Ecological aspects of upper Carboniferous – lower Permian '*Cyathaxonia* Fauna' taxonomical diversity (the Urals)

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Abstract: Some occurrences of '*Cyathaxonia* fauna', which are of latest Moscovian, Late Artinskian, and Late Kungurian age, are considered. Detailed stratigraphic data and sedimentological analyses permit the recognition of stressed environmental episodes in which the fauna occur associated with abrupt deepening of the Pre-Uralian Basin. Ecological and facies analyses show the lateral differentiation of '*Cyathaxonia* fauna' into assemblages with a predominance of euryfacies or deep-water-specific taxa. Among them, the appearance of a mostly taxonomically diverse Late Artinskian assemblage was established in the outer ramp environments in the temperate zone of the Northern Hemisphere. A review of isotopic data demonstrates a positive shift of $\delta^{18}O$, considered as a slight temperature decrease coinciding with transgressions in the Pre-Uralian Basin in the latest Moscovian and the Late Artinskian. A few new taxa from the Lophophyllididae (*Lophophyllidium interseptatum* sp. nov.) and Wannerophyllidae families (Gen. et sp. nov. 1, Gen. et sp. nov. 2) are described.

Key words: Rugosa, '*Cyathaxonia* fauna', latest Moscovian, late Artinskian-Ufimian, ecological differentiation, palaeogeography

Contents

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1. INTRODUCTION

The '*Cyathaxonia* fauna' is a well-known example of a long-ranging assemblage, which repeatedly appeared in different periods of the Upper Palaeozoic (Kullmann, 1997; Wrzołek, 2002). This fauna is reported from different facies, but abundant and variable assemblages of '*Cyathaxonia* fauna' characterize ecologically stressed environments of the carbonate platforms and their margins. This fauna is considered a recurrent assemblage without well-recognized roots, which is widespread after extinctions of the massive colonial forms in the eastern part of the Northern Hemisphere. The occurrence of morphologically similar assemblages at the end of the Mississippian (Chesterian) (Webb, 1987; Webb & Sutherland, 1993) and the latest Moscovian allows many genera to be considered as long-ranging taxa. The Late Artinskian '*Cyathaxonia* fauna' is represented by several ecologically dependent morphotypes. Variability of species composition reflects the specific features of the ecological niches. A regional correlation based on rugose corals and verified by the co-occurrences of ammonoids, ostracods and other groups, allows to synchronize the level of appearance of the Late Artinskian '*Cyathaxonia* fauna' throughout the 6.000 km extent of the Urals (Kossovaya et al., 2002). Thus, the appearance of the '*Cyathaxonia* fauna' could be considered as a correlation level with a high resolution potential.

2. STUDY AREA, MATERIAL, AND METHODS

2.1. Dalnyi T'ulkas section, the South Urals

The uppermost Moscovian coral assemblage was collected from the Dalniy T'ulkas section (56° 69' WL 53° 74' NL) situated in a quarry 3 km to the east of Krasnousolsk (southern Bashkiria) on the right bank of the Dalniy T'ulkas River (Fig. 1). The distribution of fusulinids and conodonts in this section have been previously studied (Chuvashov et al., 1983, 1990, 1991) and the upper part of the section was considered as Upper Moscovian. However, new stratigraphic results based on conodonts, fusulinids and rugose corals obtained during fieldwork carried out in 2001- 2002 (Alekseev et al., 2002) allowed to distinguish the position of the Moscovian- Kasimovian boundary, coinciding with the appearance of *Streptognathodus subexcelsus*. The collection of uppermost Moscovian '*Cyathaxonia* fauna' consists of 22 specimens (in total) of *Lophophyllidium, Soshkineophyllum, Amplexus, Amplexizaphrentis, Cyathaxonia, Wannerophyllum*? and *Neaxon*?.

2.2. Lower Artinskian – Ufimian '*Cyathaxonia* fauna'

The Lower Artinskian – Kungurian '*Cyathaxonia* fauna' was collected in the period from 1995–2000 from several sections from the Polar Urals – to the south boundary of the Southern Urals (1–6 in Fig. 1). Additional material was from the unpublished collection

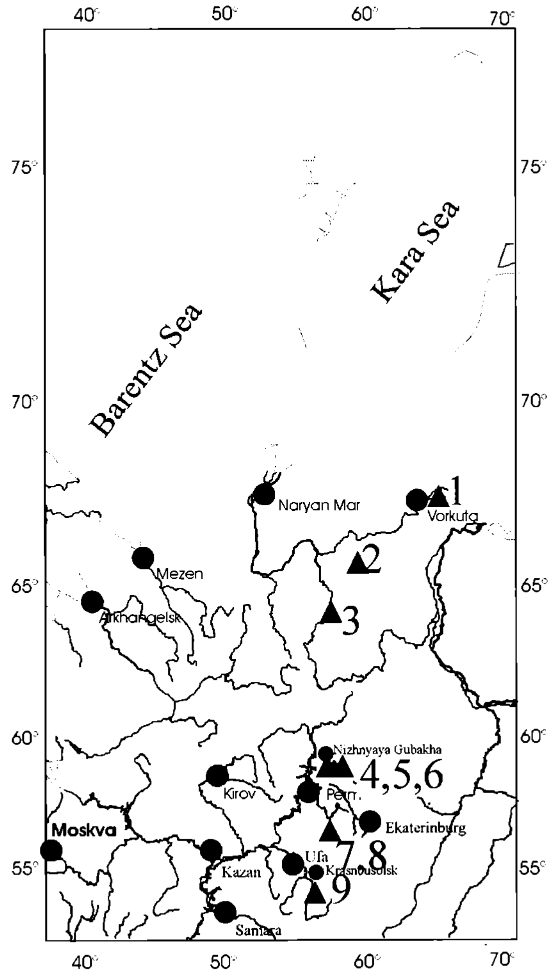


Fig. 1:
Map of the European part of Russia.
Scale 1: 35,000,000.
1–6 location of section:
1 – Vorkuta River,
2 – Kozhim River,
3 – Schugor River,
4 – Most and
5 – Karpikha sections of the Kosva River valley,
6 – Kamen' Navis'shyi section,
7 – Divya Mountain section,
8 – Ryabinov Ravine section,
9 – Dalnyi T'ulkas section.

of the Paleontological Institute RAN, doublet materials from CNIGR museum, St. Petersburg, and collections of St. Petersburg Museum of Mining Institute. The total number of the studied specimens is more than 200, and the taxonomic revision of the corals is in progress.

2.3. Geochemical data

The conclusions on environmental changes are based both on microfacies and cyclic analyses (Kossovaya et al., 2001, 2002; Kotlyar et al., 2004) and isotopic data obtained from the ^{18}O and ^{13}C analyses of brachiopod shells collected in the Urals sections (Grossman et al., 2002), and Northern Timan section (Kossovaya et al., 2001). Determination of Ca/Mg ratio used for paleotemperature analyses was done on some Upper Artinskian brachiopods shells of the Most section (Kosva River) (pers. com. Dr. G. Dorofeeva, VSEGEI).

