

NEW INTERPRETATION OF *GAUSSIA* (VOJNOVSKYALES)

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ABSTRACT

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Vojnovskyales, and not Cordaitales, have dominated the Angara floristic realm. *Gaussia*, a vojnovskyalean fructification, is interpreted as a head of flattened pistil-like structures with a single basal ovule and fairly long linear style-like portion, spatulate at the apex. The central canal of the style is expanded terminally into a funnel filled with pollination liquid. The funnel is surrounded by trichomes. The ligulate process outside the funnel is comparable with the typhaceous stigma. The Vojnovskyales had probably descended from the lagenostomalean pteridosperms.

INTRODUCTION

The Vojnovskyales are fascinating but poorly understood plants. They emerged with the discovery of *Gaussia* Neuburg in the Permian of the Kuznetsk Basin. The generic diagnosis was originally given in English (Neuburg, 1934, pp.35–36): “The reproductive organ in the shape of a radial symmetrical scutellum or disc 40 mm in diameter seats on a thick pedicel; numerous lineal laminas (microsporophylls) with a parallel nervation are going radially of the centre, tile-like disposed and seemingly in verticels or spirals; the internal laminas are short, the external — longer, at the top enlarged in shape of a horseshoe (microsporangia)”. This interpretation was evidently affected by the comparison with *Potonia*, the male fructification of pteridosperms. Later Neuburg (1948) described more specimens of the type species *Gaussia scutellata* Neuburg, noticing the “fine granulation” of the apical “microsporangia”. She compared *Gaussia* to *Taibia* (Zalessky, 1934) and *Niazonaria* (Radczenco, 1933). All these fossils are allegedly congeneric, but *Taibia* and *Niazonaria*, though published prior to *Gaussia*, were founded on poorly preserved specimens. In *Niazonaria* the apices of radial lamellae are described as bearing two tubercles. As to the leaves, Neuburg suggested association with *Pursongia* (*Glossopteris*-like leaves with anastomosing veins) or *Zamiopteris* (of the same shape, but with open venation).

In 1955 Neuburg established a new genus, *Vojnovskya*, for a shoot bearing allegedly bisexual strobili from the Permian of Pechora. The shoot axis shows

leaf scars and small-scale leaves in the upper portion. Leaves of *Nephropsis* are seen on the same slab in a position suggesting their attachment to the shoot. These leaves or cataphylls are broadly rhomboidal, with parallel venation resembling that of "cordaitalean" leaves. Strobili are axial to the leaves and consist of the overlapping radial lamellae and a seed-like body in the middle. According to Neuburg, the radial lamellae are whorled microsporophylls showing a median groove and the distal expansion with small tubercles (sporangia?). A seed-like body is a remnant of the innermost whorl of several megasporophylls. Neuburg erected the order Vojnovskyales for trees or shrubs with *Nephropsis* foliage and bisexual strobili consisting of linear microsporophylls and oval megasporophylls (megasporangia) in radially symmetrical whorls. The Vojnovskyales included also *Gaussia* which differed from *Vojnovskya* by the drooping microsporophylls on a naked stalk.

The Vojnovskyales aroused much interest as the only Palaeozoic plants with bisexual "flowers". Maekawa (1962) put *Vojnovskya* forward as a putative ancestor of angiosperms because of the "concatenation" of the pedicel, the disposition of micro- and megasporophylls, and the similarity of megasporophylls to those of *Liriodendron*, as well as the "expectance of dichotomous venation in ancient angiosperms". Subsequent authors touching on this subject (e.g., Mamay, 1978) were not sympathetic with Maekawa's suggestion. Numerous *Vojnovskya* and *Gaussia* were recorded from Pechora, to Kuznetsk Basin, Primorye and other Angara regions. Outside the Angara realm, the vojnovskyalean plants have been reported from Transvaal (Le Rous, 1970), Argentina (Archangelsky, 1971; Archangelsky and Leguizamón, 1971) and North America (Mamay, 1978). *Sandrewia* from the Lower Permian of North America comprises shoots with *Nephropsis*-like leaves, dispersed samaras and indented disc (?) with two pendulous ovules showing bifid micropyles. Meyen (1979) has preliminarily suggested a peltaspermaceous affinity of this ovuliferous structure.

