Late Permian to Middle Triassic palaeogeographic differentiation of key ammonoid groups: evidence from the former USSR

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Abstract

Palaeontological characteristics of the Upper Permian and upper Olenekian to lowermost Anisian sequences in the Tethys and the Boreal realm are reviewed in the context of global correlation. Data from key Wuchiapingian and Changhsingian sections in Transcaucasia, Lower and Middle Triassic sections in the Verkhoyansk area, Arctic Siberia, the southern Far East (South Primorye and Kitakami) and Mangyshlak (Kazakhstan) are examined. Dominant groups of ammonoids are shown for these different regions. Through correlation, it is suggested that significant thermal maxima (recognized using geochemical, palaeozoogeographical and palaeoecological data) existed during the late Kungurian, early Wuchiapingian, latest Changhsingian, middle Olenekian and earliest Anisian periods. Successive expansions and reductions of the warm–temperate climatic zones into middle and high latitudes during the Late Permian and the Early and Middle Triassic are a result of strong climatic fluctuations.

Prime Middle–Upper Permian, Lower and Middle Triassic sections in the former USSR and adjacent territories are currently located in Transcaucasia (Ševyrev 1968; Kotljar et al. 1983; Zaharov 1985; Zakharov, Biakov et al. 2005), North Caucasus (Kotljar et al. 1983; Kotlyar et al. 2004; Zakharov 1986), Mangyshlak (Astahova 1960; Ševyrev 1968, 2002; Gavrilova 1980, 1989; Balini et al. 2000), Verkhoyansk area (Zaharov 1971; Dagys & Ermakova 1996; Zakharov 2002), Arctic Siberia (Mojsisovics 1886; Lazurkin & Korčinskaja 1963; Zaharov 1978; Dagis & Ermakova 1988; Dagys & Ermakova 1996), Spitsbergen (Mørk et al. 1999; Worsley 2006) and the Far East (Russian Far East and Kitakami; Burij 1959; Kiparisova 1961, 1972; Zaharov 1968, 1978; Zaharov & Pavlov 1986a, b; Zakharov 1992, 1996, 1997; Zakharov & Oleinikov 1994; Okuneva 1976; Ehiro & Bando 1985; Ehiro et al. 1986; Ehiro 1995, 2001a, b; Ehiro & Araki 1997; Ehiro & Misaki 2005). The first reports on Permian–Triassic ammonoids from these areas were published by Buch (1831) (Bogdo Mount, Russian Platform), Keyserling (1845) (Arctic Siberia), Abich (1878) (Transcaucasia), Diener (1895b) (Russian southern Far East), Bajarunas (1936) (Mangyshlak and Kazakhstan), Popov (1939, 1958) (Russian northern Far East and Verkhoyansk area) and Kiparisova (in Voinova et al. 1947) (North Caucasus). However, our knowledge of Permian–Middle Triassic ammonoids and palaeobiogeography, and especially of the Olenekian–Anisian boundary, remains limited (Diener 1916; Zakharov 1974; Zaharov 1977; Dagys 1988; Ehiro 1997; McGowan 2005; Brayard et al. 2006; Brayard et al. 2007; Brühwiler et al. 2007; Galfetti, Hochuli et al. 2007; Brayard & Bucher 2008; Brayard et al. in press).

The purpose of this study is the analysis of diversity patterns of Permian–Early Anisian ammonoids from the former USSR area and neighbouring territories, for palaeoecological and palaeogeographical reconstructions.

Materials

Original palaeontological materials used for our investigation were obtained from the Permian of Transcaucasia, South Primorye, Kitakami (Japan) and from

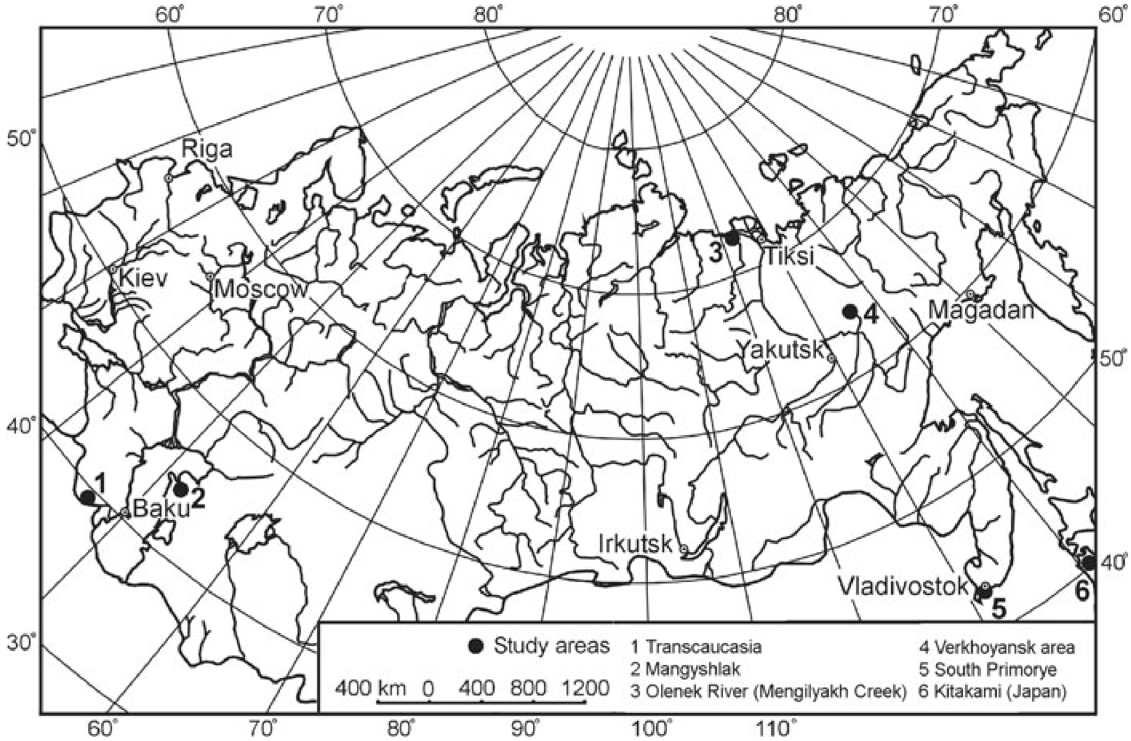

Fig. 1 Location map of sections sampled in the former USSR and Kitakami (Japan).

the Lower–Middle Triassic of the Verkhoyansk area, Arctic Siberia, South Primorye and Mangyshlak (Fig. 1).

Ammonoid successions

Within the Permian–Triassic ammonoid successions examined, some consecutive phases can be distinguished. It has been been proposed to call them megaclimaxes, confinis and pioneer phases (Zakharov 1983). The designation "megaclimaxes" (descended from Clements's [1916, 1936] biological term "climax") was proposed for the phases during which many or basic assemblage elements acquired a high diversity, and it was proposed that the phases between megaclimaxes be called confinis (from the Latin *confinis*, meaning adjacent). The confinis phases corresponding to the invasions of the first settlers can be designated as pioneer (or initial) ones.

Permian of the Far East (South Primorye and Kitakami)

The generalized stratigraphical distribution of Permian ammonoids from South Primoye and Kitakami are presented by Zakharov & Ehiro (in press). Among Permian cephalopods, cyclolobid ammonoids seem to be the most important group for phylogenetic and palaeogeographic reconstructions, because of their morphological characteristics. Specifically, they possess the most progressive suture lines among the Goniatitida, and have a wide geographical distribution. The most commonly occurring genera of cyclolobid ammonoids for the Middle and Upper Permian are *Timorites* and *Cyclolobus*, respectively, although some latest *Timorites* are also known in the lower Wuchiapingian (Ehiro & Araki 1997; Zakharov & Ehiro in press).

Wuchiapingian–Lower Induan of Transcaucasia

In the Late Permian ammonoid succession of Transcaucasia, the early Wuchiapingian and late Changhsingian possessed the most diversified and abundant ammonoid occurrences (Zakharov, Biakov et al. 2005) (Fig. 2). Goniatite *Pseudogastrioceras abichianum* (Möller) and ceratite *Paratirolites vediensis* Shevyrev ammonoids became dominant during the early Wuchiapingian and late Changhsingian, respectively.

Permian–Triassic boundary beds in the Verkhoyansk area

The Setorym River is the most important locality containing the *Otoceras* fauna in the Verkhoyansk area (Zaharov

