



Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Comparative pollen morphology and ultrastructure of modern and fossil gnetophytes

Maria V. Tekleva^{a,*}, Valentin A. Krassilov^{a,b}^a Paleontological Institute RAS, Profsojuznaya str., 123, Moscow, 117647, Russia^b Institute of Evolution, University of Haifa, Mt Carmel, Haifa 31905, Israel

ARTICLE INFO

Article history:

Received 18 December 2007

Received in revised form 8 December 2008

Accepted 11 December 2008

Available online xxxxx

Keywords:

Gnetales
gnetophytes
ultrastructure
pollen

ABSTRACT

A considerable disparity of pollen characters in the modern Gnetales (including the inaperturate and monosulcate germination types, the psilate, polyplicate and spinulose sculptural types) stands in sharp contrast with their ultrastructural uniformity. In all of the ultrastructurally studied living species of *Ephedra*, *Welwitschia* and *Gnetum*, the infratectum is granular, mostly consisting of small granules, while the endexine is uniformly thick and lamellate. The recently discovered fossil gnetophytes are a diverse group, recognized primarily on the basis of their ovulate cupules, but heterogeneous in respect to their pollen organs and pollen morphology. The pollen grains are mostly asaccate or, rarely, bisaccate (*Preflosella*, *Dinophyton*), with small ruguloid sacci (*Baisianthus*) or vestigial protosaccate structures (*Cryptosacciferites*). The germination types are inaperturate, cryptoporate, monosulcate and trisulcate. In the majority of forms the infratectum is granular, consisting of small granules, large granules, combinations of various granules, or even columella-like elements; rarely, the infratectum is alveolar. The endexine varies from distinctly lamellate to homogeneous. Our analysis of pollen grain morphology and ultrastructure of extant gnetophytes lends support to phylogenetic relatedness of extinct forms. Palaeobotanical data show a striking parallelism of morphological variations between gnetophytes and angiosperms.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Fossil gnetophytes are a morphologically heterogeneous group with supposed affinities to three living genera (*Ephedra*, *Gnetum* and *Welwitschia*) each representing a monotypic order or constituting a single order Gnetales. They first appeared in the Permian (Wang, 2004) and developed a considerable diversity of both vegetative and reproductive structures in the Triassic (Cornet, 1986, 1993; Krassilov and Ash, 1988; Anderson and Anderson, 2003). Their second peak of diversity coincided with the advent of early angiosperms (Krassilov, 1986; Crane and Upchurch, 1987; Krassilov and Bugdaeva, 1999, 2000; Rydin et al., 2003; Dilcher et al., 2005).

Fossil gnetophytes are recognized on the basis of their ovulate organs, that in both extant and extinct forms seem to represent the same basic structural type of a bracteolate cupule containing a solitary, occasionally two, erect ovules and supported by a bract, which is typically included in the disseminule ("fruit"). A distinguishing feature of gnetophytic cupules is that they are formed by fusion of sterile leafy organs, bracteoles or prophylls, whereas in the other groups of seed plants with cupulate ovules, such as pteridosperms, the cupules are of syntelomic origin or derived from fertile phyllomes, as in *Caytonia* and angiosperms (reviewed in Krassilov, 1997). Some gnetophytic cupules may resemble flowers, but the mode of polli-

nation was gymnospermous, with pollen penetrating the nucellar chamber (Krassilov, 1986).

The sporangiophores of extant gnetophytes are also distinctive: cupulate with synangiate sporangia. Such structures are found in some fossil gnetophytes, e.g., *Dinophyton* and *Baisianthus* (Krassilov and Ash, 1988; Krassilov and Bugdaeva, 2000), but in the others they are of a generalized gymnospermous type (e.g. the *Aegianthus–Loricanthus–Erdtmanitheca* group). Their affinities are inferred from association with gnetophytic ovulate structures (*Heerala*: Krassilov and Bugdaeva, 1988) or on the basis of their pollen grain morphology (Friis and Pedersen, 1996), which is highly diverse in the extant gnetophytes and even more so in the extinct forms. However the exact range of this diversity is unknown. One example is represented by the genus *Classopollis* Pflug. Indeed, this Mesozoic genus which is traditionally regarded as a conifer pollen belonging to the Cheirolepidiaceae (Stewart and Rothwell, 1993; Taylor and Taylor, 1993), is also considered a gnetophytic pollen, because of its granulate and/or columella-like ultrastructure and morphological complexity of the associated ovulate structure (Krassilov, 1982).

In this paper we attempt to outline the scope and diversity of gnetophytic pollen types (pollen of the recent gnetalean plants and the fossil plants that are related to this group on the basis of their reproductive morphology) and to assess the significance of pollen morphology and ultrastructure for demarcating this peculiar group of seed plants and elucidating their relations to the gymnosperms and angiosperms.

* Corresponding author. Fax: +7 495 3391266.

E-mail address: tekleva@mail.ru (M.V. Tekleva).

2. Material and methods

Pollen of the extant Gnetales was obtained from the palynological collection of the Department of Higher Plants, Moscow State University (*Welwitschia mirabilis* Hook. f., *Ephedra monosperma* J.G. Gmel. ex C.A. Mey., and *Gnetum indicum* Merr.) and from the herbaria of the Botanical Institute, St-Petersburg (*Gnetum africanum* Welw. and *G. funiculare* Wight) and of the Chang-Mai University, Thailand (*G. leptostachyum* Blume and *G. macrostachyum* Hook. f.).

The fossil pollen of extinct gnetophytes and related groups include:

1. In situ pollen grains from pollen organs *Dinophyton spinosum* Ash from the Late Triassic of the USA (Krassilov and Ash, 1988); *Hastystrobus muirii* van Konijnenburg-van Cittert from the mid-Jurassic of Yorkshire, England (Van Konijnenburg-Van Cittert, 1971; Tekleva et al., 2006); *Aegianthus sibiricus* Krassilov from the mid-Jurassic of Ust'-Balej, Eastern Siberia (Krassilov and Bugdaeva, 1988; Tekleva et al., 2006); *Baisianthus ramosus* Krassilov et Bugdaeva, *Loricanthus resinifer* Krassilov et Bugdaeva and *Preflosella nathania* Krassilov from the Early Cretaceous of Baisa, Transbaikalia (Krassilov and Bugdaeva, 1999, 2000; Tekleva and Krassilov, 2004); and *Bayerithea hughesii* Kvaček et Pačtová from the Late Cretaceous of Bohemia, Czech Republic (Kvaček and Pačtová, 2001; Tekleva et al., 2006).
2. Pollen grains extracted from the guts of fossil insects: *Classopollis* sp. from the Late Jurassic of Mikhajlovka, Karatau (Krassilov et al., 1997; Zavalova and Tekleva, 2005) and *Cryptosacciferites pabularis* Krassilov et Tekleva and *Alisporites alimentosus* Krassilov from the Early Cretaceous of Baisa, Transbaikalia (Krassilov and Rasnitsyn, 1982; Krassilov et al., 2003). For scanning electron microscopy (SEM), untreated mature pollen grains were mounted on SEM stubs (covered with nail varnish) and sputter-coated with platinum-palladium. Pollen was observed and photographed under a Camscan SEM and a Hitachi S-405 TEM. For transmission electron microscopy (TEM), individual pollen grains and fragments of sporangia were fixed with 1% OsO₄, dehydrated in an ethanol series, stained with uranyl acetate, dehydrated in acetone, and embedded in epoxy resin according to Meyer-Melikian et al. (2004) for the extant material and to Tel'nova and Meyer-Melikyan (2002) for the fossil material. Pollen grains were sectioned with an ultramicrotome LKB-3. The ultrathin sections were post-stained with lead citrate and examined under Jeol 100 B and Jeol 400 TEMs.

