

single megaspore but these spores are not enclosed in integuments. In this presentation we will focus on two critical aspects. First, functional aspects of the spore wall structure will be discussed with special reference to reproductive biology of the five extant genera of these ferns. Second, the development of mega- and microspores are compared in detail for these five genera: *Azolla*, *Marsilea*, *Pilularia*, *Regnellidium*, and *Salvinia*.

In this study we integrate observation of scanning electron microscopy (SEM), transmission electron microscopy (TEM), and light-microscopy (LM). By combining the observations obtained by SEM and TEM with the results of light-microscopic observations, in particular epifluorescence illumination, we are able to achieve an improved understanding of the development and structure of spores. Electron microscopic methods require in general a more or less complete dehydration of the studied material, whereas light microscopic methods allow observations of the hydrated material. Light-microscopy is today much more powerful than 20 years ago, because recent advances in image manipulation including computer controlled focus drives improved the quality of the obtained observations. This is critical if studied structures are strongly modified during the dehydration procedure.

The outer spore wall, perine, is strongly modified in the five extant genera. The three genera of the family Marsileaceae, the genera *Marsilea*, *Pilularia*, and *Regnellidium*, possess a gelatinous outer perine which is a critical adaptation to the reproduction of a free-sporing amphibious plant. The two genera of Salvinaceae, *Azolla* and *Salvinia*, have very different spore wall structures in comparison to Marsileaceae as well as in comparison to each other. Their spore walls are adaptation of free-sporing plants with a floating habit.

Very little is known about the development of the megaspores in heterosporous ferns despite earlier studies that provided critical data. We can now show that the microsporangia and megasporangia of heterosporous ferns follow a similar early developmental pathway, but after the meiosis, the developmental pathway of the megasporangium diverges significantly, culminating in the abortion of all but one megaspore tetrad. A putative mechanism of the tetrad selection is proposed which is found in all extant heterosporous ferns. The observation of the extant heterosporous ferns are compared with hypothetical explanations of similar processes in extinct ancestors of the seed plants

Session b2.1

POLLEN MORPHOLOGY AND PLANT SYSTEMATICS

Evolution of *Amorphophallus* pollen (Araceae)

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Two main Araceae pollen types exist: 1. aperturate and 2. inaperturate. The aperturate type is plesiomorphic in the family. Pollen of *Amorphophallus* (c. 200 spp.) belongs to the inaperturate type. Its exine ultrastructure (presence, size, shape and distribution of dark granules) and ornamentation are much diverse. Ten main ornamentation types are present: psilate, striate, striate with psilate caps, fossulate, areolate, verrucate, echinate, reticulate, scabrate and striate/scabrate. Two of the three echinate subtypes are much like the echinate pollen of the four closest outgroups used in molecular work on the genus (48 spp., 4 genes): *Arisaema*, *Filarum*, *Hapaline* and *Typhonium*. However, echinate *Amorphophallus* pollen is not basal in the molecular tree, which suggests that the outgroups are only distantly related to the ingroup. No pollen traits indicating the monophyly of *Amorphophallus* or any of the main clades in the molecular tree were found. The main clades are dominated either by psilate or striate pollen, which occur basally as well as distally. The less common types are found more distally and mostly in single species. This suggests that either psilate or striate ornamentation is plesiomorphic. Outgroup comparison does not allow a choice, but thin psilate exines occur more or less basally in three of the four main clades. The generally thicker striate type is ultrastructurally heterogeneous, and seems to have evolved several times. Within both striate main clades, reversals to the psilate type occur, which are mostly characterised by greater exine thickness, compared with the basal psilate type. Within the African clade, thick psilate exines seem

