PERMIAN CONIFERS OF WEST ANGARALAND AND NEW PUZZLES IN THE CONIFERALEAN PHYLOGENY

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ABSTRACT

Permian flora of West Angaraland contains many predecessors of the Mesozoic floras. Conifers of the area do not show evident links with Mesozoic members of the group, but they are phylogenetically significant because they do not fit current versions of the coniferalean phylogeny. In this respect the most interesting are representatives of the family Cardiolepidaceae (female capsules *Cardiolepis*, seeds *Nucicarpus*, leaves *Phylladoderma*, and *Vesicaspora*-like pollen), and the genera *Sashinia* gen. nov. and *Slivkovia*. Moot points of the coniferalean phylogeny proposed by Florin are discussed.

INTRODUCTION

WE rarely realize the fact that the current palaeobotanical ideas depend on historical chances. The palaeobotany originated in Europe and during more than a century Europe was the main source of the palaeobotanical materials. European fossil plants dominate in text-books. The history of vegetation in Europe is often taken as a world standard. One can often read in the literature about wet and hot climate of the Carboniferous, and many geologists and botanists are convinced that the Permian climate was dry and hot, though these characteristics cannot be ascribed to many areas outside Europe.

This misapprehension is particularly relevant in case of the Upper Permian flora. European flora of Zechstein is often regarded as the typical Upper Permian flora, though it is basically different from coeval floras of Siberia, Cathaysia and Gondwana each covering much larger areas.

I am not going to claim that Angara Permian floras are more representative. But I presume that Angara *Rufloria* whose leaves are as common in the Upper Palaeozoic throughout North Eurasia as extant conifers on the same area, deserves not less attention of scholars of past vegetation than *Cheirostrobus* known from a single specimen and mentioned in every text-book of palaeobotany. In previous papers I have treated articulates, lycopsids, cordaitalean and pteridospermous plants (Meyen, 1970, 1971c, 1976; Maheshwari & Meyen, 1975). The present paper deals with conifers which are especially characteristic for West Angaraland, i.e. its part westwards of Urals. I shall try to show that the data on these conifers pose difficult phylogenetical problems and throw doubts on current notions in coniferalean phylogeny.

West Angaraland in the Upper Permian can be divided into two parts: Pechora province and East-European area of the Angara Kingdom (Meyen, 1971b; Chaloner & Meyen, 1973). The East-European area combines features of Atlantic (Zechstein) and Pechora floras. Pechora elements are represented by cordaitalean leaves, *Phylladoderma*, ferns, articulates, mosses and *Psygmophyllum*-like plants. European elements are represented by conifers comparable to *Pseudovoltzia* and *Quadrocladus*. Pechora flora contains much more ferns, many plants common with Siberia and endemics (for detailed lists see: Meyen, 1971b; Chaloner & Meyen, 1973).

The data obtained during last decade have shown that West Angaraland yields the oldest record of some plant groups which are typical for the Mesozoic. In the upper part of the Lower Permian (Kungurian stage) there are leaves similar to ginkgoalean or czekanowskialean, typical *Peltaspermum* female discs and pteridosperms comparable to Jurassic *Pachypteris* and *Raphidopteris*. The latter are common in the Kazanian of Russian platform from Kama embayment to Fore-Timan area. In the Uppermost Permian (upper part of the Upper Tatarian substage) plant assemblages are dominated by peltaspermaceous pteridosperms (*Tatarina*, *Peltaspermum*, *Antevsia*-like male fructifications producing, however, saccate pollen) whose compressions sometimes over-fill the embedding sediment. It is possible that the Upper Permian lepidophytes *Viatcheslavia* and *Signacularia* (they may be synonyms — Meyen, 1976) are related to Triassic *Pleuromeia*. In the Lower Kazanian of the Fore-Timan area there are *Brachyphyllum*-like conifers with decussate leaves closely adpressed to the stem.

DESCRIPTION

Though, conifers described below do not show evident links with known Mesozoic forms, they are phylogenetically significant because they cannot be incorporated into the current versions of coniferalean phylogeny. Three types of Angaraland conifers are shortly described and discussed below, viz., the family Cardiolepidaceae (the genera *Cardiolepis, Phylladoderma* and *Nucicarpus*), and the genera *Sashinia* gen. nov. and *Slivkovia*.

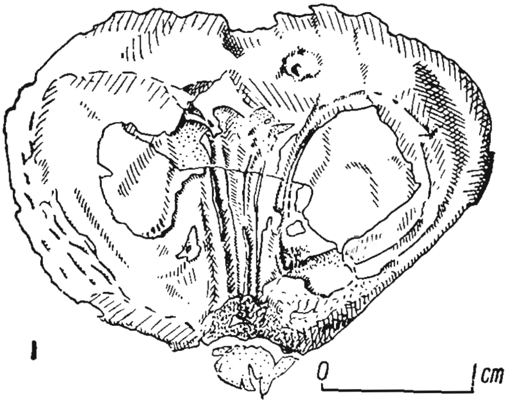
Family — CARDIOLEPIDACEAE Meyen, 1977

This family comprises plants producing female capsules *Cardiolepis*, leaves *Phylladoderma*, seeds (ovules) *Nucicarpus* and pollen of *Vesicaspora* type. These form-genera can be ascribed to the same parental plants on the following reasons:

1. All these genera are characteristic of paper coals consisting of *Phylladoderma* compressions. In small rock lenses in the coals the pollen of *Vesicaspora* type constitutes up to 80-90% of the whole miospore assemblages.
2. Dispersed *Nucicarpus* seeds are identical to those found in half-destroyed mature *Cardiolepis*. Younger intact *Cardiolepis* capsules contain ovules with a long micropylar tube. Dispersed *Nucicarpus* sometimes show tubular apex.
3. Pollen in micropyle of ovules extracted from capsules is of *Vesicaspora* type.
4. Guard cells of stomata and secretory openings in cuticle of both leaves and capsule are identical. Cuticle of these organs is characteristically thick and resistant to maceration.
5. Both leaves, capsules and even seeds are resiniferous, the external view of the resin being uniform.
6. The association *Nucicarpus-Phylladoderma-Vesicaspora* remains constant on the background of different plant assemblages of the Pechora province and East-European area.

