Arguments for a glossopterid ancestry of angiosperms

Greg Retallack and David L. Dilcher

Abstract.—Almost every living and fossil group of gymnosperms has been proposed as a possible ancestor of angiosperms. A common problem with many of these proposals is their reliance on hypothetical intermediate forms. Another common problem is finding correctly-oriented organs homologous to all the important reproductive structures of angiosperms.

These problems are least troublesome for a glossopterid origin of angiosperms. Recently discovered ovule-bearing organs of·these plants may represent evolutionary intermediates, or analogous plants, between glossopterids and angiosperms. According to recent reinterpretations of glossopterid ovule-bearing organs, they have structures in an orientation which may be homologous with both the outer ovular integument and the carpel of angiosperms. Considering the reproductive and vegetative features of glossopterids, the hypothesis that they may be part of a stock ancestral to angiosperms should be seriously considered.

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Introduction

The origin of angiosperms is as fascinating today as it was in the time of Charles Darwin. Some scientists (Krassilov 1977) reason that the past failure to find a single likely ancestral stock for all angiosperms is because angiosperms evolved polyphyletically from several separate lineages of gymnosperms. Others (Hughes 1976) feel that this failure is due to misleading concepts of early angiosperms extrapolated backwards in time from the comparative morphology of living angiosperms. Nevertheless, real progress has been made in recent years from studying the fossil record of early angiosperms (Doyle and Hickey 1976; Hickey and Doyle 1977; Doyle 1978; Dilcher 1979). An adaptive radiation and dispersal of both angiosperm-like leaves and pollen during the later Early Cretaceous is supported by what is known of early angiosperm fructifications. This is in agreement with the idea that the many distinctive features of living angiosperms, such as double fertilization, indicate that angiosperms were largely derived from one ancestral stock.

Almost every living and fossil group of gymnosperms has been proposed as a possible ancestor of angiosperms at one time or another (Wieland 1918; Thomas 1934, 1936; Melville 1962, 1969; Meeuse 1975; Long 1977; Doyle 1978). A common problem with these proposals is their reliance on hypothetical intermediate forms. Another common problem is finding correctly-oriented homologous organs for all the important reproductive structures of angiosperms. For example, both problems are evident in Doyle's (1978) proposal that the Caytoniales were ancestral to angiosperms. Among the hypothetical forms required for such an evolutionary transformation are *Caytonia*-like plants with only one seed in each fruit and neotenous plants whose fruit-bearing rachis has expanded and folded into a carpel. Doyle regarded the fruit wall of *Caytonia* as a homologue of the outer integument of angiosperm ovules. However, it requires considerable imagination to see any relationship between the rachis of *Caytonia* and the carpel of angiosperms, which Doyle suggests are homologous.

This is not the first time that glossopterids have been considered likely ancestors of angiosperms. Plumstead (1956) and Melville (1962, 1969) also claimed relationships between glossopterids and angiosperms. Such a relationship has been generally disregarded since, because the initial interpretations of glossopterid fructifications were not substantiated by later work (Surange and Chandra 1975; Schopf 1976; Gould and Delevoryas 1977) and because later analyses stressed differences between glossopterid and angiosperm leaves (Doyle and Hickey
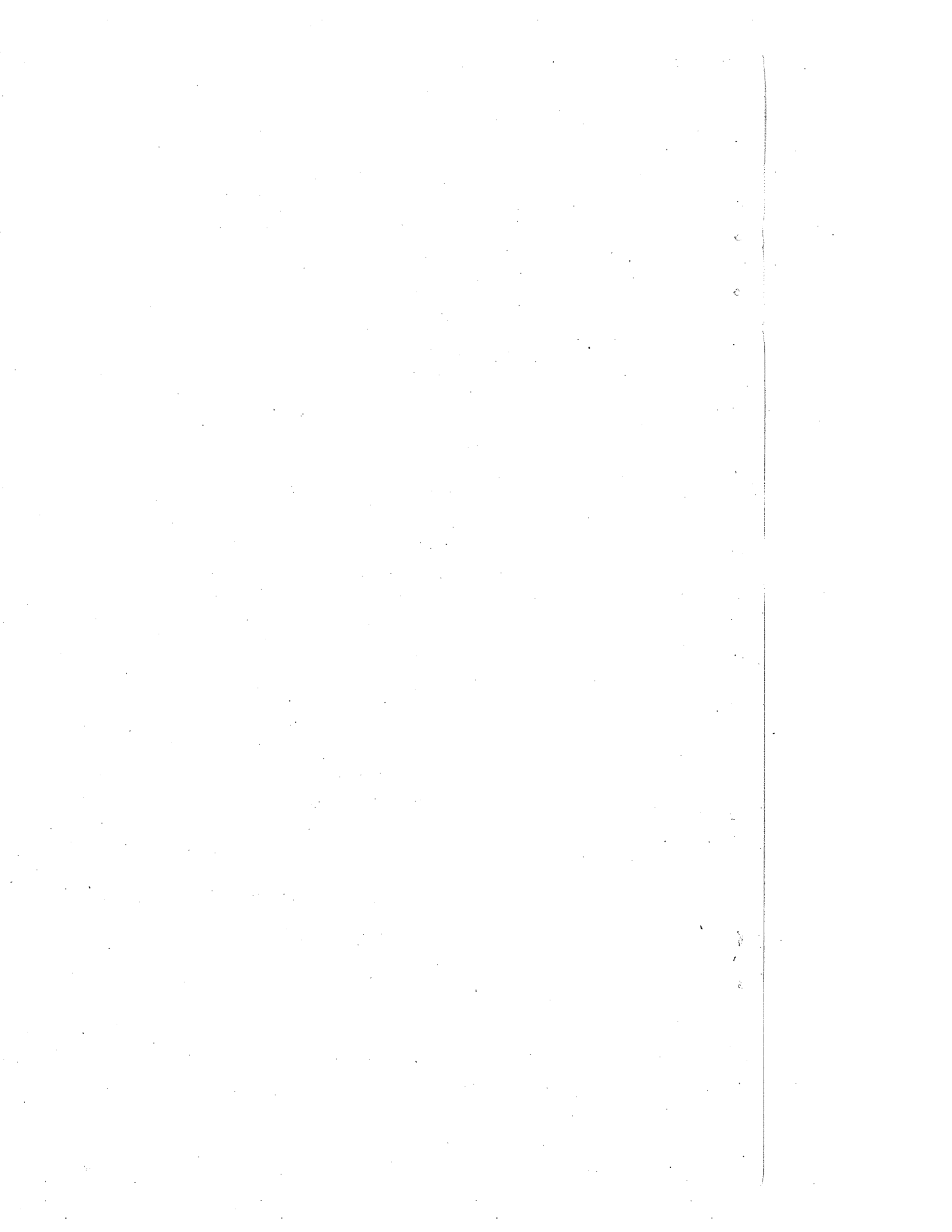
1976; Hickey and Doyle 1977). Against this mounting scepticism, Stebbins (1974) suggested intriguing homologies between different parts of the glossopterid fructification *Lidgettonia* and angiosperm ovules and carpels. There is now considerable support for Stebbins' suggestion from new discoveries and interpretations of both glossopterid and early angiosperm fructifications. We feel that the possibility that angiosperms were ultimately derived from glossopterids once again deserves serious consideration.

