

Factors of Palynomorphological Evolution

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Abstract—Sporophytic and pollen characters show only weak correlation over their evolutionary history. There are examples of parallel palynomorphological evolution associated with divergent evolution of sporophytes. In other cases, conservative pollen morphologies lag behind of the rapidly evolving sporophytes or, on the contrary, pollen evolution overtakes slowly evolving sporophytes. The coincidence of major evolutionary stages of whole plant morphology and palynomorphology resulted from global ecosystem events that simultaneously affected plant vegetative functions, reproduction strategy and pollination ecology. The most typical palynomorphological reactions to such events were a substitution of functions in multifunctional structures or paedomorphic innovations. Recurrence of pollen morphologies is a consequence of recurrent ecosystem states. Climatic and other environmental effects were indirect, mediated by structural changes in plant communities involving dominance, population densities and other variables. They triggered cyclic palynomorphological changes from simple to complex structures and *vice versa*.

INTRODUCTION

Spores and pollen grains have great potential for evolutionary morphology. These one- to four-celled haploid structures are genetically controlled by the sporophytes that produce them, while they are functionally controlled by their dispersal environments and, in seed plants, by their receptive female structures. A few palynomorphological studies deal with geological history, structural and ecological aspects, and their respective roles in defining the aperture types, sporoderm structures and surface features. Kupriyanova (1969) recognized three major evolutionary stages in apertural morphology: the Paleozoic of proximal (catasulcate), the Mesozoic of distal (anasulcate) and the Cenozoic of pericolar (por)ate apertures (this scheme focuses on the prevalent types, for each of them occasionally occurs outside their stage; thus catasulcate apertures, rather than defining "prepollen" of primitive seed plants, occur in all stages, including angiosperms).

The transition from one apertural type to another remained largely unexplained, though several attempts were made to relate the appearance of equatorial apertures to either structural changes in tetrad configuration (Wodehouse, 1935) or functional changes in dispersal environments or growth on special receptive structures (Hughes, 1976, 1994) or else to syphonic pollen tubes as different from the haustorial ones in sulcate forms. Notably, the tetrad configurations are more diverse in angiosperms than in gymnosperms which correlates with a higher diversity of apertural types. However, a causal link of tetrad types with periaperturate types is unlikely in the case of monocots that retained polar apertures despite variability of their tetrad configurations.

Pollen–stigma interactions are generally regarded as a crucial factor in determining pollen morphology of angiosperms the earliest dispersed pollen grains of which are recognized by their semitectate reticulate surface and the prevailingly columellate infrastucture—both involved in the self-incompatibility syndrome (Zavada, 1984). Recognition substances are stored in the infratectum, while periaperturate morphology provides for growth regardless of position on the stigma. These interesting considerations require verification using representative material. As yet they are not fully convincing because the typically gymnospermous alveolar infrastucture is adequate for storing recognition substances, while a correlation of stigmas with periaperturate types is inconsistent, and lacking in the case of early angiosperms with monocolpate pollen grains. In the alternative type of early angiosperms with tricolpate pollen grains the grain size was fairly small rendering their position on the much larger stigmatic trichomes irrelevant for the pollen grain selection. A harmomegathy function of symmetrically disposed apertures might be a more plausible explanation of their advantage in certain dispersal environments.

In contrast to the aperture types, certain surface structures are obviously adaptive, as in entomophilous pollen grains. Sculptural type has already been related to dispersal environment in spore plants. Nikitin (1934) noticed a disproportionate development of various outgrowths in certain Devonian spores, which he interpreted as anchoring structures. He argued that, while the area suitable for early pteridophytic plant life might have been narrow, anchoring, rather than vagility, might have been crucial for their propagules. Though this explanation seems more applicable to the pre-Devonian plants (with spores that were less conspicuously ornate) it is still noteworthy as an early attempt to

