

Palaeobiogeographical and palaeobiological aspects of mid- and Late Cretaceous ammonite evolution and bio-events in the Russian Pacific

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Key words – Ammonoidea, Cretaceous, palaeobiogeography, palaeobiology, correlations, Russian Pacific. Both faunal endemism and provincialism in the mid- and Late Cretaceous of the Pacific realm complicate the recognition of stage boundaries in that area. Correlations with other areas (e.g., Europe, United States Western Interior, Pacific coast of North and South America) therefore have to rely solely on event stratigraphy; not only extinctions, but all biotic events must be considered. During the Cretaceous, Pacific faunas were characterised not so much by the presence of typical 'Boreal' assemblages, but rather by the absence or extreme paucity of other widely distributed biota. Clearly, faunal similarities depended more on regional facies development than on their spatial distribution. The regional diversity curve reflects all global mass extinctions, faunal turnovers and radiations. A detailed analysis of ammonite evolution, based on mid- and Late Cretaceous sections from the Russian Pacific coast, plus a comparison with other provinces across the globe, fails to support a trend in decreasing ammonite diversity since the late Albian. On the contrary, ammonites demonstrated a high adaptive ability after each extinction event and recovered from each with new radiations.

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Introduction

The Late Cretaceous saw the final phase in the development of ammonoid cephalopods, one of the most important invertebrate fossil groups during the latter part of the Mesozoic. Amongst various other biota, the great majority of ammonites went extinct at the end of the Cretaceous Period and a few others slightly later, during the earliest Danian (Machalski, 2002, 2005a, b; Machalski & Heinberg, 2005; Machalski *et al.*, 2009). Moreover, Cretaceous ammonites, and Late Cretaceous ones in particular, constitute a special group, which is still very important from a biostratigraphical point of view, and

is markedly different in shell morphology and sutural details from Palaeozoic, Triassic and Jurassic taxa. In addition, they are characterised by various special morphotypes, termed heteromorphs, which flourished during this period. These so-called ‘freaks of nature’ (or, rather, ‘back to the roots’) are typical of the Cretaceous only and are the sole ammonoids to survive into the earliest Paleocene. Moreover, the generally accepted view (see, for example, Wiedmann & Kullmann, 1996) that ammonite taxonomic diversity gradually decreased from the Albian to the Maastrichtian, prior to extirpation at the Cretaceous/Paleogene (K/Pg) boundary, needs to be evaluated critically, because data for the Russian Pacific coast suggest otherwise. Following a marked crisis at the Albian/Cenomanian boundary when almost all taxa disappeared (either becoming extinct or migrating), a general increase in diversity from the Cenomanian to the Campanian is clearly seen, despite a number of critical levels during this interval. Especially interesting is the Campanian Stage during which taxonomic diversity approached the

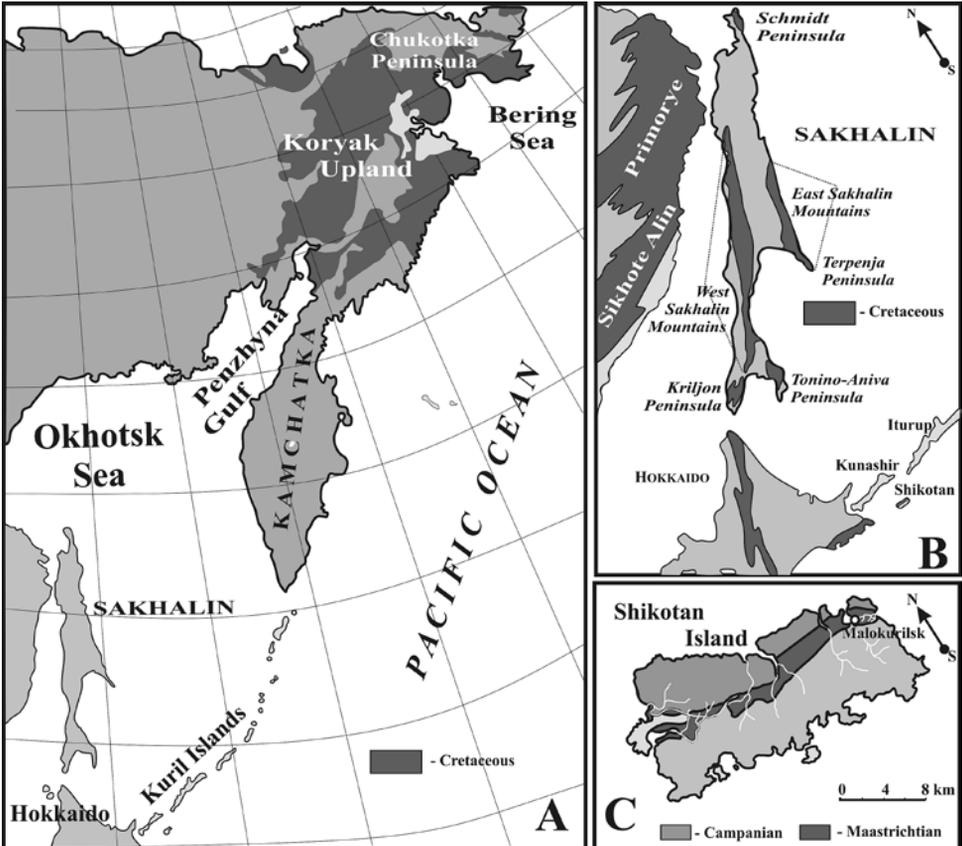


Fig. 1. Distribution of Cretaceous deposits in Far East Russia. A. Northeast Russia, Arctic Palaeobiogeographical Province (A). B. Albian-Cenomanian in Sikhote Alin and Primorje and Albian-Maastrichtian in Sakhalin Island, Northwest Pacific Palaeobiogeographical Province (NWP). C. Campanian-Maastrichtian in Shikotan Island (southern Kuril Ridge, Kuril Islands), Northwest Pacific Palaeobiogeographical Province (NWP).

high level of the Albian, thus documenting a near-complete recovery, and the Maastrichtian when numerous new species appeared to the extent that this could be termed a radiation event. Ammonite extinction at the K/Pg boundary has also been documented in Far East Russia, similar to various K/Pg boundary sites across the globe. I agree with Ward & Signor (1983) that the demise of the ammonites was sudden.

The main aim of the present work is to provide a detailed analysis of the palaeobiogeographical distribution as well as some of palaeoecological aspects of Albian-Maastrichtian ammonite faunas from the Russian Pacific coast (Fig. 1), where Cretaceous deposits are widely distributed and well characterised by different macro- and microfaunal groups. A major obstacle encountered in correlations with the type areas (mostly in Europe) of the various mid- and Late Cretaceous stages is the high degree of faunal endemism, which characterises Pacific Cretaceous faunas in general and Late Cretaceous ones in particular. This explains why most of the recently proposed criteria for the recognition of stage boundaries cannot be applied here. Moreover, macrofaunal complexes from the Russian Pacific coast are easily subdivided into endemic taxonomic groups, which illustrates the extent of local provincialism: northern (Koryak Upland, Chukotka Peninsula and Kamchatka Peninsula, mainly Penzhyna Gulf Coast) and southern (Primorye, inclusive of Sikhote Alin and the Amur River valley, as well as Sakhalin and the Kuril Islands [only Shikotan]). Therefore, all of the above-mentioned issues document the special position occupied by the Pacific realm in general, and the Russian coastal regions specifically, during the Cretaceous Period. Seen in this light, the 'extinction' of ammonoid cephalopods, based on data of Pacific representatives, certainly differ from traditional views expressed in the literature. First of all, this is a problem of endemism and provincialism in the Pacific realm in general. This has far-reaching implications for the identification of stage boundaries in Pacific sections and for attempts at global correlation, which, by necessity, need to rely on linking different kinds of events, either biotic (extinction, radiation, faunal turnover) or abiotic (volcanism, tectonics, anoxic events), in the absence of key index species used as criteria for stage boundaries. Moreover, palaeobiogeographical analyses call for a much needed clarification of terms introduced in previous papers. I here propose some new palaeobiogeographical provinces for Late Cretaceous ammonites (see below).

The present work provides an analysis of Albian-Maastrichtian ammonite faunas, and a few associated molluscan, foraminiferal and radiolarian assemblages, as well as sedimentary environments in the North Pacific Province (*sensu* Westermann, 2000), based on my own detailed studies of the Russian Pacific coast, administratively referred to as 'Far East Russia', which belonged to two palaeobiogeographical provinces, namely Boreal Pacific and Northwest Pacific (Fig. 1). The major portion of the collections studied has been amassed by myself during field work in 1986-1989 and in 1999. Field trips were organised in Sakhalin and the Shikotan islands, at Ugolnaya Bay (Chukotka Peninsula) and along the Anadyr River valley in the Koryak Upland where different groups of geologists from St Petersburg, Magadan and Juzhno-Sakhalinsk carried out geological mapping of these territories. In addition to my own collection, I obtained specimens from Professor V.N. Vereschagin's group (VSEGEI), an extensive collection made since the 1950s by numerous scientists, amongst whom were T.D. Zonova, Ju.G. Mirolubov, M.V. Titova, N.V. Salnikova and A.S. Shuvaev. Some of these specimens have already been published, but others await description.

In general, my research is based on the view that three factors – palaeoecology (evolutionary dynamics of ammonites dependent of environmental changes, taxonomic composition and possible links with lithofacies), palaeobiogeography (distribution of ammonite taxa, endemism, provinciality) and migratory/extinction patterns (bio-events such as extinction/migration, radiation and origination, faunal turnover) – can explain the above-mentioned patterns and enable long-distance correlations and comparisons with other continents, that is, to supply the ‘life history’ of ammonites (mainly North Pacific ones) through geological time. In doing so, I have attempted to take into account virtually all previous papers as well as the most recent reference works and my own collections, now housed at CNIGR Museum VSEGEI (St Petersburg, Russia; collection numbers NN 10693, 11799, 12632, 12769, 13061 and 13088), the Natuurhistorisch Museum Maastricht (Maastricht, the Netherlands; NHMM 2008 105-2008 129) and the NCB Naturalis (Leiden, the Netherlands; NCB-RGM 617946-617968). Material contained in the last-named institute is illustrated in Plates 1-13.

Ammonite faunas from the Russian Pacific and environs

All ammonite taxa recorded to date from the Albian to Maastrichtian of Sakhalin and neighbouring areas (e.g., Shikotan Island, Chukotka and Kamchatka peninsulas, the Koryak Upland, Sikhote Alin and Primorye; see Fig. 1), have been arranged taxonomically, following systematics outlined by Wright *et al.* (1996). A grand total of 198 species, inclusive of specifically indeterminate ones, denoted with ‘sp.’, ‘cf.’ or ‘aff.’, have been recorded from this area, distributed over ninety genera, twenty-two families and twenty-seven subfamilies. A detailed biostratigraphical framework has previously been proposed for Sakhalin (Yazykova, 2004), as based on papers by Russian and Japanese colleagues. Zonal subdivisions by ammonites, inoceramid bivalves and radiolarians for Sakhalin, Shikotan and Sikhote Alin are presented here in a revised version (Fig. 2), and the newest scheme for northeast Russia (Fig. 3), plus a general comparison with the Japanese ammonite zonal scheme (Fig. 4) is added.

Early Cretaceous: Late Albian – In Early Cretaceous deposits of Far East Russia, ammonites are not particularly common, having been recorded mainly from central northeast Russia, for example, at some localities in the Koryak Upland or in the Chukotka and Kamchatka peninsulas (Vereschagin *et al.*, 1965), and the Primorye region, including Sikhote Alin and the Amur River valley (Sey *et al.*, 2004). In Sakhalin, the Early Cretaceous is represented by late Albian sedimentary rocks (Pokhialajnen, 1988; Poyarkova, 1987; Zonova *et al.*, 1993), which explains why ammonite assemblages are here presented in detail starting from that substage.

Overall, the late Albian ammonite assemblage is comparatively diverse, comprising 45 species (of which 30 are in open nomenclature), distributed amongst 29 genera and eleven families. The *Cleoniceras* sp. Zone defines the latest Albian in Sakhalin, Primorye and northeast Russia (Figs. 2, 3); it has recently also been recorded from the Arctic part of Siberia (V.A. Zakharov *et al.*, 2000). It is correlated with the *Desmoceras* (*Pseudouhligella*) *dawsoni shikokuense* Zone in Japan, on the basis of a taxonomically similar assemblage (Fig. 4). The *Cleoniceras* sp. Zone also corresponds to the *Inoceramus anglicus*/*I. aiensis* Zone in Sakhalin, to the zone of *Inoceramus* ex gr. *anglicus* in Sikhote Alin and to the

Stage	Substage	Formation	Member	Sakhalin, Shikotan, Sikhote Alin		
				Inoceramid zones	Ammonite zones	Radiolarian zones
Maastrichtian	upper	Krasnoyarska Malokurilsk	5	<i>Korjalkia kociubinskii</i> <i>Shachmaticeramus kusiroensis</i> , <i>Inoceramus hetonaianus</i>	<i>Pachydiscus</i> (P.) <i>flexuosus</i> , P. (<i>Neodesmoceras</i>) <i>gracilis</i>	<i>Pachydiscus</i> (P.) <i>subcompressus</i> <i>Amphipyndax tylotus</i>
	lower		4	<i>Shachmaticeramus shikotanensis</i>	<i>Pachydiscus</i> (<i>Neodesmoceras</i>) <i>japonicus</i>	
Campaian	upper	Matakotan	3	<i>Inoceramus</i> aff. <i>balticus</i>	<i>Canadoceras multicostatum</i>	
	upper		2	<i>Schmidticeramus schmidti</i>	<i>Pachydiscus</i> (P.) spp.	<i>Pseudoaulophacus floresensis</i> - <i>Stichomitra livermorensis</i>
	lower		1	<i>Pennatoceras orientalis</i> <i>Inoceramus nagoi</i>	<i>Canadoceras kossmati</i> <i>Menuites</i> (<i>Neopachydiscus</i>) <i>naumanni</i>	<i>Spongostaurus</i> (?) <i>hokkaidoensis</i> - <i>Hexacantium</i> sp.
Santonian	upper	Bykov	9	<i>Inoceramus japonicus hokkaidoensis</i> , I. aff. <i>undulatoaplicatus</i>	<i>Menuites menu</i> <i>Texanites</i> (<i>Plesiotexanites</i>) <i>kawasakii</i>	<i>Eupachydiscus haradai</i> <i>Archaeospongoprimum bipartitum</i> - <i>Patulibracchium petroleumensis</i>
	low.		8	<i>Inoceramus amakusensis</i>		
Coniacian	upp.	Bykov	7	<i>Inoceramus mihoensis</i>	<i>Peroniceras</i> sp. <i>Forresteria</i> (F.) <i>alluaudi</i>	<i>Orbiculiforma vacaensis</i> - <i>Squinabolella putahensis</i>
	mid.		6	<i>Inoceramus uwajimensis</i> <i>Inoceramus teshioensis</i> , <i>Mytiloides incertus</i>	<i>Jimboiceras mihoense</i> <i>Subprionocyclus</i> sp.	
Turonian	upper	Bykov	5		<i>Jimboiceras planulatiforme</i>	<i>Orbiculiforma quadrata</i> - <i>O. monticelloensis</i>
	middle		4	<i>Inoceramus hobetsensis</i>	<i>Romaniceras</i> (Yubar.) <i>ornatissimum</i> <i>Scaphites planus</i>	
	lower		3	<i>Mytiloides</i> aff. <i>labiatus</i>	<i>Fagesia</i> sp.	
Cenomanian	upper	Naiba	2	<i>Inoceramus</i> aff. <i>tenuis</i>	<i>Desmoceras</i> (<i>Pseudouhligella</i>) <i>japonicum</i>	<i>Haliomma sachalinica</i> - <i>Dictiomitra multicostata</i>
	mid		1	<i>Inoceramus pennatulus</i> - I. <i>gradilis</i> <i>Inoceramus</i> (<i>Birostrina</i>) <i>nipponica</i> - I. (B.) <i>tamura</i>	<i>Turrilites acutus</i> <i>Acanthoceras</i> sp. <i>Turrilites costatus</i>	
Albian	upper	Aj	4	<i>Inoceramus</i> aff. <i>crippsi</i>	<i>Mantelliceras</i> sp.	<i>Lipmanium sacramentoensis</i> - <i>Archaeodictyomitra squinaboli</i>
	upper		3		<i>Desmoceras</i> (D.) <i>kossmati</i>	
	upper		2	<i>Inoceramus anglicus</i> , I. <i>aiensis</i>	<i>Cleoniceras</i> sp.	
			2	?	?	<i>Xitus plenus</i> - <i>Pseudo-dictyomitra lodogaensis</i>

Fig. 2. Mid- and Late Cretaceous biostratigraphical subdivisions of Sakhalin, Shikotan and Sikhote Alin. Inoceramids by Zonova (Zonova et al., 1993; Zonova & Yazykova, 1998, 2001), ammonites by Jagt-Yazykova (Yazykova, 2004, present paper) and radiolarians by Kasintzova (1988, 1992, 2000a, b).

		Northeast Russia (Koryak Upland, Pontoney Mountains, Penzhyna Gulf coast)		
Stage	substage	Inoceramid zones	Ammonite zones	Radiolarian zones
Maastrichtian	upper	<i>Korjakkia kociubinskii</i>	<i>Pachydiscus</i> (<i>P.</i>) <i>flexuosus</i> , <i>P. (Neodesmoceras)</i> <i>gracilis</i>	<i>Pachydiscus</i> (<i>P.</i>) <i>subcompressus</i>
	lower	<i>Shachmaticeramus kuroensis</i>	<i>Pachydiscus (Neodesmoceras) japonicus</i>	
Campanian	upper	<i>Inoceramus</i> aff. <i>balticus</i>	<i>Tetragonites popetensis</i>	<i>Clathrocyclas diceros-Amphipyndax tylotus</i>
	lower	<i>Schmidticeramus schmidti</i>	<i>Canadoceras</i> spp.	
	lower	<i>Pennatoceras orientalis</i> <i>Inoceramus nagoi</i>	<i>Canadoceras kossmati</i> <i>Menuites (Neopachydiscus) naumanni</i> <i>Menuites menu</i>	<i>Eupachydiscus haradai</i>
Santonian	<i>Inoceramus yokoyamai</i>	<i>Texanites</i> sp.	<i>Pseudoaulophacus florensis</i>	
Coniacian	low. m. up.	<i>Inoceramus mihoensis</i>	<i>Kossmaticeras (Natalites) penjiensis</i>	<i>Archaeospongoprimum bipartitum - Alievium superbum</i>
	low.	<i>Inoceramus uwajimensis</i>	<i>Scaphites</i> spp.	
Turonian	upper	<i>Inoceramus multiformis</i>	<i>Jimboiceras planulatiforme</i>	<i>Pseudodictyomitra pseudomacrocephala - Holocryptocanium barbui</i>
	middle	<i>Inoceramus hobetsensis</i>	<i>Scalarites scalaris</i>	
	lower	<i>Mytiloides</i> aff. <i>labiatus</i>	<i>Scaphites planus</i> <i>Zelandites mihoensis</i>	
Cenomanian	upper	<i>Inoceramus</i> aff. <i>tenuis</i> <i>I. pontonensis</i> , <i>I. pennatulus-</i> <i>Inoceramus subovatus</i> , <i>I. tychljawajemensis</i> <i>Inoceramus dunveganensis</i>	<i>M. voyanus</i> <i>M. olcostephanoides</i> <i>Turrilites acutus</i>	
	middle		<i>Marshallites compressus</i> <i>Turrilites costatus</i>	
	lower		<i>Mantelliceras</i> sp. <i>Parajaubertella kawakitana</i>	
	lower		<i>Birostrina nipponica, B. tamurai</i>	<i>Desmoceras (Pseudouligella) japonicum</i>
	upper			
Albian	upper	<i>Inoceramus anglicus</i> , <i>I. omutnensis</i>	<i>Cleoniceras</i> sp. <i>Archoplites talkeetanus</i>	<i>Marshallites cumshewaensis</i>

Fig. 3. Mid- to Late Cretaceous biostratigraphical subdivisions of northeast Russia. Inoceramids by Zonova (Zonova & Yazykova, 1998; Zonova, 2004), ammonites by Jagt-Yazykova (Yazykova, 2004, present paper) and radiolarians by Vishnevskaya (Vishnevskaya, 2001; Vishnevskaya & Filatova, 2008).

Stage	Sakhalin, Shikotan, Sikhote Alin		NE Russia	Japan		
	AMMONITE ZONE		AMMONITE ZONE	AMMONITE ZONE		
		Selected associated species		Desmoceratoidea	Selected associates	
Maastrichtian	upper	<i>Pachydiscus</i> (<i>P.</i>) <i>flexuosus</i> , <i>P.</i> (<i>Neodesmoceras</i>) <i>gracilis</i>	<i>Pachydiscus</i> (<i>P.</i>) <i>flexuosus</i> , <i>P.</i> (<i>Neodesmoceras</i>) <i>gracilis</i>	<i>Pachydiscus</i> (<i>P.</i>) <i>flexuosus</i>	<i>Gaudryceras hamanakense</i>	
	lower	<i>Pachydiscus</i> (<i>Neodesmoceras</i>) <i>japonicus</i>	<i>Pachydiscus</i> (<i>Neodesmoceras</i>) <i>japonicus</i>	<i>Pachydiscus</i> (<i>Neodesmoceras</i>) <i>gracilis</i>	<i>Gaudryceras izumiense</i>	
Campaian	upper	<i>Canadoceras multicoatum</i>	<i>Tetragonites popetensis</i>	<i>Pachydiscus</i> (<i>P.</i>) <i>awajiensis</i>	<i>Pravitoceras sigmoidale</i>	
		<i>Pachydiscus</i> (<i>P.</i>) spp. <i>Canadoceras</i> spp.	<i>Anapachydiscus arrialoorensis</i>	<i>Canadoceras</i> spp.	<i>Patagiosites laevis</i>	<i>Didymoceras awajense</i>
	lower	<i>Canadoceras kossmati</i>	<i>Damesites semicoatum</i>	<i>Canadoceras kossmati</i>	<i>Anapachydiscus fascicostatus</i>	<i>Metaplacentoceras subtilistriatum</i> <i>Hoplitoplacentoceras monju</i>
		<i>Menuites</i> (<i>Neopachydiscus</i>) <i>naumanni</i>	<i>Damesites sugata</i>	<i>Menuites</i> (<i>Neopachydiscus</i>) <i>naumanni</i>	<i>Anapachydiscus naumanni</i>	<i>Delawarella</i> sp.
Santonian	lower/upper	<i>Menuites menu</i>	<i>Menuites menu</i>	<i>Eupachydiscus haradai</i>	<i>Plesiotexanites shiloensis</i>	
		<i>Texanites</i> (<i>Plesiotexanites</i>) <i>kawasakii</i>	<i>Texanites</i> sp.	<i>Anapachydiscus sutneri</i>	<i>Plesiotexanites kawasakii</i> <i>P. pacificus</i>	
Coniacian	low/mid/upper	<i>Peroniceras</i> sp.	<i>Kossmaticeras</i> (<i>Natalites</i>) <i>penjiensis</i>	<i>Kossmaticeras theobaldianum</i>	<i>Paratexanites orientalis</i>	
		<i>Forresteria</i> (<i>F.</i>) <i>alluaudi</i>	<i>Scaphites</i> spp.	<i>Eupachydiscus keramasatoshii</i>	<i>Forresteria</i> (<i>F.</i>) <i>alluaudi</i>	
Turonian	upper	<i>Jimboiceras mihoense</i>	<i>Jimboiceras planulatiforme</i>	<i>Damesites ainuanus</i> - <i>Tongoboryceras satoi</i>	<i>Subprionocyclus neptuni</i>	
	middle	<i>Subprionocyclus</i> sp.		<i>Mesopuzosia pacifica</i>	<i>S. minimus</i>	
	lower	<i>Jimboiceras planulatiforme</i>	<i>Scalarites scalaris</i>	<i>Scalarites scalaris</i>	<i>Pachydesmoceras kossmati</i> - <i>Puzosia orientalis</i>	<i>S. bravaisianus</i>
		<i>Romaniceras</i> (<i>Yubar</i>) <i>ornatissimum</i>	<i>Scalarites scalaris</i>	<i>Scaphites planus</i>	<i>Damesites laticarinatus</i>	<i>Romaniceras deverianum</i>
Cenomanian	upper	<i>Forresteria</i> (<i>F.</i>) <i>alluaudi</i>	<i>Zelandites mihoensis</i>	<i>Marshallites olcostephanoides</i>	<i>Collignoniceras woollgari</i>	
	mid.	<i>Jimboiceras mihoense</i>	<i>Scaphites planus</i>	<i>Wellmanites japonicus</i>	<i>Fagesia thevestensis</i> - <i>Mammites</i> aff. <i>nodosoides</i>	
	lower	<i>Subprionocyclus</i> sp.	<i>Zelandites mihoensis</i>	<i>Marshallites compressus</i>	<i>Maccarthys mikasaensis</i>	<i>Pseudaspidoceras flexuosum</i>
		<i>Jimboiceras planulatiforme</i>	<i>Scaphites planus</i>	<i>Turrillites acutus</i>	<i>Mantelliceras sp.</i>	<i>? Neocardioceras juddii</i>
Albian	upper	<i>Forresteria</i> (<i>F.</i>) <i>alluaudi</i>	<i>Zelandites mihoensis</i>	<i>Marshallites compressus</i>	<i>Euomphaloceras septemseriatum</i>	
		<i>Subprionocyclus</i> sp.	<i>Scaphites planus</i>	<i>Mantelliceras sp.</i>	<i>Eucalycoceras pentagonum</i>	

Fig. 4. Mid-to Late Cretaceous biostratigraphical subdivisions of Far East Russia (present paper) and of Japan (Toshimitsu *et al.*, 1995).

I. anglicus/*I. omutnensis* Zone in northeast Russia (Figs. 2, 3). Moreover, in Sakhalin the *Xitus plenus*-*Pseudodictyomitra lodogaensis* radiolarian Zone correlates with inoceramid and ammonite zones in the latest Albian (Fig. 2).

Sakhalin – Of the 45 late Albian taxa mentioned above, only eight representatives, predominantly in open nomenclature, in seven genera and five families, have been recorded from Sakhalin (Zhuravlev, 1969a; Tarasevich, 1971; Zonova *et al.*, 1986, 1993; Matsumoto & Nishida, 2004). Some material from Sakhalin is currently being evaluated; here a few preliminary data are provided (CNIGR VSEGEI Museum, Jagt-Yazykova Collection, N 13088). This association occurs at a few localities in the south of the West Sakhalin Mountains and in the Tonina-Aniva Peninsula along the east coast (Fig. 1B). It comprises the desmoceratines *Desmoceras* (*D.*) *kossmati* Matsumoto and *Desmoceras* (*Pseudouhligella*) sp., the puzosiine *Puzosia aldersoni* Anderson, the marshallitines *Marshallites* cf. *columbianus* McLearn and *Marshallites* sp., the cleoniceratids *Breweriaceras* ex gr. *hulense* (Anderson) and *Cleoniceras* (*Neosaynella*?) sp., the anahoplite *Anahoplites* sp. and the turrilitid *Pseudhelicoceras* sp.

Northeast Russia (Koryak Upland, Penzhyna Gulf coast, northwest Kamchatka) – Albian ammonites were described from here by Vereschagin *et al.* (1965), Mikhailova & Terekhova (1975), Terekhova (1969, 1980, 1985), Terekhova & Basov (1972), Terekhova & Mikhajlova (1977), Alabushev (1987, 1995) and Alabushev & Wiedmann (1994b, 1997). Some material from the Koryak-Kamchatka area is currently being evaluated; preliminary data are presented here (CNIGR VSEGEI Museum, Jagt-Yazykova Collection, N 13088).

In comparison to Sakhalin and Sikhote Alin, this territory is characterised by the richest and most diverse Albian ammonite association, comprising 32 named species, and 13 in open nomenclature, assigned to 20 genera in ten families. These comprise the phylloceratid *Phyllopachyceras* cf. *chitinanum* Imlay, the gaudryceratid *Gaudryceras penjiensis* Vereschagin, the silesitoidine *Parasilesites orientalis* Mikhailova & Terekhova, the beudanticeratines *Beudanticeras* sp., *B.* aff. *glabrum* (Whiteaves), *B.* (*Grantziceras*) cf. *multiconstrictum* Imlay and *B.* (*G.*) *affine* (Whiteaves), the marshallitines *Marshallites olcostephanoideis* Matsumoto, *M. cumshewaensis* (Whiteaves), *M. columbianus* McLearn, *M.* cf. *miyakoensis* Obata & Futakami, *M. voyanus* (Anderson), ?*Holcodiscooides papillatus* Stoliczka (based on a doubtful identification by Vereschagin *et al.*, 1965; the specimen resembles either *Eogunnarites* or *Sounnaites*), *Eogunnarites* sp., *E. vereshagini* Terekhova and *E. unicus* (Yabe) (see Pl. 1, figs. 1-3), the kossmaticeratines *Yokoyamaoceras rarum* Terekhova and *Y. spinosum* Terekhova, the cleoniceratids *Cleoniceras* sp., *C.* (*Grycia*) *dubia* Mikhailova & Terekhova and *Arcthoplites* (*Subarcthoplites*) *talkeetnanus* (Imlay), the sonneratiine *Sonneratia* sp., and, finally, the gastropplites *Gastropplites* (*Paragastropplites*) cf. *flexicostatus* Imlay, *Neogastropplites* sp. and *N. kamchatkensis* (Alabushev & Wiedmann).

Beudanticeras (*G.*) *affine* from Albian sedimentary rocks along the Penzhyna Gulf coast, northwest Kamchatka, was illustrated by Shigeta *et al.* (1999a), but those authors failed to provide a description of their material. V.A. Zakharov *et al.* (2000) noted *Cleoniceras* cf. *bicurvatooides* in western Siberia, but, for now, this is best referred to as *Cleoniceras* (*Cleoniceras*) sp. *Neogastropplites americanus* (Reeside & Weymouth) was recorded by Alabushev & Wiedmann (1994b) from the late Albian-early Cenomanian of the Penzhyna Gulf coast (Kamchatka Peninsula). However, following views expressed by William A. Cobban (pers. comm., 2000), *N. americanus* as described by Alabushev (*in* Alabushev &

Wiedmann, 1994b) from that area rather belongs to his endemic species, *N. kamchatkensis*, which that author described as new from the Koryak-Kamchatka region (Alabushev & Wiedmann, 1994b). For this reason, the genus *Neogastrolites* in Koryak-Kamchatka is here assumed to be represented by *N. kamchatkensis* and a second, indeterminate species, *Neogastrolites* sp., which probably represents an undescribed form, is endemic as well, but in need of further study. In addition, there are the placenticeratids *Proplacenticerias?* sp. and *Proplacenticerias sutherlandbrowni* McLearn, the mortoniceratine *Mortoniceras* sp., the lyelliceratid *Stoliczkaia (Lamnayella)* cf. *japonica* (Matsumoto, Kimuka & Katto), and the turrilitids *Pseudhelicoceras carlottense* (Whiteaves), *Turrilites* sp. and *Mariella* sp.

Alabushev (in Alabushev & Wiedmann, 1997) described the new subfamily Rapidoplacenticeratinae and the new genus *Rapidoplacenticerias*, with type species *Rapidoplacenticerias sutherlandbrowni* (McLearn), from the late Albian-early Cenomanian of the Penzhyna Gulf Coast in northwest Kamchatka. However, his criteria for distinguishing this subfamily do not appear sufficient and his new genus does not differ from *Proplacenticerias*, which is why they are considered to be synonymous.

Primorye (Sikhote Alin and Amur River valley) – The Primorye palaeobasin at the southern Russian Pacific coast (Fig. 1B) differed from northeast Russia in taxonomic composition, being rather comparable to late Albian assemblages from Sakhalin (Zonova & Yazykova, 2000, 2001; Yazykova, 2001; Sey *et al.*, 2004). It has yielded 15 species, representing four genera in eight families, namely the phylloceratid *Phyllopachyceras* aff. *chitinatum* (Anderson), the lycoceratid *Protetragonites* cf. *aeolus aeolus* (d'Orbigny), the gaudryceratids *Eogaudryceras (Eotetragonites) duvalianus* (d'Orbigny) and *Gaudryceras penjiensis* Vereschagin, the puzosiine *Puzosia* cf. *lata* Seitz, the silesitoidine *Parasilesites* cf. *bullatus* Imlay, the beudanticeratine *Beudanticeras* sp., the desmoceratine *Desmoceras (Pseudouhligella)* sp., the marshallitines *Marshallites* sp. and *Eogunnarites?* sp., the cleoniceratids *Cleoniceras* (C.) sp. and *Arcthoplites (Subarcthoplites)* aff. *belli* (McLearn), the sonneratiine *Sonneratia* sp., and the turrilitids *Mariella* sp. and *M.* aff. *circumtaeniata* (Kossmat).

Late Cretaceous – Late Cretaceous deposits are widely distributed in the Russian Far East (Fig. 1), and are represented by an uninterrupted sequence from the Cenomanian to the Maastrichtian in southern Sakhalin (Naiba River valley, Kriljon Peninsula), in numerous sections in central Sakhalin (West Sakhalin Mountains or so-called Main Cretaceous Field; East Sakhalin Mountains along the Okhotsk Sea coast), isolated outcrops in the Tonina-Aniva Peninsula along the east coast and in the Schmidt Peninsula in the north (Fig. 1B). Only Campanian-Maastrichtian deposits represent the Late Cretaceous in Shikotan Island, southern Kuril Ridge (Fig. 1C). Cenomanian-Maastrichtian deposits are well characterised by ammonites in northeast Russia along the Penzhyna Gulf coast of northwest Kamchatka, in the Koryak Upland as well as in Chukotka Peninsula. In Primorye, marine sedimentation came to a halt during the Cenomanian, which explains why these are the youngest ammonite records from Sikhote Alin and Priamurye. However, Vereschagin & Pchelincev (1960) recorded the echinoid genus *Hemiaster* and the gastropod *Actaeonella* from Sikhote Alin, dating the levels which produced them as early 'Senonian' (Santonian?). However, there is no additional evidence of any age younger than Cenomanian for Sikhote Alin, so this record probably also originated

from Albian or Cenomanian deposits. Three other echinoids have subsequently been recorded from Sakhalin (Jagt-Yazykova Collection); these are currently under study.

Cenomanian – Overall, the Cenomanian ammonite fauna (Pls. 1, 2) from the Russian Far East comprises 44 species (of which 23 are in open nomenclature), representing 22 genera in nine families. Numerous ammonite finds have allowed the division of Cenomanian deposits into five zones in Sakhalin (Fig. 2), seven zones in northeast Russia (Fig. 3), and their correlation with the Japanese ammonite scheme (Fig. 4), and respective inoceramid zones in Sakhalin, Primorye and northeast Russia (Figs. 2, 3). In Sakhalin they are also comparable with two radiolarian zones, apart from the lowermost Cenomanian which has not yielded any such remains (Fig. 2).

Sakhalin – Cenomanian ammonite assemblages include representatives of seven families, comprising 16 genera, eleven named species and ten in open nomenclature. They have been described by, for example, Matsumoto (1938, 1954a, b), Vereschagin *et al.* (1965), Mirolubov in Poyarkova (1987), Zonova *et al.* (1993) and Yazykova *et al.* (2004), and comprise the phylloceratine *Hypophylloceras* (*Neophylloceras*) *seresitense* Pervinquierè, the gaudryceratids *Gaudryceras* cf. *varagurense* Kossmat, *Anagaudryceras buddha* (= *sacya* Forbes), *A.* cf. *buddha* (Forbes), *Zelandites inflatus* Matsumoto, *Z.* aff. *dozei* (Fallot), *Zelandites* sp. A, and *Z.* aff. *mihoensis* Matsumoto, the tetragonitids *Parajaubertella kawakitana* Matsumoto (see Pl. 2, figs. 2-7) and *Tetragonites makarovensis* Glasunova, the puzosiines *Parapuzosia* (*Austiniceras*) *austeni* (Sharpe) and *P.* (*A.*) *nipponicum* Matsumoto, the desmoceratines *Desmoceras* (*D.*) *kossmati* Matsumoto, *D.* (*Pseudouhligella*) sp., *D.* (*P.*) *japonicum* Matsumoto and *D.* (*P.*) cf. *japonicum* Matsumoto, the marshallitines *Marshallites olcostephanoides* Matsumoto, *Ma.* cf. *columbianus*, *Mikasaites matsumotoi* Vereschagin and *Mi. orbicularis* Matsumoto, the mantelliceratine *Mantelliceras* sp., the acanthoceratines *Calycoceras* (*C.*) sp., *C.* (*Newboldiceras*) sp. and *Acanthoceras* sp. juv., and the turrilitid *Turrilites costatus* Lamarck.

Zelandites aff. *mihoensis* was mentioned by Yu.D. Zakharov *et al.* (1984), but, according to Matsumoto (1938), *Z. mihoensis* is an early Turonian species. *Parapuzosia*(?) *ambigua* Matsumoto, recorded from Sakhalin by Matsumoto (1954b), has subsequently been regarded as a junior synonym of *P.* (*A.*) *austeni* (see Matsumoto, 1988). Vereschagin *et al.* (1965) described *Acanthoceras* ex gr. *rhotomagense* Defrance [*sic*] from middle Cenomanian deposits at the River Susuja, Naiba River valley. Later, Mirolubov in Poyarkova (1987) transferred that particular specimen to *A. sussexiense* Mantell. However, this small shell is here considered a juvenile, which cannot be readily assigned to either *A. sussexiense* or *A. rhotomagense* (Brongniart); there is no doubt that it is fact an *Acanthoceras*.

