SOME TRUE AND ALLEGED PERMOTRIASSIC CONIFERS OF SIBERIA AND RUSSIAN PLATFORM AND THEIR ALLIANCE

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ABSTRACT

Twigs *Retinosporites* ? *sibirica* and fructifications *Tomiostrbus radiatus* — *Araucarites tomiensis* from the Lower Triassic of the Kuznetz basin were tentatively regarded as belonging to the same plants. *A. tomiensis* and *T. radiatus* yield microspores (of *Aratrisporites* type) and megaspores, and belong to lepidophytes (Pleuromeiaceae). *R.?sibirica* on gross morphological and epidermal features is ascribed to *Quadrocclads*. Pollen produced by these plants were of the *Lueckisporites* type. *Quadrocclads borealis* and corresponding female fructifications *Sashinia borealis* coming from the Uppermost Permain of the Russian platform are described. *Sashinia*-plants combine very primitive female fructifications and advanced male fructifications. Taxonomical and phylogenetical corollaries of these findings are discussed. The Lower Triassic flora of Siberia seems to have come from the Subangara area of the Permian.

Key-words — Conifers, Retinosporites, Araucarites, Fructifications, Permo-Triassic, Siberia, Russia.

INTRODUCTION

In 1936, Neuburg described three species of conifers, viz., *Retinosporites* ? *sibirica* Neub., *Araucarites tomiensis* Neub. and *Tomiostrbus radiatus* Neub. from the Lower Triassic (Maltsevkaya suite) of the Kuznetz basin. The former comprised vegetative shoots which she compared with Indian *Retinosporites indica* (Oldham & Morris) Holden. *A. tomiensis* included remains interpreted as seed scales similar to Indian Mesozoic *Araucarites cutchensis* Feist. *T. radiatus*, according to Neuburg's suggestion, is a transversely broken cone consisting of *A. tomiensis* scales still attached to the axis. Although the fructifications occur in the section some 100 m below the twigs, Neuburg held that they could belong to the same plants.

Since *R. indica* has proved to be a pteridosperm *Pachypteris* (Bose & Roy, 1968) and *R.?sibirica* does belong to conifers, a problem of the generic affinity
of the latter arose. The Siberian conifers belong to the genus *Quadrocladus* hitherto known from the Upper Permian of western Europe (Schweitzer, 1960) and Russian platform (Meyen, 1978). *Q. sibiricus* (Neub.) comb. nov. also includes most of the conifers known in the Triassic volcanics of the Tunguska basin and erroneously placed into *Elatocladus* or *Voltzia*.

Female fructifications of *Quadrocladus* (genus *Sashinia* Meyen) have nothing in common with *Tomiosstrobus*. Therefore, a re-study of both *A. tomiensis* and *T. radiatus* became necessary. In 1978, Sadovnikov collected these fructifications in the type locality. During our joint study of the collection an idea arose that *A. tomiensis* is more similar to detached lepidophytalean sporophylls than to coniferalean seed scales. Later on, Sadovnikov recognized a ligule-like projection in *A. tomiensis*. His another specimen was macerated by me and it yielded spore mass from a body previously interpreted as a seed. Yaroshenko identified the microspores as *Aratrisporites*. Similar cavate and monolete microspores were recovered from sporangia of the Triassic Australian lycopod *Cylostrobus* related to *Pleuromeia*. Megaspores *in situ* were found by me in the type material of *T. radiatus*. They are trilette (?) and differ from those of both *Pleuromeia* and *Cylostrobus* in having a relief with verrucae and ribs. Krasilov and Zakharov (1975) described isolated megasporangium with megaspores *in situ* as *Pleuromea olenekensis*. Having smoothened reticulate relief, megaspores of the latter are closer to those of *Tomiotrobus* than of *Pleuromeia*. Thus *T. radiatus* merged with *A. tomiensis* (and *Pseudoaraucarites*) should be withdrawn from conifers and placed into lycopsids (*Pleuromeiaceae*). Their description and nomenclatural revision will be published elsewhere (Meyen, Sadovnikov, Yaroshenko, work in progress).

