Palaeogeography, Palaeoclimatology, Palaeoecology, 17(1975): 157—172

CLIMATIC CHANGES IN EASTERN ASIA AS INDICATED BY FOSSIL FLORAS. II. LATE CRETACEOUS AND DANIAN

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(Received June 17, 1974; accepted for publication November 11, 1974)

ABSTRACT

Krassilov, V. A., 1975. Climatic changes in Eastern Asia as indicated by fossil floras. II. Late Cretaceous and Danian. Palaeogeogr., Palaeoclimatol., Palaeoecol., 17: 157—172.

Four Late Cretaceous phytoclimatic zones — subtropical, warm—temperate, temperate and boreal — are recognized in the Northern Hemisphere. Warm—temperate vegetation terminates at North Sakhalin and Vancouver Island. Floras of various phytoclimatic zones display parallel evolution in response to climatic changes, i.e., a temperature rise up to the Campanian interrupted by minor Coniacian cooling, and subsequent deterioration of climate culminating in the Late Danian. Cooling episodes were accompanied by expansions of dicotyledons with platanoid leaves, whereas the entire-margined leaf proportion increased during climatic optima. The floristic succession was also influenced by tectonic events, such as orogenic and volcanic activity which commenced in Late Cenomanian—Turonian times. Major replacements of ecological dominants occurred at the Maastrichtian/Danian and Early/Late Danian boundaries.

INTRODUCTION

The principal approaches to the climatic interpretation of fossil floras have been outlined in my preceding paper (Krassilov, 1973a). So far as Late Cretaceous floras are concerned, extrapolation (i.e. inferences from tolerance ranges of allied modern taxa) is gaining in importance and the entire/non-entire leaf type ratio is no less expressive than it is in Tertiary floras. Since the climatic indications of a flora depend on its position relative to latitudinal climatic zones, the phytogeographical zonation is considered first.

PHYTOGEOGRAPHY

Several phytogeographic classifications are based on megafossil as well as microfossil records of Late Cretaceous plants (see Vachrameev et al., 1970; Stanley, 1970; etc.). Some of them reflect phytoclimatic zonation which is, however, disguised by a hierarchical system of "floristic provinces". Mere floristic approach is biased by the unstable taxonomy of Cretaceous angiosperm leaves. The present author prefers a combined floristic—phytoclimatic approach (e.g. Krassilov, 1972) when the principal divisions — geofloras — are delimited by a few widespread and easily recognized morphological types (or life forms) with restricted climatic tolerances. For the Late Cretaceous these are:

(1) *Phoenicopsis*; the dominant plant of "*Phoenicopsis*-forests", i.e., mesophytic deciduous forests which thrived in northern Asia from the Late Triassic up to the Early Cretaceous and then declined through the Late Cretaceous.

(2) *Ginkgo* (or *Ginkgoites*); this is most abundant in the *Phoenicopsis* zone, but spread farther south. Cenozoic representatives of the genus are restricted to the temperate zone.

(3) *Nilssonia*; the latitudinal range of this form largely overlaps that of *Ginkgo* but its optimum development is outside the *Phoenicopsis* zone.

(4) *Debeya* (*Dewalquea*); this peculiar Late Cretaceous leaf type resembles some modern Proteaceae. It is found mostly to the south of the *Phoenicopsis* zone and associates with:

(5) *Palmae*.

Diagramatically the geographic distribution of these types can be expressed thus:

Phoenicopsis

Ginkgo

Nilssonia

Debeya

Palmae

S ———————————————————— N

Four phytoclimatic units can be distinguished:

(1) Subtropical; dicotyledons of the *Debeya-Dewalquea* group are widespread and *Ginkgo* mostly absent. This zone differs from the modern tropics in the presence of taxodiaceous conifers and the smaller dimensions of prevailing angiosperm leaves. It comprises plant localities of the United States and Europe. The Dakota flora of Kansas and Nebraska (Lesquereux, 1974) grades into the next zone:

(2) Warm—temperate; *Debeya* leaves constantly present as well as *Ginkgo*

and *Nilssonia*. Cretaceous Palmae reached Central Japan and Vancouver Island whilst *Debeya* is known from North Sakhalin, the Zajsan depression, western Greenland and Vancouver Island (Fig.1).

Fig. 1. Records of *Debeya* from the warm—temperate ecotone: 1 = Sakhalin; 2 = Zajsan; 3 = Ireland (this record is from Paleogene); 4 = western Greenland; 5 = Vancouver Island.

(3) Temperate; *Debeya* absent, *Ginkgo* common, *Nilssonia* and *Phoenicopsis* occur occasionally. The principal localities are situated in Yakutia, western Siberia, western Canada, Alaska and Yukon province.

