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Permian ammonoid associations of the Verkhoyansk Region, Northeast Russia

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Abstract

On the basis of a study of the majority of Permian ammonoids known in Verkhoyansk Region, and an analysis of their age distribution, seven associations and four subassociations are established. These ammonoid associations are the Khorokyt, Arkachan, Endybal, Mysovy, Orol, Takamkyt, Delendzha and Post-*Sverdrupites* associations, in ascending order. The majority of these associations and subassociations include some complementary ammonoid Beds. The ammonoid associations and subassociations are considered as biostratigraphic divisions of regional stratigraphic extent and are useful for dating and correlating the Permian sedimentary sequences of the Verkhoyansk Region. The geographical and stratigraphic distributions of 360 Permian ammonoid shells in the Verkhoyansk Region permits us to not only diagnose each ammonoid association with specific index species, but also to elucidate the biogeographic connections and migration patterns of the Verkhoyansk ammonoid faunas in relation to these spreading throughout the entire Boreal Realm.

Keywords: Verkhoyansk; Ammonoids; Permian; Biostratigraphy; Biogeography; Northeast Russia

1. Introduction

The Permian ammonoids of the Verkhoyansk Region were first described by Popow (1958a,b, 1959). These works were based on fragmentary material that could not reveal the taxonomical composition of Verkhoyansk associations, but had a great value for the stratigraphy of the region. The main driving force for the development of the taxonomy of Permian ammonoids of the Verkhoyansk Region and of the Northeast of Asia, was the work of Ruzhencev (1961), in which some of the biostratigraphically important ammonoid genera and species from this region were first described. The results of Popow (1970) and Andrianov's (1966, 1968) researches were also significant.

The majority of Permian ammonoids of the Northeast Asia were described in Andrianov's latest monograph (1985), a volume that has been the principal work for this region. These ammonoids were classified into five associations: the Khorokyt, Echiy, Tumara, Cherkambal and an unnamed associations. These associations reflect the important stages in the development of the Permian ammonoid fauna in Northeast Asia (Kutygin, 1997) and, besides the unnamed association, characterize the Khorokytian, Echian, Tumarian and Delendzhian Horizons, respectively. However, Abramov and Grigorjeva (1988) suggested the necessity to further subdivide these associations.

Our recent field surveys (in collaboration with Budnikov and Klets) have been conducted to find more ammonoid faunas in the Permian deposits of the Western Verkhoyansk Region. The aim of these surveys was biostratigraphic substantiation of the established regional stratigraphical scheme and the elaboration of the ammonoid-based biostratigraphical scale. As a result goniatite collections were gathered from numerous stratigraphic levels, such as the Khorokytian, Echian, Tumarian and Delendzhian Horizon. The Abramov and Grigorjeva (1988) work was confirmed.

About 360 ammonoid shells were discovered from the Permian of the Verkhoyansk Region (Fig. 1) during 1953–2001, all well enough preserved to allow systematic identification (Table 1). A subsequent study was conducted for all the newly collected and most of the previously known Permian ammonoids to analyze their age distribution and taxonomic composition.

In this paper, we propose a new ammonoid-based biozonation scheme (Fig. 2) in that the Echiy 'association' of

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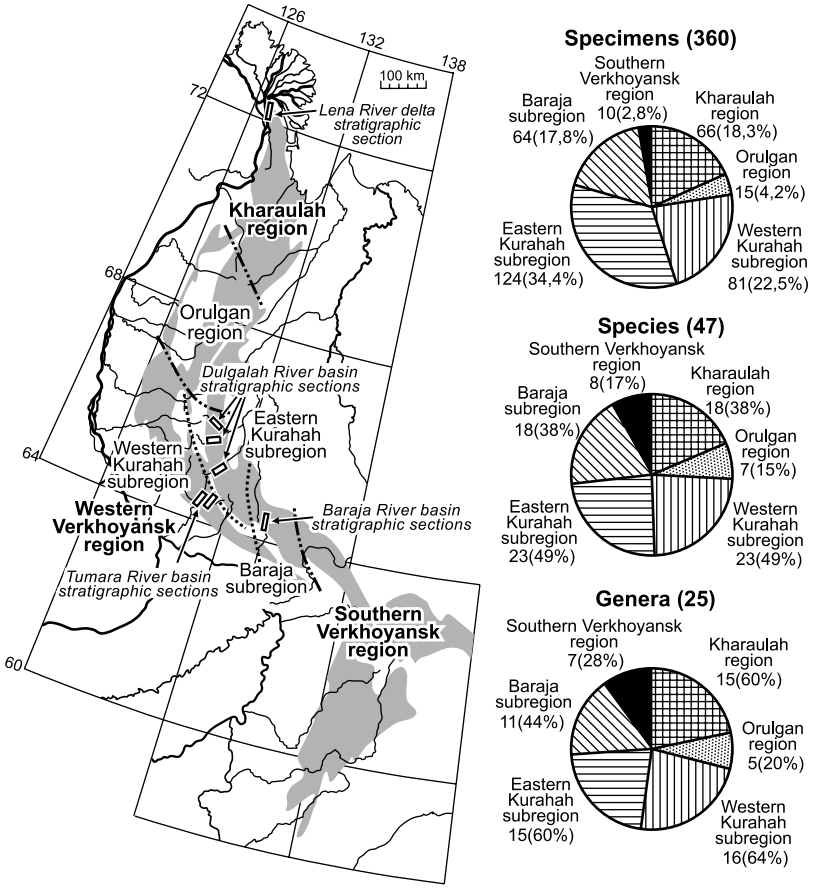

Fig. 1. Geographic demarcation of ammonoid localities and sites of stratigraphic sections and geographic regions of the Verkhoyansk Region referred to in the text. Percentages of numbers of specimen, species and genera in each region or subregion are also shown.

Andrianov (1985) is divided into three independent association: the Arkachan, Endybal and Mysovy associations; the original 'Tumara association' into two associations the Orol and Takamkyt associations; and Andrianov's 'Cherkambal association' is down-ranked as a subassociation of the Delendzha association (Fig. 3). An informal stratigraphic term, 'ammonoid Beds', is also used to characterize a subsidiary division within an association or subassociation, following Kutygin et al. (2002) (Fig. 2). For the convenience of describing the ammonoid faunas and their spatial distribution patterns, the occurrences of the Verkhoyansk ammonoids are divided into four large informal regions: the Kharaulah, Orulgan, Western Verkhoyansk and Southern Verkhoyansk (Fig. 1). At present, the biogeographic status of these ammonoid faunal regions has not been studied. Locally, the term 'subregion' is also used in the Western Verkhoyansk Region to refer to the occurrence of a localized ammonoid assemblage characteristic of a particular area.

2. Description, correlation and biogeography of Permian ammonoid associations

2.1. Khorokyt association

This ammonoid association began after the ammonoid crisis at the end of the Carboniferous (Kutygin, 1997). This recovery was marked by the appearance of new taxa among which *Bulunites* (Fig. 4) had the largest geographical expansion in the Verkhoyansk paleobasin. According to Andrianov (1985), this genus is a relict form of the Orulganitidae, a large, dominant Carboniferous endemic family. Taking into consideration the fact that *Bulunites* is not known out of the Verkhoyansk Region, it is be supposed that it appeared only in the Verkhoyansk paleobasin. Primitive forms of this genus are found in the lower parts of Tuorasis formation on the East bank at mouth of the Lena River.

The lower part of the Khorokytian Horizon in the Western Verkhoyansk Region is poor in ammonoids. Only a goniatite from 'the boundary layer of the Kygyltass and Khorokyt Formations' (Andrianov, 1981, p. 61) of the stratotype of the Khorokyt Formation (Delendzha River) has been reported (Andrianov, 1981). In Andrianov's opinion (1985), this specimen should belong to the genus *Prouddenites*. We are not sure about this identification but the discovery of this specimen in the interval under consideration is worthy of note. During the study of the stratotype of the Khorokyt Formation carried out in 2000 it was found that the 'boundary layer' marked by Andrianov (1985) must be considered to be within the Khorokyt Formation, because the numerous shells of marine invertebrates were found from this section and this level, which are not typical for the upper part of the Kygyltass Formation. The age of the basal layers of the Khorokyt

