学位論文

Paleoecological study of the earliest Cambrian biological activity evidenced by the diversification of ichnofossils

（生痕化石の多様化から探るカンブリア紀
最前期の動物活動の古生態学的解明）

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申請

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Abstract

In order to better understand the diversification of the animal activities in the earliest Cambrian than studying only body fossils, ichnofossils were comparatively studied in three different localities (Newfoundland, Canada, Yunnan, China and Gobi-Altai, Mongolia). Special attention was paid for the following topics; 1) To understand the developmental mode of the animal behaviors, the diversification patterns of ichnofossils were studied, 2) To know the adaptation processes to different environments, changes of the ichnofossil assemblages in different sedimentary facies were surveyed, 3) To reveal the body size changes of trace maker animals, size distributions of the tube-shaped ichnofossil *Planolites* were investigated, 4) To clarify the buildup processes of animal activities, densities of ichnofossils covering the bedding planes were measured.

The diversification patterns of the ichnofossils in the earliest Cambrian Chapel Island Formation, Newfoundland show that major diversification of the ichnofossils occurred twice; firstly at the almost basal part of the Pc-C boundary, secondly around the boundary of the *Treptichnus pedum* and *Rusophycus avalonensis* zones. The ichnofossil assemblages are relatively common to different depositional facies, suggesting that there was no conspicuous specialization of these assemblages to particular facies. This observation indicates that animal behaviors developed in a wider environmental spectrum

in the earliest Cambrian than in later ages. On the other hand, ichnofossil assemblages considerably differed between the late Early Cambrian Balang and Chintingshan formations in China. One possible explanation for this change would be that the animals have started to adapt and to be diversified their behavior corresponding to the environments since the late Early Cambrian.

The size (width) of *Planolites* is assumed to represent the size of the trace maker. In Newfoundland, the average size of *Planolites* in the *T. pedum* Zone is smaller than in the *R. avalonensis* Zone. Thus, there should have been an increase in the size of *Planolites* producers near the boundary of the two zones. On the other hand, the size distribution of *Planolites* in the Zhujiaqing Formation, Yunnan and the Bayan Gol Formation, Gobi-Altai showed that the variously sized animals already appeared in the *T. pedum* Zone. Besides, the densities of ichnofossils on the bedding planes were low in the *T. pedum* Zone in Newfoundland, although they became high in the *R. avalonensis* Zone. The densities in Yunnan and Gobi-Altai, however, were already high in the *T. pedum* Zone. Therefore, the animal activity became intense in the *R. avalonensis* Zone in Newfoundland, whereas they had already been intense in the *T. pedum* Zone in Yunnan and Gobi-Altai. In addition, the occurrences of specific ichnofossils show considerable differences among threes localities. *Gyrolithes* isp. was commonly observed in

Newfoundland, but was not observed in Yunnan and Gobi-Altai. *Didymaulichnus miettensis* frequently occurred in Yunnan and Gobi-Altai, but not in Newfoundland.

Therefore, there were geographical differences in the benthic animal activities between Newfoundland and Yunnan - Gobi-Altai. One possible factor of this difference can be based on the differences of the paleolatitude positions of Newfoundland and Yunnan - Gobi-Altai. The earliest Cambrian Newfoundland was located in high-latitude region, whereas Yunnan and Gobi-Altai were in low-latitude regions. Previous paleoclimatic studies show that climate in low latitudinal regions was warm whereas climate in high latitude was cold in the earliest Cambrian. In general, species generation time decrease in high temperature region, and thus biological diversification might become high in low latitude regions. Therefore, variously sized animals with intense biological activities could have firstly originated in low latitude regions in the *T. pedum* Zone. These animal activities subsequently reached to high latitude regions in the *R. avalonensis* Zone.

Contents

1. Introduction

Numerous animals of different body plans explosively appeared and radiated from the latest Precambrian to the Early Cambrian. It is assumed that all marine animal phyla appeared in this event. This abrupt adaptive radiation, called "Cambrian explosion," is known as one of the most important events in the animal evolutionary history, and many studies have been conducted in the past. However, the scenarios of morphological evolution were based on the record of body fossils such as the Chengjiang and Burgess Shale biotas in the late Early to Middle Cambrian. Therefore, the primary steps of this rapid evolution have been obscure because of poor body fossil preservations. To clarify the early stages of the Cambrian animal rapid diversification, it is important to study the ichnofossils which occurred in the earliest Cambrian all over the world.

Ichnofossils are known as the "fossil behavior" of animals and record the animal activities when the trace makers were alive. Not only the morphological changes, but also the behaviors of animals are thought to have diversified in the Cambrian radiation (ex. Jensen, 2003). Therefore, it would be the first step to study ichnofossils, in order to clarify the diversification of the animal activities in the earliest Cambrian.

Comparing ichnofossils of Phanerozoic with those of Neoproterozoic, Jensen

(2003) explained that the archetypical Neoproterozoic ichnofossils are unbranched, irregularly meandering to sinuous burrows and trails typically a few millimeters in widths, probably formed within less than 10 mm to the sediment-water interface. However in the earliest Cambrian, some more complex ichnofossils occurred. For instance, ichnofossils which show branches (like *Treptichnus* and *Phycodes*) or regular sine curves (like *Helminthopsis*) are reported from many Early Cambrian localities in the world. The type of ichnofossils with vertical structure (like *Skolithos* and *Arenicolites*), which mainly occurs in Phanerozoic, first found from the Early Cambrian. Zhu (1997) reported that the vertical tier of some ichnofossils attained 10 cm below the water-sediment interface in the earliest Cambrian.

Based on the transition of ichnofossil assemblages from the latest Neoproterozoic to the earliest Phanerozoic from sections of all over the world, Crimes (1987) firstly proposed three zonations of ichnofossil (Zones I - III). Narbonne et al. (1987) correlated these zones to the section in Newfoundland and named them on the basis of the common characteristic ichnospecies that is restricted to, or first appears in each zone, namely, *Harlaniella podolica* Zone, *Phycodes pedum* Zone and *Rusophycus avalonensis* Zone. In addition to this, MacNaughton and Narbonne (1999) modified these zonations to contain four zones, that is, Simple burrows Zone in Neoproterozoic,

Treptichnus pedum Zone, *Rusophycus avalonensis* Zone and *Cruziana tenella* Zone in Early Cambrian. Besides, Jensen (2003) divided the Neoproterozoic zone into three and described each features as shown in Figure 1.

The rapid increase of animals and diversification of animal behaviors provided heavy bioturbation on the seafloor. This turnover of sedimentary regimes into strongly bioturbated one is called "agronomic revolution" (Seilacher and Pflüger, 1994). They considered that the classic Precambrian sediments covered with microbial mats became siliciclastic and carbonatic sediments, which are comparable to those in the modern seafloor. Microbial mats formed biofilms which covered the surfaces of sand particles, and allowed expansion of habitat spaces of microbes into the deeper part of the sediments. Bottjer et al. (2000) called this sedimentary changes "substrate revolution".

According to Seilacher et al. (2005), the turning point to the agronomic revolution were an onset of many kinds of infaunal animal activities, which marked distinctive traces within the sediments, which are later recorded in the lithologic interfaces. Concerning the differences of bioturbation between the latest Precambrian (Ediacaran) and the Early Cambrian, Droser et al. (1999) studied the Upper Rawnsley Quartzite Formation, which is famous for the Ediacaran biota-bearing formation, and the overlying Early Cambrian Uratanna Formation in Flinders Ranges, south Australia. They illustrated

that bioturbation in the Ediacara Member occurred near the sediment-water interface. On the other hand, bioturbation was mainly found in the sediment (-2 cm) in the earliest Cambrian (Droser et al., 1999). However, while the agronomic revolution occurred in shallow marine environments in the Early Cambrian (Tommotian-Atdabanian), it is uncertain whether or not this evolution occurred in the same timing in the deep sea as in shallow environments (Seilacher et al., 2005). It is considered that the agronomic revolution in the deep sea was delayed and began in Ordovician (Seilacher et al., 2005).

Despite hitherto mentioned studies, some problems remain concernig the earliest Cambrian ichnofossils. First, the number of ichnological studies is still smaller than that of the body fossil studies. Second, previous studies as typified by trace fossil zonation did not always consider animal activities in different environments, because they intended to construct an index of time scale in the earliest Cambrian. Recently, Mangano et al. (2013) comparatively studied ichnofossil assemblages from different depositional facies in the Middle to Upper Cambrian of Jordan, and clarified that the animal activities had already been selectively adapted to particular depositional environments in the Middle Cambrian. However, adaptation patterns of animals in the Early Cambrian are still largely unknown. Third, although previous ichnofossil studies indicated an increase in the number of ichnofossil species, they did not explain what changes took place in certain ichnofossils

themselves. Because occurrence of body fossils is quietly rare in the earliest Cambrian, it would be of crucial significance to examine the relationships between the ichnofossils and their trace makers to clarify the early animal evolution. Fourth, it is yet to be revealed how the outset of intense bioturbation called agronomic revolution developed in Early Cambrian. Finally, it has been a difficult problem to know whether these diversifications were caused by global scale evolution of animal behavior, or by environmental differences in specific regions, because there was no comparative study of the ichnofossils between different regions. Therefore, it is necessary to clarify whether this "apparent" diversification of ichnofossils represents results of biotic evolution, or of simple environmental difference.

To answer these questions, this study focuses on the following points; 1) To survey lower Cambrian strata, and to clarify the causes that induced the diversity changes in each age and depositional facies. 2) To know the change of body sizes of trace maker animals in the Early Cambrian, the maximum widths of *Planolites* were measured. 3) To reveal the developmental processes of the early stage of the agronomic revolution, extent of bioturbation was measured by using the bedding plane bioturbation index (Miller and Smail, 1997) in the Early Cambrian strata. 4) To clarify the geological differences of these size distributions of the ichnofossils and bioturbation indexes, strata of three Early

Cambrian localities, the Chapel Island Formation, Newfoundland, Zhujiaqing Formation, Yunnan and Bayan Gol Formation, Gobi-Altai, were comparatively studied based on the ichnofossils zones (Figure 2). Finally, summarizing the outcomes of above studies, a hypothesis is proposed as to clarify what really caused the diversification of ichnofossils seen in the earliest Cambrian.

Period	Epoch	Zone name	Characteristics or first appearance of ichnotaxa	General characteristics
Cambrian	Terreneuvian	*Cruziana tenella*	*Cruziana Plagiogmus arcuatus*	Arthropod furrowing traces Large back-filled burrows
		Rusophycus avalonensis	*Taphrhelminthopsis circularis Rusophycus avalonensis*	Arthropod resting traces Large bilobed furrowing traces
		Treptichnus pedum	*Treptichnus pedum Gyrolithes Bergaueria*	Diverse branching burrow systems and anemone resting traces
Ediacaran			*Treptichnus* isp. *"Curvolithus"* isp.	First simple burrow systems First traces with three-lobed lower surface

Figure 1. General ichnofossils zones in the earliest Cambrian and characteristics of the zones (modified after Jensen, 2003). Red line shows Pc-C boundary. In this study, *Treptichnus pedum* and *Rusophycus avalonensis* zones were surveyed.

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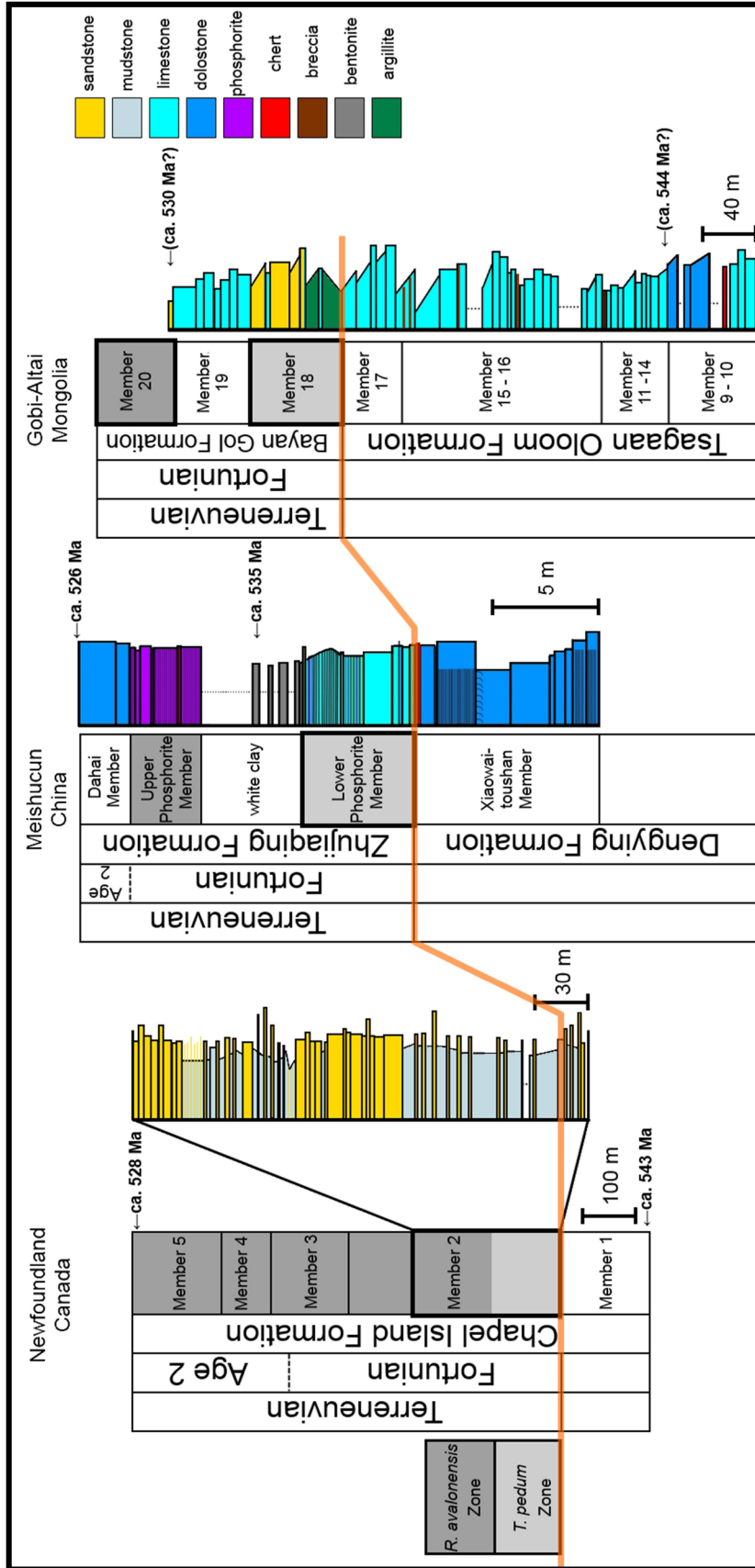
Figure 2. A Correlation of the lower Cambrian sequences in the three studying sections (Fortune Head, Newfoundland; Meishucun, Yunnan; Bayan Gol; Gobi-Altai) based on the ichnofossil zones. Orange line shows the Pc-C boundary defined by the first occurrence of *T. pedum*. Right gray members show *T. pedum* zones. Dark gray members show *R. avalonensis* zones. The members in bold flames surveyed in this study. Geological ages of the Chapel Island Formation as ca. 543 Ma is from Landing and MacGabhann (2010) and Landing and Kröger (2012); ca. 528 Ma from Schoene et al., (2006) and Landing and Kröger (2012). Geological ages of the Zhujiaqing Formation as ca. 535 Ma is from Sawaki et al., (2008) and Okada et al., (2013); ca. 526 Ma from Okada et al., (2013). Geological ages of the Tsagaan Oloom and the Bayan Gol formations as ca. 544 Ma and ca. 530 Ma are from Brasier et al., (1996b).

2. Geological settings

2.a. Chapel Island Formation, Newfoundland, Canada

The Lower Cambrian Chapel Island Formation is exposed along the coast of Fortune Head, western Burin Peninsula in Newfoundland, Canada (Figure 3). The Chapel Island Formation was first described by Widmer (1950, MS) for the sequence of siltstone and silty shale that lie conformably on the Doten Cove Formation (Hutchinson, 1962). The type section of the Chapel Island Formation is on Chapel Island in Belle Bay (Hutchinson, 1962). In 1994, the International Commission on Stratigraphy identified the section of this formation exposed in Fortune Head as the GSSP of the Precambrian-Cambrian boundary (Brasier et al., 1994).

The Chapel Island Formation is divided into five members based on the lithofacies (Bengtson and Fletcher, 1983). The uppermost part of the Member 1 and the lower to the middle part of the Member 2 were surveyed in this study. The Member 1 is a Precambrian sequence and consists mainly of gray sandstone and siltstone. Total thickness of the Member 1 is estimated about 180 m in the Fortune Head section (Myrow and hiscott, 1993).

Overlying Member 2 is almost a Cambrian sequence. The Pc-C boundary is

located 2.4 m above the base of the Member 2 (Figure 4) (Brasier et al., 1994). The beginning of the Cambrian is identified by the occurrence of the ichnofossil *Treptichnus pedum* (Figure 32d), although this ichnospecies and a different species of *Treptichnus* have also been found below the boundary (Gehling et al., 2001). The basal part of the Member 2 (15-32 m in Figure 5) is mainly composed of green siltstone with characteristic depositional structures of various sizes (gutter cast; Figure 6a) and rare thin sandstone beds. In addition to various kinds of ichnofossils, wrinkle structures, which are thought to be evidence of microbial mats (Figure 6c) (Hagadorn and Bottjer, 1999; Mata and Bottjer, 2009), were also observed on some upper bedding surfaces. These gutter cast decreases with distance from the base (36-108 m in Figure 5), and simple green siltstone beds become dominant. At about 108 m from the base of the Pc-C boundary, the beds suddenly change to reddish sandstone rocks from greenish siltstone (108-152 m in Figure 5). Parallel or cross laminations are observed in some beds. Besides, polygonal cracks frequently develop on the bedding surfaces (Figure 6b). Although the lower to the upper part of this sand layer (108-140 m in Figure 5) mainly consists of reddish sandstone, the uppermost part (140-152 m in Figure 5) is composed of green sandstone and partly siltstone beds. Ichnofossils frequently occur on the greenish beds, whereas it is rare on the reddish beds. These ichnofossils contain multiple ichnogenera that are not observed

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in the underlying beds. At about 152 m from the Pc-C boundary, the beds consist of siltstone and thicker sandstone rocks than that of the lower horizons. The rock color changes to partly red, but mainly remains green-gray (0-124 m in Figure 7). Besides, some sandstone beds show hummocky cross stratification (HCS). Ichnofossils are abundant on the lower bedding surfaces. These ichnofossils include some ichnogenera that are not seen in the lower horizons. In this study, columnar section was made from the base to middle part of the Member 2 (about 260 m in thickness). According to the previous studies, while abundant calcareous nodules were included in siltstone beds near 280 m from the base of the Member 2, lithological character is not changed to the boundary of the Member 2 and the overlying Member 3 (Myrow and Hiscott, 1993; Droser et al., 2002a). Total thichkness of the Member 2 is about 420 m (Myrow and Hiscott, 1993).

Myrow (1992) divided the Member 2 into 4 facies; gutter cast facies, siltstone dominated facies, shoreline facies and sandstone dominated facies (Figure 8). Gutter cast (GC) facies means the basal part of the Member 2 (15-32 m in Figure 5) where is observed abundant of gutter casts. Gutter casts are a kind of erosional structure which is interpreted to be formed by gravity current erosion (Myrow, 1992). Ichnofossils occur on some bottom surfaces of the gutter casts and also on the upper bedding surfaces of sandstone beds.

Siltstone dominated facies means lower part of the Member 2 (36-108 m in Figure 5). Although most of the beds consist of siltstone, some beds are composed of very fine to fine sandstone and alternating beds of sandstone and mudstone. Some sandstone beds are horizontally discontinuous. The bed thickness is generally greater than that of the GC facies. Ichnofossils occur mainly on the upper bedding surface of sandstone beds. Some bedding surfaces have wrinkle structures, as observed in the GC facies.

Shoreline deposits facies (Sh facies) is 108-152 m in Figure 5. This facies is characterized by red sandstone beds with polygonal cracks and green sandstone and siltstone beds. Although lower to upper part of the Sh facies mainly consists of reddish sandstone, the uppermost part of the Sh facies is composed of green sandstone and partly siltstone beds. Ichnofossils frequently occur on the greenish beds, whereas it is rare on the reddish beds.

Sandstone dominated (SS-D) facies constructs the uppermost part of the Member 2 in this study (0-124 m in Figure 7). The thickness of a sandstone bed becomes thicker than that of the Sh facies, and the rock color changes to partly red, but mainly remains green-gray. Besides, some sandstone beds show hummocky cross stratification (HCS).

According to the facies reconstruction by Myrow (1992), the Sh facies was a shoreline deposit from a tidal-affected peritidal environment, evidenced by the bimodal-

bipolar paleo-current and the presence of mud-chip conglomerates, desiccation cracks, and syneresis cracks. The shaly facies, which is partly shown in the Sh facies, was interpreted as the middle to upper part of the tidal flat. The GC facies was deposited in a shallow subtidal area that was a zone of throughput with high-velocity, sediment-laden flows eroding deep narrow scours (gutter casts). As storm-generated flows moved into deeper water, the casts started to decelerate, resulting in less significant erosion of the sea floor and increased deposition, to form more continuous and regular beds (SiS-D facies). At some distance from the shore, the sandstone bed attains its maximum thickness (SS-D facies). The depositional environment of the SS-D facies could be from the lower shoreface to the upper inner shelf because of the frequent appearances of HCS. To summarize these observations and the facies interpretations by Myrow (1992), Member 2 of the Chapel Island Formation were generally deposited in a shallow marine environment that was above the storm wave base (Figure 8).

Biostratigraphic zonations of the Chapel Island Formation are based on the occurrences of ichnofossils; *Treptichnus pedum* and *Rusophycus avalonensis* zones. The *T. pedum* Zone, which is thought to be the basal part of the Early Cambrian, attains a thickness of about 130 m from the Pc-C boundary to the boundary with the overlying *R. avalonensis* Zone (Figure 5) (Narbonne et al., 1987, Droser et al., 2002). The overlying

R. avalonensis Zone starts about 130 m from the Pc-C boundary (the basal part of SS-D

facies) to the uppermost part of Member 5 based on the first occurrence of *R. avalonensis*

(Narbonne et al., 1987). In this study, ichnological survey was done about 125 m from

the base of *R. avalonensis* Zone (Figure 7). The precise descriptions of the occurrences

of ichnofossils in the Chapel Island Formation are described in the Chapter 3.
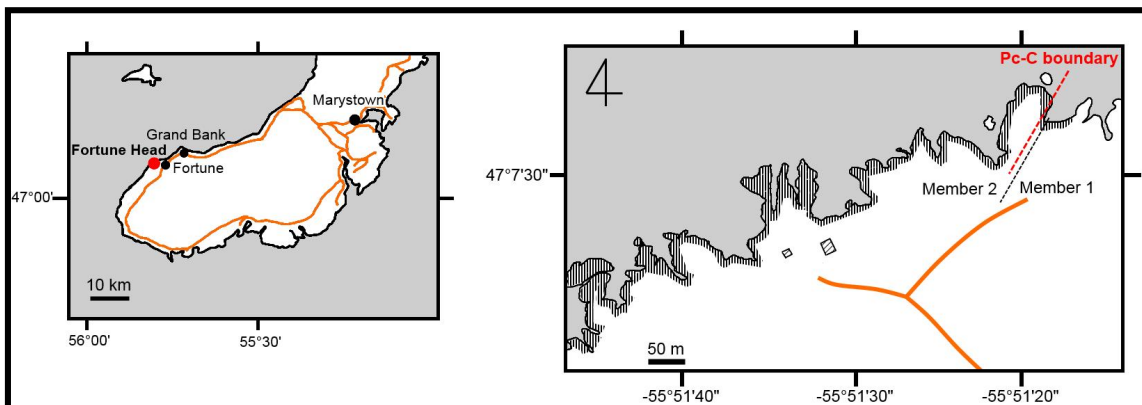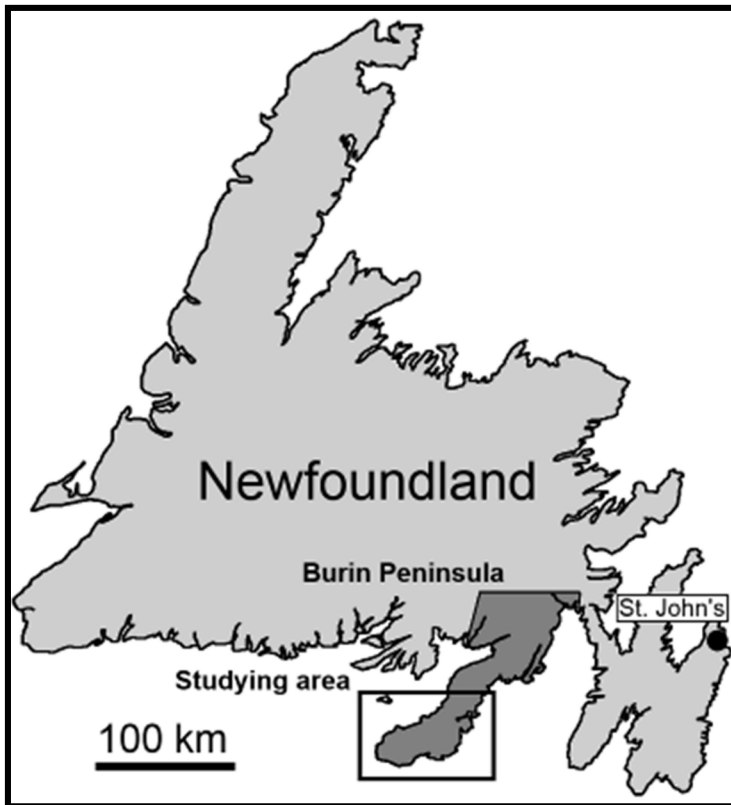
Figure 3. Location of Fortune Head in Burin peninsula, Newfoundland. Orange lines show main roads. The Chapel Island Formation outcrops along the coast (vertical lines).
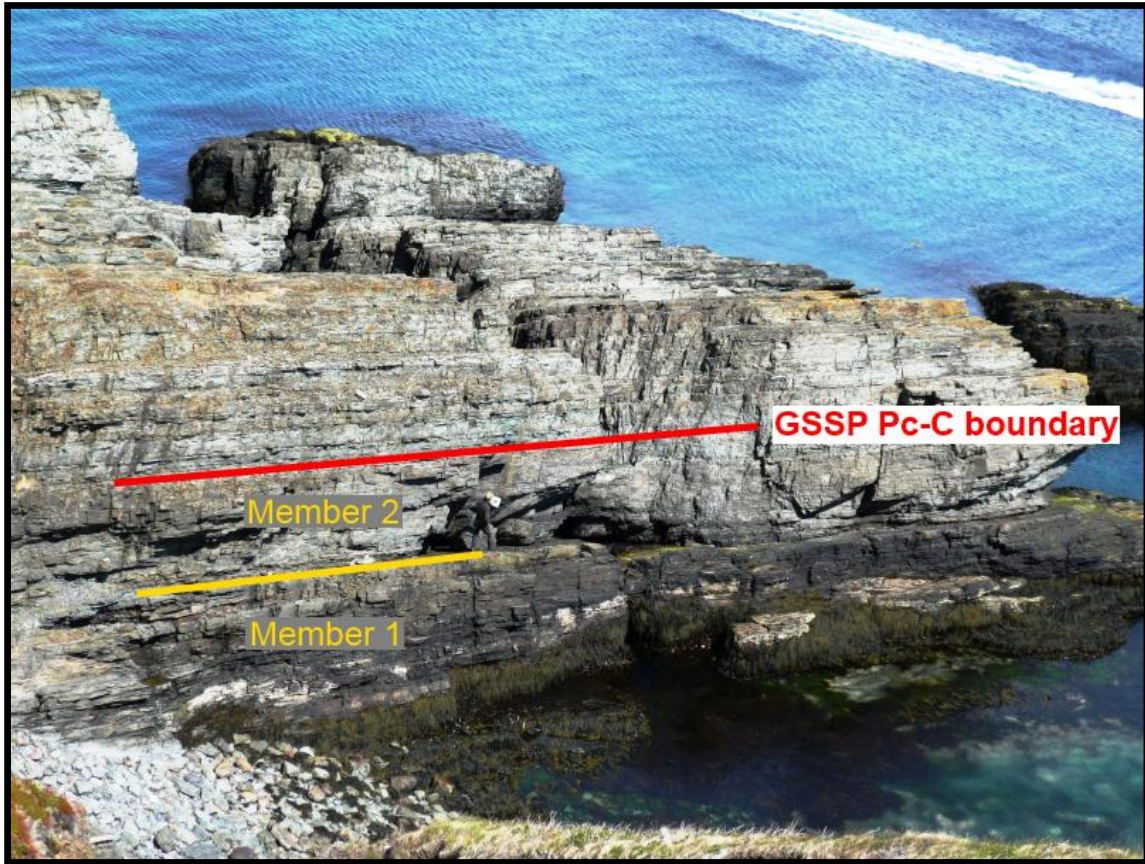
Figure 4. GSSP Pc-C boundary of the Chapel Island Formation in Fortune Head. The Pc-

