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# Ammonite faunal dynamics across bio-events during the mid- and Late Cretaceous along the Russian Pacific coast

ELENA A. JAGT-YAZYKOVA



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The present paper focuses on the evolutionary dynamics of ammonites from sections along the Russian Pacific coast during the mid- and Late Cretaceous. Changes in ammonite diversity (i.e., disappearance [extinction or emigration], appearance [origination or immigration], and total number of species present) constitute the basis for the identification of the main bio-events. The regional diversity curve reflects all global mass extinctions, faunal turnovers, and radiations. In the case of the Pacific coastal regions, such bio-events (which are comparatively easily recognised and have been described in detail), rather than first or last appearance datums of index species, should be used for global correlation. This is because of the high degree of endemism and provinciality of Cretaceous macrofaunas from the Pacific region in general and of ammonites in particular.

Key words: Ammonoidea, evolution, bio-events, Cretaceous, Far East Russia, Pacific.

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## Introduction

Cretaceous marine strata are widely distributed along the Russian Pacific coast (Fig. 1), reaching a total thickness of circa 10 km and yielding comparatively diverse macrofaunal assemblages. The emphasis in the present paper is on bio-events and a few notes on palaeoecological and palaeogeographical aspects of ammonite evolution are added for the upper Albian to uppermost Maastrichtian interval, the average thickness of which varies between 4000 and 7000 m (Vereschagin et al. 1965; Poyarkova 1987; Yazykova 2004; Zonova 2004).

A major obstacle encountered in correlations with the type areas (most of them in western Europe) of the various mid- and Late Cretaceous stages is the high degree of faunal endemicity, which characterises Pacific Cretaceous faunas in general and Late Cretaceous ones in particular (Yazykova 2004; Jagt-Yazykova 2011). This explains why most of the recently proposed criteria for the recognition of stage boundaries in the type localities cannot be applied in the study area. However, it has been demonstrated that general trends of ammonite evolution in the boreal Pacific are the same as elsewhere (Yazykova 1996, 2002, 2004; Jagt-Yazykova 2011). From bio-event to bio-event, and/or from zone to zone, overall changes in ammonite morphotypes and ecosystems are comparable to those observed in other regions, and this can be assumed to be so because the organic world is largely dependent of the global rules, which govern local environments. I support the general view that unrelated taxa with similar life habits and occurrences tend to be of a comparable morphotype, while species with a wide range of intraspecific variation, either throughout ontogeny or in the adult stage, have shell features, which reflect diverse modes of life or environments inhabited. Recently, Paul and Lamolda (2009) have argued that bio-events based on first or last appearance datums (FADs, LADs) occasionally may not be recognisable in all sections, not even within the same area, particularly when these events are based on a single taxon. In addition, whenever recognisable, they may turn out to be diachronous. Thus, morphotypes, rather than taxonomic designation, should be used for correlations because relationships between shell shapes and environments appear to be species independent (Batt 1989, 1993). Certainly, all results presented here are based on the study of adult individuals; larvae or juvenile forms were nektoplanktonic and lived elsewhere in the photic and neritic shallow zones (50–250 m; see Westermann 1989, 1996). Changes in ammonite diversity, viz. disappearance (extinction or emigration), appearance (origination or immigration) and total number of species (see Fig. 2), constitute the basis for the identification of the main bio-events.

All published data on ammonite taxa from the Albian to



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Fig. 1. Distribution of Cretaceous deposits in Far East Russia.

Maastrichtian of areas along the Russian Pacific coast (Sakhalin, Shikotan Island, Chukotka and Kamchatka peninsulas, the Koryak Upland, Sikhote Alin and Primorye; see Fig. 1), have recently been critically re-evaluated (Jagt-Yazykova 2011). In total, 200 species, inclusive of specifically indeterminate taxa, denoted with "sp.", "cf.", "aff.", have been accepted for this area, distributed over ninety genera, twenty-two families and twenty-seven subfamilies (Jagt-Yazykova 2011). A revised biostratigraphical framework, based on ammonites, inoceramid bivalves and radiolarians, has also been proposed previously for Far East Russia (mainly Sakhalin, Shikotan, and Sikhote Alin; Yazykova 2004; Jagt-Yazykova 2011), using data supplied by Russian and Japanese colleagues. In addition, the interrelationship between ammonite evolution and environmental changes in palaeobasins along the Russian Pacific coast, local bio-events, links with lithofacies types, hypothetical phylogenetic links, plus selected examples of homoeomorphy have lately been discussed in detail (Jagt-Yazykova 2011). The present paper focuses on the evolutionary dynamics of ammonites from sections along the Russian Pacific coast during the mid- and Late Cretaceous.

*Abbreviations*.—OAE, Oxygen Anoxic Event.

# Discussion

**The late Albian migration bio-event**.—Strata of late Albian age are comparatively widely distributed in all regions of the Russian Pacific, i.e., Sakhalin Island, the Sikhote Alin Mountains and in the Amur River valley, as well as in the northeasterly areas such as the Chukotka Peninsula, the Koryak Upland, and Penzhyna Gulf coast of the Kamchatka Peninsula (Fig. 1), the average thickness being between 700 and 1000 m. The general diversity amongst Russian Pacific Cretaceous ammonites is highest during the late Albian (Fig. 2), the greatest taxonomic diversity being noted amongst desmoceratids and kossmaticeratids (compare Jagt-Yazykova 2011: fig. 7). In consideration of palaeobiogeographical aspects and the taxonomically mixed composition of macrofaunal assemblages recorded, this might be interpreted as a migration bio-event, possibly correlative with similar levels elsewhere, e.g., northern California (Amédro and Robaszynski 2005), where successions yielded both Tethyan ammonites (for example, *Oxytropidoceras* and *Lyelliceras*) and Boreal taxa such as *Gastroplites* and *Pseudopulchellia*. Those authors discussed possible ammonite-based correlations between Albian sequences of northern California and the European and Arctic provinces and concluded that the stratigraphic distribution of non-endemic Albian ammonites in northern California and Europe was controlled largely by global eustatic events. In addition, they showed some possible ways of migration for endemic forms.

