Reprinted from PALAEONTOLOGY *Volume* 17 *Part* 2
June 1974

Podocarpus from the Upper Cretaceous of Eastern Asia and its bearing on the theory of conifer evolution

BY

V. A. KRASSILOV

PUBLISHED BY THE
PALAEONTOLOGICAL ASSOCIATION
LONDON

PODOCARPUS FROM THE UPPER CRETACEOUS OF EASTERN ASIA AND ITS BEARING ON THE THEORY OF CONIFER EVOLUTION

by V. A. KRASSILOV

ABSTRACT. *Podocarpus tzagajanicus* sp. nov. from the Uppermost Cretaceous (Tzagajan beds) of the Bureja River augments the Mesozoic record of the northern hemisphere Podocarpaceae. 'Northern' and 'southern' conifers grew side by side in Mesozoic and Tertiary forests. The distribution of conifers has been more deeply affected by climatic changes than by continental drift.

IN a review of the Cambridge symposium on the biogeographical aspects of continental drift, Jardine and McKenzie (1972) quoted among selected examples Florin's theory of conifer distribution. They claimed (p. 24) that 'the history of the conifers provides another striking example of the action of drifting continents as agents of dispersal. Florin showed that from the Late Carboniferous (about 300 my) to the early Eocene (about 50 my) each of the conifer genera (with the exception of Araucaria) had either a "Gondwana" distribution . . . or "Laurasian" distribution. . . . The present disjunct distribution of *Podocarpus* and other Gondwana genera may be the product of the break-up of Gondwanaland, and the Tertiary spread of them into Indonesia and Southeast Asia may result from the northward drift of Australia.' Such views on the history of conifers are widely accepted.

Rudolf Florin, an outstanding palaeobotanist and a great authority on gymnosperm taxonomy, came to his ideas of conifer evolution when describing Tertiary conifers from Chile (Florin 1940). He held then that both lineages of conifers, northern and southern, had been perfectly separated through time and space. *Paranocladus*, *Walkomiella*, *Buriadia*, Araucariaceae, Podocarpaceae, and *Athrotaxis* constituted the main body of the southern group and the rest of the conifers the northern one. Twenty years later Florin (1963) reiterated his views. The only exception made was for the Araucariaceae (but not for the genus *Araucaria*) which had been recorded from several northern localities. The works of R. Kräusel on fossil woods and of R. A. Couper on microfossils provided additional evidence in favour of Florin's theory. Although several authors (Buchholz 1948; Ferguson 1967; Krassilov 1967, 1971) objected to this theory, it became fairly popular among botanists and earth scientists and was cited in many textbooks (e.g. Stebbins 1967). In recent years it has been used as a confirmation of continental drift. It is worth mentioning that Florin himself opposed the drift theory and relied upon 'continental bridges' as pathways of conifer distribution.

The 'southern' palaeozoic conifer *Walkomiella* is hardly distinguishable from the 'northern' *Lebachia*. The early Triassic northern family Voltziaceae was represented in the southern hemisphere by the genus *Voltziopsis*. Other Mesozoic families such as Cycadocarpidiaceae and Cheirolepidiaceae were also distributed in both northern and

[Palaeontology, Vol. 17, Part 2, 1974, pp. 365–370, pl. 49.]

southern continents. *Cycadocarpidium* has been recorded from the Upper Triassic of Argentina and the generic name *Tomaxellia* was recently proposed by Archangelsky (1968) for a southern cheirolepidiaceous conifer with pollen grains of *Classopollis*-type. He also suggested the cheirolepidiaceous affinities of Patagonian Jurassic conifer *Pararaucaria*, as well as *Indostrobus* from the Cretaceous of India. The 'southern' taxodiaceous genus *Athrotaxis* (or its nearest approach *Athrotaxites*) has been repeatedly recorded from the Lower Cretaceous of Canada and U.S.S.R. (Bell 1956; Krassilov 1967).

