

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

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ABSTRACT

Twigs *Retinosporites* ?*sibirica* and fructifications *Tomioostrobus 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 *Quadrocladus*. Pollen produced by these plants were of the *Lueckisporites* type. *Quadrocladus borealis* and corresponding female fructifications *Sashinia borealis* coming from the Uppermost Permian 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.

सारांश

साइबेरिया एवं रूसी प्लेटफार्म से कुछ सत्य एवं अभिकथित पर्मियन-ट्रायैसिक कॉनिफर तथा इनके सहगण — सर्जी वी० मीयन

कुजनेत्स बेसिन के अधर ट्रायैसिक से रेटिनोस्पोराइटिस ? साइबेरिका की प्रशाखाओं तथा टॉमियोस्ट्रोबस रेडिएटस — अँराकेराइटिस टॉमियेन्सिस के फलनों को अस्थायी रूप से एक ही पौधे से संबद्ध किया गया है। अँ० टॉमियेन्सिस एवं टॉ० रेडिएटस सूक्ष्म-बीजाणु (अँराट्राइस्पोराइटिस-सदृश) एवं गुरुबीजाणु उत्पन्न करते हैं तथा लेपिडोफ़ाइट्स (प्ल्यूरोमियेसी कुल) से संबद्ध हैं। सभी बाह्य-आकारिकीय एवं बाह्य-त्वचीय लक्षणों में रे० साइबेरिका को क्वाड्रोक्लेडस से संबद्ध किया गया है। इन पौधों द्वारा उत्पन्न परागकण ल्यूकिस्पोराइटिस-सदृश हैं। रूसी प्लेटफार्म के उच्चतम पर्मियन युग से क्वाड्रोक्लेडस बोरियेलिस तथा साशीनिआ बोरियेलिस के अनु-रूप मादा फलनों का वर्णन किया गया है। साशीनिआ के पौधों में मादा फलन आदि-रूप वाले तथा नर फलन बहुत विकसित हैं। इन अन्वेषणों के जातिवृत्तीय एवं वर्गीकरणिक परिणामों का विवेचन किया गया है। साइबेरिया का अधर ट्रायैसिक कालीन वनस्पतिजात पर्मियन युग के उप-अंगारा क्षेत्र से आया हुआ प्रतीत होता है।

INTRODUCTION

IN 1936, Neuburg described three species of conifers, viz., *Retinosporites* ?*sibirica* Neub., *Araucarites tomiensis* Neub. and *Tomioostrobus radiatus* Neub. from the Lower Triassic (Maltsevskaya 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 *Tomiostrubus*. 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 *Cylostrobos* related to *Pleuromeia*. Megaspores *in situ* were found by me in the type material of *T. radiatus*. They are trilete (?) and differ from those of both *Pleuromeia* and *Cylostrobos* in having a relief with verrucae and ribs. Krassilov and Zakharov (1975) described isolated megasporangium with megaspores *in situ* as *Pleuromeia olenekensis*. Having smoothed reticulate relief, megaspores of the latter are closer to those of *Tomiostrubus* 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.

