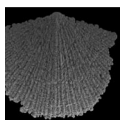


Diversity fluctuations and biogeography of Ordovician brachiopod faunas in northeastern Spitsbergen

JESPER HANSEN & LARS ERIK HOLMER



Investigations of Lower and Middle Ordovician brachiopods in northeastern Spitsbergen have revealed strong ties to faunas in North America and Greenland at the generic level, although the fauna appears mostly endemic at the species level. During the early Palaeozoic, the archipelago of Svalbard, including Spitsbergen, was located at equatorial latitudes along the northeastern margin of Laurentia. The northeastern part of Spitsbergen experienced significant sea level changes, changing from very shallow water in the Tremadocian to deep water in the Floian and slowly back to shallow-water carbonate environments in the Middle Ordovician. The Tremadocian and early Floian brachiopod fauna was of low diversity with a high proportion of cosmopolitan warm-water related rhynchonelliform genera. In the late Floian there was an abrupt diversification event, taking place against the background of the increasing isolation of Laurentia, leading to a diverse, mostly endemic fauna. This diverse fauna remained into the Middle Ordovician. A similar diversification event has been recorded in North America, but here it occurs later, in the Dapingian. The diachroneity of brachiopod diversification within different parts of a continent has previously been shown for South China, suggesting that it may be a common phenomenon. In contrast to the mostly endemic Middle Ordovician rhynchonelliform genera, the linguliform brachiopods included many genera with a wide distribution. This difference is attributed to their different dispersal strategies. • Key words: Ordovician, brachiopods, Spitsbergen, biodiversification, biogeography.

HANSEN, J. & HOLMER, L.E. 2010. Diversity fluctuations and biogeography of Ordovician brachiopod faunas in northeastern Spitsbergen. *Bulletin of Geosciences* 85(3), 497–504 (3 figures, 2 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received January 21, 2010; accepted in revised form July 1, 2010; published online July 29, 2010; issued September 30, 2010.

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The Lower Palaeozoic fossil fauna of the polar island of Spitsbergen has for decades been the subject of taxonomic, biostratigraphic, and biogeographic studies, which among other things have revealed that the fauna was part of the faunal province of Laurentia and is mostly dominated by trilobites and brachiopods (e.g. Fortey 1975, Fortey & Barnes 1977). One of the fossil groups that until now have received only limited attention is the brachiopods. At the Hinlopen Strait in the northeastern part of Spitsbergen, a Lower and Middle Ordovician succession is exposed, which in the upper part includes a rich fauna of brachiopods (Fig. 1). This succession is excellent for studying the timing and pattern of the Ordovician diversification of brachiopods and how the brachiopod fauna in the northeastern part of Laurentia related to Early and Middle Ordovician changes in global palaeogeographic configurations.

Here we present the first range chart for the complete brachiopod fauna collected from the succession. The aims of the present study are firstly to investigate whether the timing and pattern of the diversity changes are comparable with those outside of Spitsbergen. Secondly we compare

the biogeography of the Spitsbergen taxa between the Early and the Middle Ordovician in order to better understand the biogeographical trends of the Spitsbergen brachiopod fauna in a world where the continents became progressively more fragmented and disparate.

Regional geology and stratigraphy

In northeastern Spitsbergen, a Lower Palaeozoic succession is exposed in low coastal cliffs, and exposures along meltwater streams and on the Basissletta and Olenidsletta plains on each side of the Buldrebreen Glacier at the Hinlopen Strait (Fig. 1). The exact thickness of the succession is not known as the scattered exposures make precise stratigraphic measurements difficult. In the present study we use the estimates and measurements provided by Fortey & Bruton (1973) for this succession.

During the entire Ordovician, Spitsbergen was located at equatorial latitudes along the northeastern margin of Laurentia (Cocks & Torsvik 2004, 2006). Northeastern



Figure 1. Location of the investigated area in northeastern Spitsbergen.

Spitsbergen experienced significant sea level changes, but the depositional regime was mostly tidal to subtidal when not subject to subaerial exposure and erosion. Thus during the Tremadocian the area was within tidal to subtidal environments. In the Floian there was a significant transgression and highstand, giving rise to a thick unit of black shales and carbonates (Fortey & Bruton 1973, Fortey 1975). Shallow-water carbonate environments were re-established in the Middle Ordovician.

