THIRTEENTH
SIR ALBERT CHARLES SEWARD MEMORIAL LECTURE
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MAJOR PHYTOCHORIA OF THE LATE CRETACEOUS AND THE EARLY TERTIARY IN THE U.S.S.R. AND ADJACENT COUNTRIES

BY

A. TAKHTAJAN

Professor, Botany Department of the Komarov Botanical Institute
Academy of Sciences of the U.S.S.R., Leningrad

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By A. TAKHTAJAN

Madam President, Colleagues, Ladies and Gentlemen,

YOU have accorded me a great honour in inviting me here today to deliver the Thirteenth Seward Memorial Lecture at one of the most famous Palaeobotanical Centres of the world — The Birbal Sahni Institute of Palaeobotany. I was exceedingly excited when I received your invitation to give the lecture. I have *for long* wished to be in your historic country, and have sat at home in Leningrad, on many an evening, with my soul in far-away India. Often, before the mind's eye appeared the majestic peaks of the Himalayas, the virgin tropical forests of Assam and the hot deserts of Rajasthan. *And*, I am happy to say, that at last, I am really here in India amongst my friends and colleagues. I hope that my visit to your country will be fruitful and will help to strengthen the relations between Indian and Soviet Botanists.

With your permission, Madam Chairman, I will now turn to the subject of my lecture.

Introduction

During the last decade good progress has been made in the study of the fossil floras of the U.S.S.R. and other countries of the northern hemisphere. The systematic composition of the fossil angiosperm floras is now much better known than formerly and many arbitrary and fantastic identifications made in the last century have been corrected or at least called in question. All this is connected with the more critical approach to the identification of fossil material, with the greater utilization of the herbaria of living species, and the significant improvements in palaeobotanical techniques and methods. Such comparatively new fields of fossil botany as cuticular analysis, pollen analysis and the study of fossil plant debris, containing different "diaspores" (propagules), such as fruits, seeds, female cones of conifers and megaspores of heterosporous ferns, have now acquired great significance. Both pollen analysis and "diaspore analysis" (as I recently suggested calling this branch of palaeobotany) greatly broadened the possibilities of the ecological and statistical approach to the study of vegetational development in the past. Furthermore, diaspore analysis is characterized by the possibility of more exact and confident generic identification of plant remains than is the case when leaf impressions are used. During the last three decades important contributions in diaspore analysis were made by English, German, Polish, Russian and Japanese palaeobotanists, which greatly broadened and clarified our knowledge of the Tertiary floras. In several respects these new data do not agree with previous generalisations and conceptions. Thus, for example, the old idea of the origin of

angiosperms at high latitudes is now in conflict with many important palaeobotanical facts, as has been shown by Axelrod (1959). This problem is of special importance for the study of major migration routes of the Cretaceous and Early Tertiary. And no less important are the achievements of evolutionary systematics, historical geography and the ecology of living angiosperms. This is why we are in need of a new attempt to synthesize the accumulated data. But the accumulation of new facts is so rapid that it is necessary to consider any such new synthesis as only temporary.

To conclude these introductory remarks I should like to dwell on the nomenclature of the phytochoria of the past. In literature there are two kinds of designation for palaeophytochoria. One of them is based on the names of the localities of corresponding taphofloras. Such, for example, are the names of the Tertiary phytochoria " Gelindenian ", " Poltavian ", and " Turgaian ", proposed by Kryshtofovich. The other more usual way of designating past phytochoria is that which is based on the names of the geographical territories (continents and parts of continents, islands, the marine basins, and so on) occupied by them. Such, for example, are the names of the Permo-Carboniferous phytochoria " Euramerican ", " Angarian ", " Cathaysian ", and " Gondwanian ", proposed by Gothan. The second way is more in accordance with the principles of nomenclature of phytochoria accepted in neobotany, and is therefore more preferable. Such names as " Poltavian " or " Turgaian " are more expedient to keep for the designation of definite types of taphofloras. For example, we may say that the Palaeocene taphoflora of Kamyshin is of the Gelinden type, but the phytochorion itself should be named Tethyan-Tertiary (Takhtajan, 1961: 118) or Tethyan (Szafer, 1961: 193) rather than Poltavian or Gelindenian.