Macrofaunal complexes from the Russian Pacific area are characterised by similar patterns. The comparatively shallow Lower Cretaceous basins of central-northeast Russia were inhabited by numerous representatives of different bivalve groups (mainly Aucellidae, Inoceramidae, and Pectinidae) and some brachiopods (Vereschagin et al. 1965). In contrast to the numerous bivalves, ammonites are rather uncommon but represented by taxa originating from different palaeobiogeographic realms. The southern end of the vast Russian Pacific area (Amur River valley and Sikhote Alin Mountains) was also inhabited by numerous non-inoceramid bivalves and the first genuine *Inoceramus* (see Krymholz 1938; Zonova 1982; Sey et al. 2004), which were commoner than ammonites. Recently, a European cirripede, *Pycnolepas* aff. *rigida* (Sowerby, 1836), has been recorded from Primorye (Jagt et al. 2007). The Albian ammonite assemblage also has a mixed taxonomic composition, in showing both Tethyan and Boreal genera and endemic species. For example, finds of the European (Boreal) *Anahoplites* sp. and *Sonneratia* sp. can only be explained by immigration of these taxa via the Arctic. The former is confined to Sakhalin (Zhuravlev 1969), while the latter has been noted in Sakhalin, Primorye, and northeast Russia (Vereschagin et al. 1965). Members of the genus *Sonneratia* have also been described from Arctic Canada (Jeletzky 1964), as well as from California and Oregon (Anderson 1938; Jones et al. 1965), but comprise exclusively endemic species, which supports the notion of larvae and/or juveniles being taken across the Arctic by favourable cur-

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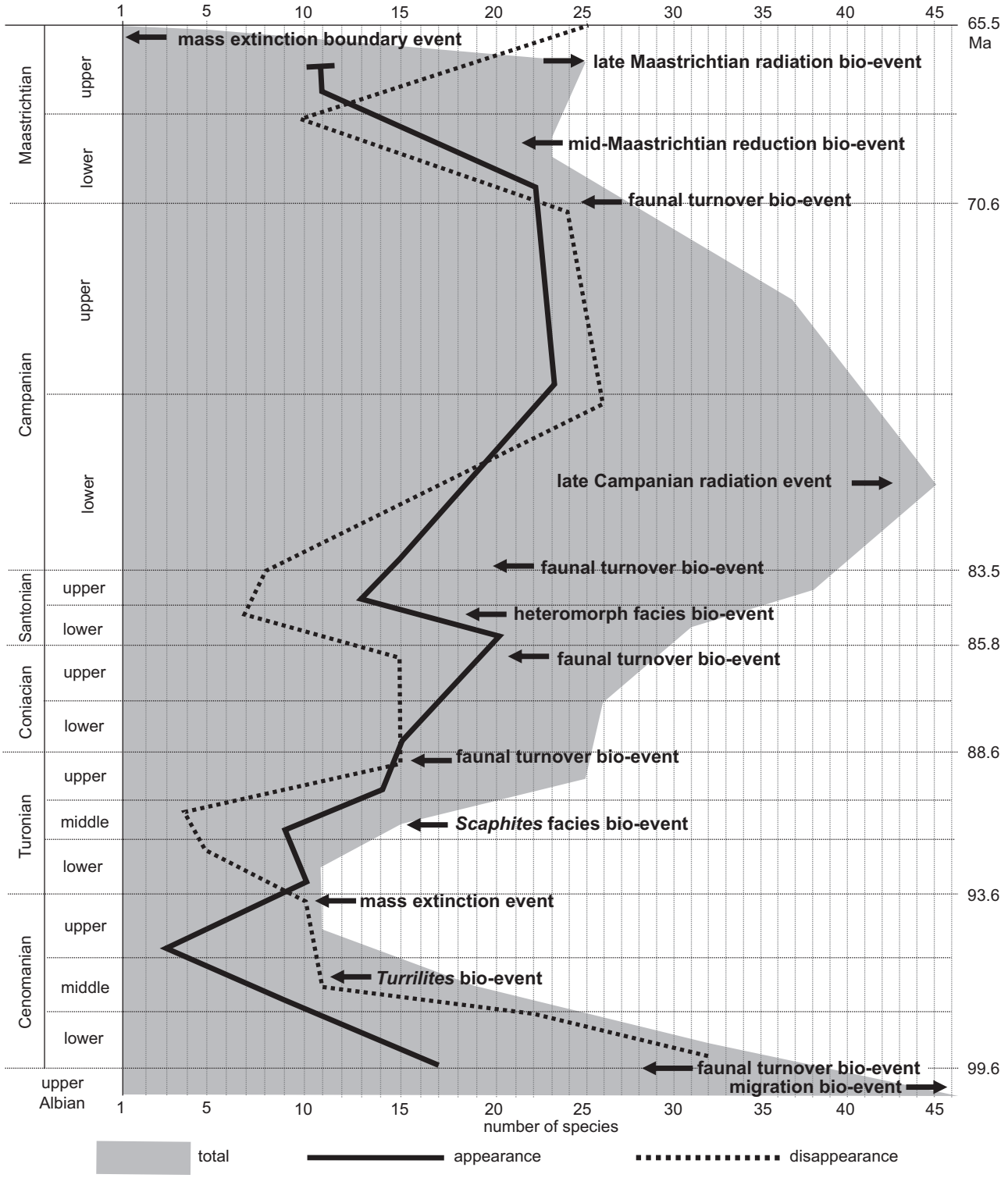



Fig. 2. Changes in Cretaceous ammonite diversity in Far East Russia: disappearance, appearance, and total number of species recorded.

rents which ultimately led to the establishment of a convergent lineage of this European genus. Representatives of *Anahoplites* and *Sonneratia* from the Russian Pacific may either belong to some new endemic species or are conspecific with those described from Arctic Canada, California, or Oregon. Similar patterns are represented by desmoceratids. Out of the ten desmoceratid taxa recorded from here only a single, truly cosmopolitan taxon is known from Albian levels, namely *Puzosia* cf. *lata* (Seitz, 1931) found in Sikhote Alin (Yazykova 2001). All remaining taxa are true endemics.