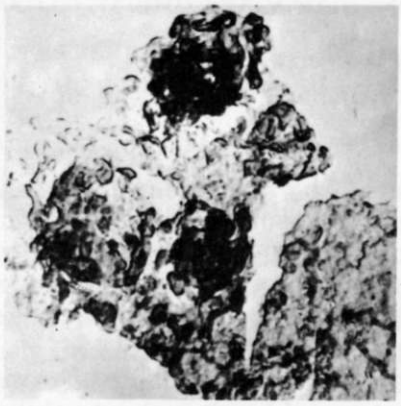
All the above-listed facts contradict the division of ancient conifers into Gondwanian and Laurasian groups. But even more important is the evidence of the Laurasian distribution of Mesozoic Podocarpaceae. Pollen grains of the podocarpaceous type are known from many northern localities. However, most of them have been recently attributed to artificial genera. I referred to Podocarpaceae several megafossils from the Lower Cretaceous of the Primorye (near Vladivostok, Far East of the U.S.S.R.). One of them, *Podocarpus sujfunensis* Krassilov, displays the characters of the *Nageia* section of the genus *Podocarpus* (Krassilov 1967). The leaves are 120 mm long and 2·2 mm broad, with numerous veins, amphistomatic. Stomata all over the surface in longitudinal files separated by several cell files, amphicyclic; the polar encircling cells shared by adjacent stomata or absent; subsidiary cells papillate. Another species, *Podocarpus harrisii* Krassilov has linear-lanceolate, shortly petiolate, single veined, hypostomatic leaves about 40 mm long and 4–6 mm wide. The abaxial epidermis with broad central stomatic band is occasionally divided into two or three parts by narrow and irregular nonstomatiferous zones. Stomata arranged in files, longitudinally orientated, amphicyclic; subsidiary cells papillate. The topography of the abaxial epidermis is rather unusual for conifers, with flat single-veined leaves. However, several living species of the subgenus *Stachycarpus* show stomata over the vein. The division of stomatic bands into 'Teilstreifen' is also known among *Stachycarpus* species (Florin 1931). Bilaterally flattened leaves have been recorded from the Lower Cretaceous of Primorye under the name *Paracmopyle florinii* Krassilov.

Primorye certainly was not the only Laurasian territory where Podocarpaceae flourished during Mesozoic time. Gomolitzky (1962) described leaves with podocarpaceous cuticle characters from the Jurassic of Central Asia. The fossil wood *Podocarpoxylon triassicum* has been found in the Keuper of Central Europe (Selmier and Vogellehner 1968). I suggested the podocarpaceous affinity of the Wealden species *Tritaenia* (*Abietites*) *linkii* (Roem.) Magdefrau and Rudolf as evidenced by stomata organization and topography of abaxial epidermis with three 'Teilstreifen' (Krassilov 1967, 1971).

Podocarpus tzagajanicus sp. nov. from the uppermost Cretaceous of the Amurland augments the record of Mesozoic podocarps. As far as I know it is the only Late Cretaceous representative of the family.

EXPLANATION OF PLATE 49

Figs. 1–8. *Podocarpus tzagajanicus* sp. nov. Upper Cretaceous, Bureja River. 1, 2, leaf fragments, × 1. 3, 4, abaxial cuticle, parts of stomatal band (slightly retouched), × 70. 5, 6, cells of adaxial epidermis, × 58 and 146. 7, 8, stomata, × 395.



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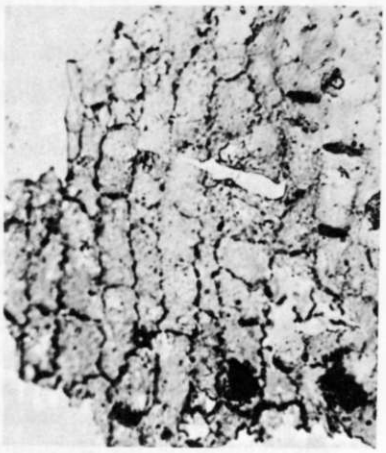

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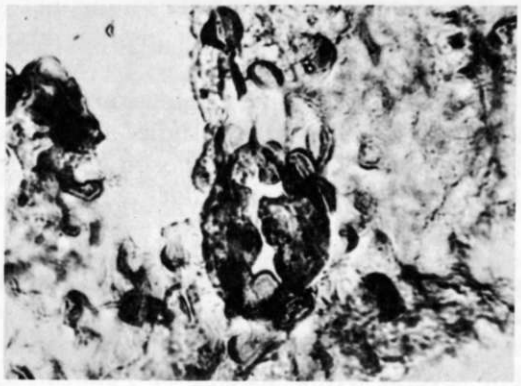

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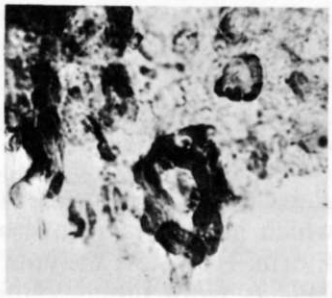

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KRASSILOV, *Podocarpus*

Genus PODOCARPUS L'Herit
Podocarpus tzagajanicus Krassilov sp. nov.

