Part I: Origins and variation

1

Fossil evidence on the evolutionary origin of tropical trees and forests

JAMES A. DOYLE
Museum of Paleontology and Department of Ecology and
Evolutionary Biology, University of Michigan, Ann Arbor, Michigan

Since early in this century, recognition of "tropical" features in the angiosperm-dominated Late Cretaceous and Early Tertiary fossil floras of the present north temperate zone has contributed to the realization that angiosperm evolution must be viewed from a tropical rather than a temperate perspective (Bews, 1927). However, it is primarily in the past two decades that advances in interpretation of the first Early Cretaceous records of angiosperms have begun to provide a solid paleobotanic (as opposed to strictly comparative morphologic) framework in which to examine such problems as the origin and specific evolutionary role of tropical trees in the initial adaptive radiation of the angiosperms. In the same period, studies of the morphology and stratigraphic distribution of early land plants of the Silurian and Devonian have shed new light on the origin and early evolution of the pteridophyte and gymnosperm groups that dominated forests prior to the rise of angiosperms, and on the origin of the basic organs and morphogenetic relations among them, which form the elements of the wide variety of architectural models seen in both living and fossil plants (Hallé & Oldeman, 1970).

Despite these encouraging advances, paleobotany is still far from providing a detailed account of the origin and evolutionary history of the vast number of lineages that make up modern tropical forests. Although studies of fossil pollen and spores (palynology) are beginning to reveal the general features of Cretaceous and Tertiary tropical floras, the most intensively studied palynofloras and essentially all the megafossil floras (which might be expected to yield the most evidence on evolution of vegetative features) are still from extratropical regions of the Northern Hemisphere. Furthermore, because the sorts of data and the problems most amenable to solution are so different in the study of living and fossil plants, the answers the paleobotanist

4   *James A. Doyle*

feels prepared to give (e.g., evolution of pollen and leaf venational characters) often do not correspond to the questions of most topical interest to the neobotanist (e.g., floral biology, growth patterns), and the paleobotanist may want answers to questions on the adaptive significance of pollen and leaf features that have been relatively little considered by neobotanists. Hence, instead of attempting a comprehensive review of the still fragmentary data, I prefer to concentrate on some selected facts and speculations about the architecture of fossil plants (in part updating the pioneering discussion of Hallé & Oldeman, 1970) and about the early ecological evolution of angiosperms that have emerged from recent paleobotanic studies, and to point out some areas where greater communication and collaboration between students of living and fossil plants might provide answers of interest to both.

### Evolution prior to the rise of angiosperms
Architecture and evolution of the earliest land plants

Recent studies of spores and plant megafossils from Silurian and Devonian rocks, summarized by Chaloner (1967, 1970), Banks (1968, 1970, 1975), Beck (1970, 1976), and Scheckler & Banks (1971), have helped correct errors in dating and morphologic interpretation that contributed to the older belief that land plants must have had a long pre-Silurian history and permit some general conclusions about the origin of organs and taxa of lower vascular plants (Fig. 1.1). Most vascular plants of the Late Silurian and Early Devonian, including both the oldest definite vascular plant, *Cooksonia* from the Late Silurian, and such Early Devonian forms as *Rhynia*, were small, herbaceous, perhaps sometimes still semiaquatic, and characterized by an organography radically different from that of modern plants, but departing only in minor respects from the prototype postulated by the telome theory of Zimmermann (1953): rootless, leafless, dichotomously branched, with terminal sporangia. The most notable exceptions, both younger than the oldest *Cooksonia*, are the order Zosterophyllales (appearing in the earliest Devonian), with lateral, reniform sporangia, and the first Lycopsida (middle Early Devonian), with both lateral sporangia and microphyllous leaves.

