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The Early Triassic ammonoid recovery: Paleoclimatic significance of diversity gradients

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Abstract

Ammonoids recovered much faster than other marine shelly invertebrates after the end-Permian mass extinction. Based on a refined global data set at the basin level, we investigate the paleobiogeographical global latitudinal and longitudinal diversity patterns in terms of climatic changes during the Early Triassic. Such analysis differs from already published qualitative or quantitative studies in that it estimates faunal patterns and endemicity at an ecologically meaningful level of spatial resolution, i.e. at the basin level. During the Early Triassic, the global first order trend in increasing ammonoid diversity was accompanied by a progressive change from cosmopolitan to latitudinally-restricted distributions. This led to the emergence of a clear latitudinal diversity gradient during most of the Smithian and Spathian stages, which entails increased steepness of the Sea Surface Temperature gradient during the late Early Triassic. However, two brief episodes of ammonoid cosmopolitanism combined with low global diversity interrupted the first order increasing trend at the very beginning of the Smithian and at its very end. The longitudinal analysis of Smithian distributions indicates a westward decrease of diversity within the Tethys, which faded away during the Spathian. Analysis of endemicity indicates a rapid biogeographical maturing and structuring of faunas concomitant with the edification of the latitudinal diversity gradient.

Keywords: Early Triassic; Ammonoids; Paleobiogeography; Generic richness; Sea surface temperature; Recovery

1. Introduction

The Permo-Triassic mass extinction drastically affected the evolution of Life with the disappearance of typical end-Paleozoic communities. The level of diversity has never been so reduced since the Cambrian with an estimated loss greater than 90% of marine species (e.g. Raup, 1979). The recovery of marine and terrestrial ecosystems was very slow compared to other mass extinctions (e.g. Erwin, 1998) and is considered to be globally ended in the Anisian (Middle Triassic). The delay in the onset of the recovery is an intriguing aspect of the Permo-Triassic mass extinction which may be due

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to the persistence of harsh and unfavourable climatic and/or oceanographic conditions (e.g. global warming, anoxia, stratified waters…).

During the survival phase of the Early Triassic, the first marine inhabitants were very particular and composed of generalist, cosmopolitan and opportunist organisms (e.g. *Lingula* for the brachiopods; *Claraia* for the bivalves) with simple communities and low diversity (Kummel, 1973b; Erwin, 1990, 1994). Even if many clades did not completely recover until the Spathian or the Anisian times (e.g. corals [Stanley, 2003], foraminifers [Tong and Shi, 2000] or radiolarians [Racki, 1999; Yao and Kuwahara, 2000; Hori et al., 2003]), some rare diversified post-extinction faunas demonstrate that marine invertebrates did found some refuges (e.g. Oman, see Krystyn et al., 2003; Twitchett et al., 2004). However, the dominant pattern is that poorly diversified and small-sized benthonic shelly faunas predominated during the Early Triassic and most of the Anisian (e.g. Fraiser and Bottjer, 2004; Fraiser et al., 2005).

The low diversity and cosmopolitan assemblages of generalist organisms until the end of Early Triassic or beginning of the Middle Triassic suggest that environmental conditions were unfavourable during the survival phase and changed during the recovery phase. Climatic simulations also indicate that the beginning of the Early Triassic should be globally and uniformly warm (e.g. Hotinski et al., 2001; Kidder and Worsley, 2004; Péron et al., 2005).

At least one exception has to be noted in the differential recovery of marine organisms: ammonoids quickly rediversified during the Early Triassic and became the most prominent part of the marine faunas during this time interval, where they became extremely widespread and abundant (Kummel, 1957, 1973a,b). Their greatest geographical differentiation was first reached during the Spathian (Kummel, 1973b; Dagys, 1988, 1997).

In this paper we investigate the global paleobiogeographical distribution of ammonoids and its relation with diversity. Patterns of distribution and diversity are discussed in terms of climatic changes during the Early Triassic.

2. Geological and paleontological settings

2.1. Position of land masses and seas

Gondwana, Laurussia and Angara were grouped in the Pangean supercontinent during the end of Permian (Elmi and Babin, 1996). The Pangea edification ended with the Ouralian orogenesis resulting from the collision between Angara and Laurussia (e.g. Smethurst et al., 1998). Later on, Gondwana slowly began to break up. The sea/land repartition was dominated by a very large oceanic domain, the Panthalassa which represented approximately 90% of the end-Permian Ocean, and a smaller ocean covering the last ~10%, the Tethys, which formed a West–East encroachment in the Pangea. The Tethys was centred on the Equator and connected to the East with the Panthalassa.

With the progressive end-Permian opening of the Neotethys, several oceanic plates (e.g. Cimmerian and Cathaysian microcontinents) shifted northward across the Tethys (e.g. Ricou, 1994; Stampfli and Borel, 2002). All these Gondwanian fragments or “transit plates” as coined by Ricou (1994) accreted to Laurasia during the Triassic (Kazmin, 1991; Besse et al., 1998). Numerous back-arc basins opened with the Northward subduction of the Paleotethys all along the southern Eurasian margin, from Austria to China (Stampfli and Borel, 2002).

During the Early Triassic, several terranes travelled through the Panthalassa and were accreted to the western margin of Pangea (see Tozer, 1982; Nichols and Silberling, 1979; Belasky and Runnegar, 1994; Belasky, 1996; Belasky et al., 2002 for Chulitna, eastern Klamath, Stikinia, Wrangellia terranes of North America) or to the eastern margin of the Pangea (e.g. Adams et al., 2002 and Kojima, 1989 for New Zealand and Japan terranes, respectively). Although many terranes were travelling across oceans, major continents and oceans remained stable during the Early Triassic, thus providing a reliable geographical frame for extracting short-term biogeographical patterns of ammonoids (Fig. 1).

2.2. Stratigraphy and timescale

The Early Triassic is commonly subdivided into two (Induan and Olenekian), three (Griesbachian, Nammalian and Spathian: see Guex, 1978) or four stages (Griesbachian, Dienerian, Smithian and Spathian: see Tozer, 1967). These subdivisions are always subject to debates (e.g. Kozur, 2003) but the Sub-Commission on Triassic Stratigraphy decided to adopt the two-fold subdivision in 1992. Yet, Induan and Olenekian are not accepted by all Triassic workers. The two-fold subdivision system was defined by Kiparisova and Popov (1956) in two different realms: Tethyan and Boreal. The Induan has its type-locality in the Salt Ranges (Tethyan realm) whereas the Olenekian is derived from the Olenek River in Siberia (Boreal realm). Because the ammonoid turnover at the Induan/Olenekian boundary

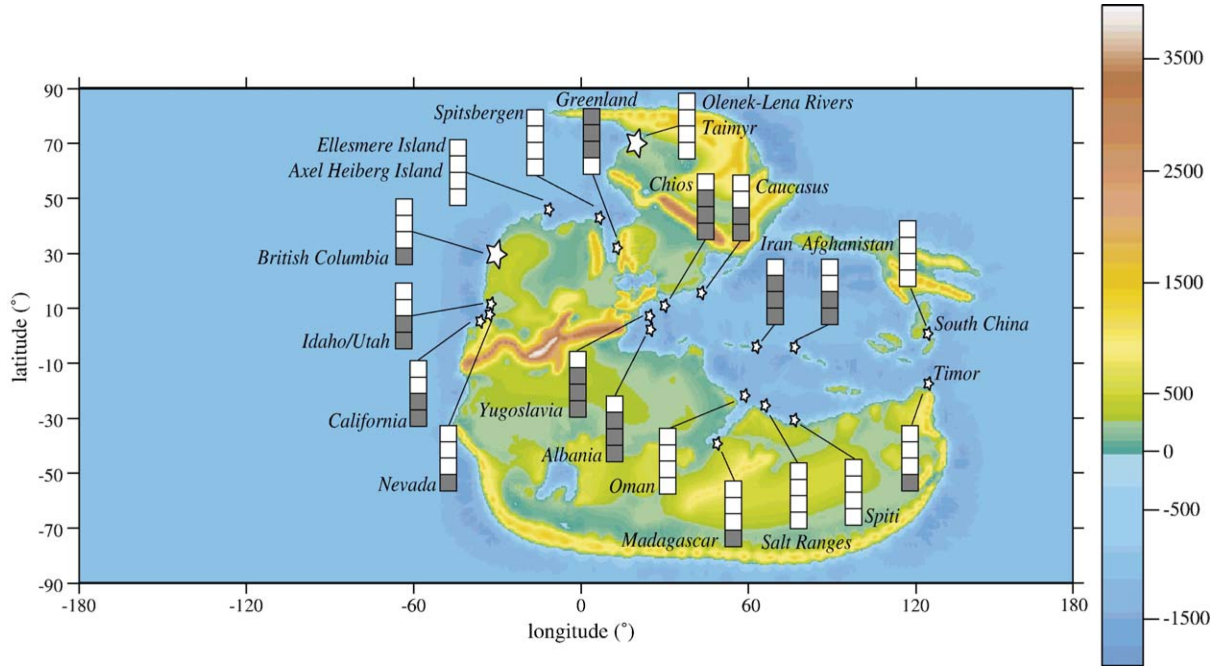

Fig. 1. Paleogeographic map of the Smithian and Spathian (modified from Péron et al., 2005) with the paleoposition of the studied basins and localities. Size of the stars indicates only the relative size of the sampling area. Small bars indicate the temporal distribution of specimens found in the studied station (from base to top: 1st square: Griesbachian, 2nd: Dienerian, 3rd: Smithian, 4th: Spathian; a grey square indicates an absence of specimens from the stage and a white square indicates presence of specimens from this stage). Right color scale bar corresponds to the altitude and bathymetry (in meters).

is comparatively minor with respect to other Early Triassic events (e.g. Smithian/Spathian boundary), correlating the Induan/Olenekian boundary across the Boreal and Tethyan realms is far from clear. Hence, in this work we use the four stage subdivision defined by Tozer (1967), whose boundaries are well-defined in terms of ammonoids (Fig. 2). Moreover, the duration of the Spathian has now been demonstrated to be of ca. 3