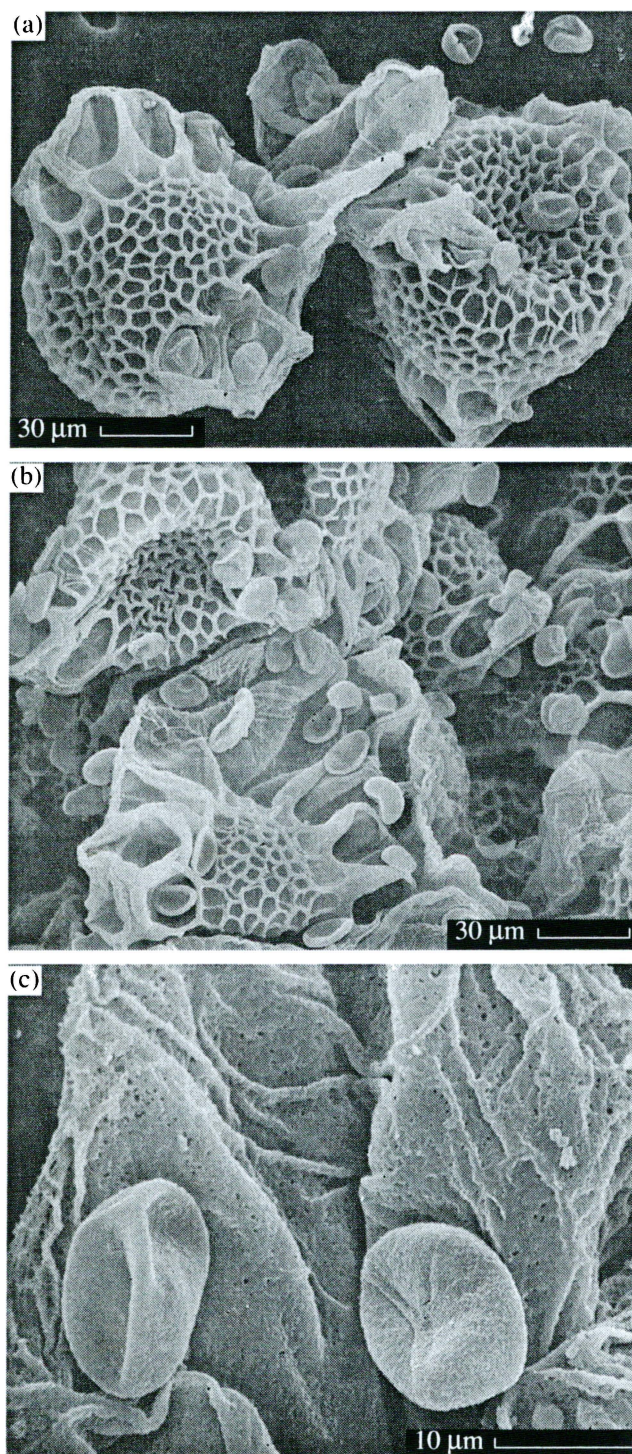


Fig. 1. Recurrent amphispores of *Heroleandra profusa* Krassilov et Golovneva from the Late Cretaceous of Western Siberia (Krassilov and Golovneva, 1999, 2000): *in situ* megaspores bearing microspores in laesural appendages, SEM.

that their producers were probably peltasperm-derived proangiosperms rather than conifers.

The counterexamples of pollen morphology changing rapidly relative to conservative sporophyte structures can be found in the geological history of pel-

tasperms and their descendant cycadophytes. Thus the end-Permian and Triassic *Lepidopteris* falls in the variability range of the Permian *Tatarina*. Both had the *Peltaspermum*-type seed-scales, whereas their sporangial clusters (*Permotheca* and *Antevsia* respectively) were closely similar. However there was a marked change

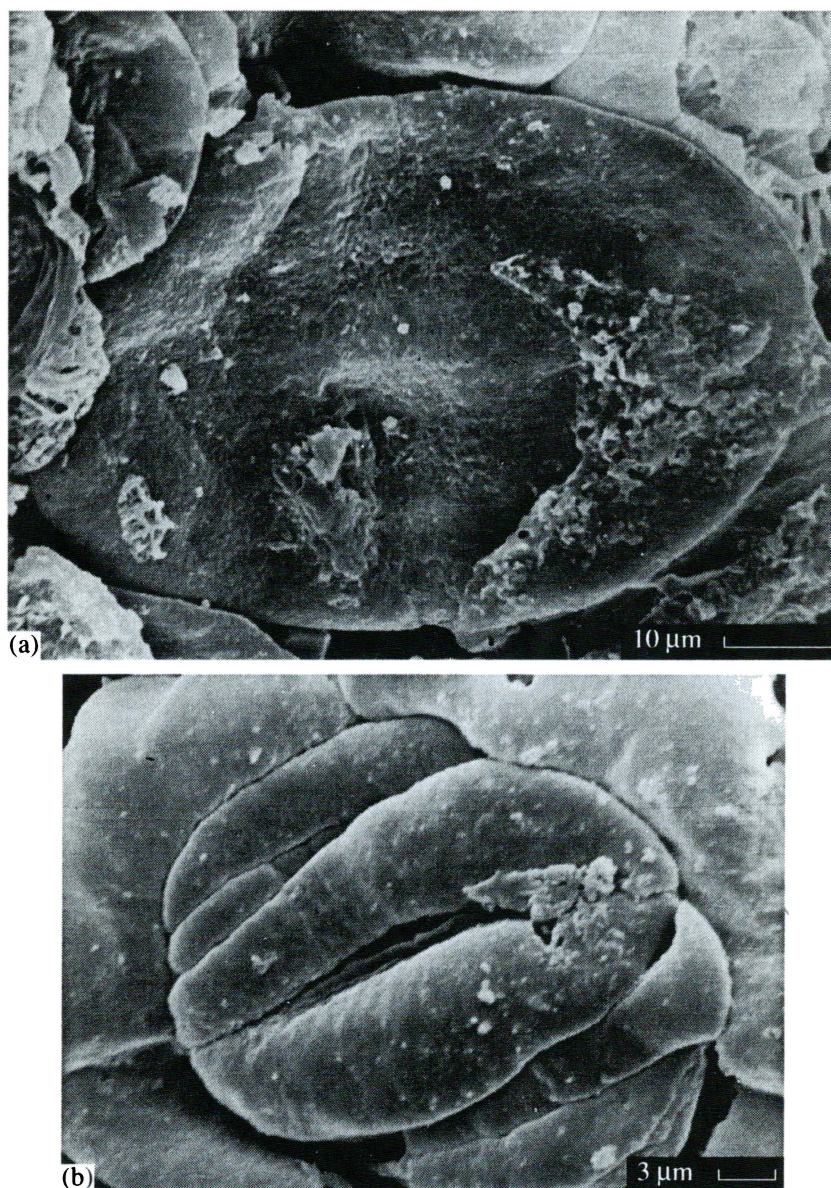


Fig. 2. Apertures of Paleozoic pollen grains, SEM: (a) porous endoaperture in *Protohaploxylinus* sp. with eroded exine from the gut content of a Permian psocid (booklouse) *Parapsocidium uralicum* Zalessky from Tchekarda locality, Fore-Urals (Krassilov *et al.*, 1999); (b) sulcus of taeniate pollen grain *Lunatisporites* sp. from the gut compression of another Permian insect, *Idelopsocus diradiatus* Rasnitsyn from the same locality (Krassilov and Rasnitsyn, 1997).

from protosaccate pollen morphotype in *Permothecca* to asaccate boat-shaped in *Antevsia*, the latter typical of Mesozoic gymnosperms. Probable reasons for such disparities are discussed below.

