
Evolutionary stages of Triassic flora in Siberia (Angarida).

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The Triassic flora of Siberia has been studied from three series of Triassic system in continuous sections. Therefore, its successive alterations and stages in the evolution throughout Triassic from the P/T boundary may be traced. Due to alternation of floristic complexes and marine deposits, the age of floristic complex may be precisely determined. The most ancient complex is studied from Induan deposits. In a single section Permian cordaitean flora is replaced.

In Siberia, the Early Triassic flora is heterogeneous. Two major floras, occupying different ecological niches, are distinguished: the lycopod flora (dominated by *Tomostrobus* and *Pleurometa*) being confined to marine plain, and the conifer fern (*Korvunbanskaya*) flora is distributed within intracontinental areas where intense volcanism had occurred at that time. The Middle Triassic flora is scanty in Siberia. The Early Ladinian flora differs from both the Early Triassic and Late Triassic ones, while the Late Ladinian flora is closely related to the Late Triassic flora.

Key-words—Evolution, Siberian flora, Triassic.

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सारांश

साइबेरिया (अंगारिडा) में ट्राएँसिक वनस्पतिजात की विकासीय अवस्थायें

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साइबेरिया के ट्राएँसिक वनस्पतिजात का तीन लगातार श्रेणियों में अध्ययन किया गया जिसके आधार पर ट्राएँसिक कल्प में इसके विकास के क्रमिक परिवर्तन एवं चरण अन्वेषित किये जा सकते हैं। वनस्पतिजात के स्वरूप में परिवर्तनों एवं समुद्री निक्षेपों के कारण वनस्पतिजात की आयु सुनिश्चित की जा सकती है। सबसे पुराना वनस्पतिजात इन्दुआन निक्षेपों से प्राप्त हुआ है। एक ही खंड में परमियन कोर्डेटियन वनस्पतिजात भी मिला है।

साइबेरिया में प्रारम्भिक ट्राएँसिक वनस्पतिजात मिश्रित प्रकार का है। इनमें लाइकोपोड वनस्पतिजात (*टोमिओस्ट्रोबस* एवं *प्लूरोमिआ* से प्रभावी) समुद्री मैदानों तक सीमित है तथा कोनिफर फर्न (*कोर्वनचान्सकया*) वनस्पतिजात अन्तरामहाद्वीपीय क्षेत्रों में वितरित है जहाँ उस समय अत्याधिक ज्वालामुखीय गतिविधियाँ हुई थीं। साइबेरिया में मध्य ट्राएँसिक वनस्पतिजात बहुत कम मिलता है। प्रारम्भिक लेडीनियन वनस्पतिजात प्रारम्भिक एवं अनंतिम ट्राएँसिक वनस्पतिजातों से भिन्न है जबकि अनंतिम लेडीनियन वनस्पतिजात अनंतिम ट्राएँसिक वनस्पतिजात से घनिष्ठता प्रदर्शित करता है।

THE Triassic flora of Siberia is of great interest for reconstruction of initiation and development of the Mesozoic flora in the Siberian paleofloristic region as well as for global correlation of Triassic sections. Hence, there is a possibility to trace subsequent changes and stages in floral evolution from the P/T boundary to the Jurassic. The presence of marine deposits with ammonites, bivalves in the Triassic sections of Siberia allows accurate age determinations of floristic complexes. The most ancient of these are from the Induan deposits of Lower Triassic. They successively

replace cordaitean flora in the continuous Permian-Triassic sections.

The Early Triassic flora greatly differs from both Permian and Late Triassic floras. It exhibits a combination of paleophytic elements with mesophytic forms being flourishing in Late Triassic and Jurassic (Table 1). The Early Triassic flora composition in Siberia is heterogeneous. Two major plant formations, the Lycopod flora and the conifer-fern flora, were distinguished. They occupied different ecological niches. The Lycopod flora occurred on the eastern margins of the Siberian Platform where in Early Tri-

Table 1—Comparison of Korvunchana flora with Late Permian, Triassic and Jurassic floras

1. Tatarina flora of Russian Platform; 2. Late Permian flora of Siberia; 3. Maltsevo floras of Kuznetsk Basin; 4. Lycopod flora of Siberia; 5. Buntsandstein flora; 6. Keuper flora; 7. Late Triassic flora; and 8. Jurassic flora.