Zonation and Major Phytochoria of the Late Cretaceous

From the very beginning of the expansion of the angiosperm floras, a definite geographical zonation and regional differentiation into distinct choria is noticeable. In the Late Cretaceous not only latitudinal zones in the distribution of angiosperm floras were expressed, but also a distinct floristic differentiation within these zones. The main differences between tropical and temperate angiosperm floras were already manifest in the Late Cretaceous, and, within the limit of the Cretaceous Holarctic flora, two great phytogeographical regions are distinctly outlined. Subsequently during the Tertiary these two regions developed into two subkingdoms of the Holarctis — Boreal and Tethyan or Ancient Mediterranean. The Boreal subkingdom, as I see it, is only a part of the Holarctis or of the Boreal Realm of Engler and Good, because it does not include the Ancient Mediterranean or the Tethyan. On the other side our Ancient Mediterranean or Tethyan subkingdom which includes only the Old World part is smaller than Popov's Ancient Mediterranean region, but it is larger than Engler's Mediterranean region. In the Tethyan subkingdom I include the following regions: Macaronesian, Mediterranean, Irano-Turanian, Central-Asiatic and Saharo-Sindian.

Now the Boreal and the Tethyan phytochoria are so much differentiated both from the floristic and geobotanical point of view, that they should be ranked higher than regions, but at the same time they are not sufficiently differentiated to be considered as kingdoms. The intermediate name of " Subkingdom ", therefore, seems to me the most appropriate for them. But certainly in the remote geological past subkingdoms and kingdoms originated as regions or even provinces. Therefore, while speaking about the Late Cretaceous

and the Early Tertiary I shall call them regions.

The northern temperate and cold parts of the Late Cretaceous Holarctis were occupied by the vast Boreal-Cretaceous region. A purely temperate flora was dominant in this region, mostly consisting of mesophilous, broad-leaved, mainly deciduous trees and shrubs, such as *Acer, Alnus, Betula, Cocculus, Corylus, Credneria, Fagus, Grewispsis, Lindera, Magnolra, Platanus, Quercus, Sassafras, Viburnum, Zizyphus*, etc., as well as *Ginkgo*, different conifers (including *Agathis borealis* Heer and *Sequoia*) and ferns. The Boreal region of the Late Cretaceous occupied the territory corresponding to Northern and North-eastern Europe, Kazakhstan, Siberia, the far east of Russia, Japan, Korea, a part of North America and the Arctic. The main fossil floras of this region of the U.S.S.R. are known from Western and Central Kazakhstan, especially along the river Kuldenen-Temir — a tributary of the Emba river, to the north-west of the Aral Sea and on the north-western extremity of the Kara-Tau mountains from the right bank of the river Ayat on the eastern slope of the Southern Urals; from Simonovo near Achinsk on the right bank of the Chulym river, and from some other localities in the same Chulym-Yeniseian basin; from the Lena-Vilui basin in Eastern Siberia, from the island New Siberia, and from many places in the far east of Russia. The leaf remains of *Sciadopitys* (*S. uralensis* Dorof. et I. Sveshn.) were found in the Cenomanian-Turonian deposits near the hamlet of Verkhniaya Siniuchika in the Sverdlovsk district. Some pollen floras have been investigated from Central Russia and from the basin of the Emba river, the Northern and Central Urals and from Transuralia, Western Siberia, the Turgai depression, the far east of Russia, etc.

Within the vast territory of the temperate Boreal flora noticeable regional differentiations into minor phytochoria were outlined in the Late Cretaceous. Thus, the Late Cretaceous temperate floras of Europe and Greenland were evidently more thermophilous than those of the Angara continent. There were also differences between the western and eastern floras of the Angara. In his paper on the Upper Cretaceous flora of North-western Kara-Tau, Jarmolenko (1935) noticed the difference between the Late Cretaceous flora of the eastern slope of the Urals, of Western Siberia, of Western Kazakhstan (which he called the Chulymian type of flora) and the so-called Ghilakian flora of Sakhalin. Later Pokrovskaya (Pokrovskaya and Stelmak, 1960), using pollen-analytical data, distinguished two regions — the Ural-Turgain-Siberian and the Far-eastern, which roughly correspond to Jarmolenko's Chulymian and Ghilakian floras. But I prefer to consider these two types of floras as two different subregions within the Boreal-Cretaceous flora. The names Western-Angarian and Eastern-Angarian would be most appropriate for them. But the actual boundary between these two subregions, as well as their floristic characteristics, is still very vague. It must be said that the subdivision of the Boreal-Cretaceous region into definite phytogeographic subregions, and especially into provinces, is still premature.