Examination of the sequence of Devonian floras reveals complex and varied modifications of the telome plan toward the normal differentiation of organs seen in modern plants, loosely correlated with a gradual increase in size and eventual attainment of the tree habit by several independent lines. Some of these modifications correspond to the elementary processes of the telome theory; others do not. For example, most groups appear to have escaped from the limitations on size inherent in a leafless, dichotomous system (mechani-

cal support, light-gathering efficiency) by the telome process of "overtopping" – a shift to unequal dichotomous (pseudomonopodial) and eventually monopodial branching, resulting in differentiation of a main trunk and lateral branches, sometimes later modified into leaves. This trend is already evident in *Psilophyton* from the middle and late Early Devonian, with pseudomonopodial branching of the main axes and dichotomous laterals (Banks, 1968, 1970). Monopodial or pseudomonopodial branching of all but the ultimate orders of branching (which often remain dichotomous) is almost universally established in Middle Devonian and younger groups of vascular plants except for Lycopsida – i.e., in all the groups Banks (1968, 1970) has postulated were derivatives of *Psilophyton*-like ancestors on the basis of branching, sporangial morphology, and anatomy.

Fig. 1.1. Stratigraphic distribution, changes in relative abundance (highly generalized), and suggested phylogenetic relations of major groups of land plants.
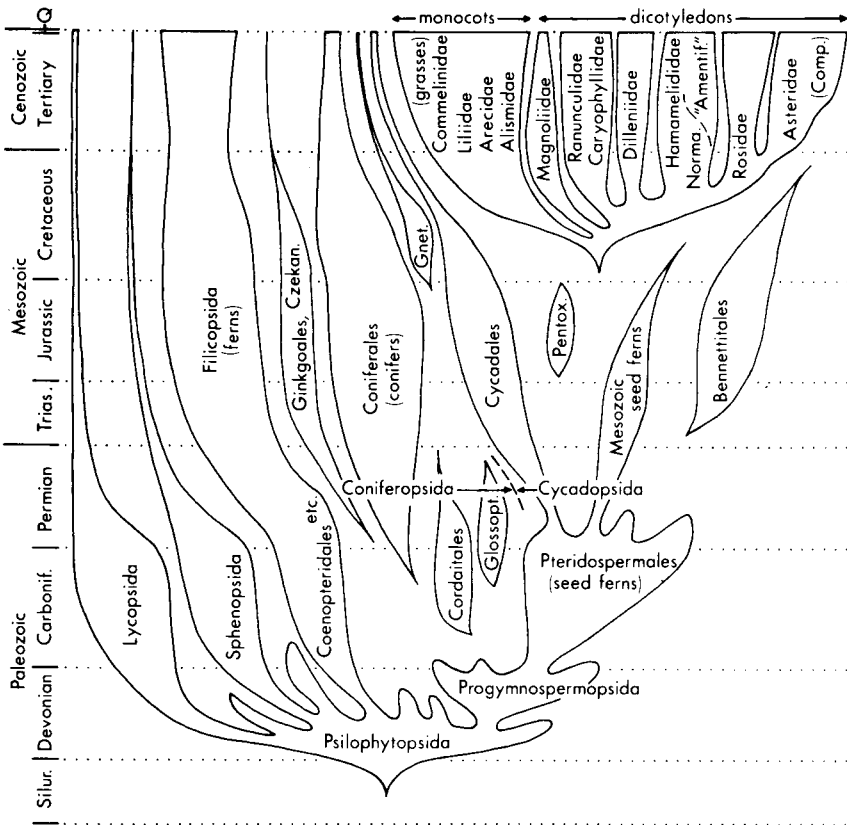
6   *James A. Doyle*

The most important Early Devonian example of a nontelome pro-
cess appears to be the origin of the leaf (microphyll) of the Lycopsida.
Their exarch stelar anatomy and sporangial morphology suggest that
the lycopsids were derived from the Zosterophyllales, many of which
have spines or enations that differ from microphylls mostly in the ab-
sence of vascular tissue (Banks, 1968; Chaloner, 1970). Interestingly,
later arborescent members of the Lycopsida (the predominantly Car-
boniferous order Lepidodendrales) are noteworthy in retaining
much of the dichotomous branching of their ancestors while enlarg-
ing their microphylls to as much as 1 m in length, as if the enation or-
igin of the leaf allowed them to compensate for the limitations of a
dichotomous system without requiring the modifications in
branching patterns seen in other groups.

