

ARAUCARIACEAE AS INDICATORS OF CLIMATE AND PALEO-LATITUDES

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ABSTRACT

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Mesozoic Araucariaceae dominated in the low-latitude (15–20° N) belt of summer-dry climate. It is suggested, that araucarian forests were the most thermophilous Mesozoic assemblages. There were no equivalents of the modern tropical rain forest. In the middle latitudes, Araucariaceae shared dominance with *Elatides* and *Classopollis*-producing plants. The northernmost Triassic records of Araucariaceae on both eastern and western Pacific coasts are at 35° N; in the Jurassic and Cretaceous time they are constantly at about 50° N. These climatically controlled chorological features are oblique to the paleolatitudes inferred from paleomagnetic data.

On the basis of material from the Jurassic of Mali, a new species of *Araucaria* is described, viz. *Araucaria africana* sp. nov.

INTRODUCTION

I contribute this paper in appreciation of Dr. Jonker's broad interest in paleoclimatology. The usefulness of pre-Quaternary plants as climate indicators is questionable because their tolerance cannot be safely deduced backward from that of their extant relatives and because intrinsic evidence of their geographic distribution is also ambiguous due to changing position of continents. Some paleobotanists are ready to accept paleomagnetic maps, while paleomagnetologists seek arrangements compatible with paleobotanical and other biological evidence. With this in mind, I considered the distribution of Mesozoic Araucariaceae. Their absence from the temperate Arctomesozoic (Siberian) province, in contrast with fairly numerous records elsewhere, is the primary evidence of climatic control and potential utility as climate indicators.

Araucarian remains in my collection came from the Jurassic and Cretaceous localities in the Far East (Tyrma, Mongolia, Primorye, Sakhalin, Amur province) and also from equatorial Africa.

DISTRIBUTION IN MODERN COORDINATES

The most important features of paleophytogeography are in descending order (1) abundance, (2) limits of distribution, and (3) diversity. While 1 is defined objectively, 2 is biased by imperfection of record and 3 depends on taxonomic judgements.

The largest Triassic locality is the famous araucarian fossil forest of Arizona. Typical cone scales were recorded as far north as Greenland (*Araucarites charcotii* Harris) and Taimir (*A. migayi* Shvedow). On the Pacific coast, araucarian woods and other remains are known from Tonkin (*Araucarioxylon zeilleri* Grie) and Japan (*A. sidugawaense* Shimakura), while they are lacking in the rich fossil-plant localities near Vladivostok (Primorye). The northern boundary of floras with Araucariaceae on both the Asiatic and the American coasts of the Pacific (South Japan and Chile) is at about 35° N.

Jurassic Araucariaceae are described from many localities, but the In-Eserin locality in the variegated Jurassic beds of the Mali—Nigerian depression in Africa is unique in its abundance of araucarian remains contrasting with a scarcity of other megafossils. Plant compressions were obtained from bore holes by bulk maceration of calcareous shales with HCl and HF. They are mostly isolated leaves (about 100 specimens), but also wood fragments, branchlets, microstrobili with pollen grains and cone scales, all attributed to a single species of *Araucaria*. Earlier, I published a preliminary description of this unnamed species, (Krassilov, 1977). Now I propose the new name *Araucaria africana* for it.

Araucaria africana sp. nov. (Plate I—III)

Diagnosis: Ultimate branchlets 1—2 mm thick. Scale-leaves imbricate, appressed or spreading. Leaf cushion rhomboidal or obovate, tapering downwards, about 3—4 mm long. Free portion clearly delimited from their base cushions, much shorter than the cushions or of equal length, triangular in section, incurved, blunt or shortly pointed or linear—lanceolate, flattened, mucronate, up to 5 mm long (average length 1.5—3 mm).