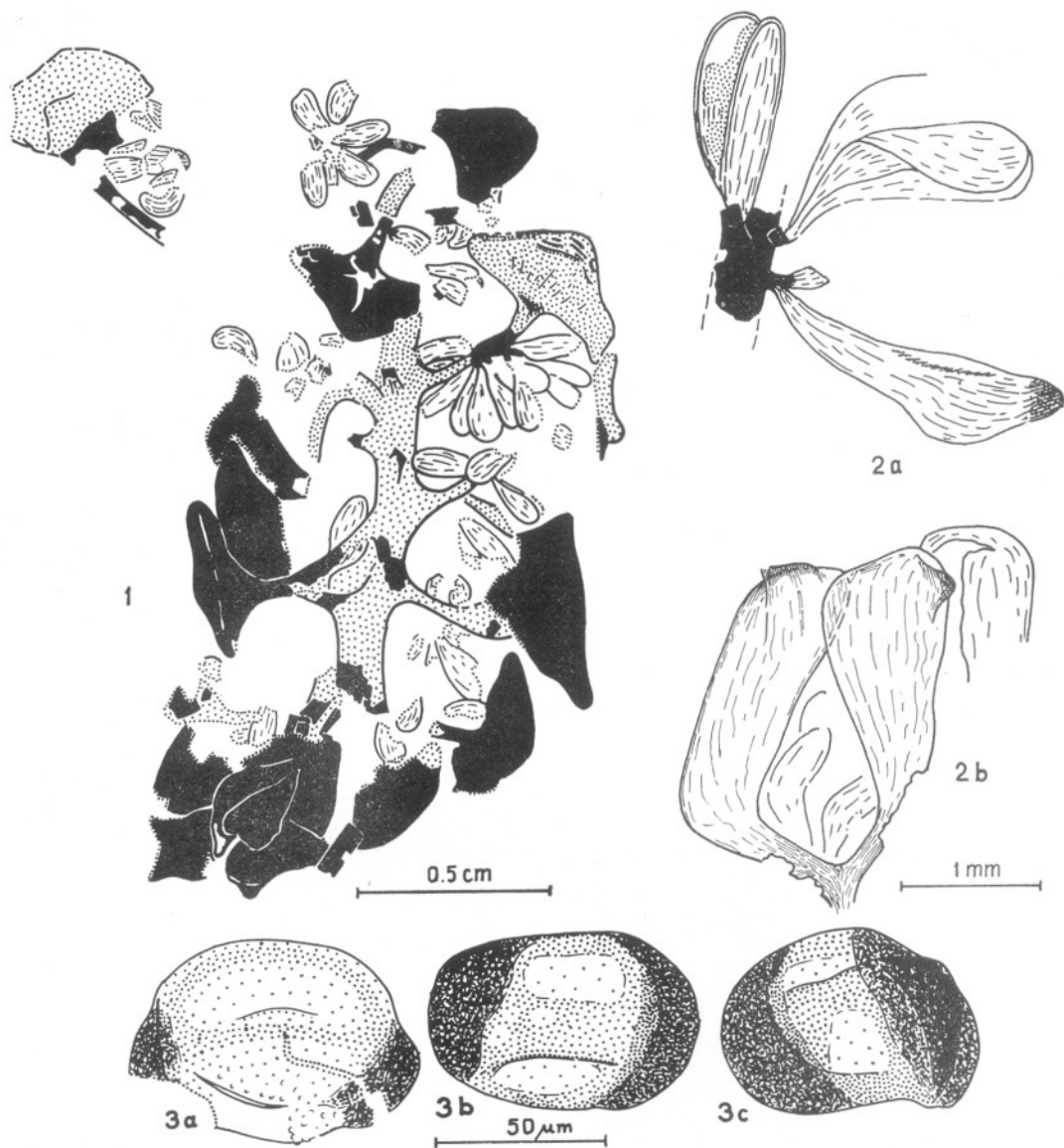
Sashinia borealis sp. nov.

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. Bracts are 1-1.2 mm wide, 6-7 mm long, linear with rounded apex. Axillary complex consists of leafy axis bearing apically 2-6 seed-bearing appendages 6-8 mm long (when measured together with inverted seeds). 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 O6, depth 139-154.5 m; Upper Permian, Upper Tatarian substage Viatsky (?) horizon.

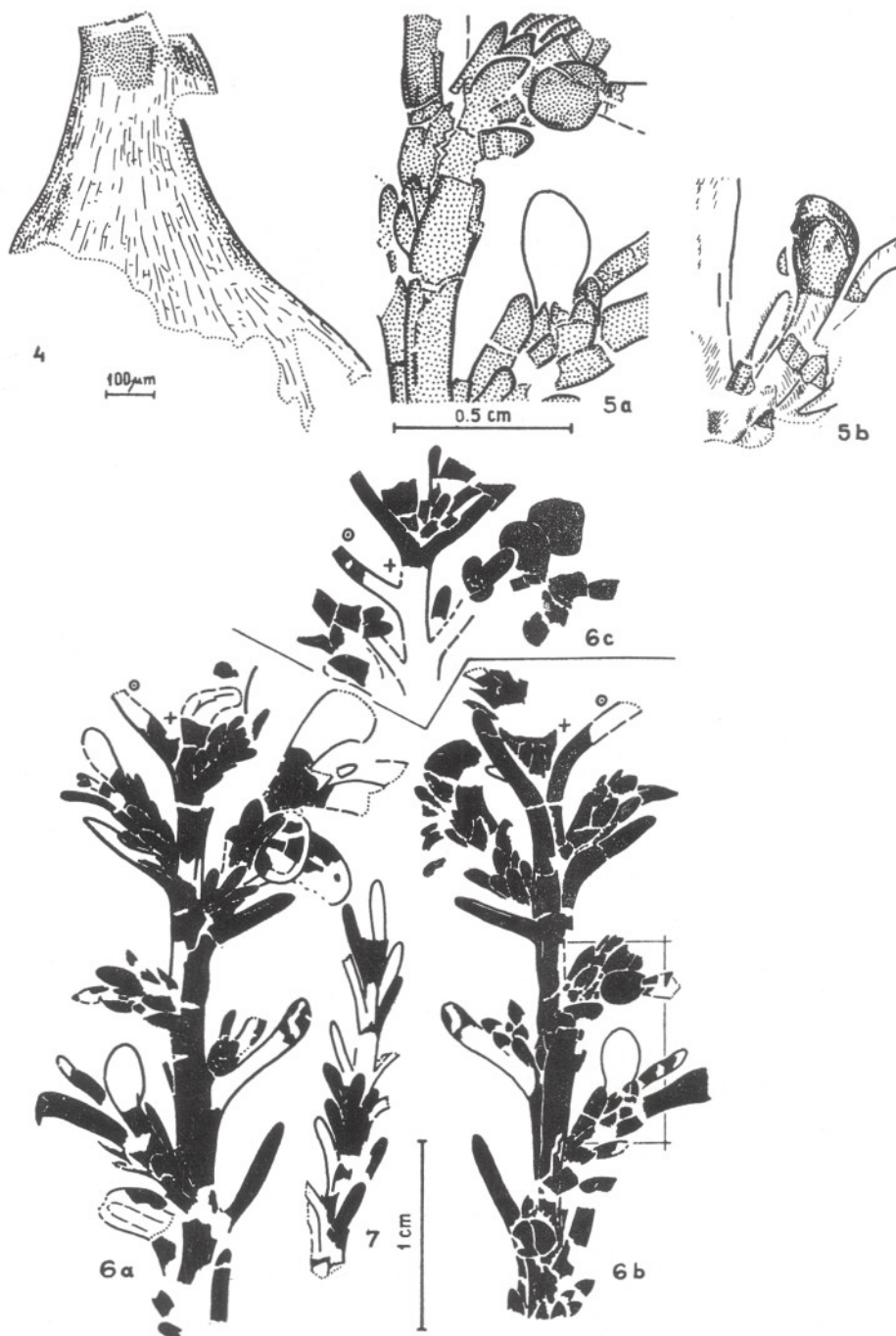
Besides the holotype, a few fragments probably belonging to the same species were found in the type locality. The holotype was transferred on a film (Text-figs 5, 6). Axillary complexes vary in size and produce various number of seed-bearing appendages (their number increases acro-