> *Progymnosperms and the origin of gymnosperms*
> Among the arborescent groups appearing in the Devonian,
the most important for our purposes are the Middle and Late Devo-
nian Progymnospermopsida – plants still pteridophytic in reproduc-
tion, but with typically gymnospermous anatomic innovations (sec-
ondary xylem, secondary phloem, periderm) and/or tendencies
(stelar anatomy, branching patterns) that support the concept that
they were ancestral to both cycadopsid and coniferopsid gym-
nosperms (Beck, 1960, 1970, 1971, 1976; Scheckler & Banks, 1971).
The older of the two principal progymnosperm orders, the Middle
and Late Devonian Aneurophytales, was characterized by several
orders of spirally or decussately arranged, orthotropic, pseudomono-
podial branches, of which the last order bore dichotomous ultimate
branchlets or ''leaves'' (Scheckler, 1976). Thus, except for the fact that
the branches had no relation to subtending leaves, the Aneurophy-
tales correspond to Attims's model; the assignment by Hallé & Ol-
deman (1970) of one genus, *Eospermatopteris,* to Corner's model is
based on older misinterpretations of the three-dimensional lateral
branch systems as fronds (Beck, 1970, 1976; Scheckler & Banks, 1971).
It may be noted that if the progymnosperms are indeed ancestral to
the gymnosperms, the almost complete suppression of dichotomous
organization (except in the ultimate appendages) even in the An-
europhytales strongly suggests that later occurrences of dichotomous
branching in seed plants (e.g., the palm *Hyphaene:* Hallé & Ol-
deman, 1970; *Flagellaria:* Chap. 7) represent secondary specializa-
tions rather than primitive holdovers, occasional claims of overen-
thusiastic telome theorists notwithstanding.
The abundant Late Devonian genus *Archaeopteris* (*Callixylon*), type
of the order Archaeopteridales, is of even greater interest as one of
the first forest-forming trees, as the first clear example of plagiotropy,

and for its bearing on the origin of the leaf architectural and habital
differences between cycadopsid and coniferopsid gymnosperms.
Detailed anatomic and morphologic studies by Carluccio, Hueber, &
Banks (1966) and Beck (1971) have shown that the apparently bipin-
nate "fronds" of *Archaeopteris* (which led earlier authors to consider
it a prefern) were actually plagiotropic branch systems: a primary
axis bearing spirally arranged, dichotomously veined, and variously
dissected wedge-shaped "leaves," and, replacing leaves at positions
in the same ontogenetic spiral, distichously arranged secondary
axes, themselves bearing spirally and/or decussately arranged leaves
(Fig. 1.2). Plagiotropy was manifested in the distichous branching
pattern, a certain dorsiventrality in leaf arrangement resulting from
deviations from normal spiral phyllotaxy (Beck, 1971), and possibly
twisting of the leaf bases (Banks, 1970). Hence, Hallé & Oldeman
(1970) are correct in assigning *Archaeopteris* to Roux's model, even
though the older restoration they cite still interpreted the phyllomor-
phic lateral branch systems as fronds.

As was first clearly proposed by Meeuse (1966) and elaborated and
modified by Beck (1970, 1971), further flattening and differentiation
from the trunk of a plagiotropic branch system like that of *Archaeop-
teris* might lead to a compound frond of the sort seen in the earliest
cycadopsid gymnosperms, the seed ferns or pteridosperms of the lat-
est Devonian and Carboniferous (Carluccio et al., 1966), whereas

