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Morphology and Systematics of Representatives of Vojnovskyales

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Abstract—The systematic position of a peculiar group of Angaran gymnosperms usually treated as cordaites is discussed. The systematics of these plants related to coniferophytes remains uncertain because of their extreme peculiarity. Possible interpretations of the generative structures of *Vojnovskya* Neub., *Paravojnovskya* Naug. et Doweld (=*Gaussia* nom. illeg.), and *Scirostrobus* Doweld et Naug. (=*Pholidophyllum* nom. illeg.), fundamentally similar genera, are considered. A significant resemblance between fructifications of *Paravojnovskya* and *Scirostrobus* and strobili of *Vojnovskya* is revealed. Such a similarity was reported earlier for representatives of *Paravojnovskya* from the Carboniferous and Permian of Angara.

INTRODUCTION

The refinement of the systematics and phylogeny of Vojnovskyales, a group of coniferophytes that was widely distributed in the geological past, but of an uncertain position in the modern system of plants, is an ongoing problem of paleobotany.

The present paper is focused on the generative morphology of peculiar gymnosperms traditionally treated in the Russian literature as Angaran cordaites. However, many leading paleobotanists, dealing with coniferophytes, noted a great peculiarity of this group and its considerable difference from the true Euramerian cordaites (the order Cordaitales, Taylor, 1981; Stewart, 1983; Rothwell, 1988; Taylor and Taylor, 1993). According to the system of higher plants proposed by S.V. Meyen (1987), this group includes two families, Rufloriaceae Ledran, 1966 and Vojnovskyaceae Neuburg, 1963. Although numerous papers are devoted to this group (Mamay, 1975, 1976; Krassilov and Burago, 1981; Meyen, 1982, 1987; Rothwell *et al.*, 1996), its systematic position remains unclear.

In studying Permian floras of western Angara, I had to interpret the fructification morphology of Angaran cordaites (e.g., Naugolnykh, 1993, 1998). There are numerous cordaite-like leaves assignable to the genera *Rufloria* S. Meyen and *Entsovia* S. Meyen, cataphylles of the genera *Crassinervia* Neub. and *Lepeophyllum* Zal., and bracts of *Nephropsis* Zalessky (*Sulcinephropsis* Zim.). Generative structures of Angaran cordaites also occur in the localities studied. In spite of their assignment to the different families accepted in the modern literature, the cordaites of the genera *Vojnovskya* Neub., *Paravojnovskya* Naug. et Doweld (=*Gaussia* Neub. nom. illeg.) and *Scirostrobus* Doweld et Naug. demonstrate a fundamental similarity.

HISTORICAL REVIEW

The serious study of the fructifications of Angaran cordaites began with the appearance of a monograph by M.F. Neuburg (1965) devoted to the leaves of cordaites and seeds from the Permian flora of the Pechora Basin. Peculiar sexual organs assigned to a new genus and two new species, *Vojnovskya paradoxa* Neub. and *V. chalmeriuensis* Neub. were described. Although little known, these species are important for adequate understanding of the morphology of the entire group. Based on the morphology of these plants, Neuburg concluded that (1) they are too specific to be referred to any known order of gymnosperms, and she introduced a new order Vojnovskyales Neub.; (2) the new order is derived from the order Cordaitales; (3) generative structures of *Vojnovskya* were bisexual and included both polliniferous and ovuliferous organs; and (4) the genera *Gaussia*, *Taibia* Zal., and *Niazonaria* Radcz. are closely related to *Vojnovskya*. It is necessary to note that the phylogenetic relationship between the orders Vojnovskyales and Cordaitales was established on the basis of the similarity between Euramerian leaves *Cordaites* Unger (the order was named after this genus) and the leaves habitually similar to those of *Cordaites* from the Pechora Basin, which were referred than to the genus *Noeggerathiopsis* Feistmantel.

Three species of the genus *Vojnovskya*, namely, *V. minima* (Chachlov et Pollack) Neub., *V. mirabilis* Gorelova, *V. usjatensis* Gorelova, were described from the Upper Permian of the Kuznetsk Basin (the Kemerovskii and Usyatskii horizons of the Ufimian). The figured specimens, which were assigned to these taxa, demonstrate a considerable variability of the length and width of the generative axes of lateral strobili (Gorelova *et al.*, 1973).

V.G. Zimina (1967, 1977) described the species *V. elegans* Zimina, *V. pacifica* Zimina, provided the

enlarged description of *Gaussia scutellata* Neub., synonimized *G. rotunda* Chachlov under *G. scutellata*, presented the extended diagnosis of the genus *Vojnovskya* and characterized developed sterile leaves of Angaran cordaites, associated with above mentioned generative structures, i.e., *Cordaites buragoi* Zimina, *C. primorskiensis* Zimina, *C.* aff. *latifolius* (Neub.) S. Meyen, *Cordaites* spp., *Rufloria derzavinii* (Neub.) S. Meyen, *R. sublanceolata* Zimina, *R.* aff. *recta* (Neub.) S. Meyen, *R.* aff. *theodorii* (Tschirk. et Zal.) S. Meyen, *R. ussurica* Zimina, and *R. (?) vassilyevii* Zimina; and the scale-like leaves of *Nephropsis (Sulcinephropsis)* spp., *Crassinervia grammii* Zimina, *C.* (?) *neuburgiana* Zimina, *C.* (?) *strelokensis* Zimina, *C. tunguscana* Scwedov, and *C.* aff. *pentogonata* Gorelova.

Zimina agreed with Neuburg's morphological interpretation of the fertile organs of *Vojnovskya* and treated them as bisexual lateral strobili with solitary ovoid megasporangia and numerous narrow linear and lanceolate leaflike microsporophylls, arranged alternately on the strobilus axis. Among the specimens, which were referred by Zimina to *Vojnovskya pacifica*, it is possible to observe a complete transition from the longitudinally elongated fructifications without terminal widening (Zimina, 1977, pl. 18, fig. 13, pl. 19, figs. 1, 4) to wider fructifications (Zimina, 1977, pl. 19, fig. 3), and finally to flattened fructifications, fitted the diagnosis of *Paravojnovskya* (=*Gaussia*) (Zimina, 1977, pl. 18, fig. 14, pl. 19, figs. 5–8). All these specimens were collected in the same locality and actually represent a monotopic sampling. These fructifications and the associated leaves *Rufloria* spp., *Crassinervia* (=*Lepeophyllum*) spp. and bracts *Nephropsis* (*Sulcinephropsis*) spp. undoubtedly belonged to plants of the same species. In addition, a figure of *Vojnovskya elegans* (Zimina, 1977, pl. 20, figs. 1–3) closely resembles *Gaussia scutellata* (Zimina, pl. 20, fig. 4).