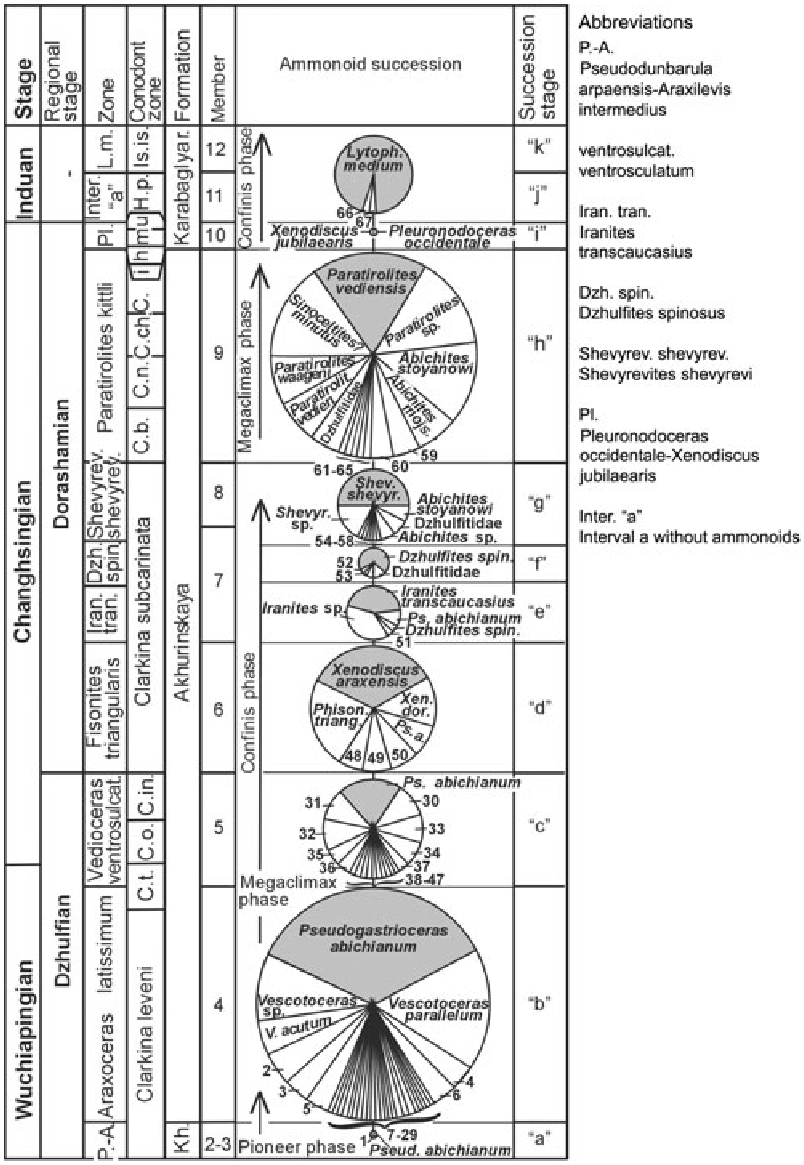

Fig. 2 Change of species composition and proportion in the Late Permian ammonoid succession of Transcaucasia: 1, *Vescotoceras parallelum* Ruzhencev; 2, *Prototoceras tropitum* (Abich); 3, *Vescotoceras serratum* Ruzhencev; 4, *Vescotoceras evanidum* Ruzhencev; 5, *Vescotoceras pessoides* (Abich); 6, *Araxoceras latissimum* Ruzhencev; 7–29, others, including *Kingoceras achurense* Zakharov, *Eumedlicottia stoyanowi* (Nassichuk, Furnish & Glenister), *Strigogoniatites* sp., *Basleoceras kotljarae* Zakharov, *Araxoceras latum* Ruzhencev, *Araxoceras varicatum* Ruzhencev, *Araxoceras glenisteri* Ruzhencev, *Araxoceras rotoides* Ruzhencev, *Araxoceras tectum* Ruzhencev, *Araxoceras trochoides* (Abich), *Araxoceras* sp., *Rotaraxoceras caucasium* Ruzhencev, *Rotaraxoceras* sp., *Prototoceras intermedium* (Abich), *Prototoceras discoidale* Ruzhencev, *Prototoceras raddei* (Arthaber), *Prototoceras fedoroffi* (Arthaber), *Prototoceras* sp., *Changhsingoceras ruzhencevi* (Zakharov), *Urartoceras abichianum* Ruzhencev, *Avushoceras* sp., *Pseudotoceras djoulfense* (Abich), *Pseudotoceras* sp.; 30, *Avushoceras jakovlewi* Ruzhencev; 31, *Vedioceras ogbinense* Ruzhencev; 32, *Vedioceras umbonovarum* Ruzhencev; 33, *Vedioceras* sp.; 34, *Vedioceras ventroplanum* Ruzhencev; 3, *Vedioceras ventrosulcatum* Ruzhencev; 36, *Dzhulfoceras fürnishi* Ruzhencev; 37, *Avushoceras* sp.; 38–47, others, including *Urartoceras abichianum* Ruzhencev, *Prototoceras tropitum* (Abich), *Pseudotoceras admirabile* Rostovcev and Azarian, *Rotaraxoceras deruptum* Ruzhencev, *Dzhulfotoceras paulum* Ruzhencev, *Dzhulfotoceras inflatum* Ruzhencev, *Changhsingoceras ruzhencevi* (Zakharov), *Pseudotoceras* sp., *Pseudotoceras djoulfense* (Abich), *Pseudotoceras armeorum* Ruzhencev; 48, *Stacheoceras tschernyschewi* (Stoyanow); 49, *Phisonites*? sp.; 50, *Xenodiscus* sp.; 51, *Xenodiscus* sp.; 52, *Stacheoceras tschernyschewi* (Stoyanow); 53, *Pseudogastrioceras abichianum* (Möller); 54–58, others, including *Pseudogastrioceras abichianum* (Möller), *Dzhulfites spinosus* Shevyrev, *Paratirolites waageni* (Stoyanow), *Paratirolites* sp., *Abichites abichi* (Shevyrev); 59, *Paratirolites kittli* Stoyanow; 60, *Abichites* sp.; 61–65, others, including *Pseudogastrioceras abichianum* (Möller), *Abichites abichi* Shevyrev, *Paratirolites trapezoidalis* Shevyrev, *Paratirolites dieneri* Stoyanow, *Pseudotirolites*? *azariani* Rostovcev; 66, *Lytophiceras* sp.; 67, Ophiceratidae gen. et sp. indet. The size of the circle plot in this and subsequent figures is proportional to the abundance of ammonoid taxa in a succession stage. Observations were from 390 (stage b), 170 (stage c), 210 (stage d), 90 (stage e), 50 (stage f), 75 (stage g), 340 (stage h) and 130 (stages j and k) samples, respectively.

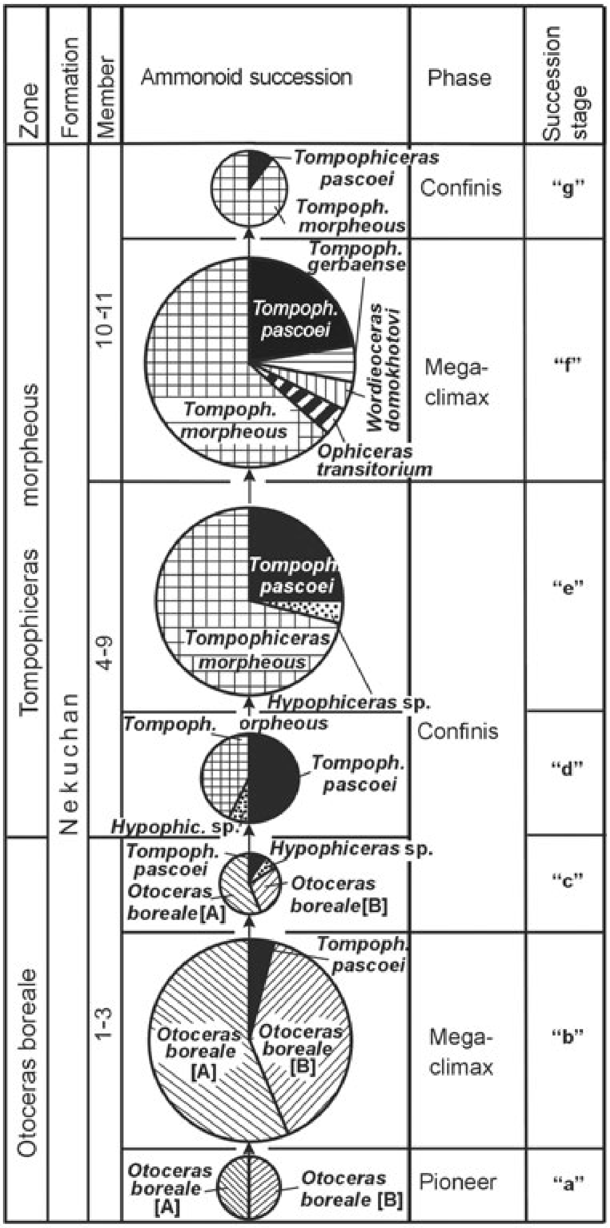

Fig. 3 Change of species composition and proportion in the early Induan ammonoid succession of the Setorym River section, Verkhoyansk area. *Otoceras boreale* (A) and *Otoceras boreale* (B) are different morphs of the same species, possibly sexual dimorphs. Observations were from 47 (stage a), 150 (stage b), 45 (stage c), 66 (stage d), 137 (stage e), 154 (stage f) and 56 (stage g) samples.

1971; Zakharov 2002). Changes of ammonoid dominance in the Setorym River section show that during the first three stages in development (stages a–c in Fig. 3), the most commonly occurring form in the assemblage is *Otoceras boreale* Spath, and during the following stages (d–g in Fig. 3) *Tompophiceras morpheous* Popow then became dominant. The population peak (megaclimax phase) of *Otoceras* occured in the development stage b represented in Fig. 3, which is characterized by some conodonts (e.g., *Hindeodus typicalis* [Sweet] and *Clarkina* cf. *changhsingensis* Wang and Wang; Kozur et al. 1995) and the first appearance of *Tompophiceras* (*Tompophiceras pascoei* [Spath]).

According to the traditional views (Griesbach 1880; Mojsisovics et al. 1895; Diener 1897; Kummel 1972; Tozer 1994), prior to definition at the Meishan Global Stratotype Section and Point (GSSP), the base Triassic in the Himalayas and other regions of the world is located at the base of the Otoceras beds. Using conodont data, Krystyn & Orchard (1996), Kozur (1998) and Orchard & Krystyn (1998) also placed the basal Triassic at the first occurrence of *Otoceras* in the Himalayas and Tibet. Basing their suggestion on their work with ophiceratid ammonoids, Krystyn & Orchard (1996) were the first to suggest that *Otoceras* species of the Otoceras woodwardi Zone were younger than Boreal *Otoceras*. Kozur (1998) has also documented that the first very primitive *Hindeodus parvus* Kozur from Greenland are found above the Otoceras boreale Zone, in the Tompophiceras pascoei Zone. As the first appearance data (FAD) of *H. parvus* in the Himalayas and Tibet are at the base of the Otoceras woodwardi Zone, Kozur (1998) believes that the conodont data confirm Krystyn & Orchard's (1996) idea concerning the younger age of the Otoceras woodwardi Zone compared with the Boreal *Otoceras* fauna. Conodont evidence with a bearing on the latest Permian age of the Otoceras boreale Zone has also been discussed (Wignall et al. 1996; Henderson & Baud 1997; Beatty et al. 2006), but all of them need additional verification, above all because Permian–Triassic conodont assemblages from the Boreal realm are significantly less abundant and diversified compared with those from the Tethys, where the Meishan GSSP is located.

Upper Olenekian–lowermost Anisian of the Olenek River area

Many localities containing late Olenekian ammonoid faunas have been discovered in the Olenek River–Olenek Gulf area, but the most abundant and diversified ammonoid occurrences are found in the Mengilyakh Creek (Mojsisovics 1886; Lazurkin & Korčinskaja 1963; Zaharov 1978; Zakharov 2007). The main known defect of the Lower Triassic Mengilyakh Creek section is its poor exposition.

Information on the upper Olenekian–lower Anisian sequence exposed along the Olenek River at the mouth of the Mengilyakh Creek is given in Table 1.

In the late Olenekian–earliest Anisian ammonoid succession of the Olenek River the highest diversity (megaclimax phase) occurs in the Olenikites spiniplicatus

Table 1 The upper Olenekian–lower Anisian sequence exposed along the Olenek River at the mouth of the Mengilyakh Creek (72°50′42.43″N, 120°58′53.94″E; Mojsisovics 1886; Lazurkin & Korčinskaja 1963; Zaharov 1978; Zakharov 2007), in descending order. The part of the Upper Olenekian exposed in this section is about 135 m thick.

Formation/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
Lower Ulakhan–Krest Formation/ Grambergia taimyrensis Zone	41	Black mudstone, intercalated with black siltstone and grey, fine-grained sandstone	>20 m		
	40	Black mudstone and siltstone with thin layers (1–20 cm) of dark grey, fine-grained sandstone	12 m		
	39	Black mudstone and siltstone with thin layers (1–20 cm) of dark grey, fine-grained sandstone	7 m	*Prohungarites tuberculatus* (Welter), *Prohungarites*? sp.	
Pastanakhskaya and Ystannakhskaya formations/ Olenikites spiniplicatus Zone	38	Black mudstone and siltstone with thin lenses of fine-grained sandstone and small, awkward-shaped calcareous nodules	3.2 m	*Prosphingites czekanowskii* Mojsisovics (dominant), *Nordophiceras euomphalus* (Keyserling), *Subolenekites altus* (Mojsisovics), *Olenekoceras middendorffi* (Keyserling), *Pseudosvalbardiceras sibiricum* (Mojsisovics)	
	37	Black mudstone with rare large calcareous nodules (in restricted and very low outcrops)	ca. 14 m		
	36	Black mudstone with large calcareous nodules	0.4 m	*Keyserlingites subrobustus* (Mojsisovics), *Boreomeekoceras keyserlingi* (Mojsisovics), *Olenikites spiniplicatus* (Mojsisovics), *Nordophiceras popovi* (Zakharov), *Nordophiceras schmidti* (Mojsisovics), *Timoceras gracialis* (Mojsisovics), *Pseudosvalbardiceras sibiricum* (Mojsisovics), *Prosphingites czekanowskii* Mojsisovics	Bivalves: *Posidonia*? sp., *Mysidioptera* sp.
	35	Black mudstone	4.5 m	*Olenikites spiniplicatus* (Mojsisovics)	
	34	Black mudstone with small calcareous nodules	0.3 m	*Olenikites spiniplicatus* (Mojsisovics), *Nordophiceras schmidti* (Mojsisovics)	
	33	Black mudstone (in small outcrops)	2.5 m		
	32	Black mudstone with large calcareous nodules	0.3 m	*Olenikites spiniplicatus* (Mojsisovics)	
	31	Black mudstone with rare calcareous nodules	1.5 m		
	30	Black mudstone with large calcareous nodules	0.4 m	*Olenikites spiniplicatus* (Mojsisovics) (dominant), *Nordophiceras schmidti* (Mojsisovics)	Brachiopod: *Lingula* sp. Bivalve: *Palaeoneilo* sp.
	29	Black, striate mudstone with rare calcareous nodules	3.2 m		
	28	Black, striate mudstone with small calcareous nodules	0.3 m	*Olenikites spiniplicatus* (Mojsisovics) (dominant), *Nordophiceras popovi* (Zakharov), *Boreomeekoceras keyserlingi* (Mojsisovics), *Olenekoceras middendorffi* (Keyserling), *Keyserlingites subrobustus* (Mojsisovics)	Nautiloid: *Trematoceras* cf. *campanile* (Mojsisovics) Belemnitid: *Atractites* sp. Nuculid bivalves