The original interpretation by Neuburg remained essentially unaltered. However, Meyen (in Maheshwari and Meyen, 1975) has questioned the interpretation of radial lamellae as microsporophylls, because any attempts to extract pollen grains from the putative sporangia had failed.

DESCRIPTION AND NEW INTERPRETATION

Recently Valentine Burago has collected *Gaussia* and *Vojnovskya* from several localities in the Lower Permian of Primorye (Far East of the U.S.S.R.), altogether about one hundred specimens evidencing the high frequency of these fructifications in the "cordaitalean" assemblages. One specimen of *Gaussia* from Russian Island (Ostrov Russkiy, near Vladivostok) is especially instructive. It allows detailed morphological study of the "microsporophyll" apices. The associated leaves are mostly *Rufloia*, *Nephropsis*, *Zamiopteris*, *Crassinervia* and *Evenkiella*.

The rosette-like compression, 60 mm in diameter, shows a receptacle 20 mm wide bearing radial rays, or lamellae 20–22 mm long (Fig. 1, Plate I, 1). The compression is several millimetres thick consisting of many layers of imbricate rays, as if flattened from an originally head-like structure. Indeed it looks much like the compressed fossil heads of *Platanus* (Plate I, 1). The receptacle shows rhombic scars of the rays. Many rays of the surface layer are crushed or broken at the base. Two of a few rays with better-preserved proximal portions, are swollen at the base, showing seed-like bodies (Plate I, 2, 3). The bodies are oval (2×1.7 mm) and finely pitted.

The ray surface is traversed by low ridges and fine longitudinal striation. Fragments of the ray incrustations have been prepared for SEM. Epidermal cells are clearly seen in these preparations (Plate III, 4; Plate IV, 2). The ridges are marked by a few rows of narrow elongate cells. The intercostal zones consist of broader cells, about $40 \times 17 \mu\text{m}$. The cell outlines are rectanguloid, with the transverse walls perpendicular or oblique to the rows. Occasional cells are wedge-shaped. The anticlinal walls are straight and conspicuously ribbed. The periclinal walls are flat. In the intercostal zones, there are pits which can be either stomata or hair bases. We believe that elliptical pits about $20 \mu\text{m}$ long are stomata (Plate IV, 3, 4). Some of them show imprints of the sunken guard cells bordered by thickened subsidiary cells. The stomata are well spaced, irregularly orientated, mostly oblique to the cell rows.