Fig. 1.2. Plagiotropic lateral branch system ("frond") of Late De-
vonian progymnosperm *Archaeopteris macilenta*. (Reproduced with
permission from Beck, 1971)
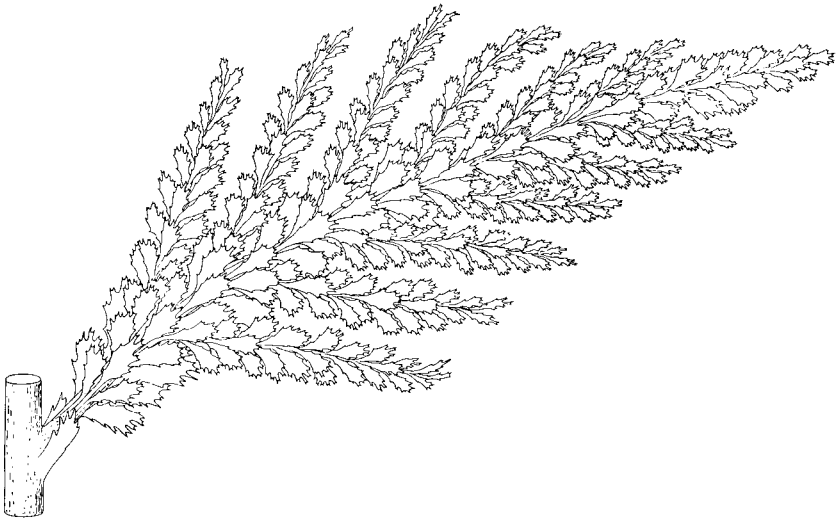
8   *James A. Doyle*

reduction of the leaves without modification of the whole system to
appendicular status might result in a plagiotropic branch system
with needlelike leaves of the sort seen in the earliest conifers of the
Late Carboniferous and Permian and in living species of *Araucaria*
(Massart's model: see Florin, 1951; Hallé & Oldeman, 1970; Beck,
1970, 1971; Chap. 10). This hypothesis has many complex corollaries,
not all of which have received the attention they require if Devonian
fossil evidence is to be related to the morphology of modern plants.
For instance, it is interesting to note that the first set of transforma-
tions postulated – essentially from Roux's model to Cook's model to
Corner's model (Hallé & Oldeman, 1970) – would be impossible in
modern angiosperms without violating the apparently obligatory as-
sociation between a branch and a subtending leaf (i.e., no matter
how phyllomorphic the branch systems of *Phyllanthus* become, they
retain their axillary position), but this would be less of a problem in
Devonian plants, where branching was rarely, if ever, axillary. Ironi-
cally, *Archaeopteris* itself may constitute an exception to this last gen-
eralization, as there are cases where the branch system appears to be
associated with a juvenile leaf on the main trunk (see Fig. 1.2). This
only underlines the arguments of Beck (1971) that *Archaeopteris* itself
has distinctively ''coniferopsid'' wood anatomic and morphologic
features (e.g., decurrent leaf bases) that indicate it is already too spe-
cialized to be the common ancestor of both cycadopsid and coni-
feropsid gymnosperms. On the other hand, any theory of the origin
of coniferopsid gymnosperms based on similarities in plan between
the compound strobili and the branch systems of *Cordaites* and early
conifers and the branch systems of *Archaeopteris* (e.g., Meeuse,
1966) must take into account the fact that branching was strictly ax-
illary in the former (Florin, 1951), but predominantly or wholly non-
axillary in the latter. These problems are less central to evolution of
early cycadopsid gymnosperms, only a few of which are known to
have had axillary rather than adventitious branching (e.g., the Penn-
sylvanian seed fern *Callistophyton poroxyloides:* Delevoryas &
Morgan, 1954), but axillary branching was to become an important
feature of later, Mesozoic cycadopsids (see below).
    Whatever the exact resolution of these problems, the morphology
of known progymnosperms and the trends inferred from *Archaeop-
teris* (if at all representative of trends in other progymnosperms) go
far toward explaining how the contrasting sparsely branched, com-
pound-leaved cycadopsid and the profusely branched, simple-
leaved coniferopsid patterns might both have been derived from a
single common ancestry. Their bearing on angiosperms is more ob-
scure because of the uncertainties concerning angiosperm ancestors
and the long time separating the Devonian and the Cretaceous. It

may be worth noting, however, that although the plagiotropy of *Archaeopteris* may be related to plagiotropy in modern conifers, it is unlikely to have anything to do with plagiotropy in angiosperms. If the anatomic evidence that suggests the angiosperms are cycadopsid rather than coniferopsid derivatives (Bailey, 1949; Takhtajan, 1969) is correct, the branch systems of *Archaeopteris* should be homologous with the leaves of angiosperms, not their branches.