The mixed character of ammonite assemblages is a feature that characterises the late Albian time slice in the Pacific realm in general. Some typically Boreal taxa such as *Arcthoplites* (*Subarcthoplites*), *Phyllopachyceras*, *Parasilesites*, *Marshal-*

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*lites*, and *Eogunnarites* from the Koryak-Kamchatka palaeobasin migrated to the south using favourable currents and later were widely distributed in Sakhalin and Japan (Matsumoto 1991). Some isolated representatives of *Marshallites* probably migrated during the Turonian–Coniacian even to the African-Indian province and later possibly continued southeasterly, towards New Zealand (compare Kennedy and Klinger 1985).

Amongst others, an interesting case is the appearance of the cosmopolitan *Eogaudryceras* (*Eotetragonites*) *duvalianus* (d'Orbigny, 1840) and a single lytoceratoid, *Protetragonites* cf. *aeolus aeolus* d'Orbigny, 1850. Both can be considered to have been good swimmers, because the occurrence in the Pacific of these European taxa cannot be explained otherwise. The former is known also from the Aptian–lower Albian of the northern Caucasus (Dagestan) (Kasansky 1914; Druschic and Mikhailova 1963). *Protetragonites aeolus aeliformis* Fallot, 1885, recorded from the Aptian of Spain (López Garrido and Orozco 1970), is similar to *P. aeolus aeolus* and *P.* ex gr. *aeolus* was recorded from the lower Albian of the western Carpathians in Slovakia (Potfaj et al. 2008). Thus, 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 likely to be found in Sakhalin. Here, probably poorly oxygenated, yet not completely anoxic, conditions prevailed, while northeasterly regions were characterised by warm, well-oxygenated waters. The Sikhote Alin palaeobasin appears to have been comparatively shallow and well-oxygenated. 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 subsequent speciation.

In conclusion, the late Albian migration event recorded in the sections of Russian Pacific coast could be linked to the middle–late Albian bio-event (Fig. 4) 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 (e.g., *Gastroplites*, *Pseudopulchellia*) and warm-temperate subtropical taxa (e.g., *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 faunal turnover bio-event**.—The late Albian anoxic-event OAE1d has been recorded in many sections of the Pacific realm (Hirano and Takagi 1995; Hasegawa 1997; Hirano and Fukuju 1997; and others). This was followed by global regression, as a result of global tectonic reconstruction and environmental changes. In turn, this again triggered changes in biodiversity at the Lower–Upper Cretaceous boundary. Some families and subfamilies disappeared altogether (i.e., Cleoniceratidae, Silesitoidinae, Beudanticeratinae, Sonneratiinae; see Wright et al. 1996). Almost all Albian ammonite taxa known from northwest Pacific provinces became extinct, except for a few species, which survived these crises but did not persist longer than the early Cenomanian. These survival taxa are best seen as failed crisis progenitor species (Kauffman and Erwin 1995; Harries and Little 1999), which did not appear until the latest Albian, and already were better adapted to changing environmental conditions. In short, changes which took place during the latest Albian to the earliest Cenomanian are best considered to illustrate a global faunal turnover bio-event.

The most drastic changes occurred in Sikhote Alin and Amur River basin. During the early Cenomanian, this basin became shallower and gradually disappeared as a result of plate tectonic movements and high volcanic activity which started in the mid-Albian (Kirillova et al. 2000). This explains why ammonite assemblages of early Cenomanian age here comprise only few survival forms, such as *Puzosia* and *Desmoceras* (*Pseudouhligella*) and the heteromorph *Mariella*. This was a small, shallow-water basin which existed only until the end of the Cenomanian, when it disappeared altogether.

However, the new early Cenomanian transgression allowed the entry of immigrant species into the Pacific region, such as *Phylloceras* (*Neophylloceras*) *seresitense* Pervinquière, 1907; *Anagaudryceras buddha* (Forbes, 1846); *Parapuzosia* (*Austiniceras*) *austeni* (Sharpe, 1855); *Mantelliceras* sp.; and *Acanthoceras* sp. These taxa probably originated from the Tethys and migrated into Sakhalin and northeast Russia. In those areas diverse micro- and macrofaunal complexes existed, in which endemics predominated. The Cenomanian shelf sea of southern Sakhalin was inhabited by representatives of sixteen genera, some of which appeared here for the first time. Cenomanian deposits of northeast Russia have yielded ammonite associations comprising thirteen genera. In taxonomic composition these are similar to those in Sakhalin, and involve mostly new taxa.

Two remarkable global bio-events can be recognised in the early Cenomanian: the taxonomic bloom of the Kossmaticeratidae (seven new genera appearing) and the entry of the family Acanthoceratidae (Wright et al. 1996). In Far East Russia, the former family was represented by ten species of two genera, *Marshallites* and *Mikasaites*, while the latter comprised four genera/subgenera, *Mantelliceras*, *Calycoceras* (*Calycoceras*), *C.* (*Newboldiceras*), and *Acanthoceras*. However, in view of the fact that all of these acanthoceratids are represented only by few examples, they probably were poorly adapted to the Pacific setting, which was likely cooler than the Tethyan realm. Only few of these taxa have been found along the Russian Pacific coast and some are known from Japan (Jimbô 1894; Matsumoto 1943; Shigeta 2001; Matsumoto and Toshimitsu 2005). Meanwhile, the Cenomanian of Western Interior of North America, as well as the European, Mediterranean, and African-Indian provinces is characterised by high diversity levels of the family Acanthoceratidae (e.g., Wright