Plate 49, figs. 1–8

Diagnosis. Leaves linear-lanceolate, flat, single-veined acuminate, with slightly thickened margins, 5–6 mm wide, hypostomatic. Abaxial epidermis with two stomatic bands about 0·8 mm wide on either side of the midrib. Stomata well spaced, arranged in discontinuous rows, longitudinally orientated, amphicyclic, with 5–6 subsidiary cells. Stomatal pit elliptical, bordered with a ridge and overarching papillae.

Cells of stomatal bands papillate. Marginal nonstomatiferous zones as wide as stomatal bands. Cells outside the stomatal bands without papillae. Anticlinal walls ridged, undulating to sinuous.

Holotype. Specimen 575-126 and slide preparation 575-126a, Institute of Biology and Pedology, Far-Eastern Scientific Centre, Vladivostok; Pl. 49, figs. 1, 3–8.

Occurrence. Outcrop of Tzagajan clays near the mouth of Bureja River, tributary of the Amur.

Age. Uppermost Cretaceous (Danian).

Description. Three incomplete leaves have been collected from the light grey Tzagajan clays. They are fossilized as yellowish-brown incrustations with small pieces of cuticle. The largest leaf fragment is more than 60 mm long (the whole length was probably 80–90 mm), 6 mm wide, tapering towards the acuminate apex. The midrib is prominent, up to 0·9 mm broad, adaxially flat, abaxially appearing as a low ridge; the margins are microscopically even. The abaxial epidermis is divided into two stomatal bands and three nonstomatiferous zones, all of nearly equal width. The stomatal bands are not sunken, not sharply delimited; stomata forming discontinuous files, longitudinally orientated, rather evenly spaced; the subsidiary cells with large papillae overarching the stomatal pit. The papillae are dorsally united into prominent ridge. Guard cells invisible. Stomatal pit including the ridge 45–63 μm long, 37–45 μm wide. The outlines of epidermal cells are rather indistinct within the stomatic bands. All cells are provided with round-elliptical papillae about 15 μm in diameter.

The cells of marginal zones are rectanguloid, arranged in files, about 54 μm long, 22 μm wide with undulating anticlinal walls. The leaf margins are bordered with narrow strips of elongated cells 13 μm wide. The cells of costal zone rectangular, up to 112×45 μm, occasionally short and square or irregular, with more distinctly sinuous anticlinal walls.

Remarks. These leaves are hardly distinguishable from the Fort Union specimens which have been identified by Brown (1962) as *Amentotaxus campbelli* (Gardner) Florin. However, the cuticle characters are different from those of *Amentotaxus*, as well as from other conifers except several living species of *Podocarpus* subgen. *Stachycarpus*, which have hypostomatic leaves. According to Florin (1931) the stomata of *Stachycarpus* are amphicyclic, with 4–6 subsidiary cells which are papillate and heavily cutinized forming a ridge around the stomatal pit. The anticlinal

walls of epidermal cells more or less undulate. In contrast, *Amentotaxus* has monocyclic, comparatively frequent stomata with 4–10 subsidiary cells. The anticlinal walls are usually straight.

Comparable leaves have been described from the Tertiary of Japan, North America (see Dilcher 1969), and Europe (e.g. *Podocarpus kinkelini* Mädler 1939) but the cuticles of the latter are not known.

Conclusions. We may conclude that there was no family of Mesozoic conifers with exclusively 'Gondwanian' or, 'Laurasian' distribution. Such genera as *Cycadocarpidium*, *Araucarites*, *Athrotaxites*, and *Podocarpus* successfully crossed the Tethys Sea long before Early Eocene time. The history of conifers has little bearing on the problem of continental drift. It seems that southern and northern conifers have been more effectively separated by equatorial temperature conditions than by water barriers. The probability of dispersal through the equatorial zone has been affected by the changing contrast between the tropical and extratropical climates. The equable Jurassic climate favoured the dispersion of conifers and the equatorial barrier was surmounted by the Araucariaceae, Podocarpaceae, Taxodiaceae, and less successfully by the more temperate Pinaceae. The *Sequoia-Taxodium* group of conifers appeared later when transequatorial migrations were barred by better-defined climatic zonation. They were confined to the northern hemisphere. The 'northern' and 'southern' conifers grew side by side during the Cretaceous and Tertiary periods, but the southern ones were gradually eliminated from Laurasia. They persisted on southern continents where the climatic conditions remained more or less comparable to those of the Jurassic period.

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V. A. KRASSILOV
Institute of Biology and Pedology
Vladivostok, U.S.S.R.

Typescript received 14 August 1972