3. Morphology and ultrastructure of gnetophyte pollen grains

3.1. Extant Gnetales

Pollen morphology and/or ultrastructure were studied in *Ephedra americana* Endl. (Hesse, 1984; El-Ghazaly et al., 1998; Doores et al., 2007), *E. californica* S. Watson (Zavada, 1984), *E. campylopoda* C.A. Mey. (Hesse, 1984), *E. distachya* L. (Van Campo and Lugardon, 1973; Kurmann, 1992; Kurmann and Zavada, 1994; Meyer-Melikian, 1994; El-Ghazaly et al., 1998), *E. equisetina* Bunqe (Meyer-Melikian, 1994), *E. foliata* Boiss. ex C.A.Mey. (Rowley, 1995; El-Ghazaly and Rowley, 1997; El-Ghazaly et al., 1998), *E. fragilis* Desf. (El-Ghazaly et al., 1998), *E. intermedia* Schrenk et C.A.Mey. (Bernard and Meyer, 1972; Meyer-

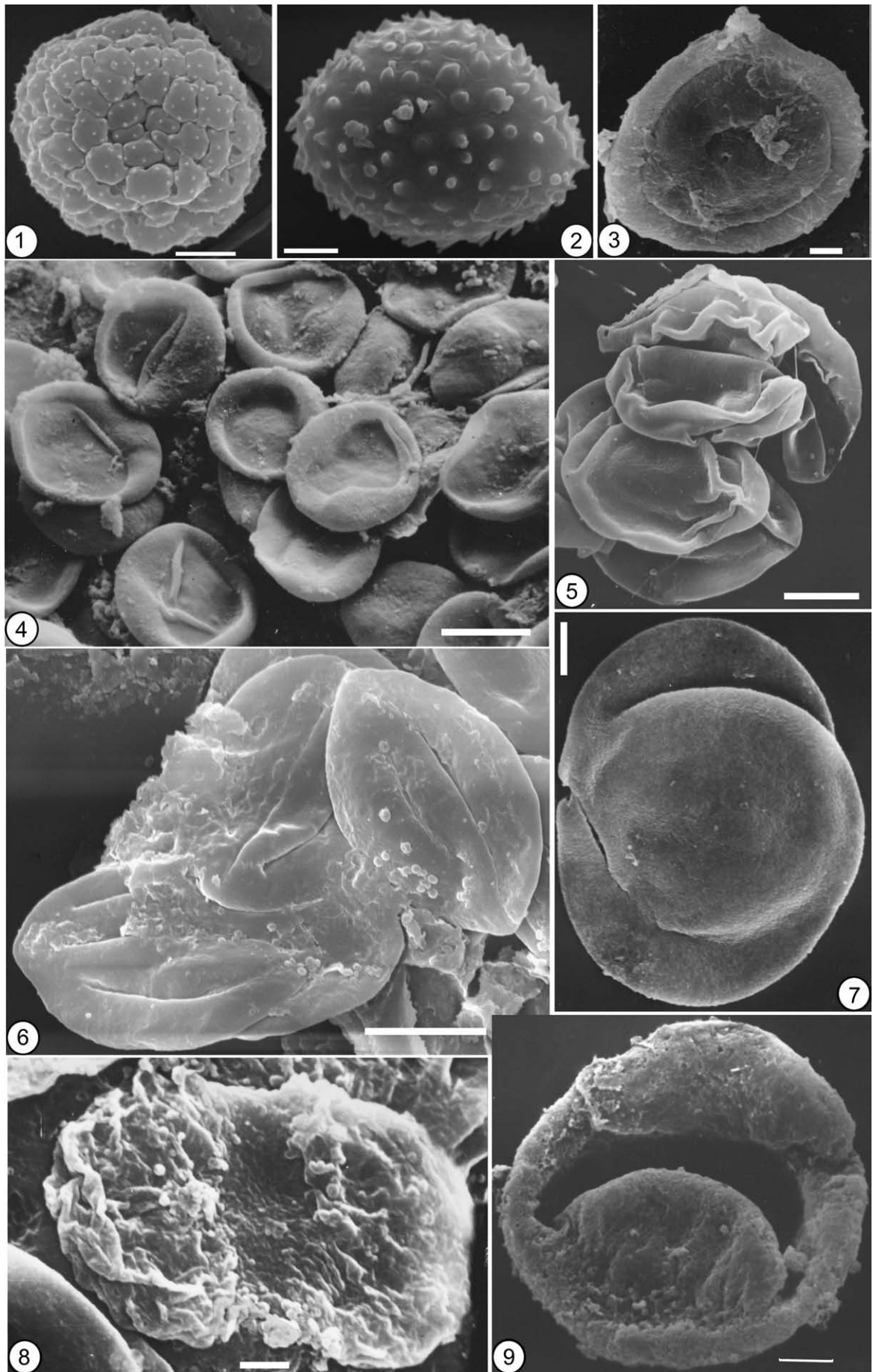
Melikian, 1994), *E. monosperma* (Afzelius, 1956; Gullvåg, 1966; Meyer-Melikian, 1994), *E. rupestris* Benth. (El-Ghazaly et al., 1998), *E. sinica* Stapf (Ueno, 1960), and *E. strobilacea* Bunqe (Meyer-Melikian, 1994); *Gnetum africanum* Welw. (Kuprianova, 1983; Orel et al., 1986), *G. cleistostachium* C.Y.Cheng (Yao et al., 2004), *G. gnemon* L. (Gullvåg, 1966; Hesse, 1980; Kurmann, 1992), *G. hainanense* C.Y.Cheng (Yao et al., 2004), *G. indicum* (Bernard and Meyer, 1972; Meyer-Melikian, 1994), *G. luofuense* C.Y. Cheng (Yao et al., 2004), *G. montanum* Markgr. (Gullvåg, 1966; Meyer-Melikian, 1994; Yao et al., 2004), *G. paniculatum* Spruce ex Benth. (Kuprianova, 1983), *G. parvifolium* (Warb.) Cheng (Yao et al., 2004), *G. pendulum* C.Y.Cheng (Yao et al., 2004), and *G. ula* Brongn. (Gullvåg, 1966), *G. sp.* (Zavada, 1984); and *Welwitschia mirabilis* (Ueno, 1960; Gullvåg, 1966; Bernard and Meyer, 1972; Hesse, 1984; Kedves, 1987; Zavada and Gabaraeva, 1991; Hesse et al., 2000; Rydin and Friis, 2005). Gnetalean pollen morphology was reviewed in Osborn (2000). For this analysis we studied the pollen morphology and ultrastructure in *Ephedra monosperma*, *Gnetum indicum*, *Gnetum africanum*, *G. funiculare*, *G. leptostachyum*, *G. macrostachyum*, and *Welwitschia mirabilis*.

The results of our study and the data from the literature show a considerable diversity of pollen morphology contrasting with a relative uniformity of the ultrastructure in the extant Gnetales.

- 1) The dimensions of the pollen grains vary from small (diameters 11–19.5 µm) in *Gnetum* and *Ephedra* to medium and large in *Ephedra* and *Welwitschia* (longer axis 30–80 µm).
- 2) The apertural types are monosulcate in *Welwitschia* and inaperturate in *Ephedra* and *Gnetum*. A leptoma was described by Kuprianova (1983) and Orel et al. (1986) in *G. africanum*, but we were unable to confirm its presence in our material.
- 3) The sculpture is spinose or spinulose in *Gnetum* and polyplicate in *Ephedra* and *Welwitschia*. Unlike angiosperms, the spinules are not supractectal, but formed both by the tectum and infratectum (Plate I, 1, 2).
- 4) The ultrastructural elements of the mature pollen grains are of the same type in all three genera. The uniformly thick tectum sharply decreases towards the furrows in *Welwitschia* and *Gnetum* (Plate II, 1, 3, 5). In *Ephedra*, the tectum is thin under the plicae and increases over the slopes (Plate II, 2). The infratectum is granular, showing variation in size and density of the granules. Bacular infratectum described by Orel et al. (1986) for *G. africanum* actually consists of large granules (Plate II, 1). By contrast, the granules are scarcely discernible in such species of *Gnetum* as *G. funiculare* and *G. montanum* (Gullvåg, 1966; Yao et al., 2004; our data). The foot layer is thin and adnate to the endexine in *Welwitschia* (Plate II, 5) and some *Ephedra* (Plate II, 2) and lacks in *Gnetum* (Plate II, 3) and some *Ephedra*. In the species of the three genera, the endexine is uniform throughout the pollen grain, of the same or lower electronic density than the ectexine, and lamellate. The apertural region of *Welwitschia* and the furrows of *Gnetum* and *Ephedra* are underlined by thin tectum and endexine or, rarely, by the endexine alone. In *Welwitschia*, the furrows are underlined by thin tectum, reduced granular layer, and endexine.
- 5) Despite the ultrastructural similarity in three genera there are several differences in the sporoderm development. The plicae and

Plate I. Pollen morphology of extant Gnetales and fossil gnetophytes. SEM.

