DEVELOPMENT OF THE EARLY CRETACEOUS FLORA IN SIBERIA

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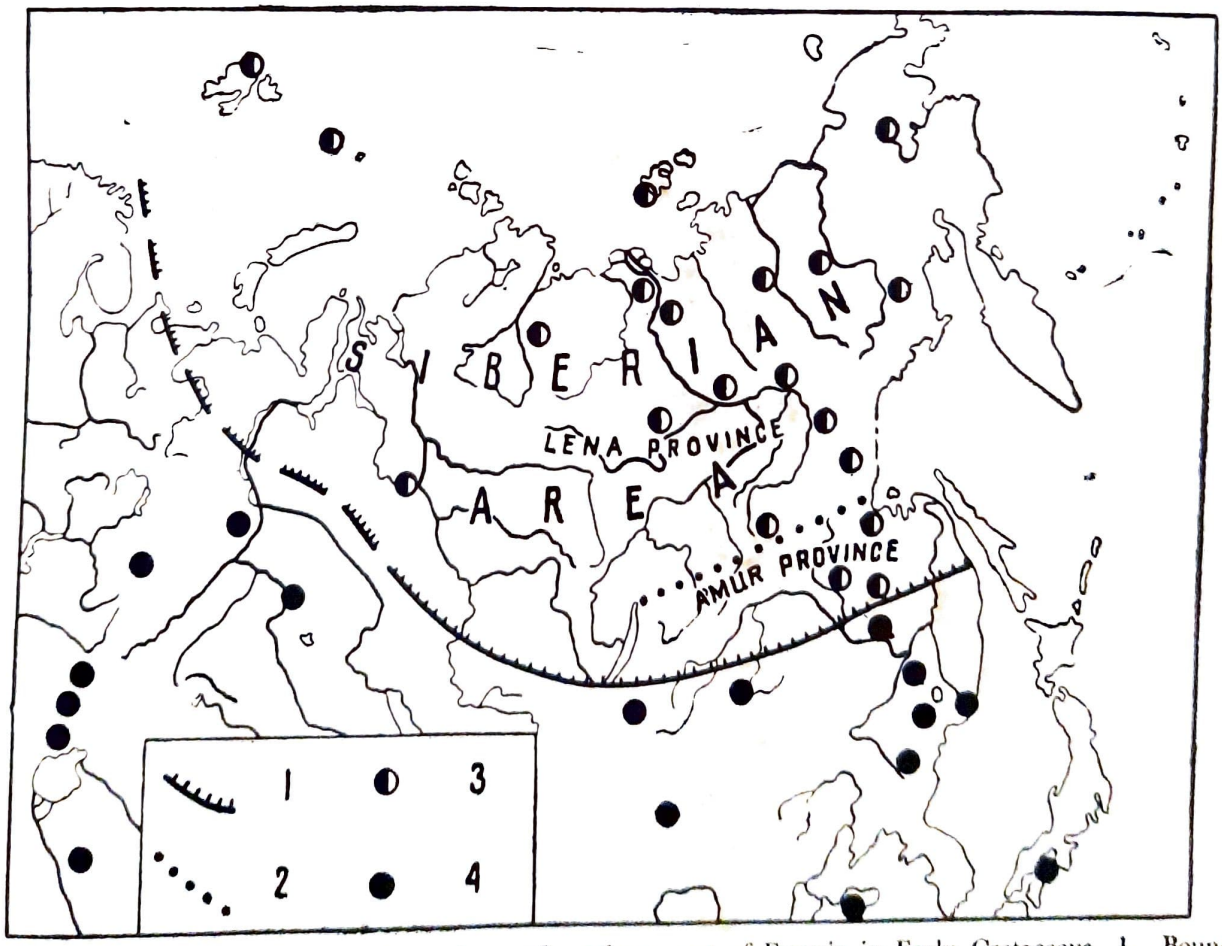
ABSTRACT

There were two palaeofloristic areas in the Early Cretaceous of Eurasia, *i.e.*, Indo-European and Siberian. The latter is divisible into Lena and Amur provinces. In the development of the Early Cretaceous floras of Siberia three main phases, corresponding approximately to the Neocomian, Aptian and Albian, can be recognized. Characteristics of these phases, lists of plants and distribution of plant-bearing beds throughout the various regions are given. Some data on the North American floras of Siberian type are also considered.