Another interpretation of the generative structures of *Gaussia* and *Vojnovskya*, including systematic conclusions for the entire group, was proposed by V.A. Krassilov (Krassilov and Burago, 1981; Krassilov, 1989). According to Krassilov, the fructifications of *Gaussia* represented head-shaped aggregations of sterile bracts and ovuliferous organs with ovules. The ovules were embedded into the ovarylike structure, on top of which a stigma with secreted pollen-catching fluid is situated. Krassilov assigns the genera *Gaussia* and *Vojnovskya* to the order Vojnovskyales. He considers this order as a very specific group of gymnosperms without close relationship to the true Euramerian cordaites. He attributes the similarity between Vojnovskyales and equatorial cordaites to homeomorphy (Krassilov, 1997).

Meyen suggested a different interpretation of generative organs of Vojnovskyales. He believed the fructifications of *Vojnovskya* to be unisexual and to produce seeds of *Samaropsis stricta* Neub. type. He assigned the fructifications of *Gaussia* to the family Rufloriaceae. According to Meyen, the families Rufloriaceae and Vojnovskyaceae are related to Euramerian cordaites and, thus, the whole group should be jointed in the order Cordaitanthales (after the genus *Cordaitanthus* of female fructifications of equatorial cordaites). However, he noted in one of his latest papers that "it should not be excluded that in the Carboniferous the fructifications of Angaran Cordaitanthales were of a single basic type" (Meyen, 1992, p. 135). Therefore, it is possible that Vojnovskyaceae and Rufloriaceae had a common origin.

Meyen's opinion on the morphology and systematics of Angaran cordaites was continued by his student I.A. Ignatiev (Ignatiev, 1988a, 1988b; Ignatiev and Meyen, 1989). Unfortunately, these papers lack new data and several ideas of Meyen, which were proposed as working hypotheses, were transformed into principles.

MATERIAL

The material available considerably extends the modern knowledge on Angaran cordaites (Figs. 1–5, Pl. 9 and 10).

The specimens discussed originate from the Kungurian (upper Lower Permian) of the Middle Fore-Urals (the localities of Chekarda-1, Krutaya Katushka) and Central Asia (the locality of Sary-Taipan). Geographic details and the exact stratigraphic position for Fore-Urals localities are given in Naugolnykh (1998), for the Sary-Taipan locality, they are given in the description of *Vojnovskya stankevichii* Sixtel. In addition to our collections, fructifications of *Paravojnovskya* (al. *Gaussia* nom illeg.) *imbricata* (Naug.) Naug. et Doweld and *Scirostrobus* (al. *Pholidophyllum* nom. illeg.) *ornatum* (Zal.) Doweld et Naug. from the collection of the Perm Regional Museum were studied. Type specimens of *Vojnovskya paradoxa, V. chalmeriuensis* Neub., *Paravojnovskya* (al. *Gaussia*) *scutellata* (Neub.) Naug. et Doweld, and *P.* (al. *Gaussia*) *cristata* (Neub.) Naug. et Doweld were restudied.

The morphology of the taxa described in Zalessky (1937), Sixtel *et al.* (1975), and Naugolnykh (1998) is discussed below. The specimens studied and quoted are housed in collections nos. 3029, 3039, 3737, 3773, 3773(11), 4559 of Geological Institute of Russian Academy of Sciences (GIN RAS).

MORPHOLOGY OF REPRODUCTIVE ORGANS OF VOJNOVSKIACEAE

Paravojnovskya (al. *Gaussia*) *imbricata* (Naug.) Naugolnykh et Doweld, a generative organ of Vojnovskyales, is represented by long sterile scales and shortened seed stalks with fused bases. Seeds were attached to the distal margins of the seed stalks at their lower side. The disk of the umbrella is asymmetric through the shift of the fructification stalk to the margin of the umbrella.