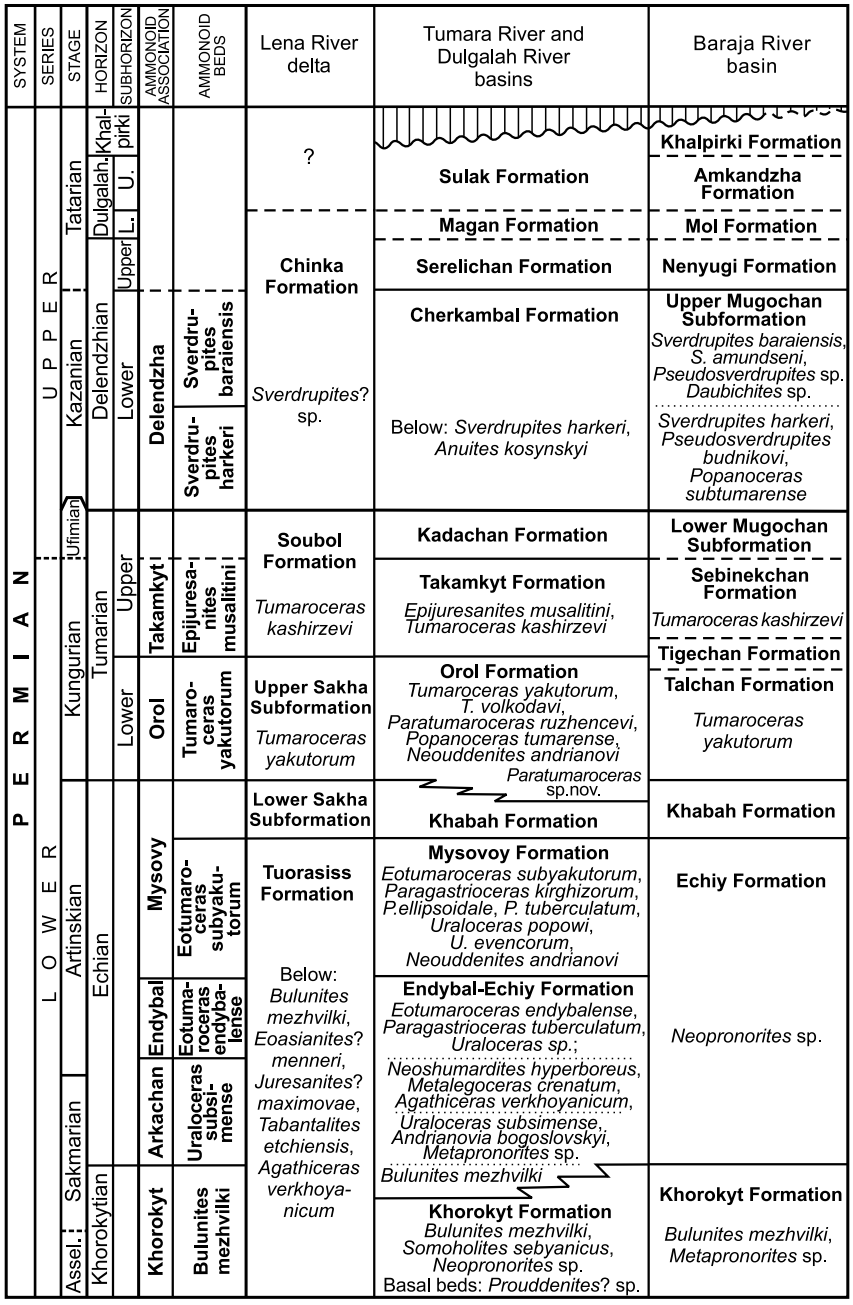

Fig. 2. A regional stratigraphical and biostratigraphical scheme for the Verkhoyansk region and a correlation of different sections based on ammonoids.

Formation is debatable. If the Andrianov's identification is correct then the sediments including *Prouddenites* should be regarded as Upper Carboniferous because this genus disappeared in the Late Carboniferous (Ruzhencev, 1949).

As the development of Permian ammonoid associations in Northeast Asia took place only during the Khorokytian time, it is proposed that the boundary between the Kygyltassian and Khorokytian Horizons should be compared with the Carboniferous–Permian boundary.

The majority of ammonoids of the Khorokyt association have been found in the middle and upper parts of the Khorokytian Horizon. *Bulunites mezhvilki* Andrianov (=*B. juferewi* Andrianov, *Uraloceras* aff. *fedorowi* Popow non Karpinsky) dominate this ammonoid association, and well known from the Northwest Kharaulah Region and from Western Verkhoyansk Region. A larger ammonoid association is found in the lower part of the Tuorasis formation distributed in the lower reaches of the Lena River where *Eoasianites menneri* (Andrianov), *Juresanites maximovae* Andrianov, *Agathiceras verkhoyanicum* Andrianov, and *Tabantalites etchiensis* Andrianov were found, besides the index species, *B. mezhvilki*.

In Bogoslovskaya's opinion (Kotlyar et al., 1987), the representatives of *Mennероceras* and *J. maximovae*, which were described by Andrianov (1985) from the lower part of Tuorasis formation, should be placed within the genus

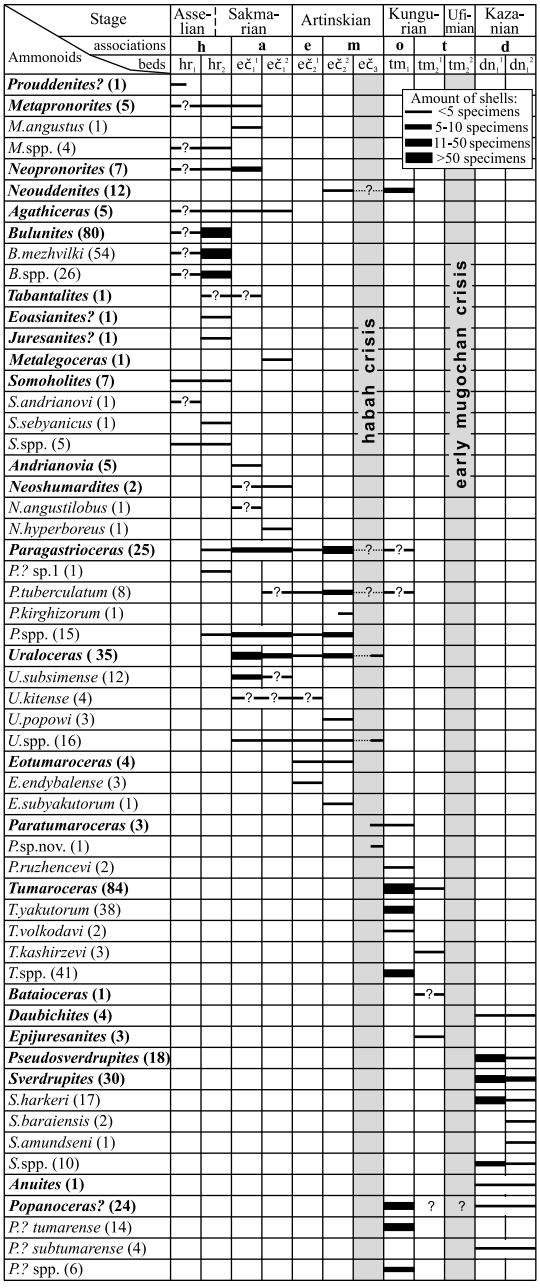

Fig. 3. Stratigraphic distribution of the Permian ammonoids of the Verkhoyansk Region: the number of known specimens is specified in parentheses pertain to the taxon name; Association: h—Khorokyt, a—Arkachan, e—Endybal, m—Mysovy, o—Orol, t—Takamkyt, d—Dielendzha; Ammonoids Beds: hr_1—lower *Bulunites mezhvilki* Beds; hr_2—upper *Bulunites mezhvilki* Beds; ec_1^1—lower *Uraloceras subsimense* Beds (*Andrianovia* Beds); ec_1^2—upper *Uraloceras subsimense* Beds (*Neoshumardites* Beds); ec_2^1—*Eotumaroceras endybalense* Beds; ec_2^2—*Eotumaroceras subyakutorum* Beds; ec_3—'khabah' Beds; tm_1—*Tumaroceras yakutorum* Beds; tm_2^1—*Epijuresanites musalitini* Beds; tm_2^2—'lower mugochan' Beds; dn_1^1—*Sverdrupites harkeri* Beds; dn_1^2—*Sverdrupites baraiensis* Beds.

Eoasianites, as they are close to the youngest forms of the last. In the case of *Mennероceras*, this opinion is followed in the current paper. However, assignment of the species *J. maximovae* to the genus *Eoasianites* is doubtful as Andrianov (1985) noted that *J. maximovae* has a distinct longitudinal lirae on the body whorl, a feature that is not typical for mature *Eoasianites* shells and these lirae are important distinguishing features of the *Juresanites* from the *Eoasianites* (Ruzhencev, 1952). The inclusion of this species to the genus *Juresanites* is also debatable as its umbilical lobe does not have any isolated 'pouch' on the outside, that is typical for all *Juresanites*. The presence of a distinct longitudinal sculpture in addition to the *Paragastrioceras* form of suture line suggests a possible connection of this unusual shell with the Paragastrioceratidae, but not the Metalegoceratidae as Andrianov (1985) considered. However, in order to change the systematic position of the species *J. maximovae* we need supplementary facts.

In Western Verkhoyansk region, ammonoids have been found in three main stratigraphic intervals (Kutygin et al., 2002): (1) the middle part of the Khorokyt Formation: *Bulunites mezhvilki* Andrianov, *B.* sp., *Somoholites sebyanicus* Kutygin and *Neopronorites* sp; (2) the upper part of the Khorokyt Formation: *Bulunites mezhvilki* Andrianov and *Metapronorites* sp.; and (3) the lower part of the Echiy Formation (only in the Eastern Kuranah Subregion): *Bulunites mezhvilki* Andrianov, and *B.* sp. nov. The Khorokyt association is very endemic at the species level to the Western Verkhoyansk Region, as it does not have any common species with other regions, including the Urals, which makes it impossible to say decide whether it contains only elements of Asselian age or not. The age of the Khorokyt ammonoid association is considered to be Asselian—early Sakmarian, because ammonoids from the overlying strata are of late Sakmarian and Artinskian age (see below).

The Khorokyt ammonoid association has a very narrow geographical distribution, only found in the Kharaulah Region and Western Verkhoyansk Region (Fig. 5). The ammonoid fauna from the Kharaulah is most similar to those described from the Asselian stage of the Southern Urals (Ruzhencev, 1951). The endemic species *Agathiceras verkhoyanicum* probably evolved, at the beginning of the Permian, from *A. uralicum* (Karpinsky), a well known species in the Upper Carboniferous of the Orulgan Region (Musalitin and Solomina, 1970). The fauna of the Khorokyt association of the Western Verkhoyansk Region is very similar to that of the Kharaulah Region, implying active biotic interchange between the two areas during this time. However, there are some differences between these two regions. The youngest representatives of *Bulunites* (*B.* sp. nov.) are known only in the middle part of the Western Verkhoyansk Region (in the Arkachan River basin). The single *Somoholites andrianovi* shell (Kutygin, 1999b), which is very close to the latest Carboniferous *Somoholites* of the Okhotsk Region (Klets, 1993) due to similarities in the contours of the suture line, was found in the Orulgan Region (the Sobopol River basin).