TEXT-FIGS 1-3 — Microstrobilus and pollen associating with *Sashinia aristovenssis* Meyen and *Quadrocladus divinensis* 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 addressed 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 were not 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. aristovensii* Meyen in lesser number and smaller size of seed-bearing appendages. Leaves at the base of axillary complex differ from those of *S. aristovensii* 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. aristovensii* and those described by Schweitzer (1960) as *Rhenania reicheltii*.

Quadrocladus Mädlér, 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 spatulate 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-

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

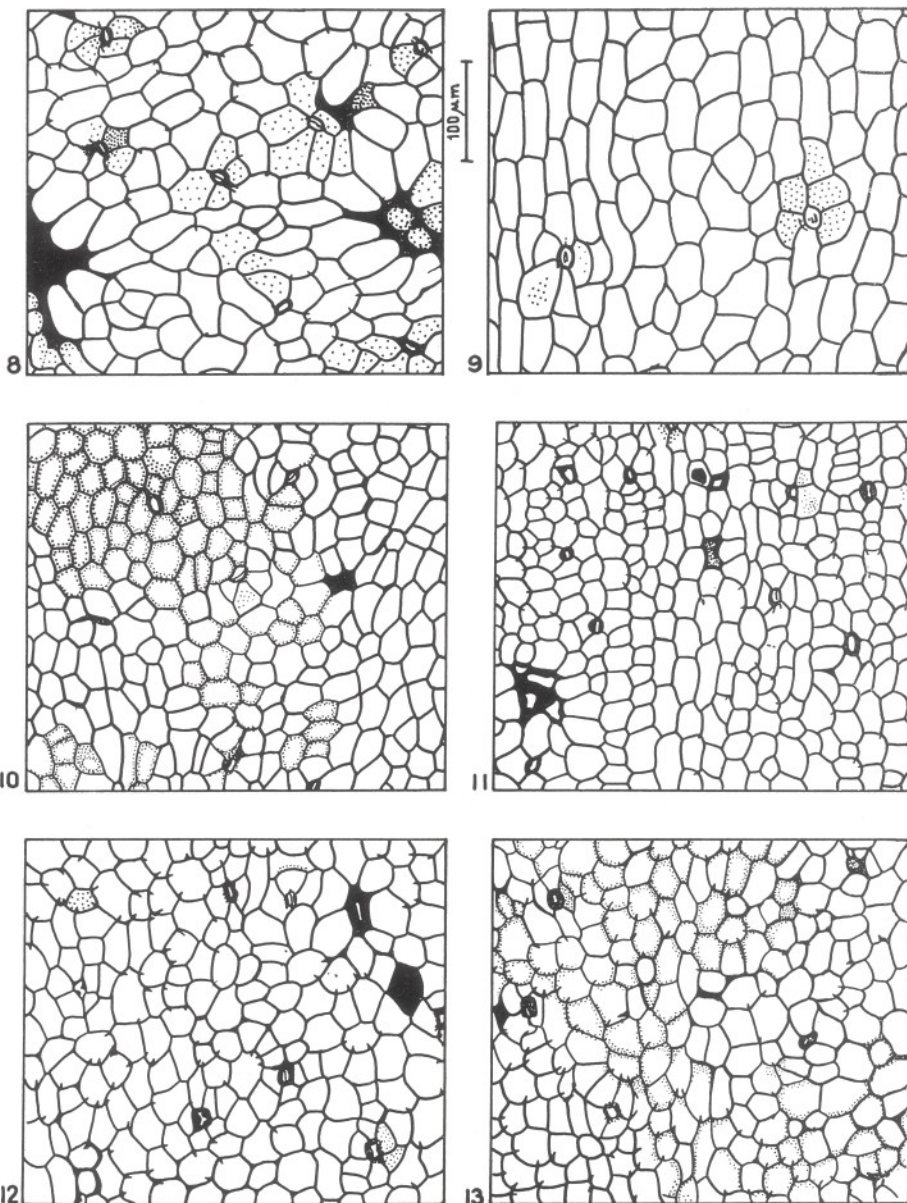
Holotype — Specimen no. 3774/1-1 (Pl. 1, figs 1-3; Text-figs 7, 15, 16).