Table 1 *continued*

Formation/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
	27	Black mudstone with numerous calcareous nodules	9 m	*Olenekoceras middendorffi* (Keyserling) (dominant), *Sibirites eichwaldi* Mojsisovics, *Nordophiceras schmidt* (Mojsisovics), *Boreomeekoceras keyserlingi* (Mojsisovics)	Plant: *Pleuromeia olenekensis* Krassilov Brachiopod: *Lingula* sp. Bivalve: *Palaeoneilo* sp. Scaphopods
	26	Black mudstone with rare calcareous lenses and nodules	13 m	*Olenekoceras middendorffi* (Keyserling) (dominant), *Pseudosageceras boreale* Zakharov, *Nordophiceras schmidti* (Mojsisovics), *Boreomeekoceras keyserlingi* (Mojsisovics), *Olenikites spiniplicatus* (Mojsisovics), *Subolenekites altus* (Mojsisovics), *Sibirites eichwaldi* Mojsisovics	
	25	Black mudstone with lenses of limestone (“cone in cone” structure) and rare calcareous nodules	20–25 m		
	24	Black mudstone with small calcareous nodules	3 m	*Nordophiceras schmidti* (Mojsisovics), *Olenikites spiniplicatus* (Mojsisovics), *Subolenekites altus* (Mojsisovics)	Bivalves Small gastropods
	Closed interval, ca. 40–45 m				
	23	Black mudstone with small, flat calcareous nodules	18 m	*Nordophiceras euomphalus* (Keyserling), *Olenikites spiniplicatus* (Mojsisovics), *Subolenekites altus* (Mojsisovics), *Olenekoceras middendorffi* (Keyserling)	
	22	Black mudstone with lenses of limestone (“cone in cone” structure) and small calcareous nodules	9 m		
	21	Black mudstone with large calcareous nodules	1 m	*Nordophiceras schmidti* (Mojsisovics), *Arctomeekoceras rotundatum* (Mojsisovics), *Sibirites eichwaldi* Mojsisovics, *Olenikites spiniplicatus* (Mojsisovics), *Olenekoceras middendorffi* (Keyserling)	Brachiopod: *Lingula* sp Bivalve: *Posidonia*? sp.
	20	Black mudstone with lenses of limestone (“cone in cone” structure) and large calcareous nodules	16 m		
	19	Greenish grey mudstone and siltstone with rare calcareous nodules	0.2 m	*Prosphingites czekanowskii* Mojsisovics	
	18	Black mudstone with lenses of limestone (“cone in cone” structure), sandy limestone and rare calcareous nodules	4 m		
	17	Black mudstone with calcareous nodules	0.3 m	*Nordophiceras schmidti* (Mojsisovics), *Pseudosvalbardiceras sibiricum* (Mojsisovics)	Nautiloid: *Phaedrysmocheilus olenekensis* (Zakharov)
	16	Black mudstone	1 m		
	15	Black mudstone with numerous calcareous nodules	0.3 m	*Olenikites spiniplicatus* (Mojsisovics), *Olenekoceras middendorffi* (Keyserling)	

Table 1 *continued*

Formation/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
	14	Black mudstone	1 m		
	13	Black mudstone with numerous large calcareous nodules	0.5 m	*Nordophiceras schmidti* (Mojsisovics), *Nordophiceras euomphalus* (Keyserling), *Olenikites spiniplicatus* (Mojsisovics), *Timoceras gracialis* (Mojsisovics), *Olenekoceras middendorffi* (Keyserling), *Keyserlingites subrobustus* (Mojsisovics)	Bivalve: *Mysidioptera aurita* Popow Nautiloids: *Trematoceras* cf. *campanile* (Mojsisovics), *Phaedrysmocheilus olenekensis* (Zakharov)
	12	Black mudstone	0.7 m		
	11	Black mudstone with lenses of limestone ("cone in cone" structure) and large calcareous nodules	0.3 m	*Nordophiceras schmidti* (Mojsisovics) (dominant), *Pseudosvalbardiceras sibiricum* (Mojsisovics), *Olenikites spiniplicatus* (Mojsisovics), *Olenekoceras middendorffi* (Keyserling)	
	9	Black mudstone with lenses of limestone ("cone in cone" structure) and calcareous nodules	0.5 m	*Nordophiceras schmidti* (Mojsisovics), *Olenikites spiniplicatus* (Mojsisovics), *Timoceras gracialis* (Mojsisovics)	Nautiloid: *Phaedrysmocheilus olenekensis* (Zakharov)
	8	Black mudstone with rare calcareous nodules	3 m	*Nordophiceras schmidti* (Mojsisovics), *Olenikites spiniplicatus* (Mojsisovics), *Timoceras gracialis* (Mojsisovics)	Bivalves: *Posidonia* sp., *Mysidioptera* sp. Nautiloids: *Trematoceras* sp., *Phaedrysmocheilus olenekensis* (Zakharov) Gastropods
	7	Black mudstone with numerous large calcareous nodules	0.5 m	*Olenekoceras middendorffi* (Keyserling) (dominant), *Pseudosageceras boreale* Zakharov, *Boreomeekoceras keyserlingi* (Mojsisovics), *Nordophiceras popovi* (Zakharov), *Arctomeekoceras rotundatum* (Mojsisovics), *Sibirites eichwaldi* Mojsisovics, *Subolenekites altus* (Mojsisovics)	Belemnite: *Atractites* aff. *boecki* (Stürzenbaum) Gastropods
	6	Black mudstone with very rare calcareous nodules	6 m		
	5	Black mudstone with numerous calcareous nodules	1 m	*Olenekoceras middendorffi* (Keyserling) (dominant), *Boreomeekoceras keyserlingi* (Mojsisovics), *Sibirites eichwaldi* Mojsisovics, *Olenikites spiniplicatus* (Mojsisovics), *Subolenekites altus* (Mojsisovics)	
	4	Black mudstone	1.5 m		
	3	Black mudstone with numerous large calcareous nodules	0.5 m	*Olenekoceras middendorffi* (Keyserlig) (dominant), *Nordophiceras euomphalus* (Keyserling), *Arctomeekoceras* sp., *Boreomeekoceras keyserlingi* (Mojsisovics), *Subolenekites altus* (Mojsisovics), *Sibirites eichwaldi* Mojsisovics	Bivalves Gastropods

Table 1 *continued*

Formation/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
	2	Black mudstone with rare small calcareous nodules	12 m	*Nordophiceras euomphalus* (Keyserling), *Arctomeekoceras rotundatum* (Mojsisovics), *Subolenekites altus* (Mojsisovics), *Boreomeekoceras keyserlingi* (Mojsisovics), *Keyserlingites subrobustus* (Mojsisovics)	
Parasibirites grambergi Zone (upper part)	1	Black mudstone with small calcareous nodules (in restricted outcrops)	30 m	*Parasibirites grambergi* Popow, *Sibirites pretiosus* Mojsisovics. In removed nodules near outcrops: *Pseudosageceras*, *Nordophiceras*, *Boreomeekoceras*, *Olenikites*, *Subolenekites*, Sibirites, Olenekoceras	

Zone, where *Olenikites spiniplicatus* (Mojsisovics) dominates the ammonoid assemblage (Zakharov 2007: fig. 3). Representatives of the genus *Olenekoceras* are more frequent in this succession than are *Keyserlingites*. In Arctic Siberia *Olenekoceras* are found within two late Olenekian zones, the Parasibirites grambergi and Olenikites spiniplicatus zones (Dagys & Ermakova 1988), which apparently correspond with the *Olenekoceras*-bearing Neocolumbites insignis–Subfengshanites multiformis interval in the middle-latitude south Russian Far East area (Zakharov 1997).

Upper Olenekian–Anisian of South Primorye (Russian Island and Atlasov Cape area)

In the late Olenekian–earliest Anisian ammonoid succession the megaclimax phase corresponds with the Neocolumbites insignis Zone (Zakharov 1997; Zakharov, Popov et al. 2005). This phase is characterized by the presence of some Boreal elements (e.g., *Olenekoceras* and *Nordophiceras*; Fig. 4). A marked increase in the abundance of *Columbites*, *Subfengshanites* and *Ussuriphyllites* took place during the stages a–c depicted in Fig. 4.

Upper Olenekian of Mangyshlak (Dolnapa)

Information on the middle Olenekian–lower Anisian sequence exposed near the Dolnapa (Angry Sister) drawwell is given in Table 2.

During the early part of the Late Olenekian megaclimax (the Columbites parisianus–Procolumbites karatauchicus interval), "*Dinarites*" *asiaticus* Shevyrev, associated with diverse articulate brachiopods (*Piarorhynchella*, *Lissorhynchia*, *Prolissorhynchia*, *Sinuplicorhynchia*, *Hustedtiella*, *Spirigerellina*, *Lepismatina*, *Antezeilleria*, *Thyratryaria*, *Proanadyrella* and others) and abundant foraminifera, dominated the ammonoid assemblage (Zakharov & Popov 2007; fig. 3). This dominance was replaced by *Stacheites undatus* (Astachova) by the end of the Olenekian. The latter species is associated with representatives of the genus *Arnautoceltites*, usually a latest Olenekian element in the Tethyan assemblages. The main peculiarity of Olenekian successions is the development of the *Tirolites* fauna. *Tirolites*, the typical tropical element in the Tethys, arose during the middle Olenekian climatic optimum, reaching a maximal population at that time. However, it continued to occur during the late Olenekian in Mangyshlak, as well as in many other low-latitude regions (Idaho, Caucasus, Alps, Iran and Albania), and at middle latitudes (South Primorye).

Discussion

Palynological, petrographical and isotopic records show that the global warming following the Permo-Carboniferous glaciation was probably caused primarily by an increase in atmospheric CO_2 (Čumakov 2004; Korte, Jasper et al. 2005; Angiolini et al. 2006). New palaeobiogeographical evidence (Figs. 5–9) suggests marked climatic changes also occurred through the post-Sakmarian Permian, and Early and Middle Triassic, when frequent expansions and reductions of the warm–temperate climatic zones in the high and middle latitudes of the Northern and Southern hemispheres apparently took place. This is consistent with some known geochemical patterns, discussed below. However, temperatures estimated from oxygen isotopic analyses on Permian and Lower–Middle Triassic biogenic carbonates (mainly brachiopod calcite), are very restricted because of the lack of well-preserved material for isotope investigation. Our recent data (Zaharov et al. 2008) suggest a warming maximum existed in the Late Kungurian, with