Unlike the Early Cretaceous floras of Europe and southern parts of U.S.S.R., which were influenced by aridity, those of Siberia inhabited warm temperate and humid climate. Lobed or dentate leaf segments are characteristic of many Siberian Cycadophytes whereas corresponding Indo-European members possessed entire leaf margins. Humid climate of the Siberian area helped in the survival for a long time of many plants which disappeared in other parts of Eurasia as early as the Late Jurassic or at the beginning of the Cretaceous.

Two paleofloristic areas were located in Eurasia during the Jurassic and Early Creataceous time: Indo-European and Siberian (VAKHRAMEEV, 1966). The boundary between them in the Early Cretaceous passed through the Petchora river and the lower Ob reaches, the southern termination of the Baikal and the lower Amur reaches northwards from Khabarovsk (Text-fig. 1).



Text.-fig. 1. Paleofloristic areas and provinces of northern part of Eurasia in Early Cretaceous. 1. Boundary between Siberian and Indo-European paleofloristic areas. 2. Boundary between Lena and Amur provinces. 3. Main localities of Early Cretaceous floras of Siberian area. 4. Main localities of Early Cretaceous floras of Indo-European area.

Study of the Early Cretaceous floras of the Indo-European areas began in West Europe as far back as in the first half of the XIX century; later the floras were discovered in the USSR, India, China and Japan. Considerably less known are Early Cretaceous floras of the Siberian paleofloristic area being distributed in Siberia and North-East of the USSR only. Investigation of these floras began 20 years ago and is associated mainly with the names of N. D. Vasilevskaya, A. I. Kirichkova, E. L. Lebedev, V. A. Samylina and the author.

Three significant steps can be outlined in the development of the Early Cretaceous floras of Siberia corresponding tentatively to the Neocomian, Aptian and Albian. Neocomian floras are known to be most widespread. Their composition is characterized by predominance of ferns, ginkgos, czekanowskias and conifers. Somewhat less distributed are cycadophytes.

Distribution of various pteridophyte and cycadophyte species within the Siberian area, and to a lesser extent representatives of other plant groups enables to distinguish within it the Lena and Amur paleofloristic provinces. The former province covers the Lena basin and the whole north-eastern part of the USSR. The latter, considerably lesser one, occupies the left shore of the Amur. The boundary between these provinces passes along the Stanovoy Range.

The most complete succession of floras from the Valanginian up to Albian age has been recognized in the Lena coal basin (Vasilevskaya, 1959; Vakhrameev, 1958, 1962; Vasilevskaya and Pavlov, 1963; Samylina, 1963; Kirichkova and Slastenov, 1968; Kirichkova and Budantsev, 1967). Another region where the Neocomian floras are predominantly presented, is the Bureya basin (Vakhrameev and Doludenko, 1961), basins of the Tyl and Uda rivers (Vakhrameev and Lebedev, 1967) and the Zeya river basin (Lebedev, 1965). Abundant Early Cretaceous floras are also described from the Kolyma river basins (Samylina, 1964, 1967). Floras with considerably poorer composition are known to be from the lower Yenisei reaches and the South-Yakut coal basin.

The Early Cretaceous floras of the Siberian area were developing just as the preceding Late Jurassic, under conditions of moderately warm, humid climate that favours intense coal formation. This peculiarity singles out the Early Cretaceous floras of the Siberian area among coeval floras of Europe and southern regions of the USSR, many of them having been influenced by arid climate.

