CLIMATIC CHANGES IN EASTERN ASIA AS INDICATED BY FOSSIL FLORAS. I. EARLY CRETACEOUS

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ABSTRACT

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The most important data for the reconstruction of Mesozoic cliseres are the life-form statistics, the phytosociological criteria and the dynamic criteria (i.e., the displacements of isoflores, the altitudinal migrations, etc.). The succession of fossil-plant assemblages in South Primorye as well as in the Bureja basin indicates a rise of temperature during the Late Jurassic Epoch up to Berriasian time, the cooling from Valanginian to Barremian and the amelioration of climate in the Aptian followed by the fall of temperatures in Albian time.

INTRODUCTION

Since Kobayashi (1942) there were few attempts to correlate the succession of Mesozoic taphofloras of Eastern Asia with climatic changes. New information on this subject has been provided by rapidly accumulating fossil records. Different methods have been applied to the climatic interpretation of taphofloras. The most important are briefly considered below.

(1) Extrapolation. This group of methods has been based on the assumption that the past conditions may be inferred from tolerance ranges of living populations of the same (or allied) species or their associations. Several refined methods of extrapolation have been proposed by Iversen (1944), Szafer (1946), Fuji (1969), Gritchuk (1969), and others. However, this "transferred palaeoecology" (Lawrence, 1971) is hardly applicable for Mesozoic plants which comprise no living species and only few extant genera.

(2) Morphological criteria. The correlation of morphology and dimensions of angiosperm leaves with climatic conditions has been demonstrated by Bailey and Sinnot, Raunkiaer and other authors (see Axelrod and Bailey, 1969). The annual rings, the Equisetalean stem diameter, the fern-frond dimensions, the degree of dissection of Ginkgoalean leaves and other climate-dependent characteristics of Mesozoic plants

have been listed by Dorf (1969). Among the epidermal characteristics the frequency of stomata and the development of adaxial stomata in proportion to abaxial ones are the most useful indicators of water regime (the thick cuticle, sunken or protected stomata and other "xeromorphic" features are of minor importance in this respect).

The ambiguity of morphological phenomena (e.g., similar leaf-size reduction in arid, alpine or oligotrophic situations) and the changes of their meaning (e.g., cauliflory in tropical plants is now correlated with chiropterophily; its former adaptive meaning is unknown) cast some limitations on this class of criteria.

(3) Chronocline. In some cases information on the climatic changes is provided by similarity between the topoclinal and chronoclinal variation. Thus, the analogy between the sequences of Madro-Tertiary chronospecies and the clines of their modern equivalents suggests the similarity of temporal and spatial climate gradients (Axelrod, 1941, 1948).

(4) Life-form statistics. Raunkiaer (1934) has classified Earth climates according to the quotients of different life forms (e.g., hemicryptophyte climate or chamaephyte climate). Such quotients may be used also for classification of palaeoclimates (e.g., "*Stigmaria* climate" or "cycadophyte climate") as well as for the reconstruction of cliseres.

(5) Phytosociological criteria. The most important criteria applicable to all taphofloras, irrespective of their geological age, are the species diversity (species number per number of specimens), the generic index, the dominance index (the percentage of dominants out of the total species number) and the homogeneity index (the number of localities with different dominant species in proportion to the total number of localities). As a rule, all these indices have higher values for humid tropical forest vegetation than for temperate.

(6) Palaeophenological criteria. Heer, Goeppert, Weber and other classical authors persistently attempted to determine the season of burial of plant remains. Later it became evident that any information on the season of burial, as well as on the seasonal changes of vegetation, might be obtained only from the distribution of plant material within seasonally laminated sequences. The indications of periodicity of growth (e.g., variations of pinnae dimensions in *Neuropteris praedentata* – Potonié, 1953) has little bearing on the reconstruction of climatic conditions, since autonomous growth rhythms are inherent to many plants of the tropical rain forest (Walter, 1964).

(7) Dynamic criteria. The changes of climate are responsible for displacements of isoflores (Chaney, 1940) and altitudinal migrations of plant communities. The upland–lowland migrations bring some plant communities nearer to the site of deposition. That is why they are manifested by pronounced variations in frequency of fossil species.

(8) Historical criteria. The increase or decrease in proportions of certain "floristic elements" (Axelrod, 1960) or the exotic/local genera ratio (Wolfe and Barghoorn, 1960) may evidence the climatic changes.

Although any judgements on palaeoclimates depend upon a whole complex of criteria only (4) the life-form statistics, (5) the phytosociological criteria and (7) the dynamic criteria are the most readily applicable for the reconstruction of Mesozoic cliseres.

The Early Cretaceous taphofloras of the Soviet Far East rank among the richest fossil-plant localities of the world. They are distributed to the north of Vladivostok (Primorye territory) and along the Amur and its tributaries (Zeja, Bureja and other rivers) see Fig.1.
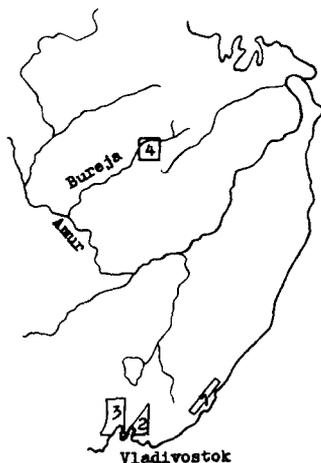

Fig.1. Map of the Upper Jurassic—Lower Cretaceous plant-bearing deposits: *1* = Berriasian deposits with the Taukhe flora, *2* = Sutschan basin, *3* = Sujfun basin, *4* = Bureja basin.