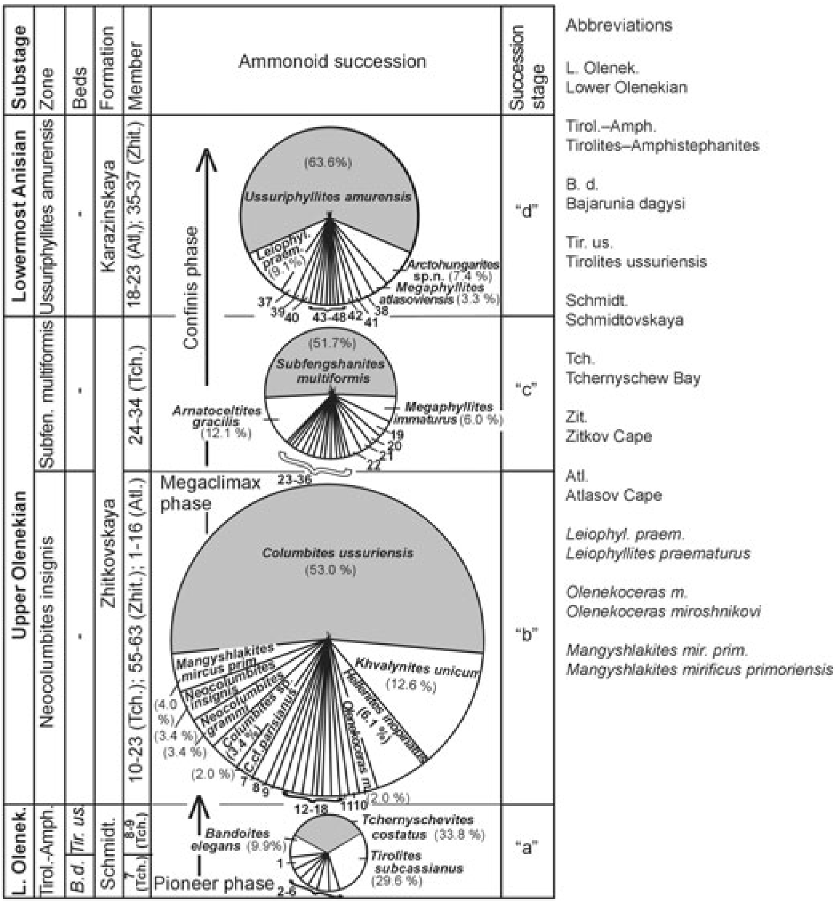

Fig. 4 Change of species composition and proportion in the Olenekian–earliest Anisian ammonoid succession of Russian Island–Atlasov Cape area, South Primorye. 1, *Tirolites ussuriensis* Zharnikova; 2–6, others, including *Amphistephanites parisensis* (Zakharov), *Kazakhstanites sonticus* (Zakharov), *Tchernyschevites subdalmatus* Zakharov, *Bajarunia dagysi* Zakharov and *Kazakhstanites zakharovi* Zharnikova; 7, *Olenekoceras tebenkovi* (Zharnikova); 8, *Procolumbites subquadratus* Burij & Zharnikova; 9, *Procolumbites* sp.; 10, *Hellenites tchernyschewiensis* Zakharov; 11, *Olenekoceras meridianus* (Zakharov); 12–18, others, including *Olenekoceras miroshnikovi* Burij & Zharnikova, "*Dieneroceras*" *spathi* Kummel & Steele, *Svalbardiceras* sp., *Svalbardiceras zhitkovense* Zakharov, *Preflorianites venustus* Zakharov, *Tirolites* cf. *subcassianus* Zakharov, *Subdoricranites*? sp.; 19, *Zhitkovites insularis* (Kiparisova); 20, *Pseudoprosphingites globosus* (Kiparisova); 21, *Isculitoides*? *suboviformis* (Kiparisova); 22, *Sulioticeras maritimus* (Kiparisova); 23–36, others, including *Columbites* sp., *Prenkites* aff. *timorensis* Spath, *Palaeophyllites superior* Zakharov, *Arnautoceltites* sp., *Pseudosageceras longilobatum* Kiparisova, *Pseudosageceras simplex* Kiparisova, *Pseudoprosphingites* aff. *globosus* (Kiparisova), *Isculitoides*? aff. *suboviformis* (Kiparisova), *Leiophyllites praematurus* Kiparisova, *Danubites* aff. *floriani* Mojsisovics, *Danubites admaris* Kiparisova, *Danubites insertus* Kiparisova, "*Dieneroceras*" *karazini* (Kummel & Teichert); 36, *Prohungarites popowi*; 37, *Arctohungarites primoriensis*; 38, *Paracrochordiceras* sp. nov.; 39, *Paradanubites* sp.; 40, *Leiophyllites* sp.; 41, *Tropigastrites sublahontanum*; 42–48, others, including *Prohungarites*? sp., *Parasageceras* sp. nov., *Salterites* sp., *Ussurites* sp., *Arctohungarites* sp., *Keyserlingites*? sp., Prionitidae gen. et sp. nov. Observations were from 75 (stage a), 300 (stage b), 130 (stage c) and 170 (stage d) samples.

palaeotemperatures in Spitsbergen of not lower than 23.1–23.8°C, and apparently also suggest short-term cooling in the latest part of the early Capitanian (Zaharov et al. 2008), as well as in the latest Wordian (Kotlyar et al. 2006; Shi 2006). This is because a sharp drop in palaeotemperatures (from 20.4 to 16.5°C; Zaharov et al. 2008) had occurred in successions of the earliest part of the late Wordian–early Capitanian interval at high latitudes of the Far East (Russkaya–Omolonskaya and Khivach areas of the Omolon River basin). Naturally, the early Capitanian temperature drop, so far documented only in the Omolon River basin, could only be localized.

Two maxima in palaeowater temperatures seem to have occurred during the Late Permian. One was during the early Wuchiapingian, with palaeotemperatures of 25.2–27.9°C calculated for the middle palaeolatitudes of Transcaucasia (Zaharov et al. 2001). The other maximum occurred during the late Changhsingian, at both the middle and high palaeolatitudes, and was characterized by somewhat lower palaeotemperatures: 22.0–24.2°C for

Table 2 The middle Olenekian–lower Anisian sequence exposed near the Dolnapa (Angry Sister) draw-well (44°21′51″N, 51°24′12″E; Astahova 1960; Ševyrev 1968, 2002; Gavrilova 1980, 1989; Balini et al. 2000; Zakharov & Popov 2007), in descending order.

Formation/ bed/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
Lower Karaduanskaya Formation (Lower Anisian)	32	Intercalation of grey, fine-grained sandstone and greenish grey mudstone	>130 m		
	31	Black and greenish grey mudstone	ca. 40 m		
	30	Intercalation of black mudstone and grey, fine-grained sandstone	ca. 100 m		
	29	Intercalation of grey, intermediate-grained and fine-grained sandstone	5 m		
	28	Grey, fine-grained sandstone	10 m		
	27	Black siltstone with thin interlayers of siliceous rocks	17 m		
	26	Grey, intermediate-grained and fine-grained sandstone	ca. 110 m		
	25	Intercalation of greenish grey, fine-grained sandstone and mudstone with interlayers of limestone–coquina (bivalve molluscs)	17 m		
	24	Brown, intermediate-grained sandstone	30 m		
	23	Brown and grey intermediate- and fine-grained sandstone	19 m		
Lower Karadzhatykskaya Formation (total thickness ca. 324 m; Upper Olenekian)/ Eumorphotis beds	22	Intercalation of greenish grey siltstone and grey, fine-grained, calcareous sandstone	34 m		Bivalves: *Pteria* sp., *Leptochondria* sp. (specimens 409-11 and 410-1 collected from different beds)
	21	Grey, fine-grained sandstone	7.5 m		
	20	Grey, fine-grained sandstone with interlayers of mudstone and rare lenses of limestone	ca. 75 m	*Pseudosageceras* sp. (specimen 409-10)	Bivalve: *Eumorphotis* sp. (specimen 409-13) Nautiloid: *Trematoceras* sp.
	19	Greenish-grey mudstone with rare interlayers (20–30 cm) of grey, fine-grained sandstone and lenses of limestone	27 m	Badly preserved specimens (409-9 and 409-10, collected from different beds)	Bivalve: *Pteria* sp. Gastropods Nautiloids (Nautilida)
	18	Grey, fine-grained sandstone with interlayers of greenish grey mudstone	8 m		
Arnautoceltites bajarunasi–Stacheites undatus Zone	17	Intercalation of greenish grey mudstone with calcareous boulders, siltstone with plant detritus and fine-grained sandstone with interlayers of light-grey limestone	ca. 165 m	From the upper part: Kashmiritidae gen. et sp. indet., *Albanites gracilis* (Kiparisova), *Preflorianites* sp., *Stacheites concavus* Shevyrev, *Stacheites undatus* (Astachova), "*Dinarites*" *orientalis* Shevyrev, *Tirolites armatus* Shevyrev (409-1, -4, -5, -6; 408-5, -6, -7 collected from several beds). From the lower part: *Pseudosageceras* sp., *Kazakhstanites dolnapaensis* Shevyrev, *Albanites gracilis* (Kiparisova), "*Dinarites*" sp., *Stacheites concavus* Shevyrev, *Stacheites undatus* (Astachova),	From the upper part: crinoids; brachiopods, *Piarorhynchella mangyshlakensis* Dagys, *Lissorhynchia* sp. nov., *Sinuplicorhynchia*? sp. nov., *Thyratryaria* aff. *pertumida* Xu and Liu, *Lepismatina* sp. nov., Spirigerellinae gen. et sp. indet. (409-3, -4, -7 collected from different beds); bivalves, *Palaeoneilo* sp., *Neoschisodus* sp. (408-5); nautiloid, *Trematoceras* sp. (409-1). From the lower part: bivalves, *Leda* sp., *Palaeoneillo* sp.,

Table 2 *continued*

Formation/ bed/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
				"*Dinarites*" *asiaticus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev, *Preflorianites* sp., *Tirolites* sp., *Kiparisovites ovalis* Shevyrev, *Tjururpites costatus* Shevyrev (408-1, -2, -3, -4; 407-13, -14, collected from several beds)[b]	*Uniites* sp., *Eumorphotis* sp. (408-1, -2, -3, -4; 407-13, collected from several beds); gastropods (408-1; 407-13); nautiloid, *Trematoceras* sp. (408-4)
	16	Greenish grey mudstone with interlayers of limestone	7 m	*Arnautoceltites bajarunasi* (Astachova), *Kazakhstanites dolnapaensis* Shevyrev, *Arctoprionites* sp., *Stacheites concavus* Shevyrev, *Stacheites undatus* (Astachova), "*Dinarites*" *asiaticus* Shevyrev, *Hyranites nodosus* Shevyrev (407-3, -4, -7, -8, -9, -10, -11, -12, -13, collected from several beds)	Bivalve: *Bakevellia* sp. (407-3) Gastropods
Tartalinskaya Formation/ Columbites parisianus–Procolumbites caratauchicus interval (total thickness ca. 274 m)	15	Intercalation of dark grey mudstone with calcareous boulders and fine-grained sandstone with cross bedding	90 m	"*Dinarites*" sp. nov. (Balini et al. 2000), rare "*Dinarites*" *asiaticus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev (407-1, -2 collected from different beds)[c]	Small bivalves Gastropods
	14	Greenish grey mudstone with rare interlayers of fine-grained, striate sandstone and calcareous boulders	38 m	*Tirolites* sp., "*Dinarites*" *asiaticus* Shevyrev (406-1, -2, -3, collected from several beds)	
	13	Intercalation of greenish grey, fine-grained sandstone (15–20 cm) and mudstone (10–20 cm)	4.9 m		
	12	Greenish grey mudstone and siltstone with interlayers of fine-grained, striate sandstone and calcareous boulders	18 m	"*Dinarites*" *asiaticus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev, *Tirolites armatus* Shevyrev, *Tirolites longilobatus* Shevyrev, *Tirolites* sp., *Doricranites acutus* Mojsisovics, *Columbites* cf. *parisianus* Hyatt and Smith, *Procolumbites karatauchicus* Astachova, *Hellenites kazakhstanicus* Shevyrev, *Leiophyllites exacudus* Shevyrev, *Kiparisovites ovalis* Shevyrev (405-18, -20, -21, -22, -23, -24, collected from several beds)	Braciopods (405-24) Nautiloid: *Trematoceras* sp. Fish remains (sample 405-19)
	11	Greenish grey mudstone with thin interlayers (2 cm) of limestone	17 m	*Mangyshlakites mirificus* Shevyrev, *Procolumbites karatauchicus* Astachova, *Columbites ventroangustus* Shevyrev, *Columbites* cf. *parisianus* Hyatt and Smith, *Columbites* sp., "*Dinarites*" *asiaticus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev, *Hellenites kazakhstanicus* Shevyrev, *Tirolites armatus* Shevyrev, *Tirolites rossicus* Kiparisova, *Tirolites longilobatus* Shevyrev, *Tirolites* sp., *Eukashmirites subdimorphus* (Kiparisova), *Kazakhstanites dolnapaensis* Shevyrev, *Tjururpites*	Nautiloid: *Sulioticeras* sp. (sample 405-15)

Table 2 *continued*

Formation/ bed/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
				costatus Shevyrev (405-14, -15, -16, -17, -18, collected from several beds)	
	10	Grey, fine-grained sandstone and greenish grey mudstone with rare lenses of limestone	6 m	*Tirolites* sp., *Hellenites kazakhstanicus* Shevyrev (405-13)	
	9	Greenish grey mudstone and siltstone with interlayers (5–15 cm) of fine-grained, striate sandstone, calcareous lenses and boulders	ca. 100 m	From the upper part: *Doricranites bogdoanus* (Buch), Prionitidae gen. et sp. indet., *Tirolites armatus* Shevyrev, *Tirolites* sp., "*Dinarites*" *asiaticus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev, *Columbites ventroangustus* Shevyrev, *Columbites* cf. *parisianus* Hyatt and Smith, *Columbites* sp., *Procolumbites karatauchicus* Astachova, *Hellenites kazakhstanicus* Shevyrev, *Hellenites* sp., *Leiophyllites exacudus* Shevyrev (405-9, -10, -11, -12, -12a, -18, -22, -23, collected from several beds). From the lower part: *Pseudosageceras longilobatum* Kiparisova, *Doricranites acutus* (Moisisovics), Prionitidae gen. et sp. indet., "*Dinarites*" *asiaticus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev, *Tirolites* sp., *Albanites gracilis* (Kiparisova), *Columbites* sp., *Preflorianites kiparisovae* Shevyrev, *Leiophyllites exacudus* Shevyrev (405-1, 404-22, -24, -25, -26, -28, -36, -41, -48, -55, -57, -59, -60, -61, -65, 405-2, -7, collected from several beds)[d]	From the upper part: crinoids (405-10); brachiopods, *Piarorhynchella mangyshlakensis* Dagys, *Lissorhynchia* sp. nov., *Hustedtiella planicosta* Dagys, *Lepismatina* sp. nov., *Prelissorhynchia* sp. nov., *Antezeilleria* sp. (405-9); bivalves, *Bakevellia* sp., *Leptochondria* cf. *minima* (Kiparisova), *Eumorphotis* sp., *Palaeoneilo* sp., Mytilidae gen. et sp. indet. (405-9, -10, -11, collected from several beds); gastropods (405-10, -14); nautiloids, *Phaedrysmocheilus* sp., Nautilidae gen. et sp. indet., *Trematoceras* sp. (405-10, -11, -12 collected from several beds). From the lower part: crinoids (404-61); brachiopods, *Lingula* sp., *Piarorhynchella mangyshlakensis* Dagys, *Spirigerellina* sp., *Lissorhynchia* sp. nov., *Spirigerellina pygmaea* Dagys, *Lepismatina* sp. nov., *Thyratryaria* sp. nov. A, *Thyratryaria* sp. nov. B, *Proanadyrella*? sp., Spirigerellinae gen. et sp. indet. (405-2, -4, -7; 404-47, -49, -50, -59, -61, collected from several beds); bivalves, *Eumorphotis* sp., *Entolium* sp. (404-19, -35, -59, -61, collected from several beds); gastropods, (404-59, -61 collected from different beds); nautiloids, *Phaedrysmocheilus* sp., *Trematoceras* sp. (405-4, 404-39, collected rom different beds)
Kiparisovites carinatus–Tirolites cassianus Zone (103 m)[a]	8	Greenish grey siltstone with interlayers (10 cm) of fine-grained sandstone calcareous boulders	17 m	*Tirolites armatus* Shevyrev, *Albanites gracilis* (Kiparisova), *Kazakhstanites dolnapaensis* Shevyrev, *Tjururpites* cf. *costatus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev (404-1, -7, -9, -15, collected from several beds)	Sea-urchins (spines) (404-5); crinoids (404-5); brachiopods, *Lepismatina* sp. nov., *Piarorhynchella mangyshlakensis* Dagys (404-1, -9, -13, collected from several