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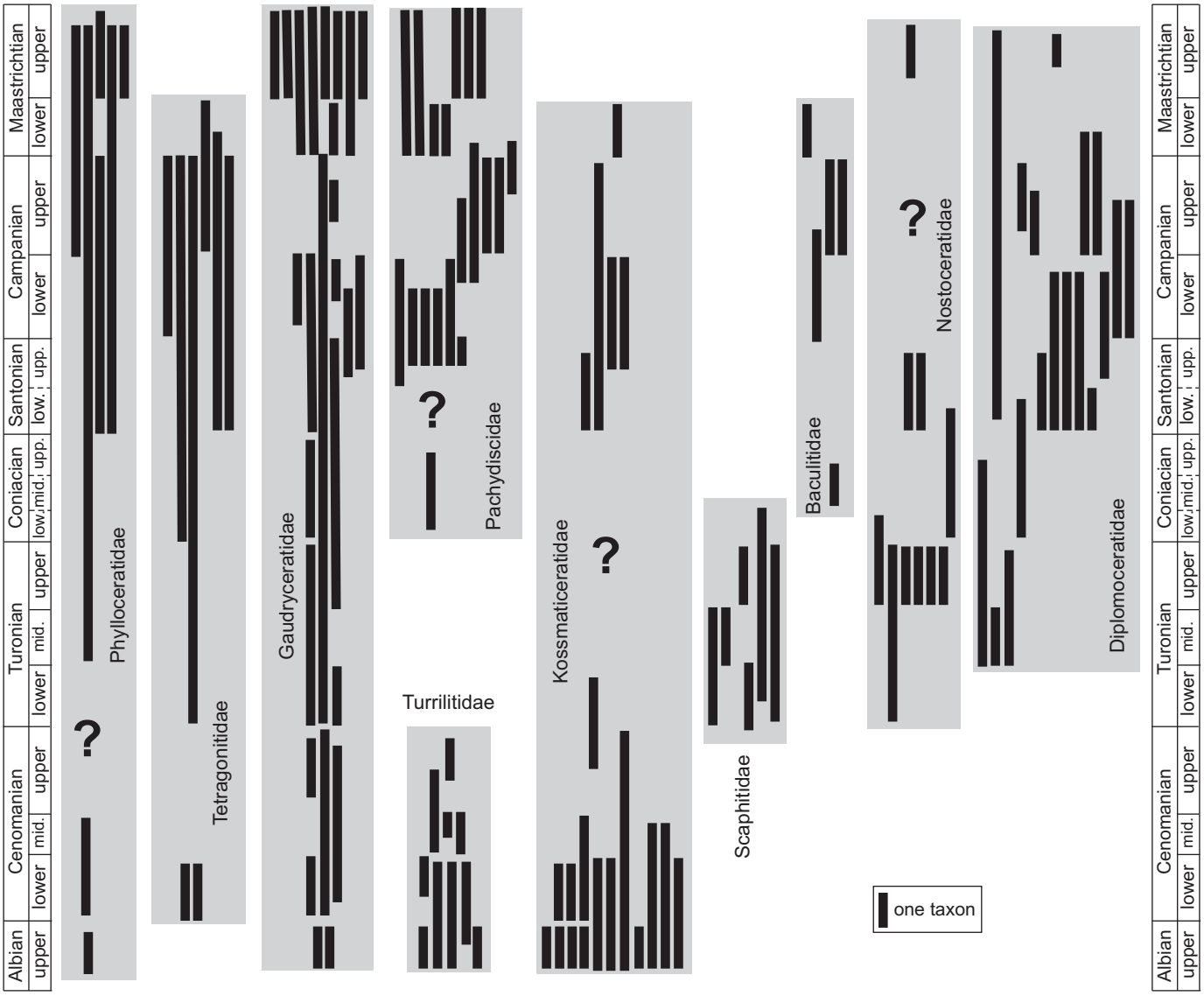



Fig. 3. Changes in the number of Cretaceous ammonite species from Far East Russia, arranged in the ten most speciose families: non-heteromorphs (Phylloceratidae, Tetragonitidae, Gaudryceratidae, Pachydiscidae, Kossmaticeratidae) and heteromorphs (Scaphitidae, Baculitidae, Turrilitidae, Nostoceratidae, Diplomoceratidae). Abbreviations: low., lower; mid., middle; up., upper.

and Kennedy 1990; Kennedy 1994; Kennedy et al. 1996; Arkadiev et al. 2000).

In summary, all but two Albian taxa disappeared at the Albian–Cenomanian boundary interval in the Russian Pacific. A short-term, global turnover in marine biota following OAE1d (Barnes et al. 1995) is characteristic of this level in many regions of the world (Fig. 3), inclusive of the Pacific as outlined above. 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. acutus* are known from middle and upper middle Cenomanian deposits (Fig. 2) of Sakhalin Island and the Penzhyna Gulf coast, respectively, as well as from the Koryak Upland (Vereschagin et al. 1965; Terekhova and Mikhajlova 1977) and Japan (Hayakawa and Nishino 1999; Shigeta 2001; Matsumoto and Takahashi 2001). These two levels could possibly be correlated (Fig. 3) with the so-called mid-Cenomanian Regressive Trough (*Turrilites costatus* event) and the mid-Cenomanian eustatic low (*T. acutus* records), respectively (Hancock 2003). This eustatic lowstand has been recorded from northwest Europe, western Kazakhstan, Texas, Colorado, and South Dakota. Monnet and Bucher (2007) proposed the last occurrence of *T. acutus* as a marker for the middle–late Cenomanian boundary since that species was abundant and widely distributed. This marker is useful in Sakhalin as well as in northeasterly regions of Russia.