(4) Boreal; *Phoenicopsis* and *Ginkgo* present, but *Nilssonia* usually absent. This zone covers northern Alaska and Chukotka.

Several plant groups occur in all zones but show quantitative correlations with climate: among the taxodiaceous conifers, *Sequoia* prevails in 1 and especially in 2, whereas deciduous *Parataxodium* ("*Cephalotaxopsis*") dominates conifer—hardwood forests of 3 and 4. Laurel-type leaves are common in 1 and rather infrequent in other zones, whereas platanoid leaf-types (i.e., *Platanus*, *Credneria*, *Paracredneria*, *Protophyllum*, *Pseudoprotophyllum*, *Aspidiophyllum* and *Pseudoaspidiophyllum*) attain their maximum diversity and numerical representation in 3 and 4.

This scheme shows some points of resemblance to that of Stanley (1970), who used the *Triprojectus* pollen-type as an indicator of a tropical—temperate ecotone. However, *Triprojectus* (*Aquillapollenites*) was controlled, not only by temperature conditions but also by humidity. According to Rouse et al. (1971), this pollen-type was less frequent in coastal than in interior regions of western North America. Thus, its uneven representation in Europe and Asia may be at least partially related to unequal land—sea distribution (Krassilov, 1971).

FLORISTIC PALAEOSUCCESSION AND CLIMATIC CHANGES

A. Cenomanian—Senonian

In eastern Asia, floras of this age (Fig.2) fall into three phytoclimatic zones: warm—temperate (Primorye, Japan and Sakhalin), temperate (Okhotsk Sea coastal region, Kolyma River, Anadyr River, Kamchatka and Anadyr Bay) and boreal (Chukotka). Their American equivalents are known from Canada and Alaska.

Primorye, Sakhalin and Japan: warm—temperate

The Albian flora of Primorye is composed mostly of ferns, cycadophytes and conifers in association with a few angiosperms (Krassilov, 1973a). Greenish-gray Albian strata are overlain by red beds of presumably Cenomanian age. They yielded a few fragments of ferns (*Onychiopsis*), cycadophytes (*Otozamites*) and *Ginkgoites*. Above the red beds there are thick series of eruptives distributed along the Sikhote-Alin Mountains and the Inner Belt of Central

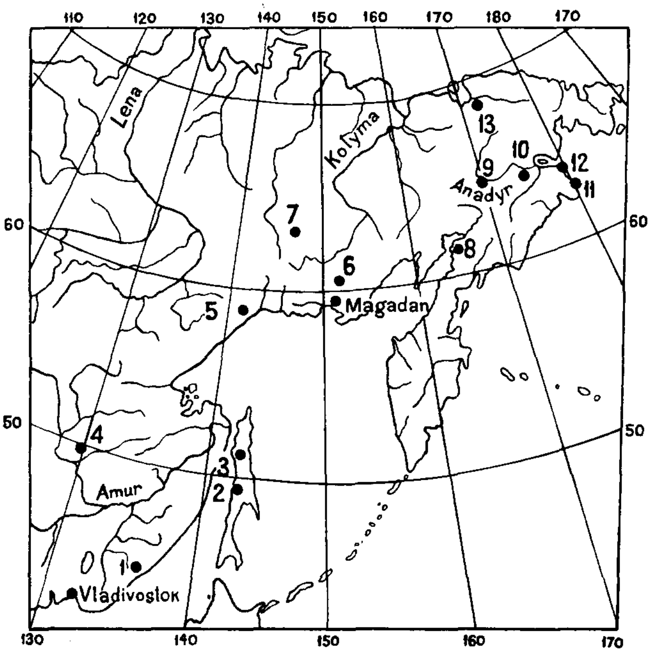

Fig. 2. Principle localities of Cretaceous plants in the Far East of the U.S.S.R.: 1 = Sikhote-Alin, Partisanian; 2 = Sakhalin, Augustovian and Boshniakovian; 3 = Sakhalin, Ajnussian, Gyliakian and Jonkiaerian; 4 = Amur Province, Tsagajan; 5 = Okhotsk coast, Ulja River; 6 = Okhotsk coast, Armanian; 7 = Kolyma basin, Arkagalian; 8 = North Kamchatka, Vali-jgenian and Bystrinskian; 9 = Anadyr basin, Grebjonka; 10 = Anadyr Basin, Rarytkin Range; 11 = Anadyr Bay, Barykovskian; 12 = Anadyr Bay, Koriakian; 13 = Chukotka, Koekwoonian.

