Ammonite Faunal Dynamics Across Bio-Events During the Mid-and Late Cretaceous Along the Russian Pacific Coast

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

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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 on 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
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 northeastern 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 *Gastropilites* 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-

Abbreviations.—OAE, Oxygen Anoxic Event.

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.

Fig. 1. Distribution of Cretaceous deposits in Far East Russia.
rents which ultimately led to the establishment of a convergent lineage of this European genus. Representatives of Ana−hoplites and Sommeratia 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−
lites, and Eogunnarites from the Koryak-Kamchatka palaeo-
basin 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 Afri-
can-Indian province and later possibly continued southeast-
erly, towards New Zealand (compare Kennedy and Klinger
1985).

Amongst others, an interesting case is the appearance of the
cosmopolitan Eogaudryceras (Eotetragonitides) duvalianus
(d’Orbigny, 1840) and a single lytoceratoid, Protetragonitides
cf. aeolus aeolus d’Orbigny, 1850. Both can be considered to
have been good swimmers, because the occurrence in the Pa-
cific 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). Protetragonitides 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 mar-
ginal shelf continental sea, and during the Albian maximum
flooding occurred as a result of a global transgression. The
deepest basin is likely to be found in Sakhalin. Here, probably
poorly oxygenated, yet not completely anoxic, conditions pre-
valued, while northeasterly regions were characterised by
warm, well-oxygenated waters. The Sikhote Alin palaeobasin
appears to have been comparatively shallow and well-oxygen-
ated. 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 a
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 am-
monite genera and species, especially in northern temperate
faunas (e.g., Gastroplites, Pseudopulchellia) and warm-tem-
perate subtropical taxa (e.g., Oxytropidoceras and Lyellii-
ceras) connected with QAElb and QAElc (Barnes et al.
1995). Thus, those ammonites which disappeared in the re-
ions mentioned could have migrated into more marginal ar-
 eas such as California, northeast Russia, Sakhalin, and Sikhote
Alin during the late Albian.

Albian–Cenomanian faunal turnover bio-event.—The late
Albian anoxic-event QAEl1d has been recorded in many
sections of the Pacific realm (Hirano and Takagi 1995; Hase-
gawa 1997; Hirano and Fukuji 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 Creta-
ceous boundary. Some families and subfamilies disappeared
altogether (i.e., Cleoniceratidae, Silesiotoidae, Beudanti-
ceratinae, Sonneratiniae; see Wright et al. 1996). Almost all
Albian ammonite taxa known from northwest Pacific prov-
inces became extinct, except for a few species, which sur-
vived 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 con-
ditions. In short, changes which took place during the latest
Albian to the earliest Cenomanian are best considered to il-
ustrate 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 Pazoasia and Des-
noceras (Pseudoulitigella) 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 al-
lowed the entry of immigrant species into the Pacific region,
such as Phylloceras (Neophylloceras) seresitense Pervin-
quière, 1907; Anagaudryceras buddha (Forbes, 1846); Para-
pazoasia (Austinerice) austeni (Sharpe, 1855); Mantelli-
ceras sp.; and Acanthoceras sp. These taxa probably origin-
nated from the Tethys and migrated into Sakhalin and north-
east 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 thir-
ten 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 Kossmati-
ceratidae (seven new genera appearing) and the entry of the
family Acanthoceratidae (Wright et al. 1996). In Far East Rus-
sia, the former family was represented by ten species of two
genera, Marshallites and Mikasaiceras, while the latter com-
prised four genera/subgenera, Mantelliceras, Calycoceras
(Calycoceras), C. (Newboldiceras), and Acanthoceras. How-
ever, in view of the fact that all of these acaenocheratids 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
(Jimbó 1894; Matsumoto 1943; Shigeta 2001; Matsumoto and
Toshimitsu 2005). Meanwhile, the Cenomanian of Western
Interior of North America, as well as the European, Mediterra-
nean, and African-Indian provinces is characterised by high
diversity levels of the family Acanthoceratidae (e.g., Wright