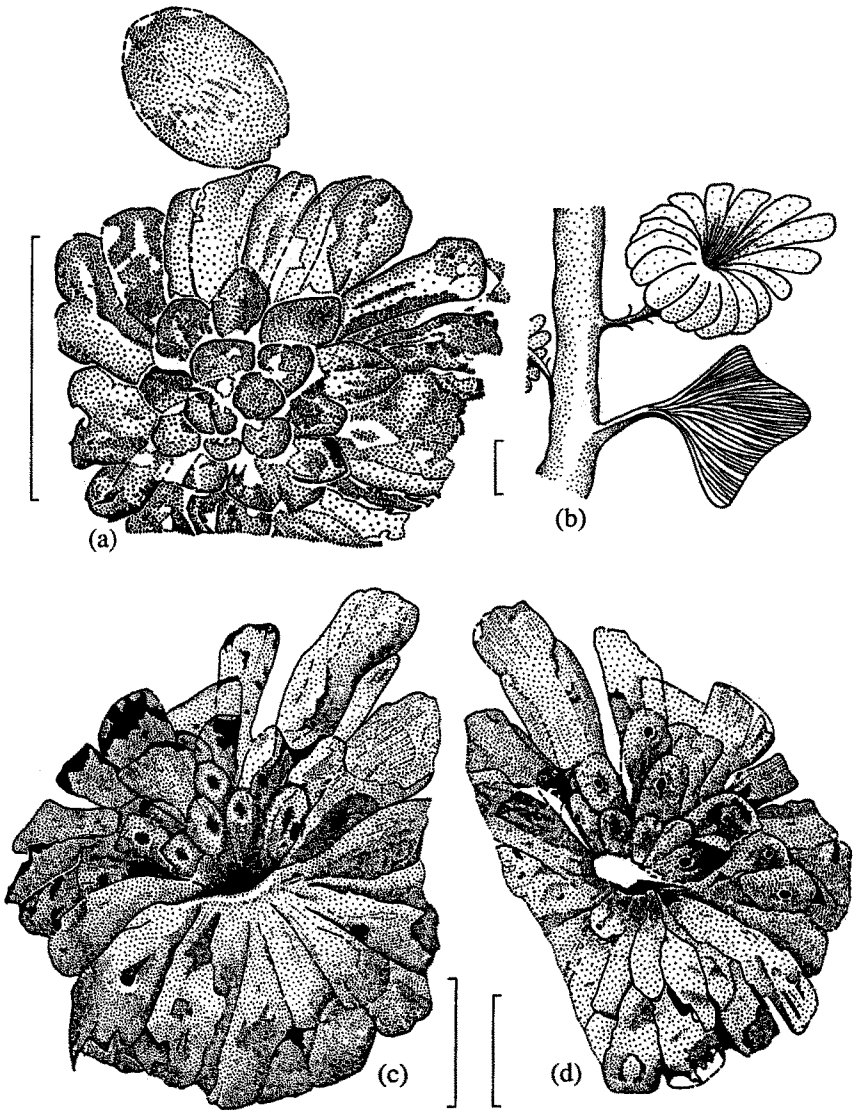


Fig. 1. Fructification morphology of representatives of Vojnovskyales: (a, c, d) *Paravojnovskya* (al. *Gaussia*) *imbricata* (Naug.) Naug. et Doweld, (a) specimen no. 3773(11)/326(92), (c, d) the specimen from the collection by Vaulev (Perm Regional Museum), (b) proposed arrangement of fructifications of *P. imbricata* on a fertile shoot, in axils of scale-form bracts of *Nephropsis* (*Sulcinephropsis*). The locality of Chekarda-1, the Kungurian, Lower Permian of the Middle Fore-Urals. Scale bar is 1 cm.

The holotype is represented by an aggregation of seed stalks and sterile scales (Fig. 1a). The sterile scales reach more than 8 mm length. The proximal regions of the seed stalk are covered by other seed stalks. Sterile scales and seed stalks are more or less distally widened, forming a circular or subrhomboidal area.

In addition to the holotype, three fructifications of the same species were studied (Figs. 1c, 1d, Pl. 9, fig. 2, Pl. 10, figs. 1, 4). Their sizes slightly exceed the size of the holotype, but all their characteristic features are identical to those of the holotype. Numerous polymorphous leaves of Angaran cordaites, assigned mostly to the genus *Rufloria*, occur in association with the fructifications of *P. imbricata* (Fig. 2a). New material, including several better preserved specimens, was collected after the establishment of *P. imbricata* (Naugolnykh, 1998). This material allowed us to extend and emend the characterization of the taxon.

There is a specimen in the available sample slightly differing from the holotype in its more asymmetrical outline, superficially resembling the genus *Scirostrobus*. This specimen bears interseminal scales, which are well developed from one side of the organ, and several longitudinally elongated structures, which may represent seeds preserved in their natural attachment.

This specimen is represented by an impression of the lower part of the fructification. Fragments of compressed material preserved in some regions allow us to study the microstructure of the fructification. A small

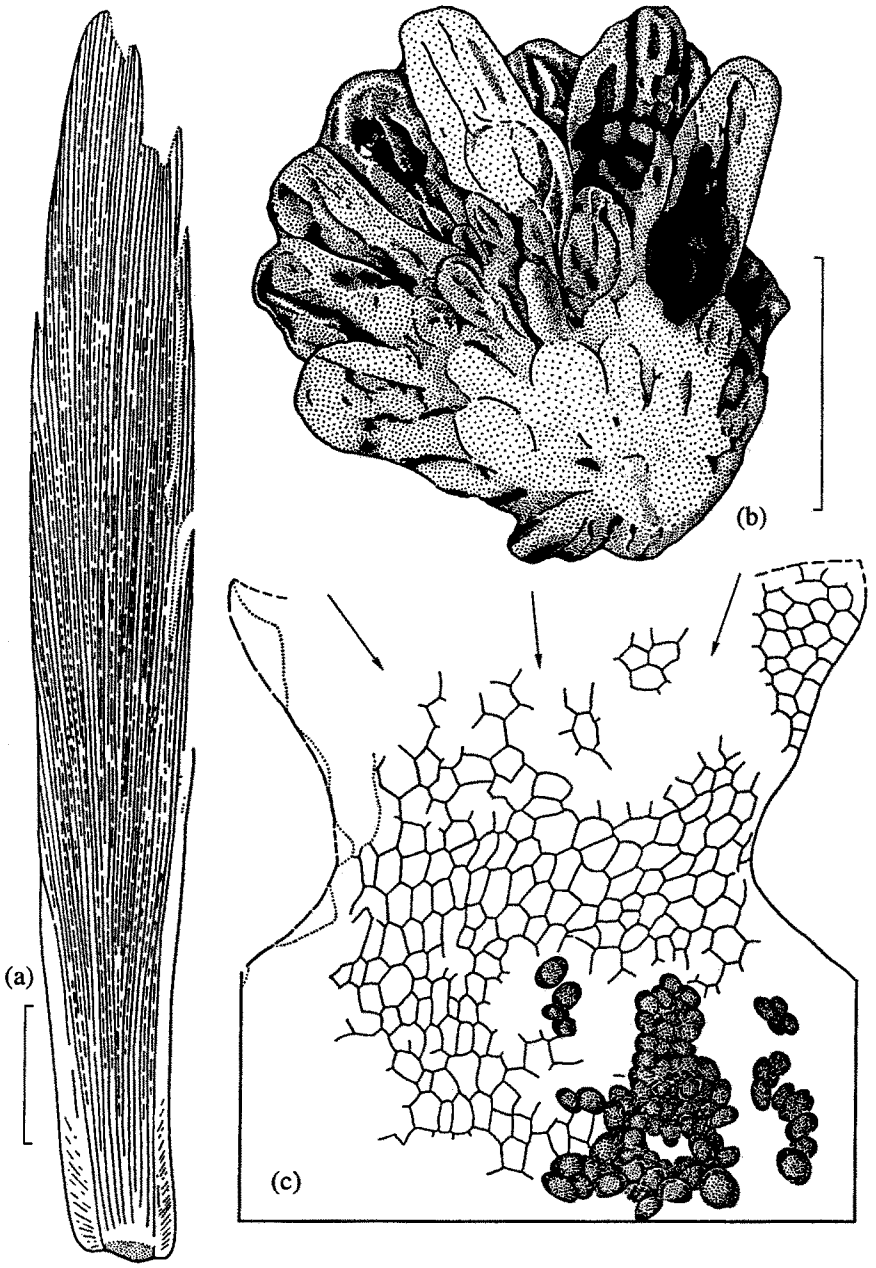


Fig. 2. Morphology of (a) vegetative and (b, c) generative structures of representatives of Vojnovskyales: (a)*Rufloria (Alatorufloria) recta* (Neub.) S. Meyen, specimen no. 3773(11)/136(89), entire leaf with partly damaged apex, note dorsal grooves (in solid lines) and true veins (in broken lines) well distinguishable only on certain regions of the compression, (b, c)*Paravojnovskya* (al. *Gaussia*) *imbricata* (Naug.) Naug. et Doweld, specimen no. 3737/205, (b) gross morphology of the fructification, (c) pollen chamber containing pollen grains (arrows indicate the direction of pollen penetration into the chamber). Scale bar is (a–b) 1 cm, (c) ×220. The locality of Chekarda-1, (a) layer 7, (b–c) layer 10, the Koshelevskaya Formation, the Kungurian, the Lower Permian.