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 epistomatal 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 differs 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.



TEXT-FIGS 8-13—*Sashinia borealis* sp. nov., holotype no. 3774/1-8. 8. Cuticle of seed in its basal part prep. no. 3774/1-8e (I), point 1 (see Pl. 1, fig. 7). 9. Cuticle of seed-bearing stalk below seed, prep. no. 3774/1-8c. 10, 11. Cuticle of different sides of sterile leaf in basal part of axillary complex, prep. 3774/1-8h (see Pl. 1, fig. 6). 12, 13. Cuticle of different sides of bract, prep. no. 3774/1-8.

Quadrocladus sibiricus (Neuburg) comb. nov.

Retinosporites ? *sibirica*: Neuburg, 1936, pp. 489-491, pl. IV, figs 1-11; Turutanova-Ketova in "Osnovy paleontologii", 1963, pp. 252, 257, fig. 115.

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

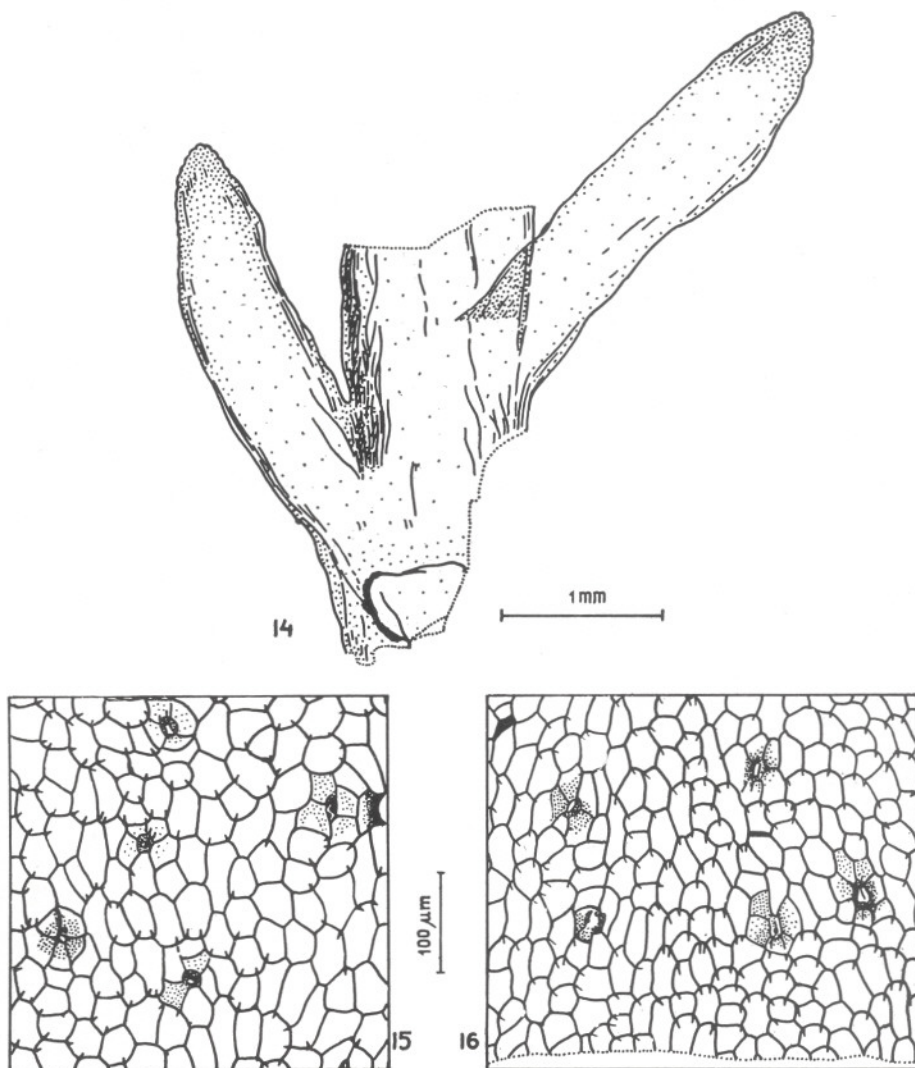
Emended Specific Diagnosis—Branches of penultimate order with larger leaves bear pinnately arranged branches of last

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.