The floras of South Primorye and the Bureja River are the most important. The former is of "Wealden" (subtropical) aspect while the latter is of "Siberian" (temperate) aspect. These floras will be considered below.

SOUTH PRIMORYE

The Upper Jurassic deposits of South Primorye are predominantly marine and contain few plant remains, whereas the Lower Cretaceous beds comprise numerous plant localities (Krassilov, 1967). They are:

(1) Taukhe flora of Berriasian age. This fossil flora is confined to a thick series of alternating sandstones and siltstones outcropping along the coast of the Sea of Japan about 160 km to the north of Vladivostok. The age is based on marine invertebrate fossils — *Neocomites, Berriasella*, etc. The principal plant species are *Alsophilites nipponensis* (Oishi) Krassil., *Coniopteris burejensis* (Zal.) Sew., *Onychiopsis psilotoides* (Stokes et Webb) Ward, *Sphenopteris nitidula* (Yok.) Oishi, *Zamiophyllum buchianum* (Ett.) Nath., *Nilssonia schaumburgensis* (Dunk.) Nath.

Several kilometers to the north there are outcrops of chiefly non-marine beds containing similar plant remains (Sibajgow flora). In addition to the above-listed species, these localities have *Ruffordia goeppertii* (Dunk.) Sew., *Sagenopteris petiolata* Oishi, *Dictyozamites falcatus* (Morris) Medl. et Blanf., *Otozamites klipsteinii* (Dunk.) Sew, *Ctenozamites* sp., *Brachyphyllum* aff. *expansum* (Sternb.) Sew. (25 species in total).

(2) Popov Creek flora of Valanginian age. The sandstones and shales of Valanginian age (Klutschevskaya Formation) are exposed along the upper reaches of the Sutschan

River and further to the north. The plant fossils from these beds are found in association with several index species of *Aucella* and other invertebrates. Among the plants occurring at Valanginian localities the fern leaves *Alsophilites nipponensis* (Oishi) Krassil., *Onychiopsis psilotoides* (Stokes et Webb) Ward and *Cladophlebis novopokrovskii* Pryn. predominate. The gymnosperm fossils are comparatively rare, only *Dictyozamites kawasakii* Tateiwa and *Podozamites* sp. are locally abundant. These assemblages probably represent fern-dominated coastal marsh communities.

(3) The Nicanian flora of Barremian–Albian age. This flora is confined to the series of predominantly fresh-water deposits named after the ancient Nican settlement at Primorye. Along the upper reaches of the Sutschan River these beds rest uncomformably upon the Valanginian strata and are probably separated from them by a considerable time interval. The Nican beds fill two depressions – the Sutschan sedimentary basin to the east and the Sujfun basin to the west. They are subdivided into three parts roughly corresponding to Barremian, Aptian and Albian stages. The age assignments are based on mega- and microfossil evidence (Verbizkaya, 1965; Krassilov, 1967). Both lower and middle members are coal-bearing and the upper one is essentially tuffaceous. At Sutschan basin the Upper Nicanian strata intercalate with *"Trigonia* beds" containing marine fauna of Albian age.

The fossil plants are collected from numerous outcrops and boreholes. There are considerable differences between contemporaneous Sutschan and Sujfun fossil floras. The former represents maritime plant assemblages dominated by Taxodiaceous conifers while the latter is rich in cycadophytes and reflects a less humid situation. The climatic differences are probably imposed by elevations separating the Sutschan and Sujfun depressions and casting a rain shadow on the latter area.

The Early Nicanian plants at Sujfun basin are *Weichselia reticulata* (Stokes et Webb) Ward, *Adiantopteris yuasensis* (Oishi) Krassil., *Hausmannia kohlmannii* Richter, *Gleichenites zippei* (Corda) Sew., *Cladophlebidium dahuricum* Pryn., *Nilssoniopteris rhitidorachis* (Krysht.) Krassil., *Ptilophyllum bajulae* Krassil., *Nilssonia densinervis* (Font.) Berry, *N.* ex *gr. brongniartii* (Mant.) Dunk., *Elatides asiatica* (Yok.) Krassil., *Araucariodendron oblongifolium* Krassil., and some other species. Near Vladivostok the Early Nicanian assemblages comprise numerous remains of Pinaceae (*Pityocladus, Pityostrobus, Pityospermum*). These localities have probably been deposited nearer to the slopes of ancient elevations. At Sutschan basin the contemporaneous localities (the old Sutschan flora) are enriched by *Polypodites verestchaginii* Krassil., *Athrotaxites sutschanicus* Krassil., *Zamiopsis dentata* (Font.) Berry and other species.