Northeast Russia (*Koryak Upland, Penzhyna Gulf coast, northwest Kamchatka*) – Ammonite faunas of Cenomanian age in northeast Russia involve nine families, comprising representatives of 13 genera and 15 named species, plus eight in open nomenclature, as described by, for example, Vereschagin *et al.* (1965), Paraketzov *et al.* (1974), Terekhova & Mikhajlova (1977), Terekhova (1969, 1980), Yazykova (1992), Alabushev & Wiedmann (1994b, 1997) and Yazykova *et al.* (2004). Added to this is ongoing work by myself on material of Albian-Cenomanian age from northeasterly regions; some preliminary data are outlined below. The assemblages includes the phylloceratine *Hypophylloceras* (*Neophylloceras*) *seresitense* Pervinquierè, the gaudryceratids *Gaudryceras* aff. *varagurense* and *Zelandites inflatus*, the tetragonitid *Parajaubertella kawakitana*, the puzosiine *Puzosia* aff.

planulata Sowerby, the marshallitines *Marshallites tumefactus* Terekhova, *M. olcostephanoidea*, *M. columbianus*, *M. cumshewaensis*, *M. voyanus*, *M. cf. miyakoensis* Matsumoto, *Eogunnarites* sp., *E. unicus* and *E. vereschagini*, the gastropplitines *Neogastropplites* sp. and *N. kamchatkensis*, the lyelliceratid *Stoliczkaia (Lamnayella) cf. japonica* (Matsumoto, Kimuka & Katto), the acanthoceratine *Calycocheras (Newboldiceras) cf. orientale* Matsumoto (see Pl. 1, fig. 4; Pl. 2, fig. 1), the mantelliceratine *Mantelliceras* sp., and the turrilitids *Turrilites* sp., *T. costatus* Lamarck, *T. acutus* Passy, *Hypoturrilites* sp., *H. anadyrensis* Mikhailova & Terekhova, *Mariella* sp. and *M. cenomaniensis* (Schlüter). Terekhova & Mikhailova (1977) first described turrilitids from the Koryak Upland; their identifications have subsequently been revised by Atabekian (1985).

Primorye (Sikhote Alin and Amur River valley) – Cenomanian ammonites from Sikhote Alin, Primorye and Priamurye are less common than in Sakhalin and Koryak-Kamchatka (Zonova & Yazykova, 2000, 2001; Yazykova, 2001; Sey *et al.*, 2004), and are comprised of only three uncertain species in three genera and two families. This explains why it was not possible to establish any ammonite zones here. Assemblages comprise the puzosiiine *Puzosia cf. lata* Seitz, the desmoceratine *Desmoceras (Pseudouhligella)* sp. and the turrilitid *Mariella aff. circumtaeniata*.

Turonian – Turonian deposits are widely distributed in the Russian Far East, in the West Sakhalin Mountains in Sakhalin, Penzhyna Gulf coast of northwest Kamchatka, Pontonei Mountains in the Koryak Upland and in the Chukotka Peninsula. In total, Turonian ammonite assemblages from these areas comprise twelve families, 24 genera and 25 named species, plus nine in open nomenclature. Five ammonite zones are recognisable in Sakhalin and can be correlated with four in northeast Russia, as well as with respective divisions in Japan (Figs. 2-4). Moreover, inoceramid zones are traceable from Sakhalin to northeast Russia, comparable with the same in Japan and match ammonite subdivisions (Figs. 2, 3). The radiolarian zonation is not detailed enough at this level because of the predominance of long-ranging taxa (Figs. 2, 3).

Sakhalin – Turonian ammonites from Sakhalin have been recorded by many authors, such as Yabe (1910), Kawada (1929), Shimizu (1935), Wright & Matsumoto (1954), Druschic & Pergament (1963), Vereschagin *et al.* (1965), Matsumoto (1954b, 1970a, 1977b, 1988), Matsumoto *et al.* (1978), Miroslubov *in* Poyarkova (1987), Alabushev & Wiedmann (1997), Yazykova (1992), Zonova *et al.* (1993), Shigeta (1989), Zonova & Yazykova (1998), Yazykova *et al.* (2004) and Shigeta & Maeda (2005). Material from Sakhalin comprises 21 named species (plus eight in open nomenclature), representing 23 genera in eleven families, as follows: the phylloceratine *Hypophylloceras (Neophylloceras) ramosum* (Meek), the gaudryceratids *Gaudryceras denseplicatum* Jimbo, *G. tenuiliratum* Yabe, *Anagaudryceras limatum* (Yabe) and *Zelandites mihoensis* Matsumoto, the tetragonitid *Tetragonites glabrus* (Jimbo), the puzosiiines *Puzosia (M.) takahashii* Matsumoto, *Jimboiceras planulatiforme* (Jimbo) (see Pl. 3, figs. 1, 2; Pl. 4, fig. 1) and *Pachydesmoceras pachydiscoide* Matsumoto, the desmoceratines *Tragodesmoceroides subcostatus* Matsumoto, *Damesites damesi intermedius* Matsumoto and *D. ainuanus* Matsumoto (see Pl. 4, figs. 4-6), and the euomphaloceratines *Pseudaspidoceras cf. armatum* Pervinquière (*sensu* Shimizu, 1935), *Romaniceras (Yubariceras) ornatissimum* Stoliczka, *R. (Romaniceras) aff. pseudodeverianum* (Jimbo) and *Kamerunoceras shimizui* (Matsumoto) (= *Polyaspidoceras shimizu* *in* Matsumoto *et al.*, 1978). Wright *et al.* (1996) synonymised *Polyaspidoceras* with

Kamerunoceras, albeit with a query. In addition, there are vascoerats (Fagesia sp.), the hourquiniine *Hourquia pacifica* Matsumoto, the collignoniceratine *Subprionocyclus* sp., and the nostoceratids *Nostoceras* (*Eubostriochoceras*) sp., *N. (E.) cf. japonicum* (Yabe), *Hypphantoceras* sp., *H. aff. reussianum* (d'Orbigny), *Nipponites mirabilis* Yabe and *N. sachalinensis* Kawada (see Pl. 3, figs. 3-5), as well as the diplomoceratine *Scalarites mihoensis* Wright & Matsumoto and the otoscapitines *Scaphites planus* Yabe, *Yezoites puerculus* (Jimbo), *Y. subplanus* Shimizu and *Y. pseudoaequalis* Yabe. Kawada (1929) distinguished *Nipponites mirabilis* var. *sachalinensis* from the Turonian of Sakhalin, noting that that variety differed from *N. mirabilis* which occurred in Hokkaido. However, Druschic & Pergament (1963) assumed distinctive features mentioned by Kawada to reflect polymorphism within a single species. Kawada's views are here subscribed to and his taxon is considered to be a distinct species.

Northeast Russia (Koryak Upland, Penzhyna Gulf coast, northwest Kamchatka) – Previously, Turonian ammonites from northeast Russia have been recorded by Vereschagin *et al.* (1965), Alabushev & Wiedmann (1997), Yazykova (1992) and Zonova & Yazykova (1998). The assemblage from Sakhalin is represented by twelve named species (plus one in open nomenclature), documenting twelve genera in eight families, as follows: the phylloceratine *Hypophylloceras* (*Neophylloceras*) *ramosum*, the gaudryceratids *Gaudryceras denseplicatum*, *G. tenuiliratum* and *Anagaudryceras limatum* (= *Gaudryceras cf. limatum* by Liverovskaya, 1959), the puzosiines *Puzosia* (*Mesopuzosia*) *indopacifica* Kossmat (probably *Kitchinites ishikawai* Jimbo, because the ornament more closely resembles that of the latter species) and *Jimboiceras planulatifforme*, the marshallitine *Marshallites tumefactus*, the euomphaloceratines *Romaniceras* (*Yubariceras*) *ornatissimum* and *R. (Romaniceras)* *aff. pseudodeverianum*, the nostoceratids *Nostoceras* (*Eubostriochoceras*) *japonicum* (= *Scalarites venustum* in Vereschagin *et al.*, 1965 and Zonova & Yazykova, 1998) and *Nipponites mirabilis*, and the diplomoceratine *Scalarites scalaris* Jimbo, as well as the otoscapitines *Scaphites planus* and *Yezoites teshioensis* Yabe.

Coniacian – Deposits of this age occur in the West Sakhalin Mountains, the Penzhyna Gulf coast of northwest Kamchatka and the Koryak Upland. However, they are comparatively less well characterised by ammonites. In total, the Coniacian ammonite assemblage from the Russian Far East involves eleven families, 16 genera and 19 named species, plus four in open nomenclature. Three ammonite zones are proposed for Sakhalin, two for northeasterly regions and both are correlated with inoceramid zones. Unfortunately, the position of substage boundaries within the Coniacian still cannot be determined (Figs. 2, 3). A similar situation has been observed in Japan (Fig. 4).

Sakhalin – Coniacian ammonites from Sakhalin were described by Yabe (1910), Vereschagin *et al.* (1965), Matsumoto (1954a, 1991a, b, 1995), Okamoto (1989), Pokhialajnen (1985), Miroslubov *in* Poyarkova (1987), Alabushev & Wiedmann (1997), Yazykova (1992), Zonova *et al.* (1993), Zonova & Yazykova (1998) and Shigeta & Maeda (2005). The complex from Sakhalin is represented by 18 named species (plus five in open nomenclature), documenting 15 genera in eleven families. Assemblages include the phylloceratine *Hypophylloceras* (*Neophylloceras*) *ramosum*, the gaudryceratids *Anagaudryceras politissimum* (Kossmat), *Gaudryceras denseplicatum* and *G. tenuiliratum*, the tetragonitids *Tetragonites glabrus* and *T. epigonus* Kossmat, the binneyitid *Binneyites*(?) sp., the puzosiines *Jimboiceras mihoense* Matsumoto (= *Pachydesmoceras mihoense* in Matsu-

moto, 1988) and *Kitchinites japonica* Spath, the desmoceratines *Damesites damesi intermedius*, *D. ainuanus* (see Pl. 4, figs. 2-6), *D. aff. sugata* (Forbes) and *D. cf. sugata*, the pachydiscid *Menuites (Anapachydiscus) sutneri* (Yokoyama), the hourcquiine *Hourcquia pacifica* Matsumoto, the barroisiceratine *Forresteria (F.) alluaudi* Matsumoto, the peroniceratine *Peroniceras* sp., the nostoceratids *Nipponites* sp., *N. sachalinensis* and *N. bacchus* Matsumoto & Muramoto, the diplomoceratine *Scalarites mihoensis*, and the polyptychoceratine *Pseudoxybeloceras (P.) obstrictum* Jimbo, as well as the otoscapitines *Yezoites puerculus* and *Y. subplanus*.

Northeast Russia (Koryak Upland, Penzhyna Gulf coast, northwest Kamchatka) – Coniacian ammonites from northeast Russia are not diverse; previous workers (Vereschagin *et al.*, 1965; Yazykova, 1992; Alabushev & Wiedmann, 1997; Zonova & Yazykova, 1998) recorded eight named species, in six genera and five families. Assemblages are comprised of the phylloceratine *Hypophylloceras (Neophylloceras) ramosum*, the gaudryceratids *Gaudryceras denseplicatum* and *G. tenuiliratum*, the puzosiine *Kitchinites ishikawai* Jimbo, and the nostoceratids *Nipponites sachalinites* and *N. bacchus*, as well as the otoscapitines *Yezoites teshioensis*, *Y. derivatum* (Alabushev & Wiedmann) and *Scaphites talovkensis* Alabushev & Wiedmann. Alabushev & Wiedmann (1994a) described the two last-named species also from the Santonian/Campanian boundary interval from the Penzhyna Gulf coast (northwest Kamchatka), the first as a new genus and species, *Eorhaeboceras derivatum*. However, diagnostic features of the new genus are unclear; it appears to be synonymous with *Yezoites* (Wright *et al.*, 1996). The Santonian-Campanian age of the strata which yielded these species resulted from misidentifications, because faunas of Turonian-Coniacian date are known from nearby. For now, *Y. derivatum* and *S. talovkensis* are accepted, but they are assumed to be of latest Turonian-early Coniacian age and, as such, they would represent the youngest representatives of scaphitids in Russian Pacific regions. However, Misaki & Maeda (2009) noted that their research in the Toyajo Formation around Mt. Toyajo (Aridagawa area, Wakayama, southwest Japan) has shown that scaphitids ranged into the Campanian. Thus, this is another matter to be revised.

Santonian – Strata of this age occur in the Naiba River valley in the south and in the Orlovka River valley in the central part of the West Sakhalin Mountains; in addition, they are known from the Koryak Upland and Chukotka Peninsula. In total, the Santonian ammonite assemblage from the Russian Far East includes 41 named species (and three in open nomenclature), documenting 24 genera in ten families. Substage boundaries have not been established in detail because the respective index species are missing. The ammonite zonation is correlated with inoceramid and radiolarian schemes in both regions of Far East Russia and can be traced to Japan (Figs. 2-4), albeit without determination of the lower/upper Santonian boundary.

Sakhalin – Santonian ammonites (Pl. 5) from Sakhalin were recorded by Yabe (1903), Kawada (1929), Matsumoto & Obata (1955), Vereschagin *et al.* (1965), Matsumoto (1954a, 1955a, b, 1970b, 1995), Matsumoto *et al.* (1990a, b), Mirolubov in Poyarkova (1987), Maeda (1993), Wright *et al.* (1996), Alabushev & Wiedmann (1997), Yazykova (1992), Zonova *et al.* (1993), Shigeta (1989), Zonova & Yazykova (1998) and Shigeta & Maeda (2005). The complex from Sakhalin includes 36 species, plus one in open nomenclature, representing 23 genera in ten families. Faunas comprise the phyl-

loceratines *Hypophylloceras* (*Neophylloceras*) *ramosum* and *Phyllopachyceras forbesianum* (d'Orbigny), the gaudryceratids *Anagaudryceras yokoyamai* (Yabe), *Gaudryceras denseplicatum*, *G. tenuiliratum* and *Zelandites kawanoi* (Jimbo), the tetragonitids *Saghalinites saghalinensis* Shimizu, *Tetragonites glabrus*, *T. epigonus* and *T. popetensis* Yabe, the puzosinines *Kitchinites ishikawai* Jimbo (see Pl. 13, figs. 3-6) and *K. japonicus* Spath, the hauericeratine *Hauericeras angustum* Yabe, the desmoceratines *Damesites damesi intermedius*, *D. d. damesi* (Jimbo) and *D. sugata*, the kossmaticeratines *Yokoyamaoceras jimboi* Matsumoto and *Y. ishikawai* (Jimbo) (as recorded by Shimizu, 1935, but probably synonymous with *Kitchinites ishikawai*), the pachydiscids *Eupachydiscus haradai* Jimbo, *Menuites* (*M.*) *menu* Forbes, *M. (M.) naibutiensis* Matsumoto, *M. (M.) japonicus* Matsumoto and *M. (M.) cf. japonicus*, the mortoniceratine *Mortoniceras? kawasakii* Kawada, the texaninites *Texanites* (*Plesiotexanites*) *kawasakii* Kawada and *Protexanites* (*P.*) *bontanti shimizui* Matsumoto, as well as the nostoceratids *Nipponites bacchus*, *Hyphantoceras orientale* Yabe and *H.(?) heteromorphum* Matsumoto, the diplomoceratids *Neocrioceras spinigerum* (Jimbo) and *Diplomoceras notabile* Whiteaves, the polyptychoceratines *Pseudoxybeloceras* (*P.*) *obstrictum* Jimbo, *P. (P.) quadrinodosum* Jimbo, *Polyptychoceras* (*P.*) *pseudogaultinum* (Yokoyama), *P. (P.) sakhalinum* Alabushev & Wiedmann, *P. (Subptychoceras) yubarensis* (Yabe) and *P. (S.) vancouverense* (Whiteaves).

Mortoniceras kawasakii was recorded from the Santonian of Sakhalin by Kawada (1929); however, representatives of *Mortoniceras* are not known from post-Albian/lower Cenomanian strata elsewhere in the world. It seems that Kawada's specimen might be assigned to the subgenus *Mortoniceras* (*Submortoniceras*), but this needs to be determined.

Northeast Russia (Koryak Upland, Penzhyna Gulf coast, northwest Kamchatka) – Santonian ammonites from northeasterly regions (Liverovskaya, 1959; Vereschagin *et al.*, 1965; Terekhova, 1980; Alabushev & Wiedmann, 1994a, 1997; Yazykova, 1992) are represented by 13 named species (plus two in open nomenclature), representing eleven genera in nine families. Faunas include the phylloceratines *Hypophylloceras* (*Neophylloceras*) *ramosum* and *Phyllopachyceras ezoense* (Yokoyama), the gaudryceratids *Gaudryceras denseplicatum* and *G. tenuiliratum*, the tetragonitid *Pseudophyllites indra* (Forbes), the puzosinine *Kitchinites ishikawai* (= *Puzosia* aff. *ishikawai sensu* Liverovskaya, 1959; *Neopuzosia ishikawai sensu* Alabushev & Wiedmann, 1994a), the kossmaticeratines *Yokoyamaoceras venustum* Terekhova and *Y. kotoi* (Jimbo), the pachydiscids *Eupachydiscus haradai* and *Menuites* (*M.*) cf. *menu*, the texaninites *Protexanites fukazawai* Yabe & Shimizu and *P.* aff. *shoshonensis* (Meek), the nostoceratid *Nipponites bacchus*, and the polyptychoceratines *Polyptychoceras* (*P.*) *pseudogaultinum*, *P. (Subptychoceras) yubarensis* and *P. (S.) vancouverense*.

Campanian – Deposits of this age occur throughout the West Sakhalin Mountains, and locally in the East Sakhalin Mountains and in Shikotan (southern Kuril Islands), as well as along the Penzhyna Gulf Coast, in the Koryak Upland and in Chukotka Peninsula. In total, the Campanian ammonite assemblage from the Russian Far East comprises eight families, 29 genera and 59 named species (Pls. 6-11), of which ten are in open nomenclature. Five ammonite zones characterise Campanian sedimentary rocks in Sakhalin (Fig. 2). They match five ammonite zones in northeast Russia (Fig. 3) and ammonite zonal schemes in Japan (Fig. 4). A detailed subdivision of the Campanian

was also provided by inoceramids, both in Far East Russia (Fig. 3) and Japan. A comparatively detailed scheme was also proposed for Sakhalin and northeasterly regions on the basis of radiolarians (Figs. 2, 3).

Sakhalin – Campanian ammonites from Sakhalin were recorded by Yabe (1909), Matsumoto (1938, 1942, 1943, 1954b, 1995), Matsumoto & Obata (1955), Vereschagin *et al.* (1965), Zhuravlev (1969b), Yu.D. Zakharov *et al.* (1984), Mirolubov *in* Poyarkova (1987), Alabushev & Wiedmann (1997), Yazykova (1992), Yazikova (1994), Zonova *et al.* (1993) and Shigeta & Maeda (2005). The complex from Sakhalin comprises 54 species, inclusive of eight in open nomenclature, documenting 27 genera in eight families. Assemblages comprise the phylloceratines *Hypophylloceras* (*Neophylloceras*) *ramosum*, *H. (N.) nera* (Forbes), *Phyllopachyceras forbesianum* and *Ph. ezoense*, the gaudryceratids *Anagaudryceras yokoyamai* (Yabe), *A. nanum* Matsumoto, *Gaudryceras tenuiliratum*, *G. mamiyai* Matsumoto & Miyauchi, *G. cf. mamiyai*, *G. striatum* (Jimbo), *G. crasscostatum* (Jimbo) and *Zelandites kawanoi* (Jimbo), the tetragonitines *Tetragonites glabrus*, *T. epigonus*, *T. pope-tensis*, *Saghalinites teshioensis* Matsumoto, *S. saghalinensis* Shimizu and *Pseudophyllites indra*, the puzosiines *Kitchinites ishikawai*, *K. japonicus* and *Puzosia* (*Mesopuzosia*) *densicostata* Matsumoto, the desmoceratines *Damesites d. damesi*, *D. sugata*, *D. cf. sugata*, *D. semicostatus* Matsumoto and *Desmophyllites diphylloides* (Forbes) (see Pl. 9, figs. 4-6), the hauericeratines *Hauericeras angustum* and *H. cf. angustum*, the kossmaticeratine *Yokoyamaoceras ishikawai* (Jimbo) (a questionable species; see above) and the pachydiscids *Canadoceras multicostatum* Matsumoto, *C. kossmati* Matsumoto, *C. mysticum* Matsumoto, *C. yokoyamai* Jimbo (see Pl. 8, figs. 1-3), *Menuites cf. menu* (see Pl. 10, figs. 1, 2), *M. japonicus* Matsumoto, *M. cf. japonicus*, *M. naibutiensis*, *M. (Neopachydiscus) naumanni* (Yokoyama) (see Pl. 5, figs. 1-8; Pl. 7, figs. 1-4), *M. (Anapachydiscus) fascicostatus* (Yabe) (see Pl. 10, figs. 3-5), *M. (A.) arrialoorensis* (Stoliczka), *Eupachydiscus haradai* Jimbo (see Pl. 6, figs. 1-7), *Urakawites rotalinoides* (Yabe) and *Pachydiscus cf. awajiensis* Morozumi (see Pl. 11, figs. 1-6). In addition, heteromorphs comprise the diplomoceratines *Neancyloceras* spp., *Neocrioceras* sp., *Neo. spinigerum*, *Diplomoceras notabile* and *D. cf. notabile*, and the polyptychoceratines *Pseudoxybeloceras* (*Schlueterella*) *kawadai* Matsumoto & Miyauchi, *P. (S.)* sp., *P. (Pseudoxybeloceras) quadrinodosum* Jimbo, *Polyptychoceras* (*Po.*) *lineatum* (Gabb), *Po. (Subptychoceras) yubarensis* (Yabe), *Po. (S.) vancouverense* (Whiteaves) and *Ryugasella ryugasense* Wright & Matsumoto, as well as the baculitids *Baculites* sp., *B. occidentalis* Meek and *B. rex* Anderson, as mentioned by Mirolubov *in* Poyarkova (1987). T.D. Zonova (pers. comm., 2008) has noted a mass occurrence of *Baculites* sp. in Member 2 of the Krasnoyarka Formation, of latest late Campanian age (*Canadoceras multicostatum* Zone). Of the above taxa, *Neancyloceras pseudoarmatum* (Schlüter) was noted by Vereschagin *et al.* (1965) and Yu.D. Zakharov *et al.* (1984). However, it is my opinion that this material in fact represents two distinct species. Klinger *et al.* (2007) likened the European *Schlueterella* aff. *pseudoarmatum* to the Japanese *S. kawadai*; these may be sibling species. As far as baculitids are concerned, Zhuravlev (1969b) described *Baculites*(?) sp., which was subsequently reidentified by Grabovskaya (*in* Yu.D. Zakharov *et al.*, 1984) as *B. cf. chicoensis* Trask. That author also erected a new species, *B. zhuravlevi*. However, the preservation of Zhuravlev's material is insufficient to allow specific identification, although he noted special features of the suture line. In short, this material also needs to be revised.

Northeast Russia (Koryak Upland, Penzhyna Gulf coast, northwest Kamchatka) – Campa-

nian ammonites from northeasterly regions (Liverovskaya, 1959; Vereschagin *et al.*, 1965; Terekhova, 1980; Alabushev & Wiedmann, 1994a, 1997; Yazykova, 1992) involve 12 named species (plus two in open nomenclature) of 11 genera in eight families. Faunas comprise the phylloceratines *Hypophylloceras* (*Neophylloceras*) *ramosum* and *Phyllophyceras* *ezoense* (see Pl. 10, figs. 6-8), the gaudryceratid *Gaudryceras* *tenuiliratum*, the tetragonitines *Tetragonites* *epigonus*, *T. crassus* (Jimbo) and *Pseudophyllites* *indra* (see Pl. 9, figs. 1-3), the puzosiine *Kitchinites* *ishikawai*, the kossmaticeratines *Yokoyamaoceras* *venustum* and *Y. kotoi*, the pachydiscid *Menuites* (*Neopachydiscus*) *naumanni*, the texanitines *Protexanites* *fukazawai* Yabe & Shimizu and *P. aff. shoshonensis* (Meek), the diplomoceratines *Neancyloceras* sp. and *Diplomoceras* *notabile*, and the polyptychoceratines *Polyptychoceras* (*P.*) *pseudogaultinum* (Yokoyama), *P. (Subptychoceras)* *yubareense* and *P. (S.) vancouverense*, as well as the baculitids *Baculites* *nitidus*, *B. singularis* and *B. sibiricus*, described by Glazunova (1955) from western Siberia (probably Enisej River Valley).

Maastrichtian – Strata of this age are known from Kriljon Peninsula in the south of the West Sakhalin Mountains and also from the central part (Pugachevka and Makarova river valleys and elsewhere), locally in the East Sakhalin Mountains and Shikotan Island (southern Kuril Islands), as well as along the Penzhyna Gulf Coast, the Koryak Upland and Chukotka Peninsula. In total, the Maastrichtian ammonite assemblage (Pl. 12; Pl. 13, figs. 1, 2) from the Russian Far East documents seven families, 17 genera, and 34 named species, and a further eight in open nomenclature. Three ammonite zones were established in Sakhalin (including two which have been recorded from Shikotan), traced to northeast Russia and correlated with the Japanese scheme. They also correspond well to inoceramid and radiolarian subdivisions (Figs. 2-4).

Sakhalin and Shikotan – Maastrichtian ammonites from Sakhalin were described previously by Yabe & Shimizu (1924a, b), Matsumoto (1936, 1954b, 1984), Vereschagin *et al.* (1965), Matsumoto *et al.* (1979), Morozumi (1985), Yu.D. Zakharov *et al.* (1984), Mirolov in Poyarkova (1987), Alabushev & Wiedmann (1997), Yazykova (1992), Yazykova (1994), Zonova *et al.* (1993), Shigeta (1993), Shigeta *et al.* (1999b) and Shigeta & Maeda (2005). Finds of Maastrichtian ammonites from Shikotan Island were briefly mentioned by Zonova & Yazykova (1994), Yazykova (1994) and Yazykova (2004); a detailed description and reinterpretation are under way (Jagt-Yazykova, research in progress). The complex from Sakhalin and Shikotan comprises 33 species, inclusive of seven in open nomenclature, documenting 15 genera in six families, as follows: the phylloceratines *Hypophylloceras* (*Neophylloceras*) *ramosum*, *H. (N.) hetonaiense* (Matsumoto), *H. (N.) victriense* Shigeta & Maeda, *H. (N.) nera* and *H. (N.) cf. nera* (= *N. aff. surya* (Forbes) *sensu* Yu.D. Zakharov *et al.*, 1984), the gaudryceratids *Anagaudryceras* *matsumotoi* Morozumi, *A. seymouriense* Macellari, *Gaudryceras* *venustum* Matsumoto, *G. denmanense* Whiteaves, *G. tombetsense* Matsumoto, *G. cf. tombetsense*, *G. hamanakense* Matsumoto, *G. makarovense* Shigeta & Maeda, *Zelandites* *japonicus* Matsumoto and *Z. varuna* Forbes, and the tetragonitines *Tetragonites* *popetensis* and *Pseudophyllites* *indra*. *Saghalinites* cf. *cala* (Forbes) was recorded by Yu. D. Zakharov *et al.* (1984) from early Maastrichtian deposits in Sakhalin. The specimen was not figured, which is why it cannot be determined whether or not this did indeed represent *S. cala* or rather one of the endemic species, *S. teshoensis* or *S. saghalinensis*. Moreover, the specimen might equally well have come from a latest Campanian level, because the provenance is not indicated clearly. In addition, there are

records of the kossmaticeratine *Brahmaites* (*Subbrahmaites*) *sachalinensis* Yabe & Shimizu, the pachydiscids *Pachydiscus* (*P.*) *cf. kobayashi* Shimizu, *P. (P.) subcompressus* Matsumoto (see Pl. 13, figs. 1, 2), *P. (P.) soyaensis* Matsumoto & Miyachi, *P. (P.) flexuosus* Matsumoto, *P. (Neodesmoceras) japonicus* Matsumoto (see Pl. 12), *P. (N.) gracilis* Matsumoto, *Canadoceras multicoostatatum* Matsumoto, *C. kossmati*, *Patagiosites cf. alaskensis* Jones and *Pseudomenuites* sp. (see by Shigeta *et al.*, 1999b), and the diplomoceratines *Neancyloceras pseudoarmatum*, *Diplomoceras notabile*, *D. cf. notabile* and *Glyptoxoceras* sp. As far as species of *Gaudryceras* are concerned, it would seem that *G. tombetsense*, *G. hamanakense* and *G. makarovense* are conspecific.

Northeast Russia (Koryak Upland, Penzhyna Gulf coast, northwest Kamchatka) – Maastrichtian ammonites from northeasterly regions (Vereschagin *et al.*, 1965; Terekhova, 1980; Alabushev & Wiedmann, 1994a, 1997; Yazykova, 1992; Yazikova, 1994) involve ten named species (plus two in open nomenclature), representing nine genera in six families. Assemblages comprise the phylloceratines *Hypophylloceras* (*Neophylloceras*) *ramosum*, *H. (N.) hetonaiense* and *Phyllopachyceras ezoense*, the gaudryceratid *Zelandites varuna*, the tetragonitine *Pseudophyllites indra*, the kossmaticeratine *Brahmaites* (*Subbrahmaites*) *sachalinensis* (= *B. (B.) brahma*, *sensu* Vereschagin *et al.*, 1965), the pachydiscids *Pachydiscus* (*P.*) *subcompressus*, *P. (P.) flexuosus*, *P. (Neodesmoceras) japonicus*, *P. (N.) gracilis* and *Patagiosites alaskensis*, the nostoceratid *Nostoceras* (*Didymoceras*) *cf. californicum* Anderson, and the diplomoceratine *Diplomoceras* sp. Alabushev & Wiedmann (1997) described a new species, *Pachydiscus* (*P.*) *denseplicatus*, but the material referred to is rather a mixture of *P. (P.) flexuosus* and *P. (N.) gracilis*.

Note that Vereschagin *et al.* (1965) described *Pachydiscus* aff. *gollevillensis* d'Orbigny and *P. neubergicus* (von Hauer) from late Maastrichtian deposits of the Penzhyna Gulf coast, northwest Kamchatka. Subsequently, Yu.D. Zakharov *et al.* (1984) recorded *P. cf. gollevillensis* and *P. cf. neubergicus* from the late Maastrichtian of Sakhalin, but did not figure the material on which these records were based. In line with Vereschagin's interpretations, Yazikova (1994) also recorded two specimens from late Maastrichtian strata in Sakhalin as *P. (P.) gollevillensis* and *P. (P.) neubergicus*. Recently (courtesy of Dr Herbert Summesberger, Naturhistorisches Museum Wien), I have obtained a cast of the holotype of the latter species, and this allows the conclusion that material was misidentified by Vereschagin *et al.* (1965) and Yazikova (1994) alike. Currently, there are also doubts over the record of *P. (P.) gollevillensis*. All specimens from Sakhalin and Penzhyna which have previously been identified either as *P. (P.) gollevillensis* or *P. (P.) neubergicus* are thus in need of revision. Some probably belong to the endemic *P. (P.) kobayashii* (Shimizu), while others resemble specimens described by Atabekian & Akopian (1969) as *P. (P.) gollevillensis armenicus* and *P. (P.) egertoni jacquoti* from the Maastrichtian of Armenia.

Ammonite evolution, bio-events and links with lithofacies, phylogeny and homoeomorphy

Introduction – The present section focuses on the evolutionary dynamics of Pacific ammonites during the mid- and Late Cretaceous (Fig. 5), as well as on palaeobiological aspects and links with lithofacies types (Fig. 6). Some phylogenetic trends (Figs. 7-14) are outlined and several examples of homoeomorphy identified. Amongst the main

results presented below is that there was a positive trend in ammonite evolution prior to their demise (Fig. 5). The dynamics of development of the seven most speciose families illustrate that at least three families reached their maximum taxonomic diversity during the Maastrichtian (Fig. 7). Palaeoecological patterns for Sakhalin and adjacent sections are based on descriptions of ammonite shell morphology by other workers such as Tanabe *et al.* (1978), Batt (1989, 1991, 1993), Westermann (1990, 1996), Tsujita & Westermann (1998) and Moriya *et al.* (2003), as well as on links with lithofacies types (see Kennedy & Cobban, 1976; Jacobs, 1992; Jacobs *et al.*, 1994).

I support the suggestion that unrelated taxa with similar life habits and occurrences tend to be of the comparable morphotype, while species with a wide range of intraspecific variation, either as adult or during ontogeny, have shell features which reflect diverse modes of life or environments inhabited. Thus, morphotypes, rather than taxonomic designation, were used because relationships between shell shapes and

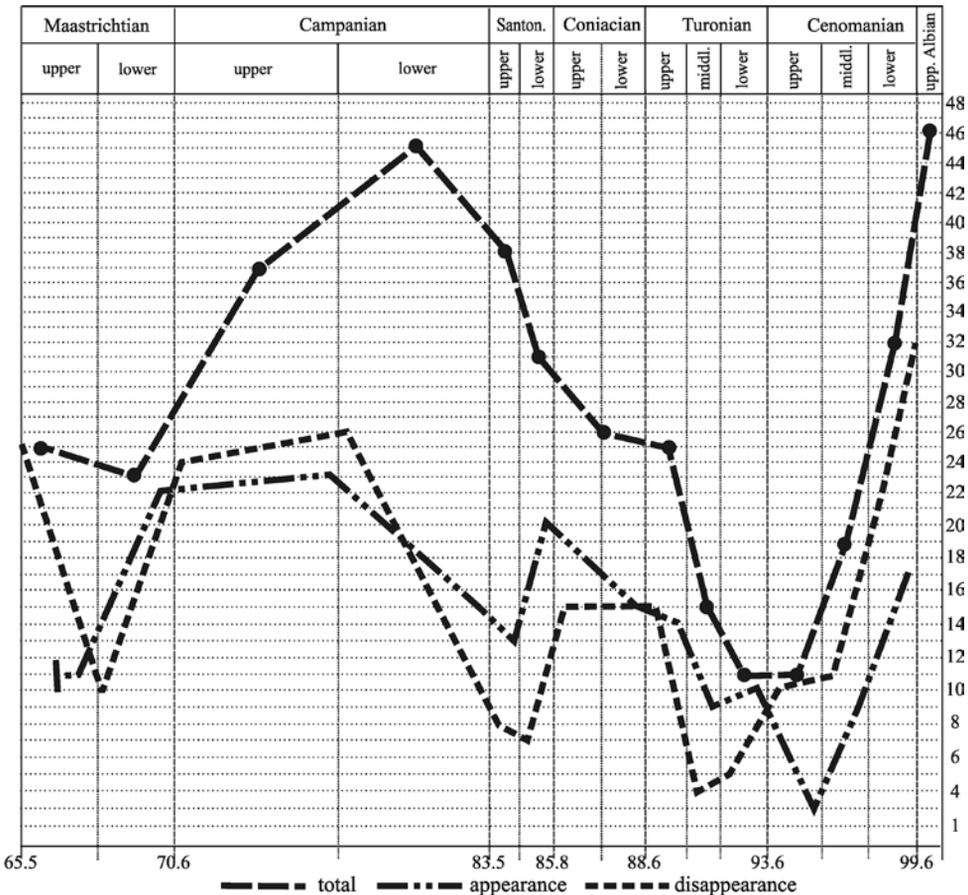


Fig. 5. Changes in mid- to Late Cretaceous ammonite diversity in Far East Russia: disappearance, appearance and total number of species recorded.

Russian Pacific genera	upper Albian	lower Cenomanian	midd. Cenomanian	upper Cenomanian	lower Turonian	middle Turonian	upper Turonian	Coniacian	lower Santonian	upper Santonian	lower Campanian	upper Campanian	low. Maastrichtian	upp. Maastrichtian
1. <i>Phyllopachyceras</i>	■								■	■	■	■	○	○
2. <i>Hypophylloceras</i> (<i>Neophylloceras</i>)	○	○	○			■	■	■	■	■	■	■	●	●
3. <i>Protetragonites</i>	○													
4. <i>Eogaudryceras</i> (<i>Eotetragonites</i>)	○													
5. <i>Anagaudryceras</i>	○	■	■	■	■	■	■	■		■	■		■	■
6. <i>Gaudryceras</i>	○	■	■	■	●	●	●	●	●	●	●	●	●	●
7. <i>Zelandites</i>		○	○	○	○					○	○		■	●
8. <i>Tetragonites</i>					○	○	○	○	●	●	●	●	○	○
9. <i>Saghalinites</i>									○	○		○		
10. <i>Pseudophyllites</i>									○	○	○	○	○	
11. <i>Parajaubertella</i>		■												
12. <i>Binneyites</i>								○						
13. <i>Puzosia</i> (<i>P.</i>)	■	■												
14. <i>Puzosia</i> (<i>Mesopuzosia</i>)						○	○		○	○	○	○		
15. <i>Parapuzosia</i> (<i>Austiniceras</i>)			■	■										
16. <i>Jimboiceras</i>					●	●	●	●						
17. <i>Pachydesmoceras</i>							■							
18. <i>Kitchinites</i>								■	■	■	■			
19. <i>Parasilesites</i>	■													
20. <i>Beudanticeras</i> (<i>B.</i>)	○													
21. <i>B.</i> (<i>Grantziceras</i>)	○													
22. <i>Desmoceras</i> s.str.		○												
23. <i>D.</i> (<i>Pseudouhligella</i>)	○	●	○	○										
24. <i>Tragodesmocerooides</i>							■							
25. <i>Damesites</i>							○	●	●	■	●	■		
26. <i>Desmophyllites</i>											■	■		
27. <i>Hauericeras</i>										○	■			
28. <i>Marshallites</i>	●	●	○	○	○									
29. <i>Holcodiscoides</i>	○													
30. <i>Eogunnarites</i>	■	○	○											

abundant (> 4) ● common (2 - 4) ■ rare (1-2 specimens) ○

Fig. 6. The stratigraphical distribution of mid- and Late Cretaceous ammonite genera and their abundance in sections along the Russian Pacific coast (in three parts).

