



# Post-tectonic limitations on Early Devonian (Emsian) reef development in the Gobi-Altai region, Mongolia

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This study investigates a Lower Devonian (Emsian) carbonate sequence from the Chuluun Formation where it is exposed in the Gobi-Altai region of southern Mongolia. Quantification of abundance patterns across guild, morphotype and general taxonomic levels was based on stratigraphical and thin-section analyses. Comparison with other Emsian carbonate platforms allowed the factors that influenced community development in the wake of a tectonic perturbation to be determined. Our evidence reveals that potential reef-building biotas preserved in the Chuluun Formation experienced rapid colonization of a newly submerged carbonate platform following an episode of tectonic uplift and the development of a coastal alluvial fan. Although critical reef-building organisms were present, colonial corals and stromatoporoids exhibited limited vertical growth and showed no significant lateral expansion of individuals or biotic assemblages. Nor did those taxa experience significant increases in abundance, density, or size. We conclude that incomplete succession and the lack of reef development occurred most likely because of an unsuitable substrate, limited accommodation space and isolation that reduced colonization potential. □ *Community succession, Emsian, palaeoecology, reef suppression.*

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Palaeontologists and ecologists have a vested interest in understanding how organisms adapt to environmental change. Response trends in marine invertebrate communities following significant changes in habitat availability (areal or spatial loss, degradation caused by pollution or siltation, etc.; Karlson & Cornell 1998) are important to study because of the widespread destruction of reef communities today (Done 1999; Gardner *et al.* 2003; but see Hughes *et al.* 2003 for alternative). In particular, investigations into the successful settlement of larvae and adults in a variety of at-risk marine habitats are especially relevant because they help document variables related to colonization and the long-term establishment of benthic communities. This helps identify the processes that influence re-colonization of previously occupied sites after conditions have returned to 'normal'. Geological deposits with well-preserved fossils provide a valuable basis for documenting the response of individual taxa and of communities to environmental change in the pre-human past.

During the Early Devonian, shallow-marine carbonate depositional systems across the world, including the Siberian, Timan-Pechora, Alberta, central

Europe, Morocco and South China platforms, supported reef development (James & Bourque 1992; Kiessling *et al.* 1999; Copper & Scotese 2003; Kiessling 2006). Generally, the reefs were constructed by a diversity of stromatoporoid sponges, tabulates and colonial rugose corals characterized by domal growth forms. The reef builders were associated with other taxa, such as branching corals and solitary rugosans, and thin, slender, branching colonies of bryozoans (Edinger *et al.* 2002; Fagerstrom & Bradshaw 2002). The high abundance of reefs in the Emsian (late Early Devonian) provides an impressive database with which to examine the factors that contributed to reef development.

This study, by contrast, examines the environmental conditions that inhibited reef growth. Stratigraphical sequences in the Gobi-Altai region are dominated by fossil-rich carbonate rocks, including Lower Silurian stromatoporoid-coral reefs exposed in the Sarchuluut Formation at Yamaan-Uus and 'Wenlock Hill' (Soja *et al.* 2010). In the Lower Devonian (Emsian) Chuluun Formation, well-preserved stromatoporoid sponges and tabulate corals secreted massive, domal skeletons but failed to produce reefs as

indicated by the low abundance and low density of colonies that form isolated ‘heads’ in well-bedded limestone. Comparative palaeocommunity composition suggests that the region was located within 35° of the equator (Copper & Scotese 2003). In addition, global sea surface temperatures are estimated to have been on average 30°C in the Early Devonian (Copper 2002), thus temperature does not explain the lack of reef development in the south Gobi.

The Chuluun Formation represents the first widespread carbonate to accumulate after tectonic uplift terminated carbonate platform sedimentation and induced alluvial fan development in the Pragian (earliest Early Devonian) (Gibson 2010; Pellegrini 2010). Our study shows that after marine habitats were re-established in the Emsian, colonization and successful settlement of invertebrate larvae occurred, but ecological succession from low- to high-diversity biotas did not take place. This study suggests that post-tectonic factors, including an unsuitable substrate, limited accommodation space and isolation of the carbonate platform, hampered reef growth in southern Mongolia in the Emsian. The results of this research add to a growing body of data about diversification patterns in marine communities, specifically those with the potential to build reefs in tectonically active areas.

## Geological setting

Near Shine Jinst in southern Mongolia, well-preserved and richly fossiliferous Ordovician–Silurian marine successions are overlain by Devonian–Triassic volcanic–sedimentary rocks (Fig. 1) (Badarch *et al.* 2002). Lithological and taxonomic studies document the basic stratigraphical relationships of Phanerozoic formations exposed across this broad region (Rozman & Rong 1993; Minjin 2000, 2001, 2002; Rozman 1999; Lamb & Badarch 2001; Minjin & Tumenbayer 2001; Wang *et al.* 2005; Lamb *et al.* 2008; Soja *et al.* 2010). Detrital zircons extracted from Upper Ordovician to Lower Devonian formations suggest that the area formed as an ocean basin, which was trapped between an unidentified continent and an offshore island-arc complex and was isolated from the Palaeo-Asian Ocean (Fig. 2) (Lamb & Badarch 1997, 2001; Lamb *et al.* 2008; Gibson 2010). Volcanic rock interbedded with terrigenous sediment, which was deposited episodically from the Late Ordovician through the Late Devonian, provides additional support for this palaeogeographical model (Lamb & Badarch 1997, 2001; Lamb *et al.* 2008; Gibson 2010). Recent work adds new details about the region’s subsequent crustal growth associated with volcanic arc activity in the

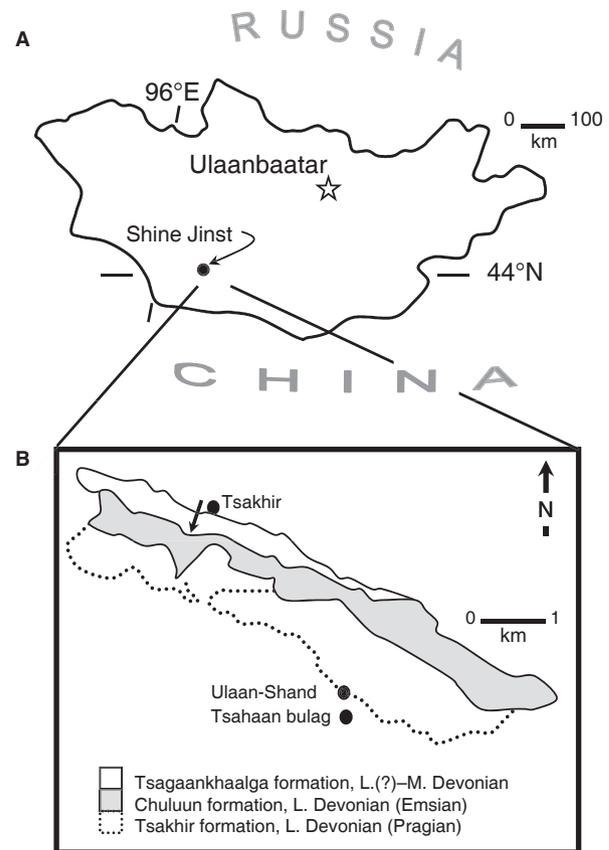


Fig. 1. Maps illustrating the field site. A, location of Shine Jinst in the Gobi-Altai region of southern Mongolia (modified from Soja *et al.* 2010); and B, geology of Tsakhir Basin (see of Shine Jinst), exposures of Lower–Middle Devonian formations in contact with the Chuluun Formation, and transect site (arrow) located at 44°21'39" N and 99°26'47" E. Modified from Wang *et al.* (2005) and Sullivan (2010).

Devonian–Carboniferous, accretion in the late Palaeozoic–Mesozoic, and multiple episodes of deformation in the Mesozoic and Cenozoic (Lamb *et al.* 2008).

