How early ferns became trees

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A new anatomically preserved fern, discovered from the basalmost Carboniferous of Australia, shows a unique combination of very primitive anatomical characters (solid centrarch cauline protostele) with the elaboration of an original model of the arborescent habit. This plant possessed a false trunk composed of a repetitive branching system of very small stems, which established it as the oldest tree-fern known to date. The potential of this primitive zygopterid fern to produce such an unusual growth form—without real equivalent among living plants—is related to the possession of two kinds of roots that have complementary functional roles: (i) large roots produced by stems with immediate positive geotropism, strongly adapted to mechanical support and water uptake from the soil; and (ii) small roots borne either on large roots or on petiole bases for absorbing humidity inside the false trunk.

Keywords: early fern; false trunk; Lower Carboniferous; Australia

1. INTRODUCTION

The tree growth habits developed by different plant lineages illustrate marked examples of convergent evolution (Chaloner & Sheerin 1979; Mosbrugger 1990; Niklas 1997). The oldest trees that have a modern 'woody' architecture belong to the Mid- and Late Devonian progymnosperms that first evolved a bifacial cambium (Beck & Wight 1988) and the ability to produce thick amounts of wood supporting the branching trunk and canopy (Meyer-Berthaud *et al.* 1999), as in modern conifers (Mosbrugger 1990). By contrast, tree-ferns known since the Carboniferous (such as *Psaronius*) are devoid of wood, but their monocaulous trunks with a crown of large compound leaves were supported by a mantle of adventitious roots (Morgan 1959). A comparable growth form persists in the extant tree-ferns in the Cyatheaceae and Dicksoniaceae. Other fossil ferns develop 'false trunks' from the intertwining of stems, petioles and roots. That structure was first described by Corda (1845) in the Cretaceous fern *Tempskya*. We report here the oldest experiment in attaining an arborescent habit through formation of a false trunk; the new plant, interpreted as a zygopterid fern, increases our understanding of the exceptional growth form that evolved independently—at an interval of 200 million years—in two groups of ferns, but which has no real equivalent among extant ferns or, generally, in other plant groups.

2. MATERIAL AND METHODS

The new fossil fern comes from the Keelbottom Group, Hardwick Formation, on the flank of Mt Saint Michael, Dotswood, Queensland. The horizon containing the fossil plants consists of clastics of volcanic origin and silica-rich mud. These beds yield a *Siphonodella crenulata* conodont zone, indicating a Mid-Tournaisian, Lower Carboniferous age (Mawson & Talent 1998). The largest specimen, 50 cm in diameter, is interpreted as the base of a trunk. Another specimen consists of three segments, totalling

more than 80 cm in length and 21 cm in diameter, which are interpreted as median portions of trunks. The basal segment, 23 cm long, was sectioned serially; photographs and camera lucida drawings of all the surfaces were prepared in order to reconstruct the complex branching system. Transverse and longitudinal thin sections prepared in the different types of organs reveal exceptionally preserved anatomical details.

3. RESULTS

The largest specimen is composed almost entirely of roots with only a few stems (5–8 mm in diameter) bearing petioles (7–10 mm in diameter) scattered near the centre (figure 1a). Roots are free but more or less densely packed and range from 1 to 5 mm in diameter. Tapering of the trunk and a very significant increase in the number of stems and petioles contrast with the organization at the base. In this mid-region of the trunk, stems and petioles are uniformly distributed within the trunk mass (figure 1b). Within an interval of 20 cm along the trunk, the numbers of stems (66–68) and of petioles (45–47) do not change significantly. Several thousand roots of very different sizes fill the spaces between vertically orientated stems and petioles (figure 1c). The petioles, also called phyllophores, have a bar-shaped or clepsydroid xylem strand ('P', figures 1c, 2b). Sections of individual stems are circular in outline ('S', figure 1c) and show solid mesarch cylindrical protostele and an outer cortex of thickened fibre cells constituting an efficient supportive tissue. The cauline branching system is highly complex and repetitive (figure 2b). Each branch of an isotomy quickly produces one phyllophore trace; subsequently, one branch may undergo a stelar dichotomy, whereas the other branch produces a second phyllophore trace. Lacinate pinnae are incompletely preserved. Small adventitious roots (1–1.5 mm in diameter) depart horizontally from both sides of the phyllophore traces; they are endogenous in origin and produced precociously after the phyllophore trace emission (figure 2b). By contrast, one large adventitious root (3–4 mm in diameter) is emergent from each branch stele; these roots are generally tetrarch ('R', figure 1c), immediately geotropic and enlarge in diameter

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Figure 1. Cross-sections showing the difference between the (a) basal and (b) median regions of a trunk concerning the distribution of small stems and petioles within the mass of roots (light stippling). (c) Detail of the anatomy (cross-section) of stems (S), petioles or phyllophores (P) and roots (R) from the median region of trunk (scale bar, 1 mm).

towards the base of the trunk. Large roots either bifurcate or produce small endogenous roots arising perpendicularly in front of a protoxylem strand. All roots are densely covered by hairs (figures 1c, 2b). Large roots appear to function as mechanical support and have an outer zone of thick-walled fibres. Excellent anatomical preservation of the tissues in the base of the trunk suggests that the oldest large roots lost epidermal hairs but retained hydraulic absorption from the soil.