to have evolved directly from thin ones. Considering this, psilate pollen might be plesiomorphic in *Amorphophallus*. The rather common fossulate type is heterogeneous, and shows transitions to the psilate as well as the striate type. Also ultrastructurally, it proved to be diverse, and its diffuse distribution in the molecular tree confirms that it is polyphyletic. Striate pollen with psilate caps, which is nested in a striate clade (continental SE Asia), is a synapomorphy of *Pseudodracontium* (Indochina). In view of its typical exine ultrastructure, the psilate caps might have evolved in an *albispatus/longituberosus*-like ancestor. Reticulate (*A. ochroleucus*, Vietnam), scabrate (*A. galbra*, Queensland) and striate/scabrate ornamentation (*A. smithsonianus*, India) are considered as autapomorphies derived from psilate or striate forms. The other types, areolate, echinate and verrucate, occur in single species in the molecular tree, but have also representatives among the species not included in the analysis. Areolate pollen (6 spp., continental SE Asia) shows two alliances, one in a psilate main clade and another in a striate main clade. Echinate pollen (5 spp., Africa and Madagascar) is heterogeneous, showing three subtypes, one of which can be easily derived from a psilate type. Verrucate pollen (Africa: 5 spp. and India: 1 sp.) is clearly diverse. Derivation from psilate forms seems most likely. Several species appeared to be distinctly polymorphic: *A. abyssinicus* (verrucate, fossulate to coarsely striate), *A. beccarii* (psilate, striate-areolate) and *A. baumannii* (fossulate, coarsely striate, psilate, with or without distinct dark granules). These observations indicate that exine features are not always rigidly fixed, which might provide possibilities for rapid selection and evolution.

Pollen morphology in the Aristolochiaceae and its implications on systematics of the family

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Aristolochiaceae consist of 4 genera and ca. 500 spp. of temperate herbs and tropical or subtropical lianas, shrubs, and subshrubs. The family has received much recent attention because of its crucial placements a basal angiosperm, either as part of the order Piperales or as sister to the monocots. An overall study of the pollen morphology of ca 120 spp. representing all genera and infrageneric taxa was carried out by LM, SEM, and TEM techniques. Pollen in the Aristolochiaceae is more or less spherical, with a diameter ranging from about 20 µm in *Saruma* to 73 µm in *Aristolochia grandiflora*. *Saruma* pollen is semitectate, per-reticulate, monosulcate, with muri sometimes discontinuous, and lumina >2 µm in width with scattered free baculae. *Asarum* pollen is porate (less often inaperturate or colpate), verrucate or gemmate, microreticulate with continuous muri and small lumina. *Thottea* pollen is inaperturate, with circular to irregular, dissected exine subunits that are punctate or imperforate, and well-developed columellae. *Aristolochia* pollen is inaperturate and highly diverse: in subgen. *Siphisia* it is fossulate, the exine is densely punctate and strongly dissected; irregular warts and/or free clavae were found in some spp. In subgen. *Pararistolochia* it is fossulate and strongly dissected, the exine is punctate, forming nearly circular insulae and a long exine ridge, the infratectum is columellate, and free clavae are present. In subgen. *Aristolochia* two types of sculpture are found, which are more or less consistent to the two sections traditionally recognized: In sect. *Diplobolus* pollen is psilate or finely fossulate and has a complete or incomplete, scarcely punctate or imperforate tectum; the exine is thinner than in the remaining *Aristolochia* spp., the infratectum is columellate, and the nexine is thin. In the greatly diversified sect. *Gymnolobus*, exine is usually strongly dissected and fossulate; the exine units are massive, irregular, "cerebriform"; in *A. grandiflora* exine subunits are flake-shaped, punctae are missing or very scarce, and the infratectum is columellate; pollen of *A. pilosa* is tectate as in some species of section *Diplobolus*, but with small and large puncta. Exine subunits in *Aristolochia* subsect. *Pentandrae* are many tightly packed, flake-like, and densely punctate, with conspicuous supracteal warts. Exine in the South American monotypic *Euglypha* and *Holostylis* is strongly dissected in irregular subunits that are scarcely punctate, and a columellate infratectum is present.

Monosulcate pollen in *Saruma* has revealed a key character that connects the Aristolochiaceae with other basal angiosperms. Apertures are not strongly differentiated in the exine of *Asarum* and *Saruma*. Inaperturate pollen of the remaining genera appears to be omniaperturate as the intine and the exine are uniform (GONZÁLEZ ET AL. 2001). Orbicules are common in Aristolochiaceae. All these results were included in phylogenetic analyses by GONZÁLEZ & STEVENSON (2002) and KELLY & GONZÁLEZ (2003), which revealed that: (1) pollen characters support the uniqueness of *Saruma* (with semitectate, per-reticulate, monosulcate pollen) and the monophyly of *Asarum* (with apomorphic porate pollen with supracteal warts), *Thottea* (with apomorphic

