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# Inflorescence with tricolpate pollen grains from the Cenomanian of Tschulymo-Yenisey Basin, West Siberia

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**Abstract**

A new taxon *Freyantha sibirica* gen. et sp. nov. is erected for a delicate racemose inflorescence from the Cenomanian of the Tchulymo-Yenisey Basin, West Siberia. The inflorescence bears male flowers of partly connate stamens that produced tricolpate reticulate pollen grains. The flowers are subtended by calyptrate bracts. The taxonomically significant features of the general inflorescence morphology, prophylls, floral bracts, stamens and pollen grains are shared with different angiosperm groups, such as the Menispermaceae and Sargentodoxaceae. Prominent glands on the floral bracts indicate pollination by nectar-sucking insects. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords*: angiosperms; inflorescence; pollen morphology; pollination; Cretaceous

## 1. Introduction

Inflorescences are relatively rare in the early angiosperm record. Though mostly preserved as impressions, they provide taxonomically significant characters that are not available in dispersed flowers or fruits (Dilcher and Kovach, 1986; Retallack and Dilcher, 1981; Krassilov, 1984; Krassilov et al., 1983). A new find in the Cenomanian of West Siberia contributes to the known morphological diversity of mid-Cretaceous angiosperms demonstrating a raceme of bracteate male flowers. Its lateral position on a stipulate axis suggests a compound inflorescence. The androecial and pollen grain morphologies combine features of different groups of modern angiosperms. In addition, this find has bearing on the pollination ecology of early angiosperms.

## 2. Material and methods

The material was collected in 1995 from an outcrop of the Kemskaya Formation on the right bank of the Kem River 16 km upstream of Podgornaya Village (about 1 km upstream of the locality that yielded a heterosporous plant described in Krassilov and Golovneva, 1999), Tchulymo-Yenisey Basin, West Siberia (Fig. 1). On the basis of stratigraphic correlation with marine deposits that are widespread in the northern part of the West Siberian Plains, the Kemskaya Formation is dated as of the Cenomanian age (Nagorski, 1939; Lebedev, 1958). The plant remains occur in the light-grey to white kaolinitic siltstones and clays. They are impressions or ferruginous incrustations that are partly covered with

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squashed compression films. The male inflorescence and detached flowers were found together with *Liriodendropsis*-type leaflets that might belong to the same plant.

The inflorescence described below is preserved on a hand-specimen of light-grey silty clay that contains also several detached flowers partly embedded in the rock matrix as if instantaneously buried by a mud flow. The stamens are conspicuous owing to the darker compressions of the filaments and the relief casts of the anthers. A few bracts subtending stamens are exposed on the rock surface. More commonly, the bracts are spreading, with the matrix penetrating between them and the stamens.

A few fragments of flowers were oxidized with nitric acid (for about an hour) and transferred to a varnish film by dissolving the matrix in hydrofluoric acid. A delicate compression film was mounted for SEM showing sporangia with pollen grains. Individual pollen grains were removed from the film and mounted for LM.

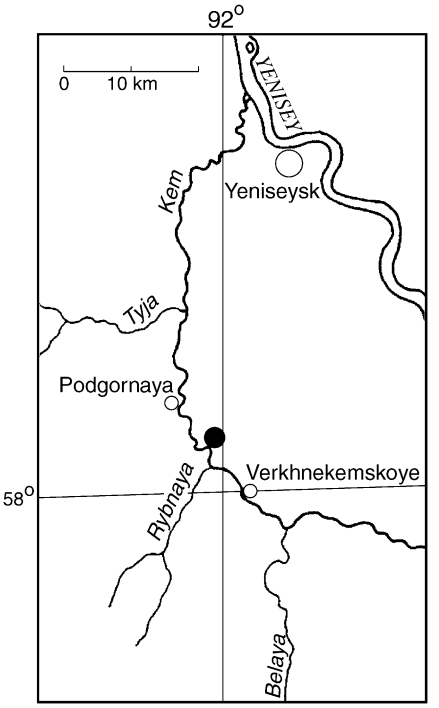



Fig. 1. Locality of *Freyantha sibirica* (black circle).

## 3. Systematics

Genus *Freyantha* Krassilov et Golovneva, gen. nov.
*Etymology:* From Freya, the northern goddess of fertility, and *anthos* (Gr.), flower.
*Type species: Freyantha sibirica* sp. nov.
*Species content:* Only type species.
*Diagnosis:* Inflorescence borne laterally on stipulate axis, racemose with a long slender peduncle bearing minute prophylls, distally with staminate flowers, arranged in two opposite rows. Flowers pedicellate, bracteate, and slightly zygomorphic. Bracts stalked, calyptral, with prominent dorsal glands. Stamens 5–6, differentiated into a short filament and bithecate anther with a slightly protruding connective. Posterior stamens spiral, free, anterior stamens — typically three — clustered, connate at base. Pollen grains tricolpate reticulate.