Carboniferous tropical forests

Although many areas covered by the *Archaeopteris*-dominated forests of the Late Devonian may have had tropical climates, the best known and first distinctively tropical Paleozoic forests were the coal swamp floras of the Late Carboniferous (Pennsylvanian) of Europe and North America. Geologic and anatomic evidence (e.g., paleomagnetic and other geologic reconstructions of positions of poles and continents, lack of growth rings) indicates that these areas were located in the wet equatorial tropics (Frederiksen, 1972; Chaloner & Lacey, 1973; Chaloner & Meyen, 1973). It is, therefore, significant that they supported a remarkable variety of architectural models known from the modern flora, many of them restricted to, or most characteristic of, wet tropical environments today, but, of course, belonging to totally unrelated, nonangiospermous groups (Hallé & Oldeman, 1970). Thus, the pachycaul tree fern or palmlike growth pattern (Corner's model), often associated with stilt roots, was exuberantly represented by *Psaronius* in the Marattiales, various coenopterid ferns, and gymnospermous seed ferns such as *Medullosa;* the models of Rauh, Attims, and Tomlinson, combined with horizontal rhizomes, were represented by arborescent sphenopsids (Calamitales); and the dichotomously branched model of Schoute, seen today in the palm *Hyphaene* and a few other monocotyledons, was represented by the arborescent lycopsid order Lepidodendrales (see Hallé & Oldeman, 1970, and above). At least some (though not all!) members of the genus *Cordaites,* the oldest definite representative of the coniferopsid gymnosperms, had stilt roots with a combination of anatomic features found only in mangroves today (Cridland, 1964). *Cordaites* corresponded to Attims's model (Hallé & Oldeman, 1970); its long, strap-shaped, parallel-veined leaves contrast with the leaves of both Paleozoic and living conifers, but they are less different from the presumed juvenile leaves (*Eddya*) of *Archaeopteris* (Beck, 1971).

Most of the bizarre groups making up European–North American Carboniferous coal swamp forests became extinct with the gradual disappearance of coal swamp conditions and evidence of increasing aridity in the following Permian period (White, 1936; Frederiksen, 1972). Their disappearance coincides with the expansion of ap-

parently more drought-resistant members of both great gymnosperm groups – coniferopsids represented by primitive conifers (e.g., *Walchia*, *Lebachia*, *Ernestiodendron:* Florin, 1951) and Ginkgoales, cycadopsids represented by new seed fern groups and forms with simple but pinnately veined leaves (*Taeniopteris,* some of which had megasporophylls suggesting relation with modern Cycadales: Mamay, 1969) – as well as ferns. As noted above, many early conifers conform to Massart's model (Hallé & Oldeman, 1970), with pseudo-whorled plagiotropic lateral branch systems as in modern *Araucaria* species, from which, however, they differed in their cone structure and the forked leaves on the main trunk. Interestingly, the influx of conifers is not seen in the then-temperate Angara province of Siberia (Chaloner & Meyen, 1973), suggesting that conifers were primitively adapted to hot and dry climates, rather than the cool, wet climates where they are most diverse today.