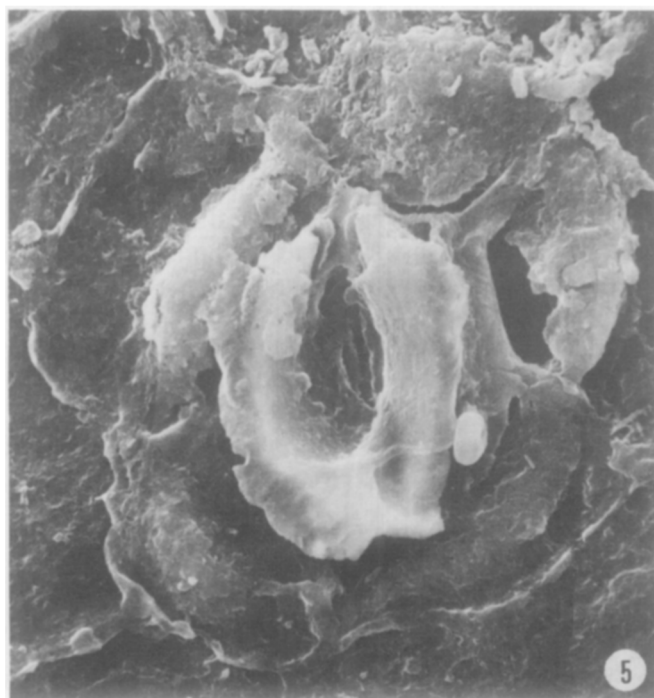
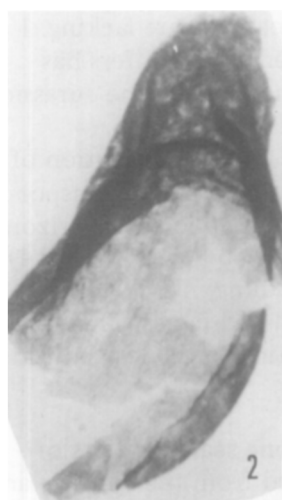
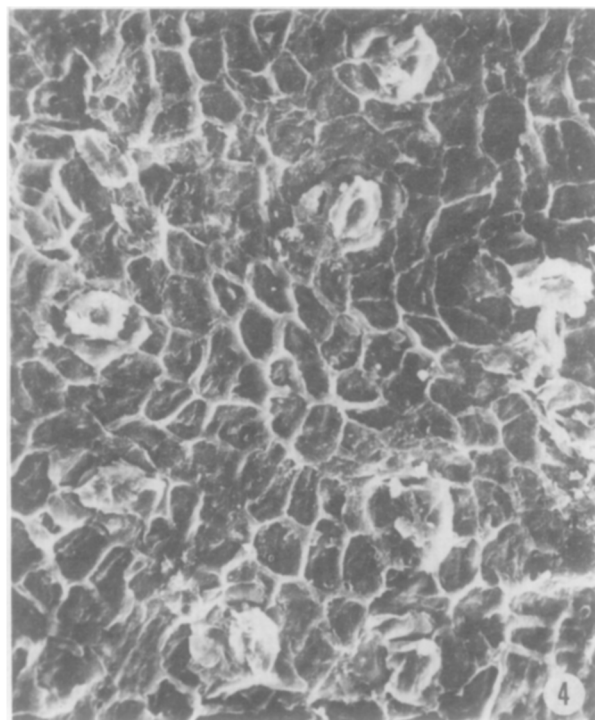
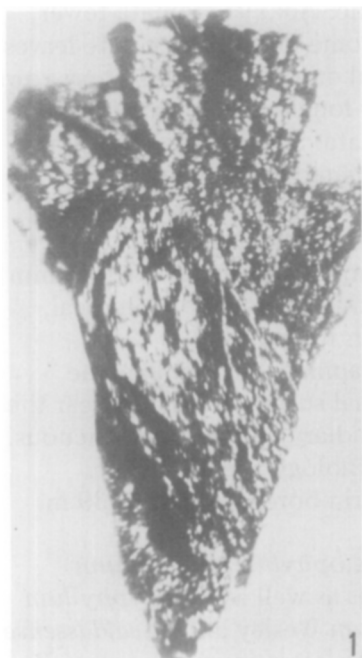
Cuticle thick, showing marginal zone of narrow thin-walled, slightly sinuous cells and central zone of rectanguloid thick-walled cells, about 50—60 × 24—30 μm (80—90 × 22—25 μm in longer leaves), arranged in short rows. Cells usually papillate. Stomata on both sides of the free portion and