Cardiolepis Neuburg, 1965 emend. Meyen, 1977

The monotypic genus *Cardiolepis* (type species *C. piniformis* Neub.) was established by Neuburg (1965) on the basis of gross morphology only. She treated the holotype (Pl. 1, fig. 3; Text-fig. 1) as an open seed scale bearing two seeds. She compared the specimen with seed scales of Pinaceae. Another specimen representing the disc with radially arranged seeds (Pl. 1, figs. 1, 2, 7, 8; Text-figs. 8, 9; comparable specimen shown in Text-fig. 6) was envisaged by her as a transverse section of a cone consisting of such scales. There are two more types of preservation of *Cardiolepis*: (i) flat disc-shaped compressions (Pl. 1, fig. 6; Text-fig. 3a, b), and (ii) round flattened bodies with open imbricated seeds (Pl. 1, figs. 4, 5; Text-figs. 2a, 7). As was shown earlier (Meyen, 1977) these modes of preservation correspond to variously flattened cupules and to various degree of their maturing (Text-figs. 10, g, h, i, j), holotype being a flattened unripe capsule dissected along longitudinal plane (cf. Text-figs. 1, 2, a, b, c). Subsequent investigations have confirmed this conclusion. I have prepared transfer-preparations from Neuburg's specimen (and its counterpart) interpreted by her as a section of cone. On the back side one can see opening with micropylar tubes inside (Pl. 1, figs. 2, 7, 8; Text-fig. 8). This opening is surrounded from one side by scars with thorn margin possibly marking attachment point of ovules under the cuticle. The place where a stalk should be attached is missing. Opposite side of the specimen was opened by me earlier (Meyen, 1977). It shows entire cuticular cover with folds (Text-fig. 9). Another transfer was prepared from longitudinally dissected capsule with imbricated seeds (Pl. 1, figs. 4, 5; Text-fig. 7; transfer preparation obtained from counterpart not shown here). A long stalk covered with thick cuticle is well seen, but unfortunately the opening of the capsule with micropylar tubes is covered with a mass of resin. Thus in none of the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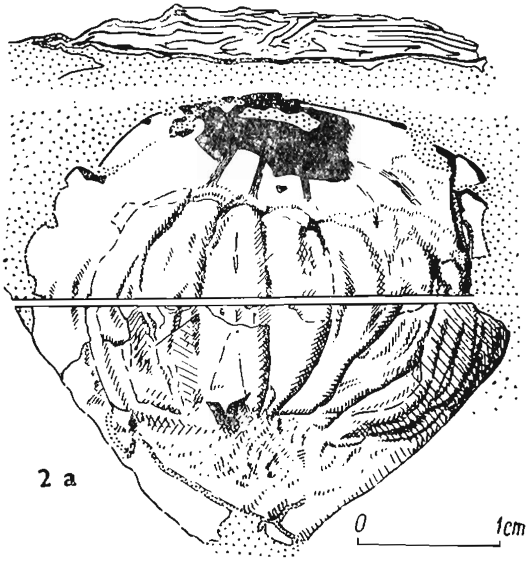
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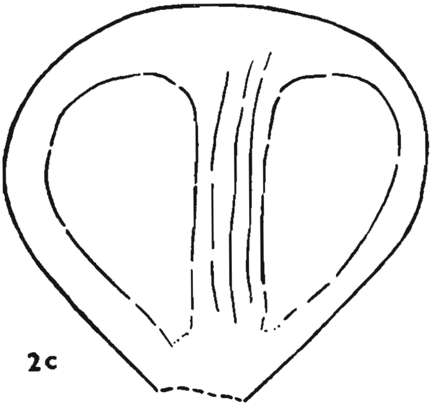
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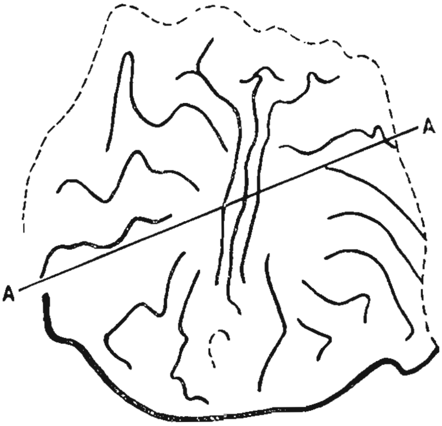
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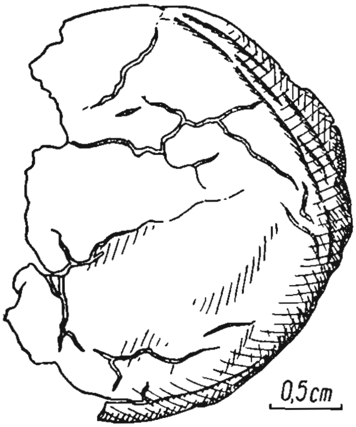
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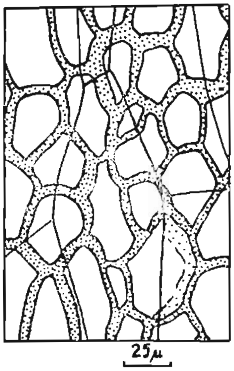
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Text-figs. 1-5

capsules both stalk and opening of the capsule can be observed.

Judging from the transferred, sectioned and macerated capsules their structure appears as follows. The capsule was flattened laterally in younger state and underwent compression in the same direction during preservation. Being splitted longitudinally, it resulted in preservation shown in Text-figs. 1 and 2. During maturation, the capsule became wider distally and hence was buried in vertical position being compressed in distal-proximal direction (Text-figs. 6, 7).

Judging from sections and results of maceration capsules contained some 14-16 ovules (Pl. 2, fig. 12; Text-figs. 2a, 2b). Outer cuticle of the integument of the ovule is very thin and is somewhat thicker around the tip of the micropylar tube. Inner cuticle of the integument and that of the nucellus are much thicker (Pl. 2, fig. 10). Both these cuticles become thinner proximally. Near chalaza, inner cuticle of the integument is very thin and show large cells. The chalaza is destroyed in all ovules extracted from capsules thus suggesting the ovules to be sessile. Micropylar tube is long (Text-figs. 5, 10d, 10e). Large amount of uniform pollen of *Vesicaspora* type (and solitary striated grains) were found both in the tube and in vicinity of nucellar tip (Pl. 2, figs. 10, 11). Micropylar tubes were grouped near the opening of the capsule and were seen from outside (Pl. 1, figs. 2, 7, 8; Text-fig. 8). It seems evident that pollen penetrated in the ovule by means of the drop mechanism as in many other gymnosperms (Caytoniales, Gnetales, Coniferales, etc.).

Phylladoderma Zalessky, 1914

The genus *Phylladoderma* consists of three species belonging to two subgenera: *Phylladoderma* subgen. *Phylladoderma* (*P. arberi* Zal., type species; *P. meridionalis* S. Meyen — Meyen & Gomankov, 1971) and *Phylladoderma* subgen. *Aequistomia* S. Meyen [*P.* (*A*) *aequalis* S. Meyen, 1977]. This genus comprises small to medium sized (up to 20 cm long) lanceolate, spathulate or nearly linear leaves with parallel veins slightly converging in obtuse apex. *Phylladoderma* was ascribed to Cordaitales by Zalessky (1914), to Ginkgoales by Neuburg (1960), and to Coniferales by me (Meyen & Gomankov, 1971). Coniferalean features of *Phylladoderma* are (i) one vein entering the leaf base, (ii) venation of the type characteristic for *Agathis*, *Araucariodendron*, *Podozamites*, and (iii) presence of resin canals between veins. In *Phylladoderma* subgen. *Phylladoderma* and from Pechora basin the stomata are freely distributed throughout both leaf surfaces. In the subgenus *Aequistomia* from the uppermost Permian of the Russian platform (a single locality is known in Pechora basin) there may be indistinct stomatal bands separated by stomata free zones. Guard cells of both subgenera are deeply sunken and have peculiar cutinization similar to that of *Bennettites*.