C boundary is located 2.4 m above the boundary of members 1 and 2.
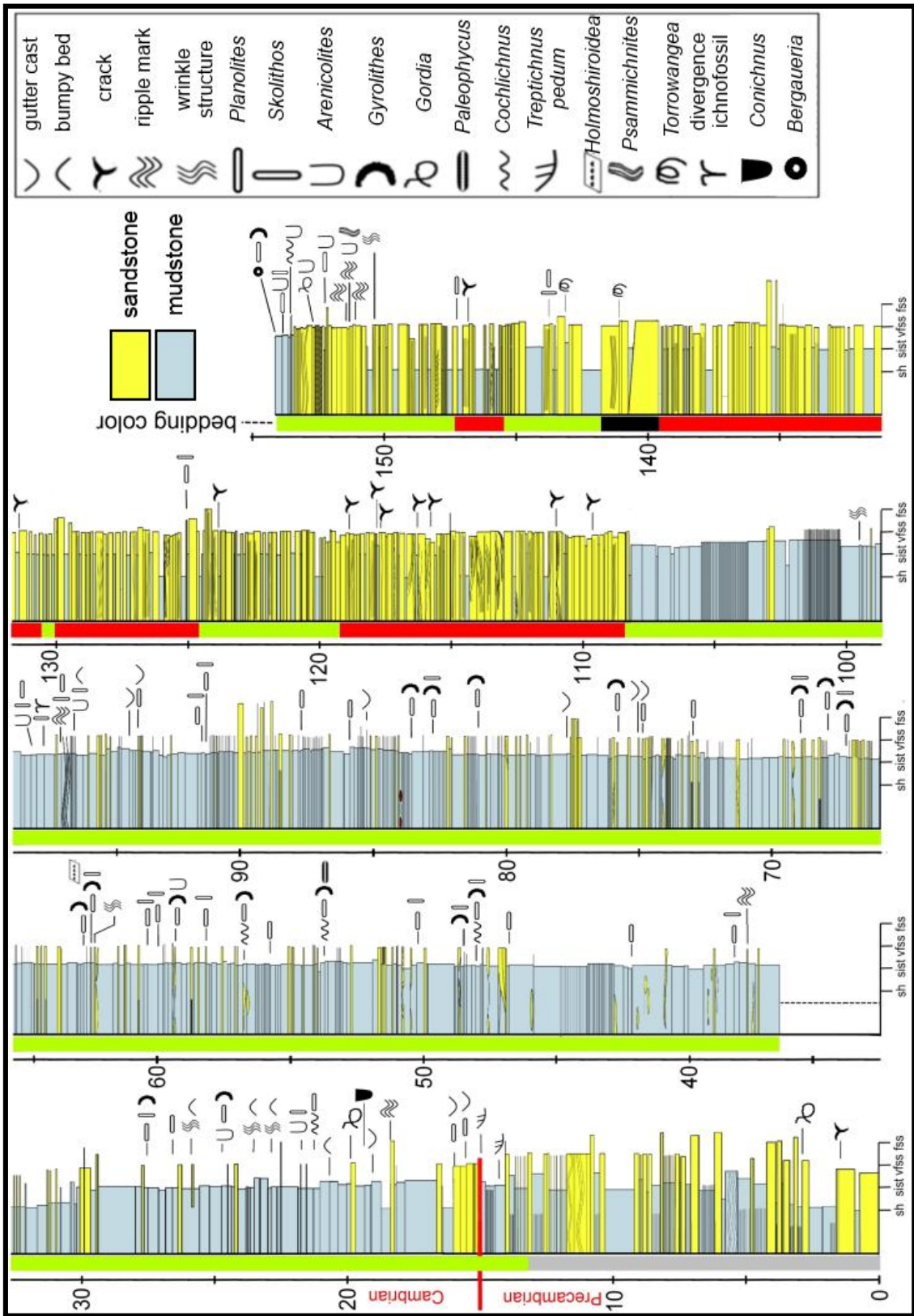
Figure 5. Columnar section of the *T. pedum* Zone in the Chapel Island Formation. Yellow beds show sandstone beds and blue ones show mudstone beds. Lateral thickness of beds show grain sizes (sh; shale, sist; siltstone, vfss; very fine sandstone and fss; fine sandstone).
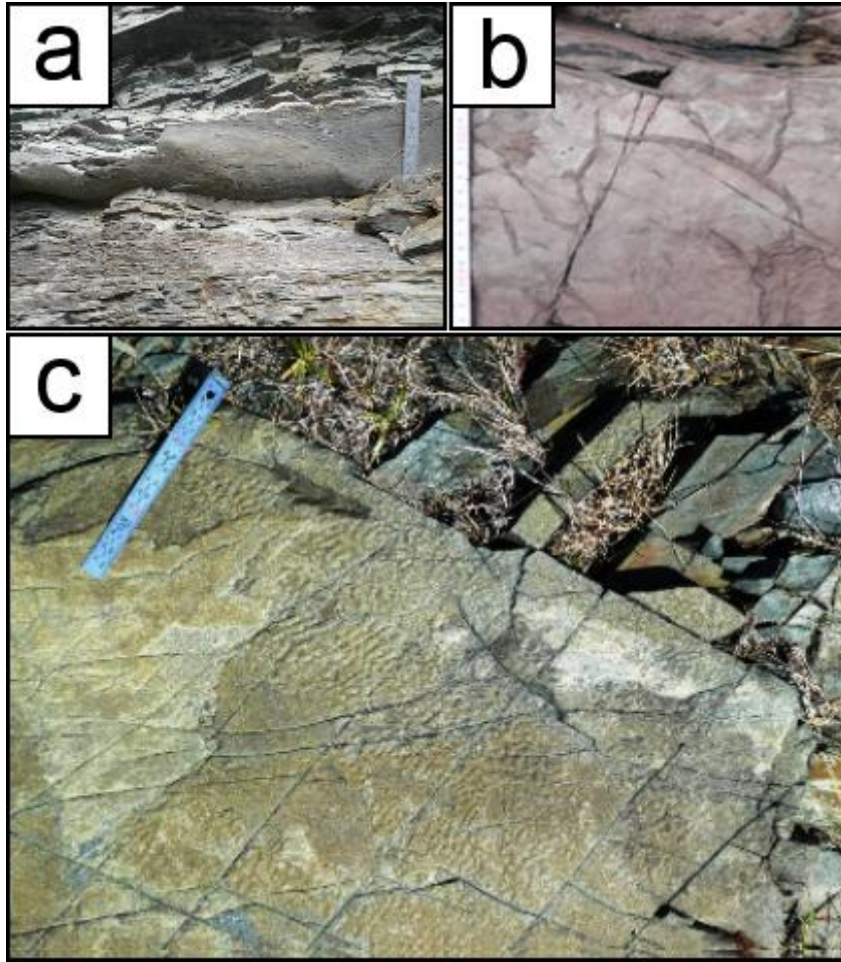
Figure 6. Characteristic structures in the Chapel Island Formation. a) Gutter cast in siltstone of GC facies. b) Mud cracks on red sandstone bedding surface of Sh facies. c) Microbial mat structure (Wrinkle structure) on the sandstone bedding plane.

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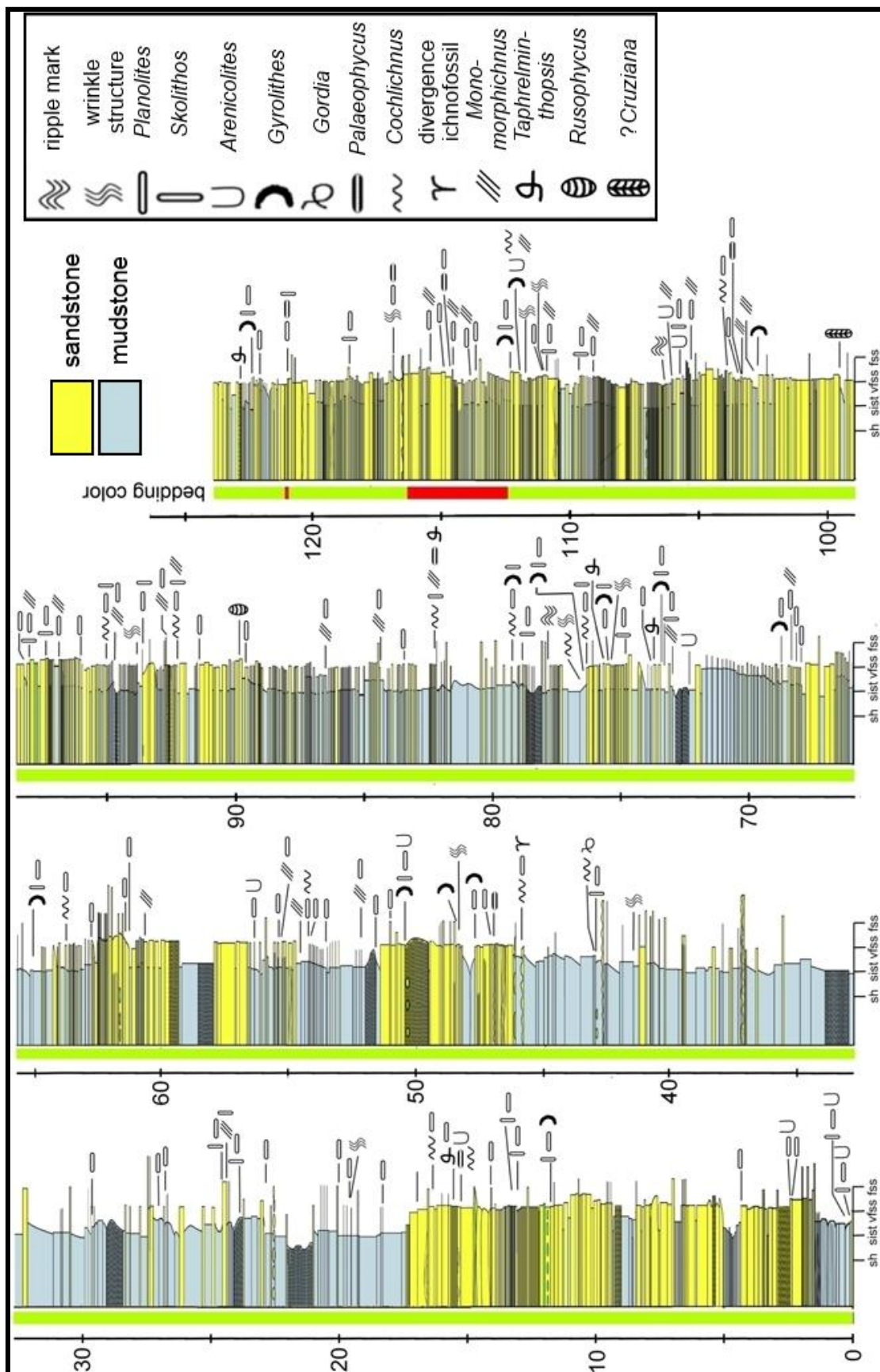
Figure 7. Columnar section of the *R. avalonensis* Zone in the Chapel Island Formation. Yellow beds show sandstone beds and blue ones show mudstone beds. Lateral thickness of beds show grain sizes (sh; shale, sist; siltstone, vfss; very fine sandstone and fss; fine sandstone).
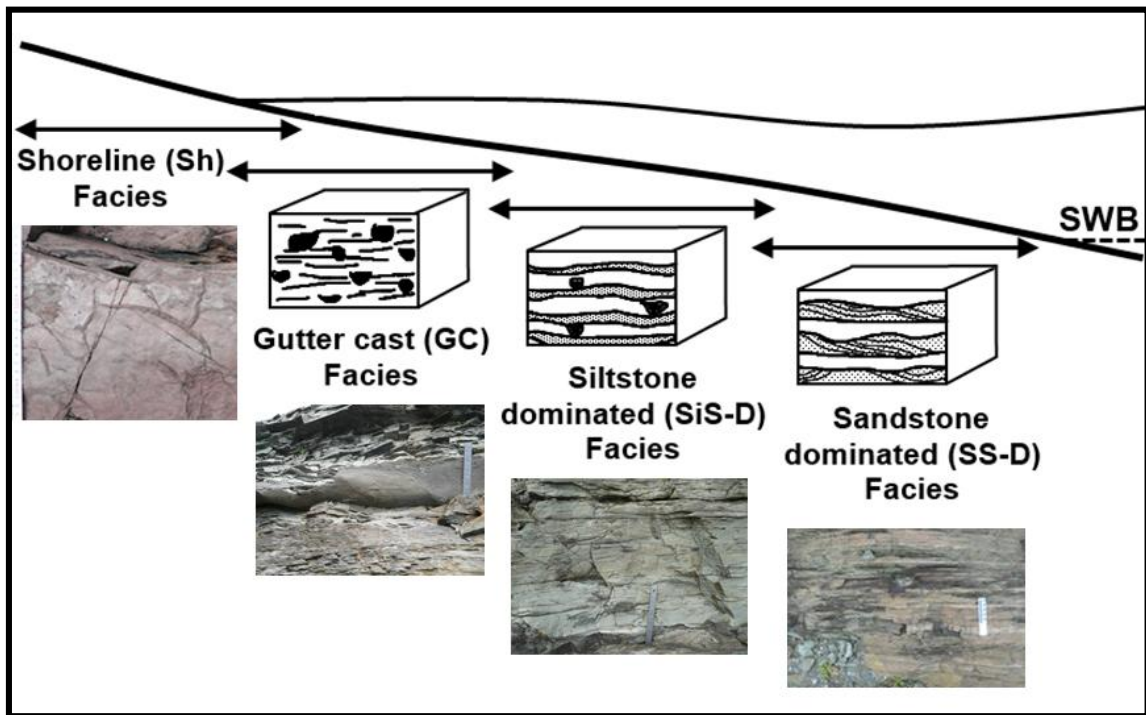
Figure 8. Facies model of the Member 2 in the Chapel Island Formation (Modified after

Myrow, 1992) and photos of outcrops in each facies.

2.b. Zhujiaqing Formation, Yunnan, China

The Lower Cambrian Zhujiaqing Formation is exposed in Kunyang phosphate mine in Jinning county, Kunming prefecture, Yunnan province, China (Figure 9). The Zhujiaqing Formation was first minutely described by Luo et al. (1982; 1984) as a Sinian (Neoproterozoic) -Cambrian boundary section in China. The type section of Zhujiaqing Formation is located about 30 km to the southwest of Kunming city (Figure 9). The columnar section is shown in Figure 10. Another quarry, which is located on the north side of the type section, was also studied.

The basal part of the type section is Xiaowaitoushan Member which is the uppermost part of Dengying Formation (Figure 10). The Xiaowaitoushan Member mainly consists of gray massive dolostone with chert bands. As the characteristic structure, parallel cross lamina is observed on one bed. Thickness in the type section is about 8.9 m. The first occurrence of small shelly fossils, *Anabarites trisulcatus*, has been reported in this member (Luo et al., 1984; Xing and Luo, 1984; Qian and Bengtson 1989; Cowie and Brasier, 1989; Xing et al., 1984). The first appearance datum (FAD) of *A. trisulcatus* is regarded as the base of the Cambrian in China. Therefore, the Xiaowaitoushan Member is sometimes included in the Zhujiaqing Formation as the earliest Cambrian (Xing et al., 1984; Li, 1986). In this study, however, due to the absence of *T. pedum*, the

Xiaowaitoushan Member is included in the latest Ediacaran Dengying Formation (Chen et al., 1996; Zhu, 1997, Weber et al., 2007).

The Early Cambrian Zhujiaqing Formation is composed of three members (Figure 10) (Chen et al., 1996; Zhu, 1997). Lower Phosphorite Member consists of the base of the Zhujiaqing Formation (Figure 10). The Lower Phosphorite Member mainly consists of parallel bedded gray limestone and limestone-phosphorite interbeds. Total thickness varies with localities; but it is about 4.3 m in thickness in the type section. The Pc-C boundary is defined as the boundary between the dolostone bed which contains the characteristic thin black siliceous beds of the underlying Xiaowaitoushan Member and the limestone bed of the Lower Phosphorite Member (Figure 11) (Chen et al., 1996; Zhu, 1997).

At 4.3 m above the Pc-C boundary, limestone beds turn to white bentonite beds, which are called White Clay Member (Figure 10). Although the bedding exposures are discontinuous, the total thickness is estimated as about 1.7 m. The White Clay Member includes a tuff layer, and numerical age was estimated as about 535 Ma from U-Pb isotopic data (Sawaki et al., 2008; Zhu et al., 2009).

The gray bedded phosphorite-limestone interbed and massive phosphate beds appear with 2 m gaps above the top of the white bentonite layer (Figure 10). These

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phosphatic beds are named Upper Phosphorite Member. The basal part of the Upper

Phosphorite Member consists of the phosphorite-limestone interbeds. The upper part is

composed of massive phosphate beds. Unlike the Lower Phosphorite Member, phosphatic

beds rather than limestone beds are developed. Total thickness is estimated to be about

3.7 m. These three members (Lower Phosphorite, White Clay, Upper Phosphorite

members) are sometime collectively designated as Zhongyicun Member (Xing et al.,

1983; 1984).

Above the phosphatic beds of the Upper Phosphorite Member is a thick massive

dolomite beds (2.4 m; Figure 10). This dolomite layer is named Dahai Member, which is

defined as the uppermost member of the Zhujiaqing Formation. The dolomite has a

coarser-grained texture toward the top of the member. Ichnofossils were not found from

this member, as in the previous report (Zhu, 1997).

Ichnofossils are rarely seen in Xiaowaitoushan Member. Only *Planolites* isp.

occurred on one bedding plane in the northern quarry section. The absence of ichnofossils

can be attributed to the lithofacies; in general, ichnofossil is mainly preserved in

siliciclastic rocks and is poorly preserved in carbonate rocks (Stanley, 1976; Zhu, 1997).

Some kind of trace fossils, however, i.e. *Planolites* isp., *Torrowangea* isp., *Arenicolites*

isp. and *Bergaueria* isp. were previously reported from this member (Zhu, 1997).

Ichnofossils were also not observed from the basal part of Lower Phosphorite Member in the type section because of the poor exposure of bedding planes. A few ichnofossils, however, occurred from the upper part, including the most abundant *Planolites* isp. and bilobed ichnofossil (?*Sellaulichnus* isp.). In the northern quarry, *T. pedum* also occurred at the upper part of Lower Phosphorite Member. A previous study reported the first occurrence of many other ichnofossils, including *Palaeophycus* isp., *Neonereites* isp., *Gordia* isp. and ?*Asteriacites* isp. from this part (Zhu, 1997). These occurrences of ichnofossils suggest that the Lower Phosphorite Member is correlated to the lower Member 2 of the Chapel Island Formation, that is, the *T. pedum* Zone (Zhu, 1997). In the White Clay Member, while abundant small shelly fossils occur on the bedding planes, ichnofossils are not observed. Ichnofossils were also rare on the bedding planes due to limited exposure in Upper Phosphorite Member. Numerous ichnofossil *Rusophycus* isp (Figure 34e), however, were found from the surface of a float. Besides, *Didymaulichnus miettensis* (Figure 32b) occurred from this member in the northern quarry. Zhu (1997) reported many kinds of ichnofossils from this member. He described 6 new specimens of ichnofossils (*Chondrites* isp., *Didymaulichnus* isp., the other kind of *Bergaueria* isp., *Monomorphichnus* isp., *Rusophycus* isp. and an unnamed ichnofossil) in addition to the existing ichnofossils. Zhu (1997) correlated these ichnofossil assemblages to the lower

part of the *R. avalonensis* Zone. Numerical age was estimated as about 535 Ma in white clay layer between Lower Phosphorite Member and Upper Phosphorite Member. Thus, it is possible that this age indicate the boundary of the *T. pedum* and *R. avalonensis* zones.
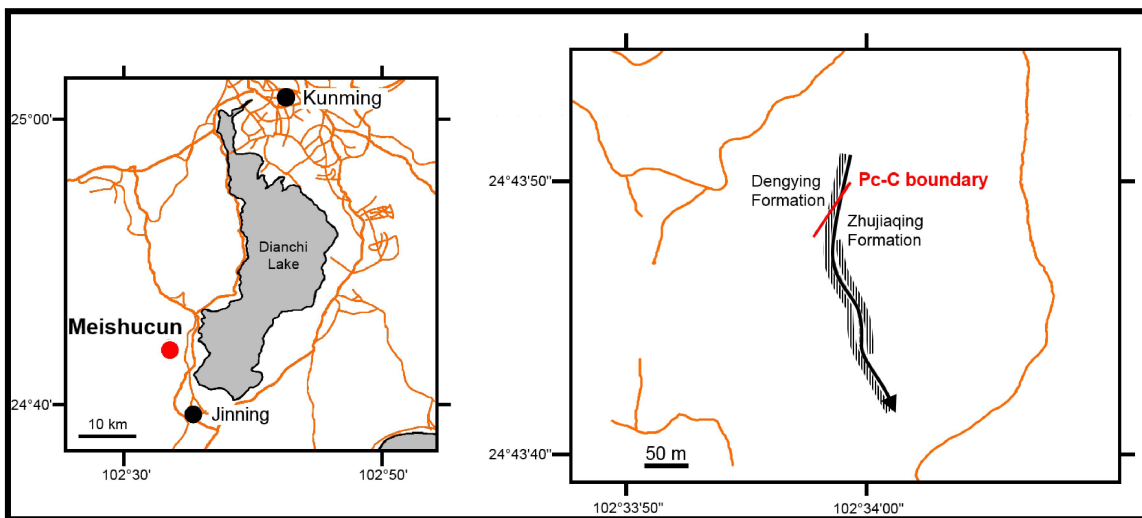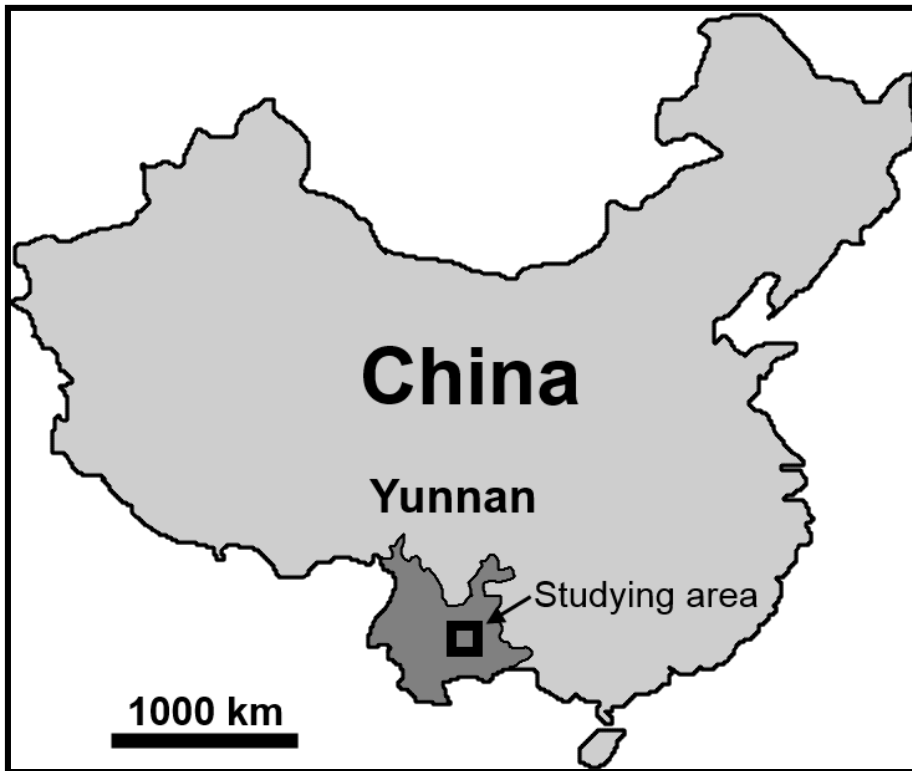
Figure 9. Location maps of the studying area of Meishucun in Yunnan province. Orange