 PLATE I

Araucaria africana sp. nov. from Mali

1. Shoot showing scale-leaves, holotype (× 25).
2. Leaf with its leaf-base cushion (× 25).
3. Stoma showing fine striation of subsidiary cells (× 330).
4. Distribution of stomata, SEM (× 300).
5. Inside view of stomatal pit and slightly sunken subsidiary cells, SEM (× 1600).

PLATE I



on the leaf-base cushion. Average leaves show 50–60 abaxial stomata distributed all over the surface except the marginal zone. Adaxial stomata fewer, concentrated in the lower portion of a leaf. In some linear–lanceolate leaves adaxial stomata more numerous than the abaxial ones. Stomata in short rows or scattered. Those in rows mostly transverse or longitudinal, while oblique orientation predominates among scattered stomata. Subsidiary cells usually five, radially arranged, slightly sunken, finely striated, conspicuous due to their lighter colour, forming stomatal pit with thickened border. Stomata elliptical, about 60 μm long, with T-shaped polar thickenings.

Microstrobili rounded, diameter about 2.5 mm, scales obcuneate, 0.8 mm long, imbricate, bearing about 10 oval pollen sacs. Pollen grains spherical, diameter about 25 μm , exine thin, smooth, often folded.

Scales of megastrobili winged, with densely papillate cuticle. Papillae conical or cylindrical in the middle part of adaxial surface, rounded near the margin. Stomata scattered, as in leaves, but subsidiary cells less conspicuous. *Holotype*: IE-44; Collection of the Institute of Biology and Pedology.

Type locality: Mali–Nigerian depression, In-Eserin borehole, 337–339 m.

Shoots of *A. africana* are comparable with *Pagiophyllum peregrinum* (Lindley et Hutton) Schenk from the British Lias as well as *Brachyphyllum tropidimorphum* Wesley, *Pagiophyllum rotzoanum* Wesley and *P. valdassense* Wesley from the Grey Limestones of Veneto. The latter species is especially similar in cuticular characters (Wesley, 1956), though papillae are lacking. I believe that close resemblance between African and Venetian conifers has some bearing on the problem of Afro-Italian land connections in the Jurassic (see Hsü, 1971).

The In-Eserin locality suggests a lowland araucarian forest. Association of shoots, leaves and cones rules out the possibility of a long-distance transportation. The facies are similar to those of the Triassic araucarian forest in Arizona.

Other low-latitude Jurassic localities — Oaxaca in Mexico (Wieland, 1914), Kutch in India (Pant and Srivastava, 1968) and Phu Kadung in Thailand (Iwai et al., 1975) — are also found in variegated or red-bed facies. They show that the araucarian forest was a dominant plant formation in the low-latitude belt of a summer-dry climate.

In middle latitudes, abundant araucarian fossils — cone scales, shoots of *Pagiophyllum* and *Brachyphyllum* types — are described from the Jurassic and Early Cretaceous localities of the eastern U.S.A. (Potomac), Portugal, France, Italy, Caucasus, Middle Asia and southern Kazakhstan (Karatau). In these

PLATE II

Araucaria africana sp. nov. from Mali

1. Inside view of a stoma, SEM ($\times 1600$).
2. Guard cells, one of the T-shaped polar thickenings is preserved, SEM ($\times 1600$).
3. Leaf cuticle showing stomata ($\times 25$).
4. Very short leaf spreading from its leaf-base cushion ($\times 25$).
5. Cleared leaf showing stomata on the leaf-base cushion ($\times 25$).