Shoots with spirally attached *Phylladoderma* leaves were found by Esaulova (Kazan University) in the uppermost Kazanian of the Volga River (between Kazan city & the mouth of Kama River). The genus *Sardykphyllum* Zalessky, 1929 from the Upper Kazanian of Tataria comprises young leaves of *Phylladoderma* and is to be considered as a later synonym of *Phylladoderma*. Another possible synonym of the genus is *Yuania* Sze, 1953 from the uppermost Permian of China. *Phylladoderma* is presently known in the Upper Permian of Primorie (Far East of the USSR; Burago, 1976). Salmenova showed me *Phylladoderma* found in the Bakalin-

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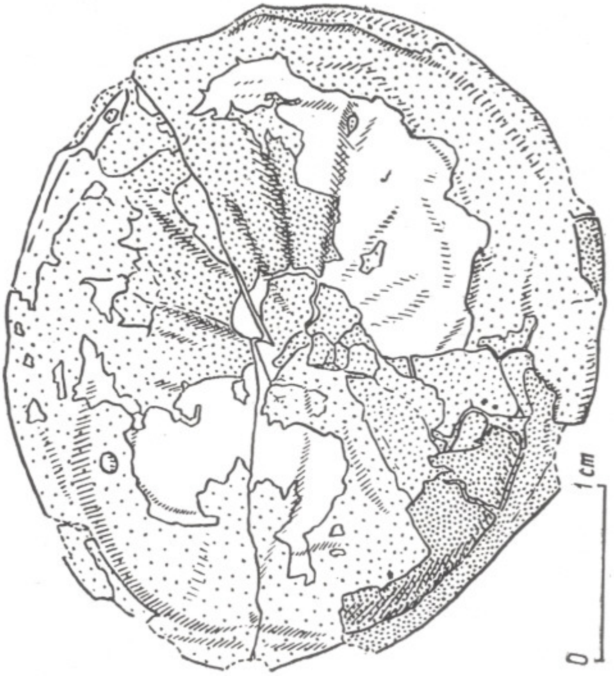
TEXT-FIGS. 1-5 — *Cardiolepis piniformis* Neub. emend. Meyen: **1**, holotype (see Pl. 1, fig. 3); **2**, opened capsule with imbricated seeds and its cross section (a); when vertical scale of the section had been enlarged 8 times, sections of ovules have become arranged radially (b), and longitudinal section of such enlarged picture along line A-A will give view as in holotype (c), no. 4548/1 (see Pl. 2, fig. 12); **3**, flattened capsule in surface (a) and lateral (b) view, no. 4548/7; **4**, superposition of nucellar (thick-walled cells) and inner integumental (thin-walled larger cells) cuticles, Prep. no. 4548/8-5; **5**, micropylar tube of ovule, Prep. no. 4548/4-5-5.



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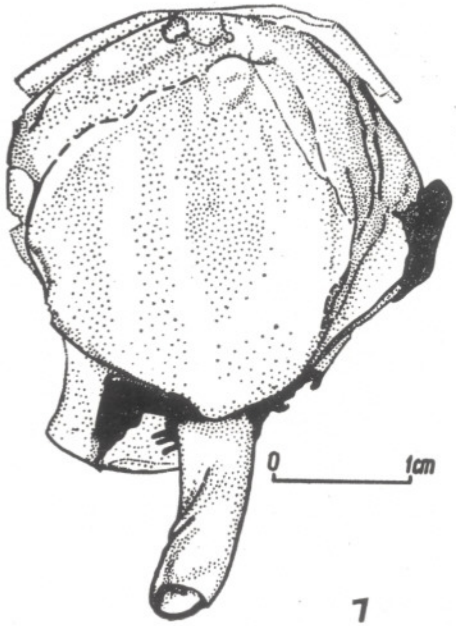

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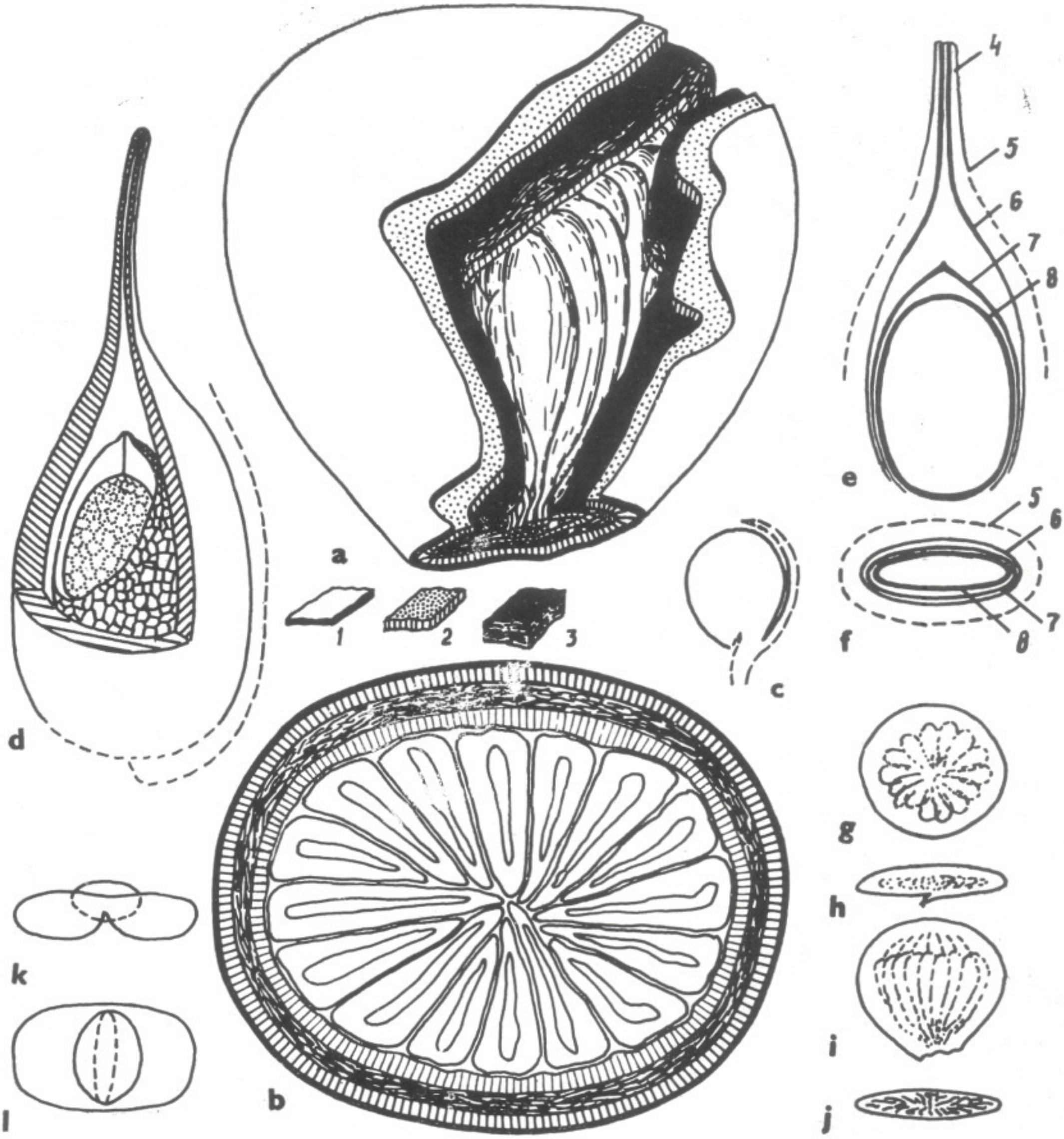
TEXT-FIGS. 6-9



TEXT-FIG. 10 — Reconstruction of *Cardiolepis piniformis* Neub. emend. Meyen: **a**, general view of dissected capsule (1, outer cuticle; 2, fleshy layers; 3, resiniferous layer); **b**, transverse section of capsule (designation of layers is same); **c**, hypothetical position of capsule in axil of bract; **d**, ovule dissected to show megaspore membrane, with imprints of nucellar cells, nucellus with beak, integument and micropylar tube; possible course of vascular strand is shown by broken line; **e**, longitudinal section of ovule (4, micropylar tube; 5, outer cuticle of integument; 6, inner cuticle of integument; 7, cuticle of nucellus; 8, megaspore membrane); **f**, transverse section of ovule (designation of layers is same); **g-j**, two types of capsule preservation depending on plane of flattening; **k, l**, pollen. All figures are not in a single scale.