1. *Gnetum africanum* Welw., extant Gnetales, from the herbarium of Botanical Institute, St.-Petersburg, Russia. Spinulose sculpture with "islands" separated by irregular gaps. Scale bar = 3 µm.
2. *Gnetum macrostachyum* Hook. f., extant Gnetales, from the herbarium of Chiang Mai University, Thailand. Spinose sculpture. Scale bar = 3 µm.
3. *Classopollis* sp. (Krassilov et al., 1997), Late Jurassic of Russia. Scabrate sculpture, rimula and pseudopore can be seen. Scale bar = 3 µm.
4. *Loricanthus resinifer* (Krassilov and Bugdaeva, 1999), Early Cretaceous of Russia. Psilate pollen with broad sulcus. Scale bar = 10 µm.
5. *Baisianthus ramosus* (Krassilov and Bugdaeva, 2000), Early Cretaceous of Russia. Psilate pollen with folded exine. Scale bar = 10 µm.
6. *Hastystrobus muirii* (Van Konijnenburg-Van Cittert, 1971), mid-Jurassic of England. Trisulcate psilate pollen. Scale bar = 10 µm.
7. *Alisporites alimentosus* (Krassilov and Rasnitsyn, 1982), Early Cretaceous of Russia. Bisaccate verrucate pollen. Scale bar = 10 µm.
8. *Dinophyton spinosum* (Krassilov and Ash, 1988), Late Triassic of the USA. Bisaccate scabrate or verrucate pollen. Scale bar = 10 µm.
9. *Preflosella nathania* (Krassilov and Bugdaeva, 1999), Early Cretaceous of Russia. Bisaccate finely foveolate pollen. Scale bar = 10 µm.



furrows are differentiated early during ontogenesis (Meyer, 1977; Zavada and Gabaraeva, 1991; Doores et al., 2007). In *Welwitschia*, the primexine is thinnest in the sulcus region, and the tectum is formed of fused granules (Zavada and Gabaraeva, 1991); whereas in *Ephedra*, the infratectal granules appear late in development, after the foot layer is formed (Doores et al., 2007). In *Ephedra americana*, incipient columellae are reported in early development, later they are only rarely discernible near the furrows (Doores et al., 2007). The exine is shed and scrolled in *Ephedra*, but persists as a cap in *Welwitschia* covering the male gametophyte (El-Ghazaly et al., 1998; Rydin and Friis, 2005).

3.2. Fossil gnetophytes and related groups

The study of fossil gnetophytes has allowed us to distinguish seven groups among their pollen (Table 1). These groups are differently related to the extant genera.

3.2.1. Group I. Plicate pollen grains (*Ephedripites* and *Equisetosporites*)

The group includes the dispersed pollen *Ephedripites* and *Equisetosporites*, pollen found in micropyles and nucellar chambers of *Eoantha* from the Neocomian–Aptian of Baisa, Transbaikalia (Krassilov, 1986), pollen associated with *Drewria* (Crane and Upchurch, 1987), *Vitimantha* (Krassilov and Bugdaeva, 1999), and *Archaeostrobilus cupulanthus* Cornet (Cornet, 1996), and pollen found in micropyles of the seeds *Ephedra portugallica* Rydin, Pedersen, Crane et Friis, *Ephedrispermum lusitanicum* Rydin, Pedersen, Crane et Friis from the Aptian–Albian of Portugal, and *Ephedra drewriensis* Rydin, Pedersen, Crane et Friis from the Aptian–Albian of USA (Rydin et al., 2006).

Dispersed pollen grains of this group are small to large, inaperturate or monosulcate, and polyplicate, psilate, scabrate, or foveolate-reticulate. The tectum is solid or perforated. The exine varies in thickness from 1.0 to 5.0 μm . The infratectum is columellate (with high or low columellae grading into large granules), or granular of small granules or with a gradation in the size of granules. The foot layer is thin and distinct, or indiscernible from the endexine, or, occasionally, lacking. The endexine is lamellate. The furrows are underlined by the endexine alone, or by the endexine and foot layer, or by the endexine, foot layer, and a vestigial tectum. Among the ultrastructurally studied pollen of the group, several subgroups are distinguished.

Subgroup 1 includes *Ephedripites* sp. (Trevisan, 1980) and *Equisetosporites* sp. (Osborn et al., 1993) and is characterized by relatively small psilate or scabrate pollen, with the tectum equal to or slightly thinner than the granular infratectum, and a thin or lacking foot layer.

Subgroup 2 includes *Equisetosporites chinleana* Daugherty (Zavada, 1984), with psilate imperforate pollen grains of medium size, the tectum thicker than the columellate infratectum, and an indiscernible from the endexine or lacking foot layer.

Equisetosporites chinleana (Pocock and Vasanthy, 1988) and *Cornetipollis reticulata* (Pocock and Vasanthy, 1988) belong to subgroup 3, which includes medium-sized or relatively large (*Cornetipollis*) pollen grains, with psilate imperforate exine (*Equisetosporites*) or foveolate-reticulate perforate taeniate exine (*Cornetipollis*). The exine is very thick (up to 5 μm); the tectum several times thicker than the columellate infratectum. The foot layer is well differentiated. A lamellate zone is present beneath the endexine.

Cornetipollis stands apart on account of its large size and peculiar sculpture. Pocock and Vasanthy (1988) and Cornet (1992) consider it as probable angiospermoid pollen.

Among these three subgroups, only the first one (*Ephedripites*) is comparable with the pollen of the extant Gnetales in the small sizes, psilate exine, granular infratectum and lamellate endexine that is uniformly developed over the pollen grain. The other two subgroups differ in the larger pollen grains, columellate infratectum, peculiar sculpture (*Cornetipollis*), and the presence of lamellate zones (subgroup 3).

The diverse taeniate grains of *Protohaploxypinus*, *Lunatisporites*, *Striatopodocarpidites*, *Striatites*, *Vittatina*, and *Weylandites* morphotypes might have been produced by conifers, glossopterids and/or peltasperms (Balme, 1995), although some of them resemble those of *Ephedripites* group. In particular, the asaccate *Weylandites* from the Permian of Russia, about 56 \times 70 μm , with a thick homogeneous tectum and granular infratectum (Zavialova, 1998) is the most similar to the gnetophytic pollen type.

3.2.2. Group II. Monosulcate pollen grains with broad sulcus, saccus-like projections, and homogeneous endexine (*Baisianthus*)

Pollen grains of this type, found in the cupulate synangia of the gnetophytic pollen organ *Baisianthus ramosus* from the Neocomian–Aptian of Baisa, Transbaikalia (Krassilov and Bugdaeva, 2000), are small, psilate, monosulcate, with the saccus-like projections, a broad sulcus and finely granular infratectum of granules that diminish toward the tectum and are partly fused with it. The endexine is less electron-dense than the ectexine, homogeneous, more or less uniformly thick, or with irregular thickenings (Plate I, 5; Plate II, 9).

Krassilov and Bugdaeva (2000) noted that pollen extracted from *Baisianthus* resemble *Retimonocolpites peroreticulatus* (Brenner) Doyle in having loosely adjoining ectexinal layers. However, these species differ since *Retimonocolpites peroreticulatus* has a columellate infratectum and lacks the endexine. Saccus-like projections, similar to those in *Baisianthus*, are described by Zavada and Dilcher (1988) in *Rugubivesiculites*, *Granamultivesiculites*, *Clavabivesiculites* and *Granabivesiculites*. Among them, the morphotype *Rugubivesiculites* has an alveolar infratectum and an endexine that is identical to the ectexine in terms of electron density. The infratectum of *Clavabivesiculites* is partly granular, as in *Baisianthus*; however, the granules are much larger and intermingled with rod-like infratectal elements, and the

Plate II. Ultrastructure of the pollen of extant Gnetales and fossil gnetophytes. TEM. Abbreviations: t=tectum; gr=infratectal granules; inf=infratectum; fl=foot layer; end=endexine; sp=saccus-like projections.

