POLLEN MORPHOLOGY OF ANGIOSPERMS AND PALEOFLORISTIC AREAS AND PROVINCES AT THE BOUNDARY OF THE CRETACEOUS AND PALEOGENE

E. D. ZAKLINSKAIA

Geological Institute of the Academy of Sciences of the U.S.S.R., Moscow

ABSTRACT

The establishment of natural affinity between ancient angiosperms and taxa of recent flora can be based on palynomorphological studies. The structure, number and distribution of apertures are important features.

At the beginning of the Late Cretaceous period angiosperms had pollen with primitive but already distinct apertures. Their relationship with Salicales, Fagales, Platanales, Eucommiales (?), can be established.

During the Late Cretaceous, pollen type with syncolpate apertures (*Duplospores-Sporopollis-Sincolporites*) become differentiated, which may be linked with the Santalales, Myrtales and Sapindales. In the Upper Senonian-Paleocene pollen with extremely complicated and varied apertures become differentiated partially with inequipolar symmetry (*Aquilapollenites, Pentapollenites, Pemphixipollenites, Betpakdalina, Kryshtofoviana, Porotrichotomosulcates* types). Some taxa of these may be associated with the families Loranthaceae, Olacaceae, Simarubaceae, Palmae (?), Euphorbiaceae etc. Genera and species included above have narrow stratigraphic ranges and distinctly outlined areals.

To the same period belongs the differentiation of pollen type with a three equatorial aperture (*Normapolles, Proteacidites, Triorites* and *Triatriopollenites*), which are links with morphological types of pollen of Proteaceae, Myricaceae, Casuarinaceae, Fagaceae, Rubiaceae, Ulmaceae, Juglandaceae and Betulaceae.

With the help of morphological groups we succeeded to establish sequential stages and phases in the history of the development of angiosperm flora and determine their role in the formation of botanical-geographical regions and provinces.

During the Late Cretaceous-Paleogene boundary period relationship is established between Pacific and Atlantic floristic areas of Eurasia on one hand the North America and the continents of the Southern Hemisphere on the other.

ONE of the most important events in the history of the vegetation of the earth — is the change of mesophytic floras of the Gymnosperms and the Pteridophytes to the predominance of Angiosperms during the Upper Cretaceous epoch. This event had been prepared much earlier, is shown by a high organization of Angiosperms of the Upper-Cretaceous as seen both in the macroscopic remnants and in the pollen spectra.

There exist many hypotheses about the place and time of the appearance of the Angiosperms, but none of them has yet received recognition. The data of the spore — pollen analysis showing an early appearance of the Angiosperms in the subequatorial area and their wide distribution in temperate areas of both hemispheres supports indirectly the hypothesis of Axelrod (1959a), who assigns the appearance of the Angiosperms to the tropical belt of the earth.

Pollen morphology is one of the methods, which helps to establish the natural affinity of ancient Angiosperms with the taxa of the recent flora. As it is known, one of the principal morphological peculiarities determining the systematic affinity (to a certain degree) with the taxa of the recent flora is the number, distribution, structure of germinal apertures of a pollen grain. The pollen-spore data show that the pollen of earlier Cretaceous Angiosperms belonged chiefly to *Tricolporites, Tricolpites, Eucommidites* and others. The information about the earlier remnants of Angiosperms according to the data of leaf impressions refer to the higher stages of the Lower Cretaceous of New Zealand, Portugal, Holland, the USSR, and other countries (AXELROD, 1959b; KRISTOFOVITCH, 1929, 1957; BERRY, 1911; SAPORTA, 1894; VACHRAMEEV, 1952; MTCHEDLISCVILI, 1961 and others).

Many findings of leaf impressions of early Angiosperms are mentioned in literature under the names approaching to the taxa in the recent floras, i.e. *Proteaphyllum, Sapindopsis, Aralia, Salix,* Menispermaceae, Nelumbonaceae, etc. Judging by these names, these findings were phylogenetically near to such taxa of the recent flora, whose pollen predominantly have a tricolporate and trisincolpate structure. Findings (which arise no doubt) undoubtedly belonging to real Angiosperms

(both by their pollen and leaf impressions) are referred to the upper stage of the Lower Cretaceous and Upper Cretaceous.