The extensive collections of Middle Nicanian flora at Sujfun basin comprise *Nathorstia pectinata* (Goepp.) Krassil., *Matonidium goeppertii* (Schimp.) Schenk, *"Polypodites"* (*Cyathea*) *polysorus* Pryn., *Gleichenites gieseckianus* (Heer) Sew., *G. porsildii* Sew., *Gleicheniopsis sujfunensis* Krassil., *Asplenium samylinae* Krassil., *Cladophlebis frigida* (Heer) Sew., *Caytonia orientalis* Krassil., *Zamiophyllum buchianum* (Ett.) Nath., *Z. ivanovii* (Krysht. et Pryn.) Krassil., *Subzamites borealis* (Heer) Halle, *Dictyozamites grossinervis* Yok., *Pterophyllum manchurense* (Oishi)

Krassil., *P. sutschanense* Pryn., *Cycadites sulcatus* Krysht. et Pryn., *Nilssoniopteris rhitidorachis* (Krysht.) Krassil., *Doratophyllum sulcatum* (Pryn.) Krassil., *Ctenis latiloba* Krysht. et Pryn., *C. yokoyamae* Krysht., *Nilssonia nicanica* Pryn., *Zamiopsis sujfunensis* (Krysht. et Pryn.) Krassil., *Araucariodendron angustifolium* Krassil., *A. heterophyllum* Krassil., *Podocarpus* (*Stachycarpus*) *harrisii* Krassil., *P.* (*Nageja*) *sujfunensis* Krassil., *Athrotaxites berryi* Bell, *Athrotaxopsis expansa* Font., *Elatides asiatica* (Yok.) Krassil., *E. curvifolia* (Dunk.) Nath., *Cephalotaxus ussuriensis* Krassil., *Torreya nicanica* Krassil. The majority of them are locally abundant. Only *Athrotaxites berryi*, *Elatides curvifolia* and few other species are abundant at several localities.

The diversity of fossil assemblages suggests the very complex structure of the Aptian vegetation. There are at least three types of cycadophyte-dominated assemblages:

(a) *Nilssoniopteris* assemblages; come from coal-bearing facies; comprise *Cladophlebis frigida, Nilssoniopteris rhitidorachis, Athrotaxites berryi, Cephalotaxus ussuriensis*; swamp habitat is suggested;

(b) *Zamiophyllum* assemblages; come from the coarse arkoses below the main coal seam; comprise large leaves of one or two *Zamiophyllum* species, crowded and overlapping, mixed with *Subzamites, Nilssonia* and a few conifers (such as *Podocarpus* and *Athrotaxites*); probably represent stream-border habitats;

(c) *Ctenis–Cycadites* assemblages; come from the fossiliferous siltstone layer just above the main coal seam (i.e., near the top of the Middle Nicanian Member); the diversity of ferns (*Gleichenites, Gleicheniopsis, Nathorstia, Matonidium*), cycadophytes (*Pterophyllum, Cycadites, Nilssoniopteris, Doratophyllum, Ctenis*) and conifers (*Araucariodendron, Podocarpus, Cephalotaxus, Torreya, Athrotaxites*) is at maximum; presumably correspond to the flood-plain communities.

It is worth mentioning that the majority of conifer genera which occur in cycadophyte assemblages (i.e., *Podocarpus, Athrotaxis, Cephalotaxus, Torreya*) are known as small trees or shrubs. It is evident that cycadophyte assemblages represent a vegetation different from Araucariaceae–Taxodiaceae-dominated forests. I think of chaparral as a probable modern equivalent.

The earliest angiosperm records at Sujfun basin are confined to *Ctenis–Cycadites* assemblages. They are *Pandanophyllum ahnertii* Krysht., presumably monocot leaf remains from the northern part of Sujfun depression and the *Onoana nicanica* fruits from its southern periphery.

At Sutschan basin the Middle Nicanian beds (or North Sutschan Formation) contain *Ostrea* shells which indicate the close proximity of a sea margin. The Middle Nicanian assemblages are dominated by *Athrotaxopsis expansa* and *Elatides asiatica*. A contrast between the abundance of these conifers at Sutschan basin and their sparse occurence at Sujfun localities may be explained by comparison with plant distributions on the slopes of the modern Sikhote-Alin Mountains. The same tree species grow at lower levels on the east (coastal) slopes than on the west (interior) ones. Analogous distribution on the slopes of the Aptian elevations which separated the Sujfun and Sutschan depressions and

provided plant debris to both would result in pronounced differences in abundance of certain plant fossils.

The first Sutschanian angiosperm, *"Aralia" lucifera* Krysht. came from the upper part of the North Sutschan Formation, approximately at the same level as the Sujfunian *Pandanophyllum* and *Onoana.*

The Upper Nicanian beds at the north of Sujfun basin are green tuffaceous sandstones. Plants occur in thin layers of yellow-grey shales. The principal species are *Teilhardia tenella* (Pryn.) Krassil., *Cladophlebis virginiensis* Font., *Adiantopteris grossidentata* Pryn., *Neozamites denticulatus* (Krysht. et Pryn.) Vachr., *Nilssonia densinervis* (Font.) Berry, *Ginkgo pluripartita* (Schimp.) Heer, *Elatides asiatica* (Yok.) Krassil., *Athrotaxopsis expansa* Font., *Podozamites tenuinervis* Heer. Several angiosperm remains — *Trochodendroides* (*"Cercidiphyllum"*) *sujfunensis* Krassil., *Laurophyllum* sp. and *Dicotylophyllum* sp. are collected from these localities.