circular area with foveolate relief, differing from the other surface of the polysperm, is situated in the basal part near the margin of the fructification. This area corresponds to the scar of the fructification attachment to the generative axis. Flattened circular, oval, or lanceolate structures diverge radially from the circular area. These structures correspond to interseminal scales or, according to Krassilov, to bracts. There is a scar at the base of some scales, apparently corresponding to the places of seed attachment. The surface of the interseminal scales is covered by longitudinal ribs and folds. The scale tops are rounded, sometimes with slightly rough margins. The scales are fused with their margins in more than half of their length.

Three structures, morphologically resembling seeds of the type *Sylvella* or *Samaropsis rectialata* Neub., are

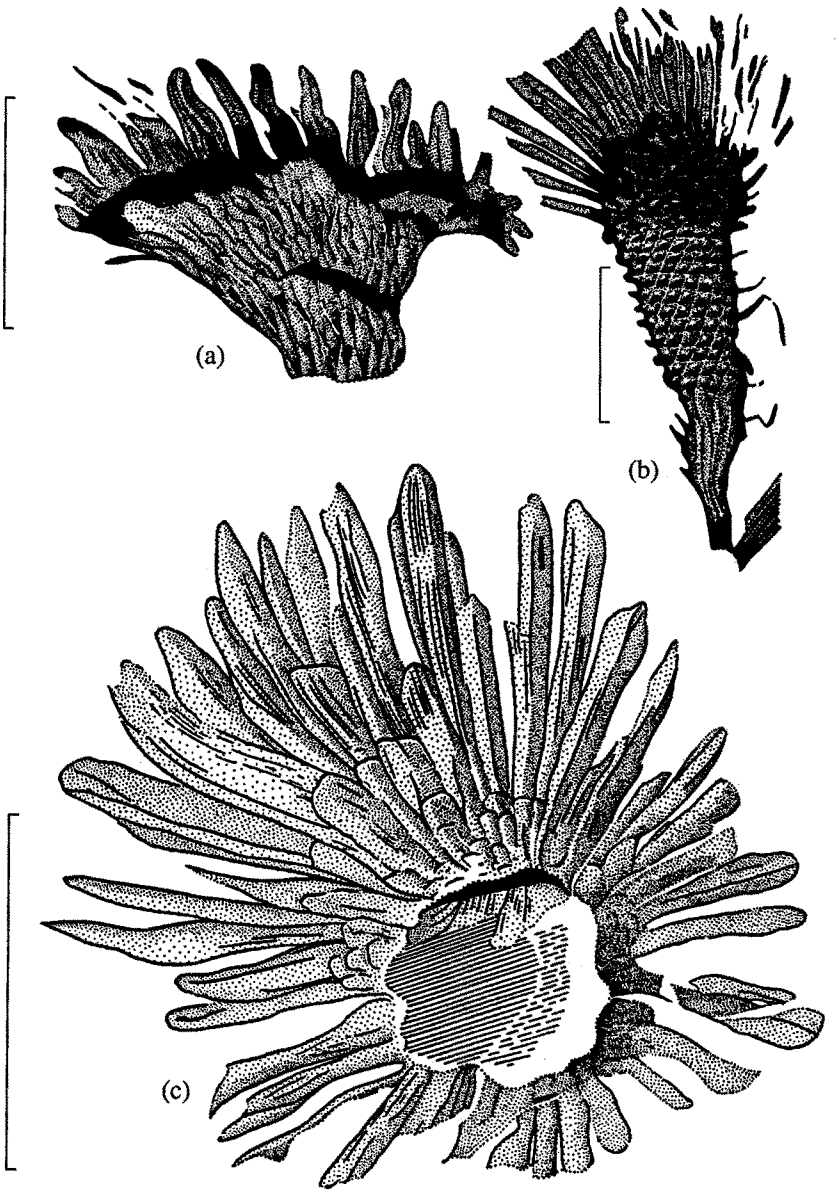


Fig. 3. Fructification morphology of representatives of Vojnovskyales: (a–b) *Vojnovskya paradoxa* Neub. The morphology of lateral strobili of two different types belonged to the same plant, (a) specimen no. 3029/379, considerably short strobilus with wide base resembling *Paravojnovskya* (=*Gaussia*) or *Taibia* after vertical deformation, (b) specimen no. 3039/194, a usual strobilus, deformed laterally, more elongated strobili of this type without apex are similar to *Suchoviella* Ing. et S. Meyen, (c) specimen no. 3039/149, *V. chalmeriuensis* Neub., vertically deformed strobilus with numerous sterile scales with occasionally visible midrib (= Neuburg, 1965, Pl. 31, Fig. 4). Scale bar is 1 cm. The locality of Khalmer'yussk Coal field, mine no. 3, the Intinskaya Formation, the Ufimian, the Upper Permian.

placed in the right part of the polysperm (see drawing). Outlines of circular or oval structures are visible at the base of these structures under oblique lighting. They may refer to the seed nucellus. Two of these presumed seeds are compressed, which is preserved better in the area of presumed nucellus. A net consisting of small cells with fine walls on the surface of this compressed material is revealed with help of a light microscope under ultraviolet light (Pl. 10, fig. 1). This net is particularly clearly distinguished by the middle seed of these three presumed seeds. In the apical region of the presumed nucellus these small cells formed a funnel-like structure. In the neck of this structure a large number of bisaccate pollen grains and a smaller number of monosaccate nonstriate pollen grains were found (Fig. 2c; Pl. 10, fig. 4). Similar pollen grains often occur on the leaves of *Rufloria, Nephropsis*, and *Lepeophyllum* from the same deposits (Pl. 10, figs. 2, 3), which is also a common member of palynoassemblages (Pl. 10, figs. 6–7). Monosaccate, bisaccate pollen, and