However, the early-cainophytic flora of the earth still distinguished greatly from the typical paleogene flora, including a great number of representatives of mesophytic Gymnosperms and Pteridophytes. The appearance of the Paleogene flora is referred to the beginning of the Cainozoic Epoch. This becomes particularly clear when using the method of spore-pollen analysis.

It is difficult to overestimate the importance of the angiospermous-pollen for stratigraphy and the history of the Upper Cretaceous flora as well as that of the early Paleogene flora.

The pollen and spore being encountered much more frequently, and taking into consideration the relative scarcity of macroscopic fossil remains in deposits between the Upper Cretaceous and lower Paleogene, the importance of the Angiosperm pollen becomes particularly great. Moreover, the method of spore-pollen analysis allows us to correlate marine and terrestrial sediments, this being practically impossible when using the data of macroscopic remains, as the findings in majority of the cases refer to the terrestrial facies only.

Judging by the data of the spore-pollen analysis, the variety of the Angiosperm species of the Upper Cretaceous in general as well as those of the early Paleogene (including, as we are inclined to believe, the flora of the Danian age) was large. In fact this variety was far greater than it was believed according to the findings of leaf impressions.

The complex Angiosperm flora of her Upper Cretaceous and early Paleogene flora in Eurasia determined according to the pollen, include to a greater extent the taxa having distant affinities with those of the recent flora of Holarctic area. We should say that they tend towards the taxa, whose areals are found within the tropical and subtropical zones, mainly in the Southern Hemisphere. The variety of the Upper Cretaceous and early Paleogene Angiosperm flora, as determined with the palynological data, is better than it could be done with the study of leaf impressions. It is possible that many plants of that time had a herbaceous habit, thus not allowing their leaves to be preserved as fossils.

In this connection Corner's (1954) hypothesis is of some interest. Corner supposes that the original Angiosperms may have been pachytual plants one part of which in the process of evolution was driven back to the undergrowth and became saprophytes and parasitic species. In fact, judging by the pollen, many taxa of the Senonian and early Paleogene flora, had their pollen very much similar to Santalaceae, Sapindaceae, Nymphaeaceae, Loranthaceae, Rafflesiaceae, Morinaceae, etc. The majority of their representatives in the recent flora of subtropics and tropics belong to the water and parasitic plants with a herbaceous habit.

Many angiosperm taxa developed at the boundary of the Upper Cretaceous and Paleogene epoch, as seen by the spore-pollen analysis, were widely distributed.

The limits of their spreading were traced simultaneously in both Hemispheres. One can also refer to the representatives of Proteales, Sapindales, a problematic group, classified in palynology as a form-genus *Aquilapollenites* (MTCHEDLISCHVILI, 1961 includes this genus in the subgroup of *Triprojectocites*), morphogenetic stemma *Normapolles* Pflug and stemma *Duplospores* Pflug, and many others taxa.

On the basis of comparison of palynological data from marine and terrestrial sediments (Cretaceous — Paleogene) one can establish a definite regularity in the development of the Angiosperm floras. The latter is expressed in a sharp change of pollen complexes belonging to different morphological types. The scheme of stages and phases established by us in the development of angiosperm floras according to palynological data is given in my earlier paper (1962) and therefore I shall not speak about it in the present paper. I shall just mention that on the basis of palynological data one can clearly trace stages in the history of Angiosperm development at the boundary of the Upper Cretaceous and Paleogene Epochs, which allows us to distinguish the Upper Cretaceous flora from the "eopaleogenic", including into the latter the floras of the so called Danian stage. The Upper Senonian floras (particularly of the Meastrichtian age) are rich in representatives in Angiosperms, whose pollen are grouped into morphological taxa like *Aquilapollenites* Rouse, *Kryshtofoviacites* Samoil. (=*Wodehouseia* Stanley), *Pentapollenites*

Pflug, *Normapolles* Pflug, *Proteacidites* Couper, *Sporopollis* Krutzsch, and others.