The Nature of Early Angiosperms

Recent finds of well-preserved early and mid-Cretaceous angiosperm fructifications (Dilcher et al. 1976; Dilcher 1979; Vakhrameev and Krassilov 1979) have clarified our understanding of early angiosperm reproduction. Previous ideas on the reproduction of early angiosperms were based largely on extrapolations from the comparative morphology of living angiosperms (Cronquist 1968; Takhtajan 1969). Even in the best preserved fossil angiosperm fructification, few of the cytological bases of angiospermy, such as double fertilization, are likely to be detected. Instead, relationships must be argued from the preserved anatomy and morphology of fossil flowers, fruits and seeds. Considering both the fossils and living angiosperms, it is likely that fructifications of numerous follicles arranged helically on elongate axes (multifollicles) and ovules with two integumentary layers are ancestral in angiosperms.

Multifollicles.—Angiosperm fructifications consisting of numerous follicles arranged helically on an elongate receptacle are called multifollicles. Each follicle is a fruit developed from a single conduplicate carpel. Multifollicles have long been considered ancestral in angiosperms (Takhtajan 1969). They are also a common kind of fossil angiosperm fructification (Fig. 1; see also Dilcher et al. 1976; Retallack and Dilcher in press a; Vakhrameev and Krassilov 1979). Typically, the individual fossil follicles are well cuticularized and have numerous ovules attached submarginally to the inner surface. The fossil follicles have several distinctive peculiarities. Unlike follicles of most living plants (but still within some definitions of follicles, such as that of Cronquist 1968, p. 378), the fossil folli-

cles have been found open adaxially, rather than abaxially. As there are no clear scars of dehiscence and an equal thickness of cuticle on the margins, inside and outside the fossil follicles, it is uncertain whether they have dehisced or were open throughout flowering and fruiting. In life the fossil follicles were probably subcarnose, the tissue of the follicles having an appearance and substance comparable with that of the pod of garden pea (*Pisum sativum*). They were neither fleshy, as in comparable fructifications of living *Schisandra,* nor were they woody, as in multifollicles of living *Magnolia.*

Stalked carpels, stigmatic crests and paracytic stomata have also been thought ancestral in angiosperms, considering their occurrence in living angiosperms (Takhtajan 1969). The evidence from fossils is not uniformly in support of this. Some of the fossils have stalked follicles with stigma-like margins (Dilcher et al. 1976). Others do not (Fig. 1; Vakhrameev and Krassilov 1979). Stomata have only been found in one of the fructifications (Fig. 1E). These are paracytic, as expected from studies of living plants (Takhtajan 1969; Baranova 1972).

Bitegmic ovules.—When suitably preserved, the seeds of fossil fructifications of early angiosperms appear to have two seed coats (Fig. 1C; see also Vakhrameev and Krassilov 1979). This supports evidence from living angiosperms that this is an ancestral feature of the group. Bitegmic ovules are most widespread in supposedly "primitive" living angiosperms (Takhtajan 1969; Stebbins 1974). The mismatch of integuments (producing a zig-zag micropyle in longitudinal section) and the rare stomata on the outer (but not inner) integument of some of these angiosperms, may indicate that the two integuments have a different origin (Stebbins 1974). Other angiosperms have a single integument around the ovule, but this integument develops either from fusion of two original primordia or cessation of growth of one of the two primordia (Maheshwari 1950).