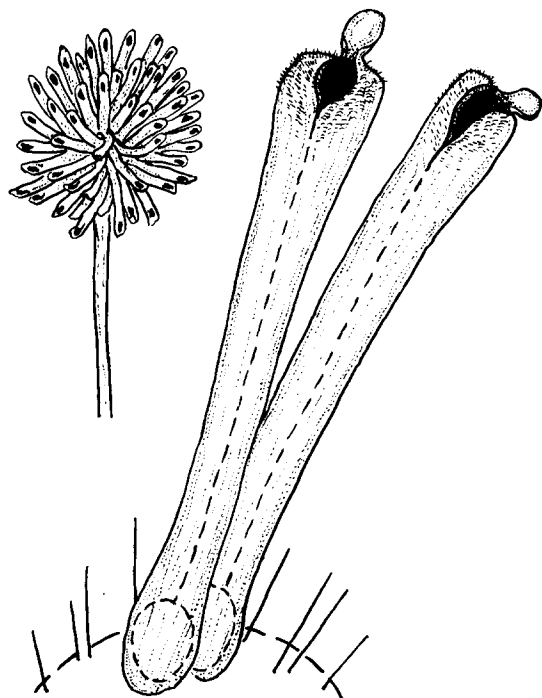
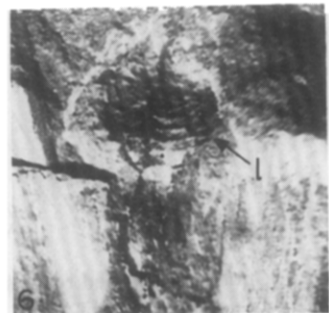
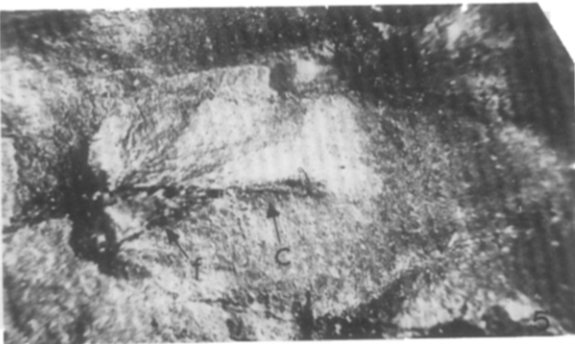
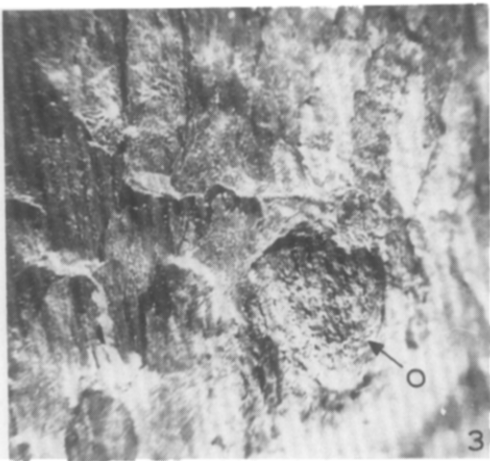
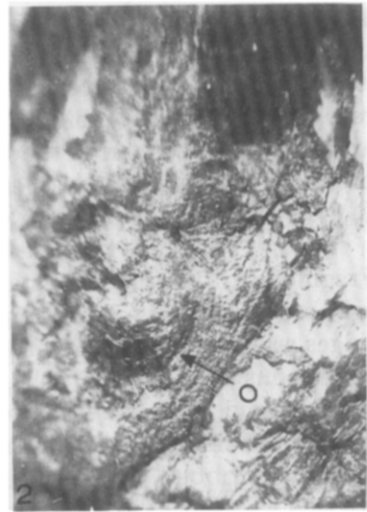
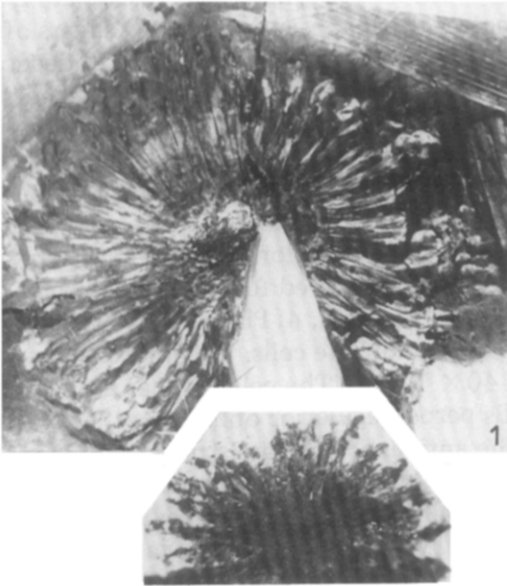


Fig. 1. *Gaussia*: sketched reconstruction of a head and the rays (not to scale).

PLATE I



The apical portions of the rays are expanded, spatulate and about 2.5–3 mm wide, showing a funnel-shaped cavity about 0.8 mm wide filled with lustrous anthraxolitic substance that is supposedly a metamorphosed pollination liquid. The funnel tapers backward into a narrow canal traceable for a short distance and then sunken below the surface. The canal is occasionally exposed well below the apex due to decay of the covering tissues. The funnel is bordered by minute pits. These features are seen on many rays under low magnifications of the dissecting microscope (Plate I, 4, 5; Plate II, 1; Plate III, 1, 2), but are especially clear under the SEM (Plate II, 2, 3; Plate IV, 1). The pits scattered over the apical expansion and crowded around the funnel are rounded, with slightly elevated borders, often filled with opaque substance. We consider these pits to be the scars of secretory hairs.

The ligulate process can be observed in favorably preserved rays distal to the funnel (Plate I, 6; Plate II, 1, 2). It is oval, about 1.5 mm long, slightly pendant, sometimes transversely wrinkled (Plate I, 6), apparently thin and fragile, showing bulging, slightly sinuous cells in the middle (Plate III, 3).

