

Permian bivalve mollusks of Northeast Asia

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Abstract

Bivalve mollusks are very important in the Permian biota of Northeast Asia. During the Permian the bivalves had different distribution patterns both in space and time, and their occurrence was governed by many factors related to water depth and geodynamic conditions. In Northeast Asia there were two main bivalve paleocommunities, shallow and deep sea bivalves. Through the Permian, the bivalves began to dominate benthic assemblages. There are five major stages in their developmental history: Asselian–Artinskian, Kungurian, Roadian–Wordian, Capitanian–Early Wuchiapingian and Late Changhsingian. The mid-Kungurian stage was characterized by a maximum in bivalve diversity, whereas the Late Kungurian, Early Capitanian and latest Permian had the lowest bivalve diversity.

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1. Introduction

Bivalves, together with brachiopods and small foraminifers, represent the most typical Permian biota throughout northeastern Asia. Studies of bivalves were conducted by Likharev (1934) in the 1930s and continued by Popov (1957), Maslennikov (1959), Kulikov (1967), Lobanova and Lyutkevich (1970), Kuznetsov (1973), Muromtseva and Gus'kov (1984), Astafieva and Astafieva-Urbajtis (1988) and Astafieva (1993).

The author of this paper has been studying this fossil group for 20 years and has recognized that the Permian bivalve faunas in northeastern Asia are important for reconstructing the Permian history of not only this vast territory, but also for the entire Boreal Realm. This study is primarily concerned with bivalve taxonomy; their significance for intra-, inter- and trans-basinal correlations; their spatial distribution in relation to depositional environments and geodynamic changes; and the dynamics of bivalve species diversity and its underlying controlling factors.

2. Paleogeography

Through the Permian, northeastern Asia (except the territory of modern Koryakia) was a set of different marine basins

forming the eastern Biarmian paleogeographic region (Biakov, 2003) (Figs. 1 and 2). Along the eastern margin of the Siberian Craton, there was a passive continental margin (the Verkhoyansk Sea) where an up to 5 km thick succession of relatively shallow-water sandstones and mudstones, often flyschoid, was deposited. The Okhotsk Microcontinent was located somewhat far to the southeast, where the Permian is characterized by continental and shallow marine sediments. The Omolon Microcontinent was separated from the Siberian Craton and Okhotsk Microcontinent by a number of marine basins, including several relatively deep seas (Ayan-Yuryakh Trough Basin and Balygychan-Sugoi Marginal Sea) (Fig. 1). Along their present southern periphery, there was the Okhotsk-Taigonoss Volcanic Arc, which had its peak development during the Gizhigian (Capitanian, Middle Permian). The southwestern part of this volcanic arc is presumed to overlie the Okhotsk Microcontinent. In the southeast, the Omolon Microcontinent was contiguous to the deep back-arc Gizhiga Sea, and in the east, to a set of relatively shallow-water back-arc seas, which at present are fragmentarily represented by Permian outcrops covering the eastern part of the Omolon Microcontinent and along the left bank of the Penzhina River near its mouth (Fig. 2). The Omulevka and Prikolya Terranes, as we may judge from their peculiar Permian sequences, seem to have been isolated from the peripheral northern part of the Balygychan-Sugoi Marginal Sea. A complicated paleogeographic environment had served as a