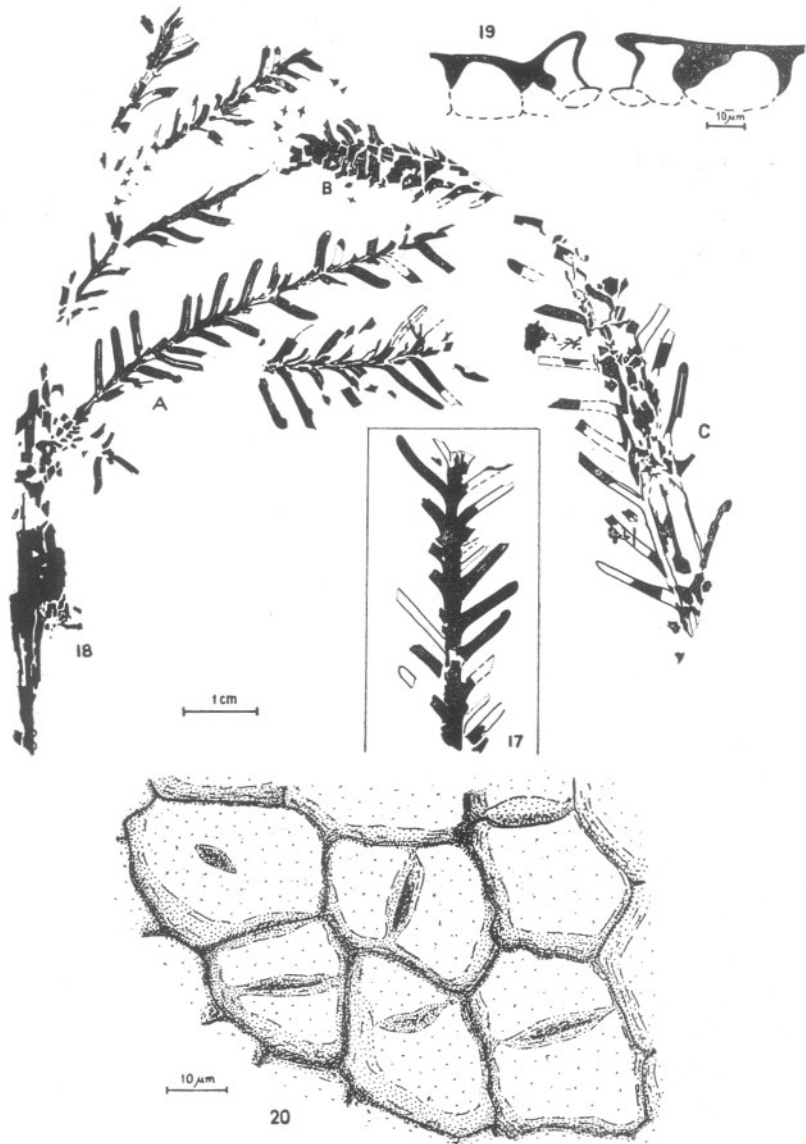
Lectotype — Specimen no. 2761/826-1, 825-1 (counterpart) figured by Neuburg, 1936, pl. 4, figs 1, 5, 7 (our Pl. 2, fig. 9; Pl. 3, figs 22-28; Text-figs 17, 19, 20).

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.



TEXT-FIGS 17-20 — *Quadrocladus sibiricus* (Neub.) comb. nov., type locality: 17. Lectotype no. 2761/826-1 (see also Pl. 2, fig. 9). 18A, B, C. Three specimens in their relative position on bedding plane (18A — branch of penultimate order with several branches of last order, specimen no. 2761/828-1, see also Pl. 2, fig. 10; 18B — branch of penultimate order with crowded leaves suggesting short shoot, specimen no. 2761/828-2, see also Pl. 2, fig. 11; 18c — branch of penultimate order with distant leaves suggesting long shoot, specimen no. 2761/828-3, its cuticle see on Pl. 3, figs 29, 30). 19. Reconstructed transverse section of stoma on Pl. 3, figs 22-24, lectotype, prep. no. 2761/826-1, point 2. 20. Cuticle of lectotype showing variously developed septae, prep. no. 2761/826-1, point 2.

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 phyllotaxis 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 (Pl. 2, figs 13, 14). 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 *Lueckisporite* type (Pl. 2, fig. 18) stuck to cuticle solitary or in groups. The pollen show a wide range of variation in body/sacci 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 bronniei* 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 aristovenssis*. 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 monotypic 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 denticulation, 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 Cardiolepidaceae. 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 Cardiolepidaceae 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 (Votzialean?) conifers *Darneya* and *Sertostrobus* (Grauvogel-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. aristovenssis* 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 *Ruflorea* 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 Voltziaceae (if *Darneya* and *Sertostrobis* 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, phyllospods 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 peltaspermeous pteridosperms producing *Tatarina* leaves (Meyen & Gomankov, 1980).