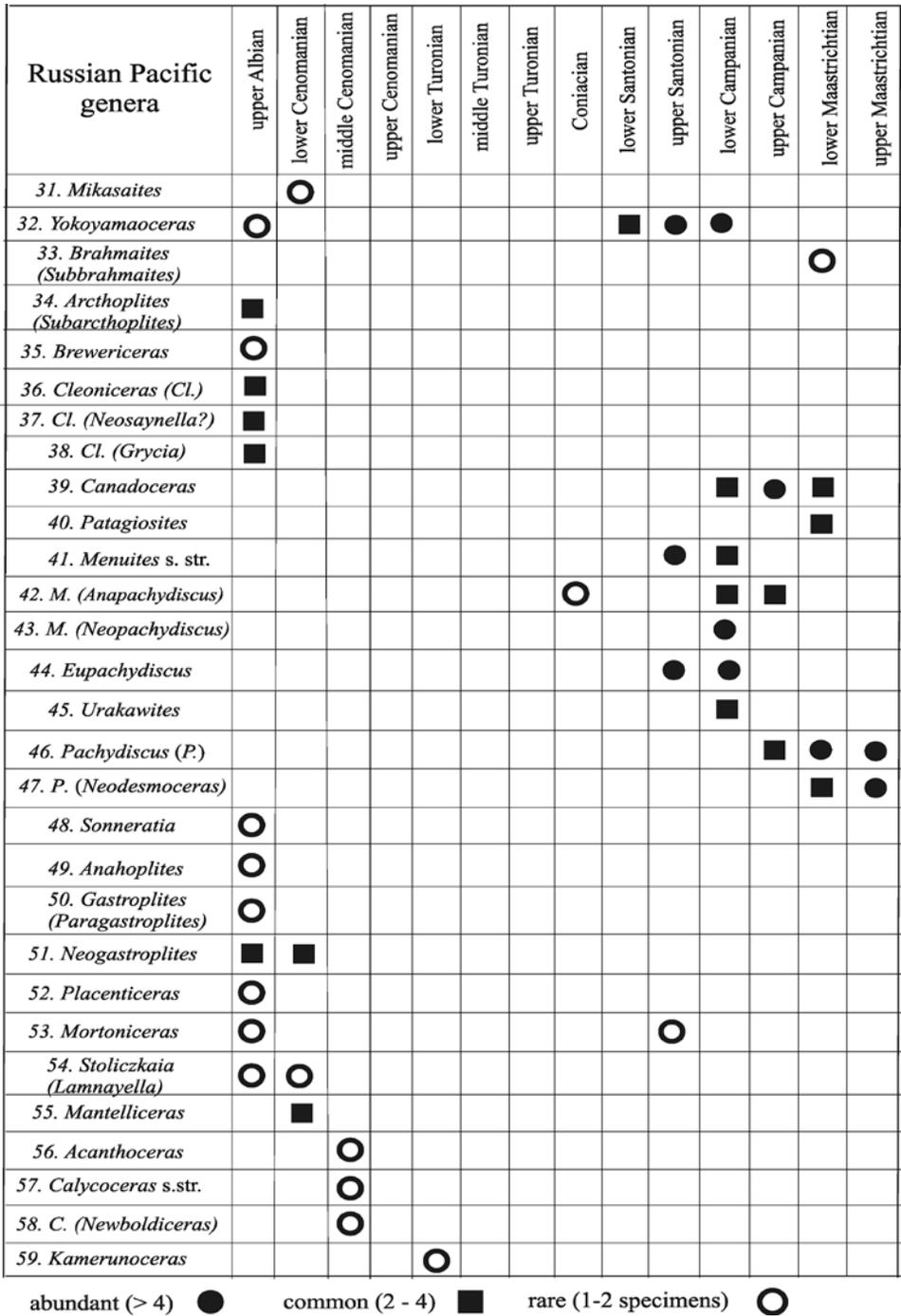


Fig. 6. Part II.

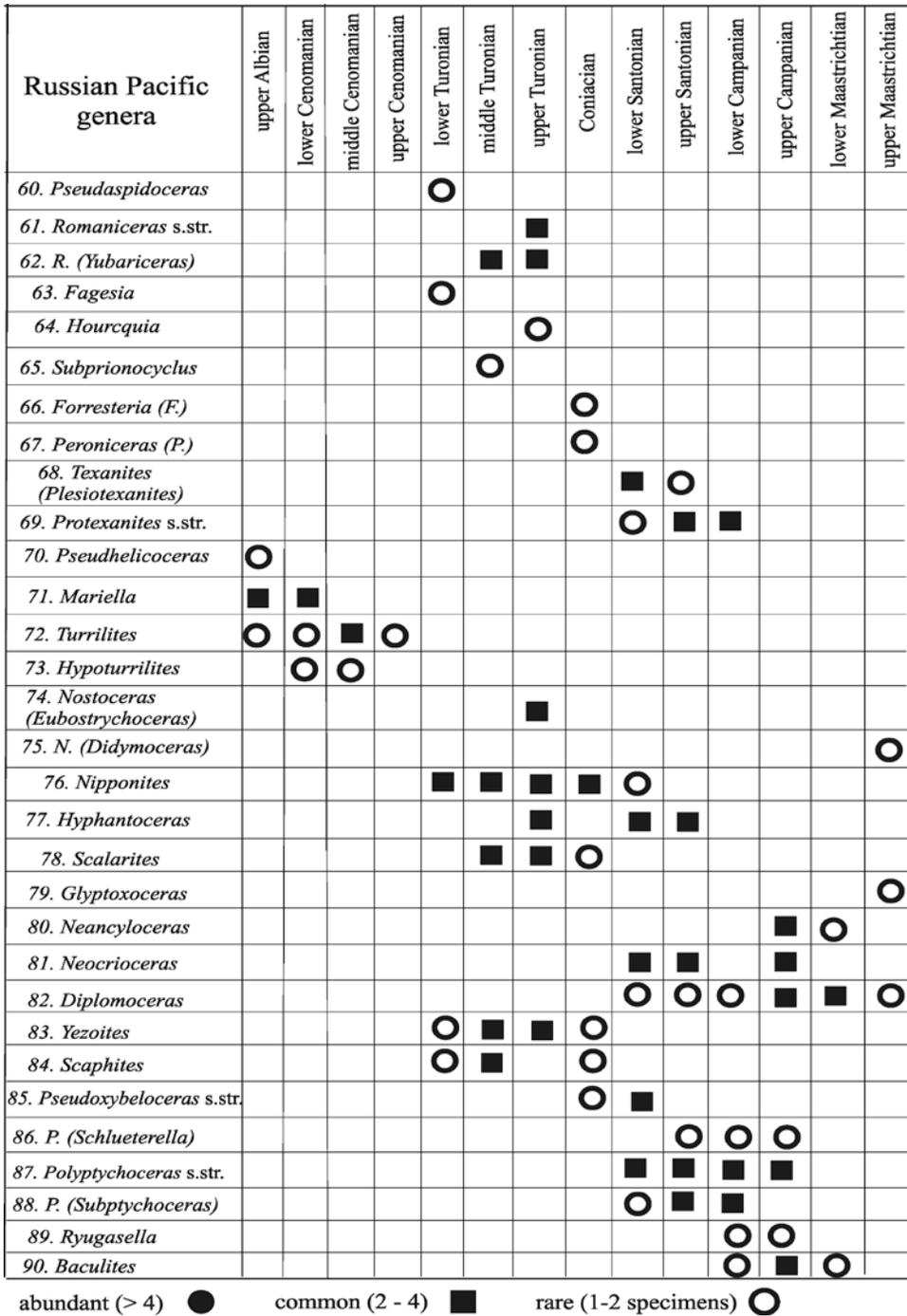


Fig. 6. Part III.

environment appear to be species independent (see Batt, 1993, p. 50, and references therein). Certainly, all results are based on the study of adult individuals; larvae or juvenile forms were rather nekto planktonic in the photic and neritic shallow zones (50–250 m) (Westermann, 1989, 1996). Changes in ammonite diversity, viz. disappearance (extinction or emigration), appearance (origination or immigration) and total number of species presented in Figure 5 constitute the basis for the identification of the main bio-events.

In Yazykova (2004), an attempt was made to count the so-called total extinction and origination rates following Raup & Sepkoski (1984). However, now I prefer to refrain from showing this herein because, according to Boucot (2006), the extinction rate represents a sampling artifact. In cases when bio-events are discussed, it should be borne in mind that some species might, in fact, have disappeared from a certain section, but that they could also not have been found yet or had migrated to adjacent areas because of some ecological changes in the basin studied. Similarly, this is relevant when discussing the origination of species. In some cases this results from migration, some taphonomic processes or these taxa have just not been recognised yet and additional field work is needed. In short, the main problems discussed in this section are the interrelationship between evolution of ammonites and environmental changes in palaeobasins along the Russian Pacific coast, local bio-events, links with lithofacies types and hypothetical phylogenetic connections, and some examples of homoeomorphy.

Palaeobiological aspects, evolution and bio-events, links with lithofacies types – First, as based on my own observations, there is the notion that facies control on ammonite distribution in the sections studied was minimal. It should be borne in mind that, as noted above, the sections studied display a rather monotonous lithology of intercalated mudstones, siltstones and sandstones with tuffaceous layers and marl concretions, which have yielded most of the fossils collected. In Figure 6, the distribution of representatives of all ammonite genera identified in the Russian Pacific is shown stage by stage, as based on the number of specimens of each genus. So, most genera and subgenera (for example, *Anagaudryceras*, *Gaudryceras*, *Hypophylloceras*, *P. (Pachydiscus)*, *Hypophylloceras* (*Neophylloceras*) and others) occur in siltstones as well as in mudstones, are rarer in sand-rich facies, but are preserved mainly in carbonate concretions. However, I agree with Kennedy & Cobban (1976, p. 44), who opined that strong facies controls suggested a benthic habit and limited post-mortem drift as factors that limit distribution. This is an additional factor which explains the high degree of endemism and provincialism of Pacific faunas in general. Genera such as *Nipponites* or *Scalarites* mostly occur in mudstones. Matsumoto & Obata (1963) studied links between sedimentary facies and the occurrence of baculitids in Japan; their results show that baculitids are much rarer in sandy than in mud-rich facies, but are present in the former anyway. In Sakhalin this picture differs even more widely. Baculitids are rare in early Campanian mudstones, but common in late Campanian and early Maastrichtian sandy facies. This suggests that nektonic groups are indeed facies independent.

Late Albian – Strata of this age occur in all regions of the Russian Pacific studied, that is, in southern Sakhalin, Sikhote Alin and Priamurye, as well as in the northeast. In Sakhalin, the comparatively low-diversity ammonite assemblage (see above) is characterised mostly by ornate forms such as the kossmaticeratid *Marshallites* and the hoplitid

Anahoplites, in addition to less ornate and smooth shell forms amongst desmoceratids (*D. (Desmoceras)*, *D. (Pseudouhligella)* and *Puzosia*) and cleoniceratids (*Brewericeras* and *Cleoniceras (Neosaynella?)*), as well as a few heteromorphs such as the turrilitid *Pseud-helicoceras*. According to Tanabe *et al.* (1978), such a combination of morphotype groups would indicate sublittoral environments along the continental slope in an offshore habitat. Westermann (1996) proposed that the well-documented neritic-oceanic gradient was paralleled by a succession of ammonoid biofacies, from shallow to deep with indication of relative abundance. In light of this interpretation, the late Albian ammonoid biofacies in Sakhalin comprised platyconic (*Marshallites*), discoconic (Desmoceratidae) and oxyconic (*Cleoniceras (Neosaynella)*, *Brewericeras* and *Anahoplites*) morphogroups (*sensu* Westermann, 1996), which, according to Jacobs (1992), had the best shape for swimming at higher velocities and belonged to planktonic (drifters and short-term vertical migrants) and nektonic groups (Westermann, 1996, p. 611, fig. 1). Moreover, the few heteromorphs mentioned above belong to the torticonic morphogroup and include short-term vertical migrants at depths of 100-150 m in the distal shelf and upper slope, but they might also have drifted post-mortem into the nearshore settings. However, hypotheses put forward by Moriya *et al.* (2003) are also significant here, in that some ammonites could have undertaken near-bottom migration from offshore to onshore habitats. Most late Albian ammonite taxa here are migrants from Tethyan and Boreal regions as described below. In addition, even benthos is represented by some non-endemic taxa such as the inoceramids *Inoceramus anglicus* Woods (Zonova *in* Poyarkova, 1987; Zonova *et al.*, 1993) and *I. aff. bohemicus* Leonhard (Matsumoto, 1942, 1943), together with endemic inoceramid species. Non-inoceramid bivalves and rare thermophilic gastropods have also been recorded; these were commoner in the central Sakhalin basin where ammonites have not been found yet. These sections are characterised by shallower-water, sandy facies with high amounts of detritic organic material as well as benthic *Orbitolina aff. shikokuense* Jabe & Hanz and other foraminifera usually indicative of shallow, warm waters (Turenko *in* Poyarkova, 1987). Planktonic foraminifera are extremely rare along the Russian Pacific coast and also in Japan. So far, no satisfactory explanation for this has been offered. Representatives of this group are closely linked with lithofacies and, in general, rarely appear in mudstones and siltstones. Perhaps too strong currents which occurred more often in the Panthalassic Ocean than in the Tethyan caused this, or yet unknown factors of temperature, salinity or bathymetry. Thus, late Albian sedimentary rocks in Sakhalin are characterised by monotonous sequences of deep-water mudstones and siltstones interbedded with sandstones and rare carbonate concretions yielding macrofossils (total thickness > 800 m), documenting an extremely high depositional rate (~ 175-180 m/myr; see Yazykova, 2004). These environments, from the open continental shelf to the upper continental slope, should be characterised by comparatively regular changes amongst factors noted and by high energy (agitation). Probably, planktonic foraminifera preferred quiet waters with stable environmental conditions.

The comparatively shallow Early Cretaceous basins of central northeast Russia were inhabited by numerous representatives of different bivalve groups (for example, Aucellidae, Inoceramidae, Pectinidae and others) and some brachiopods (Vereschagin *et al.*, 1965). In contrast to the numerous bivalves, ammonites are rather rare. They are represented by predominant trachyostracans (*sensu* Westermann, 1996), that is, costate

spherocones to planorbicones, with quadrate-rectangular whorl sections (*Phyllopachyceras*, *Sonneratia*, *Mortoniceras*, *Gastroplites* (*Paragastroplites*) and *Neogastroplites*), quasi-planktonic, costate platycones (nekctic *Gaudryceras*, planktonic *Marshallites* and *Holcodiscoides*) and torticonic heteromorphs (*Pseudhelicoceras*, *Turrilites* and *Mariella*) which were nektobenthic (Batt, 1989, 1993), pelagic or demersal vertical migrants (Westermann, 1996); rare leiostracans and mostly smooth oxycones (*C. (Cleoniceras)*, *C. (Grycia)* and *Proplacenticerias*) were mobile swimmers in offshore settings. Most oxycones were restricted to areas shallower than 40-50 m (Scott, 1940; Westermann, 1990; Batt, 1993). Thus, such ammonite biofacies, inclusive also of numerous bivalves and some brachiopods, point to sublittoral shelves of up to 100-150 m in depth, nearshore marine facies according to Tanabe *et al.* (1978). Sandy shallow facies with numerous conglomerates and tuffaceous layers (Zonova, 2004) support this environmental interpretation.

The diversity of early Albian assemblages from Primorye and Sikhote Alin gradually increases, as does that in northeasterly regions. The southern end of the vast Russian Pacific area was also inhabited by bivalves (genera *Aucellina*, *Pleuromya*, *Tancredia*, *Entolium*, *Exogyra* and the first genuine *Inoceramus*; see Krymholz, 1938; Zonova, 1982; Zonova in Sey *et al.*, 2004), which were commoner than ammonites. Recently, a European cirripede, *Pycnolepas* aff. *rigida* (Sowerby), was published from here (Jagt *et al.*, 2007). In general, the taxonomic composition represents some kind of admixture with taxa known from Sakhalin and northeasterly regions, as well as typically Tethyan forms. However, most taxa are left in open nomenclature, which makes the situation even more complicated. In previous works, a few explanations have been offered. First, such a palaeobasin could have come into existence as a result of maximum flooding and a lot of forms could have migrated via the Arctic or via Tethys into the northern Pacific (dispersal); secondly, those forms could be seen as vicariant species (Yazykova, 2001; Zonova & Yazykova, 2000, 2001, 2004; Jagt *et al.*, 2007). Certainly, to decide whether or not the present material represents a distinct species, more specimens are needed from Sikhote Alin, Primorye and Priamurye.

The Albian ammonite assemblage is represented here by spherococone *Sonneratia* and *Phyllopachyceras*, quasi-planktonic, that is, near-bottom migratory forms (Moriya *et al.*, 2003); planorbiconic to platyconic Gaudryceratidae, Kossmaticeratidae and Lytoceratidae; leiostracans with discocones such as *P. (Puzosia)*, *Desmoceras (Pseudouhligella)*, *Parasilesites* and *Beudanticeras*; oxyconic *Cleoniceras* and *Arthoplites (Subarthoplites)*; and a rare torticone heteromorph, *Mariella*. Based on such ammonite biofacies with representatives from all morphogroups, and taking into account bivalve faunas and cirripede records, these could be seen to represent the sublittoral continental shelf of a marginal sea (100-150 m depth), comparatively warm (palaeotemperature data by Yu. D. Zakharov *et al.*, 2005, show seasonal changes from 12.5-22.4°C, supported by thermophilic forms and data based on continental floras; Chumakov *et al.*, 1995; Skelton, 2003), well oxygenated and weakly agitated, because of low percentages of strongly ornamented forms, both amongst ammonites and bivalves.

In conclusion, during the Cretaceous the territory of Far East Russia belonged to a marginal shelf continental sea and during the Albian maximum flooding occurred as a result of global transgression. The deepest basin is found in Sakhalin, while northeasterly regions were characterised by warm, well-oxygenated waters. The Sikhote Alin palaeobasin appears to have been some kind of comparatively shallow, well-oxygenat-

ed bay somewhere between Sakhalin and regions in the north. This could explain the mixed character of taxonomic composition and the absence or very low numbers of juvenile forms, because most forms probably appeared here after long-distance transport with favourable currents via the Arctic and/or via Tethys, that is, successful dispersal, but without further speciation.

In comparison to northeast Russia and Sikhote Alin, probably poorly oxygenated, yet not absolutely anoxic, conditions occurred in southern Sakhalin. This is suggested by the low diversity amongst ammonite associations collected here from late Albian dark grey mudstones and sandy mudstones with rare carbonate concretions, and ammonite shell morphotypes. A well-oxygenated water column and sea floor, usually characterised by pelagic and nektobenthic forms, was disturbed by upward migration of anoxic conditions. This eliminated nektobenthic ammonites and later, continued an upward migration to within 100 m of the surface, eliminated middle-depth pelagic forms, such as torticonic heteromorphs (Batt, 1993). As noted above, the late Albian ammonite complex from Sakhalin consists mainly of planktonic (drifters and short-term vertical migrant), nektic ammonites and heteromorphs being rare, which means that the water column and bottom probably were low in oxygen, yet not anoxic. Overall, the diversity amongst Russian Pacific Cretaceous ammonites is highest during the late Albian (Fig. 5). The greatest taxonomic diversity is noted amongst desmoceratids and kossmaticeratids (Fig. 7). The palaeobiogeographical aspects and taxonomically mixed character of all described faunal assemblages could be interpreted as the migration bio-event; this issue will be discussed further below.

Cenomanian – The Early/Late Cretaceous boundary is marked by a global regression, as a result of tectonic reconstruction and concomitant abrupt environmental changes. Almost all Albian ammonite forms became extinct in the Arctic and northwest

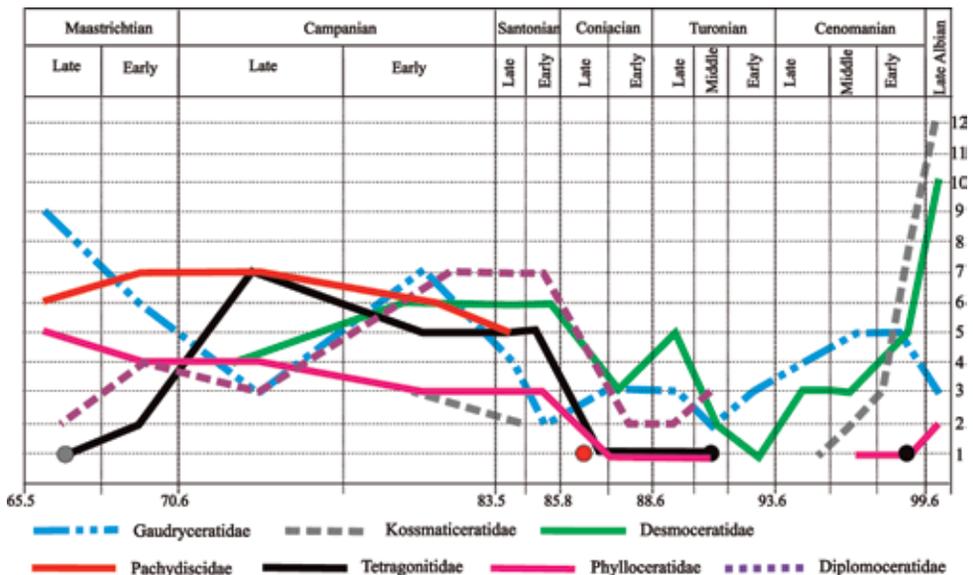


Fig. 7. Changes in the number of mid-to Late Cretaceous ammonite species from Far East Russia, arranged in the seven most speciose families.

Pacific provinces, except for a few species, which survived these crises. However, these survival taxa are failed crisis progenitor species (Kauffman & Erwin, 1995; Harries & Little, 1999), which did not appear until the latest Albian, and already were better adapted to changing conditions. Recently, Moriya *et al.* (2003) proposed that extinction and diversification of ammonites could have been achieved not only by evolution of physiological tolerance of ambient conditions, but also by a loss of habitat followed by acquisition of a new habitat and/or a new mode of life. So, the changes which took place during latest Albian through earliest Cenomanian could be determined as a global turnover bio-event.

The most drastic changes occurred in the Sikhote Alin basin. During the early Cenomanian, this basin became shallower and gradually disappeared as a result of plate tectonic reconstructions and high volcanic activity which started in the mid-Albian (Kirillova *et al.*, 2000). Along the continental margin a giant East Asian belt (up to 3,000 m) began to form. Recently, the first finds of late Albian radiolarian assemblages from volcanogenic-siliceous rocks of the Amur River have been recorded (Filippov & Kemkin, 2008), also illustrating an increase of silica concentrates in the water column. Thus, environmental conditions in the Sikhote Alin (Primorye-Priamurye) palaeobasin were not really conducive to macrofaunal development. This explains why ammonite assemblages of early Cenomanian age here comprise only few survival forms, such as the discocones *Puzosia* and *Desmoceras* (*Pseudouhligella*) and the torticone heteromorph *Mariella*. This was a small, shallow-water basin which existed only until the end of the Cenomanian.

Cenomanian sedimentary rocks occur in southern Sakhalin and comprise sandstones with conglomerates and thin layers of mudstones in the lowest part of the section (Yazykova, 2004), marking a regressive episode, and intercalated mudstones, siltstones and sandstones in the upper part of the section, documenting a change from nearshore facies at the Albian/Cenomanian boundary, via inshore facies of mid-Cenomanian age to offshore facies and anoxic conditions at the Cenomanian/Turonian boundary. In view of the comparatively rapid taxonomic origination and/or migration with favourable currents, the recovery stage in the early Cenomanian in Sakhalin was comparatively brief. The Cenomanian shelf marginal sea of Sakhalin was inhabited by representatives of 16 genera, some of which appeared here for the first time. These are platycone *Hypophylloceras* (*Neophylloceras*) and the gaudrycerarids *Gaudryceras* and *Anagaudryceras*, plus *Zelandites*, which is rather discoconic and had the best shape for swimming at higher velocities (Jacobs, 1992). The family Tetragonitidae was represented in these environments by smooth, narrowly umbilicate, spheroconic *Parajaubertella* and planorbiconic *Tetragonites*, a planktonic and probably vertical migrant; the Desmoceratidae by the discocones *Parapuzosia* (*Austiniceras*) and *Puzosia* (*Puzosia*), plus survival taxa of *Desmoceras* (*D.*) and *D.* (*Pseudouhligella*), which were probably nektobenthic. The Cenomanian is the time of taxonomic bloom of the Kossmaticeratidae in the Pacific realm. In Sakhalin, they were represented by *Marshallites* and *Mikasaites*, both of which were planktonic drifters (Westermann, 1996). The first members of the family Acanthoceratidae appeared, *Mantelliceras*, *C.* (*Calycoceras*), *C.* (*Newboldiceras*) and *Acanthoceras*, all sculpted planorbicones, usually representing warm-temperate conditions (Batt, 1993) and probably demersal, near-bottom migrants. The Mid-Cenomanian Regressive Trough, which was documented by Hancock (2003), is reflected here by the occurrences

of Turrilitidae, that is, the *Turrilites* bio-event.

During the survival interval, tetragonitids and desmoceratids predominated. However, according to Tanabe (*in Tanabe et al.*, 1978), representatives of these groups may have occupied wide habitats ranging from the nearshore to the offshore, taking into account post-mortem transportation and drift. Ward & Signor (1983) showed a wide range of morphological complexity of tetragonitids and desmoceratids which evolved a variety of shapes as well as a highly variable ornament, suggesting a capacity to adapt widely. Thus, the predominance amongst these of forms with remarkable ornament could point to relatively deep, sublittoral environments. The subsequent appearance of *Mantelliceras* and *Acanthoceras* during the recovery interval, and the occurrence of the heteromorph *Turrilites*, as well as the maximum diversity of *Pergamentia*-group inoceramids (Zonova *in Poyarkova*, 1987; Yazykova *et al.*, 2004), could be indicative of a relatively shallow inshore basin, but close to offshore, which is also suggested by some carbonate admixture in mudstones (Salnikov *in Poyarkova*, 1987). Kawabe (2003) noted that *Zelandites inflatus*, a species typical of the Cenomanian of Sakhalin and Japan, is the second-most dominant member of the most inshore facies and decreases offshore. In Sakhalin, this species is not dominant within Cenomanian associations and certainly not numerous; later, it probably decreased in numbers even further. Representatives of the bivalves *Acila* and *Nuculana* (Salnikova *in Poyarkova*, 1987) as well as rare gastropods and records of ichnofauna (Poyarkova, 1987), suggest a relatively shallow and warm environment, which changes to cooler offshore in the late Cenomanian when small-sized inoceramids of the *Actinoceras concentricus/A. nipponicus* group predominated (Zonova *in Poyarkova*, 1987; Zonova *in Yazykova et al.*, 2004); rare ammonites occurred, while gastropods and non-inoceramid bivalves disappeared. At the same time, rich and well-preserved assemblages of radiolarians have been recorded from latest Cenomanian deposits (Kasintzova *in Poyarkova*, 1987), which might point to an increase of volcanic activity during the latest Cenomanian, yielding high concentrations of silica needed for construction of radiolarian skeletons.

Northeast Russia, which is characterised by widely distributed Cenomanian deposits, has yielded ammonite associations of 13 genera, of a taxonomic composition similar to that in Sakhalin, and involving mostly new taxa. These are the platyconic and discoconic nektic swimmers *Hypophylloceras* (*Neophylloceras*), *Gaudryceras* and *Zelandites*; a planktonic vertical migrant, *Parajaubertella*, as noted above; the plankton swimmers *Puzosia*, *Marshallites*, *Eogunnarites* and *Neogastropilites*, which probably were planktonic vertical migrants; *Stoliczkaia* (*Lammayella*) and *Mantelliceras*, definitely belonging to nektobenthic, near-bottom migrants; and turrilitids (*Turrilites*, *Hypoturrilites* and *Mariella*), all nektobenthic vertical migrants. Following Westermann (1996), this assemblage represents inshore facies, above 100 m, with almost exclusively trachyostracans and torticonic heteromorphs. According to Tanabe (*in Tanabe et al.*, 1978), this is the same because of a predominance of ornamented shell morphotypes. Palaeotemperature data (Yu. D. Zakharov *et al.*, 2005) suggest a comparatively warm basin with seasonal changes between 15.9 and 21.7°C.

During the late Cenomanian, the highest taxonomic diversity is noted in the family Gaudryceratidae (Fig. 7). Overall, the taxonomically highly diverse Russian Pacific ammonites and inoceramids of early-mid Cenomanian age decrease at the end of this period (Fig. 5). In contrast, radiolarian complexes of high diversity are recorded from

the uppermost Cenomanian, which also could be explained by the onset of volcanic activity.

Turonian – The global mid-Cenomanian/Turonian transgression has also been recorded for the whole of Far East Russia; it resulted in relatively deep-water sedimentation. Anoxic conditions connected with strong active volcanism are reflected in the presence of mudstones interbedded with black, grey and green tuffaceous sandstones and siltstones as well as bentonitic clay. This ‘coloured’ interval is barren of any fossils (probably as a result of dysoxic conditions, as well as volcanic fallout) and generally reaches a thickness of some 40-50 m as in Sakhalin (see also Yazykova *et al.*, 2004) and in northeast Russia (Jagt-Yazykova, unpublished data). However, microfaunal analyses show that foraminiferal assemblages exhibit no major extinction at the Cenomanian/Turonian boundary here, but a temporary faunal restructuring did take place. The radiolarian fauna appears to have survived this interval without taxonomic change (probably because of favourable silica concentrations), with a drop in diversity occurring later, near the middle/late Turonian boundary, when volcanic activity decreased (Yazykova *et al.*, 2004). It is interesting to note that during this time numerous large-sized and heavy-ribbed inoceramids of the *Inoceramus hobetsensis* group (for details, see Yazykova *et al.*, 2004) are widely distributed, in spite of volcanic perturbations and a comparatively deep-water setting. Dundo (*in* Blank & Dundo, 1980) was of the opinion that such large and heavy-sculpted inoceramids were perfectly adapted to such environments. Amongst ammonites, new genera gradually appeared during the early Turonian survival interval, a radiation event being recorded in the mid-Turonian and a diversity maximum amongst late Turonian assemblages. New ammonite morphotypes characterised the Turonian palaeobasins.

The survival interval in the early Turonian of Sakhalin was characterised by the expansion of basins into the central part of the island (Yazykova, 2004). The ammonite assemblage consists mostly of leiostracans: platycone to discocone *Hypophylloceras* (*Nepophylloceras*), *Tetragonites*, *Gaudryceras*, *Anagaudryceras* and *Zelandites*; and planorbicone *Jimboiceras* and vermicone heteromorph *Nipponites* represent inhabitants of a rather deep (> 150-200 m depth) inshore to offshore basin. The situation changed during *Scaphites planus* Zone time (mid-Turonian radiation interval; *Scaphites* biofacies bio-event) with the appearance of the scaphitids *Scaphites* and *Yezoites* (correlated with a worldwide scaphitid bloom), and the diplomoceratid *Scalarites*.

The middle/late Turonian boundary bio-event is characterised by numerous heteromorph vermicones, scaphitocones, dominant trachyostracans with platyconic gaudryceratids, tetragonitids, phylloceratids and planorbiconic Acanthoceratidae (*R. Romaniceras*), *R. Yubariceras*), *Kamerunoceras*, *Pseudaspidoceras*; trachyostracans with planorbiconic to platyconic desmoceratids (*Puzosia* (*Mesopuzosia*), *Pachydesmoceras*); spherocone Vascoceratidae (*Fagesia*) and the *Inoceramus teshioensis* group dominated the entire, warm (15.8-17.5°C according to Yu. D. Zakharov *et al.*, 1999), about 150-200 m deep, sublittoral basin of the West Sakhalin Mountains, mostly nearshore to inshore facies. This is supported also by single representatives of hexacorals and thin carbonate layers (Poyarkova, 1987). From the mid-Turonian onwards, lithofacies consists of intercalations of mudstones and siltstones with sandstone, tuff and tuffaceous layers and turbidites, illustrating active volcanics and the predominance of storms. There were diversity and abundance peaks in the late Turonian (Fig. 5).

Bivalves, particularly inoceramids, show a high diversity during the late Turonian (Salnikova & Zonova in Poyarkova, 1987; Zonova & Yazykova, 1998). A noteworthy feature is the occurrence of numerous small-sized inoceramid species in latest Turonian deposits, namely *Inoceramus multiformis* Pergament, *I. submametensis* Zonova, *I. tenuistriatus* Nagao & Matsumoto, *I. teshioensis* Nagao & Matsumoto and others (Yazykova *et al.*, 2004).

New ammonite taxa gradually appeared: hamitocone heteromorphs (*Nostoceras* (*Eubostrychoceras*), *Hyphantoceras*), platyconic *Damesites* and *Hourcquia*, and the rare oxyconic *Subprionocyclus*. It is interesting that one new species of desmoceratid which appeared in the late Turonian, the discoconic *Tragodesmocerooides subcostatus*, inhabited offshore waters (Hirano *et al.*, 1990) and should have been a nektic swimmer, morphologically stable throughout, with no temporal fluctuation around an average. In Sakhalin, the late Turonian basin probably was sublittoral inshore to offshore, but maybe it was deeper, not only because of the occurrence of *T. subcostatus*, but also of *Nipponites*. *Nipponites occidentalis* Ward & Westermann, 1977, had a depth limit of around 500-600 m and was adapted to a passive mode of life. Packard (1972) suggested that heteromorph lytoceratine ammonites occupied the same niche as extant cranchid squids. These forms are passive, balloon-like floaters. In such a niche, selective pressure for conch streamlining and swimming ability would probably have been low (Ward & Westermann, 1977).

Because of a highstand in the Turonian, some taxonomic unification appeared in the Pacific. Thus, ammonite compositions in northeast Russia (BP) and Sakhalin (NWP) are almost identical, apart from a few taxa. These are predominantly trachyostracans with platyconic *Hypophylloceras* (*Neophylloceras*), *Gaudryceras*, *Anagaudryceras* and *Marshallites*; planorbiconic *Romaniceras* (*Yubariceras*) and *R.* (*Romaniceras*) of worldwide distribution; *Jimboiceras*; leiostracans with only planorbiconic *Puzosia* (*Mesopuzosia*) and *Kitchinites*; numerous heteromorphs such as torticonic *Nostoceras* (*Eubostrychoceras*) and vermiconic *Nipponites*; hamitoconic *Scalarites*; and scaphitoconic *Scaphites* and *Yezoites*. The environment was also similar to that in Sakhalin, that is a sublittoral basin, of about 150-200 m depth (maybe deeper), mostly inshore to offshore facies. However, it seems that the Sakhalin basin was slightly deeper, already continental slope, and the taxonomic diversity amongst ammonites higher than in northeast Russia.

Coniacian – In Sakhalin, this comparatively stable period was interrupted only by local sea level changes which are reflected in a series of intercalated mudstones and siltstones with sandstone, and possibly slight volcanic activity as evidenced by thin tuff and tuffaceous beds. However, the northerly sections in the West Sakhalin Mountains document a huge thickness of Turonian strata, in excess of 1,000 m, which means the depositional rate must have been high and closely comparable to that documented by Okada (1997) for the Turonian/Coniacian, up to a maximum of 500 m/myr in the latest Coniacian.