PLATE II

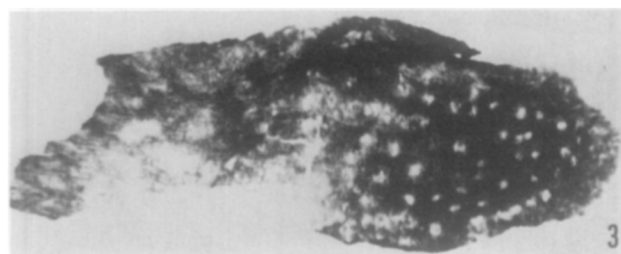
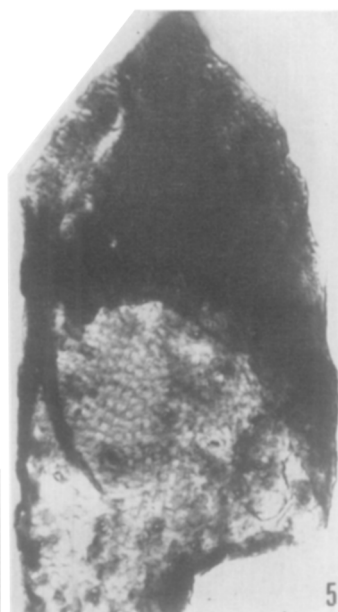
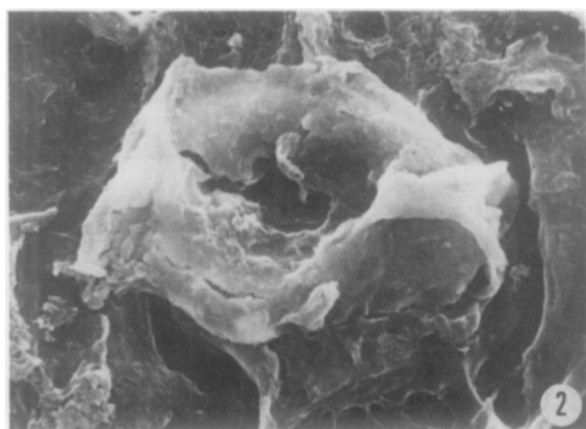
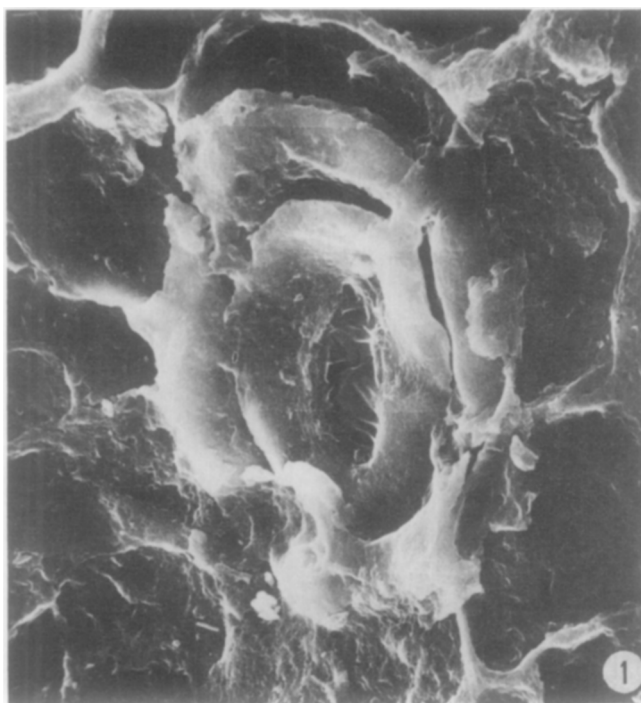
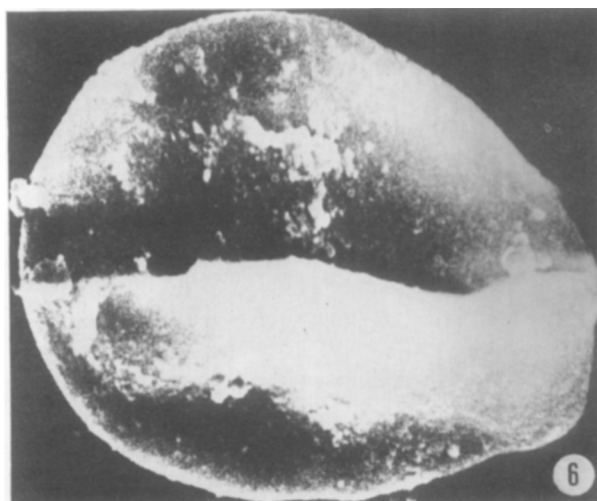
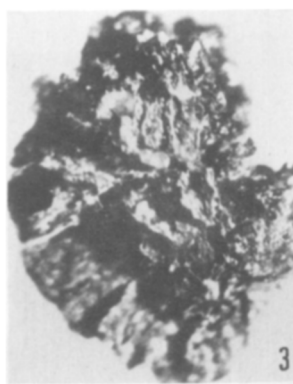
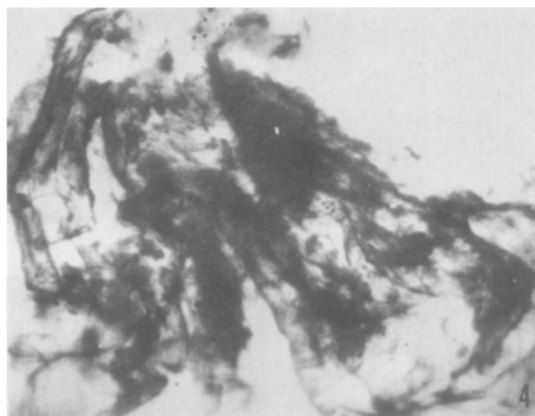
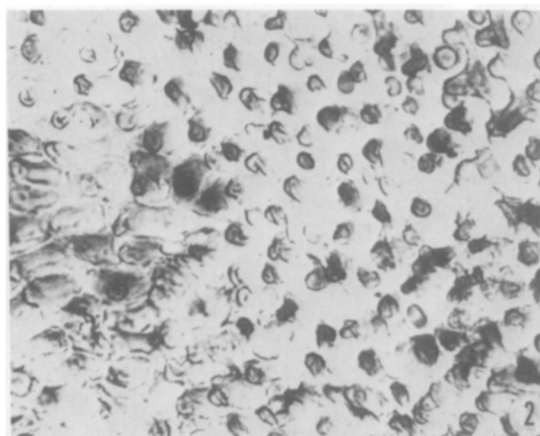