2.2. Arkachan association

The Arkachan association is typical for the lower part of the Echian Horizon (*Uraloceras subsimense* Beds). The first *Uraloceras* and *Andrianovia* appeared in the Verkhoyansk during the early Echian (Arkachan), and their presence allows

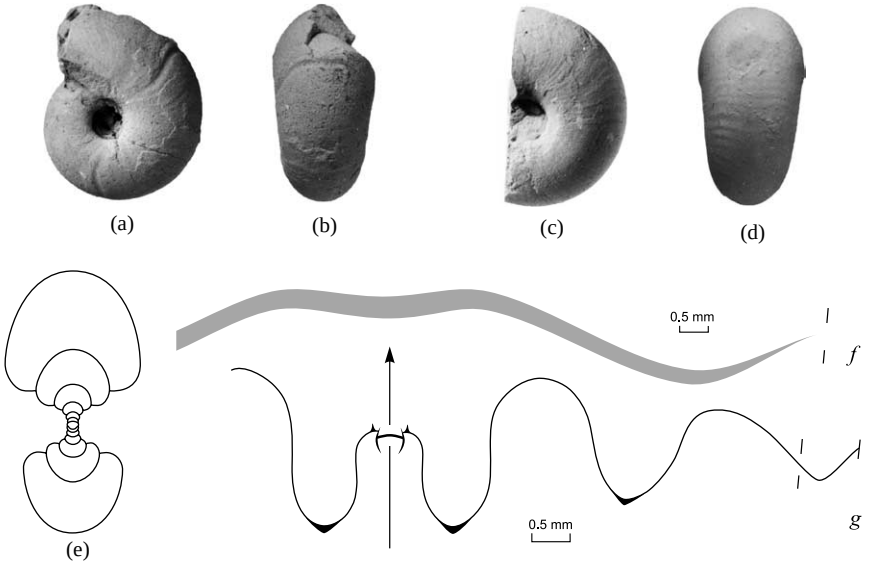

Fig. 4. *Bulunites mezhvilki* Andrianov—index species of the Khorokyt association: a, b—holotype GM IGABM no. 55/182 (×2); c, d—specimen GM IGABM, no. 175/15-1 (×2); e—cross section of the specimen GM IGABM, no. 55/185 at a conch diameter of 16.7 mm (×2.5); f—diagrammatic representation of constriction of the holotype GM IGABM, no. 55/182 at a conch diameter of 13 mm; g—suture line of holotype GM IGABM, no. 55/182 at a conch diameter 9 mm, whorl width of 5 mm, whorl height of 4 mm. Kharaulah Region, lower course of Lena River, upstream of the mouth of Kubalah Creek. Lower Permian, Khorokytian Horizon, lower part of the Tuorasiss Formation (collected by V.N. Andrianov in 1964–1965, sample 1/11).

the isolation of a distinctly Arkachan association (Kutygin, 2004). The Paragastrioceratidae took a predominant position during this time and it continued throughout the Early Permian in the region. The association can be divided into two subassociations: an older one with *Andrianovia bogoslovskyi* and a younger one with *Neoshumardites hyperboreus*.

The representatives of *Uraloceras subsimense* Kutygin (Fig. 6) have been were found from the Verkhoyansk Formation of the Kharaulah Region and from the lower part of the Endybal-Echiy Formation of the Western Verchoyansk Region. Some forms very close to this species have been know from the Munugudjak Formation of the Munugudjak River basin of the Omolonsk massif (Kutygin et al., 2002). A larger ammonoid association is found in the lower part of Endybal-Echiy Formation of the Eastern and Western Kuranah subregions where *Uraloceras subsimense*, *U. kitense* Popow, *U.* sp., *Paragastrioceras* sp., *Neoshumardites hyperboreus* Ruzhencev, *Andrianovia bogoslovskyi* (Andrianov), *Metalegoceras crenatum* Nassichuk, Furnish et Glenister, *Metapronorites* sp., *Neopronorites* sp. are found (Andrianov, 1985; Kutygin et al., 2002). Numerous *U. subsimense* and rare *A. bogoslovskyi*-bearing localities have been known in the basin of the Arkachan River. Ammonoids found in this area represent only the lower subassociation while the main species of the upper subassociation (*N. hyperboreus* and *M. crenatum*) in the Verkhoyansk Region are currently known only from the Delendzha-Tumara subregion. Rare *U. kitense* localities are known in the upper reaches of the Dianyshka River of the Kobycha subregion (Popow, 1970). One specimen of this species, according to the data presented by Budnikov (Kutygin et al., 2002), was found in the lower part of the Echian Horizon. Judging by contour of the suture line and its involute shell shape we can say that this species had the greatest resemblance with the youngest (Late Artinskian) *Uraloceras*. This fact suggests that it would be wise to try and gain more material of this species from the Kobycha subregion, so that the precision of its stratigraphic position and taxonomic placement within the family Paragastrioceratidae can be clarified. In other parts of the Verkhoyansk region the definition of the *U. subsimense* Beds remains problematic.

Among these species only *A. bogoslovskyi* and *M. crenatum* are known outside the Verkhoyansk Region. *A. bogoslovskyi* is found together with a representative of *Tabantalites* in the middle part of the 'Permian lower bench' of the Kotelny Island of the Northeast Russia (Konstantinov, 2001). *M. crenatum* is found in the Lower Permian of Yukon territory and Southwestern Ellesmere Island of Arctic Canada (Nassichuk et al., 1965). On Ellesmere Island *M. crenatum* was found together with a rather rich goniatite fauna including *Andrianovia* sp. nov. (=*Neoshumardites* cf. *sakmarae* Nassichuk, Furnish et Glenister non Ruzhencev). Nassichuk et al. (1965) considered this fauna to be late Sakmarian—early Artinskian in age. Species similar to North American *Andrianovia* with narrow branches of the ventral lobe can be found in the Munugudjak Horizon of the Omolon massif.

The presence of *Andrianovia* (=*Preshumardites* Ruzhencev, 1951 non Plummer et Scott) allows us to make a judgment on the late Sakmarian age of the Arkachan association and the *U. subsimense* Beds, as this genus is numerous in the Sterlitamakian and rare in the Tastubskian of the South Urals. This correlation is also proved by the fact that the Sakmarian species *U. simense* Ruzhencev (Ruzhencev, 1951) is the closest to the Arkachan association index species in the shell shape and sutural outline. On the other hand we can not

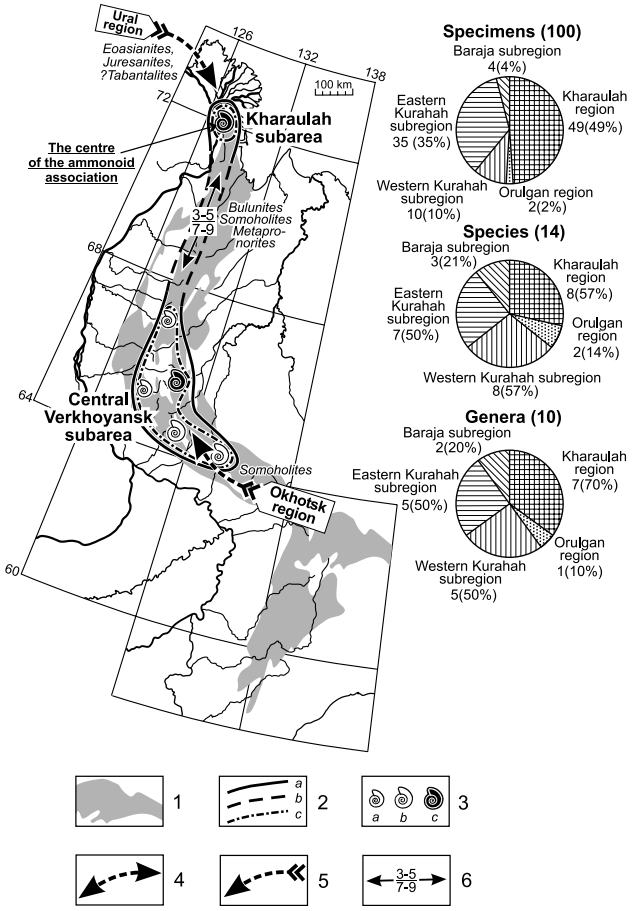

Fig. 5. Distribution and inferred migration patterns of the Khorokyt ammonoid association: 1—area of Permian deposits; 2—boundaries: *a*, *b*—Verkhoyansk ammonoid areal boundary (*a*—established, *b*—assumed), *c*—ammonoid subarea boundary; 3—ammonoid localities: *a*—occurrences of individual specimens, *b*—no more than 10 specimens, *c*—more than 10 specimens; 4—exchange of ammonoid faunas between large regions; 5—possible direction of migration the ammonoids; 6—exchange of ammonoid faunas between subareas (the number of genera and species being common for subareas is specified in numerator; the amount of kinds genera and species which are not being common for subareas is specified in a denominator).

