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ON THE SIBERIAN " ENDEMIC " CYCADOPHYTES WITH SOME PHYTOGEOGRAPHICAL IMPLICATIONS

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ABSTRACT

Such genera as *Tyrmia*, *Bureja*, *Jacutiella*, *Heilangia* and *Aldania* were supposed to constitute the endemic group of Siberian cycadophytes. However, several species of *Tyrmia* ought to be divided between *Pterophyllum* and *Pseudocycas*, *Bureja* is evidently congeneric to *Pterophyllum*, *Jacutiella* — to *Nilssoniopteris*, *Heilungia* and *Aldania* — to *Sinoctenis*, which is closely related to *Dvepanozamites*. Thus there were no Siberian endemics among the cycadophytes. The majority of them belonged to the "chaparral" group whereas the mangroves (*Ptilophyllum*) and the pachycaule group (*Cycadeoidea*) were barred from the "Siberian province" by the temperature regime. Therefore, the south boundary of this "province" was determined mainly by the climatic conditions and might be interpreted as the dividing line between the climatic zones. In contrast to this, the distinction between the Indian Mesozoic flora with its *Pentoxylales* and that of the rest of Asia is attributed to the continental drift.

INTRODUCTION

ANATHORST suggested that the Mesozoic vegetation of Siberia and the Arctic islands have constituted the distinct floristic unit — the "*Phoenicopsis* flora". This idea was elaborated by the Russian palaeobotanists V. D. Prynada and V. A. Vakhrameev (1970). They supposed that the "*Phoenicopsis*", or "Siberian" floristic province differed from the southern, or "Indo-European" one not only by the relative abundance of the *Ginkgdales* and *Bennettitales*, but also by the presence of endemic genera. According to Prynada, the majority of Siberian cycadophytes had been restricted in their distribution to this floristic province. He described the endemic genera *Tyrmia*, *Bureja* and *Heilangia* (Prynada, 1956), to which V. A. Samylina added *Jacutiella* and *Aldania*.

At present the discussions of the continental drift patterns stimulate the causal analysis of the palaeofloristic differences. The latter may be explained by the climatic barriers, or the distribution of continents, or both. The cycadophytes are believed to be the most thermophilous among the Mesozoic plants. Thus the temperature barrier effected their expansion from the south to the north but not in the opposite direction, and the endemism of Siberian cycadophytes, if existed, might not be attributed to the temperature conditions. I attempted the revision of Siberian "endemic" cycadophytes the results of which are given below.

Genus *Tyrmia* Prynada

Type-species: *Tyrmia tyrmeniis* Prynada, 1956, p. 243, Pl. 3, Fig. 3.

The type-species was described from the outcrops of the fossiliferous tuffite of the Tythonian-Berriasian age at the right bank of the Tyrma River. The leaf ribbon-shaped, evenly pinnate, up to 43 mm broad; lamina attached to the adaxial side of the rachis leaving its median portion free. Pinnae 2-4 mm broad, arising at 80-90° to the rachis, parallel sided, apices acute, margins slightly recurved. Veins mostly simple, up to 7 per segment.

The cuticle thick. Upper epidermal cells rectangular; anticlinal walls sinuous. Stomata scattered over the whole abaxial surface apart from the marginal stomata free

zone up to 1 mm broad. Stomata variously oriented, closely packed, contiguous stomata rather frequent. Subsidiary cell pair slightly reduced, thickened around the stomatal pit, distal walls not sinuous in contrast to nonspecialized epidermal cells. Guard cells variously exposed. Trichome bases mostly in close proximity to stomatal pits.

Externally these leaves resemble *Pterophyllum a'quale* Brongn. or *P.lyellianum* Dunker. According to Prynada, they differ from *Pterophyllum* in the mode of lamina attachment as well as in the thickened margins of pinnae. However, Seward (1917) maintained that the attachment of lamina to the adaxial side of rachis commonly occurred in *Pterophyllum* (and *Anomozamites*) and Thomas (1930) believed this mode of attachment to be characteristic of his genus *Leptopterophyllum*, which was subsequently merged in *Pterophyllum* (Harris, 1952a). The thickened pinna margins were observed in a number of *Pterophyllum* leaves where this feature was much more evident than in "*Tyrmia*" *tyrmensis*. The cuticular structure of *T. tyrmensis* is of the *Pterophyllum* (*Anomozamites*) *marginatum* type (see Harris, 1935; Daber, 1962). The trichome distribution is similar to that of *Pterophyllum cycadites* (Harris & Rest, 1966).