At the southern margin of Sujfun basin, near Vladivostok, the Upper Nicanian Member comprises thick bodies of unsorted gravels and conglomerates which indicate the proximity of elevations. Several miles to the west, along the Amba River (south-western border of Sujfun basin) the Upper Nicanian beds are again fine-grained sandstones and siltstones containing rich plant localities. These Amba localities provided numerous leaves of cycadophytes: *Dictyozamites cordatus* (Krysht.) Pryn., *Pterophyllum pterophylloides* (Pryn.) Krassil., *P. sutschanense* Pryn., *Neozamites denticulatus* (Krysht. et Pryn.) Vachr., *Ptilophyllum* sp., *Cycadites sulcatus* Krysht. et Pryn. and *Nilssonia densinervis* (Font.) Berry.

At Sutschan basin the beginning of the Upper Nicanian stage was marked by marine incursion (*Trigonia* sandstones) followed by deposition of black shales with abundant lacustrine invertebrates and fishes. The plant fossils occur occasionally in the *Trigonia* beds as well as in the black shales. More numerous and better-preserved specimens come from the fine-grained coaliferous sandstones 70 m thick which are transitional between the marine and lacustrine deposits. They contain the angiosperm leaves *"Aralia" lucifera* Krysht., *Cissites prodromus* Krysht., *"Sassafras" ussuriensis* Krassil., *Sapindopsis angusta* (Heer) Sew., *Artocarpidium* sp. together with *Onychiopsis psilotodes* (Stokes et Webb) Ward, *Pelletieria ussuriensis* (Pryn.) Krassil., *Cycadites* sp., *Elatides asiatica* and other Nicanian species. Angiosperms occur at approximately the same level as at Sujfun Upper Nicanian localities.

It is worth mentioning that the Albian angiosperm leaves from Sutschan basin are compound or lobed, whereas the contemporaneous Sujfun angiosperms have entire leaves. The tentative explanation is that the leaf morphology of early angiosperms reflects some differences in precipitation between these two areas.

The angiosperm increase from Middle to Upper Nicanian assemblages is clearly correlated with cycadophyte decline. The Amba flora from the southwestern margin of the Sujfun basin is the only Albian assemblage containing numerous cycadophytes. There are no angiosperm remains.

The following criteria are applicable to reconstruction of Early Cretaceous clisere at Primorye:

(1) The cycadophyte quotient. This is estimated as a proportion of cycadophytes per given assemblage in relation to the proportion of cycadophytes for the whole taphoflora. The cycadophyte quotients (Fig.2) decrease from Berriasian to Barremian (the Valanginian is omitted because the total number of species is too small), then increase and drop again at the Aptian—Albian boundary.
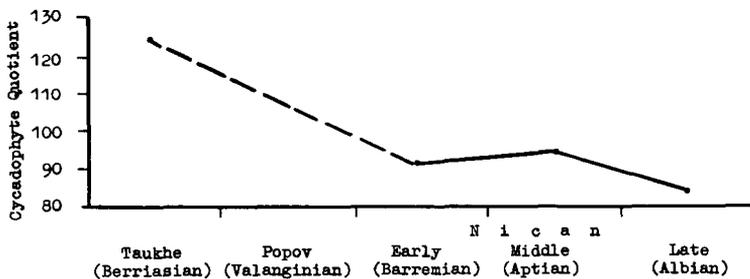

Fig.2. Cycadophyte quotient curve in the Early Cretaceous taphofloras of Primorye.

(2) The altitudinal migrations. There is some evidence that *Elatides asiatica* and *Athrotaxopsis expansa* had grown at higher altitudes on the western slopes of Nicanian elevations than on their eastern slopes (see above). The rise of these species at the Late Nicanian assemblages of Sujfun basin (which received its plant debris from the western slopes) suggests the upland—lowland migrations.

TABLE I

Phytosociological indices for Middle and Late Nicanian assemblages of Sujfun basin

	Middle Nicanian (Aptian)	Late Nicanian (Albian)
Total number of specimens, S	2,080	1,200
Total species number, N	94	29
Species diversity index, (S/N) 100	4.5	2.4
Number of genera, G	63	25
Generic index, (G/S) 100	67.0	86.2
Total number of localities, t	15	20
Number of localities with different dominants, f	7	4
Heterogeneity index, (f/t) 100	46.6	20.0

(3) Phytosociological indices. These have been counted only for the Middle and Late Nicanian assemblages of Sujfun basin (Krassilov, 1969a), see Table I.

The Middle Nicanian species diversity and heterogeneity indices are considerably higher than those of the Late Nicanian flora.

All these criteria suggest a fall of temperatures from the Berriasian to Barremian, the rise at the Aptian and rather sharp decrease in Albian time.

THE BUREJA BASIN

The plant-fossil bearing deposits of the upper reaches of the Bureja River are subdivided into six formations (the suites of Russian geologists) — Talynjan, Dublican, Soloni, Tschagdamyn, Tschemchuco, and Kyndal ranging from Upper Jurassic to Albian. The Talynjan suite rests conformably upon the marine deposits with *Arctocephalites* ammonites indicating Bathonian—Callovian age (Markov et al., 1970). The remains of Limulidae from the Talynjan suite suggest a gradual transition from a marine to a fresh-water environment.