isodiametric, densely punctate exine subunits), and three infrageneric taxa within *Aristolochia* (subgen. *Pararistolochia*; sect. *Diplobolus*; and subsect. *Pentandrae*); pollen is more heterogeneous in the remaining members of *Aristolochia* (subgen. *Siphisia*, and the bulk of Neotropical subsect. *Hexandrae*); (2) the presence of a conspicuous exine ridge is synapomorphic in *Aristolochia* subgen. *Pararistolochia*; this character was used by LOBREAU-CALLEN (1978) to support the segregation of *Pararistolochia*; (3) the dissected, massive exine that forms a fossulate sculpture is plesiomorphic in *Aristolochia*, and psilate pollen evolved independently three times, once in sect. *Diplobolus*, once in the clade *A. grandiflora*+*A. lindneri*, and once in *A. pilosa*; and (4) the suprastemal warts define *Aristolochia* subsect. *Pentandrae* although they appear independently once in *Asarum*, once in a crown clade within *Aristolochia* subgen. *Siphisia*, and once in *A. burelae*. No clear-cut differences in pollen morphology were observed between the two highly diversified Old World subsections *Euaristolochia* and *Podanthemum*, nor between *Euglypha*, *Holostylis*, and their closely relative South American species of *Aristolochia*; the latter does support the inclusion of these genera within *Aristolochia*.

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 GONZÁLEZ, F., P.J. RUDALL & C. FURNESS. 2001. Microsporogenesis and systematics of Aristolochiaceae. *Bot. J. Linn. Soc.* 137: 221-242.
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Phylogenetic relationships in Papaverales inferred from pollen ontogeny and ITS sequence data

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The order Papaverales comprises two families, Papaveraceae and Fumariaceae. In the western Mediterranean area the Papaveraceae family contains species with two basic pollen types: colpate (with from 3 to 6 colpi) in *Papaver*, *Glaucium* and *Chelidonium*, and pantoporate (with from 6 to 8 pores) in *Papaver argemone* and *Roemeria*. The Fumariaceae family contains the genera *Hypecoum*, with bicolpate pollen, *Corydalis*, with tricolpate pollen, and *Sarcocapnos* and *Ceratocapnos*, both with hexacolpate pollen grains. In *Platycapnos* the colpi are fused to form a network and in *Fumaria* and *Rupicapnos* the pollen is polyaperturate. Although the pollen from both families has been widely studied from the morphological point of view, ontogenetic studies have only been made of the pollens of *Fumaria densiflora* (ROMERO & FERNÁNDEZ, 1999) and *Hypecoum imberbe* (ROMERO *et al.*, 2003).

Attempts have been made in recent years to correlate morphological characteristics with molecular ones and thus find some phylogenetic consensus which might solve some of the many questions raised concerning taxonomical grouping among the angiosperms. As far as the Papaverales are concerned, important contributions have been made towards our answering these questions, the most recent being that by SALINAS *et al.* (2003).

A comparison of the evolutionary processes in the development of the pollen grains between different species of the Papaverales shows that, in the species studied, these processes appear to have no bearing on the morphology of the pollen. Thus the pollen of the Papaveraceae presents a common model with large orbicules showing no distinct core, a clearly developed although quite thin endexine layer and the absence of any onci. In the Fumariaceae the pollen of the genera *Platycapnos* and *Fumaria* shows a similar pattern. In these latter genera the apertures are covered in fluffy material, the origin of which is related to the remains of the endoplasmic reticulum, deriving from the decomposition of the cells of the tapetum. The endexine is always present in these cells, although it is thin and may sometimes be fragmentary. A lamellate foot layer can be discerned, this being quite distinctive in all studied taxa of the Papaverales. Although in all cases the endexine is deposited in small subunits forming glomerules, in *Sarcocapnos* it only appears around the apertural zones. The model of the genus *Hypecoum* is closer to the Papaveraceae, although it does not show formation of orbicules. From these observations we have been able to establish three models: Model 1: *Hypecoum* (*Hypecoum*, *Papaver* y *Roemeria*); Model 2: *Sarcocapnos*; and Model 3: *Fumaria* (*Fumaria* y *Platycapnos*).

A comparison of these ontogenetic models with the molecular data obtained by analysing the ITS2 sequences of the species studied, reveals considerable coincidence between the ontogeny and the phylogenetic analysis of this molecular marker. There are two clearly distinguishable clades: one corresponding to *Sarcocapnos* and one to the *Fumaria-Rupicapnos-Platycapnos* group. The latter clade corroborates our opinion that pollen morphology is not a reliable characteristic for interpreting the phylogeny of this group of plants.