PLATE III



localities, Araucariaceae are next in abundance to the taxodiaceous conifers of the *Elatides* group and *Classopollis*-producing plants. Assemblages of this type can be traced to the east in Mongolia and Primorye. The Mongolian Mesozoic flora was hitherto scarcely known, but recently the paleontologists A.G. Ponomarenko and V.N. Yakovlev have discovered structurally preserved plant material as a by-product of their search for fossil insects and fishes. The *Araucaria* on Plate IV, 1—4 came from the Shin-Khuduk and Bon-Tsagan localities of Early Cretaceous age. There are branching shoots with spirally arranged scale leaves which are crescent-shaped, carinate, and provided with a single adaxial band of fairly crowded, irregularly orientated stomata. Ovuliferous cones are elliptical, rather small. Split cones show seeds embedded in the scales with relatively thick apophyses.

In the Lower Cretaceous of South Primorye (near Vladivostok), Araucariaceae are represented by common *Araucarites* with *Brachyphyllum*-type foliage and also by two genera with bifacial pluri-nerved leaves, viz. *Araucariodendron* and *Ussuriocladus* (Krassilov, 1967). In *Araucariodendron*, stomata are in intercostal bands, longitudinally orientated, amphicyclic. Cone scales are small, wingless, consisting of completely fused bracts and ovuliferous scales, bearing one or two embedded ovules.

