

FLORISTIC ASSOCIATIONS BETWEEN EAST ASIA AND NORTH AMERICA: A STUDY OF THE RANGES OF SOME RECENT AND FOSSIL HIGHER PLANTS IN PRIMORYE, U.S.S.R.

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ABSTRACT

This paper presents a comparative study of recent and fossil (e.g. Fagaceae) floras from the temperate zones of North America and Primorye, U.S.S.R. The results showed fossil oaks from Primorye to be closely related to Asian and American species. At the same time, the former displayed some outward resemblance with European species on account of convergence.

INTRODUCTION

A COMPARISON of Cenozoic floras of North America and Primorye (Maritime Territory, U.S.S.R.) indicates a considerable number of common or very closely related species among various taxa. This mainly concerns the large family of Fagaceae, whose wide distribution among Cenozoic plant communities of North America and East Asia is common knowledge (Chaney *et al.*, 1944; Tanai, 1961; Tanai *et al.*, 1963; etc.). Our interest in Fagaceae became heightened as a result of new palaeobotanical finds in West Sikhote-Alin (Rettikhovka fossil flora). These finds not only allow existing plant collections on the Tertiary flora of Primorye to be substantially augmented, but they introduce certain corrections into relevant evolutionary concepts that had existed since Kryshtofovich (1955, 1958). Studies on the Rettikhovka flora led to the establishment of large numbers of various oak species, e.g. *Quercus* sp., very similar to *Q. endoana* Huzioka from the Miocene flora of Korea (Huzioka, 1972), *Q. protodentata* Tanai et Onoe, *Q. sinomiocenicum* Hu et Chaney and *Q. praegilva* Krysht.; *Q. lonchitis* Ung., regarded by Huzioka (1972) as part of *Castanea tanai*; and *Q. sichotensis* Ablaev et Gorovoi to-

gether with other Fagaceous genera, such as beeches, chestnut trees and, apparently, *Castanopsis* (Ablaev & Gorovoi, 1974). These finds confirm various statements on the autochthonous origin of the oak forests of Primorye (Soczava, 1945; Vassiliev, 1948; Dylis & Vipper, 1963; Kurentsova, 1968). Recent oaks do not represent a new growth, but are derivatives of former multi-component oak or chestnut-oak forests comprising the Far Eastern association of the Turgay type. Turgay forests covered considerable areas of the West Primorye plain and the Khasan-Barabash District.

The discovery of *Q. sichotensis* with compound-lobed leaves in the Rettikhovka flora is of certain interest from the botanico-geographical viewpoint. Previously, no such fossil oaks were observed in East Asia. Nor have they been found among the recent flora of East Asia, even though the genus *Quercus* is specifically very diverse there (Nakai, 1917, 1952; Ohwi, 1965; Wang, 1961; Chang Yung-Tyang, 1966; Menitsky, 1973). Thus, in the evergreen broad-leaved forests of China, over 150 *Quercus*, *Castanopsis* and *Pasania* species are observed (Wang, 1961).

The fossil *Q. sichotensis* from the section of white oaks closely resembles fossil *Q. pseudolyrata* Lesq., *Q. bretzi* Chaney and some other species, which, at one time or the other, had been identified in different localities of North America. *Q. sichotensis* differs from *Q. pseudolyrata* Lesq. (Lesquereux, 1878) only in respect to details. As a matter of fact, the two species may even be morphological variations of the same polymorphic species (Pl. 1).

North American fossil oaks of the *Q. pseudolyrata* type were time and again

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compared with recent ones from the series *Albae* (Loud.) Trel: *Q. alba* L., *Q. macrocarpa* Michx., *Q. minor* Sarg. and *Q. lyrata* Walt. (Chaney *et al.*, 1944), which are distributed solely in the southeastern United States, from Maine Bay to Missouri in the west and to Florida in the south (Sokolov, 1951).