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Pollen morphology of some platanoids

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I have studied *in situ* pollen extracted from fossil platanaceous plants *Archaranthus krassilovii* N.Maslova et Kodrul (Maastrichtian-Lower Paleocene of Amur Province; Maslova, Kodrul, 2003) and *Chemurnautia staminosa* N.Maslova (Upper Paleocene-Lower Eocene of Kamchatka; Maslova, 2002). In general pollen grains of both species have similar external morphology and ultrastructure. They are 3-colpate and elliptical, reticulate, semitricolpate, 16.0-16.8x13.3-15.3 µm (*Archaranthus*) and 13.0-16.0x11.0-13.0 µm (*Chemurnautia*). Ectexine consists of tectum, columellae and thick foot layer. Endexine is two-layered and more electronically dense than ectexine. Both endexinal layers are homogenous and equally thick all over the perimeter except the apertural region. The inner layer is electronically denser and more loosely arranged than the outer one. Towards the colpi the ectexine sharply reduces and disappears, and in apertural region pollen wall is composed only by the endexine which becomes thicker and is morphologically changed. The outer endexinal layer shows slightly thickened and finely lamellate morphology. The inner layer is granular, also gradually thickens and constitutes the most part of the apertural region. In distinction from *Chemurnautia* the colpi in *Archaranthus* pollen are bordered with a sexinal string. In addition, in *Chemurnautia* electronically dense masses of supposed tapetal origin separate individual pollen grains in the microsporangium. There are 11 species of fossil Platanaceae which pollen has been studied by means of electron microscopy. They have similar surface morphology differing in shape and size of the muri, columellae shape, thickness of the exinal layers, character of colpus margin and some structural details. All investigated species have two-layered or simply layered apertural endexine, but *Archaranthus* and *Chemurnautia* in comparison with other species differ in presence two layers of endexine with different electron density changing their fine structure towards the colpi.

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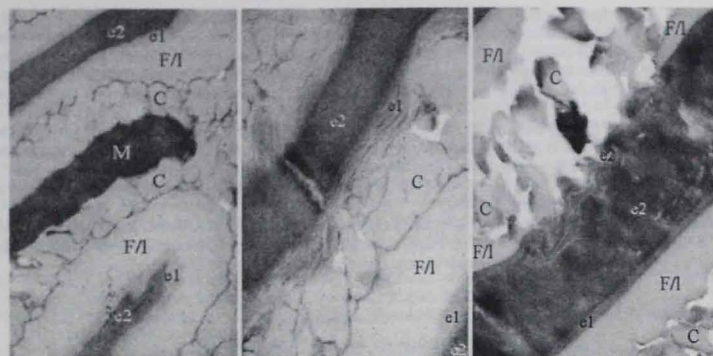


Photo 1

Photo 2

Photo 3

Photo 1 (x12000) and Photo 2 (x24700). *Chemurnautia staminosa*. Photo 3 (x19500). *Archaranthus krassilovii*. M - electronically-dense mass which separate pollen grains from each other, C - columellae, F/L - foot layer, e1 - the outer layer of endexine, e2 - the inner layer of endexine.

Pollen structure in caesalpinoid legumes

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Pollen has enduring value in providing diagnostic features towards assessments of relationships between plants. The pollen of over 900 samples, representing all 161 genera of legume subfamily Caesalpinioideae, has been examined using LM, SEM, and (selectively) TEM. Pollen data has been documented, described and the range of pollen morphological diversity in caesalpinoid legumes has been assessed. The most informed hypothesis of phylogeny available has been used to map character distribution.

Many interconnecting factors affect pollen structure: pollination syndromes, functional efficiency during dehydration, rehydration, and germination, recognition system requirements, random mutations, and protection from environmental conditions (e.g. abrasion, crushing, desiccation), all constrained by phylogenetic inheritance and developmental pathways. Summaries of the following subject areas are presented:

1. Fewer or smaller apertures are associated with slower desiccation rates and longer viability, higher numbers of apertures are associated with faster germination rates. An example of how both these factors affect the pollen morphology and success of certain related taxa in Madagascar is given.
2. A synopsis is given of the many variations in wall and aperture structure that appear to enable efficient harmomegathic mechanisms to be accommodated.
3. Tricolporate, finely reticulate or perforate pollen is widespread in eudicots and legumes, and there are many examples of reversals from more specialised pollen types. Because of this, *a priori* assumptions can be made about primitive pollen structures in Caesalpinioideae.
4. The constraint of developmental processes are explored focussing on (a) the most unusual pollen type, (b) surface ornamentation, and (c) release of mature pollen in tetrads.

