ing physical processes responsible for the radiation emitted by neutron stars.

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Palynology

Pollen and Spores. Patterns of Diversification. S. BLACKMORE and S. H. BARNES, Eds. Clarendon (Oxford University Press), New York, 1992. xii, 391 pp., illus. $120. Systematics Association Special Volume 44. From a symposium, London, March 1990.

This volume commendably attempts to put palynological research into the context of biodiversity studies. Although the book largely falls short of this goal, the editors do make a more realistic appeal for palynologists to go beyond mere static descriptive work by striving to interpret and analyze their data as part of broader systematic studies, and this aim is met in many of the chapters. In accordance with this intent, the book has three major themes: ontogenetic processes that give rise to morphologic diversity, systematic analyses of extant plants, and the fossil record of diversification through geologic time, the latter two of which have become entangled because of the increased use of both fossil and extant taxa in rigorous cladistic analyses.

With regard to ontogeny, several chapters consider developmental data in the context of a phylogenetic "survey." In one of these, Gabarayeva reviews patterns of three aspects of pollen wall development among several "primitive" angiosperms. (The term "primitive" should have been clarified; in my view it should refer only to character states, not taxa.) Gabarayeva's most interesting conclusion is that, as evidenced by careful developmental and chemical studies, endexine is present in at least several "primitive" angiosperms, perhaps refuting the oft-cited hypothesis of its secondary evolutionary origin in the flowering plants. Other chapters on ontogeny are oriented more toward describing underlying cellular or subcellular processes. Heslop-Harrison and Heslop-Harrison give a nice review of aspects of the structure, chemistry, and function of apertural intine in relation to pollen tube growth. The examples they cite point out the diversity of intine stratification and demonstrate some interesting correlations of structure with function, such as the outer, resistant pectic layer of *Eucalyptus* serving as an apparent adaptation to drought and heat stress. In another chapter, Knox and Ducker describe plant sperm cells, beginning with a thorough historical survey and ending with recent advances in descriptions and technique. Although the authors do not adequately address the "evolution of gametes" from a phylogenetic perspective, they do review recent findings on male gametes in angiospermous systems, including evidence for the "male germ unit" as a structural entity, sperm cell size or organelle dimorphism and predetermination, and sperm surface protein receptors and motility.

Paleobotanical contributions to the volume include the description of spores isolated from sporangia of several rhyniophytes of the Silurian period by Fanning *et al.* In addition to aiding in stratigraphic identification of palynomorphs, these *in situ* observations of spores with macrofossils (some newly described) could become particularly significant in analyses tracing the early evolution of land plants from "bryophyte" ancestors. In another chapter Gray summarizes our knowledge regarding fossil tetrahedral spore tetrads from the mid-Ordovician period, clarifying a past misinterpretation of morphology and suggesting a possible evolutionary transition between spore tetrads and early trilete spore monads. Gray emphasizes the significance of these tetrahedral spore tetrads in understanding land plant evolution, as they represent microfossil remains of a land flora that evolved some 40 to 50 million years prior to the first Silurian land plants known from macrofossils.

Heterospory has widely been accepted as the first step in seed evolution, on the basis of the sequence of structures appearing in the fossil record. Chaloner and Hemsley critique an alternative hypothesis that has been suggested by some authors: that endospory and retention of homosporous spores preceded heterospory. From their study of wall ultrastructure of megaspores from early free-sporing and seed fossil plants, the authors conclude that the evolution of seeds directly from homosporous ancestors was unlikely because the megaspore exine of at least some early seed plants is as thick as or thicker than that of early heterosporous plants, a primitive retention of non-seed heterosporous plants. Friis *et al.* discuss the morphology of stamens and *in situ* pollen of mid- to late-Cretaceous angiosperms. General trends include the evolution of a laminar filament-connective (in some Magnoliidae), formation of a clear differentiation between filament and connective, loss of the apical connective appendage, and evolution of strictly longitudinal dehiscence (from laterally valvate dehiscence) in Rosidae and Dilleniidae.

The determination of evolutionary polarity of pollen characters is addressed in a chapter by Zavada. One quibble with terminology is that his use of the term "outgroup method" to denote the commonality principle has, from my perspective, been defunct for some time; what Zavada terms "parsimony method" is what most systematists today just call "outgroup comparison," in which parsimony serves as a logical foundation. In any case, Zavada does a good job in applying outgroup comparison (based on parsimony) to assess the polarity of a number of pollen features in the angiosperms, utilizing several unresolved, non-angiospermous outgroups. Interestingly, he concludes that information from dispersed fossil pollen (especially pre-Cretaceous angiosperm-like pollen) may actually obscure phylogenetic relationships because it introduces additional variation in the unresolved outgroups, rendering some previously inferred polarities ambiguous. However, this limitation may be overcome by the use of additional characters and a greater number of taxonomic units (including dispersed pollen taxa) in an explicit phylogenetic analysis, in which outgroup interrelationships are better resolved. An example of such an explicit analysis is that of Doyle and Hotten, who provide a careful, detailed evaluation of early angiosperm pollen morphology and ultrastructure within a phylogenetic context. In part on the basis of a previous study (by Donoghue and Doyle), the authors place various fossil pollen types within one or another of five major angiosperm lineages, by correlation with modern forms or by hypothesizing evolutionary gradation series. Although considerable ambiguity regarding angiosperm relationships remains, this study exemplifies the insight that may be gained in studying fossil pollen in terms of a cladistic framework.

The chapters on systematic studies of extant taxa include some standard papers plus some with intriguing new approaches. An exciting methodology for quantifying variation in pollen sculpturing is presented by Vezey *et al.* The authors measure ultrastructural parameters from numerous scanning electron micrographs (using a video-interfaced image analysis system) and analyze the data using UPGMA. This study may serve as a model for quantifying data and more carefully justifying discontinuity of pollen character states in systematic studies. Finally, Cox *et al.* describe an interesting computer simulation based on three-dimensional random-search theory. Their mathematical predictions conform to the occurrence of filiform pollen grains in subsurface water-pollinated angiosperms.

In summary, this book would be worthy of selective reading to many, particularly those interested in development, land plant phylogeny, and application of new palynological techniques.

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