Ordovician to Devonian deposits in the Gobi-Altai region are dominated by limestone, which is intercalated with siliciclastic, volcanoclastic and volcanic rock. These strata exceed 3000 m in thickness and reveal abundant shallow-water indicators, including cross-bedded sandstone, stromatolites and oncoidal limestone, abundant peloids and micritized grains, and reefal limestone. This suggests that a broad, shallow carbonate ramp existed for much of the Early–Middle Palaeozoic. During the Early Silurian, reef growth appears to have produced a rimmed shelf. Tectonic-induced regression and siliciclastic sediment influx terminated carbonate platform sedimentation in the Late Silurian–Early Devonian (Soja *et al.* 2010).

The Chuluun Formation (Emsian), specifically the basal unit, is the focus of this study (Fig. 1). Conformable contact of the basal member with the underlying

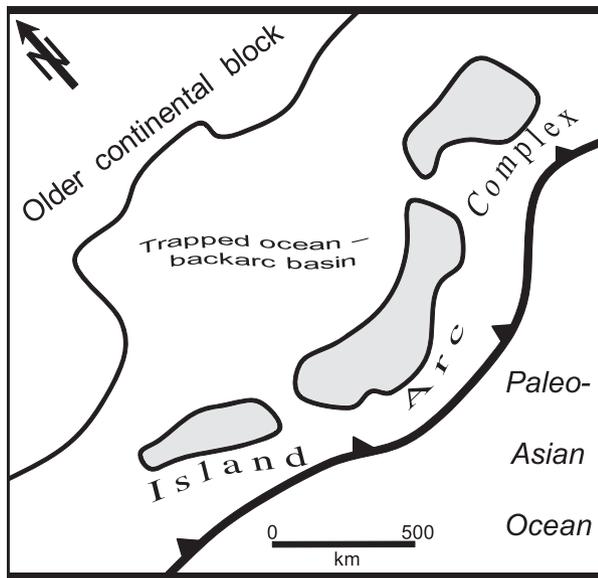


Fig. 2. Early Devonian palaeogeographical reconstruction of the Gobi-Altai region showing its isolation from the Palaeo-Asian Ocean as a back-arc basin trapped between a volcanic arc complex and an older continental block. Modified from Lamb & Badarch (2001) using base map at <http://walrus.wr.usgs.gov/infobank/gazette/jpg/regions/fr.jp.jpg>.

Tsakhir Formation indicates limestone was the first widespread sedimentary deposit to accumulate in the wake of Early Devonian tectonism. The Tsakhir Formation (540–720 m thick) comprises limestone conglomerate, siltstone, volcanoclastic sandstone, rhyolitic tuff and flows, and minor carbonate that formed during the Early Devonian (Lochkovian–Pragian) (Wang *et al.* 2005; Gibson 2010). The disconformity and massive conglomerate at the base of the Tsakhir Formation, abundance of siliciclastic strata and interbedded volcanic rock record the unfolding of a significant tectonic event in the Gobi-Altai region during that time. Clast compositions and other data suggest that a coastal alluvial wedge comprising debris flows and fanglomerate prograded from subaerial to nearshore marine environments following the regional uplift and erosion of Ordovician–Lower Devonian rock (Lamb & Badarch 1997, 2001; Gibson 2010).

## Materials and methods

A 75-m-thick section was measured from the base of the Chuluun Formation where the lower limestone member is in contact with the uppermost beds (shale) of the Tsakhir Formation (Fig. 1). Representative samples were collected every 1–2 m along a gully that bisects a prominent ridge on the western side of the Tsakhir Basin (Fig. 1). From these samples, 72 were made into thin sections. Thin sections were analysed

by identifying fossil biota – general taxonomic composition, species abundance and individual richness, and mode and state of fossil preservation – and rock type with a polarizing microscope. All samples and thin sections are housed in the Department of Geology, Colgate University. Identification numbers for all sample localities, such as AP-0.1-09, denote the height in metres above the base of the measured section followed by the year each sample was collected.

### *Guild concept*

Data from the field and thin sections were used to quantify the occurrence and relative abundance of all common organisms in the sequence. Recrystallization and partial replacement by silica precluded specific identification of most of the taxa. Rather, organisms were identified to general taxonomic group, assigned a morphotype based on skeletal properties (branching, domal, laminar, etc.) and size and then assigned to a guild.

Recognizing that competition for space shapes the development of reef communities, the guild concept, as applied to reefs (Fagerstrom 1987, 1988, 1991; see also Precht 1994; Stanley 2001), was used to group organisms based on their ecological function in a particular community. Similar morphotypes – determined objectively based on preserved skeletal material – indicate shared guild membership (Fagerstrom 1987, 1988). The analysis of functional groupings has been shown to be ecologically important because it provides a relevant metric for community diversity and sheds insight into a community's state (e.g., productivity and stability (Naeem & Li 1997; Tilman *et al.* 1997; Hector *et al.* 1999; Kiessling 2005)). Additionally, morphotypes (distinct anatomical phenotypes that are evident either across species or within species (e.g. polyphenisms) (Vollmer & Palumbi 2002)) can also be useful indicators of palaeoenvironment (e.g. Smosna & Warshauer 1979). These ecologically relevant groupings (guild/functional group and morphotype) allow a comprehensive survey to be made of community composition across localities in space and time where taxonomic composition may not be comparable. For instance, deposits that contain different taxa but similar morphotypes (such as delicate-branching corals belonging to different genera) may represent similar depositional settings and stages of community development.

Reef guilds, as defined by an organism's dominant skeletal properties, growth position and size, comprise constructors, bafflers, binders, dwellers and destroyers (Fagerstrom 1988, 1991; Fagerstrom & Weidlich 1999). As shown in table 2 in Fagerstrom (1988), we identified organisms in the constructor (framebuilder)

guild on the basis of robust, massive and domal skeletons that provided a three-dimensional structure; V:H (vertical vs. horizontal) growth dimensions were typically 0.3–0.7. For example, large domal corals and stromatoporoids ranging in size from 20 cm wide and 10 cm thick (V:H = 0.5) to 30 cm wide by 20 cm

thick (V:H = 0.7) and small spherical colonies typically 5–15 cm in diameter (V:H = 1) were classified as constructors (Figs 3D–G, 4A, B, 5C, 6–9).

Members of the baffle guild typically have slender, erect, branching skeletons, which promote sedimentation by diminishing current velocity and strength.