Understanding the impact of these factors on caesalpinoid pollen structures gives a better understanding of the evolution of pollen morphology in the group, and of their use as characters in phylogeny reconstruction.

Pollen morphology and systematics of Burseraceae

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The Burseraceae are a medium-sized family of 18 genera. A long-term project to describe the pollen morphology of each of the three widely accepted subtribes, from light, scanning electron and transmission electron microscopy, for the World Pollen and Spore Flora is nearing completion. The pollen morphology of tribe Protieae has been published (Harley & Daly 1995), as well as an account of the pollen of the African taxa (Harley & Clarkson 1999). Pollen data for the remaining tribes, Burseraceae and Canariaceae are now more or less complete.

The pollen of all the genera has been examined, with the exception of the recently described *Pseudodacryodes* Pierlot, for which there is no pollen material. There is considerable variation in exine and aperture features between, and occasionally within, genera. The distribution of pollen characteristics throughout the family is compared with previously published tribal and subtribal groupings, as well as with current ideas of generic relationships from molecular analyses (Clarkson et al. 2002).

Comparisons show that there can be surprising congruence of pollen data with molecular data. To some extent pollen morphology is different for each of the subtribes. Nevertheless, there are some notable exceptions, for example, the pollen of *Garuga* and *Boswellia* are remarkably similar, although *Garuga* has been included, somewhat tenuously, in tribe Protieae, and *Boswellia* is included in tribe Burseraceae, subtribe Boswelliinae. In the recent molecular tree of Clarkson et al. (2002) *Garuga* and *Boswellia* appear to be closely related, and this supports the conclusions of Harley & Daly (1995) who suggested, based on several macromorphological characters, as well as pollen, that *Garuga* should be transferred to tribe Burseraceae.

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CLARKSON, J.J., CHASE, M.W. & HARLEY, M.M. (2002). Phylogenetic relationships in Burseraceae based on plastid *rps16* intron sequences. Kew Bull. 57: 183-193.

Pollen Morphology of Acanthaceae from the El Bajío area and adjacent regions of México

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A morphological study of pollen grains of species of Acanthaceae from El Bajío area and adjacent regions is presented. Although this family is designated as eurypalynous it has been studied very little in Mexico. Sixty species from 18 genera have been studied with light microscopy (LM) and scanning electron microscopy (SEM). Morphological variations in shape, apertures and ornamentation were observed between genera. Nevertheless, some of the differences in pollen morphology correspond with the subfamilies established by several authors. In the sense of Bremekamp (1965), four subfamilies are represented in the area: Thunbergioideae (2 species) with spherical, spiraperturate pollen; Nelsonioideae (4 species) with spherical to prolate, tricolpate pollen, with a reticulate exine; Acanthoideae (3 species) with prolate, tricolpate pollen, and a psilate or gemmate or verrucate exine and Ruellioideae (51 species) with spherical to prolate pollen, but with variation in aperture and exine sculpturing. Within the last subfamily a major diversity of pollen morphological patterns exists. Most of the genera examined belong to subtribe Odontoneminae (10 genera, 22 species). Furthermore, most of the species can be distinguished by pollen morphology and a pollen key to the species has been constructed. It is interesting that the dimorphism of pollen grains of *Stenandrium dulce* and of *Justicia zamudioi* is similar to that found in Odontoneminae and is not like the pollen of most species of tribe Justiciaeae.

These data are potentially useful in a number of research areas, for example, in Taxonomy, pollination biology, apicultural improvement, natural resource management, and vegetation history.

A contribution to the ultrastructural knowledge of the pollen exine in tribe Inuleae Cass. (Asteraceae)

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The Inuleae *sensu stricto* comprise 38 genera and 480 species, mainly with a Eurasian and Mediterranean distribution (ANDERBERG, 1994). Using light microscopy, STIX (1960) and LEINS (1968, 1971) studied the pollen exine wall structure of five genera and 11 species included in the *Inula* pollen type, and 32 genera and 137 species representing 20 other pollen types. The only transmission electron microscope studies of pollen exine in the Inuleae were carried out by SKVARLA & TURNER (1966) (*Inula britannica*) and SKVARLA et al. (1977) (*Alagoppapus dichotomous*, *Blumea mollis*). These investigators pointed out the existence of a senecioid type wall structure in the pollen grains of the 3 taxa that they studied.