**Cenomanian–Turonian mass extinction event**.—The Cenomanian–Turonian boundary mass extinction is reflected in drop of diversity curves for all biotic groups, both at the generic and specific level. Some ammonite families and subfamilies

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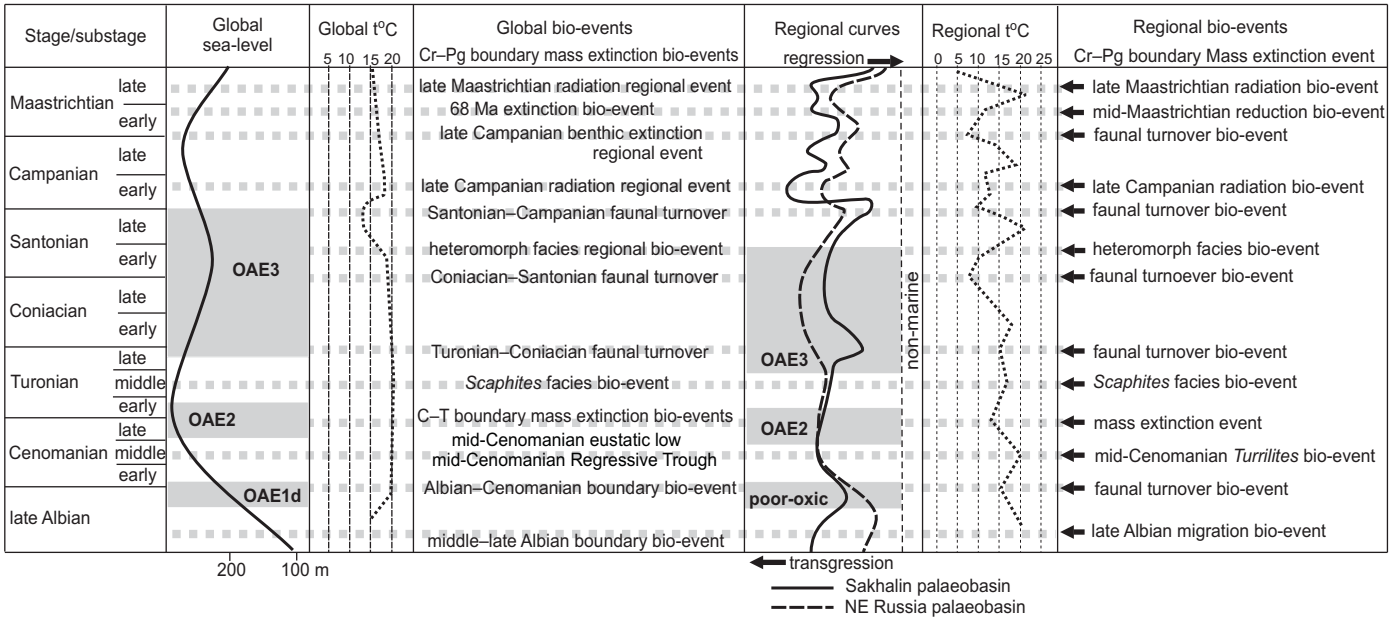



Fig. 4. Regional bio-events recorded in ammonite assemblages from Far East Russian regions (present paper); regional palaeotemperature curves modified after Zakharov et al. (1998, 1999, 2005); generalised scheme of records of transgression and regression from Sakhalin and northeast Russia; global bio-events (Kauffmann and Hart 1995); global sea level curves by Haq et al. (1987); global palaeotemperature curves by Skelton (2003). Stages are shown without calibration to absolute time. Abbreviations: C–T, Cenomanian–Turonian boundary; Cr–Pg, Cretaceous Paleogene boundary; OAE, Oxygen Anoxic Event.

disappeared altogether, for example, the Turrilitidae, Acanthoceratinae, and Lyelliceratidae (Wright et al. 1996). The late Cenomanian OAE2 event (Barnes et al. 1995; Hirano and Takagi 1995; Hasegawa 1997) was possibly the main trigger to the extirpation of many Cenomanian faunal elements near globally. In the Russian Pacific not a single Cenomanian taxon survived this crisis. Global correlation is based on OAE2 and the appearance of the ammonite genera *Fagesia* and *Jimboiceras*, as well as the inoceramid *Mytiloides*, and the appearance of new ammonite morphotypes in general. The global mid-Cenomanian–Turonian transgression has also been recorded in the entire Far East Russia and is reflected in relatively deep-water sedimentation. Anoxic conditions connected with strong active volcanism are reflected in the presence of mudstone interbedded with black, grey and green tuffaceous sandstone and siltstone as well as bentonitic clay. This "coloured" interval is barren of fossils (probably as a result of dysoxic conditions, as well as volcanic fallout) and generally reaches a thickness of some 40-50 m in Sakhalin (see also Yazykova et al. 2004) as well as in northeast Russia (EAJ-Y unpublished data).

The early Turonian survival interval is characterised by the gradual appearance of new ammonite genera. Later, following a radiation event recorded in the mid-Turonian, the general diversity of ammonites reached a maximum during the late Turonian. Moreover, because of a highstand, some taxonomic unification appeared in the Pacific and, apart from a few taxa, ammonite compositions in northeast Russia and Sakhalin are almost identical and still predominantly endemic to the western Pacific.

**The mid-Turonian *Scaphites* facies bio-event**.—A wide distribution of heteromorph ammonites (e.g., the *Scaphites* facies) during 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 the family Scaphitidae co-occur with endemic species of the genera *Scalarites* and *Hyphantoceras* (Vereschagin et al. 1965; Mirolubov in Poyarkova 1987; Zonova and Yazykova 1998; Yazykova et al. 2004). The *Scaphites* facies is one of the best correlative levels across the globe. However, all scaphitids are represented in Far East Russia by exclusively endemic species of two genera, *Yezoites* and *Scaphites*, similar to California (Matsumoto 1959). It seems that the appearance of heteromorph genus *Scalarites* would be a good marker for the early–middle Turonian boundary, coupled with *Scaphites* facies in spite of the endemic character of this assemblage.