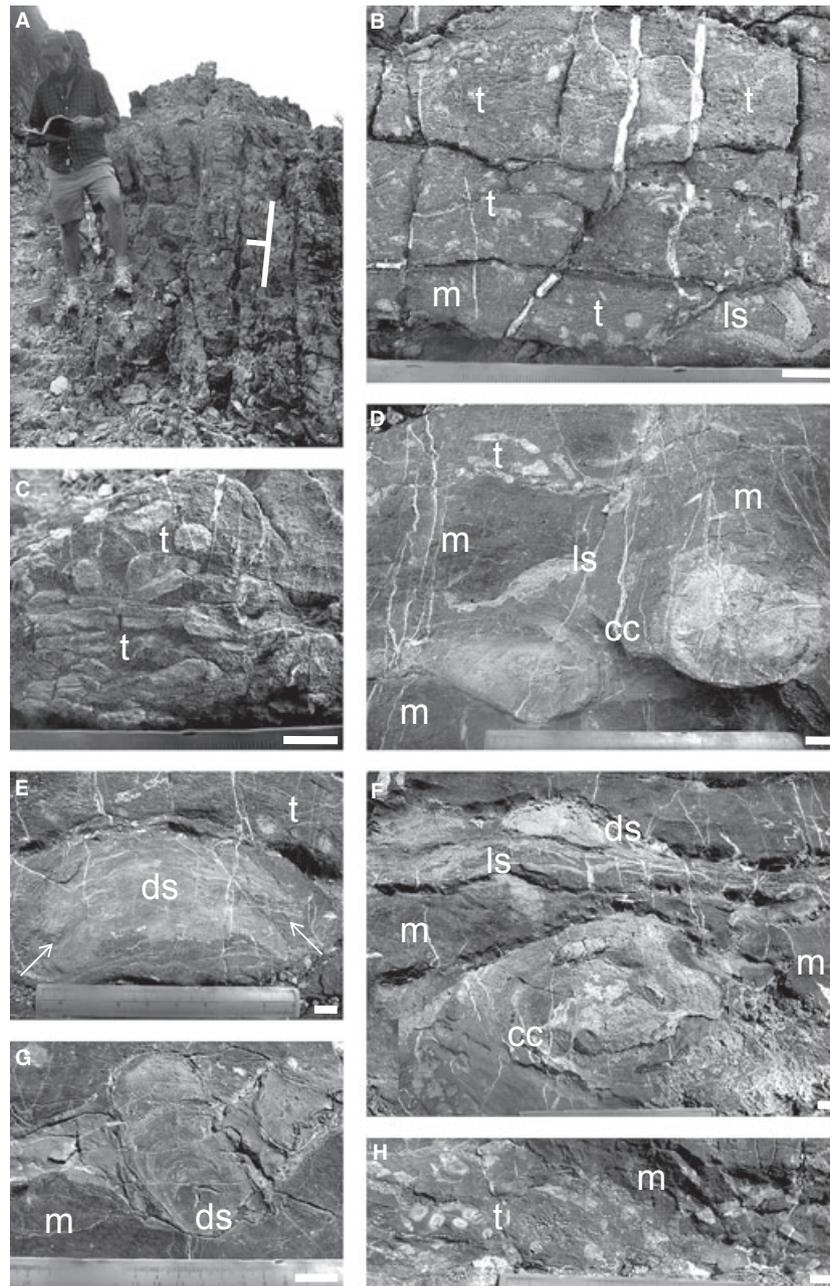


Fig. 3. Field photos showing bedding characteristics and fossils.: A, uniform thickness of beds dipping to north-northeast at high angle, AP-5-09; B, well-bedded skeletal wackestone and packstone near base of Chuluun Formation characterized by thamnoporids (t), laminar stromatoporoids (ls) and abundant micrite (m), AP-0.7-09; C, thamnoporid (t) bafflestone, AP-14-09; D, two small colonial corals (cc) closely associated with thin, laminar stromatoporoid (ls) and small lens of thamnoporids (t) surrounded by micrite (m), AP-45.6-09; E, small domal stromatoporoid (ds) with ragged margins (arrows) in micrite with scattered thamnoporids (t), AP-46-09; F, relatively large colonial coral (cc) 30 cm wide  $\times$  20 cm high overlain by micrite (m), laminar stromatoporoid (ls), and small domal stromatoporoid (ds) 5 cm wide  $\times$  2.5 cm high, AP-48.5-09; G, rare example of domal-bulbous stromatoporoid (ds) 5 cm high surrounded by micrite (m), AP-53-09; and, H, lens of thamnoporid (t) bafflestone in micrite (m), AP-68.5-09. Outcrop photos (B–H) are cross-sectional views of beds; way up is towards top of image. White scale in B–H = 2 cm.

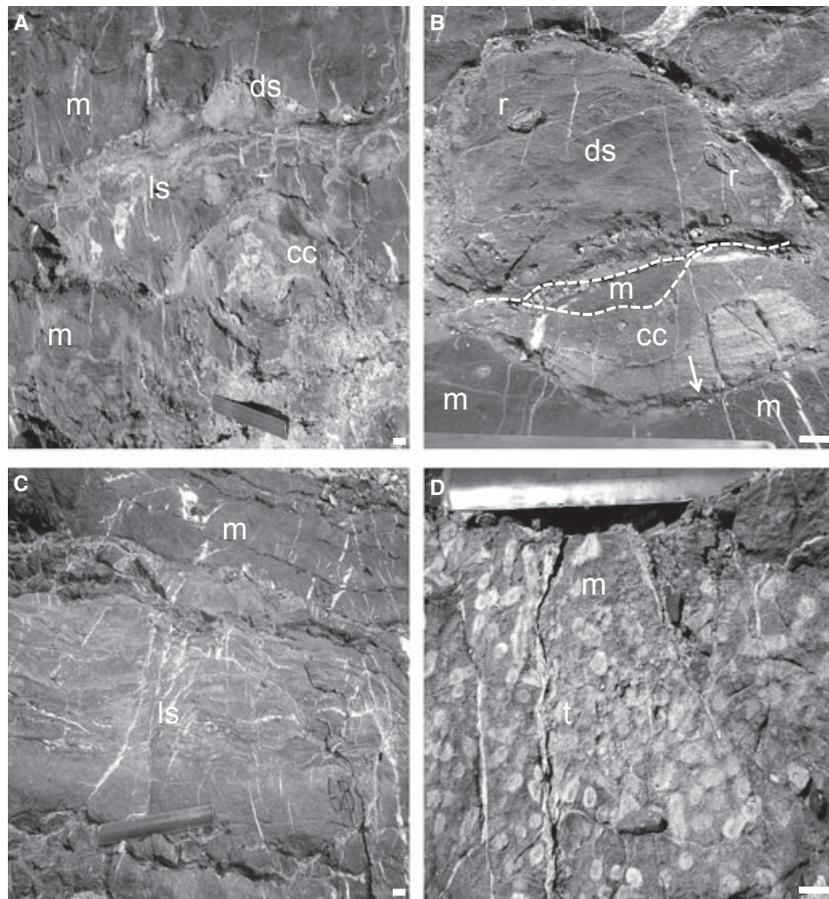


Fig. 4. Field photos showing close-up views of outcrop. A, large colonial coral (cc) (25 cm diameter) surrounded by micrite (m) and overlain by thin, laminar stromatoporoids (ls) and small, domal stromatoporoids (ds) (10 cm wide), AP-47-09. B, domal stromatoporoid (ds) with two rugosan (r) intergrowths encrusted on an overturned colonial coral (cc) in micrite (m); arrow indicates top of coral, AP-47.25-09. C, laminar stromatoporoid (ls) 30 cm thick overlain by micrite (m), AP-68-09. D, densely packed thamnoporoids (t) surrounded by micrite (m) in bafflestone, AP-72-09. Photos are cross-sectional views of beds; way up is towards top of image. White scale in all = 2 cm.

Baffles were mainly bryozoans typically with dimensions of 5 mm height  $\times$  1 mm diameter (Figs 5A, F, 6, 7); thamnoporids (Figs 3B–E, H, 5A, E, 6, 7) typically 3.5 cm long (tall) and 1–1.5 cm in diameter ( $V:H \geq 2$ ); crinoids (preserved as disarticulated columnals) (Figs 6, 7); and solitary rugose corals that ranged from 1 to 5 cm in diameter ( $V:H =$  unknown because of incomplete exposure of coral length) (Figs 4B, 6–9). Additionally, syringoporid corals (Figs 5A, D, 6, 7) were also included in the baffler guild but dimensions are not available because the fossils were incompletely exposed in the field (and in thin-section).

Binders, which exhibit more extensive lateral than vertical growth trapping and uniting sedimentary particles, were mainly thin or laminar stromatoporoids (Figs 3B, D, F, 4A, C, 5A, 6–9). These taxa were typically <5 cm thick but rarely formed crusts 15–30 cm thick (Fig. 4C). They ranged in lateral extent from 1 to 110 cm, thus exhibiting the greatest variation in  $V:H$  (<0.2–5). Dwellers and destroyers represent

diversification of marine benthos during niche specialization in reefs; as such, they vary tremendously in size, anatomy and degree of skeletonization (Fagerstrom 1988). Reefs that achieved the diversification stage are not evident at the study site. Members of the dwellers guild – brachiopods, gastropods and ostracods – are accessory constituents in the rocks under study and typically occur in such low abundance that they will not be discussed in detail (Figs 5B, E, 6, 7; Table 1).