The belief that seeds attached by long funicles are ancestral in angiosperms, suggested by Takhtajan (1969), is not supported by fossil evidence. In the early angiosperm fructification illustrated in this paper (Fig. 1G) the seeds are almost sessile and orthotropous. In another fossil the seeds have been described as anatropous
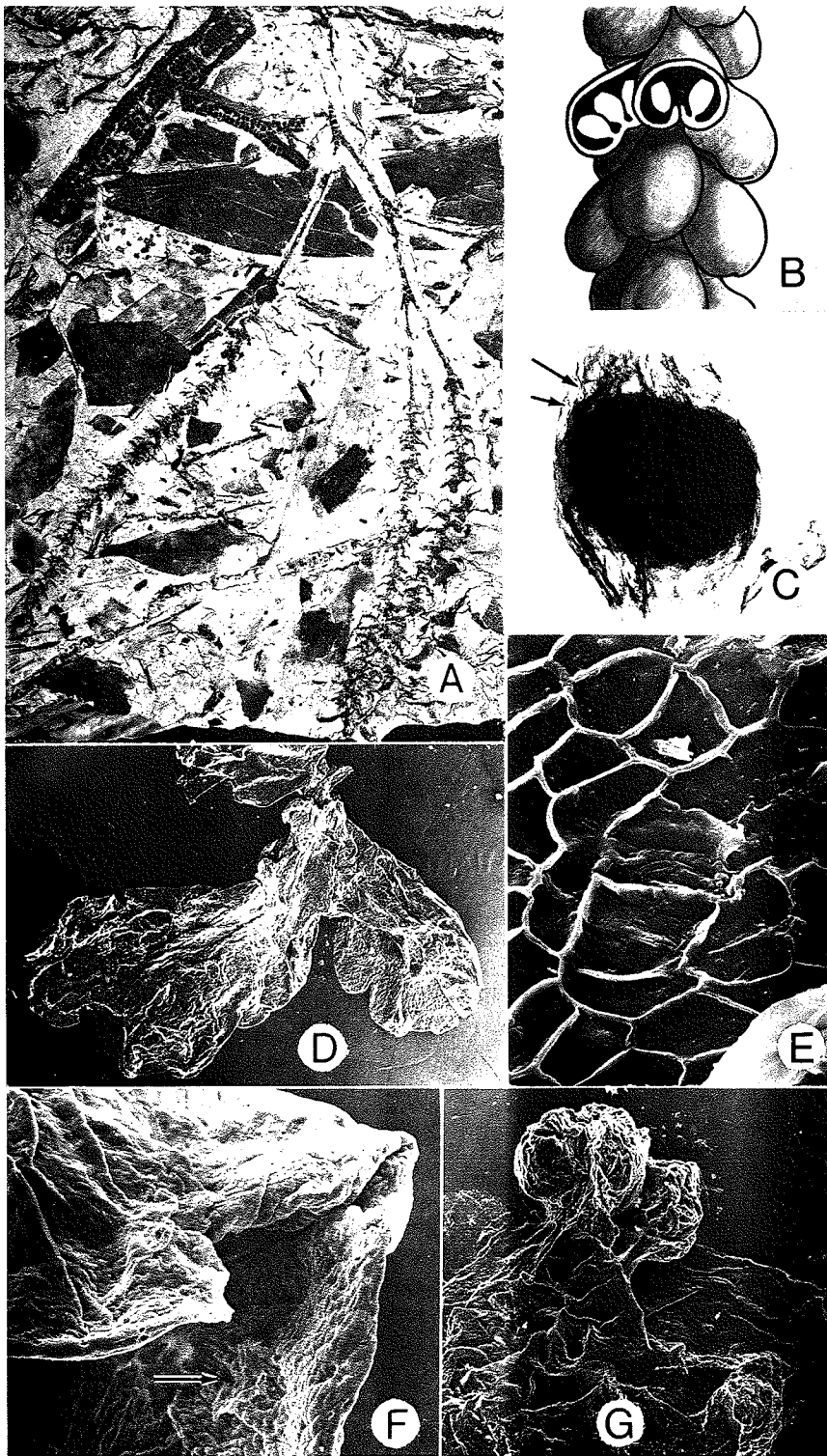
FIGURE 1. An early angiosperm fructification from the upper Dakota Formation (early Cenomanian or mid-Cretaceous) of central Kansas (described fully by Retallack and Dilcher, in press b). (A) Lax raceme of bracteate elongate multifollicles, in presumed, pendulous life-orientation (Indiana University, Geology Department, specimen IU15706-3042), ×0.8. (B)

and with a raphe, but this is not clear from the illustrations or discussion provided by Vakhrameev and Krassilov (1979).

Other features.—Traditionally the ancestral angiosperm flower has been envisaged as a large showy organ with both ovule-bearing and pollen-bearing organs on the same short shoot with bracts or perianth parts (Takhtajan 1969). However, there is no evidence from the fossil record of angiosperm fructifications that bisexual flowers are any more ancient than unisexual apetalate flowers (Dilcher 1979). These features are probably more important ecologically than phylogenetically. Bisexuality and the perianth in angiosperms are part of a syndrome of characters associated with insect pollination (Faegri and van der Pijl 1966). The radially-symmetrical bisexual strobili of some gymnosperms, such as *Cycadeoidea,* may also have been an adaption to insect pollination (Crepet 1974). The phylogenetic importance of bisexuality is also undermined by the fact that many living flowering plants have been observed, or experimentally induced, to oscillate between having flowers of only one sex on each plant and having flowers of both sexes on each plant, and also between unisexual and bisexual flowers (Heslop-Harrison 1957; Negi and Olmo 1966).

Homologous Features in Glossopterid Fructifications

Recent finds of silicified and compressed glossopterid fossils have clarified understanding of these extinct plants (Fig. 2; Pant 1977; Gould and Delevoryas 1977). Multiovulate glossopterid fructifications had been known in the past largely from poorly preserved impressions and had been interpreted as bivalved cupules (Plumstead 1956) and as bracteate strobili (Surange and Chandra 1975). Because of such interpretations, the multiovulate fructifications seemed unrelated to other glossopterid fructifications, such as *Lidgettonia* and *Denkania* (Surange and Chandra 1975). The more recent interpretations of multiovulate fructifications as laminar structures with ovules on one side (Figs. 2G–I) unites the glossopterids as a more cohesive group than previously believed.

Multiovulate fructifications.—The status of the various generic names for multiovulate glossopterid fructifications is now uncertain due to morphological reinterpretation by Gould and Delevoryas (1977). It is likely that some of the generic names proposed for impressions of these fructifications may merely be different states of preservation or stages of development of the same kind of plant. *Dictyopteridium* is the oldest generic name proposed for this kind of fructification (Banerjee 1973; Surange and Chandra 1973a). This name is used here in the broad sense of Gould and Delevoryas (1977), for multiovulate glossopterid fructifications. *Dictyopteridium* was widespread and common in Late Permian coal measures of Gondwanaland. Similar multiovulate glossopterid fructifications are also the most ancient glossopterid fructifications known (Plumstead 1956; Pant and Nautiyal 1966; Surange and Chandra 1975; Maheshwari 1976; Banerjee 1978).

In *Dictyopteridium,* two parallel laminar structures are borne together on an axis or with the upper one adnate to the lower one. Ovules are scattered over the under side of the upper laminar structure. The lower one is identical to an ordinary foliage leaf (Fig. 2G). Each ovule is typically gymnospermous, with only one integument. Some have been found with pollen in their micropyles and with well-preserved archegonia (Fig. 2I; Gould and Delevoryas 1977).

