VOJNOVSKYALES IN THE LOWER PERMIAN OF NORTH AMERICA

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ABSTRACT

Lower Permian rocks of the south-western United States contain dissociated fossil plant parts that suggest the presence of a vojnovskyalean taxon in North America. Leaves, seeds, and especially one incomplete strobiloid organ are suggestive of the original *Vojnovskya paradoxa* from the Permian of the U.S.S.R. Other reports of *Vojnovskya* in the U.S.S.R., as well as one from Argentina, are on record.

Vojnovskya is a gymnosperm of uncertain affinities. If definitely established in the future, its presence in the Palaeozoic of the U.S.S.R., North America and South America will present problems of seed-plant evolution and plant dispersal, and may add a modicum to the evidence bearing on distribution of living populations of land organisms.

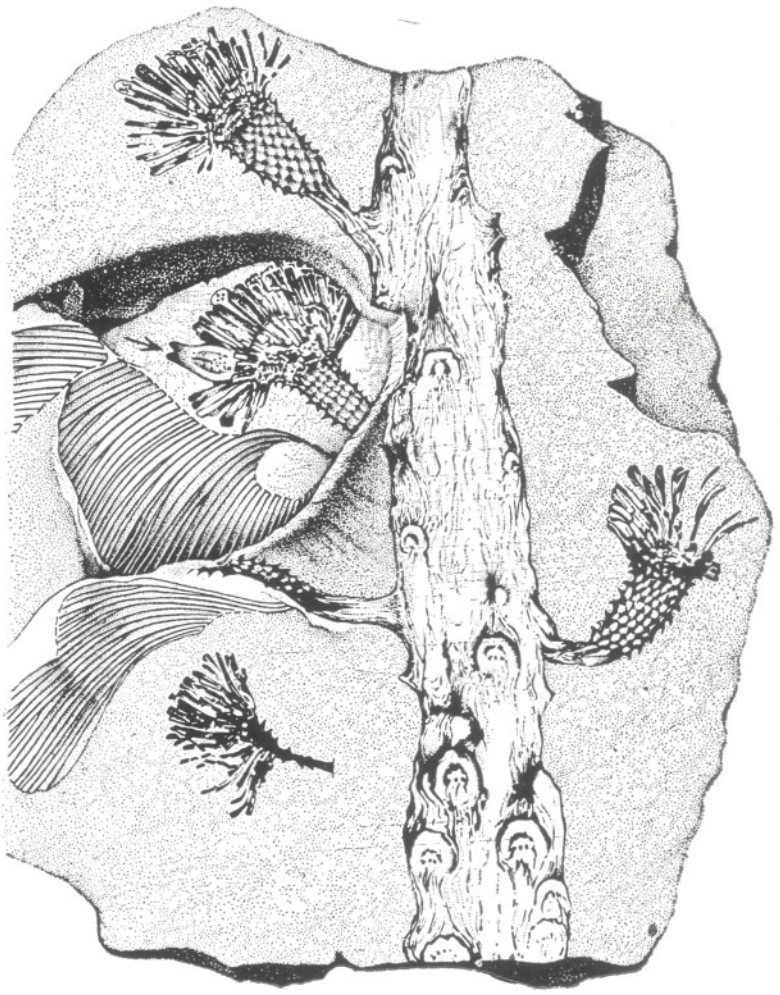
INTRODUCTION

THE Northern Hemisphere of the Old World made an important contribution to Palæozoic palæobotany in 1955, when Neuburg described an odd fossil plant from Lower Permian rocks of the Pechora Basin, U.S.S.R.; she named this plant *Vojnovskya paradoxa* n. gen. and sp. The plant was described as a shrubby or possibly arborescent gymnosperm with fairly large fan-shaped leaves similar to associated leaves known as *Nephropsis rhomboidea* Neuburg. The most interesting morphological feature of *V. paradoxa* is the reproductive system. This consists of bisexual cone-like aggregates of many units (of two kinds), arranged in a compact spiral on a thick central axis, which is attached to a vegetative branch by a short, relatively slender peduncle; excluding the peduncles, the cones are 2·50-3·0 cm long. The presumed male parts, or microsporophylls, are relatively long (about 1·0 cm) and slender, and apparently restricted to the apical part of the cone. Neuburg believed that the "microsporophylls" each bore two pairs of microsporangia near their apices, but Meyen (Maheshwari & Meyen, 1975, p. 103) subsequently claimed that these appendages". . . . .do not show sporangia, attached or embedded." Meyen did not elaborate further.