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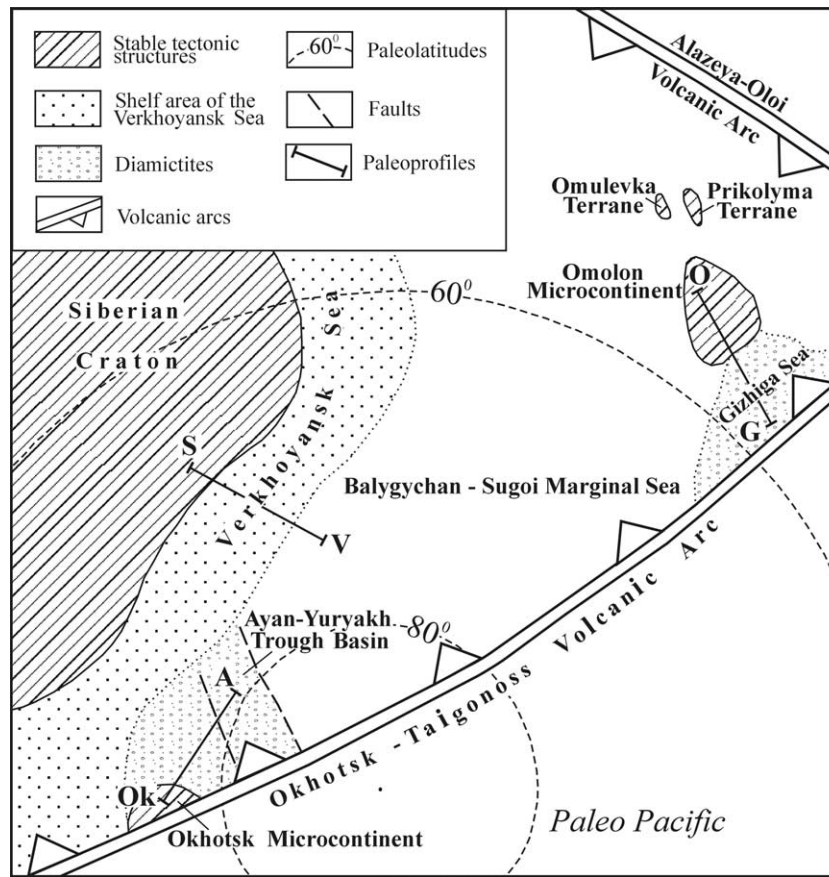


Fig. 1. Permian paleogeography of Northeast Asia for the Gizhigian (Capitanian) age in the Permian; paleolatitudes data from Khranov (1991) and Kolesov (2002).

prerequisite for different life conditions and, consequently, the development of varied bivalve paleocommunities.

3. Paleocommunities

The most diverse Permian fossils, both qualitatively and quantitatively, are found on the Omolon Microcontinent. There, the bivalve faunas have nearly all the genera typical of the entire eastern Boreal Realm. However, the situation becomes quite different in deeper seas such as in the Balygychan, Ayan-Yuryakh, Sugoi and Gizhiga seas. There, very thick (up to 7 km) and often flysch facies of sandy-clay and volcanic rocks occur, characterised by debris flow-type sedimentary processes and very low diversity biotas. The paleocommunities in these deeper marine environments are dominated by fragmentary *Inoceramus*-like bivalves, locally associated with ctenodontids and gastropods *Straparolus* sp.

Bivalves comprise about 95% of the deeper-water paleocommunities (including 95–98% Kolymiidae), the remainder being gastropods (4–5%), while other fossils comprise less than 1% of the fauna. The overall biomass of the *Inoceramus*-like bivalves, which were abundant, and among which there were large and even gigantic forms, appears to have been several orders greater than the biomass of all other fossils. Hence, a question arises: what was the source of a high biological productivity of these bivalve paleocommunities?

If we consider the deep sea environment typical of these paleobiocenoses and the peculiar hydrogen sulfide smell of the fossil shells, then we can assume a general chemotrophic source of nutrients (Ganelin, 1997; Biakov, 1999). Since the second half of the Early Permian, a new marine ecosystem had been forming throughout northeastern Asia; where benthic paleocommunities became overwhelmingly dominated by bivalves for the first time in geologic history, until, since the Early Mesozoic, this group has replaced the brachiopods.

The relationships between different bivalve taxa and sedimentary environments can be schematically represented (Fig. 3). These schematic profiles demonstrate three main shallow-to-deep water transitional types: the Omolon; Okhotsk; and Siberian types, which indicate the effect of different sea-floor topography and depositional environments in the marine basins, due to their different geodynamic settings. The Omolon Sea was a shallow marine basin encircled with islands and bounded with deep seas on all sides. The Okhotsk Sea was a marginal marine basin, bounded by the Okhotsk-Taigonoss Volcanic Arc in the modern south-east, and by the deep Ayan-Yuryakh Trough Basin in the northwest. The Verkhoyansk Sea Basin consisted of marginal to epicontinental seas located on the passive continental margin of the Siberian Craton. Each of these marine basins featured unique deep and shallow depositional environments, and was characterized by different bivalve paleocommunities. In general, two types of