The basic organization of *Dictyopteridium* is well understood, but there are at least three

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Reconstructed follicles in life orientation, showing placentation of follicles, ×6. (C) Light microscopy preparation of macerated orthotropous seed, showing inner cuticle of barrel shaped outer integument (peeled back at lower right and short arrow), outer cuticle of wrinkled inner integument (long arrow) and megaspore (central dark area) (IU15703-2609), ×8. (D) SEMG of several follicles attached helically to a short length of receptacle (IU15703-2606), ×12.5 (E) SEMG of paracytic stomate, as seen from inside of outer cuticle of follicle (IU15703-2609), ×1000. (F) SEMG of apex of follicle, showing funicle of formerly attached seed (arrow), smooth outer cuticle and adaxial crests and weakly papillate inner cuticle near margin (IU15703-2606), ×125. (G) SEMG of three orthotropus seeds (two upper center, one lower right) attached to dissected follicle, with micropylar ends of seeds shrunken back onto megaspore during drying (IU15709-2609), ×50.
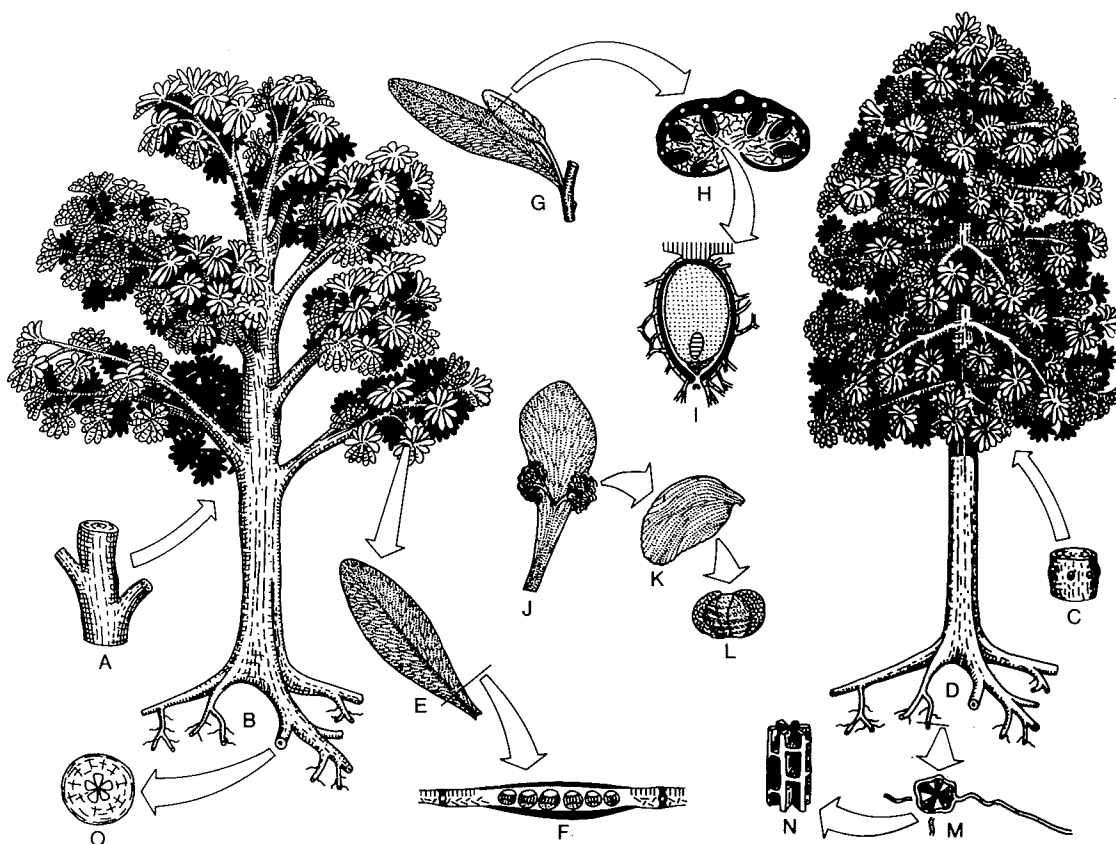
FIGURE 2. Reconstruction of glossopterid plants with fructifications of *Dictyopteridium* (modified from Gould and Delevoryas 1977 with permission from the authors and from *Alcheringa*). (A–D) Reconstruction of habit based on hand specimens. (E) Leaf venation. (F) Cross-section of leaf, with midrib showing vascular bundles of central reticulum and associated hypodermis flanked by lamina with palisade (adaxial) and spongy (abaxial) mesophyll between veins. (G) Attached ovule-bearing structure and associated leaf. (H) Cross-section of ovule-bearing structure. (I) Cross-section of ovule with associated interseminal filaments, single integument and archegonium. (J) Pollen-bearing organ. (K) Pollen sac. (L) *Protohaploxypinus* pollen. (M–O) *Vertebraria* roots. (M) Cross-section. (N) Model of septate xylem. (O) Root with considerable secondary wood. Relative to natural size, Figs. A–D approximately ×0.03, E, O and G ×0.2, M–N ×0.3, J ×0.6, H ×3, F, I and K ×12, and L ×120.

plausible botanical interpretations of this same structure (Fig. 3). All three are based on the rather secure assumptions that *Dictyopteridium* is a gymnosperm (Gould and Delevoryas 1977) and that it had axillary branching (Pant and Singh 1974 text-fig. 3, pl. 33, fig. 73). Schopf (1973, 1976) regarded the laminar ovule-bearing organ of *Dictyopteridium* as a modified axillary shoot (a cladode) and stressed affinities of the glossopterids with cordaitaleans (Fig. 3C). Gould and Delevoryas (1977) regarded the ovule-bearing organ of *Dictyopteridium* as a megasporophyll, indicating affinities with pteridosperms. By their interpretation the ovules could be either adaxial (Fig. 3A) or abaxial (Fig.

3B) depending on the position of the lateral meristem, which has not yet been located. The leaf could thus be regarded as subtending a reduced short shoot (Figs. 3A and 3B) or be an aphlebia-like lamina at the base of the megasporophyll (Fig. 3A only). There is little firm evidence to decide between these various alternatives, especially considering the different origins of fructifications adnate to leaf-like organs in modern plants, such as basswood (*Tilia*) and butcher's broom (*Ruscus*). Although fundamental to a complete understanding of the nature and origin of glossopterids, these alternatives are left open at this time. The hypothesis presented here involves such drastic re-

duction of plant parts that no remnant of vascularization or other features of older or pre-glossopterid structures would be expected in angiosperm follicles. Any of these botanical interpretations of glossopterid fructifications is compatible with the arguments and homologies presented here for the glossopterid origin of angiosperms.