In *V. paradoxa* the female parts are bilaterally symmetrical, winged *Samaropsis*-like flat seeds, about 1·0 cm long; usually they have a slightly notched apex. The seeds are said to be interspersed among the microsporophylls (Andrews, 1961, p. 35). However, the available illustrations suggest strongly that the seeds are predominantly attached at the basal part of the cone. The general features of *V. paradoxa* are shown in Text-fig. 1.

Neuburg's description of *V. paradoxa* was repeated later (Neuburg, 1965, p. 57). In the same article (Neuburg's p. 63), Neuburg described a second species, *V. chalmeriuensis*, from approximately the same geographic and stratigraphic positions as *V. paradoxa*. Any morphologic differences between *V. chalmeriuensis* and *V. paradoxa* are extremely obscure, however, and it is highly doubtful that two discrete taxa are involved.

Zimina (1967) introduced a third species, *V. pacifica*, based on specimens from the Lower Permian of the South Maritime Territory, U.S.S.R. This material consists of largely denuded, possibly fertile axes, bearing only terminal (? microsporangiate) appendages. The basal parts of the axes are covered with spirally arranged rhombic scars that probably indicate the locations of previously attached structures, some of which possibly were seeds. No seeds are shown in the illustrations, and only one incomplete foliar appendage (*Nephropsis* sp.) is illustrated in association. The basal stalks and overall appearance of the clusters of terminal appendages are to some extent similar to those of *V. paradoxa*, but there



TEXT-FIG. 1 — *Vojnovskya paradoxa* Neuburg. Specimen with fragmentary leaves and four strobilar organs with terminal "microsporangiate" organs and one seed, indicated by arrow. Note spinose emergences on bases of strobili; these are interpreted here as sites of seed attachment. Modified from Andrews (1961).

are insufficient differences to support the conclusion that Zimina's material is distinct from *V. paradoxa*.

Vojnovskya usjatensis Gorelova (in: Gorelova, Men'shikova & Khalfin, L.L., 1973), from the Permian of the Kuznetz Basin, U.S.S.R. provides no distinctive morphologic features that would confirm its taxonomic separation from the type species, *V. paradoxa*. For the time being, therefore, I regard it as a superfluous name.

The most recently named Soviet species of *Vojnovskya* is *V. stankevichii* Sikstel', 1975 from the lower Permian of Fergana, U.S.S.R. There is no apparent evidence of seeds associated with this material, and the fragmentary stem surfaces closely resemble decorticated lycopod twigs. Furthermore, the most explicit illustrated specimen (Sikstel', 1975, pl. 45, fig. 1) may only doubtfully be referable to *Vojnovskya*; it is a discoid structure composed of radiate, overlapping bract-like structures, the whole bearing a close resemblance to *Gaussia scutellata* Neuburg, 1934, a supposed microsporangiate peltate structure from the Kuznetz Basin, U.S.S.R. Thus, *V. stankevichii*, founded on an extremely meagre

suite of incomplete specimens, contributes nothing to an overall understanding of *Vojnovskya*. Despite the number of "species" reported from the Soviet rocks, *Vojnovskya paradoxa* remains the most enlightening species in this yet poorly understood genus.

The Southern Hemisphere of the New World has demonstrated evidence of vojnovskyalean plants in its fossil flora. In 1971, Archangelsky and Leguizamon described the then new species *Vojnovskya argentina* from the Upper Carboniferous of La Rioja Province, Argentina. The species is based on an association of a few sterile shoots, some bearing parallel-veined *Nephropsis*-like leaves, and one incomplete presumed fructification. The latter consists of a fairly stout axis, the base of which is clothed with a system of more or less rhombic, spiniform, and triangular scales; the basal scales are more pointed than the upper. Terminating the fructification are sparse elongate, slender appendages, diagnosed as microsporangia(?). Seeds are unknown.

Despite the several discrepancies between this material and the type material from the U.S.S.R., as well as the absence of evidence of seeds, Archangelsky has chosen to identify the Brazilian material with the Asian genus and thus has added to the specific spectrum of *Vojnovskya*.

THE NORTH AMERICAN MATERIAL

This article is based on dissociated plant parts, all from the Lower Permian of the south-western United States, and mostly from one locality in Texas. Although there is no absolute proof of affinity of these parts with each other or with Vojnovskyales, the circumstantial evidence of morphological similarity between the widely geographically separated fossils and the ages of all the taxa provides the basis for at least a tentative conclusion that these fossils all represent the same order, typified by the genus *Vojnovskya*. Foliar elements, seeds, and one compound fructification constitute the North American material.