One part of the taxa of these genera begin to disappear in the early paleogene but their morphogenetic affinities may extend to the families of Loranthaceae, Olacaceae, Proteaceae, Morinaceae, Euphorbiaceae, Onagraceae, Santalaceae, Rafflesiaceae, Rubiaceae and others.

We assign the definite differentiation and development of morphological stems of *Triorites* Cooks. & Pike, *Triatriopollenites* Pflug, *Trivestibulopollenites* Pfl. to the early Paleogene. The same can be said about other morphogenetic affinities which can be traced to the Proteaceae, Myricaceae, Ulmaceae, Betulaceae, Juglandaceae and Fagaceae.

By means of palynomorphological range one can trace not only successive stages and phases in the development of the angiosperm flora of the Upper Cretaceous and the early Paleogene, but also bring to light the part of Angiosperms in the formation of paleofloristic areas and provinces of that time.

The Eurasian flora at the boundary of the Upper Cretaceous and the Paleogene was characterized as a whole by the Phanerophytic type of vegetational cover. The latter was enriched by various angiospermous taxa of the flora alien to the recent nature of the Holarctic area (pollen *Aquilapollenites*, Bombacaceae, Proteaceae) being widely spread.

In the "eopallogene" (including the Danian) flora the whole complex of the Angiosperm flora began to appear different. Amentifereae is mostly wide spread in the far East of Asia and on the island of Sachalin. All this flora can be united into an Euroasiatic floristic area, whose southern boundary approximately runs along the 20° northern latitude. Up till now it is difficult to trace this boundary because the Meastrichti-Danian-Paleocene flora of Southern parts of the Northern Hemisphere has been little known.

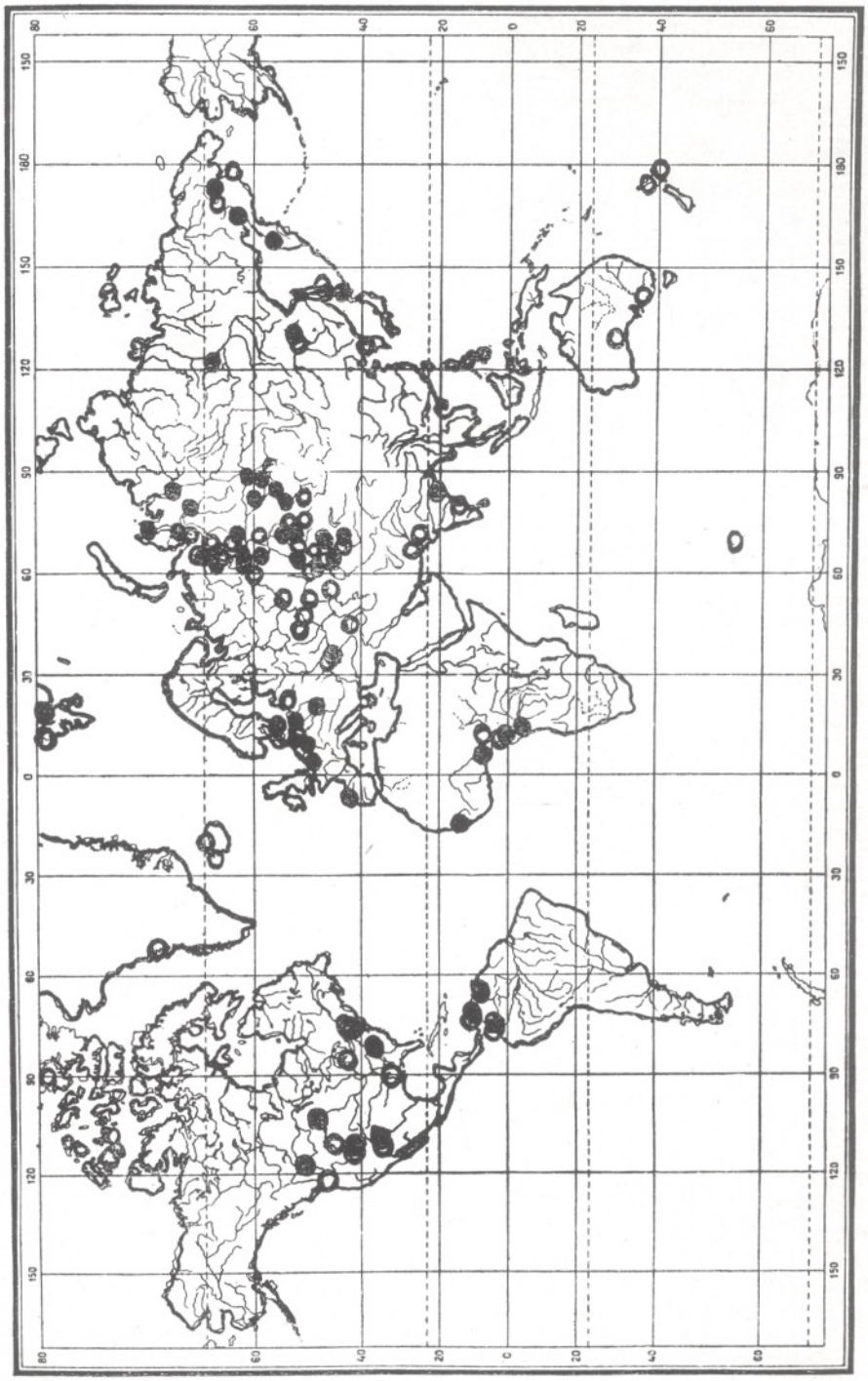
The boundary between the European (great variety of the representatives characteristic by the *Normapolles*) and the Eastern-Asiatic (a great variety of the representatives characterized by *Aquilapollenites* and Proteaceae) passed approximately between the 70 and 80° of eastern longitude. There existed a particularly xerophitic Turcmen-Kazakhstan province with the predominance of the "mixtum" palynological complex species from European and Eastern-Asiatic element and specific species of *Tricolporopollenites, Conclavipollis, Complexipollis, Lattipollis, Classopollis, Ephedripites, Triatriopollenites* and others. In the Eastern Asia there exists a Seaside-Sachalin subprovince, particularly characterized by an early appearance of Amentifereae (essentially by Betulaceae) and the representatives of Angiosperms with a pollen of a morphological type of *Trivestibulopollenites, Interoporopollenites, Tetraporopollenites* and *Triatriopollenites* in general.