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TEXT-FIGS. 6-9 — *Cardiolepis piniformis* Neub. emend. Meyen: **6**, capsule flattened in dorsiventral direction, no. 3062/69; **7**, transfer preparation of capsule with stalk (see Pl. 1, figs. 4, 5); **8-9**, transfer preparations obtained from spec. no. 3062/95 (Pl. 1, fig. 1) and its counterpart: opening with micropylar tubes is seen in fig. 8 (see Pl. 1, figs. 2, 7, 8); back side of capsule (fig. 9) is covered by entire cuticle.

skaya suite (Upper Permian) to the north of the Balkhash Lake in Kazakhstan.

Nucicarpus Neuburg, 1965

Type Species — *N. piniformis* Neuburg.

When found in dispersed state these seeds are thick, ovoid in outline, with attenuated tip or with a residue of a micropylar tube misinterpreted by Neuburg (1965) as a stalk. Some seeds exhibit a circular central patch devoid of coaly matter (Neuburg, 1965, pl. 48, fig. 6). Neuburg thought that the patch corresponds to the ovule kernel. Nucellus, however, has somewhat attenuated tip, and the patch fits better outline of megaspore membrane.

Pollen of *Vesicuspora* type was studied by me jointly with Gomankov. A single saccus is divided into two balloons with thin equatorial interconnections (Text-fig. 10k, l) which are seen only when the grain is flattened in strictly equatorial plane. When the flattening plane is oblique the pollen appears disaccate because interconnections between balloons overlap the body. In the literature the dispersed pollen of Cardiolepidaceae were erroneously described as *Ullmannia, Lebachia*, etc.

The *Cardiolepis-Phylladoderma-Nucicarpus* plexus is placed by me to conifers. Coniferalean features of *Phylladoderma* have already been enumerated. *Cardiolepis* and *Nucicarpus* if taken separately fit conifers and pteridosperms. The only conifers which are comparable to Cardiolepidaceae in female fructifications are Cupressaceae. *Cardiolepis* capsules can be compared with mature juniper cones but, according to the current codes of primitivity, they are more advanced, because the capsules are inverted and show no sign of independent cone scales. Outer cuticle of *Cardiolepis* is entire throughout the capsule, even in younger state, except for the opening where micropylar tubes are coming out. *Phylladoderma* leaves are basically different from those of Cupressaceae and are closer to those of Araucariaceae. Owing to these reasons the *Cardiolepis* plant has been separated by me into the family Cardiolepidaceae. Phylogenetic implications are given in "Discussion".

GENERA INCERTAE SEDIS

Sashinia gen. nov.

Generic Diagnosis — Twigs bearing at the apex are spirally arranged appendages with terminal inverted seeds (?). Proximal portion of twig with spirally attached leaves of *Quadrocladus* type.

Type Species — *Sashinia aristovensis* gen. et sp. nov. (Pl. 2, fig. 15; Text-figs. 11-13).

Specific Diagnosis — Short shoots with ca. 10-11 spirally arranged appendages 5-6 mm long bearing seeds ? 4-5 mm long and 2-3 mm wide with flattened tip. Foliage leaves in lower part of the fertile shoot are of *Quadrocladus dvinensis* sp. nov. type.

Holotype — Specimen no. 4552/296-1.

Locality — Right bank of Malaya Severnaya (North) Dvina River near the village of Kuznetsovo and the pier of Aristovo (see description of the locality in Efremov & Vjushkov, 1955).

Horizon—Upper Permian, Upper Tatarian Substage, Viatsky horizon.

Derivatio nominis — The genus is named in memory of late G. S. Sashina, botanist. The specific epithet is after type locality.

Five specimens (including three isolated appendages) were found in the type locality by me together with A. V. Gomankov and I. A. Ignatiev. Two fertile shoots were transferred on cellulose film and their fragments were macerated. The fertile shoots are naturally contracted below. Leaves in the lower part of the shoots correspond to dwarf sterile shoots of *Quadrocladus dvinensis* (see below).

There is no evidence of the presence of bracts.* No leaves with appropriate epidermal characters which can be treated as bracts have been found during bulk maceration of many samples from the bed. Fertile appendages are bent downwards or nearly straight. Seed-like bodies, when flattened,

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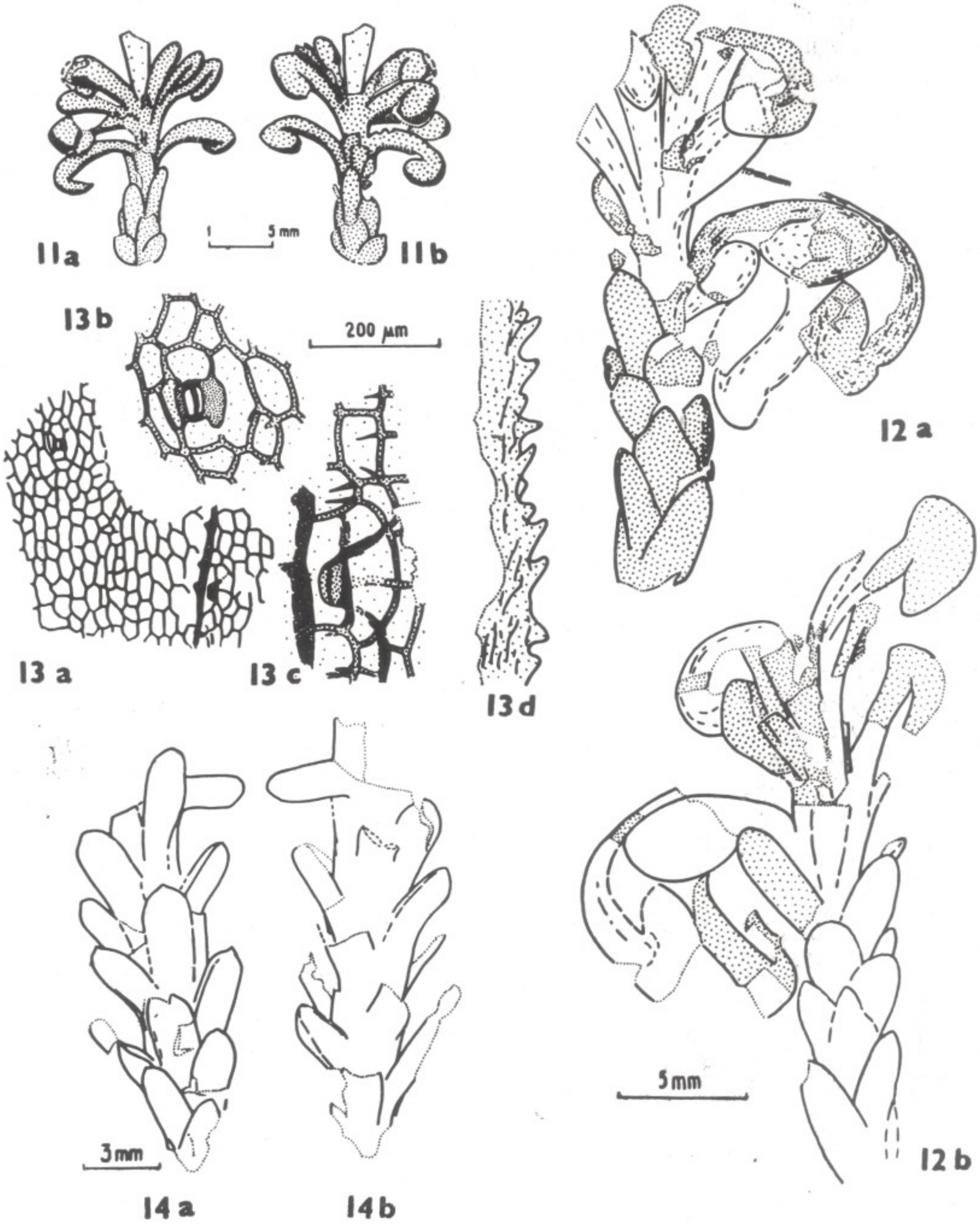
*After this study had been submitted for publication the original position of the aforesaid fertile shoots of *Sashinia* as well as its microstrobili has been discovered. These shoots were spirally arranged on a leafless axis and were subtended by bracts differing from foliage leaves only in greater length. The microstrobilus consists of an axis with spirally attached microsporophylls having terminal rhomboid lamina and bunches of sporangia in the middle portion of the stalk. Thus in these conifers primitive female fructifications are combined with advanced male ones.