The following interpretation is tentative and can be changed by better-preserved and/or better-understood material. It is radically different from the interpretation by Neuburg, but is not safer, though it is based on more detailed study. The fructification is conceived not as a rosette, but as a head flattened by compression.

The rays are not microsporophylls but ovuliferous pistil-like structures with a single basal ovule, long style and intricate apical complex for trapping the pollen grains and transmitting them through the central canal. This complex consists of a funnel filled with pollination liquid, secretory hairs bordering the funnel, and a terminal ligulate process with bulging cells on the adaxial surface. The ligular process, thin, moistened with a pollination drop, flapping against the rigid style, might have assisted the pollen-catching function.

In many specimens of *Gaussia* the basal rays have pointed apices without any traces of a funnel. We believe that these rays are sterile ones transformed into perianth bracts.

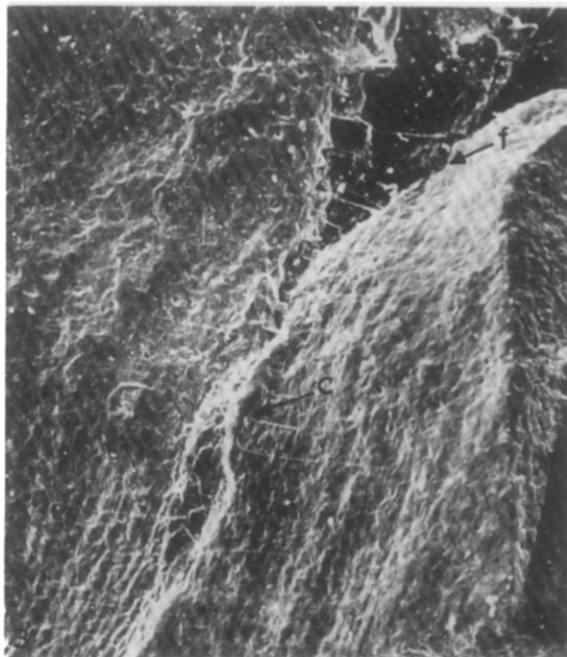
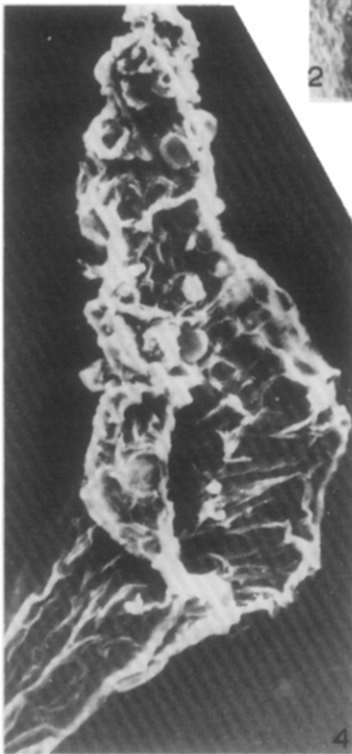
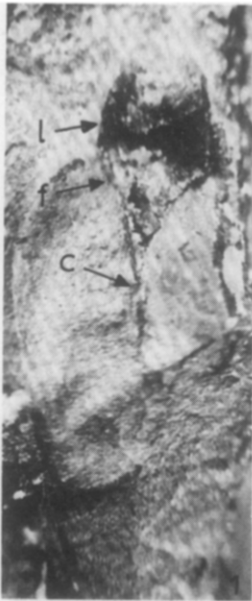
PLATE I

Gaussia sp. from the Lower Permian of Russian Island (Ostrov Russkiy)

1. Compression of a head ($\times 1$), with the parallel-veined leaves above. The compressed head of *Platanus* from the Upper Cretaceous is shown below for comparison.
2. Base of a ray showing outlines of the ovule ($\times 12$).
3. Another ovule ($\times 12$).
4. Ray apex with a funnel; minute pits — the hair scars — are seen around the funnel ($\times 12$).
5. Ray apex showing exposed distal portion of the central canal opening into the funnel with antraxolitic pollination drop substance at the end ($\times 12$).
6. Transversely plicated ligular process ($\times 12$).

