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40. This estimate is based on litter-fall data and assumes a 5-year period of leaf retention [A. Abee, thesis, Oregon State University, Corvallis (1973)].
41. We thank F. J. Swanson, P. Sollins, D. Turner, and J. Bailey for useful comments. Supported by NSF grant BSR-8514325 (Long-term Ecological Research at the H. J. Andrews Experimental Forest) and funding from the U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. Paper 2572 of the Forest Research Laboratory, Oregon State University, Corvallis.

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An Aptian Plant with Attached Leaves and Flowers: Implications for Angiosperm Origin

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Recent phylogenetic studies and fossil finds support a new view of the ancestral angiosperm. A diminutive fossil angiosperm from the Aptian of Australia has attached leaves, with intermediate pinnate-palmate, low-rank venation, and lateral axes bearing pistillate organs subtended by bracts and bracteoles that are the oldest direct evidence of flowers. A variety of data suggests a similar morphology for the ancestral angiosperm. This hypothesis explains similarities between rhizomatous to herbaceous Magnoliidae and basal monocots, scarcity of early angiosperm wood, and lack of recognition of earlier remains.

THE OLDEST UNEQUIVOCAL ANGIOSPERM remains, mostly dispersed organs, are from Lower Cretaceous strata. Fossil pollen is reported from the Hauterivian of England and Barremian of West Africa (*1*), and leaves from the Barremian to Aptian of eastern North America (*2*). Unequivocal angiosperm flowers (*3*) and wood (*4*) first appear during the Albian. These remains show affinities to taxa with diminutive stature and reproductive organs (*2, 5–7*) and to taxa with shrub to tree habit and moderate-sized, complex flowers (*2, 3*). The early and possibly oldest occurrence of the former conflicts with the existing theory that the ancestral angiosperm was a small tree or shrub, with pinnately veined, simple leaves and flowers of moderate to large size with numerous reproductive parts (*8*), though other views have been proposed (*2, 9, 10*).

We recently recognized the angiospermous affinities of a plant described by Drinnan and Chambers as a fern ("Marsileales ? indet?") (*11*) from the Aptian Korumburra Group of the Gippsland Basin at Koonwarra, Victoria, Australia (*11–13*). This fossil has leaves and attached female inflorescences (Fig. 1A), which are the oldest unequivocal angiosperm reproductive structures. The only angiospermous pollen reported from Koonwarra, *Clavatipollenites hughesii* (*12*), is of a type having the earliest range of any flowering plant. Taken together, the fossil evidence and recent phylogenetic analyses of extant plants (*10, 14*) are compatible with a new hypothesis for the ancestral angiosperm.

The fossil has two leaves attached to the axis, which bends sharply to the right at the upper node, and two axillary inflorescences (Fig. 1A). Attachment of the proximal leaf and distal inflorescence is shown by their orientation and similarity to the other clearly attached organs. The inflorescences are masses of overlapping bracts, bracteoloes, and ovaries; distinct bracts are noticeable at the apex of the lower inflorescence and along the right side of the upper, where they overlap the distal petiole.

The axis is thin (1.4 mm wide) and exhibits longitudinal ridges, which may be the remains of vascular bundles. Apparent fragility, an apparently dissected stele, and co-occurrence of fully expanded, diminutive leaves with well-developed axillary inflorescences suggest a herbaceous habit. Widely spaced yellow-brown, translucent, discoidal impressions (0.03 to 0.04 mm; Fig. 1G) occurring throughout the fossil may be the remains of ethereal oil cells.

The leaves are alternately arranged (Fig. 1A). The lower (Fig. 1E) has a long petiole that clasps the axis, and a lamina that is apparently folded over distally (Figs. 1E and 2A). Evidence for folding derives from two major veins that extend to the margin and abruptly reverse at the fold; complex, anomalously dense higher venation apparently resulting from superimposition of two levels of veins; and lack of a carbonaceous thickening along the folded margin. The leaf is simple, unlobed, slightly asymmetrical at the base, and broadly ovate, to 10.1 mm wide. The lower laminar margin is darkly stained, suggesting a thickening, and has an inferred incipient sinus (at indentation on left; Fig. 1E). The overfolded upper portion appears to be dissected into three deeply incised dentations. Evidence for dentations, rather than tears, is the symmetry of their outline and vein convergence toward their apices.

A five-stranded vascular trunk emerges into the leaf blade (Figs. 1E and 2A) with the medial strand composed of two bundles. The vein pattern qualifies equally as very loosely and irregularly palinactinodromous or weakly pinnate with three to four pairs of secondary veins. The basal two pairs are crowded proximally and arise as lateral bundles directly from the petiole at an acute angle. The festooned brochidodromous distal secondaries have irregular spacing and angles of origin, branch dichotomously to form loose and irregular loops in at least two series, and are poorly differentiated from the primary and tertiary venation.