For every metre, each guild (comprising one or more morphotypes and taxonomic groups) was assigned a value of 0 if there were no members evident or 1 if a member was present. This was done independently for all three groupings (guild, morphotype and general taxonomy) based on field data and thin sections. To facilitate the analysis of trends through the studied section, the individual metre results were grouped into an average abundance for each 10-m interval (e.g. a value of 0.66 for 0–10 m indicates that the group occurred in two-thirds of the samples from that particular section). The average relative

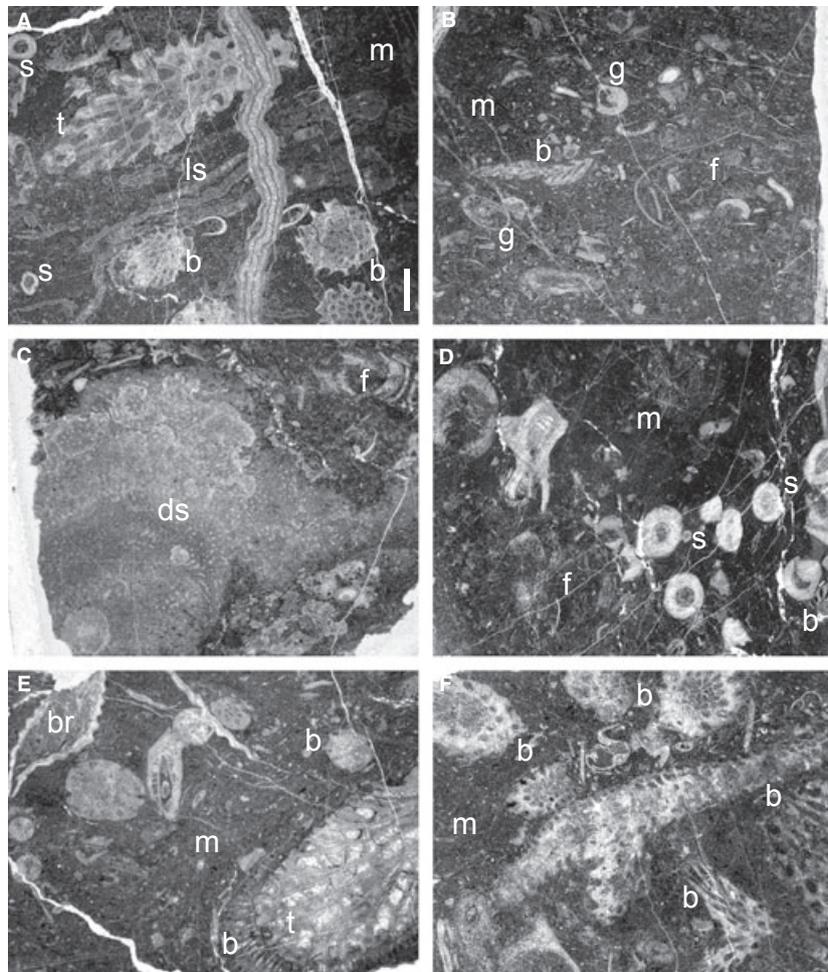


Fig. 5. Photomicrographs in plane light showing abundance of micrite and skeletal grain types. A, bryozoan wackestone–packstone with thamnoporid (t), syringoporid (s), bryozoan (b), and thin, laminar stromatoporoid (ls), AP-0.3-09; B, skeletal wackestone, characteristic of middle part of section, comprising gastropods (g) bryozoan (b), and other skeletal fragments (f), AP-41-09; C, stromatoporoid (ds) surrounded by skeletal fragments (f) in micrite, AP-57-09; D, well-preserved syringoporids (s) in micrite (m) characteristic of youngest beds, AP-70.5-09; E, bryozoan (b) encrusted on thamnoporid (t) in micrite (m) associated with spiriferid brachiopod (br), AP-71-09; F, baffestone comprising bryozoan (b) and micrite (m) in upper beds, AP-71-09. One-mm scale in (A) applies to all images.

abundance of a particular guild, morphotype and taxonomic group was calculated as the sum of the present values/number of thin sections and field observations. This measurement gives a rough estimate of relative abundances within each 10-m interval. An analysis of 300-point counts was also performed on 18 thin sections (one from each 4-m-thick interval) allowing for a more precise abundance estimate (Table 1).

Polynomial regressions were used to assess smoothed trends among data. Springer & Bambach (1985) used Markov diagrams in a more advanced mode of this type of analysis. They found that within a given section, multiple abundance peaks and trend shifts can be identified from presence–absence data. We have adopted a similar approach so that trends in organismal abundance can be quantified and compared.

## Results

The stratigraphical section is dominated by skeletal wackestone and packstone interbedded with rare thamnoporid, syringoporid, or bryozoan baffestone and stromatoporoid or coral boundstone (Fig. 7). The base of the section is characterized by the presence of small domal and laminar stromatoporoids (1 cm long by 1 mm thick) and colonial corals (average area = 50 cm<sup>2</sup>) in association with other coral taxa, bryozoans and crinoids in a skeletal wackestone (Figs 3B, 5A, 6; Table 1). From 4 to 8 m, solitary rugose, thamnoporid and syringoporid corals predominate in association with bryozoans and scattered crinoid (Fig. 6). Laminar stromatoporoids and bryozoans become more abundant at 12 m, followed by colonial corals, solitary rugosans and thamnoporids (Fig. 3C), and domal

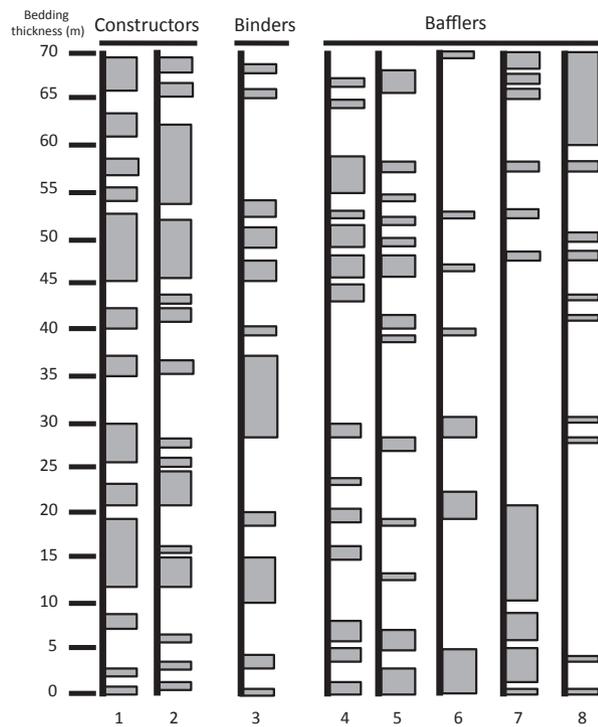


Fig. 6. Stratigraphical occurrence of organisms belonging to three guilds: constructors – domal stromatoporoids (1) and colonial corals (2); binders – laminar stromatoporoids (3); and bafflers – solitary rugosans (4), thamnoporids (5), syringoporids (6), bryozoans (7) and crinoids (8).

stromatoporoids, which form a community similar to that preserved from 0.5 to 8.0 m (Fig. 6). From 21 to 30 m, domal stromatoporoids and corals predominate but occur in patchy distribution (Fig. 6).

At 30–35 m, domal stromatoporoids and corals become less abundant, whereas laminar stromatoporoids increase in abundance (Fig. 6). The domal stromatoporoids and corals reappear at 36 m and in some beds are associated with skeletal debris (Fig. 5B). The best state of fossil preservation and the greatest abundance of individuals occur above 45 m (e.g. Fig. 3D); bryozoans, small rugosans, and thin, laminar stromatoporoids in association with domal stromatoporoids and colonial corals maintain relatively constant abundance levels until 54 m (Figs 3D–G, 4A, B, 6, 7). At that stratigraphical height, bryozoans disappear, and a lens of laminar stromatoporoids is associated with an increase in the abundance of domal stromatoporoids and corals and thamnoporids (Fig. 5C). At 62 m, thamnoporid corals decrease in abundance, and colonial corals become sparse while domal stromatoporoids and thin, laminar stromatoporoids associated with rugose corals are present (Figs 6, 7; Table 1). At the top of the section, the thamnoporid and syringoporid corals, which occur with bryozoans, rare spiriferids and laminar stromatoporoids, exhibit similar composition to the