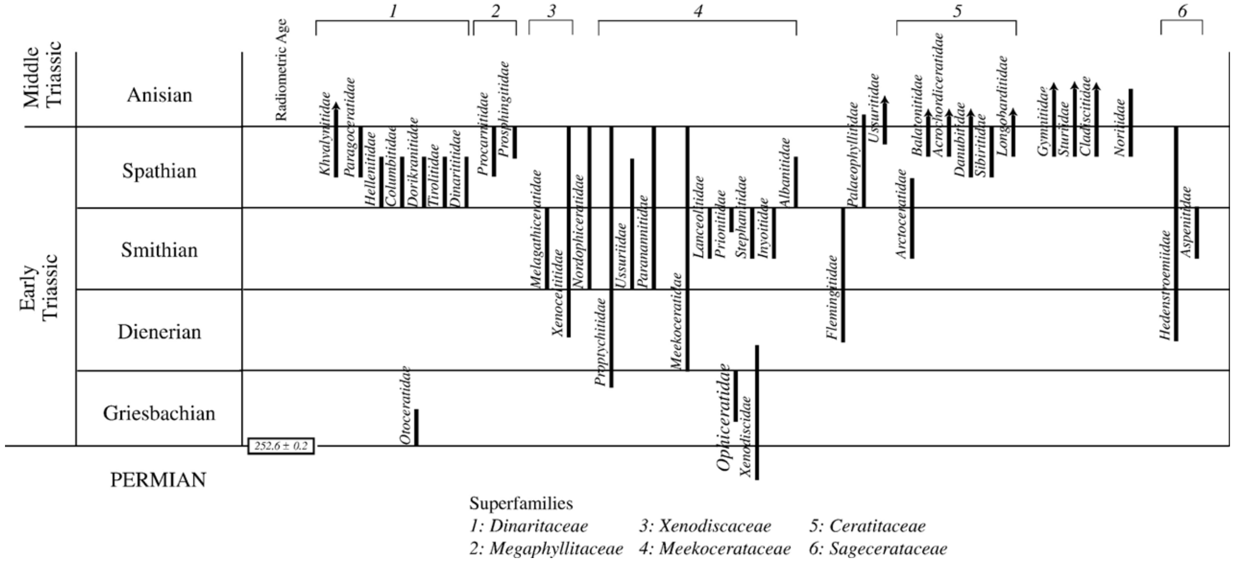

Fig. 2. Chronostratigraphic subdivisions of the Early Triassic (radiometric age by Mundil et al., 2004) and temporal distribution of the ammonoid families (modified after Tozer, 1981a,b, 1994).

myr, which amount to at least half of the duration of the Early Triassic (see Ovtcharova et al., 2006 and hereafter).

2.3. The ammonoid recovery

Ammonoids recovered and diversified faster than most other marine clades during the Early Triassic (Kummel, 1957, 1973a,b; Fig. 2). Only conodonts possibly recovered at a more or less comparable rate (e.g. Tozer in Hallam, 1996).

Otoceras, a characteristic early Griesbachian genus, was the last derivative of the Permian family Araxoceratidae. This genus only had a short existence during the earliest Triassic (Griesbachian), without further known descendents (Tozer, 1973). All other Triassic ceratitids are usually considered to derive from the Permian Xenodiscidae family, with *Ophiceras* as a bridging taxon between Xenodiscidae and Early Triassic families (Kummel, 1973a,b; Wiedmann, 1973; Kennedy, 1977; Tozer, 1981a). Hence, patterns of diversification and distribution of most if not all Early Triassic ammonoids are likely to reflect those of a monophyletic clade derived from xenodiscids such as *Ophiceras*. *Otoceras* and *Ophiceras* co-occurred during the earliest Triassic, yet *Ophiceras* was the most widespread genus.

Tethyan ammonoid faunas were generally more diverse than Boreal or Panthalassic faunas (e.g. Tozer, 1981b). A first low diversity phase spanned the Griesbachian and Dienerian. Then diversity globally increased until it dropped down again around the Smithian/Spathian boundary (Fig. 3). Boreal ammonoids were generally less diverse, with a variable endemism, and their greatest geographical differentiation was reached during the Spathian (Kummel, 1973b; Dagys, 1997). Although less severe than the Smithian/Spathian boundary event, another significant and global drop of generic richness occurred around the Spathian/Anisian boundary (Bucher, 1989).

3. Data set and method

3.1. Studied localities and ammonoid genera

The diversity and distribution patterns of ammonoids were analyzed from a data set including about twenty Tethyan and Panthalassic basins (Table 1, Fig. 1). Some of the basins were defined as early as the end of the 19th century (e.g. Spiti, Timor). The ammonoid data was compiled from published and unpublished systematic, biostratigraphical or paleobiogeographical contributions (ongoing work of Brayard–Bucher and Bucher–Guex for the Smithian and Spathian stages, respectively). Despite the fact that some of the Early Triassic ammonoid zones can be recognized at a world-wide scale, achieving global correlations at the zone level for the entire Early Triassic still requires further work. Hence, time resolution was essentially limited to the stage level in the present analysis.

We processed all the available data at the generic level in order to avoid the important taxonomic bias still pervading the species-level. Although species counts are theoretically more objective than genus richness,

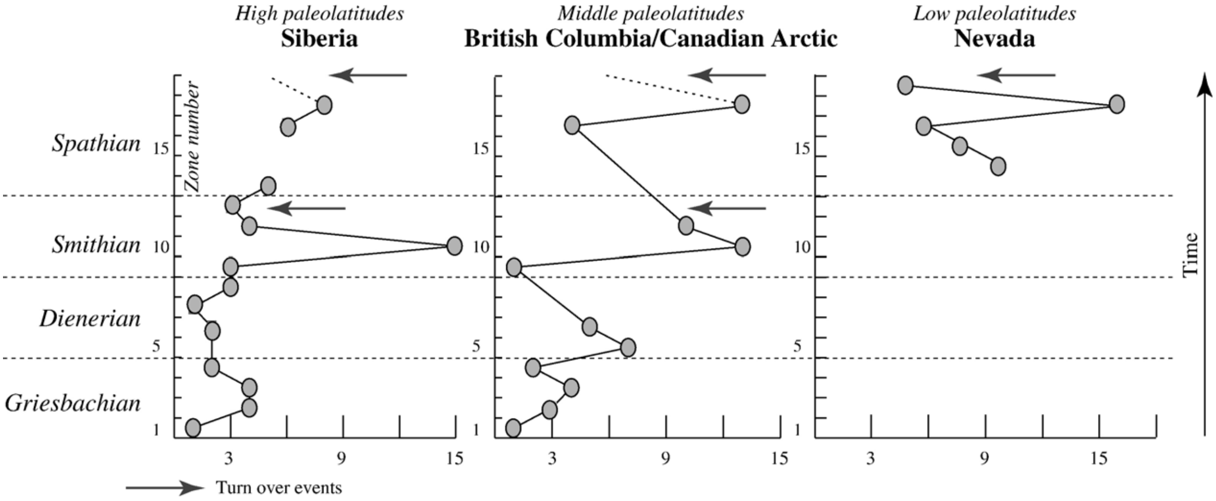

Fig. 3. Evolution of the ammonoid generic richness during the Early Triassic for low, middle and high latitudes (correlations and data for high and middle paleolatitudes after Dagys, 1999; Dagys and Ermakova, 1988, 1990, 1996; Tozer, 1994; for Nevada, data is unpublished).

Table 1
Sources for fossil data

Localities	Data					
Madagascar	Collignon, 1933–1934	Bando, 1977				
Albania	Arthaber, 1908	Arthaber, 1911	Germani, 1997			
Caucasus	Popov, 1962	Shevyrev, 1968	Shevyrev, 1995			
Yugoslavia	Petrovic and Mihajlovic, 1935	Krystyn, 1974	Posenato, 1992			
Chios	Renz and Renz, 1947	Renz and Renz, 1948	Gaetani et al., 1992	Mertmann and Jacobshagen, 2003		
Spiti and Qinghai/ Xizang Tibet	Diener, 1897	Krafft, 1900	Krafft and Diener, 1909	Kummel, 1970b		
	Wang and He, 1981	He et al., 1986	Waterhouse and Gupta, 1985	Wu, 1983		
Salt Ranges and Kashmir	Waagen, 1895	Kummel and Teichert, 1966	Kummel, 1966	Kummel, 1970a	Kummel and Teichert, 1970	Guex, 1978
	Diener, 1913	Bando, 1981	Nakazawa, 1981			
Oman	Tozer and Calon, 1990	Blendinger, 1995	Krystyn et al., 2003	Unpublished data		
Iran	Tozer, 1972					
Afghanistan	Kummel, 1968a	Kummel and Erben, 1968	Collignon, 1973			
Timor	Wanner, 1913	Welter, 1922	Kummel, 1968b	Nakazawa and Bando, 1968		
Guangxi and South China	Hsu, 1937	Chao, 1950	Chao, 1959	Wang and He, 1980	Guo, 1982	
	Wang, 1984	Wang, 1985	Unpublished data			
California Nevada Idaho/Utah	Hyatt and Smith, 1905	Smith, 1932	Kummel and Steele, 1962	Silberling and Wallace, 1969	Unpublished data	
			Mathews, 1929	Kummel, 1957		
British Columbia	Tozer, 1963	Tozer, 1965	Tozer, 1967	Tozer, 1994		
Greenland	Spath, 1930	Spath, 1935	Trümpy, 1969			
Spitsbergen	Frebold, 1929	Frebold, 1930	Kummel, 1961	Tozer and Parker, 1968	Korchinskaya, 1972	Weitschat and Lehmann, 1978
	Korchinskaya, 1982	Korchinskaya, 1983	Korchinskaya and Vavilov, 1987	Weitschat and Dagys, 1989	Mørk et al., 1999	Unpublished data
Ellesmere/Axel Heidberg Islands	Tozer, 1965	Tozer, 1967	Tozer, 1994			
Olenek/Lena River and Okhotsk/Kolyma lands	Popov, 1961	Popov, 1968	Dagys and Ermakova, 1988 Sp	Dagys and Ermakova, 1990 Sm	Dagys, 1999	Ermakova, 2001
	Dagys and Ermakova, 1996	Ermakova, 1999	Zakharov, 2002a			
General	Mojsisovics, 1886	Noetling, 1905	Diener, 1912	Spath, 1934	Kummel, 1969	Zakharov, 1971

References are given in Appendix A.

ammonoid genera are evidently more stable and conservative entities. The database contains a total of 185 genera (11 genera in the Griesbachian, 22 in the Dienerian, 61 in the Smithian, 93 in the Spathian). Taxonomy at the genus-level is based on the classification of Tozer (1981a, 1994), emended with some recently described genera. Greatest care was taken to make a consistent use of generic names. Only a few occurrences reported in the literature still lack adequate illustrations that would confirm the generic assignments, but these are unlikely to seriously modify the global patterns in diversification and distribution.

Paleolatitude measurements were taken from the published literature or interpolated from a new Early Triassic map (Péron et al., 2005). This map is a synthesis of different published reconstructions and takes into account the latest and most reliable data (see Péron et al., 2005). When a basin encompasses several localities, an average latitude and longitude was taken into account. Most of the available data are distributed within the northern hemisphere, only a few Early Triassic localities being known from the southern hemisphere (e.g. Allison and Briggs, 1993) other than those from the Tethyan encroachment. In this study, we have excluded data from allochtonous terranes whose latitudinal and longitudinal positions are too poorly constrained (e.g. the Chulitna terrane for the Smithian). Hence, the exclusion of some terranes removes some endemic genera from the data set (e.g. *Paleokazachstanites* or *Burijites* from Primorye).