The Foliar Material

The American foliar material was described as *Sandrewia texana* Mamay n. gen. and sp. (Mamay, 1975); it was found in four Permian localities in north Texas and Kansas; stratigraphic relations of the localities are presented in fig. 1 of the 1975 paper, and salient features of the species are shown in Pl. 1 (the holotype is reproduced in this paper as Pl. 1, fig. 4).

No additional material of *Sandrewia* has been found since publication of the 1975 paper.

Sandrewia was thus proposed as a new genus because only the leaves were known, and their flabelliform shapes and open venation seemed insufficient grounds upon which to relate them to species of another reasonably well-understood plant; this nomenclatural gesture seemed supported by the geographic isolation of the material, although an affinity between *Sandrewia* and *Vojnovskya* was tentatively suggested at the time. The suggestion is admittedly still only tentative because the organic connection of critical parts has not yet been found. However, at one of the Texas localities (U.S.G.S. locality 8959; Lower Permian Belle Plains Formation, Baylor County, Tex.) *Sandrewia* is associated with many detached platyspermic seeds and one presumably bisexual cone-like structure that closely resembles that depicted for *Vojnovskya paradoxa* (see Text-fig. 1). The fact that nowhere else, as far as I know, has a similar association been found gives grounds for at least a suspicion that vojnovskyalean plants existed in the Permian of Texas.

The Seeds

Seeds are of prime importance in this study because the type specimen of *Vojnovskya* was said to contain seed-like bodies of the *Samaropsis* type. One such structure, illustrated by Neuburg (1965, pl. 29), is a small (about 8 mm long & 4 mm wide), apparently winged seed with a narrowed, shallowly notched apex; it is apparently sessile on the strobilus, attached at the same level as the basal attachment of a fairly dense group of slender stalk-like structures, possibly of microsporangiate nature. The base of the seed is about twice as broad as its apex. Only one seed is shown in clear attachment, but the abundant short spine-like emergences clothing the basal halves of the strobili

may represent the stalks of other seeds, which were shed before preservation.

Many similarly sized samaropsid seeds are associated with the Texas leaves, particularly in the "Emily Irish" beds of the Belle Plains Formation (U.S.G.S. Locality 8959; see Mamay, 1975, p. 76). Of the several types of seeds found there, these are the most abundant. In many specimens they are found closely arranged in "pockets" or groups of a dozen or more (Pl. 1, fig. 3), as though they had all originally been members of a single strobilus, which dropped to the ground and lost its seeds on impact; the seeds of these "pockets" are in random positions relative to each other. The absence, among these seed masses, of fossils suggestive of male organs may indicate that the microsporangiate parts were more firmly attached than the seeds and remained attached to the cone axis after the seeds had become detached. The composition of cone remnants on *V. paradoxa*, as well as the apparent predominance of terminal, slender unseed-like structures in the single strobiloid fragment from Texas are points that seem to support the foregoing interpretation.

The Texas seeds are essentially triangular in shape, ranging from 7·0 to 10·0 mm in length and 4·0 to 6·0 mm in width. Their bases are either entire (Pl. 1, fig. 1) or somewhat convex (Pl. 1, fig. 2); sides of the seeds are mostly straight. Most seed apices are slightly notched (Pl. 1, fig. 2) or nearly entire. One seed has what appears to be a deeply trifid apex (Pl. 1, fig. 1). Whether this is a natural apical configuration or not, this specimen is the only one seen with this type of apex; although there is the possibility that it represents a species apart from the associated samaropsids, it may merely be an aberrant specimen. Both the illustrated seeds (Pl. 1, figs. 1, 2), as well as many other specimens, clearly show evidence of a conspicuous nucellar body.

The Texas seeds vary enough in minor details of size and outline that species identification is difficult at this time; thus they are simply assigned to the genus *Samaropsis*. Despite this lack of specific identity, it is important that the Texas seeds closely resemble those of Neuburg's original material, so far as the latter are known. The seed shown here (Pl. 1, fig. 2) is so similar to Neuburg's (1965, fig. 2; pl. 2b, fig. 1) that the two would be very difficult to differentiate on the species level.