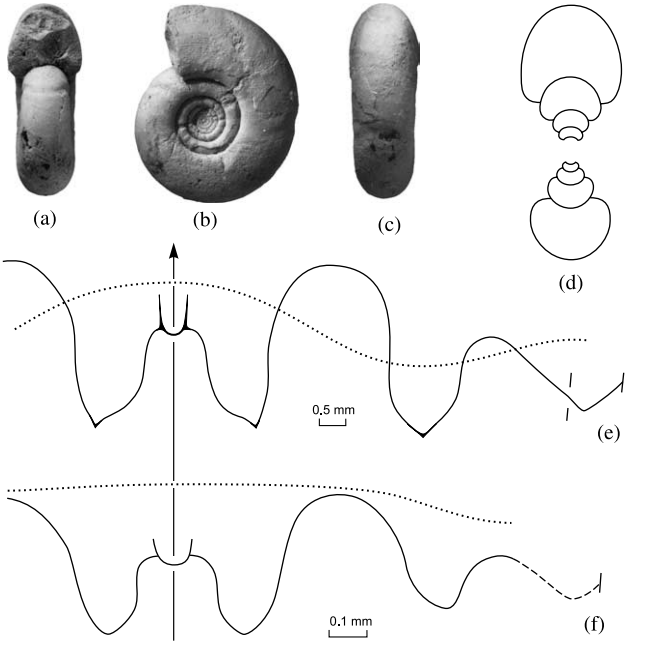

Fig. 6. *Uraloceras subsimense* Kutygin—index species of the Arkachan association: *a*–*c*—holotype GM IGABM no. 175/43; *d*—cross section of holotype GM IGABM, no. 175/43 (×1.5); e, g—suture lines and diagrammatic representations of cross ornamentation of holotype GM IGABM, no. 175/43 at a conch diameter 19 mm (*e*, mirror display) and at a conch diameter 2 mm (*f*, mirror display). Kharaulah Region, Chubukulah River basin, Nimngechaan River. Lower Permian, Sakmarian, lower part of the Echian Horizon, Verkhoyansk Formation (collected by R.V. Solomina in 1958, sample 114/997).

notice the presence of *Neoshumardites* in the Arkachan ammonoid association, a typical species known in the Lower Artinskian of the Urals. However, the systematics and stratigraphic position of the Northeastern *Neoshumardites* remain debatable. From all the above facts, the *U. subsimense* Beds are compared with the Upper Sakmarian.

There are great differences between the Khorokyt and Arkachan association in faunal composition. Only long-living Carboniferous–Permian genera such as *Agathiceras*, *Metapronorites* and *Neopronorites* continue to develop in the Verkhoyansk during the Khorokytian and Arkachanian times. A phylogenetic connection between Khorokyt Paragastrioceratids, represented by rare specimens, and various Arkachan Paragastrioceratids has not been proved. The majority of Paragastrioceratids appeared in the Verkhoyansk Region during the Arkachanian and are immigrants from the Urals. The *Neoshumardites*, a widespread genus in the Boreal Realm, appeared in the Verkhoyansk in the Early Permian, as its most ancient form (*N. angustilobus*) was found in the Lower Permian of the Kharaulah Region (Andrianov, 1985). This species could have originated from one of the Khorokyt representatives of *Somoholites*. Although it is not clear regarding the origin of the Northeastern representatives of *Andrianovia*, it is probable that they separated from *A. sakmarae*. Judging from numerous common forms of goniatites (*Uraloceras*, *Andrianovia* and *Neoshumardites*) there was an active faunal exchange between the Verkhoyansk and Omolon paleobasins during the late Sakmarian. However, it is not certain whether this exchange took place via a Northern (through the Kotel'ny zone) or a Southern route (through the Okhotsk Region). There are, however, some forms close to the Kharaulah goniatites (*Andrianovia* and *Tabantalites*) in the Lower Permian Kotelny Island (Konstantinov, 2001). This fact allows us to consider that a variant of the Northern route of faunal exchange with the Omolonsk massif is preferable.

The Arkachan ammonoid association occupied a larger area in the Verkhoyansk than the Khorokyt ammonoid association, and it can be subdivided into a number of subassociations each corresponding to a particular ammonoid subarea (Fig. 7). During the Arkachanian time, the Kharaulah ammonoid subarea expanded and its center moved closer to the Orulgan ammonoid subarea. In the Western Verkhoyansk paleobasin the ammonoid area is divided into a numerous small ammonoid

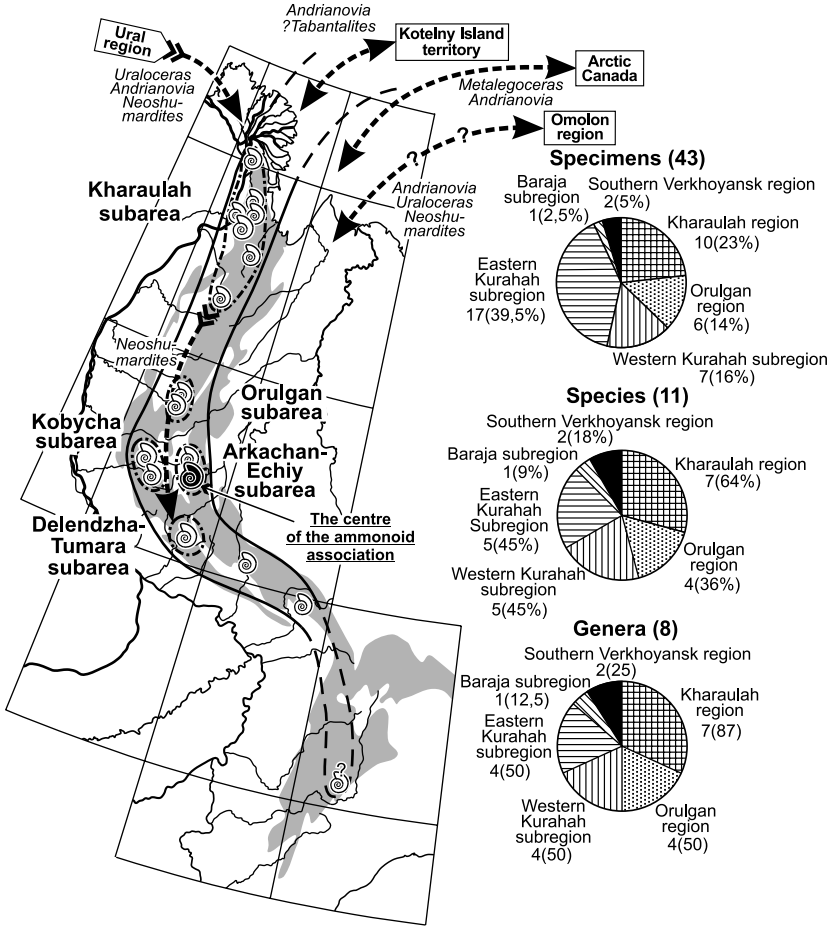

Fig. 7. Distribution and inferred migration patterns of the Arkachan association (for explanation of symbols see Fig. 5).

subareas, among which the Arkachan-Echiy ammonoid subarea was the main subarea in the whole Verkhoyansk ammonoid area. The Kobycha ammonoid subarea is rather interesting: it contains a poorly developed ammonoid fauna dominated by the exotic species *Uraloceras kitense*.

2.3. Endybal association

The Endybal association represents the middle part of the Echian Horizon. It is situated in the Arkachan-Echiy interfluve (East Kuranach subregion) where *Eotumaroceras endybalense* Andrianov (Fig. 8), *Paragastrioceras tuberculatum* (Popow), *P*. sp. and *Uraloceras* sp., are found in the upper part of the Endybal-Echiy Formation (Andrianov, 1985). The *E. endybalense* Beds with the Endybal association are correlated with the Lower Artinskian (Kutygin et al., 2002).

The period during which the Endybal association occurred in this region corresponds to a crisis in the development of the Verkhoyansk ammonoids which is thought to probably have connected with the final phase of the early Echiy transgression-regression cycle in the Verkhoyansk paleobasin. The main finds of the Endybal ammonoid association originated from the Arkachan-Echiy interfluve (Fig. 9). A very important stage of

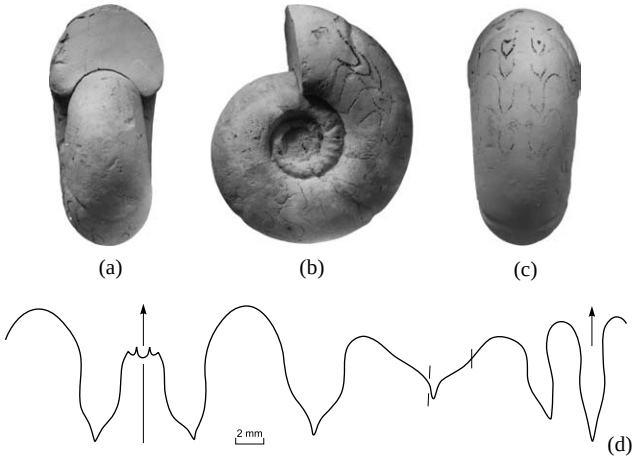

Fig. 8. *Eotumaroceras endybalense* Andrianov—index species of the Endybal association: *a–c*—holotype GM IGABM, no. 55/206; *d*—suture line of the holotype GM IGABM, no. 55/206 at a conch diameter 51.5 mm. Western Verkhoyansk Region, Dulgalah River basin, Endybal River, Chelge Creek. Lower Permian, Artinskian, middle part of the Echian Horizon, upper part of the Endybal-Echiy Formation (collected by V.N. Andrianov in 1965, sample 8/5).