3.2. Reconstructions of paleogeographical ranges, generic richness, and computational analysis

In order to assess the effects of preservation and/or sampling biases, we devised a two-level analysis of the compiled data set: (i) “real presence” where only observed occurrences are taken into account, and (ii) “real + virtual presences” where the distribution of each genus was reconstructed by taking into account its most extreme latitudinal and longitudinal occurrences. The genus was considered as “virtually” present in all basins included in this reconstructed biogeographical domain (Fig. 4). This approach would theoretically conflict with bipolar distributions. However, as data other than Tethyan are missing in the southern Early Triassic hemisphere, it does not artificially expand the latitudinal distributions of actual bipolar genera. The final generic presence/absence matrix is presented in the Table 2A–D. GIS-based approaches can also be used to reconstruct past paleobiogeographical ranges (e.g. Rode and Lieberman, 2004). However, the relatively simple Early Triassic paleogeography does not make it necessary to use such methods and occurrences can be directly plotted on the paleogeographical map.

Based on this data set, we carried out an analysis of the generic richness as a function of paleolatitude in order to test the classical “energy hypothesis” of the edification of a latitudinal diversity gradient (Rohde, 1992). At the same time, we also considered the relationship between generic richness and longitude. On the basis of the observed occurrences (“real presences”), bootstrapped 95% Confidence Intervals for latitudinal and longitudinal gradients were estimated for each basin assemblage by random resampling with replacement within the set of “virtually present + absent” genera.

In addition, we generated a generic Occurrence Ratio Profile (ORP) for each stage by computing for each genus the percentage of basins where it is actually or actually and virtually present. We consider such percentage as a proxy for the generic endemicity. Then, the frequency distribution of the *n* Occurrence Ratios corresponding to the *n* genera recorded in the data set is graphed as a ten-class histogram with a 10% binsize. The bootstrapped Confidence Intervals associated to the observed frequencies are estimated by constructing and analysing several (10,000 in this work) presence/absence pseudo-matrices generated by random resampling with

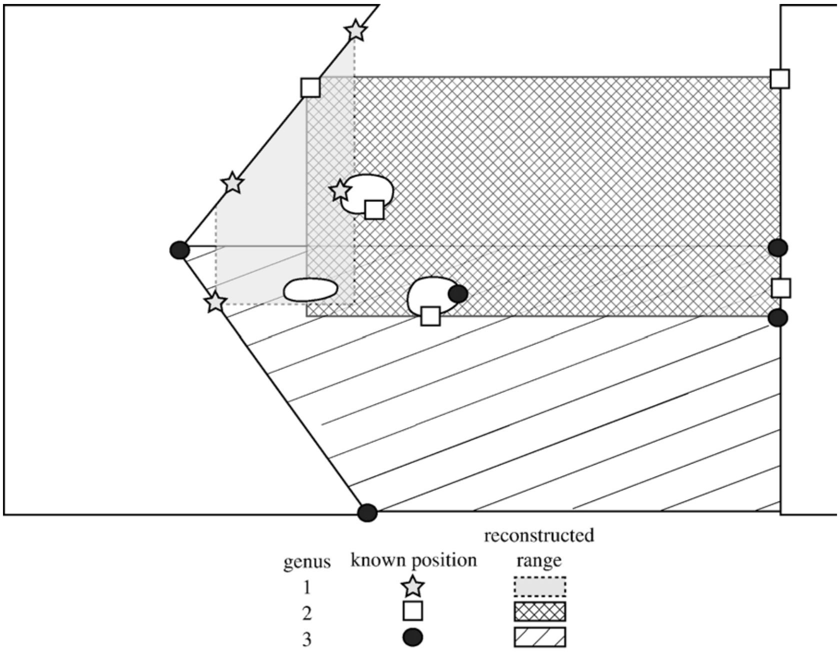

Fig. 4. Schematic range reconstructions of the ammonoid genera.

Table 2

A. Griesbachian occurrences

	Hypophiceras	*Metophiceras*	*Tompophiceras*	*Otoceras*	*Wordieoceras*	*Discophiceras*	*Ophiceras*	*Vishnuites*	*Bukkenites*	*?Anotoceras*	*Aldanoceras*
Spiti	**1**	**1**	0	**1**	0	0	**1**	**1**	0	**1**	0
Salt Ranges	**1**	1	0	0	0	0	1	1	0	1	0
Oman	0	0	0	0	0	**1**	**1**	0	**1**	**1**	0
Guangxi	**1**	**1**	**1**	**1**	0	1	**1**	1	1	0	0
Greenland	**1**	**1**	**1**	0	**1**	**1**	**1**	**1**	**1**	0	0
Spitsbergen	**1**	1	**1**	**1**	1	1	**1**	**1**	1	0	0
Ellesmere	**1**	1	**1**	**1**	**1**	**1**	**1**	**1**	**1**	0	0
Olenek	**1**	**1**	**1**	**1**	**1**	0	**1**	0	0	0	**1**

B. Dienerian occurrences

	Xenodiscoides	*Gyrophiceras*	*Kashmirites*	*Sakhaitoides*	*Eoptychites*	*Dunedinites*	*Koninckites*	*Vavilovites*	*Eovavilovites*	*Tompoproptychites*	*Proptychites*	*Kingites*	*Paranorites*	*Heibergites*	*Collignonites*	*Meekophiceras*	*Pleurogyronites*	*Ambites*	*Pleurambites*	*Gyronites*	*Prionolobus*	*Flemingites*	*Pseudosageceras*
Madagascar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	**1**	**1**	**1**
Spiti	0	0	**1**	0	0	0	**1**	0	0	0	**1**	**1**	0	0	0	**1**	**1**	**1**	0	0	**1**	**1**	**1**
Salt Ranges	**1**	**1**	**1**	0	**1**	0	**1**	0	0	0	**1**	**1**	**1**	**1**	0	0	0	**1**	**1**	**1**	**1**	1	**1**
Oman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	1
Timor	1	0	**1**	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	0	**1**	**1**	**1**
Guangxi	1	0	1	0	0	0	**1**	0	0	0	**1**	1	**1**	1	0	1	1	1	1	0	**1**	**1**	**1**
Nevada	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	1	**1**	1	0	1	1	1
Canada	**1**	0	**1**	0	0	**1**	**1**	**1**	0	0	**1**	1	0	1	0	**1**	**1**	**1**	**1**	0	**1**	**1**	1
Spitsbergen	0	0	**1**	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ellesmere	0	0	**1**	0	0	0	0	**1**	0	0	**1**	**1**	0	**1**	0	**1**	0	**1**	0	0	0	0	**1**
Olenek	0	0	0	**1**	0	0	0	**1**	**1**	**1**	0	0	0	0	0	0	0	0	0	0	0	0	**1**

C. Smithian occurrences

	Kashmirites	*Kelteroceras*	*Sakhaites*	*Pseudoceltites*	*Preflorianites*	*Eukashmirites*	*Hanielites*	*Glyptophiceras*	*Xenoceltites*	*Subvishnuites*	*Melagathiceras*	*Juvenites*	*Thermalites*	*Proharpoceras*	*Lepiskites*	*Clypeoceras*	*Clypeoceratoides*	*Pseudaspidites*	*Paraspidites*	*Lingyunites*	*Wyomingites*	*Anaflemingites*	*Meekoceras*	*Gyronites*	*Prionolobus*	*Flemingites*	*Euflemingites*	*Anaxenaspis*	*Pseudoflemingites*	*Subflemingites*	*Arctoceras*
Madagascar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	**1**	**1**	0	0	0	0	0
Spiti	**1**	0	0	**1**	0	0	0	0	**1**	0	0	0	0	0	0	**1**	0	**1**	0	0	0	0	0	0	**1**	**1**	0	0	0	0	0
Salt Ranges	**1**	0	0	**1**	0	**1**	0	**1**	**1**	0	0	**1**	0	0	0	**1**	0	0	**1**	0	0	0	**1**	0	**1**	1	0	0	0	0	**1**
Oman	0	0	0	**1**	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	**1**	0	**1**	0	1	**1**	**1**	0	0	0	0
Timor	**1**	0	0	**1**	0	**1**	**1**	0	1	**1**	0	1	0	0	0	0	0	1	0	0	1	0	1	0	**1**	**1**	**1**	0	**1**	**1**	1
Afghanistan	1	0	0	**1**	0	0	0	0	1	**1**	0	**1**	0	1	0	**1**	0	1	0	0	**1**	0	**1**	0	0	**1**	1	0	0	0	**1**
Guangxi	1	0	0	0	**1**	0	0	0	1	1	0	**1**	0	**1**	0	**1**	0	**1**	0	**1**	1	0	**1**	0	0	**1**	**1**	0	0	0	**1**
California	1	0	0	0	**1**	0	0	0	1	0	0	1	0	0	0	0	0	**1**	0	0	1	0	**1**	0	0	1	1	0	0	0	**1**
Nevada	1	0	0	0	0	0	0	0	1	0	0	**1**	0	0	0	0	0	**1**	0	0	1	**1**	**1**	0	0	1	**1**	0	0	0	**1**
Idaho	1	0	0	0	0	0	0	0	1	0	**1**	**1**	**1**	0	0	0	0	**1**	0	0	**1**	**1**	**1**	0	0	1	**1**	0	0	0	1
Caucasus	0	0	0	0	**1**	0	0	0	0	**1**	0	1	0	0	0	0	0	0	0	0	**1**	0	**1**	0	0	0	0	0	0	0	0
Canada	**1**	0	0	0	0	0	0	0	**1**	0	1	1	1	0	0	0	0	0	0	0	**1**	0	**1**	**1**	0	**1**	**1**	**1**	0	0	**1**
Spitsbergen	**1**	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	**1**
Ellesmere	**1**	0	0	0	0	0	0	0	**1**	0	**1**	**1**	**1**	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	**1**	0	0	**1**
Olenek	0	**1**	**1**	0	0	0	0	0	**1**	0	**1**	0	0	0	**1**	0	**1**	0	0	0	0	0	0	0	0	0	0	**1**	0	0	**1**

	Submeekoceras	*Ussuria*	*Metussuria*	*Parussuria*	*Oxyussuria*	*Platussuria*	*Anasibirites*	*Gurleyites*	*Hemiprionites*	*Prionites*	*Wasachites*	*Parastephanites*	*Anawasachites*	*Arctoprionites*	*Stephanites*	*Inyoites*	*Lanceolites*	*Elkoceras*	*Paranannites*	*Owenites*	*Metinyoites*	*Clypites*	*Cordillerites*	*Tellerites*	*Hedenstroemia*	*Pseudosageceras*	*Mesohedenstroemia*	*Aspenites*	*Hemiaspenites*	*Pseudaspenites*
Madagascar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**1**	0	0	0	0
Spiti	0	0	0	0	0	0	**1**	0	**1**	**1**	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**1**	0	**1**	0	0
Salt Ranges	0	0	0	0	0	0	**1**	0	**1**	**1**	**1**	**1**	0	0	**1**	0	0	0	0	0	0	**1**	0	0	**1**	**1**	0	1	0	0
Oman	**1**	**1**	0	0	0	0	**1**	0	0	0	0	0	0	0	0	**1**	0	0	**1**	**1**	0	0	0	0	**1**	**1**	0	**1**	0	**1**
Timor	**1**	**1**	0	0	0	0	**1**	0	**1**	**1**	**1**	0	0	0	1	1	0	0	1	**1**	**1**	0	0	0	**1**	**1**	0	**1**	0	**1**
Afghanistan	**1**	1	0	0	0	0	**1**	0	**1**	1	**1**	0	0	0	1	1	0	0	**1**	**1**	0	0	0	0	1	**1**	0	1	0	1
Guangxi	1	**1**	**1**	0	0	**1**	**1**	0	1	1	1	0	0	0	1	**1**	**1**	0	**1**	**1**	0	0	**1**	0	**1**	**1**	**1**	**1**	0	**1**