lines show main roads around studying section. Vertical lines show outcrops of

Precambrian Dengying and Cambrian Zhujiaqing formations.
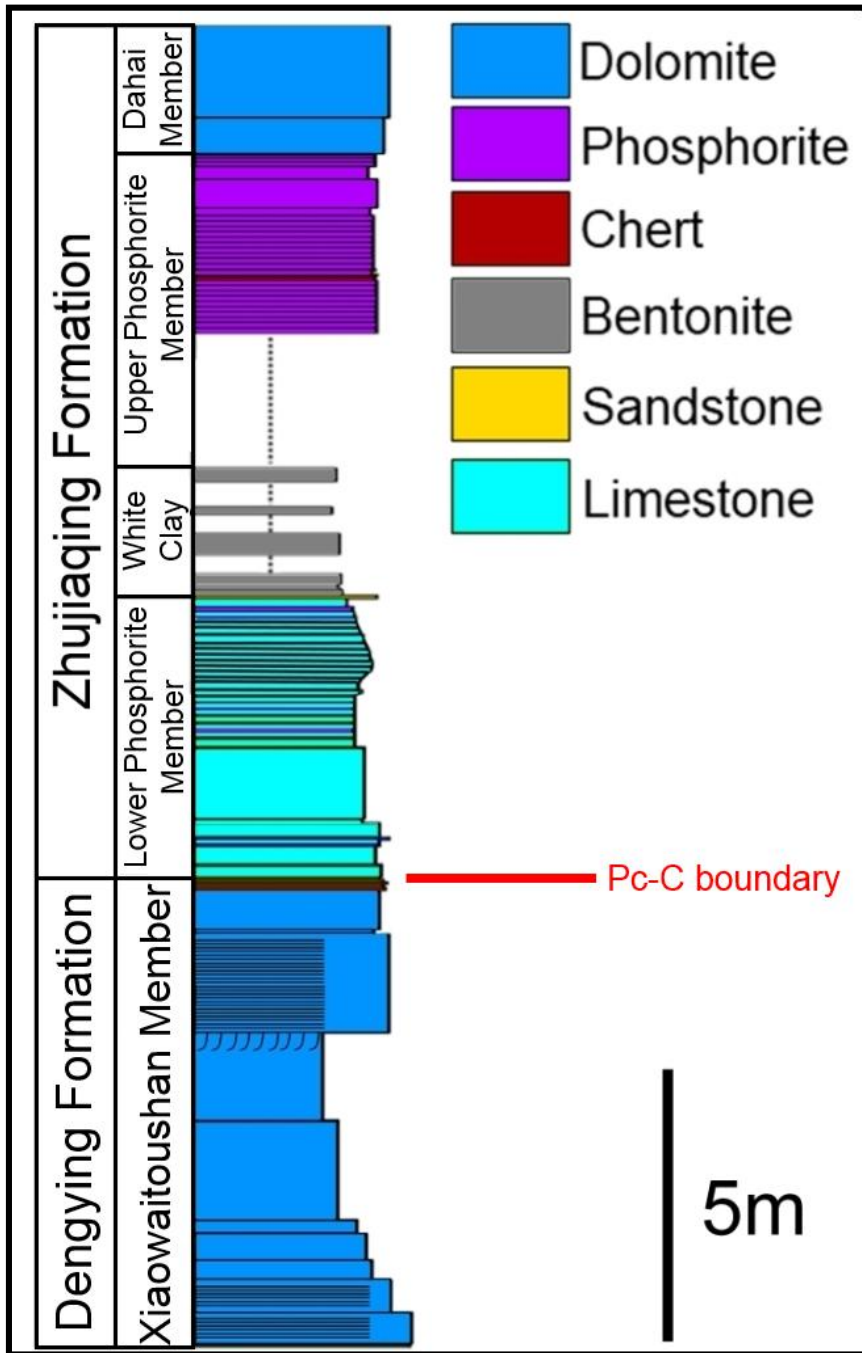
Figure 10. Columnar section of the Pc-C boundary type section in Meishucun, Yunnan. Lateral width shows the general surface morphology of the outcrops, not representing the grain size of the sediments. Pc-C boundary defines the boundary of Xiaowaitoushan and Lower Phosphorite members.
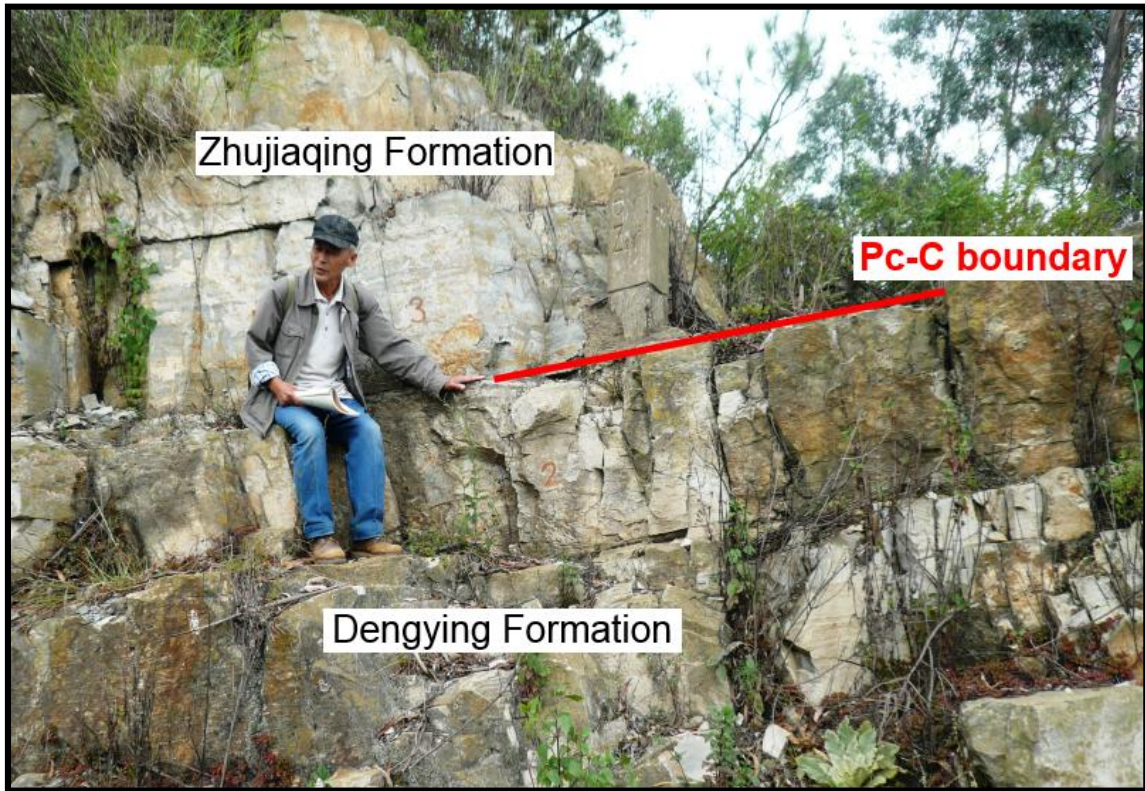
Figure 11. Outcrop of the Pc-C boundary of the type section in Meishucun. Boundary is located between the dolostone of Dengying Formation and the limestone of Zhujiaqing Formation.

2.c. Bayan Gol Formation, Gobi-Altai, Mongolia

Neoproterozoic and Cambrian rocks in western Mongolia are exposed in the Zavkhan Basin of the Gobi-Altai area (Figure 12). It is considered that the Zavkhan Basin was originally a part of the earlier Zavkhan Rift (formed during 850-650 Ma) as a result of the backup of the Baydrik-Tarbagatay microcontinent, and was formed on the continental crust as a part of a vast marginal marine back-arc basin, which developed during Neoproterozoic accretion of the Zavkhan Rift and the adjacent fragments of the Baydrik-Tarbagatay microcontinent. (Khomentovsky and Gibsher, 1996; Lindsay et al., 1996). The stratigraphical study of the Precambrian-Cambrian rocks of Zavkhan Basin was firstly described by Bezzubtsev (1963). He divided the Neoproterozoic-Cambrian geological sequences into three formations based on the lithofacies: Neoproterozoic Dzabkhan Formation, which consists of volcanic rocks, Neoproterozoic Tsagaan Oloom Formation of carbonate rocks and Early Cambrian Bayan Gol Formation of siliclastic and carbonate rocks. Total thickness of the Tsagaan Oloom Formation is estimated to be about 1000-1500 m (Kruse et al., 1996), whereas the thickness of the Bayan Gol Formation is approximately 940 m (Kruse et al., 1996). Although some minor changes have been done to the placement of formation boundaries, the basic stratigraphic scheme has been unchanged (Khomentovski and Gibsher, 1996). The Precambrian-Cambrian boundary

was not precisely defined (Brasier et al., 1996a). However, according to the first appearance of the *T. pedum* record (Goldring and Jensen, 1996), the boundary of the Bayan Gol and the Tsagaan Oloom formations is regarded as the Pc-C boundary.

In this study, Bayan Gol section was surveyed with focusing on the lithology, sedimentary structures and occurrences of ichnofossils. The columnar section of the Tsagaan Oloom and Bayan Gol formations was made. The Bayan Gol section outcrops approximately 30 km north of Altai city (Figure 12). Based on the lithological characters, sequence was locally divided into 25 members from the basement of the Tsagaan Oloom Formation to the uppermost part of the Bayan Gol Formation (Khomentovsky and Gibsher, 1996; Lindsay et al., 1996). Khomentovsky and Gibsher (1996) surveyed two separate blocks (northern and southern blocks) along the Bayan Gol valley. Because of a number of thrust faults in the northern block, the southern block was selected as the standard of the Bayan Gol section in this study. The lowermost diamictite of the Tsagaan Oloom Formation, which can be observed in other sections such as Tsagaan Oloom section, is not exposed in the Bayan Gol section (Lindsay et al., 1996). Above the volcanic units of Dzabkhan Formation, thick carbonatic beds (Members 3-10) occur with intercalations of limited siliciclastic beds (Members 1 and 2) (Lindsay et al., 1996). Because the purpose of this study is to clarify the development of biological activities in

the earliest Cambrian, columnar section was made for the interval above the top of Member 9 in the Tsagaan Oloom Formation where a number of biological signals can be seen (Figure 13).

Characteristic pink bedded stromatolitic limestones occur on the gray phosphatic limestone of the top of the Member 9 (Figure 13). Stromatolites form a thick (7 m) biostrome on the both sides of the valley. The top of the stromatolitic carbonate provides an indication of the boundary of members 9 and 10 in the Bayan Gol section (Khomentovsky and Gibsher, 1996). With an unexposed gap of 15 m thickness, the bedded phosphatic limestone and mudstone member (Member 10) overlies (34-70 m in Figure 13). Total thickness is about 35 m. Thickness of a single limestone bed is about 5-20 cm. It is noted that the flat pebble conglomerate, which is a storm deposits made of flat pebbles presumably derived from consolidate microbial mats, is observed in the upper part of the phosphatic member.

Above the phosphatic member, the amount of phosphatic beds decreases and they change to pure limestone beds (70 m- in Figure 13). Bedding thickness becomes thinner (1-3 cm) than in the lower Member. This limestone beds are the basement of Member 11. At about 82 m from the basement, intraformational foldings in large scales occur. Besides, around the horizon of 115 m, two flat pebble conglomerates are

intercalated. According to Khomentovsky and Gibsher (1996), these breccia beds are the basement of Member 15. Thus, members 11-14 are included in this interval with intraformational folding and flat pebble conglomerates (70-115 m in Figure 13). Although the boundaries from members 11 to 14 are ambiguous, total thickness of these 4 members is about 44 m.

Lithofacies is not so significantly changed from the Member 15 to 16 (115-275 m in Figure 13). Most of the beds consist of bedded limestone with 1-5 cm thickness, partly containing breccia beds. In the lower part of these members, intraformational foldings are common. These foldings disappear toward the middle to the upper part of this member. Instead, bedded limestone with calcareous nodules and massive limestone beds overlie. As observed in Member 10, flat pebble conglomerate beds are also intercalated in some horizons. In the upper part of the Member 16, oncolitic limestone beds with numerous millimeter scale oncolites overlie with clear HCS are observed. It is notable that a simple meandering ichnofossil occurred on the bedding surface of a float from the Member 15.

The Member 17 (275-323 m in Figure 13) is the uppermost Tsagaan Oloom Formation in the Bayan Gol section, and is in thrust fault contact with the Member 16. The Member 17 is composed mainly of bedded limestone with mudstone beds and a

minor amount of breccias. Some limestone beds are oncolitic. In this Member, storomatolite and HCS are also observed. This Member 17 is the uppermost Member of the Neoproterozoic Tsagaan Oloom Formation.

Above the Member 17, argillite mudstone of the Member 18 overlies (at 323 m above the base in Figure 13). This Member 18 is the basal part of the Early Cambrian Bayan Gol Formation. Because exposure of the beds is poor in this section, Pc-C boundary can not be observed (Figure 14). A characteristic stromatolite bed (in thickness) appears overlying sandstone layers. Sandstones of this Member are almost bedded. At m from the base of the Unit 18, massive limestone layer is observed. Total thickness of Member 18 is about 70 m in this section. Cambrian type ichnofossils firstly occurred from the horizon of sandstone-siltstone interbed above the argillites.

The Member 19 (394-453 m in Figure 13) consists of massive limestone beds. Ichnofossil was not found from this member. Overlying Member 20 (453 m- in Figure 13) is composed of siltstone, sandstone and limestone beds (Lindsay et al., 1996). Total thickness of Member 20 is 75 m in this section (Khomentovsky and Gibsher, 1996). Exposure of the siliciclastic rock layers of the lower part of the Member 20 is poor. Thus, only basal part of Member 20 is described in the columnar section. A number of ichnofossils were observed on the surface of floats.

Depositional environment of the Tsagaan Oloom and the Bayan Gol formations are estimated to be highly shallow marine. For example, a number of flat pebble conglomerate beds observed in the Members 10, 15 and 16. Because these flat pebble conglomerates were deposited after storm events, these members deposited at least above the storm wave base. In the Members 16 and 17, clear HCS can be observed in some beds. Thus, the uppermost part of the Tsagaan Oloom Formation was probably deposited in lower outer beach.

Ichnofossils were mainly observed in the Member 18 and 20. In the Member 18, Treptichnid ichnofossils and *Planolites* isp (Figure 33f) occurred. A storomatolitic limestone bed is intercalated in siliciclastic beds. The silisiclastic beds continue with intercalations of some limestone layers. Some kind of ichnofossils occurred from the middle to the upper part of the Member 18; ?*Psammichnites* isp. (Figure 34c), *Didymaulichnus miettensis* (Figure 32b), ?*Curvolithus* isp. (Figure 32a). In the previous study, *Helminthoida* cf. *miocenica* also appeared in this Member (Goldring and Jensen, 1996), recording the lower occurrence of this ichnotaxon. The occurrence of ichnofossils indicated that the Member 18 belongs to the *T. pedum* Zone. On the other hand, a variety of ichnofossils are observed in the Member 20; *Cochlichnus* isp. (Figure 31c), *Helminthoida* isp. (Figure 32e), *Helminthopsis* isp. (Figure 32f), *Planolites* isp. (Figure

33f), ?*Psammichnites* isp. (Figure 34c), *T. pedum* (Figure 35d) and *Rusophycus* cf.

avalonensis (Figure 34d). In addition to the above ichnotaxa, *Hormosiroidea* isp.,

Monomorphicnus isp., *Palaeophycus tubularis*, *Treptichnus* ?*bifurcus* and *T.* cf. *triplex*

were also reported from Member 20 in the previous study (Goldring and Jensen, 1996).

These occurrences of ichnofossils show that the the Member 20 is included in the *R.*

avalonensis Zone.
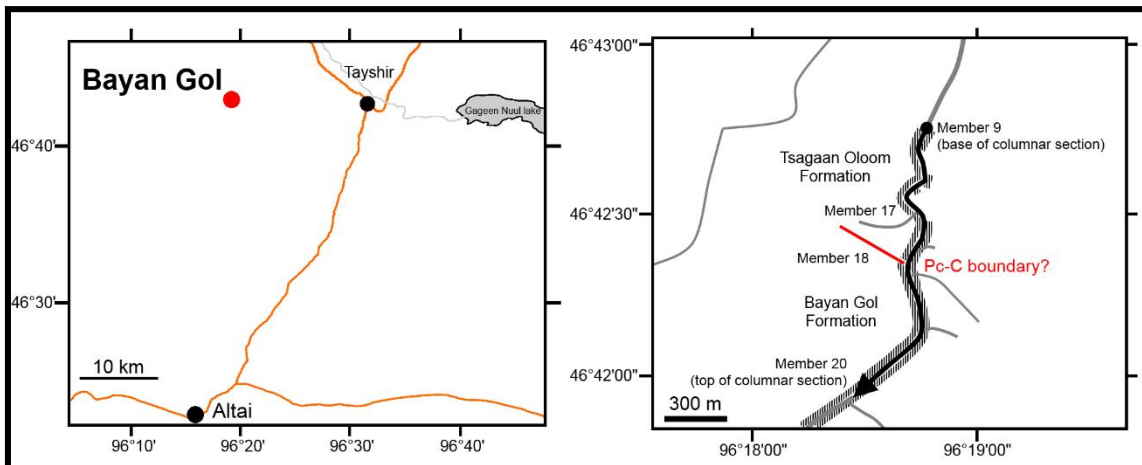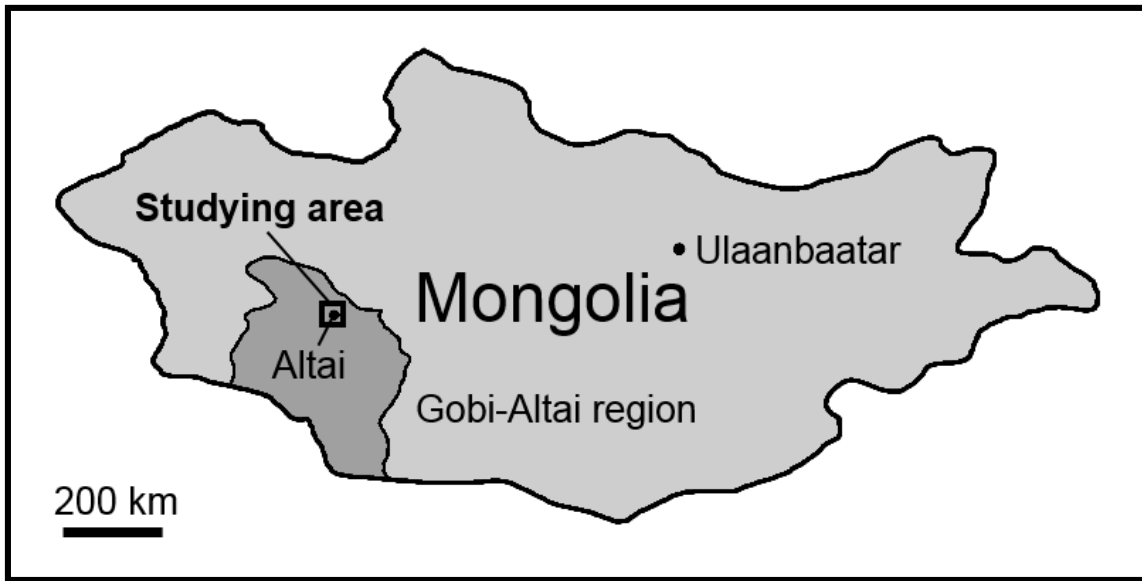
Figure 12. Location maps of the studying area of the Bayan Gol section in Gobi-Altai region. Orange lines show main roads and gray ones show river and gulley around studying section. Vertical lines show the outcrops of Precambrian Tsagaan Oloom and Cambrian Bayan Gol formations.
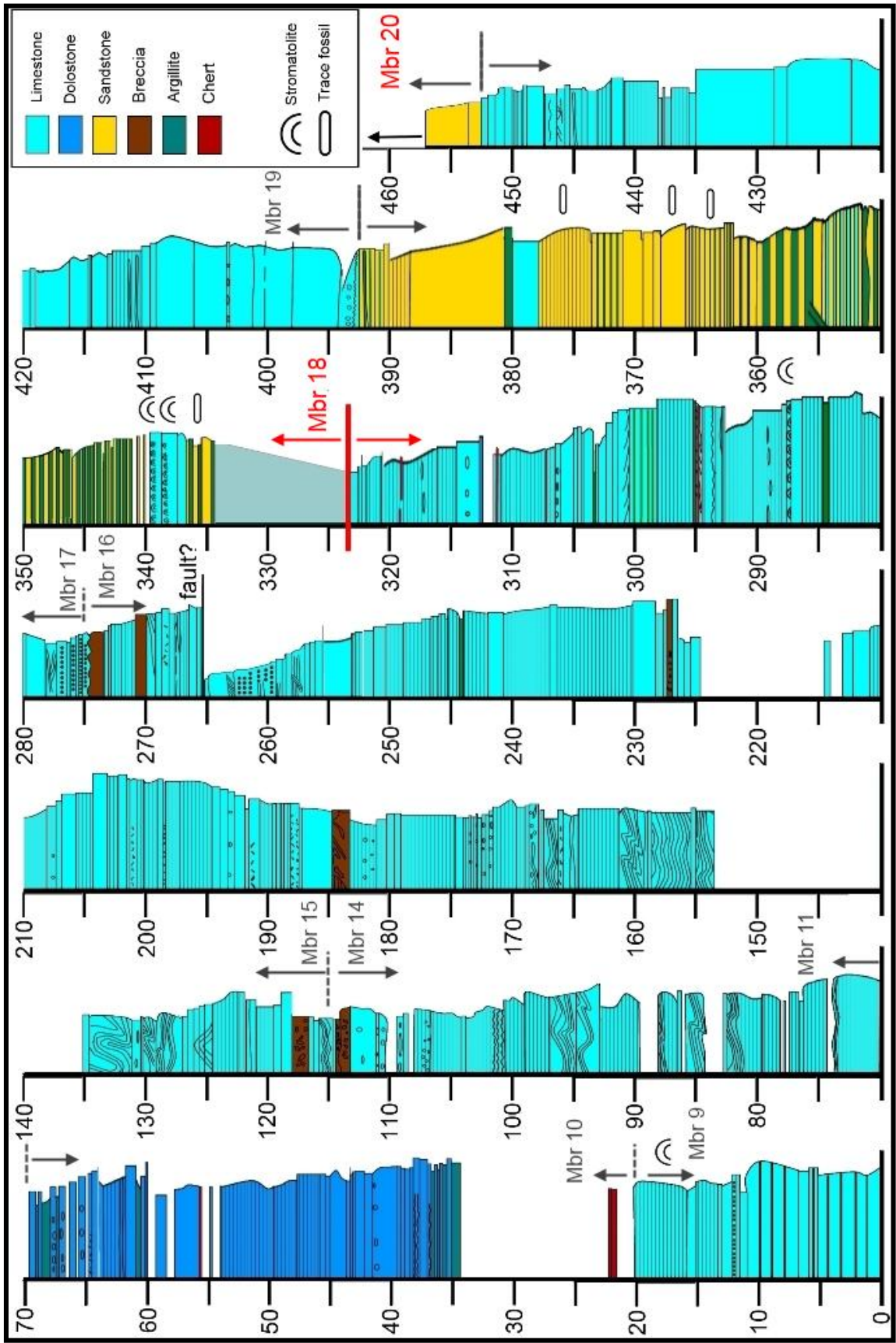
Figure 13. Columnar section of Tsagaan Oloom and Bayan Gol formations in Bayan Gol section. Lateral width shows the general surface morphology of the outcrops, not representing the grain size of the sediments. Pc-C boundary (324 m) is between the Member 17 of the uppermost Tsagaan Oloom and the Member 18 of the lowermost Bayan Gol formations. Mbr: Member.
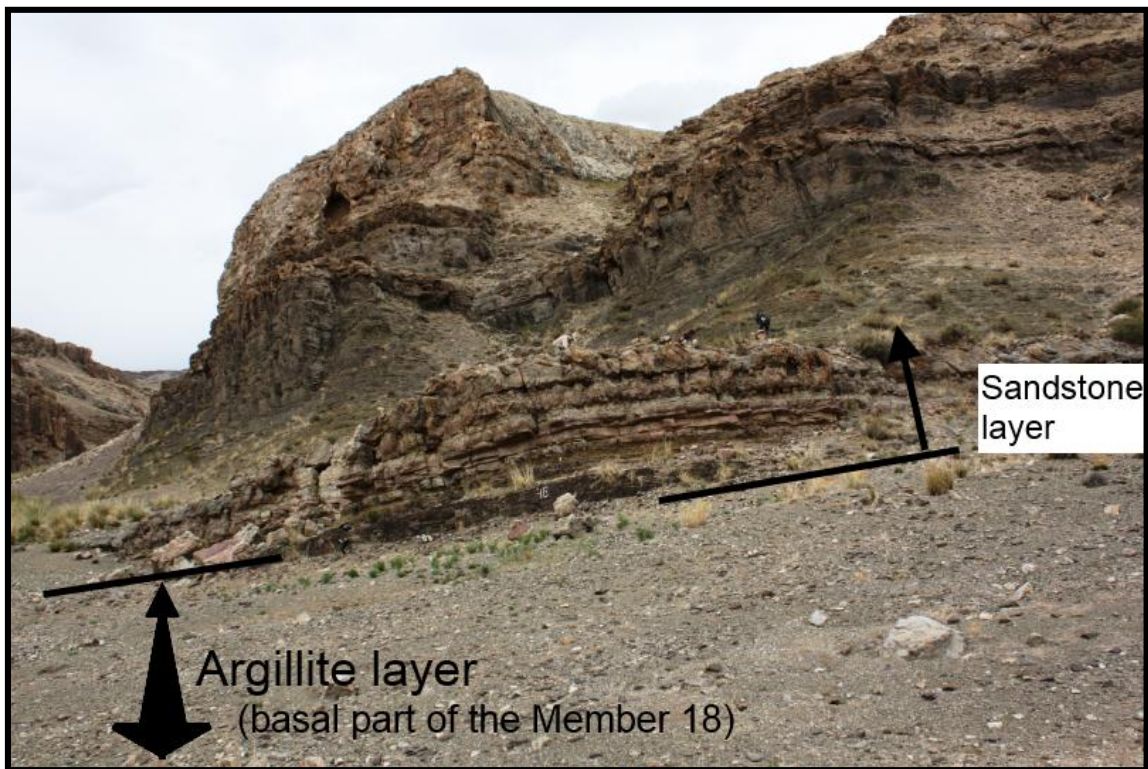
Figure 14. Outcrop of the base of the Member 18 of Bayan Gol Formation. Pc-C boundary

cannot be observed in this section because of poor exposure.

2.d. Late Early Cambrian Balang and Chintingshan formations, Guizhou, China

2.d.1. Balang Formation

The late Early Cambrian (Series 2, Stage 4) Balang Formation is distributed in the eastern Guizhou Province and western Hunan Province (Zhou et al., 1979; Yin, 1987; Yin, 1996) (Figure 15). The whole thickness is more than 600 m in central eastern Guizhou and more than 300 m in eastern Guizhou (Peng et al., 2010a). In this study, the Geyi section, about 150 km northeast of Guiyang city, was studied (Figures 15 and 16). The whole thickness of the Balang Formation in the Geyi section is estimated to be about 375 m (Peng et al., 2010a). This formation is divided into three parts: the lower part of deep-gray shale, the middle part of gray-green siltstone and shale, and the upper part of gray-green very fine sandstone and siltstone with lenticular limestone.

The base of the formation lies in fault contact with the top of the underlying Bianmachong Formation, which is composed of gray-white mudstone. In the lower part of Balang Formation (0-120 m from the base), lithofacies mainly consists of green shale and rarely contains very fine-grained sandstone. Bedding planes were unclear. At 3 m above the base, some specimens of black round-shaped fossil algae (about 5 mm in diameter) were observed. Ichnofossils are abundant at the horizons of 60 m from the base.

Middle part of the formation (121-240 m from the base) consists of siltstone, shale and minor amount of very fine-grained sandstone. Some species of trilobites including *Redlichia murakami* and algae occurred in white brown weathered shale at the horizon of the level 195 m above the base. In addition to these fossils, some species of eocrinoids, fungi, non-trilobite arthropods, palaeoscoleids and a non-mineralized naraoid also occurred from the middle-upper part of the Balang Formation in this section (Yuan et al., 2006; Zhao et al., 2007; Peng et al., 2010a; Peng et al., 2012a). These fossils are collectively called as Balang Biota (Peng et al., 2012a).

In the upper part of the formation (241-375 m), lithofacies is mainly composed of green-gray very fine sandstone and siltstone with lenticular limestone. Abundant ichnofossils occurred at the horizons of 270-295 m above the base of the formation. Detail descriptions of the occurrences of ichnofossils are described in the Chapter 4.

Generally, the Balang Formation represents a shallowing upwards sequence (Zhao et al., 2007). Depositional environment was estimated to be of a shallow marine, gentle slope basin (Pu et al., 1993).

Biological zone is based on the occurrence of trilobites (Steiner et al., 2007; Peng et al., 2012b). While the trilobite zone of this formation was assigned to the *Arthricocephalites - Changaspis - Balangia* Assemblage Zone or the *Arthricochepalus -*

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Changaspis Assemblage Zone (Zhou et al., 1980; Yin, 1987), it is now recognized that the Balang formation belongs to the *Palaeolenus - Megapalaeolenus* Zone or *Arthricochepalus chauveaui - Changaspis elongate* Assemblage Zone (Steiner et al., 2007; Qin et al., 2010; Peng et al., 2010b; Peng et al., 2012b).

