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Evolutionary and ecological perspectives of Late Paleozoic ferns Part I. Zygopteridales

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Abstract

The Zygopteridales are an extinct group of late Paleozoic ferns with distinctive morphologies, some suggesting diverse adaptations to water-stressed habitats. Anatomical and morphological details are supplemented and summarized along with illustrations in order to explore the paleoecology and evolutionary interpretations of select genera. Earliest undisputable zygopterid ferns with clear distinction between stem and megaphyllous leaf occur in the Tournaisian. Early divergence led to the *Diplolabis–Zygopteris* ferns with erect quadriseriate fronds and to *Ankyropteris* with dorsiventral biseriate fronds. Clepsydroid fern habits include both false trunk, *Symplocopteris* and *Austroclepsis*, and unbranched arborescence, *Asterochlaenopsis*. Etapteroid fern habits were mainly rhizomatous, the *Metaclepsydropsis–Diplolabis–Musatea* assemblages and *Zygopteris*. Tree habit occurs in *Zygopteris primaria*. *Zygopteris* rhizomatous assemblages (*Etapteris*, *Alloiopteris*, *Corynepteris*, *Biscalitheca*, *Nemejcopteris*) provide the strongest evidence for water stressed adaptations and responses from arrested growth or dormancy of shoots, the wood in stems and petiolar bases, distribution of tyloses in petiolar metaxylem, and the complex soral and sporangial structure of *Biscalitheca* and *Corynepteris*.

Keywords: zygopterid ferns; evolution; paleoecology; permineralization; Carboniferous–Permian; Euramerica; Australia

1. Introduction

Morphological, ecological and evolutionary perspectives of Late Paleozoic ferns have changed dramatically during the 20th century and continue to be elaborated upon. The most precipitous alterations, helping to delimit what were bona fide ferns, came with the discoveries of other vascular plant groups. The recognition of seed ferns (Oliver and Scott, 1904) and subsequent studies by many others swept away the misconception that the late Carboniferous (Pennsylvanian) was a tropical age of ferns. Nonetheless, there was no doubt that Marattialean tree ferns with complex anatomy were widespread and sometimes abundant in the late Carboniferous and Permian tropics.

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The emerging new perspectives of Late Paleozoic ferns near the turn of this past century related to the so-called "small ferns" which were known anatomically. Such plants were recognized by Seward (1910) as the Coenopterideae, then Coenopteridales; the coenopterid name implied that the ferns collectively exhibited many of the generalized character states now exhibited by some extant fern families, but in such different combinations as to not be assignable to any.

From an anatomical point of view, coenopterids were considered to have primitive protostelic stems and petiolar xylem cross sections simulating an alphabet soup of E, H, I, X, Y and inverted elaborations on the letter C. The associated or clearly attached sporangia of members of the earlier recognized, anatomically based families (Stauropteridaceae, Zygopteridaceae, Anachoropteridaceae, Botryopteridaceae) ranged from both eusporangiate and leptosporangiate osmundoid to the largest and histologically the most complex sporangia known among ferns. Added to this anatomically known sporangial morphology were numerous studies of the compression record of ferns, particularly those of *Senftenbergia* (schizaeaoid) and *Oligocarpia* (gleichenioid).

As a consequence of both informative levels available and perspectives of the primeval nature of the ferns based heavily on the antiquity of their geologic age and status (i.e. earliest ferns), the initial and sustained research perspectives of the first half century were strongly influenced by the searches for early ancestral members of the Osmundaceae (*Botryopteris*), the Schizaeaceae (*Senftenbergia*) or the Gleicheniaceae (*Oligocarpia*). This evolutionary perspective conveyed that the late Paleozoic small ferns were likely a primitive pool of morphotypes out of which arose the Filicales.

In mid-century into the 1960s there was an increased effort to anatomically document the morphology of frond origins from branch systems, influenced by Devonian discoveries of progymnosperms (Beck, 1960a,b), establishment of the Trimerophytina (Banks, 1968) and subsequent studies, as well as, by many major contributions on the coenopterid ferns. The mix of Devonian and Carboniferous studies energized evolutionary thinking about the primitive morphology of the small Carboniferous ferns we now assign to the Zygopteridales and Filicales. The available information levels provided a mixed stratigraphic base level whereby frond evolution as a focal topic really became pivotal as to whether these "ferns" were preferns, quasiferns or primitive ferns versus just ancient ferns.

In hindsight it is now evident that many of the misleading aspects of the so-called primitive nature of the vegetative morphology involving the fronds were a combination of shoots on fronds and the mixtures of foliar and cauline anatomy suggesting frond–branch systems accommodating vegetative propagation. A turning point in the morphological studies was the review paper by Phillips (1974) wherein the basic morphological attributes of the fern concept were summarized and most of the coenopterid ferns were regarded as true ferns.

Ferns are lower vascular plants (reproductive life cycle) with megaphyllous leaves, foliar-borne sporangia, circinate vernation, protostelic to polycyclic dictyostelic stems, and adventitious root systems. Recognition of the fern grade of organization in the fossil record of the Carboniferous and Permian is heavily dependent on the study of anatomically preserved assemblages, reconstructions of the representative plants, and character-state correlations with specimens in other preserved modes. Basic morphological identifications of fronds, stems, roots and sporangia are aided decisively by cellular observations of the diagnostic criteria of organs.

Early ferns of the Carboniferous and Permian, in turn, have been described systematically, based on cross-sectional foliar (non-laminate) anatomy, because the foliar members were the most commonly identifiable organs. Interestingly enough, the alphabet soup-like configurations of the foliar xylem encompass quite a divergent series of geometric patterns in cross section and have proved to be excellent guides despite expressed disparities (Stewart and Rothwell, 1993).

In this series of reviews on the paleobiology of the Paleozoic ferns, anatomically preserved assemblages are emphasized because of the necessity of such cellular observations in identifications, reconstructions and interpretations. Fortunately, much progress has been made in research utilizing anatomical preservation in relation to other modes of entombment of fossil ferns. Thus, very significant expansions of data sources have been generated from compression/coalified macrofossils as well as plant sources of spores.