FUNCTIONAL CHANGES

A lack of morphological correlation in the evolutionary development of pollen grains and the sporophytes that produce them seem to suggest that pleiotropic effects of the genes responsible for sporophytic characters scarcely played a role in major palynomorphological changes. More plausibly, these changes

were functional, related to dispersal environment and gametophyte development. In spores the conspicuous changes often associate with a shift from predominantly water-borne to predominantly wind-borne dispersal that primarily affects the area to volume ratios and ornamentation for flotation and anchoring. The dimensions and longevity of gametophytes, as well as their endosporic, aquatic, above ground or underground development might have some effect on spore size, the amount of stored nutrients and durability of sporoderm, though such correlations are as yet insufficiently studied.

As for pollen grains, the decisive factors are dispersal vectors, volume regulation, catchment facilitation,

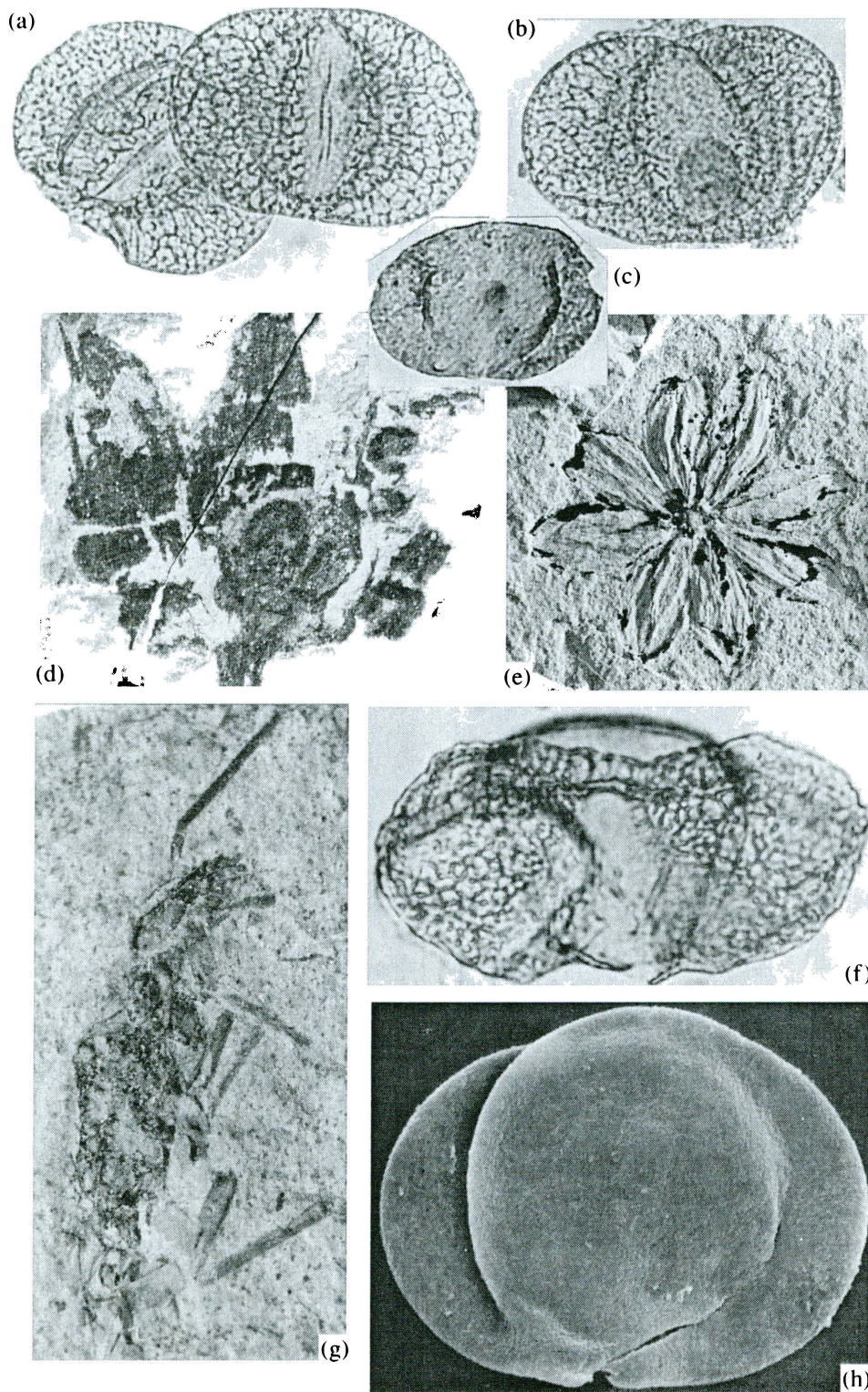


Fig. 3. An example of conservative pollen morphology: (a, b) *Vesicaspora*-type pollen grains from sporangium of *Permothecha*, a Permian peltasperm sporangial head (Krassilov *et al.*, 2000) showing transitional monosaccate-bisaccate structures, with distinct sulcus (saccus exine overlaps the capula); right grain with zoosporangium of a chitrid fungus, $\times 720$; (c) dispersed pollen grain of the same type, also with zoosporangium in the middle, from the Early Cretaceous of Mongolia (Krassilov, 1982), $\times 300$; (d) *Preflosella nathanian* Krassilov, preflower from the Early Cretaceous of Transbaikalia (Krassilov and Bugdaeva, 1999) with bracteate perianth, sporangial spikes and a central cupule, $\times 9$; (e) *Pemothecha disparis* (Zalessky) Naugolnykh, sporangial head of a Permian peltasperm, Geological Institute collection, no. 3737/202, $\times 4$; (f) *in situ* pollen grain of *Preflosella nathanian*, protosaccate with narrow lateral connection of sacci, $\times 1000$; (g) *Chaetoxxyella* sp., a xyelid from the same locality as *Preflosella*, $\times 10$, feeding on the same type of pollen grains; (h) Pollen grain from the gut compression of *Chaetoxxyella*, SEM, $\times 1000$.