**The middle–late Turonian boundary bio-event**.—The regression which began at the middle–late Turonian boundary in Russian Pacific basins is marked by the appearance of coarsely ornamented ammonites and heteromorphs (Vereschagin et al. 1965; Mirolubov in Poyarkova 1987; Zonova and Yazykova 1998; Yazykova et al. 2004), indicative of relatively shallow waters (Tanabe 1979; Westermann 1996). Heteromorphs are numerous (the new western north Pacific endemic genus *Nipponites*), alongside gaudryceratids, tetragonitids, phylloceratids, and acanthoceratids (*R.* [*Romaniceras*], *R.* [*Yubariceras*], *Kamerunoceras*, and *Pseudaspidoceras*). Desmoceratids such as *Puzosia* (*Mesopuzosia* and *Pachydesmoceras*), the cosmopolitan vascoceratid genus *Fagesia* and *Tragodesmoceroides subcostatus* predominated the entire sublittoral basin of the West Sakhalin Mountains, which was warm (15.8–17.5°C according to Zakharov et al. 1999),

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and about 150–200 m deep. This interpretation is supported also by single representatives of hexacorals and thin carbonate layers (Poyarkova 1987), which is absolutely atypical for this area. New ammonite taxa gradually appeared in the late Turonian: heteromorphs (*Nostoceras* [*Eubostrychoceras*] and *Hyphantoceras*), as well as *Damesites* and *Hourcquia*, and rare *Subprionocyclus*. There were diversity and abundance peaks in the late Turonian (Fig. 2) illustrating favourable conditions in these areas.

**The Turonian–Coniacian faunal turnover bio-event**.—The Turonian–Coniacian boundary faunal turnover bio-event in Far East Russia was marked by the entry of new ammonite and inoceramid morphotypes with a slight reduction in taxonomic diversity (Zonova and Yazykova 1998). This was a comparatively stable period, interrupted only by local sea level changes and a minimum of volcanic activity.

However, some sections display a huge thickness of Turonian strata, in excess of 1000 m, but in northeast Russia, the basin was shallower than in Sakhalin as evidenced by prevalent deposition of sandstone there. The base of the Coniacian has been defined by the last appearance of *Jimboiceras planulatiforme* (Jimbô, 1894) with thin ribs and an evolute shell shape, and the entry of *J. mihoense* Matsumoto, 1954 with coarse ribs, as well as by the first occurrence of *Anagaudryceras politissimum* (Kossmat, 1895) and *Gaudryceras denseplicatum* Jimbô, 1894. *Jimboiceras mihoense*, *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 characteristic of higher-energy environments. The appearance of small-sized inoceramids (*Inoceramus uwajimensis* Yehara, 1924; see Zonova and Yazykova 1998) supports this interpretation because later representatives of the *Inoceramus uwajimensis* group reach larger sizes and co-occur with numerous *Inoceramus mihoensis* Matsumoto, 1957 and *Jimboiceras mihoensis.* The ammonite *Forresteria* (*F.*) *alluaudi* (Boule, Lemoine, and Thevenin, 1907) was found at the same level which marks the onset of a new transgression, which is supported by other immigrant species in the latest Coniacian, namely *Peroniceras* sp. and *Binneyites* (?) sp. Thus, the appearance of coarser ornament and the abundance of heteromorphs (*Yezoites*, *Scalarites*, and *P.* (*Pseudoxybeloceras*)), as well as the first pachydiscid here, *Menuites* (*Anapachydiscus*), might be indicative of a relatively shallow-water basin with high energy, which would correspond to a lowstand period.

Approximately at the early–late Coniacian boundary, another radiation of new species of the heteromorph ammonite genera *Scaphites*, *Scalarites*, and *Nipponites* is noted, and, in total, the taxonomic diversity increased (Fig. 2). Probably this bio-event could be put forward to characterise the early–late Coniacian boundary, after it has been properly documented from other regions.

**The Coniacian–Santonian faunal turnover bio-event**.—Zakharov et al. (2005) assumed the occurrence of short-lived, subfreezing conditions periodically in the Northern Hemisphere during the late Coniacian–early Santonian, most probably in polar winter months. Moreover, basins in the Russian Pacific region became deeper and, perhaps, as a result of deepening and/or cooling, all of the Coniacian taxa above noted disappeared, although new supplements appeared comparatively rapidly. Zakharov et al. (2005) noted that the cold periods were probably never sufficiently long enough to form permanent sea ice, 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 Strait of Turgai and the Western Interior of North America. That also could be the explanation of the appearance at this time of the widespread ammonites *Polyptychoceras quadrinodosum* Jimbô, 1894, *Desmophyllites diphylloides* (Forbes, 1846) and *Phyllopachyceras forbesianum* (d'Orbigny, 1850), which co-occurred with local indexes for this boundary such as *Texanites* (*Plesiotexanites*) *kawasakii* Kawada, 1929 and *Inoceramus amakusensis* (Yazykova 1996, 2002; Yazykova and Zonova 2002). In spite of the fact that the placement of the Coniacian–Santonian boundary is still very problematic in the Russian Far East, we can recognise the principal elements of general ammonite evolution, namely the disappearance of typical Coniacian ammonites, such as *Peroniceras* sp., *Jimboiceras mihoense*, *Forresteria* (*F.*) *alluaudi* and of inoceramids of the *Inoceramus mihoensis/I. uwajimensis* group (Zonova and Yazykova 1998), as well as the common occurrence of new taxa, representing new morphotypes, plus the abundance of new heteromorph (sub)genera such as *Glyptoxoceras*, *Didymoceras*, *Pseudoxybeloceras*, *Polyptychoceras*, *Neocrioceras*, *Subptychoceras*, *Eubostrychoceras*, and *Baculites* (Poyarkova 1987; Alabushev and Wiedmann 1997; Yazykova 2004). Generally, the Santonian interval is typified by a continuous increase of taxonomic diversity amongst ammonites (Fig. 2). New migration routes which appeared during the latest Coniacian transgression were gradually widening during the Santonian and the percentage of cosmopolitan species during this time is much higher (see Yazykova 2002). This boundary is characterised also by new taxa amongst two of the most conservative families, namely the Phylloceratidae and Tetragonitidae, and by the recovery of the Kossmaticeratidae along the Russian Pacific coast (Fig. 3), where after a long period of absence two new species appeared. The tetragonitid *Pseudophyllites* could be an immigrant from the European Boreal province into the northern Pacific, via the Arctic, because *P. indra* (Forbes, 1846) first appeared in Europe and subsequently spread to the Tethys and Pacific. This species was, probably, very well adapted to a range of environments and typically occurs worldwide in abundance.