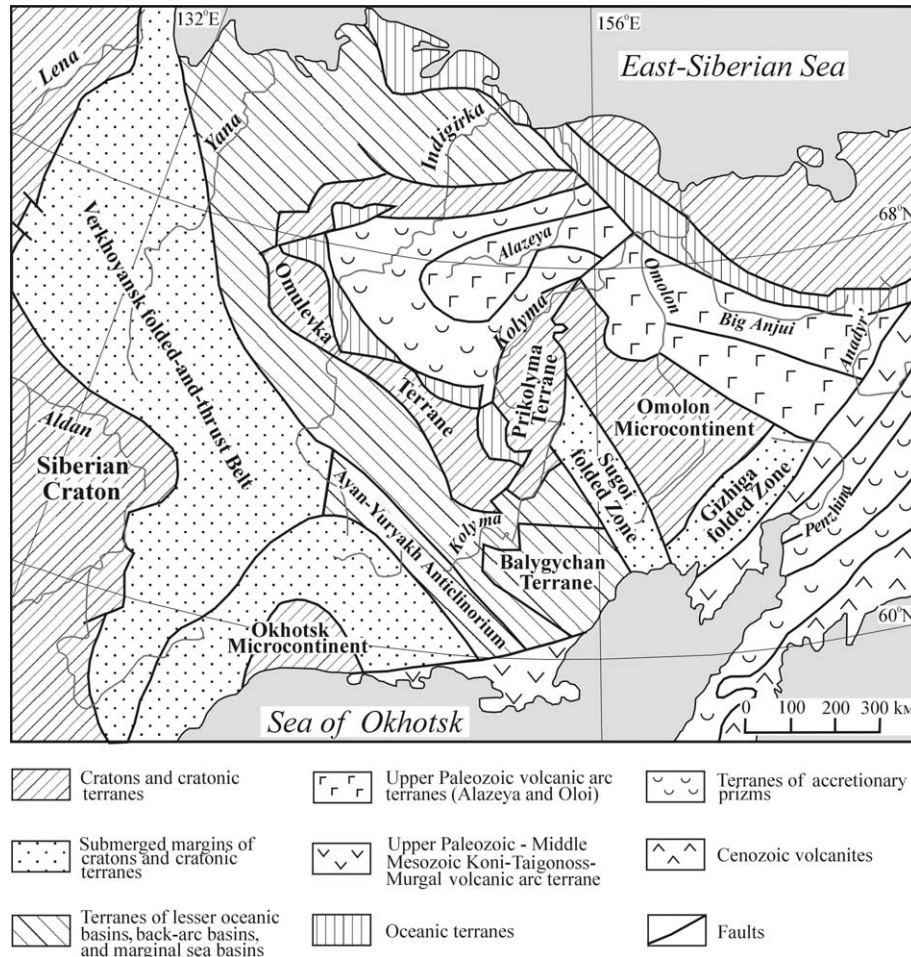


Fig. 2. Modern tectonic map showing major tectonic elements (modified from Shpikerman, (1998)).

bivalve paleocommunities may be recognized, representing respectively deep- and shallow-water environments. The deep-water paleocommunities are generally the same everywhere and are not distinguished in terms of their geographic occurrence. These paleocommunities have been reliably identified in the Ayan-Yuryakh, the Balygychan-Sugoi and the Gyzhiga basins. In the Verkhoyansk Basin they have not yet been studied in detail. On the other hand, the shallow sea paleocommunities can be differentiated into the Omolon, Okhotsk and Siberian Types, which, in turn, have sub-types characteristic of specific sedimentary environments.