It is clear from the said above that *Tyrmia tyrmensis* agrees with *Pterophyllum* in all important characters. The same may be said of "*Tyrmia*" *pectiniformis* Prynada and "*Tyrmia*" *pterophylloides* Prynada. The latter is hardly distinguishable from the Yorkshire *Pterophyllum thomasi* (Harris, 1952a). "*Tyrmia*" *polynovii* (Novopokrovsky) Prynada has thick linear pinnae 1 mm broad with single stomatal groove on the abaxial surface. Syndetocheilic stomata are closely packed and mostly transversely oriented within a groove; subsidiary cell pair with proximal papillae (Krassilov, 1969). These characters permit the assignment of "*Tyrmia*" *polynovii* to the genus *Pseudocycas* Nathorst.

Genus *Bureja* Prynada

Type-species: *Bureja rigida* Panada, 1956, p. 237, Pl. 47, Fig. 6 (Prynada assigned it to the Cycadales).

This genus is represented by a single species from the Asanovsky sequence of the Tythonian to Berriasian coal-bearing strata in the Bureja coalfield. The leaf broadly spatulate, pinnate; pinnae linear, 2.5-3*5 mm broad, slightly constricted to the base, plicate, decurrent, arising at 75-90° to the rachis. Rachis transversely wrinkled. Veins about 4 per segment. Adaxial cuticle thick, cells rectangular, anticlinal walls sinuous; costal cells not differentiated. Abaxial epidermis poorly differentiated into stomatiferous and nonstomatiferous bands; cells polygonal to irregular, anticlinal walls with jerked thickenings; stomata transversely or obliquely oriented to the veins, stomatal frequency about 70 per sq. mm. Stomatal apparatus including the subsidiary cell pair 45-55 μ broad. Subsidiary cells with proximal papillae overarching the guard cells. Guard cell thickenings about 38 μ long. Trichome bases scattered over both cuticles (Pl. 1, Figs. 6-10).

Bureja rigida is similar to *Pterophyllum zygotiacum* (Harris, 1935) both in external form and cuticular structure (apart from the nonpapillate epidermal cells) which is in general characteristic of the genus *Pterophyllum*. Prynada distinguished *Bureja* from *Pterophyllum* by the plicated pinnae and asymmetrical pinna bases, which are acropically straight (whereas in *Pterophyllum* they curve upward) and basiscopically decurrent. My observations show that the pinnae base character in "*Bureja*" is exactly the same as

in the majority of *Pterophyllum* leaves. Therefore, the new combination *Pterophyllum rigidum* (Prynada) Krassilov is proposed here.

Genus *Jacutiella* Samylna

Type-species: *Taeniopteris amurensis* Novopokrovsky, 1912, p. 6, Pl. 1, Fig. 4; Pl. 2, Fig. 5.

The type-species had been described from the same outcrop as "*Tyrma*" *tyrmensis* (see above) and was assigned to the genus *Taeniopteris*. Samylna (1956) instituted for it, a new genus *Jacutiella*. According to her, *Jacutiella* differed from *Taeniopteris* by the attachment of lamina, which completely covered the rachis from above. The cuticular structure of *Jacutiella* was incompletely known (only adaxial cuticle fragments with sinuous cell walls). The type material had been deprived of the coaly substance and the cuticle was obtained from the specimens found in the Bureja coalfield. These leaves are indistinguishable from the holotype.

The leaf is ribbon-shaped, simple, up to 300 mm broad. Lamina attached to the adaxial side of thick rachis and the opposite halves of lamina drawn together over the rachis. Lamina margins recurved. Veins thick, arising at 80° to rachis, about 1 mm apart, simple or forking mostly close to the margin.