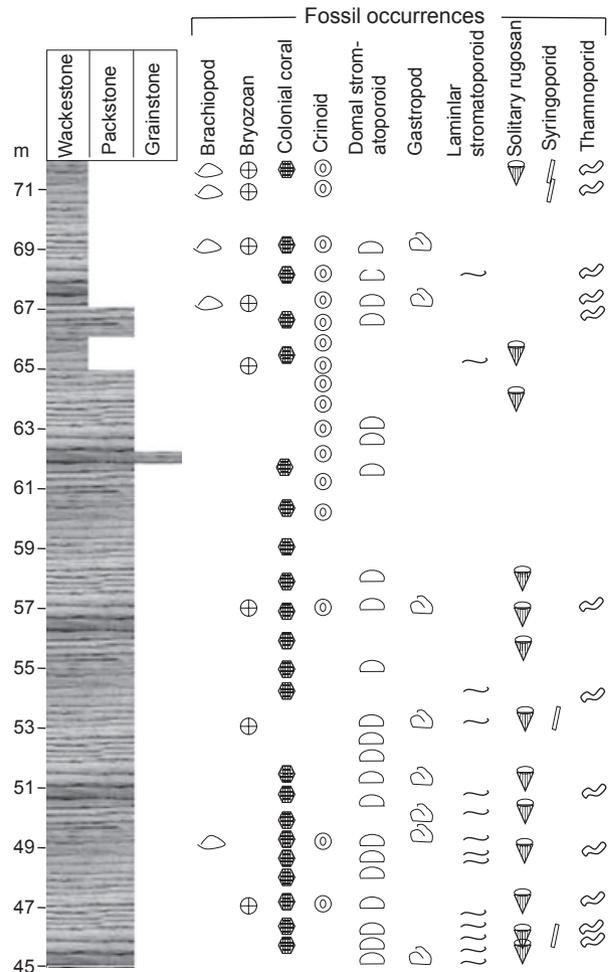


Fig. 7. Lithology and fossil occurrences in the upper part of the stratigraphical section (45–72 m) where skeletal preservation is best and organismal abundance is highest.

communities preserved at the base of the formation (Figs 3H, 4C, D, 5D–F, 6, 7).

There were no evident patterns of change in average organism size throughout the section (Figs 3, 4). Smaller organisms, such as solitary corals and bryozoans (no larger than 5 cm in diameter) and laminar stromatoporoids (1 cm thick and 5 cm wide), were present throughout most of the section. Tabulate corals ranged from 15 to 600 cm<sup>2</sup> in area but on average were 150–250 cm<sup>2</sup>. Domal stromatoporoids ranged from 10 to 600 cm<sup>2</sup> but were on average 300–400 cm<sup>2</sup> in diameter. Thin, laminar stromatoporoids ranged from 10 to 750 cm<sup>2</sup> in total area and generally did not exceed 5 cm in thickness.

## Discussion

The section under study documents the colonization of a newly submerged shallow carbonate platform by

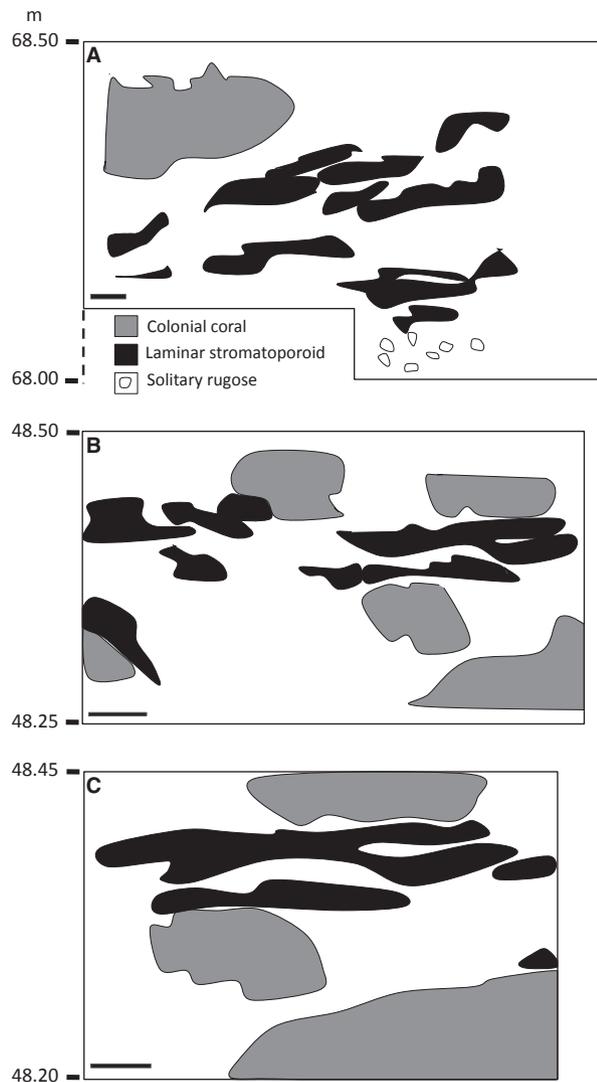


Fig. 8. Sketches done to scale on the outcrop showing the high abundance of micrite (white) and low density of organisms. All scales = 5 cm.

potential reef-building biotas (primarily massive stromatoporoids and colonial coral constructors in association with corals and bryozoan bafflers and stromatoporoid binders) in the wake of a significant tectonic event, as recorded in the underlying Tsakhir Formation (Gibson 2010). To determine the factors that appear to have dampened reef growth, we compare data from a guild-, morphotype- and taxonomic-based perspective with evidence from other Early Devonian marine benthic communities.

### Palaeoenvironment

The well-preserved, whole and unabraded fossils of stenohaline organisms (brachiopods, stromatoporoids, corals, bryozoans and crinoids), coated grains

and skeletal fragments micritized by endolithic borers, lack of deep-water biotas, such as abundant cephalopods (Lubeseder 2008) and siliceous sponge spicules (Pohler 1998), and the continuous, gradational transition from the underlying subaerial–nearshore deposits of the Tsakhir Formation suggest that the palaeoenvironment was a shallow-marine ramp. The abundance of lime mud, stromatoporoids and corals in growth position, complete solitary rugose corals, bryozoans comprising long, thin branches, and the occurrence, albeit rare, of intact crinoid columnals indicate that the environment was calm (Williams 1980; Zhen 1996; Ernst & May 2009). No wave ripples, interbedded siliciclastics, or intertidal indicators are evident, but variable wave energy is suggested by the high abundance of small skeletal fragments and the rare occurrence of overturned coral heads in some beds (Fig. 4B). There is no evidence for a gradual shallowing or deepening through time: well-bedded limestone (on average 50 cm thick) (Fig. 3A), overall fossil composition, and preservational state remain consistently uniform. However, cycles of organism abundance may record cyclical changes in the palaeoenvironment (Figs 6–8; Tables 1–3).

As suggested by the widespread development of limestone and by faunal affinities, south Mongolia was most likely located at 30–35° latitude in the Early Devonian, an interval in which warm-water conditions most likely prevailed at mid-to-high latitudes because of the overall elevated global temperature in the Early and Middle Devonian (Lethiers & Whatley 1994; Copper 2002; Copper & Scotese 2003; Königshof *et al.* 2010). This is supported by the presence of stromatoporoids, which prefer shallow water and are generally intolerant of cool temperatures associated with higher latitudes or deeper water (Embry & Klován 1972; Bjerstedt & Feldmann 1985; Zhen 1996; Kershaw 1988; Pohler 1998). The similarity in community composition between the Chuluun Formation and Emsian subtropical and tropical reefs comprising domal stromatoporoids and colonial corals suggests that the Chuluun Formation formed under similar climatic conditions (Sharkova 1981).