As some pollen-analytical data clearly show, there was a warming trend in Siberia which began at the end of the Turon and continued during the Senon and Danish.

To the south of the temperate Boreal-Cretaceous region there extended the subtropical Ancient Mediterranean or Tethyan region of the Late Cretaceous. The boundary between the Boreal-Cretaceous and Tethyan-Cretaceous regions crossed Europe through the middle of England, the southern part of the Scandinavian peninsula, the Baltic Sea, Middle Russia, the northern coast of the Caspian Sea,

and extended further through the Aral Sea, lake Balkhash, and possibly Mongolia and the northern part of China.

Over all the territory of the Tethyan-Cretaceous flora the subtropical climate dominated, with a more or less dry summer (particularly clearly expressed in its eastern part), and it was characterized by the significant role of evergreen trees and shrubs, among which there were many Lauraceae and Fagaceae. Palms were also characteristic of this region. There were also some deciduous plants, usually comparatively narrow-leaved, which here and there reached a high percentage. Ferns of the Tethyan-Cretaceous region were of a more thermophilous type than in the Boreal-Cretaceous region, and among gymnosperms there were in some places rather many Araucariaceae and even Bennettitales. The differences between the two regions were not very great, though they were distinct enough. They were expressed mainly in the species composition and to a lesser extent in the generic composition.

The Tethyan-Cretaceous subtropical flora was particularly characteristic for the islands situated on the territory corresponding to modern South Europe and the Caucasus. A rich flora of this type is known from the Cenomanian beds of North-western Czechoslovakia. But in spite of some special papers devoted to this flora our knowledge of it is far from satisfactory. A considerable part of the identification is wrong, as for example *Dryandra*, *Grevillea*, *Eucalyptus* and others, and all the flora needs a revision using modern palaeobotanical methods and techniques. But though there are many erroneous identifications, the whole appearance of the flora leaves no doubt but that there were many "exotic" subtropical elements among the angiosperms, as well as among the gymnosperms and ferns. Cenomanian floras of more or less similar type are known from Niederschona near Freiburg, from Portugal, and from Southern Transcaucasia (between the villages of Gnishik and Aush).

The Transcaucasian Cenomanian (probably the Lower Cenomanian) flora was studied by Palibin (1937) and has recently been revised by me. Among the angiosperms *Comptonia yakovlevii* (Palib.) Takht. (= *Dryandra yakovlevii* Palib.) and species of *Platanus* predominate. There are also *Lindera jarmolenkoi* Imch., *Cocculus extinctus* Velen., *Cassia*(?) *atavia* Velen., *Aralia*(?) *daphnlphyllum* Velen., *Myrica zenkeri* (Ett.) Velen., *Populus daralagensis* Palib., *P.*(?) *hyrcanica* Palib., *Proteophyllum saportanum* Velen., *P. laminarium* Velen., *Betulites obovatus* Palib., *Paliurinella paffenholzii* Palib., *Myrtus*(?) *araxena* Palib., *V. burnum* sp., *Smilax praeexcelsa* Palib., an enigmatic form-genus *Pseudoginkgo bohemica* Velen. et Vinicl., etc. There are various conifers such as *Widdringtonites reichii* (Erringsh.) Heer and *Sequoia rechenbachii* (Geinitz) Heer (which are the most abundant), *Araucaria angusta* (Palib.) Takht. (= *Protodammara angusta* Palibin), *Brachyphyllum araxenum* Palib. and *B. obesiforme* Sap., leaves of *Pinus*, and only one fern, *Gleichenia shaparenkoi* Takht. Species of *Comptonia*, *Myrica* and *Proteophyllum* were sclerophyllous whereas *Platanus*, *Populus* and *Betulites* were broad-leaved. The Fagaceae and evergreen species of Lauraceae are absent in this flora.