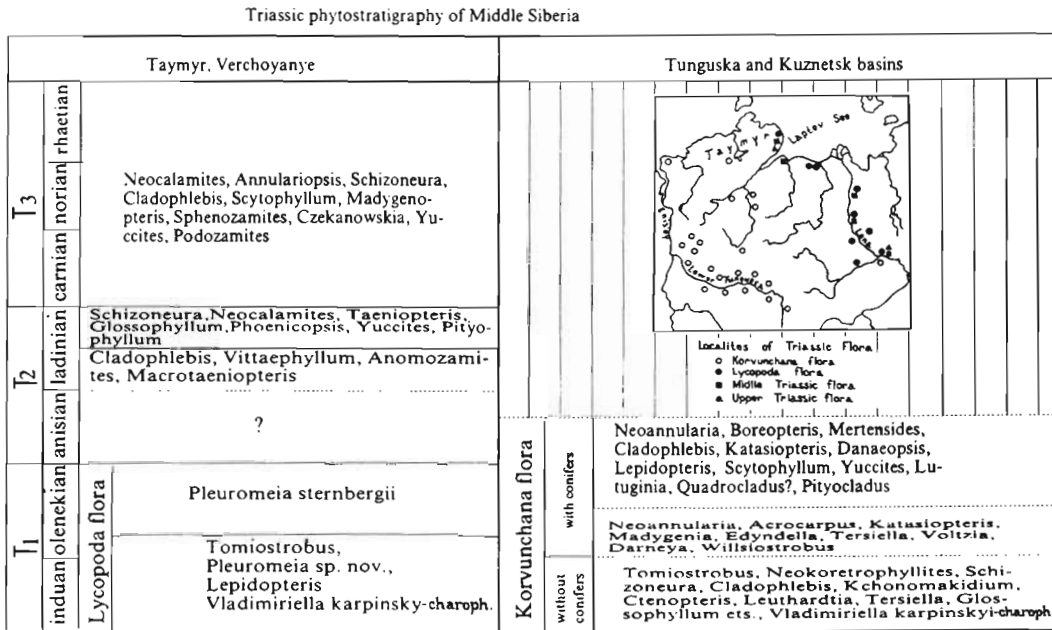
Korvunchana flora	1	2	3	4	5	6	7	8
	P ₁	P ₂	T ₁	T ₂	T _{1,2}	T _{2,3}	T ₃	J
Mesenteriophyllum			+	+		+		
Tomiostrabus			+	+	+			
Neokoretrophyllites		+	+	+				
Gamophyllites		+						
Tschernovia		+						
Phyllothea								+
Neoannularia							+	
Neostachya							+	
Lobatannularia			+				+	
Neocalamites			+				+	
Schizoneura			+			+	+	+
Prynadaia					+	+	+	
Equisetites					+	+	+	
Paracalamites		+	+	+		+	+	
Osmundopsis							+	+
Todites		+	+	+	+	+	+	+
Danaeopsis						+	+	
Boreopteris			+				+	
Mertensides			+				+	
Acrocarpus							+	
Eboracia							+	+
Lobifolia			+				+	+
Cladophlebis		+	+	+		+	+	+
Pecopteris		+	+		+	+	+	+
Sphenopteris		+	+			+	+	+
Katasiopteris			+				+	
Kchonomakidium			+				+	
Prynadaeopteris		+	+				+	
Rhaphidopteris			+				+	+
Madygenia			+			+	+	
Scytophyllum			+			+	+	
Edyndella			+			+	+	
Tersiella-Tatarina	+	+	+				+	
Lepidopteris			+	+		+	+	
Peltaspermum	+		+	+		+	+	
Yavarskiya		+	+				+	
Taeniopteris			+	+	+	+	+	+
Tomia		+	+				+	
Leuthardtia	+					+		
Ctenopteris							+	+
Glossophyllum			+			+	+	
Ginkgo						+	+	+
Sphenobaiera						+	+	
Rhipidopsis		+	+				+	
Izostrobis							+	+
Yuccites			+				+	
Volzia			+	+	+	+	+	
Darneya					+	+	+	
Williamsoniella					+	+	+	
Pityocladus					+		+	
Lutuginia			+				+	
Elatocladus			+	+			+	
Quadrocladus?	+		+				+	