Arrows: *o* = ovule; *l* = ligule; *f* = funnel; *c* = canal.

PLATE II



DISCUSSION

Though much more work is needed for a decisive conclusion, we suggest at present that *Gaussia*, *Vojnovskya*, *Taibia* and *Niazonaria* are pistillate heads of the same basic structure. In major Siberian localities, these fructifications associate with *Nephropsis* and *Crassinervia* cataphylls as well as with leaves of *Rufloria* and *Zamiopteris*.

The leaves of *Rufloria* (taeniate, with subparallel venation and distinct stomatal grooves between the veins) and allied morphotypes are traditionally classified as "cordaitalean", though the genuine cordaitalean fructifications have never occurred in association with these leaves, and the *Gaussia* — *Vojnovskya* ovuliferous organs have little in common with *Cordaitanthus*. The implication is that the Late Palaeozoic vegetation of Siberia was dominated not by the cordaitalean but by the vojnovskyalean plants. This possibility was previously recognized by Neuburg (1965) and Meyen (Maheshwari and Meyen, 1975). The pollen cones of the Vojnovskyales are supposedly represented by *Cladostrobus* (Maheshwari and Meyen, 1975).

According to our interpretation, the Vojnovskyales had little in common with cordaites. Their affinities were rather with the lagenostomalean pteridosperms. In the Lagenostomales, the pollen chamber is swollen into the lagenostome which has an apical tubular extension, the salpinx, for funneling the pollen grains. *Salpingostoma dasu* Gordon has a comparatively long salpinx not unlike the apical funnel of *Gaussia*. Leisman (1964) showed the shortening of the salpinx in the *Salpingostoma*—*Eurystoma*—*Conostoma* morphocline. The vojnovskyalean ovuliferous organs were dissimilar to those of the glossopterides as interpreted by Gould and Delevoryas (1977), though both groups might be descended from the Lagenostomales. Some fructifications in the *Glossopteris* realm, such as *Rigbya arberioides* (Rigby, 1978) resemble *Gaussia*, at least superficially.

Vojnovskyales were linked to angiosperms mainly because of the misinterpreted "bisexual flowers". Though *Gaussia* and presumably also *Vojnovskya* are unisexual, they are not unlike the pistillate heads of some angiosperms, e.g., *Pandanus*, *Sparganium*, *Juncus* or *Luzula*. The pollen-catching device with the ligulate process can be compared, among angiosperms, with the stigma of *Typha*. These wind-pollinated marsh herbs with robust stems and linear distichous leaves have small unisexual flowers massed in spicate inflorescences subtended by the leaf-like bracts. The unicarpellary ovary narrows into a very long filiform style showing the funnel-like terminal expan-

PLATE II

Gaussia sp. from the Lower Permian of Russian Island (same specimen as in Plate I)

1. Ray apex with the ligular process ($\times 12$).
 2. Ligular process of the same ray, SEM ($\times 60$).
 3. Central canal and the funnel of the same ray, SEM ($\times 60$).
 4. *Typha* sp. the funnel-shaped stylar apex and the ligular stigma, SEM ($\times 350$).
- Arrows as in Plate I.

PLATE III (Description on p. 236)