Japan. Lower members of the volcanic series in Japan contain Asuwa and Omichidani floras assigned to Late Turonian—Early Coniacian (Matsuo, 1962, 1970). These floras consist of ferns (including *Onoclea* cf. *sensibilis* L.), *Nilssonia* spp., *Ginkgoites*, pinaceous and taxodiaceous conifers, rather sparse small-leafed terrestrial angiosperms and aquatic *Quereuxia ("Trapa") angulata*.

The Partisan flora of Sikhote-Alin (Kryshtofovich, 1939) occupies a similar stratigraphic position. Ferns and conifers associate here with small-leafed *Viburnum* and *Quereuxia*.

In Sakhalin, plant remains occur in a paralic sequence overlying marine Turonian shales and grading southward into marine beds. Several successive plant assemblages have been recognized by Kryshtofovich (1918, etc.) and revised by Vachrameev (1966) and Krassilov (1973b):

(1) Ajnussian; *Gleichenites sachalinensis* Krysht., *Sequoia reichenbachii* (Gein.) Heer, and platanoid leaves (mostly *Protophyllum* ex gr. *sternbergii* Lesq. and *P. ignatianum* Krysht. et Baik.) predominate. Records of *Inoceramus uwajimensis* in marine interbeds indicate a Coniacian age (Vereshagin, 1970).

(2) Gyliakian; *Sequoia reichenbachii* predominate. The gymnosperms *Cycas* and *Araucarites* are locally abundant. Platanoid leaves play a subordinate role. *Trochodendroides sachalinensis* (Krysht.) Krysht., *Laurophyllum sakhalinense* Krassil., *Araliaephyllum polevoi* (Krysht.) Krassil., *Bauhinites cretacea* (Newb.) Sew., and *Debeya tikhonovichii* with small to medium-sized ovate, lanceolate, trilobate, and trifoliate leaves are the principal angiosperm elements (see Krassilov, 1973c). Numerical representations have been calculated for the Mgachi locality, which is *locus classicus* for the Gyliakian flora (Table I). Upper horizons with Gyliakian plants contain the Late Santonian—Early Campanian ammonite *Annapachydiscus naumanni* Yok. Thus, the most probable age for the Gyliakian is Santonian. It is worth mentioning that Japanese geologists use Kryshtofovich' term "Gyliakian" for marine Cenomanian—Turonian strata from its original (now amended) age assignment in Sakhalin.

(3) Jonkiaerian; *Sequoia reichenbachii* retains its dominant position. *Nilssonia* and ferns occur abundantly. Among them *Saccoloma gardneri* (Lesq.) Knowlt. makes its first appearance. Characteristic angiosperms are *Magnoliaephyllum magnificum* (Dawson) Krassil., *Myriciphyllum yokoyamae* (Krysht.) Krassil., and "*Rulac*" *quercifolium* Hollick (the affinities of the latter are with *Koelreuteria* or *Cupanites* rather than with *Rulac* or *Acer*). Plant-bearing strata are intercalated with marine beds which yielded *Inoceramus schmidti* Mich., *I. orientalis* Sok. and other invertebrate fossils of Campanian age.

(4) Augustovian; differs from older assemblages by the presence of *Osmunda*, *Elatocladus (Parataxodium) intermedius* (Holl.) Bell, *Macclintockia* and especially *Trochodendroides arctica* (Heer) Berry. Platanoid leaves and *Ginkgoites* are more frequent than in the Gyliakian and Jonkiaerian. This assemblage occurs in paralic beds resting on marine stata with *Pachydiscus* aff. *gollevillensis* Orb. and *P. subcompressus* Mat. of Late Maastrichtian age.

(5) Boshniakovian; is described below with the Danian assemblages.

In Japan, the Kamogata flora with platanoid leaves presumably corresponds to the Ajnussian. The Izumi flora (Campanian according to Matsuo, 1970) is of Jonkiaerian aspect and the Omichidani flora with *Cladophlebis frigida*, *Asplenium dicksonianum*, *Nilssonia* spp., *Glossozamites*, "*Sequoia heterophylla*" (? *Parataxodium*), *Protophyllum*, and *Trochodendroides arctica*

(Endo, 1925) is similar to the Augustovian assemblage.