In their summary report on Mio-Pliocene floras of California and Oregon, Chaney *et al.* (1944) cited a successive series of oaks and a continuity between the extinct *Q. winstanleyi* Chaney and *Q. columbiana* Chaney, on the one hand, and the existent East American *Q. bicolor* Willd., *Q. muhlenbergii* Engelm. and *Q. prinus* L.; the European *Q. sessiliflora* Salisb.; and the East Asian *Q. aliena* Blume, *Q. fabri* Hance. and *Q. mongolica* Fisch., on the other. The said continuity is still more apparent when comparing the above species with fossil oaks of the Rettikhovka flora, primarily *Q. sichotensis* and *Q. pseudolyrata*, which are ancestral forms of the present *Q. alba* and *Q. lyrata*.

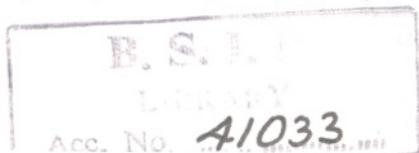
Such facts are readily explicable by postulating the existence of associations between continents. In the past, there appeared to be frequent situations which led to migrations of certain animal and plant species between Asia and North America. They essentially involved individual migrants, not whole floras (or faunas), whose development, as we see it, took place *in situ* on the basis of autochthonous transformations of the mother floras (faunas).

DISCUSSION

Fossil oaks of the *Q. sichotensis* type with compound-lobed leaves most probably belong to fossil North American elements discovered in Asia. Generally speaking, a favourable climatic situation must have conditioned the penetration of North American and Asian elements across the Bering Land Bridge. Such fluctuations as cooling in Paleocene, maximum warmth in Late Eocene, repeated strong cooling in Oligocene and warming in Mid-Miocene followed by worsening of the climate in Pliocene were shown to have taken place over the entire Cenozoic (Tanai, 1961, 1967; Tanai & Huzioka, 1967; Mai, 1967; Wolfe & Hopkins, 1967; Wolfe, 1970; Addicott, 1969; Nemejc, 1970).

According to available evidence (Wolfe, 1972), a par-tropical rain forest with laurels, palms, dryophylla, the soap bark tree and other Early Ravenian flora grew in Eocene on the territory of present Alaska. In Miocene (Wolfe & Leopold, 1967; Wolfe, 1972), evergreen species were no longer observed there; however, climatic conditions were favourable enough for such trees as the hazel, the alder, the oak, the beech, the amber tree, the platan, the water-elm, various maple species, the nut-tree, etc. (Seldovian flora). It was precisely in Seldovian time that various oak species, including *Q. pseudolyrata* Lesq. (Chaney *et al.*, 1944; Chaney, 1959), were widely distributed in North America, climatic obstacles for their penetration to the north being absent. In all probability, in Early and Middle Miocene, a rather lively exchange of migrants took place across the Bering Land Bridge. It is not accidental, therefore, that Seldovian flora is closely related simultaneously to both Early and Middle Miocene floras of Central North America, e.g. to those of Oregon and Japan (Wolfe, 1972). Japanese Miocene floras of the Aniai, Daijima and Mitoku types are best known and, without any exaggeration, may be considered as exemplary of the Far Eastern floras of the same age (Tanai, 1961, 1971; Tanai *et al.*, 1963; Tanai & Suzuki, 1965, 1972; Huzioka, 1964; O.100, 1966; Murai, 1969; Suzuki, 1970). On the background of the temperate mesophyte Aniai and Mitoku floras, the Early and Middle Miocene Daijima is conspicuous by its warm-temperate composition comprising a large number of evergreen species. Daijima is widely represented by different Fagaceous species, especially of the genus *Quercus*. The variety of oaks appears to be sufficiently high also in the Late Miocene Mitoku flora. Taxonomically, the Rettikhovka flora of Primorye resembles the Japanese flora, in general, and Mitoku, in particular.