Other fructifications.—In *Dictyopteridium* there is only one ovuliferous structure for each leaf. Fossil impressions of *Jambadostrobus* (Chandra and Surange 1977), from Late Permian coal measures of India, have two and possibly three adnate ovule-bearing structures on each leaf (Figs. 4I, J). These ovule-bearing structures appear identical to those which are solitary in *Dictyopteridium*. In its greater number of ovule-bearing structures, *Jambadostrobus* is morphologically intermediate between *Dictyopteridium* and other glossopterid fructifications such as *Lidgettonia,* also of Late Permian age.

Lidgettonia has cordate, stalked ovule-bearing structures each bearing six gymnospermous ovules (Figs. 4C, K). Up to six of these ovule-bearing structures are borne adnate to the adaxial surface of a leaf (Surange and Chandra 1974, 1975). Lacey, Van Dijk and Gordon-Gray (1975) have described comparable fructifications, which they referred to two genera, *Lidgettonia* and *Mooia.* In both these genera, the leaf and attached ovule-bearing structures are smaller than comparable structures in *Dictyopteridium* and *Jambadostrobus.*

Other fossil impressions of glossopterid fructifications are less well understood. They appear to have had a similar organization but are smaller than those already discussed. Surange and Chandra (1973b, 1975) have interpreted impressions called *Denkania* (Fig. 4D) as leaves bearing up to six adnate, stalked uniovulate cupules. Lacey et al. (1975) interpret comparable fossils, called *Rusangea,* as leaves bearing stalked scales, each with one sessile fleshy ovule. Both interpretations have a typically glossopterid organization, although much reduced.

Homologues with angiosperm multifollicles.— One problem confounding many previous hypotheses of angiosperm origins has been to find homologous organs for both the outer integument of the ovule and the carpel. Glossopterids
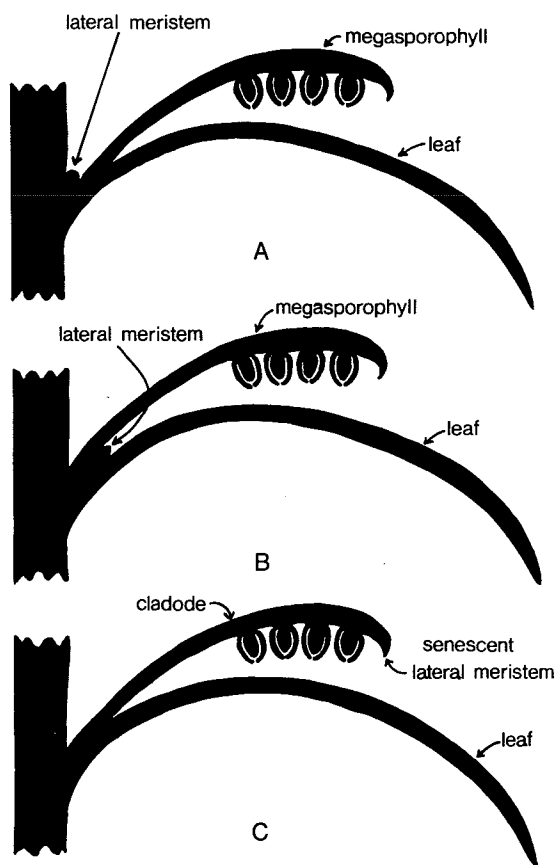

FIGURE 3. Alternative botanical interpretations of the glossopterid ovule-bearing fructification, *Dictyopteridium.* (A, B) Alternatives for the megasporophyll interpretation of Gould and Delevoryas (1977). (C) Cladode interpretation of Schopf (1973, 1976).

not only have homologous organs for both, but they also have a similar orientation. The outer integument of angiosperm ovules could be considered homologous with the ovule-bearing structure of glossopterids and the carpel of angiosperms homologous with the associated leaf of the glossopterids. The fructifications of glossopterids are known to have been borne in a helix on short shoots (Pant and Singh 1974; White 1978), like the multifollicular axes of early angiosperms and some living angiosperms.