Figure 15. Location map of the studying area (Weiganping and Geyi sections) in Guizhou

province, South China. Orange lines show main roads, and gray ones show river around

the studying areas.
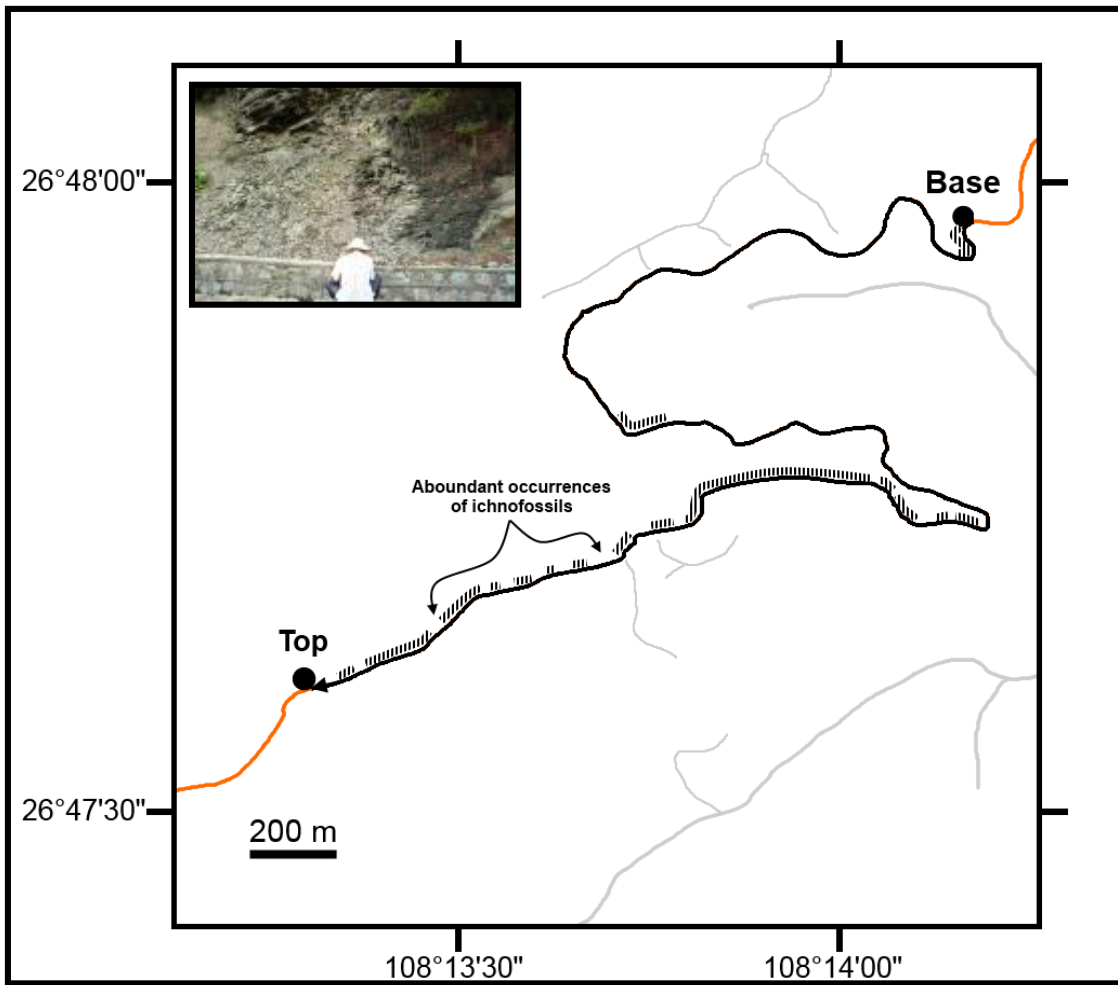
Figure 16. Map and outcrop photo of Geyi section. Orange line shows road. Vertical lines show the outcrops of the Balang Formation.

2.d.2. Chintingshan Formation

The late Early Cambrian (Series 2, Stage 4) Chintingshan Formation is distributed in northern-central Guizhou Province (Zhang, 1989) (Figure 15). The studied section is in the Weiganping area, about 50 km northeast of Guiyang City, Guizhou Province (Figure 16). Whole thickness of the formation is unknown because of the poor exposure and small number of previous studies about the Chintingshan Formation. The boundary with underlying Mingxinsi Formation, which is characterized by gray shale and mudstone, was covered by vegetation and could not be confirmed. Previous report described that the lower part of the Chintingshan Formation consists of gray massive or thick-bedded limestone and greenish-yellow shale with rich archaeocyathid fossils (Zhang, 1989). The middle to the upper part of the formation is mainly composed of massive very fine-grained green-gray sandstone, with interbeds of siltstone. No HCS was confirmed in the sandstone beds.

It is suggested that the Chintingshan Formation was deposited in a shallower environment than the Balang Formation because of the sedimentary characteristics (thick sandstone beds with siltstone interbeds and coarse grain size), although it was deeper than the storm wave base. Ichnofossils were mainly observed on the surface of floats.

Biological zone is also constructed of the occurrence of trilobites (Steiner et al.,

2007; Peng et al., 2012b). Based on the trilobite zone, Chintingshan Formation was deposited almost same age as Balang Formation, that is, *Palaeolenus - Megapalaeolenus* Zone or *Arthricochepalus chauveaui - Changaspis elongate* Assemblage Zone (Steiner et al., 2007; Qin et al., 2010; Peng et al., 2010b; Peng et al., 2012b).
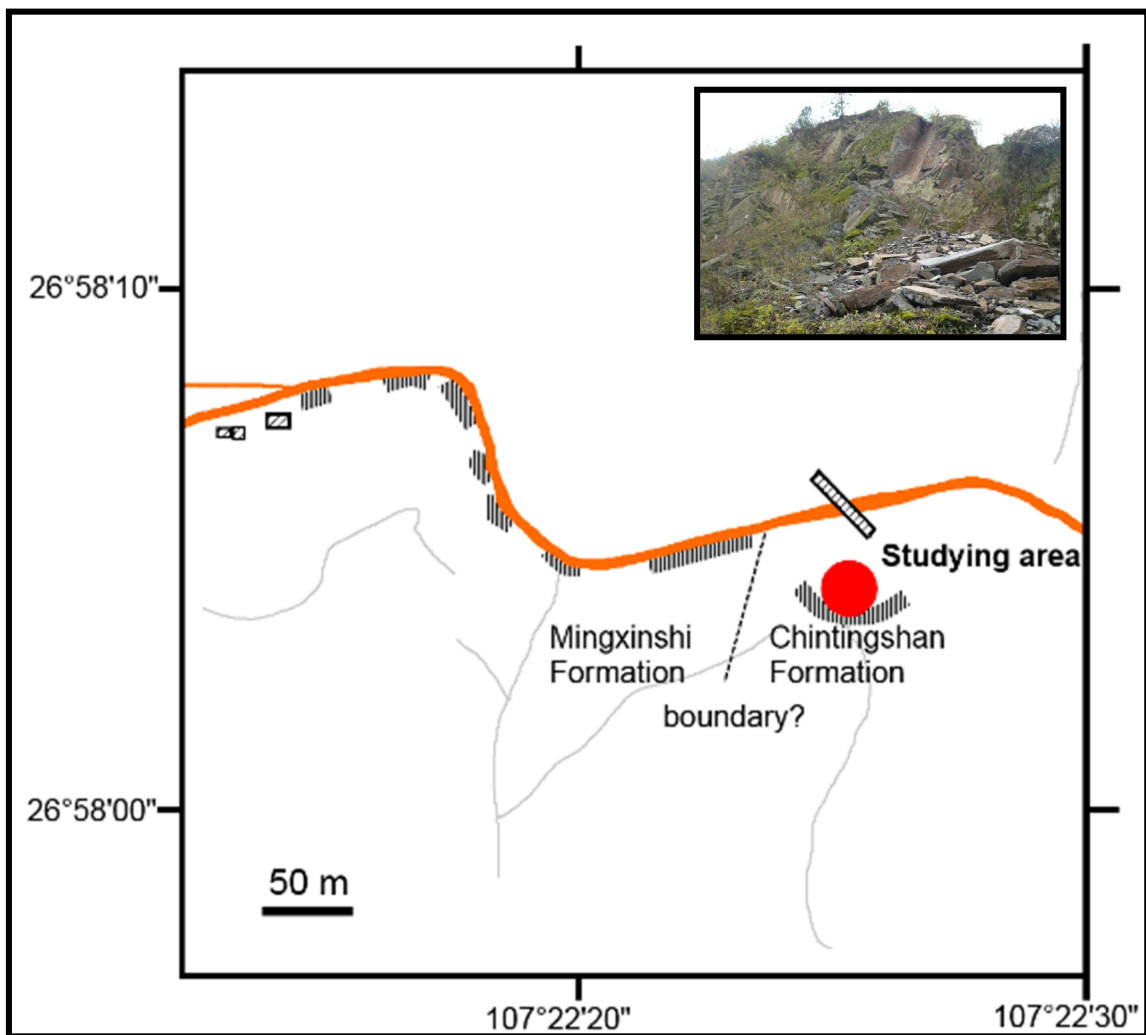
Figure 17. Map and outcrop picture of Weiganping section. Orange line shows road.

Vertical lines show the outcrops of the Chintingshan and the underlying Mingxinshi

formations. The boundary of the Chintingshan and the Mingxinshi formations is unclear

because of vegetation. Red circle shows the main studying area of the Chintingshan

Formation.

3. The Diversification Patterns of Ichnofossils in the Earliest Cambrian Chapel Island Formation

3.a. Introduction

This chapter focuses on the diversification pattern of ichnofossils in the basal part of the Cambrian, and clarifies if these ichnofossils assemblages are controlled by environmental factors, or how strongly these assemblages are influenced by environmental factors. In order to fulfill these purposes, the Chapel Island Formation exposed on the coast of Fortune Head is well suited for this study, because ichnofossils are abundant, the sequence is excellently continuous and multiple sedimentary facies suggesting different sedimentary environments are all represented in this formation.

3.b. Methods

Log sections were made for the *T. pedum* and *R. avalonensis* zones, focusing on the sediment types, sedimentary structures, and occurrences of ichnofossils. Ichnofossils seen in the outcrops were photographed, and the ichnofossils were identified in the field and laboratory. Based on the multiple occurrences of ichnofossils within the columnar section, the ranges for individual ichnofossils were determined.

3.c. Results

The ranges of common ichnofossils in the earliest Cambrian *T. pedum* and *R. avalonensis* zones are shown in Figure 18. The black lines show the occurrences of ichnofossils in this study, whereas the gray lines show the occurrences of ichnofossils reported by the previous study (Narbonne et al., 1987). Below the Pc-C boundary, only one ichnogenus *Gordia* isp. (Figure 32c) was identified on the bedding surface at approximately 11 m below the boundary. The *T. pedum* Zone above the Pc-C boundary witnessed a sudden increase of various ichnotaxa such as *Planolites* isp. (Figure 33f), *Skolithos* isp. (Figure 34f), *Gyrolithes* isp. (Figure 32d), *Conichnus conicus* (Figure 31d), *Arenicolites* isp. (Figure 31a) and *Cochlichnus* isp. (Figure 31c). Other ichnotaxa such as *Palaeophycus* isp. (Figure 33e), *Hormosiroidea* isp. (Figure 33a), and undeterminable divergent traces (Figure 36a) occur in the middle to the upper part of this zone. These ichnotaxa occur in multiple sedimentary facies, including not only SiS-D facies but also Sh facies.

The following two stepwise increases in ichnofossil diversity and abundance were detected at two horizons in the *T. pedum* and *R. avalonensis* zones: the first increase is identified at the horizon immediately above the Pc-C boundary, and the second around

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the boundary of the *T. pedum* and the *R. avalonensis* zones. In the lowermost part of the

T. pedum Zone, *Treptichnus pedum* was discovered from the bed approximately 1 m

below the Pc-C boundary. Other ichnofossils occurred at the level 6 m above the Pc-C

boundary. Most ichnofossils occurred mainly on the bedding surfaces and bottom surfaces.

In addition to the horizontal ichnofossils such as *Planolites* isp. and *Cochlichnus* isp.,

ichnofossils that penetrated into sediments such as *Skolithos* isp.   and *Gyrolites* isp. also

occur at 6 m above the Pc-C boundary.

Although a few new forms of ichnofossils were found from the middle part of

the *T. pedum* Zone, an increase in the number of ichnogenera was not as conspicuous as

that observed at the base and at the uppermost parts of the zone. Therefore, ichnofossil

assemblages in the *T. pedum* Zone were regarded as almost uniform throughout the zone,

despite the changes in the depositional facies. Ichnofossils were almost absent from the

reddish sandstone of the Sh facies that occur in the middle to the upper part of the zone.

Five new ichnogenera and one ichnoshape appeared in the uppermost part of the

T. pedum Zone and the lower part of the overlying *R. avalonensis* Zone. This ichnofossil

assemblage contains *Torrowangea* isp. (Figure 35c), ?*Psammichnites* (Figure 34b),

Bergaueria isp. (Figure 31b), an unidentified radial bi-lobed ichnofossil (Figure 36b),

Monomorphichnus lineatus (Figure 33b), and *Taphrhelminthopsis circularis* (Figure 35b),

none of which were observed in the section below. From the middle to the upper part of

the *R. avalonensis* Zone in the Fortune Head section, two characteristic ichnogenera,

Rusophycus cf. *avalonensis* (Figure 35d) and *Cruziana* isp. (Figure 31e) are also present.

Compared with the occurrence of ichnofossils in the previous study (Narbonne

et al., 1987), some ichnofossils, i.e. *Hormosiroidea* isp. and *Cruziana* isp., were newly

found in this study. Besides, *Cochlichnus* isp., *Bergaueria* isp. and *Gyrolithes* isp. were

observed at lower horizons than the previous report. On the other hand, some ichnogenera,

such as *Palaeopascichnus* isp., *Helminthopsis* isp. and *Curvolithus* isp., were not

observed in this study.

3.d. Discussions

3.d.1. Diversification of Ichnofossils in the Earliest Cambrian

Analysis of the ichnofossils in the *T. pedum* Zone and the lower part of the *R.*

avalonensis Zone shows that increases in ichnofossil diversity occurred twice; first near

the basal part of the *T. pedum* Zone and the second around the boundary between the *T.*

pedum and *R. avalonensis* zones (Figure 18). No remarkable increase was detected in

other parts of the *T. pedum* and *R. avalonensis* zones. This pattern of increase suggests

that the diversification of ichnofossils was stepwise, with each diversification occurring

within a relatively short time period from the *T. pedum* Zone to *R. avalonensis* Zone. These diversifications, especially the second one, were not clearly demonstrated in previous work (Narbonne et al., 1987). There are three possible reasons for this discrepancy. First, the two kinds of ichnofossils (?*Psammichnites* isp. and unidentified radial bi-lobed trace fossils), which were not reported in previous studies, were newly observed in this study. Second, some ichnofossils, e.g., *Gyrolithes* isp., *Hormosiroidea* isp. and especially *Bergaueria* isp., were newly observed in the lower horizons of the formation. Third, the ichnofossil *Torrowangea* isp. did not appear below the upper part of the *T. pedum* Zone at Fortune Head, although it was reported below the Pc-C boundary in Grand Bank Head (Narbonne et al., 1987).

The ichnofossils involved in the second diversification have some features that were not observed in the ichnofossils from the first diversification. First, some ichnofossils had more complex structures than those from the lower horizons. The ichnofossils in the first diversification had simple shapes; they had almost no walls and no ornamental structures. On the other hand, ?*Psammichnites* isp. and unidentified ichnofossils, which first appeared in the second diversification, display bank-like structures on their sides. Similar structures were observed in *Taphrhelminthopsis circularis*, a common ichnogenus in the *R. avalonensis* Zone. It is thought that this

structure was made by animals that moved in the upper part of the sediment just below

the sea bottom (Jensen, 2003). Second, compared with the ichnofossils from the lower

horizon, these ichnofossils are generally larger in size. For example, ?*Psammichnites* isp.

and *Torrowangea* isp. are 5-9 mm in width, while the common ichnogenus *Planolites* isp.

from the *T. pedum* Zone is 1-2 mm in width (see Chapter 5). This general increase in size

of ichnofossils may indicate that the second diversification of ichnofossils involved

appearance of new animals and/or the development of new behaviors that were not seen

in the *T. pedum* Zone.

3.d.2. Development of Animal Activity in Response to Change of Depositional

Environments in the Chapel Island Formation.

In the lower to the middle part of the *T. pedum* Zone, the dominant sedimentary

facies changes from gutter cast facies to sandstone-dominated facies. Myrow (1992)

interpreted that this facies change reflects a change in depositional environments. He

further assigned the SiS-D facies to the deposits in a deeper environment beyond the reach

of the storm-laden flow, which produced the gutter casts on the seafloor. As described

above, alternating sandstone and siltstone, which also suggests a deep environment, are

found in the upper part of SiS-D facies. Despite the differences in the depositional

environments (gutter cast facies vs. SiS-D facies), the ichnofossil assemblages are not

significantly different (Figure 18). This consistency of the occurrence of ichnofossils

through two different sedimentary facies suggests that there was no strong link between

the composition of ichnofossil assemblages and depositional environments in the lower

part of the Fortune Head section. The first increase in ichnofossil diversity in the *T. pedum*

Zone was also not likely to have been influenced by the change in depositional facies in

the shallow marine environment, because there was no remarkable change in sedimentary

facies across the lower boundary of the *T. pedum* Zone.

On the other hand, ichnofossils were rare in the red Sh facies. This red sandy

facies had a number of cracks on the bedding surfaces, with parallel or cross-laminated

beds. Myrow and Hiscott (1993) suggested that these features indicate deposition along

a periodically subaerially exposed, high-energy, sandy nearshore and shoreline zone.

Therefore, there was a high degree of environmental stress for marine organisms at the

time of the deposition of the red sandy facies. Also as a result of the high-energy

environment, horizontal ichnofossils might have had a lower chance of preservation in

this facies.

In the SS-D facies in the *R. avalonensis* Zone, *Monomorphichnus lineatus* and

Taphrhelminthopsis circularis are common. The major ichnogenera that were associated

with the ichnoassemblage, consisting of *Planolites* isp., *Skolithos* isp., *Cochlichnus* isp., *Arenicolites* isp. and *Gyrolithes* isp., however, were not significantly different from the GC and SiS-D facies in the *T. pedum* Zone. Therefore, although these two new ichnofossils could indicate the diversification of animals and/or their behaviors, animal behaviors had not yet been specialized to occur in particular environmental settings in the lower part of the *R. avalonensis* Zone (Figure 19). This means that the benthic fauna that left traces had a wider spectrum of environmental tolerance than the fauna of the later ages. In conclusion, the earliest Cambrian animals did not yet fully develop their behaviors with changing environments surrounding them.
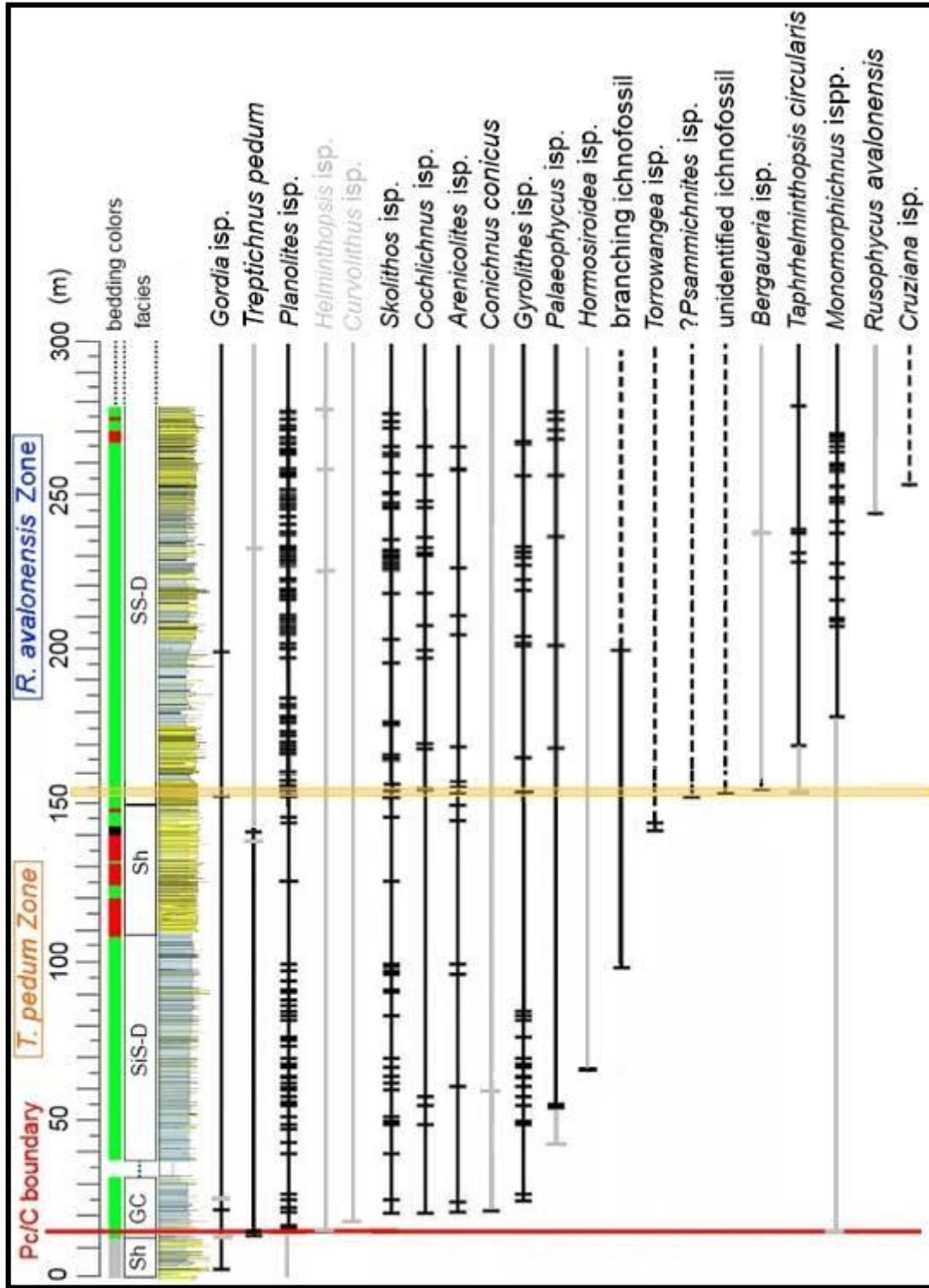
Figure 18. The occurrences of ichnofossils of the *T. pedum* and *R. avalonensis* zones in the Chapel Island Formation. The boundary of *T. pedum* and *R. avalonensis* zones is 155 m above the Pc-C boundary. Horizontal bars show the horizons of each ichnofossil occurrence. Black horizontal bars and ichnofossils can be observed in this study. Gray bars and ichnofossils were shown in Narbonne et al. (1987).
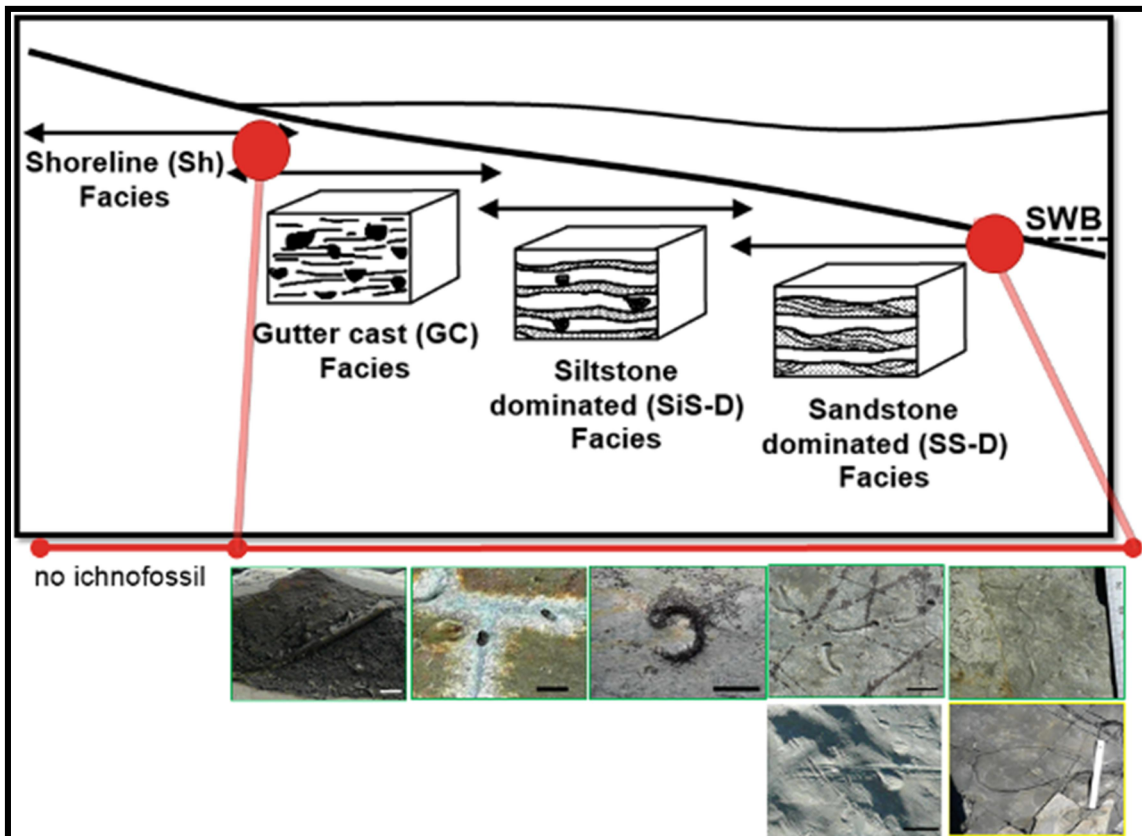
Figure 19. Facies of the Chapel Island Formation (modified after Myrow, 1992) and common ichnofossils which can be observed in each facies. The ichnofossil assemblage was almost unchanged between the GC, SiS-D and SS-D facies.

4. Development of Animal Activity in Response to Change of Depositional Environment in the Early Cambrian.

4.a. Introduction

As the analysis of the Chapel Island Formation clarified, animal activities had relatively wide tolerance to different environments, and they were not adequately adapted to the surrounding environments in the earliest Cambrian. Thus, to specify the timing when the animal activities finely adapted to different environments, occurrences of ichnofossil assemblages were comparatively studied in the coeval two formations in the southern China block; the Early Cambrian Balang and Chintingshan formations in Guizhou province, China.

4.b. Methods

The occurrence of ichnofossil assemblages was comparatively studied in the Early Cambrian Balang and Chintingshan formations. Besides, It is also clarified what kind of behavior developed in different depositional environment to compare the character of ichnofossils in each formations.