Possibly the Senonian flora of Potylicz in the Western Ucraine (near Rava-Russka in the Lovov district), described by Novak (1907), also borders upon this type. This flora, which unfortunately has not yet been revised, is less xerophilous than that of Transcaucasia, but its floristic composition is in general subtropical.

The subtropical zone undoubtedly also passed through Central Asia and a considerable part of China, but the Upper Cretaceous plant-remains from these countries are almost unknown. The dominant types

of vegetation here were probably of a xerophilous character (Kryshtofovich, 1954). As is now evident on the basis of some lithological data, the aridization of climate in some regions of the northern hemisphere, which was so characteristic of the Late Jurassic, continued into the Cretaceous. During the Late Cretaceous there was an extensive belt of arid climate which stretched from Spain and North Africa through Western and Central Asia to Eastern China and North-eastern Indo-China (Strakhov, 1960), embracing both the southern parts of the subtropical and the northern parts of the tropical zones. On the territory corresponding to South Europe, North Africa and Western Asia, there were no extensive land masses but only islands, and the xerophilous vegetation probably had no favourable conditions for development. On the contrary, the arid belt occupied a vast territory on the Angara continent, including Central Asia and a considerable part of China, especially its north-western and northern regions. This arid zone of the Angara continent was probably one of the most ancient centres of development of the xerophilous angiosperm flora.

The data on the existence of arid territories with xerophilous vegetation within the Tethyan-Cretaceous region are mainly indirect. This is explained by the unfavourable conditions for plant fossilization in dry climates. Therefore, the study of the past history of xerophilous vegetation must still be based upon indirect data, in particular upon palaeozoological data. Very important results were obtained also from studies of the modern floras of arid regions, the study of their endemism and the systematic and geographic relations of their most important components. From these phytogeographic and taxonomic investigations many authors have already attributed a great antiquity to the desert floras of Asia.

The Development of the Early Tertiary Phytochoria

By the beginning of the Tertiary the geographic differentiation of the angiosperm floras is stronger and the phytochoria are differentiated more clearly. All the subsequent history of the Tertiary floras is characterized by their increasing zonal and regional differentiation. The vast Boreal-Cretaceous region develops into the Boreal-Palaeocene, and the Tethyan-Cretaceous region develops into the Tethyan-Palaeocene. The Boreal-Palaeocene region more or less corresponds to Kryshtofovich's (1955) Greenlandian province, whereas our Tethyan-Palaeocene region corresponds only to a small part of the Gelindenian province. These two regions were certainly not the only phytogeographic regions of the Early Tertiary, even in the extratropical part of the northern hemisphere. For example, in the east, the Boreal and Tethyan Tertiary regions possibly passed imperceptibly into the East Asiatic region; and in the arid regions of North America the " Madro-Tertiary " flora was developing, the pattern of whose history was given by Axelrod (1958). But it is necessary to notice that the phytogeographical " regions " of the Cretaceous and of the Tertiary are virtually zones of vegetation rather than real floristic regions. The data are too scarce for satisfactory floristic characterization of these " regions ". Therefore, we must look upon all these " regions " as very provisional.

The Boreal-Palaeocene angiosperm flora consisted of many deciduous genera, many of which grow over almost all the territory of this huge region. In deciduous Boreal-Palaeocene forests, especially in warm temperate parts of the region, there were possibly also some evergreen species. Some deciduous arborescent plants reached Northern Siberia, the Arctic islands, and even the Polar area where, as the palaeobotanical data indicate, a cold temperate

climate of the oceanic type dominated. To the south the cold temperate climate gave place to a warm temperate one, which further south still passed very gradually into the subtropical climate of the Tethyan-Palaeocene region. The latitudinal zonation was clearly expressed during the Early Tertiary, but in contrast to the present time the zones were more or less shifted northwards. The boundaries between these zones, however, were not stable and underwent significant changes.

To the south of the Boreal-Palaeocene region stretched the subtropical Tethyan-Palaeocene region. A typical subtropical flora was characteristic for this chorion, which consisted predominantly of evergreen trees and shrubs with some admixture of thermophilous deciduous species. The herbaceous cover in subtropical forests of the Tethyan-Palaeocene region was probably considerably poorer than in the temperate forests, although there were many more lianas and possibly also some epiphytes. In the majority of cases the greatest role in these forests was played by numerous members of the Lauraceae and thermophilous and mostly evergreen representatives of Fagaceae. The most characteristic genera were *Cinnamomum, Litsea, Neolitsea, Persea, Laurus* and *Quercus* (incl. *Cyclobalanopsis*); various subtropical palms were also very characteristic.