The fossil glossopterid fructifications discussed here may be examples of intermediates between the more common multiovulate glossopterid fructifications and early angiosperm follicles (Figs. 4A–E). Whether this represents an evolutionary lineage within the glossopterids
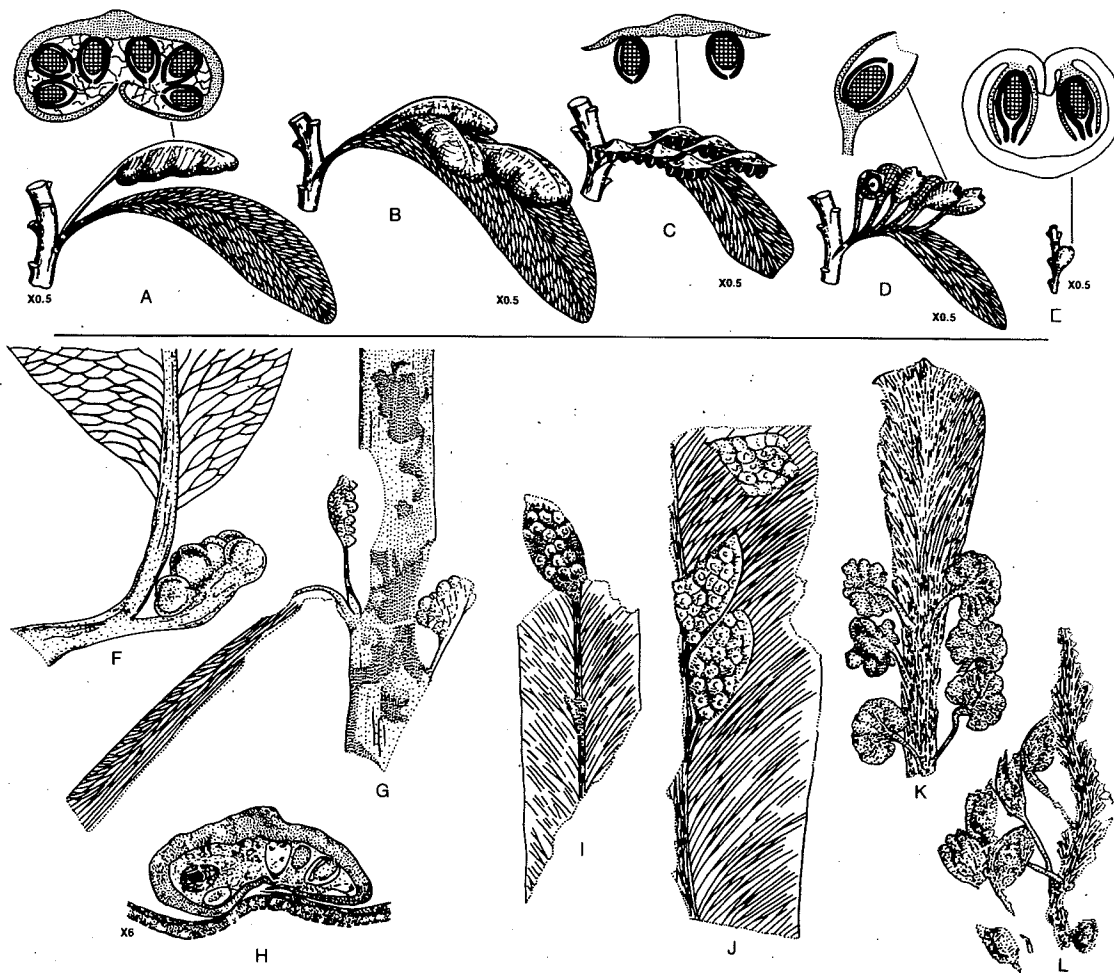
FIGURE 4.   Reconstructions (A–E) of selected glossopterid and early angiosperm fructifications and some fossils (F–L) on which they are based. (A–E) Reconstructions all 0.4 times natural size. In transverse sections of ovule-bearing structure, the megaspore and nucellus are cross-hatched, integument is solid, ovule-bearing structure is stippled and subtending leaf blank. (A) *Dictyopteridium* sp. (after Gould and Delevoryas 1977). (B) *Jambadostrobus pretiosus* Chandra and Surange 1977 (original re-interpretation based on similarities with *Dictyopteridium*). (C) *Lidgettonia mucronata* Surange and Chandra 1974. (D) *Denkania indica* Surange and Chandra 1973b. (E) Early angiosperm fructification from mid-Cretaceous of Kansas (Fig. 1). (F–L) Representative hand specimens and a thin section (Fig. 4H) of glossopterid ovulate fructifications, all 0.9 times natural size excepting Fig. 4H which ×5. (F) "*Austroglossa*" *walkomii* Holmes 1974, after Holmes. (G) Fertile *Glossopteris taenioides* Feistmantel 1882, after Pant and Singh (1974; also refigured by Pant 1977). (H) Transverse section of silicified multiovulate fructification *Dictyopteridium* after Gould and Delevoryas (1977). (I, J) *Jambadostrobus pretiosus* Chandra and Surange 1977, after Chandra and Surange. (K) *Lidgettonia mucronata* Surange and Chandra 1974, after Surange and Chandra. (L) *Denkania indica* Surange and Chandra 1973b, after Surange and Chandra.

remains to be established by more comprehensive studies. However, some glossopterid fructifications show several features comparable with angiosperm follicles. *Denkania* can easily be described using terminology commonly applied to angiosperms. According to the interpretation of Surange and Chandra (1975), it could be described as having orthotropous bitegmic ovules with long funicles and adaxial laminar placentation on a flat open carpel.

Glossopterid short shoots have also been found bearing two or more kinds of leaf-like structures (Etheridge 1899; White 1978). However, it is still uncertain whether fertile glossop-

terid short shoots were bisexual or unisexual, so comparison with angiosperms on this basis is not possible.

Other Features of Glossopterids

The other features of glossopterid plants neither preclude them as possible ancestors of angiosperms nor strongly support a glossopterid origin of angiosperms.

Pollen organs.—The pollen organs of glossopterids are profusely-branched axes with terminal pollen sacs. Several of these branching structures are attached adaxially to more or less modified leaves (Fig. 2J; see also Surange and Chandra 1975; Lacey, Van Dijk and Gordon-Gray 1975; Gould and Delevoryas 1977). Only a few living angiosperms, such as *Ricinus* and *Eucommia,* have even superficially similar pollen organs. Angiosperm anthers are fundamentally different in having more than one kind of tissue, unlike the structurally-preserved glossopterid pollen sacs illustrated by Gould and Delevoryas (1977, fig. 8). As we have argued here, the derivation of angiosperm follicles from glossopterid ovule-bearing structures would involve considerable reduction. Comparable reduction, adnation and perhaps even embedding of glossopterid pollen organs in their associated leaf could have resulted in laminar stamens of the type commonly thought ancestral in angiosperms (Takhtajan 1969). There is little fossil evidence in support of this idea. Late Permain glossopterid bract-like structures with fewer attached pollen sacs than usual have been reported by White (1978). Mid-Cretaceous angiosperm inflorescences with laminar stamens have also been reported by Dilcher (1979). Although this indicates the antiquity of laminar stamens, it does not prove that they are more ancient than filamentous stamens. These are not the oldest fossil angiosperm reproductive structures. Moreover, we have recently found (with the assistance of R. Pabian, H. Reynolds and J. F. Basinger) fossil flowers with filamentous stamens in deposits of the same age in Nebraska.

Pollen.—The bisaccate striate pollen of glossopterids (Fig. 2L) is quite unlike anything found in angiosperms. This is not as serious an objection to the glossopterid origin of angio-

sperms as it might first appear. Bisaccate pollen is widespread among gymnosperms, especially the extinct Mesozoic seed ferns. Thus, similar difficulties beset hypotheses deriving angiosperms from most gymnospermous groups. Sacci are commonly interpreted as "wings." Serious doubt was first cast on this interpretation by Wodehouse (1935, p. 254). He observed that the sacci of modern conifers collapse rapidly as they dry out after release. It is more likely that the sacci are adaptations for either flotation or orientation in micropylar fluids of the ovule (McWilliam 1958; Chaloner 1976). Conifers in which the pollen grain does not enter the micropyle do not have saccate pollen. These conifers, such as *Eutsuga* and *Araucaria,* have a crude kind of stigmatic pollination. Pollen grains adhere to the cone scale and only the pollen tube enters the micropyle of the ovule (Doyle 1945). Similarly, the lack of sacci may have been a natural consequence of the development of stigmatic pollen reception in early angiosperms and so not a feature of phylogenetic significance in itself.