The Talynjan plants have been described by Heer (1876), Zalessky (1904), Seward (1912), Vachrameev and Doludenko (1961) and Krassilov (1968, 1969a, 1969b, 1970a, 1970b and 1971). About 170 m of Talynjan sandstones, dark-grey siltstones, and pale-grey to white tuffites crop out along the right bank of the Bureja near the mouth of its tributary the Umalta River. Abundant plant remains are obtained from numerous fossiliferous layers throughout the sequence. They are grouped into several assemblages:

(1) Czekanowskio-Pseudotorellietum. The dominant leaf-species are *Czekanowskia aciculata* Krassil. and *Pseudotorellia angustifolia* Dolud. together with fructifications of the same plants — *Leptostrobus, Ixostrobus* and *Umaltolepis* (Krassilov, 1970b, 1971). *Raphaelia diamensis* Sew., *Coniopteris burejensis* (Zal.) Sew. and *Dicksonia nympharum* (Heer) Krassil. are most abundant among the ferns. Cycadophytes occur in small numbers. Bulk maceration of *Czekanowskia—Pseudotorellia* beds reveals numerous remains of liverworts (Krassilov, 1970a), mosses, fern sori, sporangia and spores, bisaccate pollen grains, as well as the small twigs, scale-leaves, cuticles and seeds of *Elatides ovalis* Heer. This conifer occurs there mainly as small fragments among the products of bulk maceration. Its larger twigs and complete cones predominate a few meters above the *Czekanowskia—Pseudotorellia* beds, forming the second assemblage.

(2) Elatidetum. Few species have been recognised from the *Elatides* beds. The fern *Raphaelia diamensis* is the most prominent among them.

(3) Pityophylletum. This assemblage, dominated by *Pityophyllum* leaves together with *Pityocladus* shoots and *Pityospermum* seeds, associates with coal seams. It presumably represents a swamp forest producing bisaccate pollen grains which occur abundantly at other assemblages.

(4) Stephenophylletum. The assemblage is dominated by *Stephenophyllum burejense* Krassil. leaves together with *Leptostrobus mollis* Pryn. strobili which probably belong to the same plant. The subdominants are *Sphenobaiera huangii* (Sze) Krassil., *Sphenobaiera umaltensis* Krassil., *Karkenia asiatica* Krassil., *Pterophyllum sensinovianum* Heer, *Nilssonia schmidtii* (Heer) Sew. Ferns play a subordinate role.

The Czekanowskio-Pseudotorellietum → Elatidetum (Pityophylletum) → Stephenophylletum succession may probably be related with the retreat of the sea.

The Dublican suite has thick conglomerates at the base and is presumably uncon-formable with the underlying Talynjan suite. It is composed most of arkosic sandstones

with numerous coal seams. The Dublican flora is similar to the Talynjan in having
the fern *Raphaelia diamensis* which disappears at higher horizons. However, it is
characterized by the first appearances of *Hausmannia leeiana* Sze, *Eboracia kataevensis*
Vachr., *Cladophlebis orientalis* Pryn, and other ferns; it is rich in cycadophytes.

The dominant Dublican assemblages are Stephenophylletum, Pityophylletum and
Pityo-Pseudotorellietum. The latter is dominated by *Pseudotorellia angustifolia* Dolud.
which is known also from the Talynjan suite. However, the mean width of Talynjan
Pseudotorellia leaves is 5–6 mm against the 3–4 mm of Dublican ones.

The plant-bearing deposits of the western (Asanowski section) and the southern
(Tyrma depression, Alanap section) margins of the Bureja basin are probably contempor-
aneous with the Dublican suite of the central part of the basin. The major assemblages
are Pityophylletum with occasional occurrence of *Baiera manchurica* Yabe et Oishi,
Pityo-Pseudotorellietum and Pityo-Czekanowskietum (Asanowski section only). There
are also assemblages dominated by cycadophytes *Pterophyllum* (*"Tyrmia"*) *tyrmense*
(Pryn.) Krassil., *P. pectinatum* (Pryn.) Krassil., *P.* (*"Bureja"*) *rigidum* (Pryn.) Krassil.,
Pseudocycas (*"Tyrmia"*) *polynovii* (Novopokr.) Krassil., *Nilssoniopteris* (*"Jacutiella"*)
amurensis (Novopokr.) Krassil., and *Ctenis burejensis* Pryn. in association with *Torreya*-
like conifers. They probably correspond to plant communities of shrubby aspect. I refer
to this type of Mesozoic vegetation as "cycadophyte chaparral". Several fruit-like capsules
provided with glochidia are obtained from the cycadophyte beds (Krassilov, 1973).

The Soloni suite rests conformably on the Dublican deposits and is similar to them
in comprising a number of cyclothems which consist of coarse arkosic sandstones
(lower member) grading upward to fine-grained sandstones and siltstones (upper member).
The Soloni flora is less diverse than the Dublican. Several species of ferns, *Pterophyllum*
and *Ctenis*, as well as *Pseudotorellia angustifolia* disappear at the Dublican–Soloni
boundary. The dominant assemblages are Stephenophylletum and Pityophylletum with
increased frequency of *Baiera manchurica* (Baiero-Pityophylletum). Allochtonous
remains of *Ginkgoites* occur in small numbers. They are mostly confined to the lower
members of cyclothems.