The floristic composition as a whole undergoes insignificant changes through the Late Cretaceous. However, some variations are of stratigraphic as well as of climatologic importance:

(1) The frequency of *Nilssonia* increases in coastal environments, i.e. in

TABLE I

Numerical representation of vascular plant species per 500 rock slabs in Mgachi locality, North Sakhalin

	Number of specimens	%
Filicales		
Gleichenites sachalinensis (Krysht.) Krassil.	10	0.6
Anemia (*"Asplenium"*) *dicksoniana* (Heer)	32	2.8
Cladophlebis frigida (Heer) Sew.	40	2.4
Cladophlebis oerstedii (Heer) Sew.	4	0.2
Sachalinia sachalinensis Vakhr.	25	1.5
Caytoniales		
Sagenopteris variabilis (Velen.)	20	1.2
Cycadales		
Nilssonia serotina Heer	31	1.8
Ginkgoales		
Ginkgoites ex gr. *adiantoides* (Unger)	25	1.5
Coniferales		
Araucarites pilosistomus Krassil.	308	17.7
Sequoia reichendachii (Gein.) Heer	605	34.7
Cupressinocladus cretaceus (Heer) Sew.	87	4.9
Protophyllocladus polymorphus (Lesq.) Berry	244	14.0
Angiospermae		
Araliaephyllum polevoi (Krysht.) Krassil.	127	7.2
Debeya tikhonovichii (Krysht.) Krassil.	60	3.5
Trochodendroides sachalinensis (Krysht.)	77	4.4
Trochodendrocarpus sp.	2	0.1
Protophyllum ignatianum Krysht. et Baik.	42	2.4
Bauhinites cretaceus (Newb.)	2	0.1
Total	1741	100

Japan and Sakhalin localities in relation to Primorye, and in Jonkiaerian and Augustovian assemblages in relation to the Ajnussian and Gylikian.

(2) The frequency of *Ginkgoites* leaves increases in the Ajnussian and Augustovian assemblages. Since *Ginkgoites* is a temperate element, its frequency is believed to be negatively correlated with temperature trends. Deeply dissected *Ginkgoites* of "Jurassic" aspect makes its last appearance in the Turonian.

(3) The platanoid element is at maximum in the Ajnussian; it decreases through the Gyliakian and Jonkiaerian, and begins to rise again in the Augustovian. As this element achieves its optimum development in northern regions, the negative correlation with temperature is to be expected. However, this correlation can probably be influenced by changes of local topography. Plants with platanoid leaves dominated a flood-plain vegetation and their numerical representation therefore depended on the development of flood-plains. The Turonian Partisan and Asuwa assemblages in Primorye and Japan mostly accumulated in lakes bordered by volcanoes, hence an extreme reduction of the platanoid element.

(4) The percentage of angiosperm leaves with entire margins in Sakhalin floras is at its maximum in the Jonkiaerian and drops in the Augustovian (Fig. 3).

All these criteria suggest a temperature optimum in the Campanian and cooling in the Coniacian and Maastrichtian.

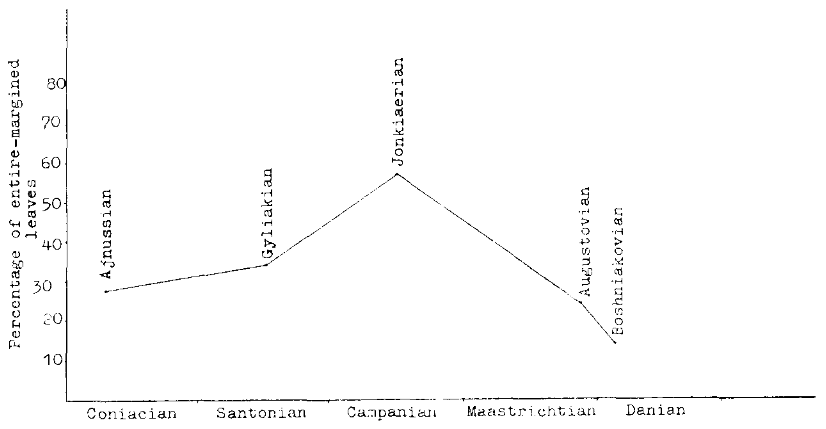

Fig.3. Percentages of entire-margined angiosperm leaves in the Late Cretaceous floras of Sakhalin.

Northern regions : temperate and boreal

The Albian floras of Kolyma are much like those of Primorye. They are replaced by impoverished assemblages with characteristic Late Cretaceous conifers (*Sequoia reichenbachii*) and platanoid leaves. These assemblages, exemplified by the Toptan flora of Kolyma (Samylina, 1962, 1974, etc.) have no equivalents in the Primorye—Sakhalin area and correspond to the latest Albian—Early Cenomanian Nulato flora of Alaska (see below). They reflect the first stage of the Late Cretaceous floristic succession.

The second stage is represented by assemblages of various conifers (*Sequoia, Parataxodium, Cupressinocladus*, Pinaceae) which dominate small-leafed angiosperms (*Trochodendroides, Celastrophyllum, Menispermites, Quereuxia*), ferns, *Ginkgoites* with both entire and deeply divided leaf blades, *Sphenobaiera, Czekanowskia* and *Phoenicopsis*. These assemblages occur in the lower horizons of the volcanic series, e.g. the Ulja locality on the Okhotsk coast (Kryshtofovich, 1937), the Arkagalian Formation of Kolyma (Samylina, 1962), and the Koekwoonian Formation of Chukotka (Vachrameev, 1966, Filippova, 1972a,b). They agree with Turonian floras of Primorye and Japan in general aspect and in a depositional environment of pyroclastic sedimentation in lakes.