The adaxial epidermal cells rectangular with sinuous walls. Coastal cells narrower than those between the veins. The abaxial cuticle differentiated into stomatiferous and nonstomatiferous bands of almost equal width. Cells irregular, anticlinal walls sinuous, surface walls with median papillae. Stomata transversely oriented to the veins, forming indistinct transverse files, 4-6 per file. Stomatal apparatus, including the subsidiary cell pair, immersed below the level of epidermal cells. Proximal walls of surrounding epidermal cells more or less thickened forming the outer opening of the pit 50 μ long \times 35 μ wide. Subsidiary cells with proximal papillae. Trichome bases scattered mainly over veins (Pl. 1, Figs. 1-5).

The cuticular structure of *Jacutiella amurensis* is characteristic of *Nilssoniopteris Nathorst* and closely resembles *N. jourdyi* (Zeill.) Florin which differs only in smaller sinuosities of cell walls and the absence of trichomes (Harris, 1935). However, the large cell wall sinuosities as well as the presence of trichomes commonly occur in other *Nilssoniopteris* leaves. The lamina attachment in *Jacutiella* is like that of *Nilssoniopteris glandulosa*. According to Florin in this species "lamina aus der Oberseite der Rhachis befestigt und ihre beiden Hälften in der Medianlinie fast zusammenstossend" (p. 7). I believe that the joining of the lamina halves over the rachis have been exaggerated by the bending of thick petiole under compression.

Therefore, "*Jacutiella*" agrees with *Nilssoniopteris* in all important features and the new combination *Nilssoniopteris amurensis* (Novopokrovsky) Krassilov is proposed here.

Genus *Heilungia* Prynada

Type-species: *Pseudoctenis amurensis* Novopokrovsky 1912, p. 10; Pl. 1, Figs. 2, 3, 6; Pl. 2, Fig. 1.

The genus *Heilungia* was instituted by Prynada (1956) for the leaves described as *Pseudoctenis amurensis* (Novopokrovsky) from the Tythonian-Berriasian of Tyrma. The leaves large, pinnate, with comparatively slender rachis. Pinnae up to 20 mm broad, gradually tapering to the apices, with more or less conspicuous basispicous auriculae at

the base, overlapping, arising at 90° to the rachis. Two veins enter the pinnae close to the basisopic margin. They branch copiously giving rise to a system of subparallel veins.

Prynada evidently overlooked that the same plant had been described from the Jurassic of Kiangsi Province, China by Sze (1931) who instituted for it the new genus *Sinoctenis* with type-species *Sinoctenis grabauiana* Sze. The relation of *Sinoctenis* to *Drepanozamites* (Harris, 1935) remains uncertain. The both genera are closely related having the veins diverging from the point close to the basisopic margin of the pinnae. However, *Drepanozamites* differs from *Sinoctenis* in the conspicuous acrosopic basal auriculae. The importance of this feature is questionable.

Genus *Aldania* Samylna

Type-species: *Aldania auriculata* Samylna, 1959, p. 1337; 1963; p. 81, Pl. 16, Figs. 8-10.

According to Samylna (1963), *Aldania* differs from *Sinoctenis* ("Heilungia") in having only two veins at the pinna base. Since Lebedev (1965) recognized the same style of venation in "Heilungia" the distinction between these genera became rather doubtful. Lebedev maintained that the pinnae of "Heilungia" were more elongated than those of *Aldania*. However, the pinnae of "Heilungia" *zejensis* Lebedev are 30 mm long X 9 mm wide whereas those of "Aldania" *auriculata* are 14-20 mm long x 5-10 mm wide. Therefore, these genera intergrade with each other and "Aldania" is even closer to *Drepanozamites* in having the acrosopic basal auriculae.