The Soloni sequence is truncated by Tschagdamyn conglomerates. The Tschagdamyn
and Tschemchuco suites consist of thick layers of homogeneous siltstones alternating
with greenish-gray polymict sandstones easily distinguishable from the arkosic sandstones
of the Soloni suite. The change in lithology correlates with adequate change in the
composition of the fossil flora. *Dicksonia arctica* (Pryn.) Krassil., with finely dissected
pinnules, dominates among the ferns. The cycadophytes are comparatively rare being
represented mostly by *Nilssonia sinensis* Yabe et Oishi, which has rather small leaves
divided into narrow pinnae. However, the upper part of Tschemchuco suite includes
one or a very few cycadophyte beds with *Nilssoniopteris amurensis* (Novopokr.)
Krassil.

There is an immense increase in frequency of *Ginkgoites* which evidently achieves the
status of principal dominant of the lowland vegetation (Ginkgoitetum). The composition
of Ginkgoitetum assemblages is fairly uniform throughout the basin. The subdominants

are *Eretmophyllum glandulosum* (Samyl.) Krassil., *Hartzia* sp. and *Athrotaxopsis expansa* Font. Another Tschagdamyn–Tschemchuco assemblage, Pityophylletum, is subordinate to Ginkgoitetum.

The Tschemchuco deposits are overlain by conglomerates and sandstones (Kyndal suite) containing brackish invertebrate fossils and a few angiosperm leaves. The composition of the post-Tschemchuco fossil flora is but little known.

The Talynjan suite being conformable with the underlying *Arctocephalites* beds, is arbitrarily assigned to the Callovian–Oxfordian Stages. The disconformity at the top of Talynjan suite is suggested by thick basal conglomerate of the overlying Dublican suite that rests directly on the erosion surface of the Palaeozoic granitic rocks along the western and southern borders of the Bureja basin. Judging from the marked change in the composition of the fossil flora the disconformity between Talynjan and Dublican suites represents a long period of nondeposition.

The Dublican flora is similar to the Taukhe flora of South Primorye and to the Wealden (Berriasian) flora of England. The dominant Dublican species, *Pseudotorellia angustifolia* with narrow leaves, is hardly distinguishable from the Wealden *Pseudotorellia* described by Watson (1969). Thus, the age of the Dublican flora is thought to be Berriasian or Tithonian–Berriasian.

The Soloni flora is correlated with Valanginian floras of North Siberia (Sachs and Schulgina, 1962; Vachrameev and Lebedev, 1965) whereas the Tschagdamyn–Tschemchuco flora is equivalent to the Barremian–Aptian floras of this region. The presence of *Athrotaxopsis expansa* reconciles the correlation of the Tschemchuco suite with Middle Nicanian (Aptian) deposits of South Primorye, whereas the Late-Nicanian deposits of Albian age probably correspond to the Kyndal suite of the Bureja basin. The time-gap represented by the disconformity at the contact of the Soloni and Tschagdamyn suites presumably embraces most of the Hauterivian Stage.

The changes of climate are indicated by the following characteristics of Bureja taphofloras:

(1) The cycadophyte quotients (Fig.3) rise from Talynjan (Callovian–Oxfordian) to Dublican (Tithonian–Berriasian), decrease at Soloni (Valanginian), reduce to minimum values at the Tschagdamyn (Barremian) and increase again up to the end of the Tschemchuco (Aptian).

(2) The diversity of bryophytes and Czekanowskiales is at a maximum in the Talynjan and Tschagdamyn–Tschemchuco taphofloras, i.e., negatively correlates with the diversity of cycadophytes. The Talynjan deposits contain at least four hepatic and two moss genera. All of them are revealed by bulk maceration. The rocks of the Dublican and Soloni suites being equally subjected to bulk maceraton yielded no bryophytes. The Tschagdamyn–Tschemchuco rocks yielded two hepatic and two moss genera. According to Townrow (1964) the proportion of bryophytes in Mesozoic taphofloras is negatively correlated with temperature. The Czekanowskiales include several genera of phanerophytes with deciduous short-shoots (i.e., *Czekanowskia, Hartzia, Phoenicopsis* and *Arctobaiera*, see Krassilov,1970) representing the most "temperate" element in the Mesozoic taphofloras.
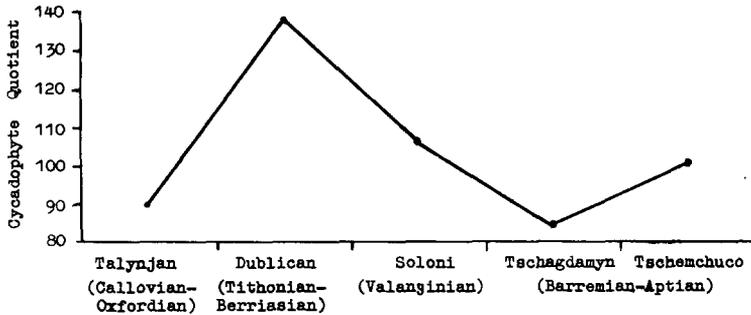
Fig. 3. Cycadophyte quotient curve in the Late Jurassic—Early Cretaceous taphofloras of the Bureja River.