The distinction of floristic area and provinces for the time between the Upper Cretaceous and Paleocene epochs fill up gaps in the records of the early Paleogene flora. As it is known, the floristic areas of the Upper Cretaceous epoch re-established by Vachrameev (1957) according to the macro-flora remains are assigned to the time dated as Senonian-Turonian. Kryshtofovitch (1955) distinguished the Greenland and Gelinden provinces of the Paleogene for the Northern Hemisphere, only on the basis of the Paleogene and the so-called "Danian" floras known at that time.

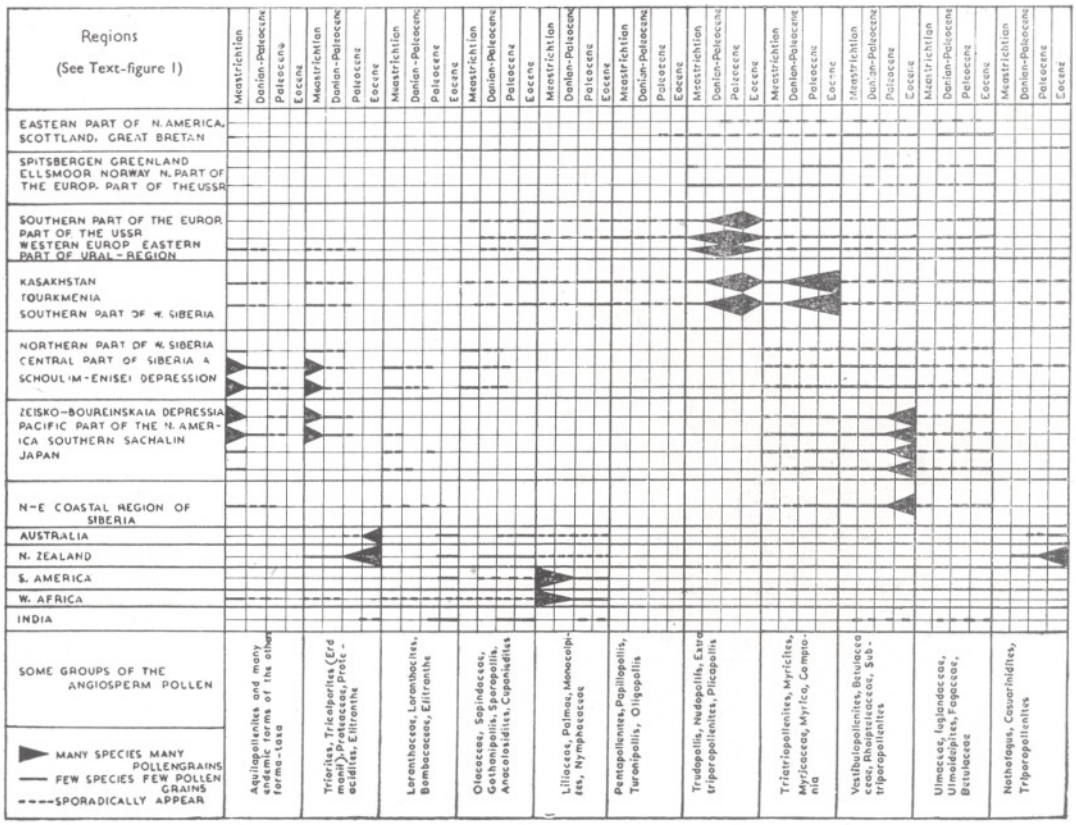
Thus the geography of the upper Senonian flora of Eurasia and Northern Hemisphere is not clear up till now.

If one adds to all the palynological data known at the present time from the territory of the Soviet Union, the information about the Meastrichian, Danian, Paleogene and Paleocene-Eocene floras, known at present for S. America, Africa, N. America, Spitzbergen, Greenland, Scandinavia, W. Europe, New Zealand, Australia, Antarctics, Japan and India (TEXT-FIG. 1) there will appear rather clear intercontinental floristic bonds (TEXT-FIGS. 2, 3). As for instance, rather clear floristic relationships between European province and Atlantic coasts of Northern America will be outlined. The Turcmen-Kazakhstan province has many common taxa with the floras of Africa (W. Africa-Gabon, Nigeria, Senegal, BELSKY, C. & BOLTENHAGEN, E., 1963) and partly of the Northern part of South America. A later flora (Paleocene-Eocene) confirms these relationships spreading into India.

The floras of Eastern-Siberian province reveal close relationships and affinities with floras of the same age of Japan and Pacific coasts of N. America. The data of the



TEXT-FIG. 1 — Position of the point of the Meastrichtian and Early-Paleogene sediments with the pollen-spore spectra. ●, Meastricht; O, Danian Paleocene.