Table 2 (*continued*)

	Submeekoceras	*Ussuria*	*Metussuria*	*Parussuria*	*Oxyussuria*	*Platussuria*	*Anasibirites*	*Gurleyites*	*Hemiprionites*	*Prionites*	*Wasachites*	*Parastephanites*	*Anawasachites*	*Arctoprionites*	*Stephanites*	*Inyoites*	*Lanceolites*	*Elkoceras*	*Paranannites*	*Owenites*	*Metinyoites*	*Clypites*	*Cordillerites*	*Tellerites*	*Hedenstroemia*	*Pseudosageceras*	*Mesohedenstroemia*	*Aspenites*	*Hemiaspenites*	*Pseudaspenites*
California	1	0	1	1	0	0	1	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	1	0	1	1	0	1	0	0
Nevada	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	0	1	1	0
Idaho	1	0	1	0	0	0	1	1	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	0	1	1	0
Caucasus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0
Canada	0	0	0	0	1	0	1	0	1	1	1	0	1	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0
Spitsbergen	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0
Ellesmere	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Olenek	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0

D. Spathian occurences

	?Xenodiscoides	*Sulioticeras*	*Hemilecanites*	*Paranoritoides*	*Proptychitoides*	*Evenites*	*Koninckitoides*	*Arctomeekoceras*	*Boreomeekoceras*	*Neomeekoceras*	*Pseudosvalbardiceras*	*Bajarunia*	*Nordophiceras*	*Boreoceras*	*Pseudokymatites*	*Subinyoites*	*Isculitoides*	*Chiotites*	*Chioceras*	*Protropites*	*Zenoites*	*Vickohlerites*	*Popovites*	*Albanites*	*Byrrangoceras*	*Hyrcanites*	*Kiparisovites*	*Tozericeras*	*Pseudosageceras*	*Cordillerites*	*Metasageceras*	*Beatites*
Madagascar	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	0	0	0	1	0	0	0
Spiti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Salt Ranges	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	1	1	0	0	0
Oman	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	0	0	0	1	0	0	0
Timor	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0
Afghanistan	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0
Iran	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0
Guangxi	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0
Albania	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1
California	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Yugoslavia	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nevada	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Idaho	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Chios	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1	1	1	0
Caucasus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	0	0
Canada	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0
Spitsbergen	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
Ellesmere	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
Olenek	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0

	Dinarites	*Pseudodinarites*	*Dagnoceras*	*Stacheites*	*Balkanites*	*Tirolites*	*Diaplococeras*	*Dorikranites*	*Columbites*	*?Tirolites*	*Procolumbites*	*Pleurocolumbites*	*?Ceratites*	*Hellenites*	*Pallasites*	*Pseudoharpoceras*	*Paragoceras*	*Epiceltites*	*Epiceltitoides*	*Subcolumbites*	*Fengshanites*	*Prenkites*	*Tunglanites*	*Khvalynites*	*Metadagnoceras*	*Metahedenstroemia*	*Procarnites*	*Doaboceras*	*Neopopanoceras*	*Digitophyllites*	*Procarnitoides*	*Prosphingites*
Madagascar	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	0	0	0	0	0	0	0
Spiti	0	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	0	0	0
Salt Ranges	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Oman	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Timor	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0
Afghanistan	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	1	1	0	0	0	0
Iran	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0
Guangxi	0	0	1	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	1	0	0
Albania	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	0	1	1	1	0	0	0	0	0
California	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0
Yugoslavia	1	1	0	1	1	1	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
Nevada	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0
Idaho	0	0	0	1	0	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Chios	1	1	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	0	0
Caucasus	1	1	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Canada	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1
Spitsbergen	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	0	0	0	0	0	0	0
Ellesmere	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	0	0	0	0	0	0	1
Olenek	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	0	0	0	0	0	1	1

(continued on next page)

replacement of taxa. Then, the observed profiles were compared to their respective null distribution models as generated by random reshuffling of taxa occurrences among localities (this permutation model corresponds to the third method of permutation of a taxon × locality occurrence matrix as discussed by Legendre et al., 1997).

Table 2 (*continued*)

	Sibirites	*Parasibirites*	*Tjururpites*	*Kazakhstanites*	*Olenikites*	*Svalbardiceras*	*Keyserlingtes*	*Olenekoceras*	*Monacanthites*	*Prohungarites*	*?Middlemissites*	*Qilianshanites*	*Dalmatites*	*?Prohungarites*	*?Hungarites yatesi*	*Eodanubites*	*Preflorianitoides*	*Proacrochordiceras*	*?Acrochordiceras*	*Eoacrochordicereas*	*Eogymnites*	*Ziyunites*	*Procladiscites*	*Paleophyllites*	*Eophyllites*	*Mangyshlakites*	*Meropella*	*Leiophyllites*	*Ussurites*
Madagascar	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	0	0	0	0
Spiti	0	0	0	0	0	0	**1**	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	**1**	0
Salt Ranges	0	0	0	**1**	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Oman	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Timor	0	0	0	0	0	0	**1**	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	**1**	0
Afghanistan	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	**1**	0	0	1	0
Iran	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	**1**	0	0	**1**	0
Guangxi	0	0	0	0	0	0	1	0	0	1	0	**1**	0	0	**1**	**1**	**1**	0	0	**1**	0	**1**	**1**	1	0	0	0	**1**	0
Albania	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	**1**	0	**1**	0	0	0	0
California	0	0	0	0	0	0	**1**	0	0	1	0	0	1	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Yugoslavia	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0
Nevada	0	0	0	0	0	0	1	0	0	**1**	0	0	1	**1**	**1**	0	0	0	**1**	0	0	0	0	0	0	0	0	1	0
Idaho	0	0	0	0	0	0	1	0	0	**1**	0	0	**1**	**1**	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0
Chios	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	**1**	**1**	**1**	0	**1**	**1**	0
Caucasus	0	0	**1**	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	**1**	0
Canada	0	0	0	0	0	**1**	**1**	0	**1**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**1**
Spitsbergen	0	0	0	0	0	**1**	**1**	0	**1**	**1**	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	1	**1**
Ellesmere	0	0	0	0	**1**	**1**	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**1**
Olenek	**1**	**1**	0	0	**1**	0	**1**	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**

Bold numbers indicate real presences.
Normal numbers indicate interpolated presences. See Appendix 1 for references.

This method of permutation generates the null hypothesis that for each basin, a fixed number of genera (preserved by the permutation model and corresponding to a first order to a fixed number of ecological niches) randomly colonize the basin through a lottery where the exact identity of each genus does not matter. Hence, this null hypothesis implicitly assumes that the geographical location and physical and environmental characteristics of the basin do not control the detailed taxonomic composition of its generic assemblage, but only control its generic richness, i.e. its number of colonisable "niches".

Such basin level based analysis departs from already published qualitative or quantitative studies (e.g. Dagys, 1988; McGowan, 2005) in that it estimates faunal endemicity at an ecologically meaningful level of spatial resolution. Indeed, taxonomic assemblages recorded within basins, i.e. areas ranging in most cases between surface scales of 10^4 to 10^6 km^2, correspond to a first order to metacommunities, i.e. "sets of local communities that are linked by dispersal of multiple interacting species" (see Leibold et al., 2004). The variations of taxonomic composition at this regional scale of γ diversity (Whittaker, 1977) are known to be independent from local processes controlling α diversity but strongly depend on historical and biogeographical constraints (e.g. origination, extinction and migration rates; Brown, 1995; Rosenzweig, 1995; Gaston and Blackburn, 2000; Lieberman, 2000; Hillebrand and Blenckner, 2002) as well as on global physiographic and environmental conditions (Arita and Rodríguez, 2004). This makes the regional metacommunity level an ecologically meaningful level of functional organization with its own dynamic and own interaction rules partly emerging from local community integration. Moreover, the metacommunity level is also partly determined by globally controlled physical and historical parameters (Ricklefs, 1987, 2004; Leibold et al., 2004).

4. Results

4.1. Griesbachian

During Griesbachian time, no latitudinal or longitudinal generic richness gradient can be recognized (Figs. 5A, 6A). The bootstrapped Confidence Intervals associated with these generic richness transects suggest that this feature is not an artefact generated by the meagre amount of Griesbachian data. The ammonoid fauna appears very cosmopolitan and homogeneous (Figs. 7A and 8A), as illustrated by the respective distributions of *Ophiceras*, *Hypophiceras* or *Otoceras*. The rest of the Griesbachian genera are preferentially found in middle or high-latitude basins (e.g. *Tompophiceras*), but the comparatively scarce data from the Early Triassic southern hemisphere prevents further in-depth comparisons.

4.2. Dienerian

A weak latitudinal diversity gradient emerges and marks the onset of a change in the paleogeographical distribution of ammonoids (Fig. 5B). A weak longitudinal diversity gradient cannot be excluded in the Tethys (Fig. 6B). Many genera are longitudinally distributed across the entire Panthalassa, thus indicating the onset of a latitudinal zonation (e.g. *Pleurogyronites*, *Ambites*, *Pleurambites*). Hence, a weak endemism emerges during the Dienerian (Figs. 7B and 8B). It involves genera confined to northern Siberia or to the southern border of the Tethys (e.g. *Eovavilovites*, *Tompoproptychites*, *Collignonites*).

4.3. Smithian

A clear unimodal latitudinal diversity gradient first emerges during the Smithian (Fig. 5C), whereas the longitudinal analysis of Smithian distributions suggests a flat gradient across the Panthalassa and a marked westward decrease of the diversity gradient within the Tethys (Fig. 6C). This longitudinal gradient in the Tethys suggests that different factors influenced the modes of distribution and dispersal of ammonoids between the Tethys and the Panthalassa. Some genera such as *Aspenites*, *Lanceolites*, *Inyoites* or *Owenites*, which are essentially restricted to the intertropical belt, indicate strong longitudinal similarities between the Tethyan and the tropical eastern Panthalassic basins (California, Nevada, Idaho).