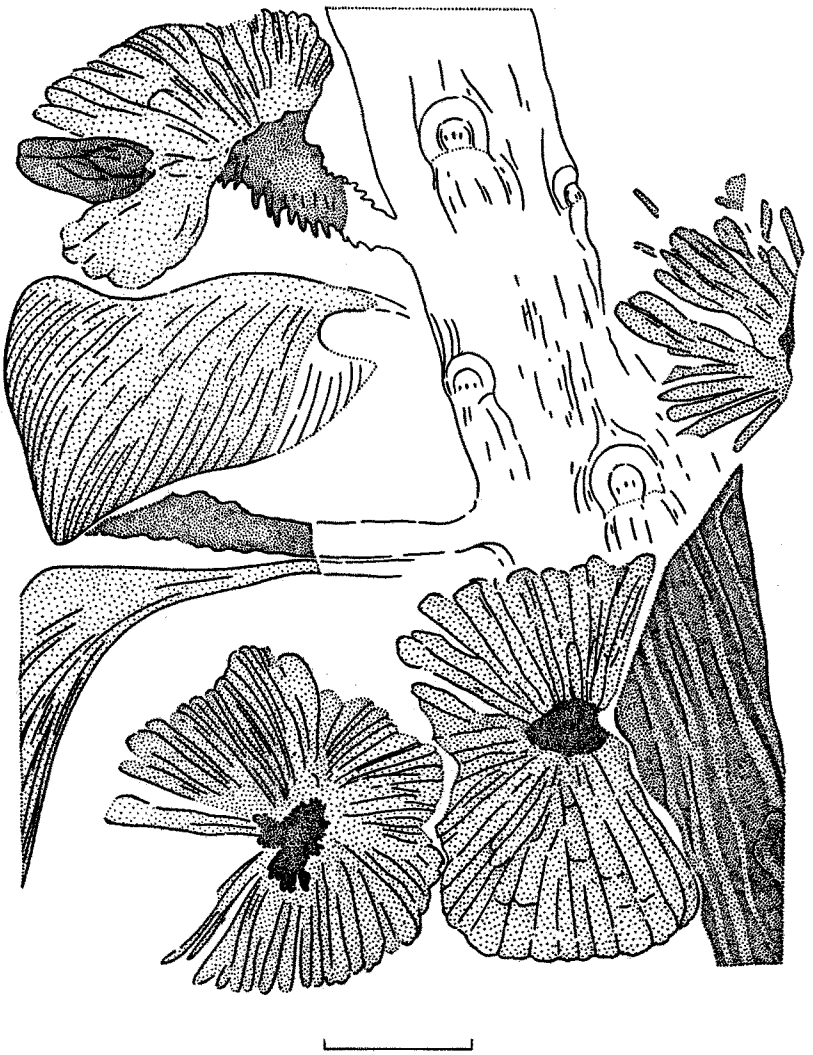


Fig. 4. *Vojnovskya paradoxa* Neub., specimen no. 3039/194, the holotype before preparation (see also Neuburg, 1965, pl. 27), note the occurrence on the same fertile shoot a laterally deformed strobilus with a seed of *Samaropsis stricta* or *S. rectialata* type in natural attachment (above to the left) and two vertically deformed strobili resembling *Paravojnovskya* (=*Gaussia*) (below to left). Scale bar is 1 cm. The locality of Khalmer'yussk Coal field, mine no. 3, the Intinskaya Formation, the Ufimian, the Upper Permian.

even pollen grains with three sacci occur rather often within one and the same sporangium of fossil gymnosperms (e.g., Lindstrom *et al.*, 1997). Thus, it is logical to treat this structure as a salpinx containing pollen. During ovule fertilization, pollen penetrated into the pollen chamber placed in the apical area of the nucellus.

Considering the asymmetrical umbrella, the generative structures under description represent an intermediate link between typical members of *Paravojnovskya* and representatives of the genus *Scirostrobus*. This point supports a phylogenetic relationship between these genera.

The species described above differs from the most closely related *P. cristata* and *P. scutellata* by the asymmetrical umbrella, numerous well-developed sterile interseminal scales, and the absence of well-defined scars of seed attachment.

The general morphology of *P. imbricata* as well as other representatives of this genus resemble that of fructifications assigned by many competent paleobotanists to the genus *Vojnovskya* (Betekhtina and Sukhov, 1968; Sixtel *et al.*, 1975; Durante, 1976). It proves the reliable systematic relationship of these genera.

The habitus of generative organs of Vojnovskyales depends greatly on preservation and especially on the plain of compression of a fructification during sedimentary diagenesis. Reinvestigation of type material of *Vojnovskya paradoxa* and *V. chalmeriuensis* (Figs. 3, 4) revealed that in case of not lateral but apical deformation of generative structures, they look like umbrella-like structures (e.g., Neuburg, 1965, pl. 26, fig. 1, note