1. *Gnetum africanum* Welw., extant Gnetales, from the herbarium of Botanical Institute, St.-Petersburg, Russia. Plicae region. Scale bar=1 μm .
2. *Ephedra monosperma* J.G.Gmel. ex. C.A. Mey., extant Gnetales, from the palynological collection of the Department of Higher Plants, Moscow State University, Russia. Plicae region. Scale bar=0.67 μm .
3. *Gnetum macrostachyum* Hook. f., extant Gnetales, from the herbarium of Chiang Mai University, Thailand. Plicae region. Scale bar=0.5 μm .
4. *Classopollis* sp. (Krassilov et al., 1997), Late Jurassic of Russia. t1 and t2 – outer and inner parts of a "complex" tectum. Scale bar=1 μm .
5. *Welwitschia mirabilis* Hook. f., extant Gnetales, from the palynological collection of the Department of Higher Plants, Moscow State University, Russia. Plicae region. Scale bar=1 μm .
6. *Loricanthus resinifer* (Krassilov and Bugdaeva, 1999), Early Cretaceous of Russia. Nonaperture region. Scale bar=0.5 μm .
7. *Bayeritheca hughesii* (Kvaček and Pacltová, 2001), Late Cretaceous of Czech Republic. Scale bar=0.5 μm .
8. *Hastystrobilus muirii* (Van Konijnenburg-Van Cittert, 1971), mid-Jurassic of England. Sporoderm structure on the distal side. Scale bar=1 μm .
9. *Baisianthus ramosus* (Krassilov and Bugdaeva, 2000), Early Cretaceous of Russia. Arrow head indicates the aperture region. Scale bar=1 μm .
10. *Alisporites alimentosus* (Krassilov and Rasnitsyn, 1982), Early Cretaceous of Russia. Transition to the saccus region. Scale bar=1.5 μm .
11. *Cryptosacciferites pabularis* (Krassilov et al., 2003), Early Cretaceous of Russia. Equatorial region with protosaccate structure. Scale bar=1.5 μm .
12. *Dinophyton spinosum* (Krassilov and Ash, 1988), Late Triassic of the USA. Corpus part, arrow head indicates the gametophyte cavity. Scale bar=0.78 μm .
13. *Preflosella nathania* (Krassilov and Bugdaeva, 1999), Early Cretaceous of Russia. Corpus part, arrow heads point to the foot layer. Scale bar=3.66 μm .
14. *Hastystrobilus muirii* (Van Konijnenburg-Van Cittert, 1971), mid-Jurassic of England. Sporoderm structure on the proximal side. Scale bar=0.5 μm .

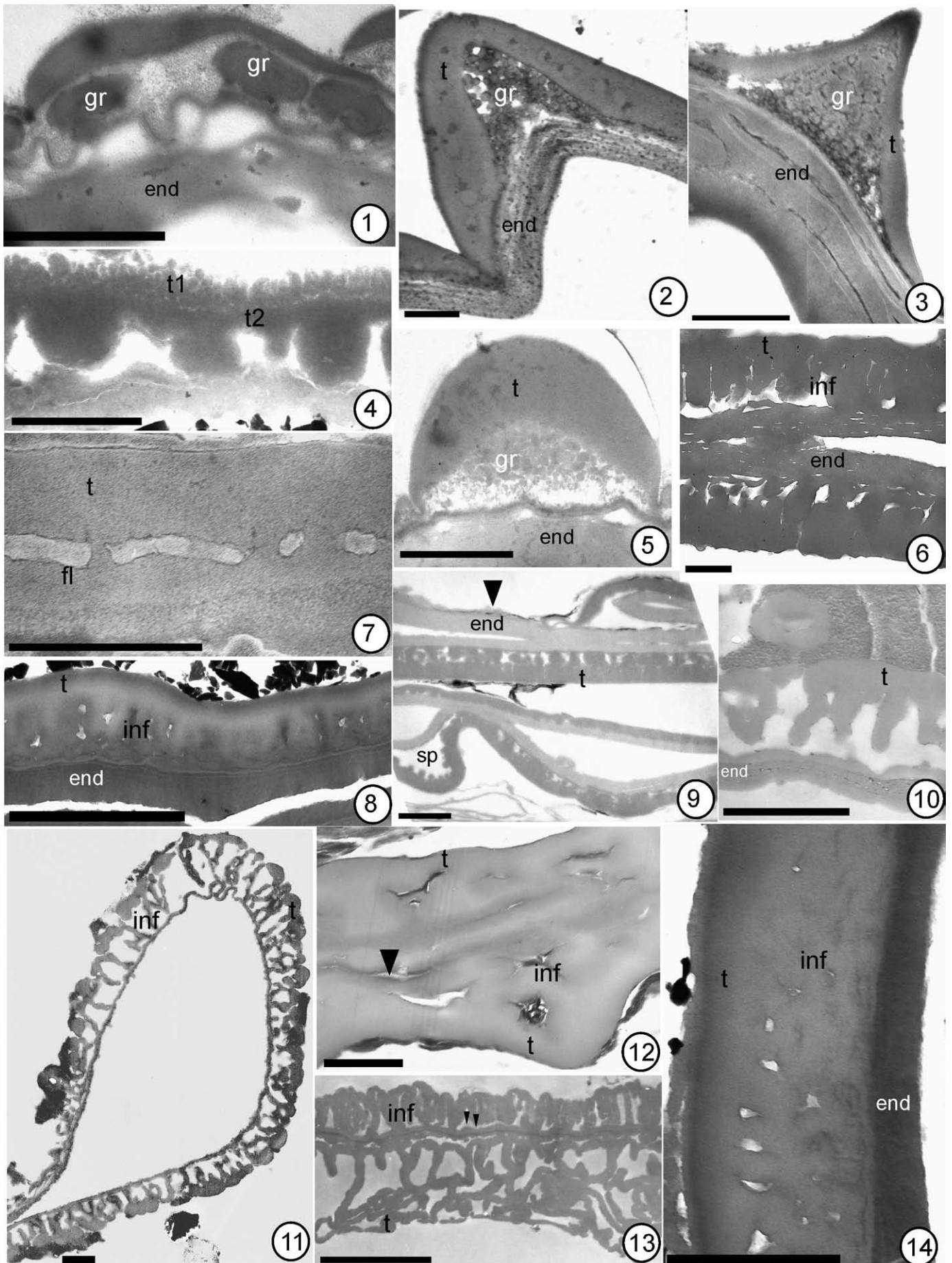


Table 1
VII groups of pollen grains assigned or related to extinct gnetophytes

Group	Size	Aperture type	Sculpture	Infratectum	Foot layer	Endexine (if present)
I. <i>Ephedripites</i> , <i>Equisetosporites</i>	Small to large	Inaperturate, monosulcate	Polyplicate psilate, scabrate or foveolate-reticulate	Columellate or finely granular	Thin and distinct, indiscernible or absent	Lamellate
II. <i>Baisianthus</i>	Small	Monosulcate, with saccus-like projections	Psilate	Finely granular	Thin and distinct	Homogeneous
III. <i>Loricanthus</i> , <i>Aegianthus</i> , <i>?Sahnia laxiphora</i>	Small or medium-sized	Monosulcate	Psilate, finely foveolate	Granular of large granules or columella-like elements	Thin and distinct	Lamellate
IV. <i>Classopollis</i>	Small	Rimulate, with proximal Y-mark, pseudopore	Psilate, granulate or spinulate, with a "complex" tectum	Granular of large granules or columella-like elements		Lamellate
V. <i>Eucommiidites</i>	Small to medium-sized	Trisulcate with asymmetrical furrows	Psilate or slightly scabrate	Granular or columella-like	Thin and distinct or weakly differentiated	Lamellate
VI. <i>Cryptosacciferites</i> , <i>Zolerella</i>	Large	Trisulcate with asymmetrical furrows	Psilate or slightly scabrate	Alveolar, with protosaccate structure in the equatorial region	Thin and distinct	Lamellate
VII. <i>Preflosella</i> , <i>Dinophyton</i> , <i>?Alisporites</i>	Large	Bisaccate, with a distal leptoma	Psilate, scabrate, foveolate-verrucate or verrucate	Alveolar	Thin and distinct	Lamellate

endexine is lacking or not preserved. *Granabivesiculites* is most similar to *Baisianthus* in having a thick tectum and granular infratectum, although the latter consists of fewer tiers of granules; the foot layer is much thicker, and the presence of endexine is questionable. In sum, *Baisianthus* shares its peculiar pollen morphology with a number of dispersed forms, some of which might have been related to gnetophytes.

3.2.3. Group III. Monosulcate pollen grains with infratectum of large granules and/or columella-like elements (*Loricanthus* and *Aegianthus*)

The in situ pollen grains extracted from gnetophytic pollen organs *Loricanthus resinifer* and *Aegianthus sibiricus* are monosulcate, small or medium-sized, and psilate or finely foveolate. The infratectum consists of large granules or columella-like elements; the foot layer is thin, but distinctive. The aperture regions are underlined by endexine sometimes contacting the foot layer (Plate I, 4; Plate II, 6).

This ultrastructural type is comparable with *Classopollis*, except for the tectum, which is much more complex in the latter pollen genus. Pollen of *Sahnia laxiphora* Drinnan et Chambers from the Early Cretaceous of Australia (Osborn et al., 1993) can be included in this group.

Granamultivesiculites (Zavada and Dilcher, 1988) from the Cenomanian of USA is similar in its relatively thick perforated tectum and infratectal ultrastructure, but differs in its numerous small saccus-like projections, a considerably thicker foot layer, and the absence of endexine.