The "Strobilus"

Although the Texas collection consists of several tons of carefully searched slabs containing several leafy axes of *Sandrewia* and literally hundreds of the samaropsid seeds described here, just one *Vojnovskya*-like strobiloid fragment is present (Pl. 1, figs. 5, 6). Even though it is preserved as a faint impression with little surficial relief, oblique lighting reveals that certain important comparisons with the fructification of *V. paradoxa* may be made.

The Texas specimen (Pl. 1, fig. 6) is a strobilus-like structure slightly more than 5·0 cm long; approximately the terminal two-thirds is seemingly fertile. The basal sterile part is apparently a stout (0·6-0·7 mm thick) peduncle, on whose surface no appendicular scars or otherwise distinguishing feature appear. The upper or terminal part of this structure is a globose "head-like" object, nearly 3·5 cm broad at its widest point. This appears to be an aggregate of more or less pointed slender appendages, which are about 1·0 cm long and 2·0 to 3·0 mm broad. The number of these appendages can only be estimated, but there might have been 25 to 30. They apparently radiate out from a central receptacular area upon which no distinguishing features are seen other than shallow vague depressions that could represent points of attachment of other structures; a few small flakes of coalified residue are also evident here. For convenience of reference, and admitting the lack of any knowledge of the morphological nature of these terminal stalk-like objects, they are referred to here as "microsporophylls." If indeed they are microsporophyllar, then an important step toward establishing identity with *V. paradoxa* will have been made. However, no convincing evidence has been presented of microsporophyllar function for these structures in *V. paradoxa*, and Meyen (Maheshwari & Meyen, 1975, p. 103) has already made a contrary statement on this point.

An important additional feature of the Texas strobilus-like object is the presence of two, possibly three, pendant seed-like objects, showing evidence of bifid apices

(tooth-like protrusions extending from the bottom of the specimen shown on Pl. 1, fig. 5). Points of their attachment or other details thereof cannot be observed in the specimen, but these objects appear to have the remains of an originally thicker substance than the surrounding areas, a fact that substantiates their interpretation as seeds; they are also about the same size as many of the detached seeds previously described here. The apical notches in these seeds are deeper than those of most of the associated detached seeds (Pl. 1, fig. 2), but not significantly deeper than those in the apparently trifid seed shown in Pl. 1, fig. 1.

Although the "microsporophylls" of the Texas specimen are oriented in the same manner as those of *Vojnovskya paradoxa*, relative to the strobilar axes, the seed-like bodies on the Texas specimen, if correctly represented here, are oriented oppositely to those of *V. paradoxa;* seeds of the Texas specimen appear to point toward the base of the strobilus, whereas those of *V. paradoxa* point toward the strobilar apex (compare Text-fig. 1 with Pl. 1, fig. 5). Inadequacy of preservation of the Texas specimen permits only a speculative approach to this difference. If a real structural difference is represented here, it becomes all the more important that additional material of the Texas strobili be found and investigated. Differences in orientation of the seeds may, of course, reflect positional distortion during compaction of the sediments.

Although only one certainly identifiable seed is shown attached to Neuburg's type specimen of *V. Paradoxa* (Text-fig. 1), the numerous spinose emergences at the basal parts of the strobili may be a significant feature in support of comparison between the Texas strobilus and those of Neuburg's type. I think that these "spines" may actually represent the remnants of short seed stalks, the mature seeds having been more loosely attached than the terminal "microsporophylls". The seeds thus could have been detached more or less simultaneously by a blow of another object against a mature strobilus, denuding the basal part of the receptacle and leaving most of the "microsporophylls" still attached. This sort of differential attachment of parts could explain the concentrations or "pockets" of seeds commonly found in the Texas sediments, as well as the generally seedless condition of the specimens from the U.S.S.R. and Argentina.

DISCUSSION

Although Neuburg's original material of *Vojnovskya* is by far the most informative of any of the suites or specimens tentatively referred to this taxon, it is intriguing to consider the possibility that all the other reported materials are truly vojnovskyalean, even though based upon fragmentary or dissociated parts. As previously stated, the additional Soviet material (excepting *V. stankevichii* Sikstel') is not convincingly separable from *V. paradoxa* because of paucity of material and absence of critical parts. Nonetheless, the Soviet reports add a few localities to the geographic distribution of the Vojnovskyales. *V. argentina*, from Argentina shows no evidence of bisexuality in the one strobiloid specimen known but the terminal appendages and associated leaves probably are sufficiently like those of the specimens from the U.S.S.R. to allow speculation that the specimens from South America are at least ordinally, if not generically related to those from the U.S.S.R. This relationship is important because it would extend the global range of Vojnovskyales from the Northern to the Southern Hemisphere and from the Old World to the New.