The Turonian/Coniacian boundary faunal turnover bio-event in Sakhalin was marked by the entry of new ammonite and inoceramid morphotypes with a slight reduction in taxonomic diversity (Zonova & Yazykova, 1998). The base of the Coniacian has been defined by the last appearance of *Jimboiceras planulatiforme* with thin ribs and an evolute shell shape, and the entry of *J. mihoense* with coarse ribs, as well as by the first occurrence of *Anagaudryceras politissimum* and *Gaudryceras denseplicatum*. *Jimboiceras mi-*

hoense, *A. politissimum* and *G. denseplicatum* demonstrate the appearance of new morphotypes as a result of adaptation within their phylogenetic lineages to new ecological conditions, demanding thicker shells and coarse ornament because of, probably, higher-energy environments. The appearance of small-sized inoceramids (*Inoceramus uwajimensis* Yehara; see Zonova & Yazykova, 1998) supports that interpretation because later representatives of the *Inoceramus uwajimensis* group reach larger sizes and co-occur with numerous *Inoceramus mihoensis* Matsumoto and *Jimboiceras mihoensis*. *Forresteria* (*F. alluaudi*) was found at the same level. In the latest Coniacian, *Peroniceras* sp. and *Binneyites*(?) sp. have been recognised; these are migrant species which mark the beginning of a new transgression. Thus, the appearance of coarser ornament and the abundance of heteromorphs (*Yezoites*, *Scalarites*, *Nipponites* and *P. (Pseudoxybeloceras)*), and coarsely sculpted *Forresteria*, *Peroniceras* and *Hourcquia*, with the first pachydiscid *Menuites* (*Anapachydiscus*) in the lower part of the section, could indicate a relatively shallow-water basin with high energy, which would correspond to a lowstand period. However, representatives of planorbiconic to platyconic Phylloceratidae (*Hypophylloceras* (*Neophylloceras*)), Gaudryceratidae (*Anagaudryceras*, *Gaudryceras*), Tetragonitidae (*Tetragonites*) and Desmoceratidae (*Jimboiceras*, *Kitchinites* and *Damesites*), which predominate, definitely belonged to drifting planktonic groups. Such a mixed set of morphotypes rather suggests depths of >150-200 m, open continental shelf, nearshore to inshore facies and, as noted above, a high-energy environment of warm water with seasonal changes from 11.3-22.4°C (Yu.D. Zakharov *et al.*, 2005); the basin became deeper during the latest Coniacian.

In northeast Russia, the basin probably was shallower. Representatives of planorbiconic to platyconic phylloceratids, gaudryceratids, tetragonitids, desmoceratids and heteromorphs (nostoceratids, scaphitids) predominated there, too. However, the taxonomic diversity amongst ammonites is lower; in contrast, small-sized inoceramids of the *Inoceramus uwajimensis* group are more abundant. Thus, I interpret this as the same open continental shelf, but a rather nearshore facies of around 150 m in depth.

Yu.D. Zakharov *et al.* (2005) assumed the occurrence of short-lived, subfreezing conditions occasionally in the Northern Hemisphere, most probably during polar winter months in the early Valanginian, late Coniacian/early Santonian and early Maastrichtian. However, those authors underlined that it was probably never sufficiently cold for long enough for permanent sea ice to form because of the absence of a continent in the North Pole region and a significant ameliorating effect of oceanic heat-transport towards the pole, mainly via the straits of Turgai and the Western Interior of North America.

Santonian – Placement of the Coniacian/Santonian boundary is still very problematic in the Russian Far East. The FADs of *Texanites* (*Plesiotexanites*) *kawasakii* and *Inoceramus amakusensis* are the two best criteria for the base of the Santonian in Sakhalin (Yazykova, 1996, 2002; Yazykova & Zonova, 2002), in spite of the fact that both are endemic. However, lending support to this interpretation is the co-occurrence of these taxa with the widespread ammonites *Polyptychoceras quadrinodosum*, *Desmophyllites diphylloides* and *Phyllopachyceras forbesianum*. In the Naiba River reference section (Sakhalin), the Coniacian/Santonian boundary as currently understood is placed at the base of Member 8 of the Bykov Formation. At the top of Member 7 there is a good marker, namely a light grey sandstone with abundant plant debris and green-grey tuff

intercalations, which is also traceable in Japan (Hirano & Takagi, 1995). The last Coniacian ammonite, *Peroniceras* sp., has been found just above these tuffs. Typical Coniacian species, such as *Jimboiceras mihoense*, *Forresteria* (*F.*) *alluaudi* and inoceramids of the *Inoceramus mihoensis*/*I. uvajimensis* group, occur just below the tuff intercalations (Zonova & Yazykova, 1998).

New taxa, representing new morphotypes, characterise the Santonian as does the abundance of new (sub)genera of heteromorphs such as *Glyptoxoceras*, *Didymoceras*, *Pseudoxybeloceras*, *Polyptychoceras*, *Neocrioceras*, *Subptychoceras*, *Eubostrochoceras* and *Baculites*. Representatives of these were published in only three previous papers (Poyarkova, 1987; Alabushev & Wiedmann, 1997; Yazykova, 2004). Generally, the Santonian interval is typified by a continuous increase of taxonomic diversity amongst ammonites (Fig. 5). The clear predominance of morphotypes of heteromorphs and ornate shell forms (compare Tanabe, 1979) points to a comparatively shallow-water basin probably similar to that in the latest Coniacian. New migration routes which appeared during the latest Coniacian were gradually getting wider during the Santonian and the percentage of cosmopolitan species during this time is much higher (see Yazykova, 2002). However, details of this boundary still need additional research.

The distribution during the Santonian is similar to the Coniacian, for example, planorbiconic to platyconic *Hypophylloceras* (*Neophylloceras*), *Anagaudryceras*, *Gaudryceras*, *Tetragonites*, *Saghalinites*, *Kitchinites*, *Damesites* and *Nipponites*, *Hyphantoceras*, and co-occurring gastropods (Poyarkova, 1987). This supports the notion that the environment did not change noticeably, being still around 200 m in depth, an open continental shelf, nearshore to inshore facies with warm water and high energy. The latter is suggested also by the appearance of thick, coarsely ornamented shells of the families Collignoniceratidae, Texanitidae (*Texanites* (*Plesiotexanites*) and *P.* (*Protexanites*)) and Brancoceratidae (*Mortoniceras*), which rather belonged to near-bottom migration taxa. On the other hand, some demersal forms are known here as well, such as Kossmaticeratidae (*Yokoyamaoceras*) and Pachydiscidae (*Eupachydiscus*, *M.* (*Menuites*)), the latter occasionally represented by numerous specimens in central Sakhalin (Yazykova, 2004), where the facies points to shallower-water conditions. Interestingly, the northeasterly regions during this time are represented practically by the same complex of morphotypes apart from the appearance of *Pseudophyllites*, and the absence of *Tetragonites* and *Saghalinites* (all Tetragonitidae). It seems that *Pseudophyllites* could be a migrant from the European Boreal province into the northern Pacific, via the Arctic Ocean, because *P. indra* first appeared in Europe and subsequently spread to the Tethys and Pacific. However, it is a long way to reach the northern part of the Pacific where this species has also been found in Santonian strata, which is why I assume that it, too, came via Arctic ocean. Discocone *Zelandites* and oxycone *Hauericeras* probably were more efficient nektonic swimmers which appeared only in the south of the Sakhalin basin during the Santonian.

During the late Santonian transgression, new species of inoceramids with a new type of radial shell sculpture appeared; the index *Inoceramus* (*Platyceramus*) *japonicus* and single records of '*Inoceramus*' sp. aff. *Cladoceramus undulatoplicatus* (Yazykova, 2002), as some kind of precursor of the late Campanian inoceramid subfamily Sachalinoceraminae with radial shell sculpture, and a new, complex and highly typical ligament apparatus (Zonova, 1984). However, these inoceramids appeared only in

northern Pacific regions; they have never been found in the Arctic province, although members of the Sachalinoceraminae did appear there during the Campanian.

In taxonomic composition, the Santonian ammonite assemblage of the northeastern regions (mostly the Koryak Upland) is similar to that from Sakhalin, albeit less diverse and with a predominance of trachyostracans (non-heteromorphs as well as heteromorphs), pointing to shallower waters. Numerous inoceramid and non-inoceramid bivalves, some brachiopods and echinoids, isolated corals and plant detritus substantiate such an interpretation, as does the wide distribution there of thermophilic gastropods, mostly herbivorous genera which preferred depths of no more than 70 m (Blank & Dundo, 1980).

Campanian – The Santonian/Campanian boundary in Sakhalin is characterised by an abrupt regressive pulse which interrupted deep-water sedimentation and triggered notable environmental changes, causing a regional biotic event which is evident in different parts of the world. Yu.D. Zakharov *et al.* (1998) recorded negative $\delta^{18}\text{O}$ values indicating some increase in temperature during approximately the early late Santonian. However, the total number of ammonite taxa increases and reaches its maximum in the early Campanian. Thus, the Santonian/Campanian regional biotic event entailed the disappearance of Santonian forms and the rapid appearance of a new assemblage with novel ammonite and inoceramid morphotypes (for Sakhalin this boundary has been described in detail; see Yazykova *et al.*, 2002).

In general, the early Campanian assemblages in Sakhalin represent offshore to nearshore faunas. This part of Member 10 of the Bykov Formation records initially quiet sedimentation in a relatively deep-water, marine environment, as suggested by the predominance of planktonic radiolarians, and nektonic and benthic heteromorphs: cyrticone, orthocone and hamiticone (*Baculites*, *Neancyloceras*, *Neocrioceras*, *Diplomoceras*, *Pseudoxybeloceras* (*Schlueterella*), *Ps.* (*Pseudoxybeloceras*), *Polyptychoceras* (*Po.*), *Po.* (*Subptychoceras*) and *Ryugasella*), and planispiral ammonites (mostly Desmoceratidae and Pachydiscidae), which are relatively large and have platyconic, discoconic and spheroconic shell shapes. However, planorbicone and platycone Phylloceratidae, Tetragonitidae and Gaudryceratidae are also abundant. These shell forms suggest open, offshore marine settings (Tsujita & Westermann, 1998). The taxonomic diversity maximum amongst Campanian ammonites occurs at this level, especially in the families Pachydiscidae, Tetragonitidae and Diplomoceratidae. However, the absolute maximum of diversity within these three families was reached in late Campanian deposits. The abundance of radiolarians also points to high levels of silica and other nutrient loads (see Racki & Cordey, 2000), so the next increase in volcanic activity is noted here. The most abundant radiolarian assemblages have been collected from siliceous mudstones in the Terpenja Peninsula (Fig. 1), where macrofaunal records are extremely scanty. The appearance of new inoceramid species provides evidence of warm water of normal salinity. Nearly 70 taxa of foraminifera, most of them benthic and stenobiotic, indicate a well-oxygenated basin (Turenko *in* Poyarkova, 1987). This interpretation is supported by the appearance of new gastropod species and the occurrence of non-inoceramid bivalves (Poyarkova & Salnikova *in* Poyarkova, 1987).

Fossil associations of the *Canadoceras kossmati*/*Pennatoceras orientalis* zones, in the uppermost part of Member 10, show continuous changes in the local environment. Several lines of evidence suggest a well-oxygenated sea of normal salinity and a steady

shallowing: a relative fall in ammonite diversity, reflected in the disappearance of some heteromorphs and the last representatives of *Menuites*; a rise in inoceramid diversity (the appearance of the first radially ribbed *Pennatoceras*); a rise in the abundance of foraminifera; and a decrease in the radiolarian abundance. A continuous rise of temperature in the northern Pacific region could have been caused by some increase of volcanic activity (Kirillova *et al.*, 2000), as reflected in the tuff layers of the uppermost part of Member 10 of Bykov Formation.

Member 1 of the Krasnoyarka Formation (*Pachydiscus* (*P.*) sp. aff. *egertoni*/*Schmidti-ceramus schmidti* zones) was deposited during a time of lowstand and highest temperatures in the Campanian. The occurrence of tuffaceous mudstone interlayers, glauconitic sandstones and bentonitic clays points to relatively high volcanic activity. Conglomerates at the base of Member 1 may indicate some hiatus at the early/late Campanian boundary. Yu.D. Zakharov *et al.* (1998) documented a relatively abrupt drop in temperature (from 13° up to 18°C) across the conglomerates. Faunal assemblages from Member 1 record a peak of diversity of benthic organisms and a high diversity of planktonic invertebrates. The waters must have been relatively shallow and warm, agitated, well oxygenated and of normal salinity, thus enabling proliferation of inoceramids, gastropods and non-inoceramid bivalves. Perhaps, the gigantic sizes and radial ribs of most inoceramids and gastropods reflect high energy levels in the basin. However, the origin of radial ribbing, and the repeated evolution of radial sculpture in the inoceramid group throughout the Cretaceous probably had multiple causes.

The predominance of the subfamily Sachalinoceraminae, at times reaching giant size, and large-sized gastropods (*Gigantocapulus*, *Helcion giganteus* and others; Poyarkova, 1987), and the abundance of non-inoceramid bivalves, characterise this interval everywhere in the northwest Pacific province. The absence of foraminifera may result from stressful life conditions and/or may be a taphonomic signature. The elevated diversity and abundance of planispiral ammonites, the overall predominance of pachydiscids, the reduced importance of heteromorphs and the sandy lithofacies point to rather high-energy, nearshore deposition. Interestingly, this interval is characterised by maximum taxonomic diversity of radiolarians, which may relate to a eutrophic regime (Racki & Cordey, 2000). The richest radiolarian assemblage is from late Campanian siliceous shales in section at the Terpenja Peninsula. It is possible that the East Sakhalin Mountains occupied a deeper part of the basin, and volcanic and tectonic activity was much higher. The majority of inoceramids and ammonites are ill-preserved and rare here. In summary, optimum environmental conditions for benthic and planktonic groups could be assumed. In total, 92 taxa in six faunal groups have been identified from Member 1 of the Krasnoyarka Formation.

Latest Campanian sedimentary rocks were deposited during an episode of transgression, falling temperature and probably a change of salinity level, judging from a decrease in benthic faunal diversity (Fürsich *et al.*, 1995). As compared to the underlying zone, the faunal assemblage from this interval is markedly reduced as a result of these environmental changes to fifty-four species. A mass occurrence of *Baculites* was observed in Member 2 of the Krasnoyarka Formation (T.D. Zonova, pers. comm., 2008), but probably all of them belong to one or two species. In general, during the late Campanian, all taxa of inoceramids and ammonites typical of this interval gradually disappeared. Faunas are dominated here by ammonites and contain few radiolarians; one new inoceramid spe-

cies, *Inoceramus* aff. *balticus*, appears and 17 species of benthic foraminifera have been identified (Turenko in Poyarkova, 1987). Waters probably were of varying depth, but cold and poorly oxygenated, with a tendency to low levels of salinity during this depositional phase. Comparatively poor faunal assemblages characterise the late late Campanian; a significant biotic recovery in Sakhalin is not apparent until the mid-Maastrichtian.

A few species of *Cymatoceras* (Nautilidae) have been described from Campanian sedimentary rocks in Sakhalin (Shimanski, 1975; Matsumoto & Muramoto, 1983; Wilmsen & Yazykova, 2003). Westermann (1971) showed that extant *Nautilus* had a strength value of about 12 and withstood internal pressure equivalent to a depth of about 700 m, while Ammonitina had values ranging from 2-9 and Phylloceratina and Lytoceratina values between 12 and 19. Representatives of *Cymatoceras* were found in Sakhalin mostly co-occurring with Ammonitina, a *Canadoceras* acme and an acme of radially ribbed inoceramids, *Schmidticeras* (Wilmsen & Yazykova, 2003, fig. 2).

In comparison to the Campanian ammonite succession of Sakhalin, that in north-east Russia was not so varied and taxonomic diversity was lower. This was an even shallower nearshore basin with a predominance of trachyostracans represented even by Collignoniceratidae and a rich complex of gastropods which usually are common in brackish waters (Blank & Dundo, 1980). However, the deepest late Campanian level with *Canadoceras* spp., various representatives of the subfamily Sachalinoceraminae and thick-shelled gastropods (*Helcion giganteus* Schmidt), has also been documented in the Koryak Upland (see, amongst others, Dundo & Efremova, 1974; Blank & Dundo, 1980; Poyarkova, 1987).

Near the end of the late Campanian, the onset of tectonics resulted in an overall uplift of the region (Kirillova, 2003), with the new regression-transgression pulse leading to global environmental changes. Moreover, some cooling effect which, for example, recorded from this interval in the North Atlantic (Linnert & Mutterlose, 2009) and also noted in the Pacific (Yu.D. Zakharov *et al.*, 1999, 2005), led to changes in oceanic circulation and caused climatic oscillations. In general, almost all Campanian ammonite and inoceramid taxa disappeared in the areas studied, with the exception of a few rare occurrences at the base of the Maastrichtian. A reduction of diversity and a slow recovery in the early Maastrichtian have been also recorded for foraminiferal assemblages (Kalishевич *et al.*, 1981; Turenko in Poyarkova, 1987).

Maastrichtian – Sedimentary rocks of this age were studied not only in Sakhalin and northeast Russia, but also in Shikotan Island (southern Kuril Ridge) where they are widely distributed. In Sakhalin, the Campanian/Maastrichtian boundary corresponds to the base of Member 4 of the Krasnoyarka Formation in the West Sakhalin Mountains, and to the boundary between the Zaslonoysk and Turovsk formations in the East Sakhalin Mountains, based on the disappearance of most Campanian ammonites and inoceramids and on the first occurrence of *Pachydiscus* (*P.*) *subcompressus* and *P.* (*Nedesmoceras*) *japonicus*, both widely distributed Pacific species (Yazykova, 1991; Yazikova, 1994 and references therein). In Shikotan Island, the Campanian/Maastrichtian boundary is placed 5-6 m above the boundary between the Matakotan and Malokurilsk formations, within the lowest portion of the latter unit, as based on the first appearance of *Shachmaticeras* *shikotanensis* and *P.* (*P.*) *subcompressus*, and the highest records of *Canadoceras multicoatum* and *Inoceramus* aff. *balticus* Böhm (Zonova & Yazykova, 1994).

Recently, this placement has been supported by data on radiolarians (Palechek *et al.*, 2008). Following those authors, the last representatives of Campanian radiolarians occur 5-6 m above the lithological boundary between the Matakotan and Malokurilsk formations within a tectonic unconformity, that is at approximately the same level as the highest finds of *Canadoceras multicoatum* and *Inoceramus aff. balticus* made by Zonova & Yazykova (1994). This level is matched by a similar horizon in Japan (Toshimitsu *et al.*, 1995).

During the early Maastrichtian, the south of the island saw the deposition of shallow-water sandstones. Salnikov *et al.* (1980) noted that late Campanian-early Maastrichtian complexes of foraminifera and non-inoceramid bivalves were typical of lower to upper sublittoral environments. However, a gradual facies change may be observed going from south to north. The early Maastrichtian sequence in the Aleksandrovsk-Sakhalinskij region is composed of mudstones and sandy mudstones. In the southern part of East Sakhalin, volcanogenic siliceous rocks of Campanian age are overlain by deep-water mudstones with silica tuffs illustrating strong tectonic activity and the highly complex sedimentary sequence. Possibly, this represented the ultimate interval of strong tectonic 'rearrangements' of the Sakhalin Mountains; meanwhile, the late Maastrichtian comprised quiet, deep-water sedimentation of mudstones with carbonate concretions, elongated along bedding planes and forming concretion layers in some sections in the south of the island. It seems that the occurrence of such concretions might be linked to storm events during the taphonomic process. Wani (2001) stressed that shell accumulations in the shelf facies in Hokkaido, which are often visible in calcareous concretions, were related to storm events. Some increase in temperature was also recorded (Yu.D. Zakharov *et al.*, 1999).

During the late Maastrichtian, the northern Pacific ammonites again underwent an 'explosion' of new taxa, with the evolution of new species in the families Pachydiscidae, Phylloceratae, Gaudryceratae and Tetragnostidae (Yazykova, 1994; Yazykova, 1996; Hirano *et al.*, 2000) against the background of a global late Maastrichtian transgression. Some species are immigrants from the European and Mediterranean realms, for example *Pseudophyllites indra* and *Zelandites varuna*. The genus *Hypophylloceras* (*Neophylloceras*) comprised long-lived *Hypophylloceras* (*Neophylloceras*) *ramosum*, but in the late Maastrichtian *H. (N.) hetonaiense* and *H. (N.) victriense* appeared. Along the River Krasnoyarka (Naiba River valley), at almost 2 m below the Maastrichtian/Danian boundary, numerous representatives of small-sized, smooth involute discocone *Zelandites* have been found (Zonova *et al.*, 1993; Yazykova, 1994). Wiedmann & Kullmann (1996, p. 807) claimed that, "just eight genera are recorded 15 meters (~150,000 years) below the boundary" at the "two most complete boundary sections, Zumaya and Hendaye", that is, *Neophylloceras*, *Gaudryceras*, *Saghalinites*, *Pseudophyllites*, *Vertebrites*, *Anapachydiscus*, *Pachydiscus* and *Diplomoceras*. I add to these records the Naiba section in Sakhalin, because, with the exception of *Vertebrites* and *Anapachydiscus*, all genera listed above have been recorded here from the late Maastrichtian and, as noted above, numerous individuals of *Zelandites japonicus* have been collected by myself from about 2 m (~20,000 years) below the Maastrichtian/Paleocene boundary.

The last kossmaticeratid is *Brahmaites* (*Subbrahmaites*) *sachalinensis*, a platycone demersal taxon. The family Pachydiscidae is highly diverse, with four new species of *Pachydiscus* (*P.*) and one new subgenus, *P. (Neodesmoceras)*, comprising two new spe-

cies, plus new species of *Patagiosites* and *Pseudomenuites*. Heteromorphs are represented by species of *Diplomoceras*, *Neancyloceras*, *Nostoceras* (*Didymoceras*) and *Glyptoxoceras*. It should be noted also that an important element in the Maastrichtian ecosystem in Sakhalin is the linuparid genus, *Linuparus* (Poyarkova, 1987; Shigeta & Maeda, 2005).

In contrast to the ammonites, inoceramids do not reveal such a diversity pattern. Taxonomic diversity as well as abundance gradually decreased during the Maastrichtian. However, some interesting interval should be noted. A new genus appeared in the late Maastrichtian, *Shachmaticeramus* (Zonova *et al.*, 1993), with a peculiar chess-board construction of the ligament strip, unknown in any pre-Maastrichtian inoceramids. Nearly all Maastrichtian inoceramids from Far East Russia have this type of ligament strip. If this feature is seen as a novel phylogenetic modification, unfavourable taphonomic conditions for this group of inoceramids need to be taken into account, which precluded shell preservation. It is interesting to see that inoceramid ligament strips and prismatic layers are commoner than complete individuals.

Interestingly, Blank & Dundo (1980) noted rich assemblages of small-sized gastropods, non-inoceramid bivalves, common brachiopods, rare hemiasterid echinoids and crustaceans, mainly crabs, on which evidence they assumed the late Maastrichtian basin of the Koryak Upland to have been shallower, brackish, well oxygenated, but slightly cooler than during the Campanian and early Maastrichtian, and somewhat separated from the ocean. However, those authors also noted oceanic taxa of gastropods and rare nautiloids, which demonstrate that this basin cannot have been isolated completely from the ocean. The Koryak Upland basin was similar to that in southern Sakhalin, on account of rich complexes of non-inoceramid bivalves, gastropods and brachiopods (Poyarkova, 1987). Along the entire range of sections in Sakhalin and northeast Russia, isolated finds of shark teeth and fish vertebra are known that await description.

The Cretaceous/Paleogene boundary in the Russian Pacific is characterised by a global regression, strong volcanic activity and, as a consequence, drastic environmental changes, which are here reflected in the total annihilation of ammonites and inoceramids, and by some remarkable changes in other groups of organisms. In the West Sakhalin region, deposition of green-grey clays, 1-2 m in thickness, was recorded. The East Sakhalin region and northeasterly areas show volcanic activity, reflected in glauconitic material within the basal Danian sandstone in Sakhalin (Shuvaev, 1965) and basal Danian volcanogenic-terrigenous-silica deposits in the Koryak Upland (Dundo, 1974). The Kuril Islands are positioned within a zone of strong tectonic activity, and the boundary between Maastrichtian and Paleocene rocks is within the tectonic contact (Zonova & Yazykova, 1994). During the Danian, shallow-water sandstones with bentonitic and tuffaceous material were laid down in the Russian Far East. Yu.D. Zakharov *et al.* (2002) noted a general temperature drop, which was also supported by data on average annual temperatures based on palaeoflora analyses by Herman *et al.* (2009). Based on these, a generally abrupt and strong (less than 5°C above freezing) climatic cooling appears feasible.

Twitchett (2006, p. 195) suggested that global cooling was not necessarily less detrimental than global warming to the biosphere. In his opinion, "recent evidence shows that the climate of the Maastrichtian was rather variable: a long term cooling trend gave way to a brief interval of warming in the latest Maastrichtian, followed by the onset of cooling just before the K/Pg boundary. Cooling is also considered to be one possible

consequence of extraterrestrial impact". However, he also noted (p. 196) that global "cooling should promote oceanic circulation and mixing and lead to the oxygenation of marine ecosystems. Ocean productivity is also higher under icehouse conditions". Recently, during the 8th International Symposium on the Cretaceous System (Plymouth, September 2009), a wealth of new data on climate changes during the Cretaceous and especially in the latter part of that period, were presented. Some scientists still support previous ideas of greenhouse conditions and abrupt cooling during the latest Cretaceous, while others presented evidence to suggest a long-term cooling trend. Amongst others, Moriya *et al.* (2009, pp. 144, 145) discussed a Late Cretaceous thermal structure in the northwest Pacific and centred on the question: "How does the earth turn into an icehouse mode after a greenhouse"? Those authors presented oxygen isotope records for the late Turonian to early Campanian from pristinely preserved planktonic and benthic foraminifera from the mid-latitude northwest Pacific, and claimed that global climate suffered progressive cooling. Therefore, they argued that their data indicated an increase in heat transport northwards in the northwest Pacific during a cooling episode under greenhouse climatic conditions.

Thus, it appears that of all currently known stressed-environment factors, that is, climatic variation, anoxia, regressions and major volcanic eruptions, the most important to ammonites were regression-transgression cycles and volcanic activity. However, as is clearly seen from studies of their evolution and phylogeny in the Russian Pacific, recovery after environmental stress usually was rapid enough and a radiation event invariably followed.

In short, ammonites as a group (characterised by exceedingly rapid evolutionary rates and a very wide range of morphologies reflecting a marked degree of environmental adaptation), which existed for over 300 million years, would not be driven to extinction merely by cooling, anoxia or volcanic eruptive phases. Stress suffered across the K/Pg boundary had to be strong and sudden, and probably comprised all detrimental factors taken together, in particular a high concentration of different toxic gases in the atmosphere and ocean water. Such an event could only have been triggered by an impact (or multiple ones?), followed by hypercanes and giant tsunamis, widespread wildfires, plus heightened tectonic and volcanic activity on land as well as on the seafloor.

Homoeomorphy, dynamics and phylogenetic relationships – Matsumoto (1955a, b, 1991b) drew attention to the similarities apparent between several species or genera within the subfamilies Marshallitinae (Albian-Cenomanian) and Kossmaticeratinae (post-Cenomanian). Klinger & Kennedy (1997) assumed the genera *Ryugasella* and *Madagascarites* to be heterochronous homoeomorphs. I wish to follow up on this issue by using my own material and personal observations.

Some similarities are easily seen between *Cleoniceras* (*Neosaynella*) and *Zelandites*, genera which, phylogenetically, are not closely related. The former is a typical Albian index taxon, while the latter ranges from the Albian to the end of the Maastrichtian. These genera appeared almost simultaneously, more specifically in the Pacific realm (the Arctic province, mainly), from where they subsequently extended into other provinces, for example, European or Mediterranean. They are characterised by a number of closely similar morphological features, such as weak or no ornament (near-smooth shell

surface), with mostly involute to semi-involute discoconic to oxyconic shape and of comparatively small size, but, in general, representatives of *Zelandites* are slightly smaller than species of *Cleoniceras* (*Neosaynella*). On these features, representatives of these two genera could be interpreted to have been adapted to similar environmental conditions. However, *Cleoniceras* (*Neosaynella*) disappeared in the Cenomanian, whereas *Zelandites* continued to develop, reaching its greatest geographical distribution during the late Maastrichtian, when abundant, albeit taxonomically not very diverse, representatives of this genus occurred mainly in the northwestern and Arctic provinces of the Pacific realm. Here, it should be noted that, during its comparatively short time span (Albian), apart of *C.* (*Neosaynella*), the genus *Cleoniceras* was represented in total by four subgenera, while the long-lived *Zelandites* comprised merely ten species for its entire stratigraphic range (Albian-Maastrichtian). Interestingly, Maastrichtian *Zelandites japonicus* in some way 'repeats' the general shell shape of the Albian *Z. odiensis* (Kossmat). This notable trend in the evolution of *Zelandites* came to a halt at the Cretaceous/Paleogene boundary. The youngest representatives of *Zelandites* have been collected from between 1-2 m below that level. More than likely, environmental conditions during the late Maastrichtian in the Northern Hemisphere were similar to those in the Southern Hemisphere during the Albian, where this group reached its maximum diversity. This could also explain the high rate of origination and total taxonomic diversity at that time, as documented from Sakhalin and the northeasterly regions of the Russian Pacific, as well as from Japan. In general, smooth, compressed forms predominate in late Maastrichtian ammonite assemblages. New species amongst Pachydiscidae, such as *P.* (*P.*) *flexuosus* or even the new subgenus, *Pachydiscus* (*Neodesmoceras*), demonstrate a near-complete absence of ornament. The family Gaudryceratidae was also represented by species with numerous, fine ribs on thin delicate shells, for example, *Gaudryceras hamanakense*. All morphotypes are extremely close to those from the Albian. Ammonite evolution at that time had just reached a new stage in development which replicated in some way a previous success story. Smooth or very fine ribbing actually may have reduced drag (Chamberlain, 1991) and such compressed-involute forms could have been better swimmers (Westermann, 1996); perhaps this was their way to success. Anyway, first of all, this shows that the group was viable and 'developing', and that their extinction was abrupt.

Phylogenetic links and dynamics – Current views on the evolution of mid- and Late Cretaceous ammonite species known from the Russian Pacific coast are shown here for the best-represented groups, that is, the (super) families Desmocerotidae, Pachydiscidae, Lytoceratoidea, Phylloceratidae, Kossmoceratidae, Nostoceratidae, Diplomoceratidae, Baculitidae, Turrilitidae and Scaphitidae. Endemic and migrant taxa are indicated; they clarify the picture of extinction and origination because migrating forms can be excluded.

During mid- to Late Cretaceous time, the lowest dynamics of development in the Russian Pacific was displayed by the family Phylloceratidae (Figs. 7, 8), although the maximum diversity is noted during the late Maastrichtian, just prior to the mass extinction event. Exactly at this moment appeared a new character of ornament which suggests the family to have been evolving rather than degrading. *Hypophylloceras* (*Neophylloceras*) *hetonaiense* is morphologically similar to *H. (N.) surya* from Crimea and the Caucasus, and shows the same character of thin, delicate lirae (Zonova *et al.*, 1993; Yazikova, 1994). Probably, *H. (N.) nera*, an immigrant from the Mediterranean-Caucasian province, is an-

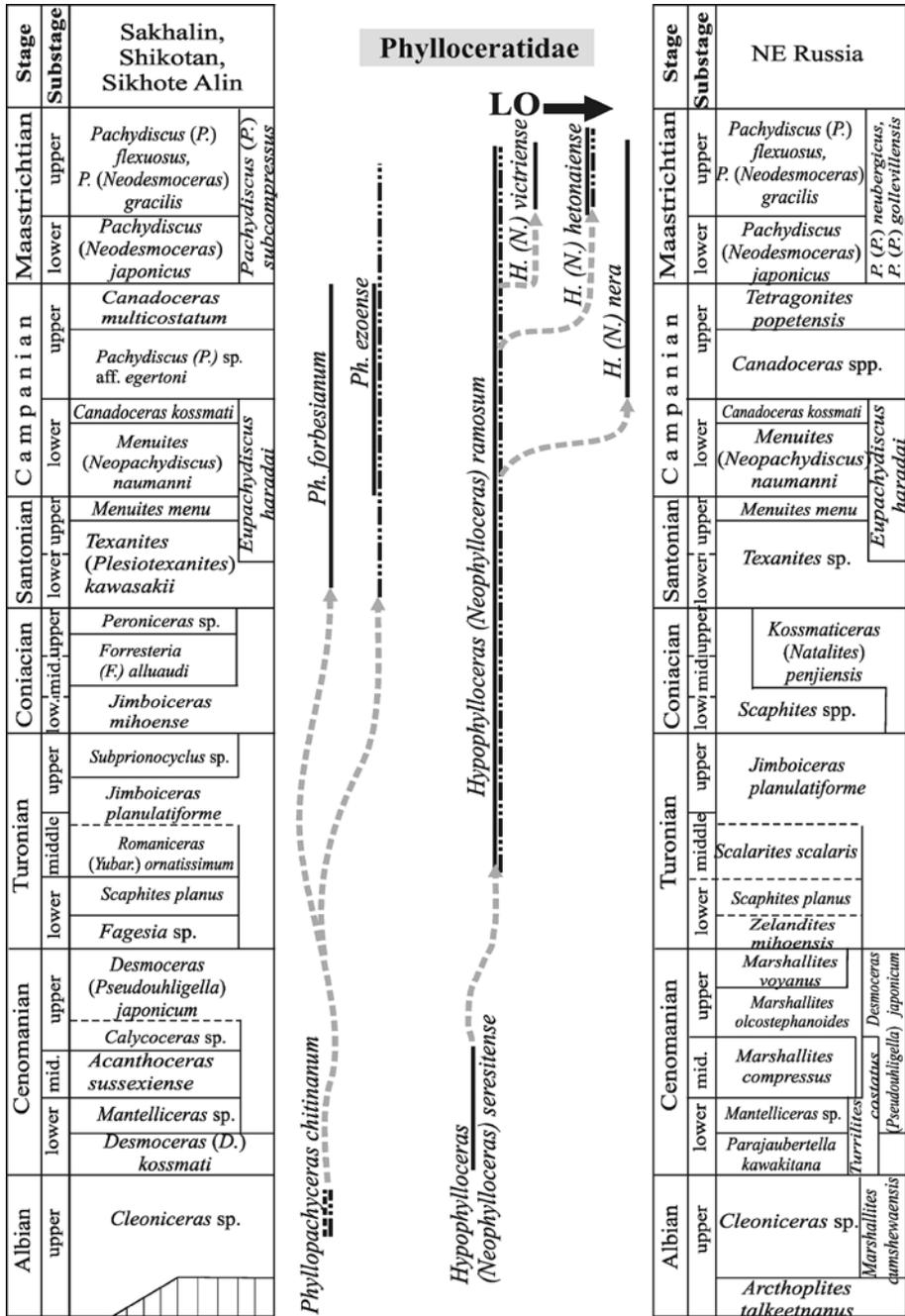


Fig. 8. Hypothesised evolution of the Phylloceratidae from the Russian Pacific coast during the mid- and Late Cretaceous.

cestral to *H. (N.) surya*, a Mediterranean taxon, as well as to *H. (N.) hetonaiense*, a north Pacific form.

The family Gaudryceratidae shows the highest degree of adaptation and comparatively high dynamics of development (Figs. 7, 9). During the whole interval studied, this family was represented by five genera, whose members succeeded each other as a result of environmental changes. Interestingly, this family reached a diversity maximum during the late Maastrichtian, similar to Phylloceratidae and Pachydiscidae (Fig. 7). Of note is that Maastrichtian endemic Pacific representatives of the Pachydiscidae are characterised by a lack of genuine ribs and by more evolute shells. The same trend is seen in the *Gaudryceras* lineage. For example, *Gaudryceras tenuiliratum* is replaced by *G. hamanakense* with numerous thin ribs and a thin, delicate shell. The family Tetragonitidae shows a maximum diversity during the Campanian (Figs. 7, 9).

In general, Phylloceratidae, Gaudryceratidae and Tetragonitidae show "great evolutionary conservatism throughout their range from lowest Jurassic to the uppermost Cretaceous" (Page, 1996, p. 763). However, as noted above, in sections along the Russian Pacific coast I have observed at least some trends to change this tendency and produce either some new morphological features (*Hypophylloceras* (*Neophylloceras*) *hetonaiense* and *H. (N.) surya*) or to replicate morphology that, in some way, had already proved successful previously (*Zelandites*). Moreover, specimens of *Gaudryceras* are abundant in the late Maastrichtian and *Tetragonites* is common in the early Campanian. Phylloceratidae, in association with Gaudryceratidae and Tetragonitidae, mostly occurred in deeper-water facies (Page, 1996). However, it appears that of these three, gaudryceratids were the best adapted during environmental crises and recovered rapidly. Interestingly, during some episodes of environmental stress (for example, the Santonian/Campanian boundary), long-lived species such as *Gaudryceras tenuiliratum* were represented by specimens smaller than normal size, a possible Lilliput effect.

Desmoceratid predominance gradually declined; the family died out at the end of Santonian (Figs. 7, 10). However, it was characterised by high evolutionary dynamics and a marked degree of sensitivity to environmental changes. Following Hirano *et al.* (1990), *Tragodesmoceroides subcostatus*, for example, following its evolution from *Desmoceras* (*Pseudouhligella*) *japonicum*, constituted a new phylogenetic form as a result of environmental changes. Those authors also suggested that *T. matsumotoi*, which seems to occur most abundantly in the late Turonian of Japan, but which is still unknown in Sakhalin, never co-occurred with *T. subcostatus* and continued the lineage in shallower-water settings. The timing of speciation of *T. subcostatus* from *D. (P.) japonicum* and that of *T. matsumotoi* from the former is in accordance with oceanic events, with an oceanic anoxic event for the former and a marine regression for the latter (see Hirano *et al.*, 1990, p. 405). The last representatives of desmoceratids in Russian Pacific sections have been noted in the late Campanian. Probably strong environmental changes, as mentioned above, were too drastic for this group to cope with. In general, this family shows the widest range of morphological features. During the Albian-Campanian interval, it consisted of four subfamilies and 15 genera. The invasion of Tethyan forms during the Albian provided opportunities for subsequent speciation of numerous endemic taxa. In the case of this family, facies control can be established.