Moderately-warm seasonal climate is also evidenced by a wide distribution of remains of pycnoxylic stems with well pronounced growth rings. Stems of arborescent ferns known from the Cretaceous of West Europe, as well as barrel-shaped stems *Cycadeoidea* in the Siberian area have not been found yet. An abundance in some layers of brachyblasts with *Czekanowskia* and *Phoenicopsis* leaves and *Podozamites* shoots also testifies to seasonal leaves abscission by these trees. In the north of the Lena basin of the Neocomian age is the flora of the Kigilyakh, Kyusyuz and Bulun suites, the latter being confirmed by Valanginian ammonites findings in the lower part of the Kigilyakh suite. In the southern part of the Lena basin the Batylikh suite flora, and in the Bureya basin, the flora of the Solony suite belong to it. To the Aptian can be ascribed floras of the Ogoner-Yuryakh and Eksenyakh suites from north and southern parts of the Lena basin respectively. Suites containing the Albian flora will be discussed below.

Among the ferns that occurred in the Neocomian of the whole Siberian area, the most typical are: *Coniopteris burejensis* (Zal.) Sew., *C. nymphaeum* (Heer) Vachr., *C. saportana* (Heer) Vachr. *C. vsevolodii* E. Lebed., *Hausmannia leeiana* Sze, *Cladophlebis argutula* (Heer) Font., *C. williamsonii* (Brongn.) Brongn. Worth attention is the fact that only the last species of this list is known within the Indo-European area where it can be found in Jurassic deposits.

Species known from the Lena province only are: *Coniopteris setacea* (Pryn.) Vachr., *Gonatosorus ketovae* Vachr., *Cladophlebis pseudolobifolia* Vachr., *C. atyrkanensis* (Heer) Vassil.,

Jacutopteris lenaensis Vassil., and other less distributed species (Table 1). A number of species found within the Amur province are also distributed in the adjacent part of the Indo-European areas (KRASSILOV, 1967). These are *Marattiopsis sp.*, *Klukia exilis* (Phill.) Racib., *Anemia asiatica* Vachr., *Eboracia lobifolia* (Phill.) Thomas, *Nathorstia* sp., *Dictiophyllum* sp., *Lobifolia novopokrovskii* (Pryn.) Rasskaz. et Lebed.

Bennettites and cycads of the Siberian area are extremely peculiar. Only (or almost) within this area are known genera *Neozamites* Vachr. (Bennettitales), *Aldania* Samyl. and *Heilungia* Pryn. (Cycadales), *Butefia* Dobrusk. and *Encephalartites* Vachr. (Cycadophyta). In the Neocomian these are represented by species: *Neozamites verchojanensis* Vachr., *Aldania auriculata* Samyl., *A. umanskii* Vachr. et Lebed., *A. vachrameevii* Samyl., *Heilungia amurensis* (Novopokr.) Pryn., *H. sangarensis* Vassil., *Butefia burejensis* (Pryn.) E. Lebed., *Encephalartites lepzigii* Vachr.

Of special interest are the genera *Aldania* and *Heilungia* that can be attributed to the order Cycadales (concerning structure of epidermis) having pinnate leaves. Most important for both genera is type of venation. Two veins enter the segment near its catadromic side. A shorter one follows the posterior rounded edge of the segment; another, a longer one, is directed upwards, almost parallel to the rachis. The secondary veins (LEBEDEV, 1968) diverge from both the veins inside the segment.

Besides the above-mentioned genera, in the Neocomian of the Siberian area are widespread various *Pterophyllum*, *Nilssoniopteris*, *Ctenis*, *Nilssonia* represented mostly by local species. Among them peculiar are: *Pterophyllum acuta* (Vassil.) Vachr., *P. tyrmensis* (Pryn.) Krassil., *P. pectiniforme* (Pryn.) Krassil., *Ctenis burejensis* Pryn., *C.nana* Samyl., *C. tigyensis* Vassil., *Nilssonia jacutica* Samyl., having dentate margin, and *N. magnifolia* Samyl., and *N. prynadae* Vachr.

In the Lena province, in the right tributary of the lower Aldan river, there has been recently found *Dictyozamites cordatus* (Krysht.) Pryn. that is likely to have penetrated here from the East-Asiatic province of the Indo-European area.