*Sashinia* fructifications, originally described on isolated axillary fertile shoots, are now known in detail. A new species *S. borealis* alongwith a corresponding new species of sterile twigs, *Q. borealis*, are described here. Microstrobili of these plants were also discovered (Meyen, 1978, p. 304). The best specimen, reproduced on Text-figs 1, 2, 3a, is a loose cone with spirally attached microsporophylls having distal rhomboid lamina and bunches of sporangia in the middle of the stalk. Pollen is disaccate with a single proximal taenia and equatorial taenia-like band (Text-fig. 3a). There is a certain similarity between the microstrobili and those described by Schweitzer (1960) from West European Zechstein as *Rhenania reicheltii*.

**DESCRIPTION**

*Sashinia* Meyen, 1978

*Emended Generic Diagnosis*—Female fructification consists of axis bearing spirally attached distant bracts differing from foliage leaves in larger size. Bract subtends fertile dwarf shoot (axillary complex) producing usual foliage leaves (*Quadrocladus* type) which are replaced upwards by the seed-bearing appendages. Seeds are apical, inverted. Their outer cuticle is similar to that of leaves, bracts and appendages.

*Sashinia borealis* sp. nov.

*Specific Diagnosis*—Loose female cone consists of 2 mm wide and more than 40 mm long axis bearing spirally arranged distant bracts with decurrent basis. Bract subtends fertile dwarf shoot (axillary complex) producing usual foliage leaves (*Quadrocladus* type) which are replaced upwards by the seed-bearing appendages. Bracts, appendages and leaves in axillary complex have cuticular structure common with that of *Q. borealis* (see below). Boundary between seed and its bearing appendage is gradual. Seed apex is acute.

*Holotype*—Specimen no. 3774/1-8 (Pl. 1, figs 5-7; Pl. 2, figs 19-21; Text-figs 4-6, 8-13); collected by M.A. Stepanenko, 1965.

*Locality & Horizon*—Arkhangelsk area, Vilegod District, village Pavlovskoe, near bridge across Viled River, borehole 06, depth 139-154·5 m; Upper Permian, Upper Tatarian substage Viatsky (?) horizon.

Besides the holotype, a few fragments probably belonging to the same species were found in the type locality. The holotype was transferred on a film (Text-figs 5, 6). Axillary complexes vary in size and produce various number of seed-bearing appendages (their number increases acro-
TEXT-FIGS 1-3 — Microstrobilus and pollen associating with *Sashinia aristovensis* Meyen and *Quadrocladus dvinensis* Meyen: 1. General view of microstrobilus, specimen no. 4552/494-1, Locality Aristovo. 2a. The same specimen, attachment of microsporangia to stalk of microsporophyll, left sporangium is longitudinally dehisced. 2b. The same specimen, furcation of sporangial stalk, thickened swellings on sporangia. 3a. Pollen in situ in equatorial view, specimen no. 4552/164-5a, point 1. 3b, c. Dispersed pollen from the same locality, polar view, specimen nos. 4552/371-4-44, 4552/371-4-51.

petally along the cone axis). Seeds increase in diameter in the same direction thus suggesting different degree of maturity. Seeds are round or elliptical, transversely or longitudinally elongated. One of them was macerated. After treatment with alkali a seed apex adpressed to the seed-bearing appendage was seen (Pl. 2, figs 19, 20). Outer cuticle of the seed in its middle and lower parts is of the same type as that of
TEXT-FIGS 4-7 — Sashinia borealis sp. nov., holotype no. 3774/1-8: 4. Seed apex, prep. no. 3774/1b-8. 5a, b. Portion of holotype with two axillary complexes bearing inverted seeds (5a — part of transfer preparation; 5b — counterpart of transferred specimen, macerated seed is figured on Text-fig. 4 and Pl. 2, figs 19-21). 6a. General view before transferring. 6b. Transfer preparation (frame corresponds to portion on fig. 5a). 6c. Transfer preparation of apical portion of counterpart (black cross and circle with dot mark corresponding points in 6a, b, c). 7 — Quadrocladus borealis sp. nov., holotype no. 3774/1-1 figured together with Sashinia borealis (Text-fig. 6a) as preserved on bedding plane.
appendage (Pl. 1, fig. 7; Text-figs 8, 9) and no distinct boundary between seed and appendage can be seen both macro — and microscopically. Only small fragments of internal seed cuticles were obtained (Pl. 2, fig. 21; Text-fig. 4). Cuticles of the nucellus and inner surface of the integument are closely adpressed suggesting their at least partial fusion. Megaspore membrane is thin and minutely granular, only 0.3 mm wide. Pollen in micropyle werenot observed.