*Freyantha sibirica* Krassilov et Golovneva, sp. nov. (Plates I and II)
*Etymology:* From Siberia.
*Holotype:* No. 1198-7-42 (Plates I and II).
*Repository:* Botanical Institute, St. Petersburg, collection no. 1198.
*Type locality:* The Kem River 16 km upstream of Podgornaya Village, Tchulymo-Yenisey Basin, West Siberia; Kemskaya Formation.
*Age:* Cenomanian.
*Material examined:* Part and counterpart of inflorescence and four detached flowers on the same hand-specimen.
*Diagnosis:* As for the genus.
*Description:* The holotype shows a bracteate axis bearing laterally a single raceme spread in the bedding plane (Plate I, 1). The main axis is 9 mm long, 0.4 mm thick, straight, with a sheathing bract 5 mm long. A small thickening at the end of the axis suggests a second inflorescence node. The sheathing bract is lanceolate, apically curved around the axis, convex, with a smooth surface that does not show venation (Plate I, 2). The lateral raceme departs at a right angle 6 mm above the bract, bends down, then curves to bring the fertile part in erect position nearly parallel to the main axis. It is 20 mm long, with a peduncle 12 mm long, and a preserved fertile part 8 mm long. The peduncle is slender, 0.4 mm thick, longitudinally striate, apparently flexible and bearing two small

Fig. 2. *Freyantha sibirica*, schematic drawing of staminate flowers with subtending bracts showing glands, same as in Plate I, 4–6.

acroscopic appendages (prophylls): the basal one 2 mm long, the next one 1 mm long. These appendages are flat, decurrent, with the anterior margin minutely serrate.

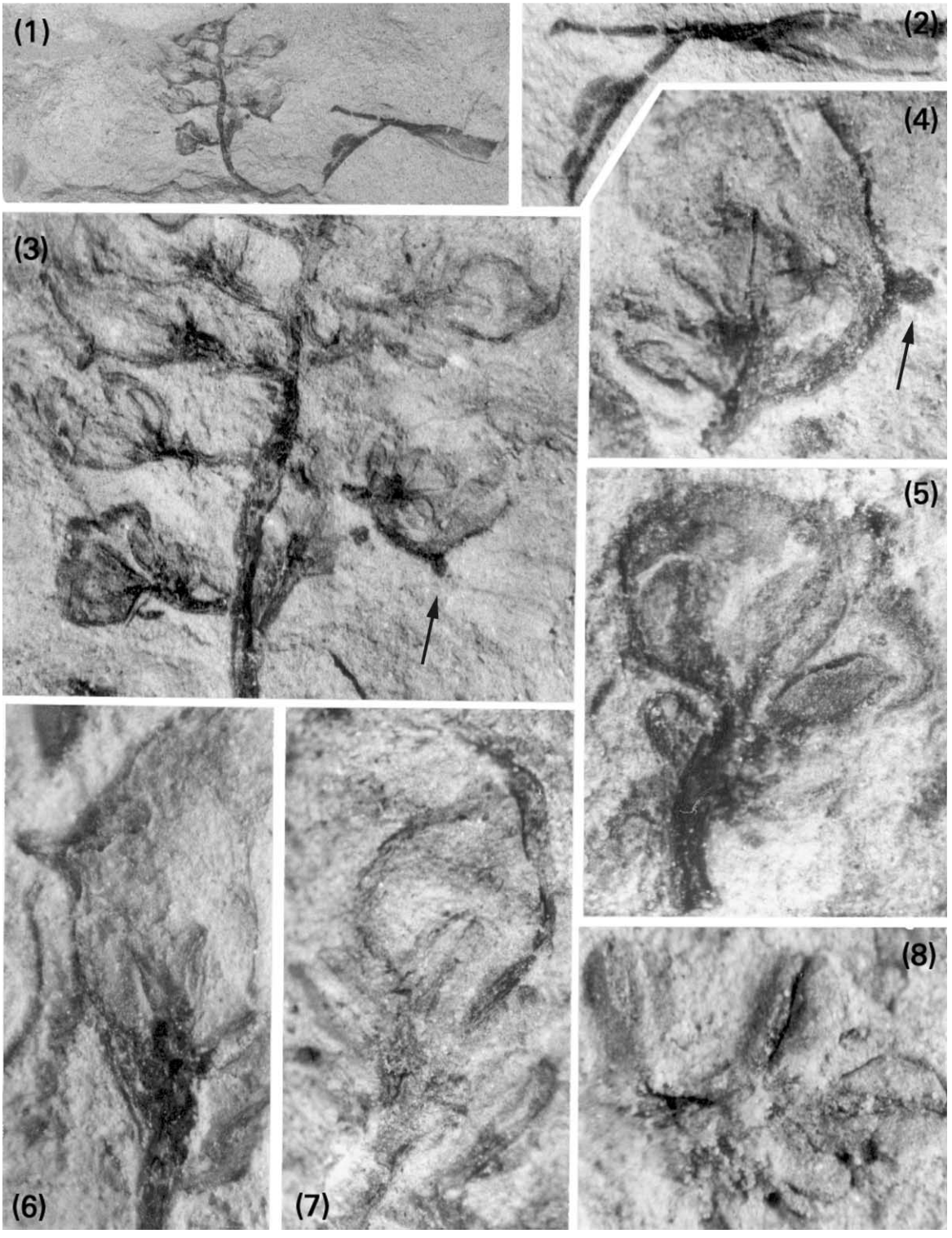
Distally the peduncle continues into the inflorescence axis without any appreciable change of thickness. The inflorescence consists of eight stalked flowers that are arranged in two opposite rows. We infer from twisting of the pedicels that the flowers were borne spirally, but this is difficult to ascertain in the impression material. The pedicels arise at intervals of about 1 mm, proximally at a right angle, distally obliquely to the axis (Plate I, 3). A basal flower on the abaxial side of the raceme is 3 mm long, the next four flowers are 4 mm long, the distal flowers are incompletely preserved. The pedicels are uniformly 1 mm long.