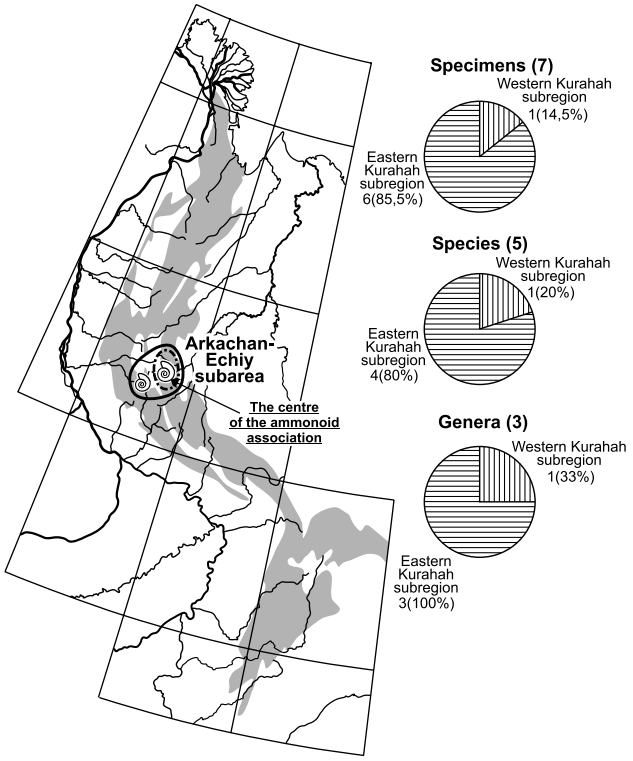

Fig. 9. Distribution and inferred migration patterns of the Endybal association (for explanation of symbols see Fig. 5).

the ammonoid development is connected with the occurrence of the Endybal association. The species *E. endybalense* appeared at this time, marking the beginning of the phylogenetical branch *Eotumaroceras* → *Tumaroceras* → *Epijuresanites* → *Sverdrupites*.

2.4. Mysovy association

This association is found in the middle part (Pre Khabah) of the Upper Echian subhorizon (*subyakutorum* Beds). Most representatives of this association came from the Mysovy Formation of the Kuranah Region and contain *Eotumaroceras subyakutorum* (Andrianov) index species of the Mysovy association (Fig. 10), *Paragastrioceras kirghizorum* (Voinova), *P. tuberculatum* (Popow), *P.* spp., *Uraloceras popowi* Andrianov, *U.* spp. and *Neouddenites andrianovi* Ruzhencev (Andrianov, 1985; Kutygin et al., 2002). Specimens of *N. andrianovi* and *Uraloceras* sp. will probably be found in the equivalent strata of the Echian Horizon in the Baraja River basin (Andrianov, 1985), but this needs to be confirmed in future study. *Paragastrioceras verneuili* Ruzhencev, *P.* aff. *kirghizorum* (Voinova) and *P. kharaulakhense* Popow (Popow, 1970), were found in the Kharaulah Region in the 'Verkhoyansk Formation' (Popow, 1970), while *P. tuberculatum*, *P.* sp. and *Uraloceras* sp. have been reported from the Echiy Formation and in the lower part of the Khaldzin Formation of the Orulgan Region (Andrianov, 1985). *Paragastrioceras jossae* (Verneuil) was described by Popow (Umitbajev, 1963) from the Ingychan Formation of the Nyut

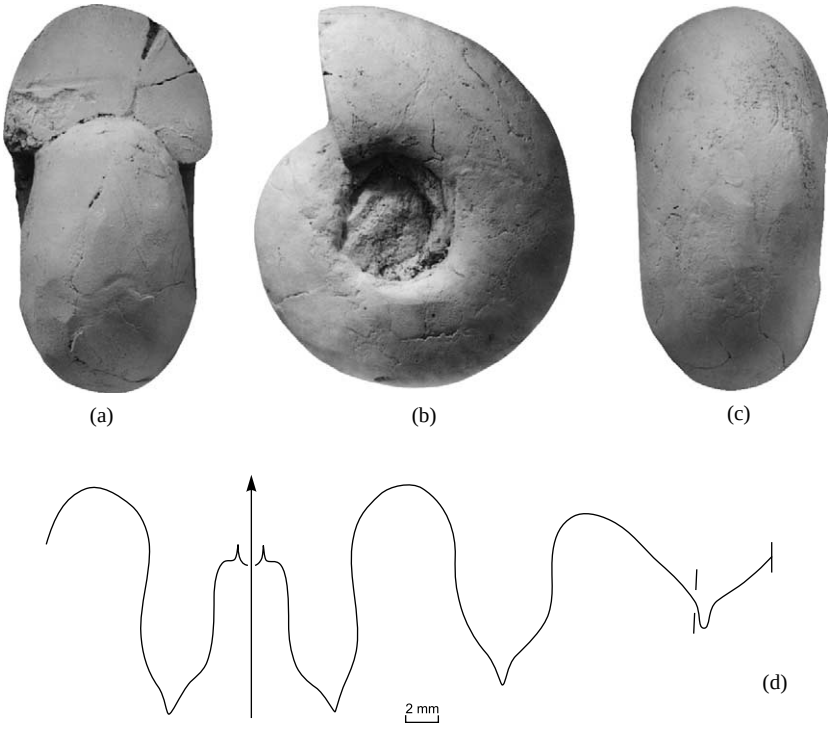

Fig. 10. *Eotumaroceras subyakutorum* (Andrianov)—index species of the Mysovy association: *a–c*—holotype GM IGABM, no. 55/282; *d*—suture line of the holotype GM IGABM, no. 55/282 at a conch diameter 55 mm. Western Verkhoyansk Region, Tumara River basin, Delendzha River, Topolinaya Creek. Lower Permian, Artinskian, upper part of the Echian Horizon, upper part of the Mysovy Formation (collected by V.N. Andrianov et al. in 1967, sample 19/1).

River basin of the Okhotsk Region. The representatives of *U. popowi* are known in the Artinskian of Pechora basin (Bogoslovskaya and Shkolin, 1998). The majority of the *Paragastrioceras* species listed above are typical for the Sakmarian and Artinskian Stages of the Urals, while the mass spreading of *P. kirghizorum* appears to correspond to the Upper Artinskian. For these reasons, the *E. subyakutorum* Beds are correlated with the Upper Artinskian.

From the composition and sites of the Echiy association presented above, it can be seen that in the Verkhoyansk paleobasin the Mysovy transgression was a beneficial influence on the development and diversification of ammonoids during this time, as the ammonoids of this association became very widespread (Fig. 11). This association is characterized by a predominance of various species of *Paragastrioceras* and also by the appearance of a number of new *Uraloceras* and *Eotumaroceras* species. During the Mysovian time the first representatives of *Neouddenites* appeared in the Verkhoyansk Region and became widespread in the Boreal seas during the Kungurian (Kutygin, 2004). The Central Verkhoyansk ammonoid subarea had the most species of this association, and the diversity center of the ammonoid association appears to have moved from the Arkachan-Echiy zone to the Delendzha-Tumara zone (Fig. 11). During the Mysovian time the Verkhoyansk ammonoid faunas had only limited relations with those of the Taymyr province, and the Ural and Pechora basins in Western Russia. There was active migration of various *Paragastrioceras* species from the Ural basin across the Taymyr province. An exchange of *Uraloceras* occurred with the Pechora basin. Perhaps, species of *Paragastrioceras* and some *Uraloceras* were migrating across the Verkhoyansk paleobasin towards the Okhotsk and Omolon regions. The evolutionary development of the endemic genus *Eotumaroceras* was proceeding within the paleobasin, and *Eotumaroceras* species acquired many morphological signs characteristic in its Kungurian descendent—*Tumaroceras*.

There have been no authentic ammonoid specimens in the 'Khabah Beds' (upper part of the Echiy series), which is tentatively compared with the upper part of the Artinskian (Klets et al., 2001a). The specimen noted by Andrianov in the upper part of the Khabah Formation of the Orol River (Andrianov, 1985, p. 54–55), really came from the lower part of the Orol Formation ('pre *Tumaroceras yakutorum* Beds'). The change from the Mysovy transgression to the Khabah regression, the largest one in the Early Permian of the region, led to the complete disappearance of ammonoids. Rare specimens of Paragastrioceratidae (Andrianov, 1985; Kutygin et al., 2002) occurring in the base of the Orol Formation in the Orol River (Eastern Kuranah Subregion) probably represent the terminal part of the Mysovy phase of ammonoid development.

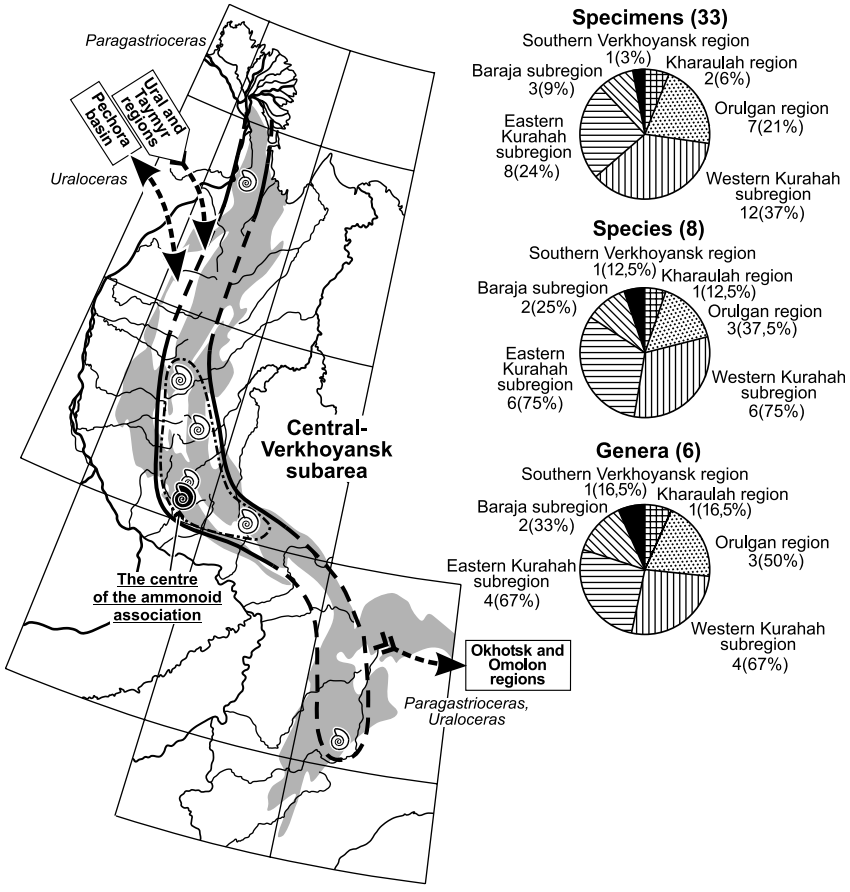

Fig. 11. Distribution and inferred migration patterns of the Mysovy association (for explanation of symbols see Fig. 5).