The third stage is marked by the expansion of platanoid types which dominate, e.g. in the Valijgenian flora of North Kamchatka. Other angiosperms are *Magnolia, Macclintockia, Menispermites, Trochodendroides, Cissites* and *Viburnum* (Vachrameev, 1966). This flora is assigned to the Turonian—Coniacian on the marine invertebrate evidence. The Grebjonka flora of Anadyr has a similar composition although its age is in dispute. It comprises *Pseudocycas hyperborea* Krysht. in addition to minor Cretaceous gymnosperms (Kryshtofovich, 1958a,b). Both Valijgenian and Grebjonka assemblages agree with the Ajnussian flora of Sakhalin.

The next stages are characterized by a decline of platanoid types, which are subordinate to *Macclintockia, Trochodendroides, "Rulac" quercifolium, Vitis* and *Viburnum*. In Kamchatka, the Valijgenian is overlain by the Bystrinskaya Formation of Santonian age, yielding plant assemblages of Gyliakian aspect (Vachrameev, 1966). A similar assemblage was recorded recently by Filippova (in press) from the Armenian locality north of Magadan. The younger Barykovskian flora of Anadyr Bay (Campanian) is enriched by *Onoclea, Pterophyllum validum* and *Magnoliaephyllum* (Vassilevskaya, 1962; Vachrameev, 1966) and corresponds to the Jonkiaerian flora of Sakhalin.

Thus, the palaeofloristic succession in the northern regions is parallel to that of Primorye, Sakhalin and Japan but supplements the latter by the initial stage of the impoverished assemblages with platanoid leaves suggesting Early Cenomanian cooling.

Alaska and Canada

In northern Alaska, Smiley (1969, 1972, etc.) recognized several floristic zones. Arborial angiosperm fossils started in zone III (Late Albian—Early Cenomanian). Zone IV (Early Cenomanian) contained ill-preserved platanoid leaves. The sequence is interrupted by a Late Cenomanian interval of nondeposition. Zone V (Turonian) is characterized by the presence of *Celastrophyllum* and *Laurophyllum*, together with platanoid leaves and the last records of the Mesozoic conifer *Podozamites*. Platanoid leaves are abundant in zone VI (Coniacian—Campanian) which is marked also by the first appearance of *Parataxodium* and *Trochodendroides*; these achieved dominant status in zone VII (Late Campanian—Maastrichtian). The percentage of angiosperm leaves with entire margins, and other climatic criteria, suggest a temperature optimum in Campanian times (zone VI), and cooling in the Coniacian (the beginning of zone VI) and Maastrichtian (zone VII), which agrees well with Asiatic data.

In the Yukon Province, Hollick (1930) described fossil plants from the Melozi, Kaltag and Nulato Formations. Marine fossils probably of Albian age came from the Nulato, which was placed between the paralic Melozi and the Kaltag. Correspondingly, the age of the Melozi was believed to be Albian. This age assignment influenced the stratigraphy of Cretaceous continental deposits, not only in North America but also in Asia. Recently the Melozi was proved to be the equivalent of the Kaltag, i.e. above the Nulato, which yielded not only Albian but also Cenomanian invertebrate fossils (Patton, 1973). Thus, the Nulato flora is Late Albian—Early Cenomanian. It contains only a few platanoid leaves and differs considerably from the essentially platanoid Melozi—Kaltag flora with *Parataxodium* ("*Cephalotaxopsis*"), *Protophyllum*, *Trochodendroides*, *Macclintockia*, *Araliaephyllum* ("*Sassafras*"), etc. It has little in common with the Cenomanian or Turonian floras of Eastern Asia and much resembles the younger Ajnussian flora of North Sakhalin, as well as the zone VI assemblage of Smiley. A sudden change in floristic composition between the Nulato and the Melozi—Kaltag may point to a disconformity, probably equivalent to the Late Cenomanian disconformity of northern Alaska. This suggestion allows a post-Cenomanian age for the Melozi—Kaltag.

Senonian floras are known from the middle and upper parts of the Chignik Formation (Hollick, 1930). Platanoid leaves only play a subordinate role in the Chignik flora. The middle Chignik with *Trochodendroides* and "*Rulac*" *quercifolium* may correspond to the Gyliakian of North Sakhalin (Santonian). *Magnolia* and Lauraceae occur mostly in the upper Chignik, suggesting a correlation with the Jonkiaerian.