3.2.4. Group IV. Rimulate pollen of *Classopollis*/Circumpolles type

The in situ and dispersed pollen grains of this type are small, spheroid, having an annular equatorial girdle, subequatorial groove or rimula, proximal Y-mark with exinal filaments, and a distal pore-like depression (pseudopore or cryptopore). They are dispersed in monads, dyads or tetrads. The exine surface is psilate, granulate or spinulate. The ectexine includes a "complex" tectum, in which the outer layer differs in electronic density from the inner layer and is probably of a tapetal origin. The infratectum consists of columella-like elements and/or large granules. The endexine is lamellate or not preserved/absent (Plate I, 3; Plate II, 4).

Classopollis and a number of dispersed morphotypes (*Eurollina*, *Paracorollina*, *Lobelina*, *Echinulina*, *Eocorollina*, *Corollina*, *Aporina*, *Classoidites*, *Gliscopollis*, *Circulina*, *Paracirculina*, *Praecirculina*, *Camerospores*, *Gemmulina*, *Granuloperculatipollis*, *Dicheiropollis*, *Rhaetipollis*, *Exesipollenites*, etc.) are members of the group Circumpolles (Médus, 1970; Pocock et al., 1990; Zavialova and Roghi, 2005). In spite of differences in the aperture types, *Circulina* and *Classoidites* (Pettitt and Chaloner, 1964; Médus, 1977) share with *Classopollis* a similar infratectal ultrastructure (Taylor and Alvin, 1984), while in

Duplicisporites granulatus (Leschik) Scheuring and *D. verrucosus* (Leschik) Scheuring the infratectum consists of densely packed small to medium-sized granules (Zavialova and Roghi, 2005).

A layer similar in structure and electronic density to the outer tectum of *Classopollis* was described in some *Eucommiidites* (Trevisan, 1980; Zavada, 1984). Such complexity of tectum is not matched by any other gymnosperms, being remotely similar to that of some modern Ranunculaceae (*Anemone*; Nowicke and Skvarla, 1979, 1982) and Asteraceae (Meyer-Melikian et al., 2004), in which the ectexine consists of two columellate layers, but, unlike *Classopollis*, these layers are better developed and of the same electronic density.

Most palaeobotanists assign *Classopollis*-producing plants to conifers. Our assignment of the pollen type to gnetophytes is based on the interpretation of the ovulate organs *Hirmeriella* given in Krassilov (1982), and its pollen morphology and ultrastructure which has no similarity to that of known conifers, being instead comparable to that of gnetophytes on the basis of the granulate and/or columella-like ultrastructure.

3.2.5. Group V. Triapertural pollen with asymmetrical furrows and granular infratectum (*Eucommiidites*)

In situ pollen grains of *Hastystrobus muirii*, *Eucommitheca hirsuta* Friis and Pedersen, *Bayeritheca hughesii* and *Erdtmanitheca texensis* Pedersen, Crane and Friis and dispersed *Eucommiidites* are characterized by three asymmetrical and irregularly developed sulci or furrows. However, their ultrastructures are highly heterogeneous (Tekleva et al., 2006). The pollen grains are small to medium-sized (long axis less than 40–45 µm, mostly under 36 µm), psilate or slightly scabrate, and with irregularly scattered foveolae and verrucae. Of three asymmetrical apertures, the central one is definitely sulcate, with rounded ends, and the two lateral ones are slit-like with pointed ends. The exine is thin (less than 1.7 µm, most below 1.3 µm). The infratectum is granular or columella-like; the endexine (if present) is lamellate. The foot layer is thin, distinct or weakly, if at all, differentiated (Plate I, 6; Plate II, 7, 8, 14).

Pollen grains found in the pollen chamber of *Erdtmanispermum balticum* Pedersen, Crane and Friis (Pedersen et al., 1989) differ by the exine that is nearly twice as thick as in other *Eucommiidites*, three nearly symmetrical apertures, foveolate sculpture, and a relatively thick tectum (atypical of *Eucommiidites*) and probably represents an independent morphological group.

3.2.6. Group VI. Large cryptosaccate triaperturate pollen with alveolar infratectum (*Cryptosacciferites* and *Zolerella*)

Pollen grains *Cryptosacciferites pabularis* from the gut content of a fossil xyelid insect, from the Neocomian–Aptian of Baisa, Transbaikalia (Krassilov et al., 2003), are large, psilate or slightly scabrate, with

irregularly scattered foveolae and verrucae, and three asymmetrical apertures, as in *Eucommiidites*. The angle between the central sulcus and each of two lateral furrows is less than 90°. The infratectum is alveolar, slightly thicker in the equatorial region, where it is inflated into a protosaccate structure. The endexine is less electronically dense than the ectexine, finely lamellate, and the aperture regions are underlined by the endexine and filamentous elements of the foot layer (Plate II, 11).

Another putative member of the group, *Zolerella tricolpata* Scheuring from the Triassic of Switzerland, has large (70–80 µm), psilate, spheroid pollen grains with three asymmetrical sulci (Scheuring, 1978). The sexine is up to 5 µm thick (measured in transmitted light), supposedly alveolar, and the central aperture is shorter than the lateral ones. *Zolerella* differs from *Cryptosacciferites* in its spheroid shape, much thicker sexine, and the apparently better developed protosaccate structure. A more detailed comparison requires ultrastructural study of *Zolerella*.

The group resembles *Eucommiidites* on account of three apertures, though differing in a larger size, residual protosaccate structure, and alveolar infratectum.

3.2.7. Group VII. Bisaccate pollen with alveolar infratectum (*Preflosella* and *Dinophyton*)

The pollen is of the *Alisporites*-type (Jansonius, 1971), large and bisaccate, with psilate, scabrate, foveolate-verrucate or verrucate exine, a distal leptoma, alveolar infratectum, and a thin foot layer; the endexine is finely lamellate (*Alisporites*), absent, or not preserved (*Preflosella* and *Dinophyton*). The aperture region is underlined by a foot layer and endexine (if present) (Plate I, 7, 8, 9; Plate II, 10, 12, 13).

In general morphology, these pollen grains are comparable to a number of saccate morphotypes, such as those found in situ in *Permotheca* (Krassilov et al., 1999), *Pteruchus* (Townrow, 1962, 1965; Taylor et al., 1984; Osborn and Taylor, 1993; Xuanli et al., 1995; Axsmith et al., 2000), and *Caytonanthus* (Harris, 1941; Krassilov, 1977; Zavada and Crepet, 1985; Pedersen and Friis, 1986), yet differing in their ultrastructural organization.

The ultrastructure of the pollen grains from Triassic conifers assigned to the genus *Alisporites*, such as *A. circulicarpus* Clarke (Taylor and Grauvogel-Stamm, 1995), also differs from that of the pollen studied by us. Indeed, they have a thinner tectum and an alveolae pattern while those assigned to *Alisporites* in the present study have an endexine and a foot layer clearly differentiated and a distinctly lamellate endexine.

We consider *Alisporites* as a morphotaxon possibly including pollen grains of various natural affinities but discussed here owing to the findings of this type of pollen grains in the pollen organs of *Dinophyton* and *Preflosella* assigned to gnetophytes on the basis of their macromorphology.

4. Evolutionary trends in gnetophyte pollen morphology

The Mesozoic Gnetophytes differ from conventional gymnosperms in the elaboration of exine structures that approaches the angiosperm level of structural complexity ornamentation, additional apertures, and ultrastructural differentiation. The pollen grains are mostly asaccate, rarely bisaccate (*Preflosella* and *Dinophyton*), with small ruguloid sacci (*Baisianthus*), or with vestigial protosaccate structures (*Cryptosacciferites*). They are inaperturate, cryptoporate, monosulcate or trisulcate. The sculpture is psilate, scabrate, weakly (or, occasionally, distinctly) verrucate or foveolate (e.g., *Ephedripites*, *Aegianthus*, *Hastystrobis*, *Bayeritheca*, *Sanmiguelia*, *Praecolpites* and *Sahnia*). The tectum is variably perforate in *Eucommiidites*, some species with rather large perforations (Batten and Dutta, 1997). Usually, the infratectum is granular, composed of small to large granules or their combinations, as well as of columella-like elements, rarely alveolar. The endexine varies from distinctly lamellate to homogeneous.

The modern representatives of the group – Gnetales – are characterized by lower diversity in pollen. The pollen grains are monosulcate or inaperturate, the sculpture is spinose/spinulose or polyplacate. The infratectum is granular, the endexine is uniform in thickness and lamellate.