4.c. Results

4.c.1. The occurrence of ichnofossils in the Balang Formation

Ichnofossils were abundant in very fine-grained sandstone beds at 60 m from the base. Most common ichnofossil was *Planolites* isp. (Figure 33f), which occurs from the bottom to the top of the Balang Formation. In the lower horizons, tubular structures of *Planolites* were almost straight, or slightly curved. The other ichnofossils included two forms of *Monomorphichnus* (Figures 33b and c) and pellet like ichnofossils (Figure 36d). Because one *Monomorphichnus* had bold 6 straight lines, it is considered that this ichnofossil could be *Monomorphichnus lineatus*. On the other hand, another *Monomorphicnus* shows thin radiated lines. Ichnospecies was not identified for this specimen. Generally, these *Monomorphichnus* were considered to be the scratching marks of arthropods (Martinsson, 1965; Crimes, 1970; Alpert, 1976; Crimes and Anderson, 1985). In addition, two species of trilobites (*Redlikia murakamii* and *Arthrococephalus chauveaui*) occurred near the same horizon.

In the middle part of the formation (121-240 m), ichnofossils are less abundant than in the lower part. A few *Planolites,* however, were observed.

In the upper part of the formation (241-375 m), ichnofossils were abundant in the silty sandstone from the horizons of 270-295 m. The most common ichnofossil was

Planolites isp., and these *Planolites* specimens had more diversified shapes than those of the lower horizons. Interestingly, some *Planolites* specimens show that the ichnofossil producers had up and down movements in the sediments, while other specimens show ordinary horizontal burrows. These pieces of evidence suggest that there were several different types of producers of *Planolites* in Balang Formation. In the upper part of the formation, a number of shapes of ichnofossils newly appeared. For example, *Tricophycus* isp. (Figure 35e), *Neonereites uniserialis* (Figure 33d), ?*Treptichnus pedum*, ?*Conichnus* isp. and branching burrow were observed. *Tricophycus* isp. is a curved branching burrow with nubby structures. *Neonereites* is a straight or slightly curved trail with consecutive grained structures. ?*Conichnus* isp. is a pot shaped trace which vertically penetrated into the sediment. While many kinds of ichnofossils occurred, many of these ichnofossils had the movements not only parallel to the surface but also up and down movements in the sediment.

4.c.1. The occurrence of ichnofossils in the Chintingshan Formation

Diversity of the ichnofossils was lower in the Chintingshan Formation than in the Balang Formation. Because the bedding plane exposures were poor in Weiganping section (Chintingshan Formation), ichnofossils were mainly observed on the surfaces of

floats. The most common ichnofossil was *Cruziana* isp. (Figure 31f). *Cruziana* had straight or meandering bilobed horizontal trails with V angles of almost 180º. It is generally considered that *Cruziana* is a moving trail of arthropods such as trilobites. *Planolites* isp., which abundantly occurred in the Balang Formation, also appeared in Chintingshan Formation, whereas the number of occurrences was smaller. As to other ichnofossils, *Bergaueria* isp. (Figure 31b) and *Spirorhaphe* isp. (Figure 35a) occurred. *Bergaueria* is a rounded ichnofossil with a central depression. *Bergaueria* is considered that as a dwelling burrow of actinians (Seilacher, 1956, 1989; Zhu, 1997). In this section, two different sizes of *Bergaueria* appeared. *Spirorhaphe* is a spiral shaped horizontal trail which coils inwards, loops back, and coils outwards along the inward trail (Pickerill and Mitchell, 1999). Only one specimen was observed on the same surface of float with *Cruziana* isp.. The general tendency of the ichnofossils in the Chintingshan Formation is that most specimens are horizontal and observed on the bedding plane.

4.d. Discussions

In the Balang Formation, many shapes of ichnofossils were observed on the bedding. In addition, the ichnofossil assemblages changed from the bottom to the top of the formation, that is, with the sedimentary environment shallowing upward (Zhao et al.,

2007); more shapes of ichnofossils occurred in the upper horizons than in the lower part. Besides, various shapes of *Planolites* also appeared in the upper part of the formation. Therefore, it is indicated that benthic animals, which left many kinds of ichnofossils, lived in the seafloor, and these animals could freely move into the deposits. The transition of the ichnofossil assemblage, through the formation also suggests that the animal activities varied along with the changes of the sea depth and diversified with environmental change, that is, shallowing of the sea depth.

On the other hand, in the Chintingshan Formation, diversity of ichnofossils was lower than in the Balang Formation, indicating that the variety of animals and their activities were limited. Besides, most ichnofossils were observed on the bedding planes rather than in the sediments, suggesting that the benthic animal activities were mostly epifaunal and rarely infaunal.

These observations indicated that animal activities adapted to different environments already existed in the late Early Cambrian. In the shallow sandy facies, animals generally lived on and rarely moved into the sediments. On the other hand, in a deeper muddy facies, animals not only moved on but also dived into the sediments. This difference could be attributed to the difference in the hardness of the sediments and living animals in these two environments. When the sediments were soft and soupy, animals

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were easy to move into and through the sediments for having nutrient. On the other hand, when the sediments were hard, animals were hard to dive into the sediments. However, it became easy for actinid animals to attach their bodies on firm sediments. Other animals grazed on the hard substrate.

Therefore, it is suggested that the animals had already differentiated into those adapted to epifaunal as well as infaunal life habitats in the upper Early Cambrian. These differences of animal activities were shown as the difference of ichnofossil assemblages between the Balang and Chintingshan formations.

5. Geographical Difference of Diversification of Animal Activities in the Earliest Cambrian

5.a. Introduction

In spite that numerous studies about Cambrian animal diversification have been done, it is still unknown when the diversification occurred in the first phase of the Cambrian explosion, and expanded to all over the world. One reason of this question is due to a small amount of comparative study between regions in the earliest Cambrian. Geographical differences of climate and oceanic component could affect the diversification of animals. Previous study suggests that either rapid plate movements or rapid true polar wander occurred during the Early Cambrian (Mitchell et al., 2010). If that in fact occurred, the oceanic environments of specific regions could have changed in a relatively short period of time. Moreover, animals would evolve with such rapid environmental changes. In this study, to clarify the geographical differences of the process of animal diversification in the earliest Cambrian, two topics (size distributions of ichnofossils and bedding plane bioturbation indices) are comparatively studied with focusing the paleo-latitudes in different regions.

The size of animals depends on many factors, such as age, temperature and

oxygen level of surrounding environments, and so on. It would be difficult to single out a factor causing a size increase. As for the skeletal organisms, a clear size increase occurred in the early Cambrian. In the early Cambrian, the first skeletal fossils are small shelly fossils, millimeter scale fossils of various, mostly unknown kinds of animals. Then large-sized animals such as brachiopods and various arthropods, including trilobites appeared in a wide geographic range. This increase could be postdated the increase of size represented by the ichnofossils. Therefore, first, when and how did the size increase of animals, which were represented by various kinds of ichnofossils occur, should be studied based on the size distribution of ichnofossils. Second, the timing of these increases, in other word, possible timing of diversification of benthic animals, is compared between different regions.

Activity of animals should be different among different animal taxa. Primitive metazoans such as monoblastic animals (ex. sponge) usually do not move, and diploblastic animals such as cnidarians have very limited ability for movements. However, many triploblastic clades (Bilateria) have ability for powerful movements. Of course there are wide variations in the degree of movements among bilaterians. Therefore one possibility of active move should derive from the evolution of animal taxa. In addition, behavioral complexity should also evolve to achieve active movements. Lastly, animal

activity would also depend on the physical environment, such as oxygen levels in the habitats.

By examining numerous bedding planes in different areas, a general pattern of increase in animal activities was revealed by the ichnofossil study herein. It appears most probable that the activity increase was influenced by the evolution of animals themselves, rather than by other factors (physical factors). This in mind, the pattern of increase in the animal activity and the geographical difference in the timing of such increase are examined and discussed below.

5.b. Methods

First, in order to clarify the diversificational pattern of animal activities in the earliest Cambrian, the occurrence of ichnofossils, the size distributions of ichnofossil and the bedding plane bioturbation indices were comparatively studied between three sections; the Chapel Island Formation, Newfoundland, the Zhujiaqing Formation, Yunnan and the Bayan Gol Formation, Gobi-Altai. The depositional environment in these three localities was shallow sea which was from the shoreline to lower outer beach.

Second, to clarify the patterns of change in the animal body size, the maximum diameters of *Planolites*, which was the most common ichnogenus from the early

Cambrian, were measured on bedding surfaces (Figure 20a). The ichnogenus *Planolites* has the following characteristics: a straight or slightly curved tubular burrow without divergence or ornaments on its walls. Therefore, it is easy to identify and measure the maximum diameter. The maximum diameter of *Planolites* should represent the size (body width) of the producer. The diameter of *Planolites* was mainly measured by using caliper; measurement accuracy is 0.1 mm. Only the diameter of the *T. pedum* Zone in the Chapel Island Formation was measured by sensitive ruler (measurement accuracy is 0.5 mm). Therefore, measurement precision is less than 1 mm in either approach. The size distributions of *Planolites* in the earliest Cambrian were compared among three regions. The measured diameters of *Planolites* were grouped into 10 intervals; 1 to less than 2 mm, 2 to less than 3 mm, and so on. The largest group consists of those with diameter equal to or greater than 10 mm.

Third, in order to understand and compare the intensities of benthic biological activity in the earliest Cambrian, the bedding plane bioturbation index (BPBI) (Miller and Smail, 1997; Marenco and Bottjer, 2010) was used (Figure 20b). The photographs of bedding planes with ichnofossils were scanned into a computer, and the density of ichnofossils on the bedding planes were calculated from the number of pixels they occupied within the photos. Based on the density of the ichnofossils, the bedding plane

bioturbation index was determined; index I represents no observable bioturbation on the bedding plane; II, the density of ichnofossils covers 1-10% of the bedding plane; III, 10-40%; IV, 40-60%; and V, 60-100%. Finally, these indices were also compared between the three earliest Cambrian sections.

Finally, global diversificational process of the earliest Cambrian animal is discussed based on animal body sizes and animal activity evidenced by ichnofossils.

Correlation of the geological age in each formation was important to compare the geological differences. The major way of the comparison consists of three different methods in the previous studies; ichnofossil zone, small shelly fossil zone and carbon isotopic change. In this study, ichnofossil zones (*Treptichnus pedum* and *Rusophycus avalonensis* zones; Figures 1 and 2) are chosen to correlate the geological age, because these ichnofossil zones have been established in all three sections by previous studies (Narbonne et al., 1987; Goldring and Jensen, 1996; Zhu, 1997).

Beside, some geochronological data are added on these ichnofossil zones (Figure 2). In the Chapel Island Formation, geological ages near the boundary between the base of Member 1 and underlying Recontre Formation (ca. 543 Ma; Landing and Macgabhann, 2010; Landing and Kröger, 2012), and uppermost part of Chapel Island Formation are studied in southern New Brunswick region (ca. 528 Ma; Schoene et al., 2006; Landing

and Kröger, 2012). Geological ages in the Zhujiaqing Formation are also estimated in white clay Member (ca. 535 Ma; Sawaki et al., 2008; Okada et al., 2013), and near the boundary of Dahai Member and overlying Shiyantou Formation (ca. 526 Ma; Okada et al., 2013). White Clay Member is located between the *T. pedum* (Lower Phosphorite Member) and *R. avalonensis* (Upper Phosphorite Member) zones. Therefore, this could indicate the boundary age of the *T. pedum* and *R. avalonensis* zones. On the other hand, there is no geochronological data in the Tsagaan Oloom and Bayan Gol formations in Gobi-Altai region. Based on the correlations of $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ curves with Siberia, however, the geological age of Member 11 indicates ca. 544 Ma, and the lower Member 20 shows ca. 530 Ma (Brasier et al., 1996b). Therefore, studying horizons seems to be deposited during the period of 544 Ma to 526 Ma, i.e., Fortunian age.

In addition to the ichnofossil zonation and the strontium correlation above, in order to evaluate the simultaneity of these ichnofossil zones, carbon isotopic data are compared between different regions. Previous studies (ex. Fan et al., 2011) showed that there is a major carbon isotopic anomaly (BACE event) near the Pc-C boundary. This BACE (Basal Cambrian Carbon Isotope Excursion) event represents a large negative $\delta^{13}C$ excursion which has been documented near the Pc-C boundary from many localities of the world (Fan et al., 2011). Minimum $\delta^{13}C$ values are between -3‰ and -12‰ with a

magnitude about 5‰-10‰ (Fan et al., 2011). This negative excursion is also observed in the top of the Dengying Formation in South China and the upper part of the Tsagaan Oloom Formation in Gobi-Altai (Brasier et al., 1996b; Li et al., 2009; Fan et al., 2010). Because the carbon isotopic data of Bayan Gol and Meishucun sections are poor, the data of Tsagaan Gol and Salaany Gol sections in Gobi-Altai, and Laolin section in Yunnan are supplementarily used in this study (Figure 21). Based on these isotopic data, both the *T. pedum* Zones of the Member 18 of the Bayan Gol Formation and the Lower Phosphorite Member of the Zhujiaqing Formation are safely assigned to the earliest Cambrian, because a large negative δ^{13}C excursion is reported below these members (Brasier et al., 1996b; Li et al., 2009; Fan et al., 2010). Both the *R. avalonensis* Zones (Member 20) of the Bayan Gol Formation and the Upper Phosphorite Member of the Zhujiaqing Formation were thus concluded to have been deposited after 535 Ma from the geochronological data (Figure 2). On the other hand, it is difficult to identify whether the Member 18 of the Bayan Gol Formation was deposited before 535 Ma or not; in other words, the Member 18 could actually be included in the *T. pedum* Zone or in a part of the *R. avalonensis* Zone. This uncertainty comes from the carbon isotope data of the Bayan Gol Formation (Brasier et al., 1996b) that there are two negative excursions in the upper part of the Tsagaan Oloom Formation, and it is difficult to assign which of these two

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excursions were the BACE event. The previous study, however, did not report the occurrence of the *R. avalonensis* from the member 18 (Goldring and Jensen, 1996). Besides, considering the enormous thickness of the Member 19, it is suggested that the Member 18 should have been deposited before 535 Ma; namely during the time of the *T. pedum* Zone. Thus, it would be the most plausible interpretation that the ichnofossil zones of these two regions should be regarded as representing almost the same age.

On the other hand, almost no data about the carbon isotopes were available from the Chapel Island Formation because of the weak thermal alteration of the formation (Fan et al., 2010). However, a stratigraphic comparison with considering the thickness of the formations, as well as the geochronological data (Schoene et al., 2006; Landing and Macgabhann, 2010; Landing and Kröger, 2012) suggests that the *T. pedum* and the *R. avalonensis* Zones of the Chapel Island Formation and these two zones of the Zhujiaqing and Bayan Gol formations should be almost coeval.

5.c. Results

5.c.1. Occurrences of the ichnofossils

Almost all ichnofossils commonly occurred in studied sections, whereas a few ichnofossils occurred in limited regions. The common ichnofossils include *Cochlichnus*

isp. (Figure 31c), *Planolites* isp. (Figure 33f), *Rusophycus* isp. (Figures 34d and e),

Taphelminthopsis circularis (Figure 35b) and *Treptichnus pedum* (Figure 35d). According

to the previous reports, *Arenicolites* isp. (Figure 31a), *Bergaueria* isp. (Figure 31b),

Cruziana isp. (Figures 31e and f), *Gordia* isp. (Figure 32c), *Hormoshiroidea* isp. (Figure

33a), *Monomorphichnus* isp. (Figures 33b and c), *Palaeophycus* isp. (Figure 33e) and

Skolithos isp. (Figure 34d) were also commonly observed (Goldring and Jensen, 1996;

Zhu, 1997). On the other hand, the ichnofossils of limited geographical distribution

include *Gyrolithes* isp. (Figure 32d) and *Didymaulichnus miettensis* (Figure 32b).

Gyrolithes isp was quite often observed in the Chapel Island Formation, Newfoundland.

This ichnofossil, however, did not appear in the Zhujiaqing Formation, Yunnan, nor in

the Bayan Gol Formation, Gobi-Altai. On the other hand, *Didiymaulichnus miettensis*

commonly occurred in the Zhujiaqing and the Bayan Gol formations, whereas it was not

observed in the Chapel Island Formation. According to the past study, Crimes and

Anderson (1985) recorded *Didymaulichnus* isp. from Member 2 to 5 of the Chepel Island

Formation. However, these specimens were now suspected to be of *Taphelminthopsis*

circularis (Goldring and Jensen, 1996). Therefore, locally limited occurrences of these

two ichnofossil species were supported by the evidence from the previous report of the

ichnofossils (Goldring and Jensen, 1996; Zhu, 1997; Narbonne et al., 1987).

5.c.2. Size distribution of *Planolites* in three regions

There was a clear increase in the diameters of *Planolites* from the *T. pedum* Zone

to the overlying *R. avalonensis* Zone in the Chapel Island Formation (Figures 22, 23 and

24). In the *T. pedum* Zone, more than 80% of 263 measured specimens had diameters of

1-2 mm. Other larger sizes, especially with diameters greater than 4 mm, were extremely

rare. The average size of the measured diameters was 1.5 mm. On the other hand,

specimens with various diameters were observed in the *R. avalonensis* Zone (396

specimens were measured). Although the most common diameters were also 1-2 mm, the

range of sizes was wider, with diameters between 1 and 6 mm in this Zone. The average

size of diameter was 2.7 mm. The result of median test shows that there was a significant

difference of the size distributions between the *T. pedum* and the *R. avalonensis* zones

(the median value is 1.7 mm, $p < 0.025$). Besides, boxplots are made by the quartiles of

the diameters of *Planolites* in each bedding plane (Figure 23). Boxplots show clear

discrepancies between the *T. pedum* and the *R. avalonensis* Zones; variation of sizes is

greater in the *R. avalonensis* Zone than in the *T. pedum* Zone. Boxplots also show abrupt

increase of the size distribution from the *T. pedum* Zone to the *R. avalonensis* Zone (250-

260 m in Figure 23). However, there were no significant variations of the size distribution

between the horizons in the *T. pedum* and the *R. avalonensis* zones, because the range of boxplots is overlapped in a number of horizons; 1-2 mm in the *T. pedum* Zone and 2-3 mm in the *R. avalonensis* Zone. No significant difference of the size distributions is also shown by the size data of *Planolites* from sandstone beds and those from mudstone beds in the *R. avalonensis* Zone according to the results of median test (median value = 2.6 mm, *p* = 0.9473). Therefore, the influence of compaction derived on the different sediments is concluded to be quite small.

In contrast to the result from the Chapel Island Formation, a wide size range of *Planolites* already appeared in the *T. pedum* Zone in the Zhujiaqing and Bayan Gol formations (Figure 24).

In the Zhujiaqing Formation, although the most frequent width of *Planolites* was 2-3 mm, the frequency was no more than 30% of 131 measured specimens. The difference in frequency from the second most common width (3-4 mm) was only 3 specimens. Besides, a number of specimens with 1-6 mm in width also occurred in the *T. pedum* Zone. The average diameter is 3.5 mm. In this study, the data from *R. avalonensis* Zone is not shown, because there was no good exposure of bedding planes with ichnofossils in this section.

In the Bayan Gol Formation, general tendency of size distribution in *T. pedum*

Zone (184 specimens in total) is similar to that of the Zhujiaqing Formation. The most

common diameters are 2-3 and 3-4 mm, and the third most common range of diameter is

1-2 mm. Most of the *Planolites* observed were within the range between 1 to less than 5

mm, but some reach greater than 10 mm in diameter, with an average diameter of 3.3 mm.

In the *R. avalonensis* Zone (149 specimens in total), the range of size distribution became

narrow. However, various sizes (1-7 mm) of *Planolites* appeared, and the average

diameter is 2.9 mm.

Based on the median test, significant differences were observed from the size

distributions of the *T. pedum* Zone between Chapel Island and Zhujiaqing formations (the

median value is 1.5 mm, $p < 0.025$), and between Chapel Island and Bayan Gol formations

(the median value is 1.5 mm, $p < 0.025$). On the other hand, no significant differences

were shown in the *R. avalonensis* Zone between Chapel Island and Bayan Gol formations

(the median value is 2.6 mm, $p = 0.4317$).

5.c.3. bedding plane bioturbation indices among three regions

A clear increase in bioturbation intensity is also observed in the *R. avalonensis*

Zone in the Chapel Island Formation (Figures 25, 26 and 27). In the *T. pedum* Zone, a

total of 10 bedding surfaces were studied. The BPBI in the *T. pedum* Zone is I on six beds

and II on four beds. The maximum density of ichnofossils shows 7%. The average density is as low as 2%. On the other hand, a total of 18 beds were studied in the *R. avalonensis* Zone. Although two beds have BPBI I, fourteen beds show II and two show III. The maximum density of ichnofossils in this Zone is over 35%, and the average density is 7%. Because three beds in *R. avalonensis* Zone had large bedding planes, densities of these three beds were calculated from the average densities among three random compartments. The densities including errors (2σ) are shown in Figures 25 and 26; $0\pm0.3\%$ (from 153 m), $4\pm3\%$ (from 265 m) and 8 ± 1 (from 268 m). All three values do not exceed threshold value of BPBI I (nearly 0%) and II (1-10%). Only one bed (265 m in Figure 26) have a large margin of error ($\pm3\%$) compared with other two beds. However, error of the bed of BPBI I (153 m in Figure 26) is quite small ($\pm0.3\%$). Thus, it is unlikely that the bed of BPBI I becomes BPBI II by measurement error. Median test show that the BPBI distributions between the *T. pedum* and the *R. avalonensis* zones were significantly different (the median value is BPBI II, $p < 0.025$).

On the other hand, intense bioturbations were already observed in the *T. pedum* Zone in the Zhujiaqing and Bayan Gol formations (Figure 27). In the Zhujiaqing Formation, a total of 10 bedding surfaces were surveyed in the *T. pedum* Zone. Only one bedding plane showed BPBI I. However, intense bioturbations were observed on the other

bedding planes; BPBI II on five beds and III on four. The maximum density of ichnofossils is 36%, and the average density is 12%. Because the outcrop was not well exposed, the BPBI in the *R. avalonensis* Zone could not be studied in this section.

In the Bayan Gol Formation, a total of 11 bedding surfaces were studied in the *T. pedum* Zone (Figure 27). As in the case of the Zhujiaqing Formation, only a small number of bed showed BPBI I. The other beds, however, were heavily bioturbated; BPBI II on three beds and III on six. Moreover, one bed was quite heavily bioturbated (BPBI V). The maximum density is 96%, and the average density is 19%. Among a total of 12 beds from the *R. avalonensis* Zone, both of the maximum and average densities decreased (maximum 23% and average 10%), intense bioturbation was observed on almost all bedding planes. Thus, intense bioturbation was confirmed both in the *T. pedum* and *R. avalonensis* zones.

There were significant differences of the BPBI distribution of the *T. pedum* Zone between the Chapel Island and Zhujiaqing formations (the median value is BPBI II, $p < 0.025$), and also between Chapel Island and Bayan Gol formations (the median value is BPBI II, $p < 0.025$). On the other hand, no significant differences were observed from the *R. avalonensis* Zone between Chapel Island and Bayan Gol formations (the median value is BPBI II, p-value = 0.4063).

5.d. Discussions

5.d.1. Limited occurrences of ichnofossils *Gyrolithes* and *Didymaulichnus*

In this study, it became clear that the occurrence of *Gyrolithes* isp. and *Didymaulichnus miettensis* were limited in specific regions; *Gyrolithes* occurred in Newfoundland, *Didymaulichnus miettensis* appeared in Yunnan and Gobi-Altai. These limited occurrences of ichnofossils indicate that the living animal and/or animal behavior differed from region to region in the earliest Cambrian. In a previous study from other areas, *Gyrolithes* isp was abundant in the lower Cambrian units of Baltica (Droser et al., 2002b). On the other hand, *Didymaulichnus* isp. was reported from the lower Cambrian Rocky Mountains of Canada (Young, 1972), India (Parcha and Singh, 2010) and central Australia (Graessner, 1969) as molluscan trail. Interestingly, both occurrence of Gyrolithes and Didymaulichnus were reported in the Early Cambrian strata in Estonia (Jensen and Mens, 2001). Therefore, it is indicated that *Gyrolithes* isp. was abundant in the earliest Cambrian west Avalonia (including Newfoundland) and Baltica, whereas *Didymaulichnus* isp. mainly occurred in the earliest Cambrian south China, Mongolia, Laurentia, Australia and Baltica (Figure 28).

The reason for these biogeographical differences could be related to a

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palaeogeographical factor of studied sections. Previous studies indicate that west

Avalonia was located in a high latitude region, whereas south China and Mongolia were

located in a low latitude region in the earliest Cambrian (Steiner et al., 2007). Based on

the paleomagnetic data from the Neoproterozoic and the Cambrian, southeastern

Newfoundland was situated at 34°S +8°/-7° paleolatitude at ca. 580-570 Ma and moved

to higher southerly latitude (60°-54°) during the Late Cambrian (McCabe et al., 1992;

Trench et al., 1992; McNamara et al., 2001; Hibbard et al., 2007). Therefore, the position

of Newfoundland was in the middle to high latitudes in the early Cambrian. On the

contrary, South China was located near the equator in the early Cambrian. According to

the paleomagnetic study by Huang et al. (2000; Figure 2), the South China Block was

located near the equator, between 0-15°N. Not many studies on the Cambrian

paleogeographic position of western Mongolia are available, but some studies (e.g. Wood

et al., 1993) show that the Zavkhan microcontinent (where the Bayan Gol Formation is

located) was located between 10°N and 10°S. Thus, different occurrences of specific

ichnofossils could be influenced by these differences in paleo-latitude. Indeed, the

sections where *Didymaulichnus miettensis* was commonly reported are located in low

latitude areas in the earliest Cambrian (South China, Mongolia, Laurentia and Australia).

On the other hand, *Gyrolithes* isp. is commonly observed in west Avalonia which was

located from middle to high latitude area. In Baltica, which was located middle latitude, both ichnofossils were observed in the Early Cambrian strata. These observations also suggest that the development of animal behavior, or possibly living animals, differed between low and high latitude regions in the earliest Cambrian.

5.d.2. Diversification of benthic animal body sizes in three regions

Geographical differences were also shown in the size distribution of the ichnofossil (Figure 24). The analysis of width distribution of *Planolites* shows that various sizes of *Planolites* firstly occurred in the *R. avalonensis* Zone in the Chapel Island formation. Therefore in Newfoundland, it is indicated that the trace makers of *Planolites* firstly achieved various body sizes in the *R. avalonensis* Zone, while their body size was small in the *T. pedum* Zone. On the other hand, the analysis in the Zhujiaqing and Bayan Gol formations shows a different trend. In both areas, various sizes of *Planolites* are already observed in the *T. pedum* Zone. Besides, there is no extreme bias toward a specific size, which can be observed in the *T. pedum* Zone in the Chapel Island Formation. Thus, in Yunnan and Gobi-Altai regions, *Planolites* producers already diversified in the *T. pedum* Zone. These results also suggest that there is a regional difference for the process of diversification of animal body sizes in the earliest Cambrian.

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The size of *Planolites* can be influenced by environmental rather than evolutionary factors (Marenco, 2006 MS). Dominant sizes of *Planolites* are different among nearby bedding surfaces, suggesting that the size of *Planolites* is partly controlled by environmental factors. However, accumulation of data from multiple bedding surfaces representing varied facies allowed us to estimate a general pattern of body size change.

