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Archaeopteris is the earliest known modern tree

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Archaeopteris* is an extinct plant which is of botanical interest for two reasons. It was the main component of the earliest forests until its extinction around the Devonian/Carboniferous boundary[1–3], and phylogenetically, it is the free-sporing taxon that shares the most characteristics with the seed plants[4,5]. Here we describe the largest group of anatomically preserved *Archaeopteris* remains ever found, from the Famennian marine beds of south-eastern Morocco[6], and provide the first evidence that, in terms of development and branching strategies, these 370-million-year-old plants were the earliest known modern trees. This modernization involved the evolution of four characteristics: a lateral branching syndrome similar to the axillary branching of early seed plants; adventitious latent primordia similar to those produced by living trees, which eventually develop into roots on stem cuttings; nodal zones as important sites for the subsequent development of lateral organs; and wood anatomy strategies that minimize the mechanical stresses caused by perennial branch growth.

Archaeopteris is thought to have been an excurrent tree, with a single trunk producing helically arranged deciduous branches growing almost horizontally[7]. All studies relating to the development of *Archaeopteris* support the view that these ephemeral branches arise from the pseudomonopodial division of the trunk apex[8–11]. Apical branching also characterizes all other contemporaneous non-seed-plant taxa including those that had also evolved an arborescent habit, such as lepidosigillarioid lycopsids and cladoxylalean ferns. This pattern, which can disadvantage the tree if the trunk apex is damaged, contrasts with the axillary branching reported in early seed plants[12]. Analysis of a 4 m-long trunk from the Famennian of Oklahoma has shown that *Archaeopteris* may produce adventitious organs[13]. These have been interpreted as being branches of limited lifespan that increase the survival potential of the plant.

About 150 specimens were collected in three localities of the Mader Basin and Tafilalt Platform in eastern Anti-Atlas[6]. They were found in dark-grey shales with calcareous concretions of the lowermost Famennian age (Kellwasser facies, *crepida* zone). They range from 2.5 mm-wide distal axes to portions of trunks nearly 40 cm in diameter. Developmental analyses were conducted on one 5 m-long decorticated portion of trunk, which was presumed to be that of a young individual given its proximal diameter of less than 10 cm (ref. 14). Three types of appendage were identified from the size, structure, length and spatial arrangement of vascular traces along a 40 cm-long portion of its distal part (Fig. 1a). Developmentally, type A organs correspond to the ephemeral, apically produced branches previously recognized in *Archaeopteris*. We interpret them as being physiologically homologous to seed-plant leaves and assume that they were not significant in the large-scale architectural structure of the tree.

Type H adventitious organs are also short-lived. Their traces, which occur singly or in serial groups, compare well in size, structure and horizontal course with traces to small adventitious appendages in Trivett's[13] *Archaeopteris* trunk from Oklahoma. New
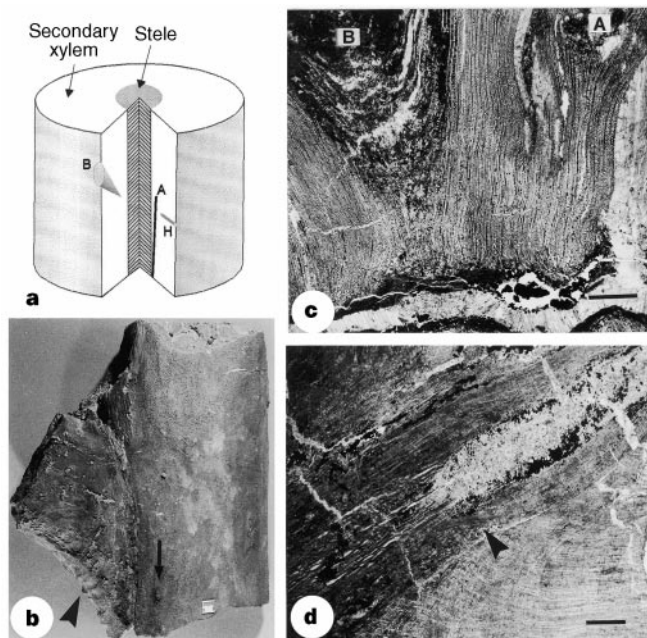

Figure 1 *Archaeopteris*, Early Famennian of Morocco. **a**, The relative arrangement of type A, B and H traces in the trunk. **b**, Trunk exterior with a large branch on the left that has a pronounced collar of trunk wood surrounding its base, showing transverse waves of wood on the branch bottom (arrowhead) and a cluster of small buried traces on the branch flank (arrow). **c**, Cross-section of trunk showing a type B trace lateral to a type A one at the level of occlusion. **d**, Type B trace in radial section showing trace to lateral appendage (arrowhead). Scale bars: **b**, 1 cm; **c**, **d**, 1 mm.

information from our specimen reveals that they usually occur on the same radius as a type A branch and that they are similar to the radial bands of tissue that differentiate in the wood of living trees when latent primodia are produced[15]. These tissue bands are generally associated with the development of roots for vegetative propagation.