The laminar organs subtending the androecium are described here as bracts for they do not form a perianth with any regular arrangement of members relative to the stamens. They are flabellate with a stalk-like base, folded, with digitate striation and with a prominent dorsal gland (Fig. 2) at about the base of the laminar expansion. The flowers on the left side (Plate I, 5 and 6; Fig. 2) show a flabellate bract concave beneath the androecium. In an opposite flower (Plate I, 3) the bract is upcurved over the androecium, showing a stalk-like base attached almost at the level of a posterior stamen. A flower twisted obliquely to the bedding plane (Plate I, 7) shows tips of two bracts imbricate over the androecium.

The stamens are not in a regular whorl but arise spirally in a loose cluster. The anterior stamens are joined constantly in a group of three (Plate I, 3–5) and are perhaps connate at the base. The posterior stamens are more distant, often reflexed. Such an arrangement of the stamens makes the androecium slightly zygomorphic (Plate I, 8). The stamens consist of a short filament and a massive anther 7 mm long, with an apically produced connective (e.g. left stamen in Plate I, 4).

The cuticle of the connective is thick and rugulate, while that of the sporangia is delicate and fragile (Plate II, 1). The sporangial walls appear single-layered. The pollen grains are nearly spherical, slightly prolate, equatorial axis 16–18 μm, polar axis 17–19 μm, equatorial aspect elliptical to rounded-elliptical, polar aspect trilobate, with the

PLATE I



lobes broadly triangular (Plate II, 2 and 3). The colpi are slit-like, invaginate, long, nearly reaching to the poles, with smooth margins, gaping in the middle as if over an incipient porous mesoaperture (Plate II, 6 and 7) which, however, is not discernible in transmitted light (Plate II, 4). The colpus membrane is not preserved. The mesocolpia are slightly depressed in the middle, reticulate with irregular smooth patches (Plate II, 5). Muri of the reticulum are prominent, uniformly thick, and smooth. The lumina are elliptical, rounded-polygonal, irregularly curved, about 1 μm long in the middle of the mesocolpia, smaller towards the periphery, forming an irregular pattern, but indistinctly concentric over the mesocolpia (Plate II, 5).

## 4. Discussion

Staminate inflorescences are rare in the Cretaceous, except in the Platanaceae. Moreover, in *Freyantha* the flowers are devoid of perianth and are subtended by floral bracts. In conjunction with a distinctly spiral arrangement of posterior stamens, these features may suggest an archaic floral structure.