assic existed a marine plain recurrently flooded by the sea. The inland areas of the rest part of Siberia, where active volcanic activity occurred, flourished the conifer-fern flora. Though these floras sharply flourished, differ in dominant elements; they have common elements too.

The principal components of the Lycopod flora are represented by lycopsids *Tomiostrabus* (subgenus of genus *Annalepis* after Dobruskina 1995) and *Pleuromeia* sp. nov., occasional pteridosperms *Lepidopteris* and *Peltaspermum*, individual fragmentary remains of sphenophyta (*Neokoretrophyllites*,

Paracalamites, *Equisetites*), ferns (*Cladophlebis*, *Sphenopteris*, *Kchonomakidium*), cycadophytes (*Taeniopteris*), ginkgophytes (*Rhipidopsis*) and seeds (*Carpolithus*, *Samaropsis*). Floras of such a composition are found in the Induan and Lower Olenekian deposits. In the Upper Olenekian the floral composition changes. It shows an absence of *Tomiostrabus*, and the presence of *Pleuromeia* similar to *P. sternbergii* (Munster) Corda, which is characteristic of the Olenekian-Anisian Buntsandstein flora. Remains of equisetaceous plants (*Paracalamites*, *Neocalamites*, *Equisetites*), ferns (*Cladophlebis*) and pteridosperms (*Peltaspermum*) are rare. No similar plant associations are found in the Middle Triassic. Thus, the Lycopod flora is limited in Early Triassic. This flora substituted the cordaitan one, but inherited less of the latter in composition. The genera *Neokoretrophyllites*, *Paracalamites*, *Sphenopteris*, *Rhipidopsis* are common for both, however, common species are absent in both floras. The evolution of the lycopod flora reveals two stages: (i) biozone containing *Tomiostrabus*, *Pleuromeia* sp. nov., *Lepidopteris*, and (ii) biozone containing *Pleuromeia sternbergii* and no *Tomiostrabus*. The first biozone is of the Induan-Early Olenekian age, the second is of Late Olenekian. A similar stage pattern in the *Pleuromeia* flora evolution is found in China (Wang & Wang, 1982).

The rich and diverse conifer-fern flora, known as the Korvunchana flora, was abundant in Early Triassic of Siberia. It includes almost all primary groups of Mesozoic plants. Its individual elements are present in the Lycopod flora. The Korvunchana flora comprises more elements, common to the cordaitan flora but strongly differs from it in both dominants and composition, and total absence of common species. It already contains many Mesozoic elements a part of which is widely distributed in the younger floras. Most of them reveal their first and the earliest emergence in the geological history, for example, *Lobatannularia*, *Neoannularia*, *Neocalamites*, *Neostachya*, *Acrocarpus*, *Eboracia*, *Mertensides*, *Diplazites*, *Danaeopsis*, *Madygenia*, *Scytophyllum*, *Williamsoniella*, *Leuthardtia*, *Glossophyllum*, *Pityocladus* and others. Some of these genera of the Korvunchana flora are found in the Late Triassic floras of West and East Europe, Middle Asia, China, Vietnam. Furthermore, the Korvunchana and lycopod floras include elements in common with



Text-figure 1—Triassic phytogeography of Middle Siberia.

those of the Buntsandstein flora of Vosges (*Schizoneura*, *Voltzia*, *Darneya*, *Willsiostrobos*, *Elatocladus*, *Yuccites*, *Pleuromeia* and *Tomiostrabus*, the latter being subgenus of the genus *Annalepis*).