3. LATEST MOSCOVIAN ASSEMBLAGE

3.1. Stratigraphic setting

The Tashly Fm. (Stepanov, 1941) is exposed in the lower part of the Dalniy T'ulkas section (Fig. 2). This formation comprises two lithological units (Units 1 and 2). The lower unit (Unit 1) is light-grey and white dolomitized crinoid packstones with numerous chert nodules. Beds are separated by wavy surfaces with localized accumulations of yellow crinoid grainstones near by. Corals of the lower unit were collected from 3 levels and are most abundant at the top of second bench of the quarry and from the base of the third bench. In the latter they were found forming thin lenses near bedding surfaces. In Unit 1 the conodont assemblages contain: – *Idiognathodus* aff. *podolskiensis*, *Idiognathodus* sp. A, and *Gondolella levis*. Fusulinids recorded include -*Wedekindellina uralica*, *W. excentrica magna*, and *W. dutkevich*. Rugose corals recovered include – *Pseudotimania irregularis* Gorsky, *P. kasimovi* Dobrolyubova & Kabakovich, *Siedleckia mutafii* (Gorsky), *'Caninia' remotetabulata* Gorsky, and *'Axophyllum'* sp. Based on the all the data from the faunal groups the age of the enclosing limestone is considered as Podolskian (Alekseev et al., 2002). Outside the Uralian Basin, a similar coral fauna is known from the northern Timan region, Moscow Basin, Novaya Zemlya, and Spitsbergen. The overlying beds (9 m from the base of the section; Fig. 2) are characterized by *Idiognathodus podolskiensis*, *Id. obliquus*, *Id. inaequalis*, which are also characteristic of the Podolskian. The lower boundary of the Myachkovian is not easily recognized. Unit 2 of the Tashly Fm. includes clays, mudstones, and tuffs. The late Myachkovoan age of Unit 2 is supported by the presence of *Neognathodus roundyi* and *Gondolella magna*. The *'Cyathaxonia* fauna' found in the upper Myachkovian strata is characterized by *Lophophyllidium* (*Lophbillidium*) *interseptatum* sp. nov., *Lophophyllidium* sp. ('cyathaxonimorph' type), *Wannerophyllum? incertum* Rodríguez & Kullmann, *Cyathaxonia* aff. *cornu* Michelin, *Neaxon*? *multitabulatus* Rodriguez & Kullmann, *Soshkineophyllum* sp.1. The taxonomic change coincides with the abrupt change of lithology from carbonates

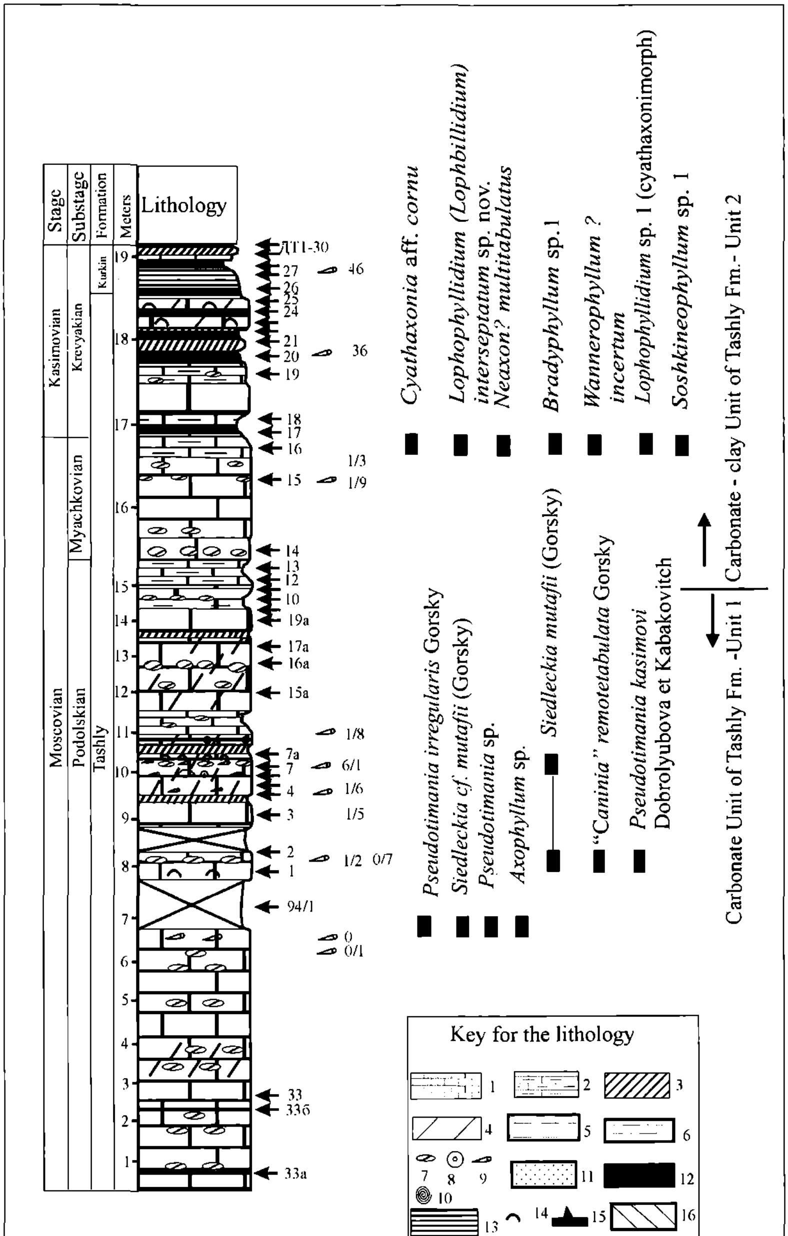


Fig. 2: Distribution of corals in the Talniy T'ulkas section, southern Bashkiria.
Legend for lithology for Figs. 2–6:
1 – limestone, 2 – clay limestone, 3 – siliceous layer, 4 – dolomite, 5 – claystone, 6 – siltstone, 7 – chert nodules, 8 – crinoids, 9 – rugose corals, 10 – ammonoids, 11 – sandstone, 12 – clay, 13 – tuffs, 14 – brachiopods, 15 – coal layers, 16 – marl.

to sedimentation with a major input of terrigenous and siliceous material trigged by deepening of the basin. Comparison with the assemblage from the coeval deposits of the upper part of the Picos de Europa Fm. (Spain) shows a similar generic and species composition (Rodríguez & Kullmann, 1999).

The overlying Kurkin Fm., is characterized by the intercalation of predominant black cherty layers, clay, tuff, and rare mudstone. It is exposed in the upper part of the quarry (Fig. 2). Its Kasimovian age is supported by the occurrence of *Streptognathodus subexcelsus* and others (Alekseev et al., 2002).

3.2. Taxonomical structure of rugose coral assemblage

There is only one level characterized by the '*Cyathaxonia* fauna' in the latest Myachkovian (Fig. 2), but the presence of a similar fauna in the coeval deposits in the Cantabrian Mountains (Rodríguez & Kullmann, 1999) and Mid-Continent USA (Jeffords, 1947) increases the correlation potential of this assemblage. The collection comprises of Laccophyllidae Grabau, 1928, Lophophyllidiidae Moore & Jeffords, 1945, Polycoeliidae Fromentel, 1861, Wannerophyllidae Fedorowski, 1986.

The family Laccophyllidae is represented by only one specimen (Pl. 1, Figs. 1–4), which is similar to *Neaxon*? *multitabulatus* Rodriguez & Kullmann, 1999. The similar features are: (1) a thin cardinal septum similar in length to that of other major septa; (2) an aulos that consists of chyathotheca and phyllotheca; (3) the axial part of the long counter septum that continues into the chyathotheca; (4) a phyllotheca formed by the axial edges of major septa; and (5) very short minor septa, but some of them project out of the septotheca. The specimen in our collection differs from *Neaxon* by the absence of trabeculae (Weyer, 1989).

Two specimens of the family Polycoeliidae Fromentel, 1861 are determined as *Soshkineophyllum* sp. 1. (Pl. 1, Figs. 21–23). The early ontogenetic stage (Pl. 1, Fig. 21) characterized by a shortened cardinal septum, long counter septum, two long lateral protosepta, allows the recognition of the genus, but the remains of four extremely long axial parts of septa separated in the axial part of the coral does not allow attribution to any known species. The axial structure shows some similarity with lophophyllidid corals, but early ontogenetic features are considered as more important for generic diagnosis. It is comparable to *Soshkineophyllum corisense* de Groot (de Groot, 1963), which shows also similar remains of a pseudoaxial structure (de Groot, 1963, Pl. 2, Fig. 6).