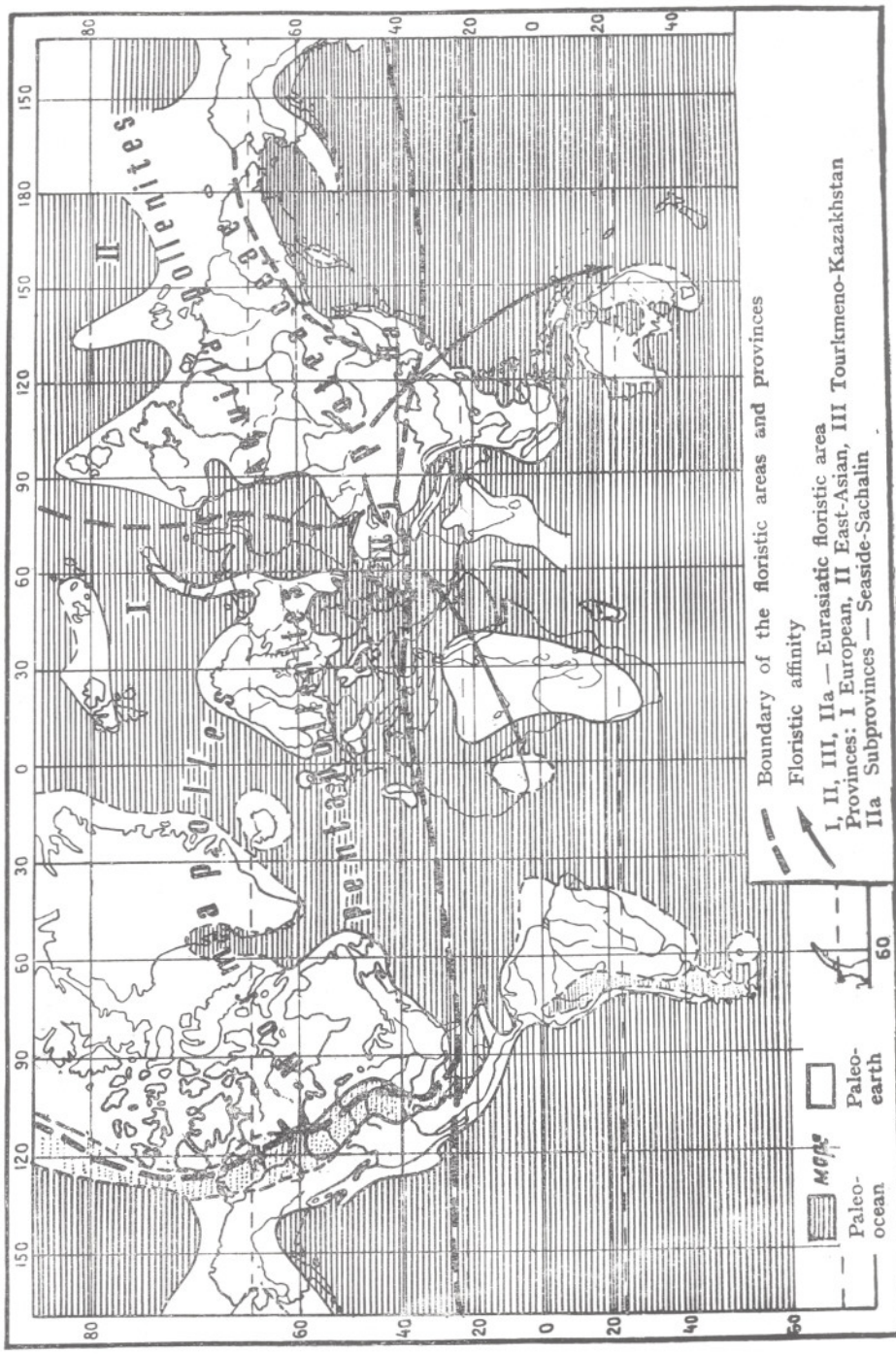
TEXT-FIG. 2 — Pollenstratigraphy of Upper Cretaceous — Paleogene boundary of Northern Hemisphere and some regions of the Southern Hemisphere.

pollen-spore analysis also confirm relationship of Late-Cretaceous floras of Eastern Siberian area with the paleogene floras of Australia and New Zealand.

The palynological material accumulated at the present time permits to correlate not only deposits of different facies within the same or various floristic provinces of N. Hemisphere.

Gradually it becomes possible to find ways for an intercontinental comparison. The main criteria for this comparison is of course a definite staging in the development of floras, which are expressed in different floristic areas and provinces by a different complex of taxa. At the same time there is gradually becoming known a number of genera and species, which can be found in various quantities in geofloras of the same age.

This fact puts them in the range of real guide fossils in stratigraphy. A number of species of *Aquilapollenites*, Proteaceae, *Tricolporites* Erdtm., *Triatriopollenites*, *Kryschtofoviacites*, *Sporopollis* etc. can be referred to such taxa. A number of them or in any case the nearest to them enter the complex of floras of tropical areas, islands and continents of the Southern Hemisphere, which are reservations of "living fossils", with a wide distribution within "Praeurasias" separated in the Upper Cretaceous epoch by the waters of the ancient Tethys.



TEXT-FIG. 3 — Floristic areas and provinces of the boundary of the Cretaceous and Paleogene.

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