At the complete stage level, the generic assemblages become more and more endemic (Figs. 7C and 8C), even if some successive distinct biogeographical configurations can be distinguished. At the very beginning of the Smithian the widespread and very abundant genus *Hedenstroemia* indicates a short phase of high cosmopolitanism. For the following phase, the Tethyan and Equatorial basins include more endemic genera than the high-latitude ones. This illustrates an intensification of the geographical differentiation despite the fact that some cosmopolitan genera still do persist (e.g. *Arctoceras*, *Flemingites*, *Pseudosageceras*). Finally, this pattern of biogeographical distribution is markedly altered during the very end of the Smithian (*Anasibirites* Zone and its high-latitude correlative, the *Anawasachites tardus* Zone), with a severe drop in diversity (Figs. 3 and 5D) accompanied by a return to essentially cosmopolitan distributions as shown by *Xenoceltites* and Prionitids (Fig. 9).

4.4. Spathian

An even steeper latitudinal gradient finally characterizes Spathian times (Fig. 5E). However, it differs from the Smithian one in being asymmetrically bimodal instead of unimodal, with two maxima separated by ca. 20° in latitude, thus delineating a marked peri-Equatorial decrease. A special attribute of this gradient is the increase of generic richness in the Boreal realm. Unlike the latitudinal gradient, the longitudinal differentiation previously observed between the Panthalassa and the Tethys fades away (Fig. 6D). This suggests that the primary environmental factors controlling the spatial distribution of the ammonoids may become identical again in the two oceanic realms. At the entire stage level, the generic endemicity reached its maximum value (Figs. 7D and 8D). Few genera such as the long-ranging genus *Pseudosageceras* do actually display a cosmopolitan distribution.

4.5. Interpolated generic richness maps

The generic richness for the Smithian and Spathian basins can be interpolated to visualize preliminary diversity contours (Fig. 10A, B). For this purpose, we used the simple Delaunay triangulation as implemented in the Isopaq software (Monnet et al., 2003a). This method of interpolation is well suited here because the values interpolated for sampled basins are the observed ones by definition and only intervening values are interpolated. This method avoids the over or underestimation effect often observed with more complex interpolation methods such as the Thin Plate Splines or Kriging. In the case of the Smithian and Spathian, the number of basins is still too small for a reliable interpretation of a worldwide interpolation (Brayard et al., 2004). Yet, these contours allow first order estimates of the diversity pattern evolution. The Smithian interpolated map clearly highlights the latitudinal and longitudinal diversity gradients. The Spathian interpolated map illustrates the complexity of the distribution of ammonoid genera and indicates the existence of a western Tethyan diversity hot-spot including a high proportion of endemic genera (e.g. *Diaplococeras*, *Meropella*, *Protropites*, *Pseudokymatites*).

5. Discussion

5.1. End-Permian versus Early Triassic climates: data and models

After the Carboniferous–Permian glaciation, the Late Paleozoic marine biogeographical provinces were well differentiated, with a pronounced provincialism (e.g. Bambach, 1990; Nie et al., 1990; Shen and Shi, 2004) suggesting a steep latitudinal temperature gradient, possibly coupled with an intensive thermo-haline

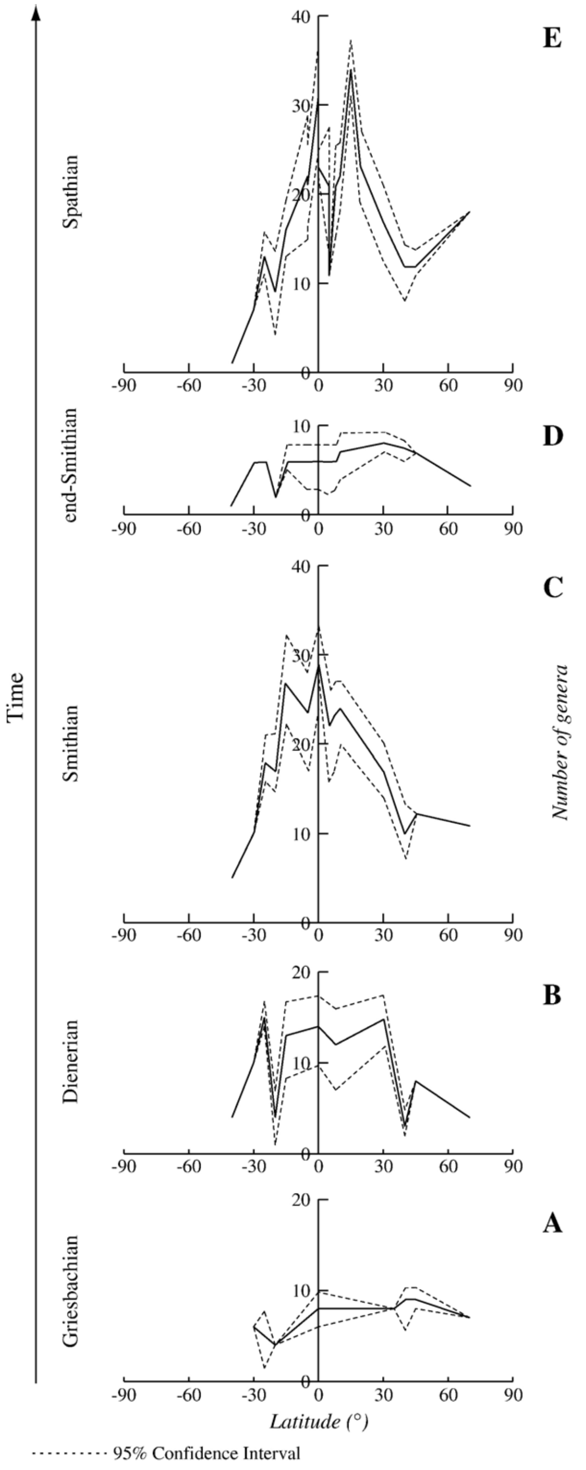

Fig. 5. Latitudinal diversity patterns during the A) Griesbachian, B) Dienerian, C) Smithian, D) end-Smithian, E) Spathian.

oceanic circulation (e.g. Beauchamp and Baud, 2002). Floras and climate-sensitive sedimentary rocks also indicate a relatively marked latitudinal temperature gradient showing the complete spectrum of temperature biomes (Rees, 2002; Gibbs et al., 2002; Rees et al., 2002).

Moreover, climatic models of the end-Permian indicate a steep temperature gradient coupled with a high seasonal variability (e.g. Crowley et al., 1987, 1989;

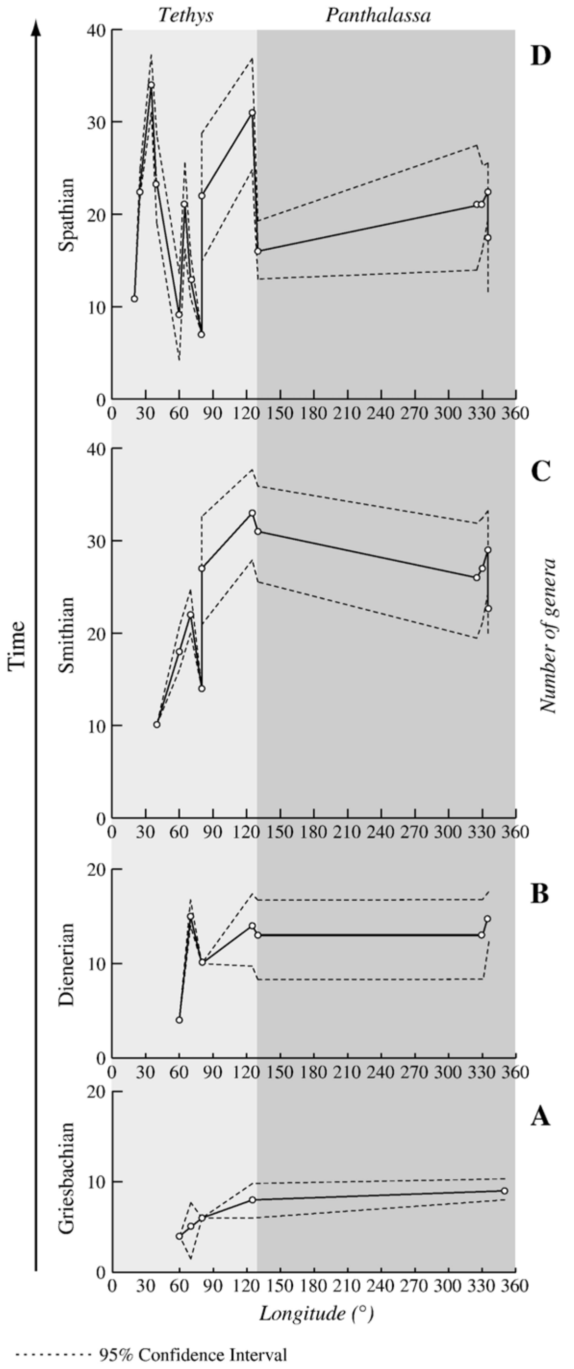

Fig. 6. Longitudinal diversity patterns for intertropical basins (30°N–30°S) during the A) Griesbachian, B) Dienerian, C) Smithian, D) Spathian.