Sporophylls similar to *Tomioctrobis* are known outside Kuznetz basin in Pechora basin, Tajmyr peninsula and Verkhoyan mountains. The relation between *Tomioctrobis* and Gondwana Triassic *Cylostrobis* 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 *Viat-cheslavia* 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 rearrangement 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

- BOSE, M. N. & ROY, S. K. (1968). On the occurrence of *Pachypteris* in the Jabalpur Series of India. *Palaeobotanist*, **16** (1): 1-9.
- CHALONER, W. G. & MEYEN, S. V. (1973). Carboniferous and Permian floras of the northern continents, pp. 169-186 in Hallam, A. (Ed.)—*Atlas of Palaeogeography*. Elsevier Sci. Publ. Co., Amsterdam.
- FLORIN, R. (1951). Evolution in Cordaites and conifers. *Acta Hort. Bergiani*, **15** (11): 285-388.
- GRAUVOGEL-STAMM, L. (1978). La flore du grès à Voltzia (Buntsandstein supérieur) des Vosges du Nord (France). Morphologie, anatomie, interprétations phylogénique et paléogéographique. *Univ. L. Pasteur de Strasbourg, Inst. Géol., Mém.*, **50**: 1-255.
- KRASILOV, V. A. & ZAKHAROV, YU. D. (1975). *Pleuromeia* from the Lower Triassic of the Far East of the USSR. *Rev. Palaeobot. Palynol.*, **19**: 221-232.
- MALOVETSKAYA, I. M., NOVOZHILOV, N. I. & SADOVNIKOV, G. N. (1976). Stages in development of flora and fresh-water fauna of the Tunguska basin in the Late Permian and Early Triassic. *Trudy XIII i XIV sessij Vsesoyuznogo Paleontologicheskogo Observatoria (Pyatidesyatiletie sovetsskoi paleontologii i voprosy sistematiki drevnikh organizmov)*. Publ. Office "Nauka", Leningrad: 296-302 (in Russian).
- MEYEN, S. V. (1973a). The Permian-Triassic boundary and its relation to the Paleophyte-Mesophyte floral boundary, pp. 662-667 in Logan, A. & Hills, L. V. (Eds)—*The Permian and Triassic Systems and their Mutual Boundary*. (Canad. Soc. Petrol. Geologists, Mem., 2). Calgary.
- MEYEN, S. V. (1973b). Plant morphology in its nomothetical aspects. *Bot. Rev.*, **39** (3): 205-260.
- MEYEN, S. V. (1978). Permian conifers of the West Angaraland and new puzzles in the coniferalian phylogen. *Palaeobotanist*, **25**: 298-313.
- MEYEN, S. V. (1979). Permian predecessors of the Mesozoic pteridosperms in Western Angaraland. *Rev. Palaeobot. Palynol.*, **28**: 191-201.
- MEYEN, S. V. & GOMANKOV, A. V. (1980). Pteridosperms of the genus *Tatarina*. *Paleontol. Zh.*, **2**: 116-132 (in Russian).
- NEUBURG, M. F. (1936). On the stratigraphy of the coal-bearing deposits of the Kuznetsk basin. *Bull. Acad. Sci. USSR, cl. sci., mathém. et natur.*, **4**: 469-510 (in Russian, English summary).
- OBONITSKAYA, E. K. (1974). Spore and pollen assemblages of volcanogenous deposits of the central part of the Tunguska syncline. *Trudy Tomsk. Univ.*, **232**: 160-165 (in Russian).
- SADOVNIKOV, G. N. (1964). On the age of volcanogenous formations of Tunguska syncline. *Izvestiya Akad. Nauk SSSR, ser. Geol.*, **11**: 68-77 (in Russian).
- SCHWEITZER, H. J. (1960). Die Makroflora des niederrheinischen Zechsteins. *Fortschr. Geol. Rheinld. Westf.*, **6** (Vorausdruck): 1-46.
- SCHWEITZER, H. J. (1963). Die weibliche Zapfen von *Pseudovoltzia liebeana* und seine Bedeutung für die Phylogenie der Koniferen. *Palaeontographica*, **113B** (1-4): 1-29.
- VISSCHER, H. (1970). The Permian and Triassic of the Kingscourt outlier, Ireland. A palynological investigation related to regional stratigraphical problems in the Permian and Triassic of Western Europe. *Geol. Surv. Ireland, spec. paper No. 1*: 1-114.

EXPLANATION OF PLATES

PLATE 1

- 1-3. **1**, *Quadrocladus borealis* sp. nov., cuticle of holotype. Stoma with proximal papillae on subsidiaries, prep. no. 3774/1-1. $\times 1000$. **2**, Stoma without proximal papillae, thin corner spines on left side, prep. no. 3774/1-1. $\times 1000$. **3**, Marginal denticulation, prep. no. 3774/1-1a, point 1. $\times 300$.
4. *Quadrocladus borealis* sp. nov., cuticle of shoot apex, prep. no. 3774/7-10. $\times 100$.
- 5-7. **5**, *Sashinia borealis* sp. nov., cuticle of holotype. Stoma on bract with proximal papillae on

subsidiaries, corner spines are thick, prep. no. 3774/1a-8, point 2. $\times 1000$. **6**, Cuticle of sterile leaf in basal part of axillary complex (see also Text-figs 10, 11), prep. no. 3774/1-8h, point 1. $\times 300$. **7**, Outer cuticle of seed in its lower part (see also Text-fig. 8), prep. no. 3774/1b-8, point 3. $\times 300$.