The detached Permian structures from Texas — leaves (*Sandrewia*), seeds and strobiloid structure — are enough like the various parts of Neuburg's *Vojnovskya paradoxa* to permit serious consideration that the Texas fossils are parts of one plant, and that said plant is a vojnovskyalean entity. Other factors, such as relatively comparable geologic ages, close association of the Texas fossils, and the suggestion of similarly loosely attached seeds on basal parts of the strobili tend to support the idea that *Vojnovskya* and the Texas fossils are closely related, at least ordinally, *Sandrewia* representing foliage of the American plant. Because of the speculation involved, however, no systematic formalities are presented here.

Should the necessary organic attachments eventually be found and demonstrate a vojnovskyalean relationship for the Texa

fossils — and assuming that the plant from Argentina has been correctly assigned — the already disjunct geographic distribution of this group of strange gymnosperms would be extended to include both the Southern and Northern Hemispheres of the New World, as well as the Northern Hemisphere of the Old. This distribution would place a singularly odd type of plant in locations in both the Gondwanan and Laurasian land areas, and would pose a difficult problem regarding geographic origin and dispersal of the group.

This report of North American *Vojnovskya*-like material invites a short review of possible affinities of these interesting plants, even though the new material sheds no additional light on the question. *Vojnovskya* has tentatively been regarded as possibly related to either the Cordaitales or Bennettitales, although any resemblances are scarcely close. An important step toward an understanding of the morphology of the vojnovskyalean fructification would be made by unqualified certification of the nature of the terminal "microsporophylls". This certification has been challenged by Meyen (Maheshwari & Meyen, 1975, p. 103) and none of the material described thus far under the name *Vojnovskya* has been proven to have polleniferous organs. T. M. Harris (personal communication, 1977) informed me that those organs may be comparable with the "armor-like" sterile interseminal scales of Bennettitales, but he took no positive stance on the affinities of *Vojnovskya*; nor did he offer any explanation of the possible function of these "armor-like" appendages.

A startling misinterpretation of *Vojnovskya* was offered by Maekawa (1962, p. 152), who proposed *Vojnovskya* as a "presumable ancestor of angiosperms". This interpretation arose from Maekawa's ideas (1962, p. 152) involving "Deffinite [sic] disposition of microsporophylls and macrosporophylls which is fundamentally equal to stamen-pistil relationship*** "Similarity of the form of macrosporophyll with that of *Liriodendron*", etc. These self-evident fallacies demonstrate the difficulties in taxonomic interpretations of *Vojnovskya* or other plant types that need not necessarily have left recognizeable lineages. At most, the best phylogenetic interpretation of *Vojnovskya* is that it probably represents some bizarre, short-lived group of Late Palaeozoic gymnosperms that attained a sparse but geographically broad distribution.

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EXPLANATION OF PLATE

PLATE 1

Illustrations of *Vojnovskya*-like fossils from the Lower Permian Belle Plains Formation, Texas, U.S.A.

1. Detached samaropsid seed, with apparently trifid apex. × 2 (from specimen U.S.G.S. 8959-5, seen in fig. 3).
2. Detached samaropsid seed, with shallowly bifid apex. × 2. Compare with seed of *Vojnovskya paradoxa*, shown in Text-fig. 1. U.S.G.S. 8959-6.
3. Mass of detached samaropsid seeds, presumably all from one shattered strobilus. Elongate mass of small sporangia in upper right quadrant is an unknown fructification. × 1. U.S.G.S. 8959-5.
4. Leafy axis (holotype) of *Sandrewia texana*. × 2. U.S.G.S. 8959-4.
5. Line tracing of strobilar specimen shown in fig. 6. m, " microsporophyll "; S, seed.
6. Strobilar specimen found associated with seeds and foliar material. Structure resembles strobilus of *Vojnovskya* in fundamental features (line tracing in fig. 5). × 2. U.S.G.S. 8959-7.

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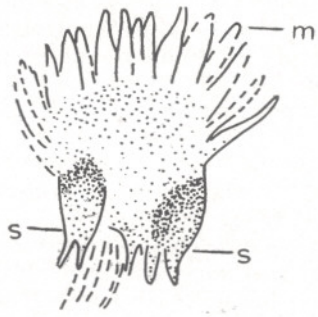

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PLATE 1