Table 2 *continued*

Formation/ bed/ zone	Member	Lithology	Thickness	Ammonoids	Other fossils
					beds); small gastropods (404-9); nautiloids, *Trematoceras* sp., *Phaedrysmocheilus* sp. (404-6, -9, collected from different beds). Upper part of the *Tirolites* beds contains foraminiferal remains (Vuks 1997)
	7	Greenish grey siltstone with calcareous boulders and lenses (15 cm) of limestone	11 m	*Tirolites* sp., "*Dinarites*" *asiaticus* Shevyrev, "*Dinarites*" *orientalis* Shevyrev (404-1, -2, -3, collected from several beds)[e]	Brachiopod: *Piarorhynchella mangyshlakensis* Dagys (404-1); bivalves (404-1); gastropods (404-1)
	6	Intercalation of greenish grey siltstone (50 cm), fine-grained, calcareous, wavy and cross-bedding sandstone (5–10 cm)	3 m		
	5	Greenish grey siltstone with thin interlayers (2–5 cm) of brown limestone	40 m	*Kiparisovites carinatus* Astachova, "*Dinarites*" *orientalis* Shevyrev (403-37, -38, -38a, collected from several beds)	Bivalves Small gastropods
	4	Greenish grey mudstone with thin interlayers (5–6 cm) of fine-grained sandstone and calcareous boulders	ca. 30 m	<u>From the upper part</u>: *Pseudosageceras* sp., *Tirolites* cf. *cassianus* Quenstedt, *Tirolites rossicus* Kiparisova, *Tirolites longilobatus* Shevyrev (403-26, -27, -28, -32, -34, collected from several beds). <u>From the lower part</u>: *Pseudosageceras* sp., *Tirolites* cf. *cassianus* Quenstedt, *Tirolites* sp. (403-14, -17, -19, -21, -25, collected from several beds)	<u>From the upper part</u>: bivalves, *Neoschizodus* cf. *laevigata* (Zieten), *Leda* sp. (403-32, -36, collected from different beds); gastropods (403-31) <u>From the lower part</u>: bivalve, Mytilidae gen. et sp. indet. (403-21); gastropods (403-21); amphibian remains (403-21)
	3	Intercalation of greenish grey siltstone (0.5 m) and fine-grained sandstone	2 m		
	2	Greenish grey siltstone with calcareous boulders	4 m		Bivalves: *Myophoria* sp., Ostreidae gen., sp. indet. (403-2, 8 collected from different beds); fish remains (scales) (403-2)
	1	Intercalation of greenish grey mudstone, siltstone, brown, fine-grained sandstone with calcareous interlayers (10–15 cm) at 1–2 m above the base of the member	6 m	*Pseudosageceras longilobatum* Kiparisova, *Tirolites* cf. *cassianus* Quenstedt, *Tirolites* sp. (403-3, -5, collected from different beds)	Bivalves: Mytilidae, Monotidae (403-1, -4, collected from different beds)

[a]Dorikranites beds, characterized by the conodont *Neospathodus* cf. *brevissimus* Orchard (Balini et al. 2000) and rare foraminifera (Vuks 1997), have not been found by us in the block investigated.

[b]*Procarnites* sp. (Balini et al. 2000) and "*Dinarites*" *astachovae* Gavrilova (Gavrilova 1989) were apparently discovered in the upper and lower parts of Member 17, respectively.

[c]Conodonts *Neospathodus* sp., *Neospathodus* sp. C, *Neospathodus hommeri* (Bender), *Neospathodus abruptus* Orchard, *Neospathodus symmetricus* Orchard, *Neospathodus dolnapae* Nicora (Balini et al. 2000) were apparently found in Member 15.

[d]Conodonts *Neospathodus abruptus* Orchard, *Neospathodus dolnapae* Nicora and *Neospathodus* sp. (Balini et al. 2000) and foraminifera *Nodosaria hoae* (Trifonova) (Vuks 1997) were apparently discovered in the upper part of Member 9.

[e]Conodonts *Neospathodus hommeri* (Bender), *Neospathodus* sp. A, *Neospathodus* sp. B and *Neospathodus dolnapae* Nicora (Balini et al. 2000) were apparently discovered in the lower part of Member 7.

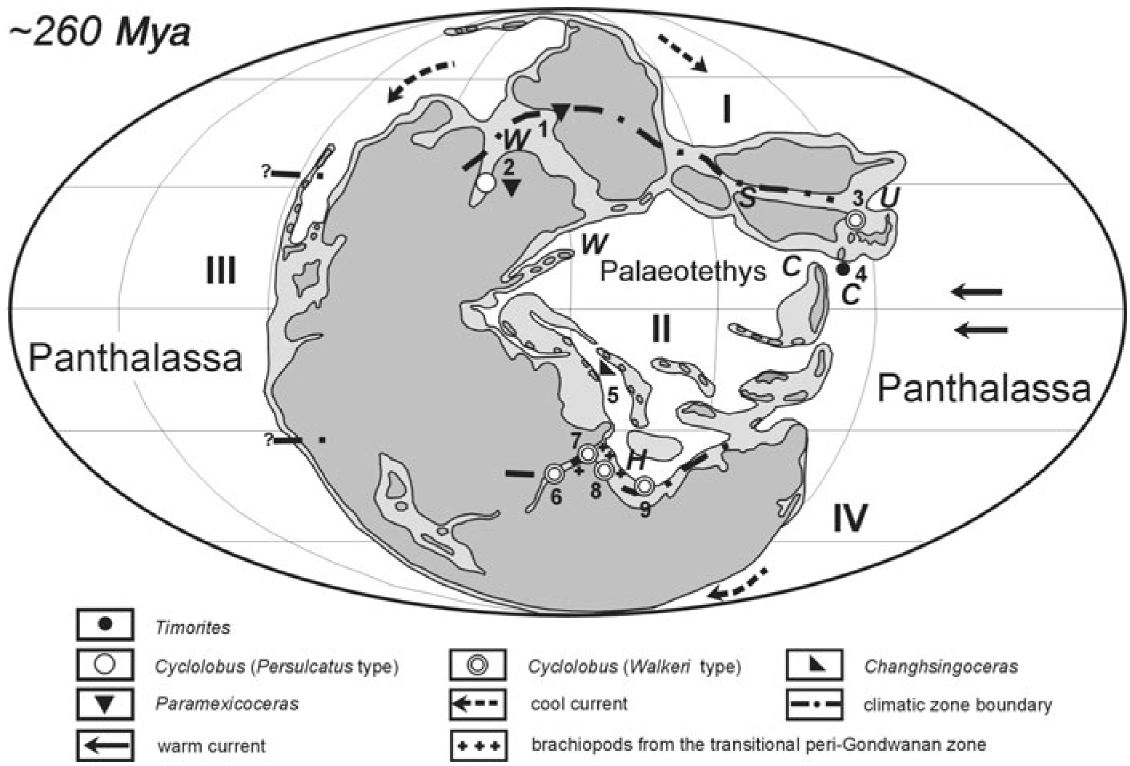

Fig. 5 Expansion of the tropical–subtropical zone during the Early Wuchiapingian (base map after Ziegler et al. 1999): 1, Verkhoyansk area (Popov 1970); 2, East Greenland (Frebold 1932; Nassichuk et al. 1966; Nassichuk 1995); 3, South Primorye (Zaharov 1983); 4, Kitakami (Ehiro & Bando 1985); 5, Transcaucasia (Zaharov 1985); 6, Madagascar (Furnish & Glenister 1970); 7, Salt Range (Furnish & Glenister 1970); 8, central Himalayas (Diener 1903); 9, Tibet (Leonova 2002). Climatic zones/realms: I, Boreal warm–temperate; II, Tethyan tropical–subtropical; III, American tropical–subtropical; IV, Gondwanan warm–temperate. Provinces: C, Cathasian; H, Himalayan; U, Ussurian; W, western Tethyan.

the upper part of the Paratirolites kittli Zone in Transcaucasia and North Caucasus, and 23.1°C for the upper part of the Itomodesma costatum Zone (Zakharov, Biakov et al. 2005), which are confirmed by the data on ammonoid diversity (Fig. 2). Very high palaeotemperatures for the Lopingian age Joulfa section in Iran (23–34°C) and the Meishan section in South China (26–32°C) were similarly obtained by Korte, Jasper et al. (2005). Some of these facts seem to be in disagreement with Beauchamp & Baud's (2002) hypothesis that the northwest margin of Pangea was under the influence of cold to very cold waters for nearly 30 My of the post-Sakmarian Permian, which was the period of chert accumulation in this area.

Late Permian expansions of the tropical–subtropical zone may be linked to both the Early Wuchiapingian and the Late Changhsingian temperature maxima. This is supported by the wide geographical distribution of thermophilous cyclolobid ammonoids (Zakharov & Ehiro in press) and conodonts (Mei & Henderson 2001) in the early Wuchiapingian (Fig. 5). Our ammonoid data agree with the data on early Wuchiapingian ammonoids from the Kitakami area, which Ehiro (1997, 1998, 2001b) considered to be similar to ammonoids from the tropical Cathaysian province. Latest Changhsingian ammonoids of South Primorye are especially similar to those from the Cathaysian province (Zakharov & Oleinikov 1994). The wide distribution of Cathaysian elements may also be explained by latitudinal expansion of the tropical–subtropical zone at that time. The southward invasion of abundant warm-water brachiopods, conodonts, calcareous sponges and gastopods in the Southern Hemisphere during the latest Changhsingian has been confirmed by Shen et al. (2000) and Shen et al. (2006). However, no Changhsingian ammonoids have been discovered at high latitudes (if our assumption concerning the earliest Induan age of all *Otoceras* and *Tompophiceras*, and associated *Hypophiceras*, from the Setorym section, Verkhoyansk area, is correct), which is still unexplainable.