Beyond Japan, Miocene floras were found in several localities. In South Primorye, they are represented by the Ustj-Suifun and Bolotninsk floras (Kryshstofovich, 1946; Ablaev, 1973); in Khabarovsk Territory by the Botchinsk flora (Akhmetyev, 1965, 1973); in Sakhalin by the Kurasiisk and Verkhneduisk floras (Fotyaynova, 1964, 1967); in Kamchatka by the Pyroshnikova River and Medvezhkinsk floras (Chelebayeva, 1968;



1971); in Korea by the Hamjing, Changjin and other floras (Huzioka, 1972); and in China by the Shangwang flora (Hu & Chaney, 1940; Sung, 1959).

Thus, a huge range, comprising almost the same type of broad-leaved Mesophyte flora, is apparent. In addition to the typically temperate genera *Alnus*, *Betula*, *Juglans*, *Acer*, *Salix*, *Populus* and *Cercidiphyllum*, the above-mentioned flora especially Daijima, quite often comprises the warm-temperate and subtropical genera *Fothergilla*, *Styrax*, *Sassafras*, *Hamamelis*, *Mallotus*, *Sapindus*, *Koelreuteria* and others. Such a wide distribution was caused by favourable climatic conditions at the end of Early- and the beginning of Middle Miocene, which, in turn, promoted the penetration of numerous thermophilic species far to the north. Unfortunately, palaeobotanical evidence for northeast Asia is very scarce. Actually, the northern borderline of the distribution of thermophilic species lies at 60° N.Lat. near the locality where the Medvezhinsk flora of North Kamchatka evolved (Chelebayaeva, 1971). In this connection, Kartasheva's (1973; 1974) reports on the results of spore and pollen analyses for Middle Miocene deposits in the lower reaches of Yana and Omoloy Rivers proved to be very interesting. These reports proved the existence of coniferous — broad-leaved forests in the region, beeches, chestnuts and oaks being dominant. Morphologically, beeches were exceedingly varied, and their content in the spore and pollen complex amounted to 32 per cent.

The above-cited evidence on the Miocene flora and vegetation of East Asia and North America are similar in that the climatic optimum in Miocene epoch of levelled off the various latitudinal zones to make way for large-scale areal displacements of certain plant species.

Available comparative materials on recent floras of North America and East Asia ostensibly indicate repeated floristic associations between the two regions. It was back in 1840 that Gray pointed out the similarity of the two floras in his review on "Florae of Japan" (Siebold & Zuccarini) and cited the following examples of amphipacific associations of vicarious species: *Illicium religiosum* and *I. parviflorum*, *Aralia edulis* and *A. racemosa*, *Viburnum tomentosum* and *V. lantanoides*, *Wistaria japonica*

and *W. frutescens*, etc. Six years later, he again indicated that similarity (Gray, 1846). Referring again to the same book by Siebold and Zuccarini, he wrote that it is interesting to note how many typically American genera inhabit Japan, not to speak of strikingly similar forms. Gray further cites a large number of genera, whose species bridge the Pacific from Asia to America, e.g. *Rhus*, *Lespedeza*, *Sieversia*, *Acer*, *Stuartia*, *Tilia*, etc.