The trisulcate pollen of *Eucommiidites* and *Cryptosaccites*–*Zolerella* group represents an aperture type unique for seed plants, with no close analogies among dicotyledons, but resembling such monocotyledons as *Tinantia anomala* C.B. Clarke, *Tradescantia pendula* (Schnizl.) D.R. Hunt (Harley, 2004) and some Cyripedioideae (Burns-Balogh and Hesse, 1988).

Among gymnosperms, *Gnetum* and *Sciadopitys* (Taxodiaceae) are unique in having spinulose sculpture (Yamazaki and Takeoka, 1962; Kuprianova, 1983). Among angiosperms, *Peperomia* (Piperaceae) and *Ceratostigma abyssinicum* Aschers. (Plumbaginaceae) show a striking similarity to *Gnetum* in sculpture. *Peperomia* is also characterized by the inaperturate pollen and granular infratectum (Walker, 1976; Kuprianova, 1983), while *Ceratostigma* differs considerably from *Gnetum* in the aperture type (tricolpate) and columellate infratectum (Nowicke and Skvarla, 1979).

The plicate pollen of the *Ephedra*, *Welwitschia* and *Ephedripites* group resemble some members of the angiosperm orders Arales (Araceae: *Spathiphyllum*, *Holochlamys*, *Amorphophallus*, *Pseudodracontium*, *Arisarum*, *Ambrosina*, *Stuednera*, *Protarum* and *Pistia*), Laurales (*Hortonia* and *Dahlgrenodendron*), and Zingiberales (*Zingiber* sect. *Cryptanthium*) (Hesse et al., 2000; Tarasevich, 2002). Plicae surface of the species is psilate, slightly ornamenting, or foveolate; pollen grains are ranging from 21 to 80 µm; the infratectum is columellate or granulate; the endexine is spongy, thin, thick or absent. Hesse et al. (2000) showed that these species resemble polyplacate pollen of Gnetales superficially and only a few of them are resistant to destruction. The degree of the superficial similarity differs. Polyplacate pollen grains of some representatives (e.g., *Spathiphyllum*) are nearly identical to those of *Ephedra* and *Welwitschia*; *Spathiphyllum* pollen is highly resistant to acetolysis, though differs considerably from the Gnetales in having a columellate infratectum, thin non-lamellate endexine, discontinuous ectexinal plicae and some other features. Tarasevich (2002) reported on monosulcate (*S. patini* N.E.Br. and *S. commutatum* Schott) and polycolpate (*S. blandum* Schott) aperture types within *Spathiphyllum*. Pollen grains of *Pistia* and *Amorphophallus* are also similar to *Ephedra* and *Welwitschia*, but their plicae are destroyed completely after chemical treatment. Other polyplacate species (*Hortonia*, *Dahlgrenodendron*, *Zingiber* sect. *Cryptanthium* and *Holochlamys*) differ from the Gnetales in pollen morphology. Thus, inaperturate polyplacate condition in different taxa shows only a superficial similarity, concealing more important characters which distinguish species: infratectal type, chemical resistance of the plicae, and endexine structure.

Asaccate pollen prevails in both gnetophytes and angiosperms. Yet extinct gnetophytes *Dinophyton spinosum* and *Preflosella nathania* had saccate pollen grains of *Alisporites*-type. Such forms as *Cryptosacciferites pabularis* and *Zolerella tricolpata* show a tendency for reduction of sacci. *Baisianthus ramosus* with saccus-like projections, expressed both in morphology and ultrastructure, differs from other saccate forms by its granular infratectum. A parallel tendency is exhibited by the angiosperm *Lactoris fernandeziana* Phil. (Lactoridaceae) with vestigial sacci (Zavada and Taylor, 1986) or folds on both sides of the aperture (Walker, 1976; Sampson, 1995, 2000). The infratectum is composed of rounded or irregular granules and columella-like elements that are rooted in the foot layer in the equatorial region, but are pendant in the region of sacci or folds (Zavada and Taylor, 1986). Zavada (1984) has described several palynomorphs from the Late Triassic of the USA, Jurassic of England, and Cenomanian of North America with rudimentary sacci and a granular infratectum that can be compared with *Baisianthus ramosus* on the one hand and *Lactoris fernandeziana* on the other.

Such designations as columella-like or pseudocolumellate refer to irregular disposition of rod-like elements that are pendant, occasionally touching the foot layer, or their association with granules, as in *Loricanthus*, *Aegianthus*, some *Eucommiidites*, *Classopollis*, *Crinopollis* and *Polycolpopollis* (Vasanthi et al., 2004). The structures occur also in such angiosperm pollen as *Tricolporopollenites miniverrucatus* Roche from the Early Eocene of Hungary (Kedves and Párdutz, 1973) and can be precursory to a regular columellate infratectal structure typical of angiosperms. A transformation of a one-tiered alveolar infrastructure into pseudocolumellate is also a possibility worth considering with accumulation of data on the gnetophytic pollen ultrastructure.

5. Conclusions

Seven morphotypes of pollen grains are assigned or related to extinct gnetophytes on the basis of their in situ or nucellar chamber occurrences in sporangiate or ovulate organs of gnetophytic morphology or on account of their intrinsic morphological complexity. Several groups of supposedly gnetophytic pollen are distinguished representing distinctive lines of morphological differentiation in respect of their external features and ultrastructure.

At this preliminary stage of morphological analysis, the ultrastructure appears more uniform than external morphology and of a primary importance for recognition of extinct gnetophytes. Yet no clear-cut demarcation can be drawn between gnetophytic pollen morphologies and those of gymnosperms and angiosperms. Multiple origins are suspected for a number of traits in pollen morphology. The analysis highlights parallel tendencies in morphological evolution of gnetophytes and angiosperms, such as the saccate to asaccate, mono- to polyaperturate, granular to columellate, and possibly also alveolar to columellate, transformations.

Acknowledgments

We are grateful to the reviewers for their valuable comments on the manuscript. The study was supported by the Russian Foundation for Basic Research, projects numbers 06-04-49577 and 06-04-48534. V.A. Krassilov is supported by the German Israeli Science Foundation project number 1-888-159.8/2005.

References

Afzelius, B.M., 1956. Electron-microscope investigations into exine stratification. *Grana Palynol.* 1 (2), 22–37.

Anderson, J.M., Anderson, H.M., 2003. Heyday of the gymnosperms: systematic and diversity of the Late Triassic Molteno Formation, South Africa. *Strelitzia*. 15. National Botanical Institute, Pretoria.

Axsmith, B.J., Taylor, E.L., Taylor, T.N., Cuneo, N.R., 2000. New perspectives on the Mesozoic seed fern order *Crostospermales* based on attached organs from the Triassic of Antarctica. *Am. J. Bot.* 87, 757–768.

Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Rev. Palaeobot. Palynol.* 87 (2–4), 81–323.

Batten, D.J., Dutta, R.J., 1997. Ultrastructure of exine of gymnospermous pollen grains from Jurassic and basal Cretaceous deposits in Northwest Europe and implications for botanical relationships. *Rev. Palaeobot. Palynol.* 99, 25–54.

Bernard, V.V., Meyer, N.R., 1972. Pyl'tsevie zerna *Ephedra*, *Welwitschia* i *Gnetum*. *Vestnik Moskovskogo universiteta. Serija 6. Biologija, povovedenie* 27, 86–88.

Burns-Balogh, P., Hesse, M., 1988. Pollen morphology of the cyripedioid orchids. *Plant Syst. Evol.* 158, 165–182.

Cornet, B., 1986. The reproductive structures and leaf venation of a Late Triassic angiosperm, *Sanmiguelia lewisii*. *Evol. Theory* 7, 231–309.

Cornet, B., 1992. Why do paleobotanists believe in a Cretaceous origin of angiosperms? PhD. <http://bcornet.tripod.com/Cornet92/why.htm>.

Cornet, B., 1993. Dicot-like leaf and flowers from the Late Triassic tropical Newark Supergroup rift zone, USA. *Mod. Geol.* 3, 81–99.

Cornet, B., 1996. A New Gnetophyte from the Late Carnian (Late Triassic) of Texas and its bearing on the origin of the angiosperm carpel and stamen. In: Taylor, D.W., Hickey, L.J. (Eds.), *Flowering Plant Origin, Evolution and Phylogeny*. Chapman and Hall, pp. 32–67. Chapter 3.

Crane, P.R., Upchurch Jr., R., 1987. *Drewria potomacensis* gen. et sp. nov., an early Cretaceous member of Gnetales from the Potomac Group of Virginia. *Am. J. Bot.* 74, 1722–1736.