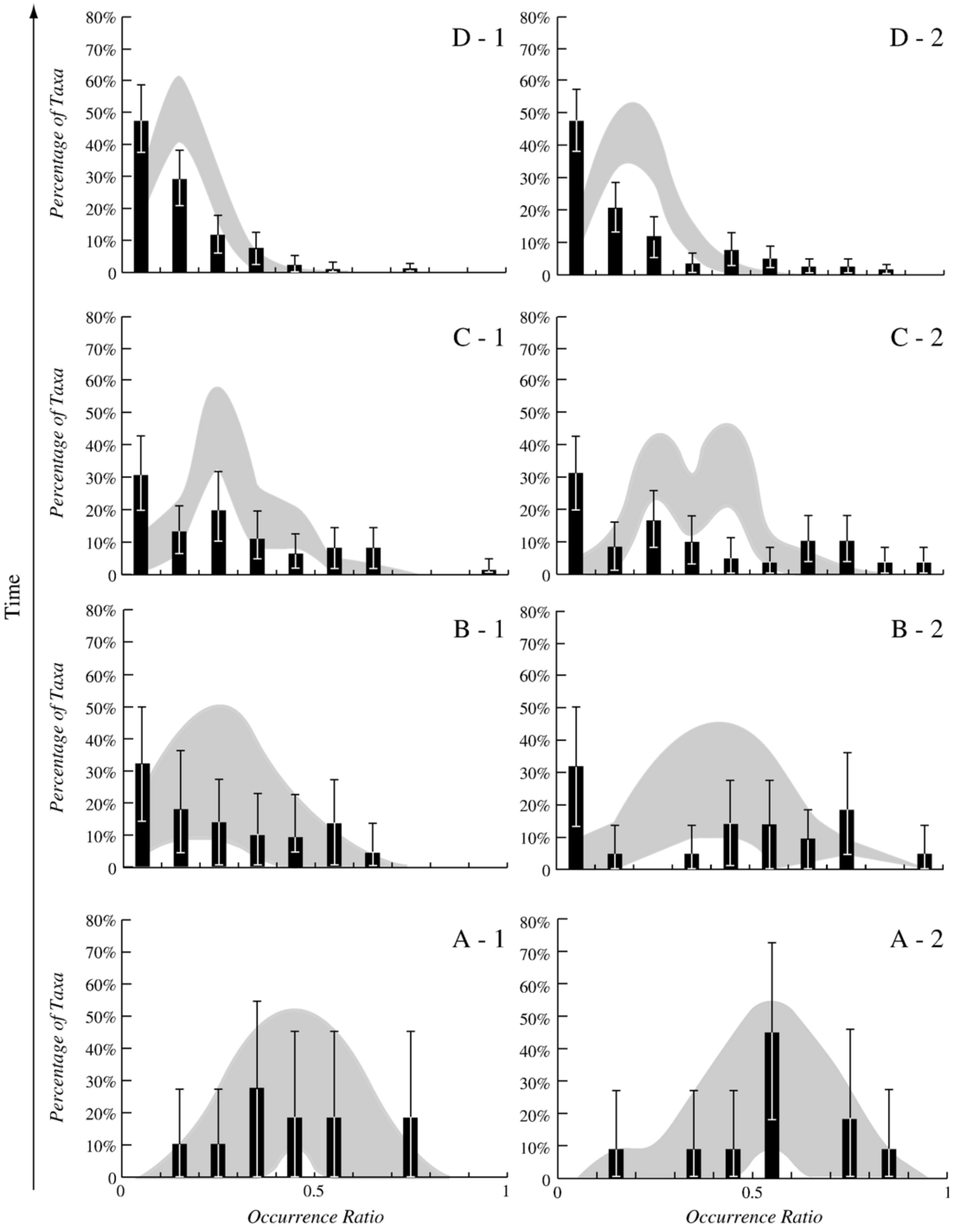

Fig. 7. Generic Occurrence Ratio Profiles for Early Triassic ammonoids. A) Griesbachian, B) Dienerian, C) Smithian, D) Spathian; 1) ORP computed from observed genera only, 2) ORP computed from observed and interpolated genera. Bootstrapped 95% Confidence Intervals associated to the observed Occurrence Ratios (error bars on the histogram) estimated with 10,000 iterations; 95% ORP null distribution (shaded area) estimated with 10,000 iterations under a lottery permutation model (see text for details).

Kutzbach and Gallimore, 1989; Kutzbach and Ziegler, 1993; Fluteau et al., 2001). During the end of the Permian and the beginning of the Early Triassic, simulated temperature gradients suggest warm waters in high latitudes (Kutzbach et al., 1990). Recent computer simulation by Hotinski et al. (2001; see Hotinski et al., 2002; Zhang et al., 2003 for a discussion) adopts this scenario, assuming a latitudinal

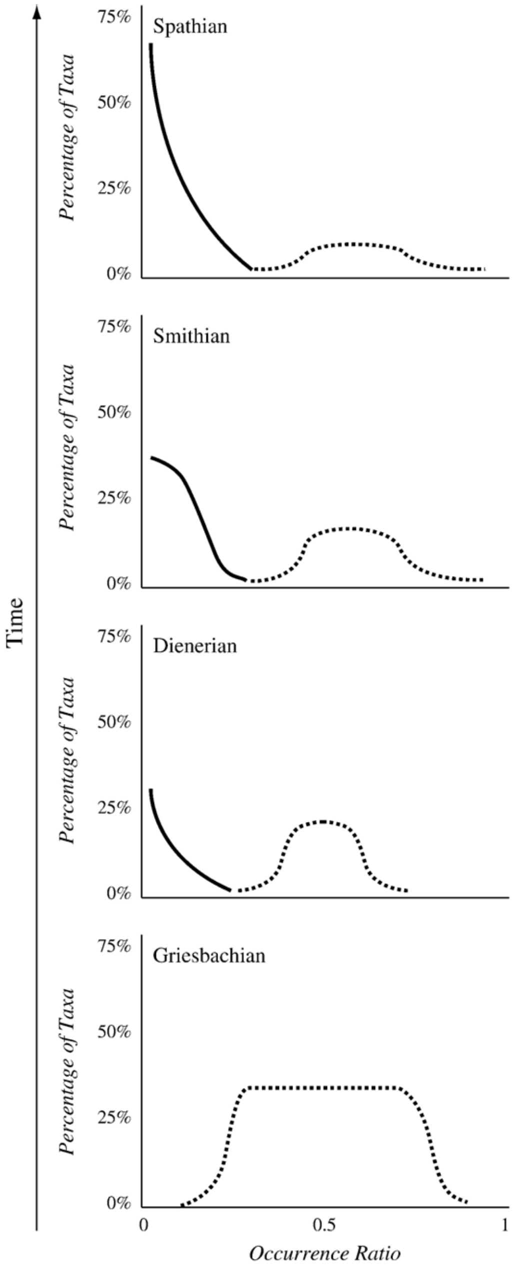

Fig. 8. Simplified generic ORP (Fig. 7) evidencing the Early Triassic trend toward increasing endemicity and decreasing cosmopolitanism. Based on the ORP shapes, genera are empirically divided in two groups: endemic (ER<ca. 1/4; continuous line) and cosmopolitan (OR>ca. 1/4; dotted line).

sea surface temperature (SST) gradient of only 16 °C (with polar temperature of 12 °C). Such a weak SST gradient may have slowed down the deep oceanic circulation and ultimately lead to anoxia which has been put forward as a possible cause of the Permo-Triassic mass extinction and the delayed recovery (e.g. Wignall and Hallam, 1992; Wignall and Twitchett, 1996, 2002; Isozaki, 1997; Kato et al., 2002; Twitchett et al., 2004). Recent hypothetical and simplified climatic scenario for the end-Permian and the beginning of the Early Triassic assumed a restricted oceanic-surface circulation and a weaker latitudinal temperature gradient (e.g. Kidder and Worsley, 2004).

The characteristically Equatorial symmetrical position of Pangea during the Late Permian also affects the Tethyan climatic conditions by creating a “megamonsoon” around the Tethys (e.g. simulations by Kutzbach and Gallimore, 1989; Parrish, 1995; Fluteau et al., 2001). In response, interior climates of Pangea should be drier with an increase of seasonal rainfalls along the circum-Tethyan coasts. However, the only Early Triassic climatic simulation available to date (Péron et al., 2005) indicates the disappearance of the “megamonsoon” possibly due to the northward drift of Gondwana.

Some paleontological and geological data support the simulation results, for instance:

- ice caps are absent from the very end-Permian, indicating that the latitudinal temperature gradient is less steep than the present-day one;
- some Spitsbergen rocks indicate that some warm-water algae migrated from low to high-latitudes by the Early Triassic (Wignall et al., 1998);
- the demise of biogenic cherts during the Late Permian indicates that Pangean coasts were bathed by cold currents before the mass extinction but not during the recovery interval, suggesting a complete or partial stop of the thermo-haline oceanic circulation during this period (Beauchamp and Baud, 2002);
- the Early Triassic biomes are also less distinct, with warm temperate floras extending to high latitudes (Rees, 2002). Temperate biomes migrate poleward during the Permo-Triassic boundary indicating a global warming trend (Ziegler et al., 1993). Coal forming plants are replaced by plants adapted to drier conditions (Rees, 2002);
- the loss of the Late Permian provinciality and the cosmopolitan distribution of many species in the marine realm are the predominant trait and also suggests a high warming trend during the earliest Triassic (Kummel, 1973b; Bambach, 1990).

All cited paleontological data and the unique Early Triassic computer simulation (Péron et al., 2005) lead to the general statement that the latitudinal temperature gradient was probably weak during the earliest Triassic, as a result of a global warming. The end-Permian mass extinction recovery is generally considered to have lasted until

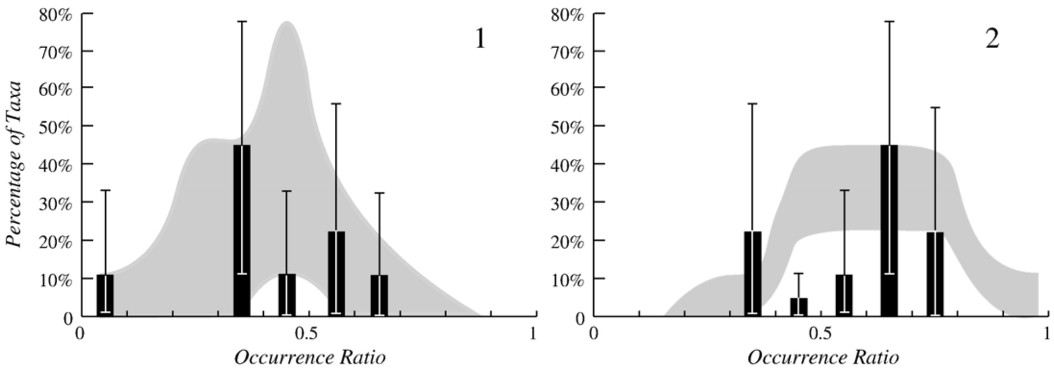

Fig. 9. Generic Occurrence Ratio Profiles for end-Smithian ammonoids (see Fig. 7 for legend). 1) ORP computed from observed genera only, 2) ORP computed from observed and interpolated genera. These ORP illustrate a short faunal event which markedly affected the biogeographical structuring of ammonoids by strongly decreasing the global level of endemicity (compare with Fig. 7C). Comparisons with the associated latitudinal gradient pattern (Fig. 5D) suggest that this event is of climatic origin (see text for details).

the end-Spathian or the Early Anisian, but ammonoid diversity recovered much earlier than many other marine clades. How does this differential recovery relate or reflect climatic changes during the Early Triassic?