4. DISCUSSION

The new Australian fern has a number of characters consistent with the extinct group of ferns known as Zygopteridales (Taylor & Taylor 1993), which include: (i) anatomical distinction between a radially symmetrical stem and a foliar member where the petiole or phyllophore has two perpendicular planes of symmetry; and (ii) a clepsydroid phyllophore anatomy ('P', figure 1c) representing a primitive character and, in these new fossils, the stem actually shows the simplest stelar organization known among zygopterid ferns. It is also significant that the stele is very similar to the solid terete and centrarch protostele of basal members of Devonian Euphyllophytina such as *Psilophyton* (Banks *et al.* 1975; Kenrick & Crane 1997). In contrast to a primitive cauline anatomy, the new fern shows an advanced level of morphological organization with branching stems bearing leaf members (phyllophores) and roots, two organs known to have evolved in only a few other basal euphyllophytes (e.g. the prefern *Rhacophyton* and the progymnosperm *Archaeopteris*).

The new fern represents the oldest known example of a false trunk (figure 2a) in ferns and in plants in general. Only two other fossil fern genera exhibit this unusual growth form. One is *Austroclepsis* (Sahni 1928), a zygopterid fern from rather later in the Lower Carboniferous (Upper Viséan) of Australia, which differs by a number of anatomical features of individual stems, roots and phyllophores.

The interval of time (15–20 million years according to Harland *et al.*'s (1990) time-scale) separating the two taxa was certainly adequate for the transition from a small solid protostele to the large medullated actinostele present in *Austroclepsis*, and perhaps supports the idea that the two ferns are successive members of the same Australian clade of zygopterid ferns. Interestingly, false trunk morphology evolved again more than 200 million years later, during the Cretaceous, in an unrelated group of ferns, the Tempskyaceae (Filicales). In the genus *Tempskya* Corda (Corda 1845), which comprises a large number of species from Europe, North America and Japan (Tidwell & Ash 1994), the false trunk was also composed of many small dichotomizing stems embedded in a mass of roots and petiole bases, but they differ markedly from the new fern in stem and petiole anatomy. In the new fern, as in *Tempskya*, the largest—supposedly basal—portion of trunks contains the fewest axes, which probably result from a single original stem. Although it is difficult to reconstruct the development of these plants, it is possible that the young fern quickly produced an obconical, erect, branching system supported mechanically by the large reflexed adventitious roots arising from the numerous branches. Stems and phyllophores have an outer cortex with thickened cells equivalent to the hypodermal sterome of *Psilophyton* (Speck & Vogellehner 1994); however, without the mechanical support of roots, the hypodermal architecture might not have been sufficient to support the highly branched system developing in the young plant. In the mature plant, the false trunk consisted of more than 60 axes maintaining a constant diameter above the mantled base. This organization shows a remarkable convergence with living tree-fern construction (Mosbrugger 1990), in extant Cyatheaceae and Dicksoniaceae a crown of fronds and many roots initially develop obconically at ground level, followed by extension of a single-stem trunk, which maintains a relatively constant diameter (Hallé *et al.* 1978). This living tree-fern construction differs slightly from that of the Upper Carboniferous–Permian *Psaronius*,

Figure 2. (a) Reconstruction of the false trunk habit of the new fern. (b) Detail of a portion of the branching system inside the trunk with erect isotomous stems (S) that bear petioles (P) and reflexed or lateral hairy roots (R). For clarity, only some roots and bases of petioles have been shown.

in which the single-stem diameter increases distally (Morgan 1959). In *Psaronius*, adventitious roots emerge some distance below the apex and extend downwards, forming a stiff mantle of roots with sclerenchymatous cortex, bonded by an interstitial tissue of proliferated root hairs, which constitute the mechanical support (Mosbrugger 1990; Niklas 1997). In the new tree-fern from Australia, roots are intermixed with stems and petioles along the entire trunk, originating continuously along branches and therefore near the top of the trunk as well, which is another marked difference from *Psaronius*. The false trunk of the new Australian fern represents an original and very light construction in which roots are

filling the available space between stems and petioles; their dense covering of root hairs is an indication that a high level of humidity existed inside the trunk, creating a favourable ecosystem for some herbivores, the coprolites of which are abundant in hollowed-out organs in the trunk.

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