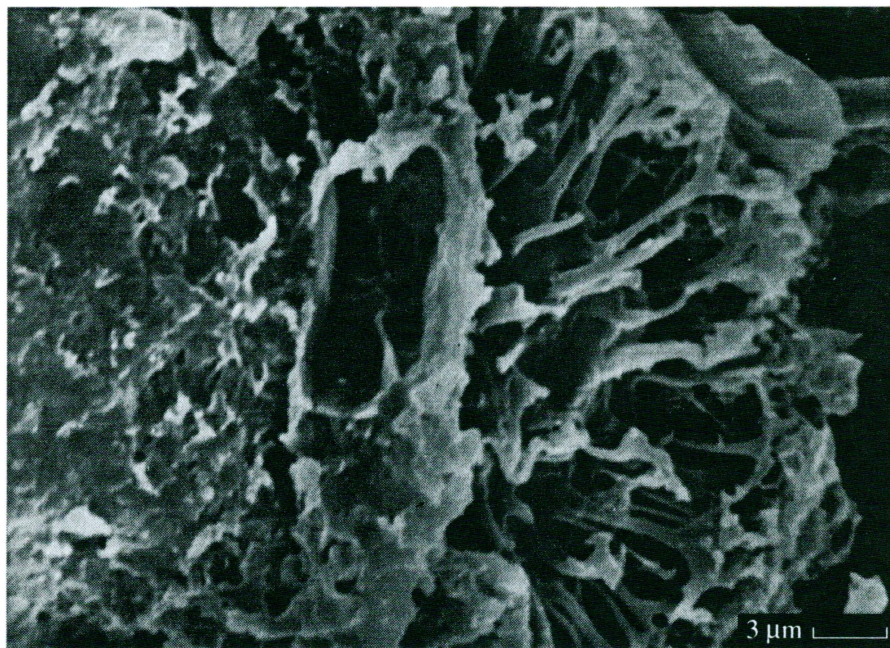


Fig. 4. Protosaccate structure in *Lunatisporites* sp. with eroded exine from the gut content of a Permian booklouse *Parapsocidium uralicum* Zalesky from Tchekarda locality, Fore-Urals (Krassilov *et al.*, 1999), SEM.

recognition by receptive structures and pollen tube development inside or outside the ovules. Pollen morphology results from adaptation to a certain combination of these functional factors. Any of the latter potentially affects pollen grain morphology, but at what extent the scale of morphological changes was adequate to functional changes might have depended on flexibility or multifunctional nature of the characters involved.

Sacs or bladders provide the best examples of multifunctional structures. Their commonly recognized function, for wind dispersal, may not be the major one and is certainly not the only one. The hollow eusaccate structures serve for flotation as well. They regulate pollen volume during dispersal and, when distally inclined, protect the aperture. They also facilitate pollen catchment causing the pollen grain to spin in the air vortices between spiral cone scales. The protosaccate structures, filled with sexinal elements (Fig. 4), increase the quality of edible pollen. Both types play a role in competition for space on receptive structures and in sperm competition (which is analogous to sexual selection in animals) by filling the micropyle and by promoting an ascending motion of captured pollen grains over the micropylar canal. With a change of functional environments, one or another aspect comes forth which does not necessarily lead to morphological changes.

Actually, multifunctional pollen structures might adapt to environmental changes affecting their dispersal, catchment, reception, gametophyte development or all these not by morphological innovation, but

rather by abandoning certain functions while enhancing others. This explains their morphological conservatism. However, profound changes at major geological boundaries involved not only functions, but also morphology, affecting even such multifunctional structures as bladders that in many seed plant lineages were modified or lost.