In western Canada the platanoid Dunvegan flora (Bell, 1963) is equivalent to the Kaltag—Melozi. Younger Bad Heart (Santonian) and Milk River (Early Campanian) floras are lacking in platanoid leaves. The Milk River contains *Magnolia* and *Saccoloma gardneri* which are known also from the Jonkiaerian of North Sakhalian. Termophilous ferns (*Anemia fremontii*, *Saccoloma*, etc.) and angiosperms (*Geonomites*, *Artocarpus*, *Liriodendron*, *Cinnamomum*, etc.) are even more prominent in the Nanaimo flora of Vancouver Island (Campanian according to Bell, 1957). Various *Cupanites* and *Koelreuteria* described from Nanaimo by Bell are probably conspecific with "*Rulac*" *quercifolium* from the Chignik of Alaska and Jonkiaerian of Sakhalin.

The Augustovian flora of Sakhalin has its counterpart in the lower Edmonton flora of Alberta, with *Nilssonia serotina*, *Sequoiites artus*, *Elatocladus intermedius*, *Trochodendroides arctica*, *Dombeyopsis nebrascensis*, *Vitis stantoni*, etc. (Bell, 1949).

Thus, the floristic evolution in Alaska and Canada is parallel to that of Eastern Asia, indicating similar climatic changes and almost synchronous tectonic events. The most important among the latter are the Turonian orogeny and volcanism in Eastern Asia and Late Cenomanian (? also Turonian) diastrophism in Alaska. Tectonic and igneous activity coupled with sea-floor spreading is widespread in the western Pacific (see, e.g., McDougal and Van der Lingen, 1974) in Cenomanian—Turonian time.

B. Danian

A consensus of opinion now indicates that Danian biota have a Paleogene aspect. In freshwater and paralic deposits the Danian is no longer recognized as a separate unit, but merges into the Paleocene. However, taking into account the great importance of Danian evolutionary events, it seems expedient to retain the Danian as a separate stage of the Paleogene. There are better grounds for delimiting the Danian in nonmarine sequences than any other stage unit.

The Danian of Denmark falls into two natural divisions — the Early—Middle Danian (Fish clay, *Cerithium* limestone, Fakse coral limestone, etc.) and the Upper Danian which corresponds, at least partially, to the Montian of Belgium (see Hansen, 1970, for discussion). The lowermost "Tertiary" plant-bearing beds of Spitsbergen, as well as the Agatdal Formation of western Greenland, have been assigned recently to the Upper Danian (Hansen, 1970; Rosenkrantz, 1970; Vonderbank, 1970). Rich fossil floras from these beds constituted the main part of Oswald Heer's *Flora fossilis arctica* and have been revised by Nathorst (1910—1911), Schloemer-Jäger (1958), Manum (1962) and Koch (1963, 1972).

In western North America rich plant localities are known from the Lance Formation and Fort Union Group. The Cannonball Member of the lower Fort Union in North Dakota yielded foraminifera of Early Danian age (Fox and Olsson, 1969). Plant megafossils occur abundantly in the Cannonball and its lateral equivalents (Brown, 1962). Thus, there are reference floras of both Early and Late Danian.

Plant microfossils have been described from the Danian of Oiching (Kedves, 1970), from the type Montian (Roche, 1969) and its equivalents in the Crimea (Rotman, 1971), Ukraine (Korallova, 1966), etc. Nonmarine Danian deposits of Spitsbergen, Greenland and western North America have been extensively studied by palynologists (Manum, 1962; Stanley, 1965; Hall and Norton, 1967; Norton and Hall, 1969; Leffingwell, 1971). They revealed a floristic turnover between the Maastrichtian and the Danian, separated by a transitional zone embracing the uppermost Lance and the lowermost Fort Union. Fine palynological work has been done by Srivastava (1969, 1970, etc.) on the Edmonton Formation of Alberta. The upper Edmonton, resting on the Kneehills Tuff, contains both dinosaurian and mammalian faunas. The radiometric age of the Kneehill Tuff is 66 m.y. (Folinsbee et al., 1961). The lower part of the upper Edmonton, up to the Nevis coal seam, is referred to the *Wodehousea spicata* zone, traceable also in the Hell Creek Formation (latest Maastrichtian) of South Dakota and Montana. Above the Nevis seam, dinosaur records are extremely rare. This part of the upper Edmonton section (also assigned to Maastrichtian) contains the Ardley coal seam, with a radiometric age of 63 m.y. (within the limits of the Danian) and microfossils of the *Wodehousea fimbriata* zone. The index pollen type of this zone is recorded also from the lower Fort Union (Ludlow Formation of South Dakota, Tullock Formation of Montana, etc.). I doubt whether this evidence of the Early Danian age should be abandoned for the sake of few dinosaur bones.