### Platform colonization and community development

Palaeontological and ecological studies have identified multiple factors that can affect reef development during various stages of growth (Brett *et al.* 2007). For instance, suitable water depths maintained by slow changes in sea level or rates of platform subsidence (Copper 1988, 1994; Copper & Scotese 2003); substrate stability (Isaacson & Curran 1981; Zhen 1996; Königshof *et al.* 2010); location downcurrent from

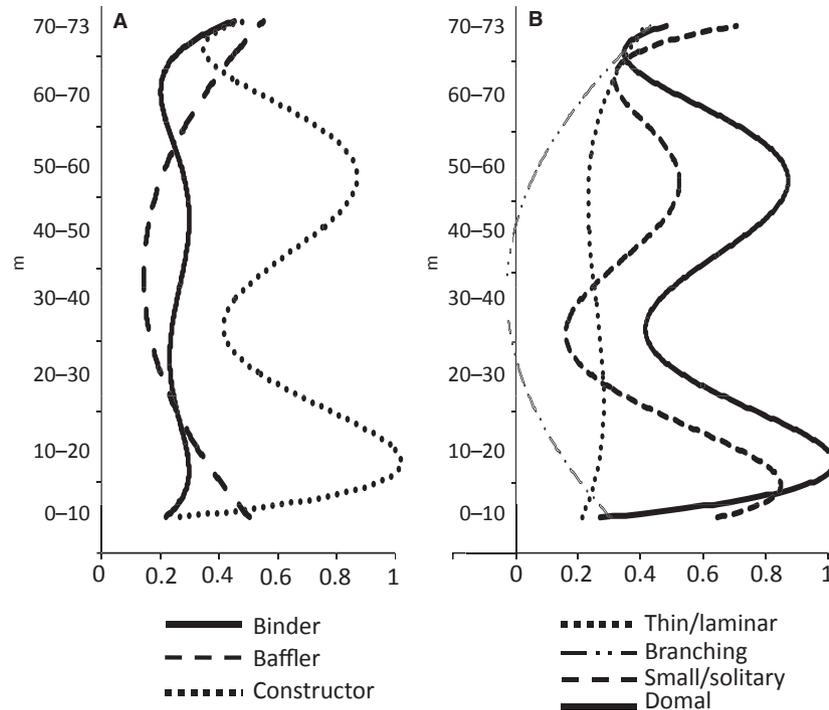


Fig. 9. Abundance polynomials fit to histogram plots based on abundance grouping data derived from field and point count analyses. A, guild groupings include constructor (colonial corals and domal stromatoporoids), baffler (branching syringoporoids, thamnoporids, solitary rugosans and bryozoans) and binder (laminar stromatoporoids); x-axis = number of samples in which a taxonomic group is present divided by total number of samples in that portion of the section and averaged across all taxonomic groups for a given guild. B, morphotype groupings include thin, laminar stromatoporoids, small/solitary (solitary rugosans and bryozoans), large/branching (thamnoporid and syringoporid corals) and large/domal (domal stromatoporoids and colonial corals).

biologically rich source areas of larvae, species diversity, and an abundance of key organisms, functional groups, and guilds (Smosna & Warshauer 1979; James & Bourque 1992; Da Silva & Boulvain 2004; Kiessling 2005); interruptions in volcanic activity or limited tectonic activity (Kittredge & Soja 1993; Soja & Gobetz 1994; Soja 1996; Soja & Krutikov 2008; Königshof *et al.* 2010); and intrinsic (evolutionary) aspects of reef communities, including macroevolutionary resilience (Kiessling 2009), have been shown to be significant factors in promoting reef development.

Reefs tend to reach a 'diversity stage', as shown by the abundance and taxonomic richness of fossils achieved relatively rapidly following stabilization and colonization (Copper & Scotese 2003). In comparison, isolation from sites of reef growth, the lack of suitable climatic conditions, muddy or unstable substrate, turbid or poorly oxygenated water, excess nutrients, changes in sedimentation rate or depth, and other factors have been shown to contribute to partial or 'aborted' reef growth (Williams 1980; Smith & Stearn 1987; Copper 1988; Rogers 1990; Zhen 1996; Pohler 1998; Pomar 2001). Thus, these factors require consideration to ascertain the conditions that facilitated

colonization but hampered reef growth when carbonate sedimentation resumed in the Gobi-Altai region after tectonic disturbance in the Early Devonian.

The occurrence of stromatoporoids, corals and bryozoans in the lowest beds of the Chuluun Formation is evidence for rapid colonization of the newly submerged ramp by potential reef-building biotas (Figs 3B, 6). However, the overlying deposits do not record growth trends similar to other Lower Devonian reefs (Tables 1–3) (Smith & Stearn 1987; Clough & Blodgett 1989; Edinger *et al.* 2002). For example, Emsian deposits on Ellesmere Island in the Canadian Arctic represent a reef complex 10 km long and 100 m thick (Smith & Stearn 1987). An Early to Middle Devonian deposit from the South China landmass has massive corals and stromatoporoids that formed extensive reefal boundstones 1000–2000 m thick unlike those we examined in the Chuluun Formation (Shen *et al.* 2008; but see Sharkova 1981). Additionally, 25- to 30-m-thick stromatoporoid-coral reefs in the Urals show similar reef growth to South China but not to our site in the Chuluun Formation (Antoshkina & Königshof 2008). Similarly, Early–Middle Devonian reefs in Australia achieved a thickness of 18 m

Table 1. Point count data (%) showing relative abundances of all lithological components.

Bed height in metres above base	Micrite	Domal stromatoporoid	Laminar stromatoporoid	Colonial coral	Syringoporid	Thamnoporid	Bryozoa	Crinoid	Brachiopod	Ostracod	Gastropod	Unid. skeletal debris	Fracture fill
73	80.0	8.3	0.0	8.3	1.3	8.3	4.7	2.0	2.3	1.0	0.0	0.3	0.0
72	62.4	19.9	0.0	0.0	2.6	0.0	8.8	2.6	1.2	0.0	0.0	2.6	0.0
68	27.7	72.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
65	86.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	11.0	0.0
60	94.3	0.0	0.0	0.0	0.3	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0
57	64.7	0.0	0.0	0.0	0.0	0.0	20.0	0.0	0.0	0.0	1.3	1.7	12.3
53.5	83.3	0.0	0.0	15.0	0.7	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0
47	86.7	0.0	0.0	0.0	0.0	0.0	2.0	5.0	0.7	0.0	0.0	5.7	0.0
45	97.0	0.0	0.0	0.0	0.0	0.0	0.7	1.3	0.3	0.7	0.3	0.0	0.0
41	79.7	0.0	0.0	0.0	0.0	0.0	2.3	2.0	0.0	0.3	7.7	5.0	3.0
37.5	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
33	28.7	22.3	47.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
28	85.3	0.0	0.0	4.7	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0
21	51.7	0.0	3.3	45.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15.6	74.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	6.0	12.0	6.0
11	97.7	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.3	0.0	0.0	0.0	0.0
4	32.0	50.3	0.0	13.0	2.3	0.0	0.7	0.0	0.0	0.0	0.0	1.7	0.0
0.3	78.3	0.0	1.7	8.7	0.7	0.0	10.7	0.0	0.0	0.0	0.0	0.0	0.0

Table 2. Average abundance values grouped by 10-m intervals for guilds (averaged across morphotypes).

Bed height in metres above base	Binder	Constructor	Baffler
70–73	0.45	0.5	0.6
60–70	0.22	0.44	0.22
50–60	0.22	1	0.28
40–50	0.33	0.67	0.29
30–40	0.25	0.33	0.04
20–30	0.21	0.71	0.14
10–20	0.3	0.9	0.4
0–10	0.21	0.29	0.48

Table 3. Average abundance values grouped by 10-m intervals for morphotype (averaged across taxonomy within morphotype groupings).

Bed height in metres above base	Thin/laminar	Large/domal	Large/branching	Small/solitary
70–73	0.45	0.50	0.50	0.70
60–70	0.22	0.44	0.06	0.39
50–60	0.22	1.00	0.17	0.39
40–50	0.33	0.67	0.00	0.58
30–40	0.25	0.33	0.00	0.08
20–30	0.21	0.71	0.00	0.29
10–20	0.30	0.90	0.10	0.70
0–10	0.21	0.29	0.32	0.64

and comprise domal stromatoporoids 1–2 m high that grew on a coarse-grained skeletal substrate (Pohler 1998).

Although the Chuluun Formation contains large stromatoporoids (45 cm in diameter) and tabulate corals (30 cm in diameter) – comparable in size to coral and stromatoporoid colonies evident in some Devonian reefs (Zhen 1996; Shen *et al.* 2008), organisms in the Chuluun Formation never reached a high enough density to create extensive boundstone (Fig. 8), as recorded at those other sites. For example at AP-45.6-09, only four domal colonial corals with average dimensions of 15 cm wide × 5 cm thick (high) are evident across a 1–1.5 m wide area; similarly at AP-68-09, a few solitary rugosans, ca. 1–2 cm in diameter, occur in low density forming the only cluster in a 80-cm-wide zone (Fig. 8A). Thamnoporid corals are commonly densely packed, but typically they are concentrated in small lenses 10–35 cm wide and 4–10 cm thick (Figs 3C, H, 4D).