Dilcher, D.L., Bernerdes-de-Oliveira, M.E., Pons, D., Lott, T.A., 2005. *Welwitschiaceae* from the Lower Cretaceous of Northeastern Brazil. *Am. J. Bot.* 92, 1294–1310.

Doores, A.S., Osborn, J.M., El-Ghazaly, G., 2007. Pollen ontogeny in *Ephedra americana* (Gnetales). *Int. J. Plant Sci.* 168 (7), 985–998.

El-Ghazaly, G., Rowley, J.R., 1997. Pollen wall of *Ephedra foliata*. *Palynology* 21, 7–18.

El-Ghazaly, G., Rowley, J.R., Hesse, M., 1998. Polarity, aperture condition and germination in pollen grains of *Ephedra* (Gnetales). *Plant Syst. Evol.* 213, 217–231.

Friis, E.M., Pedersen, K.R., 1996. Angiosperm pollen in situ in Cretaceous reproductive organs. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: principles and applications*, vol. 1. American Association of Stratigraphic Palynologists Foundation, pp. 409–426.

Gullvåg, B., 1966. The fine structure of some gymnosperm pollen walls. *Grana Palynol.* 6, 435–475.

Harley, M.M., 2004. Triaperturate pollen in the monocotyledons: configurations and conjectures. *Plant Syst. Evol.* 247, 75–122.

Harris, T.M., 1941. *Caytonanthus*, the microsporophyll of Caytonia. *Ann. Bot.* 5, 47–58.

Hesse, M., 1980. Pollenkitt is lacking in *Gnetum gnemon* (Gnetales). *Plant Syst. Evol.* 136, 41–46.

Hesse, M., 1984. Pollenkitt is lacking in Gnetales: *Ephedra* and *Welwitschia*; further proof for its restriction to the angiosperms. *Plant Syst. Evol.* 144, 9–16.

Hesse, M., Weber, M., Halbritter, H., 2000. A comparative study of the polyaperturate pollen types in Arales, Laurales, Zingiberales and Gnetales. In: Harley, M.M., Morton, C.M., Blackmore, S. (Eds.), *Pollen and spores: morphology and biology*. Royal Botanic Gardens, Kew, pp. 227–239.

Jansonius, J., 1971. Emended diagnosis of *Alisporites* Daugherty 1941. *Pollen Spores* 13, 349–357.

Kedves, M., 1987. LM and EM studies on pollen grains of recent *Welwitschia mirabilis* Hook. and *Ephedra* species. *Acta Bot. Hung.* 33, 81–103.

Kedves, M., Párdutz, B., 1973. Ultrastructure investigations of angiospermatophyte pollens from the Lower Eocene. *Acta Bot. Acad. Sci. Hung.* 18 (1–2), 135–154.

Krassilov, V.A., 1977. Contributions to the knowledge of the Caytoniales. *Rev. Palaeobot. Palynol.* 24, 155–178.

Krassilov, V.A., 1982. On the ovuliferous organ of *Hirmerella*. *Phyta. Pant Commemorative Volume*, pp. 141–144.

Krassilov, V.A., 1986. New floral structure from the Lower Cretaceous of Lake Baikal area. *Rev. Palaeobot. Palynol.* 47, 9–16.

Krassilov, V.A., 1997. Angiosperm origins: morphological and ecological aspects. *Pensoft, Sofia*.

Krassilov, V.A., Ash, S.R., 1988. On *Dinophyton* – protognetalean mesozoic plant. *Palaeontogr., Abt. B* 33–38 (Bd. 208, Lfg. 1–3).

Krassilov, V.A., Bugdaeva, E.V., 1988. Gnetales plants from the Jurassic of Ust-Balej, east Siberia. *Rev. Palaeobot. Palynol.* 53, 359–374.

Krassilov, V.A., Bugdaeva, E.V., 1999. An angiosperm cradle community and new proangiosperm taxa. *Acta Palaeobot., Suppl.* 2, 111–127.

Krassilov, V.A., Bugdaeva, E.V., 2000. Gnetophyte assemblage from the Early Cretaceous of Transbaikalia. *Palaeontogr., Abt. B* 139–151 Bd. 253, Lfg. 4–6.

Krassilov, V.A., Rasnitsyn, A.P., 1982. A unique finding: pollen in the intestine of Early Cretaceous sawflies. *Paleontol. Zhurn.* 4, 83–96 (in Russian, translated into English in *Paleontol. J.* 16 (4), 80–94).

Krassilov, V.A., Zherikhin, V.V., Rasnitsyn, A.P., 1997. *Classopollis* in the guts of Jurassic insects. *Paleontology* 40 (4), 1095–1101.

Krassilov, V.A., Afonin, S.A., Naugolnykh, S.V., 1999. *Permothea* with in situ pollen grains from the Lower Permian of the Urals. *Palaeobotanist* 48 (1), 19–25.

Krassilov, V., Tekleva, M., Meyer-Melikyan, N., Rasnitsyn, A., 2003. New pollen morphotype from gut compression of Cretaceous insect, its bearing on palynomorphological evolution and palaeoecology. *Cretac. Res.* 24, 149–156.

Kuprianova, L.A., 1983. *Struktura pyl'cy gnetuma – shodstvo ili rodstvo?* *Priroda* 12, 70–71 (in Russian).

Kurmann, M.H., 1992. Exine stratification in extant gymnosperms: a review of published transmission electron micrographs. *Kew Bull.* 47, 25–39.

Kurmann, M.H., Zavadá, M.S., 1994. Pollen morphological diversity in extant and fossil gymnosperms. In: Kurmann, M.H., Doyle, J.A. (Eds.), *Ultrastructure of fossil spores and pollen*. Royal Botanic Gardens, Kew, pp. 123–137.

Kvaček, J., Pacltová, B., 2001. *Bayeritheca hughesii* gen. et sp. nov., a new *Eucommiidites*-bearing pollen organ from the Cenomanian of Bohemia. *Cretac. Res.* 22, 695–704.

Médus, J., 1970. Contribution a la classification des grains de pollen du groupe des *Circumpolles* (Pflug) Klaus. *Pollen Spores* 12, 205–216.

Médus, J., 1977. The ultrastructure of some *Circumpolles*. *Grana* 16, 23–28.

Meyer, N.R., 1977. Svravnitel'nomorfologicheskie issledovanija razvitiia i ul'trastrukturny sporodermy golosemnykh i primitivnykh pokrytosemnykh. Avtoref. na soiskanie uch. st. d.b.n. Leningrad. (in Russian).

Meyer-Melikian, N.R., 1994. Pyl'cevye zjorna gnetovykh. *Palinologija v stratigrafii*. Nauka, Moskva, pp. 30–33 (in Russian).

Meyer-Melikian, N.R., Bovina, I.Y., Kosenko, Y.V., Polevova, S.V., Severova, E.E., Tekleva, M.V., Tokarev, P.I., 2004. Atlas morfologii astrovykh (Asteraceae). *Palinomorfologija i razvitie sporodermy predstavitelej semejstva Asteraceae*. KMK, Moskva (in Russian).

Nowicke, J.W., Skvarla, J.J., 1979. Pollen morphology: The potential influence in high order systematics. *Ann. Mo. Bot. Gard.* 66, 633–700.

Nowicke, J.W., Skvarla, J.J., 1982. Pollen morphology and the relationships of *Circaea*, of *Kingdonia*, and of *Sergentodoxa* to the Ranunculales. *Am. J. Bot.* 69, 990–998.

Orel, L.I., Kuprianova, L.A., Golubeva, E.A., 1986. Ul'trastrukturna acetolizirovannykh obolechek tapetal'nykh kletok i pyl'cevykh zjoren u *Gnetum africanum* (Gnetales). *Botanicheskij zhurnal* 71, 750–754 (in Russian).

Osborn, J.M., 2000. Pollen morphology and ultrastructure of gymnospermous anthophytes. In: Harley, M.M., Morton, C.M., Blackmore, S. (Eds.), *Pollen and Spores: morphology and biology*. Royal Botanic Gardens, Kew, pp. 163–185.