3.1. Deep-water paleocommunities

The deep water paleocommunities are distinguished as bathyal and abyssal types. These paleocommunities are usually rare and poor in taxonomic diversity. There are scarce *Inoceramus*-like bivalves (*Maitaia*, to a lesser extent *Intomodesma*, and very rare *Kolymia*, which are usually byssiferous and free-lying benthic forms) and creeping solitary Ctenodontida (*Glyptoleda*, less frequent *Polidevcia*, *Nuculopsis* and *Palaeoneilo*). Other deep-water forms are extremely scarce. The deep-water Okhotsk Type of bivalve paleocommunity is

specifically characterised by rare but relatively large deep water ‘bioherms’, which appear to have been controlled by submarine hydrothermal effects. The proof of the hydrothermal nature of these ‘bioherms’ is their very large size (on average 40–50 m across). These ‘bioherms’ consist of accumulations of *Inoceramus*-like bivalves buried in deep-water sediments without any sign of redeposition.

3.2. Shallow water paleocommunities

This type of paleocommunities displays some paleogeographical differences. The shallow-water bivalve paleocommunities are more common and much more diverse in their taxonomy compared with deep-water paleocommunities. Three shallow-water paleocommunities can be recognized: the Omolon; Okhotsk; and Siberian types.

3.3. The Omolon type

This type includes the paleocommunities inhabiting the clayey to sandy carbonate substrate of the outer shelf, submarine rises within the shelf area, the inner shelf (including depressions within the inner shelf area) and also the clay-sand