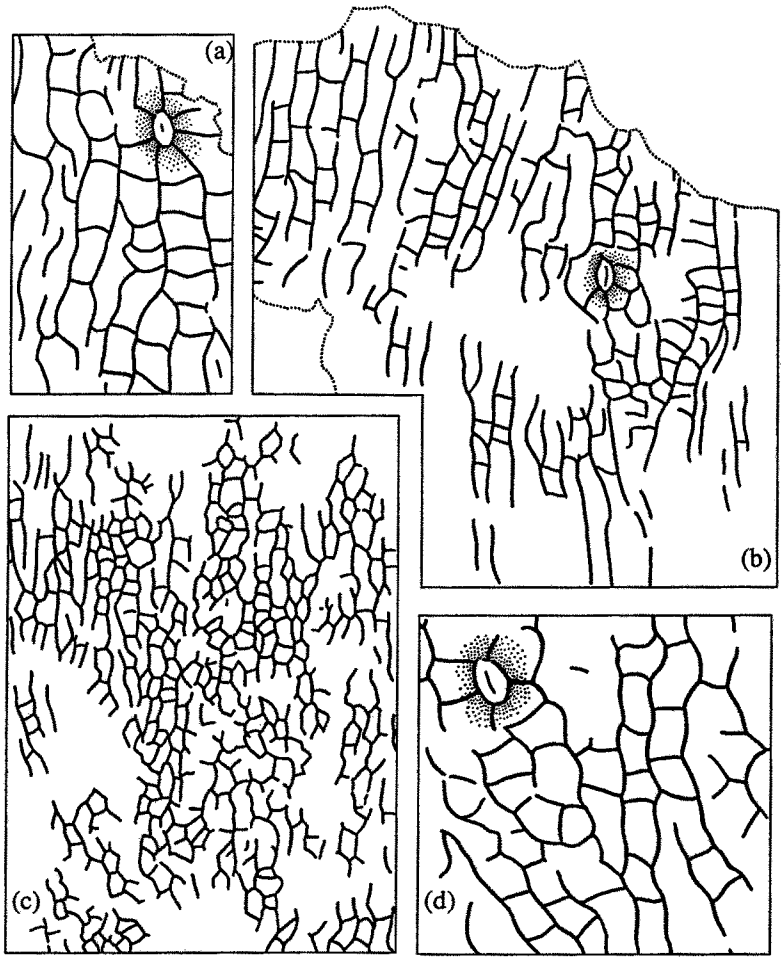


Fig. 5. *Scirostrobus ornatus* (Zalessky) Doweld et Naug., specimen from the collection housed in Perm Regional Museum, epidermal structure of sterile scales, note the longitudinally orientated upper cells of epidermis with rare stomatal apparatus, (a, d) ×300, (b) ×150, (c) ×100. The locality of Chekarda-1, layer 10, he Koshelevsk Formation, the Kungurian, the Lower Permian.

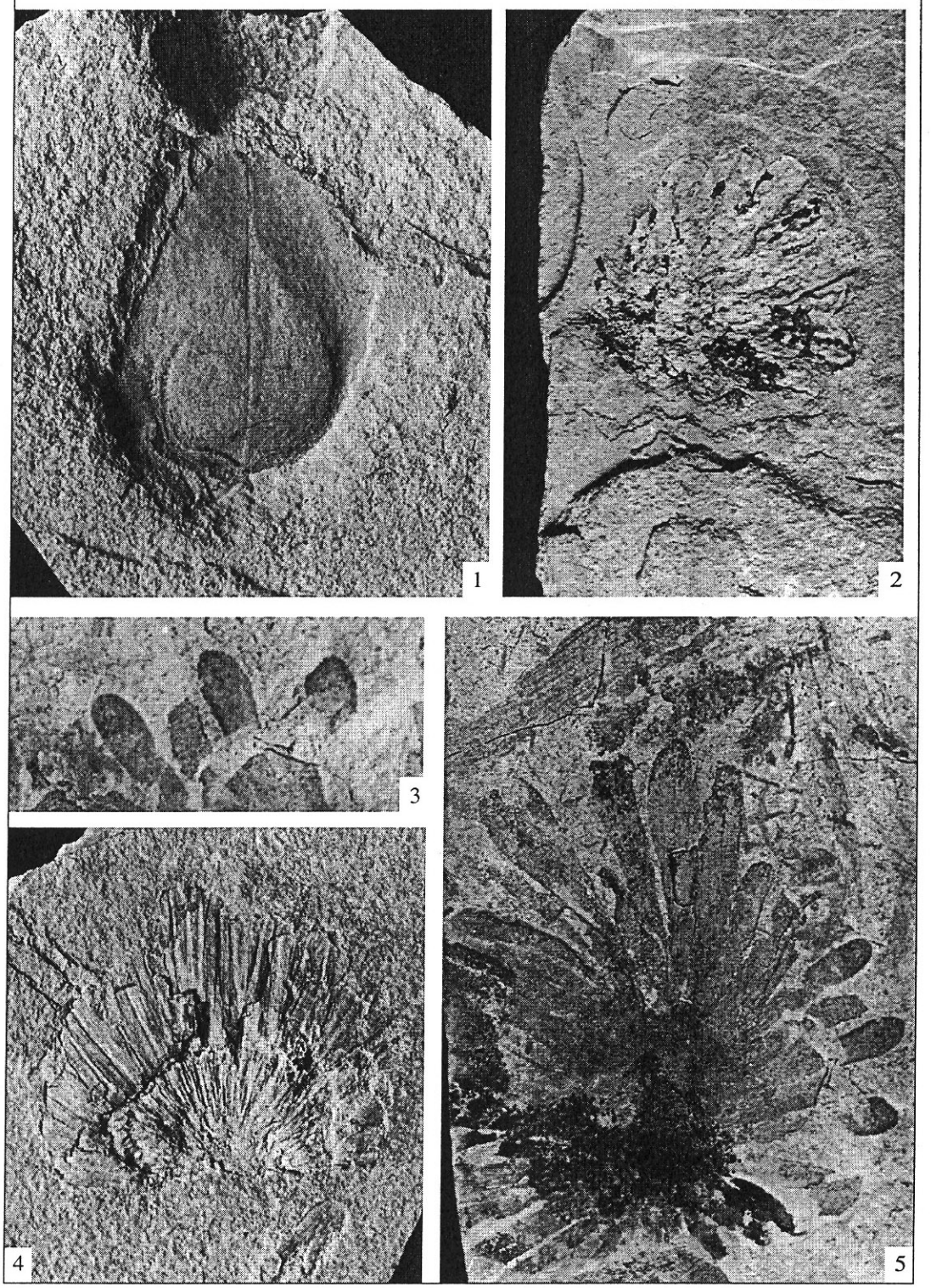
a polysperm below to the right; pl. 27, fig. 1, note polysperms in the lower part of the photograph) and, thus, found dispersely, may be referred to the genus *Paravojnovskya*. This proposition holds true for the holotype of *V. chalmeriuensis* Neub. (Fig. 3c; Neuburg, 1965, pl. 31, figs. 1, 1a).

A similar phenomenon is observed on the material of *V. stankevichii* (Pl. 9, figs. 3, 5; Pl. 10, fig. 5). The holotype of this species is represented by an isolated polysperm, which was described in the protologue as a microsporophyll aggregation (Sixtel *et al.*, 1975, pl. 45, fig. 1). The plain of its compression was orientated transversely to the polysperm axis, giving it an umbrellalike outline. Considering this type of preservation, this fossil might also be assigned to the genus *Paravojnovskya*. Nevertheless, other ovuliferous organs of this species, which were deformed laterally, are identical to obconical polysperms, usually considered to be characteristic for the genus *Vojnovskya* (Sixtel *et al.*, 1975, pl. 45, fig. 4).