Some studied argued that the diameter of *Planolites* became reduced in some environmental factors, such as low oxygen levels (Savrda and Bottjer, 1987), low saline levels (Pemberton et al., 1982) and low nutrient supplies (Jumars and Wheatcroft, 1989). These studied indicate that the sizes of *Planolites* became small under stress environment for animals (Pruss and Bottjer, 2004). Although there is no conclusive evidence that the Chapel Island Formation was deposited under such a stressful environment in the age of *T. pedum* Zone, it is possible that oxygen level in Newfoundland was lower than in Meishucun and Gobi-Altai in the earliest Cambrian. A piece of corroborate evidence for this hypothesis is the presence of wrinkle structures in the Chapel Island Formation. It is generally recognized that wrinkle structures were formed by microbial mats developed under a stressful environment in Phanerozoic (Pflüger, 1999). However, it is doubtful whether this theory can be applied to the Cambrian environment or not. Because Cambrian is the transitional regime from Proterozoic to Phanerozoic, the microbial mat

structures were sometime reported in the Cambrian strata all over the world (Hagadorn and Bottjer, 1999). In fact, abundant wrinkle structures can be observed in the Middle Cambrian Wolsey Shale Formation in Clarks Fork Canyon, Wyoming. The size distribution of *Planolites*, however, shows wide range of diameters (Figure 29). Thus, frequent occurrences of microbial mat could not indicate that the stratum was always deposited under stressful environment in Cambrian.

Another possible explanation is that the various sizes of *Planolites* are attributed to the earliest Cambrian benthic animal evolution. In general, animal body sizes tend to diversify through the process of evolution (Hayami, 1978). Payne et al., (2009) study the fossil body sizes of various ages and show that rapid animal size increase occurred twice in history of life; first occurred in the middle of the Paleoproterozoic, second from Ediacaran to Ordovician. Thus, diversification of benthic animals due to rapid evolution in the earliest Phanerozoic could be preserved as various sizes of ichnofossil. If that in fact occurred, various sizes of *Planolites* indicate that rapid diversification of the animals firstly occurred in low latitude regions including Yunnan and Gobi-Altai in the age of the *T. pedum* Zone. On the other hand, it is also suggested that this diversification occurred late in high latitude regions as Newfoundland, that is, in the age of the *R. avalonensis* Zone.

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5.d.3. Development of intense animal activities in three regions

The analysis of BPBI in the *T. pedum* Zone of the Chapel Island Formation shows that the animal activities were generally weak at the beginning period in the earliest Cambrian in Newfoundland (Figures 25 and 27). Moreover, the biological activities frequently disappeared. This trend, however, dramatically changed in the *R. avalonensis* Zone. As the BPBI showed, the bioturbations were observed on almost all bedding planes, whereas one bedding plane showed no bioturbation. Thus, there was a relatively rapid increase in benthic animal activity from the earliest Cambrian *T. pedum* to the *R. avalonensis* zones in Newfoundland. In addition to the rapid increase of animal activity, decrease of the bedding plane with no bioturbation indicates that the biological activity occurred more frequently in the *R. avalonensis* Zone than that of in the *T. pedum* Zone. Besides, all the bedding plane with bioturbation in the *T. pedum* Zone show BPBI II (Figures 25 and 27). On the other hand, a number of bedding planes (N = 14) show BPBI II and 3 bedding planes show BPBI III (Figures 25 and 27) in the *R. avalonensis* Zone. These results indicate that the intensity of benthic animal activity sometimes varied in the *R. avalonensis* Zone, whereas the intensity was almost same in the *T. pedum* Zone.

These Ichnofossil densities of bedding planes were actually influenced by

sedimentation rate. Based on the result from Chapel island Formation, however, the densities were different within same facies (ex. GC facies, Sh facies and SS-D facies in Figure 25). Because depositional rate could not change rapidly in single depositional facies, these differences of densities should show the active level of benthic animals at the time. Besides, sedimentation rate is generally low in mudstone settings. If BPBI was influenced by the depositional rate, index would be commonly higher in muddy facies (GC and SiS-D facies) than in sandy facies (SS-D facies). However, results of this study show higher densities of ichnofossils in SS-D facies of the *R. avalonensis* Zone than that of in GC and SiS-D facies of the *T. pedum* Zone. Thus, it is reasonable to suppose that the change of densities of ichnofosils can be correlated with the intensity of benthic animal activity rather than the sedimentation rate.

On the other hand, in the Zhujiaqing and Bayan Gol formations, many bedding planes showed high ichnofossil densities in the *T. pedum* Zone (Figure 27). This observation indicates that the biological activity was already intense in the earliest Cambrian *T. pedum* Zone in Yunnan and Gobi-Altai regions. In addition, the bedding plane with BPBI I was quite few. Therefore, it is indicated that the biological activity constantly occurred in the *T. pedum* and the *R. avalonensis* zones in these two regions. Moreover, the intensity of the biological activity was heavier than that in the *R.*

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avalonensis Zone of Newfoundland. These observations suggest that there is a regional difference in the biological activities similar to the one observed for the size distribution of *Planolites*.

The main factor of development of intense biological activity is unclear. However, this may be derived on biological productivity and nutrient supply from surface water mass to benthic layer, because amount of organic matter supply should influence benthic biological activities (Wetzel, 1984).

Previous study indicated that the planktonic ecological system, which is as complex as in the modern ocean, was already constructed in the earliest Cambrian (Casenove, 2010 MS). It is also implied that prey-predator system was formed in same age evidenced from the occurrence of probable fossil chaetognatha in South China (Vannier et al., 2007; Casenove, 2010 MS). To construct a certain level of complex ecosystem, primary productivity should have been already high in the earliest Cambrian. Besides, biological productivity thereby would be increased in marine surface layer, and supply the nutrient to sea floor. These processes might promote intense benthic animal activities in the earliest Cambrian. Delay of the occurrence of heavy bioturbation in the Chapel Island Formation may suggest that surface ecological system first developed in the age of the *R. avalonensis* Zone in high latitude region such as Newfoundland, whereas

it had been already constructed in the age of the *T. pedum* Zone in low latitude region

(Yunnan and Gobi-Altai).

5.d.4. Expansion of the earliest Cambrian benthic animal diversification

To summarize the above discussions, the most probable explanation for the

geographical difference of the occurrences, sizes and densities on the bedding plane of

ichnofossils should be the difference of latitudes between three regions. Other

possibilities include the difference of host rock types of ichnofossils among studying

sections; the Zhujiaqing Formation mainly consists of phosphorite whereas the Chapel

Island and the Bayan Gol formations consist of mudstone and sandstone. Existence of

variously sized *Planolites* and intense bioturbation, however, are confirmed both in the *T.*

pedum Zone of Meishucun and Gobi-Altai sections. Considering the different lithologies

of these two formations yet the both have intense bioturbations with large-sized *Planolites*,

it would be difficult to think that these different lithologies causes differences of

ichnofossil sizes and the digree of bioturbations.

Seawater composition might be another possible factor for causing the different

sizes and activities of ichnofossil producers. The three formations surveyed are regarded

as representing a shallow but open marine environment. Abundance of carbonate rocks

in the Meishucun and Bayan Gol formations suggest such an interpretation. The Chapel

Island Formation almost lacks carbonate rocks but the most part has also been assigned

to open marine environment by the typical sedimentary structures (gutter casts, storm

beds; Mylow, 1992). Thus difference of sea water composition is not plausible for

explaining the difference of ichnofossil sizes and abundances. On the other hand, it is

reasonable to suppose that the different paleo-latitudes between studying regions can be

a major factor for the difference of sedimentary environments; previous studies showed

that the paleo-latitudes are quite different between Newfoundland, and Yunnan and Gobi-

Altai (ex. Steiner et al., 2007).

Based on these discussions above, it would be reasonable to suggest that the

diversification of *Planolites* producers and intense biological activities should start earlier

in the low latitude regions than in the high latitude regions in the earliest Cambrian *T.*

pedum Zone. After a brief interval, diversified sizes of animals and heavy biological

activities followed and spread to the high latitude regions in the *R. avalonensis* Zone

(Figure 30).

The reason why the various sizes of animals and the intense biological activities

first appeared in low latitude regions remains unclear. However, a possible explanation

may include different climates between low and high latitude regions in the earliest

Cambrian. Dolomites, microbialites, oolites and flat pebble breccias, which are frequently observed in the Zhujiaqing and the Bayan Gol formations, suggest warm depositional environments after the Varangian glaciation (Brasier, 1992). On the other hand, these sediments are rarely observed in the Chapel Island Formation. Besides, presence of drop stone was reported in the middle Member of Chapel Island Formation (Landing and MacGabhann, 2010). These observations indicate that there were climate differences between low latitude regions and high latitude in the earliest Cambrian; warm temperature in low latitude regions and cold temperature in high latitude regions.

In the modern world, temperature strongly correlates with biological diversity (Currie, 1991). Because Biochemical metabolism kinetics is faster at high temperature region, species generation time decrease (Kirschvink and Raub, 2003). Therefore, rapid animal diversification in the earliest Cambrian might first start in low latitude regions. If this in fact occurred, preceding appearance of various sizes of animals in low latitude regions can be interpreted as the result of rapid evolution of animals. As a basis for this prediction, first small shelly fossils appeared with, or sometimes before, the first occurrences of *T. pedum* in some low latitude regions (Khomentovsky and Gibsher 1996, Steiner et al., 2007), suggests that planktonic ecological system would be constructed at least in warm low latitude regions in the time of *T. pedum* Zone. On the other hand, small

shell fossils are first observed in Members 3 and 4 (Terreneuvian Stage 2) in the Chapel Island Formation, Newfoundland (Landing et al., 1989; Steiner et al., 2007). No occurrence of small shelly fossil in Members 1 and 2 might be attributed to the delay start of animal penetrating into high latitude regions from low latitude; of course, facies control could have the strongest influence on preserving of small shelly fossils. This construction of ecosystem could provide intense benthic animal activities in low latitude region in the age of *T. pedum* Zone.

However, appearance of various sizes of *Planolites* and intense bioturbations were also observed in the Chapel Island Formation of the *R. avalonensis* Zone. This observation indicates that the appearance of various animals and construction of ecosystem could spread to middle and high latitude after a short while. If so, it is also suggested that the earliest Cambrian diversification expanded all over the world in a quite short period from the time of *T. pedum* to the *R. avalonensis* zones in Fortunian, that is, 544 – 535 Ma (Figures 1 and 30).
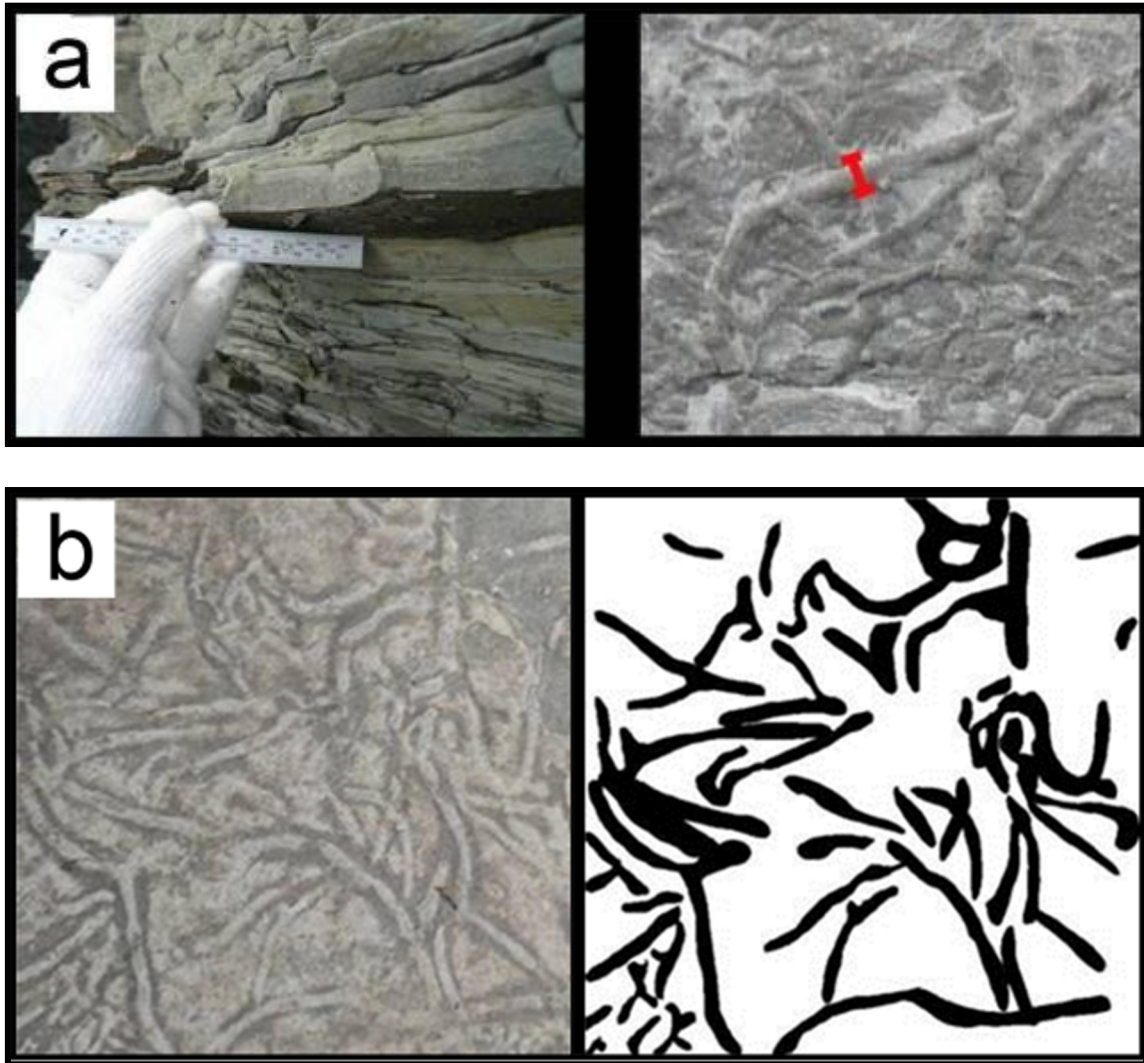
Figure 20. a) Measurement method of ichnofossil *Planolites*. The thickest positions of tubes were measured by using calipers. b) Measurement method of bedding plane bioturbation index (BPBI). Sole bedding surfaces were taken by photo and scanned their outlines into a computer. The densities of ichnofossil were calculated from the number of pixels by using a paint program.
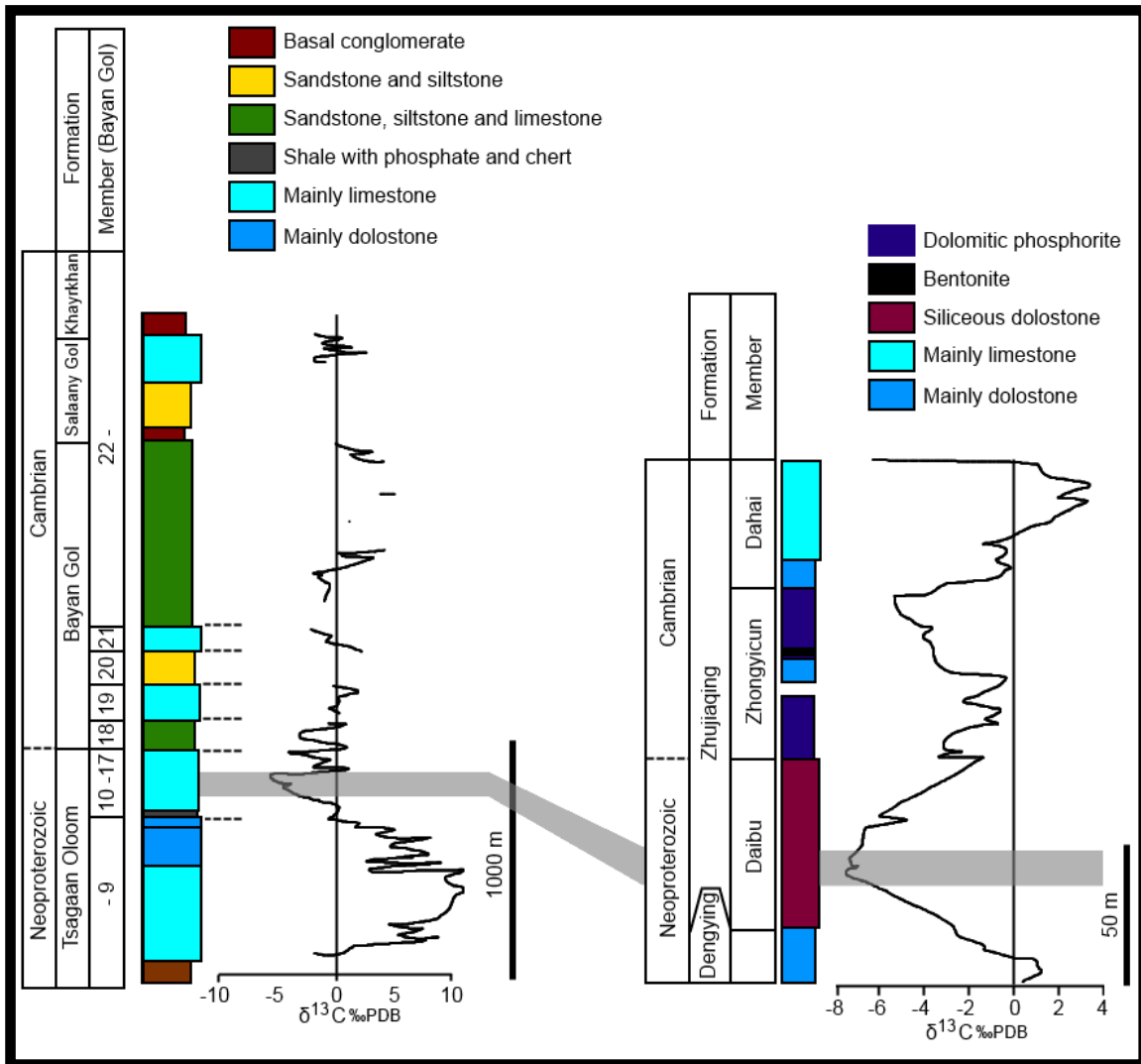
Figure 21. δ¹³C curve from the latest Neoproterozoic to the earliest Cambrian between Gobi-Altai and Yunnan (modified after Brasier et al., 1996b; Li et al., 2009; Fan et al., 2010). Gray band shows the large negative anomaly of the BACE event. Correlation of the BACE is referred from Li et al. (2009).
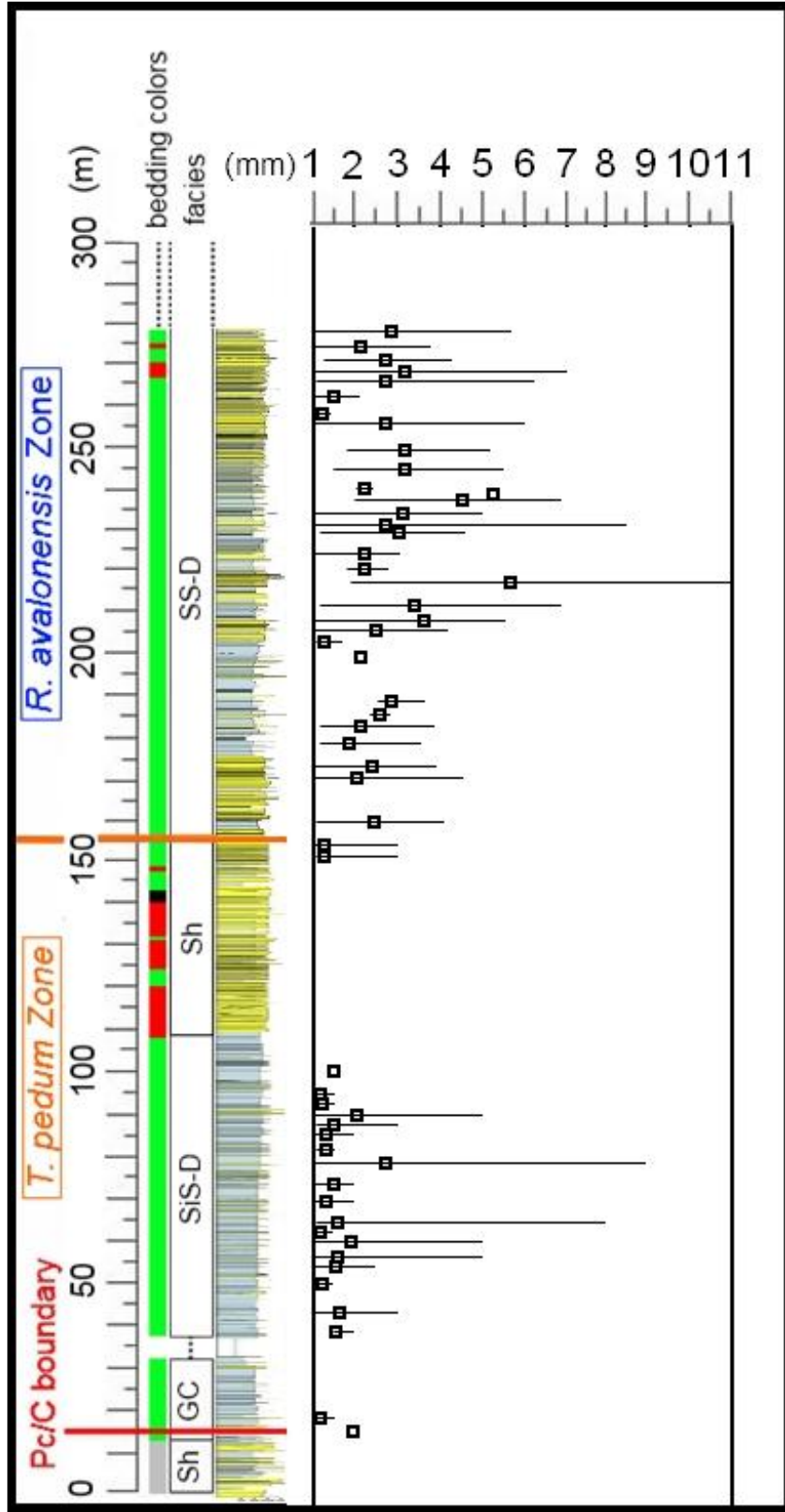
Figure 22. Change of the size distribution of *Planolites* in the Chapel Island Formation. Vertical axis shows the levels of horizon from the base. Horizontal axis shows width of *Planolites*. Lateral bars show the size distributions of the *Planolites*; left-most side shows the minimal diameters of *Planolites*, and right-most side shows the maximum diameters of *Planolites* in each horizon. The square marks indicate average sizes of *Planolites* in each horizon.
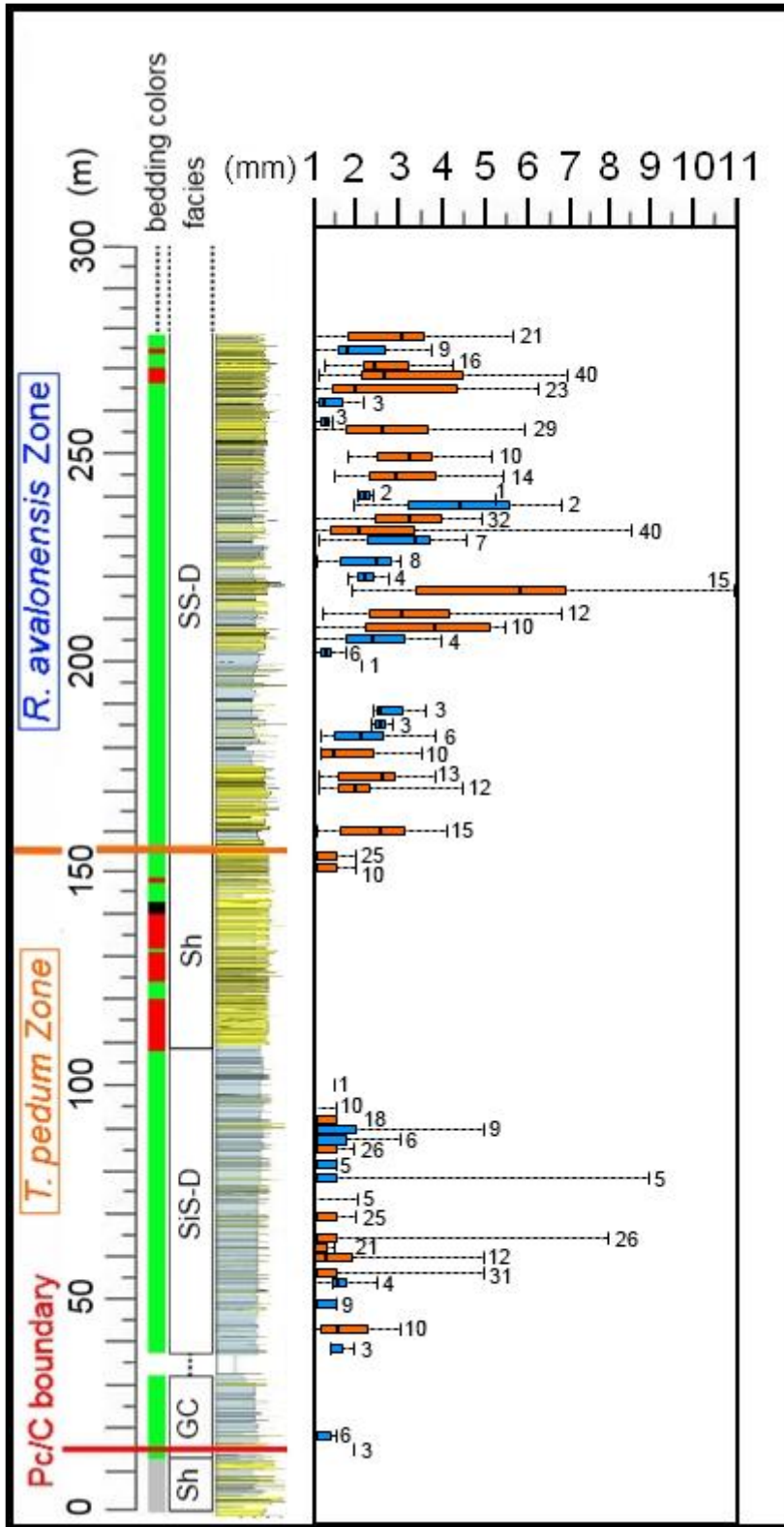
Figure 23. Change of the size distribution of *Planolites* in the Chapel Island Formation shown by boxplot of quartile. Vertical axis shows the levels of horizon from the base. Horizontal axis shows width of *Planolites*. Lateral bars show the size distributions of the *Planolites*; left-most side shows the minimal diameters of *Planolites*, and right-most side shows the maximum diameters of *Planolites* in each horizon. Orange box shows the horizon which has more than 10 specimens of *Planolites*, blue box shows less than 10 specimens. Left-most side of box shows 25 percentile, and right-most side of box shows 75 percentile. Black band in the box shows median value. The numbers next bars show the number of individuals in each horizon.
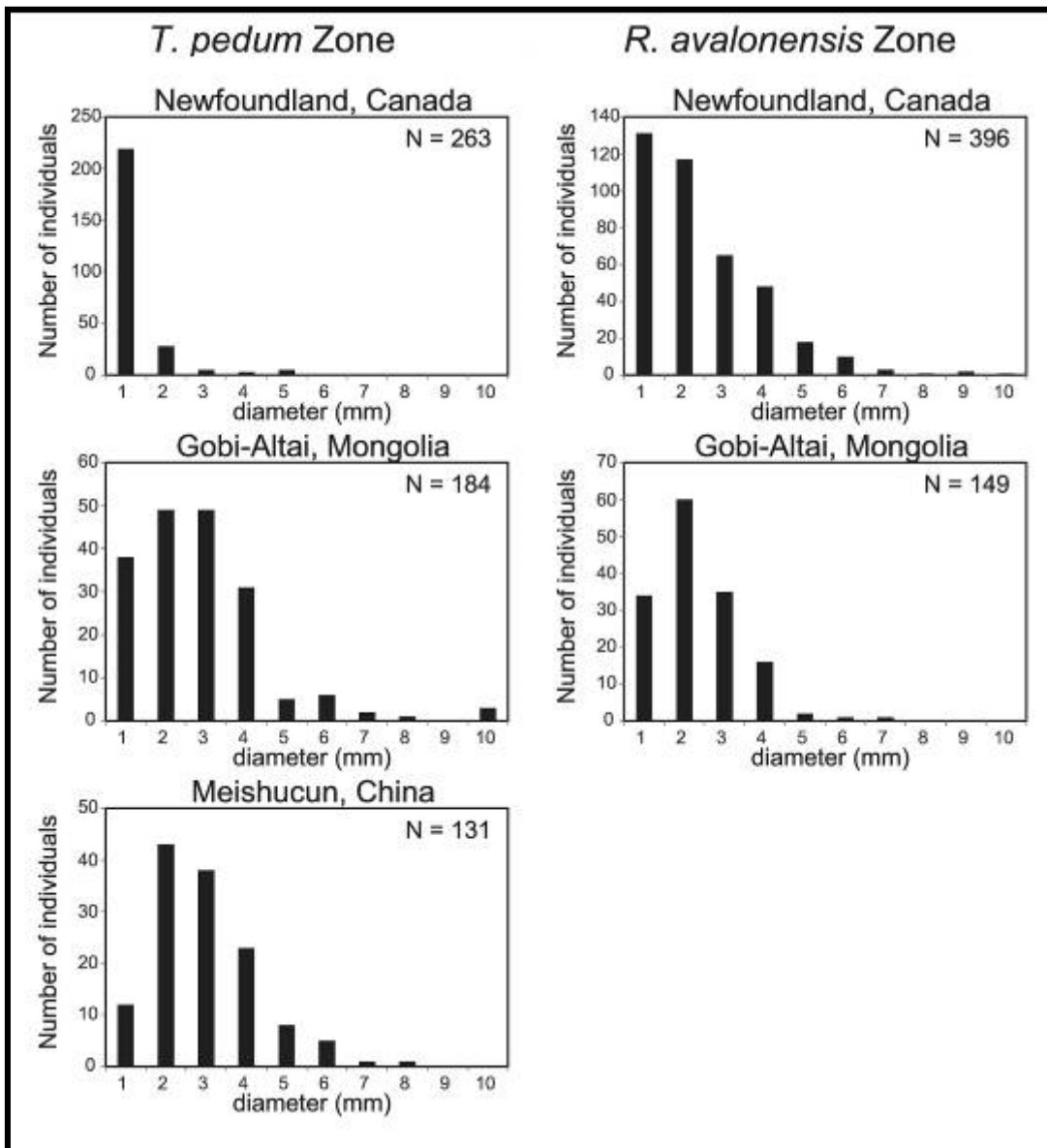
Figure 24. Comparison of size distributions of *Planolites* between 3 regions. Vertical axis shows the number of individuals of *Planolites*. Horizontal axis shows maximum diameters of *Planolites*.
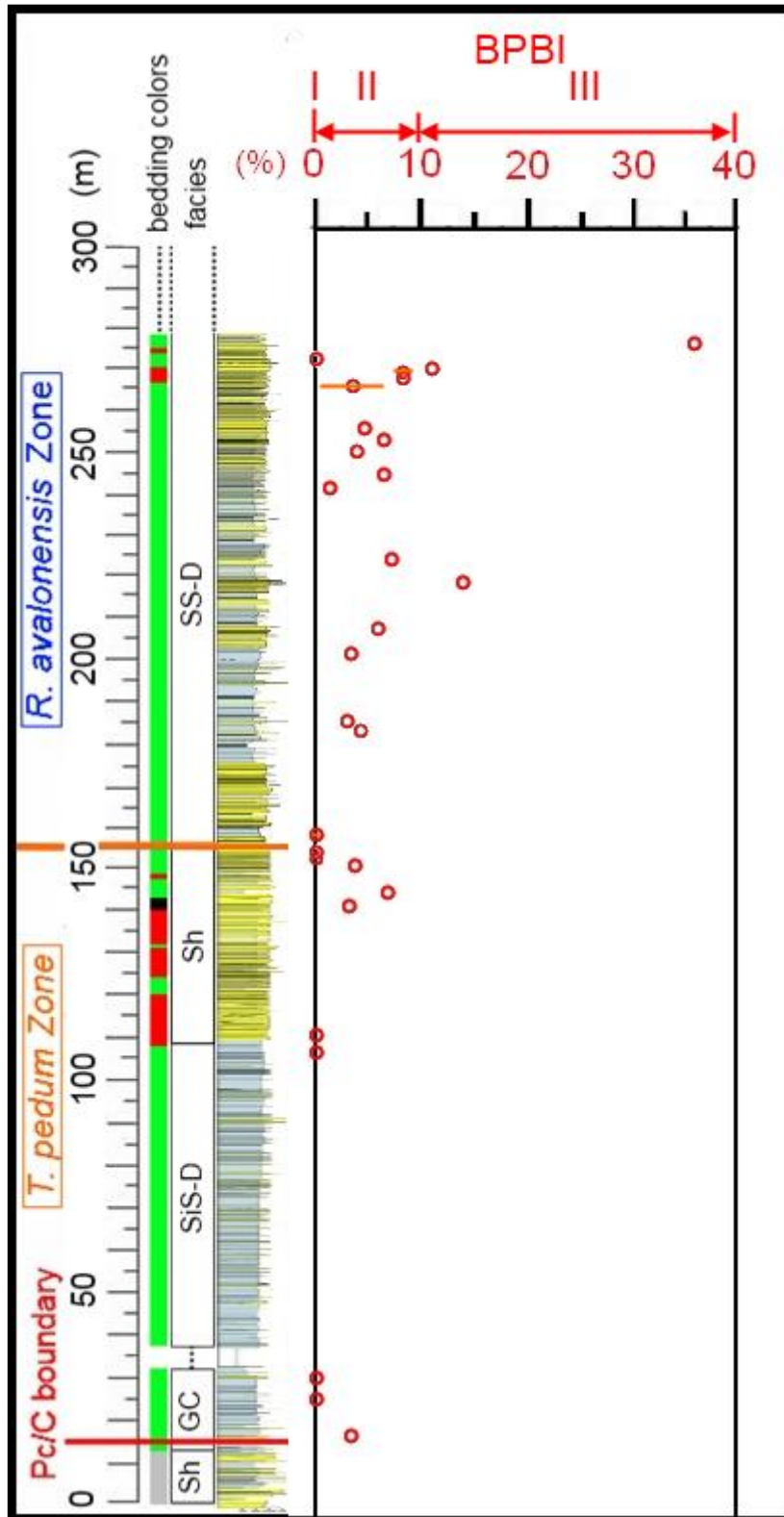
Figure 25. The densities of ichnofossils in each horizon of the Chapel Island Formation. Vertical axis shows levels of horizon from the base. Horizontal axis shows densities of ichnofossils and bedding plane bioturbation index on bedding planes. Lateral bars on markers around 150 and 270 m show the standard errors which are calculated by average densities of ichnofossils from 3 measurement compartments on wide bedding planes.
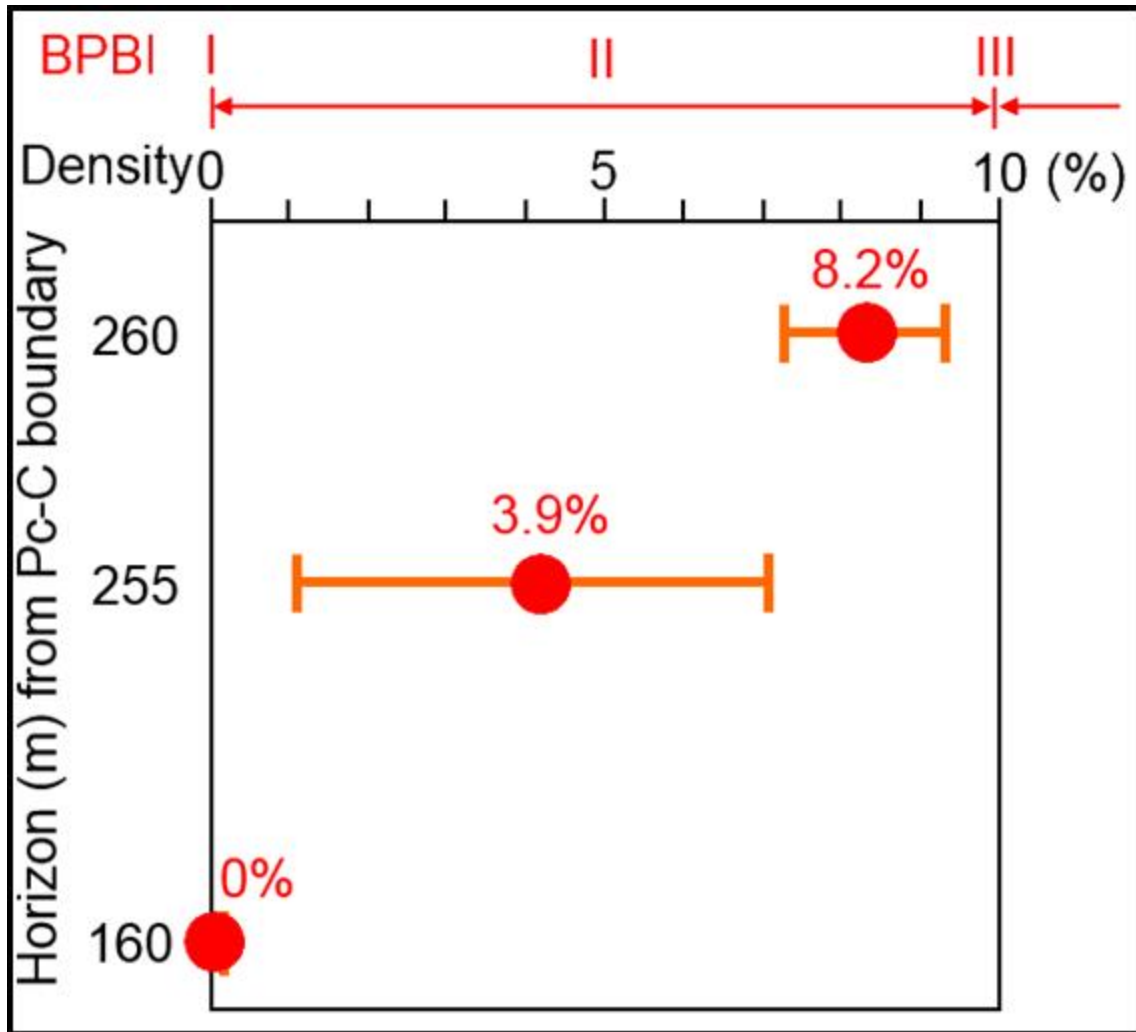
Figure 26. Average density of ichnofossils on the large bedding plane and its error bars