The Korvunchana flora evolved distinctly connected to the geological stages of the region (Mogutcheva, 1982), i.e., Tutonchana, Dvurogy, and Putorana. The Tutonchana flora including more than 60 forms shows a wide distribution of arthropytes and pteridophytes associations. Ferns (about 30 species) belong to the genera *Astherotheca*, *Osmundopsis*, *Todites*, *Schvedopteris*, *Lobifolia*, *Cladophlebis*, *Pecopteris* and *Sphenopteris*, *Kchonomakidium*, *Korvunchania* and *Katasiopteris* appeared to be the basic dominant taxa. Arthropytes were less important, but their composition was rather varied. *Neokoretrophyllites*, *Gamophyllites*, *Tschernovia*, *Paracalamites*, *Neocalamites*, *Equisetites*, *Schizoneura* and *Prynadaia* are commonly found. The Tutonchana arthropytes and ferns demonstrate direct relation to the cordaitean, Madygen, Buntsandstein and the younger floras. Pteridosperms such as *Madygenia*, *Rhaphidopteris*, *Leuthardtia*, *Tersiella*, *Peltaspernum* were of limited distribution. Relatively diverse cycadophytes (*Taeniopteris*, *Ctenopteris*, *Yavorskyia*, *Tomia*, *Glossozamites*) and ginkgophytes (*Rhipidopsis*) were of minor importance. The presence of lycosids (*Tomiostrabus* and

Gagariostrobos) and absence of conifers are the peculiar features of the Tutonchana flora.

The major development of the Korvunchana flora took place in the Dvurogy horizon. Conifers *Voltzia*, *Elatocladus*, *Quadrocladus*, *Darneya* and *Willsiostrobos* appeared in this stage for the first time, *Yuccites* were rare as in the Tutonchana flora. Arthropytes reduced in number and diversity; *Neokoretrophyllites*, *Phyllotheca*, *Paracalamites*, *Neoannularia*, *Lobatannularia* were differentiated. Ferns partially changed in species and generic composition. *Acrocarpus*, *Mertensides* and *Boreopteris* appeared for the first time. The last two genera are of significant importance for the younger Putorana flora. In the Dvurogy flora *Madygenia* was widely distributed and *Tersiella* became more abundant in species. Also, the genus *Edyndella* appeared. Cycadophytes (*Taeniopteris*, *Parajacutiella*, *Yavorskyia*) and ginkgophytes (*Rhipidopsis*) were still of little importance. Besides, there were occasional lycosids (*Tomiostrabus*, *Taxhtajanodoxa*) there.

The Putorana flora differs from the Dvurogy flora in different dominant plant groups and in their species composition. Ferns became more abundant and diversified (more than 35 species). Conifers were widely spread. *Pityocladus* and *Lutuginia* also appeared. *Yuccites* occurred more frequently. The specific composition of some conifer genera changed. *Voltzia* was absent.

In ferns, *Cladophlebis* dominated; *Sphenopteris*, *Katasiopteris* were rather diversified; *Boreopteris* and *Mertensides* were common; *Eboracia*, *Eleganopteris* were present. *Arthrophytes* were not abundant, but represented by *Trizygia*, *Lobatannularia*, *Neoannularia*, *Neostachya*, *Phyllotheca* and *Paracalamites*. *Madygenia* was absent in pteridosperms, whereas *Scytophyllum* appeared for the first time. *Cycadophytes* were not widely distributed too and represented by the genus *Yavorskiya*. There were occasional occurrences of *Williamsoniella*. It is the earliest finding of this genus.

The Korvunchana flora appears to be coeval and parallelly evolved with the Lycopod flora. The finding of the *Tutonchana* type flora in the Lower Induan of Verkhoyanye and *Tomiostrubus* in the lowermost Tutonchana horizon (including the Maltsevskaya Formation from Kuzbass) suggests the Tutonchana horizon to be Induan. The Dvurogy horizon is conventionally correlated to the Upper Induan-Olenekian, whereas the Putorana horizon - to the Upper Olenekian and Anisian.