The carbonate-dominated Lower Palaeozoic succession ranges from the Lower Cambrian and up into the Middle Ordovician. However, the succession is far from complete, including a hiatus covering the Middle and Upper Cambrian and possibly the basal Ordovician (Fortey & Bruton 1973). Three formations are recognized. The succession begins with the mainly Lower Cambrian Tokammane Formation (Harland *et al.* 1966) composed of quartzitic sandstone and dolostone. Above follows the Tremadocian to Floian Kirtonryggen Formation (Harland *et al.* 1966), which changes from a lower unit dominated by dolostones and common stromatolites to an upper unit of

fossiliferous carbonates. At the top is the upper Floian to Middle Ordovician Valhallfonna Formation (Vallance & Fortey 1968) dominated by black, graptolite-rich shaly carbonates in the lower part changing to more massive, fossiliferous carbonates in the upper. Lithological descriptions are provided by Fortey & Bruton (1973) and Kosteva & Teben'kov (2006).

The chronostratigraphic and biostratigraphic framework used here is based on Fortey & Bruton (1973), Fortey & Barnes (1977), Maletz & Bruton (2007, 2008), Bergström *et al.* (2009), and Svend Stouge (pers. comm. 2010).

Material and methods

The study is based on more than 13,500 brachiopod specimens representing the faunas of the entire studied succession. Most of the brachiopods were collected by the authors during field work in 2008, but material collected during the Cambridge University Expedition in 1967 and the joint expedition by the Norwegian Polar Institute and the Palaeontological Museum in Oslo, Norway, in 1971 has also been included. The material contains both crack-out specimens and specimens extracted by dissolving rock samples from horizons throughout the succession. A solution of 10 percent acetic acid was used for dissolving samples collected during the 2008 expedition.