PLATE 2

- 8-12. **8**, *Quadrocladus sibiricus* (Neub.) comb. nov., external view of leafy shoots. Lateral shoot

- in leaf axil, no. 2761/831-1. $\times 5$. **9**, Detail of lectotype no. 2761/826-1. $\times 5$ (see also Text-fig. 17). **10**, Detail of syntype no. 2761/828-1 (I). $\times 5$ (see also Text-fig. 18A). **11**, Dwarf shoot, no. 2761/828-2. $\times 5$ (see also Text-fig. 18B). **12**, Dwarf shoot, no. 2761/826-2. $\times 5$.
- 13,14. **13**, *Quadrocladus sibiricus* (Neub.) comb. nov., cross sections of leafy twigs. Note variations in leaf outline in section view. No. 2761/829-1. $\times 5$. **14**, No. 2761/835-2. $\times 10$.
- 15,16. **15**, *Quadrocladus sibiricus* (Neub.) comb. nov. cuticles of fragmentary leafy twigs obtained by bulk maceration. Prep. no. 2761/828-31. $\times 5$. **16**, Prep. no. 2761/828-32. $\times 5$.
17. *Quadrocladus sibiricus* (Neub.) comb. nov. Cuticle of leaf basal part with rhomboid opening corresponding to attachment plane. Prep. no. 2761/828-19. $\times 30$.
18. Pollen of *Leuckisporites* type stuck to cuticle of *Quadrocladus sibiricus* (Neub.) comb. nov. Prep. no. 2761/828-26. $\times 300$.
- 19-21. **19,20**, *Sashinia borealis* sp. nov. Seed cuticle after treatment with alkali, before mounting, stereophotographs, prep. no. 3774/1b-8. $\times 10$.
- 21**, Internal cuticle of integument adpressed to nucellar cuticle, prep. no. 3774/1b-8, point 2. $\times 300$.

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. $\times 1000$.
- 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). $\times 100$.
- 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). $\times 300$.