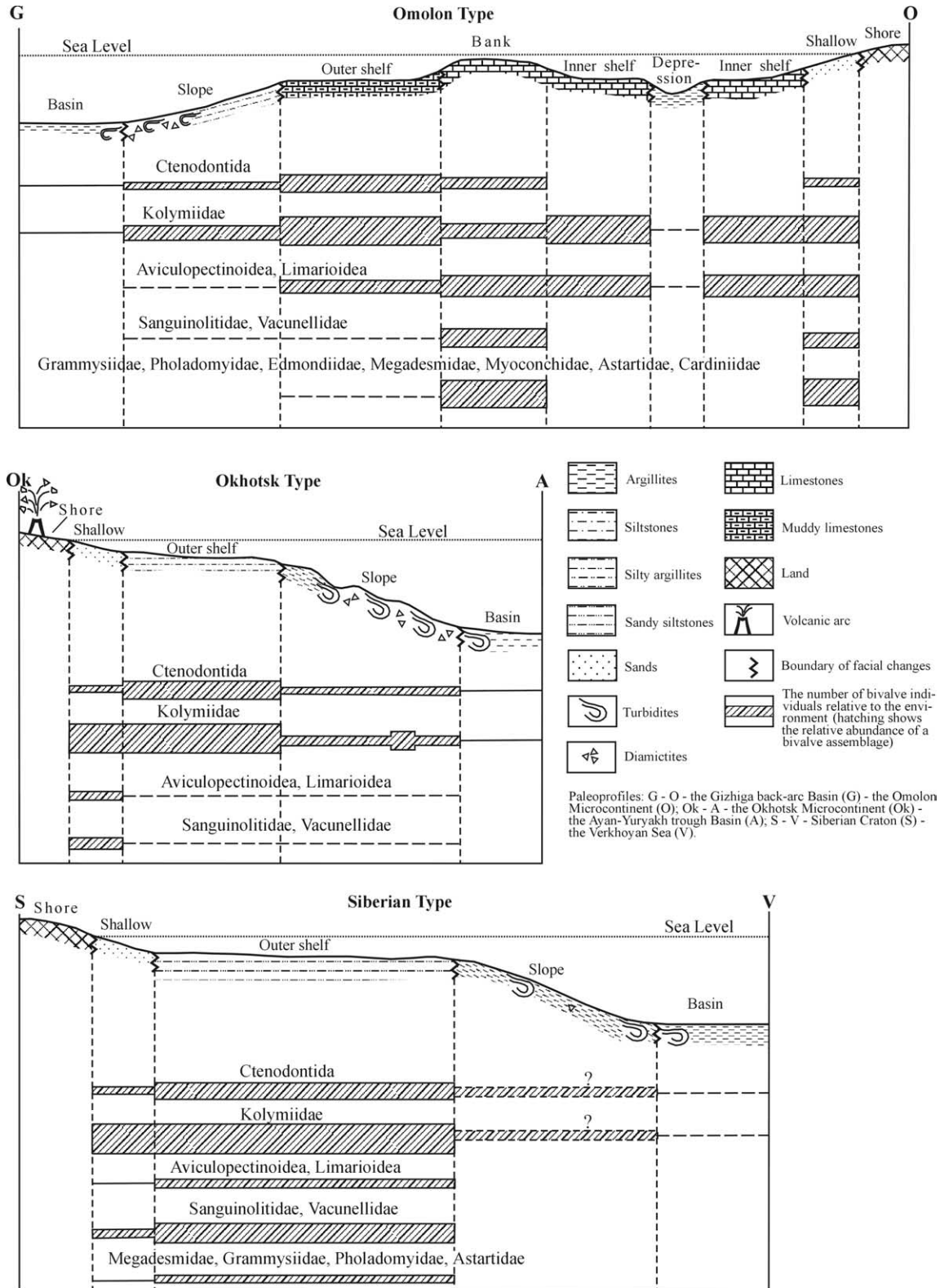


Fig. 3. Different bivalve paleocommunities and their living environments in the Permian throughout Northeast Asia.

and carbonate–sand substrata of the nearshore zone. The most thriving paleocommunities were those inhabiting submarine rises (banks) over the shelf area and those living in clay–sand substrata in the nearshore zone; they were composed

exclusively of bivalve forms. However, those inhabiting submarine rises were dominated by Aviculopectinoidea (*Heteropecten*, *Omolonpecten*, *Vorkutopecten*, *Vnigripecten*, *Streblopteria*, *Streblochondria*, etc.), Limarioidea

(*Palaeolima*), Vacunellidae (*Myonia*, *Vacunella*), Cardiniidae (*Cypricardinia*), Sanguinolitidae (*Myophossa*, *Praeundulomya*, *Sanguinolites*), Astartidae (*Astartella*), Pholadomyidae (*Wilkingia*, *Solenomorpha*), Edmondiidae (*Edmondia*) and others. Somewhat less frequent were Ctenodontida (*Nuculopsis*, *Polidevcia*) and Kolymiidae (*Kolymia*, *Praekolymia*, *Intomodesma*, *Maitaia*). Unlike the submarine rise paleocommunities, the nearshore paleocommunities were typically characterized by *Permophorus*, *Parallelodon*, *Solemya*, *Pyramus*, *Solenomorpha*, *Lithophaga*, *Edmondia* and some other forms; locally the Kolymiidae became dominant and extremely abundant (e.g. *Maitaia*, *Intomodesma*).

Paleocommunities inhabiting the inner shelf areas and depressions had a very low diversity. The paleocommunities in the inner shelf environment were dominated by *Inoceramus*-like bivalves (*Aphanaia*, *Kolymia* and, to a lesser extent, *Maitaia* and *Intomodesma*), which formed ‘kolymic’ (‘atomodesmic’) limestones, which have a specific smell of hydrogen sulfide. These rocks nearly all consist of minute (less than 1 mm across) fragmented shells of Kolymiidae, and often may form rock units up to several tens of meters thick. Aviculopectinoidea (*Heteropecten* and *Streblopteria*) are less frequent. Other bivalves are unknown. Depressions within the inner shelf area are barren of fossils.

3.4. The Okhotsk type

These paleocommunities are less diverse than the Omolon Type. There are two basic sub-types within this type of paleocommunity: those living on a clay and sandy substrate in the nearshore zone and those living on a clay–silt–sand substrate of the outer shelf. The former is typically represented by Kolymiidae (*Maitaia*, *Intomodesma*, less frequent *Aphanaia*, *Praekolymia*, *Kolymia* and *Cyrtokolymia*). Relatively scarce are Vacunellidae (*Pachymyonia*), Sanguinolitidae (*Praeundulomya*), Ctenodontida (*Polidevcia*) and Aviculopectinoidea (*Heteropecten*, *Streblopteria*, *Streblochondria*). The second sub-type is characterized by the dominance of Kolymiidae (*Aphanaia*, *Cyrtokolymia*, less frequent *Kolymia*, *Maitaia*, *Intomodesma*) and Ctenodontida (*Nuculopsis*, *Polidevcia*).