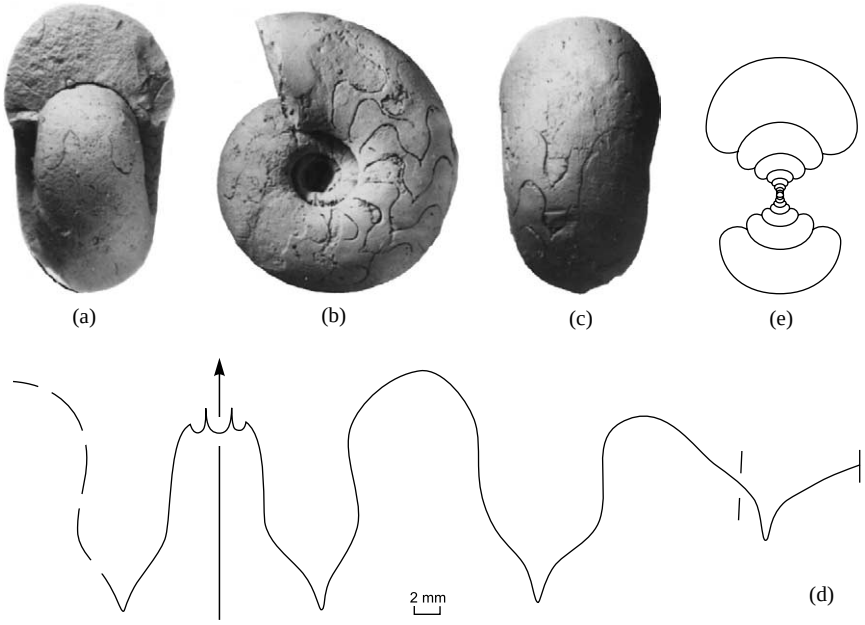

Fig. 12. *Tumaroceras yakutorum* Ruzhencev—index species of the Orol association: *a–c*—specimen GM IGABM, no. 55/274; *d*—suture line of the specimen GM IGABM, no. 55/274 at a conch diameter 38 mm; Western Verkhoyansk Region, Dulgalah River basin, Orol River. Lower Permian, Kungurian, lower part of the Tumarian Horizon, Orol Formation (V.N. Andrianov, L.G. Tyutyunnikov et al. in 1967, sample 1/53); e—cross section of the specimen GM IGABM, no. 55/277 at a conch diameter 22.9 mm (×1.5). The locality same (collected by V.N.Andrianov and V.A.Yarkov in 1961, sample 9/31).

2.5. Orol association

The Orol ammonoid association is found in the Lower Tumarian Subhorizon (*Tumaroceras yakutorum* Beds). Sections of the Orol Formation in the upper reaches of the Tumara and Dulgalah Rivers yield most characteristic species of this association. The index species of the association is *Tumaroceras yakutorum* Ruzhencev (Fig. 12), and other characteristic species are *T. volkodavi* Andrianov, *Paratumaroceras ruzhencevi* Kutygin, *Popanoceras tumarense* Ruzhencev and *Neouddenites andrianovi* Ruzhencev. The species *T. yakutorum* has been known in the upper part of the Sakha Formation in the lower reaches of the Lena River (Andrianov, 1985) and in the Tel'ga Formation of the Yudoma River basin (Reshenija…, 1982), and is the most abundant among the listed species. The index species and the majority of accompanying species form a goniatite fauna that is not known outside the Verkhoyansk Region. Outside of this region, only *N. andrianovi* has been found from the Omolon massif (Ganelin et al., 1990) and, probably also on the Northeastern side of the Okhotsk massif (Biakov and Vedernikov, 1990). However, the occurrence this species does not provide a basis for correlating precisely with the *T. yakutorum* Beds, because its stratigraphic range is wider. The ammonoid association characterizing the *T. yakutorum* Beds is Kungurian in age (Andrianov, 1985; Kutygin et al., 2002).

In the beginning of the Orolian in the Verkhoyansk paleobasin there was an almost complete change of taxonomic composition of the ammonoid fauna. The important development in the new association was the appearance of *Tumaroceras*, which occupied the predominant position in the evolution of the Boreal ammonoids during the Kungurian (Kutygin, 1999a). The appearance of this genus, diverged from the Mysovy genus *Eotumaroceras*, possibly happened at the boundary between the Khabahian and Orolian in the Dulgalah-Tumara zone. The appearance of the *Popanoceras tumarense* in the Verkhoyansk paleobasin is probably conditioned by migratory factors. In any case, there is not a representatives of the family Popanoceratidae in the underlying sediments (Artinskian) in the whole of Northeast Russia. Perhaps numerous *Popanoceras* were obliged to exploit new areas due to the beginning of the closure of the Ural basin at the end of the Artinskian. Only a few representatives of this genus could reach the Northeast seas where they formed isolated groups with low abundance, and could evolve slowly during the Kungurian and Kazanian.

The Central Verkhoyansk ammonoid subarea appears to represent the area where this association was most abundantly developed (Fig. 13). Here, for example, in the upper reaches of the Dulgalah River, the Orol association is predominantly represented by abundant *Tumaroceras* accompanied by rare *Popanoceras*. A very similar ammonoid assemblage is also found from the same stratigraphic level in the Tumara River and Delendzha River basins. Ammonoids of this association represented by rare materials are also known in other parts of the Verkhoyansk Region (e.g. lower reaches of the Lena River, the Arkachan-Echiy Rivers interfluve, the Baraja River, Uyana River basins and etc.), but the authenticity of the presence of the Orol ammonoid association outside the Verkhoyansk Region demands more accurate definition.

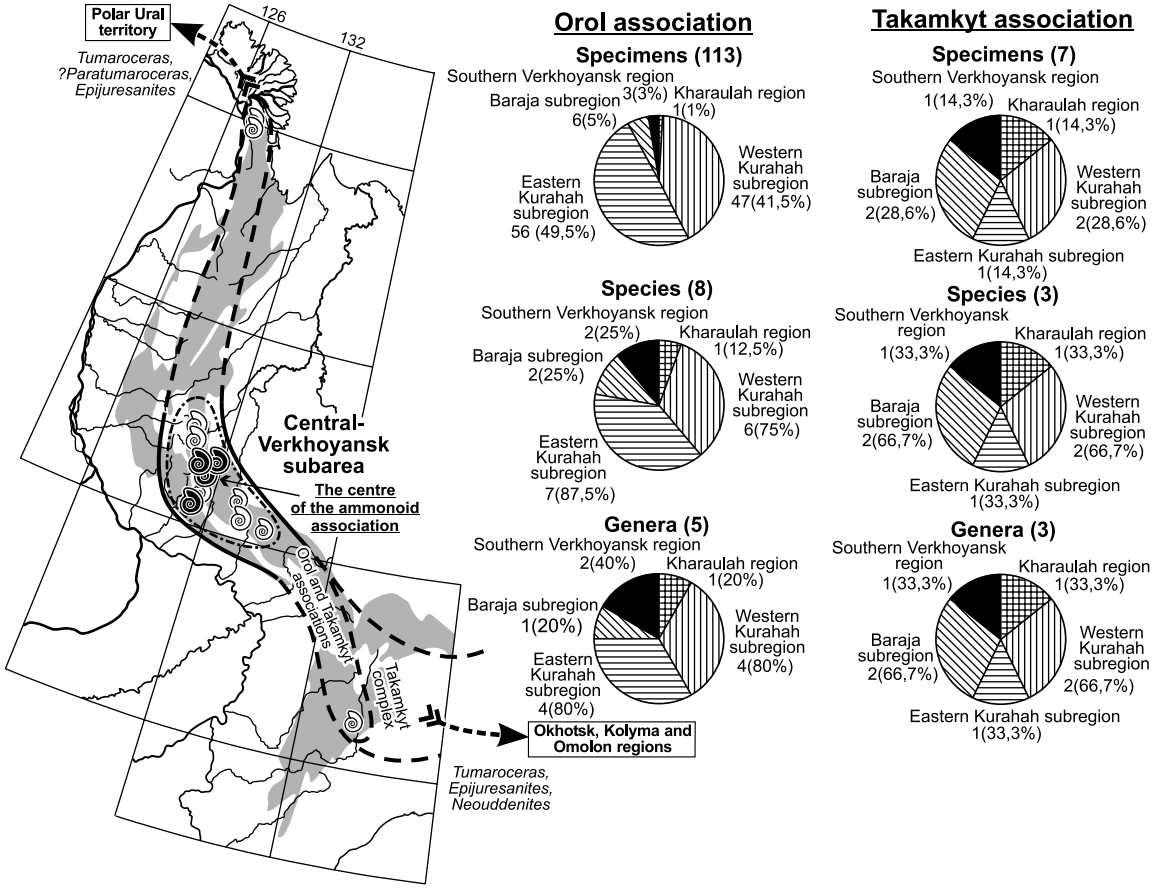

Fig. 13. Distribution and inferred migration patterns of the Orol and Takamkyt association (for explanation of symbols see Fig. 5).