The type B branches of *Archaeopteris* represent a major innovation (Fig. 1c–d); five are recorded in the portion of trunk analysed. These laterals do not arise in the same ontogenetic spiral as the type A branches. They represent a new category of organ, of possibly adventitious origin, where the innermost part of its vascular trace, although close to the outer edge of the trunk primary vascular cylinder, apparently does not connect to it. Their sequence of production is irregular and currently unpredictable but the site where they originate is spatially determined, as they always occur on a radius next to the site of attachment of type A branches (Fig. 1c). Type B branches correspond to the largest traces running into the trunk, which suggests that they had a larger morphogenetic potential than the type A ones. Type B traces depart at approximately 30° from the horizontal and protrude on the outer surface of the trunk (Fig. 1d). They produce regularly arranged lateral appendages. The occurrence of short internodes in the basal part supports the view that type B organs had a delayed development. We interpret these branches as being long-lived structures that probably represent significant permanent constructional units of the tree architecture.

The earliest evidence of axillary branching was reported for Tournaisian seed plants of the family Calamopityaceae[12]. Branches of *Calamopitys* are inserted in the axils of leaves but their traces connect to the closest vascular traces, not necessarily to the main stem, which suggests some period of branch primordium dormancy. The new *Archaeopteris* lateral branching syndrome, which involves the evolution of an extra type of branch and its spatial dependence on a leaf-type organ, apparently needs only a few positional adjustments to fit with the axillary branching of Calamopityaceae. It represents a major breakthrough from pseudomonopodial types of branching and may correspond to an evolutionary step towards the axillary branching of basal seed plants.

Several trunk fragments from Morocco bear the bases of large branches at wide angles. These show characteristic waves of undulating wood at their bottom points of attachment and collars of extra wood surrounding the sides and upper surface (Fig. 1b). The points of attachment of these perennial branches are reinforced by these external collars and by internal sockets for compressional and tensional load-bearing, just like modern tree limbs[16–18] that grow heavier each year.

New information on branching patterns in *Archaeopteris* shows that this Devonian tree evolved most of the developmental features subsequently selected in the vegetative body of most derived seed plants. These features allowed the emergence of new growth forms which lived longer and could occupy space more efficiently, thereby increasing their fitness. They may partly explain the worldwide dominance of *Archaeopteris* forests on Late Devonian floodplains. □

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Fungus-growing ants use antibiotic-producing bacteria to control garden parasites

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The well-studied, ancient and highly evolved mutualism between fungus-growing ants and their fungi has become a model system in the study of symbiosis[1–5]. Although it is thought at present to involve only two symbionts, associated with each other in near isolation from other organisms[1–5], the fungal gardens of attine ants are in fact host to a specialized and virulent parasitic fungus of the genus *Escovopsis* (Ascomycotina)[6]. Because the ants and their fungi are mutually dependent, the maintenance of stable fungal monocultures in the presence of weeds or parasites is critical to the survival of both organisms. Here we describe a new, third mutualist in this symbiosis, a filamentous bacterium (actinomycete) of the genus *Streptomyces* that produces antibiotics specifically targeted to suppress the growth of the specialized garden-parasite *Escovopsis*. This third mutualist is associated with all species of fungus-growing ants studied, is carried upon regions of the ants' cuticle that are genus specific, is transmitted vertically (from parent to offspring colonies), and has the capacity to promote the growth of the fungal mutualist, indicating that the association of *Streptomyces* with attine ants is both highly evolved and of ancient origin.

Because few organisms cultivate their own food, fungus-gardening by ants (Attini: Formicidae) is considered to be a major breakthrough in animal evolution[7]. These ants forage on a variety of substrates that they use for the cultivation of the vegetative mycelium of a fungus, their dominant food source. Fungus cultivation evolved apparently only once in the attines, over 50 million years ago, with the domestication of a fungus in the family Lepiotaceae (Agaricales: Basidiomycotina)[3,4,8]. Other lepiotaceous lineages, and in one case a distantly related non-lepiotaceous basidiomycete, were