In the general habit of racemose, probably compound, inflorescence *Freyantha* is comparable with *Prisca* (Retallack and Dilcher, 1981) and *Hyrcantha* (Krassilov et al., 1983) in which the flowers are either carpellate or bisexual. *Freyantha* is more delicate, with a slender axis and supple peduncle. While pollen-feeding was widespread in the Mesozoic (Krassilov et al., 1997), in *Freyantha* the androecial flowers had conspicuous glands on the floral bracts suggesting pollination by nectar-sucking insects, a newly acquired feature of pollination ecology.

Among the mid-Cretaceous angiosperms, inflorescences of small staminate flowers most commonly occur in the platanoid complex. The stamen morphology with a short filament, relatively massive anther and protruding connective is typical of the latter group. So are the tricolp(or)ate reticulate pollen grains. However, in the Cretaceous platanoids, the inflorescences are capitate as in the living *Platanus*, while the flowers are tetra- to pentamerous, with perianth members variously developed, but usually shorter than stamens (Krassilov and Shilin, 1995).

In the Chloranthaceae, the inflorescences are compound spikes with the lateral spikelets bearing prophylls. However, the male flowers are typically reduced to a single scale-like stamen and the pollen morphology is different (Endress, 1987).

On the other hand, the racemose inflorescences of numerous small flowers with nectariferous tepals, androecia of six stamens and tricolpate pollen grains are typical of extant ranunculids (reviewed in Hutchinson, 1926; Cronquist, 1981; Goldberg, 1986). Among these, the conspicuous inflorescence prophylls are characteristic of the Menispermaceae (*Cissampelos*). This family provides also examples of zygomorphic flowers, two bracteate petals (*Antisoma*), variously connate stamens, anthers with produced connectives (*Chondrodendron*) and small tricolpate reticulate pollen, but the anthers are typically shorter relative to filaments (Imkhanitskaya, 1980; Thanikaimoni, 1986).

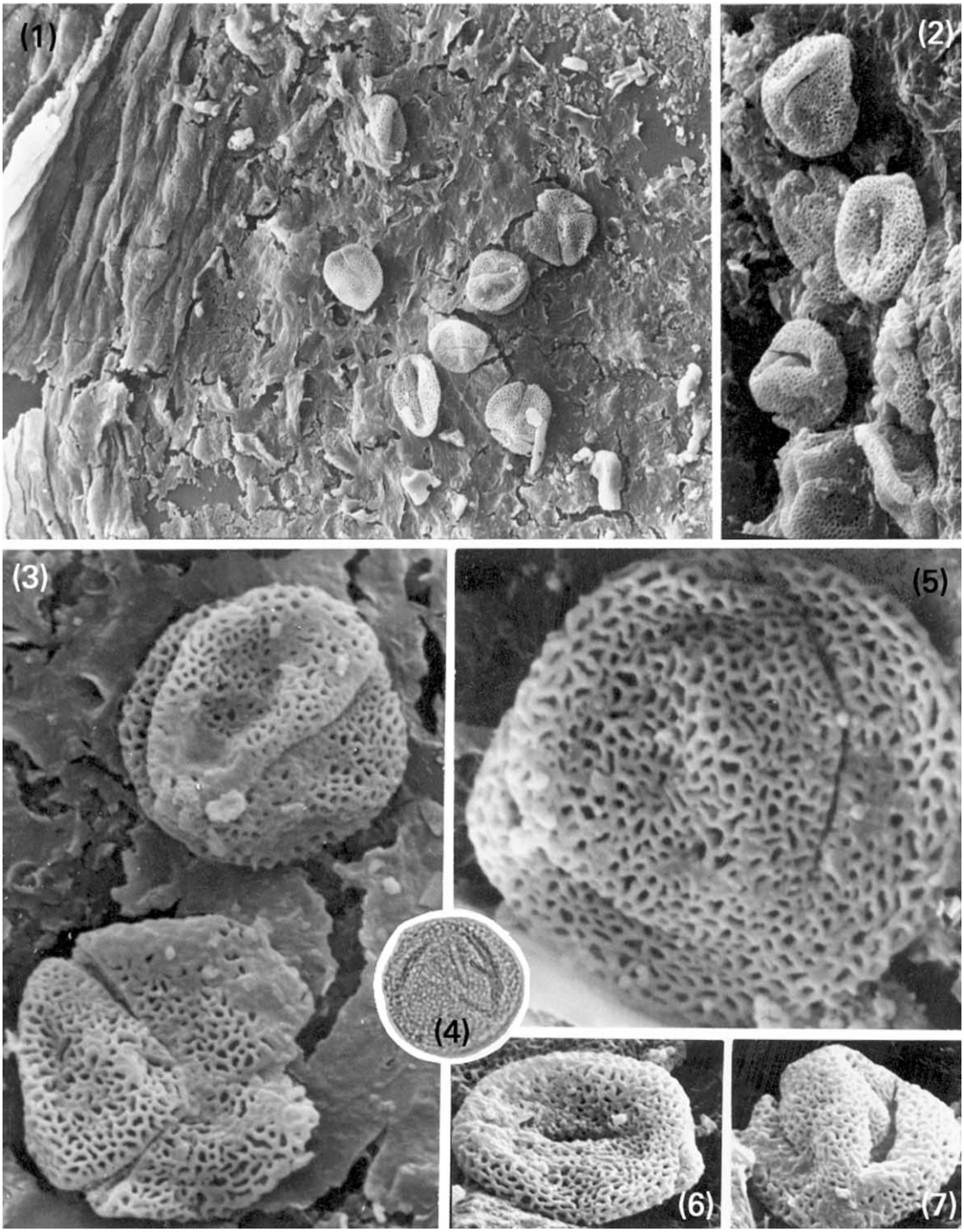
A similar stamen morphology can be found in the Lardizabalaceae (*Decaisnea*), Sargentodoxaceae (*Sargentodoxa*) and Berberidaceae (*Nandina*), while the latter family also provides examples of naked flowers (*Achlys*) and sepaloid bracts (Leinfellner, 1955; Sastri, 1969; Terabayashi, 1985). Large