TEXT-FIGS. 11-14 — *Sashinia aristovensis* gen. et sp. nov.: **11**, transfer preparation obtained from holotype as seen from both sides (**11b** — Pl. 2, fig. 15); **12**, paratype no. 4552/92 **(12a)** and its counterpart no. 4552/92a **(12b)**; **13**, epidermal characters of sterile leaf of holotype (a — general view of epidermis; b — stoma; c — stoma in lateral position, and corner spines; d — denticulate margin), prep. no. 4552/296-1b. **14**, *Quadrocladus dvinensis* sp. nov.: transfer preparation of specimen no. no. 4552/32a as seen from both sides.

bear lip-like termination faced to the stalk. The bodies are profusely veined by calcite and this prevents the obtaining of satisfactory preparations to reveal the relation between different cuticular membranes within the bodies. Outer cuticle is similar to that of foliage leaves. Two different kinds of cuticular membranes were found inside suggesting inner cuticle of integument and nucellar cuticle, but their interrelation was not observed. No megaspore membrane was found. Between cuticles many striated disaccate pollen are preserved. I am not sure that these bodies are naked terminal seeds. One cannot exclude that they represent seed-bearing cupules. Looking like duck head they are externally similar to cupules of *Umkomasia* and *Caytonia*, and to inverted arillate cones of Podocarpaceae.

Due to the uncertain nature of seed-like bodies of *Sashinia* it is impossible to provide its full comparison with coniferalean family. But in any case it stands separately among Coniferales. If the bodies are naked seeds, the whole system of fertile appendages can be compared with dwarf fertile shoot of *Lebachia* and *Ernestiodendron*, but it seems hardly possible that the fertile shoots of *Sashinia* were organized in *Walchiostrobus*-like cones. There are no data, both direct or indirect, that the fertile shoots were subtended by a bract and were accompanied by scales. If the bodies represent seed-bearing cupules, they will be different from one-seeded coniferalean cones in the absence of bract or other accompanying specialized scaly leaves. *Sashinia* is comparable to those fertile dwarf shoots of *Cordaitanthus* which have unbranched seed-bearing stalks (e.g. *C. williamsonii*), but differs in having unspecialized leaves in basal part. Sterile shoots of *Sashinia* are quite unlike *Cordaites*.

***Quadrocladus* Mädler, 1957**

Quadrocladus dvinensis sp. nov.

Specific Diagnosis — Shoots with spirally arranged fleshy leaves, which are tongue-shaped in long shoots and obovate in lateral dwarf shoots. Margins are minutely denticulated. Cuticular structure of dorsal and ventral sides is identical. Stomata are rare, monocyclic or incompletely bicyclic. Guard cells are sunken. Corners of cells bear long cutinized spines faced inside leaf.

Holotype — Specimen nos. **4552/277-1, 277a-1**(part & counterpart).

Locality & Horizon — The same as in *Sashinia aristovensis* (see above).

Several dozen of specimens were collected in the type locality by me together with A. V. Gomankov and I. A. Ignatiev. Some specimens being pyritized are not flattened. Ventral side is narrower and less convex than dorsal one. Therefore denticulate margin is displaced ventrally when leaf is compressed. Correspondingly the apical part of leaf can be displaced proximally and the apex becomes obtuse (Text-fig. 14). Position of lateral dwarf shoots is seen in the holotype (Pl. 2, figs. 13, 14; Text-fig. 15). The cuticle is thinner to the leaf base. Stomata (Text-fig. 13) are more frequent in the upper portion of the leaf. Cuticle of subsidiary cells forms a short tube on the bottom of which guard cells are located (Text-figs. 16b, 16c, 19). Corner spines are particularly well seen near the margin (Text-fig. 17). Marginal teeth are inclined both upwards and downwards (Text-fig. 18a). In very rare cases papillae are observed on subsidiary cells (Text-fig. 16b). Otherwise epidermal cells are without papillae.

Comparison — These shoots agree well with *Quadrocladus* in leaf arrangement, outline, cross section and stomatal characters.