The family Lophophillidiidae Moore & Jeffords, 1945 are the most representative group including *Lophophyllidium* sp.1, characterized by 'cyathaxoniamorphic' features (Pl. 1, Figs. 8–9), and *Lophophyllidium* (*Lophbillidium*) *interseptatum* sp. nov. (Pl. 1, Figs. 10–16). The Upper Chesterian *Lophophyllidium* species of Arkansas (Webb & Sutherland, 1993) differs from the late Moscovian ones by very splintered inclined tabulae. The biform tabularium also is not present in the American species. The trend from splintered type of tabulae (as in *L. imoense* Webb & Sutherland) to flatter ones (as in *L.* (*Lophophyllidium*) Fedorowski, 1987) seems to be possible. A second trend, which could be interpreted, is the appearance of a biform tabularium as in *L.* (*Lophbillidium*).

The family Wannerophyllidae Fedorowski, 1986 is represented by *Wannerophyllum*? *incertum* (Pl. 1, Figs. 17–20) with three specimens characterized by small size (9.5–10 mm, number of septa 22 x 2), short cardinal and counter septa in the mature stage,

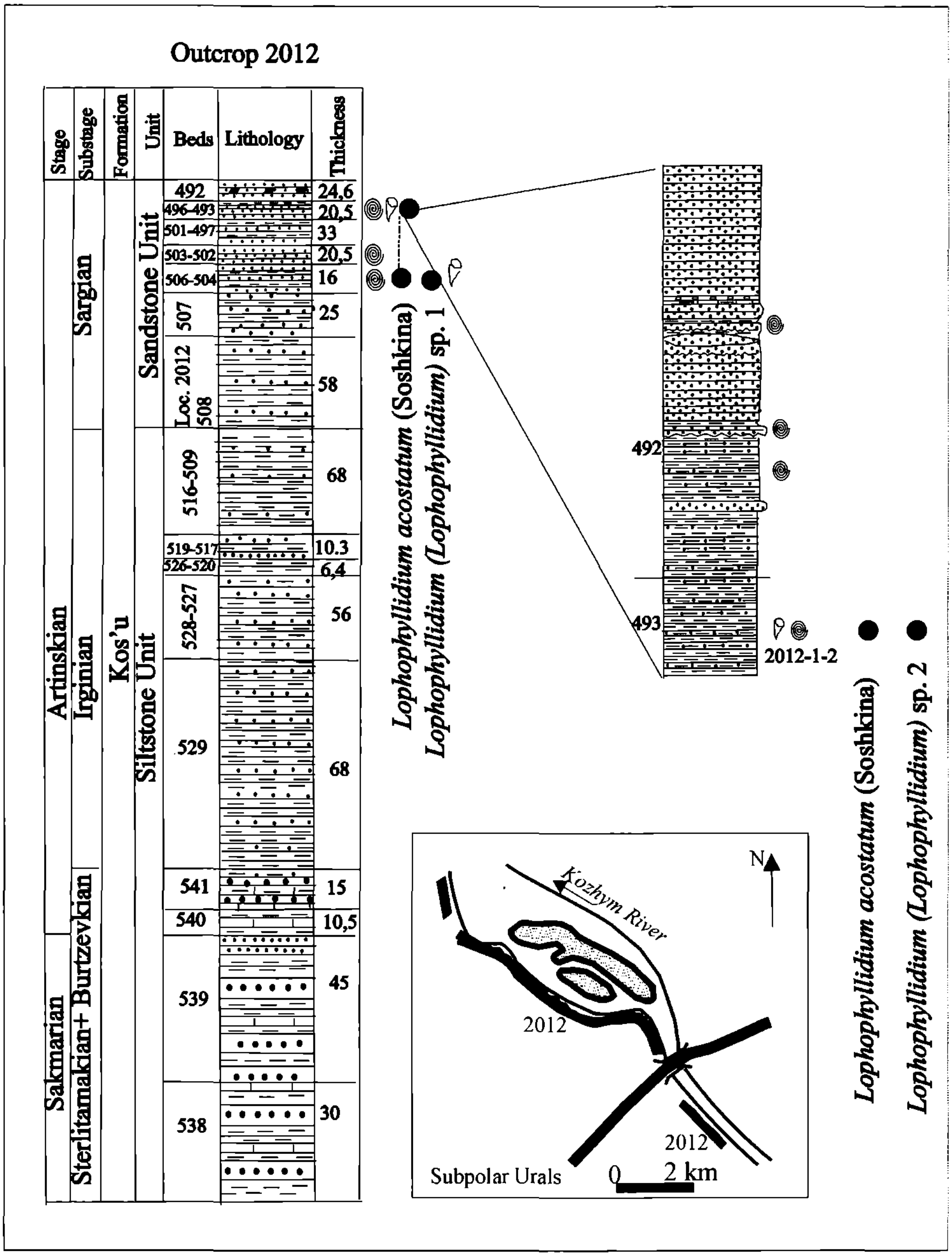


Fig. 3: Rugose coral distribution in the Upper Artinskian deposits of the Kozym River section. (Log based on CHUVASHOV et al., 1995 and pers. com. of Dr. A. ZHURAVLEV).

and well-developed minor septa. Long minor septa and distinct biform tabularium demonstrate a similarity with *Pseudowannerophyllum differens* FLÜGEL (FLÜGEL, 1975).

The Antiphyllidae ILINA, 1970 are represented by three specimens attributed to *Bradyphyllum* sp. (Pl. 1, Figs. 5–7). A similar specimen was described from Picos de Europe Fm., Westphalian D, Austuria (RODRIGUEZ & KULLMANN, 1999, Pl. 7, Figs. 17–19).

The comparison of the studied interval shows the existence of a morphologically similar approximately coeval assemblage in the South Urals, Cantabrian Mountains (RODRIGUEZ & KULLMANN, 1999; DE GROOT, 1963) and in the Mid-Continent USA (JEFFORDS, 1942, 1947).

3.3. Environmental changes

Besides the Dalnyi T'ulkas section, the latest Myachkovian '*Cyathaxonia* fauna' is known in a few outcrops in the Cisuralian (GORSKY, 1978), usually accompanied by the appearance of deep-water deposits. The upper Myachkovian in the Kamen'Perevalochnyi section shows an increase in the value of ^{18}O and a decrease of ^{13}C (GROSSMANN et al., 2002). These geochemical trends are interpreted as a deepening of the Pre-Uralian foredeep accompanied by a slight decrease of temperature. Such abiotic change seems to be the reason for the appearance of the '*Cyathaxonia* fauna' in the Dalniy T'ulkas section.

4. LATE ARTINSKIAN – UFIMIAN '*CYATHAXONIA* FAUNA'

4.1. Previous investigation

SOSHKINA described the Upper Artinskian corals of the Central Urals (SOSHKINA, 1925), the Polar Urals (SOSHKINA, 1928), the Ufimian plateau (SOSHKINA, 1932), and the Aktyubinsk region (SOSHKINA, 1936). Most of these description were summarized later in SOSHKINA et al. (1941). More recently, some specimens have been described by SIMAKOVA (in GORSKY & KALMYKOVA, 1986). Remarks on the type material of *Ufimia carbonaria* STUCKENBERG, 1895 were made by FEDOROWSKI (1973) and ILYINA (1984). The latter author re-described *Hexalasma hexaseptatum* (SOSHKINA) (referring it to *Pentaphyllum*), *Ufimia carbonaria* and *Soshkineophyllum artiense* (SOSHKINA), and mentioned some other Late Artinskian species in her revision (ILYINA, 1984). Using the data from co-existing ammonoids, ostracodes and brachiopods, the coral assemblages found in the Most, Karpihka, Dyvia Mountain, and Kozhim sections correspond to the Upper Artinskian (KOSSOVAYA et al., 2001, 2002). Two assemblages collected in the Kungurian and Ufimian deposits of Kozhim River section are also discussed.