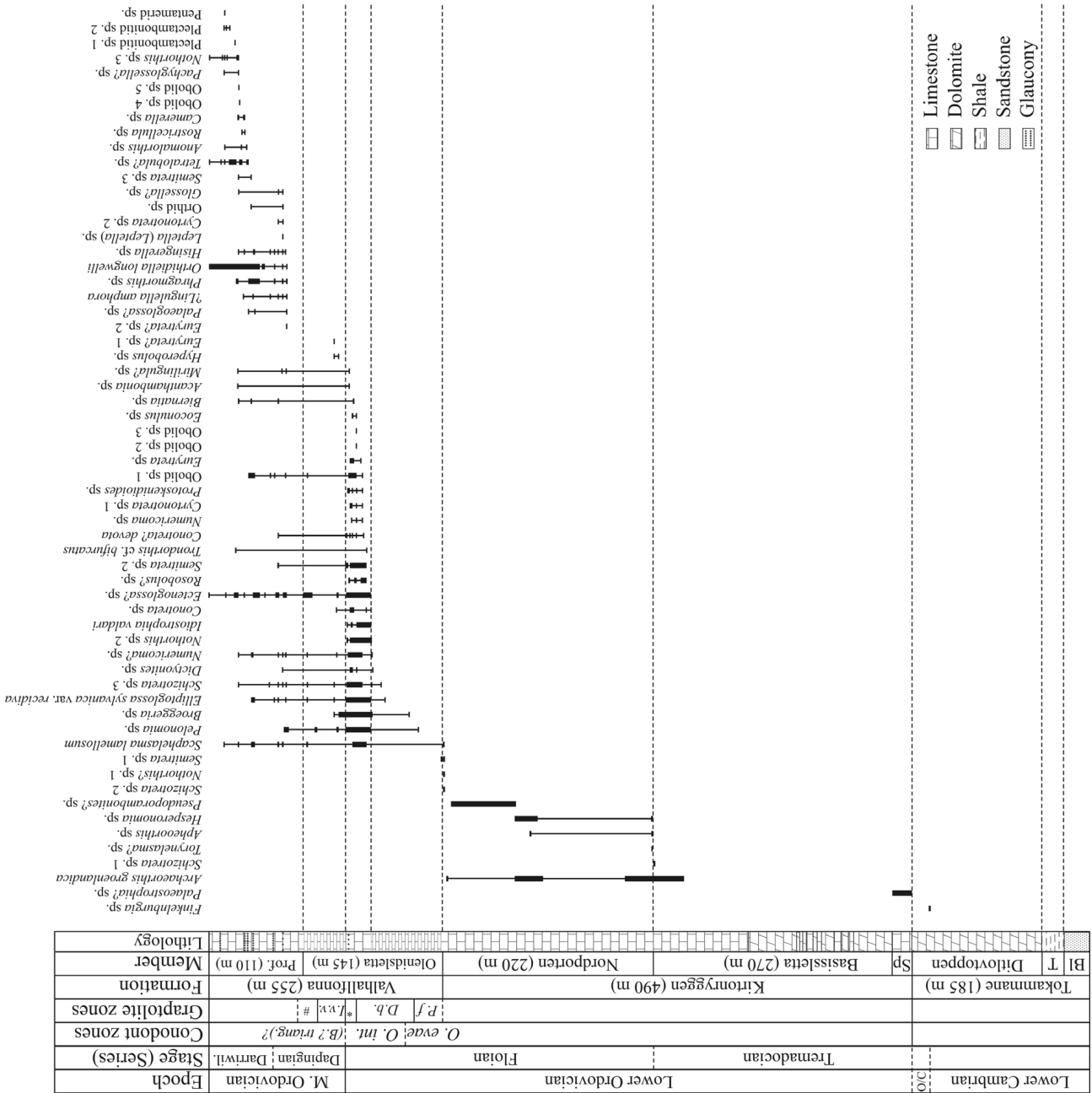
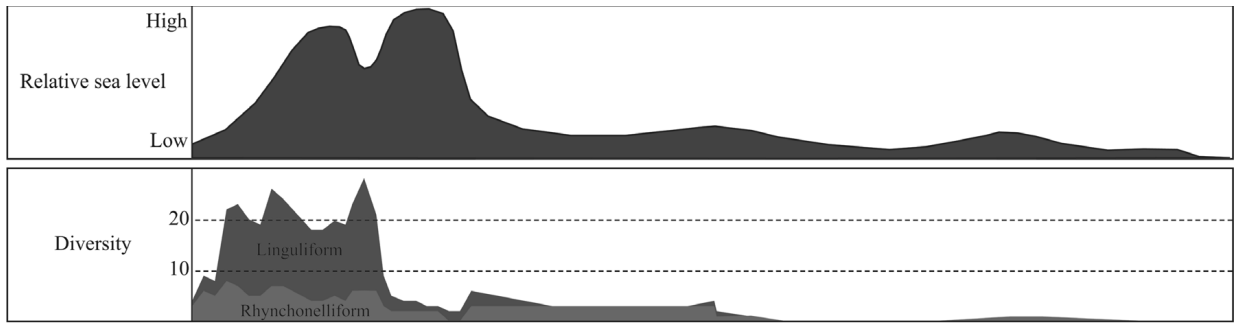
The fossils are presently deposited in the Tromsø University Museum, Norway, the Sedgwick Museum in Cambridge, and the Natural History Museum of London.

Diversity was calculated by first dividing the lithological units into smaller intervals. The well-sampled units of the Valhallfonna Formation were divided into ten-metre intervals. Data on the brachiopods from samples within each of the intervals were then accumulated, and finally diversity was calculated by the software program PAST (Hammer *et al.* 2001).

Results

A detailed systematic study of the Lower Palaeozoic brachiopods from northeastern Spitsbergen reveals that the α -diversity along northeastern Laurentia increased dramatically in the late Floian and remained high well into the Middle Ordovician (Fig. 2). This change is seen in the upper part of the *D. bifidus* graptolite biozone in time

Figure 2. Range chart and diversity curve for the brachiopods, and sea-level curve for the Lower Palaeozoic succession in northeastern Spitsbergen. The lithological column and thicknesses are in accordance with Fortey & Bruton (1973). Diversity was calculated using the software program PAST (Hammer *et al.* 2001). C/O – Upper Cambrian/Lower Ordovician; *O. int.* – *O. intermedius*; *B.?* *triang.* – *Baltoniodus? triangularis*; *P.f.* – *P. fruticosus*; *D.b.* – *D. bifidus*; * – *L. lunatus*; *I.v.v.* – *I. victoria victoria*; # – *I. v. maximus*; Prof. – Profilbekken; Sp – Spora; Bl – Blårevbreen; T – Topiggane.



slice 2C. Prior to the diversification event, α -diversity had increased from 0–1 in the Tremadocian Basissetta Member to about 5 in the Nordporten Member, representing the late Tremadocian to mid Floian. In the uppermost part of the succession, the diversity appears to return to a low level. However, as the diversity at any given level is calculated by adding the taxa known to occur both below and above to the number of taxa counted from the level itself, the endpoints will generally always show diversities which are too low. Although the linguliform and rhynchonelliform brachiopods both diversified, the dramatic diversification in the late Floian is mostly related to the appearance of linguliform taxa, which in the area were virtually absent during the Tremadocian. Similarly, the decrease in diversity is associated with a return to a fauna dominated by rhynchonelliform brachiopods as the diversity of rhynchonelliform taxa stays rather high.