PLATE I.

*Freyantha sibirica*, a male inflorescence from the Cenomanian of West Siberia, LM

1 Lateral raceme attached to a slender axis, 3×.
2 Axis and peduncle of the lateral raceme magnified to show bract and two prophylls, 7×.
3 Raceme with two rows of pedicellate flowers with glandular appendage (arrow), 10×.
4 Flower with a bract attached by a stalk-like base and showing a glandular appendage (arrow) at the level of laminar expansion; anterior stamens are joined in a group of three, 20×.
5 Flower with a bract beneath the anterior stamens apparently joined by their filaments; posterior stamens are reflexed, 24×.
6 Flower with a bract showing glandular appendage and a spiral arrangement of stamens, 20×.
7 Flower showing two bracts imbricate over the androecium, 20×.
8 Detached flower with a zygomorphic arrangement of stamens, 20×.

PLATE II



nectaries occur in a number of ranunculids, but they are prevalently perigonous or staminate (Werth, 1941).

Diagnostic palynological characteristics of ranunculids include a sculpturing of the colpus membrane that is not preserved in our material. However, the surface reticulum and colpi are as in the extant genera *Sargenthodoxa*, *Helleborus* and *Hydrastis* (Wodehouse, 1936; Kumasawa, 1936; Echlin, 1972; Nowicke and Skvarla, 1982; Savitsky, 1982) that are commonly considered as primitive members of the Ranunculaceae.

Thus, the mid-Cretaceous *Freyantha* shows characteristics that are scattered among various extant angiosperm families. However, most characteristics are shared with the Menispermaceae and Sargentodoxaceae. The latter family, first appearing in the Palaeogene (Tiffney, 1993), includes a single extant species of a climber with deciduous palmate leaves occurring today in China, Laos and Vietnam. The flowers are diclinal, in pendent axial racemose inflorescences. The flower parts are transitional spiral to cyclic, a supposedly primitive condition. The perianth consists of relatively large, petaloid sepals and the much smaller scaly petals that are transformed into nectaries. The androecium consists of six free stamens differentiated into a short filament and a relatively massive extrorse anther with a slightly protruding connective. The anthers dehisce longitudinally. The pollen grains are tricolporate reticulate with a network of small irregular lumina. In the closely related family Lardizabalaceae, the petals are likewise transformed into nectaries, the stamens are connate by their filaments, and the anthers often bear conspicuous connectives. *Freyantha* is not assignable to either of these families perhaps representing an extinct family of an ancestral complex.

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PLATE II

*Freyantha sibirica*, a male inflorescence from the Cenomanian of West Siberia

1 Cuticle of connective (left) and theca with pollen grains, SEM, 400×.

2 Group of in situ pollen grains, 1200×.

3 Pollen grains, equatorial and polar aspects, SEM, 2700×.

4, 5 Pollen grains, oblique equatorial view, with colpi converging to poles. The reticulum lumina radiate from a central depression of mesocolpium, LM, 1300× and SEM, 6000×.

6, 7 Pollen grains with gaping colpi in equatorial and tilted polar position, 2300×.

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