V. stankevichii originates from the Lower Permian (Kungurian?) deposits of the stow of Sary-Taipan (mountains of southern Fergana, Uzbekistan). I have studied the collection of plant remains collected by N.N. Kalandadze (PIN RAS) in this locality and housed in Vernadsky Geological Museum and GIN RAS. The collection contains numerous polysperms of *V. stankevichii* with well-developed sterile interseminal scales and rare short seed stalks. Associated plant remains allow us to hypothesize the connection between ovuliferous organs of this type, leaves of *Rufloria recta*, and *R. ensiformis* (Neub.) S. Meyen, and scalelike bracts of *Nephropsis* (*Sulcinephropsis*) sp. abundant in this locality.

Flattened radial polysperms were figured without description by Durante (1976, pl. 56, figs. 1–4). In spite of the absence of obconical bases and their obvious umbrellalike outline, Durante assigned them not to *Paravojnovskya*, but to *Vojnovskya*. This example emphasizes the morphological similarity of these gen-

Plate 9



Explanation of Plate 9

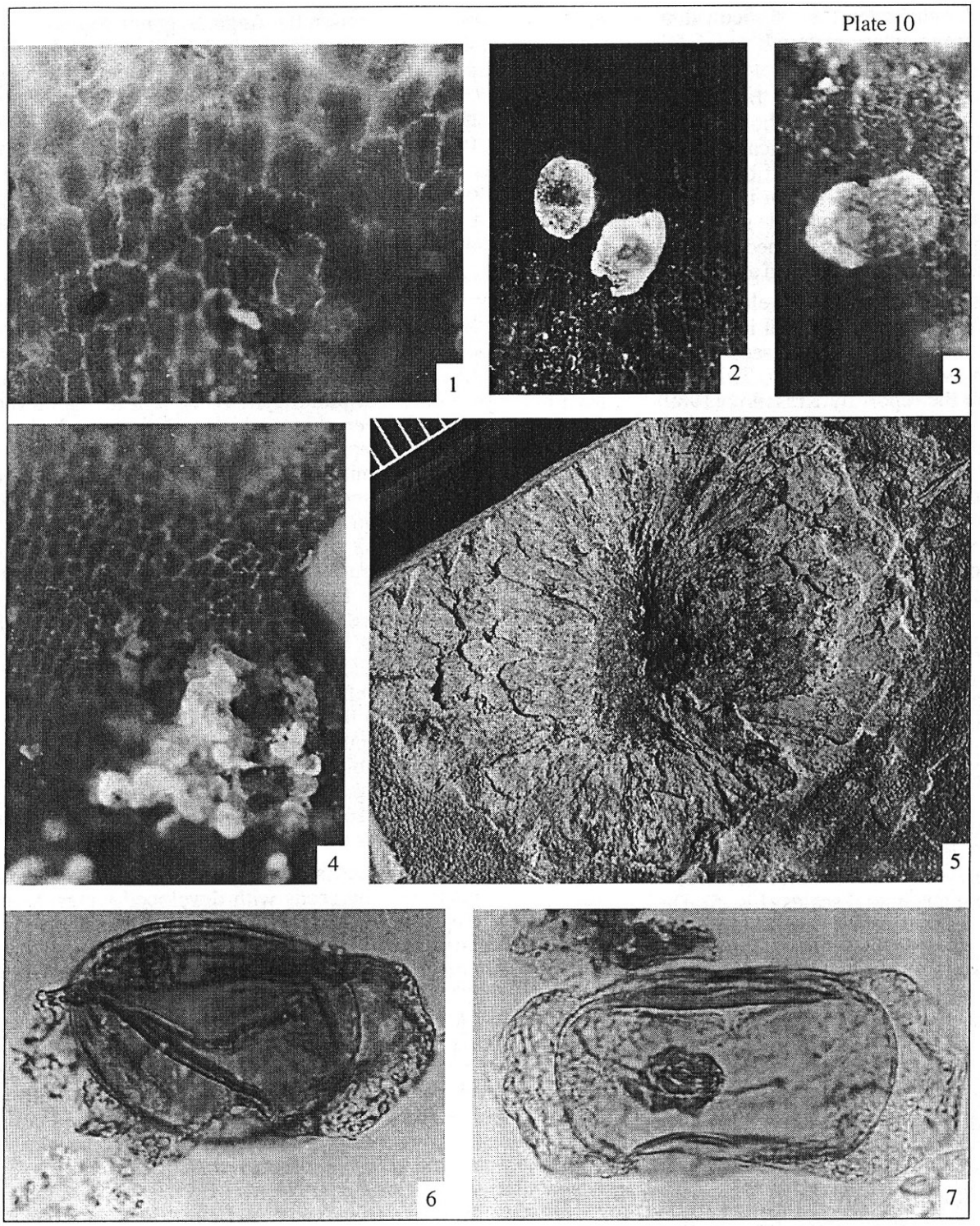
Fig. 1. *Samaropsis karamasarensis* Sixtel (a species close resembling *S. rectialata* Neub.), specimen no. 4559/19, ×3.

Fig. 2. *Paravojnovskya* (al. *Gaussia*) *imbricata* (Naug.) Naug. et Doweld, specimen no. 3737/205, ×2.

Figs. 3 and 5. *Vojnovskya stankevichii* Sixtel, specimen no. 4559/3, (3) ×3, (5) ×2, note numerous sterile scales.

Fig. 4. *Scirostrobus pterocerum* (Naug.) Doweld et Naug., specimen no. 3773/457a, ×2.

The localities of (1, 3, 5) Sary-Taipan, (2) Chekarda-1, layer 10, (4) Krutaya Katushka, the Kungurian, the Lower Permian.



Explanation of Plate 10

Figs. 1 and 4. *Paravojnovskya* (al. *Gaussia*) *imbricata* (Naug.) Naug. et Doweld; Fig. 1. Cells of nucellus, ×300; Fig. 4. A fragment of pollen chamber containing pollen, ×150.

Fig. 2. Pollen grains on the epidermis of *Rufloria* sp., ×200, analogous to pollen grains represented in figs. 6, 7.

Fig. 3. A pollen grain on the epidermis of *Rufforia* sp., ×300, identical to that in Fig. 7.

Fig. 5. *Vojnovskya stankevichii* Sixtel, a vertically deformed strobilus similar to *Paravojnovskya* (=*Gaussia*), ×3.