The Tremadocian to lower Floian brachiopod fauna in the top of the Tokammane Formation and the Kirtonryggen Formation as well as the Dapingian to mid Darriwilian brachiopod fauna in the Profilbekken Member of the Valhallfonna Formation were split between linguliform and rhynchonelliform genera. The genera determined are listed in tables together with information on their geographic distribution (Tables 1 and 2). The numbers of genera occurring in other parts of the world were then calculated as percentages of the total numbers found in northeastern Spitsbergen and plotted in the palaeogeographical reconstructions presented in Fig. 3A–C. The figure and tables are based on data from Poulsen (1927, 1937), Ulrich & Cooper (1938), Cooper (1956a, 1956b), Lochman (1966), Ross (1967, 1972), Neuman & Bruton (1974), Krause & Rowell (1975), Havlíček & Branisa (1980), Laurie (1980), Nazarov & Popov (1980), Babin *et al.* (1982), Sevirgina (1984), Yadrenkina (1984), Laurie (1987), Holmer (1989), Loch *et al.* (1993), Freeman & Stitt (1996), Holmer & Popov (2000), Benedetto (2001a), Holmer *et al.* (2001), Robson & Pratt (2001), Mergl (2002), Benedetto (2003), Zhan *et al.* (2005), Benedetto & Cech (2006), Zhan & Harper (2006), Nikitina *et al.* (2006), Gutiérrez-Marco & Villas (2007), Cocks (2008), and Popov *et al.* (2008). The Lower Ordovician distribution of linguliform genera is omitted, as three of the four genera did not have representatives of similar ages in the researched literature. For the rhynchonelliform genera within the topmost part of the Tokammane Formation and the Kirtonryggen Formation, the greatest similarities are with faunas from the USA, Canada, and Greenland within Laurentia and with faunas in a belt connecting Siberia, Kazakhstan, and South China (Fig. 3A). With the exception of South China, which was located at low middle latitudes, all these regions were located at low latitudes.

In the Middle Ordovician, the rhynchonelliform genera as a group are markedly more restricted to Laurentia than

earlier (Fig. 3B). Even within Laurentia the distribution of the Svalbard genera is more restricted. Like earlier, the highest similarities are found in the regions close to the Equator. Precordillera of Argentina and South China are the only regions outside Laurentia, which have as many as three genera or more in common with Spitsbergen.

The Middle Ordovician linguliform genera show a more curious distribution (Fig. 3C). Within Laurentia the distributional pattern resembles that of the rhynchonelliform genera. Outside, however, neither Siberia nor Australia was found to have any genera in common with Spitsbergen, while continents at higher southern latitudes frequently have genera in common with Spitsbergen. Like the rhynchonelliforms, the linguliform brachiopod faunas of South China and Kazakhstan have unusually many genera in common with Spitsbergen compared to the surrounding continents.

Discussion

Diversity

Locally the brachiopod fauna had a low level of diversity with a high proportion of cosmopolitan genera during the Tremadocian and early Floian (Fig. 2). With the initiation of middle Floian *O. evae* drowning this fauna was completely replaced. The following regressive event in the late Floian opened the way for an abrupt and significant diversification of a partly endemic Laurentian fauna. This change is seen in the upper part of the *D. bifidus* graptolite biozone in time slice 2C. More than 40% of the identified species that appeared at that time and during the continued influx of new taxa are among the earliest known representatives of their respective genera. It can therefore be assumed that the observed diversification not only was a result of local environmental changes opening the area for settlement of taxa living elsewhere, though that was undoubtedly an important factor, but also reflects diversification on at least a regional scale. The greater part of the appearing brachiopods is linguliform taxa, which characterizes the Cambrian Evolutionary Fauna, but also includes typical Ordovician rhynchonelliform taxa such as plectambonitids and camerelloids characteristic of the Palaeozoic Evolutionary Fauna replacing the Cambrian Evolutionary Fauna during the Great Ordovician Biodiversification Event (Bassett *et al.* 2002 with references). A research in the literature on brachiopods in North America indicates that nowhere there did the diversification take place before the Dapingian. This diachroneity in diversification between different parts of Laurentia is similar to what Zhan & Harper (2006) found in South China, suggesting it is a common phenomenon. They attributed that diachroneity to bathymetric factors with shallow-water faunas diversifying before the deep-water faunas. At present the same does