THE PALAEOECOLOGY OF THE MESOZOIC CYCADOPHYTES

The following ecological groups may be provisionally distinguished among the Mesozoic cycadophytes:

1. The "Mesozoic chaparral". The cycadophyte dominated assemblages termed the "Pterophyllum beds", "Ctenis beds", etc., have been widespread in the Mesozoic coal-bearing deposits. These fossil assemblages evidently reflected the profuse growth of the leptocaul bennettites with forked stems and the plants of *Ctenis* — *Nilssonia* group, which might have been the forest undergrowth or might constitute the formation of its own. Working on the Early Cretaceous "Ctenis beds" of Primorye (Far East) I found that the latter possibility was more probable since the remains of forest dominants — the *Araucariaceae*, the *Taxodiaceae* (apart from *Athrotaxites*), the *Ginkgoaceae* — have been exceedingly rare in these beds. The cycadophyte leaf material have associated with the remains of those conifers which displayed not only the tall tree but also the low tree or shrubby habit, i.e. *Podocarpus*, *Torreya*, *Cephalotaxus* and *Athrotaxites* (Krassilov, 1967).

These observations were confirmed by the palaeoecological study of the Bureja coal field localities (the Siberian province). The majority of these localities have been dominated by the leaf remains of such trees as *Czekanowskia*, *Phoenicopsis*, *Pseudotorellia*, *Ginkgoites* and *Elatides* but the "Ctenis beds" also occurred repeatedly through the several cyclothems. The assemblage of the "Ctenis beds" comprised *Ctenis* (up to three species), *Pterophyllum*, *Nilssoniopteris*, *Pseudocycas* and the conifer *Torreya* and was almost deprived of the remains of the forest dominant species. It was suggested that this fossil assemblage corresponded to the chaparral-like vegetation.

2. *P. achy caul bennettites*. *Cycadeoidea* and its allies dominated the rich fossil plants localities in the Western North America (the Black Hills of Dakota, the Freczout Hills of Wyoming, etc.). They extended into the Western Europe and Eastern Asia (Mongolia and Japan). The equivalents of this pachycaul cycadophyte growth hardly exist today.

3. *Mangroves*. Harris (1952b) suggested that *Pachypteris*, *Stenopteris* and the bennettites *Ptilophylkim* and *Zamites gigas* had been the most probable representatives of mangrove vegetation in the Yorkshire Jurassic. They associated rather frequently with the marine plankton. As to the *Ptilophyllum*, this suggestion was confirmed by my observations in the Jurassic beds of Kamenka (Ukraine). At the transition from the marine glauconitic sandstones to the on delta silstones and clays containing the rich assemblage of fossil plants, there was a layer of the gypsiferous clay filled with the *Ptilophyllum* compressions. The *Ptilophyllum* and *Otozamites* leaves of exceptionally good preservation are known from the dolomitic paper shales of the Jurassic salt lake (or lagoon) of Kara-Tau (South Kazakhstan). Although *Ptilophyllum* is common in a number of the continental localities, it is much more abundant in the paralic situations. In Asia *Ptilophyllum* reached its highest development in India and extended along the Pacific coast up to the South Primrye and Japan, which is not far from the northern limit of mangroves at present. It was not found in the *Phoenicopsis* zone.

CONCLUSION

The cycadophytes of the "Siberian floristic province" belonged mostly to the "chaparral" group, whereas the mangroves (*Ptilophyllum*) and the pachycaule group (*Cycadeoidea*) were barred from extending there by the temperature regime. There were no Siberian endemics among the cycadophytes. Thus the southward extention was not limited for them and the south boundary of the "Siberian province" had been determined by the climatic conditions only. Therefore, it was not the proper province boundary, but rather a dividing line between the climatic zones. The distribution of the *Pentoxylales*, known from New Zealand (Harris, 1962) and in the northern hemisphere restricted to India, seems to be the only floristic feature which may be attributed not to the climatic differences, but to the Mesozoic arrangement of continents.

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EXPLANATION OF PLATE

Nilssoniopteris amurensis (Novopokr.) com. nov.

- 1-2. Leaf portions. x 1
3. Lower epidermis, x 146
4. Stomatal apparatus, x 395
5. Cells with papillae, x 395

Pterophyllum rigidum (Pryn.) comb. nov.

6. Leaf, x 1
7. Upper epidermis, x 146
- 8-9. Stomata. x 395
10. Stomatal band. X 146