In the north and on the mountains the subtropical forests gradually passed into forests of the temperate type, and on the shores of the Tethys Sea they contained a considerable number of tropical elements. In the Palaeocene and the Eocene the northern limit of subtropical vegetation was shifted to rather high latitudes (but generally no more than 15°), while tropical vegetation was shifted to a lesser degree (no more than 10°). Already Berry (1929) came to the conclusion " that none of the fossil floras of the Temperate Zone that palaeobotanists have termed tropical, are in the strict sense of the word ' tropical '." The same idea was even more forcefully expressed by Barghoorn (1953). Other palaeobotanists as well as geologists (see, for example, Strakhov, 1960: 1963) are now coming to the same conclusion. Numerous palaeobotanical data show clearly that on the territory of Europe, and even more on the territory of Northern Asia, there was no zone of purely tropical vegetation, though many tropical elements, and even some associations of them (as, for example, the stemless palm *Nipa* and its associates), sometimes penetrated rather far north. But unfortunately in literature the botanical myth of the existence of a tropical zone on the territory of Europe and the Caucasus during the Palaeogene is still maintained. In reality the evergreen subtropical vegetation was present and was in many places luxuriously developed. It consisted of Holarctic elements, though in certain places there was considerable admixture of Palaeotropical elements, as may still be observed, for example, in the subtropical zone of South and Southwest China. From these facts one may conclude that to judge the general character of the plant societies and vegetational and climatic zones of the past it is necessary to take into consideration the whole composition of each flora, not only its separate representatives.

Palaeocene Floras

There are comparatively few fossil floras of definite Palaeocene age in Eurasia and particularly in the U.S.S.R., and unfortunately not all of them have been satisfactorily studied. In the European part of the U.S.S.R. there are a few floras of the Late Palaeocene (Sparnacian or Saratovian) age in the Povolzhye. The main localities are (1) Ushi mountain near Kamyshin, (2) near the village of Akshuat near the sources of the river Sviyaga in the Korsun

region, (3) near Toporkino and Lesnoe Matunino in Syzran region, (4) in the environs of Saratov and Volsk, and some other places. Also of the Palaeocene age are the sandstones to the east of Lebedyan in the Lipetsk district, from where the so-called *Dryophyllum rossicum* L. Kretsch. was described. Further to the east the Palaeocene (and probably also the Sparnacian) floras occur on the eastern slopes of the Urals near Chelyabinsk at the village of Smolino and in the basin of the river Or in the Khalilovo region of the Orenburg district, in the southern Urals along the brook Ramankul and on the spurs of the Mugodjaras and probably in the chocolate clays of Kiin-Kerish mountain situated on the eastern extremity of the Zaisan lake in Eastern Kazakhstan. Unfortunately there are not any certain Palaeocene floras in Siberia and Middle Asia; and only in the far east of Russia are there some localities of more or less certain Palaeocene age on the western coast of Kamchatka, on the Zee-Bureyan Plain and possibly also near the village of Raichikha and on the Rarytkin Range. Lastly there are many angiosperm floras of more or less definite Palaeocene age in the Arctic. From the palaeophytogeographical point of view, of special importance are the floras of Greenland, Spitsbergen, Franz Josef Land, the vicinity of Tiksi (near the Lena delta), New-Siberian Islands and lake Tastakh in North-eastern Siberia. This last flora was studied by Kryshtofovich (1958), who considered it (as well as the Rarytkin flora) to be " undoubtedly Palaeocene ".