Bell (1949) described, from the upper Edmonton, *Platanus raynoldsii*, *Anona robusta*, *Fraxinus leii* and other plant megafossils indicative, in his opinion, of a Lancian (Maastrichtian) age. However, these species are also known from "Paleocene" strata. *Platanus raynoldsii* can be seen as one of the few guide plant megafossils of the Danian, since it occurs chiefly in post-Lancian floras of North America (Fort Union, Paskapoo, etc.) and their equivalents in Asia (see below). Others with similar ranges are *Taxodium olriki* (Heer) Brown (the Danian of Spitsbergen, western Greenland, western U.S.A., eastern Asia) and *Ginkgo spitsbergensis* Manum (together with presumably conspecific *G.wyomingensis* Manum and *G.tsagajanica* Samylina).

It is worth mentioning that *Nilssonia* occurs only in the lower Edmonton, but not in the top layers. This cycadophyte was reported mainly from Lancian and older floras. However, it was identified also from the Sifton Formation of British Columbia in association with *Metasequoia occidentalis*, *Trochodendroides arctica*, *Celastrinites wardii* and the essentially Paleogene pollen type *Pistillipollenites*. Rouse (1967) admitted the possibility of a Danian age for the Sifton beds.

In Sakhalin, the Maastrichtian paralic beds with an Augustovian flora (see above) are overlain by the tuffaceous Boshniakovian Formation which yielded abundant plant remains. No marine fossils have been found hitherto in the Boshniakovian Formation, though its lateral equivalents contain a monotonous fauna of small bivalves of Danian aspect, replacing diverse Maastrichtian assemblages with *Pachydiscus*. The Boshniakovian flora resembles those of the upper Edmonton, Sifton, etc. The principal species are *Anemia* sp., *Woodwardia* sp., *Cladophlebis columbiana* Dawson, *C. frigida* (Heer) Sew., *Nilssonia gibbsii* Newb., *Ginkgoites adiantoides* (Unger), *Metasequoia occidentalis* Newb.) Chaney, *Nymphaeites* sp., *Macclintockia kanei* (Heer) Sew. et Conw., *Trochodendroides arctica* (Heer) Berry, *Platanus heeri* Lesq., *Corylites insignis* Heer, *Celastrinites* sp., *Bauhinites cretaceus* (Newb.) and some other angiosperms.

Of the above species, *Cladophlebis frigida*, *Nilssonia gibbsii*, *Ginkgoites adiantoides* and *Bauhinites cretaceus* occur throughout the Senonian sequence, whereas *Macclintockia kanei* and *Trochodendroides arctica* pass up from the preceding Augustovian flora. However, these species occur in small numbers. More significant is the disappearance of the major Senonian dominants *Se-*

quoia reichenbachii (Gein.) Heer and *Protophyllum ignatianum* Krysht. et Baik., which are replaced by *Metasequoia* and *Platanus*. Also there is the appearance in abundance of a new dominant type, *Corylites insignis* Heer, completely alien to the Senonian floras. These events increased proportions of both deciduous trees and non-entire-margined leaves, thus pointing to considerable cooling. Similar changes are displayed by the latest Maastrichtian—Early Danian Koriakian flora of Anadyr Bay (Vassilevskaya, 1962) when compared with the Campanian Barykowskian flora of the same area (see above). The Koriakian flora shares with the Boshniakovian the genera *Woodwardia*, *Metasequoia*, *Trochodendroides*, *Platanus* and *Corylites*. It includes also various *Cissites*, which are lacking in the Sakhalin floras.

Being older than the Agatdal and Fort Union floras, the Boshniakovian flora and its equivalents in eastern Asia are therefore restricted to the Early Danian. The Boshniakovian sequence is truncated unconformably by Paleogene conglomerates. A more complete Danian sequence is known from the Amur Province, where the plant-bearing Tsagajan Formation rests on Senonian beds with dinosaur remains. Lower horizons of the Tsagajan Formation yielded only microfossils of allegedly Maastrichtian age (Bratzeva, 1969, etc.), whereas plant megafossils came from: (1) clay lenses and fine sandstones of the uppermost middle Tsagajan, and (2) clay and sandstone interbeds of the upper Tsagajan pebblebeds.

A small collection from (2) was described by Heer (1878), who assigned it to the Miocene. Konstantow (1914), Pojarkova (1939) and especially Kryshtofovich and Baikovskaya (1966) carried out a more comprehensive study and unanimously claimed the "Laramie" affinities of the Tsagajan flora.