EVOLUTIONARY GRADES

As mentioned above, Kupriyanova (1969) has defined three major stages of pollen grain evolution based on apertural characters. A transition from the Paleozoic to Mesozoic pollen morphologies was marked by a shift of proximal to distal apertural dominance. This process had already started in the Pennsylvanian and extended to the early Mesozoic times. It involved several lineages that showed parallel developments. It was accompanied by other changes, such as a loss of taeniae as a dominant surface feature, a decline of monosaccate and, in particular, zonosaccate morphotypes, a transition from protosaccate to eusaccate structures and, eventually, by a parallel reduction of bladders in the rising Mesozoic gymnosperm orders. These changes, though gradual rather than abrupt, accelerate at about the Permian–Triassic boundary.

Actually none of the Paleozoic pollen morphologies disappeared at the boundary as a result of replacement of archaic gymnosperms by their Mesozoic descendants. Rather there was a shift of dominance from one morphotype to another, with a long persistence of archaic characters. For example, degradation of proxi-

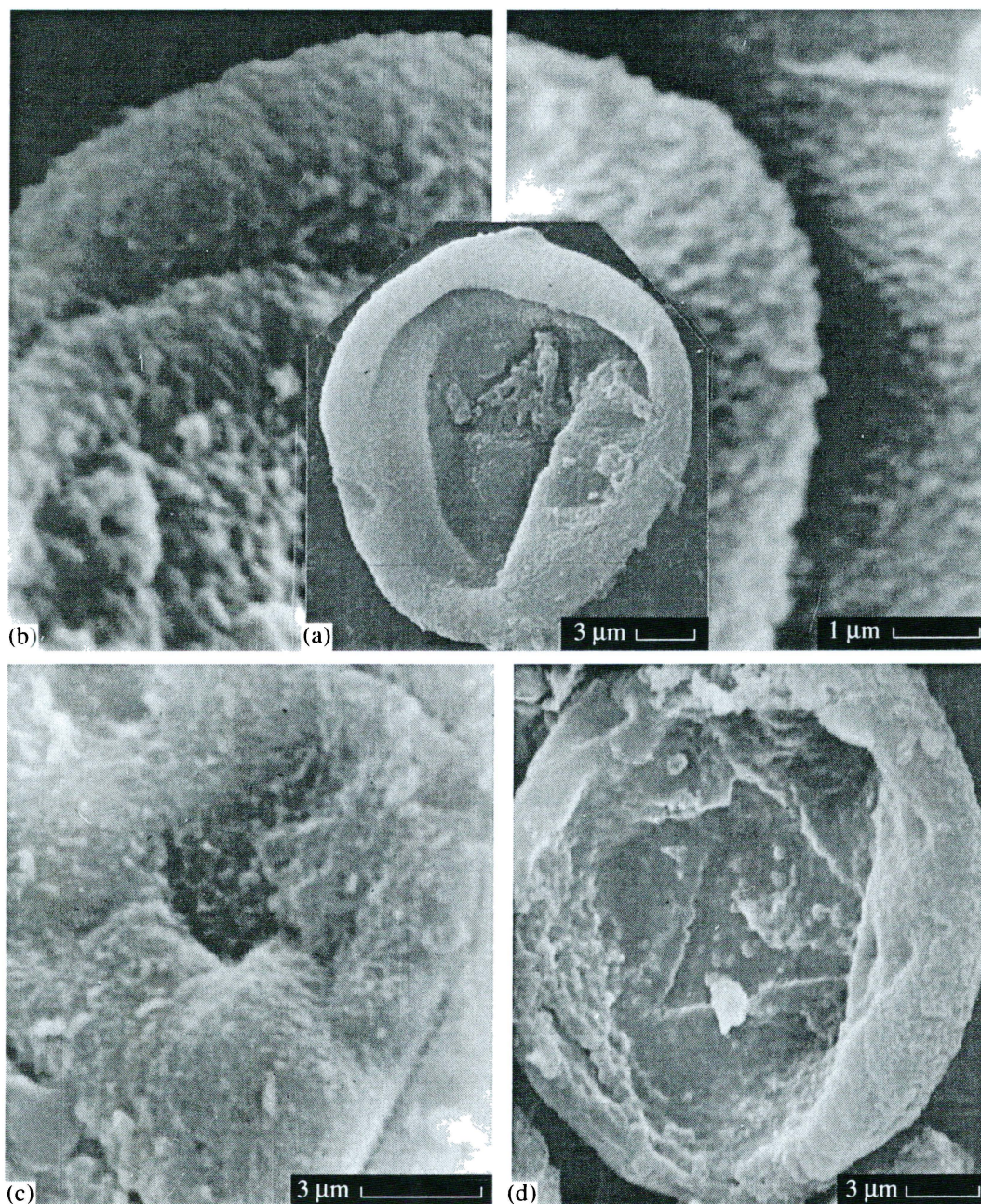


Fig. 5. *Classopollis* from the gut compression of *Aboilus* from the Late Jurassic of Kazakhstan (Krassilov *et al.*, 1997). SEM: (a) proximal face with Y-mark showing exinal filaments; (b) infratectate structure protruding through the tectum; (c) distal pore with a porous membrane; (d) triangular tetrad mark covered with a granular membrane.

mal apertures started long before the boundary, while in such morphotypes as *Vesicaspora* Y-mark gradually disappeared over the Pennsylvanian already (Millay and Eggert, 1970). In the Triassic the vestigial Y-marks are still common in the pollen morphotypes with distal apertures. In *Classopollis*, a widespread Mesozoic pollen genus, individual pollen grains were joined in persistent tetrads by exinal filaments (Fig. 5) protruding from a triangular Y-mark covered with a granular membrane. Similar membrane was developed over the distal

porous aperture (Krassilov *et al.*, 1997) perhaps indicating a bipolar germination. These forms also had an equatorial belt of striate exine and subequatorial groove, or rimula, perhaps inherited from an annular zonosaccus of *Cordaitina*-like Paleozoic prototype that already became rare in the Tatarian. In *Classopollis* the zonosaccus was modified as a volume-regulating structure related to entomophily.