The holotype is buried together with two sterile twigs of *Q. borealis* (one of the twigs is the holotype) lying parallel to each other (Text-fig. 7). This orientation suggests that all they might originally belong to the same individual.

**Comparison** — *S. borealis* differs from *S. aristovensis* Meyen in lesser number and smaller size of seed-bearing appendages. Leaves at the base of axillary complex differ from those of *S. aristovensis* in the same way as foliage leaves of *Q. borealis* sp. nov. differ from *Q. dvinensis*.

Schweitzer (1960, pp. 31-32, pl. 13, fig. 1) figured and briefly described a female (?) fructification tentatively referred to *Q. solmsii*, because its scales resemble the former species in epidermal structure. The relation between this fructification and *Sashinia* is obscure. I do not exclude, however, that the above mentioned scales may belong to distal laminae of a male strobilus. If so, this fructification may be comparable with microstrobilus associating with *S. aristovensis* and those described by Schweitzer (1960) as *Rhenania reicheltii*.

**Quadrocladus** Mädler, 1957

**Quadrocladus borealis** sp. nov.

**Specific Diagnosis** — Shoots with spirally attached leaves 0.6-1.3 mm wide and up to 5 mm long, linear in long shoots and spathulate in lateral (?) dwarf shoots. Leaf margins smooth or (very rare) minutely denticulate. Cuticle uniform, without distinction between lower and upper surfaces. Leaves decurrent and grade into stem without distinct boundary. Leaf apex obtuse or slightly sharpened. Stomata monocyclic or incompletely bicyclic. Guard cells sunken, orientated mainly along leaf axis. Sub-

sidiary cells exceptionally bear proximal papillae. In corners of cells small cutinized spines faced inside leaf.

**Holotype** — Specimen no. 3774/1-1 (Pl. 1, figs 1-3; Text-figs 7, 15, 16).

**Locality & Horizon** — Arkhangelsk area, Vilegod District, village Pavlovskoe, near bridge across Viled River, borehole 06, depth 139-154.5 m, Upper Permian, Upper Tatarian substage, Viatsky ? horizon.

The species is represented by fragments of twigs of the last order (Pl. 1, fig. 4; Text-figs 7-14). Some of them, including the holotype, bear elongated narrow (less than 1 mm) leaves ascending at acute angle to the axis. Others, less frequent are short bunches of leaves which are broader and tightly arranged. These may be lateral dwarf shoots comparable to those known in *Q. dvinensis* Meyen, or to the underdeveloped axillary complex of *Sashinia*. Bulk maceration yielded an apical portion of a twig (Pl. 1, fig. 4) and many isolated leaves of both kinds along with a number of larger leaves comparable to *Sashinia* bracts in size.

Epidermis is uniform throughout leaf surfaces (Text-figs 15, 16). Judging from longitudinal cuticular folds along the compression margins leaves were fleshy (Text-fig. 14). Leaf margin can be recognized only if it is minutely denticulate (Pl. 1, fig. 3), that is very rare. Stomata are eventually arranged into indistinct files. Proximal walls of subsidiaries are usually thickened as a narrow lip (Pl. 1, fig. 2). This might be resulted from a folding of the cuticle covering epistomal chamber. The latter is often displaced and shows barrel-shaped outline. In a few cases proximal papillae on subsidiaries were observed (Pl. 1, fig. 1). The percentage of stomata with different number of subsidiaries (A) is: 7A-2%, 6A-12%, 5A-56%, 4A-30%. Cuticular corner spines are common (Pl. 1, fig. 2; Text-figs 15, 16). Guard cells bear lateral thickenings as in *Q. dvinensis* (Meyen, 1978).

**Comparison** — *Q. borealis* differs from *Q. solmsii, Q. orobiformis, Q. florinii* and *Q. sibirica* in the absence (or rarity) of proximal papillae on subsidiaries, and in less frequent stomata. It differes from *Q. dvinensis* in regular absence or very poor development of marginal denticulation and in twice lesser leaf width. Corner spines in *Q. dvinensis* are larger.
**Quadrocladus sibiricus** (Neuburg) comb. nov.


1970 *Elatocladus pachyphyllus*: Prynada, p. 68, pl. 4, fig. 4

*Emended Specific Diagnosis* — Branches of penultimate order with larger leaves bear pinnately arranged branches of last
order with smaller leaves. Leaves rhomboid or round in cross section. Epidermis is uniform without cell bands corresponding to margins. Stomata frequent, irregularly orientated, exceptionally arranged in short indistinct files, otherwise freely scattered. Four-five (solitary 6) subsidiaries bear proximal papillae elevating above stomatal pit. Covering (i.e. not belonging to stomata) epidermal cells are polygonal, irregularly orientated, often divided by septae.