The first representatives of the Pachydiscidae appear along the Russian Pacific coast during the Coniacian, but the maximum of taxonomic diversity has been recorded from

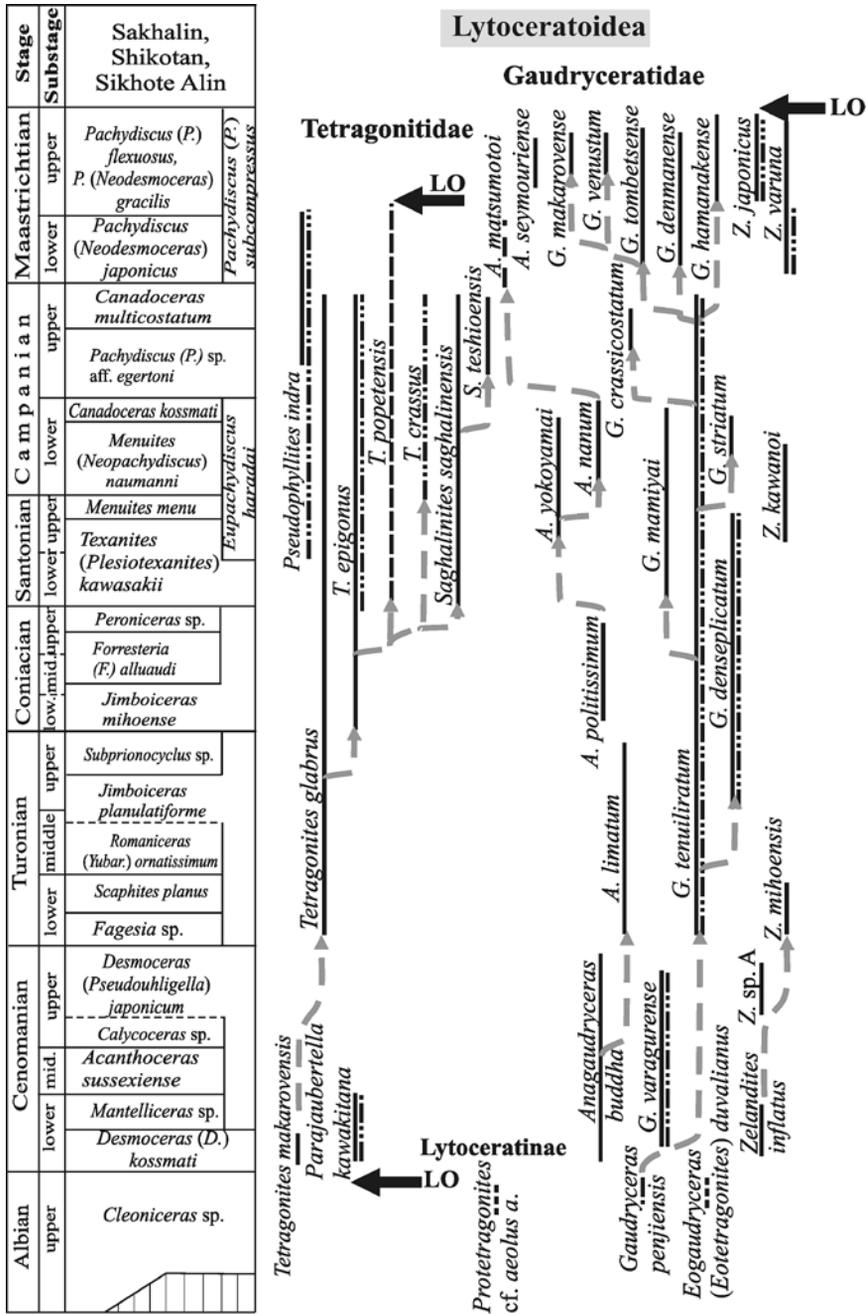


Fig. 9. Hypothesised evolution of the Lytceratoidea from the Russian Pacific coast during the mid- and Late Cretaceous.

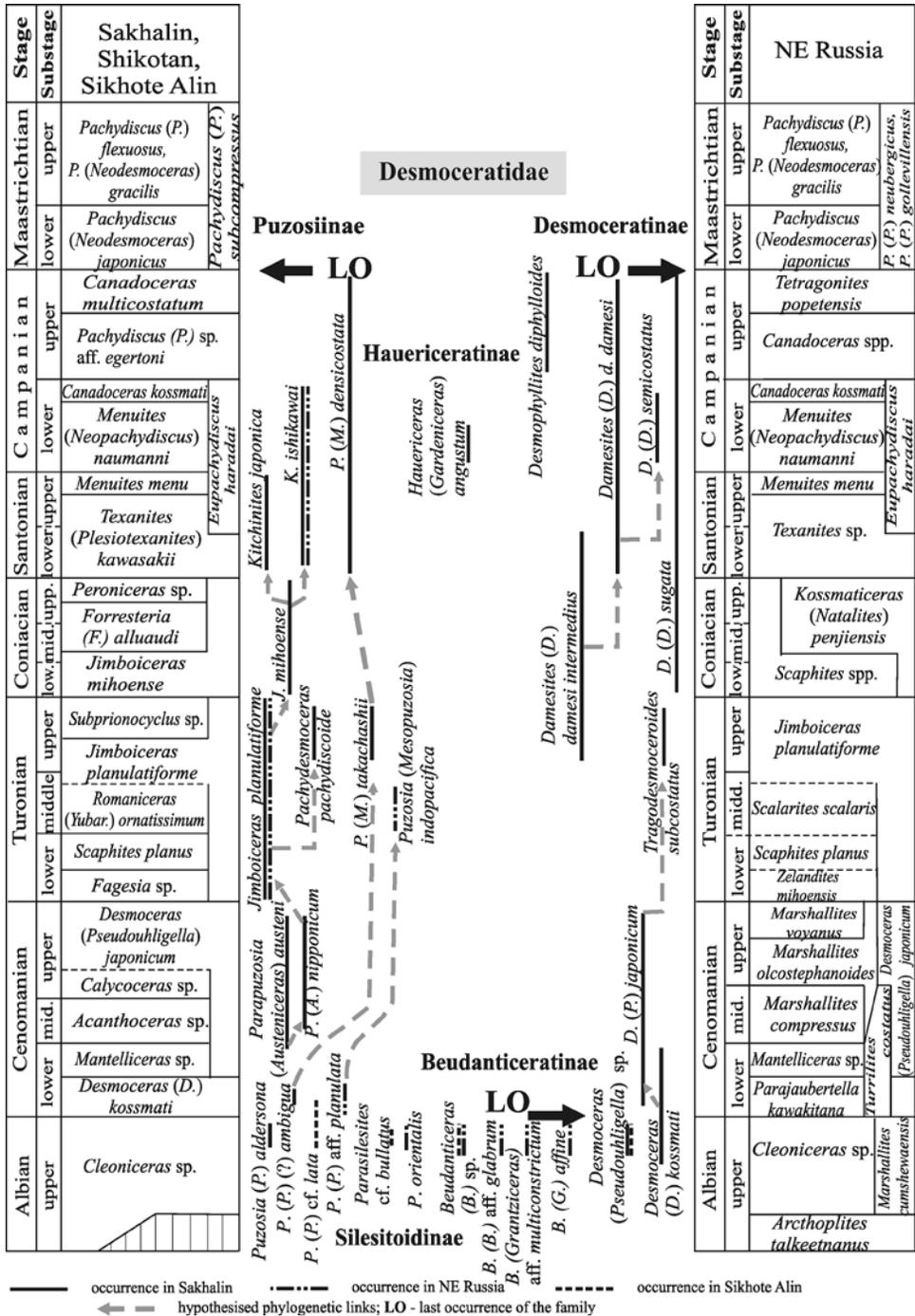


Fig. 10. Hypothesised evolution of the Desmoceratidae from the Russian Pacific coast during the mid- and Late Cretaceous.

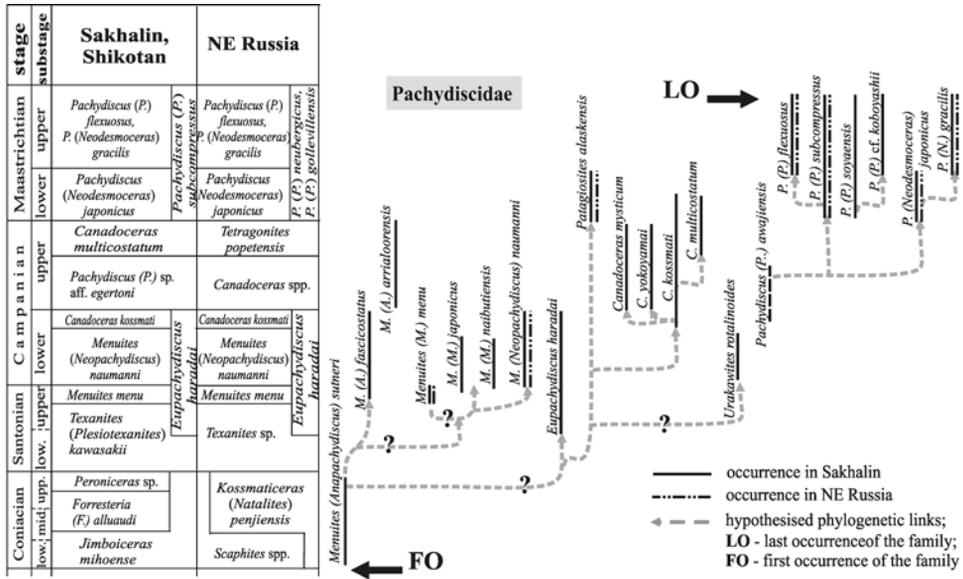


Fig. 11. Hypothesised evolution of the Pachydiscidae from the Russian Pacific coast during the mid- and Late Cretaceous.

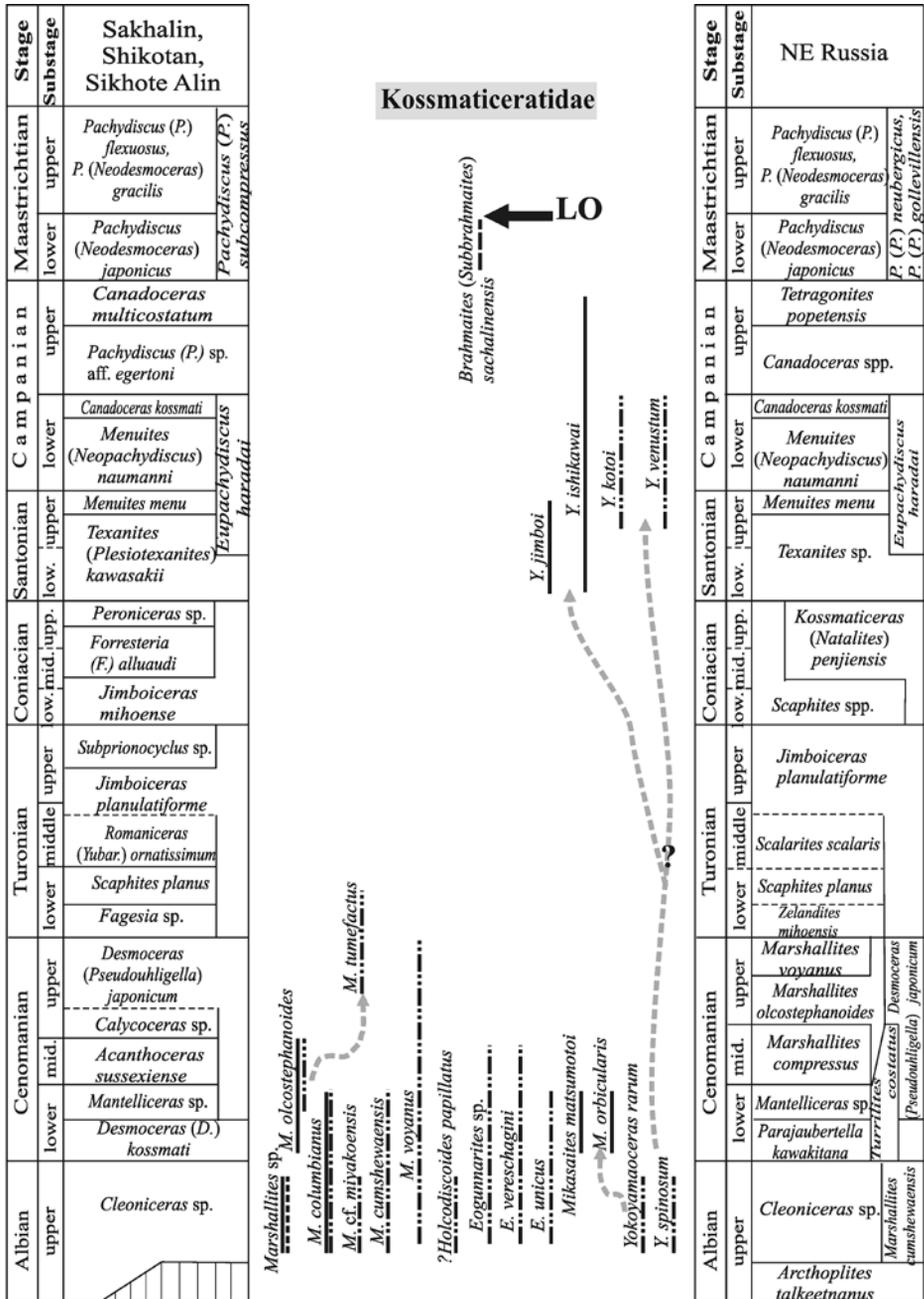
the late Campanian and early Maastrichtian (Figs. 7, 11). Moreover, during the Maastrichtian, and in particular during the latest phase of that stage, a new subgenus and several new species appeared. The perfect preservation of a number of specimens documents no degradation features for the group, thus providing additional evidence for an abrupt extinction of ammonites at the K/Pg boundary.

The closest links with lithological facies, in my opinion, are revealed by the family Kossmaticeratidae (Figs. 7, 12). Representatives occur exclusively in shallow-water sandstones or sandy mudstones; this family is also characterised here by a 100 per cent predominance of endemic forms. In addition, it should be noted that species found in Sakhalin have never been collected in the northeasterly regions and *vice versa*.

The evolutionary development of Pacific heteromorph ammonites shows three important peaks of high diversity (Figs. 7, 13, 14): the *Scaphites* facies and an abundance of nostoceratids in the Turonian; an explosion of diplomoceratids in the Santonian; and a maximum diversity of heteromorphs during the Campanian when this complex consisted of three families, namely Baculitidae, Nostoceratidae and Diplomoceratidae. Immigrant taxa appeared during the Albian and early Cenomanian (Turrilitidae), and later all complexes of heteromorphs were characterised by a predominance of endemic taxa. A new immigration event is recorded in the early Campanian.

Palaeobiogeographical aspects

Introduction – The present section discusses the palaeobiogeographical distribution of mid- and Late Cretaceous ammonites from the Russian Pacific, focusing in detail on endemism and provincialism of macrofaunas, plus possible migration routes and com-



— occurrence in Sakhalin - - - - - occurrence in NE Russia ······ occurrence in Sikhote Alin
 ◀ — — — hypothesised phylogenetic links; LO - last occurrence of the family

Fig. 12. Hypothesised evolution of the Kossmaticeratidae from the Russian Pacific coast during the mid- and Late Cretaceous.

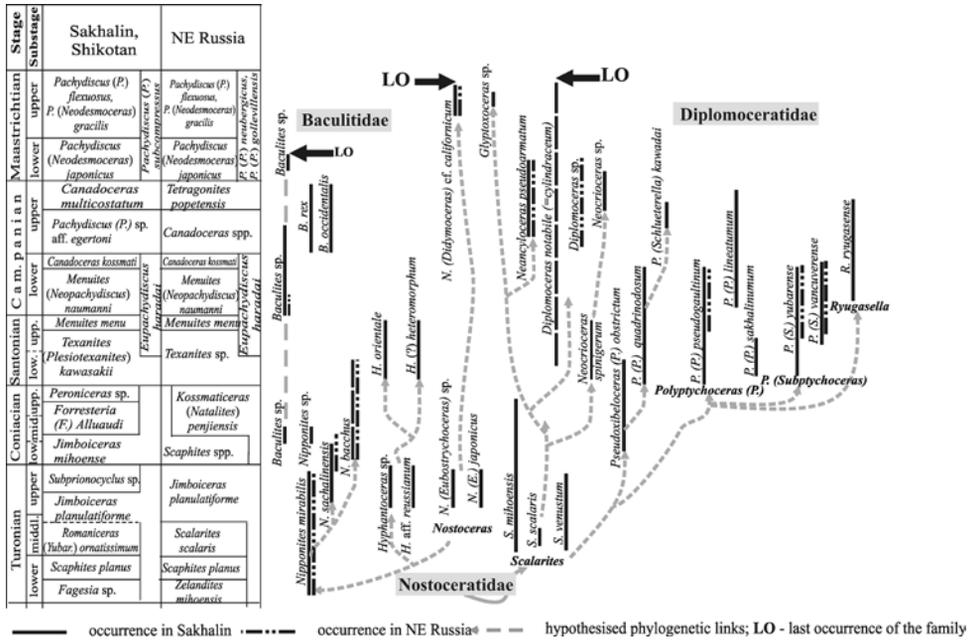


Fig. 13. Hypothesised evolution of the Nostoceratidae, Diplomoceratidae and Baculitidae from the Russian Pacific coast during the mid- and Late Cretaceous.

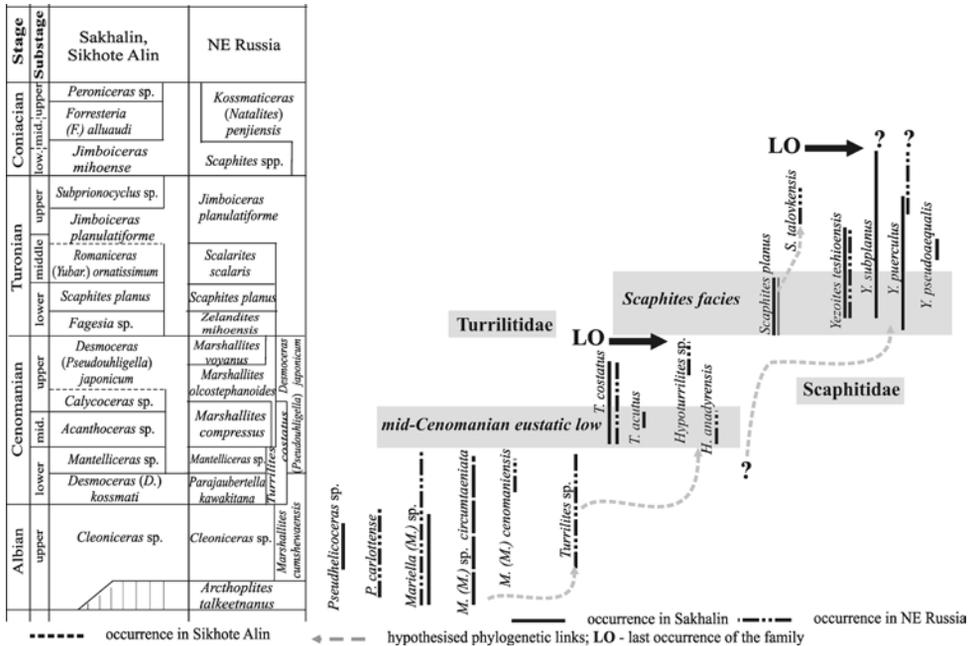


Fig. 14. Hypothesised evolution of the Turrilitidae and Scaphitidae from the Russian Pacific coast during the mid- and Late Cretaceous.

parisons with other palaeobioprovinces. According to Bengtson & Kakabadze (1999), the most important criteria for distinguishing 'bioprovinces' as biogeographical units showing biogeographical partitioning are determination of taxonomic composition (such as presence *vs* absence of taxa), of taxonomic diversity at a given systematic level and of population structure (that is, relative abundance of taxa). Such a framework is provided in the first part of this introduction. The stratigraphical distribution of mid- and Late Cretaceous ammonite genera, and their abundance in sections along the Russian Pacific coast, are shown in Figure 6. The palaeobiogeographical provinces, as based on ammonites and here proposed, are illustrated in Figure 15, while the palaeobiogeographical distribution of all taxa identified is outlined in supplementary material available from my website (www.paleo.uni.opole.pl).

Page (1996) noted that, during the Early Cretaceous, ammonite distributions were essentially similar to those during the latest Jurassic, with a relatively high degree of endemism and provincialism. Later in the Cretaceous, continental separation increased considerably and, as a result, more migratory pathways were opened up and endemism was significantly reduced. That author assumed that the hallmark of Late Cretaceous ammonite faunas was the virtually pandemic distribution of genera, and occasionally also of species, and the main control on early to early Late Cretaceous faunal distributions appeared to have been latitude. However, Page (1996) underlined that, in comparison to other groups (for example, belemnites), a Boreal Realm ceased to be recognisable for ammonites after the Cenomanian. Moreover, he concurred with Kauffman (1977) that a Tethyan Realm, interpreted in a very wide sense, included also nearly the entire ammonite and inoceramid bivalve faunas from the north and south Pacific.

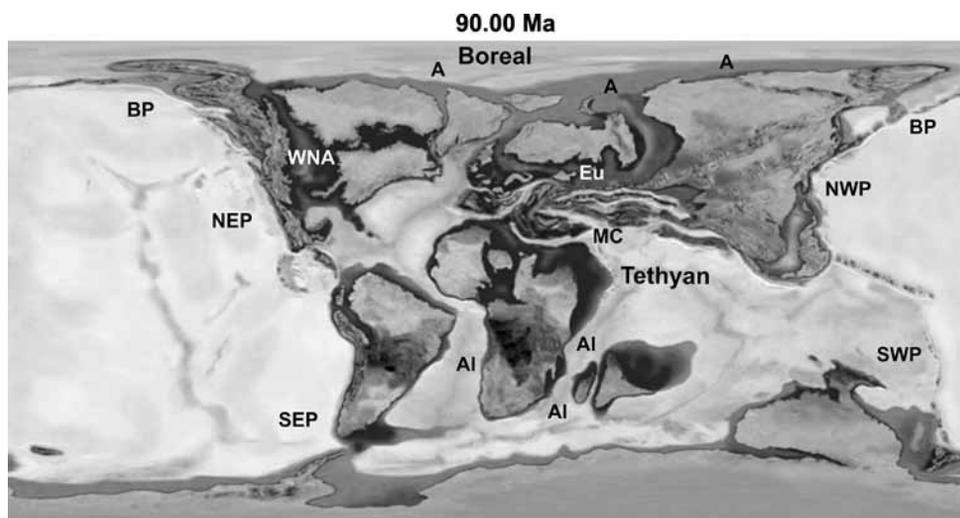


Fig. 15. Generalised mid- and Late Cretaceous provinces and realms based on ammonites (modified after Vereschagin, 1977; Khudoley & Rzhosnickaya, 1976; Page, 1996; Westermann, 2000). Boreal – Boreal palaeogeographic Realm; Tethyan – Tethyan palaeogeographic Realm. A – Arctic Province; BP – Boreal Pacific Province; NWP – North West Pacific Province; NEP – North East Pacific Province; SWP – South West Pacific Province; SEP – South East Pacific Province; WNA – Western Interior of North America; Eu – European Province; AI – African-Indian province; MC – Mediterranean/Caucasian Province.

Furthermore, Page (1996) stated that there was virtually but a single faunal province which could be recognised during the Late Cretaceous, namely the Western Interior of the United States and Canada, from where high levels of endemism at both specific and generic levels have been well documented (e.g., Kennedy & Cobban, 1976; Kauffman, 1986). However, in spite of 'reduced' endemism, Page (1996) introduced fourteen ammonite biogeographical provinces for the Late Cretaceous! Specifically, I find fault with his note that the West Pacific faunal Province (WP) within the Tethyan Realm was barely recognisable on the basis of data available for Japan and the Far East of the former Soviet Union. Using relatively outdated papers by Matsumoto (such as Matsumoto, 1973; Matsumoto *et al.*, 1978) and a single Russian author (Pergament, 1977), Page (1996, p. 786) suggested that only few endemic taxa in those areas, including *Nipponites* in the Coniacian and Santonian, and "some faunal differentiation, perhaps at a provincial level, had occurred. Associated are typical circum-Pacific taxa including Desmocerataceae and Tetragonitaceae...". However, these data are erroneous and need to be corrected. In general, it involves the problem of endemism and provincialism in the Pacific, as well as in other provinces, during the Late Cretaceous.

Kennedy & Cobban (1976) discussed factors which may have controlled ammonite distribution patterns and recognised five basic categories of distribution; pandemic, latitudinally limited, endemic and provincial, disjunctive, and post-mortem. Cecca (1999) outlined the main reasoning behind these and assigned them to two groups, namely factors dependent of ammonite biology (such as post-mortem drift, palaeoecology and dispersal) and those linked to physical factors (that is, high temperature, currents, upwelling and food supply). Naidin (2001) discussed meridian links amongst Late Cretaceous biota of the Northern Hemisphere and illustrated opportunities for faunal migration through the palaeo-Arctic basin, and compared these with the "traditional" views of migrations through the Mediterranean-Atlantic basin. The distribution of some Pacific taxa studied here illustrates trans-Arctic migration. Volkov & Naidin (1994) discussed variations in solar activity during the Late Cretaceous, which led to changes in climate zones, and offered reconstructions of global surface currents. They also proposed that faunal migration through longitudinal seaways which connected with the Arctic basin had been feasible. Spicer (*in* Skelton, 2003) insisted that the Arctic Ocean was effectively an enclosed basin, isolated from the deep-water global system by connections that were shallow (that is, only a few 100 m deep) and that oceanic heat transport during the Cretaceous was limited. However, I see no problem in postulating that migrations of marine faunas from the Pacific into the Arctic, and *vice versa*, were possible, generally during highstand phases such as the Albian or late Campanian.

The first scientist to describe the specific character of Cretaceous faunas from Pacific regions was Vereschagin (1963). He noted significant macrofaunal differentiations, not only between Pacific and European assemblages, but also within the Pacific Realm and proposed to use the term "Pacific Palaeobiogeographic Province". He also discussed some differences between its northern (including Alaska, the Koryak Upland, Kamchatka, Sakhalin, Kuril Islands, Japan, California and British Columbia) and southern (Australia, New Zealand, Antarctica) limbs. Subsequently, Vereschagin (1977) recognised some differences in taxonomic composition between Sakhalin, the Kuril Islands and Japan on the one hand, and Alaska, the Koryak Upland and Kamchatka on the other. In the meantime, Jeletzky (1964) had introduced a new term, "North Pacific

Realm", on the basis of his studies of Jurassic and mainly Early Cretaceous molluscs from the Koryak Upland, Chukotka and Kamchatka peninsulas, and from the Pacific slopes of North America. A decade later, an extensive study programme was set up by a group of Russian scientists, headed by K.M. Khudoley (Khudoley & Rzhosnickaya, 1976). This group prepared the *Palaeobiogeographic Atlas of Pacific Mobile Belt and Pacific Ocean*, using data on the distribution of all ammonites then known from Pacific regions, and illustrated some possible trends in ammonite migrations.

Westermann (2000) reviewed the confused terminology of Early Cretaceous palaeobiogeography. He took into account the drastic changes which occurred following Albian-Cenomanian plate tectonic activity and recommended a reduction of terms used to make the overall picture clearer. Here, I propose a compilation of terms introduced in previous papers (Vereschagin, 1977; Khudoley & Rzhosnickaya, 1976; Page, 1996) and adopt Westermann's (2000) suggestions, using the most recent publications. In my view, the Northwest Pacific Province (NWP, new name) is comprised of Priamurye and Sikhote Alin, Sakhalin and the Kuril Islands, plus Japan, while northeast Russia (the Koryak Upland, Chukotka and Kamchatka peninsulas) and northern North America (Alaska Peninsula, Arctic Canada and British Columbia) constitute the Boreal Pacific Province (BP; after V.A. Zakharov & Rogov, 2003; V.A. Zakharov *et al.*, 2003). Palaeobiogeographical provinces are shown in Figure 15 and the geographical distribution of ammonites is plotted on palaeomaps (Scotese, 2001; see <http://www.scotese.com>) for each stage (Albian to Maastrichtian), and separately for genera and species (see supplementary material available from my website, www.paleo.uni.opole.pl). In my interpretations of the palaeobiogeographical distribution of species, I have treated material that has been assigned to a particular taxon with a query (as indicated by the use of cf., aff. and ex gr.) as indeed belonging to that nominal species, with the exception of those forms which have been commented on specifically.

As noted above, it is possible to subdivide the Pacific into various provinces on the basis of mid- and Late Cretaceous ammonite faunas. In general, this subdivision can be recognised only at the species level; however, there are some intervals where it is even demonstrable at the generic level.

Early Cretaceous (pre-Albian) ammonites and associated macrobiota: a brief review – Rocks of Early Cretaceous age have been recorded mainly from the northeasterly regions of Russia (Fig. 1A) and from Sikhote Alin and Primorye-Priamurye (Fig. 1B), which are characterised by a complex depositional history (Kirillova *et al.*, 2000). Broad connections between the Tethyan and Boreal realms existed during the Berriasian-Hauteriviian. The most diverse macrofaunal assemblage was recorded from Sikhote Alin and Primorye-Priamurye (NWP), characterised by ammonites (*Pseudosubplanites*, *Berriasella*, *Dalmasiceras*, *Substerceras*, *Parodontoceras* and *Fauriella*) and bivalves, such as *Buchia* and *Anopea*. The Valanginian complex includes the ammonite genera *Olcostephanus*, *Neocomites* and *Sarasinella*, in addition to *Buchia* and rare inoceramids (Sey *et al.*, 2004).

In comparison to the southern coast of Russian Pacific regions (NWP), Valanginian macrofaunas from the Koryak Upland are utterly different and can be assigned to the Boreal Pacific province (BP). Bivalves, mainly of the genus *Aucella*, predominate, while belemnites such as *Spanioteuthis* and *Acroteuthis* are rare, and ammonites of the genera *Tollia* and *Polyptychites* even rarer (Vereschagin *et al.*, 1965; Pergament, 1969). I have re-

cently acquired some specimens collected by I.P. Vasecki in the Anadyr River Valley (Koryak Upland) in 1958 and identified as *Olcostephanus* sp. Unfortunately, these specimens are poorly preserved. Belemnites may have reached this area subsequent to a transgressive pulse from the Arctic Province (Russian Platform, Timan Peninsula), where these genera were common during the Early Cretaceous (Gustomesov, 1979; Mutterlose, 1998). Then, following the Hauterivian regression, only in some areas did marine sedimentation take place and the general taxonomic composition of marine biota markedly decreased in diversity. Marine Hauterivian deposits are known exclusively from southeastern Primorye (NWP), where they yield only representatives of the inoceramid genus *Coloniceramus*, as well as along the Penzhyna Gulf coast and at Pekulnej Ridge in the Koryak Upland (BP), where the last belemnites have been collected (Vereschagin *et al.*, 1965; Kirillova *et al.*, 2000; Sey *et al.*, 2004). Members of the genera *Cylindroteuthis* and *Lagonibelus* occurred in the Koryak Upland during that stage, in association with some typically Boreal ammonites such as the *Simbirskites* (Vereschagin *et al.*, 1965). Later, only single representatives of *Cylindroteuthis* are known from the Albian in Alaska (Imlay, 1961), marking the final phase of belemnite occurrence in Pacific regions. However, Yu. D. Zakharov *et al.* (2007) have recently recorded some belemnite remains (listed as Dimitobelidae gen. et sp. indet., *Belemmella?* sp. and Belemnitidae? gen. et sp. indet.) from Santonian-Maastrichtian deposits of the Magellan Rise (central Pacific), whose preservation was such that detailed identification proved impossible. In my view, it is still possible to collect Late Cretaceous belemnites from the Pacific province, as the examples below illustrate. A few years ago, I worked on Cretaceous collections made by other scientists at the CNIGR Museum (VSEGEI) and came across a strange-looking specimen (collected by T.D. Zonova in the 1960s) from Turonian strata at the Penzhina Gulf Coast. Larisa Doguzhaeva (pers. comm., 2009) thinks the specimen looks like an enigmatic belemnite phragmocone, but a detailed microanalytical study needs to be performed. Košťák & Wiese (2008) described *Praeactinocamax* aff. *plenus* (de Blainville), collected in 1973 by the late Dmitry P. Naidin, from the early Turonian of northwest Siberia (Taimyr Region, Arctic province). Those authors proposed that the geographic position of this record could offer explanations for the occurrence of the genus *Praeactinocamax* in the Turonian of the United States Western Interior by migration from the Arctic Ocean. Therefore, the occurrence of belemnites would be even obvious in the Late Cretaceous seas of Far East Russia as, for example, some kind of so-called migration islands or stepping stones. Here I wish to note that the palaeobiogeographical map of the Northern Hemisphere, in North Pole projection, presented by those authors (see Košťák & Wiese, 2008, p. 675, fig. 5), would appear to exclude any Late Cretaceous marine faunas from the areas of Chukotka and the Koryak Upland, since only land is shown for Turonian and especially Maastrichtian time. This begs the question where all those Turonian-Maastrichtian ammonites and inoceramid bivalves came from. I disagree with such palaeogeographical interpretation and present data to the contrary below.

The Barremian-middle Albian time interval is characterised by a gradual sea level rise, reflected in deep-water sedimentation in the Sikhote Alin Basin, along the Penzhyna Gulf coast and in the Koryak Upland, and with a temperature maximum (24.5°C) during the early Barremian (Yu.D. Zakharov *et al.*, 2002). A gradual transgression and climate amelioration consequently caused a gradual increase of biodiversity. The Bar-

remian, shallow epicontinental sea in the Koryak Upland was characterised by a diverse bivalve fauna (*Aucellina*, *Pleuromya*, *Nuculana*, *Tancredia* and *Entolium*), and by the ammonites *Aspinoceras kajgorodzevi* Vereschagin (Vereschagin *et al.*, 1965) and *Eugaudryceras* (*Eutetragonites*) *duvalianus* (d'Orbigny) (Vereschagin *et al.*, 1965; Zonova & Yazykova, 2000). The latter species is also known from Sikhote Alin, Priamurye and Primorye (Zonova & Yazykova, 2000), where it co-occurs with *Spitidiscus* aff. *rotula* (J. de C. Sowerby) and *Pseudohaploceras chinense* Sey & Kalacheva, as well as representatives of the bivalve *Aucellina* (Sey *et al.*, 2004), which become more abundant later during the Aptian. Yu.D. Zakharov *et al.* (1999, 2002) noted the continuation of high temperatures (18.4–25.9°C) at that time and increased levels of biological productivity ($\delta^{13}\text{C}=3.6\text{--}6.8\text{‰}$), in particular during the early Aptian, as based on macrofauna from the Koryak Upland. Takashima *et al.* (2007) presented the first Pacific record of the late Aptian warming event, indicating extreme warmth at mid-latitudes as well. The next temperature maximum (12.5–21.6°C) in the Pacific was documented by Yu.D. Zakharov *et al.* (2002) during the early Albian.