Tertiary and higher (to fifth) order veins (Figs. 1E and 2A) form a random reticulum in which vein orders cannot be consistently determined, and the angle of tertiary vein origin is irregular but mostly acute. A fimbrial vein appears to be present. Areolation is apparently incomplete or possibly lacking over some of the leaf. The leaf-rank (*15*) is very low first rank, the lowest of any leaf described or examined among basal angiosperms (*16*).

The inflorescence (Fig. 1A) is pedunculate and cymose, probably a thryse (to 9 mm long), with ovate bracts (to 3.5 mm long; b in Fig. 1, A and F) attached to a primary axis. There appear to be two axillary bracteoles (br in Fig. 1F) and within these is at least one ovary. The small, oblong ovaries (Fig. 1C; 0.57 mm wide) have a short stigma (Fig. 1C) and no style. There is no evidence of a suture, and, although the specially placed stigma is typical of ascidate carpels, the ovary could be syncarpous.

Leaf characters alone reveal the angiospermous affinities of the fossil. Random-reticulate venation with anastomoses at several vein orders, a multistrand splaying out into the laminar base forming an indeterminate actinodromous-brochidodromous venation, and incomplete areoles occur in combination only in angiosperms (*5, 16*). In addition, the morphology of the reproductive

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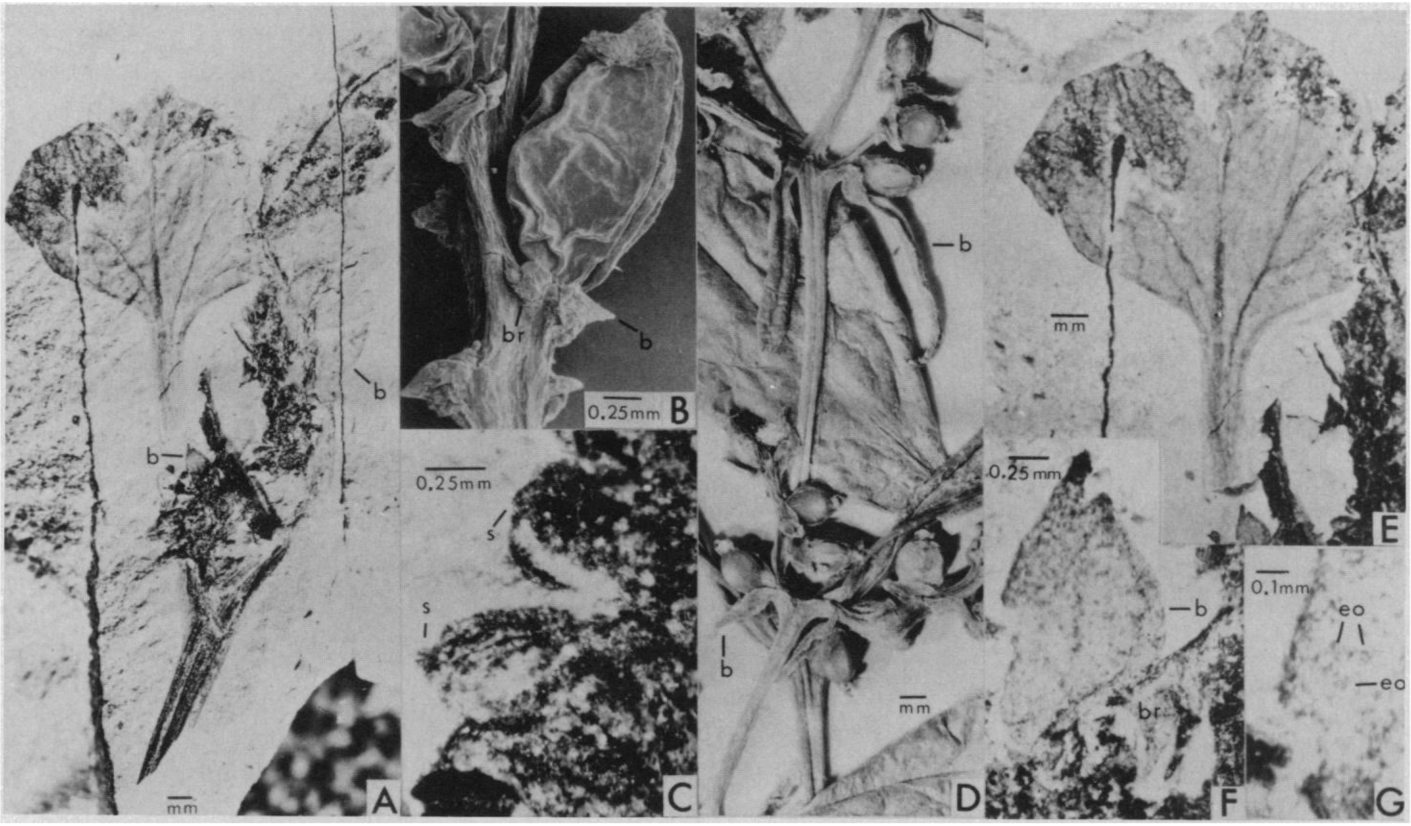