Lectotype — Specimen no. 2761/826-1, 825-1 (counterpart) figured by Neuburg, 1936, pl. 4, figs 1, 5, 7 (our Pl. 2, fig. 9; Pl. 3, figs 22-28; Text-figs 17, 19, 20).

Locality & Horizon — Kuznetz basin, right bank of Tom River below Sosnovka Creek, cliff “Babi Kamen”, layer 55 (Maltsevskaya Suite, Lower Triassic; stratigraphic setting is given by Neuburg, 1936).

The species is represented by mass accumulation of fragments on bedding planes.

Text-figs 14-16 — *Quadrocladus borealis* sp. nov. type locality: 14. Cuticular preparation of twig fragment showing two attached leaves and opening left by shed leaf, prep. no. 3774/7-1a. 15, 16. Cuticle of different leaf sides, holotype, prep. no. 3774/1-1.
The complete specimen (Pl. 2, fig. 10; Text-fig. 18A) is a branch of penultimate order with pinnately arranged twigs of the last order. Branches of penultimate order (Pl. 2, figs 11, 12; Text-fig. 18B, C) bear larger leaves and show portions with crowded or more distant leaves suggesting the alternation of short (dwarf) and long shoots,
Leaves greatly vary in proportions (Pl. 2, figs 15, 16) and are attached at acute angle. Neuburg erroneously treated the phyllo-taxis as two-ranked. Spiral arrangement is evident from cross section of leafy shoots (Pl. 2, fig. 13) and macerated fragments (Pl. 2, figs 15, 16). Leaves are linear with obtuse apex eventually having an indistinct "mucro". Both rhomboid and circular leaf cross sections are observed in a single shoot. The rhomboid and circular leaf cross sections are observed in a single shoot. It seems that the original cross section might be circular (as also evidenced by uniform epidermis) and the rhomboid ones arose as a result of preservation. Some specimens, however, obtained by bulk maceration show basal opening in the cuticle suggesting rhomboid original outline (Pl. 2, fig. 17). Leaves on twigs of the last order are 6-10 mm long and 0.8-1.3 mm wide (when flattened), those of penultimate branches are 10-12 mm long and 1.2-1.5 mm wide. The lectotype (Pl. 2, fig. 9; Text-fig. 17) is a fragment with better preserved cuticle (Pl. 3, figs 22-28). Covering cells are polygonal with thick radial walls. In some cells thick septae are present eventually underdeveloped (Text-fig. 20). Subsidiaries may be more cutinized than covering cells. The percentage of stomata with different number of subsidiaries (A) is: 6A-4%, 5A-48%, 4A-48%. Guard cells are badly preserved (Pl. 3, fig. 22).

In most of specimens the subsidiaries are damaged and show openings instead of periclinal walls (Pl. 3, figs 28-30), proximal walls are also destroyed and hence lack papillae. Cuticle of axes is the same as in leaves, but cell files are more distinct and stomata are less frequent. Available specimens of *Q. sibiricus* are petrified in various degree, but their anatomy is still to be studied.

Many leaves show pollen of *Lueckisporites* type (Pl. 2, fig. 18) sticked to cuticle solitary or in groups. The pollen show a wide range of variation in body/sacchi proportion and equatorial outline (from elliptical to nearly circular). Surprisingly no male sporangia were found in bulk maceration.

Comparison — *Q. sibiricus* differs from *Q. dvinensis* in pinnate arrangement of twigs of the last order (they are furcating in *Q. dvinensis*). Mode of branching of remainder species is unknown. Unlike *Q. florinii*, *Q. dvinensis* and *Q. borealis* the denticulate margin in the present species is absent. *Q. sibiricus* is peculiar in having septate covering cells. It differs from *Q. dvinensis* and *Q. borealis* in much better pronounced proximal papillae on subsidiaries.

**DISCUSSION**

**Taxonomical Problems** — *Q. sibiricus* differs from the Permian species of the genus in characters, used to serve for establishing genera. I held, however, that for generic distinctions in case of these conifers we need more essential characters, especially as variations of epidermal characters in better known species of *Quadrocladus* is unusually high. The generic unity of the enumerated species is indirectly supported by association with pollen of the same basic organization. The association is retained on a back-ground of fundamentally different plant assemblages.