4.2. Stratigraphic setting

4.2.1. Subpolar Urals

The northernmost outcrop, containing the Upper Artinskian fauna is situated in the Kozhym River Valley (Fig. 3). A few species were documented earlier from this section: *Soshkineophyllum breve* (SOSHKINA), *Lophophyllidium acostatum* (SOSHKINA), *Calophyllum gerthi* (SOSHKINA), *Ufimia rhizoides* (SOSHKINA), *Soshkineophyllum lophophylloides*

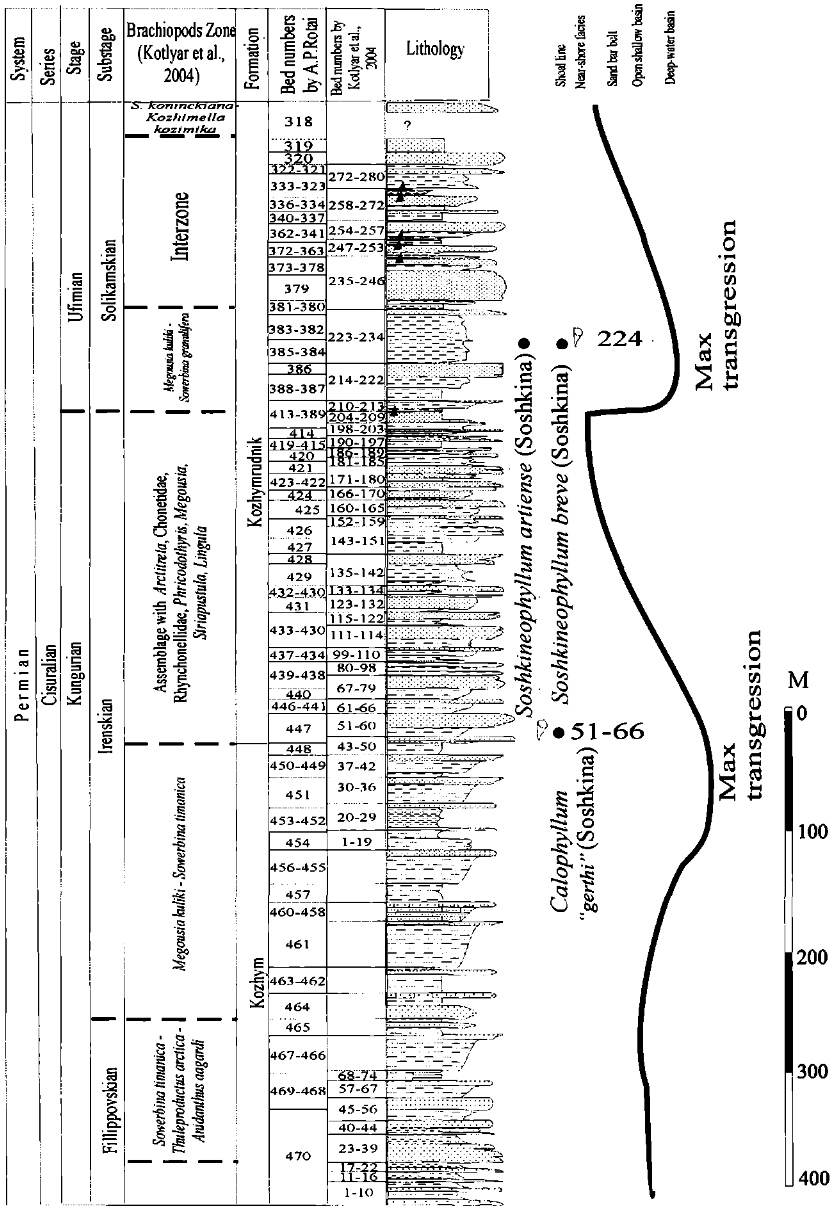


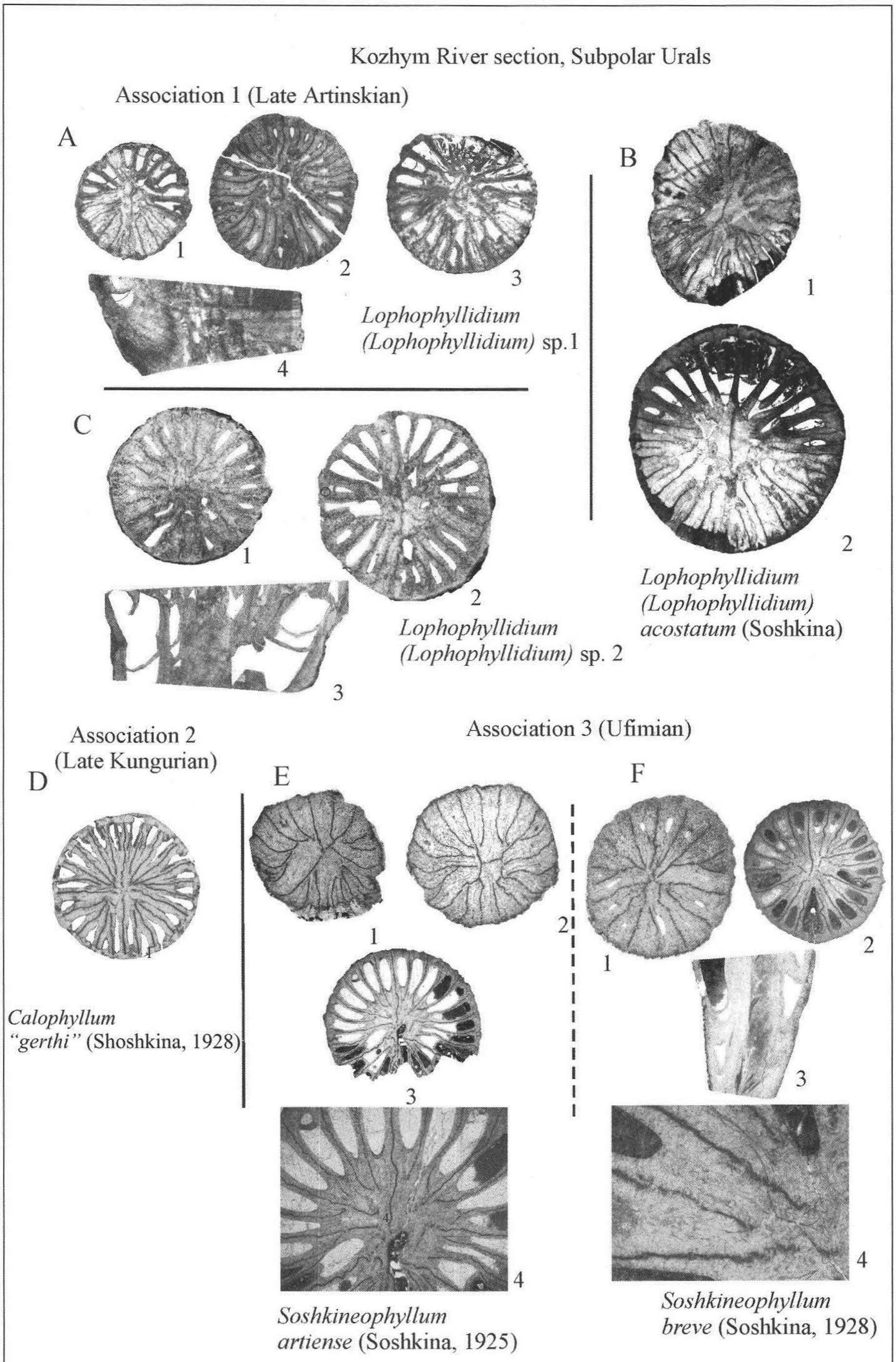
Fig. 4: Distribution of corals in the Kungurian – Ufimian deposits of the Kozhym River section. (Log based on Chuvashov et al., 1995 and Kotlyar et al., 2004).