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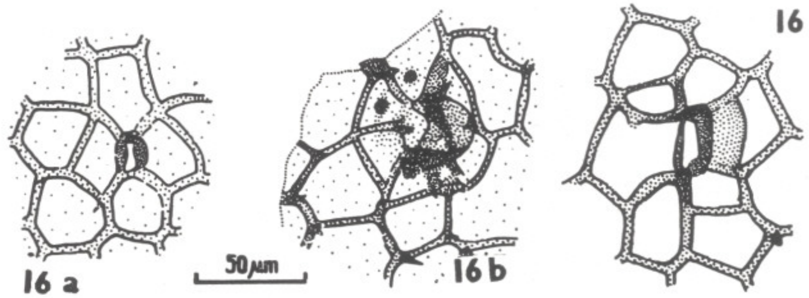
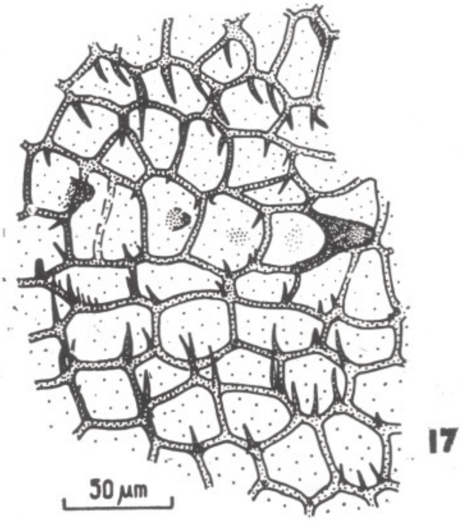
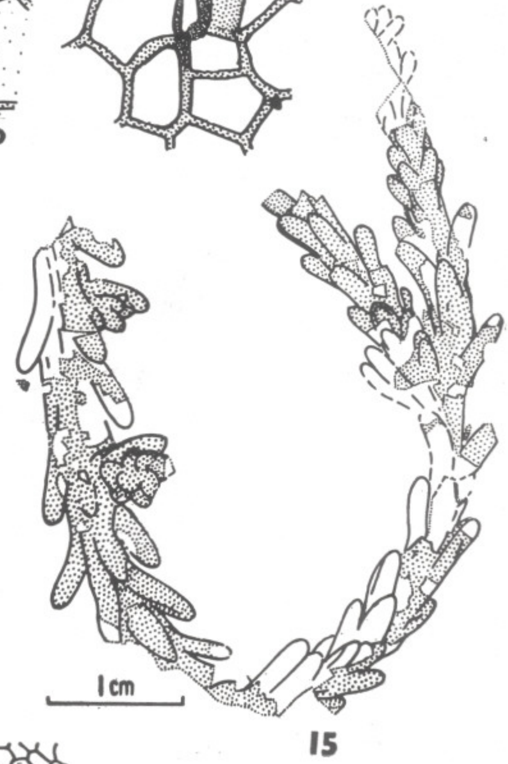
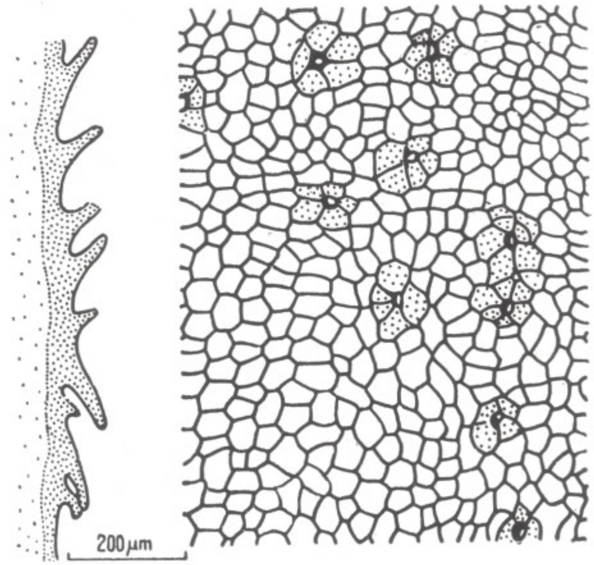
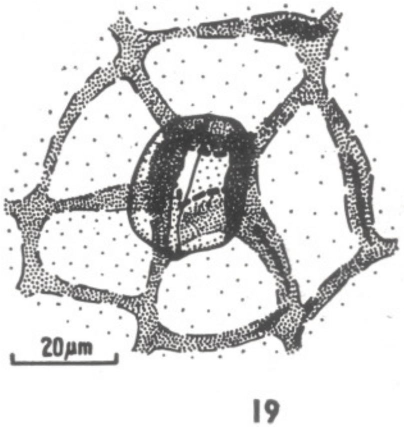
TEXT-FIGS. 15-19 — *Quadrocladus dvinensis* sp. nov.: **15**, holotype no. **4552/277a-1** (see Pl. 2, figs. 13, 14); **16**, stomata (in b polar parts of guard cells appear as spines), prep. no. **4552/277a-1**; **17**, leaf margin with minute trichome-like teeth, corner spines of both surfaces are faced to margin, prep. no. **4552/277a-1**; **18**, denticulate margin (a — prep. no. 4552/277a-1a) and general view of cuticle (b — prep. no. 4552/277a-1); **19**, stoma, prep. no. 4552/453-a.











TEXT-FIGS. 15-19

The type species *Quadrocladus florinii* Mädler (1957) shows denticulate margin which character is not mentioned in the description of *Q. solmsii* (Goth. et Nagalh.) Schweitzer and *Q. orobiformis* (Schloth.) Schweitzer (1960). My specimens differ from previously described species of *Quadrocladus* in absence of regular proximal papillae on subsidiary cells, in much less frequent stomata which are never arranged in rows even short ones, and in the presence of spines in corners of cells.

It seems justified to refrain from placing such shoots into *Sashinia*, because for other shoots fitting the diagnosis of *Quadrocladus* fructifications are unknown. Schweitzer (1960) figured a female cone possibly belonging to *Q. solmsii* and fundamentally different from *Sashinia*. Therefore, it is more reasonable to have independent nomenclature for sterile and fertile shoots, the more so, as we are ignorant of the fructifications of the type species *Q. florinii*.

Slivkovia Meyen, 1969

The monotypic genus *Slivkovia* (type species *S. petschorensis* Meyen) comprises shoots with closely adpressed and spirally arranged scale-like leaves bearing multiple stomatal furrows on dorsal sides (Text-figs. 20, 21). Leaf margins are minutely denticulate. Judging from the pattern of dorsal furrows (Text-fig. 21), veins entered the margin from the lower third of the leaf. During bulk maceration, a peculiar leaf was found showing shorter and more irregularly spaced furrows and a circular area on ventral side (Pl. 2, fig. 9; Text-figs. 22, 23). In this area the cuticle was either absent or extremely thin to be obtained by maceration. The area is bordered by a thick cuticular fold. I presume that this leaf represents seed scale, the position of the seed being corresponded to the aforesaid cuticle free area.

Slivkovia is known in the upper part of the Upper Permian (upper part of the Pechora Series in vicinity of the town of Pechora; the Tatarian deposits of Southern Bashkiria, South Fore-Urals).

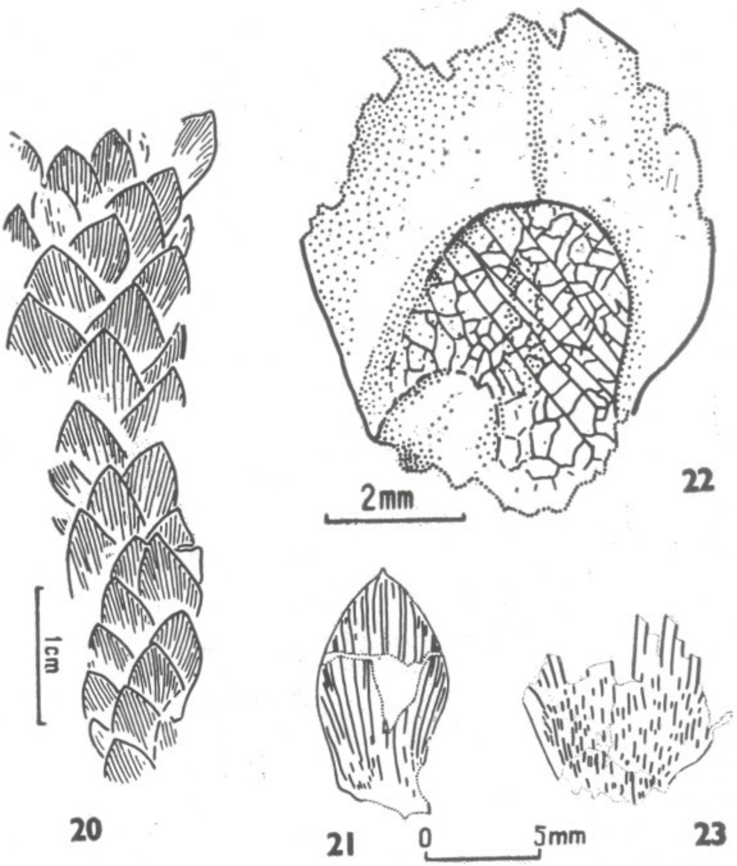
In having multiple dorsal furrows *Slivkovia* resembles *Rufloria* but differs in denticular margin and scale-like habit of foliage leaves (scaly leaves are also known in *Rufloria* but usually they accompany normal foliage leaves with broad lamina and are connected with them by a gradual transition — Maheshwari & Meyen, 1975). In none of the localities with dominating *Rufloria* leaves, seed scales with dorsal furrows were found.