Though the Palaeocene flora of the Arctic has not been studied enough, its general features are already more or less clear. According to Kryshtofovich (1955) " the most characteristic feature of the Palaeocene flora of the northern zone is the gigantic size of the leaves of some dicotyledons — up to 40 cm. in length with great width and delicate consistency ". These dimensions and the consistency of the leaves indicate the great humidity of the purely oceanic climate of that time. One of the most characteristic elements of the flora of the northern zone was *Trochodendroides arctica* (Heer) Berry, which is known also from the Late Cretaceous. It belongs to the Cercidiphyllaceae and according to Brown's opinion (Brown, 1939) must be combined with the natural genus *Cercidiphyllum*. It was a very widely distributed plant known from many localities in the northern zone, though it is hardly probable that it was one of the dominants in the Late Cretaceous and Palaeocene forests. The fern genus *Onoclea*, which is now monotypic and distributed in East Asia and North America, was very characteristic. *Ginkgo*, and such branch-deciduous conifers as *Metasequoia*, *Taxodium* and *Glyptostrobus*, were widely distributed. Species of *Platanus*, *Quercus*, *Alnus*, *Corylus*, *Betula*, Vitaceae, Tiliaceae and Juglandaceae, as well as *Macclintockia* spp., were also very characteristic of this zone. These North Siberian large-leaves floras were considered by Kryshtofovich (1953) as a separate Yakutian province.

Rather different from the Yakutian floras was a most interesting and unfortunately very incompletely studied flora found on the Lozva river on the eastern slope of the Urals north of 61st parallel (Kryshtofovich, 1933). It contains *Sequoia langsdorfii* Brongn. (*Metasequoia disticha*? A.T.), *Sequoia reichenbachii* (Gein.) Heer, *Potamogeton uralense* Kryst., *Trochodendroides richardsonii* (Heer) Krysht., *Corylus macquarrii* Forbes, *Ficus*(?) *uralica* Krysht., *Magnolia inglefieldii* Heer, *Ilex longifolia* Heer, *Macclintockia trinervis* Heer, *M. lyellii* Heer, *Quercus* sp., etc. According to Kryshtofovich this flora is of the Palaeocene or more probably of the Late Cretaceous age. But he indicates a clearly expressed similarity between the Lozva flora and those

of the praebasaltic strata of West Greenland, the Palaeocene age of which is now definitely established (Koch, 1963). Baranov (1959) is also inclined to recognize the Palaeocene age of this flora. If this is right, we must say that the Palaeocene flora of Greenland continued as far as the Northern Urals and following Kryshtofovich we may recognize two provinces in Arctic and Subarctic Eurasia during the Palaeocene: Yakutian and Greenlandian or Thulean (Kryshtofovich, 1933).

The third type of Palaeocene fossil flora within the limits of the Boreal-Tertiary region is that of the Zee-Bureyan plain in the far east of Russia. It is the only certain Palaeocene flora known from the temperate zone of Siberia and the far east of Russia. Like the Late Cretaceous floras of the far east of Russia this flora was almost entirely deciduous and predominantly narrow-leaved. It consisted of species of *Salix*, *Myrica* and *Juglans*, *Populus balsamoides* Goepp., *Ficus ratonensis* Knowlt., a large-leaved deciduous *Magnolia gigantea* Baik., *Lindera venusta* Lesq., *Litsea*, *Cercidiphyllum*, *Platanus*, *Gymnocladus*, *Robinia amurensis* Baik., *Sophora*, *Ailanthus*, *Cotinus*, *Acer*, *Paliurus*, *Actindia*, *Cornus*, *Vaccinium praeatrococcum* Baik., *Diospyros ficoidea* Lesq., and many leaf-impressions of *Hovenia thunbergii* (Nath.) Baik. and *Zizyphus matutina* Krysht. As Baikovskaya (1950) points out, this flora in spite of its antiquity shows a great similarity with the modern flora of Japan and China. A very remarkable feature of this fossil flora is that it has more similarity with the modern warm temperate East Asiatic flora than with the younger Tertiary floras of the far east of Russia. It is possible that this flora indicates the existence of a distinct palaeophytogeographic province in the warm temperate part of the far east of Russia.

In the Palaeocene the northern boundary of the subtropical Tethyan region crossed Europe through Southern England, Belgium, the Baltic Sea, the Syzran and Chelyabinsk districts and the South Urals. Further to the east the northern boundary possibly crossed South Kazakhstan, North China and Japan, but we have no direct evidence of it yet. Thus the northern limit of the subtropical flora was shifted in Europe rather far to the north. This is explained by the tropical Tethyan currents.