Fig. 1. Fossil angiospermous plant of Aptian age from the Koonwarra locality, Victoria, Australia, and some female inflorescences of extant Chloranthaceae. (**A**) Whole Koonwarra plant with two attached leaves each subtending an inflorescence with bracts (b). (National Museum of Victoria, P167565). (**B**) Female flower of *Ascarina lanceolata* Hook, f., *Christophorsen and Hume 2014* (YU), note single ovary subtended by two bracteoles (br) and bract (b). (**C**) Fossil ovaries with stigmatic surfaces (s). (**D**) Female inflorescence of *Hedyosmun nutans* Swz., *Wright 1416* (YU); the subtending bract is elongate. (**E**) Detail of the lower leaf of the fossil. (**F**) Bract (b) from the lower inflorescence of the fossil with remains of the bracteoles (br) and possibly the ovary. (**G**) Detail of the bract in F showing the inferred ethereal oil cells (eo).

structures is similar to angiosperm inflorescences and ovaries.

Generally, the fossil shares the greatest number of states with living members of Magnoliidae [sensu Cronquist (*17*)] and basal monocots [sensu Dahlgren *et al.* (*18*)]. Specifically, the splayed multistrand, intermediate palmate to pinnate primary venation, incomplete areoles, and generally low leaf-rank are shared with some Saururaceae, Piperaceae, Aristolochiaceae, Dioscoreaceae, Smilacaceae, and Barclayaceae (Fig. 2, B to D). Closest similarities are with the first three families, though none are dentate. Saururaceae and Aristolochiaceae leaves (Fig. 2) usually have cordate bases, whereas those of Piperaceae either have different primary venation or are thickened.

Diminutive apetalate flowers subtended by bracts in spicate inflorescences are found in Saururaceae, Piperaceae, and Chloranthaceae (*17*), but bracteoles occur only in Chloranthaceae (*19*) (Fig. 1, B and D). Ovaries consisting of a single carpel with a terminal truncate stigma are found in Piperaceae, some Dioscoreales, and Chloranthaceae (Fig. 1B) (*17*).

Although the Koonwarra pollen flora is

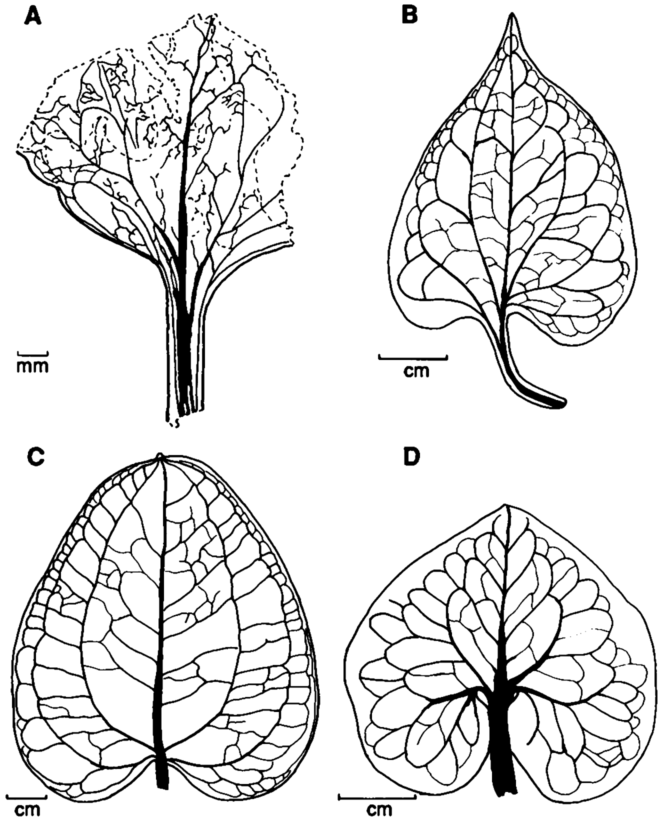

Fig. 2. Leaf architectural comparison of lower order venation of the Koonwarra fossil to several extant angiosperms. (**A**) Detail of the lower leaf of the fossil. Overfolded portion outlined with dashed line. (**B**) *Houttuynia cordata* Thunb., *Tsiang 9913* (NY) (Saururaceae). (**C**) *Smilax glauca* Walt., *Moldenke 6118* (NY) (Smilacaceae). (**D**) *Asarum canadense* L., *Tweedy 22* (YU) (Aristolochiaceae).