5.2. Modes of life, distribution and dispersion

Many of the present-day marine organisms such as bivalves, brachiopods or gastropods possess at least one

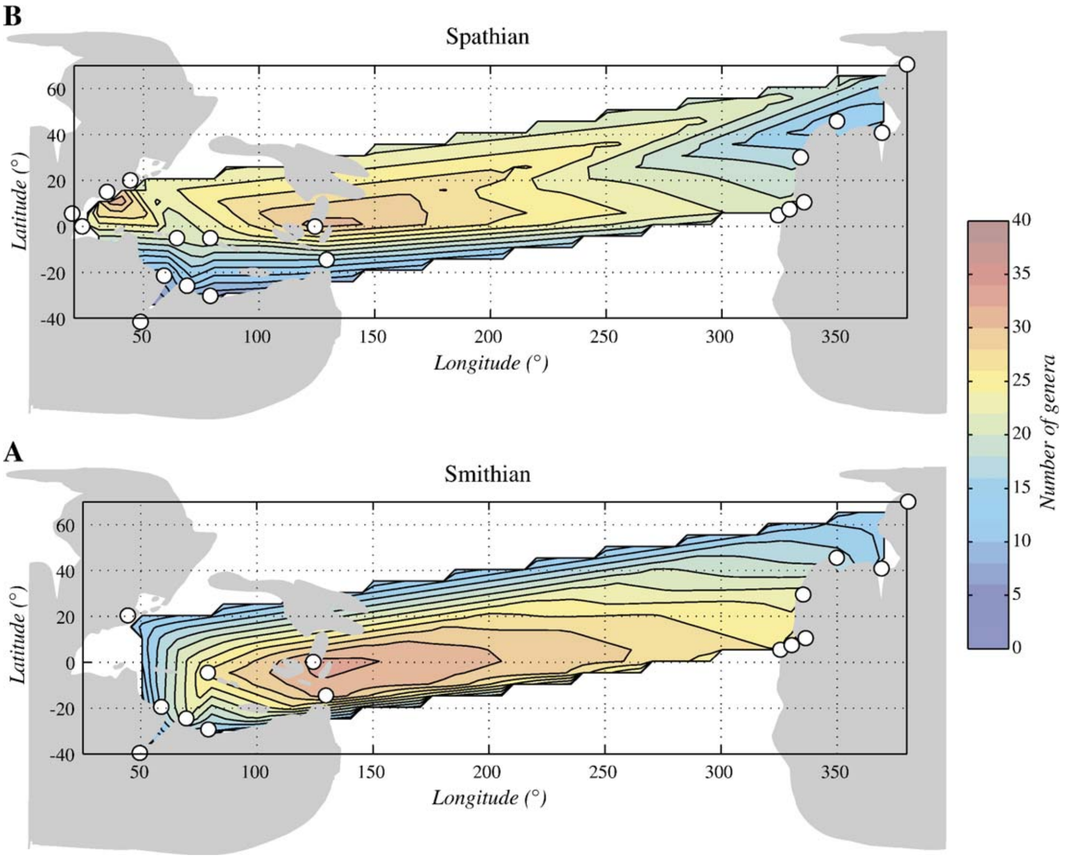

Fig. 10. Preliminary diversity contours for the A) Smithian, B) Spathian. Interpolation was realized using the software Isopaq© (Monnet et al., 2003a) and the Delaunay Triangulation method.

juvenile planktonic stage allowing their passive dispersal by ocean currents along coastlines of continents and across ocean basins (e.g. Scheltema, 1968, 1979, 1986). The exact mode of dispersal of ammonoids is unknown but the comparison with present-day coleoids (the best candidate as an ammonoid sister group; Boletzky, 2004) strongly suggests that they had also a juvenile planktonic phase (e.g. Tozer, 1982; Tanabe et al., 1993). An active long-distance migration of the adult form has to be brushed aside due to their morphology (e.g. Jacobs, 1992; Jacobs and Chamberlain, 1996), and because broad and deep oceanic basins such as the Panthalassa may have represented severe biogeographical barriers. A second possibility is the dispersal by rafting. Without evidence supporting that juveniles or egg capsules of ammonoids were able to attach to floating objects, this mode of transport can only be considered as minor.

Furthermore, the Spathian ammonoid latitudinal diversity gradient evidenced in this work (Fig. 5E) presents an asymmetrically bimodal shape centred on the thermal Equator. Such gradient closely mimics the present-day bimodal latitudinal gradients of taxonomic richness as observed for organisms possessing at least one planktonic stage (see Section 5.3.2.). This typical pattern reinforces the hypothesis of a juvenile planktonic phase for ammonoids as observed in many groups of their phylum (coleoids, bivalves). A passive dispersal mode during early growth stages appears to be a necessary explanation with respect to the observed distributions and very long distance crossing within paleolatitudinal belts. The ammonoid distributions observed during the Smithian and Spathian stages show that several genera are only encountered within narrow latitudinal bands. This point is well illustrated by *Aspenites*, *Lanceolites*, *Pseudaspidites*, *Hanielites* (Smithian), *Tirolites*, *Fengshanites*, *Hellenites*, *Columbites*, *Proptychoides* (Spathian) which are confined to the Equatorial belt. Such zonal distributions indicate that a wide ocean such as the Panthalassa is not an obstacle to ammonoid dispersion and strongly suggest that SST could be a preponderant controlling parameter, even when compared to sea-level fluctuations. Indeed, ammonoid distribution and dispersion are often considered to be linked to sea-level changes or the opening of oceanic corridors (e.g. Enay, 1980; Hallam, 1989; Hantzpergue, 1995; O'Dogherty et al., 2000), but the deterministic causal relationship between sea-level changes and diversity appear complex to determine (e.g. Macchioni and Cecca, 2002). Time intervals characterized by reduced epicontinental seas such as the Early Triassic are likely to favour temperature as the prime controlling factor as opposed to time intervals characterized by vast epicontinental seas and paleogeographical fragmentation (e.g. Cretaceous).

It is also worth noting that the Early Triassic Panthalassa was straddled with terranes (Tozer, 1982) which could also enhance the capacity of long-distance dispersal of ammonoids (the Panthalassa covered more than 20,000 km in width). Hence, even if a precise location of the centres of speciation and diversification is always difficult — if not impossible — to attest, the following biogeographical scenario emerges from available evidence on ammonoid diversity and distribution.

From the Dienerian on, the intensification of the SST gradient and winds surely increases possible North and South Equatorial currents (in comparison to the present-day Pacific Ocean configuration, see Pickard and Emery, 1990). In this case, every Panthalassic terrane can be considered as a stepping-island facilitating a westward dispersal of ammonoids. On the one hand, the West coasts of Pangea may act as a centre of dispersion in the direction of the Tethys across the Panthalassa, the Tethys being a receptacle of migration but also a cradle for new endemic genera (especially during the Spathian). On the other hand, the existence of a potential Equatorial Countercurrent (although deeper and involving a smaller water volume than the North and South Equatorial current) may also make it possible for some genera to migrate eastward across the Panthalassa, as already proposed by Newton (1988) in her theory of pantropic distribution.

5.3. Diversity patterns

5.3.1. Latitudinal gradient of diversity: the classical pattern

The latitudinal gradient of diversity is one of the most studied patterns of both past and present-day global biodiversity (e.g. Dobzhansky, 1950; Stehli et al., 1969; Currie and Paquin, 1987; Rosenzweig, 1995; Roy et al., 1998; Gaston, 2000; Rex et al., 2000; Cecca et al., 2005). It is known to occur in the majority of taxonomic groups and is manifested by a decreasing number of taxa (in most cases, species, genera or families) from low to high latitudes. The latitudinal diversity cline is usually described as unimodal with a taxonomic richness monotonically increasing from the Pole to the Equator, and centred near the Equator (e.g. Pianka, 1966; Gaston, 2000). Yet, a second pattern often interpreted as a particular derivative of the unimodal cline must be considered. It consists of a bimodal gradient of taxonomic richness with two maxima centred near the Tropics of Cancer and Capricorn and a drop of taxonomic richness near the Equator (e.g. Rutherford et al., 1999; Kiessling, 2002; Shen and Shi, 2004; Worm et al., 2005; Dolan et al., 2006). This Equatorial low is frequently observed for extant and past marine organisms.

The ecological and evolutionary mechanisms explaining the spatial structure and temporal variability of latitudinal gradients of diversity are still contentious (see Rohde, 1992 for a review of the different classical factors). About thirty possible explanations have been proposed to explain the origin of the latitudinal gradients of diversity. Most of them imply empirically derived, direct or indirect relationships between taxonomic richness and climatic gradients and can be regrouped within the energy-hypothesis (Currie, 1991). The climate and especially the temperature are known to influence directly the dispersal and the distribution of species (see Brayard et al., 2004, 2005). Other explanations can involve evolutionary and dispersal rates (e.g. Pianka, 1966) or parameters such as predation or competition levels. Nevertheless, the majority of these last hypotheses cannot be used for the purpose of a general or unique explanation. Moreover, most of them contain various degrees of circularity or are not supported by sufficient evidence (Rohde, 1992).

5.3.2. Temporal variability of the latitudinal diversity gradient

Considering the stable and relatively simple Early Triassic paleogeography, SST is likely to have been the major first order parameter controlling the distribution of ammonoids. Based on this hypothesis, the absence of a latitudinal diversity gradient, the global low diversity, and the high cosmopolitanism observed during the Griesbachian (Figs. 5A, 6A, 7A) are compatible with a flat SST gradient, possibly implying a weak oceanic surface-circulation. At this time, dispersion of genera was certainly slow and ended into uniform distributions.

The first latitudinal differentiation occurred during the Dienerian (Fig. 5B), which correlatively suggests the onset of a contrasted SST gradient. This early phase ended with the beginning of the Smithian (*Hedenstroemia hedenstroemi* Zone of the Canadian Arctic and Siberia). This time interval is characterized by an impoverished and cosmopolitan fauna, suggesting a brief return to a poorly contrasted SST gradient. Increasing trend in latitudinal gradient of taxonomic richness quickly resumed during Mid-Smithian times (*Meekoceras gracilitatis* Zone of the Nevada and its approximate higher latitude correlative, the *Flemingites romunderi* Zone) until it was again severely interrupted during the latest Smithian time (*A. tardus* Zone of the Canadian Arctic and Siberia and its low latitude correlative, the *A. pluriformis* Zone). The latest Smithian diversity dropdown was also accompanied by marked cosmopolitan distributions (e.g. *Xenoceltites*, prionitids), which again suggests a major and brief climatic event leading to an almost flat SST gradient (as modelled by Brayard et al., 2004, 2005). Extremely contrasted diversity gradients resumed shortly after the Smithian/Spathian boundary and persisted during the entire Spathian. The Smithian/Spathian boundary also corresponds to the biggest evolutionary turnover of ammonoids throughout the entire Early Triassic (see Fig. 2). Latitudinal biogeographical differentiation (Figs. 7D and 8D) and global diversity values (Fig. 5E) peaked during the Spathian. A global transgression at the beginning of this stage may also have contributed to the rise of the global diversity of ammonoids. However, whatever its amplitude, sea-level only cannot account for the observed pronounced latitudinal distributions. Again, the preponderant controlling parameter seems to have been a contrasted SST gradient.

The clearly bimodal Spathian gradient of latitudinal diversity differs from the classically recognized unimodal one (e.g. Stehli et al., 1969; Gaston, 2000), but closely mimics the extant or fossil gradients observed for foraminifers, radiolarians, brachiopods or predator fishes (e.g. Rutherford et al., 1999; Kiessling, 2002; Shen and Shi, 2004; Worm et al., 2005, respectively). In the literature, this type of diversity gradients is explained by many hypotheses: (i) possible mesothermal waters in low-latitudes; (ii) less habitable areas (Shen and Shi, 2004); (iii) Equatorial water mixing-assemblages; (iv) Equatorial current effect or (v) extreme Equatorial temperatures (Rutherford et al., 1999). Yet, another possible explanation to this drop of generic richness near the Equator is the influence of geometric constraints on the distribution of organisms (Colwell et al., 2004). These constraints act by combining a geographic mid-domain effect with a thermal mid-domain effect to engender the Equatorial drop of diversity (Brayard et al., 2005). The geographic mid-domain effect generates the first order increasing of taxonomic richness from high to low latitudes, and then the thermal mid-domain effect divides it in two hemispheric gradients peaking near the Tropics. This hypothesis applies very well to marine organisms, notably those possessing at least one planktonic stage, and illustrates the overall importance of SST on the differentiation and distribution of ammonoids. From this point of view, the intertropical drop of generic richness has nothing to do with differential extinction of tropical forms (e.g. due to a sudden cooling event) but is the direct consequence of the geographic constraints imposed by the SST on living organisms.