The most western localities for fossil remains of the Palaeocene subtropical flora are those of the south of England. The British Palaeocene floras are of the Thanetian age (Thanet Sands of Herne Bay, Kent) and Sparnacian age (Reading and Woolwich Beds). The material is too scanty to suggest any definite conclusions on the climate, but according to Chandler (1961), all the recorded facts taken together suggest that the climate during the deposition of the Woolwich and Reading Beds must have been very warm and damp, though it was subtropical rather than tropical, which had already been suggested by Gardner (1878). The only definitely tropical angiosperms among the known plant remains of the British Sparnacian Beds are *Oncoba variabilis* (Bowerb.) E.M. Reid et Chandl. of the Flacourtiaceae, which is near to living African and Arabian species *O. spinosa* Forsk. (Chandler, 1961), and *Mastixia* sp. (Chandlner, 1964). As to *Natsiatum eocenicum* Chandl., which is also considered by Chandler as a tropical plant, it must be assigned to *Hosiea* a subtropical genus closely related to the tropical genus *Natsiatum*. There are only two living species of *Hosiea*—*H. sinensis* (Oliv.) Hemsl. in Central China (Hunan, Hupeh and Szechaun) and *H. japonica* (Makino) Makino in Japan. According to Chandler, the living Chinese species *Hosiea sinensis* (which she names *Natsiatum sinense* Oliver) appears to be most nearly related to the fossil. Thus the systematic relations of *Hosiea eocenica* (Chandl.) Takht. indicate a definite

subtropical affinity. The majority of other species, mentioned by Chandler, have extratropical (subtropical and partly temperate) affinities, such as *Sequoia couttsiae* Heer, *Libocedrus adpressa* J. Gardner, *Carpinus davisii* Chandl., *Liquidambar palaeocenica* Chandl., *Trochodendroides smilacifolia* (Newb.) Krysht. (mentioned by Chandler under " Hamamelidaceae Genus? "), *Phellodendron costatum* Chandl., *Vitis pygmaea* Chandl., *Abelia palaeocenica* Chandl., *Sambucus* sp.

The Palaeocene flora of North-eastern France was also subtropical with an admixture of tropical elements. The predominant families were Fagaceae and Lauraceae represented by different genera, both evergreen and deciduous.

One of the most interesting Palaeocene floras of Western Europe is that of Gelinden in Belgium which is of the Early Thanetian age and is somewhat older than the Thanet Sands of England (Chandler, 1964). Unfortunately, there has been no revision of this flora since the classical works of de Saporta and Marion (1873, 1878), and we have to use the old data, but with some corrections of identification. As in the Palaeocene floras of North-eastern France, the dominant families here are also Fagaceae and Lauraceae, which underlines the subtropical character of the flora. The Fagaceae are represented by several evergreen and deciduous species of *Quercus*, mainly by *Q. diplodon* Sap. et Marion, and some species of the organ-genus *Dryophyllum*. The Lauraceae consist of *Cinnamomum* spp., *Apollonia tetrantheroidea* (Sap.) Takht. (= *Phoebe*? *tetrantheracea* Schimp.), *Persea palaeomorpha* Sap. et Marion, *Ocotea apicifolia* (Sap. et Marion) Takht. (= *Oreodaphne*? *apicifolia* Sap. et Marion), *Litsea* spp., *Laurus omalii* Sap. et Marion and *Neolitsea* sp. (" *Daphogene sezanuensis* Sap."). Also very frequent in this flora are *Celastrophyllum crepinii* Sap. et Marion, with its characteristic coriaceous leaves, and especially *Dewalquea gelindenensis* Sap. et Marion — an enigmatic dicotyledonous organ-genus which most probably belongs to the family Araliaceae.