Another possible explanation for the existence of warm conditions in the south Far East during the Late Permian and possibly the Early Triassic is the location of the South Kitakami and South Primorye near the equator. This is

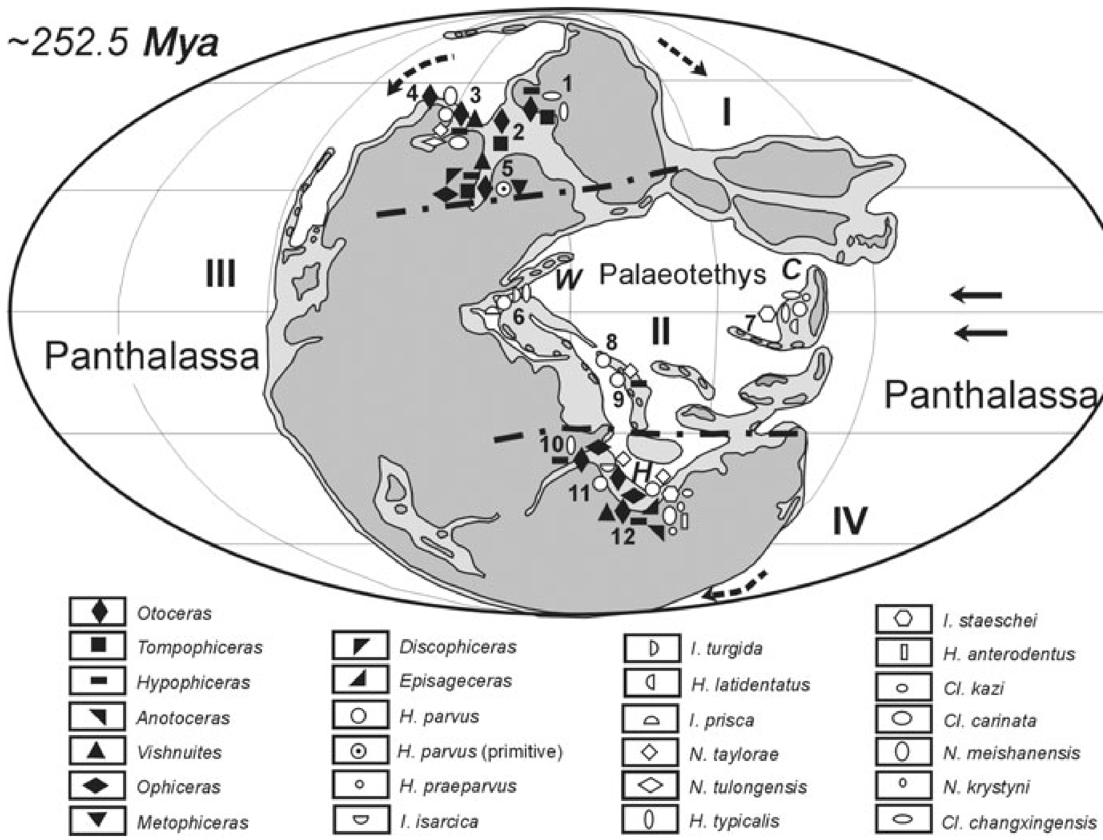

Fig. 6 Reduction of the topical–subtropical zone during the earliest Induan (base map after Ziegler et al. 1999): 1, Verkhoyansk area (Zakharov 2002); 2, Svalbard (Korčinskaja & Vavilov 1987); 3, Arctic Canada (Orchard 1994; Tozer 1994; Orchard & Tozer 1997); 4, Alaska (Kummel's data; Zaharov 1968); 5, eastern Greenland (Spath 1930; Ševyrev 2000; Kozur 1998); 6, Alps (Perri & Farabegoli 2003); 7, South China (Yin et al. 1996; Mei et al. 1998; Mei & Henderson 2001); 8, Transcaucasia (Zakharov, Biakov et al. 2005); 9, Iran (Bando 1979; Kozur 2004); 10, Kashmir (Nakazawa 1981, 1993; Nakazawa & Kapoor 1981; Ševyrev 1999); 11, southern Tibet (Jin et al. 1996); 12, Himalayas (Kummel 1972; Orchard & Krystyn 1998; Ševyrev 1999). Other designations are as listed in Fig. 4. The latest radiometric data (Mundil et al. 2004; Menning et al. 2007) have been used.

based on the palaeomagnetic data from South Primorye (Zaharov & Sokarev 1991a, b), or on both palaeontological and the aforementioned palaeomagnetic data from the south Far East (Ehiro 1997, 1998, 2001b; Brayard et al. in press). It seems to be debatable because of the strong Early Cretaceous remagnetization of Permian and Triassic rocks in the Russian Far East and Japan, which are used for palaeomagnetic investigation (Kodama, pers. comm.). It is clear that the palaeoposition of South Primorye and Kitakami within a palaeoclimatic zone cannot be determined precisely without having reliable palaeomagnetic data.

The extensive loss of ammonoid species took place during the Permian–Triassic boundary (PTB) ecological crisis. Many hypothetical processes have been proposed to explain PTB events, which have recently been reviewed by Berner (2002), Kidder & Worsley (2004) and Richoz (2006). A question that remains is the impact of temperature, because there is no information on seawater palaeotemperatures for the PTB beds: no well-preserved fossils suitable for oxygen isotopic investigation have been discovered within this interval. However, data with a bearing on the main trends in temperature changes have been obtained using the Ca/Mg ratio method for carbonate sequences. According to Zaharov et al. (2001), the PTB transition in the Karabaglyar-2 and Akhura sections in Transcaucasia (located between low and middle latitudes at the very end of the Changhsingian) shows a Ca/Mg ratio in carbonates rising from 170–178, in the upper part of the Paratirolites kittli Zone, to 185 in the overlying Pleuronodoceras occidentale–Xenodiscus jubilaearis interval, which is interpreted as a gradual temperature drop during the latest Changhsingian. The highest Ca/Mg ratio (197–204), reflecting the lowest magnesium content at the PTB in Transcaucasia, falls in interval "a" (Fig. 2), which is a stromatolitic limestone characterized by the first appearance of the conodont *H. parvus*. In overlying limestones of the Isarcicella

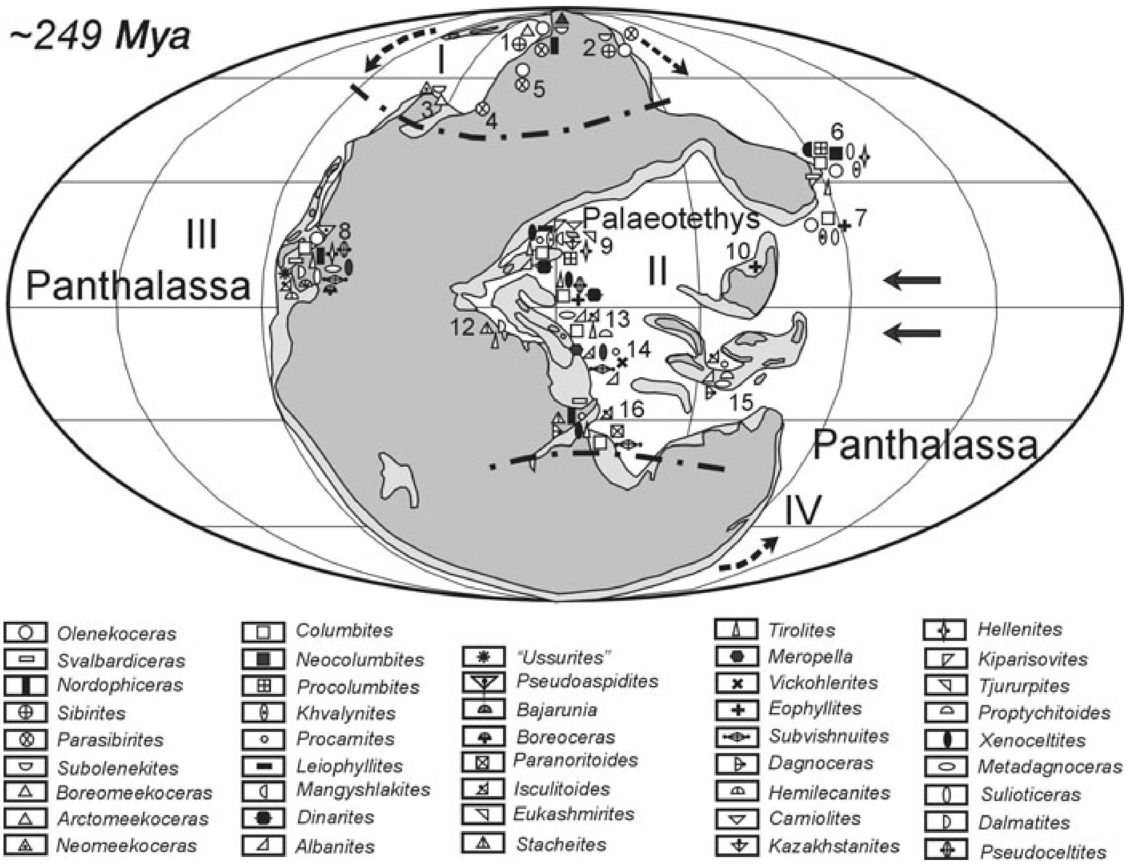

Fig. 7 Expansion of the tropical–subtropical zone during the early part of the late Olenekian Parasibirites grambergi Zone (base map after Ziegler et al. 1999): 1, Arctic Siberia (Dagis & Ermakova 1988); 2, Kolyma area (Byčkov 1972; Zaharov 1978); 3, Arctic Canada (Tozer 1994); 4, Svalbard (Tozer & Parker 1968; Korčinskaja 1970); 5, Verkhoyansk area (Zaharov 1978); 6, South Primorye (Zakharov 1997); 7, Kitakami (Bando & Ehiro 1982); 8, Idaho and Nevada (Kummel 1969); 9, Mangyshlak (Astahova 1960; Ševyrev 1968, 1990; Gavrilova 1980); 10, South China (Tong et al. 2004); 11, North Caucasus (Ševyrev 1990); 12, Alps (Krystyn 1974); 13, Iran (Ševyrev 1990); 14, Afganistan (Kummel 1969); 15, Timor (Kummel 1969); 16, Salt Range (Kummel 1969). Other designations are as listed in Fig. 4. The latest radiometric age by Galfetti, Bucher, Ovtcharova et al. (2007) has been used.

isarcica Zone in the Karabaglyar-2 section (yielding the ammonoid *Lythophiceras medium* Griesbach), the Ca/Mg ratio is lowered (174–176), reflecting a rise in magnesium content. We interpret the lowest magnesium content as a short-term fall of the palaeo-seawater temperature at the very end of the Changhsingian, and particularly at the beginning of the Induan (FAD *H. parvus*), just after the significant negative carbon isotope excursion (Baud et al. 1989; Zakharov, Biakov et al. 2005). It may also be caused by a fundamental change in PTB sedimentation, as expected by Baud et al. (2007). However, Kozur (2007) discovered a cool-water conodont fauna in the Pleuronodoceras occidentale–Xenodiscus jubilaearis interval of Transcaucasia and Iran (the discovery of volcanic microsphaerulites in this level in Iran, and in the Germanic Basin, documents volcanic activity only occuring during its habitation in cool conditions). These palaeontological and volcanological patterns are consistent with what we propose.

The abrupt decline in heavy carbon isotope concentrations just prior to the PTB (Baud et al. 1989; Magaritz 1989; Yin & Zhang 1996; Musashi et al. 2001; Korte, Jasper et al. 2005) reflects a global reduction in primary biological productivity (Alcala-Herrera et al. 1992). This might have been induced by increasing oxygen deficiency in response to a dramatic decline in phytoplankton photosynthesis (Hallam 1994). Short-term cooling, following significant warming, and a possible reduction of atmospheric oxygen during the PTB were the likely consequences of the release of CO_2 from the Siberian traps (Conaghan et al. 1994; Kozur 2007; Payne & Kump 2007; Riccardi et al. 2007), and also of methane from seafloor gas hydrates (clathrates) (Martin & Macdougall 1995; Berner 2002; Kidder & Worsley 2004; Krull et al. 2004; Payne et al. 2004).