Reef development is a complex process involving organisms living in guilds that form spatially and temporally structured communities (Fagerstrom 1988). Four major stages may occur during the development of reefs: stabilization, colonization, diversification and domination (Walker & Alberstadt 1975). Although the degree of autogenic succession is debated (in many cases, allogenic factors regulate community succession

Table 4. Average abundance values grouped by 10-m intervals for morphotype and taxa.

Bed height in metres above base	Thin/laminar	Large/domal		Large/branching		Small/solitary		
	Thin stroms.	Domal stroms.	Large coral	Syringoporid	Thamnoporid	Rugose coral	Bryozoan	Crinoid
70–73	0.90	0.10	0.90	0.70	0.30	0.70	0.70	1.00
60–70	0.44	0.44	0.44	0.00	0.11	0.33	0.44	0.20
50–60	0.44	1.00	1.00	0.33	0.00	0.33	0.44	0.30
40–50	0.67	0.50	0.83	0.00	0.00	0.50	0.67	0.00
30–40	0.50	0.33	0.33	0.00	0.00	0.00	0.17	0.10
20–30	0.43	1.00	0.43	0.00	0.00	0.14	0.43	0.10
10–20	0.60	0.80	1.00	0.00	0.20	0.40	1.00	0.00
0–10	0.43	0.36	0.21	0.43	0.21	0.64	0.64	0.20

(Gould 1980)), ecological succession in reefs is evident based on empirical data (see Copper 1988). During the stages in reef succession, taxa belonging to specific ‘guilds’ play functional roles in community development.

In the Chuluun Formation, members of several reef guilds are evident (constructor, baffler, binder and dweller), but individuals and colonial organisms grew relatively isolated from one another (Figs 3D,F, 4A, 8). There is no direct evidence of either a linear change in organismal composition or density throughout the section nor is there any change in the lithology of the deposits (e.g. micritic limestone is not interbedded with shale, for example; Table 4). Similar to incipient reefs reported from an Emsian island arc in Australia, the potential frame-building reef constructors did not form the dense clusters that are so common in other Lower–Middle Devonian reefs (Williams 1980; Zhen 1996; Pohler 1998; Copper & Scotese 2003). This suggests that environmental conditions, such as substrate, subsidence rate and accommodation space, were not optimal for the extensive growth of these organisms.

One apparent trend from the fitted polynomials is the abundance of bafflers and binders relative to constructors throughout most of the section (Figs 7–9; Table 2). In reefs, bafflers and binders entrap sediment, reduce water currents and induce sedimentation (Williams 1980; Fagerstrom 1991); typically they may be opportunistic taxa with high recruitment rates that are capable of gaining rapid establishment on shifting substrates of mixed composition (Zhen 1996). Their survival seems to be a critical step in the formation of reefs because following the initial colonization of initially barren, soft or mobile substrate by binders and bafflers, lateral skeletal growth as well as the bafflers’ roots and holdfasts stabilize the sediment. For example, some low-diversity reefs reveal the importance of baffler abundance for successful larval colonization. The Lankey Limestone (Reefton, New Zealand) is similar to the Chuluun Formation in that it formed in a shallow but calm water setting and comprises relatively low taxonomic diversity

(Fagerstrom & Bradshaw 2002). The Lankey, however, displays reef development that the authors attributed to the positive influence of bafflers on larval colonization and filtration efficiency, which has been shown to be important by others (Wildish & Kristmanson 1997).

Once hard surfaces (skeletal material, etc.) become available for larval attachment, colonization by constructors requiring a stable surface for growth takes place (Zhen 1996; Berkowski 2006). After a three-dimensional structure is created and if ecological succession is not interrupted, large, robust, constructor species continue to build upon and strengthen the accreting reef edifice (Williams 1980; Copper 1988; Fagerstrom & Bradshaw 2002; Copper & Scotese 2003). Thus, the relative abundance of bafflers – branching corals, bryozoans and crinoids – and of stromatoporoid binders cannot entirely explain the limited reef growth evident at the study site (Table 4).

Members of the baffler guild may play only local roles and not affect overall reef development when there is a high abundance of binders and constructors (Fagerstrom & Weidlich 1999). For example, some Lower Devonian reefs have a much greater abundance and density of constructors, which in some cases preceded the colonization of extensive binders and bafflers. The Upper Keyser Limestone Member in Virginia (Lower Devonian) has levels of taxonomic diversity similar to the Chuluun Formation (Isaacson & Curran 1981), but it hosts a greater volume of domal stromatoporoids (80% in Keyser Member vs. 10% in Chuluun Formation). Smosna & Warshauer (1979) identified the high density of domal stromatoporoids as being critical for reef development because of their functional role in reef construction. Thus at our study site, the presence of various members of the baffler and binder guilds and of potential reef frame-builders (domal stromatoporoids and colonial corals) suggests that colonization was successful, allowing some individuals to settle, become established, and grow. Throughout the section, however, the low density and abundance of established

individuals belonging to three important reef guilds suggest that other factors must have limited subsequent widespread establishment of flourishing, complex, shallow-marine communities.

### *Substrate, sedimentation rate and accommodation space*

Binders, bafflers and constructors exhibit limited lateral growth in the Chuluun Formation. The lack of such growth suggests that an unsuitable or unstable substrate precluded most organisms from expanding laterally, binding the matrix and substrate components into a boundstone fabric. For example, successive growth in an Eifelian patch reef in central New York State occurred after crinoids and rugosans colonized the area. The skeletal remains of these organisms produced a stable substrate that allowed domal tabulates and stromatoporoids to initiate reef development (Williams 1980). During the Late Silurian, the lateral growth of stromatoporoid-dominated reefs up to 5 m thick on Gotland was facilitated by a hard substrate, typically crinoidal grainstone, and by low clastic sediment influx (Kershaw & Keeling 1994). Zhen (1996) noted that some colonial corals, but not solitary rugosans, from a Givetian intracratonic basin in north Queensland required firm seafloor sediment and were incapable of growth on moving or unstable sediment.

A similar pattern of reef succession is documented in the Middle Devonian of Germany where reefs grew on submarine volcanic edifices near the southern margin of the Old Red Continent. Intercalated beds of reefal and volcanoclastic detritus indicate that incipient reefs were buried episodically. Subsequent transgression and a hiatus in volcanoclastic sedimentation promoted the growth of stromatoporoid and coral reef complexes up to 400 m thick on sediment comprising the skeletal remains of branching coral and stromatoporoid binders (Königshof *et al.* 2010). In southeastern Spain during the Tertiary, patch reefs up to 15 m thick grew on a quartz-rich substrate of submarine deltaic fan lobes when siliciclastic sediment influx was diminished (Reinhold 1995). In addition, the distribution of substrate types (calcareous vs. siliciclastic) has been shown to result in spatial heterogeneity of benthic communities (Kershaw 1988; Pohler 1998; Testa & Bosence 1999; Leinfelder *et al.* 2005; Purkis & Kohler 2008). For example, Zhen (1996) and Leinfelder *et al.* (2005) demonstrated that stromatoporoids preferred offshore sites because terrigenous clastic sediment deleteriously affected their growth.

At our site, the dominance of fine-grained lime mud (micrite) (Table 1) and the lack of abundant hard surfaces (no evidence of concentrated shells, grainstone horizons, hardgrounds, etc.) appear to

have prevented widespread larval settlement and also hampered the subsequent lateral growth of most colonizing taxa. Organisms that grew in small clusters and achieved only modest vertical development are associated in some beds with encrustations on individual skeletons and organismal intergrowths, particularly above 45 m in the section. For example, a small domal stromatoporoid 5 cm in diameter is overgrown by a laminar stromatoporoid (AP-45.25-09); a colonial coral 15 cm wide × 5 cm high is encrusted by a laminar stromatoporoid (AP-45.6-09); an overturned colonial coral 25 cm wide × 8 cm high is encrusted by a spherical stromatoporoid 17 cm in diameter into which are grown two solitary rugosans (AP-47.25-09) (Fig. 4B); and a solitary rugose is encrusted by a laminar stromatoporoid (AP-53-09).