In the Neocomian of the Siberian area abundant are the remains of ginkgos—(*Ginkgo*, *Baiera*, *Sphenobaiera;* in the Amur province—*Pseudotorellia*), czekanowskias (*Czekanowskia*, *Phoenicopsis*) conifers (*Pityophyllum*, *Podozamites*) and seeds of various gymnosperms (*Pityosperum*, *Schizolepis*, *Ixostrobus*, *Stenorachis*, etc.).

A number of species of these gymnosperm groups is considerably less than that of ferns and cycadophytes. This appears to be related to the fact that morphological variety of leaves of ginkgos, czekanowskias and conifers is not great, and the species distinguished by paleobotanists are based, as a rule, on leaf remains. Study of cuticles of Ginkgoales, Czekanowskiales and conifers has revealed a great diversity of epidermal structures as compared to morphological variety of leaves. This will enable in the future to distinguish a larger number of species especially among such genera as *Ginkgo*, *Phoenicopsis*, *Pityophyllum*.

The other reason may be accounted for by the fact that under conditions of moderately warm climate peculiar to the Siberian area in the Early Cretaceous, the variety of species among arborescent plants is always less than that of herbs and shrubs. As mentioned above, there are good reasons to believe that ginkgos, czekanowskias and conifers were represented by arborescent, often large, forms, whereas an underbrush consisted of various herbaceous ferns and short bennettites and cycas.

Among Neocomian conifers the genus *Rhipidiocladus* Pryn., should be mentioned that has been found up till now within the Siberian area only.

At the beginning of the Aptian the composition of the Siberian flora underwent changes. A new genus *Arctopteris* (*A. kolymensis* Smayl., *A. rarinervis* Samyl.) appears, which is native to the Lena province, and representatives of *Asplenium* (*A. dicksonianum* Heer, *A. rigidum* Vassil.)

and *Adiantopteris* (*A. gracilis*, *A.* aff. *sewardii* Yabe.) Representatives of *Onychiopsis* and *Gleichenia* (=*Gleichenites*), widespread in the Indo-European area, penetrated into the Siberian area, their occurrences however, being rather scarce.

Along with the appearance of new forms in the Aptian, many fern species become extinct (Table 1). Cycadophytes become scarce, *Aldania* disappears, and variety of *Pterophyllum* decreases sharply. Composition of *Ctenis* is changed considerably. Among other gymnosprems of the Aptian floras is present *Ginkgo* ex gr. *adiantoides* (Ung.) Heer which can be observed together with *Coniopteris onychioides* in small amounts already in the upper part of the Neocomian.

In the Aptian we find *Parataxodium jacutense* Vachr. Especially diverse are *Podozamites*; among these worth attention are *P. reinii* Geyl., *P. gracilis* Vassil.

Reconstruction of Aptian floras was carried out on the basis of plant remains localities in the Lena province, since the floras of this age in the Amur province are represented not fully enough yet.

The younger floras whose age being determined by me as the Albian, are very closely related to the floras of the Aptian, and therefore they cannot always be well distinguished from one another. Appearance of angiosperms serves as the main characteristic feature of the Albian floras. There are many data, however, showing that their appearance in various regions of the paleofloristic area of Siberia, as well as in the other parts of the Earth, did not take place simultaneously.

This asynchronism may be likely seeming and depend on conditions of burial of plant remains. In the Albian age the angiosperms were not yet a predominant plant group, as they became at the beginning of the Late Cretaceous. Up till now we have no reliable data for elucidation of conditions for the growing plant assemblages including the first angiosperms.

Many palaeobotanists, including the author, believe that the latter grew on upland conditions instead of lands where accumulation of continental sediments took place. If this point of view is true, appearance of angiosperm remains in continental deposits depended on a number of causes. In many localities of plant remains the absence of angiosperms may be accounted for by the fact that they did not grow near by owing to unfavourable conditions (absence of suitable relief producing favourable microclimate). When leaves of angiosperms are transported from more remote regions by water flows, they could have been ground and transformed into small fragments.