(SOSHKINA), representing a mixed Artinskian-Kungurian assemblage (SOSHKINA, 1928). Recent detailed stratigraphic work allows to specify the stratigraphic distribution of corals and to identify three stratigraphic associations: (a) (First association) – *Lophophyllidium acostatum, L. colummelare* (SOSHKINA), *Hexalasma primitivum* (SOSHKINA), and *Soshkineophyllum lophophylloides* which occurs in the middle part of the Kos'yu Fm. together with numerous ammonoids *Paragastrioceras* sp. and *Waagenina subinterrapta* (KROTOW) (pers. com. of K. Borisenkov) and minute disintegrated fasciculate bryozoans in siltstone including rare carbonate-clay concretions (KOTLYAR et al., 2004). Ammonoids support the Upper Artinskian age of these deposits; (b) (Second association) – only one specimen of *Calophyllum "gerthi"* was found in the Kozhym Fm. of the Kungurian (Irenskian Regional Substage); (c) (Third association) *Soshkineophyllum breve* and *S. artiense* characterize the middle part of the Kozhimrudnik Fm. (Solikamskian Regional Substage) (Figs. 4, 5). According recent studies of brachiopods in the Kozhim River section, the Solikamskian Regional Stage was included in Kungurian. By the official point of point of view it is a part of the Ufimian Stage of the Russian Stratigraphic Chart of the Permian System. Also, the Ufimian Stage is corresponded to Kungurian Stage of the International Stratigraphic Chart. Thus, we consider third assemblage as the Ufimian (= Late Kungurian in the International Stratigraphic Chart). Facies analysis shows that all the associations occupied relatively deep water, but the first association was found in open shelf facies, whereas the second and third associations occur in turbidites. One of the most diverse associations of the first type was found at the Schugor River, downstream of the outcrop 'Middle Gates' and 4 km upstream from the mouth of the river. The deposits, considered as Orlovka Fm. (CHUVASHOV et al., 1999) contain: *Soshkineophyllum schematicum* (SOSHKINA), *S. tenuiseptatum* (SOSHKINA), *S. breve, Hexalasma hexaseptatum, H. primitivum, Ufimia rhizoides, U. carbonaria, Cyathaxonia cornu, Cyathocarinia tuberculatum* SOSHKINA, *Pseudowannerophyllum* sp. nov. 1, *Lophophyllidium shtchugoriense* (SOSHKINA), Gen. et sp. nov. 1, Gen. et sp. nov. 2.

4.2.2. Central Urals

After E. D. SOSHKINA's publication on the Upper Artinskian corals from Lytva River and Sylva rivers (SOSHKINA, 1925), corals have been collected from a few outcrops in the

Fig. 5: Taxonomic composition of Late Artinskian – Ufimian corals in the Kozhym River section. All specimens are kept in CNIGR museum (St. Petersburg).
A: Figs. 1–2: specimen Koz-5/109–2, x 2; Fig. 3: specimen Koz-5/109–3, x 2; Fig. 4: specimen Koz-5/109–2, x 3, Kos'u Fm., bed 504–506, collection of Dr. V. Saldin;
B : Figs. 1–2, specimen Koz-5–106; Fig. 1: x 4; Fig. 2: x 2
C: Figs. 1–3, specimen 2021–1/2 collection of Dr. A. Zhuravlev, Kos'u Fm., bed 493
D: Specimen 51–42/99, x 4, Kozhym Fm., bed 51–66
E: Figs. 1–4, specimen 224/5, Kozhymrudnik Fm., bed 224, collection of Dr. S. Shishlov;
Fig. 1–2: x 4; Fig. 3: x 2; Fig. 4: x 4, alar septa are longer than others
F: Figs. 1–3: specimen 224/7, Kozhymrudnik Fm., bed 224, collection of Dr. S. Shishlov;
Fig. 1: x 4; Fig. 2: x 2; Fig. 3: x 10.


Kozhym River section, Subpolar Urals
Association 1 (Late Artinskian)
A
1
2
3
4
Lophophyllidium (Lophophyllidium) sp.1
B
1
2
Lophophyllidium (Lophophyllidium) acostatum (Soshkina)
C
1
2
3
Lophophyllidium (Lophophyllidium) sp. 2
Association 2 (Late Kungurian)
D
Calophyllum "gerthi" (Shoshkina, 1928)
Association 3 (Ufimian)
E
1
2
3
4
Soshkineophyllum artiense (Soshkina, 1925)
F
1
2
3
4
Soshkineophyllum breve (Soshkina, 1928)

Kosva River basin (Most, Karpikha) and in the Navis'shiy sections (Us'va River). The Upper Artinskian strata bearing corals consist of wackestone, mudstone and spiculite packstone overlying tempestites of the Irginian Substage. This unit termed 'marl unit' is situated between carbonate deposits with chlorozoan association (Kossovaya et al., 2002) and typical turbidite fans. In the Navis'shiy section the 'marl unit' is characterized by the ammonoids *Waagenina subinterrapta* (Chuvashov et al., 1990, p. 305). The Sargian age of the 'marl unit' is well documented by different faunas (Kossovaya et al., 2002). The coral assemblage consists of *Lophophyllidium* sp. 1. *Pseudowannerophyllum* sp. 2, *Cyathaxonia* ex gr. *C. cornu*, *Cyathocarinia multituberculata* Soshkina, *Paralleynia permiana* Soshkina, *Ufimia carbonaria, U.* sp. nov. 1, and *Soshkineophyllum artiense.*

4.2.3. Southern Urals

Upper Artinskian corals from the Divya Fm. of the Divya Mountain and Riabinov Ravine – the classical Upper Artinskian deposits – are known from the work of Soshkina (1936). Most of the fauna is from the inter-reef deposits and only two species were found in the massive sponge-bryozoan reef – Divya Mountain (Kossovaya et al., 2002). The fauna includes: *Soshkineophyllum breve, S. artiense, Ufimia carbonaria, Lophophyllidium colummelare, Paralleynia biseptata* Soshkina, *Amplexocarinia muralis minuta* Soshkina, *Cyathocarinia multituberculatum*, and *Ufimia rhizoides*.

4.3. Taxonomical composition of coral assemblages

The comparison of the taxonomic composition of the Late Artinskian coral assemblages from reef to the outer shelf and ramp environments shows the maximum diversity in the deep–water sediments of the open-ramp, where the siliciclastic input is rather considerable (Fig. 6). In addition to euryfacies *Soshkineophyllum, Ufimia, Cyathaxonia,* and *Amplexocarinia*, the numerous corals with columella are characteristic of the deep-water environments. They are represented by *Lophophyllidium, Pseudowannerophyllum,* Gen. et sp. nov. 1, and Gen. et sp. nov. 2. Besides the columellate forms, the occurrence of *Hexalasma* is also limited to the deep-water facies (Kozhim, Most, and Karpikha sections). Most species in the assemblage are represented by a few specimens, with *Soshkineophyllum, Lophophyllidium* and *Pseudowannerophyllum* being the most abundant ones. The number of specimens of each taxon is more than 10 in every section.

Hexalasma hexaseptatum was described by E. D. Soshkina (Orlov, 1962) and later transferred to *Pentaphyllym hexaseptatum* by Iliyna (1984). The main features distinguishing *Hexalasma* from *Pentaphyllum* are the well-developed cardinal, counter and lateral protosepta, the virtual absence of metasepta and a specific microstructure, composed in the lateral part of septa by numerous lamellae of stereoplasma. Counter-lateral septa are also rather well developed. However, the genus *Pentaphyllum* de Koninck has a well- developed cardinal septum, alar septa and counter-alar septa. The counter septum is short.

Pseudowannerophyllum sp. nov. 1. The comparison with *Pseudowannerophyllum* Flügel (Flügel, 1975; Fedorowski, 1987) shows a less developed biform tabularium (Pl. 2, Figs. 11–14).