3.5. The Siberian type

Shallow-water paleocommunities of the Siberian Type have much in common with the Okhotsk paleocommunities and can be also separated into two main sub-types: those living in the clay–sand substrate of the nearshore zone and those living in clay–silt–sand substrate of the outer shelf. But, unlike the Okhotsk Type paleocommunities, the Siberian Type is much more diverse in species composition, although it is less diverse than the Omolon Type. The most typical forms of the nearshore paleocommunities are Kolymiidae (*Praekolymia*, *Kolymia*, *Intomodesma* and less frequent *Aphanaia* and *Maitaia*). Other bivalve groups are less common and have a taxonomic

composition similar to the Okhotsk Type, although somewhat more diverse. Kolymiidae were also the most typical forms of the outer shelf paleocommunities (*Aphanaia*, *Praekolymia*, *Kolymia*, less frequent *Maitaia*, *Cyrtokolymia*, *Intomodesma*), as well as Ctenodontida (*Polidevcia*). Less widespread bivalve groups include Aviculopectinoidea (*Heteropecten*), Vacunellidae (*Myonia*, *Pachymyonia*, *Australomya*), Sanguinolitidae (*Myophossa*, *Praeundulomya*, *Sanguinolites*), Megadesmidae (*Pyramus*, *Megadesmus*), and others.

4. Biozonation of Permian bivalve faunas in northeastern Asia

The most ample data available are those obtained from the Omolon Massif. It was there that the first bivalve-based biostratigraphical zones were established and these have now been used in many other locations, including the Kolyma-Omolon, Verkhoyansk and Transbaikal region (Biakov, 2000a, 2002b), as well as in many other areas of the Boreal Realm.

The bivalve-based biozonation scale (except in its lowermost part) demonstrates, as its basis of construction, the developmental stages of *Inoceramus*-like bivalves of the Kolymiidae (Biakov, 1995, 1997). These developmental stages were established by morphogenic changes of the Kolymiidae through the Permian, and by reconstructing the phylogeny of this group. Such an approach allows us to avoid faunal breaks in the scale and make area- and region-wide correlations using evolutionary trends. The Kolymiidae are not found in the Munugudzhakian Superhorizon, nor in the lowermost Dzhigdalinian Superhorizon of the Lower Permian, therefore the bivalve biozones in these areas are based on other groups. The description and a detailed substantiation of the bivalve-based biostratigraphic scale and the problems associated with the correlation of this scale have been discussed in several previous studies (Biakov, 2000a,b; Biakov and Ganelin, 2002; Ganelin et al., 2003).

The bivalve-based biozones and their correlation with brachiopod faunas, as well as with the East European and International Permian timescales, are summarized in Ganelin and Biakov (2006).

5. Developmental stages and species diversity

The evolutionary history of Permian bivalves, like many other fossil groups, was much affected by paleoenvironment (Ganelin et al., 2001) and by different geological events in the territory of northeastern Asia. Modeling the evolution of the bivalve faunas and examining their species diversity through the Permian (Biakov, 2001, 2002a) have allowed us to establish five major stages in their development. The developmental stages are signified by important biotic events, and usually reveal drastic changes in bivalve species diversity (Table 1, Ganelin and Biakov (2006)). There are more than 210 bivalve species established, representing 62 genera and 30 families.