Mid-Cretaceous; Albian-Cenomanian ammonites – From the late Albian onwards, links between the Boreal and Tethyan realms were interrupted by a short-term regression and by active tectonic movements. The Arctic, Boreal Pacific and NWP provinces are more easily recognised, in spite of the just partially occupied territory of Sakhalin Island. This was a comparatively shallow sea, inhabited by only few ammonites, as discussed above. In general, Albian ammonite assemblages from Sakhalin, Primorye and Sikhote Alin (NWP) gradually differentiated from those of northeasterly regions of the Russian Pacific (BP). Iba & Sano (2007a, b) described a bloom of carbonate-platform biota during the Berriasian to early Albian interval in the northwest Pacific, indicating that this area clearly belonged to the Tethyan Realm at the time and documenting a stepwise demise of Tethyan biota during the latest Aptian to middle Albian. Those authors linked that demise, as well as an expansion event in the South Atlantic and Western Interior seaway, to global changes in the ocean current system (especially a change in warm-water circulation) and, possibly, in ocean heat transport triggered by the formation of a new ocean gateway in the mid-Cretaceous. In light of that, it is possible to explain the episodic appearance of 'Arctic' species in NWP, such as *Arcthoplites* (*Subarcthoplites*), *Phyllopachyceras*, *Parasilesites*, *Marshallites* or *Eogunnarites*, which could migrate from the Koryak-Kamchatka palaeobasin in the Arctic province using favourable currents. However, it was not a mass event because these taxa are rather rare in the early Albian of Sikhote Alin and Hokkaido, and extremely rare in Sakhalin. *Arcthoplites* (*Subarcthoplites*) sp. is known also from Albian deposits in the Queen Charlotte Islands, western British Columbia (McLearn, 1972), and from the lower Albian of West Siberia, Arctic province (V.A. Zakharov *et al.*, 2000). Thus, the most obvious path of migration was from Greenland via the Arctic. Iba & Sano (2008; see also Iba, 2009) opined that the demise of the pectinid bivalve genus *Neithea* and the appearance of *Arcthoplites* indicated an early Albian 'cooling' episode during the time of a mid-Cretaceous greenhouse Earth. Some other authors recorded a cooling phase in the latest Aptian-early Albian in the North Sea basin (Mutterlose & Bornemann, 2005; Rückheim *et al.*, 2006). However, as noted above, Yu.D. Zakharov *et al.* (2002, 2004), on the basis of macrofauna from the Koryak Upland and Kamchatka Peninsula, documented high temperatures (12.5–

21.6°C) during the early Albian and a maximum (32-33°C) for the late Albian. This is in correspondence with oxygen isotopic records of calcareous fine-fraction, bulk sediments and rudistid bivalve shells (for example, Steuber *et al.*, 2005), which show that oceanic temperature increased continuously from the early Albian onwards, and reached a maximum in the Turonian. Moreover, numerous scientists assume the Arctic basin to have been fairly warm throughout the Cretaceous (including Kirillova *et al.*, 2000; Skelton, 2003). Palaeobiogeographical data do not suffice in this particular case, especially so because Iba & Sano (2008) did not take into account the occurrence of other 'Arctic' genera such as *Marshallites* and *Eogunnarites*; the palaeobiogeographic distribution of the genus *Arcthoplites* is wider than that of *Eogunnarites* or *Marshallites*. Such a 'cooling' episode should also be backed up by geochemical data. In my view, the late Albian demise in the Pacific was caused by a gradual cessation of links between the Boreal and Tethyan realms, changes in the ocean current system and a shallowing of palaeobasins as a result of plate tectonic reconstructions, and last, but not least, increased volcanic activity which started in the mid-Albian (formation of the giant East Asian belt; see Kirillova *et al.*, 2000). The last-named event explains high temperatures and a concomitant decrease in biotic diversity. However, some Albian taxa survived and continued into the Cenomanian, yet in Sikhote Alin and the Primorye basin existed only during the Cenomanian.

In addition, those so-called 'Arctic' species were distributed widely in Sakhalin, northeast Russia and Japan later, during the early Cenomanian when the Sikhote Alin basin gradually ceased to exist. First of all, the highly diverse, latest Albian-Cenomanian complex of *Marshallites* known from Japan (Matsumoto, 1991b) comprises no fewer than nine species, *M. cumshewaensis*, *M. olcostephanoides*, *M. miyakoensis*, *M. compressus*, *M. hendersoni*, *M. virgatoides*, *M. involutus*, *M. rotundatus* and *M. kossmati*. Assemblages of *Marshallites* are taxonomically diverse in Japan and Koryak-Kamchatka especially during the Cenomanian, consisting of at least ten species (Terekhova, 1969; Matsumoto, 1991b; Alabushev & Wiedmann, 1997; Jagt-Yazykova, research in progress). At the same time, few *Marshallites* have been recorded from the latest Albian in Sakhalin and Sikhote Alin (Yazykova, 2001), and *M. olcostephanoides* is known from the early Cenomanian in Sakhalin. *Marshallites cumshewaensis* and *M. columbianus* have also been recorded from the late Albian-early Cenomanian of British Columbia, Alaska and California (Matsumoto, 1959a, b, 1991b). Matsumoto (1991b) described *Marshallites* as a latest Albian-late Cenomanian genus which occurred in the Indo-Pacific region, but he also noted that some examples from South Africa probably belonged to it, such as '*Gunnarites kalika*' from the Campanian-Maastrichtian as described by Kennedy & Klinger (1985, fig. 34A-C). *Marshallites cf. cumshewaensis* from the Coniacian of Zululand, recorded by the same authors, definitely belongs to this genus. Moreover, Kennedy & Klinger (1985), in their comments on this genus, suggested that *Marshallites* may also occur in New Zealand (with reference to Henderson, 1970), which, when accepted, means that this genus also occurred during the Santonian-Campanian, and also in other provinces of the Tethyan Realm. Probably, some isolated representatives of *Marshallites* really did migrate during Turonian-Coniacian time to the African-Indian (AI) province and later possibly continued southeast towards New Zealand (SEP). This would enlarge the stratigraphical distribution of this genus even further, from the late Albian to the Maastrichtian. However, during the Albian-Cenomanian interval, *Marshallites* occurred only in the

northerly provinces of the Pacific (BP and NWP) and should thus be considered a Pacific endemic. In addition to *Marshallites*, the family Kossmaticeratidae is represented here by *Eogunnarites* sp., *E. vereshagini*, *E. unicus*, *Yokoyamaoceras rarum* and *Y. spinosum*, and all taxa are endemic to northeast Russia.

Migration from Europe via the Arctic is also hinted at by the presence in the Russian Pacific of taxa such as the hoplitids *Anahoplites* sp. and *Sonneratia* sp., with the latter having been found in all three regions (Sakhalin, Primorye and northeast Russia), and the former being restricted to Sakhalin. Representatives of *Sonneratia* were also described from Arctic Canada (Jeletzky, 1964), as well as from California and Oregon (Anderson, 1938; Jones *et al.*, 1965), but comprise only endemic species, which supports the notion of larvae and/or juveniles across the Arctic via favourable currents and, subsequently, successful dispersal, which led to a convergent lineage of this European genus. I believe that representatives of *Anahoplites* and *Sonneratia* from the Russian Pacific probably also belong to some new endemic species or conspecific with those described from Arctic Canada or California and Oregon, but that issue is best deferred to another occasion.

In addition to *Sonneratia*, the family Hoplitidae is represented by gastropplites, that is, *Gastropplites* (*Paragastropplites*) cf. *flexicostatus*, *Neogastropplites* sp. and *N. kamchatkensis*, which are confined to the Arctic province. However, *N. kamchatkensis* is morphologically similar to *N. americanus*, which is widely distributed in the Western Interior and could be its geographical sibling species.

The palaeogeographical distribution of cleoniceratids known from Russian Pacific sections show interesting results as well. First of all, they are represented mostly by species endemic to the north Pacific, and in some case even by genera and subgenera. Thus, in Sakhalin we have recorded *Brewericeras* ex gr. *hulenense* and *Cleoniceras* (*Neosaynella*?) sp.; in Sikhote Alin, *Cleoniceras* (C.) sp. and *Arcthoplites* (*Subarcthoplites*) aff. *belli*; and in northeast Russia, *Cleoniceras* (C.) sp., *C. (Grycia) dubia* and *Arcthoplites* (*Subarcthoplites*) *talkeetnanus*. V.A. Zakharov *et al.* (2000) recorded *C. cf. bicurvatooides* and *Arcthoplites* (*Subarcthoplites*) sp. from West Siberia (Arctic province). Based on data supplied by Jacobs (1992) and Westermann (1996), *Cleoniceras* (C.) and *Arcthoplites* (*Subarcthoplites*) might have been good swimmers, which travelled at greater speeds than other coeval genera (see above), and probably also migrated at some ontogenetic stage from Greenland and Europe via the Arctic, after which successful settlement led to the rise of a new, convergent line of endemic species which characterised the BP, NWP and NEP provinces in the north Pacific realm.

Desmoceratids are widely distributed along the Russian Pacific coast. First of all, these are mostly Pacific taxa, for example, *Desmoceras* (*Pseudouhligella*) from Sakhalin and Sikhote Alin, and *Parasilesites*. *Parasilesites* cf. *bullatus* has been recorded from the Sikhote Alin-Primorye region, but *P. orientalis* appears to be endemic to northeast Russia. Interestingly, the subgenus *D.* (*Desmoceras*), which is worldwide in distribution, is known only from Sakhalin where it is represented by *D. (D.) kossmati*, which is absolutely endemic to Sakhalin and Japan. In addition, there is *Beudanticeras* which is on record from all three regions, but in northeast Russia encompasses more species than in the other two areas, namely *B. aff. glabrum*, *B. (Grantziceras) cf. multiconstrictum* and *B. (G.) affine*, and these three are Pacific (even exclusively Boreal Pacific) species. Only a single, truly cosmopolitan taxon amongst desmoceratids is known from Albian levels,

namely *Puzosia* cf. *lata* from Sikhote Alin. Another representative of this genus, *P. alder-sona* (recorded from Sakhalin), is endemic to the north Pacific and has also been described from California. Thus, the picture is very similar to the previous one, that is, printed over the near-absolute predominance of endemic taxa in general, a few cosmopolitan taxa appeared, but almost exclusively at the generic level, apart of *Puzosia* cf. *lata*, which encompassed endemic species. However, desmoceratids did migrate (either as larvae or juveniles) from AI and MC provinces (a few cases from Eu) via Tethys during this time, and again, after successful dispersal, led to a new, endemic lineage which characterised the north Pacific. At the same time, the difference between Arctic and NWP (and even within NWP, between Sakhalin and Sikhote Alin) is even clearer in desmoceratids than cleoniceratids, because the former probably were not such good swimmers.

The endemism of the north Pacific provinces is very clear also when Phylloceratiidae are considered, represented by the endemic species *Phyllopachyceras chitinatum*, known from Sikhote Alin and northeast Russia. It should be added that *Hypophylloceras* (*Neophylloceras*) *seresitense*, which appeared in Far East Russia during the early Cenomanian, has been recorded from the late Albian in Japan. Moreover, from the Guadalupe Guyot a new, endemic species, *H. (N.) pacificum* Grabovskaya, Mikhailova & Zakharov, was described (see Poyarkova *et al.*, 1988).

The family Gaudryceratidae in the late Albian consists of two species, namely the endemic *Gaudryceras penjiensis* (northeast Russia and Sikhote Alin) and cosmopolitan *Eogaudryceras* (*Eotetragonites*) *duvalianus*, identified only in Primorye from the Aptian-Albian interval. The appearance of the latter species is of note, as is the single lycocera-toid *Protetragonites* cf. *a. aeolus*, collected from the late Albian of Sikhote Alin (which, according to Westermann, 1996, could inhabit depths down to 500 m). Both would have had to be good swimmers, because the occurrence in the Pacific of these European taxa cannot be explained otherwise. *Eogaudryceras* (*Eot.*) *duvalianus* is also known from the Aptian-early Albian of the northern Caucasus, Dagestan (Kasansky, 1914; Druschic & Mikhailova, 1963). *Protetragonites a. aeliformis* Fallot, known from the Aptian of Spain (López Garrido & Orozco, 1970), is similar to *P. a. aeolus* and *P. ex gr. aeolus* was recorded from the early Albian of the western Carpathians, Slovakia (Potfaj *et al.*, 2008), meaning that migration via the Tethys would have been feasible.

Some taxa were identified exclusively from northeast Russia (BP province), having no records (yet) in Sakhalin or Sikhote Alin, namely *Proplacenticerias sutherlandbrowni* (widely distributed also in NEP; see McLearn, 1972), the widespread *Mortoniceras* and *Stoliczkaia* (*Lamnayella*) cf. *japonica*, endemic to the Pacific. Interestingly, that last-mentioned form is also known from Japan, but not from Sakhalin.

An assemblage of Albian heteromorph ammonites, recorded from the Russian Pacific coast, is comprised exclusively of turrilitids, namely *Mariella* sp., *M. aff. circumtaeniata*, *Turrilites* sp., *Pseudhelicoceras* sp. and *P. carlottense*. There is no doubt that these are cosmopolitan genera, but in most cases, identification at species level is fraught with difficulties because of poor preservation. For now, it cannot be stated whether these forms comprised endemics or more cosmopolitan forms, in addition to *P. carlottense*, which is known from the Arctic, BP and NEP provinces.

Supporting the hypothesis of larval/juvenile dispersal via the Arctic, albeit indirectly, is the absence of all above-mentioned species from the southern provinces of the

Pacific realm (SWP and SEP). It appears that the huge Pantalassa Ocean during the Albian was divided into two by some barrier(s) which should have been long lived and comparatively stable, for example, currents either too cold or too strong, or, alternatively, high volcanic activity emersion (volcanic islands?; Magellan mountains?). However, sea level was very high and the absence of north Pacific forms in the south could also be connected with superplumes and dysoxic conditions, which would have hindered ammonite larvae in distributing. The late Albian OAE1 event has been recorded from many sections in the Pacific realm (Yazykova, 2004).

As noted above, the Albian/Cenomanian boundary interval was marked by some abiotic events, including anoxia, tectonic movements, volcanic activity and a global regression, which led to a decrease in biotic diversity. For example, some families and subfamilies disappeared completely (Cleoniceratidae, Silesitoidinae, Beudanticeratinae, Sonneratiinae; see Wright *et al.*, 1996). However, the early Cenomanian transgression saw the entry of immigrant species, such as *Phylloceras* (*Neophylloceras*) *seresitense*, *Anagaudryceras buddha*, *Parapuzosia* (*Austiniceras*) *austeni*, *Mantelliceras* sp. and *Acanthoceras* sp. The formerly diverse palaeobasin of Primorye (Amur River valley and Sikhote Alin) almost stopped to exist, following global tectonic perturbations. Only single representatives of two desmoceratids, *Puzosia* cf. *lata* and *Desmoceras* (*Pseudouhligella*) sp., and the turrilitid, *Mariella* aff. *circumtaeniata*, make up the Cenomanian ammonite assemblages here. At the end of the Cenomanian, the basin disappeared altogether. In contrast, Sakhalin and northeast Russia supported diverse complexes of macro- and microfaunas. The above-mentioned cosmopolitan taxa probably migrated here via Tethys, but endemics still predominate. The widest distribution in the Russian Pacific is recorded by representatives of Pacific genera which appeared during the late Albian, but reached their maximum development in the Cenomanian, that is, *Marshallites*, *Eugunnarites* and *Neogastrolites*. During the Cenomanian, connections with other basins must have been severely limited, especially across the *Turrilites costatus* and *T. acutus* levels, the so-called Middle Cenomanian Eustatic Low (Hancock, 2003). It is truly amazing to see that, at exactly the same time, the same species occur in so many, distant regions (England, Crimea, Mangyshlak, Western Interior, Russian Far East), in particular since these are benthic heteromorph species. The only explanation is that larval and/or juvenile dispersal during the short-term early Cenomanian was highly successful in establishing these species in all these areas that were already well and truly separated at the time. A prime example of a global correlative level.

The late Cenomanian OAE2 (Yazykova, 2004) probably was the main trigger to the extirpation of Cenomanian faunas. The Cenomanian/Turonian boundary mass extinctions reflected in the diversity of every biotic group, both at the generic and specific level. Some ammonite families and subfamilies disappeared, for example, Turrilitidae, Acanthoceratinae and Lyelliceratidae. Amongst species known from the Russian Pacific, not a single Cenomanian taxon survived this crisis.

Late Cretaceous; Turonian-Maastrichtian ammonites – The Cenomanian/Turonian highstand is also characterised by a temperature increase, which some scientists indicated to be, with seasonal changes, between 15.9 and 21.7°C (Yu. D. Zakharov *et al.*, 2005) and, subsequently, a high level of biological productivity ($\delta^{13}\text{C}=3.2\text{--}4.3\%$) in the middle-late Turonian (Yu. D. Zakharov *et al.*, 2002). However, some recent data propose that an ice

cap up to ~60 % the size of that of the modern Antarctic ice sheet was probably located on the South Pole during the Turonian (Bornemann *et al.*, 2008), but that view is highly contested.

The euomphaloceratine *Kamerunoceras shimizui* is known exclusively from Sakhalin and Japan (Matsumoto *et al.*, 1978). This is a typically endemic species, but other representatives of this genus are known from elsewhere in the Boreal Realm, for example, Eu, WNA (Western Interior of North America) and NEP, and also from the Tethys (AI, MC and SEP; see Fig. 15). Other acanthoceratids found in Sakhalin rather belong to cosmopolitan taxa which are known from different regions in the world, that is, *Pseudaspidoceras* cf. *armatum*, *Romaniceras* (*Yubariceras*) *ornatissimum* and *R.* (*R.*) aff. *pseudodeverianum*. Migrating in from AI and MC provinces, they first occupied NWP and only some of them appeared in the Arctic province. However, their representation is not abundant, either in Sakhalin or in northeast Russia. Similarly, single specimens only document the families Collignoniceratidae (*Subprionocyclus* sp.) and Vascooceratidae (*Fagesia* sp.) in Sakhalin, whereas there was successful dispersal distribution and speciation in Japan. There are no collignoniceratids or vascooceratids in northeast Russia.

In general, the palaeobasin of Penzhina Gulf coast (Kamchatka Peninsula, Koryak Upland) was inhabited by endemic taxa during the Turonian, to almost one hundred percent. Cosmopolitan forms are known only from Sakhalin; however, there are many taxa in common between these two areas. Phylloceratids include *Hypophylloceras* (*Neophylloceras*) *ramosum*, gaudryceratids comprise *Gaudryceras denseplicatum*, *G. tenuiliratum*, *Anagaudryceras limatum* and *Zelandites mihoensis*, and tetragonitids *Tetragonites glabrus*. All are widespread, yet Pacific species.

The global *Scaphites* facies can be clearly traced in northeast Russia and Sakhalin, from where only endemic representatives are known: *Scaphites planus*, *Yezoites puerculus*, *Y. subplanus*, *Y. pseudoaequalis* and *Y. teshioensis*. Species of *Yezoites* predominate, while at the same time *Scaphites* is the dominant genus in Eu or MC (see, amongst others, Atabekian & Akopian, 1970; Kaplan *et al.*, 1987; Wiese *et al.*, 1996).

In comparison to the Cenomanian when the family Desmoceratidae was represented by a few widely distributed taxa, in the Turonian this group included only endemics, that is, *Puzosia* (*M.*) *takahashii*, *Jimboiceras planulatiforme*, *Pachydesmoceras pachydiscoide*, *Tragodesmoceroides subcostatus* and *Damesites damesi intermedius*, while in northeast Russia only *Kitchinites ishikawai* and *J. planulatiforme* are known. The sole member of the Pseudotissotiidae, *Hourcquia pacifica*, is endemic to NWP.

Heteromorphs are comparatively diverse in the Turonian. Of note is that of four nostoceratids identified, namely *Nostoceras* (*Eubostrychoceras*) *japonicum*, *Nipponites mirabilis*, *N. sachalinensis* and *Hyphantoceras* aff. *reussianum*, only the first two are known from northeast Russia, but all of them occur in Sakhalin, including the only one which is truly cosmopolitan, *H. reussianum*. Two endemic forms represent the family Diplomoceratidae, one of them occurring in Sakhalin, *Scalarites mihoensis*, the other in northeast Russia, *S. scalaris*. In total, the degree of endemism rose during the Turonian and continued this trend in the Coniacian.

The family Phylloceratidae is still represented by the Pacific species *H.* (*N.*) *ramosum* as well as the gaudryceratids *Gaudryceras denseplicatum* and *G. tenuiliratum*, joined now, however, by *Anagaudryceras politissimum*, an immigrant from southern India, which much later, during the Maastrichtian, was widely distributed in AI, SWP, SEP and NEP,

but in NWP it is confined either to the Coniacian (Sakhalin) or to the late Campanian-early Maastrichtian (Japan). This could also be connected with some temperature maximum, recorded for the Coniacian and Campanian (Yu.D. Zakharov *et al.*, 2002).

Tetragonitids are represented by *Tetragonites glabrus*, which probably appeared already in the Cenomanian of Alaska (BP), and later extended into the NWP, NEP and AI provinces. A similar way of distribution can be determined for *T. epigonus*, which first appeared in the Turonian of Japan (NWP) and later extended to the Eu, AI and SWP provinces.

The appearance of *Binneyites* in Sakhalin is interesting. This genus was held to be endemic to the northern Western Interior of North America (WNA province). Since only a single specimen is known from the northwest Pacific, probably, this is an example of post-mortem drift distribution (compare Kennedy & Cobban, 1976).

Of the family Desmoceratidae only *Kitchinites ishikawai* survives, but new (sub)species appeared as well, such as *K. japonica*, *Jimboiceras mihoense*, *Damesites damesi intermedius* and *D. sugata*. All of them are Pacific endemics, with the exception of *D. sugata*, which is also known from the AI and south Eu provinces. *Hourcquia pacifica*, the endemic pseudotissotiid, survived into the Coniacian.

The Coniacian of Sakhalin and Japan sees the first member of the family Pachydiscidae, an endemic to NWP, *Menuites (Anapachydiscus) sutneri*. This constitutes one of the earliest appearances of *Menuites (Anapachydiscus)*; an even earlier one was noted from post-Turonian strata in Durban, South Africa (Kennedy *et al.*, 1973).

Immigrant taxa in the Coniacian are the collignoniceratids *Forresteria (F.) alluaudi* and *Peroniceras*, which probably appeared here by favourable warm currents across the Pacific from NEP. The family Scaphitidae presents a high degree of provincialism; of five scaphitids occurring in the Coniacian, two are known from Sakhalin (*Yezoites puerculus*, *Y. subplanus*) while the others are from northeast Russia (*Yezoites teshioensis*, *Y. derivatum* and *Scaphites talovkensis*). All representatives of the family Nostoceratidae are endemic, that is, the genus *Nipponites* with two species, *N. sachalinites* and *N. bacchus*, as are diplomoceratids (*Scalarites mihoensis* and *Pseudoxybeloceras (P.) obstrictum*).

In the Russian Pacific, the Santonian was characterised by a continued increase of taxonomic diversity, in spite of an abrupt temperature drop across the Coniacian/Santonian boundary (Yu.D. Zakharov *et al.*, 2002), which is reflected in the disappearance of many Coniacian forms. However, as noted before, ammonites did not really depend of climate changes and usually rapidly recovered following such environmental crises.

Some long-lived species still occur, such as the phylloceratid, *Hypophylloceras (Neophylloceras) ramosum*, and the gaudryceratids *Gaudryceras tenuiliratum* and *G. denseplicatum*. However, these two families also are represented by new species in northeast Russia, that is, *Phyllopachyceras forbesianum* (Phylloceratidae), and, in Sakhalin, *Phyllopachyceras ezoense* (Phylloceratidae), *Anagaudryceras yokoyamai* and *Zelandites kawanoi* (Gaudryceratidae).

The family Tetragonitidae is represented by the endemic *Saghalinites saghalinensis*, *Tetragonites glabrus*, *T. epigonus* and *T. popetensis*, and one immigrant species, *Pseudophyllites indra*, which appeared only in northeast Russia. In Far East Russia, collignoniceratids are represented by the subfamily Texanitinae, also with a high degree of provincialism. *Texanites (Plesiotexanites) kawasaki* and *Protexanites (P.) bontanti shimizui* are known only from Sakhalin, the latter being an immigrant from Eu province, while *P. (P.)*

fukazawai and *P. (P.) shoshonensis* have been recorded exclusively from northeast Russia (BP Province).

Desmoceratids are still represented by species and subspecies which appeared earlier, that is, *Kitchinites ishikawai*, *K. japonica*, *Damesites sugata* and *D. damesi intermedius*. Two others, *D. d. damesi* and *Hauericeras angustum*, are new and both are endemic. *Hauericeras angustum* probably originated from *H. gardeni*, after migrating in from AI to Japan.

There is a markedly wide distribution of pachydiscids, comprising *Eupachydiscus haradai*, *Menuites (M.) menu*, *M. (M.) naibutiensis* and *M. (M.) japonicus*. It appears that *M. (M.) menu* first appeared in the Koryak Upland, later in Sakhalin and Japan, and gave rise to two endemic species, *M. (M.) naibutiensis* and *M. (M.) japonicus*, which in turn disappeared from the Pacific and migrated elsewhere, more specifically South Africa and southern India (AI province), where they appeared during the Maastrichtian (Forbes, 1846; Kennedy & Henderson, 1992a, b; Kennedy & Klingler, 2006).

The family Kossmaticeratidae shows the highest degree of provincialism, with three species of *Yokoyamaoceras* known from northeast Russia only, namely *Y. venustum*, *Y. jimboi* and *Y. kotoi*. In Sakhalin only two of these, *Y. jimboi* and *Y. ishikawai*, have been recorded.

One of the most interesting events in the Santonian is the appearance of the mortoniceratine (brancoceratid) *Mortoniceras? kawasakii*, recorded by Kawada (1929). Elsewhere in the world, representatives of *Mortoniceras sensu stricto* are completely unknown from post-Albian/lower Cenomanian strata. Probably, Kawada's specimen is best reassigned to the subgenus *Mortoniceras (Submortoniceras)*, which is known from the Campanian of California and Oregon (Anderson, 1958), and could thus represent the precursor of species of *Mortoniceras (Submortoniceras)* in California.

Interestingly, all heteromorphs known from the Santonian are endemic to BP and NWP provinces. Nostoceratids include *Nipponites bacchus*, *Hyphantoceras orientale* and *H.(?) heteromorphum* (found in Sakhalin and Japan), and *H. reussianum* and *H. yabei* (found in Sakhalin and the Koryak Upland), while the family Diplomoceratidae is represented by mostly Sakhalin endemics. Only two species were found in northeasterly regions, viz. *Polyptychoceras (Po.) pseudogaultinum* and *Po. (S.) vancouverense*, while others are known from Sakhalin (*Neocrioceras spinigerum*, *Diplomoceras notabile*, *Pseudoxybeloceras (Ps.) obstrictum*, *Ps. (Ps.) quadrinodosum*, *Ps. (Ps.) sakhalinum* and *Ps. (Subptychoceras) yubarensis*) and only two were found in Japan (*Polyptychoceras (Po.) pseudogaultinum* and *Po. (Subptychoceras) yubarensis*).

As noted above, the Campanian was characterised by the greatest taxonomic diversity amongst Russian Pacific Cretaceous ammonites and a temperature maximum (20.6-26.1°C) (Yu.D. Zakharov *et al.*, 2002). A high level of diversity characterises the family Gaudryceratidae, which is represented by seven species: *Anagaudryceras yokoyamai*, *A. nanum*, *Gaudryceras tenuiliratum*, *G. mamiyai*, *G. striatum*, *G. crassicostatum* and *Zelandites kawanoi*. However, all of these are endemic to the NWP province, with the exclusion of *G. tenuiliratum*, which also occurs in the Arctic province and is known from South Africa, where it appeared in the Coniacian.

The family Tetragonitidae appears to have evolved furthest, with seven species known from Campanian deposits in Far East Russia. Two of these are cosmopolitan (*Pseudophyllites indra* and *Tetragonites epigonus*), another two (*T. glabrus* and *T. popetensis*) are characterised by wider distribution than the remaining three, *T. crassus*, *Saghalinites*

teshioensis and *S. saghalinensis*, which are endemic to the north Pacific. Representatives of *Saghalinites* have not yet been found in northeast Russia.

The family Phylloceratidae demonstrates a particularly interesting picture. On the one hand, three Santonian taxa survive (*Hypophylloceras* (*Neophylloceras*) *ramosum*, *Phyllophyceras forbesianum* and *Ph. ezoense*), but on the other, a new species made its appearance in the late Campanian in Sakhalin, *H. (N.) nera*, which previously was known only from the latest Maastrichtian of southern India, Japan and northeast Mexico. It is possible that *H. (N.) nera* was derived from *H. (N.) ramosum*, and later distributed into the SEP and AI provinces, similar to *H. (N.) ramosum*, known also from Maastrichtian deposits of those provinces. Thus, I interpret *H. (N.) ramosum* as the precursor of *H. (N.) nera*, *H. (N.) hetonaiense* and *H. (N.) surya*. In this way, the similar character of morphological features between the two-last named makes sense. They originated from the same ancestor, but in different environments, representing vicariant species. However, there is one locality where both these species have been identified, namely central Chile (Salazar *et al.*, 2010), which, as I see it, can only be ascribed to a misidentification. *Hypophylloceras (N.) surya* has previously been recorded from Chile (Stinnesbeck, 1986) and *H. (N.) hetonaiense*, as interpreted by Salazar *et al.* (2010), might be also *H. (N.) surya*.

Amongst desmoceratids, represented by *Hauericeras angustum*, *Kitchinites ishikawai*, *Puzosia* (*Mesopuzosia*) *densicostata*, *Damesites d. damesi*, *D. sugata*, *D. semicostatus* and *Desmophyllites diphyloides*, only the last-named one is cosmopolitan, having migrated in from the MC and AI provinces, probably across the Pacific. Skelton & Wright (1987) described a Caribbean rudistid bivalve from the Campanian-Maastrichtian of Oman and explained its appearance by larval dispersal along a corridor of shallow staging posts like islands and/or seamounts which served as stepping stones. This means that other groups could have migrated via similar routes across the Pacific Ocean.

During the Campanian, kossmaticeratids demonstrated absolute endemism and provincialism. Three species are known from northeasterly regions, namely *Yokoyamaoceras jimboi*, *Y. venustum* and *Y. kotoi*, while only one (*Y. ishikawai*) was found in Sakhalin.

A diverse lot of pachydiscids (*Canadoceras multicoatum*, *C. kossmati*, *C. mysticum*, *C. yokoyamai*, *Menuites menu*, *M. japonicus*, *M. naibutiensis*, *M. (Neopachydiscus) naumanni*, *M. (Anapachydiscus) fascicostatus*, *M. (A.) arrialoorensis*, *Eupachydiscus haradai*, *Urakawites rotalinooides* and *Pachydiscus (Pachydiscus) aff. egertoni*) is on record, with almost all of them endemic. Excluded are *P. (P.) aff. egertoni*, an immigrant from the AI province with records from the late Campanian of Nigeria (Zaborski, 1985; Cobban & Kennedy, 1995), and the Maastrichtian of Madagascar (Collignon, 1938), Nigeria, southern India and Mississippi (Cobban & Kennedy, 1995). Further, *M. (A.) arrialoorensis* is also known from Madagascar and *Eupachydiscus haradai* has been recorded from South Africa, Madagascar and southern India (Collignon, 1938; Cooper & Greyling, 1996).

Representatives of the Collignoniceratidae are known only from the Koryak Upland, being the endemics *Protexanites fukazawai* and *P. aff. shoshonensis*. These record the last appearance of this family and of the subfamily Texanitinae, both here as elsewhere in the world (Wright *et al.*, 1996).

The diversified heteromorphs comprise representatives of the families Diplomoceratidae (*Neancyloceras aff. pseudoarmatum*, *Neancyloceras sp.*, *Neocrioceras sp.*, *Diplomoceras notabile*, *Pseudoxybeloceras (Schlueterella) kawadai*, *Ps. (Ps.) quadrinodosum*, *Polyptychoceras*

(*Po.*) *lineatum*, *Po.* (*Subptychoceras*) *yubarense*, *Po.* (*S.*) *vancouverense* and *Ryugasella ryugasense*) and Baculitidae (numerous *Baculites* sp. in Member 2 of the Krasnoyarka Formation in southern Sakhalin, of latest Campanian age; T.D. Zonova, pers. comm., 2008), plus *B. occidentalis* and *B. rex*. These show a comparatively low degree of endemism.

Following reduction of taxonomic diversity at the Campanian/Maastrichtian boundary interval and a relatively low diversity during the early Maastrichtian, the assemblage of Pacific ammonites almost completely recovered. Two families witnessed their highest diversity in the whole of the Late Cretaceous, viz. Gaudryceratidae and Phylloceratidae, and pachydiscids are both diverse and numerous with new morphological types. In spite of high endemism of Maastrichtian faunas in the Russian Pacific in general, some taxa really did show a wide distribution. For example, amongst phylloceratids, *Hypophylloceras* (*Neophylloceras*) *ramosum*, *H. (N.) nera* and *H. (N.) hetonaiense* are known from elsewhere across the globe, and only *H. (N.) victriense* and *Phyllopachyceras ezoense* are restricted to the north Pacific. New evolutionary trends and a high speciation rate have been recorded for the family Gaudryceratidae, which is represented by nine species (*Anagaudryceras matsumotoi*, *A. seymouriense*, *Gaudryceras venustum*, *G. denmanense*, *G. tombetsense*, *G. hamanakense*, *G. makarovense*, *Zelandites japonicus* and *Z. varuna*), the last-named being truly cosmopolitan.

Representatives of the family Tetragonitidae, *Tetragonites popetensis*, *Pseudophyllites indra* and *Saghalinites* sp., are characterised by a relatively wide distribution. Also interesting is the appearance of the kossmaticeratid *Brahmites* (*Subbrahmaites*) *sachalinensis*, which clearly is an endemic subgenus and species, but this event is correlative with the FAD of *Brahmites* (*B.*) *brahma* Forbes in southern India, southwest France, Madagascar (Collignon, 1938) and Tunisia (Goolaerts *et al.*, 2004), and also with the occurrence of *B. (B.) kossmati* in Western Australia (Henderson & McNamara, 1985).

The family Pachydiscidae is represented by ten endemic species, with *Canadoceras multicosatum*, *C. kossmati*, *P. (Pachydiscus) subcompressus* and *P. (Neodesmoceras) japonicus* characterising the early Maastrichtian, whereas *Pachydiscus* (*P.*) *kobayashii*, *P. (P.) soyaensis*, *P. (P.) flexuosus*, *P. (Neodesmoceras) gracilis*, *Patagiosites alaskensis* and *Pseudomenuites* sp. are common in the late Maastrichtian. These species are all widely distributed in the Koryak and Chukotka uplands, in Sakhalin and Japan, but only two of them, *P. (P.) kobayashii* and *Patagiosites alaskensis*, have been recorded from Alaska (Matsumoto, 1959a; Toshimitsu *et al.*, 1995). However, it should be borne in mind that endemic representatives of the subgenus *Neodesmoceras* are known from Alaska, southern India, Madagascar, South Africa, southern France and the northern Western Interior. In general, pachydiscid faunas in the late Maastrichtian of the Russian Pacific contain solely endemic taxa. Interestingly, in different areas of the world, *Pachydiscus sensu stricto* typically reveals maximum diversity during the late Maastrichtian, but in every province mostly endemic species predominate. To date, *Pachydiscus* (*P.*) *neubergicus* (von Hauer), *P. (P.) j. jacquoti* Seunes, *P. (P.) gollevillensis* (d'Orbigny) and *P. (P.) armenicus* Akopian & Atabekian appear to be the only pachydiscids with a (near-)worldwide distribution. In this respect, it is particularly important to realise, as shown by various workers during recent years, that the first appearance of *P. (P.) Neubergicus* is highly diachronous. Moreover, confusion with another late Maastrichtian taxon, *P. (P.) noetlingi* Kennedy, with records from Baluchistan and the Netherlands, may have occurred, in particular for records from, for example, Crimea. I am certain that not all material re-

ferred to *P. (P.) neubergicus* is properly identified. For instance, records from Far East Russia would be best assigned either to *P. (P.) kobayashii* or *P. (P.) soyaensis*. Indeed, morphological features of *P. (P.) kobayashii* closely resemble those of members of the 'jacquoti group' (including *P. (P.) noetlingi*), of which it might be a vicariant.

In comparison to the Campanian, heteromorph ammonites are not so diverse, with only two families and four species in all: *Nostoceras (Didymoceras) cf. californicum* Anderson, *Neancyloceras pseudoarmatum*, *Diplomoceras notabile* and *Glyptoxoceras* sp. Many sea-mounts have now been charted, inclusive of data on their fossil records, for example, *Zelandites japonicus*, *Saghalinites* sp. and indeterminate belemnites, the latter from the Magellan Rise, Ioan Guyot (Yu.D. Zakharov *et al.*, 2007).

In summary, as a result of present analyses of the palaeobiogeographical distribution of mid- and Late Cretaceous ammonites from the Russian Pacific coast, it is apparent that, first of all, migration routes for ammonites, and some other faunal groups, across the Pacific Ocean, and via the Arctic, rivalled those via Tethys, which are the ones most often postulated in the literature. During some periods, one of these routes was more important than the other, and some taxa appear to have preferred one way above the other. Secondly, but no less important, is that it has proved absolutely necessary to provide a new interpretation of the palaeobiogeography of the Arctic Ocean in general, and the Russian Arctic in particular. First and foremost, this concerns the Maastrichtian when there must have been a connection between the Pacific and the Arctic, perhaps in the form of numerous temporary (maybe seasonal) channels via the Koryak Upland, Pontonei Mountains and Penzhyna Gulf Coast similar to those which definitely existed between the Arctic and the north of the Western Interior of North America. In this respect, I stress that the future Bering Strait could have played a significant role – this might have opened up temporarily already during the Maastrichtian, because intense tectonic activity and numerous palaeogeographical transformations have been recorded for the Pacific and Tethys peripheral zones during the latest Cretaceous (Zharkov *et al.*, 1998).

Mid- to Late Cretaceous regional bio-events compared to allegedly global events

Introduction – Kauffman (1986; see also Kauffman *et al.*, 1996) demonstrated that mass extinction events ranked amongst the most important correlative tools in global bio-events. He presented the Western Interior of North America as an example of the various types and levels of bio-events, and their probable causes, as well as their importance to high-resolution regional and global correlations. Since 1996 the same principles have been applied to the Cretaceous of the Russian Pacific coast in an attempt to demonstrate that, in spite of the high degree of faunal endemism and provincialism, there are possibilities for global correlation (see, for example, Noda & Matsumoto, 1998; Zonova & Yazykova, 1998; Yazykova, 2004). The general trends in ammonite evolution (or in any biotic group, for that matter) in the boreal Pacific are the same as elsewhere (Yazykova, 1996, 2002, 2004). Bio-event by bio-event (and/or zone by zone) changes in morphotypes and ecosystems in total are closely comparable to those observed in other regions, because it is assumed that the organic world is largely dependent of the global rules which govern local environments. Kauffman (1977) did not consider the Russian Pacific and Japan as regions characterised by high endemism. In fact, data for the West-

ern Interior (Kauffman, 1986) are the most closely comparable to the present results.