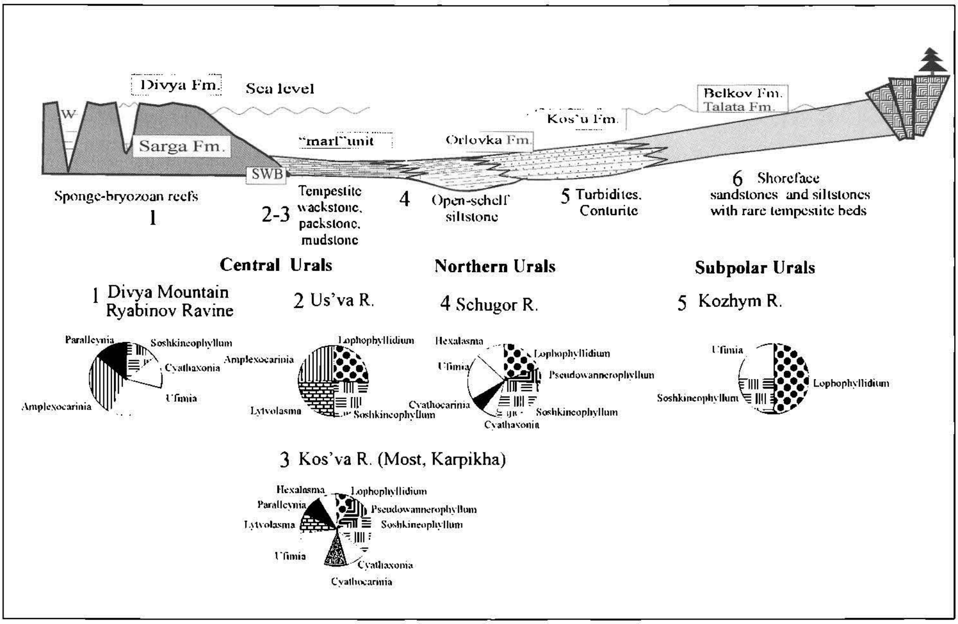


Fig. 6: Dynamics of the taxonomical composition of Late Artinskian '*Cyathaxonia* fauna' in the different facies from eastern margin of carbonate platform to south-western ramp of the Urals. SWB – storm wave base.

Gen. et sp. nov. 1. (Pl. 2, Figs. 15–21) – the more closely related genus is *Wannerophyllum* SCHOUPPÉ & STACUL, 1955 (SCHOUPPÉ & STACUL, 1955; FEDOROWSKI, 1986). Distinctions in early ontogeny include: counter septum is longer then the cardinal, but joined, as in *Wannerophyllum*; all septa thicker; septal increase is approximately equal for counter and cardinal quadrants, or even more septa appear in counter quadrants. Additionally, perpendicular lamellae in axial structure also resemble those in *Wannerophyllum*. One of the distinguishing features is a thick stereotheca. It cannot be included in *Pseudowannerophyllum* FLÜGEL, 1975 because it lacks a biform tabularium, and the species has a different tabularium structure.

Gen. et sp. nov. 2 – these corals are represented by another type of columellate form, more closely related to *Verbeekiella* in the origin of the columella, but the counter and cardinal septa also participate in forming the columella. The initial part (Pl. 2, Fig. 22) is comparable with that demonstrated by FEDOROWSKI (1986, Pl. 3, Fig. 5a), but the multitrabecular structure of the septa and the lamellar wall type are the main differences from *Wannerophyllum* SCHOUPPÉ & STACUL, 1955 (Pl. 2, Fig. 26). Carinate septa are considered a specific feature (Pl. 2, Fig. 24).

The rather unique Kungurian and Ufimian assemblages are distinctly impoverished and include only a few species of *Calophyllum* and *Soshkineophyllum* (Fig. 4, Fig. 5 D, F). Their occurrences coincided with transgressive pulses established in the siliciclastic inner-shelf deposits, which accumulated in the carbonate-starved basin.

4.4. Facies analysis and environmental changes

The Upper Artinskian – Lower Kungurian coral-bearing deposits embrace a wide facies spectrum from the north to the south and from the west to the east. They change from typical temperate-water carbonates, such as sponge-bryozoans reefs or marls in the inter-reef depressions of the South Urals (edge of the carbonate platform) to an alternation of thin-bedded mudstones and spiculites, observed in the contemporaneous deposits in central Urals. The carbonate starvation in the northerly disposed parts of the basin resulted in the accumulation of siltstones and mudstones. To the east some coral-bearing siltstones are the parts of turbidites, which accumulated in the siliciclastic shelf of the eastern part of the basin, situated close to the Uralian orogenic belt.

The abrupt setting of the specific and abundant late Artinskian corals could be explained by several reasons. The end of the Sakmarian – Early Artinskian is a time of widespread regression triggered by glaciations in the Southern Hemisphere. The end of the Early Artinskian is correlated with the beginning of a transgression displayed in the widespread tempestites and deep-water spiculites in different parts of the Uralian Basin (Kossovaya et al., 2002). Also, some data on isotope shifts have been obtained, based on the brachiopod shells collected from the Artinskian – Kungurian deposits in the northern part of the Russian Platform (Sula River section, Northern Timan) (Kossovaya et al., 2001). The results show a positive trend from –8.5 ‰ to -8 ‰ PDB of ^{18}O and from +3.1 ‰ to +3.5 ‰ ^{13}C. The increase of $\delta^{18}O$ values is interpreted as a result of a fall in temperature in the Late Artinskian. The palaeotemperature data based on Ca/Mg 1986ratio shows the average value for Late Artinskian between + 15 °C and + 17 °C in Northern Timan and + 19 °C in the Central Urals, Most section (pers. com. Dr. L., Dorofeeva, VSEGEI).

5. DISCUSSION

The diversity of shallow warm-water assemblages characterized by a predominance of colonial or complex solitary corals is more abundant in the inner shelf or upper part of the outer shelf slope. These corals are rare or absent in deep-water. Compared with shallow-water corals, which dwelt in the carbonate shelves of Pangea during Middle Asselian – Early Artinskian time and represented by numerous species of fasciculate, cerioid and asteroid corals, the diversity of cool-water corals seems to be very restricted. The occurrences of the Asselian – Early Artinskian '*Cyathaxonia* fauna' are well known from Mid-Continent USA (Fedorowski, 1987), but rarely recorded from the Uralian Basin. Only Early Asselian assemblages could be identified (Gorsky & Kalmykova, 1986). But after the extinction of most of the colonial corals in the end of Early Artinskian, the '*Cyathaxonia* fauna' assemblage became widespread. Possibly well adapted to cool temperature, mud substrate and deep water, they demonstrated their adaptiveness over the shallow and warm water dwellers. Comparison of the relatively warm shallow-water Mid-Artinskian '*Cyathaxonia* fauna' and deep-cool-water fauna of the same age shows the more diverse taxonomic composition of corals in cool-water. Rare occurrences of corals in the reef facies may be explained by the occupation of their niches by bryozoans and poriferans, which became free after elimination of colonial forms.

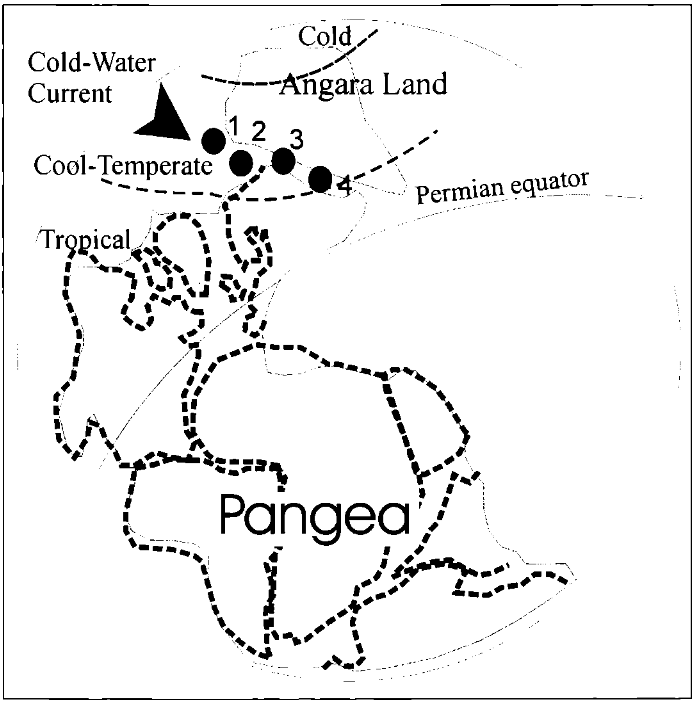


Fig. 7:
Artinskian palaeoclimatic map with the occurrences of rugose corals (based on Ross & Ross, 1984; Mei et al., 1999; Paleomap, 2004): cool water assemblages – Polar Urals (1), Northern Urals (2) and Central Urals (3), warm water assemblage - Southern Urals.