The Lycopod and Korvunchana conifer-fern floras have also genera in common with those of the known European and Chinese floras, that makes possible the comparison of the Siberian Triassic floras with them. The most important of these are *Pleuromeia*, *Tomiostrubus*, *Schizoneura*, *Equisetites*, *Lepidopteris*, *Peltaspermum*, *Glossophyllum*, *Voltzia*, *Darneya*, *Willisostrobos*, and others. There are also genera of the Madygen flora of Middle Asia and similar to the Late Triassic floras of Eurasia.

The Middle Triassic flora of Siberia is very scanty because plant remains in the alluvial Middle Triassic are rare and in small amounts. In Verkhoyanye of the Unguokhtakh R. Basin, the lower Middle Triassic (the Tolbonskaya Formation) is found to contain *Paracalamites* sp., *Neocalamites* sp., *Equisetites* cf. *sixteliae* Mogutch., *Cladophlebis* sp., *Sphenobaiera*? sp., *Yuccites* ex gr. *spathulatus* Pryn. and *Carpolithus* sp. In the upper Middle Triassic partially penetrated into the Karnian there are *Neocalamites carrerei* (Zell.) Halle, *Schizoneura grandifolia* Krysh. et Pryn. *Equisetites* sp., *Podozamites* sp. There is an interesting finding of lycopsids, i.e., *Cylomeia* aff. *undulata* (Burges) White, which indicates a direct relation to the Lycopod flora. There are *Neocalamites uralensis* Tur.-Ket., *Paracalamites* aff. *taradanica* Vlad., *Dictyophyllum*? sp., *Cladophlebis* sp., *Lepidopteris* aff.

strombergensis (Sew.) Town. *Taeniopteris* cf. *ensis* Oldh., *Glossophyllum* sp. and *Podozamites distans* (Presl) Braun in other sections (Dobruskina, 1982). Representatives of both the Early Triassic and Late Triassic floras are present in this assemblage. In northern Siberia plant remains were found in the Ladinian which is also supported by the marine fauna. The Anisian deposits are marine and contain no plant remains.

Two different assemblages were found from the Upper and Lower Ladinian. The first one is derived from the Lower Ladinian in association with marine fauna on the Anabar Bay Coast (Mogutcheva, 1981). Not numerous plants of this assemblage are encountered there, such as *Cladophlebis* aff. *chantajkensis* Mogutch., *Cladophlebis* sp., *Sphenopteris* sp., *Vittaephyllum anabarense* Mogutch., *Anomozamites parvifolius* Mogutch. and *Macrotaeniopteris* sp. The assemblage is characteristic by the presence of pteridosperm *Vittaephyllum* which is one of the typical representatives of the *Scytophyllum* flora of Eurasia, and the presence of cycadophytes *Anomozamites* and *Macrotaeniopteris* uncommon to the Siberian Triassic flora. Just these very peculiarities make the assemblage look unlike the known floristic assemblage of the Siberian Triassic ones but similar to the Middle-Late Triassic flora of Novaya Zemlya (Vassilevskaya, 1984). As a whole, the northern Siberian Triassic is sometimes marked by the increase of cycadophytes in the floras. Thus, in Eastern Taimyr in the vicinity of the Tulai-Kiryak Uplift the following remains were found: *Equisetales* gen. et sp. ind., *Cladophlebis* sp., *Scytophyllum*? sp., *Nilssonia* sp., *Macrotaeniopteris* cf. *novozemelica* Vassil., *Taeniopteris* cf. *kryshstofovichii* Vassil. *Taeniopteris* ex gr. *stenophylla* Krysh., *Taeniopteris* sp., *Phoenicopsis* ex gr. *angustifolia* Heer and *Czekanowskia*? sp. As cycadophytes are dominant in the collection, this assemblage shows a highest similarity to that from Novaya Zemlya and is likely to be close to it in age, i.e., the uppermost Middle Triassic-early Late Triassic.