(2σ) from the Chapel Island Formation. Horizontal axis shows densities of ichnofossils

and bedding plane bioturbation indices on the bedding planes. Horizontal axis shows the

horizon from the Pc-C boundary. Average density is measured by three compartments

(single compartment is 600 cm^2). Red circle and number shows average density in each

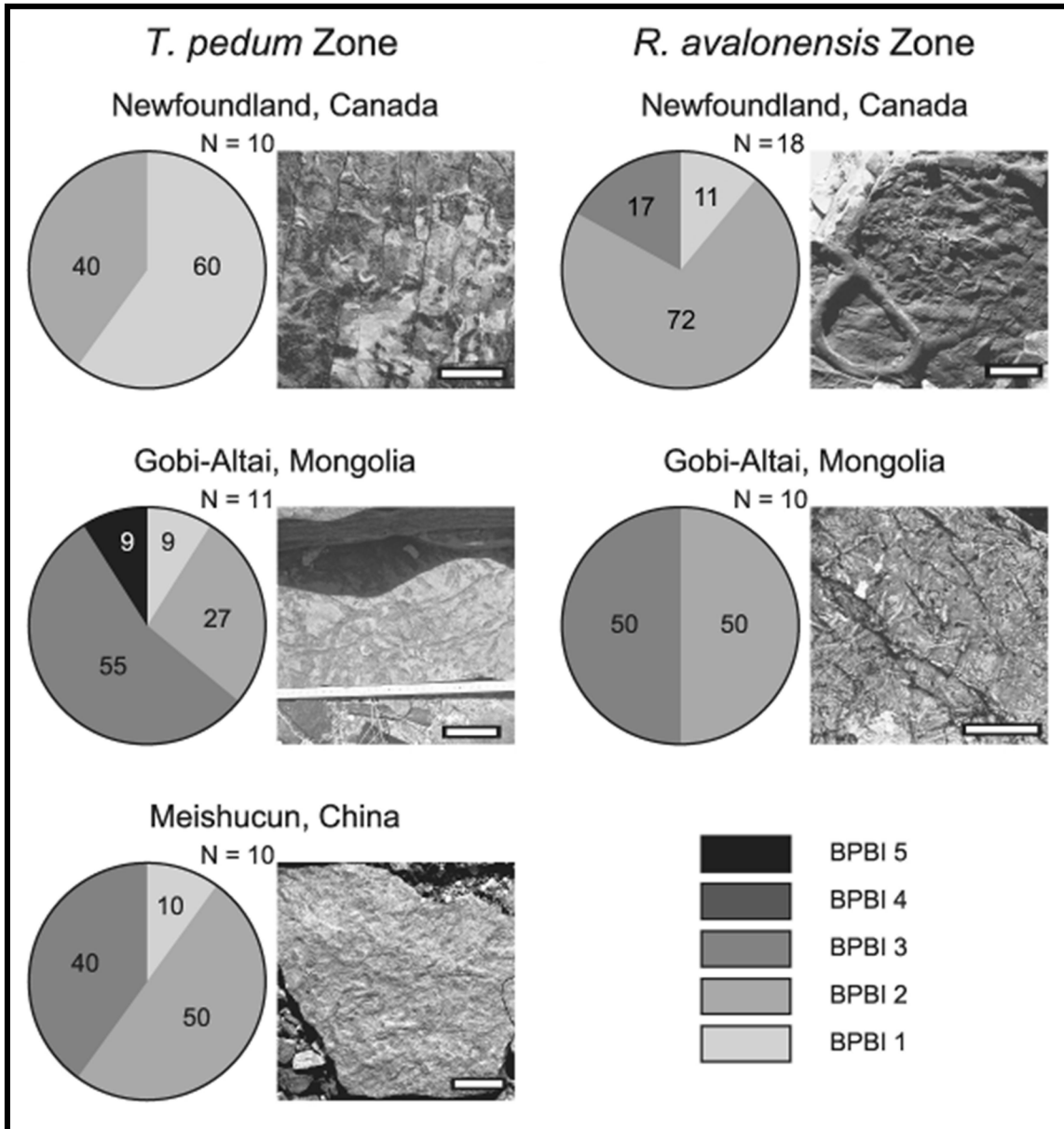bedding plane. Orange bar show error bar.

Figure 27. Comparison of the BPBI between 3 regions. Bars show 5 cm. Index I represents no observable bioturbation recognized on the bedding plane; II, the density of ichnofossils covers 1-10% of the bedding plane; III, 10-40%; IV, 40-60%; and V, 60-100%.
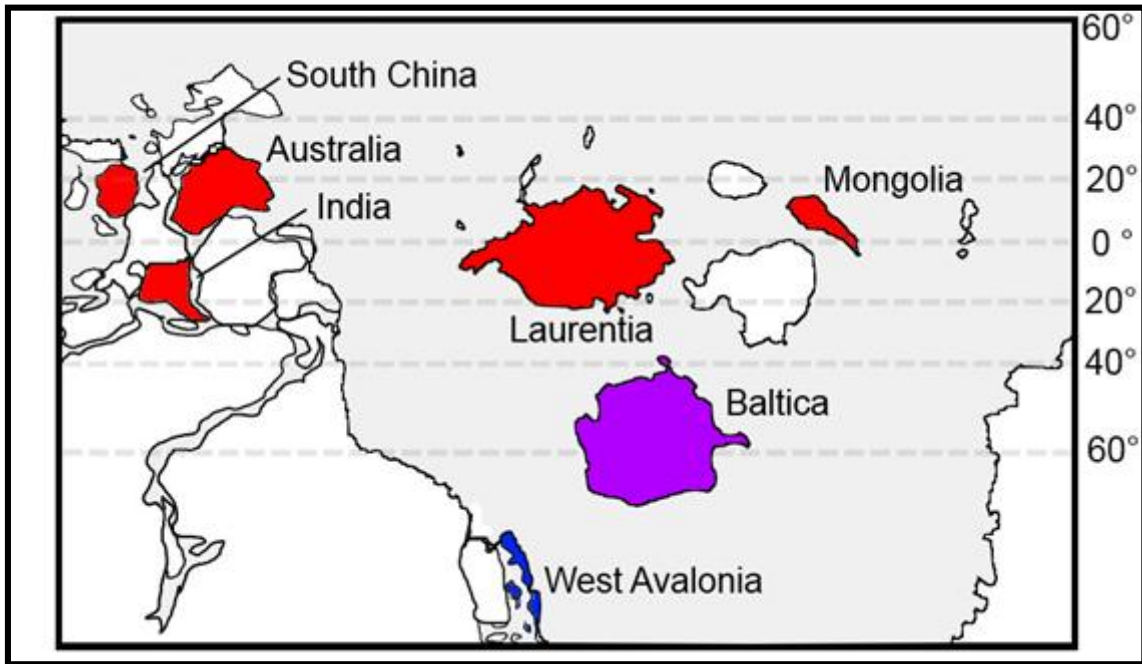
Figure 28. Eatimated paleomap of the earliest Cambrian (modified after Steiner et al., 2007). Red areas show that the occurrences of ichnofossil *Didymaulichnus* have been reported by previous studies (Graessner, 1969; Young, 1970; Goldring and Jensen, 1996; Zhu, 1997; Parcha and Singh, 2010). Blue area shows that the occurrences of ichnofossil *Gyrolithes* (Narbonne et al., 1987) have been reported by previous studies. Purple area shows that the occurrences of both ichnofossils were reported (Jensen and Mens, 2001).
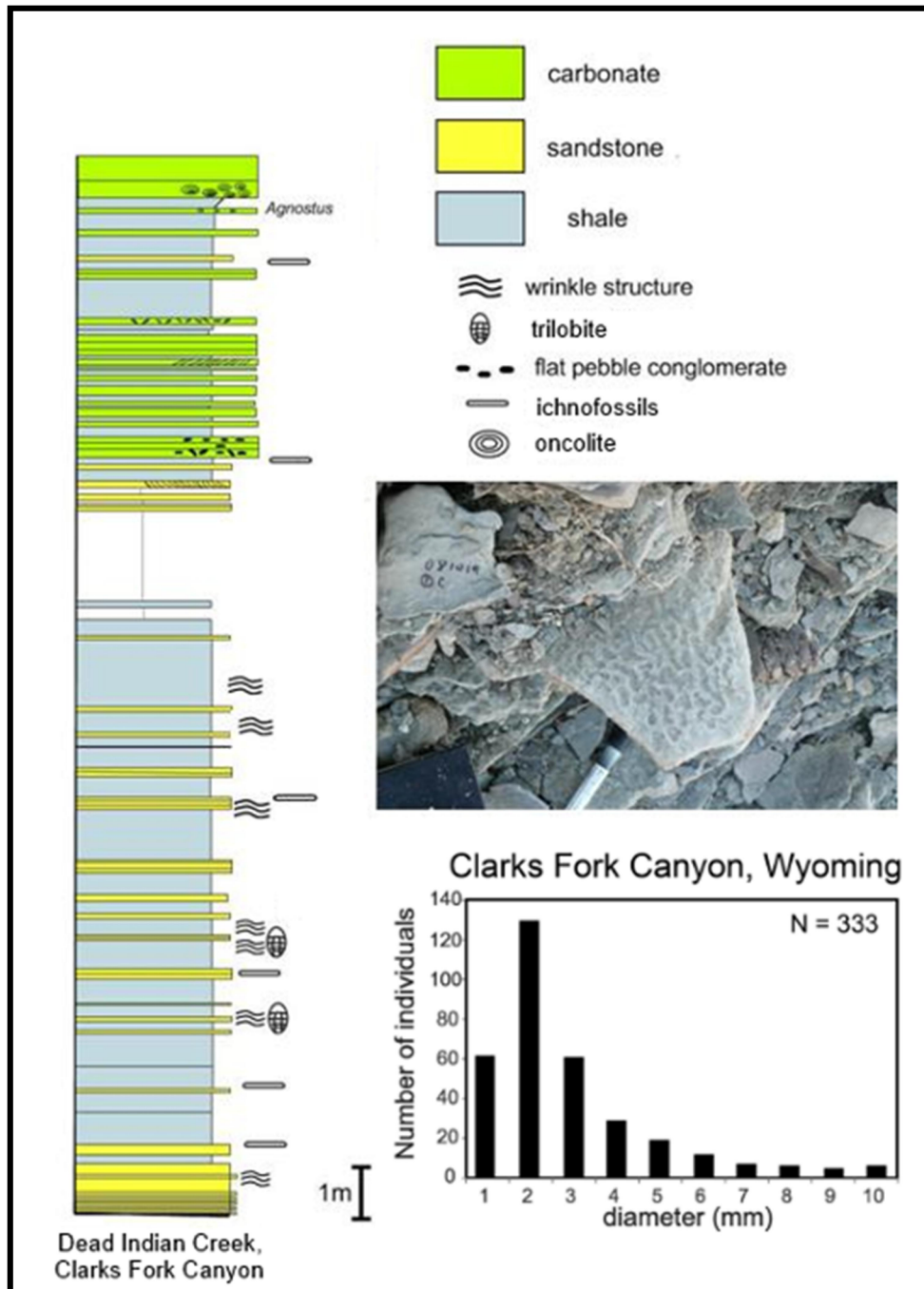
Figure 29. Columnar section of Middle Cambrian Wolsey Shale Formation in Clarks Fork

Canyon, Wyoming. Lateral thickness of beds shows concavity and convexity of the

outcrop. Photo indicates the occurrence of wrinkle structure on the outcrop. Chart shows

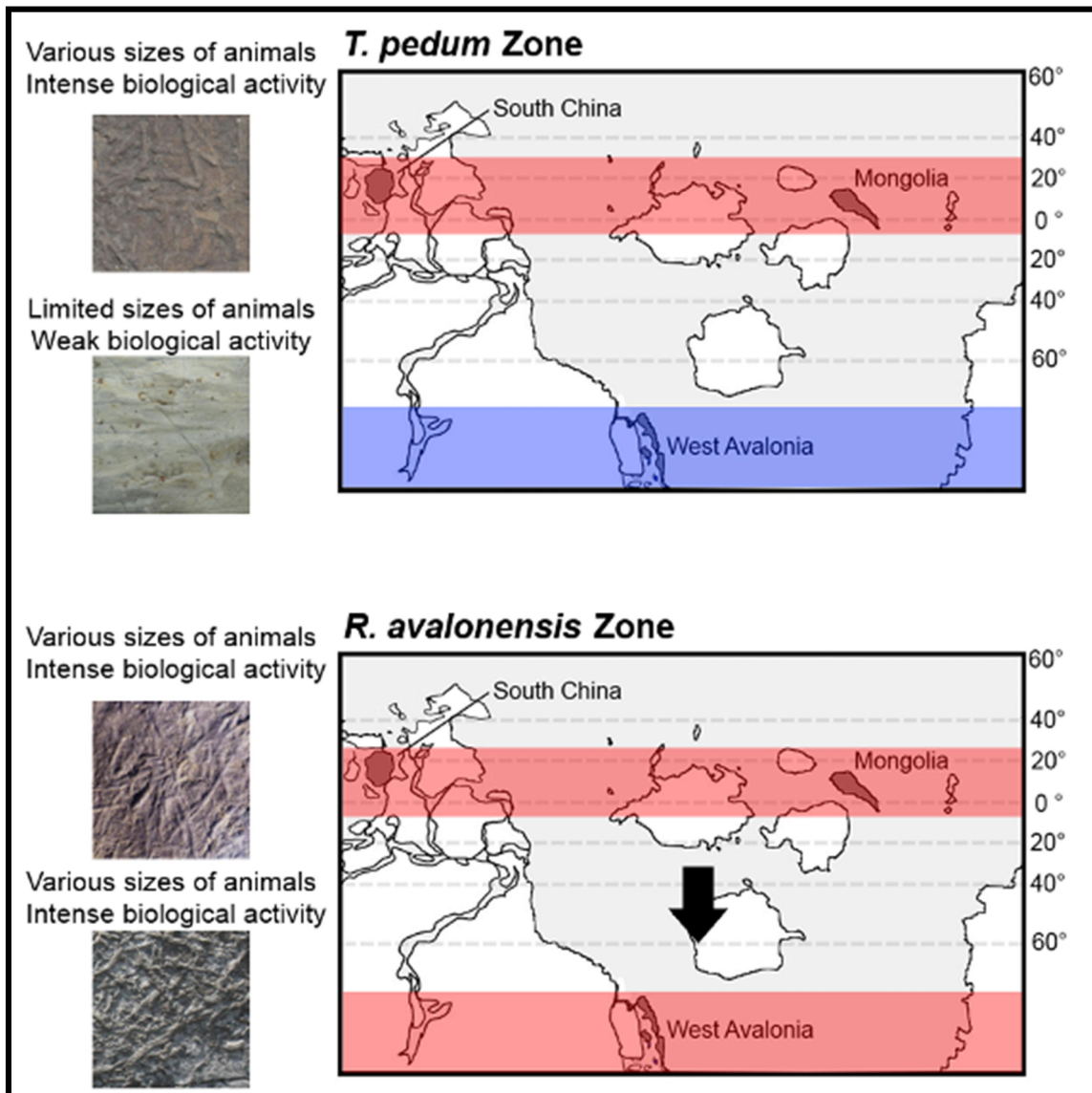the diameters of *Planolites* in this Formation.

Figure 30. The presumed expansion model of the diversification of animal body sizes and intense biological activities from the time of *T. pedum* to *R. avalonensis* zones. Red bands show the regions with various sizes of animals and intense biological activities. Blue band show the regions with limited (small) sizes of animals and weak biological activities.

8. Conclusions

1. The diversification pattern of ichnofossils in the earliest Cambrian Chapel Island Formation, Newfoundland shows that the major diversification of the ichnofossils occurred twice; first at the almost basal part of the Pc-C boundary, second around the boundary of the *Treptichnus pedum* and *Rusophycus avalonensis* zones.

2. Based on the ichnofossil assemblages from the Chapel Island Formation, there was no remarkable difference in the ichnofossil assemblages from different depositional facies. Therefore, the animal behavior occurred in a wider environmental spectrum in the earliest Cambrian than those of the later ages.

3. The ichnofossil assemblages were considerably differed in the late Early Cambrian Balang and Chintingshan formations in China. The animals could have started to adapt and to be diversified their behavior corresponding to the environment since the late Early Cambrian.

4. Variously sized *Planolites* appeared in the *R. avalonensis* zones, suggesting that a general size increase of *Planolites* producers firstly occurred in the *R. avalonensis* zone in Newfoundland. On the other hand, the size distribution of *Planolites* in Yunnan and Gobi-Altai showed that the various sizes animals already appeared in the *T. pedum* Zone.

These differences indicate that a rapid evolution in the earliest Cambrian could first occur in low latitude regions.

