

Pollen and spore research: morphology, ecology and phylogeny

ABSTRACTS

How plants conquered the land: an EvoDevo analysis of the spore wall

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Many theories have been advanced regarding the key innovations required to enable plants to successfully colonise terrestrial habitats. One such proposed innovation is the development of a durable spore wall structure to withstand a dry and UV rich environment. A significant amount of study has been conducted with regards to the molecular genetics of pollen wall (the derived homologue of the spore wall) development in angiosperms, particularly *Arabidopsis thaliana* (L.). However, research into the molecular genetics of spore wall development in basal plants has thus far been extremely limited. By examining the results of a fully replicated microarray analysis at early and mid stages of moss sporogenesis, up and down regulated genes have been compared with those known to be involved in pollen wall development, therefore allowing the identification of candidate genes likely to be involved in the development of the spore wall and consequently the ability of the sporophyte to survive in the terrestrial environment. The involvement in spore wall development of selected candidate gene(s) will be verified by conducting gene knock-out and gene swap experiments between the moss model species *Physcomitrella patens* and the higher plant, *A. thaliana*. Ultimately this experimental approach will test the hypothesis that the biochemical and developmental pathway required for pollen wall development in higher plants is ancient and highly conserved.

Small RNAs and the male gametophyte: great leaps in small steps

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Small RNAs are found in all eukaryotes and are comprise an ancient, highly conserved mechanism of gene regulation. These small RNAs do not encode proteins themselves but act through protein complexes that include small RNA-binding proteins. These small RNAs can have effects at the level of the chromosome (such as guiding changes to chromatin) that result in gene expression changes as well as post-transcriptional effects on messenger RNAs. These effects include repressing translation of messenger RNAs and guidance of their destruction by endonuclease 'cleavage'.

In flowering plants, small RNAs are essential for normal developmental processes. However, until recently nothing was known about small RNAs in the gametophytic stage of the life cycle. Here, I will present our work demonstrating that a great diversity of small RNAs are present in the male gametophyte. We have discovered a novel class of small RNAs in *Arabidopsis thaliana* pollen and we will present compelling evidence that they have a critical function in late pollen development, including germination and pollen tube growth. From an evolutionary perspective, small RNA-based regulatory systems may have been critical in the transition of the more complex and slow-growing gymnosperm male gametophytes to the highly reduced and fast-growing male gametophyte of advanced angiosperms.

Constraints and selection on pollen aperture determination

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Microsporogenesis is a key event in pollen development during which aperture pattern is determination takes place. A number of features of microsporogenesis have been shown to play a role in the relative distribution of apertures on the surface of the pollen grain. These features include the type of cytokinesis, the way intersporal callose walls are formed, the resulting tetrad shape, as well as the way additional callose is deposited within tetrad. We discuss the relative contribution of these features to the design of aperture pattern. In addition, we investigate the respective roles of constraints and selection acting on these microsporogenesis features by comparing aperturate and inaperturate species.

Pollen of early-divergent monocots

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Pollen and anther characters including microsporogenesis, tapetum and pollen apertures have been shown to be key characters in monocot phylogenetics, especially in the lilioid orders Aparagales and Liliales. This talk reviews these features in the order Alismatales, and compares them with other early-branching and lilioid monocot lineages. Many Alismatales are characterized by thin-walled or exineless, inaperturate (omniaperturate) pollen with a smooth or reticulate surface. In contrast, pollen of most Pandanales and Dioscoreales has an exine and is spheroidal or ellipsoidal and aperturate, though exceptions occur, such as inaperturate pollen in Triuridaceae. Current phylogenetic data indicate that the characteristic smooth, exineless pollen of Alismatales has evolved iteratively within the order, probably related to the aquatic or semi-aquatic habit that is characteristic of many alismatid species. Microsporogenesis is successive in most Alismatales (as also in *Acorus*, the sister to all other monocots) and the tapetum is plasmodial. Remarkably long (up to 1500 μm), filamentous pollen occurs in three closely related alismatid families (Cymodoceaceae, Posidoniaceae and Zosteraceae), associated with hydrophilous pollination in these taxa.

Fly pollination in *Ceropegia* (Apocynaceae: Asclepiadoideae): Biogeographic and phylogenetic perspectives