(3) The succession Czekanowskio-Pseudotorellietum → Elatidetum (Pityophylletum) → Stephenophylletum, following the retreat of the sea is conceived as reflecting the relative proximity of these communities to a sea margin in Talynjan time. The Czekanowskio-Pseudotorellietum community disappears from the lowlands and the Stephenophylletum expands in Soloni time. Simultaneous appearances of allochtonous *Ginkgoites* leaves probably indicate the existence of Ginkgoitetum at higher levels. The subsequent expansion of Ginkgoitetum in Tschagdamyn time can be related to upland— lowland migrations.

(4) Leaf-size reduction in *Pseudotorellia angustifolia* in Dublican time suggests some decrease in humidity.

(5) The heterogeneity index:

$$m = (f/t) \, 100$$

(where f = number of localities with different dominant species and t = total number of localities) decreases from 30 for the Soloni taphoflora to 15.4 for that of the Tschagdamyn—Tschemchuco.

It appears from these data that the temperatures have fallen from the Berriasian to the Barremian. This suggestion is in harmony with the evidence from the Taukhe— Nicanian succession in South Primorye.

CONCLUSIONS

The succession of fossil floras of two areas with different Mesozoic climates suggests a rise of temperatures during the Late Jurassic epoch up to the Berriasian time, followed by a cooling in the Valanginian.

The Hauterivian orogenic episodes are evident at many places within the Circum-Pacific belt. They are responsible for the intervals of non-deposition between the

Valanginian and Barremian strata and probably also for the deterioration of Barremian climates that is indicated by the Early Nicanian and Tschagdamyn taphofloras. The subsequent Middle Nicanian and Tschemchuco taphofloras are indicative of the amelioration of climate in Aptian time.

The Albian Stage is marked in the Far East by increased orogenic and vulcanic activities. The Albian ignimbrites and tuffites, of immense thickness, are exposed southeast of the Bureja basin and at other places. The floristic change at the Aptian–Albian boundary in South Primorye appears to be related to a fall of temperatures.

These conclusions are more or less in agreement with the reconstructions of the Late Jurassic–Early Cretaceous climates based on isotope palaeotemperatures and marine-invertebrate evidence. Several measurements reveal the rise of palaeotemperatures during the Late Jurassic and Berriasian (Bowen, 1961; Teis et al., 1968). The cooling of the North Siberian sea in Late Tithonian–Early Berriasian time is interpreted as a local phenomenon (Sachs and Nalnjaeva, 1968). There is a sharp rise of water temperatures in Late Berriasian time followed by the Valanginian cooling. The fall of sea-water palaeotemperatures at the Berriasian–Valanginian transition is believed to be universal. The Berriasian marine fauna is rather of Late Jurassic aspect. Some authors place the Jurassic–Cretaceous boundary between the Berriasian and Valanginian (e.g., Wiedmann, 1969).

There are probably causal relationships between the Albian deterioration of climate, the decline of cycadophytes and certain groups of dinosaurs and the rise of early angiosperms and mammals.

REFERENCES

Axelrod, D. I., 1941. The concept of ecospecies in Tertiary paleobotany. *Proc. Natl. Acad. Sci. U.S.*, 27: 545–551.
Axelrod, D. I., 1948. Climate and evolution in western North America during Middle Pliocene time. *Evolution*, 2: 127–144.
Axelrod, D. I., 1960. The evolution of flowering plants. In: S. Tax (Editor), *Evolution after Darwin*, 1. Univ. Chicago Press, Chicago, Ill., pp. 227–305.
Axelrod, D. I. and Bailey, H. P., 1969. Paleotemperature analysis of Tertiary floras. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 6: 163–195.
Bowen, R., 1961. Paleotemperature analysis of Mesozoic Belemnoidea from Germany and Poland. *J. Geol.*, 69: 75–83.
Chaney, R., 1940. Tertiary forests and continental history. *Bull. Geol. Soc. Am.*, 51: 469–499.
Dorf, E., 1969. Paleobotanical evidence of Mesozoic and Cenozoic climatic changes. *Proc. North Am. Paleontol. Conv.*, Pt. D: 323–346.
Fuji, N., 1969. Fossil spores and pollen grains from the Neogene deposits in Noto Peninsula, Central Japan, 3. *Trans. Proc. Palaeontol. Soc. Jap.*, 76: 185–201.
Gritchuk, V. P., 1969. Essai de la reconstruction de quelques éléments du climat à l'hémisphère septentrionale pendant le période atlantique du Holocène. In: M. J. Neustedt (Editor), *Holocene.* Nauka, Moscow, pp. 41–57 (in Russian).
Heer, O., 1876. Beiträge zur Jura-Flora Ostsibiriens und des Amurlandes. *Mém. Acad. Imp. Sci. St. Pétersbourg*, 22: 1–122.
Iversen, J., 1944. *Viscum, Hedera* and *Ilex* as climate indicators. *Geol. Förh.*, 66: 463–483.
Kobayashi, T., 1942. On the climatic bearing of the Mesozoic floras of eastern Asia. *Jap. J. Geol. Geogr.*, 18: 157–196.