Current knowledge on the floristic associations studied was substantially augmented in recent years chiefly due to numerous lists of recent species with amphipacific distribution (Hara, 1952, 1956, 1972; Kawano, 1971; Constance, 1972; Iwatsuki, 1972; Kurokawa, 1972; Li, 1972; Mizushima, 1972; Sharp, 1972; Yurtsev, 1972). Comparisons of recent floras of North America (Britton & Brown, 1936; Hultén, 1968) and Primorye (Vorobiev *et al.*, 1966; Voroshilov, 1966) revealed the following common species: *Osmunda cinnamomea* L., *O. claytoniana* L., *Onoclea sensibilis* L., *Adiantum pedatum* L., *Coptis trifolia* (L.) Salisb., *Sanguisorba sitchensis* C.A. Mey., *Smilacina trifolia* (L.) Desf., *Majanthemum dilatatum* (Howell) Nels. et Macbr., *Fritillaria camtschatcensis* (L.) Ker.-Gawl., *Streptopus streptopoides* (Ledeb.) Nels. et Macbr., *Calyptso bulbosa* (L.) Rehb., *Brasenia schreberi* Gmel., *Monotropa uniflora* L., and *Cornus canadensis* L. Among those closely related to the above-mentioned species are the following (first name in the pair represents American species): *Phyllitis scolopendrium* (L.) Newm. — *Ph. japonica* Kom., *Clintonia borealis* (Ait) Raf. — *C. udensis* Trautv. et Mey., *Alnus maritima* (Marsch.) Muhl. — *A. japonica* Sieb. et Zucc., *Corylus rostrata* Ait. — *C. mandshurica* Maxim., *Atragene americana* Sims. — *A. ochotensis* Pall., *Menispermum canadense* L. — *M. dahuricum* DC., *Caulophyllum thalictroides* Michx. — *C. robustum* Maxim., *Astible biternata* (Vent.) Britton — *A. chinensis* (Maxim.) Franch. et Savat., *Philadelphus coronarius* L. — *P. tenuifolius* Rupr. et Maxim., *Aruncus americanus* Rafin. — *A. asiaticus* Pojark., *Echinopanax* (= *Oplopanax*) *horridum* (Sm.) Decne. et Planch. — *E. (=O.) elatum* Nakai, *Osmorhiza depauperata* Phil. — *O. aristata* (Thunb.) Makino et Yabe, *Sanicula trifoliata* Bien. — *S. chinensis* Bunge, *Heracleum lanatum* Michx. — *H. moellendorffii* Hance, *Acer penn-*

sylvanicum L.—*A. tegmentosum* Maxim. and *Doellingeria amigdalina* Nees—*D. scabra* (Thunb.) Nees. The species listed above are found in ranges embracing Primorye (and part of South Priamurye) and North America. They belong to a special group of Asian-American species from temperate zones of recent *Quercus*, whose ranges are considerably disjunct, though morphologically much alike. These plants comprise a special group, and do not belong to circumpolar, amphi-Pacific or Beringian species.

Our study of American and Primorye Fagaceae and the search for their analogues showed that oak species were not observed among the nearest western Central Asian arid flora (Grubov, 1972). However, they have been frequently mentioned in the lists of Turgay-type floras of Western Asia (Iljinskaya, 1967). Boitsova (1966) even admitted the possibility of oak forests growing in the West Siberian lowlands and the Turgayan trough during Late Oligocene. At the same time, beeches, maples, limes, magnolias, nut-trees, etc. also grew there. In Ashutas, the most representative flora of the Turgay type, *Q. alexejevii* Pojark., *Q. antipovii* Kryshch. and *Q. furuhjelmii* Heer (Kryshchovitch *et al.*, 1956) were noted; however, they proved to be quite different from the Rettikhovka-type oaks with compound-lobed leaves. The same may be said of European oaks, the only exceptions being the following cerric oak species: *Q. cerris* foss. Kolak., *Q. kubinyii* (Kov.) Czecz., *Q. kuschukensis* Kornilova, *Q. pliovariabilis* Kolak., *Q. pseudocastanea*

Goepp., *Q. sosnowskyi* Kolak. and *Q. cerris* var. *caucasica* Kutuzk. (Sitar, 1969; Kolakovskiy, 1972; Kutuzkina, 1974). Of the above-said species, the strongest resemblance to *Q. sichotensis* is borne by *Q. cerris* foss. Kolak., among whose synonyms we find *Q. macranthera* Fish. et Mey., distinguished by Palibin (1906) for the Late Pliocene of Western Georgia. The series of morphologically resembling leaves can be continued. Thus, Straus (1956) described *Q. prae-eruceifolia* Straus from the Pliocene flora of the Willershausen District of Osterode (Harz). He included as synonyms of that species those with leaf imprints previously determined for *Q. alba* L. foss., *Q. macranthera* Fish. et Mey. foss., also noted by Straus in the same work, is morphologically closely related to *Q. protodentata* Tanai et Onoe. Somewhat resembling *Q. sichotensis* is the Mio-Pliocene species *Q. hispanica* aff. *sessiliflora* Smith (Brice, 1965) found in the south of France.