Sterile leaves of *Slivkovia* are similar to *Ullmannia* in general outline, denticulate margin and stomatal structure (large proximal papillae on subsidiary cells overhanging the stomatal pit). Seed-bearing (?) leaf of *Slivkovia* can be compared to the seed scale of *Ullmannia bronnii*, though in *Slivkovia* the leaf is more foliage in habit and the seed seems to have been more closely adpressed to the subtending surface and its place was bordered by a fold absent in *Ullmannia*.

Ullmannia Goeppert 1850 and *Voltziopsis* H. Potonié, 1899

Ullmannia was repeatedly mentioned in the Permian plant assemblages of West Angaraland (J. F. Schmalhausen; M. D. Zalessky; see Meyen, 1971b). Cuticular studies have not supported so far the presence of *Ullmannia* in these assemblages. Some of the shoots coming from Tatarian stage were ascribed by me to *Ullmannia* on the basis of gross morphology (Meyen, 1971b). Subsequent cuticular studies have shown that these shoots should be referred to *Quadrocladus*. It is suggestive that in miospore assemblages of the embedding rocks, there are no pollen of *Illinites*-type known in male fructifications of *Ullmannia* (Schweitzer, 1960; Grebe & Schweitzer, 1962). In my collection, there are *Ullmannia*-like shoots from the Kazanian Stage associating with *Pseudovoltzia*-like female fructifications. Undisputable *Illinites* pollen were not found during preliminary palynological study of the Kazanian beds yielding shoots traditionally referred to *Ullmannia*. The presence of the latter in the Permian of West Angaraland remains uncertain.

I erroneously recorded (Meyen, 1971b) *Voltziopsis* in the Upper Tatarian substage of the Russian platform. I had mistaken for cone scale of *Voltziopsis* a laterally compressed *Peltaspermum* disc, marginal lobes of which simulate distal lobes of a coniferalean seed scale.



TEXT-FIGS. 20-23 — *Slivkovia petschorensis* Meyen: **20**, holotype no. 3749/56, intercalating lines corresponding to stomatiferous dorsal furrows are shown diagrammatically; **21**, distribution of dorsal furrows on sterile leaf, no. 3753/140-1; **22**, fertile (?) scale with cuticle free area bordered with fold (see Pl. 2, fig. 9), no. 3753/25-2; **23**, dorsal cuticle of the same scale with dorsal furrows (magnification as in Text-fig. 21).

DISCUSSION

Florin's now classical phylogeny of conifers is very popular among botanists and palaeobotanists. His phyletic sequence from *Cordaitanthus* via. *Lebachia*, *Ernestiodendron*, *Pseudovoltzia* and *Ullmannia* to Mesozoic and modern conifers looked quite convincing. As was rightfully noted by Harris (1976), *Pseudovoltzia* was a key genus for Florin, who believed that this genus has fertile axillary complex consisting of five partly united lobes and of three finger-like megasporophylls with terminal seeds. Schweitzer (1963) "has broken the thread of Florin's story for now there is a gap between ... *Lebachia* and *Ernestiodendron* and the Permian *Pseudovoltzia*" (Harris, 1976, p. 126). He has shown that the finger-like megasporophylls are absent. There are instead surface ridges on the adaxial side of seed scale. The situation of *Voltziopsis* remains unclear, though it is possible that its female cone is basically similar to that of *Pseudovoltzia* (Townrow, 1967).

There are other doubts that the sequence of genera suggested by Florin is an authentic phylogeny:

1. It is not evident that *Lebachia* can be safely ascribed to conifers. In many respect *Lebachia* is closer to cordaites (Kras-

silov, 1971; Meyen, 1971a) than to typical conifers. Actually, there are only two characters in favour of its coniferalean affinity, i.e. needle-shaped leaves and peltate microsporophylls. Both characters are not quite reliable. Conifers produce leaves of four basic types (Laubenfels, 1953) and there are no grounds to admit that among Cordaitanthales (this order was proposed instead of Cordaitales — Meyen, 1972) could be leaves of one basic type only. Coniferalean microsporophylls are of 10 main types (Ueno, 1960). There are data that plant with cordaitalean habit of leaves may show coniferalean type of microsporophylls. I mean association of *Rufloria* leaves and *Cladostrobus* male fructifications (Meyen & Maheshwari, 1975).

2. The genus *Buriadia* from Lower Gondwana does not fit at all the Florin's sequence (Pant & Nautiyal, 1967).

3. According to Florin's ideas, Cardiolepidaceae should be envisaged as having the most advanced female fructifications. Since the latter play the decisive role in Florin's phylogenetic interpretation of conifers, Cardiolepidaceae must be placed at the topmost position in coniferalean phylogeny. But the stratigraphical range of genera constituting *Phylladoderma-Nucicarpus-Cardiolepis* plexus does not support such conclusion. First two genera appear before undisputable *Ullmannia* and coexisted with *Pseudovoltzia*. To derive all younger conifers from *Cardiolepis* is much easier (than from *Pseudovoltzia* & *Ullmannia*) involving only reduction of certain elements of the seed-bearing capsule.

4. In Florin's admittedly phylogenetic sequence, there is no room for the Upper Permian *Sashinia* and *Slivkovia*.

I am not going to claim that Florin's ideas are altogether misleading. Together with Harris (1976, p. 127) I "great hope further work bridges this gap" between *Lebachia* and *Pseudovoltzia*. Florin's interpretation of female axillary complex remains convincing in many respects, though I am not sure that this interpretation is applicable to all the conifers. I do not take seriously the aforesaid possibility to derive Mesozoic and modern conifers from Cardiolepidaceae. But the acquaintance with *Slivkovia*, *Sashinia* and *Cardiolepis* do not permit me to take seriously none of the previously suggested phylogenetic schemes of conifers. These genera along with Gondwana *Buriadia* and *Walkomiella* illustrate the significant diversity of the Upper Palaeozoic conifers. Taking in consideration the incompleteness of fossil records and the possibility that conifers could inhabit upland areas one can suggest that this diversity was even more significant.