A decline of taeniate morphotypes was likewise gradual, with few surviving over the Mesozoic. Eusaccate



Fig. 6. *Cycandra profusa* Krassilov et Delle from the Middle Jurassic of Georgia (Krassilov *et al.*, 1996), with pollen grains released from sporangium through the narrow apical beak, $\times 240$ and $\times 600$.

morphotypes of the Mesozoic and later conifers might evolve from protosaccate ones that occurred in their Paleozoic predecessors. While a spread of protosaccate pollen types in the Permian might have been related to pollinivory and entomophily (above), their eusaccate modifications, with the saccus infrastructure separated from the corpus, might arise in response to wind-pollination. Insect feeding on saccate pollen became less common than in the Permian. The Mesozoic pollinivorous insects, with a few exceptions, had switched to the rising bennettites, gnetophytes and other proangiosperms (including *Preflossella* and hirmerebrids that produced *Classopollis*-type pollen grains). Their insect retinue was partly inherited by the early angiosperms. Today only Lepidoptera larvae and some Coleoptera feed on saccate pollen grains.

Vestigial sacchi occasionally develop in pollen grains of ginkgo and cycads indicating origin from a saccate prototype (Herzfeld, 1927). These groups, simultaneously raised to dominance in the Mesozoic, might have been phylogenetically related, but their nearly identical pollen morphologies are more likely a result of parallel evolution.

Then what was the reason of such a radical change in dominant pollen morphologies at the Paleozoic–Mesozoic transition? It is commonly related to climatic changes, in particular to a widespread aridity that placed emphasis on harmomegathy and respective morphological structures. A shift of apertures from a proximal to distal position might provide for their protection by the distally inclined bladders, but this effect was already achieved in the Paleozoic. At the onset of Mesozoic, however, the volume-regulating structures, such as the taeniate exine and protosacci, were lost or simplified in the dominant gymnosperm groups. In the most widespread asaccate anasulcate morphotypes, the apertures were protected by the margins of involute boat-shaped grains alone. Additional cingulate or leptomate structures developed in a few morphotypes, such as *Ephedripites* or *Classopollis*, apparently in relation to entomophily (Krassilov *et al.*, 1997). Such morphotypes were most prominent in the tropical “elater” zone of prevalently entomophilous pollination.

Whatever the environmental changes, a vegetational turnover at about the Permian–Triassic boundary is well recorded in the fossil record. It started with decline of the dominant Paleozoic cordaites and voynovskians in the mid-Tatarian time and proceeded, over a succession of intermediate steps, to a new stable state of the mid-Triassic time, dominated by cycadophytes, ginkgoids and modern conifers. The transitional stages were relatively short-leaved and less diverse, indicating a simpler vegetational structure. Conceivably, a cut-off of the former climax phase in unstable environments put forth the pioneer and successional forms. Populations of the latter typically use a mixed pollination strategy of autogamy, anemophily and entomophily involving unspecialized pollinators. Pioneer species typically produce small seeds, a considerable number of which are lost during dispersal.

A change in vegetational structure triggers a chain of events that eventually lead to morphological changes. Incidentally, with a loss of specialized pollinators, such attraction features as taeniae were no longer advantageous, whereas a transition to anemophily demanded an instantaneous shedding of free-flowing pollen grains, hence a loss of sticky surface structures and substances. Small ovules also favor a decrease of pollen size compensated by increase in numbers. Finally, a widespread autogamy makes self-incompatibility structures superfluous.

Thus climatic and other environmental events, rather than directly affecting pollen morphologies, alter them by their destabilizing effect on plant communities and, thereby, on reproductive strategies of their constituent species. The pioneer strategies do well with simple morphologies. Subsequent stabilization and recovery of climax vegetation set on the opposite tendencies of morphological complexity and recurrence of characters related to specialized entomophily and self-incompatibility. New apertural types and harmomegathy structures, as in *Classopollis* and *Ephedripites*, appeared in the process.

This explanation seems difficult to apply to simple pollen morphologies, such as smooth asaccate boat-