Bando (1973, 1979, 1980) considered that the Dorashamian genus *Julfotoceras* was most intimately related to *Otoceras*, the ammonoid index fossil for the

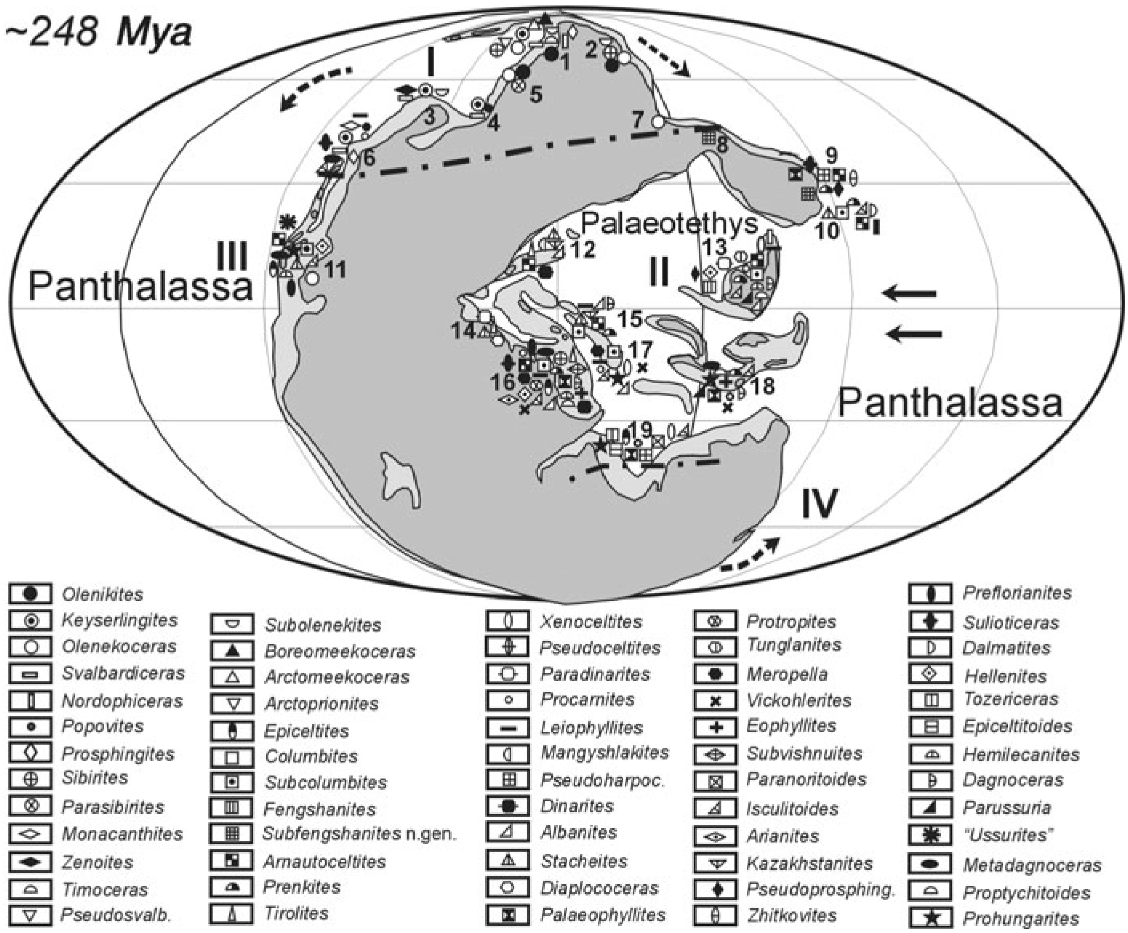

Fig. 8 Reduction of the tropical–subtropical zone during the late part of the late Olenekian Olenikites spiniplicatus Zone (base map after Ziegler et al. 1999): 1, Arctic Siberia (Mojsisovics 1886; Zaharov 1978); 2, Kolyma area (Byčkov 1972; Zaharov 1978); 3, Arctic Canada (Tozer 1994); 4, Svalbard (Korčinskaja 1970; Mørk et al. 1999); 5, Verkhoyansk area (Zaharov 1978); 6, British Columbia (Tozer 1994); 7, Uda River basin, Amur River basin (Ehiro et al. 2006); 8, Bolshiye Churki, Lesser Hingan (Okuneva 1976); 9, South Primorye (Zakharov 1997); 10, Kitakami (Bando & Shimoyama 1974; Bando & Ehiro 1982); 11, Nevada (Kummel 1969); 12, Mangyshlak (Astahova 1960; Ševyrev 1968, 2002; Gavrilova 1980, 1989); 13, South China (Chao 1959; Kummel 1969); 14, Alps (Krystyn 1974); 15, Iran (Ševyrev 1990); 16, Chios and Albania (Kummel 1969); 17, Afghanistan (Kummel 1969); 18, Timor (Kummel 1969); 19, Salt Range (Guex 1978). Other designations are as listed in Fig. 4. The latest radiometric age by Lehrmann et al (2006) and Galfetti, Bucher, Ovtcharova et al. (2007) has been used.

PTB beds in both the Himalayas and the Boreal realm. However, our morphological analysis shows that the ancestor of the genus *Otoceras* apparently originated from the Dzhulfian–Dorashamian *Avushoceras*, which was an inhabitant of the tropical–subtropical climatic zone (i.e., such as that in Transcaucasia). These two genera (*Avushoceras* and *Otoceras*) have very similar suture lines; besides, the juvenile *Otoceras* shell looks like the adult *Avushoceras* (Zaharov 1971; Zaharov & Pavlov 1986a), which reflects a possible anabole in the phylogenetic line *Avushoceras*–*Otoceras*. We can hypothesize that the ancestral form migrated into higher northern latitudes, following phytoplankton, crustaceans and other organisms, probably to restore its food supply that had been disrupted by short-term cooling, as documented by Ca/Mg studies in Permian–Triassic carbonates in Transcaucasia (Zaharov et al. 2001), and possibly the oceanic superanoxia of the Permian–Triassic boundary transition (Hallam 1994; Wignall & Twitchett 2002), and/or other factors exerting a stronger influence in some low–middle latitude areas.

We suggest that the wide distribution of the cool-water *Otoceras* faunas at high palaeolatitudes of the Northern Hemisphere (Boreal realm), and at middle palaeolatitudes of the Southern Hemisphere (Himalayan province), reflects the short-lived expansion of the warm–temperate zone, and the favourable reduction of the tropical–subtropical climatic zone, which would have been a result of the aforementioned short-term cooling that mainly

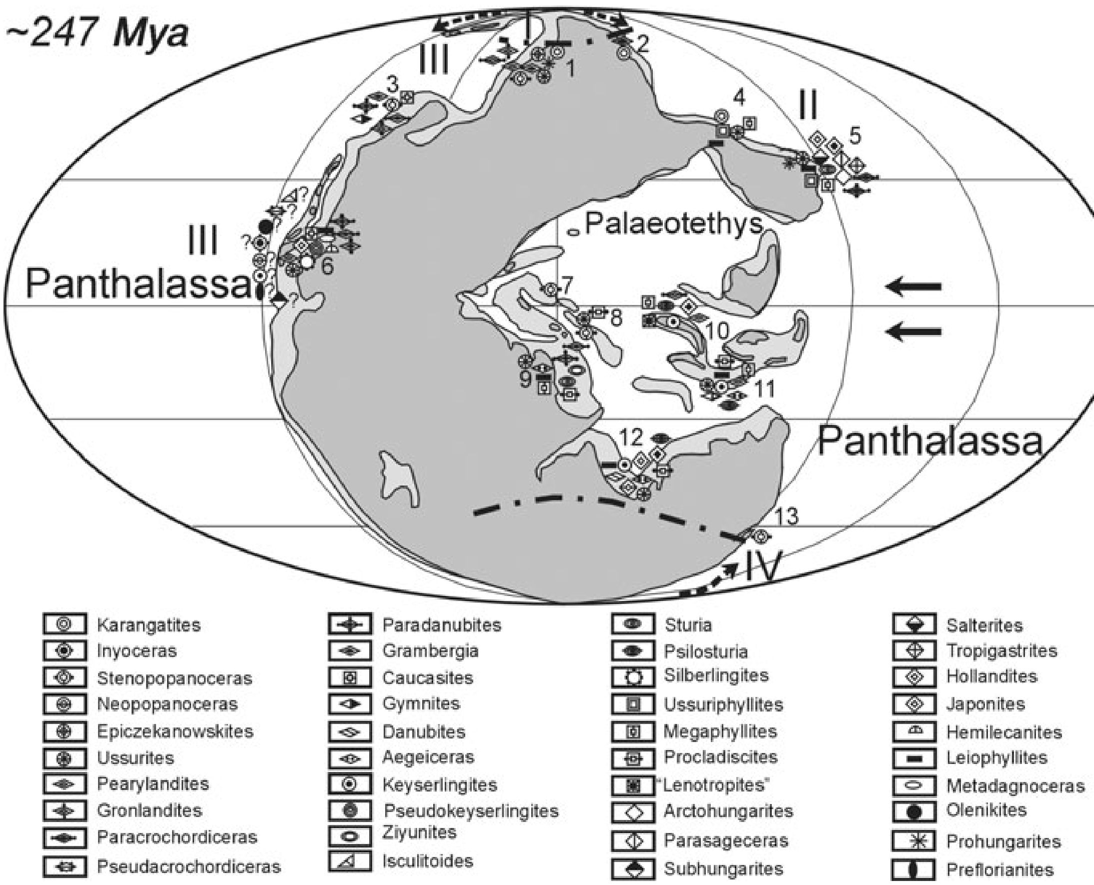

Fig. 9 Expansion of the tropical–subtropical zone during the earliest Anisian Karangatites evolutus beds (base map after Ziegler et al. 1999): 1, Arctic Siberia (Popov 1968; Zaharov 1978); 2, Kolyma area (Byčkov 1972); 3, British Columbia (Tozer 1994); 4, Bolshiye Churki, Lesser Hingan (Okuneva 1976); 5, South Primorye (Zakharov, Popov et al. 2005); 6, Nevada and Idaho (Bucher 1989; Ševyrev 2002); 7, North Caucasus (Ševyrev 1990); 8, Iran (Ševyrev 1990); 9, Chios (Fantini Sestini 1981; Gaetani et al. 1992); 10, Qinghai (Wang 1985; Bucher 1989); 11, Timor (Welter 1915; Ševyrev 1990); 12, Himalayas (Diener 1895a; Ševyrev 1990); 13, New Zealand (Kummel 1965). Other designations are as listed in Fig. 4. The last radiometric age by Lehrmann et al. (2006) has been used for the base of the Anisian.

occurred at the very beginning of the Induan (FAD *Hindeodus parvus*) (Fig. 6).

According to Brayard et al.'s (2006) calculation, no latitudinal or longitudinal ammonoid generic richness gradient can be recognized during early Induan (Griesbachian) time, but a weak latitudinal diversity gradient emerges during late Induan (Dienerian). In contrast, the Olenekian is characterized by a stronger latitudinal diversity gradient, showing a less uniform climate tendency during the Early Triassic.

According to our oxygen isotope temperature determinations (Zakharov et al. 1999), late Olenekian and late Anisian climates in Arctic Siberia seem to be about 7.4 and 6.6°C warmer, respectively, than early Olenekian temperatures. The calculated middle–late Anisian isotopic palaeo-seawater temperatures of about 15°C for Arctic Siberia (Kurušin & Zaharov 1995; Zakharov et al. 1999) approach those of the late Olenekian at about 16.2°C (Zakharov et al. 1999). No oxygen isotopic palaeotemperature data have been obtained for other levels of the Lower–Middle Triassic.

Additional information on Early–Middle Triassic marine environments may be obtained from data on carbon isotopic anomalies. As suggested by Alcala-Herrera et al. (1992), some variations in the $^{13}C/^{12}C$ ratios recorded in deep-water marine carbonates might be controlled by the carbon budget, upwelling and primary productivity. It is difficult to separate the effect of each of these factors in deep-water conditions, but when worldwide carbon isotope shifts are observed in shallow-water carbonates they can generally be attributed to changes in primary biological productivity, most likely in the phytoplankton. The peculiarities in the distribution of phytoplankton, one of the main organisms that utilize solar energy in today's oceans, have been thoroughly investigated (Bogorov 1974). As photosynthesizers, phytoplankton are concentrated in the upper 100 m of the water column, but their geographical distribution depend on the degree of hydrological intermixing of water under the influence of thermal gradients and winds. Phytoplankton productivity is high in areas characterized by an intensive vertical circulation, such as in upwelling areas. The small numbers of plankton in recent Arctic and Antarctic seas is probably connected with the short summer growth interval of phytoplankton at high latitudes. However, during times when polar ice was absent, the hydrological conditions were probably considerably different from those of the present day, in that poleward transport of large equatorial warm-water masses and weaker vertical circulation of waters probably occurred in some climatic zones. Therefore, the actual causes of Phanerozoic carbon isotopic anomalies can only be evaluated under conditions of poor constraints. Our data show that the positive $\delta^{13}C$ anomalies at different levels of the Permo-Triassic younger than the Sakmarian are usually characterized by a high Mg content (Zaharov et al. 2001). These seem to be mainly related to times of high biological productivity in the ocean basins, caused by conditions stimulated by transgressions and warm climate.

The carbon isotope and Ca/Mg data from Transcaucasia, North Caucasus, South Primorye, South China, Iran, Pakistan, Oman and the Alps suggest a recurrent warming trend, beginning in the latest parts of the early Induan (Lythophiceras medium Zone) (Zakharov et al. 2000), and continuing into Anisian times, reaching temperature maxima in the Middle–Late Induan (Zakharov, Biakov et al. 2005), early Olenekian (Richoz 2006; Horacek & Abart 2007), Middle Olenekian (Tirolites–Amphistephanites Zone) (Zakharov et al. 2000; Korte, Kozur et al. 2005; Richoz 2006; Lehrmann et al. 2006; Galfetti, Bucher, Brayard et al. 2007; Galfetti, Bucher, Ovtcharova et al. 2007; Horacek & Abart 2007) and in the beginning of the Anisian (Zakharov et al. 2000; Korte, Kozur et al. 2005; Richoz 2006). Hence, it is anticipated that there was a general reduction (in latitudinal extent) of the warm–temperate climatic zone throughout the late Induan to earliest Anisian (Figs. 7, 9), which more or less agrees with data on Early Triassic–earliest Anisian ammonoid and brachiopod diversity (Figs. 3, 4) (Xu & Lui 1983; Brayard et al. 2006; Brayard et al. 2007; Zaharov et al. 2008).