Remains of older angiosperms, known at present in the Siberian area, seem to be associated to the Buor-Kemiuss suite protruding along the Zyryanka river, the left tributary of the Kolyma river. Here there were found remains of undoubtful angiosperms mainly represented by small-leaved forms, together with Early Cretaceous ferns peculiar to Aptian deposits of the Lena basin (*Coniopteris onychioides*, *Onychiopsis psilotoides*, etc., and various *Nilssonia*, *Ginkgo*, *Baiera*, *Sphenobaiera*, *Phoenicopsis*, *Czekanowskia* and *Podozamites*).

Hence are described representatives of genera *Ranunculaecarpus*, *Cercidiphyllum*, *Crataegites*, *Dalbergites*, *Celastrophyllum*, *Cariopsis*. The list of species is given in the paper by Samylina (1968). Samylina believes that the age of the Buor-Kemyuss suite could embrace the time from the Late Aptian to Middle Albian inclusive. On the right shore of the Kolyma river are developed the Omsukchan and overlying it Toptan suites. In the lower of them composition of ferns and gymnosperms is similar to the type composition from the Buor-Kemyuss suite of the Kolyma left shore. Here are encountered fruit of angiosperms *Kenella harrisiana* Samyl., as well as conifers *Cephalotaxopsis magnifolia* Font. and *Elatocladus manchurica* (Yok) Yabe. This flora seems to have the same age as the flora from the Buor-Kemyuss suite.

A considerable amount of ferns and gymnosperms disappear when passing to the Toptan suite; these ferns and gymnosperms belong mostly to the forms that had appeared as early as the Neocomian. Preserved are *Onychiopsis sp.*, *Coniopteris onychioides*, *Asplenium dicksonianum*, *Elatocladus manchurica*, i.e., the species that appeared approximately from the Aptian or the very end of the Neocomian. Along with them were found certain conifers, *Elatocladus smittiana* (Heer) Sew., and *Sequoia fastigiata*, that had developed in the Late Cretaceous already, and angiosperms: *Cinnamomoides ievlevii* Samyl., *Nelumbites* aff. *minimus* Vachr., *Celastrophyllum* aff. *hunteri* Ward, *C. serrulatus* Samyl. Samylina (1968) regarded the age of the Toptan suite as the Late Albian.

In the Lena basin the angiosperms were encountered in deposits of the Khatyryk suite, occurring above the Eksenykh suite that contains the Aptian plant assemblages. Unlike the latter, in the Khatyryk suite there appear angiosperms: *Prototrochodendroides jacutica* Budants. et Kiritchk., and *Morophyllum dentatum* Budants. et Kiritchk., as well as conifers—*Cyparissidium gracila* Heer being widespread in the Late Cretaceous. At the same time in the Khatyryk suite somewhat decreased is diversity of ferns and cycadophytes. The composition of the latter is confined to various *Nilssonia* and two species of *Neozamites* only.

In coeval deposits of the Ukin suite developed in the north of the lower Lena no remains of angiosperms were found despite a very similar composition of ferns and gymnosperms.

The Boskhin suite flora overlying the Khatyryk suite (Kirichkova, 1970) may have the Late Albian or even Early Senomanian age. Only sporadic ferns were found in it (*Coniopteris sp.* and *Asplenium dicksonianum* Heer), cycadophytes being absent at all. Among conifers some forms were found that appeared in the second half of the Early Cretaceous, many of them being still widely spread in the Late Cretaceous. To these belong: *Cephalotaxopsis heterophyalla* Holl., *Parataxodium wigginsii* Arnold et Lowt., *Sequoia fastigiata* Heer, etc. Rather numerous were reprints of angiosperm leaves, a part being determined up to a genus only, owing to their poor preservation. Hence the following can be recorded: *Delbergites sp.*, *Crataegites cf. borealis* Samyl., *Celastrophyllum ovale* Vachr., *C. kolymensis* Samyl., *Cissites spp.*, *Dicotylophyllum spp.* (Kirichkova, 1970).