In a recent paper, Paul & Lamolda (2009) argued that bio-events based on first (FAD) or last appearance (LAD) datums sometimes may not be recognisable in all sections, not even within one region particularly when these events are based on a single taxon. In addition, whenever recognisable, they may turn out to be diachronous. Such data support the proposal of present work for a revised global correlation by: 1 – a choice of regional key sections and production of detailed biostratigraphical schemes based on different faunal groups with precise regional correlation (using some regional stages or horizons); 2 – determination in regional key sections of all known types of biotic and abiotic events; and 3 – global correlation on the basis of both biostratigraphical zonation and events between key sections and identification of a GSSP section.

A regional key section for Sakhalin was described from the south of the island in the valley of the River Naiba. For northeast Russia there are three areas where key sections should be accepted, but only after proper documentation of events: the Penzhyna Gulf Coast (partially described in Zonova, 2004), the Koryak Upland (partially described in Dundo *et al.*, 1971, 1974) and Chukotka Peninsula, inclusive of Chukotka Upland (not described to date).

Below, a brief description for some of the regional bio-event levels recorded for each (sub)stage in Russian Pacific sections is presented. All bio-events recorded on the Russian Pacific coast are compared to those from other regions in the world, which have often been assumed to be global in nature, but, with some exceptions, have not yet been studied in detail.

Late Albian migration bio-event – The late Albian migration event is best recognised in Sikhote Alin and northeast Russia. The basin which existed in Sikhote Alin during late Albian-early Cenomanian time was inhabited by ammonites of both Tethyan and Boreal realms, as were Sakhalin, Japan and northeast Russia, plus taxa which are never found in all three regions at the same time (Zonova & Yazykova, 2000, 2001, 2004). The Sakhalin palaeobasin is characterised by a taxonomically rather poor complex of ammonites in comparison to Sikhote Alin and northeast Russia, but, in total, the late Albian ammonite assemblage shows a maximum diversity (Fig. 16).

A closely similar pattern has been outlined (Amédro & Robaszynski, 2005) for northern California where the succession yielded both exotic ammonites of the Tethyan realm (for example, *Oxytropidoceras* and *Lyellicerias*) as well as taxa from the Boreal realm (*Gastrolites*, *Pseudopulchellia*). Those authors discussed possible correlations by ammonites between the Albian sequences of northern California, and European and Arctic provinces. A succession of confinement periods, with numerous endemic faunas, followed by periods of open communications and the appearance of cosmopolitan forms was determined. Amédro & Robaszynski (2005) concluded that the stratigraphic distribution of Albian, non-endemic ammonites of northern California and Europe was largely controlled by global eustatic events, and showed some possible ways of migration for endemic forms.

Probably, the late Albian migration event is linked to the middle/late Albian bio-event that has been recorded from North America, Europe, India and North Africa, and which is characterised by short-term extinctions among ammonite genera and species, especially in northern temperate faunas (for example, *Gastrolites* and *Pseudopulchellia*)

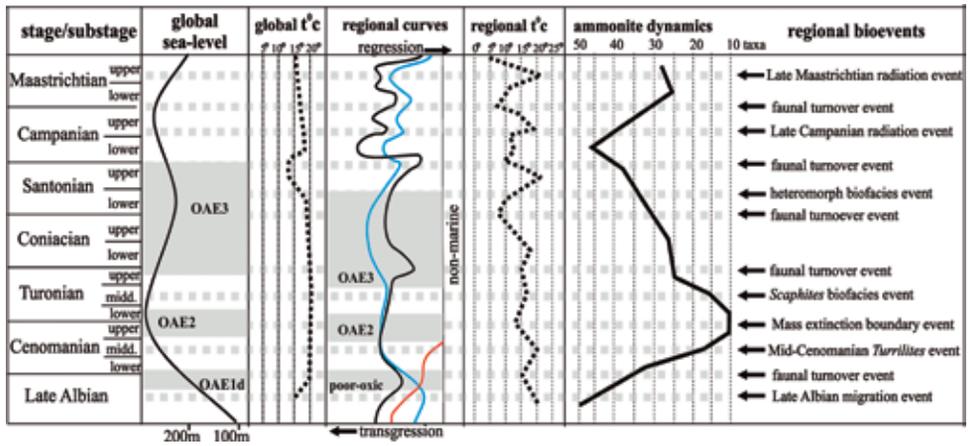


Fig. 16. Regional bio-events recorded in Far East Russian regions and changes of total number of species of mid- and Late Cretaceous ammonites in the area (present paper); global sea-level curves by Haq *et al.* (1987), global palaeotemperature curves by Skelton (2003) and regional palaeotemperature curves modified after Yu.D. Zakharov *et al.* (1996, 1998, 2006); generalised scheme of records of transgression and regression from Sikhote Alin (red line), Japan, Sakhalin (black line) and Arctic palaeobasins (blue line) based on Matsumoto (1977a, 1980). Stages are shown without calibration to absolute time.

and warm-temperate subtropical taxa (for example, *Oxytropidoceras* and *Lyelliceras*) connected with OAE1b and OAE1c (Barnes *et al.*, 1995). Thus, those ammonites which disappeared in the regions mentioned could have migrated into more marginal areas such as California, northeast Russia, Sakhalin and Sikhote Alin during the late Albian.

Albian/Cenomanian bio-event: global faunal turnover event – The Early/Late Cretaceous boundary is marked by a complete disruption of links between the Pacific and European realms, and, coincidentally, between the Boreal and Tethyan realms. From the early Cenomanian onwards, the Far East Russian region can be divided into a southern and a northern Pacific province. During the Late Cretaceous, the northern Pacific province may be described generally as Boreal (Far East Russia, Alaska, Japan, California, Queen Charlotte Islands), whereas the southern Pacific province is Tethyan (New Zealand, Australia). The palaeobasin of Primorye and Sikhote Alin emerged during the Cenomanian.

An abrupt faunal turnover marks the Albian/Cenomanian boundary (Fig. 16). In the Russian Pacific, with the exception of two species, all Albian taxa disappeared at this boundary. A short-term, global turnover in marine biota following OAE1d (Barnes *et al.*, 1995) characterises this level in many regions of the world (Fig. 16). The OAE1d (Fig. 17) has been recorded from Japan and Sakhalin as well (Hirano & Takagi, 1995; Hasegawa, 1997; Hirano & Fukuji, 1997; Toshimitsu & Hirano, 2000; Hasegawa *et al.*, 2003). The disappearance of Albian forms and the first occurrence of new species and even genera, as well as of new morphotypes amongst ammonites and inoceramids, is also typical of this boundary in the Pacific Realm.

Mid-Cenomanian Turrilites bio-event – Representatives of *Turrilites costatus* and *T. acu-*

tus are known from middle and late middle Cenomanian deposits of Sakhalin Island and the Penzhyna Gulf coast, respectively, as well as from the Koryak Upland (Verezhagin *et al.*, 1965; Terekhova & Mikhajlova, 1977) and Japan (Hayakawa & Nishino, 1999; Shigeta, 2001; Matsumoto & Takahashi, 2001). These two levels could possibly be correlated with the so-called mid-Cenomanian Regressive Trough (*Turrilites costatus* event) and the mid-Cenomanian eustatic low (*Turrilites acutus* records), respectively (Hancock, 2003). This eustatic lowstand has been recorded from northwest Europe, western Kazakhstan, Texas, Colorado and South Dakota. Monnet & Bucher (2007) proposed the last occurrence of *T. acutus* as a marker for the middle/late Cenomanian boundary since that species was also abundant and widely distributed. This marker is useful in Sakhalin as well as for northeasterly regions of Russia.

Cenomanian/Turonian boundary extinction bio-event – At the Second International Symposium on Cretaceous Stage Boundaries in Brussels in 1995, it was recommended that the main criterion for recognition of the Cenomanian/Turonian boundary be the first appearance datum of the ammonites *Watinoceras devonense* Wright & Kennedy (see Bengtson *et al.*, 1996). Kennedy *et al.* (2000, 2005) have suggested the first occurrence of the inoceramid *Mytiloides puebloensis* Walaszczyk & Cobban for the base of the Turonian. Neither of these species has been recorded from Far East Russia. A single specimen has been noted from the late Cenomanian in Japan, as *Watinoceras(?)* sp., but with the remark that it was “somewhat questionable” (Toshimitsu & Hirano, 2000, p. 580). The first detailed analysis of correlation between Turonian sequences in Japan and those in northwest Europe was performed by Hancock *et al.* (1977), who demonstrated the numerous difficulties that arose during attempts to determine any possible correlative criteria on the basis of appearance and/or disappearance of zonal indexes.

The Cenomanian/Turonian boundary remains one of the best-studied major extinctions in the world and is a perfect event-correlative level, albeit occasionally with its own specific character in each biogeographic province and region. Recently, a first attempt to analyse that bio-event in Sakhalin has been carried out (Yazykova *et al.*, 2004 and herein). No Cenomanian taxa survived this crisis, not in Sakhalin nor in northeast Russia. Correlation is based on association with OAE2 (Fig. 17), the appearance of the ammonite genera *Fagesia* and *Jimboiceras*, and the inoceramid *Mytiloides*, thus the appearance of new ammonite morphotypes in general. Kauffman (*in* Barnes *et al.*, 1995) referred to this bio-event as the most dynamic, second-order, stepwise mass extinction during a sea level highstand. The disappearance of the *Pergamentia* group amongst inoceramids in Far East Russia (Yazykova *et al.*, 2004) can be correlated with the extinction of the *Inoceramus pictus* group in European areas and/or the Western Interior of North America (Kennedy & Cobban, 1991a, b; Harries *et al.*, 1996; Kauffman & Harries, 1996; Kennedy *et al.*, 2000) as well as western Siberia (Khomentovsky *et al.*, 1999; V.A. Zakharov *et al.*, 2003). This could be used as an additional criterion for this boundary.

Mid-Turonian Scaphites biofacies event – The criterion recommended at the Second International Symposium on Cretaceous Stage Boundaries in Brussels in 1995 for the lower/middle Turonian boundary, namely the FAD of *Collignoniceras woollgari* (Mantell) (Bengtson *et al.*, 1996), cannot be accepted in the Russian Far East, because this species has not been yet found there. Meanwhile, *C. woollgari* and some other representatives of this genus have been found in Japan. So, probably, these taxa may also be demonstrated

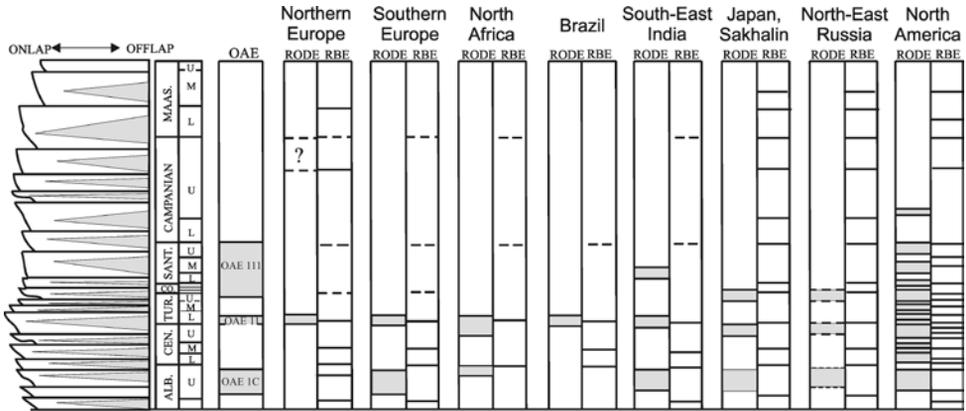


Fig. 17. Global cycle chart (Haq *et al.*, 1987), together with global oceanic anoxic events (OAE), regional oxygen depletion events (RODE) and regional bioevents (RBE) in northern and southern Europe, North Africa, Brazil, southeast India, North America (modified from Kauffman & Hart, 1995) and Japan

in future to occur at least in Sakhalin, which was in close proximity to the Japanese islands, or, alternatively, *C. woollgari* just did not migrate further than Japan. This is coincident with other differences in the taxonomic composition of macrofaunal complexes from Sakhalin and Japan, which also could be explained by the appearance of temporary biogeographical barriers between these two areas.

A wide distribution of heteromorph ammonites, particularly the development of the *Scaphites* facies in the late early/middle Turonian, has been recorded from numerous regions in the world, occurring at the same level (Tanabe, 1979; Kaplan *et al.*, 1987; Hirano *et al.*, 2000). In Far East Russia, numerous representatives of *Scaphites* co-occur with species of the genera *Nipponites* and *Hyphantoceras* (Vereschagin *et al.*, 1965; Mirolubov in Poyarkova, 1987; Zonova & Yazykova, 1998; Yazykova *et al.*, 2004). The *Scaphites* facies is one of the best global correlative levels. However, in the northwest Pacific at the same level appeared another heteromorph genus, *Scalarites*, which would be a good marker for the early/middle Turonian boundary here.

Middle-late Turonian boundary bio-event – The regression at the end of the Turonian in Russian Pacific basins is marked by the appearance of trachyostracans, that is, coarsely ornamented ammonites, and heteromorphs indicative of relatively shallow waters (Tanabe, 1979; Westermann, 1996). However, the taxonomic diversity of ammonites decreased at this level (Fig. 16). The warm, shallow-marine basin was conducive to inoceramid development, a group which showed a high diversity during the boundary interval (Zonova & Yazykova, 1998). Numerous small-sized inoceramid species occur in the early/late Turonian boundary interval (*Inoceramus teshioensis*, *Mytiloides incertus* Zone in Sakhalin and *Inoceramus multiformis* Zone in northeast Russia) (Zonova & Yazykova, 1998; Yazykova, 2004). Usually, all inoceramid species which appeared in the early and middle Turonian are of average size typical of most inoceramid species. In the latest Turonian all of them are small and numerous. Commonly, fossil taxa in the immediate aftermath of mass extinction events are smaller compared to those of pre-extinction as-

semblages – probably the ‘Lilliput effect’ (Harries & Wani, 2009). In the study area, there is a level just prior the next faunal turnover at the Turonian/Coniacian boundary. This level is traceable from northeast Russia to Sakhalin and Japan, and possibly could be correlated with the *waltersdorfensis* II Event in the late Turonian of Germany and Poland (Walaszczyk & Wood, 1999), which is also characterised by the occurrence of small-sized inoceramids of the *waltersdorfensis* group. Bivalves are sensitive ecologically, and the presence of small-sized inoceramids could both signify a mass extinction and environmental changes such as higher salinities or temperature.

Turonian/Coniacian faunal turnover event – The main criteria for the recognition of the Turonian/Coniacian stage boundary proposed at the Second International Symposium on Cretaceous Stage Boundaries in Brussels in 1995, such as the first occurrence of *Forresteria* (*Harleites*) *petrocoriensis* for Europe and of *F. peruana* and *F. brancoi* for North America, and the first occurrence of *Cremnoceramus rotundatus* (*sensu* Tröger, *non* Fiege) (see Kauffman *et al.*, 1996), which is now referred to as *C. deformis erectus* (Meek) (compare Walaszczyk & Wood, 1999; Walaszczyk, 2000), cannot be applied to the Russian Pacific because the index species are absent. Moreover, it has been suggested that representatives of the genus *Forresteria*, in fact, make their first appearance in the latest Turonian (Kennedy & Cobban, 1991b; Walaszczyk & Cobban, 2000; Kennedy & Walaszczyk, 2004). This means *Forresteria* can no longer be used as an index for the base of the Coniacian, leaving the first occurrence of *Cremnoceramus deformis erectus* as the sole criterion (Kauffman *et al.*, 1996; Walaszczyk & Wood, 1999; Walaszczyk & Cobban, 2000).

So far, In Russian Pacific sections, only a single specimen of *Forresteria* has been collected from the upper part of the Coniacian sequence there (Mirolubov *in* Poyarkova, 1987). This boundary In Russian Pacific sections is based on some local criteria, such as the LAD of *Jimboiceras planulatiforme* and the FAD of *J. mihoense*, as well as on the first occurrence of *Anagaudryceras politissimum* and *Gaudryceras denseplicatum*. Also, the base of the Coniacian is marked by the occurrence of a new *Scaphites* assemblage (endemic species) in Sakhalin and northeast Russia, similar to Europe (Kauffman & Hart, 1995; Kauffman *et al.*, 1996).

In North America, as well as in Europe (Kauffman & Hart, 1995), this bio-event is marked, first of all, by the loss of the cosmopolitan *Mytiloides* inoceramid group lineage and the widely distributed ammonite genus *Prionocyclus*. These inoceramids are replaced by the *Cremnoceramus erectus* group. Amongst ammonites, *Peroniceras* is a newcomer.

The appearance of various representatives of the *Inoceramus uwajimensis* group marked the base of the Coniacian in the Russian Far East and Japan together with *Peroniceras*, which ousted *Subprionocyclus*, and *Jimboiceras mihoense* replacing *J. planulatiforme* (Zonova & Yazykova, 1998). That event may be coincident with the mass occurrence of inoceramids of the *Volviceras* group in western Siberia (Khomontovsky *et al.*, 1999; V.A. Zakharov *et al.*, 2003) and with the *Cremnoceramus erectus* fauna (Walaszczyk & Wood, 1999; Walaszczyk, 2000) in Europe. *Inoceramus uwajimensis* Yehara is probably a vicariant species of *Cremnoceramus erectus*.

Approximately at the early/late Coniacian boundary interval, another radiation of new species of the heteromorph ammonite genera *Scaphites*, *Scalarites* and *Nipponites* is noted, and, in total, the taxonomic diversity increased (Fig. 16). Probably this bio-event could be put forward to characterise the early/late Coniacian boundary, after it has been

properly documented from other regions. All of these mentioned taxa disappeared at the end of this stage in the Russian Pacific.

Coniacian/Santonian faunal turnover event – The exact position of the Coniacian/Santonian boundary is still very problematic in the Russian Far East (Yazykova & Zonova, 2002) as well as in Japan (Toshimitsu *et al.*, 2007). The first appearance of the ammonite genus *Texanites* was rejected as the main marker for this boundary at the Second International Symposium on Cretaceous Stage Boundaries in Brussels in 1995. The prime marker recommended there, that is the FAD of *Cladoceramus undulatopticatus*, cannot be applied in Far East Russia, nor in Japan. Isolated occurrences of *Inoceramus* sp. aff. *Cl. undulatopticatus* are known from the late Santonian of Sakhalin, co-occurring with *I. (Platyceramus) kawasakii* (Zonova *et al.*, 1993). The Coniacian/Santonian boundary in Japan is situated at the limit between the *Inoceramus uwajimensis/I. mihoensis* and *Inoceramus amakusensis* zones, which is equated with the base of the *Texanites collignonii/T. quinquenodosus* Zone (Toshimitsu *et al.*, 2007).

In western Siberia, a mass occurrence of species of the inoceramid genus *Sphenoceramus* was recorded from the earliest Santonian, together with *Oxytoma tenuicostata* (Roemer) (Khomentovsky *et al.*, 1999; V.A. Zakharov *et al.*, 2003). The FADs of *Inoceramus amakusensis* and *Texanites (Plesiotexanites) kawasakii* are the two best criteria for the base of the Santonian Stage in Sakhalin (Yazykova, 1996, 2002), in spite of the fact that both are endemic. However, lending support to this interpretation is the co-occurrence of these taxa with the cosmopolitan ammonites *Desmophyllites diphylloides* and *Phyllopychyceras forbesianum*. The former is widely distributed in the Santonian-Campanian, with records from Oman, southern India, North Africa, Western Australia, North America (inclusive of the Western Interior), southern Argentina, Angola, Pondoland and Madagascar (Collignon, 1969), as well as the Campanian of Corbières (southern France) and Crimea (Henderson & McNamara, 1985; Kennedy, 1995; Arkadiev *et al.*, 2000; Klingler *et al.*, 2001). The latter appeared in the Pacific and later extended in the Santonian to earliest Maastrichtian of Alaska, Spain (Bay of Biscay), southern India, Madagascar, British Columbia (Jones, 1963), California, New Zealand, Western Australia, Antarctica, Argentina, northern Germany, Austria, Galicia (Henderson, 1970; Ward & Kennedy, 1993), as well as the Maastrichtian of northeast Mexico (Ifrim *et al.*, 2004) and central Chile (Salazar *et al.*, 2010).

Correlation problems again might be resolved by refined studies of bio-events. The gradual decrease in ammonite and inoceramid taxonomic diversity, as observed in the Coniacian succession and possibly triggered by a renewed regression and a slight temperature drop (Yu.D. Zakharov *et al.*, 1996, 1998, 2002), came to a halt at the beginning of the Santonian. The Coniacian/Santonian faunal turnover, characterised by the same evolutionary trends, has been documented from many places across the globe (Kauffman & Hart, 1995; Hallam & Wignall, 1997).

Late Santonian heteromorph biofacies event – Near the early/late Santonian boundary, macrofaunal taxonomic diversity increased again, linked to a global sea level rise and an increase in temperature. New taxa, representing new morphotypes, appeared, especially new genera of heteromorphs. This bio-event could be proposed for the early/late Santonian boundary as soon as it has been documented in detail from regions elsewhere.

Santonian/Campanian faunal turnover event – None of the criteria recommended at the Second International Symposium on Cretaceous Stage Boundaries for Santonian/Campanian boundary, that is, the extinction of the crinoid genus *Marsupites*, the FAD of the ammonite *Placenticerus bidorsatum* and the belemnite *Goniotentis granulataquadrata* (see Hancock & Gale, 1996), is applicable either in Sakhalin, northeast Russia or Japan, because the taxa in question have not been recorded from these areas. The Santonian/Campanian boundary in Sakhalin as currently marked by the first appearance of the inoceramid bivalve *Inoceramus nagaoi* Matsumoto and the ammonite *Anapachydiscus* (*Neopachydiscus*) *naumanni* (Yazykova, 2002; Yazykova *et al.*, 2002); these two criteria are also applicable in Japan (compare Toshimitsu *et al.*, 1995). Additionally, the base of the Campanian can be defined, both in Sakhalin and adjacent Hokkaido (Matsumoto, 1977a; Toshimitsu *et al.*, 1995), by the LAD of *Texanites* and the FAD of *Phyllopachyceras ezoense* (Yazykova, 1996, 2002).

Vishnevskaya & Basov (2007) recorded a mass extinction event amongst radiolarians at the Santonian/Campanian boundary and the appearance of new taxonomic assemblages in the earliest Campanian in the sections along the Russian Pacific coast and compared this bio-event with other regions in the world. Recent magnetostratigraphic analyses for Sakhalin, Hokkaido, Shikoku, the Western Interior and California (Kodama, 2003) show a good match across the Santonian/Campanian boundary, as well as for two levels within the Campanian.

The bio-event of near-total disappearance of inoceramids at the Santonian/Campanian boundary occurs in western Siberia. There is just a single record of *Inoceramus nagaoi* Matsumoto & Yeda from the earliest Campanian, which is a criterion in Sakhalin, northeast Russia and Japan, and an explosion in taxonomic diversity of dinocysts in the upper water levels (Khomentovsky *et al.*, 1999; V.A. Zakharov *et al.*, 2003) and anoxia close to the sea floor. It seems that, in many other regions, Campanian assemblages of marine dinocysts are diverse and abundant (see for example Soliman *et al.*, 2009), while assemblages of different macrofaunal groups (Yazykova, 1996, 2002, 2004) occur in the early survival period following the Santonian/Campanian biotic crisis.

Early/late Campanian radiation bio-event – A distinct level of faunal radiation recorded across the early/late Campanian boundary (Yazykova *et al.*, 2002) is traceable from northeast Russia, through Sakhalin and Japan, and into Europe, for example, in southern Poland (Jagt-Yazykova, research in progress). In the Russian Far East this level is marked by the onset of a shallow-water facies with abundant ammonites, new morphotypes of inoceramids, and new taxa of gastropods and non-inoceramid bivalves. The highest diversity is found amongst benthic groups and some planktonic forms are associated. Representatives of some biotic groups form coquina-like beds. In southern Poland, in sections in the Miechów area, the early/late Campanian interval is marked by a regressive hardground surface and the lower Campanian is characterised by an abundance of fossils (Jagt *et al.*, 2004). The biotic event(s) at the early/late Campanian level in different regions of the world may constitute a good correlative marker level, but need further study.

Schmidticeramus schmidti is known from the late Campanian of Alaska and British Columbia (recorded under the name of *Sphenoceramus schmidti* by Haggart *et al.*, 2009). It is the main constituent at this late Campanian level along the western Pacific coast.

However, on the other side of the Pacific, *S. schmidti* occurs in the late Santonian together with another species of radially ribbed inoceramid and different ammonites, forming coquina beds. Again, it is not possible to correlate on the basis of this taxon only, but one has to consider the entire complex of biological and lithological features. The level described from British Columbia and Alaska may be correlative with the *Hoplitoplacentoceras vancouverense* Zone (Ward, 1978; Haggart *et al.*, 2009).

The early/late Campanian boundary can be recognised in other groups as well, for example, mosasaurs, which appeared in many regions at this level, so that there is evidence of a wide-ranging biotic event throughout the water column, from plankton to the top of the food chain (Lindgren, 2004; Jagt, 2005). Vishnevskaya (2009) noted remarkable taxonomic changes in early and late Campanian radiolarian associations, which may reflect environmental changes within the palaeobasins of Sakhalin, the Koryak Upland and Kamchatka. During Campanian time, a general reduction in taxonomic diversity amongst heteromorphs is typical of Russian Pacific regions.

Campanian/Maastrichtian faunal turnover event – The first occurrence of *Pachydiscus* (*P.*) *neubergicus*, the marker for the Campanian/Maastrichtian boundary, cannot be applied in Sakhalin. The few finds from the Russian Far East (Vereschagin *et al.*, 1965; Zonova *et al.*, 1993; Yazykova, 1994) stem from late Maastrichtian deposits. It is possible that the Pacific specimens are either not conspecific with *P. (P.) Neubergicus* and previous identifications are erroneous, or that they are conspecific, but appeared in the Pacific much later. Alternatively, there is also the possibility of misidentification and it could be that these finds from the Russian Pacific actually belong to different species (A. Alekseev, pers. comm., 2004). A revision of all specimens from Sakhalin, the Koryak Upland and Kamchatka that have been labelled *Pachydiscus* (*P.*) *neubergicus* and *P. (P.) gollevillensis*, with detailed comparisons with the holotypes of both principally European species is in preparation.

The FAD of *P. (P.) Neubergicus* as definition of the base of the Maastrichtian was ratified by IUGS (Odin & Lamaurelle, 2001). Instead of using just a single faunal event, an arithmetic mean of twelve biohorizon levels is now employed, and level 115.2 at the quarry at Tercis les Bains (Landes, France) is the recommended level for placement of the GSSP for the boundary (Odin, 2001). None of these biohorizons (ammonites, dinoflagellates, planktonic and benthic forams, inoceramids and calcareous nannofossils) can be applied in Far East Russia. Calcareous nannofossils have not been recorded yet here, and planktonic foraminifera are both extremely rare and poorly preserved (Turenko *in* Poyarkova, 1987; Peryt *in* Yazykova *et al.*, 2004; D. Peryt, pers. comm., 2009).

However, there are biohorizons specific to the Pacific, marking a bio-event which is correlatable with the Campanian/Maastrichtian boundary in that area. First of all, there is the disappearance of most Campanian ammonite and inoceramid taxa, and the FADs of *Pachydiscus* (*P.*) *subcompressus* and *P. (Neodesmoceras) japonicus*. Both pachydiscids are widely distributed Pacific species (Yazykova, 1991; Yazykova, 1994, with references therein). This level is matched by a similar horizon in Japan (Toshimitsu *et al.*, 1995). Moreover, this boundary can be recognised by the appearance of the inoceramid *Shachmaticeramus* (Zonova *et al.*, 1993) characterised by a peculiar chess-board construction of the ligament strip.

Early/late Maastrichtian inoceramid extinction event and late Maastrichtian ammonite radiation event – The early/late Maastrichtian boundary is marked by the worldwide demise of most inoceramid bivalve lineages (Ward *et al.*, 1991; MacLeod, 1994), an abrupt extinction of rudistid bivalve-dominated ecosystems (Johnson & Kauffman, 1990) and a great reduction in the diversity of shallow, warm-water, level-bottom communities, the so-called 68 Ma Extinction bio-event *sensu* Kauffman & Hart (1995). Those authors also noted a general cooling and eustatic fall under way at this time (Kauffman & Hart, 1995, p. 301). Nifuku *et al.* (2009) described the stratigraphically youngest finds of *Pachydiscus (P.) flexuosus* and '*Inoceramus*' *awajiensis* Matsumoto from the early late Maastrichtian, around 300 m below the Cretaceous/Paleogene boundary in Japan. Based on those data, they claimed that the mass extinction of inoceramids and ammonites took place in the North Pacific 2.3-5.0 myr prior to the K/Pg boundary.

In the Russian North Pacific, a decrease of inoceramid diversity is also recorded at this level; only a few new species appeared, but their representatives are not numerous and the youngest amongst them have been collected from 100 m below the Cretaceous/Paleogene boundary in Sakhalin (Zonova *et al.*, 1993). However, *Tenuipteria(?) awajiensis* and *Korjakkia kociubinskii* Pokhialajnen have been recorded from the late late Maastrichtian in Sakhalin and Koryak Upland, respectively (Pokhialajnen, 1988; Zonova *et al.*, 1993).

A bloom and radiation event for the ammonite families Pachydiscidae, Phylloceratidae and Gaudryceratidae marks the early/late Maastrichtian boundary in the Russian Far East. Phylloceratidae and Gaudryceratidae predominated, and reached their maximum species diversity in the Late Cretaceous. Most early Maastrichtian forms disappeared during the late early Maastrichtian, possibly as a result of short-lived, subfreezing conditions which, as Yu.D. Zakharov *et al.* (2002, 2004, 2006) noted, could occasionally have occurred in the Northern Hemisphere. However, new species appeared at the base of the late Maastrichtian (a temperature maximum was recorded here by Yu.D. Zakharov *et al.*, 2006; see Fig. 16 herein) and rapidly distributed across the entire northwest Pacific provinces, extending even to the northeast Pacific coast (Ifrim *et al.*, 2004). That radiation was one of the fastest during the Late Cretaceous. The taxonomic diversity of ammonites reached levels of the late Turonian (Fig. 16).

A migratory pathway must have existed between the western Tethys and the Pacific Ocean during Maastrichtian time, allowing faunal interchange through northeast Mexico, and leading to a mixture of cephalopod assemblages from different latitudes and an increase in faunal diversity (Ifrim *et al.*, 2004). Pacific ammonites (mostly from northerly regions) and the coleoid *Naefia neogaeia* were interpreted by Ifrim *et al.* (2004) as cold-water faunal elements, indicative of a minor cooling event in the northeast Pacific. The appearance in the late Maastrichtian in Sakhalin of warm-water species such as *Brahmaites*, *Zelandites varuna* and *Pseudophyllites indra* may be indicative of a warming event. Of note, in this respect, is also the occurrence of *Diplomoceras cylindraceum* in the late Maastrichtian of Far East Russia and Mexico, as elsewhere in the world.

However, the youngest ammonites in Sakhalin were found in the highest 1.5 m below the 20-cm bed of green clay in the Sinegorsk Formation at the Naiba section, which represents the Cretaceous/Paleogene boundary in Sakhalin (Yazykova, 2004). Concretions from this level yielded well-preserved representatives of *Zelandites japonicus*, *Gaudryceras* sp., *Neophylloceras* sp. and *Tenuipteria(?) awajiensis*. This is the highest bed of

concretions (a temperature minimum having been recorded by Yu.D. Zakharov *et al.*, 2005; Fig. 16 herein); such beds occur comparatively regularly (every 2-3 m) in Member 5 of the Krasnoyarka Formation. The next youngest concretion layer, approximately 4-5 m below the K/Pg boundary, yields representatives of seven ammonite (sub)genera, that is, *P. (Pachydiscus)*, *P. (Neodesmoceras)*, *Hypophylloceras (Neophylloceras)*, *Gaudryceras*, *Anagaudryceras*, *Zelandites* and *Diplomoceras*. At the Zumaya (Spain) and Hendaye (France) sections (Wiedmann & Kullmann, 1996 with references; see also Ward & Kennedy, 1993), eight genera were recorded 15 m below that boundary, namely *Neophylloceras*, *Gaudryceras*, *Saghalinites*, *Pseudophyllites*, *Vertebrites*, *Anapachydiscus*, *Pachydiscus* and *Diplomoceras*. In the uppermost 0.5 m below the boundary at Zumaya, *Neophylloceras ramosum*, and at Hendaye, *Gaudryceras* sp., *Pachydiscus gollevillensis* and *Pachydiscus* sp. have been recorded. In general, deep-water, long-lived phylloceratids and lycoceratids were dominant among the last ammonoids (Wiedmann & Kullmann, 1996). Probably, the extinction of these two long-lived stocks, which had survived various previous perturbations during the whole Cretaceous, left other groups highly vulnerable and prone to extinction.

Cretaceous/Paleogene mass extinction bio-event – Above the green clay bed in the Sinegorsk Formation at the Naiba section in Sakhalin, sandy mudstones yield a Danian fauna (spores and pollen, and bivalves; see Poyarkova, 1987). There are no ammonite finds known above this level in Sakhalin, nor are there in northeast Russia and Shikotan Island (Kuril Islands), where the last inoceramids and ammonites have been found in the Malokurilsk Formation. In Shikotan, the contact between the Malokurilsk and Zelenovsk formations is considered to equate with the Cretaceous/Paleogene boundary, but it has not been described in detail.

Conclusions

1. Endemicity and provincialism in the Pacific realm make determination of stage boundaries in the region difficult. Correlation with other areas (such as Europe, United States Western Interior, Pacific coast of North and South America) can only be based on event stratigraphy; not just extinction events, but all types of biotic events need to be considered.
2. The above-mentioned issues also concern other areas where it is difficult to find representatives of the proposed boundary criteria for the various stages. This underscores the usefulness of the definition of local stages within local key sections, to improve the usefulness of the standard (GSSP) sections to many different areas across the globe. For example, the usage of New Zealand regional stages (alongside the worldwide stage names) is one such an example, as are the old Russian and Japanese stratigraphic subdivisions, now obsolete, but nevertheless highly useful (Yazykova, 2004).
3. A detailed analysis of ammonite evolution, based on mid- and Late Cretaceous sections from the Russian Pacific coast and a comparison with other provinces across the globe, fails to find support for a decreasing trend in ammonite diversity since the late Albian, as outlined in textbooks and numerous other publications. On the contrary, ammonites displayed a high adaptive ability after each extinction event, from each of which they recovered and re-radiated.

4. During the mid- and Late Cretaceous, fourteen regional bio-events were recorded and compared to those from other regions in the world (Figs. 16, 17), viz. the late Albian migration bio-event; Albian/Cenomanian bio-event: global faunal turnover event; mid-Cenomanian *Turrilites* event; Cenomanian/Turonian boundary extinction bio-event; mid-Turonian *Scaphites* biofacies event; mid/late Turonian boundary bio-event; Turonian/Coniacian faunal turnover event; Coniacian/Santonian faunal turnover event; late Santonian heteromorph biofacies event; Santonian/Campanian faunal turnover event; early/late Campanian radiation bio-event; Campanian/Maastrichtian faunal turnover event; early/late Maastrichtian inoceramid extinction event and late Maastrichtian ammonite radiation event; Cretaceous/Paleogene mass extinction bio-event.
5. The final demise of ammonites must have been sudden, that is, catastrophic. Only a small number of heteromorph species briefly extended into the Paleocene in some places (for example, New Jersey, Denmark, the Netherlands).

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Plate 1

Figs. 1-3. *Eogunnarites unicus* (Yabe, 1904), NCB-RGM 617946 (leg. V.P. Pokhialajnen, 1962); early Cenomanian (*Parajaubertella kawakitana* Zone) at locality 2163 (River Izvilistyj), upstream portion of River Es-gichninvaam, Penzhyna Gulf coast, northeast Russia.

Fig. 4. *Calycoceras (Newboldiceras) cf. orientale* Matsumoto, 1959c, NCB-RGM 617947 (leg. E.D. Volkonskaya, 1960); early Cenomanian (*Parajaubertella kawakitana* Zone) at locality 2016 (Pekulnej Ridge) in the River Vesnovannaya valley, northeast Russia (see also Pl. 2, fig. 1).

Scale bars represent 10 mm.