2.6. Takamkyt association

This ammonoid association is found in the middle part of the Tumarian Horizon (*Epijuresanites musalitini* Beds) and characterized by *Epijuresanites musalitini* Popow (index species of the association) (Fig. 14) and *Tumaroceras kashirzevi* Andrianov. This association has been known from the Takamkyt Formation in the Kuranah Region and in the middle part of the Soubol Formation in the lower reaches of the Lena River (Andrianov, 1985). We have also found *T. kashirzevi* from the middle part of the Sebinekchan Formation in the Southern tributary of the Nadi River (Baraja River basin). The species *E. musalitini* was found from the Dognikan Formation, in the Southern Verkhoyansk Region and the Okhotsk massif (Reshenija…, 1982), and from the lower part of the Ozerny Formation in the Prikolymsk Region (Andrianov, 1985). More numerous Takamkyt ammonoids occur in the middle Dzhigdali Formation of the Omolon massif. The *E. musalitini* Beds with the Takamkyt association are correlated with the Upper part of the Kungurian (Kutygin et al., 2002).

During the Takamkytian time three species, *T. kashirzevi*, *E. musalitini* and probably *Baraioceras stepanovi* Andrianov, appeared in the Verkhoyansk paleobasin. The species *T. kashirzevi* represents a final stage of the evolution of *Tumaroceras*. The species *B. stepanovi* is phylogenetically connected to the Ural species *B. kungurense* (Mirskaya) (Bogoslovskaya and Shkolin, 1998). These two species of *Baraioceras* represent a short deadend phylogenetical branch in paragasrioceratid evolution. The appearance of *E. musalitini* represented new possibilities in the evolution of the Kungurian-Kazanian goniatites. This species is considered to be a progenitor of the family Spirolegoceratidae (Ruzhencev, 1974) which was the dominant ammonoid family in the Boreal Realm at the beginning of the Late Permian.

The geographic distribution of the Takamkyt ammonoid association expanded in comparison with the Orol association (Fig. 13). There was an active migration of *Tumaroceras* and *Epijuresanites* among the basins of the polar Urals, Kolyma and Okhotsk regions. Ammonoids are not known from the upper part of the Tumarian Horizon ('Lower Mugochan beds') of the Verkhoyansk Region. There was a great crisis in the ammonoid development in the region during the deposition of the Lower Mugochan subformation. However a distinct succession from the Takamkyt to younger Delendzha association testifies that even during the early Mugochan crisis the ammonoid-living areas existed, probably as very small subareas, allowing the continuation of the evolution of the Spirolegoceratidae and Popanoceratidae. Perhaps, the latest *Epijuresanites* discovered in Vaygach Island (Bogoslovskaya,

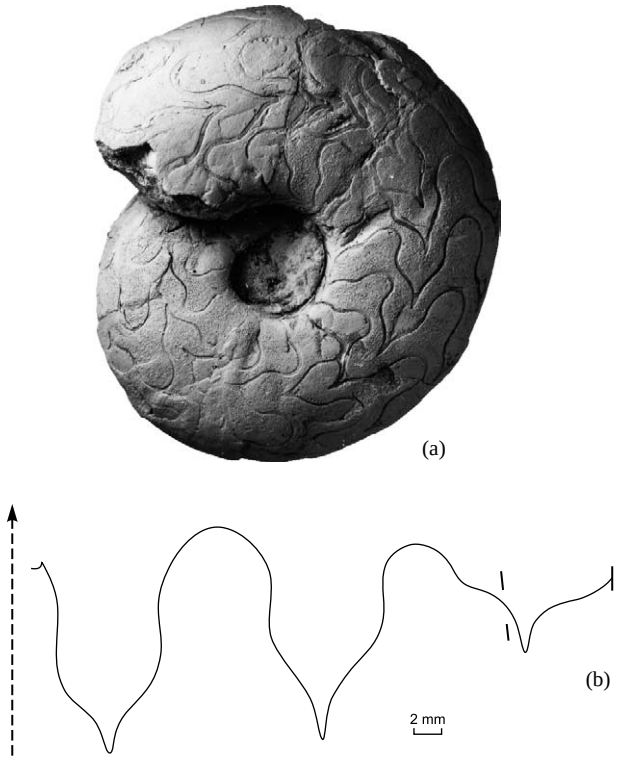

Fig. 14. *Epijuresanites musalitini* Popow—index species of the Takamkyt association. For explanation of symbols follows that for Fig. 5. *a*—holotype CGM, no. 48/8717; *b*—suture line of the holotype CGM, no. 48/8717 at conch diameter 70.5 mm (mirror display); Western Verkhoyansk Region, upper part of the Tumara River. Lower Permian, Kungurian, Tumarian Horizon (collected by L.A. Musalitin in 1964, sample 6).

1997) and in Southern Primorie (Zakharov et al., 1997) are connected with the lower Mugochan stratigraphic level.

2.7. Delendzha association

The Delendzha ammonoid association occurs in the Lower Delendzhian Subhorizon and can be divided into two successive subassociations—the Cherkambal (*Sverdrupites harkeri* Beds) and the Baraja (*S. baraiensis* Beds) subassociations. The stratigraphic interval containing the Cherkambal subassociation includes the lower part of the Lower Delendzhian Subhorizon and is best represented in the Baraja River basin where *S. harkeri* (Ruzhencev) (index species of the subassociation, Klets et al., 2001b), *Pseudosverdrupites budnikovi* Kutygin and *Popanoceras subtumarense* Andrianov have been found from the lower part of Upper Mugochan Subformation. Ammonoids are rare in the Cherkambal Formation in the upper reaches of the Dulgalah and Tumara Rivers, where only three shells, identified as *S. harkeri*, *S.* cf. *harkeri* and *Anuites kosynskyi*, occur. A large association of brachiopods (Klets et al., 2001b) characterizing the *Mongolosia russiensis* zone (Klets et al., in press), was collected together with *S. harkeri* and *P. budnikovi* in the upper reaches of the Baraja River.

The stratigraphic interval containing the Baraja subassociation includes the upper part of the Lower Delendzhian Subhorizon. This subassociation was considered formerly to be poorer in diversity than the Cherkambal subassociation (Kutygin, 1996; Kutygin et al., 2002). Only two specimens of *Sverdrupites baraiensis* Kutygin (index species of the subassociation, Kutygin, 1996) and some small Spirolegoceratids with obscure specific and generic positions were known. The shell from the Beglin Formation of the Northeastern side of the Okhotsk massif (Khuren River), described by Popow (1970), text-Fig. 23, pl. XVII, Fig. 3) as *Spirolegoceras* aff. *harkeri*, can be compared taxonomically with the *S. baraiensis*. Other species of this subassociation include *P.* aff. *budnikovi*, found by Biakov in 1985 and a large shell of *Sverdrupites amundseni* Nassichuk in the upper part of the Mugochan Formation.

New records given by the studies of the sections of the Delendzhian Horizon allow us to consider that the Baraja ammonoid subassociation is more diverse than the Cherkambal subassociation. A number of shells, previously found from the Lower Delendzhian Subhorizon and assigned to the same stratigraphic level (Cherkambal level), in reality are common to both subassociations. The interval of the Baraja subassociation probably represents a period of maximum taxonomic diversity for the genus *Sverdrupites*. It is a period when *S. harkeri* continued to develop with new species (*S. baraiensis* and *S. amundseni*) with more complicated suture lines and more involute and narrower shell. Probably, the Baraja ammonoid subassociation of Northeastern Asia and diverse ammonoid association in the Kazanian of the Volga-Ural Region (Leonova et al., 2002) are close in age. The *S. baraiensis* Beds are compared with the lower part of the brachiopod *Olgerdia zavodowskyi* zone (Klets et al., 2001b), or with the *Terrakea korkodonensis* Beds.

A single goniatite shell, first identified by Andrianov (1985) as '*Spirolegoceras* sp.', was found in 1964 from the Chinka Formation in the lower reaches of the Lena River. At that time the genus *Sverdrupites* was not yet defined and all its current representatives were assigned by researchers to *Spirolegoceras*, as was the case for the lower Lena specimen. On evidence derived from Egorov and Andreev (1981) and from Solomina's material, two *Daubichites* sp. shells were found in the 'bench number 4' or in the Kharauluh Formation of the Eastern Kharaulah. *Sverdrupites harkeri* and *S.* sp. are common in the Upper Permian of Northeastern side of the Okhotsk massif (Biakov and Vedernikov, 1990).

