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Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction

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Abstract

Information on the fossil record of angiosperms has expanded dramatically over the past twenty-five years, and in particular the discovery of numerous mesofossil floras with fossil flowers has added a completely new element into the study of angiosperm history. A review of the phylogenetic diversification of angiosperms through the Cretaceous is given based mainly on the extensive record of fossil flowers and other reproductive organs. Several major phases in the Cretaceous angiosperm radiation can be distinguished. These are recognised primarily by structural and functional traits of the flowers and by pollen features, as well as distinct changes in the systematic composition of the floras. ANITA grade angiosperms and Chloranthaceae, as well as other magnoliids, early monocots and early eudicots, differentiated almost simultaneously during the Early Cretaceous. There is also strong evidence for extensive diversification of core eudicots during the Late Cretaceous. In addition to patterns of phylogenetic diversification, the fossil record of angiosperm flowers also provides insights into the timing of floral evolution in terms of the functions of the various kinds of floral organs, as well as accompanying patterns of ecological diversification.

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1. Introduction

While most major groups of land plants have a fossil history extending back to at least the Early Mesozoic, the first unequivocal evidence of angiosperms is from the Early Cretaceous. Nevertheless, despite their relatively late geological appearance, angiosperms are hugely diverse. With perhaps as many as 420,000 extant species (Govaerts, 2001), there are many more species of angiosperm than all other species of land plants combined.

The extraordinary species diversity of angiosperms is also matched by exceptional structural diversity. In habit angiosperms range from minute free floating aquatics to massive forest trees, while their propagules range from the dust seeds of orchids to the giant double coconut. The diversity of angiosperm functional types is overwhelming and underpins their ecological success. Angiosperms dominate the vegetation of most land ecosystems.

Angiosperm flowers also exhibit enormous diversity ranging from the minute male flowers of *Hedyosmum* to the giant blossoms of *Rafflesia*. The diversity of angiosperm flowers reflects extraordinary developmental and evolutionary plasticity (e.g., Endress, 1994). Since the earliest scientific studies it has been clear that these structures provide a great range of features by which different groups of angiosperms may be distinguished and compared. And since Darwin the characteristics of flowers have also been widely

used to interpret evolutionary relationships among different angiosperm lineages. Flowers are also of central importance to angiosperm reproductive biology and have been highlighted as key innovations that perhaps facilitated angiosperm diversification through their influence on speciation and extinction rates.

Over the last twenty-five years, information on the flowers of ancient angiosperms has expanded dramatically with the discovery and investigation of fossil floral material from Cretaceous deposits. It is these studies that are mainly reviewed in this work. Together with new insights into angiosperm phylogeny based on analyses of DNA sequences (see references in Soltis and Soltis, 2004), these data now permit critical evaluation of previously hypothesised patterns of angiosperm floral evolution. This, in turn, facilitates a clearer understanding of the developmental and evolutionary processes responsible for angiosperm floral diversity (e.g., Endress, 2001b).

In this paper we review the patterns of floral diversification revealed by our current understanding of the relationships among extant angiosperms and the emerging fossil history of the group. We then discuss the major morphological innovations and recurrent themes that can be detected in the early evolution of angiosperm flowers. In particular, we draw on current hypotheses of angiosperm phylogeny based on molecular data, and the results of our own research on Cretaceous angiosperm flowers.

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