Table 1. Brachiopod genera from the Tremadocian and lower Floian succession and their co-occurrence in other parts of the world. East Baltic, Iran, Novaya Zemlya and Perunica are not included in the table as they have no genera in common with Spitsbergen. Abbreviation: A – *Apheoorthis*, B – *Archaeoorthis*, C – *Finkelburgia*, D – *Hesperonomia*, E – *Nothorthis*, F – *Palaeostrophia*, G – *Pseudoporambonites*, H – *Scaphelasma*, I – *Schizotreta*, J – *Semitreta*, K – *Torynelasma*.

	A	B	C	D	E	F	G	H	I	J	K
Spitsbergen	1	1	1	1	1	1	1	1	1	1	1
Canada	1	1	1	0	1	1	0	0	0	0	0
Greenland	1	1	1	0	0	0	1	0	0	0	0
Scotland	0	1	1	0	0	0	0	0	0	0	0
USA	1	1	1	1	0	1	0	0	0	0	0
Precordillera	0	1	0	1	1	0	0	0	0	0	0
Avalonia	0	1	0	0	0	0	0	0	0	1	0
Poland	0	0	0	0	0	0	0	0	0	1	0
Siberia	1	1	1	0	1	0	0	0	0	0	0
Kazakhstan	1	1	1	1	1	0	0	0	0	0	0
South China	1	1	1	0	1	0	1	0	0	0	0
Australia	1	1	1	0	0	0	0	0	0	1	0
Puna	0	0	1	1	0	0	0	0	0	0	0
Bolivia	1	0	0	0	0	0	0	0	0	0	0

not appear to be the case for Laurentia, as the succession in Spitsbergen is thought to represent an off-shore setting as compared to most of the deposits in North America (see Fortey & Droser 1996, 1999). An interpreted offshore setting for most of the Valhallfonna Formation is supported by the dominance of linguliform brachiopods (see Patzkow-

sky 1995). In Spitsbergen the start of the diversification was later than in South China, where it took place in the early Floian (Zhan *et al.* 2005), but still earlier than for the first major diversification of the rhynchonelliform brachiopods globally and in Baltica, taking place in the Dapingian to early Darriwilian (Harper *et al.* 2004, Rasmussen *et al.* 2007). On a global scale the micromorphic linguliform brachiopods already diversified in the late Tremadocian, but this stage appears to be missing in Laurentia (Harper *et al.* 2004).

Palaeobiogeography

At the generic level the Ordovician brachiopods in northeastern Spitsbergen reveal strong ties to faunas in North America and Greenland, although the fauna appears rather endemic at the species level. No more than 13 of the approximately 60 species are found to be identical to those outside the archipelago of Svalbard. The 13 species are the linguliform *Conotreta? devota* Krause & Rowell, *Cyrtotreta* sp. (= *Conotreta* sp.; Krause & Rowell 1975), *Ectenoglossa? sp.* (= *Ectenoglossa? sp.*; Krause & Rowell 1975), *Elliptoglossa sylvanica* var. *recidiva* Krause & Rowell, *?Lingulella amphora* Krause & Rowell, *Numericoma* sp. (= *Ephippelasma spinosum* Biernat in Krause & Rowell 1975), obolid sp. (= *?obolid* gen. et sp. nov.; Krause & Rowell 1975) and *Scaphelasma lamellosum* Krause & Rowell, and the rhynchonelliforms *Anomalorthis* sp. (= *Anomalorthis* n. sp. A; Ross 1970), *Archaeoorthis groenlandica* Poulsen, *Idiostrophia valdari* Ross, *Orthidiella longwelli* Ulrich & Cooper, and *Trondorthis* cf. *bifurcatus*