Patagonian localities may represent the Southern Hemisphere counterpart of the Araucariaceae—*Elatides*—*Classopollis* belt. Conifers from these localities are now much better understood due to the excellent work of Stockey (1975).

The Jurassic Araucariaceae have been recorded from Grahamland, and the southern limit of their distribution is not known. In the Northern Hemisphere, their numerical representation decreases towards the northern limits of the Araucariaceae—*Elatides*—*Classopollis* belt. The Yorkshire (*Araucarites esto-nensis* Kendall) and Ukrainian records are evidently situated near the boundary, since they are lacking from the Jurassic of Greenland, Bornholm and Sweden. In Asia, no araucarian remains are known from the Arctomesozoic, or Siberian province dominated by deciduous *Phoenicopsis* forests (fossil woods of *Araucariopitys* described from various northern localities are now transferred to *Protocedroxylon*). The northernmost records are from the Tyrma River, a tributary of the Bureja, at about 50° N.

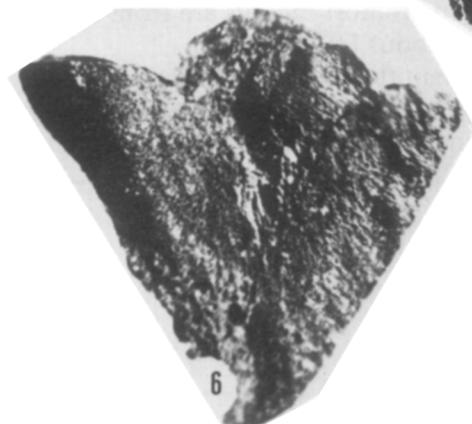
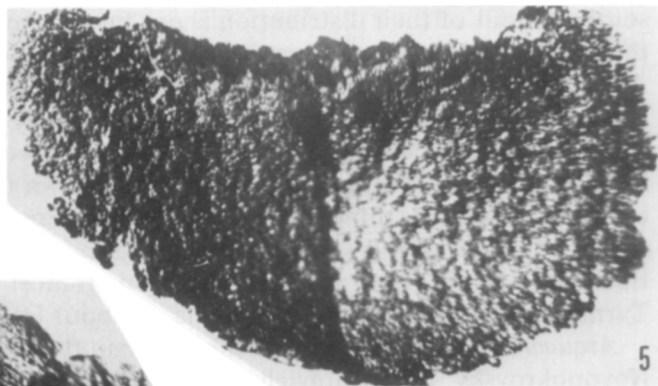
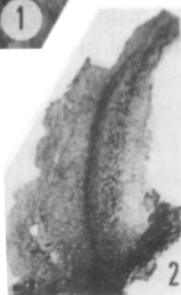
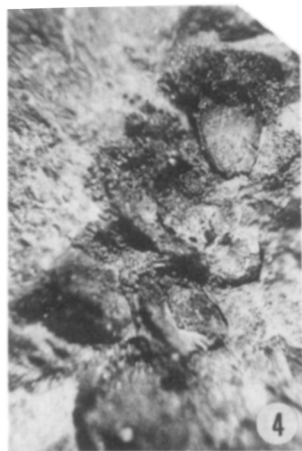
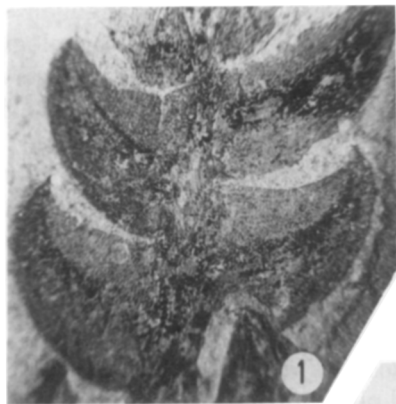
Araucaria is a new element in the Tyrmian flora studied by Seward, Novopokrovsky, Kryshstofovich and other authors. It is represented, mostly in the products of bulk maceration, by small fragments of shoots, isolated