Leaves.—Melville (1969) argued for angiospermous affinities of glossopterids on the basis of their reticulate venation (Fig. 2E). More recently Hickey and Doyle (1977) have suggested that the venation of glossopterids is typically gymnospermous, lacking several orders of finer veins. However, it is possible that the secondary veins of angiosperms are homologous with the veins of a small leaf with glossopterid venation of one row of vein loops each side of the midrib. Studies of both living (Kaplan 1973) and fossil angiosperm leaves (Samylina 1968; Krassilov 1973; Hickey and Doyle 1977) have indicated that early angiosperms had very small leaves.

The cuticle of *Glossopteris* and *Gangamopteris* leaves has been examined by many paleobotanists (Srivastava 1957; Surange and Srivastava 1957; Høeg and Bose 1960; Saksena 1963; Maithy 1965; Pant and Gupta 1968; Banerjee 1971; Srivastava 1969; Lele and Makada 1974; Pant and Singh 1974). These leaves mainly have stomata on one side only (hypostomatic), although some have them on both sides (amphistomatic). Stomata with an unspecialized ring of subsidiary cells (anomocytic) are most common, but paired lateral subsidiary cells (paracytic)

and other arrangements are found, often on the same piece of cuticle. The unspecialized nature of the subsidiary cells in glossopterids is generally similar to that of some of the oldest fossil angiosperm leaves (Upchurch 1978, 1979).

Other features of glossopterid leaves are widespread among vascular plants and probably of little phylogenetic value. The multi-stranded arc of vascular bundles in the petiole of *Glossopteris* leaves (Gould and Delevoryas 1977) is similar to that of living angiosperms (Bailey and Nast 1945, 1948), and is also a feature of other gymnosperms (Sahni 1948; Maheshwari and Vasil 1961). The differentiation of palisade and spongy mesophyll within the leaf of *Glossopteris* is also a feature found in both angiosperms (Eames and MacDaniels 1947) and several other groups of gymnosperms (Chamberlain 1919; Maheshwari and Vasil 1961; Ramanujam, Rothwell and Stewart 1974).

Wood.—Neither the stelar nor nodal anatomy of glossopterids nor the nature of pitting in glossopterid protoxylem and metaxylem are known. A variety of primary structures are found in trunks associated with glossopterid leaves (Kräusel, Maithy and Maheshwari 1962; Maheshwari 1972), but it is not yet certain which of these are glossopterid and which coniferous. The secondary wood of glossopterids is largely known from petrified roots (Schopf 1965; Gould 1975) and maceration of woody axes bearing leaves (Pant and Singh 1974; Pant 1977). This wood, usually identified as *Araucarioxylon*, is pycnoxylic, vessel-less and has well-developed growth rings. Rays are homogeneous (with procumbent cells) and are mainly uniseriate but rarely multiseriate. On the tracheid walls are circular or oval groups of three to nine circular or polygonal bordered pits. There are fewer oval pits in the cross field.

Wood like that of the living vessel-less angiosperms is generally regarded as the ancestral type in angiosperms (Takhtajan 1969), a conclusion supported by limited fossil evidence (Wolfe, Doyle and Page 1975). Like glossopterid wood, vessel-less angiosperm wood is pycnoxylic and sometimes also has growth rings. Unlike glossopterid wood, vessel-less angiosperm woods have mainly multiseriate rays in addition to uniseriate rays, heterogeneous rays (with

erect as well as procumbent cells) and a tendency towards scalariform pitting in certain areas of the tracheids (Bailey 1944; Bailey and Nast 1945; Carlquist 1975). These differences have traditionally been used to ally angiosperms with seed ferns, cycads and related plants rather than with conifers and *Ginkgo* (Bailey 1944; Bailey and Nast 1945), although these arguments now seem less clear (Carlquist 1975; Doyle 1978).

It is true that secondary wood like that of glossopterids occurs in living conifers and *Ginkgo* (Beck 1971) and in fossil cordaitaleans (Lepekhina 1972). However, the reproductive organs of glossopterids, as presently understood (Gould and Delevoryas 1977), indicate affinities with seed ferns. Similar secondary wood has also been found in corystosperm seed ferns (Archangelsky and Brett 1961; Archangelsky 1968; Schopf 1973) and in the cycad-like pentoxylaleans (Sahni 1948). Perhaps it is best, as indicated by Beck (1971), to regard this kind of secondary wood as ancient and conservative in gymnosperms and so of limited phylogenetic significance.

Habit.—Many vegetative features of glossopterids are found in angiosperms. Since they are also found in other gymnosperms, they probably have no phylogenetic value.

Both fertile and sterile leaves of *Glossopteris* have been found in a helix of variable pitch on short shoots attached to long shoots (Pant and Singh 1974). Larger trunks found in association with *Glossopteris* may be irregularly branched (Fig. 2A; Plumstead 1958; David 1907). Other trunks with whorled branches have also been found (Fig. 2C; Gould and Delevoryas 1977). Perhaps younger trees were conical and older trees had more irregular crowns. This and the long and short shoot arrangement are patterns of organization widespread among conifers and in *Ginkgo,* and also common in angiosperms, such as *Cercidiphyllum, Liquidambar* and *Nothofagus.*

The abundance of abscised *Glossopteris* leaves in coarser (possibly spring) layers of varved shales, together with other evidence for seasonal climate (such as prominent growth rings in associated fossil wood), may indicate that *Glossopteris* was seasonally deciduous (Plumstead 1958; Gould and Delevoryas 1977; Retallack, in press). A large number of modern

angiosperms are seasonally deciduous but so are some modern gymnosperms, such as *Ginkgo, Taxodium* and *Larix.*