The Coniacian–Santonian boundary was very important also for the development of the Diplomoceratidae (Fig. 3). Six new species appeared in the earliest Santonian, which marked the onset of the future bloom which this family experienced during the Campanian in Far East Russian regions as well as in many other regions of the world (Wright et al. 1996).

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**The late Santonian heteromorph facies bio-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. Heteromorphs present a special case. They are represented by eight species, in six genera/subgenera such as *Hyphantoceras*, *Neocrioceras*, *Diplomoceras*, *Pseudoxybeloceras*, *P.* (*Polyptychoceras*), and *P.* (*Subptychoceras*). This bio-event could be proposed for the early–late Santonian boundary, awaiting detailed documentation elsewhere. The following examples appear to support the distinctiveness of this event: representatives of *Hyphantoceras* appeared at the same level in Japan (Matsumoto 1977), southeast France (Thomel 1988), Westfalen, Germany (Kennedy and Kaplan 2000), Zululand and Pondoland (Kennedy et al. 1995) and members of *Necrioceras* are known from this level in Japan and British Columbia (Haggart and Higgs 1989; Shigeta 2001). This list will undoubtedly be longer after detailed study of this interval in different regions across the world. Interestingly, at the same level new representatives of the family Pachydiscidae make their appearance in the Pacific region. For that basin, this particular moment marks the start in the development and wide distribution of this family (Fig. 3).

**The Santonian–Campanian faunal turnover bio-event**.—In Far East Russia, the Santonian–Campanian boundary 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 regions across the world. Zakharov et al. (1998) recorded some increase in temperature during the early late Santonian which could have had an impact on the disappearance of many Santonian taxa (Fig. 4). However, the total number of ammonite taxa increased and reached its maximum in the early Campanian (Fig. 2). Thus, this is another example of rapid recovery amongst ammonites (Yazykova et al. 2002).

In general, the early Campanian in the Russian Pacific region was characterised by a high diversity of diplomoceratids, pachydiscids, gaudryceratids, and tetragonitids (Fig. 3). The two last-named families are not only diverse but also greatly abundant. This was a fairly warm-water basin with normal salinity. Meanwhile, nearly seventy taxa of foraminifera, most of them benthic and stenobiontic, indicate a well-oxygenated basin, which also hosted new species of gastropod, inoceramid and non-inoceramid bivalves (Poyarkova 1987; Yazykova et al. 2002). Thus, during the early Campanian this basin was very conducive to the development of numerous marine biotic groups.

The end of the early Campanian was characterised by a relative fall in ammonite diversity, reflected in the disappearance of some heteromorphs and the last representatives of *Menuites*, and also a rise in inoceramid diversity, i.e., the appearance of the first radially ribbed *Pennatoceramus* providing evidence of higher energy in the basin, coupled with a rise in the abundance of foraminifera and a decrease in radiolarian abundance (Yazykova et al. 2002).

**The late Campanian radiation bio-event**.—The faunal impoverishment at the end of early Campanian was followed by a radiation at the start of the late Campanian (Figs. 2–4), which is well traceable from northeast Russia, through Sakhalin and Japan, and into Europe, for example, in southern Poland (EAJ-Y unpublished data). In the Russian Far East this level is marked by the onset of shallow-water facies with abundant ammonites, new morphotypes of inoceramids and new taxa of gastropods and non-inoceramid bivalves. 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; the highest diversity is found amongst benthic groups and some associated planktonic forms. Representatives of several macrofauna 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 early 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 is (are) in need of further study. Similar features can be seen at this level in British Columbia (Canada) and Alaska (Ward 1978; Haggart et al. 2009). On the other hand, the late Campanian time slice was a period of general reduction in taxonomic diversity amongst heteromorphs in Russian Pacific regions (Fig. 3).

The latest Campanian regression and temperature drop (Fig. 4) caused the gradual disappearance of all taxa amongst inoceramids and ammonites typical of this interval, with the exception of a few rare occurrences at the base of the Maastrichtian. Kirillova (2003) noted the onset of tectonic activity near the end of the late Campanian which resulted in an overall uplift of the whole region with the new regression-transgression pulse. Moreover, some cooling effect at this time, which has been documented in the North Atlantic (Linnert and Mutterlose 2009) and also in the Pacific (Zakharov et al. 1999, 2005), led to changes in oceanic circulation and caused climatic oscillations. A reduction of diversity and a slow recovery in the early Maastrichtian have also been recorded for benthic foraminiferal assemblages (Kalishevich et al. 1981; Turenko in Poyarkova 1987); this bio-event could be correlated with the late Campanian benthic extinction regional event (Fig. 4) described by Kauffmann and Hart (1995).

**The Campanian–Maastrichtian faunal turnover**.—The Russian Pacific coast is characterised by a relatively widespread distribution of Maastrichtian sedimentary rocks. They have been studied not only in Sakhalin and northeast Russia, but also in Shikotan Island, the smallest island of the southern Kuril Ridge. The disappearance of most Campanian ammonites and inoceramids, noted above, and the first occurrence of *Pachydiscus* (*P.*) *subcompressus* Matsumoto, 1959 and *P.* (*Neodesmoceras*) *japonicus* (Matsumoto,

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1947), both widely distributed Pacific species (Yazykova 2004) are the criteria for placement of this boundary. This is supported by data on inoceramids and radiolarians (Palechek et al. 2008), this level being matched by a similar horizon in Japan (Toshimitsu et al. 1995). In total, twenty-two new taxa appeared in the early Maastrichtian, mainly pachydiscids and gaudryceratids (Fig. 3). General ammonite diversity is lower even than during the late Campanian but still comparatively high (Fig. 2).