Figs. 6 and 7. Pollen grains apparently belonging to Vojnovskyales, ×600. **Fig. 6.** Protomonosaccate modification; **Fig. 7.** Protobisaccate modification of the Pityosporites-Piceapollenites type.

The localities of (1–4, 6, 7) Chekarda-1, bed 10, (5) Sary-Taipan, Kungurian, Lower Permian.

era and demonstrates their difficult distinction, especially on fragmentary material.

Scirostrobus pterocerum (Naug.) Doweld et Naug. has flattened umbrellalike bilateral fructifications formed by sterile scales and short seed stalks. The seed stalks are fused at the fructification base. The base of the generative organ is placed on one of the umbrella margins. The seed stalks form irregular crossed parastichies. Distal parts of the sterile scales and those of seed stalks may be free. Wing-shaped structures of the margins of the umbrella are situated at the fructification base.

A seed impression with an elongated micropyle and asymmetrical wing was found in the basal part of the fructification. Obviously, the seed was in natural connection with the fructification. This observation coincides with the report by Krassilov (1989) that fructifications of *Vojnovskya-Paravojnovskya* (=*Gaussia*) contained seeds of *Sylvella* Zal. with elongated apices and long micropylar channels through a hypertrophied wing. Seeds of *Samaropsis danilovii* Such. and *S. stricta* Neub. are possibly similar to the seeds of *Sylvella*. Seeds of *S. stricta* were discovered attached to lateral strobili of *Vojnovskya paradoxa* (Neuburg, 1965).

Sterile wings that extend around the polysperm base represent a characterizing feature of *Scirostrobus pterocerum*. The presence of this feature, visible on the holotype and several syntypes (Pl. 9, fig. 4), as well as other peculiarities, i.e., numerous sterile interseminal scales with well-developed midribs and the general proportions of the umbrella, precludes the identification of this species with *S. ornatum* (Zal.) Doweld et Naug.

Epidermal morphology supports the theory that the long well-developed structures of fructifications of *S. pterocerum* and *S. ornatum* represent not seed stalks, but sterile interseminal scales (Fig. 5). During maceration seed scars were not revealed in the apices of proposed long seed scales, although they always remain on the cuticle of a seed-bearing organ, appearing as circular luminae free of a cuticle.

DISCUSSION

During the last decade, much additional data on leaves and fructifications from the Late Paleozoic of Gondwana, similar in both morphology and micromorphological features to Angaran cordaites, have appeared. This similarity is very surprising considering the widespred opinion about the lack of phylogenetic relationships between many Carboniferous and Permian taxa of Angara and Gondwana (e.g., Meyen, 1977). The most important findings of cordaitelike leaves, significantly similar to typical Angaran genera, and associated fructifications and seeds are discussed below.

The majority of cordaitelike leaves from the Upper Paleozoic Gondwana is usually referred to the genus *Noeggerathiopsis*, which was formerly considered to differ strongly from the Angaran genus *Rufloria* by the absence of stomatal grooves. However, data reliably supporting the presence of dorsal grooves of *Noeggerathiopsis*, identical to those of *Rufloria*, have been published recently (McLoughlin and Drinnan, 1996). A thorough description of these Gondwanan leaves was accompanied by excellent photographs and drawings. Moreover, leaves from the Permian of Southern America were described by Guerra (1989) with direct assignment to the genus *Rufloria* (*R. gondwanensis*).

Zalessky (1912) observed the extraordinary similarity between the Angaran species *Cordaites aequalis* Schmalh., described in detail by I.F. Schmalhausen, complemented later by Zalessky, and undeservedly forgotten and almost unused by modern paleobotanists, (who preferred junior synonyms) and the Gondwanan species *Noeggerathiopsis hislopii* Feistmantel. Generative organs, represented by rosettes of radially fused sterile interseminal scales and seed stalks, were discovered in the same assemblages as the leaves of *N. hislopii* (Anderson and Anderson, 1985, p. 149, text-fig. 4, p. 343, pl. 168, figs. 1–6). Anderson and Anderson linked these fructifications with the pinnate leaves of *Botryochiopsis* Kurtz. Considering the list of taxa and their occurrence in the localities (Anderson and Anderson, 1985), the connection of these fructifications and leaves of *N. hislopii*, abundant in these localities, seems to be more well founded. These fructifications were first figured to be *Lerouxia transvaalensis* Plumstead, but were not published (Plumstead, 1961). They are undistinguishable from Angaran *Paravojnovskya*. Some of the figured specimens (Anderson and Anderson, 1985, pl. 168, figs. 1–6) also considerably resemble deformed fructifications of *Vojnovskya*.

As was discussed above, Angaran cordaites are characterized by seeds with developed wings. Leaves of *Rufloria* are traditionally associated with seeds of *Samaropsis triquetra* Zal., *S. macroptera* Naug., *S. vorcutana* Tschirk., characterized by equally developed wings, and allied to the *Samaropsis* species. Leaves of *Cordaites* are usually associated with seeds of *Samaropsis rectialata, Sylvella* spp. and allied species, which are characterized by an asymmetrical wing strongly developed near the micropyle. A partly destroyed female fructification was described from the Permian deposits of India characterized by dominant glossopterids and occasional leaves of *Noeggerathiopsis* (Surange and Chandra, 1974, text-fig. 1). The fructification contains numerous seeds of *Indocarpus elongatus* Surange et Chandra, the general morphology of which closely resembles that of *Sylvella* and *Samaropsis rectialata*.

Summarizing the points previously discussed, I can conclude that Angaran and Gondwanan plants with cordaitelike leaves (or at least, some of them), in spite of their different position in primary assemblages, may be united in a single order.

In studying the fructifications of *Vojnovskya stankevichii, Paravojnovskya* (al. *Gaussia*) *imbricata*

and *Scirostrobus pterocerum* from the Kungurian of middle Fore-Urals, their considerable similarity with polysperms of *Vojnovskya paradoxa* and *V. chalmeriuensis* was revealed. Such a resemblance was also reported for the representatives of *Gaussia* from the Carboniferous and Permian of Angara (Neuburg, 1965; Krassilov, 1989).

The presence of a seed in the presumably natural attachment at one of the specimens of *Scirostrobus pterocerum* confirms our opinion about the morphology of fructification containing seeds with stylelike micropyle.

The considerable archetypical similarity between the fructifications of *Vojnovskya, Paravojnovskya* and *Scirostrobus* precludes the assignment of these genera to different families of the order Vojnovskyales.

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