PLATE III

Araucaria africana sp. nov. from Mali

1. Wing-like extension of a bract ($\times 10$).
2. Papillate bract cuticle ($\times 130$).
3. Microstrobilus ($\times 25$).
4. Several cleared pollen sacs borne on a microsporophyll ($\times 130$).
5. Tetrad from a pollen sac ($\times 660$).
6. Pollen grain, SEM ($\times 3500$).

PLATE IV



leaves and a single cone scale (Plate IV, 5–7). There are also numerous pollen sacs, yet unassigned, but probably belonging to this plant. The scale-leaves are spreading, straight or hooked, about 3.5 mm long, fringed by dense microscopic hairs. Stomata are on the adaxial side only, scattered, orientated along the cell rows or somewhat oblique. The cone scale is sammara-like, 5 mm wide, with broad ligule and median groove. Cuticle is thickened in the median portion, where a seed was embedded. Cuticular characters are like those of the leaves.

The latest Jurassic or Berriasian flora of Tyrma is ecotonal between the *Phoenicopsis* and *Cycadeoidea* provinces (Krassilov, 1972) and contains such southern plants as *Klukia* and *Pachypteris*.

In the Late Cretaceous, *Sequoia* replaced *Elatides* and other archaic Taxodiaceae in the middle latitude coniferous forests, while Araucariaceae maintained their position and were still common in eastern U.S.A. (Raritan), Bohemia, Caucasus and Kazakhstan. “*Dammara*” or “*Dammarites*” have been often quoted from higher latitudes (e.g., from West Greenland), but in my opinion they have nothing to do with the Araucariaceae (in fact, most of them are isolated cone scales of *Sequoia*). In eastern Asia, the northernmost records are from the Tsagajan beds of the Amur province (Danian) and northern Sakhalin (Senonian), both at about 50° N. *Araucarites pojarkovae* (Plate V, 5–7) from Tsagajan has cylindrical shoots with imbricate obovate leaves about 11–13 × 10–11 mm. Megastrobili are globose, about 20 mm in diameter, scales obcuneate, lingulate, indehiscent, with a rather long awn and vestigial wings (Krassilov, 1976a). This species is related to the section *Columbea*, now restricted to South America.

Araucaria from Sakhalin also resembles extant species of *Columbea*, but the stomatal structure is very peculiar. Each stoma is provided with a stout process overhanging the stomatal pit (Plate V, 1–4). Such unique characters, together with outstanding versatility of the Early Cretaceous Araucariaceae from Primorye (see above) suggests the Pacific region as an area of primary diversity of this group. On the American coast, *Araucaria* is known from the Lance Formation and Fort Union Group of Dakota, but not from the equivalent strata in western Canada. Thus, the northern boundary roughly coincides with the line of latitude 50° N.

PLATE IV

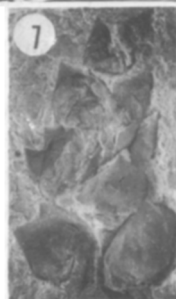
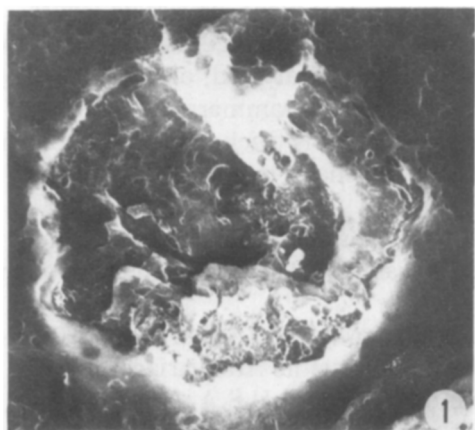
Araucaria from the Lower Cretaceous of Mongolia

1. Shoot with scale-leaves (× 7).
2. Cleared leaf showing stomatal band (× 7).
3. Part of the same stomatal band, SEM (× 550).
4. Split cone showing seeds (× 7).