Habitat.—For reasons outlined by Stebbins (1974) and Hickey and Doyle (1977), the earliest angiosperms appear to have been derived from plants with several xeromorphic adaptations, including very small leaves. Unlike this hypothetical ancestral angiosperm, most glossopterids had medium to large leaves and were evidently dominant plants of extensive coastal swamplands which accumulated most of the economically-mineable coal of the southern hemisphere (Retallack, in press). The smaller fructifications (such as *Lidgettonia* and *Denkania*) may be products of evolutionary reduction in some glossopterid lineages but could not be regarded as xeromorphic. Although xeromorphism is more common in areas outside swamps and marshes, such as intertidal mudflats, salt pans and coastal sand dunes, it may also be found in swampland plants as adaptations to substrates of acid humus or low nutrients (Schimper 1903). There was a gradual diversification of glossopterid plants as climate ameliorated following the earliest Permian glaciations (Retallack, in press). This may have been accompanied by expansion into a variety of coastal habitats. However, it is unlikely that glossopterids ever successfully colonized drier inland and upland habitats. These areas were largely vegetated by conifers and seed ferns during the late Permian (Carpentier 1935; Retallack 1977). Although Axelrod (1952, 1960) has advocated an upland origin and evolution of angiosperms, more recent findings and reinterpretation of early angiosperm fossils are compatible with a coastal origin and evolution of angiosperms (Hickey and Doyle 1977; Raven 1977; Retallack and Dilcher, in press a).

Distribution.—Glossopterids were most abundant in and characteristic of Gondwanaland, the Permian supercontinent including modern South America, Africa, Madagascar, India, Australia, New Zealand and Antarctica. Some may have penetrated into New Guinea and Turkey, but none of the previous records of *Glossopteris* from the U.S.S.R. have been accepted by later investigators (Meyen 1969; Chaloner and Lacey 1973; Chaloner and Meyen 1973).

Many authors have regarded southeast Asia as the "cradle of the flowering plants" (Takhtajan 1969). However, recent palynological work indicates that west Gondwanaland is a more likely center of angiosperm origin. In the sediments of rift valley bottoms then connecting Africa and South America, angiosperm-like pollen appears as early as anywhere else in the world and is also precociously diverse (Hickey and Doyle 1977; Doyle et al. 1977).

Age.—The time interval of about 120 Myr between the last abundant Permian glossopterid fructifications and the first Barremian (middle Early Cretaceous) angiosperm-like fossils has been cited as an obstacle to the glossopterid origin of angiosperms. This time gap is considerably narrowed by the likely survival of *Glossopteris* and related plants into the Triassic. In South Africa and eastern Australia, fossil leaves indistinguishable from *Glossopteris* persist in Middle Triassic coal measures (Thomas 1952; Retallack, in press). These are rare and a group of low diversity. Some have been found attached to axes in the characteristic close helix of glossopterids. It is also possible that *Linguifolium* was a Triassic descendant of *Glossopteris* (Retallack 1977, 1980, in press). These leaves are similar to *Glossopteris* but lack anastomoses of the dichotomizing secondary veins. In New Zealand, *Linguifolium* appears to have formed low diversity freshwater swamp woodland communities. Also like *Glossopteris, Linguifolium* was evidently seasonally deciduous and is associated with pycnoxylic wood with marked growth rings. Fragments of *Linguifolium* have been found in marine rocks of New Zealand as young as the Rhaetian stage at end of the Triassic (Retallack 1977).

On more general grounds, it is difficult to assess the importance of the time between positively identifiable glossopterids and angiosperms. The most pronounced adaptive radiation of fishes occurred during the Silurian (Romer 1966), but rare Ordovician (Ritchie and Gilbert-Tomlinson 1977) and even Cambrian (Repetski 1978) fossil fish are still being found. Although the most pronounced adaptive radiation of mammals occurred during the earliest Tertiary, it is likely that they had differentiated from reptiles by the Triassic (Romer 1966). The significance of gaps in the fossil record has also

been shaken by the discovery of living coelacanth fish (*Latimeria*), thought to have been extinct since the Cretaceous (Romer 1966) and of living monoplacophorans (*Neopilina*) which still have no post-Paleozoic fossil record (Runnegar and Jell 1976). Thus the long time between the last glossopterids and the first angiosperms cannot be considered a serious objection to the glossopterid origin of angiosperms.

Uncertainties

Glossopterid fructifications can be arranged in a series of morphological intermediates, suggestive of the course of evolution of angiosperm multifollicular axes (Fig. 4). However, a concrete phylogenetic scheme linking glossopterids with angiosperms is still premature for several reasons. Knowledge of other glossopterid and early angiosperm fructifications is incomplete. Angiosperm-like pollen has been found in Late Triassic rocks, some 80 Myr before the appearance and diversification of angiosperms during the later Early Cretaceous (Cornet 1977; Doyle 1978). There are also many other kinds of poorly understood Mesozoic pollen, such as *Eucommiidites* (Hughes 1961; Brenner 1967; van Konijnburg-van Cittert 1971). Bizarre extinct gymnosperm pollen is characteristic of early Cretaceous palynofloras of west Gondwanaland, in which some of the earliest angiosperm-like pollen appears (Jardiné, Kieser and Reyre 1974; Jardiné, Doerenkamp and Biens 1974; Doyle et al. 1977). As with these fossil plants, little is known of the ancestry of *Gnetum*, *Ephedra* and *Welwitschia,* living plants with a tantalizing blend of angiospermous and gymnospermous features. Most of these uncertainties also apply to theories deriving angiosperms from other gymnospermous groups.

Conclusions

Recent finds of fossil fructifications have clarified our understanding of glossopterids and early angiosperms. Early angiosperms probably had multifollicular fruits and bitegmic ovules. The unitegmic ovules of glossopterids were borne on the under side of a laminar organ which was more or less adnate to the adaxial surface of a leaf. This leaf may be homologous with the carpel of angiosperms, and the ovule-bearing structure homologous with the outer integument of angiosperm ovules. Some support for these homologies is apparent in a series of morphologically intermediate glossopterid fructifications, which may represent evolutionary changes between multiovulate glossopterid fructifications and early angiosperm follicles.

Other features compatible with a glossopterid origin of angiosperms are the morphology and anatomy of glossopterid leaves and the habit and distribution of glossopterids. The pollen organs, pollen, wood, habitat and age of glossopterids do not preclude them as angiosperm ancestors, but neither can they be regarded as support for the idea. We hope that the hypothesis presented here will stimulate more detailed investigations of these various uncertainties.

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