Mesozoic gymnosperms

Coniferopsids, cycadopsids, and ferns (represented, of course, by a variety of successively evolving and radiating subgroups) continued to dominate land floras until, and in some areas even after, the mid-Cretaceous rise of angiosperms. Understanding of their growth patterns and ecology is important both in searching for possible ancestors of the angiosperms and in attempting to explain the pattern of angiosperm occupation of Mesozoic communities. Although Mesozoic coniferopsids did include large, monopodial trees with needlelike, simple leaves, and Mesozoic cycadopsids included squat, unbranched, manoxylic forms with crowns of pinnately compound leaves (e.g., *Cycadeoidea*), it would be a serious mistake to visualize them solely in terms of modern conifers and cycads. As Hughes (1976) emphasizes in his stimulating, though controversial, review of Jurassic and Early Cretaceous seed plants, modern gymnosperms are clearly relict and restricted to their present niches by competition with angiosperms; before the rise of angiosperms, they undoubtedly covered a much greater spectrum of ecologic and architectural types.

Among the coniferopsids, a prime example of Hughes's concept is provided by the great group of Jurassic and Early Cretaceous conifers represented in the pollen record by *Classopollis* and in the megafossil record by several genera, including *Brachyphyllum* (branch systems with tightly appressed, rhomboidal, xeromorphic scale leaves) and *Frenelopsis* (with the exserted portions of the opposite-whorled leaves so reduced that the stems have a jointed appearance: Hluštík & Konzalová, 1975). These "Mesozoic brachyphylls" are often but misleadingly compared with Araucariaceae or Cupressaceae, from

which they are quite distinct in cone and pollen morphology (Hughes, 1976). In the Jurassic, *Classopollis* dominates palynofloras from most areas of the world except Siberia and adjacent Arctic regions (Vakhrameev, 1970). In the Early Cretaceous, it becomes somewhat less abundant at middle paleolatitudes, but it is still dominant, along with newly appearing "ephedroid" pollen grains, in an African–South American belt straddling the paleoequator (Kuyl, Muller, & Waterbolk, 1955; Herngreen, 1974; Jardiné, Kieser, & Reyre, 1974; Brenner, 1976). These plants were clearly the most successful group of tropical forest-forming trees in the Jurassic and Early Cretaceous, but they were so completely replaced during the phenomenal mid-Cretaceous radiation of angiosperms that their closest tropical analogs on which to base speculations about growth habit are in totally unrelated groups (e.g., *Casuarina*?). At the same time, the Ginkgoales, which dominated northern latitudes, included genera with leaf architecture (long, ribbonlike leaves) quite removed from that of modern *Ginkgo biloba*; however, even some of the ribbon-leaved forms are known to have had a pronounced long-shoot–short-shoot dimorphism (Florin, 1936) that, together with the abundance of detached leaves, suggests a winter-deciduous habit.

The Mesozoic cycadopsids included an even greater variety of extinct groups – the orders Bennettitales and Pentoxylales; the seed fern families Corystospermaceae, Peltaspermaceae, and Caytoniaceae; and extinct Cycadales (Nilssoniales) – which exhibited a far greater range of morphology than the relict living Cycadales. In particular, as emphasized by Harris (1961), Delevoryas & Hope (1971, 1976), and Hughes (1976), many had smaller leaves, more slender stems, and more profuse branching than modern cycads. Examples are Cycadales such as the Late Triassic *Leptocycas* (Delevoryas & Hope, 1971) and the Cretaceous *Nilssoniocladus*, with a remarkable *Ginkgo*-like shoot dimorphism (Kimura & Sekido, 1975); Bennettitales such as the Late Triassic *Wielandiella* (Nathorst, 1909), the Jurassic *Williamsoniella* (Thomas, 1915), and the Late Triassic *Ischnophyton* (Delevoryas & Hope, 1976); and, judging from the small size of its palmately compound leaves and a single slender, branched twig with scale leaves, the Jurassic seed fern *Caytonia* (Harris, 1964). However, there are intriguing hints that one of the most distinctive architectural features of modern Cycadales (and many angiosperms!) – sympodial branching, as opposed to the predominantly (though not exclusively) monopodial branching of both Mesozoic and modern conifers – was widely distributed in other, less closely related Mesozoic cycadopsid groups. In the bennettitalian genera *Wielandiella* and *Williamsoniella*, upward growth of each stem segment was terminated by flowering, but upward growth of the plant