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 Mikhailova 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
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 and siltstone as well as bentonitic clay. This “coloured” interactive volcanism are reflected in the presence of mudstone water sedimentation. Anoxic conditions connected with strong Cenomanian–Turonian transgression has also been recorded in of new ammonite morphotypes in general. The global mid-

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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 (Vere–shagin 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, tetragonids, phylloceratids, and acanthoceratids (R. [Romaniceras], R. [Yubariceras], Kameruniceras, and Pseudaspido- ceras). Desmoceratids such as Pucoxia (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),
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 [Eubostryhoceras] and Hyphantoceras), as well as Damesites and Houriqueta, 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 ammonites 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 (Jimbo, 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 (Kossat, 1895) and Gaudryceras denseplicatum Jimbo, 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 Jimbo, 1894, Desmophyllites diphyloides (Forbes, 1846) and Phyllopachyceras forbesianum (d’Orbigny, 1850), which co-occurred with local indexes for this boundary such as Texanites (PlesioteXanites) kawasakiKawada, 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/L. 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, Ditymoceras, Pseudoxybeloceras, Polyptychoceras, Neoetriceras, Subptychoceras, Eubostryhoceras, and Baculites (Poyarkova 1987; Alabashev 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 Kossmaticsitidae along the Russian Pacific coast (Fig. 3), where after a long period of absence two new species appeared. The tetragonitid Pseudoephyllices 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).
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 *Hyphantocteceras*, *Neocteceras*, *Diplomoceras*, *Pseudoxybeloceras*, *P. (Polyptychocheceras)*, and *P. (Subptychocheceras)*. 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 *Hyphantocteceras* 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* (Kennedy et al. 1995) and members of many others (Kennedy and Kaplan 2000), Zululand and Pondoland regions across the world. Interestingly, at the same level new representatives of the family Pachydiscicidae 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 stenobiotic, 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 *Menefites*, and also a rise in inoceramid diversity, i.e., the appearance of the first radially ribbed *Pennatoceras* 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 (Kalishевич 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 northeastern 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) jonicus* (Matsumoto,
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 Pseudophyllites (Meek, 1857). The gaudryceratids comprised nine endemic species: Anagaudryceras matsu−motoi Morozumi, 1985; A. seymouriense (Forbes, 1846) and Zelandites varuna (Forbes, 1846). The subgenus Hypophylloceras (Neophyllloceras) is represented by the new H. (N.) Hetonaiense Matsumoto, 1942 and H. (N.) Victrienense Shigeta and Maeda, 2005, alongside the long-lived H. (N.) Ramousum (Meek, 1857). The gaudryceratids comprised nine endemic species: Anagaudryceras matsu−motoi 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. makarovenense Shigeta and Maeda, 2005; and Zelandites japonicus Matsumoto, 1938. The last kossmaticeratid, Brahmaites (Subbrahmaites) Sachalinensis Yabe and Shimizu, 1924, was probably a demersal taxon. The family Pachydiscidae is highly diverse, probably with four new species of P. (Pachydiscus) and two new species of a new subgenus, P. (Neodesmoceras), plus new species of Patagiosites and Pseudomenataes. Heteromorphs are represented by species of Diplomoceras, Neancyloceras, Nostoceras (Didymoceras), and Glyptoxoceras.

The Cretaceous–Palaeogene mass extinction event.—The Cretaceous–Palaeogene 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–Palaeogene 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, Anaphyloceras, Pachydiscus, and Diplomoceras. To these records I here add the Naiba section in Sakhalin, because, with the exception of Vertebrites and Anaphyloceras, 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 hamana−kense (Matsumoto and Yoshida, 1979) have been collected by myself about 2 m (~20 000 years) below the Cretaceous–Palaeogene 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 Turritites event; Cenomanian–Turonian boundary extinction bio−event; mid–Turonian Scaphites facies bio−event; 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–Palaeogene 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–Palaeogene boundary had to be really strong and relatively sudden, and probably comprised all detrimental factors taken together, including
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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