5.1. The Munugudzhakian—earliest Dzhigdalinian developmental stage

This developmental stage encompasses the Asselian, Sakmarian and Artinskian. The beginning of this developmental stage and, correspondingly, the Carboniferous–Permian boundary, is marked by a certain change in bivalve species. The change, however, is not obvious at the generic level and supposedly manifests itself only by the appearance of the new genus *Myophossa*. Through the first developmental stage, bivalve genera such as *Merismopteria*, *Pyramus* and *Vorkutopecten* emerged, and the total number of species increased from 11 to 23, with maximum species diversity occurring at the end of the Sakmarian (the *Jakutoproductus terekhovi*–*Cypricardinia eopermica* time) (Table 1). Munugudzhakian time was prolific, with Carboniferous faunas including other fossil groups. Bivalves of this time are numerically subordinate to brachiopods. In general, this bivalve fauna has much similarity with coeval bivalve assemblages from Western and Eastern Australia (Dickins, 1963; Runnegar, 1967) and New Zealand (Waterhouse, 1969) and is dominated by *Palaeoneilo*, '*Aviculopecten*', *Heteropecten*, *Omolonopecten*, *Streblochondria*, *Schizodus*, *Permophorus*, *Pyramus*, *Myophossa*, *Dulunomya*, *Palaeocosmomya*, *Vacunella*, and *Cypricardinia* (Biakov, 2001). However, this bivalve fauna lacks peculiar Gondwanan genera such as *Eurydesma*. The first developmental stage can be subdivided into three substages. Each corresponds approximately to a stage of the East European Early Permian.

5.2. The Dzhigdalinian developmental stage

This developmental stage represents the Dzhigdalinian Horizon (except the *Jakutoproductus burgaliensis*–*Lithophaga gigantea* Lone, see Ganelin and Biakov (2006) for definition of 'lones') and corresponds to the Kungurian and the Ufimian. Its beginning was signified by a change in the ecosystem. The most important event at this stage was the emergence of the *Inoceramus*-like bivalves, mainly *Aphanaia*. Throughout the rest of the Permian, *Inoceramus*-like bivalves dominated the benthic paleocommunities. Dominant genera characteristic for this developmental stage include *Polidevcia*, *Parallelodon*, *Solemya*, *Praeundulomya*, *Pyramus*, *Aphanaia*, *Praekolymia*, *Heteropecten*, *Vorkutopecten*, *Undopecten*, *Streblopteria*, *Palaeolima*, *Cypricardinia*, *Astartella* and *Schizodus*. It was during this period of the Late Paleozoic that the first deep-sea paleocommunities living on the continental slope and adjacent basinal environments became established in northeastern Asia. Ctenodont bivalves formed the core of these paleocommunities. Since the Kazanian, *Inoceramus*-like bivalves and gastropods such as *Straparolus* sp. also occurred. In the *Megousia kuliki*–*Aphanaia andrianovi* Lone of the Kungurian, the number of species reached 31, which was the period of greatest taxonomic diversity for the Permian. This biotic event has been reported from other faunal groups in many parts of the world (Leven et al., 1996; Leonova, 1999). The end of the Dzhigdalinian stage (*Kolymaella ogonerensis* Lone) was

signified by an important extinction event, when about 70% of the bivalve species died out, with no new forms. This event may serve as a basis for us to support the idea held by many researchers that the Ufimian Stage could just be a part of the Kungurian.

5.3. The Omolonian developmental stage

The Omolonian developmental stage includes the Kazanian and Early Tatarian (the Urzhumian). The bivalve paleocommunity at this time was dominated characteristically by *Kolymia* s. s. These were often rock-forming organisms producing 'kolymic' ('atomodesmic') limestones. Besides *Kolymia*, other common forms include *Polidevcia*, *Aphanaia*, *Heteropecten* (s. l.), *Streblopteria*, and, at the end of this stage, also *Myonia* and *Maitaia*. At the beginning of the Omolonian, bivalves began to replace brachiopods, and their species diversity through this period increased from 14 to 26 species. From the viewpoint of the Permian bivalve history, the Omolonian stage appears to consist of two substages corresponding approximately to the Roadian and Wordian Stages respectively (see table 1 of Ganelin and Biakov, 2006). The pectinid *Vnigripecten* sp., a form close to *Vnigripecten phosphaticus* (Girty) from the Phosphoria Formation of USA (Ciriacks, 1963), has been reported from the *Aphanaia dilatata* Zone of the Omolon Massif, and '*Aviculopecten*' cf. *girtyi* Newell and 'A.' cf. *gryphus* Newell, both typical of the Word Formation (Newell, 1938), are also known from the *Kolymia multiformis* Zone of the Omolon Massif. The idea expressed by some researchers (Molostovsky et al., 2002; Lozovsky et al., 2002) that the Urzhumian Stage should be recognized as an individual unit seems quite reasonable. The Urzhumian Stage corresponds presumably to the Wordian Stage.