5. The densities of ichnofossils suggest that animal activity firstly became intense in the *R. avalonensis Zone in Newfoundland, whereas these were already intense in the T. pedum* Zone in Yunnan and Gobi-Altai. These differences would be derived from the different timing of construction of the earliest Cambrian ecology in marine surface layer and increase of nutrient supply in these areas.

6. There were geographical differences in the animal activity between Newfoundland and Yunnan - Gobi-Altai. One possible factor of the geographical difference could be based on the difference of climate between low and high latitude regions. Moreover, a rapid evolution of animals and their intense activities could have firstly occurred in warm low latitude regions (Meishucun and Gobi-Altai) in the *T. pedum* Zone. These animal activities subsequently reached high latitude regions (Newfoundland) in the *R. avalonensis* Zone.

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Supplemental Figures
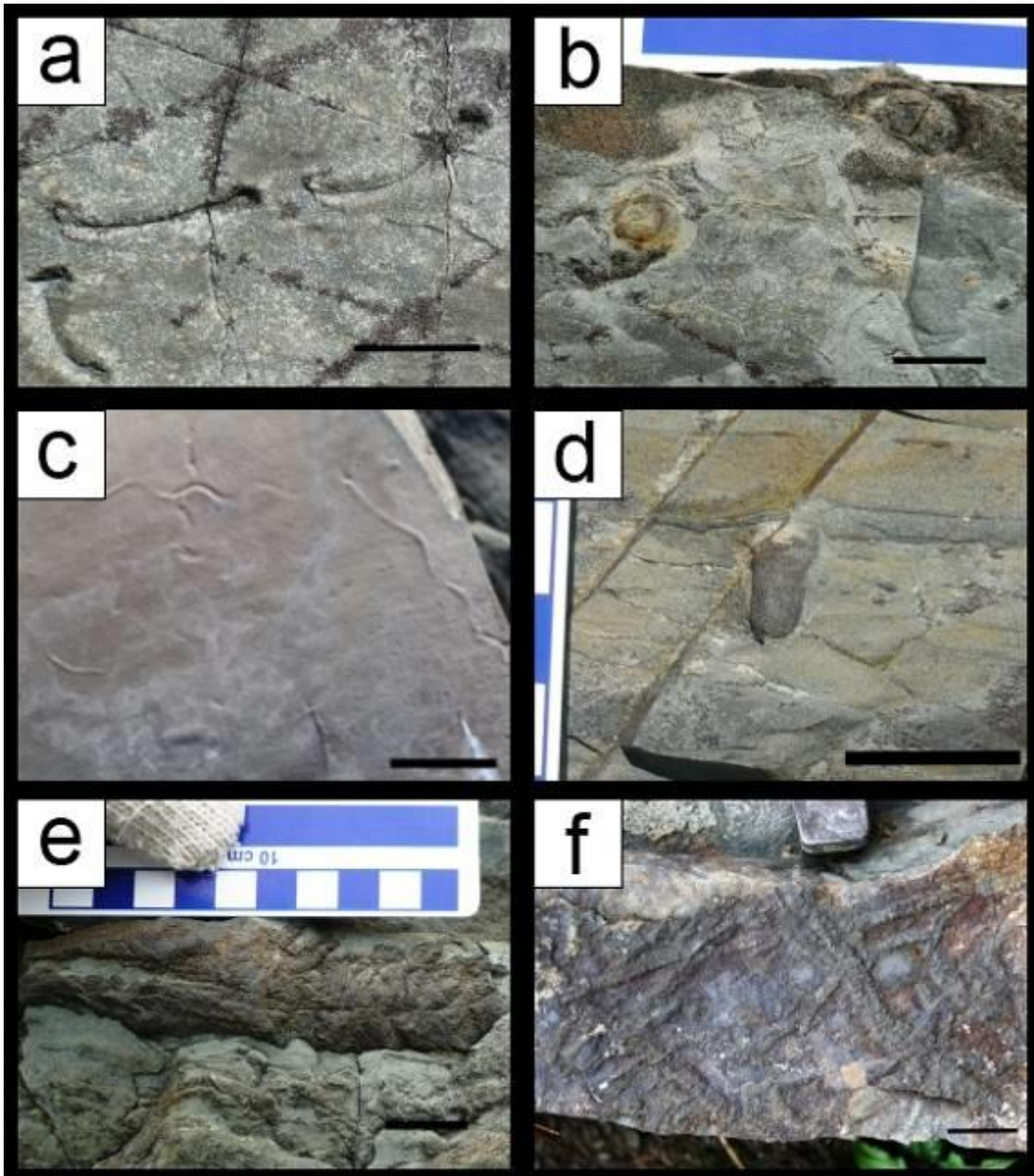
Figure 31. a: *Arenicolites* isp., top view, uppermost part of the *T. pedum* Zone of the

Chapel Island Formation, Newfoundland, bar; 2 cm. b: *Bergaueria* isp., top view,

uppermost part of the *T. pedum* Zone of the Chapel Island Formation, Newfoundland, bar;

2 cm. c: *Cochlichnus* isp., float, *R. avalonensis* Zone of the Chapel Island Formation,

Newfoundland, bar; 2 cm. d: *Conichnus conicus*, side view, near the basal part of the *T.*

pedum Zone of the Chapel Island Formation, Newfoundland, bar; 2 cm. e: *Cruziana* isp.

type a, sole view, upper part of the *R. avalonensis* Zone of the Chapel Island Formation,

Newfoundland, bar; 2 cm. f: *Cruziana* isp. type b, float, Chindingshang Formation,

Guizhou, bar; 2 cm.
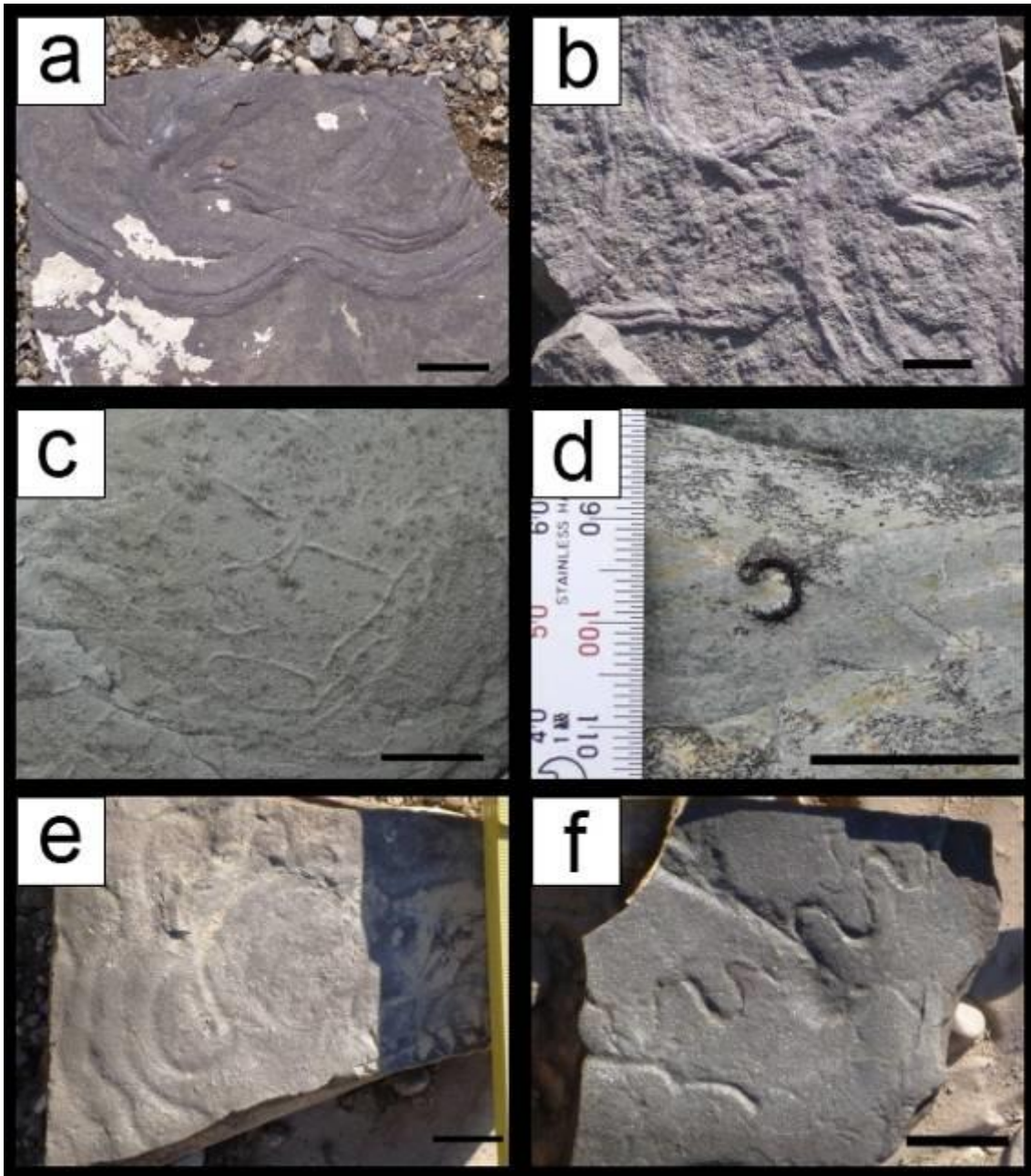
Figure 32. a: ?*Curvolithus* isp., float, *T. pedum* Zone of the Bayan Gol Formation, Gobi-

Altai, bar; 2 cm. b: *Didymaulichnus miettensis*, float, *T. pedum* Zone of the Bayan Gol

Formation, Gobi-Altai, bar; 2 cm. c: *Gordia* isp., top view, basal part of the *R. avalonensis*

Zone of the Chapel Island Formation, Newfoundland, bar; 2 cm. d: *Gyrolithes isp*., top

view, near the basal part of *T. pedum* Zone of the Chapel Island Formation, Newfoundland,

bar; 2 cm. e: *Helminthoida* isp., float, *R. avalonensis* Zone of the Bayan Gol Formation,

Gobi-Altai, bar; 2 cm. f: *Helminthopsis* isp., float, *R. avalonensis* Zoneof the Bayan Gol

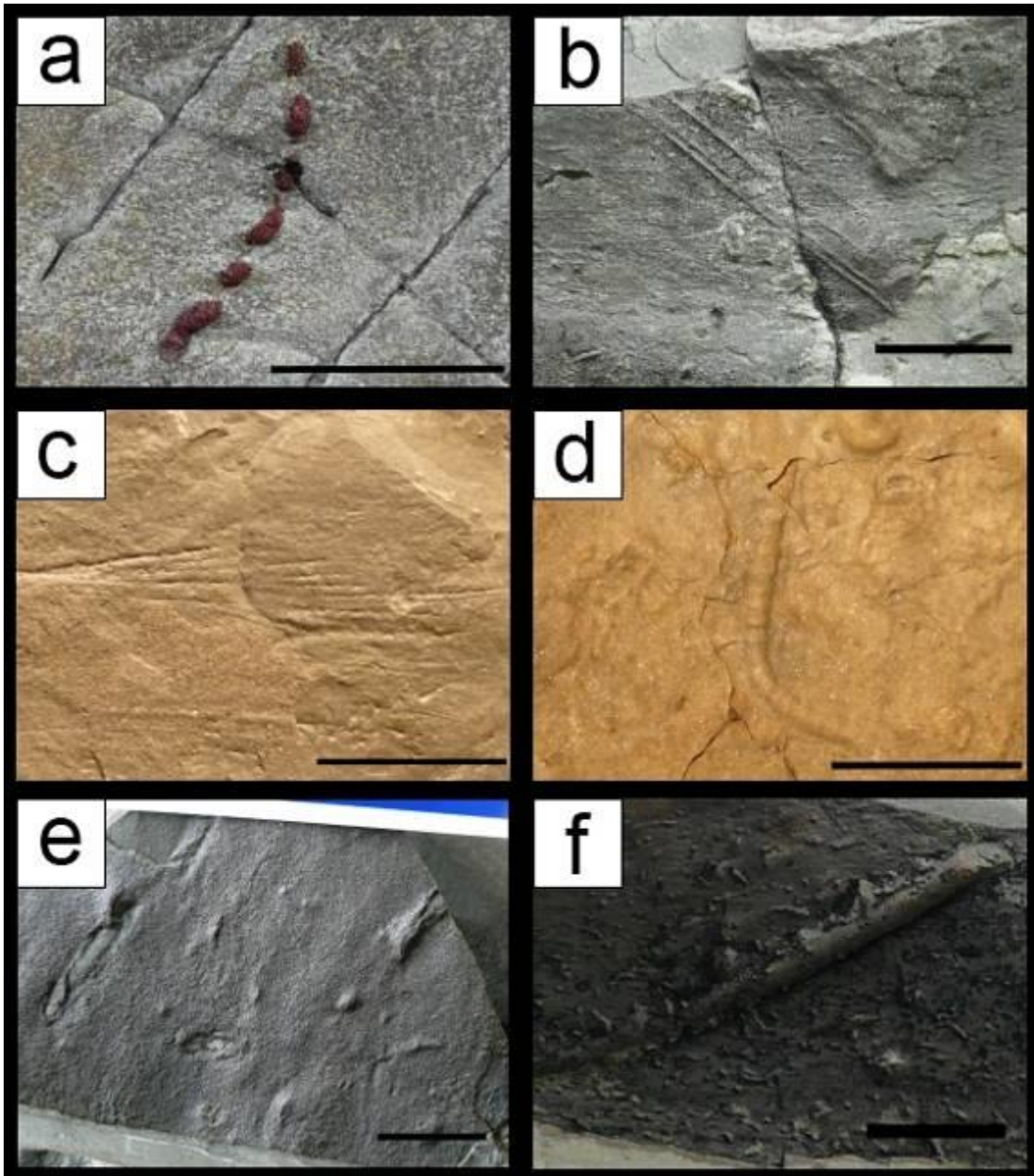Formation, Gobi-Altai, bar; 2 cm.

Figure 33. a: *Hormosiroidea* isp., top view, middle part of the *T. pedum* Zone of the

Chapel Island Formation, Newfoundland, bar; 2 cm. b: *Monomorphicnus lineatus*, sole

view, middle part of the *R. avalonensis* Zone of the Chapel Island Formation,

Newfoundland, bar; 2 cm. c: *Monomorphicnus* isp., top view, lower part of the Balang

Formation, Guizhou, bar; 2 cm. d: *Neonereites uniserialis*, counter part, upper part of the

Balang Formation, Guizhou, bar; 2 cm. e: *Palaeophycus* isp., sole view, middle part of the *R. avalonensis* Zone of the Chapel Island Formation, Newfoundland, bar; 2 cm. f. *Planolites isp.* type a, sole view, lower part of the *T. pedum* Zone of the Chapel Island Formation, Newfoundland, bar; 2 cm.
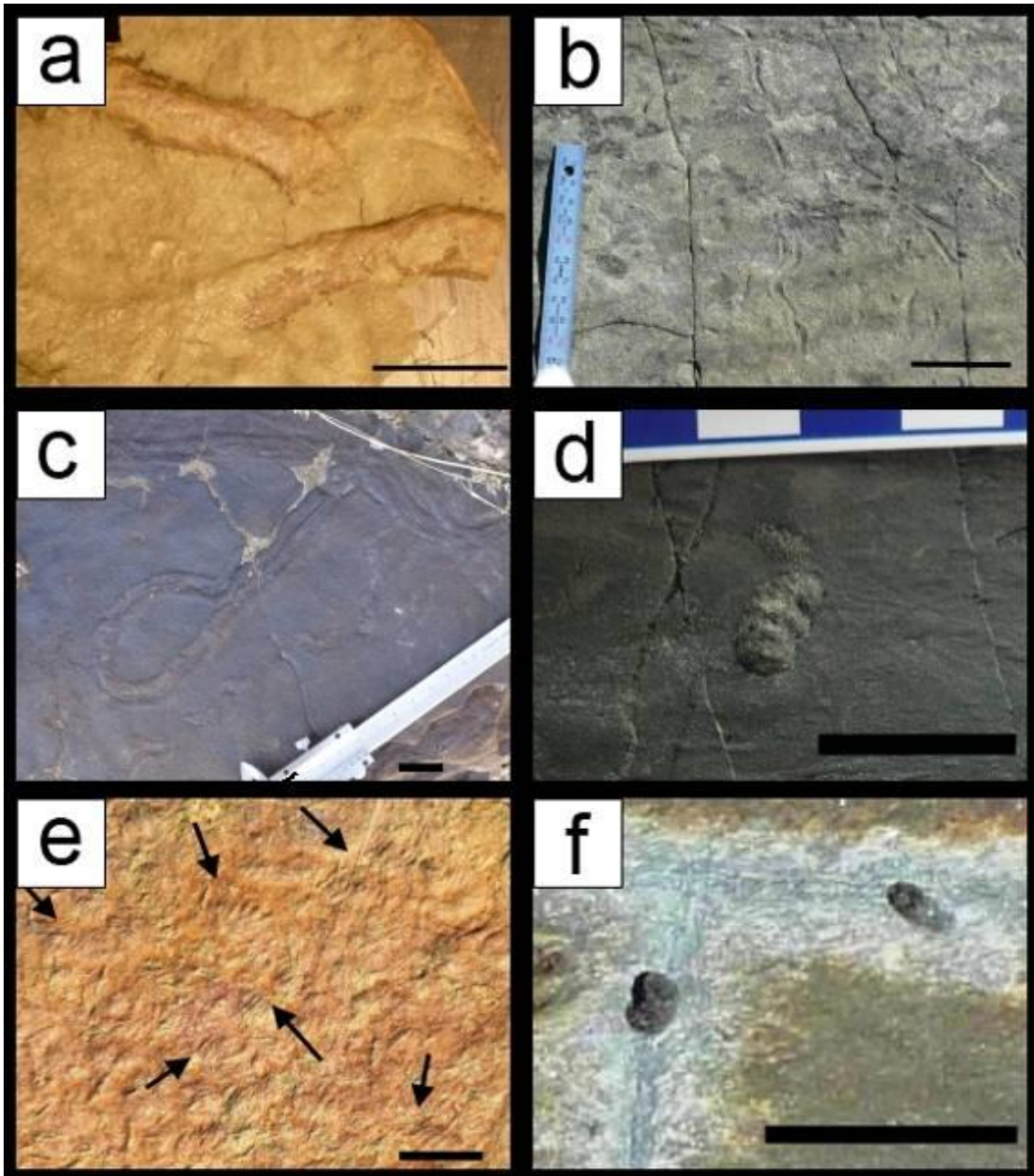
Figure 34. a: *Planolites* isp. type b, top view, upper part of the Balang Formation, Guizhou,

bar; 2 cm. b: ?*Psammichnites* isp. type a, top view, uppermost part of the *T. pedum* Zone

of the   Chapel Island Formation, Newfoundland, bar; 4 cm. c: ?*Psammichnites* isp. type

b, top view, *T. pedum* Zone of the Bayan Gol Formation, Gobi-Altai, bar; 2 cm. d:

Rusophycus cf. *avalonensis*, sole view, middle part of the *R. avalonensis* Zone of the

Chapel Island Formation, Newfoundland, bar; 2 cm. e: *Rusophycus* isp., float, upper part

of the *R. avalonensis* Zone of the Zhujiaqing Formation, Yunnan, bar; 2 cm. f: *Skolithos*

isp., top view, near the basal part of the *T. pedum* Zone of the Chapel Island Formation,
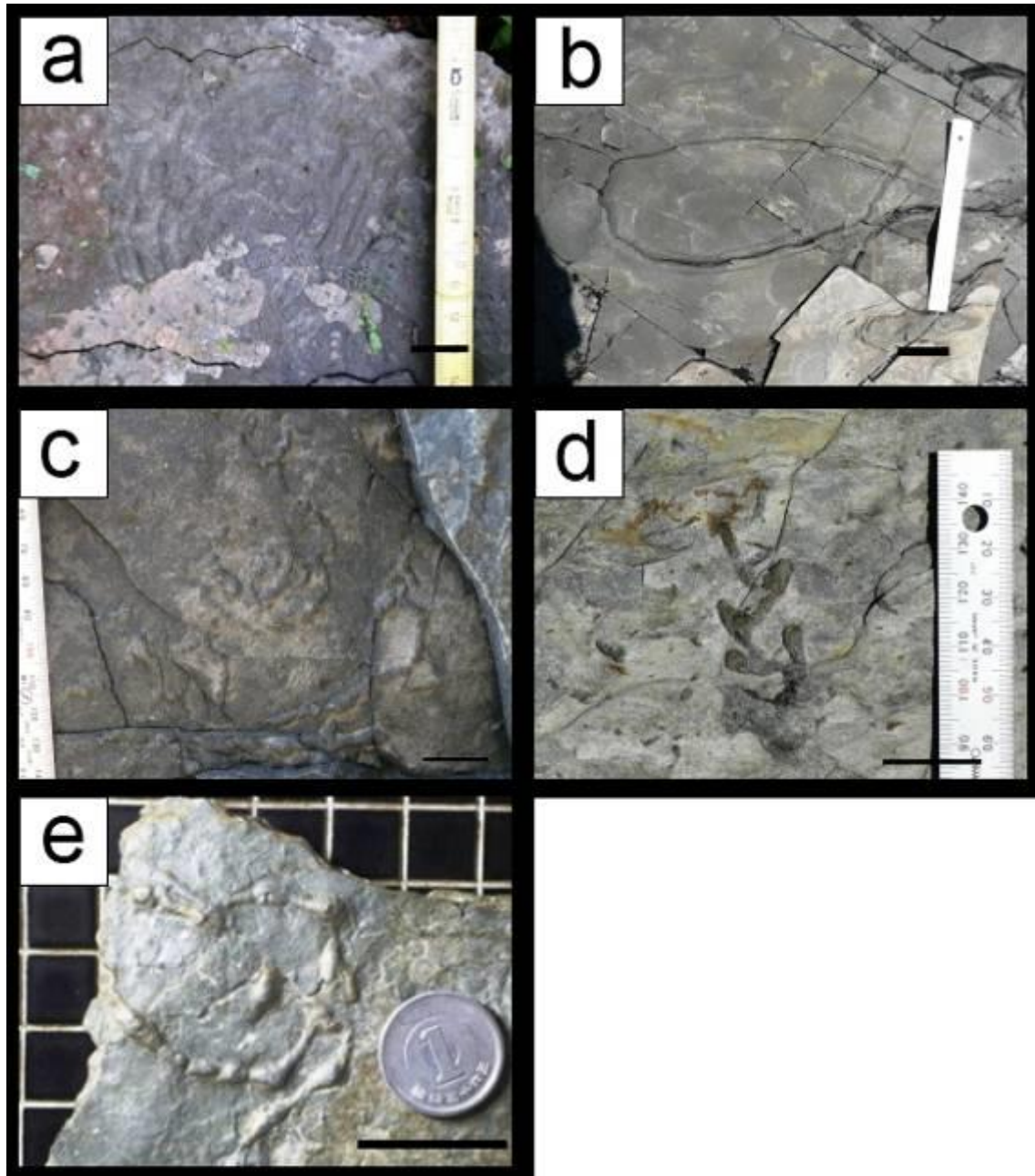
Newfoundland, bar; 2 cm.

Figure 35. a: *Spiroraphe* isp., float, Chintingshang Formation, Guizhou, bar; 2 cm. b:

Taphelminthopsis circuralis, top view, middle part of the *R. avalonensis* Zone of the

Chapel Island Formation, Newfoundland, bar; 4 cm. c: *Torrowangea* isp., sole view upper

part of the *T. pedum* Zone of the Chapel Island Formation, Newfoundland, bar; 2 cm. d:

Treptichnus pedum, top view, near the basal part of the *R. avalonensis* Zone of the Chapel

Island Formation, Newfoundland, bar; 2 cm.   e: *Tricophycus* isp., top view, middle part
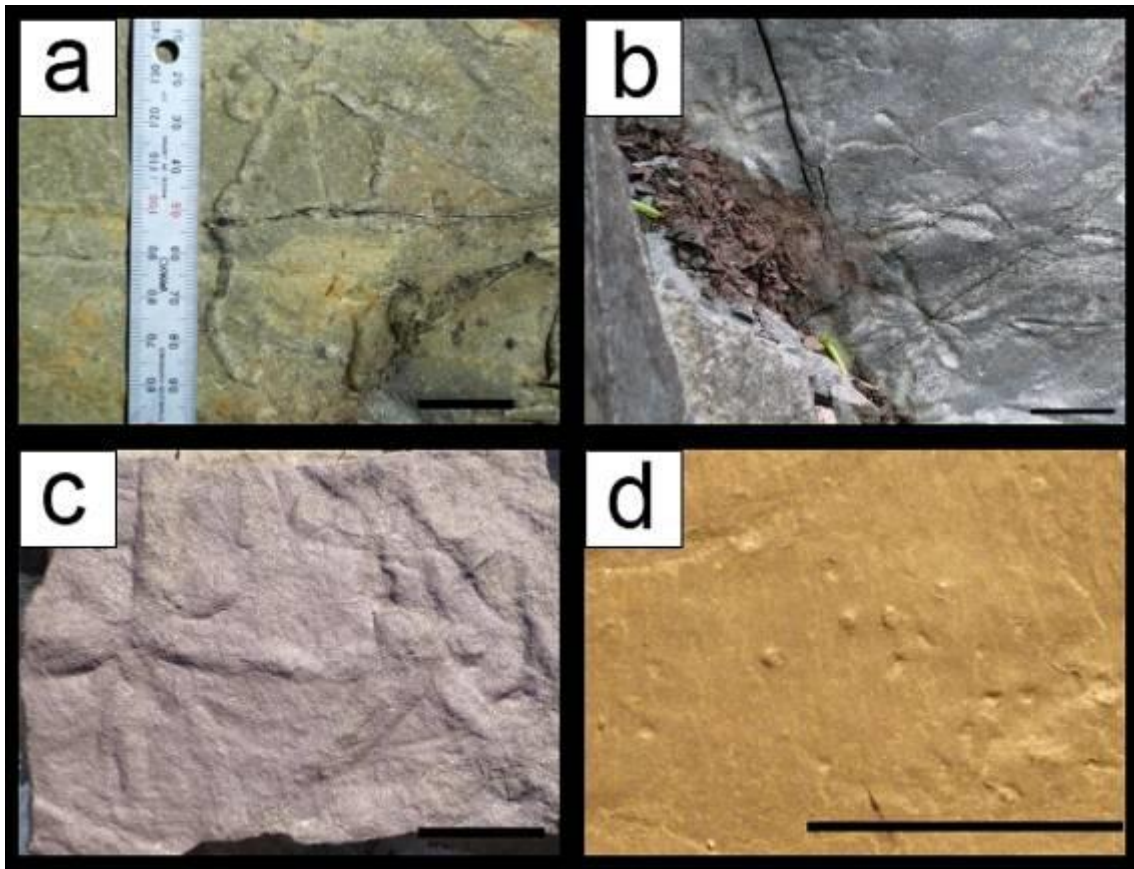
of the Balang Formation, Guizhou, bar; 2 cm.

Figure 36. a: unnamed branching ichnofossil, top view, middle part of the *T. pedum* Zone

of the Chapel Island Formation, Newfoundland, bar; 2 cm. b: unnamed radial ichnofossil,

type a, top view, near the uppemost part of the *T. pedum* Zone of the Chapel Island

Formation, Newfoundland, bar; 2 cm. c: unnamed radial ichnofossil, type b, float, the *T.*

pedum Zone of the Bayan Gol Formation, Gobi-Altai, bar; 2 cm. e: pellet like ichnofossil,

top view, lower part of the Balang Formation, Guizhou, bar; 2 cm.