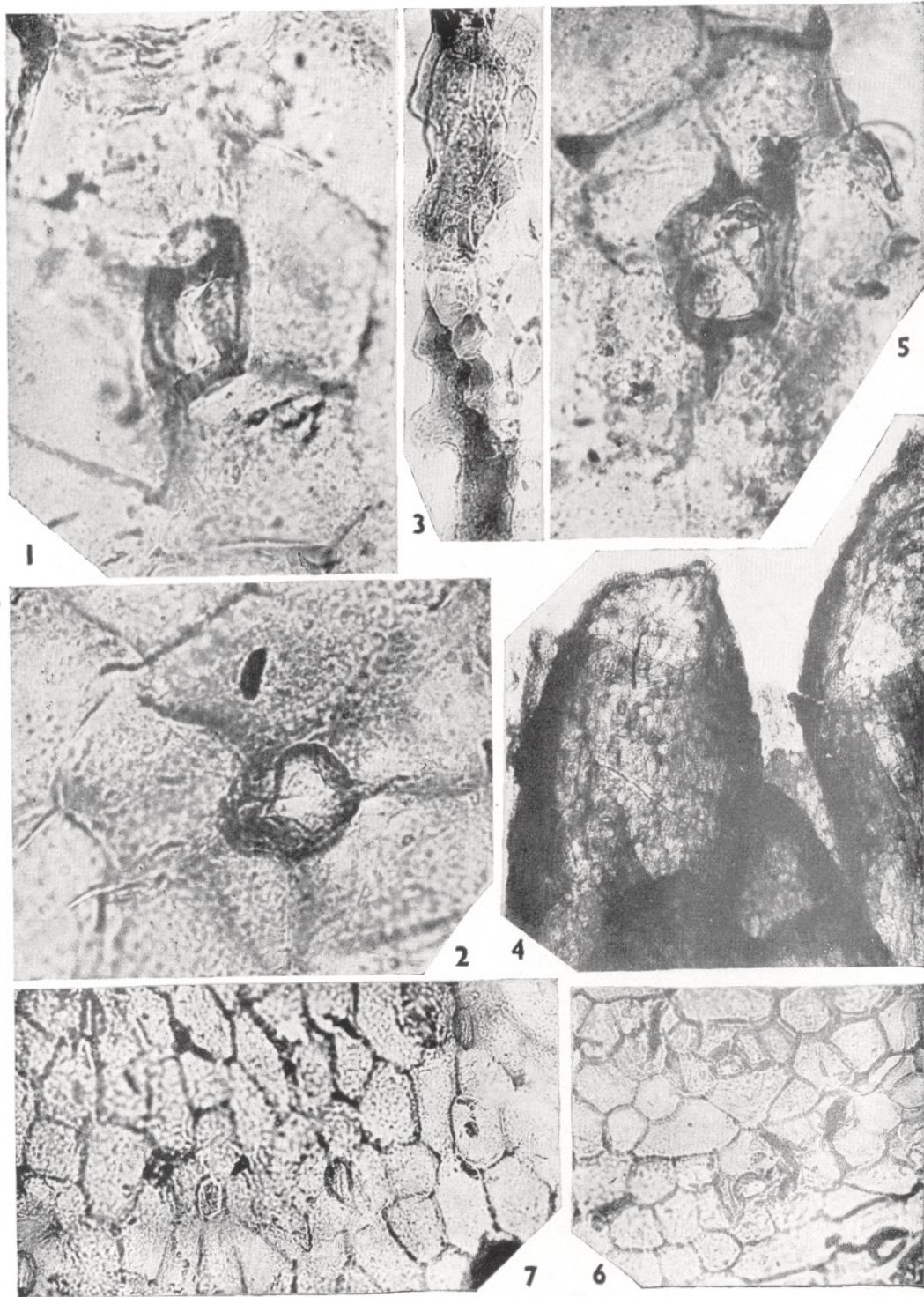


PLATE 1

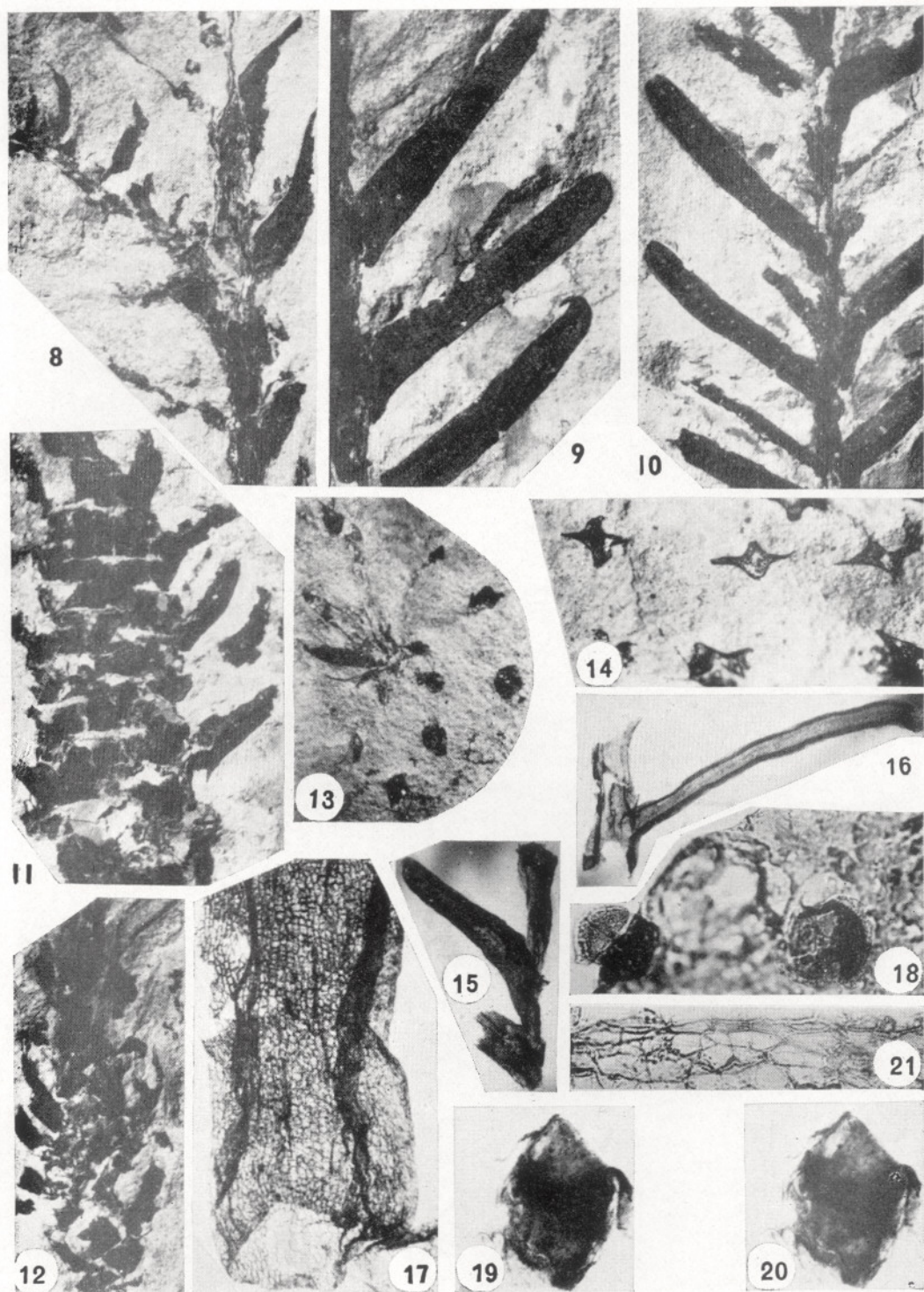


PLATE 2