5.4. The Gizhigian—early Khivachian developmental stage

This developmental stage seems to correspond to the Severodvinian (Capitanian and Early Wuchiapingian). The beginning of this stage was signified by a major biotic crisis (Biakov and Ganelin, 1998), probably as the first phase of the great end-Permian extinction event. At that time, 85% bivalves became extinct, including those which dominated the previous stage (e.g. *Kolymia* s. s.). Through this stage, occurrences of bivalves and other faunas were stratigraphically scattered. Bivalves were dominated by *Maitaia*, and at the beginning of the stage, those in relatively shallow environments of the Omolon Massif were dominated by *Merismopteria* and *Cypricardinia*. The typical bathyal forms were *Polidevcia* and *Glyptoleda*. Through this developmental stage, the taxonomic diversity of bivalves was the lowest for the whole Permian, with only 5–8 species (especially in the *Maitaia tenkensis* Zone). The *Maitaia tenkensis* Zone (the beginning of the Wuchiapingian) can be compared with the second phase of the end-Permian extinction. Presumably, there is a correspondence between the early Khivachian biotic crisis and the Midian–Dzhulfian mass extinction event reported from many other faunas all over the world (Shi et al., 1999; Tong et al.,

1999; Kotlyar and Kossovaya, 2000; Shen and Shi, 2002; Leven, 2003).

5.5. The late Khivachian stage

This is the terminal stage in bivalve development in northeastern Asia. The beginning of this development stage (the *Intomodesma hurenensis* and *I. costatum* subzones) was characterized by a significant increase of taxonomic diversity in all faunas, including bivalves. In the case of the bivalves, the number of taxa became as high as that before the crisis, with 25 species and 14 genera in the following *Intomodesma evenicum* Subzone. The late Khivachian bivalve paleocommunities were dominated by *Intomodesma*, which was especially typical of the terrigenous and deep sea facies. *Polidevcia* was also common, whereas *Maitaia* was uncommon. Typical shallow-water forms were mainly pectinoids such as *Vnigripecten*, *Streblopteria*, *Streblochondria* and *Cyrtorostra*. Other groups were represented by *Myonia*, *Praeundulomya*, *Wilkingia*?, *Conocardium* and *Nuculopsis*. The late Khivachian taxonomic rise is comparable to that in the Vyatkian Stage of the East European Platform, which also displays a significant increase in the taxonomic diversity (Molostovsky et al., 2002). The terminal stage of the Permian Period (*Intomodesma post-evenicum* subzone), corresponding to the very end of late Khivachian time, was characterized by an abrupt elimination of all Permian paleocommunities. At that time, there were just some bivalves of *Intomodesma* and solitary *Claraioides* remaining.

At the beginning of the Triassic, sedimentary basins became deeper throughout northeastern Asia. The Permian–Triassic crisis caused the extinction of most benthic paleocommunities, and only a few survived through to the end of the Induan. The survivors are exclusively solitary ctenodontids and kolymiids (e.g. *Maitaia*). In the Early Induan, there were only four bivalve species (Kurushin, 2001), which inhabited only the eastern Verkhoyansk areas.

6. Conclusions

The Permian bivalves of northeastern Asia display a high degree of regional endemism. However, through the Permian, this region appears to have had some short-term biotic exchanges with other biochores. For example, there were invasions of non-Boreal bivalves (*Atomodesma variabile* Wanner in the Wuchiapingian), as well as migrations of Boreal bivalves through contiguous sea basins into this region (e.g. *Maitaia bella* Biakov in the Capitanian). Besides, there is also evidence of probably parallel development in the bivalve faunas between Northeast Asia and Australia. For instance, there is much similarity between the Lower Permian bivalve assemblages of the Omolon Massif and Western Australia. There are also some genera (some *Polidevcia*, *Merismopteria*, *Maitaia*, etc.), which are similar to those reported from Eastern Australia, Tasmania and New Zealand. In order to furnish well-grounded explanations to these inter-hemispheric biogeographical phenomena, further studies must be continued.

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