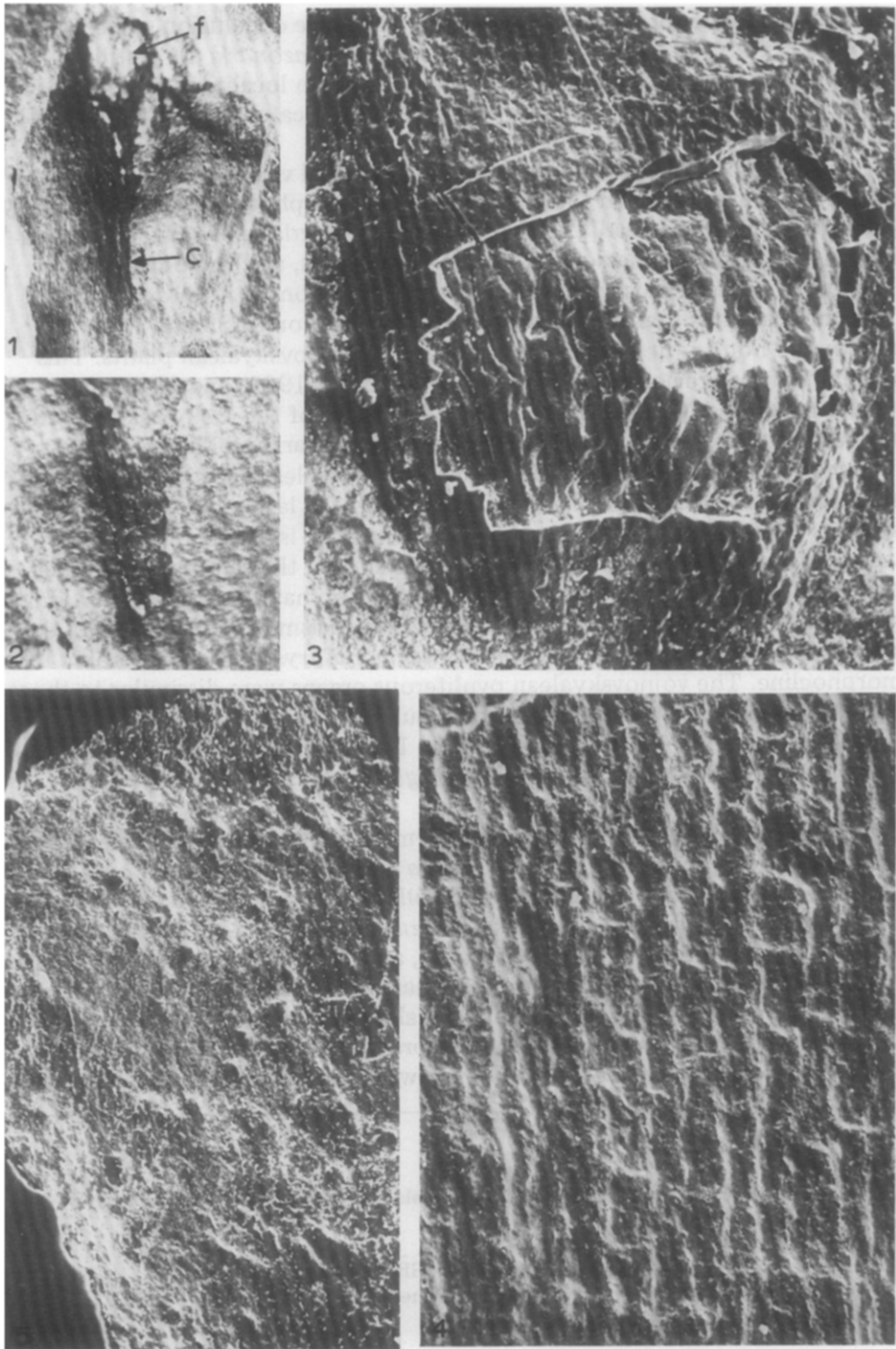


PLATE IV (Description on p. 236)