The pollen intimately associating with *Quadrocladus sibiricus* is currently referred to *Lueckisporites* (Obonitskaya, 1974). Visscher (1970) is of the opinion that the latter genus might belong to plants producing sterile shoots of *Ullmannia bronni* Goeppert. The only grounds for this suggestion, however, is (i) the dominance of both fossils in the plant assemblages, and (ii) general similarity between *Lueckisporites* and pollen found in situ in microstrobili of *U. frumentaria* (Schloth.) Goeppert. The latter pollen, when found dispersed, is referred to *Illinites delasaucei* (Potonié & Klaus) Grebe & Schweitzer. However, an attribution of *Lueckisporites* to *Quadrocladus*, in Zechstein of West Europe also agrees with their association. *Lueckisporites* and *Q. sibiricus* are two dominant fossils in the Lower Triassic of Siberia where *Ullmannia* was never recorded. Besides, *Lueckisporites* pollen profusely occur attached to the cuticle of *Q. sibiricus*. There are though some complicating observations which should be kept in mind. There is a difference between *Lueckisporites* associating with *Q. sibiricus* and pollen found in situ in microstrobili associating with *Q. dvinensis* and *Sashinia aristovensis*. Both these pollen types were found in miospore assemblages of beds yielding *Quadrocladus* and *Sashinia* in the uppermost Permian of the Russian Platform.
Another taxonomical problem is involved by delimitation of species within Quadrocladus. Gross morphological features have little value due to a significant variation of characters in a monotropic sampling. In some cases the dimensions of leaves may play a role, e.g. in case of Q. dvinensis and Q. borealis. In Q. sibiricus a continuous variation in leaf sizes is observed, on a single bedding plane, on a background of the uniform epidermal characteristics. According to Schweitzer (1960) Q. orobiformis differs from Q. solmsii in leaf cross section (round in solmsii & rhomboid in orobiformis). In Q. sibiricus both kinds of cross section occur in a single twig. Q. borealis are peculiar in having lateral dwarf shoots with shorter leaves. Such shoots are rare in Q. sibiricus and were never recorded in West European species.

Epidermal characters delimiting the species are presence of septate cells, degree of development of marginal dentillation, dimensions (or absence) of proximal papillae on subsidiaries, thickenings in distal walls of subsidiaries, corner spines, etc. None of the characters is constant within a single species. In some leaves of Q. sibiricus septae are very rare or, when preservation is poor, unrecognizable. In Q. dvinensis and Q. borealis large papillae on subsidiaries overhanging stomatal pit are usually absent, but occur in solitary stomata. In Q. sibiricus rare stomata lack papillae, the presence of which also depends on preservation.

This situation exemplifies once more that differences between species attain statistical nature when the sampling is representative enough (Meyen, 1973b). It means that a single specimen, even very well-preserved, may principally be unassignable to a certain species without a support of the monotypic sampling. 

Phylogenetic Implications—In a paper, where the original description of Sashinia was given (Meyen, 1978), I briefly treated the phylogenetical significance of this and other Angara conifers. Some of my statements now need both corrections and additions. The most important correction relates to Cardiolepis and Cardirolepidaceae. My student, H.G. Smoller (Ukhta), showed me a specimen of Cardiolepis which was studied by us jointly. Previously I concluded that the stalk of the seed-bearing capsule is attached at a distance from the capsule mouth. The reason of such assumptions was given in the above mentioned paper. The maceration of the Smoller's specimen has convinced us that the stalk entered the mouth and micropylar tubes of ovules were closely adpressed to the stalk being arranged around it. The stalk easily separated from the capsule. That is why I could not find the stalk when the mouth was well seen. When the stalk was still attached, it prevented seeing the mouth. A detailed description of new material will be published elsewhere.

Thus, the previous interpretation of Cardiolepis (as an inverted capsule comparable with multiovulate epimathium) has proved to be erroneous. Smoller and I tentatively interpret Cardiolepis as a semiclosed peltate structure, the margin of which is bent down and embraces the stalk. In fundamental organization it is similar to peltasperms. Spirally arranged foliage leaves of these plants (genus Phylladoderma) having resin ducts between (?) parallel veins converging at the apex, and longitudinally orientated stomata are alien to any known pteridosperms and look much more conifer-like. They are closely similar to Podozamites and Araucariodendron. The combination of such leaves and seed-bearing capsules is unique among gymnosperms. Therefore, their previous separation into the family Cardirolepidaceae remains valid. But everything said on the bearing of the family to the coniferalian phylogeny now should be abandoned.