Comparison of the Early Cretaceous floras of the Indo-European and Siberian areas reveals considerable differences between them. The Early Cretaceous of the Indo-European area is characterized by ferns *Weichselia*, *Onychiopsis*, *Ruffordia*, *Gleichenia*,*Nathorstia* distributed from England up to the Pacific Ocean, as well as cycadophytes: *Zamites*, *Otozamites*, *Dictyozamites*, *Ptilophyllum*, *Cycadites*. Up till now no *Weichselia*, *Zamites*, *Otozamites*, *Ptilophyllum* have been found in the Siberian area. However, findings of representatives of other genera are sporadic and tend to occur mostly towards its southern margin.

Among ferns of the Siberian area widespread are various *Coniopteris* species. This genus, so common for the Middle Jurassic of the Indo-European area, began to disappear rapidly from its territory at the beginning of the Late Jurassic, probably due to aridization of climate. By the beginning of the Early Cretaceous it was preserved in the north of the East-Asiatic province only that was directly adjacent to the Siberian area, and in small numbers in India.

However, in the Siberian area in the Late Jurassic and Early Cretaceous a new burst of *Coniopteris* speciation took place, it being represented here by almost 20 new species. New genera of ferns appeared here as well, e.g., *Arctopteris* and *Jacutopteris*.

Cycadophytes of the Siberian area are extremely peculiar; their composition is characterized by some genera which are either not known at all outside the area (*Aldania*, *Butefia*, *Encephalartites*, *Heilungia*, *Jacutiella*), or have penetrated in the adjacent East-Asiatic province of the Indo-European area (*Neozamites*).

Comparison of specific composition of ferns and cycadophytes presented by genera

common for the Siberian and Indo-European areas (*Adiantopteris*, *Coniopteris*, *Cladophlebis*, *Eboracia*, *Ctenis*, *Nilssonia*, *Pterophyllum*, etc.) shows that there are very few common forms between them.

There are certain species among cycadophytes of the Siberian area whose leaf segments have dentate or lobed margins. Among these are *Aldania umanskii* Vachr. et Lebed., *A. vachrameevi* Samyl., *Neozamites verchojanensis* Vachr., *Encephalartites leipzigii* Vachr., *Nilssonia prynadae* Vachr. and *N. jacutica* Samyl., described during the last decade. Cycadophyta leaves from the Indo-European area have very seldom dentate or lobed margins (only in *Nilssonia*).

Regularity supposed in distribution of cycadophytes with various leaf types can be correlated to the regularity that was established long ago for dicots. It is known that in tropics and subtropics among arborescent dicots prevail forms with entire-margined leaves, whereas in a moderate zone they give way to dicots with leaves having lobed or dentate margins.

With beginning of Late Jurassic, ginkgos and czekanowskias, that were widespread almost throughout Eurasia, remain predominant in the Siberian area only. In the Early Cretaceous representatives of their genera, but *Ginkgo* itself, disappear almost completely from the Indo-European area. Even in the Lower Cretaceous of the South Primorye and North China these groups are represented by sporadic remains of *Baiera*, *Sphenobaiera*, *Czekanowskia*.

In the Early Cretaceous of the Siberian area representatives of these groups still prevail in plant composition along with such conifers as *Podozamites* and *Pityophyllum* (Pinaceae ?). This can be evidenced by a great number of remains of these plants found in Lower Cretaceous deposits of East Siberia and North-East of the USSR.

The above material shows a quite extraordinary position of Early Cretaceous floras of the Siberian paleofloristic area among coeval floras of other Eurasian regions. The whole complex of palaeobotanical, palaeozoological and lithological data enables to confirm that they were developing under conditions of stable moderately-warm and humid climate.

In the Siberian area many ferns and Ginkgoales found their last refuge, as well as *Nilssonia* and czekanowskias that had been growing in the Jurassic almost throughout Eurasia and became extinct on vast territories in the Late Jurassic and at the beginning of the Early Cretaceous. The main cause of this extinction was formation of the belt of arid climate and its influence on climate of neighbouring territories (Vakhrameev, 1964).