Table 2. Identified brachiopod genera from the Dapingian to mid Darriwilian succession and their co-occurrence in other parts of the world. Armorica and Peru are excluded from the table as they had no genera in common with Spitsbergen. Abbreviation: A – *Anomalorthis*, B – *Camerella*, C – *Leptella*, D – *Nothorthis*, E – *Orthidiella*, F – *Pelonomia*, G – *Phragmorthis*, H – *Rostricellula*, I – *Tetralobula*, J – *Trondorthis*, K – *Acanthambonia*, L – *Biernatia*, M – *Conotreta*, N – *Cyrtotreta*, O – *Dictyonites*, P – *Ectenoglossa*, Q – *Elliptoglossa*, R – *Eurytreta*, S – *Glossella*, T – *Hisingerella*, U – *?Lingulella*, V – *Mirilingula*, W – *Numericoma*, X – *Pachyglossella*, Y – *Palaeoglossa*, Z – *Scaphelasma*, a – *Schizotreta*, b – *Semitreta*.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	a	b	
Profilbekken	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Canada	0	1	1	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0
NW Ireland	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	
Scotland	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Trondheim	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
USA	1	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1	0	0	1	0	1	1	1	
Precordillera	0	0	1	0	0	1	0	0	0	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Avalonia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	
Baltica	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	1	0	0	
Siberia	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Kazakhstan	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	
South China	0	0	1	1	0	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	
Australia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Iran	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	
Perunica	–	–	–	–	–	–	–	–	–	–	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	

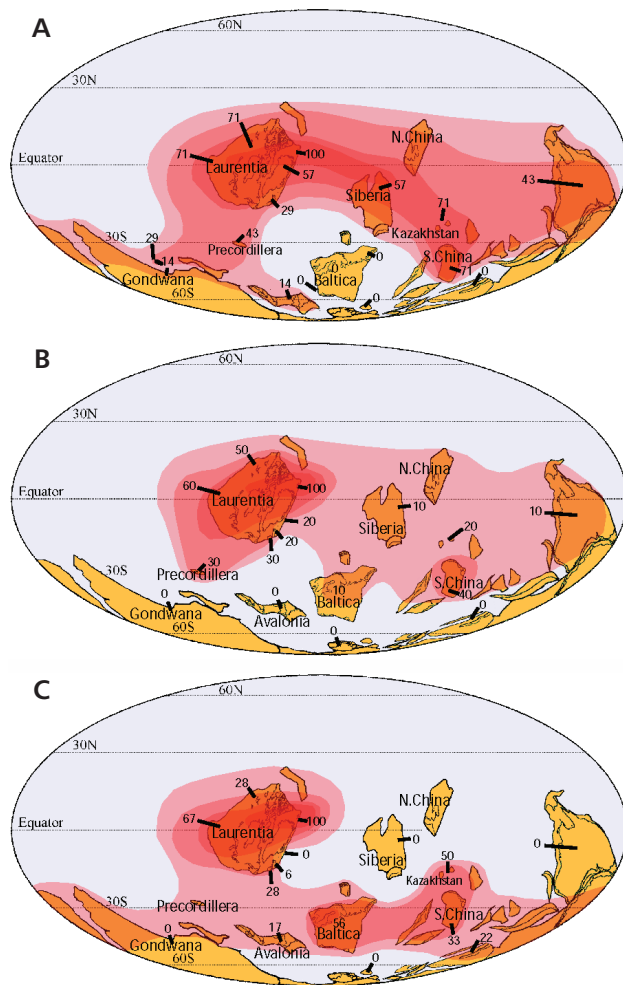


Figure 3. Biogeographic distribution of the rhynchonelliform genera found in the Tremadocian–early Floian of northeastern Spitsbergen. Numbers indicate percentages of genera from the Spitsbergen fauna found in other areas. Red grading divided into 25% intervals. • A – the 7 rhynchonelliform genera in the Tremadocian–early Floian. • B – the 10 determined rhynchonelliform genera in the Dapingian to mid Darriwilian. • C – the 18 determined linguliform genera in the Dapingian to mid Darriwilian. Globes modified from Cocks & Torsvik (2004, 2006).

Cooper. With the exception of the Tremadocian *A. groenlandica* known from Greenland and the Darriwilian *Trondorthis bifurcatus* Cooper from Nevada, all species were previously described from the Dapingian of Nevada. ?*L. amphora* is also reported from Newfoundland by Robson & Pratt (2001).

