

# Diversification of Eupolypods in Mid-Cretaceous—Evidenced by Myanmar Amber Forest

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**How to cite this paper:** Li, C.X. and Zhang, L.B. (2019) Diversification of Eupolypods in Mid-Cretaceous—Evidenced by Myanmar Amber Forest. *Open Journal of Geology*, 9, 726-730.

<https://doi.org/10.4236/ojg.2019.910086>

**Received:** August 30, 2019

**Accepted:** September 24, 2019

**Published:** September 27, 2019

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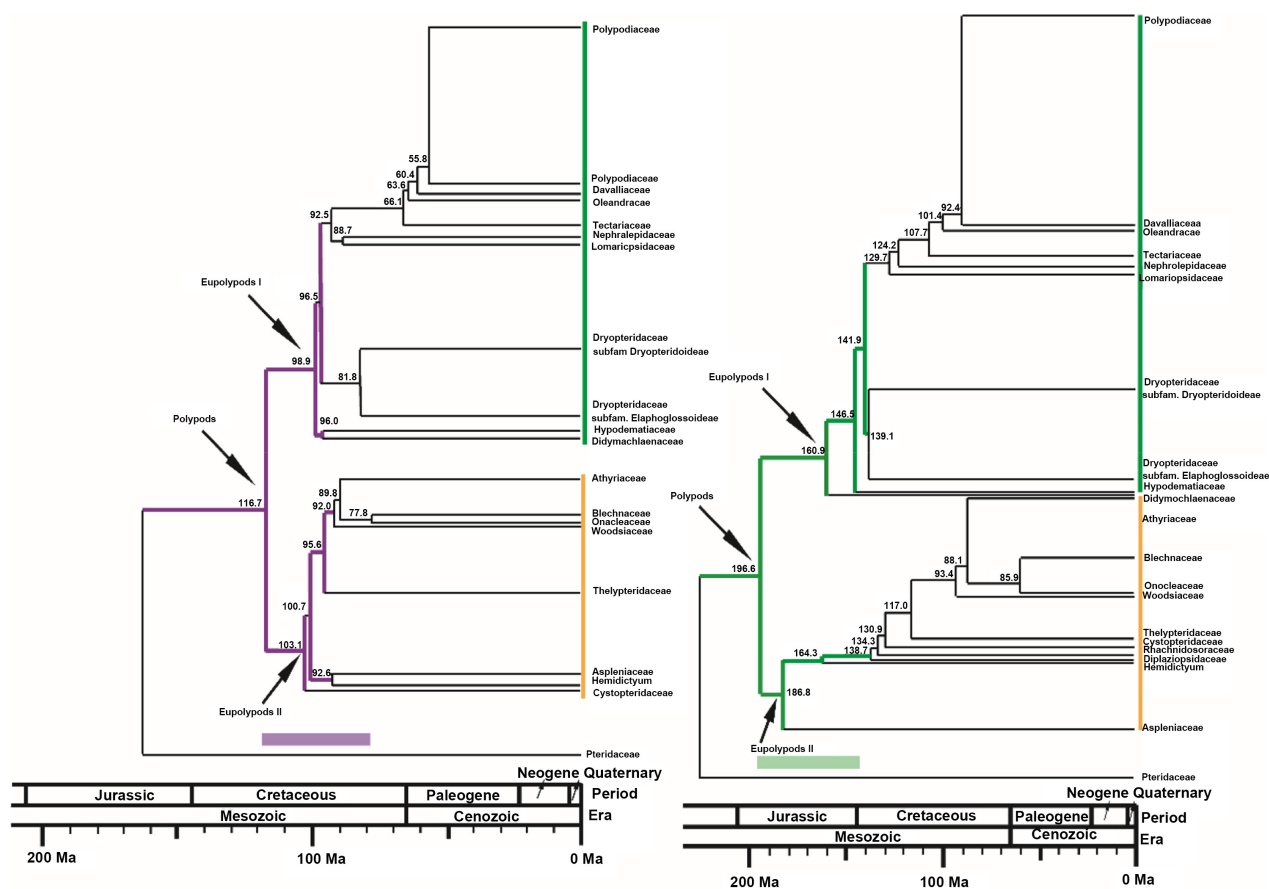
## Abstract

The evolutionary history of Eupolypods still remains unclear, especially on its diversification scenarios. In recent years, it has been found that approximately 100 million-year-old Myanmar amber provides a unique source of polypod fossils. Different families and numerous sporangia, spores, and scales have been found in Myanmar amber. These discoveries are nevertheless important because they provided the first unequivocal fossil evidence that the diversity of eupolypod ferns was present already in the mid-Cretaceous Myanmar amber forest. This clearly shows that Eupolypods originated before mid-Cretaceous, probably as early as the Early Jurassic, which is consistent with the recent divergence time estimate based on molecular dating.