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Plant-pollinator interactions involving small, cryptic pollinators such as micro-diptera are relatively poorly studied compared to those involving larger, charismatic pollinators such as bees, butterflies or birds. *Ceropegia* (Apocynaceae subfamily Asclepiadoideae) is an Old World plant genus of more than 180 spp., all of which possess distinctive flask-shaped flowers that temporarily trap pollinators, and (like all asclepiads) pollen presented as structurally coherent pollinia. The taxonomic diversity of pollinators, biogeographic and phylogenetic patterns of pollinator exploitation, and the level of specificity of interactions were assessed in order to begin to understand the role of pollinators in promoting diversification within the genus. Flower visitor and pollinator data for c. 60 *Ceropegia* taxa were analysed with reference to the main centres of diversity of the genus and to a cpDNA-nrDNA molecular phylogeny of the genus. *Ceropegia* spp. interact with flower visiting Diptera from at least 26 genera in 20 families, of which 11 genera and 11 families are pollinators. Size range of flies was 0.5 to 4.0 mm and c. 94% were females. *Ceropegia* from particular regions do not use specific fly genera or families, though Arabian Peninsula species are pollinated by a wider range of Diptera families than those in other regions. The basal-most clade interacts with the highest diversity of Diptera families and genera, largely due to one hyper-generalist taxon, *C. aristolochioides* subsp. *deflersiana*. Species in the more derived clades interact with a smaller diversity of Diptera. Approximately 60% of taxa are so far recorded as interacting with only a single genus of pollinators, the remaining 40% being

less conservative in their interactions. *Ceropegia* spp. can therefore be ecological specialists or generalists. The genus *Ceropegia* has largely radiated without evolutionary shifts in pollinator functional specialization, maintaining its interactions with small Diptera. Intriguing biogeographic and phylogenetic patterns may reflect processes of regional dispersal, diversification and subsequent specialization onto a narrower range of pollinators, though some of our findings may be caused by inconsistent sampling. Comparisons are made with other plant genera in the Aristolochiaceae and Araceae that have evolved flask-shaped flowers that trap female flies seeking oviposition sites.

***Narthorstia* versus *Konijnenburgia* - why introduce a new taxon?**

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Narthorstia angustifolia from the Lower Cretaceous of Greenland was revised and the true status of the genus *Narthorstia* has been verified in 2007 (Kvaček & Dařková). *Narthorstia* was redefined as a morphogenus of fern foliage recalling the family Matoniaceae, but lacking diagnostic characters of this family: sori consisting of radially arranged sporangia having *Matoniaceae* spores *in situ*. It was the first step in establishing the new genus of unequivocal Cretaceous fossil Matoniaceae: a new genus *Konijnenburgia* was introduced in 2010 (Kvaček & Dařková) for fertile, well preserved ferns of the family Matoniaceae, which were previously assigned to the genus *Narthorstia*. *Konijnenburgia bohémica* is described from the Upper Cretaceous, Cenomanian of the Czech Republic and compared to *Konijnenburgia latifolia* and other Cretaceous members of the family. Each sorus of *Konijnenburgia bohémica* is covered by a massive circular persistent indusium. The indusium is relatively smooth, flat, showing delicate radial striation and biseriate margin. Distance between two sori is 2–2.5 mm. A sorus consists of 12–14 radially arranged wedge-shaped sporangia 500 µm long. Spores of *Matonisporites* type are trilete, triangular in equatorial outline, with slightly convex sides, leasurae raised, extending 75% of the spore radius, interradial thickenings are well pronounced, equatorial thickening (crassitude) is present. Exine is psilate and perispore is not preserved. Spores mean diameter in equatorial view is 47 µm.

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Kvaček, J., Dařková, J. 2007. Revision of the type material in the genus *Narthorstia* Heer (Filicales). Journal of the National Museum (Prague), Natural History Series, 176 (7): 117–123.

Kvaček, J., Dařková, J. 2010. *Konijnenburgia*, a new genus of the fern family Matoniaceae. Review of Palaeobotany and Palynology, 158 (3–4): 308–318

The nature of tropical expansion during global greenhouse climatic phases

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The tropics have an established role as a global biodiversity ‘pump’ through deep-time, maintaining ancient and modern biogeographic patterns such as the latitudinal diversity gradient. The tropical climatic belt has varied in size throughout the Phanerozoic, and during the early Cenozoic warm interval (~65-45 million years ago) tropical vegetation may have occupied as much as three times its current area. It is therefore vital to understand the patterns and processes of diversification within this ancient, expanded tropical biome. Global mean annual temperature (MAT) has previously been shown to correlate well with sporomorph (pollen and spore) standing diversity and turnover in the Palaeogene equatorial neotropics. We test the generality of this result in the middle latitude paratropics using sporomorph data from the US Gulf Coastal Plain (GCP). Our time-series extends across ~ 18 Ma from the late Early Paleocene to the Middle

Eocene. The GCP was geographically separate and floristically distinct from the South American tropics at this time.

Richness and turnover remain relatively stable throughout this interval, and there is no clear relationship with global or regional MAT. There is no shift in abundance to taxa with tropical affinities during warming, or taxa with temperate affinities during cooling. Intra- and intercontinental migration of plant taxa from higher latitudes was a more important driver of diversification than speciation on the GCP. This demonstrates that within an expanded tropical climatic zone, controls on floral speciation and extinction are not uniform through space. In a warmer world, species richness in tropical marginal areas may only increase with temperature through immigration from lower latitudes, rather than from enhanced *in situ* speciation.