326.
- Zenger, D.H., 1979. Primary textures in dolostones and recrystallized limestone: a technique for their microscopic study. *J. Sediment. Petrol.* 49, 677–678.