On the other hand, new data on Sashinia corroborate to previously made statements. Sashinia-plant (I use this designation for reconstructed plant) had loose female cones resembling sterile shoots. Both bracts and sterile leaves of the axillary complex are unspecialized showing no difference from foliage leaves. If one assumes the leafy nature of specialized bracts and sterile leaves in the axillary complex of Cordaitanthus, Lebachia and Ernestiodendron, the Sashinia-plant becomes more primitive than all these genera. At the same time, Sashinia-plant produced advanced microstrobili comparable with those of Triassic (Voltzialean?) conifers Darneya and Sertostrobus (Grau-vogel-Stamm, 1978). Hence, Sashinia-plant may be envisaged as a member of separate phylogenetic line rooting in more primitive
ancestors, i.e. Cordaitanthus, Lebachia and Ernestiodendron. In this case the acquisition of conifer-like male fructifications can be treated as an example of parallelism.

An alternative hypotheses involves an admission that female cones of Sashinia-plant are despecialized, and the similarity between bracts, sterile leaves of the axillary complex and foliage leaves is secondary in origin. From this viewpoint the similarity of seed-bearing appendages and leaves in S. aristovensis deserves mentioning. In a fusainized specimen of the species, the appendage is round in cross-section and is very similar to leaves of associating Q. dvinensis. In S. borealis the epidermal structure of seed-bearing appendages and leaves is the same (Text-figs 8-13). One can interpret these similarities as secondary as well. But if such increasing uniformity of different organs is possible we lose reliable criteria for phylogenetic reconstructions. Data on other parts of the plant body cannot help. Indeed the advanced nature of male fructifications of Sashinia-plant may lead to two controversial conclusions: (i) parallelism in male fructifications advancement together with retained primitiveness of female cones, or (ii) true advanced status of the the former together with despecialized status of the latter. Any additional character involved for the solution of the phylogenetic problem may bring similar alternatives, each of them being equally plausible.

Principal possibility of despecialization of parts and, on the other hand, the equal possibility of parallel development resulting in remarkably similar structures (e.g. a striking parallelism in gross morphology between coniferalean male fructifications and the Upper Permian Cladostrobus of Siberia associating with Rufioria leaves and Cladaitina pollen) leave very few chances to restore an authentic phylogenetic sequence of taxa.

When reconstructing phylogenies of living organisms we usually hope that competing versions can be “selected” by fossil records. Unfortunately the latter also provide alternative versions as exemplified by phylogenies of conifers quite differently restored by Florin (1951) and Schweitzer (1963). It seems that reliable phylogeny of conifers (and of many other plant groups) to be restored need much fuller sequence of genera in the geochronological scale than presently available.

An unusual combination of characters in Sashinia-plant poses a difficult problem in assigning these conifers to a certain family. Female cones suggest their proximity to very primitive Lebachiaceae, whereas male cones and pollen are closer to those of Voltziaeae (if Darneya and Sertostrous do belong to this family). Having a peculiar combination of characters Sashinia-plant may form a family of its own. To select one of the alternatives right now seems impossible.

Phytogeographical and Florogenetical Implications — Q. sibiricus belong to one of the dominating plants in the Lower Triassic of Siberia. The age of the beds is based on ostracods, phyllopods and bivalves (Sadovnikov, 1964; Malovetskaya et al., 1976). In indisputable Upper Permian beds of Siberia Quadrocladus is altogether absent. It is known with confidence in the Upper Permian of western Europe, Russian platform and South Fore-Urals, i.e. in the Atlantic kingdom and East-European area of the Angara kingdom (Chaloner & Meyen, 1973). Recently many data appear that the flora of the East-European type extended further to the south and east. M.V. Durante (personal communication) found that the flora of the Bexell’s zone C of Nan-Shan Range in China contains many elements (including Quadrocladus-like conifers and peltasperms) characteristic of the Upper Tatarian of Russian platform. The belt encircling the territory with the typical Angara flora of the Pechora-Siberian type may be regarded as an independent ecotonous area for which the name “Subangara” seems appropriate.