6. CONCLUSIONS

Three types of '*Cyathaxonia* faunal' assemblages have been established appearing due to their response to palaeotemperature and bathymetry of the basin.

1. Warmer-water assemblages appeared during the transgressive pulse of the basin in the Late Moscovian (latest Myachkovian). Indirect evidence of rather warm temperature is the co-occurrence with fusulinids and conodonts. The number of columellate and non–columellate corals is nearly equal. Corals with a columella have very small diameters (typically < 1 cm).
2. Late Artinskian cool water assemblages can be subdivided into two types: (a) Shallow-water assemblages include mostly non-columellate taxa, and (b) Deep-water assemblages with predominant columellate species are more diverse. Variability increased in cooler environments and is commonly expressed by the increase of morphological elements of axial structures. The Late Artinskian fauna seems to be a phase of short–time duration explosive diversification in the first transgressive cycle of cold water in the expanded Boreal Province (Fig. 7). The palaeotemperature differentiation of the assemblages of deep-water corals is similar to the distribution of temperate and tropical conodonts. The boundary between temperate and tropical assemblages of conodonts was shown at the latitude of Perm (Mei et al., 1999).
3. The subsequent Kungurian- Ufimian shallowing resulted in the abrupt restriction of diversity, distribution of non-columellate forms and diminution of coral size.

7. APPENDIX

7.1. Description of new species

Lophophyllidium (Lophbillidium) interseptum Kossovaya sp. nov.
(Pl. 1, Figs. 10–16)

Holotype: Specimen 21–12 (Pl. 1, Figs. 10–13), CNIGR Museum, St. Petersburg, uppermost Myachkovian, Dalnyi Tuylkas Section, bed 16, Tashly Fm., Unit 2.

Material: 3 small solitary corals with diameter less then 10 mm and height 15 mm, 7 thin sections.

Occurrence: Dalnyi Tuylkas Section, bed 21, uppermost Myachkovian, Tashly Fm., Unit 2.

Description: Small solitary *Lophophyllidium* with short cardinal septum, which does not join the columella. Counter septum joins the columella. Major septa are weakly rhopaloid in adult stages and separated from each other, but their rhopaloid character is clearly visible in the late neanic stage. The well-developed separated radial plates in the columella within the calyx resemble the axial structure '*Pseudowannerophyllum*'. Minor septa are contratingent. Columella consists of the axial parts of the short medial plate, radial plates split in the early ontogenetic stages, major septa reinforced by stereoplasma comes close to the columella and form semi-closed circle around the columella in the neanic stage (Pl. 1, Fig. 10). In the longitudinal section the columella consists of round-shaped hemispherical medial plates and occupies 1/3 of tabularium (Pl. 1, Figs. 11, 15). Tabularium is biform. Tabulae are steeply inclined and splintered in the middle part of the tabularium. A main fossula with short cardinal septum is distinct.

Comparison: Closely similar with *Lophophyllidium minutum* Jeffords (Jeffords, 1942, Pl. 7, Fig. 2), known from the Wapanicka Fm. of Texas by its diameter (near 10 mm), number of septa (21 major septa), and the short cardinal septum. It differs considerably, however, by separated radial plates in the columella and longer minor septa. From *L. plummeri* Jeffords, 1947 it is distinguished by the large number of septa, shorter minor septa, and a smaller size. The new species differs from *L. coniforme* Jeffords, 1947 from the Lansing and Pedee Group of the Missourian series (Pennsylvanian) by absence of permanent alar fossula. *Lophophyllidium interseptum* Kossovaya sp. nov. differs from species described recently from coeval deposits in the Cantabrian Mountains (Rodríguez & Kullmann, 1990, 1999) which do not have as well-developed minor septa.

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Plate 1

Late Myachkovian rugose corals, Dalnyi T'ulkas Section, bed 16, Tashly Fm., unit 2.

Figs. 1–4: *Neaxon? multitabulatus* RODRIGUEZ & KULLMANN. Specimen 21–2, x 3,5; CNIGR Museum, St. Petersburg, Russia. Fig. 1: early ontogenetic stage with well developed aulos. Fig. 2: longitudinal section. Fig. 3: mature stage. Fig. 4: microstructure of septa, x 20.

Figs. 5–7: *Bradyphyllum* sp. Specimen 21–13, x 3, CNIGR museum, St. Petersburg, Russia. Fig. 5: early ontogenetic stage with 'zaphrentoid' arrangements of septa. Fig. 6: longitudinal section. Fig. 7: late neanic stage.

Figs. 8–9: *Lophophyllidium* sp. Specimen 21–1-1, x 3, CNIGR Museum, St. Petersburg. Specimen with cyathaxoniamorphic features. Fig. 8: mature stage. Fig. 9: longitudinal section.

Figs. 10–16: *Lophophyllidium (Lophbillidium) interseptum* KOSSOVAYA sp. nov. Specimen 21–12, x 3; CNIGR Museum, St. Petersburg. Fig. 10: early ontogenetic stage. Fig. 11: longitudinal section. Fig. 12: microstructure of septa, x 35 (detail of Fig. 16). Figs. 14–15: specimen 21–1/2 (holotype), CNIGR museum, St. Petersburg. Fig. 13: early ontogenetic stage, x 4. Fig. 14: mature stage, x 3. Fig. 15: longitudinal section, x 3.

Figs. 17–20: *Wannerophyllum? incertum* RODRÍGUEZ & KULLMANN, 1999. Specimen Dt-21kn-1, x 3. Fig. 17: late neanic stage. Fig. 18: mature stage. Fig. 19: longitudinal section.

Figs. 21–23: *Soshkineophyllum* sp. 1. Specimen 21/9, CNIGR Museum, St. Petersburg. Fig. 17: early ontogenetic stage, x 5. Fig. 18: longitudinal section, x 3. Fig. 19: mature stage, x 3.

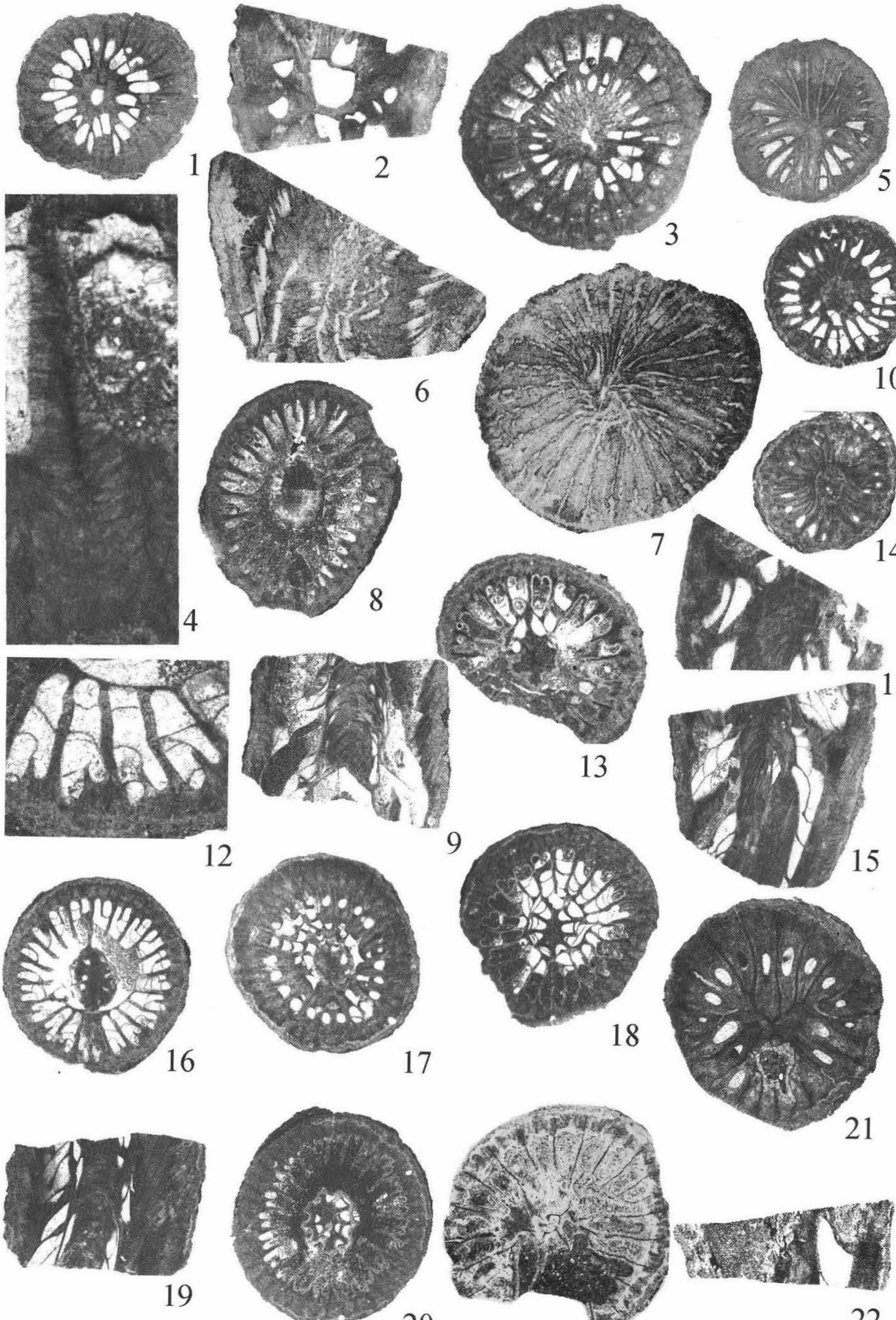
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Plate 2