In the middle and earliest part of the late Olenekian, as in the early Wuchiapingian and late Changhsingian, the tropical–subtropical climatic zone was very extensive. Typical Tethyan *Tirolites* faunas appeared in the middle Olenekian, approximately 2 Mya, after the PTB mass extinction (Ovtcharova et al. 2006), and continued to play a significant role in the earliest part of the late Olenekian ammonoid assemblages in the western Tethys. Ammonoids of Tethyan type inhabited a tropical–subtropical climatic zone in the earliest part of the late Olenekian, and were very abundant and diversified: among them, columbitid ammonoids seem to be one of main indicators of the tropical–subtropical climatic zone for that time (Fig. 4). *Subolenekites*, *Olenekoceras*, *Svalbardiceras*, *Nordophiceras*, *Parasibirites*, *Sibirites*, *Boreomeekoceras*, *Arctomeekoceras* and *Neomeekoceras* are usually characteristic of the northern warm–temperate climatic zone (Boreal realm) in the earliest part of the late Olenekian, but some of them (*Olenekoceras*, *Nordophiceras* and *Svalbardiceras*) may possibly have migrated southwards along the eastern and western areas of Pangea, to middle-latitude (South Primorye and Kitakami) and low-latitude (Idaho and Nevada) areas of the Northern Hemisphere. Three ammonoid genera common in Boreal assemblages (*Nordophiceras*, *Svalbardiceras* and *Arctomeekoceras*) have been discovered in the middle latitudes of the Southern Hemisphere (i.e., the Salt Range) (Kummel 1969), in association with typical Tethyan ammonoids *Tirolites*, *Columbites* and *Procolumbites*.

The data on the geographical distribution of ammonoids of the latest part of the late Olenekian show that cooling apparently took place (in the Subfengshanites multiformis Zone) just before the earliest Anisian climatic optimum, initiating expansion of the warm–temperate climatic zone southwards in the Northern Hemisphere. The southern boundary of the Boreal realm reached the northern part of the Khabarovsk area in the east, and the southern part of British Columbia in the west (Fig. 8). Abundant endemic ammonoid elements, such as *Olenikites*, *Olenekoceras*, *Keyserlingites*, *Nordophiceras*, *Svalbardiceras*, *Prosphingites*, *Popovites*, *Sibirites*, *Parasibirites* and *Monocanthites* were present in the Boreal realm in the latest part of the late Olenekian, showing the lack of any remarkable faunistic relations between the Tethys and the Boreal realm at that time.

Fossiliferous sedimentary rocks of earliest Anisian are comparatively restricted in distribution in Eurasia, and their global correlation is still uncertain. (Following Hyatt & Smith's [1905] original proposal, we continue to consider that the Neopopanoceras haugi Zone in North America is earliest Anisian, in spite of the recent tendency to expect it to be latest Olenekian [Bucher 1989; Tozer 1994; Ševyrev 2000].) However, faunal connections between the Boreal realm and Tethys (via the distribution of juvenile invertebrate individuals, possibly by oceanic currents) were undoubtedly more active in the early Anisian compared with the late Olenekian, possibly because of the extension of a more homogeneous climate at the beginning of the Middle Triassic. The existence of the earliest Anisian (Ussuriphyllites amurensis Zone) temperature maximum is confirmed by the wide latitu-

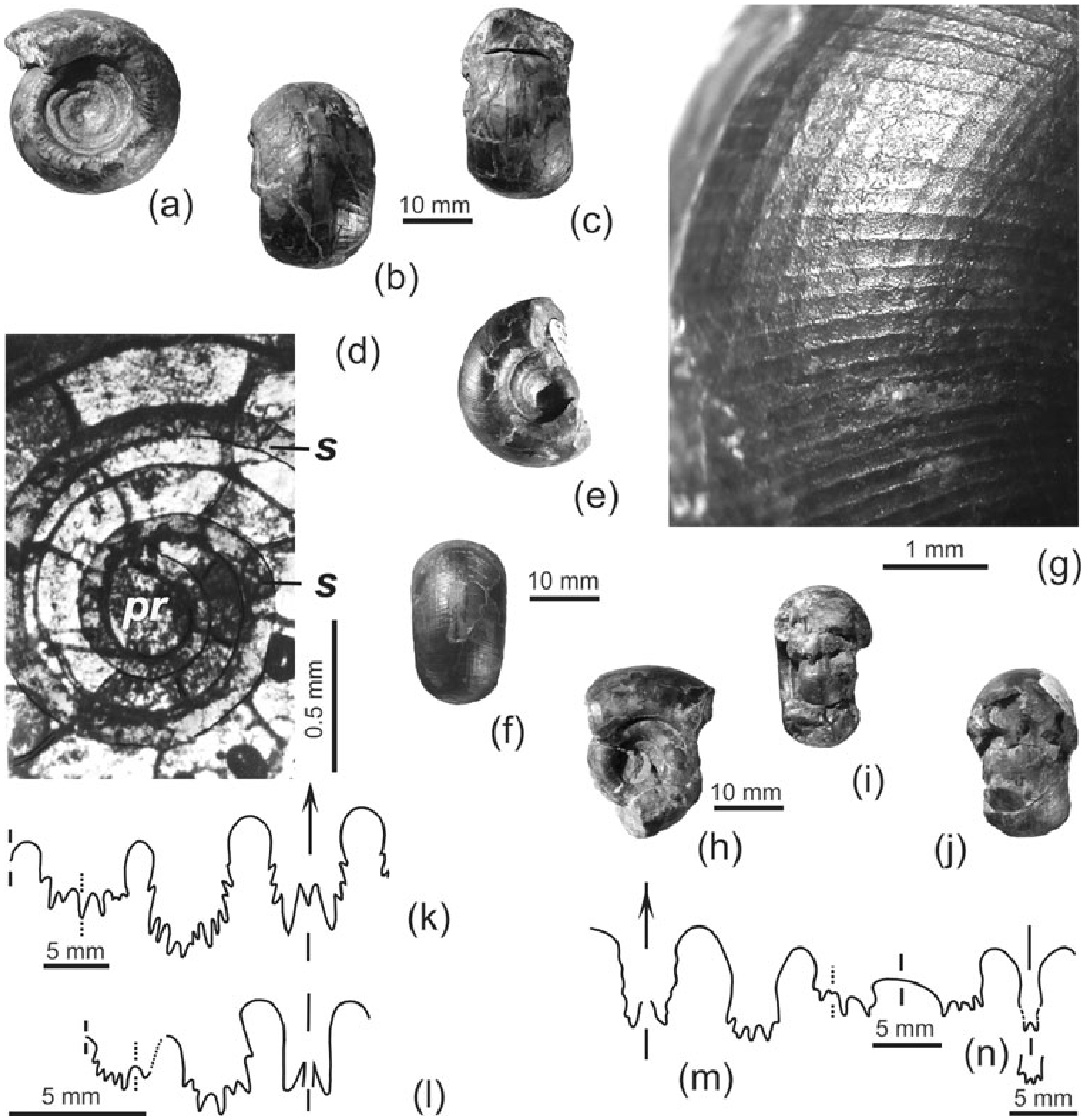

Fig. 10 *Subfengshanites multiformis* (Kiparisova). (a–c) Dal'nevostočnyj Geologičeskij Institut (Far Eastern Geological Institute) (DVGI) 449/801: lateral, ventral and apertural views. (d) DVGI 71/801: inner shell structure, showing dorsal position of siphuncle at the first whorl, and its subdorasal position at the second whorl (pr, protoconch; s, siphuncle). (e and f) DVGI 452/801: lateral and ventral views. (g) DVGI 452/801: reticulate ornamentation. (h–j) DVGI 451/801: lateral, ventral and apertural views. (k–n) Suture lines. (k and l) VSEGEI 126/5504 (holotype). (k) Height 10 mm; width 18.9 mm. (l) Height 4.8 mm; width 13.6 mm. (n) DVGI 456/801, dorsal lobe: height 6.8 mm; width 16 mm. Upper Olenekian, the uppermost part of the Zhitkov Cape Formation. Samples 126/5504 (holotype), 71/801, 449/801, 451/801, 452/801 and 456/801 were collected from the lens of calcareous marl, 0.3 m thick, located at the base of the Subfengshanites multiformisone Zone, Russian Island, Zhitkov Cape.

dinal extent of the tropical–subtropical climatic zone (Fig. 9). Many earliest Anisian ammonoids, such as *Stenopopanoceras, Karangatites, Prohungarites, Pearylandites, Paracrochordiceras, Paradanubites* and *Grambergia* are cosmopolitan, being common in the tropical–subtropical climatic zone in low, middle and high latitudes. However, earliest Anisian ammonoids as a whole were less diverse at high latitudes: among the earliest Anisian endemics of high latitudes, only forms of *Gronlandites* are known. Typical late Olenekian ammonoid elements of the Boreal realm, such as *Keyserlingites,* disappeared before the earliest Anisian assemblages at high latitudes because they apparently migrated to the middle and low latitudes in both hemispheres (Nevada, Timor, Tibet, Himalayas and possibly Primorye). Their unchecked advance, similar to the global migration of *Stenopopanoceras* and some 18 other ammonoid genera, may be explained by a warm and uniform climate during the earliest Anisian.

Conclusions

Correlation of palaeontological and geochemical data suggests that most evident thermal maxima existed during the late Kungurian, early Wuchiapingian, latest Changhsingian, middle Olenekian and earliest Anisian. Successive latitudinal expansions and reductions of the tropical–subtropical zone during the Late Permian, and the Early and Middle Triassic, are a result of significant climatic fluctuations. The wide distribution of the cool-water *Otoceras* faunas at high palaeolatitudes of the Northern Hemisphere (Boreal realm), and at middle palaeolatitudes of the Southern Hemisphere (Himalayan province), reflecting the short-lived expansion of the warm–temperate and the favourable reduction of the tropical–subtropical climatic zones, seems to be a result of short-term cooling at the very beginning of the Induan. In contrast, the unprecedented expansion of the tropical–subtropical climatic zone to higher latitudes at the beginning of the Anisian suggests that the earliest Anisian was a time of stable and warm climatic conditions.

Description of a new genus

Superfamily Columbitoidea Spath, 1930
[nom. transl. Zaharov, 1978 (ex Columbitidae Spath, 1930)]
Family Columbitidae Spath, 1930
Genus ***Subfengshanites* gen. nov.**

Type species. *Subcolumbites multiformis* Kiparisova (Voinova et al. 1947: 144, pl. 32, figs. 8–11; Kiparisova 1961: 121, pl. 27, figs. 1–7; Zaharov 1968: 108, pl. 21, figs. 1–3); Upper Olenekian, Subfengshanites multiformis Zone, South Primorye.

Diagnosis. Semi-evolute to evolute cadicone, with broadly arched veter without any tendency of carination, but characterized by marked development of reticulate ornamentation; position of the sifuncle in the first two whorls is dorsal to subdorsal (Fig. 10a–j). Suture line consists of five lobes: (V_1V_1) $UU^1 : I$ (D_1D_1) (Fig. 10k–m). Lobes U, U^1 and I are broad and significantly denticulated at the base. Dorsal lobe has tendency to become a four-indented lobe (Fig. 10n).

Occurrence. Uppermost Olenekian, South Primorye.

Species composition. Single species (*Subfengshanites multiformis* [Kiparisova] = "*Subcolumbites*" *solites* Kiparisova and "*Subcolumbites*" *anomalus* Kiparisova) from the upper Olenekian of South Pimorye.

Comparison. The new genus is identified by the most complicated suture among known columbitid ammonoids. Denticulated head-like lateral saddles differentiate it from *Fengshanites* Chao. A broadly arched venter without any tendency of carination, significantly stronger spiral striae and denticulated lateral lobes differentiate it from *Subcolumbites* Spath. A broadly arched venter, significantly stronger spiral striae, denticulated head-like lateral saddles and dorsal to subdorsal position of the siphuncle in the second whorl differentiate it from *Columbites* Hyatt and Smith (*Columbites* is characterized by its subdorsal to central position in the same stage; Zaharov 1978).

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