## Keywords

Mid-Cretaceous, Myanmar Amber, Eupolypods, Divergence Time

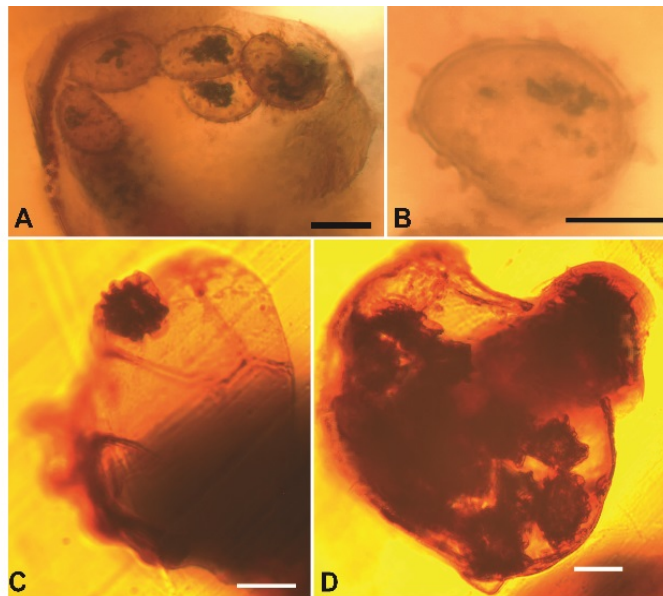
In the last two decades, unprecedented progress has been made by employing DNA sequence data and phylogenetic approaches toward a full understanding of the relationships that shape the major branches of the fern tree of life. In 2006, these phylogenetic hypotheses were consolidated and presented in a revised classification for ferns [1]. Smith *et al.* [1] recognized a monophyletic order Polypodiales (“Polypods”, **Figure 1**), and most species within the order belong to the Eupolypods, composed of two clades: Eupolypods I and Eupolypods II [2] [3]. Together, the eupolypod lineages include nearly 6000 species—more than half of extant fern diversity.



**Figure 1.** Eupolypod phylogenetic chronology based on the study of [4] (left) and [5] (right). Divergence time estimates for eupolypod lineages are indicated on the left side of the time tree.

However, the evolutionary history of the ferns remains incompletely understood, especially on its diversification scenarios, for example, most DNA-based divergence-time studies indicate that Eupolypods diversification occurred in the Late Cretaceous [2] [4], but Testo and Sundue [5] demonstrated that Eupolypods originated as early as in the Early Jurassic (Figure 1). The latter authors thought their age estimates to be much more realistic because they used more taxa (4000 taxa), a more advanced dating algorithm, and many more fossil calibrations with different placements. Although a range of molecular dating methods is now available, they all share a vital dependence on fossils as one of important age calibrations. It is therefore of prime importance to thoroughly document and critically evaluate new and informative fern fossils, especially those fossils from those periods of geologic time that are believed to represent important phases in the establishment and/or radiation of new fern lineages [6]. However, so far, no single study based on fossils from stratigraphic depositions has provided unequivocal evidence for a Cretaceous or pre-Cretaceous occurrence for Eupolypods [2] [7] [8] [9].

In the recent years, it has been found that approximately 100 million-year-old Myanmar ambers provide a unique source of polypod fossils. Eight fossils of



**Figure 2.** Eupolypod spores (monolete with distinct perine) in Cretaceous Myanmar amber ((A) (B), #2016-03; CD, #2018-67). Scale bars = 20  $\mu$ m (A) (C) (D), and 10  $\mu$ m (B).

different families and numerous sporangia, spores, and scales have been found in Myanmar ambers [6] [10]-[15], including eupolypod-like fossil *Cretacifilix fungiformis* [10], the first compelling eupolypod fossil *Holtumopteris burmensis* [6], eupolypod fossil scales, and spores (Figure 2). All these findings suggest that a diversity of eupolypod ferns was present already in the mid-Cretaceous Myanmar amber forests, clearly showing that Eupolypods originated before mid-Cretaceous, probably as early as the Early Jurassic, consistent with the divergence time estimates from the study of Testo and Sundue [5]. Myanmar amber is about to become the most important source of new information on mid-Cretaceous fern diversity, as work on the Myanmar amber deposits continues, new fossils will be discovered and described and can be used to refine reconstructions of fern evolution during this important period of geologic time (*i.e.*, the Cretaceous Terrestrial Revolution, [16]), and eventually can be used to piece together the steps and stages in the evolution and radiation of the eupolypod ferns [6].

### Acknowledgements

The research was supported by projects of State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of geology and Palaeontology, Chinese Academy of Science) (Grant No. Y626040108) and Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDB26000000). This is a contribution to UNESCO-IUGS IGCP Project 679.

### Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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