- Osborn, J.M., Taylor, T.N., 1993. Pollen morphology and ultrastructure of the Crystospermales: permineralised in situ pollen from the Triassic of Antarctica. *Rev. Palaeobot. Palynol.* 79, 205–219.
- Osborn, J.M., Taylor, T.N., de Lima, M.R., 1993. The ultrastructure of fossil ephedroid pollen with gnetalean affinities from the Lower Cretaceous of Brazil. *Rev. Palaeobot. Palynol.* 77, 171–184.
- Pedersen, K.R., Friis, E.M., 1986. *Caytonanthus* pollen from the Lower and Middle Jurassic. In: Muller, J.T. (Ed.), 25 Years of Geology in Aarhus. *Geoskrifter*, vol. 24, pp. 255–267.
- Pedersen, K.R., Crane, P.R., Friis, E.M., 1989. Pollen organs and seeds with *Eucommioides* pollen. *Grana* 28, 279–294.
- Pettitt, J.M., Chaloner, W.G., 1964. The ultrastructure of the Mesozoic pollen *Classopollis*. *Pollen Spores* 6, 611–620.
- Pocock, S.A.J., Vasanthy, G., 1988. *Cornetipollis reticulata*, a new pollen with angiosperm features from upper Triassic (Carnian) sediments of Arizona (USA), with notes on *Equisetosporites*. *Rev. Palaeobot. Palynol.* 55, 337–356.
- Pocock, S.A.J., Vasanthy, G., Venkatachala, B.S., 1990. Pollen of *Circumpollis* – an enigma or morphotrends showing evolutionary adaptation. *Rev. Palaeobot. Palynol.* 63, 179–193.
- Rowley, J.R., 1995. Are the endexine of pteridophytes, gymnosperms and angiosperms structurally equivalent? *Rev. Palaeobot. Palynol.* 85, 13–34.
- Rydin, C., Friis, E.M., 2005. Pollen germination in *Welwitschia mirabilis* Hook. f.: comparing differences between the polylicate pollen producing genera of the Gnetales. *Grana* 44, 137–141.
- Rydin, C., Mohr, B., Friis, E.M., 2003. *Cratonia cotyledon* gen. et sp. nov.: a unique Cretaceous seedling related to *Welwitschia*. *Biol. Lett.* 270, 29–32.
- Rydin, C., Pedersen, K.R., Crane, P.R., Friis, E.M., 2006. Former diversity of *Ephedra* (Gnetales): evidence from Early Cretaceous seeds from Portugal and North America. *Ann. Bot.* 98, 123–140.
- Sampson, F.B., 1995. Pollen morphology of Lactoridaceae: a re-examination. *Grana* 34, 100–107.
- Sampson, F.B., 2000. Pollen diversity in some modern magnoliids. *Int. J. Plant Sci.* 161 (Suppl. 6), 193–210.
- Scheuring, B.W., 1978. Mikrofloren aus den Meridekalken des Mts. San Giorgio (Kanton Terrsin). *Schweiz. Paläontol. Abh.* 88, 1–119.
- Stewart, W.N., Rothwell, G.W., 1993. *Paleobotany and the evolution of plants*, 2nd edition. Cambridge University Press, Cambridge.
- Tarasevich, V.F., 2002. Morfologija i ul'trastruktura pyl'cy triby Spathiphyllae v svjazi s ee položeniem v semejstve Araceae. *Materialy X Vserossijskoj palinologičeskoj konferencii*. IGIRGI, Moscow, Russia, pp. 246–248 (in Russian).
- Taylor, T.N., Alvin, K.L., 1984. Ultrastructure and development of Mesozoic pollen: *Classopollis*. *Am. J. Bot.* 71, 575–587.
- Taylor, T.N., Grauvogel-Stamm, L., 1995. The ultrastructure of voltzialean pollen. *Rev. Palaeobot. Palynol.* 84, 281–303.
- Taylor, T.N., Taylor, E.L., 1993. *The biology and evolution of fossil plants*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Taylor, T.N., Cichan, M.A., Baldoni, A.M., 1984. The ultrastructure of Mesozoic pollen: *Pteruchus dubius* (Thomas) Townrow. *Rev. Palaeobot. Palynol.* 41, 319–327.
- Tekleva, M.V., Krassilov, V.A., 2004. Sporoderm Ultrastructure in Early Cretaceous Proangiosperms. *Paleontological Zhurnal* 38 (1), 97–102.
- Tekleva, M.V., Krassilov, V.A., Kvaček, J., van Konijnenburg-van Cittert, J.H.A., 2006. *Eucommioides*: ultrastructure and affinities. *Acta Palaeobot.* 46 (2), 137–155.
- Tel'nova, O.P., Meyer-Melikian, N.R., 2002. Spory v reproduktivnyh organah devonskih rastenij. Nauka, St-Petersburg.
- Townrow, J.A., 1962. On some desiccated pollen grains of Permian to Middle Jurassic age. *Grana Palynol.* 3 (2), 13–44.
- Townrow, J.A., 1965. A new member of Crystospermaceae Thomas. *Ann. Bot. (Gr. Brit.)* 29 (115), 495–511.
- Trevisan, L., 1980. Ultrastructural notes and considerations on *Ephedripites*, *Eucommioides* and *Monosulcites* pollen grains from Lower Cretaceous sediments of southern Tuscany (Italy). *Pollen Spores* 22, 85–132.
- Ueno, J., 1960. On the fine structure of the cell walls of some gymnosperm pollen. *Biol. J. Nara Women's Univ.* 10, 19–25.
- Van Campo, M., Lugardon, B., 1973. Structure grenue infratectale de l'ectexine des pollens de quelques gymnospermes et angiospermes. *Pollen Spores* 15, 171–187.
- Van Konijnenburg-van Cittert, J.H.A., 1971. In situ gymnosperm pollen from the Middle Jurassic of Yorkshire. *Acta Bot. Neerl.* 20 (1), 1–96.
- Vasanthy, G., Cornet, B., Pocock, S.A.J., 2004. Evolution of proangiosperms during Late Triassic: pre-Cretaceous pollen trends towards mono- and dicotyledonous taxa diversification. *Geophytology* 33 (1–2), 99–113.
- Walker, J.W., 1976. Comparative pollen morphology and phylogeny of the Ranalean Complex. In: Beck, C.B. (Ed.), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York, pp. 241–299.
- Wang, Z.-Q., 2004. A new Permian gnetalean cone as fossil evidence for supporting current molecular phylogeny. *Ann. Bot.* 94 (2), 181–188.
- Xuanli, Y., Taylor, T.N., Taylor, E.L., 1995. The crystosperm pollen organ *Pteruchus* from the Triassic of Antarctica. *Am. J. Bot.* 82 (4), 535–546.
- Yamazaki, T., Takeoka, M., 1962. Electron-microscope investigations of the fine details of the pollen grain surface in Japanese gymnosperms. *Grana Palynol.* 3 (2), 3–12.
- Yao, Y.F., Xi, Y.Z., Geng, B.Y., Li, C.S., 2004. The exine ultrastructure of pollen grains in *Gnetum* (Gnetaceae) from China and its bearing on the relationship with the ANITA Group. *Bot. J. Linn. Soc.* 146, 415–425.
- Zavada, M.S., 1984. Angiosperm origins and evolution based on dispersed fossil pollen ultrastructure. *Ann. Mo. Bot. Gard.* 71, 444–463.
- Zavada, M.S., Crepet, W.L., 1985. Pollen grain wall structure of *Caytonanthus arberi* (Caytoniales). *Plant Syst. Evol.* 153, 259–264.
- Zavada, M.S., Dilcher, D.L., 1988. Pollen wall ultrastructure of selected dispersed monosulcate pollen from the Cenomanian, Dakota Formation, of central USA. *Am. J. Bot.* 75, 669–679.
- Zavada, M.S., Gabaraeva, N.I., 1991. Comparative pollen wall development of *Welwitschia mirabilis* and selected primitive angiosperms. *Bull. Torrey Bot. Club* 118, 292–302.
- Zavada, M.S., Taylor, T.N., 1986. Pollen morphology of Lactoridaceae. *Plant Syst. Evol.* 154, 31–39.
- Zavialova, N.Z., 1998. Morfologija i ul'trastruktura iskopaemyh pyl'cevnyh zeren (iz verhnepernskih otlozhenij verhovij reki Vjatka i nizhnepernskih otlozhenij Zapadnoj Sibiri). *Avtoref. diss... kand. biol. nauk (in Russian)*.
- Zavialova, N.E., Roghi, G., 2005. Exine morphology and ultrastructure of *Duplicisporites* from the Triassic of Italy. *Grana* 44, 337–342.
- Zavialova, N.Z., Tekleva, M.V., 2005. Ul'trastruktura jekziny pyl'cevnyh zeren roda *Classopollis*, izvlečennyh iz zheludkov nasekomyh jurskogo vozrasta. *Materialy XI Vserossijskoj palinologičeskoj konferencii «Palinologija: teorija i praktika»*. APEC, Moskva, Russia, pp. 86–87 (in Russian).