Late Artinskian rugose corals

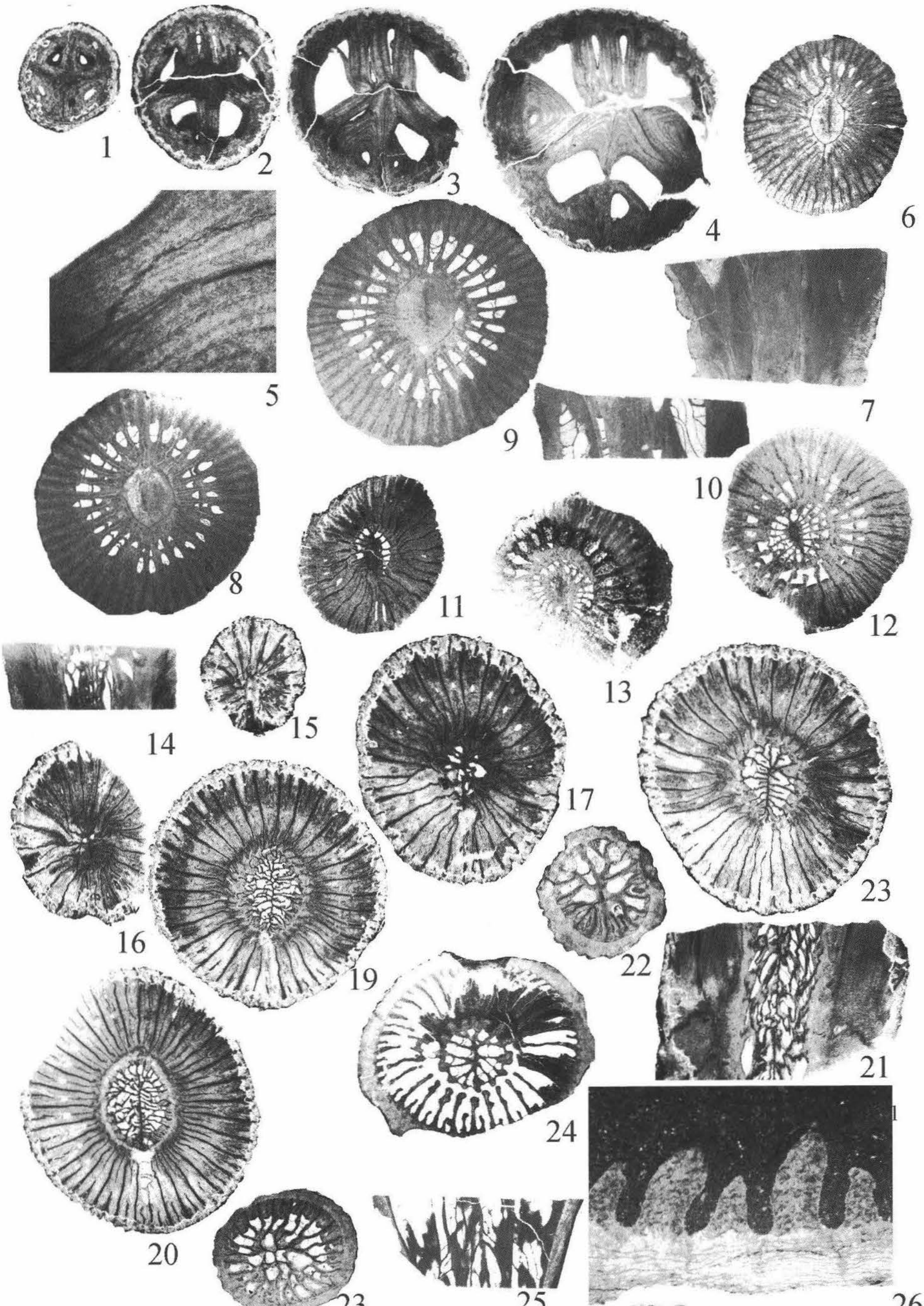
Figs.1–5: *Hexalasma hexaseptatum* (Soshkina), x 35. 146/1051, 4 km above mouth of Northern Urals, Schugor River, Orlovka Formation; Sargian Regional Stage, Museum of Paleontological Institute of Russian Academy of Science, Moscow. Figs. 1–3: transversal sections of early ontogenetic stages, x 3. Fig. 4: transversal section of the mature stage, x 2,5. Fig. 5: microstructure of septa, x 8; layers of stereoplasm are well visible.

Figs. 6–10: *Lophophyllidium (? Lophbillidium)* sp. nov. 1, specimen 184, CNIGR museum, St. Petersburg, Central Urals, Karpikha section, River Kos'va, 'marl unit'- analogues of Divya Formation, Sargian R.S., x 2. Fig. 6: an early ontogenetic stage: Fig. 8: the late neanic stage. Fig. 7: longitudinal section of the early stage. Fig. 9: transversal section of the mature stage. Fig. 10: specimen 184/3, longitudinal section of mature stage, x 2, location and residence – the same.

Figs. 11–14: *Pseudowannerophyllum* sp. nov. 1, specimen 134/5, CNIGR Museum, St. Petersburg, Central Urals, Most section, River Kos'va, 'marl unit'- analogues of Divya Formation, Sargian R.S., x 3. Fig. 11: transversal section of the early ontogenetic stage. Figs. 12–13: transversal sections of the mature stages. Fig. 14: longitudinal section.

Figs. 15–21: Gen. et sp. nov. 1, Central Urals, Schugor River, Orlovka Formation, 'Middle Gates', loc. 7, Sargian Regional Stage, collection of Dr. T.G. Ilyna, Specimen 2899/502, Museum of Paleontological Institute of Russian Academy of Science, Moscow. Figs. 15–17: successive transversal sections of early ontogenetic stages, x 3. Figs. 19–20: successive transversal sections of mature ontogenetic stages, x 2,5. Fig. 21: longitudinal section of specimen 2899/500, x 3; location and residence – the same.

Figs. 22–26: Gen et sp. nov. 2, Central Urals, Schugor River, Orlovka Formation, 'Middle Gates', loc. 31, Sargian Regional Stage, collection of Dr. T.G. Ilyna, Specimen 2899/374, Museum of Paleontological Institute of Russian Academy of Science, Moscow. Figs. 22–23: transversal sections of early ontogenetic stages, x 3. Fig. 24: transversal section of mature stage, x 2. Fig. 25: longitudinal section, x 2. Fig. 26: microstructure of septa with well visible multitrabecular structure. Microstructure of wall possesses features of lamination, x 10.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