diverse, only one known angiosperm-type grain is reported, and it is monosulcate, spherical, tectate-columellate, and reticulate (*12*). This type occurs in *Saruma* (*20*) (Aristolochiaceae), Chloranthaceae (*21*), and Dioscoreales (*20*) (reticulum uneven).

The fossil clearly has a mosaic of states distributed in different extant families. The leaves are similar to the entire margined leaves of Saururaceae, Piperaceae, and Aristolochiaceae (some Aristolochiaceae have lobed leaves). Reproductive organs subtended by bract-bracteole complexes occur only in Chloranthaceae. Other early Cretaceous dispersed organs also show similarity to those in the same suite of taxa. Thus *Clavatipollenites*-type pollen is similar to that of Chloranthaceae and Aristolochiaceae. Contemporaneous dispersed leaves (*2*) share the intermediate pinnate to palmate primary venation found in these families, excluding Chloranthaceae, and some leaf cuticles are similar to those of Chloranthaceae (*6*). In addition, flowers similar to those of Chloranthaceae (*7*) are found in slightly younger sediments.

These data, combined with analyses of leaf (*16*), flower (*22*), ovule, and carpel (*23*) characters, support the hypothesis that the ancestral angiosperm was a small, rhizomatous perennial (with secondary growth), which had diminutive reproductive organs arranged cymosely and subtended by a bract-bracteole complex. Further support is indicated by recent phylogentic analyses of RNA sequences (*14*), and morphology and anatomy (*10*) of basal angiosperms. In the former the shortest or nearly shortest trees have members of Saururaceae or Piperaceae basal, whereas the latter has nearly shortest trees rooted near these families. This hypothesis explains the numerous similarities between the basal monocots (*18*) and these rhizomatous-herbaceous dicots, suggesting that they probably diverged quite early. It also suggests that the lack of pre-Albian fossil angiosperm wood (*4*) is due to their diminutive habit and that the failure to recognize protoangiosperm fossils results from their diminutive size and an incorrect search image.

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Expression of β-Nerve Growth Factor Receptor mRNA in Sertoli Cells Downregulated by Testosterone

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Nerve growth factor (NGF) is synthesized in male germ cells. The NGF receptor (NGFR) mRNA was found in the Sertoli cells of rat testis. Hypophysectomy increased both NGFR mRNA in testis and the number of NGFR hybridizing cells in seminiferous tubules. This was suppressed by treatment with chorionic gonadotropin or testosterone, but not with follicle-stimulating hormone. The NGFR mRNA also increased after destruction of Leydig cells or blocking of the androgen receptor. This suggests that NGF produced by male germ cells regulates testicular function in an androgen-modulated fashion by mediating an interaction germ and Sertoli cells.

TESTICULAR FUNCTION DEPENDS ON local cellular interactions that are influenced by pituitary secretions of luteinizing hormone (LH) acting on Leydig cells and secretions of follicle-stimulating hormone (FSH) acting on Sertoli cells. Leydig cells produce testosterone that regulates both Sertoli and germ cell function. Developing germ cells are supported by Sertoli cells that synthesize several essential components, including energy metabolites (*1*) and transport proteins such as transferrin (*2*), ceruloplasmin (*3*), and androgen-binding protein (ABP) (*4*). Several peptide growth factors have been detected in Sertoli cells, including insulin-like growth factors I and II (*5*), transforming growth factor β (*6*), and a testicular interleukin-1–like factor (*7*). However, the target cells in testis for these growth factors have not been identified, and their physiological roles in testis are poorly understood.

β-Nerve growth factor is a target-derived neurotrophic factor that is essential for the development and maintenance of sympathetic and sensory peripheral neurons, as well as central cholinergic neurons (*8*). Nerve growth factor (NGF) is also present at relatively high concentrations in bull semen and seminal vesicle (*9*). The NGF mRNA is detectable in testis, primarily in spermatocytes (*10*), and the NGF protein is in germ cells from primary spermatocytes to

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