The Russian subtropical Palaeocene floras are very near to that of Gelinden and have some common or closely related species and similar ecological features. One of the richest floras is that of Ushi mountain near Kamyshin in Povolzhye, which in spite of the series of papers published by Palibin, Krasnov and Baranov, is still very insufficiently studied. As in Gelinden the main role here is played by various species of Fagaceae and Lauraceae. Very frequent in this flora are species of *Quercus*, especially *Q. kamyschinensis* (Goepp.) Ung. The Lauraceae are represented by *Cinnamomum* spp., *Litsea magnifira* Sap., *Persea palaeomorpha* Sap. et Marion, *Persea* (*Laurus*) *delessii* Sap. Different species of *Magnolia* are characteristic, as well as *Betula gypsicola* Sap., *Fagus deucalionis* Ung., *Ilex stenophylla* Ung., *Viburnum volgense* Krassn., several species of the organ-genus *Dewalquea*, an enigmatic fruit(?) impression *Oxycarpia fibaria* Trautsch. *Chamaecyparis belgica* Sap. et Marion, *Podocarpoxylon* spp., *Osmundites kamyschinensis* Krassn., etc. On the eastern slopes of the Urals in the eastern region of the Orenburg district in the basin of the Or river there are some rich floras of the Kamyshin type containing remains of *Chamaecyparis belgica* Sap., *Dewalquea grandifolia* Krassn., *Quercus* cf. *diplodon* Sap. et Marion, *Viburnum giganteum* Sap., *Dryophyllum dewalquei* Sap. et Marion, *Comptonia schrankii* (Sternb.) Berry, *Magnolia* sp., *Ficus* sp., etc.

Of the same Kamyshin type are also the Palaeocene floras of the Southern Urals (along the brook Romankul) and of the spurs of the Mugodjaras. Noticeable in the Romankul flora are a large-leaved *Viburnum giganteum* Sap. var. *uralense* Baran., *Dewalquea gelindensis* Sap. et Marion, *Aralia*(?) cf. *venulosa* Sap. et Marion, different species of *Cornus*, a remarkable *Camelia*

(*Ternstromiacites*) *uralensis* Vasilevsk. ex Baran., *Magnolia* sp., various Lauraceae (*Cinnamomum*, *Daphnogene*, *Persea*), *Quercus* sp., *Ficus uralica* Vasilevsk., *Grewiopsis uralensis* Vasilevsk. and *Chamaecyparis belgica* Sap. et Marion (wood). The majority of Lauraceae species are large-leaved, especially *Daphnogene gigas* Baran., *D. vasilevskajae* Baran. and *Cinnamomum uralicum* Baran. Leaf impressions of *Viburnum giganteum* predominate in this flora (Baranov, 1959). By its composition the Romankul flora is rather near to the Kamyshin one, but is characterized by the unusually large leaves of many species, which indicates more humid climate. Unfortunately this most interesting flora has been studied even less than that of Kamyshin.

The rich flora of the Mugodjaras, which is very near to those of Povolzhye (Palibin, 1936), is also very weakly studied. Characteristic for this flora are: *Quercus* cf. *diplodon* Sap. et Marion, *Dewalquea grandifolia* Krassn., *Chamaecyparis belgica* Sap. et Marion, some species of *Cinnamomum*, *Cornus mugodscharica* Krysht. and some other species, which are identical with those of the Kamyshin flora. In the Mugodjaras we have possibly the eastern boundary of the subtropical flora of the Gleinden-Kamyshin type (Palibin, 1936).

The Palaeocene floras of Europe from the Paris Basin and Belgium to the Southern Urals and the Mugodjaras apparently constituted a separate phytogeographical province. The flora of this province resembles that of some regions of the modern Eastern Himalayas and South-west China. Taxonomical and adaptive relations of this flora suggest that it was derived from the subtropical flora of Sino-Himalayan type.

Unfortunately very little is known about a very interesting flora from the horizon of chocolate clays of the mountain Kiin-Kerish in Eastern Kazakhstan, which is probably either of the Late Cretaceous or more likely of the Palaeocene age (Iljinskaja, 1963). Here are found *Nitophyllites zaisanica* Iljinskaja (a probable representative of Podostemaceae), *Leucothae*(?) *kushkensis* (Vassilevsk.) Iljinskaja, *Phragmites ceningensis* A. Br., *Ilex palaeogena* Iljinskaja, *Carex schenchzeri* Heer, *Cyperites custeri* Heer, *Dryophyllum curticellense* (Wat.) Sap. et Marion, *Lindera vassilenkoi* Iljinskaja, *Protoacerophyllum perforatum* Romanova (Platanaceae), *Pterospermites minor* Ward, *Poacites* sp., *Torreya* sp. and *Salvinia natanella* Shap. It is interesting that *Ilex palaeogena* is near to the Chinese *I. dipyrena* Wall (Iljinskaja, 1963).