The equatorial distribution of the rhynchonelliform genera (Fig. 3A, B) suggests that temperature related factors were one of the major controls on the distribution of these brachiopod taxa occurring in Spitsbergen. Temperature or latitudinal relationship has previously been reported by Thomsen (1990) for Recent brachiopods and by Harper *et al.* (1996) and Benedetto (2001b) among others for Lower and Middle Ordovician rhynchonelliform brachiopods. Many rhynchonelliform brachiopods have very short pelagic larval stages and thus often problems crossing the

environments of the deep seas (Thomsen 1990, Richardson 1997, Harper *et al.* 2004, Popov *et al.* 2007), which makes the existence of relatively shallow seas connecting the continents during the dispersal history of the genera highly probable. That islands and archipelagos existed in the Iapetus Ocean and probably functioned as stepping stones along migrational routes have already been established (Harper & Mac Niocail 2002 with references). Scotland and Trondheim, part of marginal Laurentia, had remarkably few genera in common with Spitsbergen when compared with regions outside Laurentia. If temperature-related factors were indeed major controls on brachiopod distribution, it may suggest that cold-water currents influenced the southeastern margin of Laurentia. During the Ordovician biodiversification, the fauna of northeastern Laurentia became much more endemic at the generic level even though the relative sea level was higher than during the Tremadocian and early Floian. This increased endemism may be attributed to both a greater isolation of the continent and a shorter dispersal history of the new genera.

The distribution of the Middle Ordovician linguliform brachiopods shows some surprising differences from that of the rhynchonelliform. Outside Laurentia they are missing from the continents closest to the equator, although in both actual and relative numbers the genera occur more abundantly at higher southern latitudes (Fig. 3C). We expected them to have a wider distribution as compared with the rhynchonelliform brachiopods as they have a long pelagic larval stage allowing for transport with the current systems, and linguliform taxa are known to generally have a wider distribution than the rhynchonelliform taxa (Emig 1997, Harper *et al.* 2004). We believe the main reason for their absence from the equatorial latitudes outside Laurentia is a lack of data more than any real pattern, as biogeographic knowledge about the group is still patchy. The high number of genera that Kazakhstan has in common with Spitsbergen supports this view.

Conclusions

The diversification of the linguliform and to a lesser degree the rhynchonelliform brachiopods seen in the upper Floian of northeastern Spitsbergen took place against a background of increasing isolation of the brachiopod fauna in Laurentia and following the maximum highstand of the late Early Ordovician. As in South China, the diversification of the brachiopods in Laurentia was diachronous, starting earlier in Spitsbergen than in the central parts of North America. The diversification of the rhynchonelliform taxa was later than in South China, but still earlier than the main global diversification and the diversification in the extremely isolated Baltica.

The biogeographic pattern of the rhynchonelliform brachiopods from Spitsbergen suggests that temperature-related factors were one of the major controls on the

distribution of these brachiopods. Due to the limited dispersal capability of most rhynchonelliform brachiopods, the cosmopolitan distribution of the genera in the Lower Ordovician also indicates that shallow seas connected the continents at one time or another. In the Middle Ordovician the rhynchonelliform brachiopod fauna in northeastern Laurentia had become endemic even in the offshore setting represented by Spitsbergen. In contrast, the linguliform faunas, with their better dispersal strategies, included many cosmopolitan genera. The different dispersal strategies did not, however, become expressed as a markedly differentiated diversification of the two groups in Spitsbergen.

Acknowledgements

We thank the University of Tromsø and the European Synthesis Fund (ref: GB-TAF-3876) for financial and technical support. The fieldwork was kindly funded by Det norske oljeselskap ASA, the Norwegian Petroleum Directorate, the Amundsensenteret (Project 200706248), and the Swedish Research Council (VR) as well as the Swedish Polar Research Secretariat. We are indebted to the participants of all the expeditions on which this study is based. Helpful comments from D.A.T. Harper, L.R.M. Cocks and an anonymous reviewer improved the manuscript. We also thank S. Stouge for valuable new information on the conodont biostratigraphy. The paper was presented as a poster at the IGCP 503 meeting in Copenhagen in 2009, and we acknowledge comments from M. Calner, O. Lehnert and T. Servais.

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