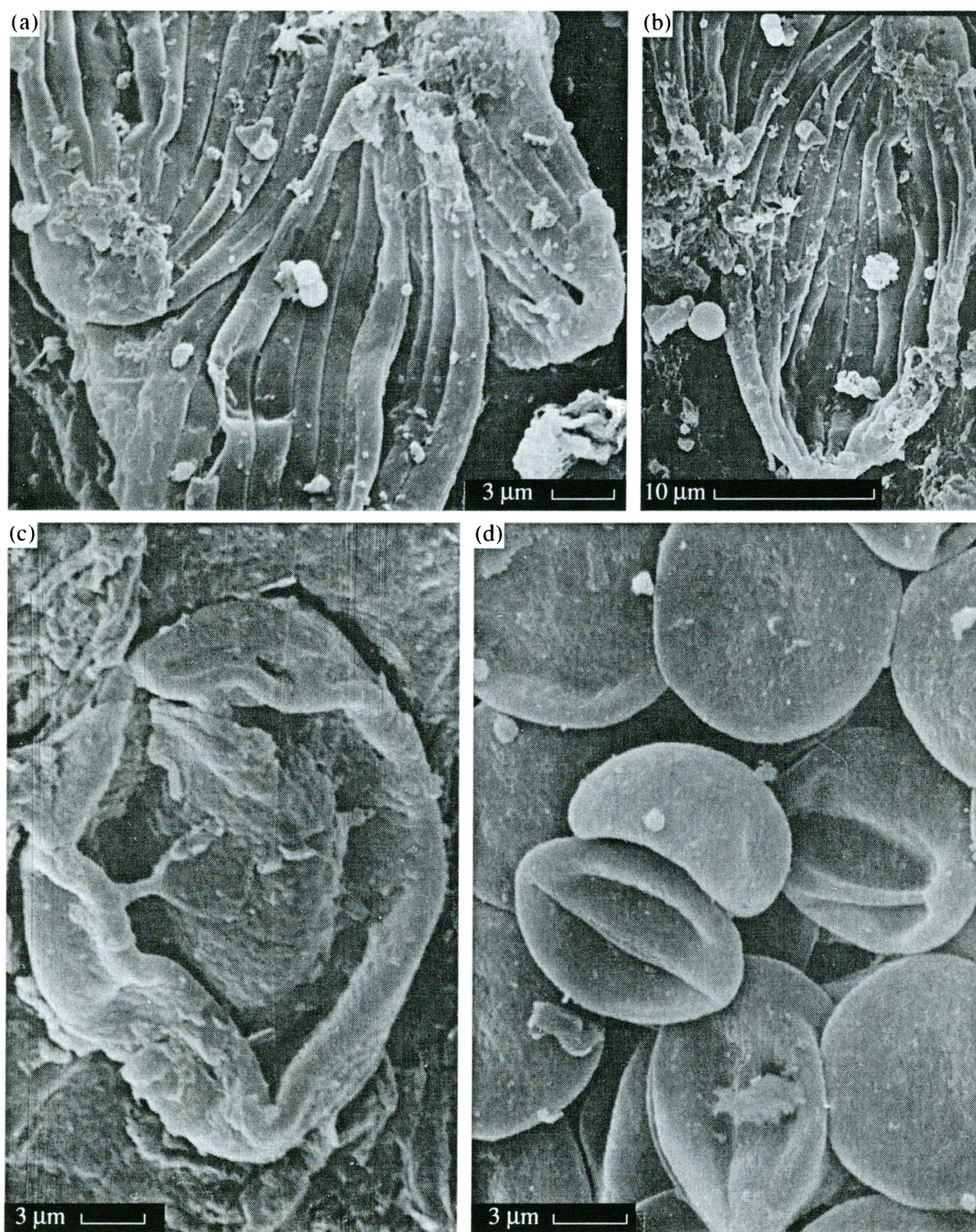


Fig. 7. Proangiosperm pollen grains from the Early Cretaceous of Baisa, Transbaikalia, SEM: (a, b) *Ephedripites*-type pollen grains from preflowers *Vitimantha crypta* Krassilov et Bugdaeva; (c) *in situ* pollen grain from a male spike of *Baisianthus ramosus* Krassilov et Bugdaeva, showing a nexinal body with a sac-like sexine attached at the poles; (d) *in situ* pollen grains from a male cone *Loricanthus resinifer* Krassilov et Bugdaeva, with partly preserved tetrad configuration; the contact area appears bisulcate, transected by a ridge (Krassilov and Bugdaeva, 1999, 2000).

shaped *Cycadopites*-type grains retained in advanced forms of Mesozoic gymnosperms. In the advanced bennettites, a retention of the pollen morphotype that appeared at an early evolutionary stage might have been related to cleistocarpic preflowers and autogamy as a prevailing pollination mode. In the Jurassic *Cycandra* (Krassilov *et al.*, 1996), large male cones produced

a great number of inconspicuous pollen grains that were released in small portions through a narrow beak at the apex of thick-walled sporangia (Fig. 6). This peculiar mechanism of partial exposure (as contrasted to instantaneous dispersal of wind-born pollen grains) make sense in the case of a long-lived male cone providing a continuous supply of pollen grains for sequen-