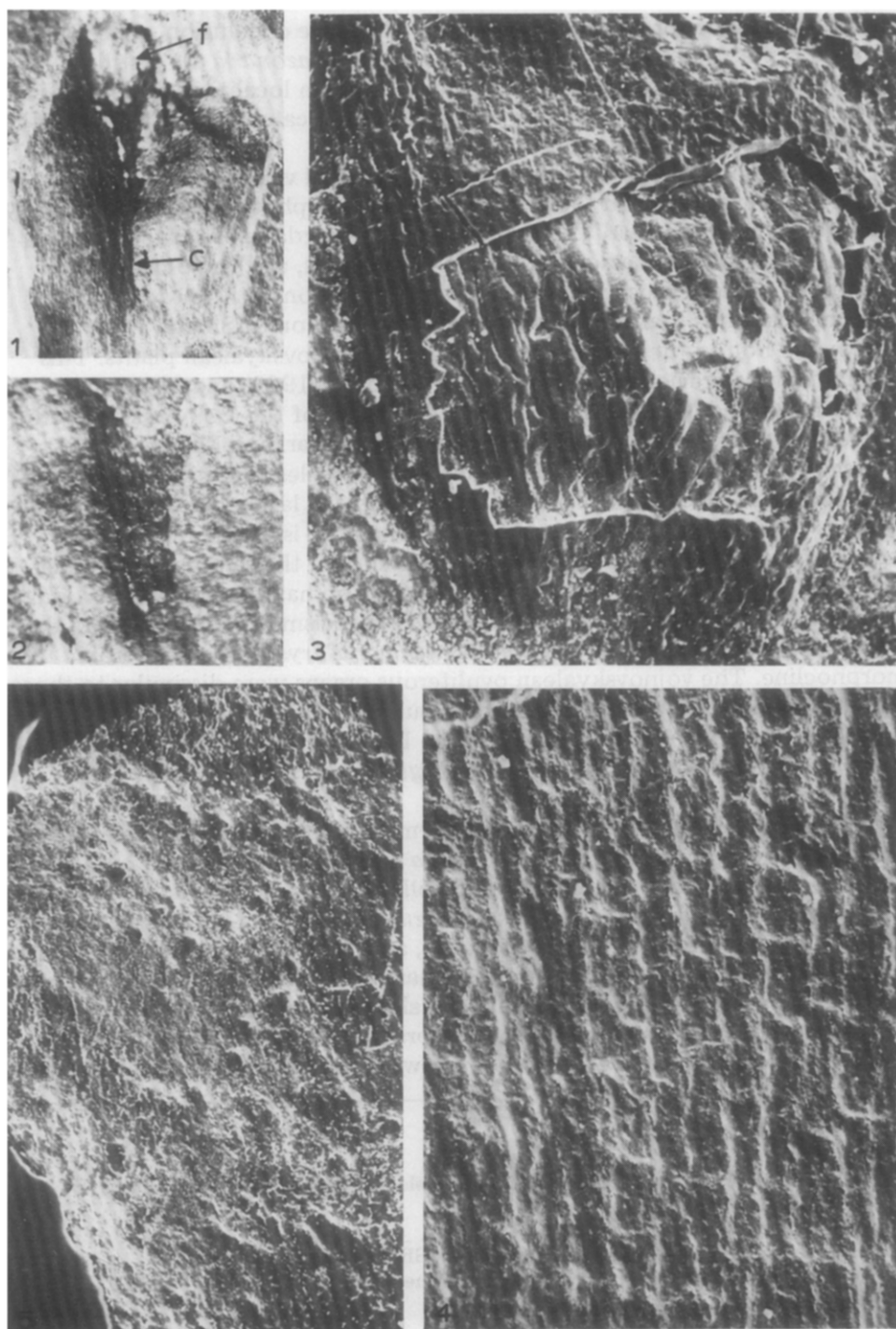


PLATE III (p. 234)

Gaussia sp. from the Lower Permian of the Russian Island (same as in Plate I).

1. Ray apex with distally exposed central canal and the funnel ($\times 12$).
2. Funnel filled with metamorphosed pollination liquid, surrounded by the pustulate hair bases ($\times 20$).
3. Ligular process (same as in Plate II, 2) showing bulging epidermal cells, SEM ($\times 120$).
4. Epidermal cells of the ray, SEM ($\times 400$).
5. Ray apex with the hair scars, SEM ($\times 100$).

Arrows as in Plate I.

PLATE IV (p. 235)

Gaussia sp. from the Lower Permian of the Russian Island (same specimen as in Plate I).

1. Ray apex with distorted ligular process, SEM ($\times 60$).
2. Ray surface showing a ridge zone of narrow cells flanked by broader intercostal cells, SEM ($\times 200$).
3. Imprints of the stomata showing sunken guard cells, SEM ($\times 400$).
4. Stoma surrounded by a thickened ring of subsidiary cells ($\times 400$).

sion and the ligulate unilateral stigma (Plate IV, 4). We are not suggesting the vojnovskyalean ancestry of *Typha*, but we believe that the Vojnovskyales might have contributed to the character pool of pro-angiosperms (cf. Krassilov, 1977).

Finally, we must stress again that our interpretation of *Gaussia* is based on imperfect material. Much is still to be learned about *Gaussia* and its allies.

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