The "Laramie" of classical authors includes both the Lance and the Fort Union of the Rocky Mountains. Now it is evident that the Tsagajan flora agrees with the Fort Union and has little in common with the Lance flora. Taxonomic revision undertaken recently by the present author (Krassilov, 1970, 1973c, 1974) has revealed a number of species shared with the Fort Union: *Onoclea hebridica* (Forbes) Johnson, *Dryopteris lakesii* (Lesq.) Knowlt., *Ginkgo spitsbergensis* Manum (probably conspecific to *G. wyomingensis* Manum), *Taxodium olrikii* (Heer) Brown, *Androvettia catenulata* Bell, *Cupressinocladus interruptus* (Newb.) Krassil., *Limnobiophyllum scutatum* (Dawson) Krassil., *Trochodendroides arctica* (Heer) Berry, *Platanus raynoldsii* Newb., *Viburniphyllum finale* (Ward) Krassil., "*Credneria*" cf. *daturaefolia* Ward, and *Quereuxia angulata* (Newb.) Krysht. This makes about 1/4 of all the (47) Tsagajan species. The uppermost middle Tsagajan beds with *Gleichenites* and *Protophyllum* of Senonian aspect is believed to be the equivalent of the lowermost Fort Union, whereas the upper Tsagajan corresponds to its higher horizons.

The revision resulted in the exclusion from the Tsagajan flora of genera with predominantly tropical—subtropical modern equivalents, e.g. *Ficus*, *Celastrus*, *Zizyphus*, *Pterospermites*, etc.

The general aspect of the Tsagajan vegetation was temperate and it was evidently dominated by deciduous trees. Species with entire-margined leaves or leaflets amount to less than 30% of the total number of dicotyledon species. The Tsagajan localities usually yield countless leaves of two or three dominant species, together with their reproductive organs and occasional remains of other species. The number of species per locality varies from one to eighteen, but localities with three or four species are most common. Schmidt collected four species from the *locus classicus* in 1862 and only one species was added as a result of repeated visits of various workers in 1912, 1914, 1939, 1966 and 1970. Several plant communities have been recognized: (1) an aquatic community with *Potamogeton*, *Hydrocharis*, *Nuphar*, *Nymphaeites*, *Limnobiophyllum* and *Quereuxia*; (2) a reed-sedge community with *Phragmites* ex gr. *alaskana* and *Carex* spp.; (3) a *Taxodium—Nyssa* swamp forest; (4) a *Trochodendroides—Platanus* riparian forest with *Myrica* and *Viburniphyllum* shrubs; (5) an upland forest with *Metasequoia*, *Pinus*, *Araucarites*, *Podocarpus*, *Tiliaephyllum tsagajanicum* (Krysht. et Bail.) Krassil., *Celtis*, *Cyclocarya*, Menispermaceae, Leguminosae, etc.

An increase in the numerical representation of *Pinus*, *Araucarites* and especially *Tiliaephyllum* in the upper Tsagajan localities indicates upland—lowland migrations induced by cooling. Serrate *Tiliaephyllum* leaves, arising in abundance, add to the overwhelming preponderance of non-entire leaf types. Thus, the middle—upper Tsagajan boundary is marked by a notable change in the composition of the lowland forests as well as the elimination of such Senonian relics as *Protophyllum*.

In the northeast, similar changes are displayed by the Rarytkin flora of the Anadyr basin, compared with the Early Danian Koriakian flora of adjacent territory. According to Kryshtofovich (1958b, with some recent emendations), the Rarytkin flora is dominated by *Taxodium olrikii*, *Metasequoia disticha*, *Platanus raynoldsii* (= *Grewiopsis orientalis* Krysht.), and *Trochodendroides arctica*, which agree with the Tsagajan population in leaf polymorphism. The record of *Potamogeton* from Rarytkin by V. N. Vassilevskaya (personal communication) reinforces the resemblance to the Late Danian floras of Tsagajan and Spitsbergen.

It appears that the climatic deterioration which commenced in the Maastrichtian had progressed in Early Danian time and culminated in the Late Danian, bringing about a major replacement of dominant genera at the Maastrichtian—Danian boundary and subordinate replacement as well as extinction of Senonian relics at the Early—Late Danian boundary. This conclusion is consistent with that of Srivastava (1970, etc.), who claimed a cooling trend in the Late Maastrichtian, Dorf (1942), Hall and Norton (1967) and other authors who demonstrated a temperature fall at the Lance (or Hell Creek)—Fort Union transition. Late Danian floras may be viewed as ancestral to the Arcto-Tertiary geoflora. Some communities (especially the aquatic) passed into the Arcto-Tertiary vegetation essentially unchanged. Others underwent both segregation (especially in respect to conifers, since in the Danian forests, pines and podocarps grew side by side). There was also integration of floristic elements from various florogenic sources.

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