As a contribution to the knowledge of pollen wall structure in this tribe, we have investigated, with transmission electron microscopy, the pollen exine in the following taxa: *Asteriscus maritimus*, *Dittrichia viscosa*, *Pallenis spinosa*, *Limbaria crithmoides*, *Nauplius aquaticus*, and *Pulicaria paludosa*. In some cases, this study was complemented by scanning electron microscope observations of fractured exines. In the pollen of all the taxa examined, a well-defined senecioid pattern is noted. The spines are not solid, but have distinct structural modification for about 1/2-3/4 of their length. The only exception is the pollen of *A. maritimus* where only very reduced caecae were observed.

In general our results agree with those of LEINS (1968, 1971) and SKVARLA & col. (1966, 1977).

According to BOLICK (1978), EL-GHAZALY & ANDERBERG (1995), and ZAVADA & VILLIERS (2000), the reduction of the caecae and foramina indicates that the pollen of the Inuleae is primitive within the Asteroideae.

In our opinion, the unusual development of the caecae of *Asteriscus maritimus*, when compared with that of the other Inuleae, represents an adaptation to the especially harsh conditions of habitat for this species (seaside rocks exposed to the action of sun and salty wind). In fact, greater caecae constitute an efficient harmomegathic device, and are a good place for the accumulation of hydrophobic substances, for preventing the dessication of the male gametophyte.

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Orbicules: intriguing features of the anther

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In the anthers of flowering plants, gymnosperms, and seed ferns, tiny ($\pm 1 \mu\text{m}$) granules may occur on the radial and innermost tangential wall of secretory tapetum cells. These granules are called orbicules or Ubisch bodies. Orbicules develop simultaneously with the growing pollen exine and are composed of sporopollenin, similar to the pollen exine.

In higher plants, the ornamentation of the pollen exine and that of the orbicule wall often show striking analogies. These parallelisms are rooted in the homology of tapetum and sporogenous tissue. Since ornamentation of the pollen exine offers useful characters for systematics, orbicules might also have taxonomic value. We studied the ontogeny, diversity and systematic importance of orbicules in the order Gentianales with scanning and transmission electron microscopy. A typology based upon the morphological and ultrastructural diversity was worked out. The proposed typology offered a useful tool to evaluate the systematic importance of orbicule characteristics in the families of Gentianales. In Apocynaceae s.l. and Gentianaceae orbicule characters seemed to be strongly correlated with evolutionary trends in pollen and tapetum type features.

As mentioned above, orbicules are considered to be a general feature of species characterised by a secretory tapetum. An interesting fact is that hay-fever-causing angiosperms are characterised by the presence of secretory tapeta. We investigated the possible role orbicules may play as vector of allergens. The presence of orbicules was studied in 15 important European allergenic species. In all Betulaceae, Chenopodiaceae, Poaceae, and Urticaceae species, orbicules were attached to the pollen exine, indicating the possibility of dispersal of orbicules into the atmosphere during anthesis. The localisation of homologs of the new birch allergen *Bet v 7* was studied at the ultrastructural level in Hazel anthers using immunocytochemical staining methods. The results of this study showed that orbicules of Hazel might act as effective vectors for homologs of *Bet v 7* and that the debris of Hazel anthers represent another vector of allergens after the pollen season.

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EVOLUTION OF ANGIOSPERM POLLEN CHARACTERS

Pollen evolution in cordaites and early conifers

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Modern conifers, according to S.V. Meyen (1984), represent the "summit" of evolution among gymnosperms possessing the most advanced seeds. It can be confirmed by the realizing the fact that they possess the most advanced pollen too. The origin of two main features of modern conifer pollen grains – strict distal germination and the eusaccus in bisaccate condition – should be understood to reveal the trend of pollen evolution in the clade of pinopsids.

Since R. Florin (1938 – 1945) it is generally accepted that conifers has originated from Euramerian cordaites (the Cordaitanthaceae). Florin has derived *Potomiesporites*, monosaccate pollen of the earliest conifers from the cordaitalean pollen *Florinites*, but now it is highly doubtful, as *Florinites* possesses an eusaccus and a