In North America the analogues of the floras of the Siberian area are floras of Canada (Bell, 1956) and especially that of Alaska. Study of the latter has just begun (Smiley, 1969 a, b). Preliminary identifications, however, testify to the presence in them of certain peculiar representatives of Early Cretaceous floras of the Siberian area (*Arctopteris*, *Neozamites*, *Jacutiella*). In Alaska, as well as in the Lena province, *Czekanowskia rigida* Heer and *Phoenicopsis angustifolia* Heer remain up to the Albian.

The main cause that determined peculiarity of the Early Cretaceous floras of Siberia and similar floras of Alaska and West Canada, was climatic zonation. The influence of the latter on distribution of floras of various composition in the north hemisphere was well pronounced as early as the Carboniferous (Vakhrameev, Dobruskina, Zaklinskaya and Meyen, 1970).

Table 1—The distribution of some typical fossil plants of Siberian area in Early Cretaceous

Name of Plants	Age		
	Neocomian	Aptian	Albian
	1	2	3
Ferns:			
Adiantopteris gracilis Vassil. (×)		—	
A. polymorphus Vassil. (×)			—
Arctopteris lenaensis Vassil. (×)		—	
A. rarynervis Samyl. (×)		—	—
A. kolymensis Samyl. (×)		—	—
Asplenium dicksonianum Heer			—
A. rigidum Vassil. (×)		—	—
Cladophlebis argutula Heer	—		
C. lenaensis Vachr. (×)	—		
C. pseudolobifolia Vachr. (×)	—	—	—
C. sangarensis Vachr. (×)	—	—	
Coniopteris burejensis (Zal.) Sew.	—		
C. nympharum (Heer) Vachr.	—	—	—
C. onychioides Vassil. et K.-M.	—	—	—
C. setaceae (Pryn.) Vachr. (×)	—		
C. saportana (Heer) Vachr.	—	—	
C. vachrameevii Vassil. (×)		—	—
Jacutopteris lenaensis Vassil. (×)	—		
Gleichenia lobata Vachr. (×)	—	—	
Gonatosorus ketovae Vachr. (×)	—		
Onychiopsis elongata (Geyl.) Yok.		—	—
Cycadophyta:			
Aldania auriculata Samyl. (×)	—		
A. umanskii Vachr. et E. Lebed. (×)	—	—	
A. vachrameevii Samyl. (×)	—		
Anomozamites arcticus Vassil. (×)		—	—
A. angulatus Heer	—	—	
Ctenis burejensis Pryn.	—		
C. nana Samyl. (×)	—		
C. tigyensis Vassil. (×)	—		

Name of Plants	Age		
	Neocomian	Aptian	Albian
	1	2	3
Heilungia amurensis (Novopokr.) Pryn.	—	—	
H. sangarensis Vassil. (×)	—		
H. sobopolensis E. Lebed. (×)		—	
Jacutiella amurensis (Novopokr.) Samyl. (×)	—	— ? —	
Neozamites verchojanensis Vachr.	—	—	—
Nilssonia jacutica Samyl. (×)		—	
N. lobatidentata Vassil. (×)..	—		
N. prynadae Vachr.		—	—
Pterophyllum acuta (Vassil.) Vachr. (×)..	—		
P. polynovii (Pryn.) Krassil...	—		
P. tyrmensis (Pryn.) Krassil	—		
Ginkgoales:			
Ginkgo paraadiantoides Samyl.	—	—	—
G. polaris Nath. (×)		—	—
Sphenobaiera angustiloba Heer	—	—	—
S. flabellata Vassil. (×)		—	—
Czekanowskiales:			
Czekanowskia rigida Heer	—	—	—
Phoenicopsis angustifolia Heer	—	—	—
Coniferales:			
Cephalotaxopsis borealis Samyl.		—	—
Cyparissidium gracile Heer			—
Parataxodium spp.		—	—
Podozamites gracilis Vassil. (×)		—	—
P. gramineus Heer	—	—	—
P. reinii Geyl.		—	—
Rhipidiocladus flabellata Pryn.	—		
Angiospermae—mainly forms with small leaves		—	—

(x) Only in Lena province.

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