The situation with conifers is not unique. We often confuse two things: our possibility to derive one plant group from another by means of 'phylogenetic game' beautifully described by Harris (1976), and the real phylogenetical processes which remain nearly unknown and reconstructions of which cannot principally be proved.

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EXPLANATION OF PLATES

Plate 1

Cardiolepis piniformis Neub. emend. Meyen

1. Open capsule erroneously treated by Neuburg (1965) as transverse section of a female cone with radially arranged seed scales. The capsule was flattened as shown in Text-figs. 10g, h. No. 3062/95a. × Nat. size.

2. Transfer preparation of the same capsule showing opening, with micropylar tubes, at the bottom (see also figs. 7, 8; Text-figs. 8, 9). × 2.

3. Holotype no. 3062/59 (see also Text-fig. 1). × 1.

4. Surface view of capsule before transferring. No. 3062/206. × 2.

5. Transfer preparation of the same capsule showing stalk. (see also Text-fig. 7). × 2.

6. Flattened capsule with stalk. No. 4548/3. × 2.

7, 8. Stereophotographs of the opening with micropylar tube. The same specimen as in figs. 1, 2; Text-figs. 8, 9. × 5.

Plate 2

9. *Slivkovia petschorensis* Meyen. Ventral surface of a scale showing cuticle free area possibly corresponding to position of a seed (see also Text-fig. 22). No. 3753/25-2. × 10.

10. *Cardiolepis piniformis* Neub. emend. Meyen. Ovule extracted from a capsule. Many pollen in the upper part of nucellus are seen. Nucellar cuticle is surrounded by inner cuticle of integument. Prep. no. 4548/8-5. × 100.

11. *Cardiolepis piniformis* Neub. emend. Meyen. Pollen of *Vesicaspora* type between inner cuticle of integument in vicinity of nucellar tip. Prep. no. 3090/287-1-4. × 500.

12. *Cardiolepis piniformis* Neub. emend. Meyen. Cross section of capsule shown in Text-fig. 2. No. 4548/1. × 3.

13, 14. *Quadrocladus dvinensis* sp. nov. Holotype no. 4552/277a-1. Furcating part of twig (fig. 13), and two dwarf shoots on twig (fig. 14). See also Text-fig. 15. × 3.

15. *Sashinia aristovensis* gen. et sp. nov. Transfer preparation from holotype no. 4552/296-1. See also Text-fig. 11. × 3.


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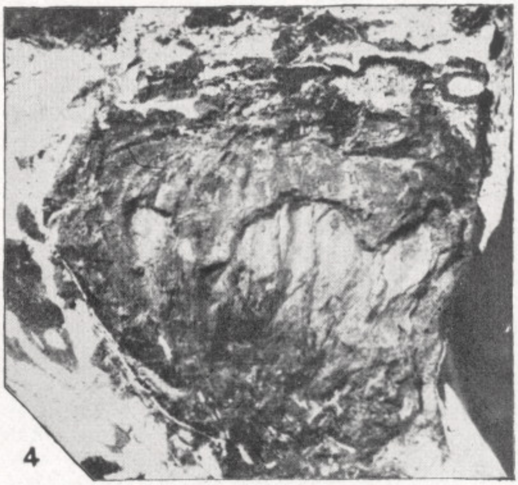
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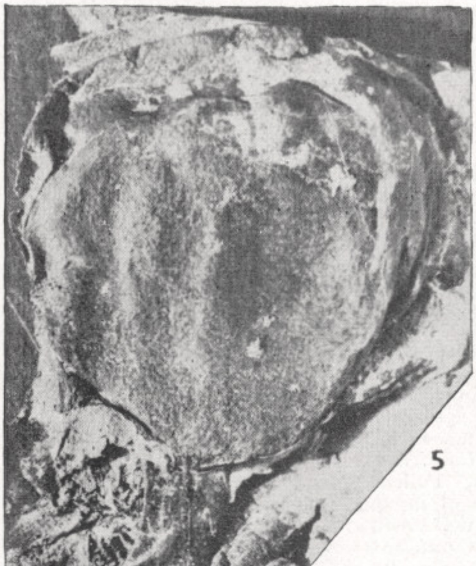
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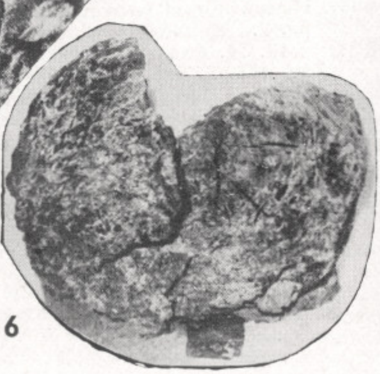
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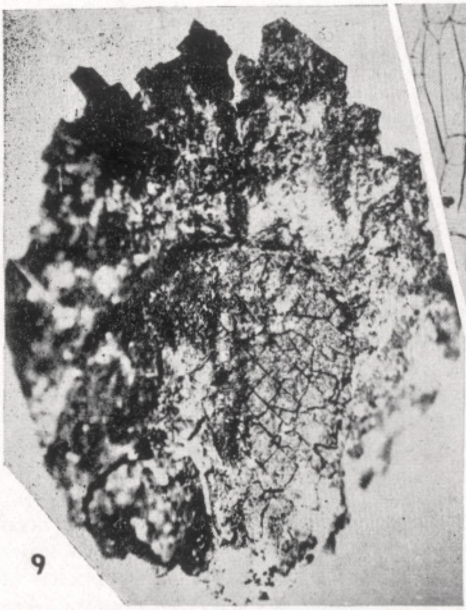
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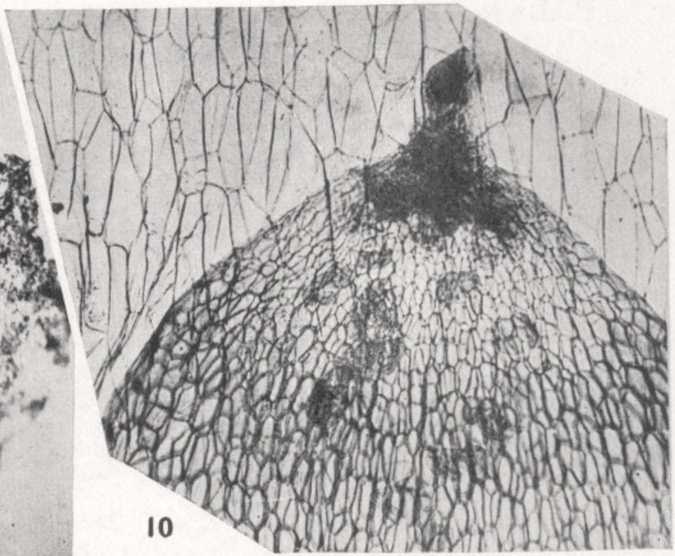
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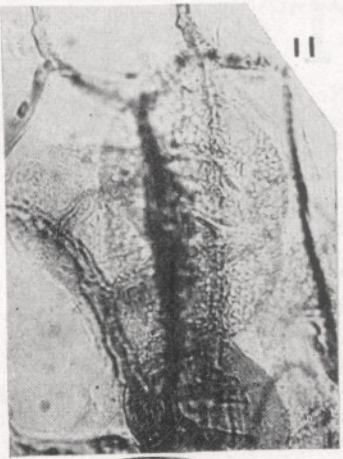
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PLATE 2