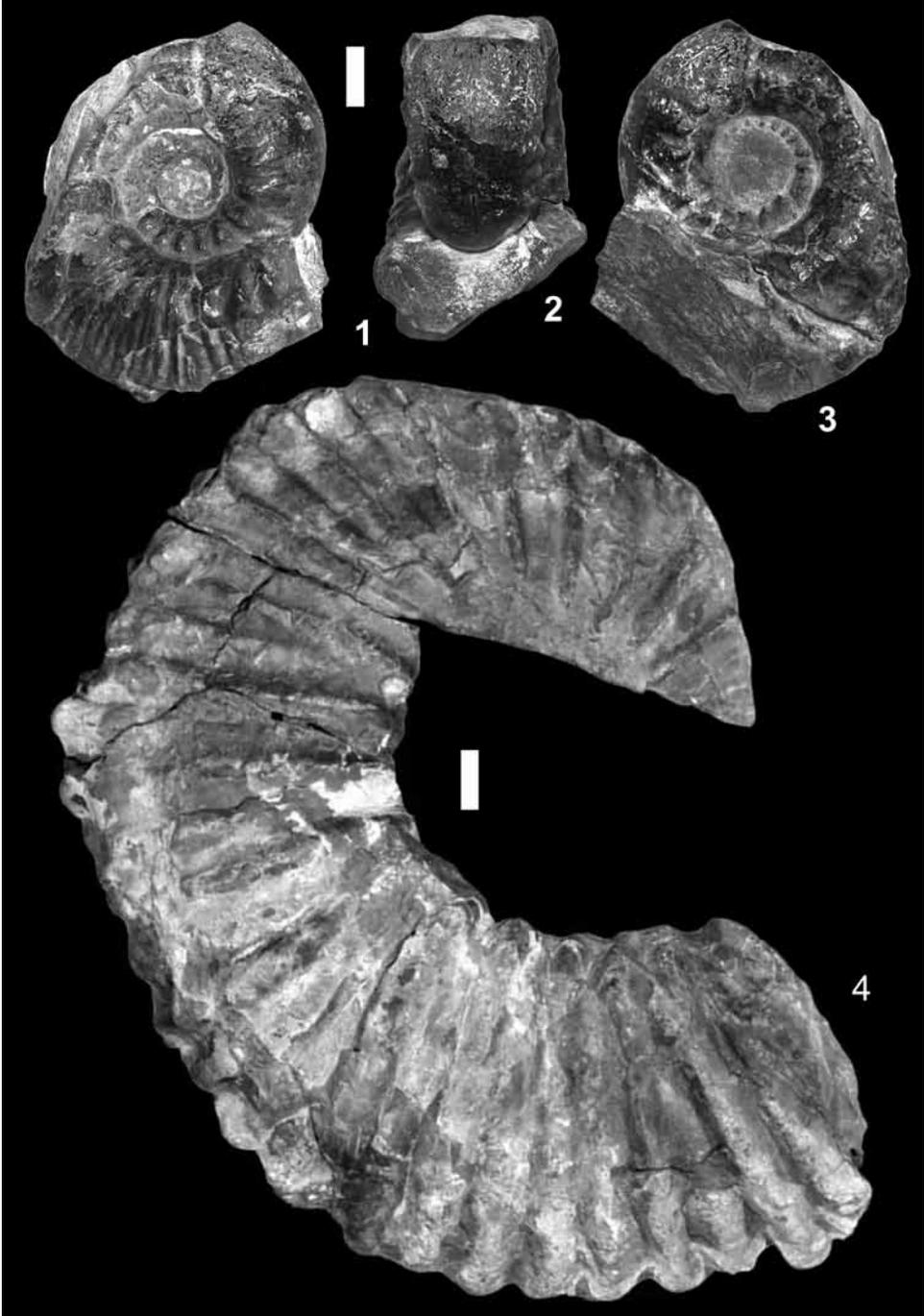


Plate 2

Fig. 1. *Calycoceras* (*Newboldiceras*) cf. *orientale* Matsumoto, 1959c, NCB-RGM 617947 (leg. E.D. Volkhonskaya, 1960); early Cenomanian (*Parajaubertella kawakitana* Zone) at locality 2016 (Pekulnej Ridge) in the River Vesnovannaya valley, northeast Russia (see also Pl. 1, fig. 4).

Figs. 2-7. *Parajaubertella kawakitana* Matsumoto, 1942, NCB-RGM 617948 (leg. T.D. Zonova, 1972); early Cenomanian (*Parajaubertella kawakitana* Zone) at locality 104 (River Golodnyj in the River Penzhyna valley), northeast Russia.

Scale bars represent 10 mm.

Plate 3

Figs. 1, 2. *Jimboiceras planulatiforme* (Jimbo, 1894), NCB-RGM 617949 (leg. E.A. Yazykova, 1999); middle Turonian, Bykov Formation, Member IV (*Jimboiceras planulatiforme* Zone) at locality 2, River Kluch Najdenova in River Naiba valley, Sakhalin.

Figs. 3-5. *Nipponites sachalinensis* Kawada, 1929, NCB-RGM 617950 (leg. T.D. Zonova, 1970), late Turonian, Bykov Formation, Member IV (*Jimboiceras planulatiforme* Zone) at locality 213, River Naiba, near the village of Chetwertjy uchastok.

Scale bars represent 10 mm.

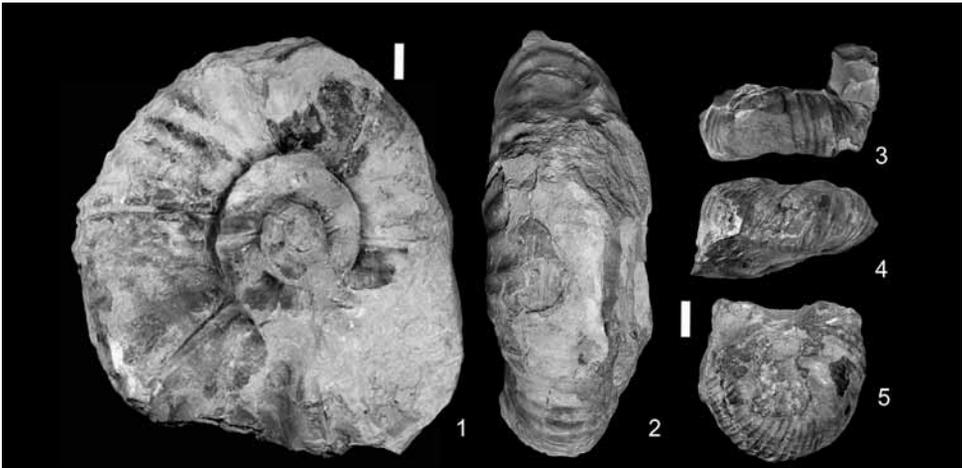
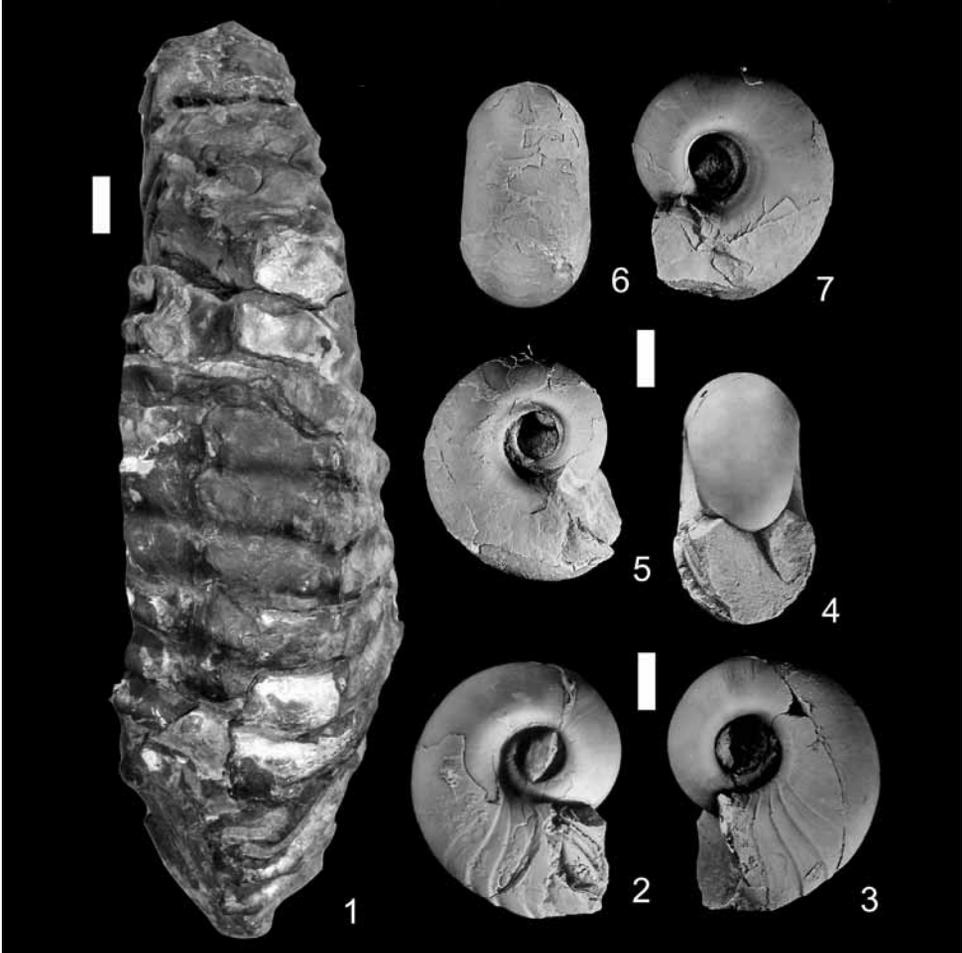


Plate 4

Fig. 1. *Jimboiceras* cf. *planulatiforme* (Jimbo, 1894), NCB-RGM 617951 (leg. T.D. Zonova, 1960), late Turonian, Bykov Formation, Member V (*Jimboiceras planulatiforme* Zone) at locality 0128, River Gurjevka in the River Naiba valley, Sakhalin.

Figs. 2-6. *Damesites ainuanus* Matsumoto, 1957.

Figs. 2, 3. NCB-RGM 617952 (leg. A. Zhyljakov, 1979), early Coniacian, Bykov Formation, Member VI (*Jimboiceras mihoense* Zone) at locality 2249, River Firsovka, Sakhalin.

Figs. 4-6. NCB-RGM 617953 (leg. T.D. Zonova, 1960), late Turonian, Bykov Formation, Member V (*Jimboiceras planulatiforme* Zone) at locality 0128, River Gurjevka in the River Naiba valley, Sakhalin.

Scale bars represent 10 mm.

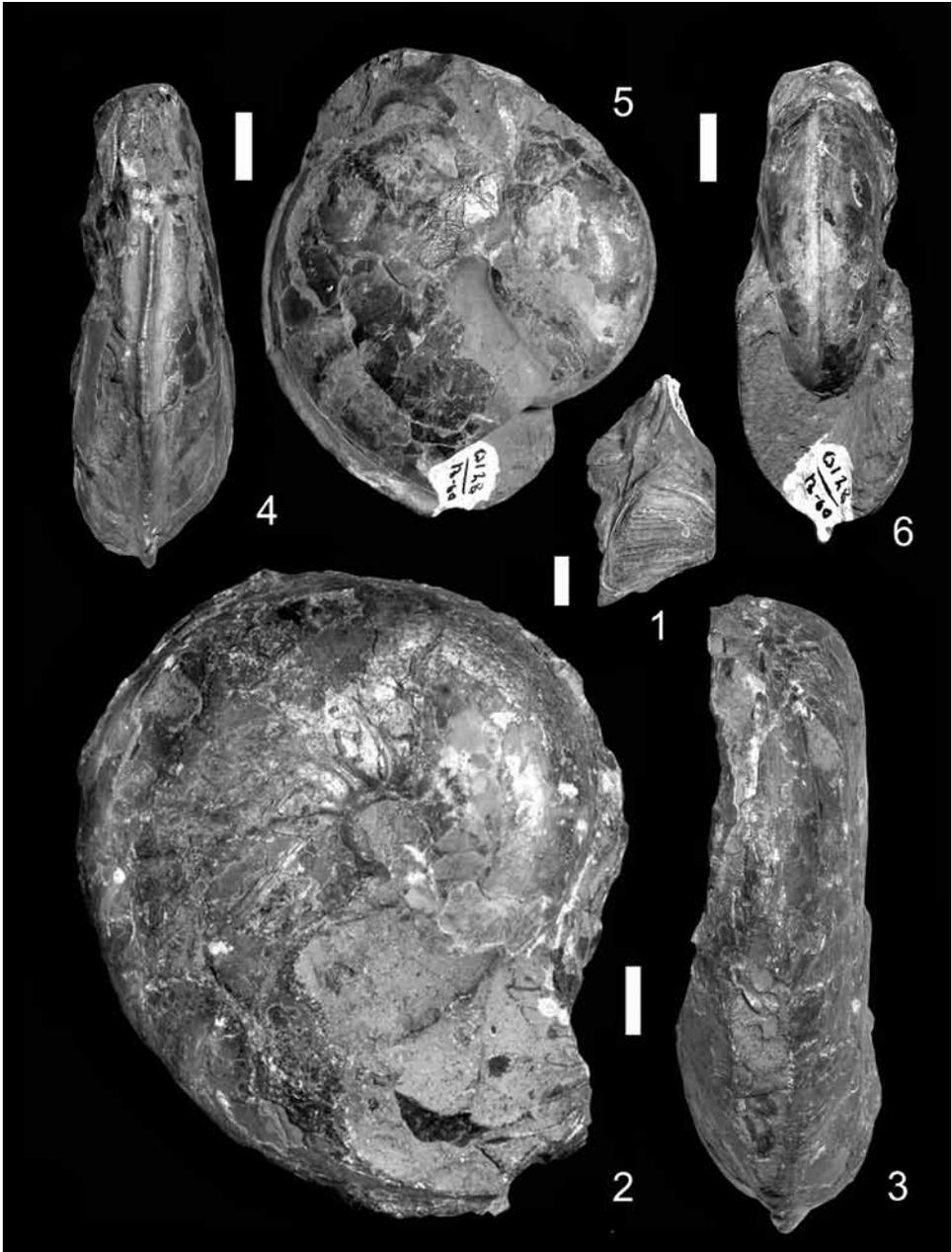


Plate 5

Figs. 1-8. *Menuites (Neopachydiscus) naumanni* (Yokoyama, 1890).

Figs. 1-4. NCB-RGM 617954 (leg. V.E. Bevz, 1959), early Campanian, Bykov Formation, Member 10 (*Menuites (Neopachydiscus) naumanni* Zone) at locality 16, Kholmsoke Shosse, Sakhalin.

Figs. 5-8. NCB-RGM 617955 (leg. V.N. Vereschagin, 1960), late early Campanian, Bykov Formation, Member 10 (*Menuites (Neopachydiscus) naumanni* Zone) at locality 55, River Ul'yanovka, Kriljon Peninsula, Sakhalin.

Scale bars represent 10 mm.

Plate 6

Figs. 1-7. *Eupachydiscus haradai* (Jimbo, 1894); early Campanian, Bykov Formation, Member 10 (*Menuites (Neopachydiscus) naumanni* Zone) at locality 045, River Susuya in the River Naiba valley, Sakhalin.

Figs. 1-3. NCB-RGM 617956 (leg. V.N. Vereschagin, 1970).

Figs. 4-7. NCB-RGM 617957 (leg. V.N. Vereschagin, 1970).

Scale bars represent 10 mm.

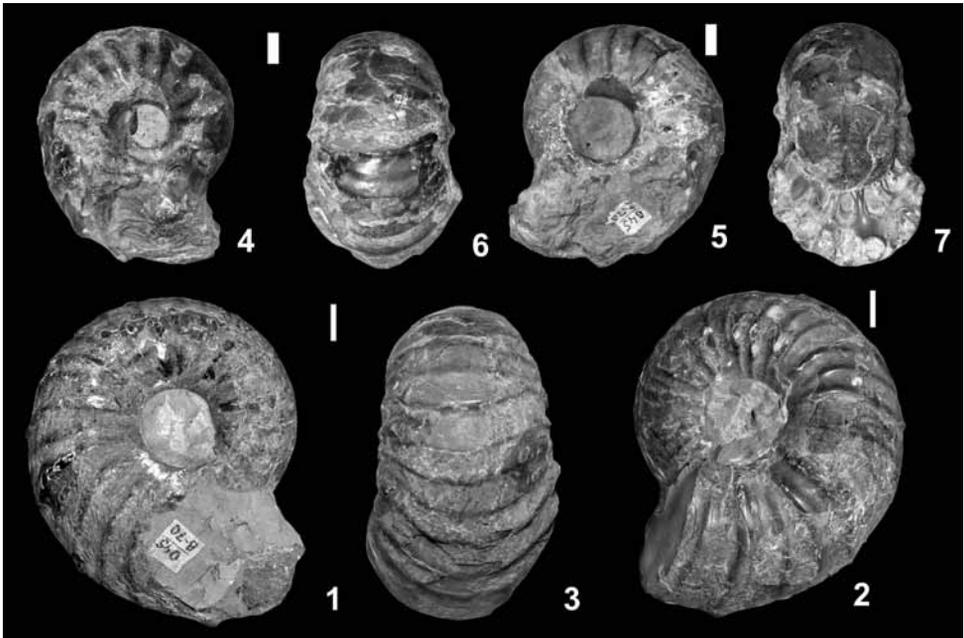
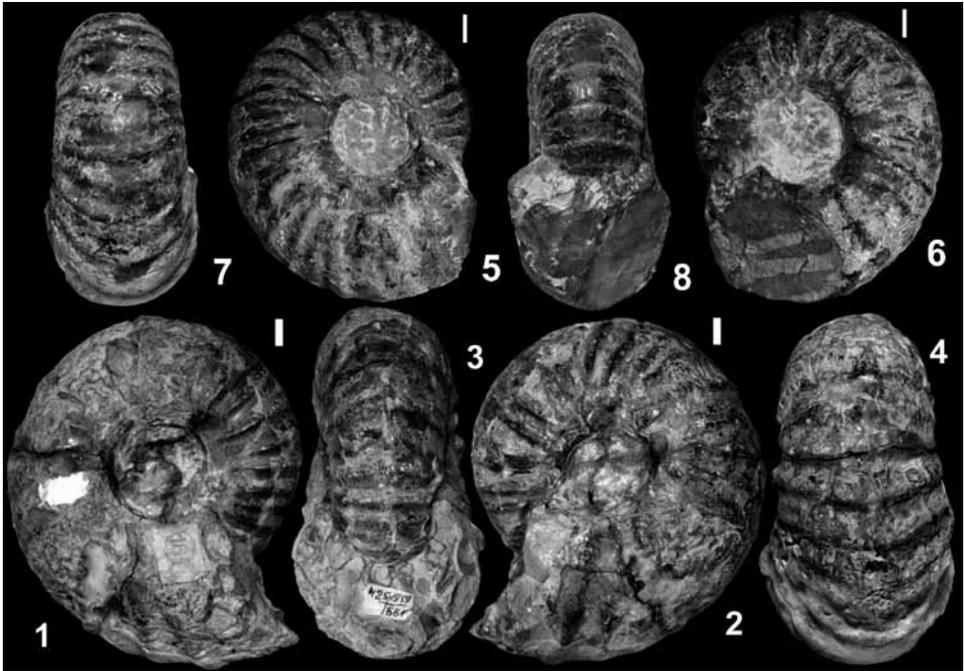


Plate 7

Figs. 1-4. *Menuites (Neopachydiscus) naumanni* (Yokoyama, 1890), NCB-RGM 617958 (leg. V.N. Vereschagin, 1960), early Campanian, Bykov Formation, Member 10 (*Menuites (Neopachydiscus) naumanni* Zone) at locality 9, River Kluch Zaprudny near the village of Sinegorsk, Sakhalin.

Scale bar represents 10 mm.

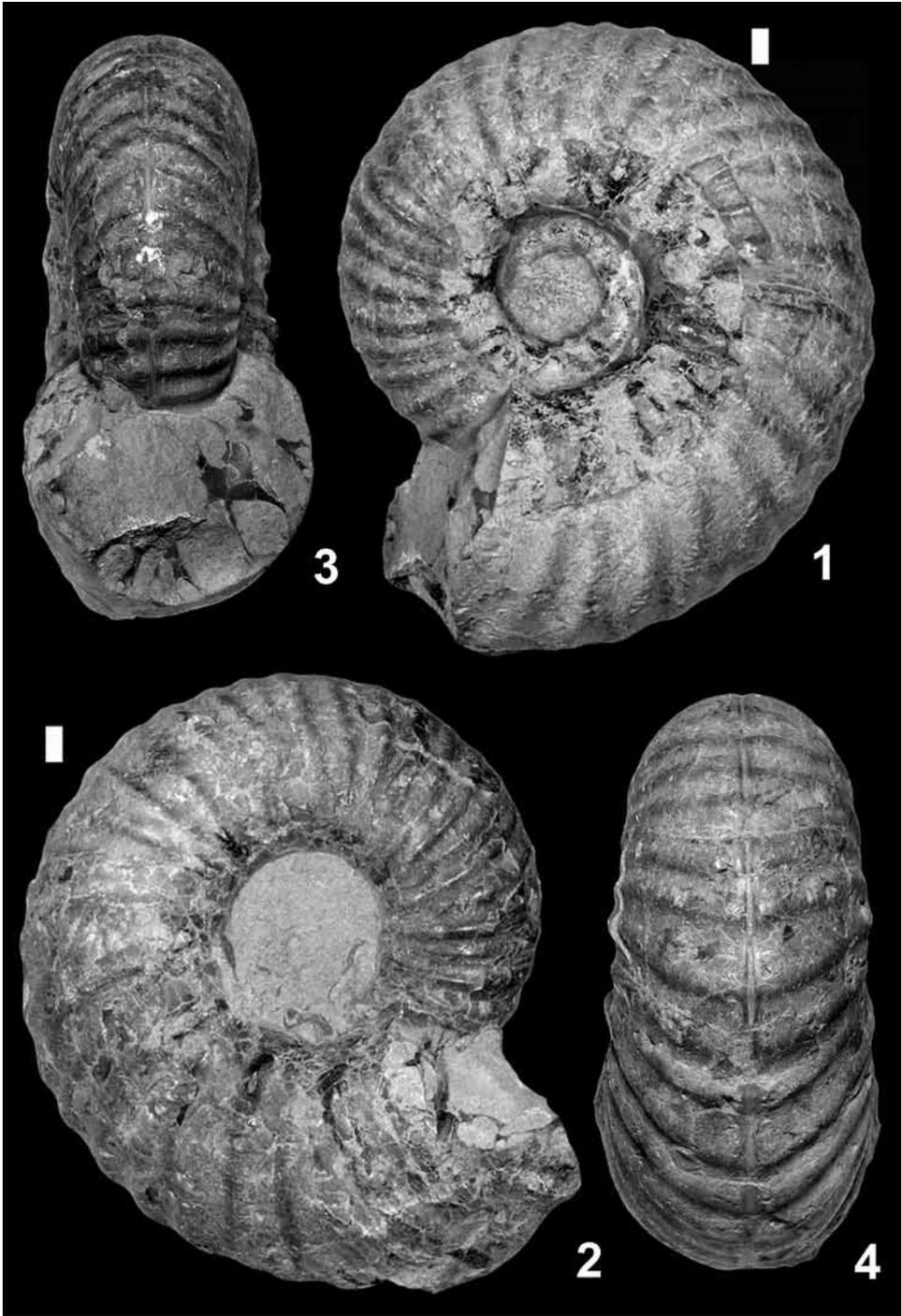


Plate 8

Figs. 1-3. *Canadoceras yokoyamai* (Jimbo, 1894), NCB-RGM 617959 (leg. B.A. Salnikov, 1970), late Campanian, Krasnoyarka Formation, Member 1 (*Tetragonites popetensis* Zone) at locality 601, River Gorbusha, Kriljon Peninsula, Sakhalin.

Scale bar represents 10 mm.

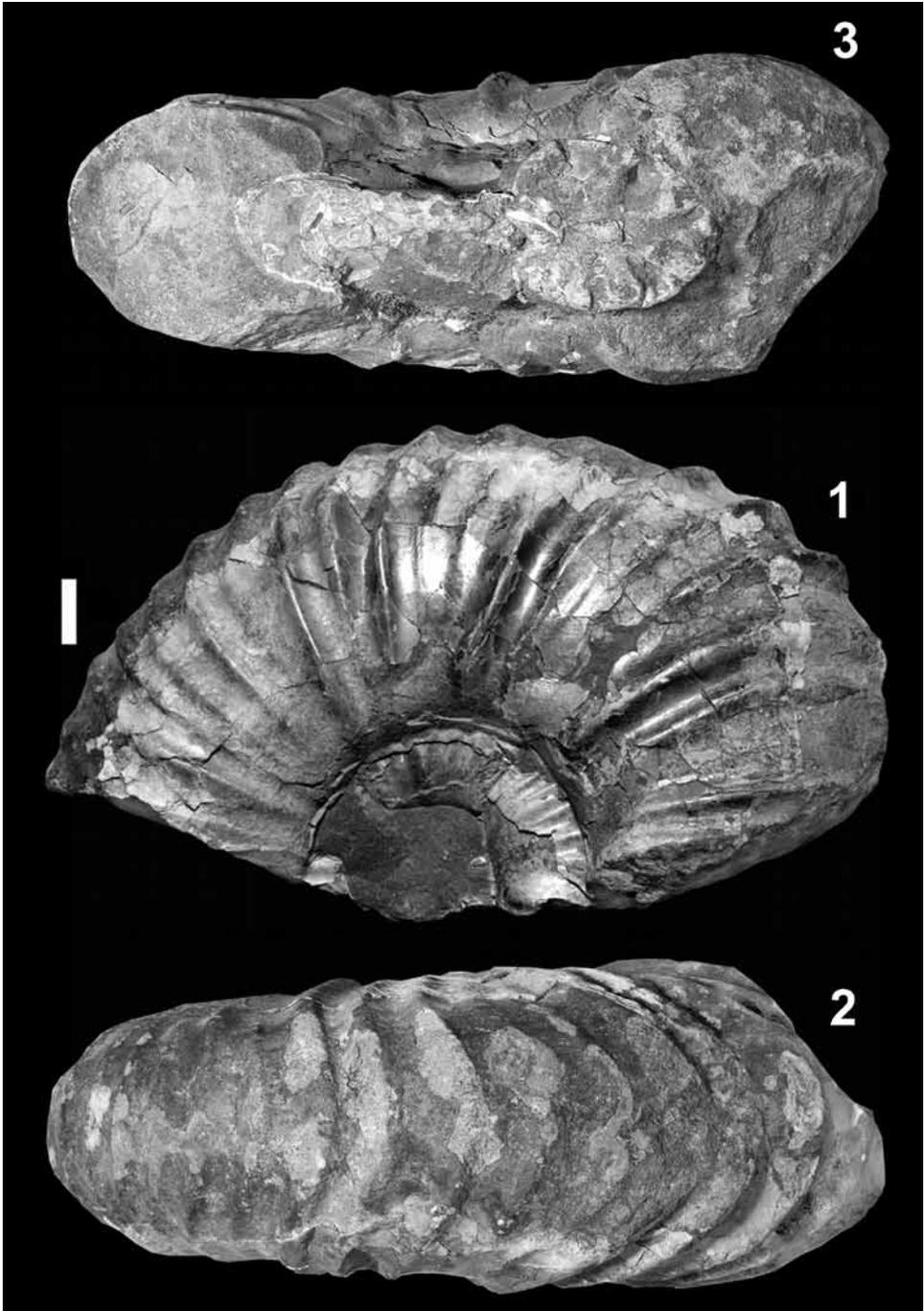


Plate 9

Figs. 1-3. *Pseudophyllites indra* (Forbes, 1846), NCB-RGM 617960 (leg. Ju.I. Tikhomolov, 1966), late early Campanian, Bykov Formation, Member 10 (*Canadoceras kossmati* Zone) at locality 3016, River Tura (left tributary of River Madera, in turn a right tributary of River Lesnaja), Sakhalin.

Figs. 4-6. *Desmophyllites diphylloides* (Forbes, 1846), NCB-RGM 617961 (leg. I. Mytarev, 1968), late Campanian, Krasnoyarka Formation, Member 1 (*Pachydiscus* (*P.*) sp. aff. *egertoni* Zone) at locality 215, River Kura, Kriljon Peninsula, Sakhalin.

Scale bars represent 10 mm.

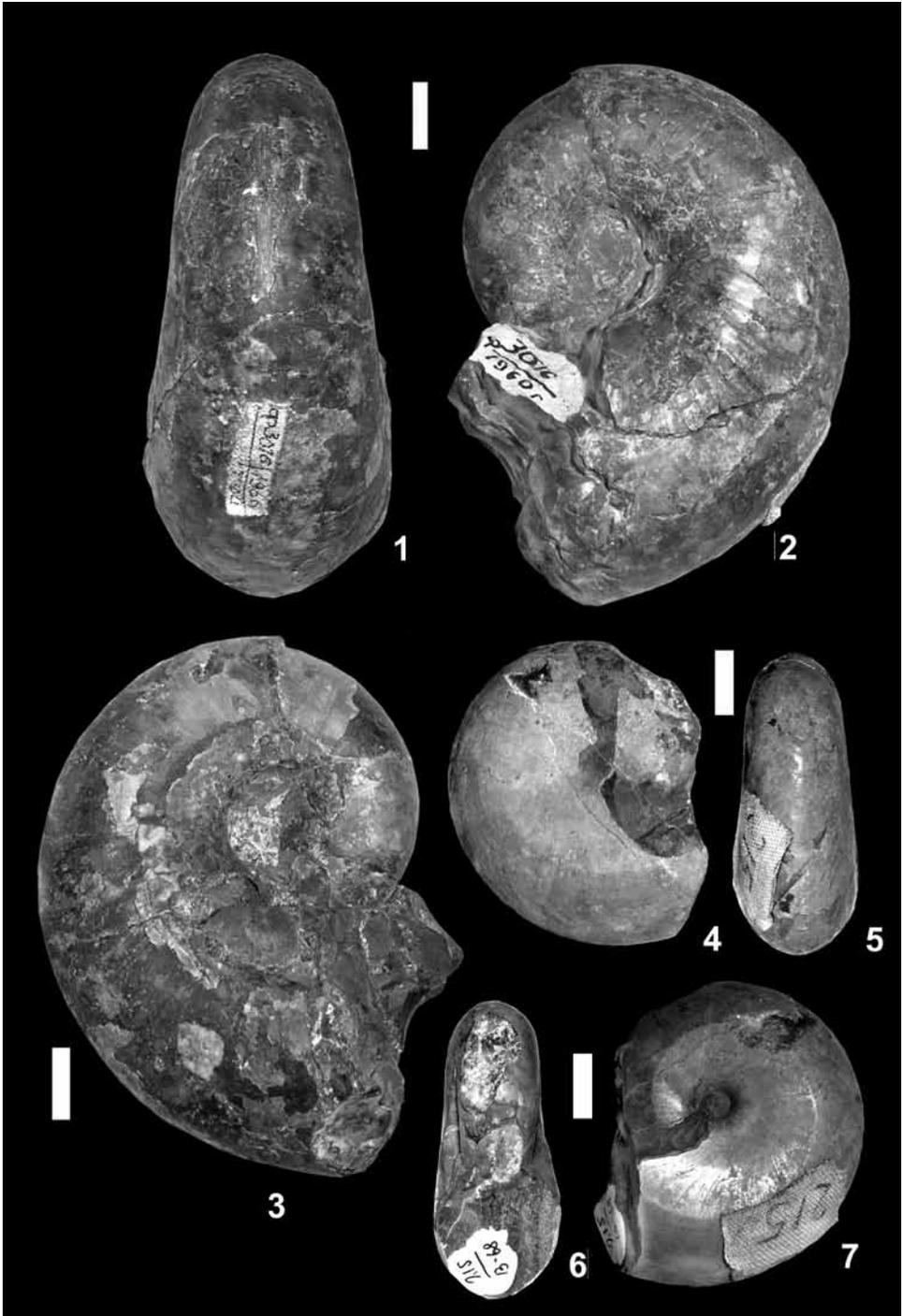


Plate 10

Figs. 1, 2. *Menuites (Menuites) cf. menu* (Forbes, 1846), NCB-RGM 617962 (leg. B.A. Salnikov, 1970), late Campanian, Krasnoyarka Formation, Member 2 (*Canadoceras multicosatum* Zone) at locality 366, River Kuchino, Kriljon Peninsula, Sakhalin.

Figs. 3-5. *Menuites (Anapachydiscus) fascicostatus* (Yabe, 1921), NCB-RGM 617963 (leg. V.N. Vereschagin, 1960), early late upper Campanian, Zhonkier Formation (*Pachydiscus (P.)* sp. aff. *egertoni* Zone) at locality 2a, River Orlovka, Sakhalin.

Figs. 6-8. *Phyllopachyceras ezoense* (Yokoyama, 1890), NCB-RGM 617964 (leg. B.A. Salnikov, 1963), late Campanian, Krasnoyarka Formation, Member 1 at locality 65, River Naiba, Sakhalin.

Scale bars represent 10 mm.

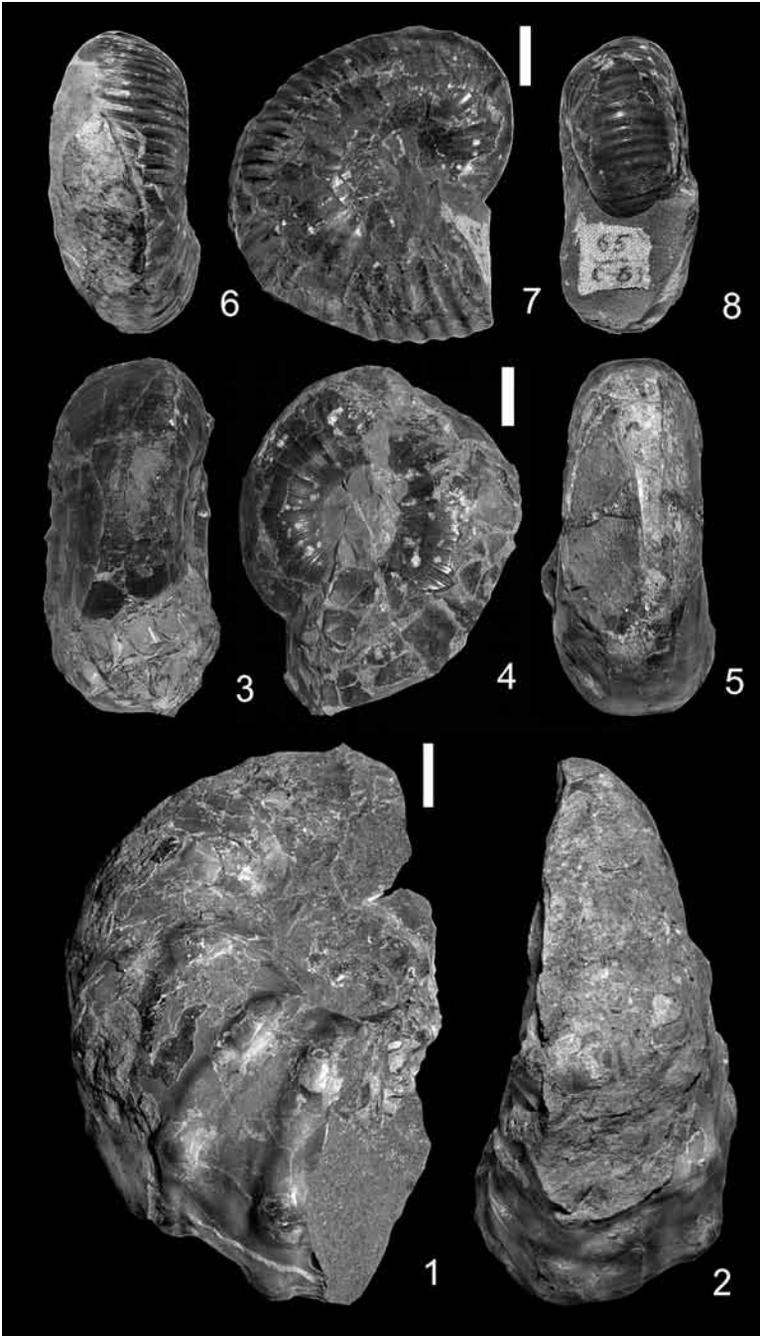


Plate 11

Figs. 1-6. *Pachydiscus* (*P.*) cf. *awajiensis* Morozumi, 1985, NCB-RGM 617965 (leg. V.N. Vereschagin, 1960), late Campanian, Krasnoyarka Formation, Member 1 (*Pachydiscus* (*P.*) spp. Zone) at locality 0111A, River Naiba, Sakhalin.

Scale bar represents 10 mm.



Plate 12

Figs. 1-3. *Pachydiscus (Neodesmoceras) japonicus* Matsumoto, 1947, NCB-RGM 617966 (leg. M. A. Pergament, 1953), early Maastrichtian (*Pachydiscus (Neodesmoceras) japonicus* Zone) at locality 170, Penzhyna Gulf coast, northeast Russia.

Scale bar represents 10 mm.



Plate 13

Figs. 1, 2. *Pachydiscus (Pachydiscus) subcompressus* Matsumoto, 1954b, NCB-RGM 617967 (leg. T.D. Zonova, 1979), early Maastrichtian, Krasnoyarka Formation, Member 4 (*Pachydiscus (Neodesmoceras) japonicus* Zone) at locality 189, River Krasnoyarka in the River Naiba valley, Sakhalin.

Figs. 3-6. *Kitchinites ishikawai* (Jimbo, 1894), NCB-RGM 617968 (leg. M.A. Pergament, 1954), Santonian (*Menuites menu* Zone) at locality 147, Penzhyna Gulf coast, northeast Russia.

Scale bars represent 10 mm.