Krassilov, V. A., 1967. *Early Cretaceous Flora of South Primory and its Stratigraphic Significance.* Nauka, Moscow, 248 pp. (in Russian).

Krassilov, V. A., 1968. The Czekanowskiales – a new group of gymnosperms. *Dokl. Acad. Sci. U.S.S.R.*, 178: 942–945 (in Russian).

Krassilov, V. A., 1969a. Types and causes of palaeofloristic successions. *Palaeontol. J.*, 3: 7–23 (in Russian).

Krassilov, V. A., 1969b. Taxonomical revision of the genus *Tyrmia*. In: M. N. Gramm and V. A. Krassilov (Editors), *Fossil Fauna and Flora of the Far East.* Vladivostok, pp. 95–116 (in Russian).

Krassilov, V. A., 1970a. Leafy hepatics from the Jurassic deposits of the Bureja basin. *Palaeontol. J.*, 3: 131–142.

Krassilov, V. A., 1970b. Approach to the classification of Mesozoic "Ginkgoalean" plants from Siberia. *Palaeobotanist*, 1: 12–19.

Krassilov, V. A., 1971. On the morphology and taxonomy of Ginkgoales and Czekanowskiales. *Palaeontol. J.*, 1: 113–118 (in Russian).

Krassilov, V. A., 1973. Mesozoic plants and the problem of angiosperm ancestry. *Lethaia*, in press.

Lawrence, D. R., 1971. The nature and structure of paleoecology. *J. Paleontol.*, 45: 393–607.

Markov, V. A., Trofimuk, A. A. and Shcherbakov, V. S., 1970. Relationship between marine and coal-bearing sediments in Bureja depression. *Dokl. Acad. Sci. U.S.S.R.*, 191: 647–649.

Potonié, R., 1953. Zur Paläobiologie der karbonischen Pflanzenwelt. Geologische Zeugnisse der Karbonflora zur Kohlenbiogonie. *Naturwissenschaften*, 40: 119–127.

Raunkiaer, C., 1934. *The Life Forms of Plants and Statistical Plant Geography.* Clarendon, Oxford, 631 pp.

Sachs, V. N. and Nalnjaeva, T. I., 1968. Alterations in composition of belemnites at boundary between Jurassic and Cretaceous periods in the Boreal and Arctic zoogeographic regions. In: V. N. Sachs (Editor), *Mesozoic Marine Faunas of the U.S.S.R. North and Far East and their Stratigraphic Significance.* Nauka, Moscow, pp. 80–89 (in Russian).

Sachs, V. N. and Schulgina, N. I., 1962. Cretaceous system in Siberia. Proposals of subdivision on stages and zones. *Geol. Geophys.*, 10: 28–39.

Seward, A. C., 1912. Jurassic plants from Amurland. *Mém. Com. Géol. St. Pétersbourg* (N.S.), 81: 1–34.

Szafer, W., 1946. Flora pliocenska z Kroscirnka nad Dunajcem. *Rozpr. Wydz. Mat. Przyr.*, 72.

Teis, R. V., Naidin, D. P. and Sachs, V. N., 1968. Determination of Late Jurassic and Early Cretaceous paleotemperatures by isotopic composition of Oxygen in rostra of belemnites. In: V. N. Sachs (Editor), *Mesozoic Marine Faunas of the U.S.S.R. North and Far East and their Stratigraphic Significance.* Nauka, Moscow, pp. 51–71 (in Russian).

Townrow, J., 1964. A speculation of the Rhaeto–Liassic climate of Tasmania. *Pap. Proc. R. Soc. Tasmania*, 98: 113–118.

Vachrameev, V. A. and Doludenko, M. P., 1961. Late Jurassic and Early Cretaceous flora of Bureja basin and their stratigraphic significance. *Trans. Geol. Inst. Acad. Sci. U.S.S.R.*, 54: 136 pp. (in Russian).

Vachrameev, V. A. and Lebedev, E. L., 1967. Paleobotanical characterization and the age of coal-bearing Upper Mesozoic deposits of Far East (between the Amur and Uda Rivers). *Proc. U.S.S.R. Acad. Sci., Geol. Ser.*, 1967 (2): 120–133 (in Russian).

Verbizkaya, Z. J., 1965. Spore and pollen complexes from the Cretaceous deposits of the Sujfun coal field. In: Z. J. Verbizkaya et al. (Editors), *Cretaceous Vegetation and Coals of the Primorye Basin.* Nauka, Moscow-Leningrad, pp. 41–86 (in Russian).

Walter, H., 1964. *Die Vegetation der Erde in Öko-Physiologischer Betrachtung*, 1. Fischer, Jena, 550 pp.

Watson, J., 1969. A revision of the Wealden flora, pt. 1, Charales–Ginkgoales. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, 17: 207–254.

Wiedmann, J., 1969. Zur Frage der Jura–Kreide-Grenze. *Ann. Inst. Geol. Hung. Publ.*, 54: 149–154.

Wolfe, J. A. and Barghoorn, E. S., 1960. Generic changes in Tertiary floras in relation to age. *Am. J. Sci.*, A, 258: 388–399.