The growth of closely related (or identical) species in the temperate zones of North America and East Asia may be ascribed to lengthy transformation of the principal and most ancient type of flora, which occupied a transregional position in the times when polychronous floras were dominant. This position is also confirmed by evidence on recent and fossil oaks. On the other hand, the morphological similarity with European oaks may be explained by the widespread phenomenon of convergence, since there is at present insufficient evidence testifying to the presence of white oaks in Europe in the geological past.

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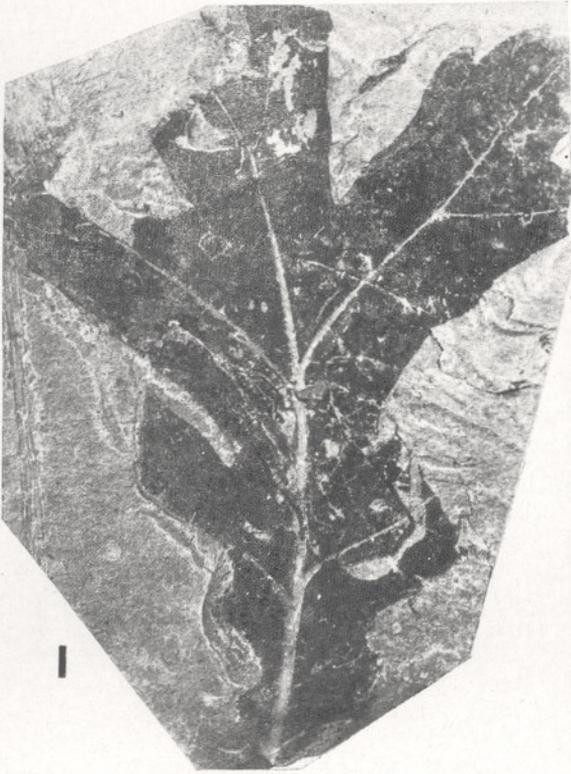
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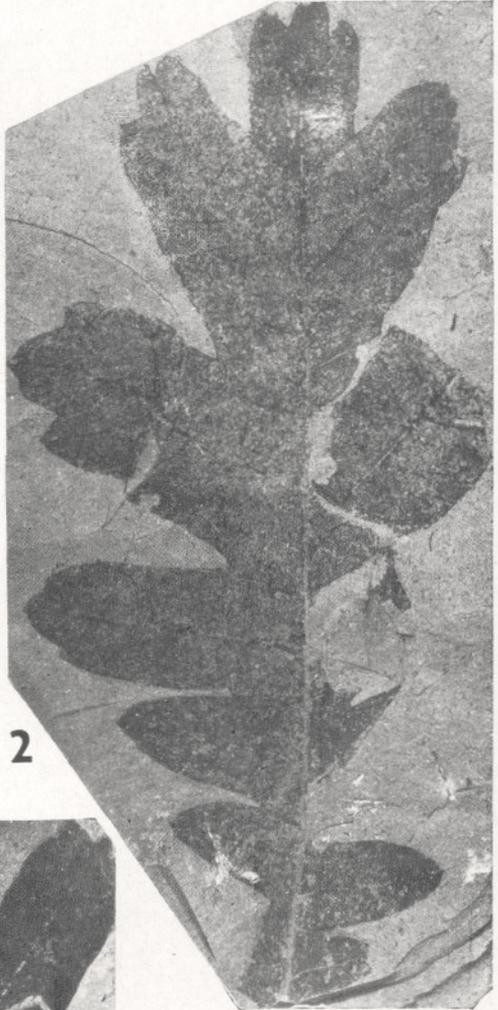
EXPLANATION OF PLATE

1-6. *Quercus sichotensis* Ablav et Gorovoi, leaves ($\times 1$); 1-sp. no. 560/100; 2-560/36; 3-560/IIa; 4-560/IIb; 5-560/73; 6-560/II; Rettikhovka

fossil flora, Primorye, U.S.S.R., coal-bearing sediments, Miocene.



1



2



5



3



4



6