The ammonoids of the Delendzha association had a large geographical distribution. The species *Sverdrupites harkeri* has been known from the upper part of Dzhigdali Formation (Kotlyar et al., 1987), perhaps from the lower part of the Omolon Formation of the Omolon massif (Andrianov, 1985), from the middle part of the Kochergin Formation of Novaya Zemlya (Bogoslovskaya et al., 1982), and from the Assistance Formation in the Sverdrup Basin, Arctic Canada (Nassichuk, 1970). The species *Sverdrupites amundseni* is known from the Assistance Formation in the Sverdrup Basin (Nassichuk, 1970), from the base of the Gerke Formation in Novaya Zemlya (Bogoslovskaya et al., 1982) and from the lower part of

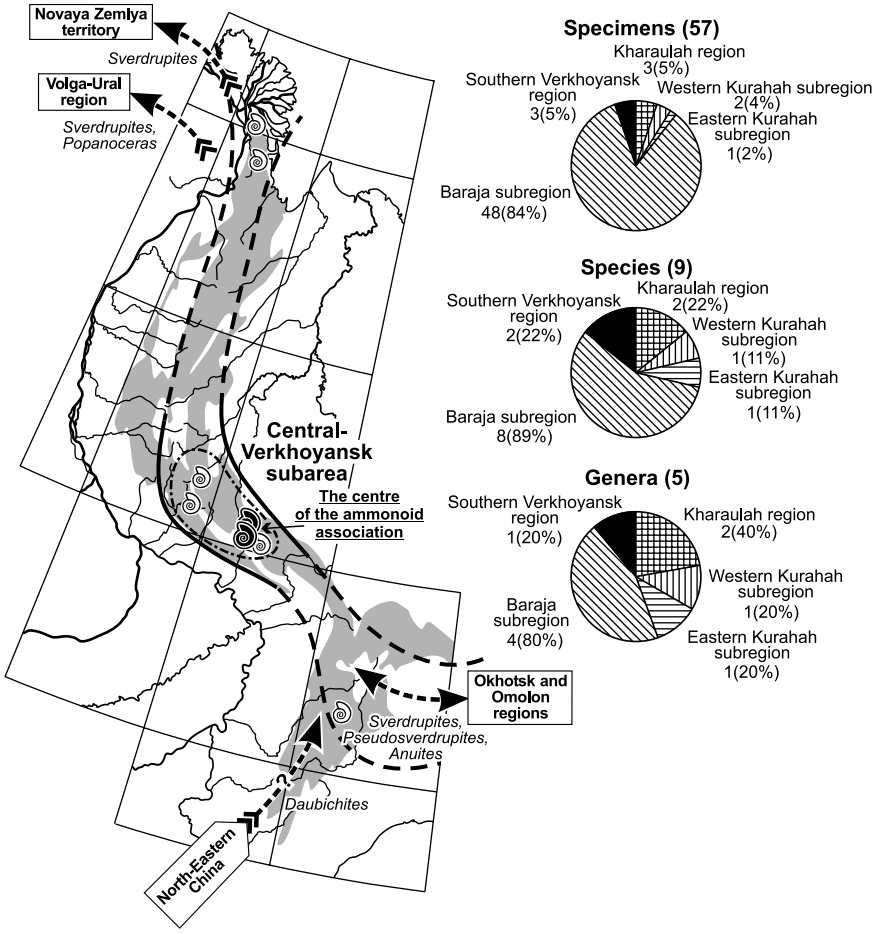

Fig. 15. Distribution and inferred migration patterns of the Delendzha association (for explanation of symbols see Fig. 5).

the Omolonian Horizon of Kolyma-Omolon Province (Ganelin et al., 1990). *Daubichites goochi* has been known from the Upper Mugochan Subformation of Baraja River; it is and characteristic of the Upper Permian of Western Australia (Glenister and Furnish, 1961). Forms close to this species are known also from Northeastern China (Zhao and Zheng, 1977).

The Delendzha association has been previously considered to be the Ufimian (Andrianov, 1985; Kutygin, 1999a). However, the recent discovery of *Sverdrupites* ex gr. *harkeri* and *Popanoceras* spp. in a section of Kazanian strata on the Nemda River in the Volga-Ural Region (Esaulova et al., 2002; Leonova et al., 2002) indicates that the age of the Lower Delendzhian Subhorizon needs to be revised. Hence, this should be considered to be Kazanian in age.

A complete turnover of the Verkhoyansk ammonoid species occurred at the beginning of the Delendzhian. The appearance of the short lived genus *Sverdrupites* is important. This genus occupied a large geographic range extending from the Ural basin to the Canadian Arctic. The short lived nature and widespread occurrence have made *Sverdrupites* very useful as a tool to date the boundary between the Early and Late Permian (Kutygin, 1999a; Kotlyar et al., 2002). During the Delendzhian the ammonoid faunas spread very widely across the entire Verkhoyansk paleobasin (Fig. 15) and passed into the Okhotsk Region to the south via the South Verkhoyansk Region.

2.8. Post-Sverdrupites association

No ammonoids have been found above the Lower Delendzhian Subhorizon in the Verkhoyansk Region. A shell fragment of the Wordian-Capitanian goniatite *Mexicoceras* (= *Paramexicoceras*) is found only in alluvium in the vicinity of the Chamba and Imtachan Formations of the Tatarian of the Vostochnaya Khandyga River basin in the Southern Verkhoyansk Region (Popow, 1970). The shell, (Popow, 1970, pl. XIX, Fig. 5) of this mainly North American genus is the youngest among all known goniatites in the Permian of Northeast Russia, but its stratigraphic position remains unknown. Judging by the discovery of the shell fragment of *Mexicoceras* (*Paramexicoceras*) in the Vostochnaya Khandyga River basin and taking into consideration the presence in this region of Early Triassic ammonoids (Ermakova and Kutygin, 2000), it is supposed that the center of the Verkhoyansk ammonoid area was situated in the South Verkhoyansk Region during the Tatarian (Fig. 16).

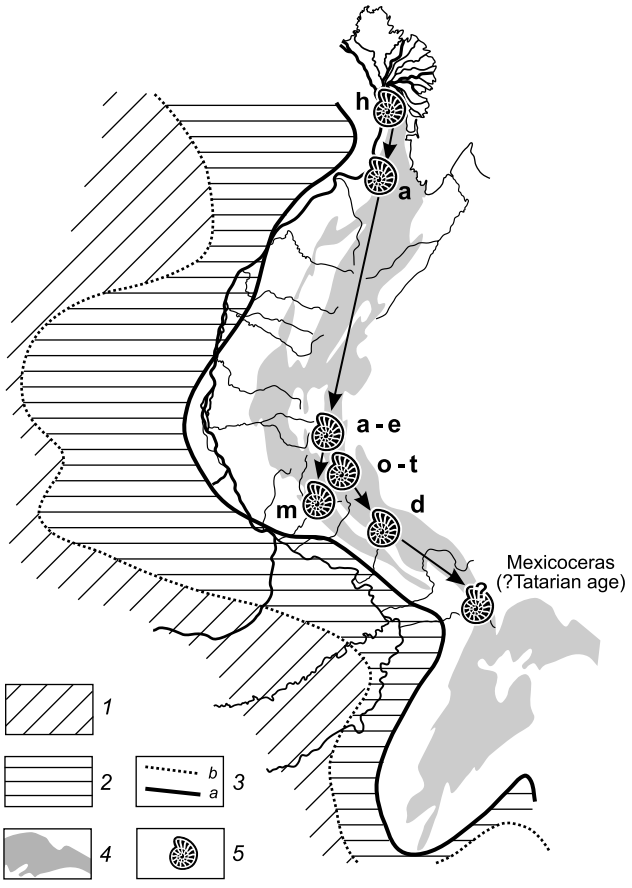

Fig. 16. Inferred migration directions of the center of the Verkhoyansk ammonoid associations during the Permian: 1—the hilly plains; 2—the low coastal plains which were periodically shallow marine during transgressive events;; 3—boundaries: a—between areas of mainly continental and mainly marine conditions, b—between low coastal and hilly plains; 4—area of Permian deposits; 5—prospective arrangement of the centers of the Verkhoyansk ammonoid association for various age intervals; Age intervals: h—Khorokyt (Asselian—Early Sakmarian ages), a—Arkachan (Lower Sakmarian age), e—Endybal (beginning of the Artinskian age), m—Mysovy (middle—end of the Artinskian age), o—Orol (Early Kungurian age), t—Takamkyt (Lower Kungurian age), d—Delendzha (Kazanian age); The map of generalized paleogeographical conditions is executed on the basis of paleogeographical maps made by V.N. Andrianov, V.A. Andrianova and I.I. Tuchkov (Tuchkov, 1973).

3. Conclusions

As a result of the analysis of the stratigraphic distribution and of faunal composition of ammonoids of the Permian of Verkhoyansk Region, eight associations are established: Khorokyt, Arkachan, Endybal, Mysovy, Orol, Takamkyt, Delendzha and Post-*Sverdrupites* associations. These associations are characterized by distinct stratigraphic intervals, which are designated as an ammonoid Bed. The ammonoid Beds are considered as biostratigraphic divisions of a regional stratigraphic scale.

During the Permian in the Verkhoyansk paleobasin a large ammonoid belt extended along the coastline. During the Khorokytian time (Asselian—Early Sakmarian) there was an evolutionary development of endemic ammonoids inside the Verkhoyansk paleobasin and migration of fauna from the Ural and Okhotsk Regions. The export of ammonoids from the Verkhoyansk paleobasin in Khorokytian time is not established. In the Arkachanian time (Late Sakmarian) the Verkhoyansk ammonoid area was divided in many subareas. During the Arkachanian time (Late Sakmarian) and during the Mysovian to Early Delendzhian times (Late Artinskian—Kazanian) there was an active exchange of the ammonoid faunas between Verkhoyansk and Omolonsk Regions. In the Artinskian and Kungurian the main direction of ammonoid migration was to the Omolonsk paleobasin. The ammonoid associations became geographically reduced and existed only in closed subareas in such stages as in the Endybalian (Early Artinskian) time, during the Khabah crisis (termination of the Artinskian) and Early Mugochan crisis (Ufimian).

During the Permian the flourishing center of the ammonoid of the Verkhoyansk paleobasin appeared to have progressively moved southward along the shoreline from Northern Kharaulah zone to the Southern Verkhoyansk zone.

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