Araucaria from Tyrma

5. Cone scale (× 7).
6. Shoot fragment with scale-leaves (× 7).
7. Leaf margin fringed by hairs (× 146).

PLATE V



RELATION TO PALEOLATITUDES

Smith et al. (1973) produced a series of world maps based on topographic, tectonic, and paleomagnetic data. In their words, the pertinent test is whether distributions of latitude-dependent sedimentological and paleobiological features are parallel or oblique to the latitude lines on these maps.

Among the features defined above, the low-latitude records (Oaxaca, Mali, Kutch, Phu Kadung, 15–20° N) and the middle latitude Araucariaceae—*Elatides*—*Classopollis* belt (optimal development at 40–45° N) are displaced to the south and somewhat more scattered on the Jurassic paleomagnetic map (0–10° N and 20–30° N, respectively). The northern boundary of the Triassic floras with Araucariaceae extends across the Pacific from 55° N in the west (southern Japan) to 20° N in the east (Arizona). On the Cretaceous map, the northernmost records of Araucariaceae are scattered between 25 and 70° N. They are at 40° N in eastern Asia (North Sakhalin) and 70° N in western North America. Thus, both Triassic and Cretaceous isoflors based on the northernmost occurrences of Araucariaceae are oblique to paleolatitudes, especially so in the Pacific region. These isoflors are parallel to the lines of modern latitudes 35 and 50° N.

CONCLUSIONS

The major chronological features of the Mesozoic Araucariaceae in the present-day coordinates are:

(1) Araucariaceae dominated in the low-latitude (15–20° N) belt of predominantly summer-dry red-bed climate. There was no evidence of a plant assemblage more thermophilous than the araucarian forests. Thus, the tropical zone was probably much cooler than at present. No equivalents of the modern tropical rain forest have existed.

(2) Araucariaceae were common in the middle latitudes. Araucariaceae—*Elatides*—*Classopollis* forests stretched from Potomac and Portugal to Mongolia and Primorye. These forests reached their optimal development at about 40–45° N. In the Southern Hemisphere, the equivalent plant formations occupied symmetrical position.

(3) The northern limit of Triassic floras with Araucariaceae is at about 35° N on both the Asiatic and the American Pacific coasts. In Jurassic and

PLATE V

Araucaria from the Late Cretaceous of Sakhalin

1. Stomatal pit with a hair-like process, SEM ($\times 1500$).
2. Guard cells, the foot of a hair is seen above, SEM ($\times 1500$).
3. Leaf cuticle showing stomata ($\times 12$).
4. Outside view of stomatal pits ($\times 1000$).

Araucarites pojarkovae Krassilov from the Danian of the Amur province

5. Longitudinally split cone ($\times 2$).
6. Cone scale ($\times 2$).
7. Shoot apex ($\times 1$).

Cretaceous time, their northernmost occurrences are constantly at about 50° N. It appears that this boundary was not sensitive to minor climatic changes. In the Southern Hemisphere, the equivalent boundary is displaced to the south, probably due to dispersal of continents.

(4) Morphological versatility of Araucariaceae from eastern Asia suggests the primary centre of diversity to be in the Pacific region.

The features 1—3 are parallel to the modern latitudes, while their position on paleomagnetic maps is less regular and 3 is markedly oblique to the latitudes of contemporaneous reassemblies orientated by rotation bringing their geographic poles into coincidence with the mean paleomagnetic poles. These data would be more consistent with a method of orientation assuming minimal latitudinal shift of major continents. To reconcile drift with stable latitudinal position of continents, the outsider hypotheses of an expanding Earth or flattening of the geoid must be re-evaluated. I prefer the latter hypothesis for the reasons given elsewhere (Krassilov, 1976b).

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