Noted by Zhen (1996) to be most common in Middle Devonian stromatoporoid reefs, encrusting and intergrowth relationships arise because of competition for space, especially where hard surfaces may be limited. Small, incipient reefoid-like clusters at our site appear to reflect successful growth on hard surfaces of limited availability (either scattered fossil debris or individual skeletons). Similar adverse conditions are reported from the Emsian of Australia where an unstable slope, siliciclastic input and other factors led to stunted growth forms and hindered the establishment of true reefs (Pohler 1998). In southeastern Spain during the Tertiary, a low-diversity pioneer community of stabilizers and colonizers grew into shallow water but did not achieve a climax phase in reef growth because of fluctuating sedimentation rate and eventual smothering by sediment (Reinhold 1995). In our study, stromatoporoids with ragged growth margins occur at AP-46-09 (Fig. 3E), AP-48.25-09 and AP-49-09. This is evidence of episodic sedimentation, shifting sediment and organismal re-growth (Kershaw 1988; Luczynski *et al.* 2009), thus indicating that unstable conditions on the seafloor and the lack of abundant hard surfaces hindered organismal growth.

At tropical and subtropical latitudes where temperature regimes are conducive to reef growth today, sedimentation rate has also been identified as influencing the development of modern benthic fauna and reef assemblages (Testa & Bosence 1999). Sedimentation rates are likely to have fluctuated to some extent during deposition of the Chuluun Formation because of variations in the growth morphology of stromatoporoids and colonial corals, which range from laminar to domal to erect branches throughout the measured section (Fig. 7). Massive, domal stromatoporoids and colonial rugosans in the Chuluun Formation were most likely adapted to shallow water and higher sedimentation rates (Isaacson & Curran 1981; Zhen 1996; Pohler 1998). Sedimentation rates were most likely

lower in the micrite-dominated beds where thin, laminar stromatoporoid morphotypes prevailed (mainly from 30 to 35 m; Fig. 6), as they would have been susceptible to burial when sedimentation was high (Pohler 1998).

Accommodation space – the amount of space that can be occupied by sediments or water in aquatic habitats – can also influence the vertical development of reef communities (Bosscher & Schlager 1993; Copper & Scotese 2003). The Coeymans Formation comprises similar deposits (uniformly bedded micritic wackestone) to the Chuluun Formation, but as corals (*Favosites*, *Tryplasma* and *Briantelasma*) increased in dominance, they developed into a reef that culminated with large planar *Favosites* boundstone (Isaacson & Curran 1981). This upward transition suggests that a flat growth form was favoured as the accreting reef eventually occupied the space between the seafloor and the ocean's surface. In the Knoxboro buildup, there is a concurrent increase in large colonial corals and bedding thickness, which suggests that accommodation space allowed reefs to keep pace with rates of subsidence and (or) eustatic sea-level rise. Similarly, ecologic succession in Middle Devonian, coral-dominated biostromal reefs of central New York State was controlled by changes in water depth and turbulence (Wolosz 1992).

Regardless of organismal abundances and lithologic compaction, bedding thickness in the Chuluun Formation is roughly constant (0.1–0.5 m) through the 75-m-thick sequence. This suggests that accommodation space, achieved through a balance of subsidence, eustasy and sedimentation rates, remained uniform and may have placed limitations on the extent to which organisms could grow vertically between the seafloor and mean sea level (Bosscher & Schlager 1993; Leinfelder *et al.* 2005). However, the overall depauperate nature of the biotas, the lack of abundant functional morphotypes and the low abundance levels suggest that isolation may have been a compounding factor that reduced the potential for the widespread colonization by organisms (or their larvae) and, consequently, for reef formation.

### Isolation

When considered in the context of the regional geology of central Asia, the volcano-sedimentary stratigraphical profile of the Shine Jinst region indicates it is an allochthonous crustal fragment that formed as a back-arc basin (Badarch *et al.* 2002; Lamb *et al.* 2008). Influenced by episodic volcanism and influxes of siliciclastic detritus, deposition occurred in a small ocean, which was trapped between an unknown continent and a deeply eroded volcanic arc in the Early

Devonian, as indicated by detrital zircons (Gibson 2010). The shallow-marine carbonate ramp system that evolved in the ocean basin was isolated from the Palaeo-Asian Ocean by the island-arc complex (Fig. 2) (Lamb *et al.* 2008; Gibson 2010).

Geographic isolation results in fewer successful colonizing events because of the dispersal limits of planktonic larvae (Underwood *et al.* 2009). Given the palaeogeographical setting of the Gobi-Altai region and its distinctive assemblage of detrital zircons (Gibson 2010), it seems likely that isolation from biologically rich source areas contributed to the slow recovery and limited expansion of marine biotas in the wake of the Early Devonian tectonic event. Support for this idea stems from the post-tectonic colonization of the platform by low-diversity and low-density suites of depauperate shallow-marine biotas in the Chuluun Formation. The taxonomic affinities of Silurian brachiopods, which cannot be closely allied with other fossil assemblages from areas outside of Mongolia, also support this interpretation. The provincial nature of those faunas appears to reflect evolution in an isolated terrane (Badarch *et al.* 2002), palaeocontinent (Copper 2002), or endemic centre within the Mongolo-Okhotsk Subprovince of the Uralian-Cordilleran Region (Rozman 1999). Additional support for these hypotheses may be available in the future once the taxonomy of the corals and other taxa can be determined from better-preserved material.

The restricted number of species preserved in the Chuluun Formation and the muted, post-tectonic development of community complexity are similar in part to the evolution of marine benthic communities in the Alexander terrane of Alaska, which formed as a volcanic arc in the Uralian Seaway (proto-Arctic Ocean basin) in the early–mid Palaeozoic (Soja 2008; Soja & Krutikov 2008). Silurian–Devonian fossils from that terrane are among the best-studied organisms that evolved in Palaeozoic island-arc settings. In the Late Silurian–Early Devonian, reef communities were affected by regression and the widespread deposition of coarse conglomerate. Similar to the Tsakhir Formation, the conglomerate represents a significant interruption in carbonate platform sedimentation and the development of a coastal alluvial fan (Soja & Krutikov 2008).

Upper Silurian limestone that overlies the conglomerate records the rejuvenation in carbonate platform evolution during subsequent transgression, similar to the Chuluun Formation (Soja & Krutikov 2008). In contrast to the Chuluun Formation, larval exchange along a marine corridor (Uralian Seaway) promoted the re-establishment of reefs after tectonic disturbance in the Alexander terrane (Antoshkina & Soja 2006; Soja & Krutikov 2008). In the wake of environmental

perturbances, no such seaway appears to have facilitated colonization and diversification of marine communities in the Chuluun Formation, suggesting isolation from potential sources of larval dispersants.

## Conclusions

This study documents the influence of tectonism and environmental factors on marine benthic palaeoecology and community evolution during deposition of the Chuluun Formation in the Gobi-Altai region of Mongolia. It examines which organisms became re-established and how communities evolved in marine sites during sea-level rise following tectonic uplift and marine regression. Specifically, it provides new insights into communities that had the potential to build reefs in the Early Devonian but failed to do so.

After prolonged intervals of siliciclastic influx and volcanism associated with deposition of the Tsakhir Formation, potential reef-building organisms colonized level-bottom habitats during marine transgression, as indicated by the occurrence of massive stromatoporoids, colonial corals and bryozoans in the basal beds of the Chuluun Formation. These low-diversity biotas, characterized by low abundance and low density, are preserved in well-bedded micritic limestone, which also comprises depauperate suites of brachiopods, gastropods, crinoids and ostracods. Although organisms that were common in Early Devonian reef guilds successfully colonized shallow-marine areas, they grew predominantly as small, isolated clusters that did not experience significant vertical or lateral growth. Nor is there evidence of ecological succession from colonizing to diversification or domination reef stages. The lack of reef development appears to reflect an unsuitable substrate for widespread larval settlement, insufficient accommodation space for expanded growth of successful colonizers, and isolation from biologically rich source areas.

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