The second assemblage is known from the Upper Ladinian in the Triassic section on the eastern coast of Taimyr (Mogutcheva, 1982). *Schizoneura grandifolia* Krysh. et Pryn. and *Neocalamites carrerei* (Zeiller) Halle are common there and *Glossophyllum*, *Podozamites*, *Yuccites*, *Phoenicopsis*, *Pityophyllum* are in abundance, whereas *Cladophlebis*, *Adiantopteris*, *Madygenia*, *Scytophyllum*, *Peltaspermum*,

Sagenopteris, *Taeniopteris* are occasional. The generic and species composition of the Late Ladinian assemblage is very close to that of the Late Triassic Siberian flora. The Late Ladinian is most likely to be considered as the onset of the Late Triassic stage in the Siberian floral history. The first appearance of Czekanowskiales (*Phoenicopsis*) and conifers (*Podozamites*, *Pityophyllum*) is in favour of such a consideration. These genera exhibit the widest distribution in the Jurassic flora of the Siberian paleofloristic region.

The Late Triassic flora is typically mesophytic. It is closely related to the Early-Middle Jurassic floras, but its general composition is similar to the Early-Middle Triassic floras. It was studied from Eastern Taimyr and Verkhoyanye. The age of the Taimyr assemblages is strictly dated by the intercalated marine layers in the plant containing deposits and that of the Verkhoyanye is determined through correlation.

In the Carnian deposits of Verkhoyanye, plant remains are not frequent. They are represented only by *Neocalamites carrerei* (Zeiller) Halle, *Equisetites*, *Cladophlebis*, *Madygenopteris irregularis* Sixt., *Phoenicopsis* and *Podozamites*. In the Norian *Cladophlebis* occurs more often and *Cycadocarpidium* is found in good number. Among conifers, *Elatocladus* and *Treematostrobos* occur together with *Podozamites*. Of the Rhaetian, the only one location of plant remains is known. *Cladophlebis nebbensis* (Brongn.) Nath. is dominant there and *Yuccites*, *Borysthenia*, *Podozamites* and *Elatocladus* occur in subdominance.

A more rich assemblage (more than 30 species) was found in the Lower Norian of Taimyr (Mogutcheva, 1982). Conifers (2 species of *Podozamites* and *Yuccites*) and ferns (15 species of *Cladophlebis*) prevail there. *Dictyophyllum* and *Kugartenia irregularis* Sixt. are found. Among Equisetales *Neocalamites carrerei* (Zeil.) Halle is the most abundant, whereas *Annulariopsis* is rare. Pteridosperms (*Scytophyllum*, *Rhaphidopteris*), ginkgo-phytes (*Gingko*), cycadophytes (*Taeniopteris*, *Sphenozamites*) and Czekanowskiales (*Czekanowskia*, *Ixostrobus*) are not common, but *Glossophyllum*, *Yuccites* and *Lepeophyllum* in association with these are rather abundant.

This Early Norian assemblage is similar to the Late Ladinian one but differs in the dominance of ferns, *Yuccites* and *Podozamites* and in the absence of pteridosperms — *Madygenia*.

The Early Norian assemblage shows a closest similarity with the Late Triassic floras of Eastern Ural (Kiritchkova, 1969) and Gorny Altai (Mogutcheva & Batyaeva, 1987). These floras have many species in common (*Cladophlebis crenulata* Kiritch., *C. jolkinensis* Pryn., *C. uralica* Pryn. *Yuccites nanus* and others). They are also similar in the dominance of *Cladophlebis* and in having a close composition of Equisetales, abundant *Yuccites* and insignificant cycadophytes.

Thus, the Siberian flora has little in common with the Late Triassic floras from other regions (Pechora Basin, Southern Priuralye, Kazakhstan, Kirghizia, Southern Primorye, China, Swabland) and, as a whole, greatly differs from these. There are two major stages in the history of the Siberian Triassic flora: (i) Early Triassic and, probably, Anisian, and (ii) Late Ladinian-Late Triassic.

The Early Ladinian flora appears to hold a somewhat isolated position. It considerably differs from both the Late Ladinian flora and the Koryvchana flora, though it has elements in common with them. It is possible that further evidence will suggest a more correct position for this flora.

If the floral evolution during the second stage was progressive, the Koryvchana and Lycopod flora were to have undergone essential reconstructions.

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