The relative important amount of Early Spathian genera in the Boreal domain is an intriguing point. A relative isolation of the Boreal seas, promoting speciation of endemic taxa appears as a possible explanation.

5.3.3. Longitudinal gradient: what cause?

Although interrupted by several episodes of cosmopolitanism, the progressive emergence of a steep latitudinal gradient of generic richness is the first order biogeographical trend observed during the recovery of Early Triassic ammonoids. Yet, another interesting biogeographical pattern of Early Triassic ammonoids is the existence of a longitudinal gradient within the Tethys during Smithian times.

Contrary to the latitudinal diversity gradient which is linked to the SST gradient, a longitudinal diversity gradient cannot be directly explained by the SSTs because the solar energy supply does not vary significantly with longitudes. Present-day longitudinal gradients (e.g. best exemplified by corals) are generally explained by the eastward deepening of the mean SST and thermocline, with the added difficulty of larvae having to cross the Pacific without a sufficient number of stepping islands (Belasky, 1996).

Concerning the Early Triassic ammonoids, the existence of a longitudinal gradient seems to have been possible within the Tethys during the Smithian and to lesser degree during the Dienerian. The number of terranes within the Tethys was sufficient to allow the westward ammonoid dispersion. Nevertheless, a limiting factor may have been the absence or a sluggish surface circulation within the Tethys.

In some distant Tethyan sections (e.g. Spiti on the northern Gondwanian margin and Guangxi in the South China Block), an abrupt facies change is recorded at the Smithian/Spathian boundary. It is manifested by a drastic reduction of the clastic input (dryer conditions) and the end of anoxic water–sediment interface (strengthening of the oceanic circulation and stronger ventilation; Galfetti et al., 2004). This paleoceanographic change is compatible with the rise of highly contrasted SST gradient as inferred from ammonoids. It is also congruent with a Spathian sea-level change, which may have led to additional opportunities for biogeographical partitioning and speciation of ammonoids. These marked changes in facies and biodiversity may have resulted from modifications of the Tethyan circulation. From the Spathian on, the Tethyan oceanic circulation may have intensified and true latitudinal temperature belts established. The end of anoxia around the Smithian/Spathian boundary on several Tethyan outer platforms (Galfetti et al., 2004) could be the sign of an intense SST gradient (strong oceanic circulation and ventilation) or an indication of the end of the relative isolation between Panthalassic and Tethyan water masses. However, this hypothesis is still difficult to verify and requires further investigations.

Another hypothesis explaining the longitudinal gradient in the Tethys can also be derived from a geometric mid-domain effect generated by the global narrow triangular shape of the Tethyan encroachment (Colwell et al., 2004; Brayard et al., 2004). Yet, this hypothesis does not explain why all ammonoid genera do not latitudinally colonize the western part of the Tethys and is somewhat in contradiction with the fact that endemic genera are confined to the easternmost part of the Tethys.

This last point could be the combined outcome of the lack of western Tethyan basins and a potential less efficient sampling in this part of the Tethys. Our present-day knowledge is not sufficient to completely rule out this hypothesis.

5.3.4. Evolution of the generic occurrence ratio profile

Another, complementary way to look at the evolution of the biogeographical structuring of the Early Triassic ammonoid faunas relies on the computation and statistical analysis of Occurrence Ratio Profiles as proxies for the structure and dynamic of the global taxonomic endemicity level through Early Triassic times (Figs. 7 and 8). Distinct situations characterize each stage and evidence a global trend starting from a cosmopolitan configuration (Griesbachian) to a marked endemic configuration (Spathian). When compared to the ORP null distributions under a lottery model of random “niche” colonization (permutation model 3 in Legendre et al., 1997; see Section 3.2.), this trend appears to be the consequence of an increasingly heterogeneous biogeographical structuring of faunas. In practice, this evolution is expressed by a significantly higher than predicted percentage of very sparsely distributed (OR < ca. 0.1) as well as highly widespread (OR > ca. 0.5) genera, compensated by a significantly lower than predicted percentage of “intermediate” genera (OR between ca. 0.1 and 0.5). Hence, based on the selected null model, the biogeographical global configuration appears to be initially random (neither under nor over-“distributed”) and then more and more non-random throughout the Early Triassic. Such biogeographical maturing is fully coherent with respect to the emergence and increasing steepness of the latitudinal SST gradient as suggested by the latitudinal diversity gradient (Fig. 5) and by the interpolated generic richness maps (Fig. 10). Moreover, when latitudinal diversity gradient flattened again during the latest Smithian, the biogeographical distribution of genera becomes random again, as evidenced by the ORP (Fig. 9).

5.4. Phases of recovery

Cosmopolitan faunas at the beginning of the Griesbachian are likely to correspond to a short survival interval sensu Kauffman and Erwin (1995) with generalist and opportunistic genera. For ammonoids, this phase seems extremely reduced and ends before the Dienerian. The Dienerian stage marks the real start of the recovery interval with several new genera branching off from the *Ophiceras* stock. The Early Triassic radiation of ammonoids was largely shaped by the evolution of the SST gradient and its fluctuations. The ammonoid recovery was completed in the middle Spathian.

The formation of a pronounced latitudinal diversity gradient from the Smithian on also indicates that the rates of recovery were probably not homogeneous in time and space (contra McGowan, 2005). The latest radiometric ages obtained from South China indicate a total duration of the Early Triassic ca. 5 myr and a possible duration of the Spathian of ca. 3 myr, i.e. more than half the entire Early Triassic (Ovtcharova et al., 2006). Thus, the four Early Triassic stages are of extremely uneven duration, making the two fold subdivision of the Early Triassic even more inadequate. Hence, we believe that Early Triassic paleobiogeographical studies should preferably be based on the four stage subdivision which provides better time constraints. This new calibration also clearly illustrates the very high tempo of the ammonoid recovery during the Griesbachian, Dienerian and Smithian.

5.5. Climatic significance

The current understanding of the extremely warm climates of the Early Triassic (e.g. Hotinski et al., 2001; Kidder and Worsley, 2004) should be refined and adjusted in the light of the ammonoid paleobiogeography. They are apparently the first marine invertebrates to fully recover. They clearly indicate rapid changes in their distributions and diversity patterns which are highly suggestive of climatic modifications. These sudden faunal biogeographical changes are more easily explained in terms of climatic changes than eustatic changes alone.

As in the simple model of Kidder and Worsley (2004), the Griesbachian appears as a stage of extreme warm and uniform climate. The same model for the Dienerian/Smithian suggests a more intense but always warm climatic gradient. For these stages, ammonoids also indicate an intensification of the SST gradient but with brief reversed phases during the earliest and the latest Smithian. The Griesbachian hothouse climate and the weakly pronounced Dienerian SST gradient may have led to a weak oceanic circulation and a prolonged Early Triassic anoxia (e.g. Wignall and Twitchett, 1996, 2002). So, if the duration of anoxic bottom waters on the platforms may have influenced the timing of recovery of benthic organisms (e.g. Fraiser and Bottjer, 2005), it did not influence that of epipelagic organisms such as ammonoids. However, the edification of a clear bimodal latitudinal diversity gradient for Spathian ammonoids and the end of anoxia on outer platforms are both compatible with a steeper SST gradient. A new normal oceanic circulation was able to re-oxygenate oceanic waters during the Spathian.

6. Conclusions

The recovery in time and space of Early Triassic ammonoids was largely shaped by the latitudinal SST gradient and its short-term fluctuations. Previous suggested correlations between diversity and sea-level (e.g. Hallam and Wignall, 1999) or anoxia (e.g. Wignall and Hallam, 1992) should be considered more as indirect causes or supplementary mechanisms. Other causal relationships proposed between the Permian–Triassic mass extinction and trap volcanism (e.g. Bowring et al., 1998; Reichow et al., 2002; Mundil et al., 2004) or hydrate gas release (e.g. Morante, 1996; de Wit et al., 2002; Dickens, 2003) have to be seriously taken into account due to their multiple feedbacks on climates and especially in the cause of long-trend warming.

In this context, we show that the global recovery of Early Triassic ammonoids proceeded together with the emergence of a latitudinal gradient of generic richness. This first order global increasing trend in ammonoid diversity was interrupted by two short-term events characterized by diversity downs combined with cosmopolitan distributions. The most dramatic of these events occurred at the very end of the Smithian and ended with a major evolutionary turnover at the Smithian/Spathian boundary. This sequence of global biogeographical patterns strongly suggest that an increase of the steepness of the SST gradient is the general climatic trend for the Early Triassic (Fig. 11)

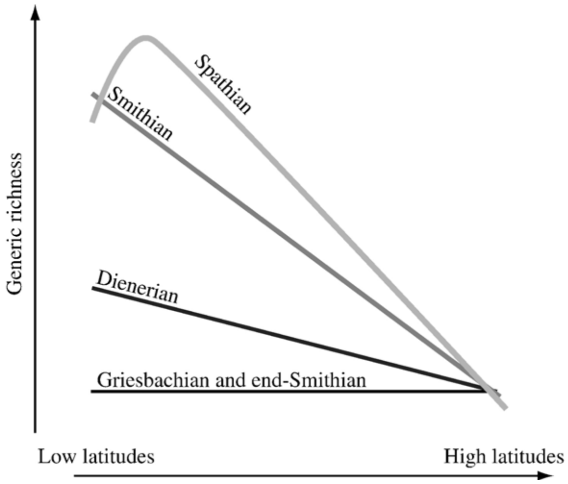

Fig. 11. Schematic evolution of the latitudinal gradient of ammonoid generic richness corresponding to the variations of the SST gradient during the Early Triassic.

with brief interruptions characterized by weak SST gradient (or more uniform climate) as suggested by short-lived and low-diversity cosmopolitan faunas.

Moreover, patterns of generic distributions seem to have been influenced by oceanic currents, especially within the Tropics where the ammonoid dispersal across the Panthalassa is clearly observed.

From another point of view, this study underlines the remarkable ability of ammonoids to recover very quickly from the Permo-Triassic mass extinction. Indeed, global diversity levels equal to or greater than pre-crisis ones were reached ca. 3 to 4 myr after the Permo-Triassic crisis, which involve extremely high origination rates at all infra-ordinal levels. Such unusual reactivity strongly calls for further paleoecological investigations, especially with regard to the nature of Early Triassic oceanic primary producers that enabled the precocious evolutionary rebound of the ammonoids. It also highlights that ammonoids were comparatively less affected by anoxic conditions on outer platforms (see Monnet et al., 2003b for the Cenomanian–Turonian anoxic event) than most other marine invertebrates.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2006.02.003.

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