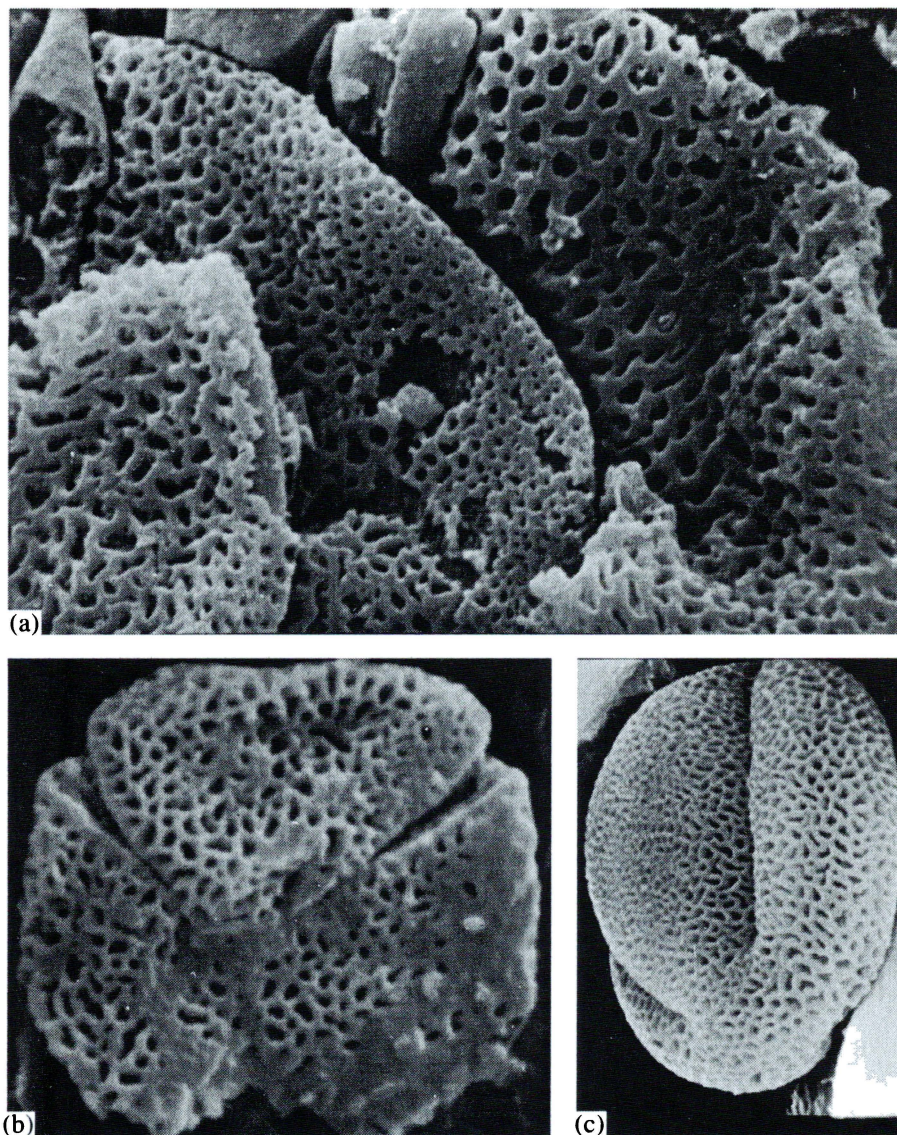


Fig. 8. Similar infratectal structures in Permian gymnosperms and semitectate structures in early angiosperms, SEM: (a) *Luna-tisporites* sp. from the gut compression of Permian insect *Idelopsocus diradiatus* Rasnitsyn from the Tchekarda locality, Fore-Urals (Krassilov and Rasnitsyn, 1997), infratectal structures, somewhat different in the sacchi and on the corpus (middle) are exposed through gaps in eroded tectum, $\times 2000$; (b) reticulate pollen grain of *Freyantha sibirica* Krassilov et Golovneva, male flower from the Cenomanian of Western Siberia), $\times 2700$; (Krassilov and Golovneva, 2000b); (c) reticulate pollen grain from a male head *Sarbaya radiata* Krassilov et Shilin, the Cenomanian of Kazakhstan, $\times 4000$ (Krassilov and Shilin, 1995).

tially developing ovulate structures. Such system also implies an availability of pollinators all year round.

Early angiosperms might evolve in the pioneer proangiosperm communities with various pollen morphologies, none of which appeared as angiospermous (Fig. 7) (Krassilov, 1986; Krassilov, Bugdaeva, 1982, 1999a, 1999b). Angiosperms lack pollination drop that attracted insects to ovulate organs of their gymnosperm ancestors. Therefore, before the appearance of nectaries, insects came for the pollen grains alone which promoted bisexual reproductive structures. Since in the pioneer populations autogamy is not prevented, self-incompatibility is scarcely a necessity. Rather, this

stage favored a premature development of pollen grains in which bladders were lost and tectum was reduced (in *Classopollis* already, see Fig. 5). Semitectate surface structures of early angiosperms resemble infratectate reticulum of saccate gymnosperm morphotypes suggesting their pedomorphic origin (Fig. 8). New pollen morphologies might also evolve from pedomorphic tetrades (Krassilov, 1997).

Later on, with angiosperms entering advanced seral stages, pollination ecology was radically changed by the development of nectaries (recently found in male flowers from the Cenomanian of Siberia: Krassilov and Golovneva, 2000b). With them, harmomegathy, as well

as sticky pollen surfaces, became once again important in the newly evolved entomophilous outcrossing systems. Scars of reduced bladders and other vestigial exinal structures were involved in volume regulation and were modified as rugate or colpate apertures. The appearance, parallel in the early angiosperm lineages (Fig. 8), of structural characters related to self-incompatibility syndrome gave this stage a peculiar morphology widely recognized as typically angiospermous (Zavada, 1984). These palynological "first appearances" thus mark a fairly advanced stage of angiosperm origins.

In conclusion, sporophyte–pollen grain correlation was not a leading factor of pollen evolution. Divergent plant lineages show convergent palynomorphological characters. Rapid sporophyte evolution associates with conservative palynomorphology and *vice versa*. Coincidence of major stages in evolution of sporophytes and pollen grains results from very general and mostly indirect environmental impacts that induce independent, but roughly simultaneous change of both vegetative and reproductive functions, including pollination ecology. Palynological characters typically react to such changes by substitution of functions as well as by pedomorphic innovations.

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