It appears that Triassic Quadrocladus of Siberia were rooted in the Upper Permian ancestors inhabited the Subangara area. Another Siberian Triassic plant group of the same origin might be peltaspermaceous pteridosperms producing Tata-rina leaves (Meyen & Gomankov, 1980).

Sporophylls similar to Tomiosstrobus are known outside Kuznetz basin in Pechora basin, Tajmyr peninsula and Verkhoyan mountains. The relation between Tomiosstrobus and Gondwanan Triassic Cylostrobus is still uncertain, but both are presumably the members of Pleuromeiaceae. Palaeozoic ancestors of the family are unknown,
They may be searched among Subangara and Pechora Permian lycopods like Viaticheslavia and Signacularia.

Subangara flora might well be one of the most important sources of the Mesozoic floras in general (Meyen, 1979) and of the Triassic flora of Siberia in particular. The appearance, in the Siberian Triassic, of some plants characteristic for the Subangara Upper Permian suggests a re-arrangement of migration roots and phytogeographical barriers near the Permian-Triassic boundary. The significance of these events for the transition from the Palaeophyte to Mesophyte were analysed by me earlier (Meyen, 1973a).

### REFERENCES


### EXPLANATION OF PLATES

**PLATE 1**

1-3. 1. *Quadroc!adus borealis* sp. nov., cuticle of holotype. Stoma with proximal papillae on subsidiaries. prep. no. 3774/1-1. × 1000. 2. Stoma without proximal papillae, thin corner spines on left side, prep. no. 3774/1-1. × 1000. 3. Marginal denticulation, prep. no. 3774/1-1a, point 1. × 300.

4. *Quadroc!adus borealis* sp. nov., cuticle of shoot apex, prep. no. 3774/7-10. × 100.

5-7. 5. *Sashinia borealis* sp. nov., cuticle of holotype. Stoma on bract with proximal papillae on apex, prep. no. 3774/1a-8, point 2. × 1000. 6. Cuticle of sterile leaf in basal part of axillary complex (see also Text-figs 10, 11), prep. no. 3774/1b-8, point 1. × 300. 7. Outer cuticle of seed in its lower part (see also Text-fig. 8), prep. no. 3774/1b-8, point 3. × 300.

**PLATE 2**

8-12. 8. *Quadroc!adus sihricus* (Neub.) comb. nov., external view of leafy shoots. Lateral shoot
in leaf axil, no. 2761/831-1. x 5. 9, Detail of lectotype no. 2761/826-1. x 5 (see also Text-fig. 17). 10, Detail of syntype no. 2761/828-1 (1). x 5 (see also Text-fig. 18A). 11, Dwarf shoot, no. 2761/828-2. x 5 (see also Text-fig. 18B). 12, Dwarf shoot, no. 2761/826-2. x 5.


15,16. 15, *Quadrocladus sibiricus* (Neub.) comb. nov. cuticles of fragmentary leafy twigs obtained by bulk maceration. Prep. no. 2761/828-31. x 5. 16, Prep. no. 2761/828-32. x 5.


18. Pollen of *Leucitesporites* type stuck to cuticle of *Quadrocladus sibiricus* (Neub.) comb. nov. Prep. no. 2761/828-26. x 300.

19-21. 19,20. *Saschnia borealis* sp. nov. Seed cuticle after treatment with alkali, before mounting, stereophotographs, prep. no. 3774/1b-8. x 10. 21. Internal cuticle of integument adpressed to nucellar cuticle, prep. no. 3774/1b-8, point 2. x 300.

PLATE 3

*Quadrocladus sibiricus* (Neub.) comb. nov.

22-24. Lectotype, stoma photographed at different foci. Guard cells (Fig. 22), papillae on subsidiaries (Fig. 23), epistomatal chamber (Fig. 24) (see also Text-fig. 19). Prep. no. 2761/826-1, point 2. x 1000.

25,26. Cuticle of opposite leaf surfaces with badly pronounced (Fig. 26) and absent (Fig. 25) stomatal files. Lectotype. Prep. no. 2761/826-1, point 3 (Fig. 25), point 4 (Fig. 26). x 100.

27,28. Cuticle with variously preserved periclinal walls, in some subsidiaries periclinal walls are perforated. Lectotype, prep. no. 2761/826-1, point 1 (Fig. 27) and point 2 (Fig. 28). Prep. no. 2761/828-3a, point 1 (Fig. 29) and point 2 (Fig. 30). x 300.
Plate 2