**The mid-Maastrichtian reduction bio-event**.—Around 50% of ammonite taxa became extinct at this time, and this holds true for almost all inoceramids as well. The last representatives of the Tetragonitidae and Kossmaticeratidae, and, probably, also the Baculitidae have been found in the latest early Maastrichtian. A slight increase in temperature was recorded by Zakharov et al. (1999). This bio-event can be correlated (Fig. 4) with the 68 Ma extinction bio-event of Kauffmann and Hart (1995).

**The late Maastrichtian radiation bio-event**.—The global late Maastrichtian transgression triggered maximum diversity in the families Pachydiscidae, Phylloceratidae, and Gaudryceratidae (Fig. 3 here; Hirano et al. 2000; Yazykova 2004), and during the same time, the northern Pacific ammonites again witnessed a "surge" of new taxa. In contrast, inoceramids did not recover after the decimation noted above. Some Russian Pacific ammonite species are immigrants from the European and Mediterranean realms, e.g., *Pseudophyllites indra* (Forbes, 1846) and *Zelandites varuna* (Forbes, 1846). The subgenus *Hypophylloceras* (*Neophylloceras*) is represented by the new *H*. (*N*.) *hetonaiense* Matsumoto, 1942 and *H*. (*N*.) *victriense* Shigeta and Maeda, 2005, alongside the long-lived *H.* (*N.*) *ramosum* (Meek, 1857). The gaudryceratids comprised nine endemic species: *Anagaudryceras matsumotoi* Morozumi, 1985; *A. seymouriense* Macellari, 1986; *Gaudryceras venustum* Matsumoto, 1984; *G. denmanense* (Whiteaves, 1901); *G. tombetsense* Matsumoto, 1984; *G*. cf. *tombetsense* Matsumoto, 1984; *G. hamanakense* Matsumoto and Yoshida, 1979; *G. makarovense* Shigeta and Maeda, 2005; and *Zelandites japonicus* Matsumoto, 1938. The last kossmaticeratid, *Brahmaites* (*Subbrahmaites*) *sachalinensis* Yabe and Shimizu, 1924, probably was a demersal taxon. The family Pachydiscidae is highly diverse, with four new species of *P.* (*Pachydiscus*) and two new species of a new subgenus, *P*. (*Neodesmoceras*), plus new species of *Patagiosites* and *Pseudomenuites*. Heteromorphs are represented by species of *Diplomoceras*, *Neancyloceras*, *Nostoceras* (*Didymoceras*), and *Glyptoxoceras*.

**The Cretaceous–Paleogene mass extinction event**.—The Cretaceous–Paleogene boundary in the Russian Pacific region was characterised by a global regression and strong volcanic activity with drastic environmental changes; these are here reflected in the total extinction of ammonites and inoceramid bivalves, and by some remarkable changes in other groups of organisms (Kalishevich et al. 1981; Turenko in Poyarkova 1987; Zonova et al. 1993; Yazikova 1994; Yazykova 2004; Jagt-Yazykova 2011).

In Sakhalin the youngest ammonites were found almost 2 m below the Maastrichtian–Paleogene boundary along the River Krasnoyarka (Naiba River Valley). These are numerous representatives of small-sized *Zelandites* (Zonova et al. 1993; Yazikova 1994) and one poorly preserved *Gaudryceras*. Wiedmann and Kullmann (1996: 807) suggested 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*. To these records I here add the Naiba section in Sakhalin, because, with the exception of *Vertebrites* and *Anapachydiscus*, all genera listed above have also been recorded here from the latest Maastrichtian. In addition, numerous individuals of *Zelandites japonicus* Matsumoto, 1938 and a single specimen of *Gaudryceras hamanakense* (Matsumoto and Yoshida, 1979) have been collected by myself about 2 m (~20 000 years) below the Cretaceous–Paleogene boundary.

# Conclusions

Ammonite evolution dynamics during the mid- and Late Cretaceous along the Russian Pacific coast reflected periods of crisis and bloom (radiation and recovery) as well as other bio-events. The majority of these probably have a global character and could possibly be used for correlation. In the Far East Russian sections the following bio-events have been recorded: the late Albian migration bio-event; Albian–Cenomanian faunal turnover bio-event; mid-Cenomanian *Turrilites* event; Cenomanian–Turonian boundary extinction bio-event; mid-Turonian *Scaphites* facies bio-event; mid–late Turonian boundary bio-event; Turonian–Coniacian faunal turnover bio-event; Coniacian–Santonian faunal turnover bio-event; late Santonian heteromorph facies bio-event; Santonian–Campanian faunal turnover bio-event; late Campanian radiation bio-event; Campanian–Maastrichtian faunal turnover bio-event; mid-Maastrichtian reduction bio-event and late Maastrichtian radiation event; Cretaceous–Paleogene mass extinction bio-event (Figs. 2, 4).

Moreover, studies of ammonite evolution and phylogeny in the Russian Pacific region show that recovery after environmental stress usually was rapid enough within this faunal group and a subsequent radiation event invariably followed. It seems that ammonites were characterised by rapid evolutionary rates and a wide range of morphologies which reflect a marked degree of environmental adaptation. This group existed for over 300 million years and likely would not be driven to extinction merely by cooling, anoxia or volcanic eruptive phases. Such kind of "drawbacks" were successfully dealt with. Stress suffered across the Cretaceous–Paleogene boundary had to be really strong and relatively sudden, and probably comprised all detrimental factors taken together, including

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high concentrations of toxic gases in the atmosphere and dissolved in ocean water. Such an event could only have been triggered by an impact or even multiple impacts, followed by hypercanes and giant tsunamis, widespread wildfires, plus intensified tectonic and volcanic activity, probably across the globe.

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