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Enigmatic gymnosperms? Structurally preserved Permian and Triassic seed ferns from Antarctica

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Abstract

Representative organs from the seed fern groups Glossopteridales and Corystospermales are commonly found in Gondwana during the Permian and Triassic, respectively. To date, both groups have been reconstructed predominantly on the basis of compression fossils and, in the case of the glossopterids, impressions. As a result, many details of their morphology remain unclear, and their taxonomic status and relationship to other groups are somewhat enigmatic. Collections of anatomically preserved fossils from permineralized peat in the central Transantarctic Mountains, Antarctica include a number of organs assignable to these two orders. Anatomical characters provide an opportunity to correlate isolated plant organs and to develop new reconstructions of these plants. Combined with paleoecological data, these fossils are beginning to provide a more accurate picture of the habitat and life history of these unique seed plants.

1. Introduction

The term enigmatic is used often in paleobotany, but what exactly is meant by this designation? The traditional definition for paleobotanists is a group of plants that is difficult to classify, i.e. it is enigmatic in the taxonomic sense of the word. Such groups are usually extinct; have unusual vegetative, and more commonly, reproductive structures; and often seem to be unique when compared to other groups. Additionally, because of their uniqueness they often appear in the fossil record with no likely ancestors and no generally accepted descendants.

There are many fossil plants that potentially could be included in a discussion of "enigmatic" gymnosperms. This contribution will concentrate only on members of two groups that are usually classified as seed ferns: the Glossopteridales, which existed almost exclusively in the Southern Hemisphere during the Permian, and the Corystospermales, another Gondwana group that is generally restricted to the Triassic. In addition to reviewing the current level of information about each group, this paper will primarily focus on anatomically preserved fossils from Antarctica and the details this material has contributed to the current understanding of these groups. Both groups show interesting features, many of which are considered to be enigmatic, either in their reproductive biology, their relationship (or lack of relationship) with other groups, their distribution, and their geologic history. Each group has been considered enigmatic for varying reasons, not all of which are taxonomic. Therefore, this paper will consider the following features: adaptations in

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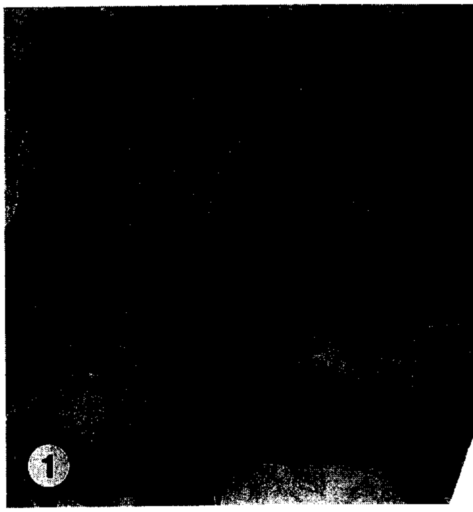
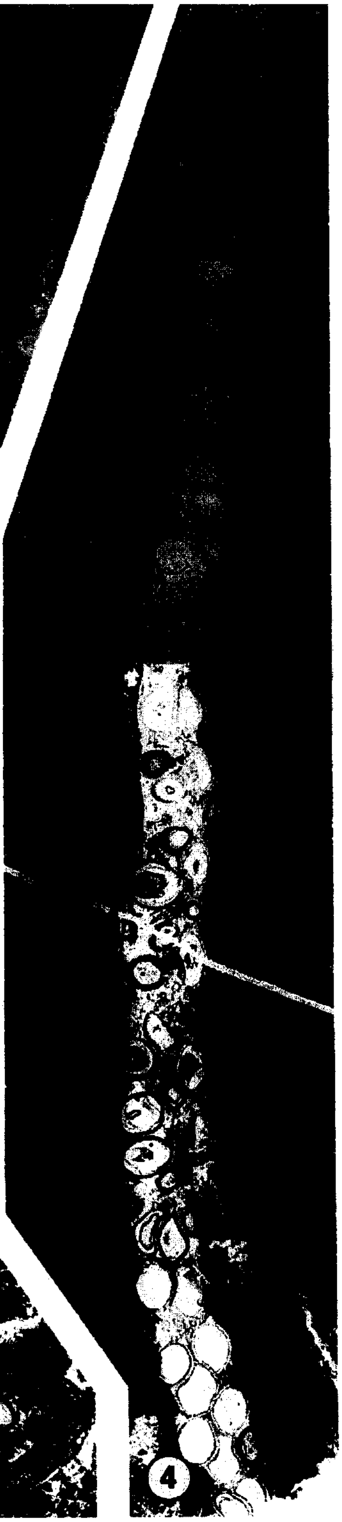
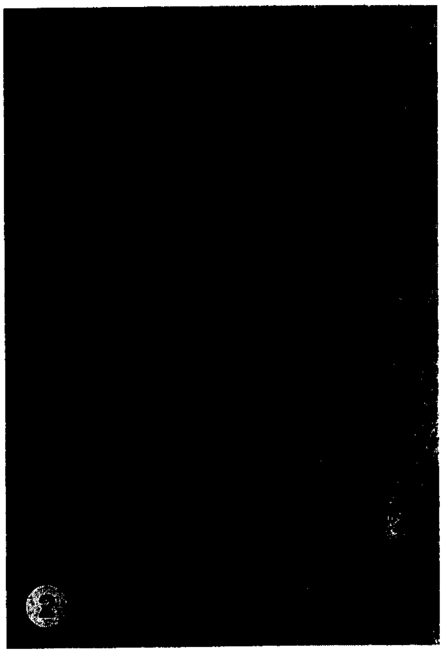
PLATE I







vegetative organs, morphology and interpretation of reproductive structures, paleobiogeography, and paleoecological significance, where applicable.

2. Materials and methods

Anatomically preserved material comes from two localities in the central Transantarctic Mountains (Queen Alexandra Range), Antarctica (Taylor et al., 1989). The Skaar Ridge site is within the Buckley Formation and is probably Late Permian; the Fremouw Peak site occurs in the uppermost Fremouw Formation (Smoot et al., 1985) and is dated as early Middle Triassic, based on palynomorphs within the peat (Farabee et al., 1990). The fossils are silicified and were prepared using standard cellulose acetate peel techniques.

3. Glossopteridales

The Glossopteridales first appeared in Gondwana in the Late Carboniferous/Early Permian and by the Late Permian dominated the landscape in this area. Although *Glossopteris* leaves have been found in the Early Triassic of India and possibly even the Jurassic of Mexico (*Mexiglossa*; Delevoryas and Person, 1975), it is predominantly a Permian group. *Glossopteris* is the most diverse and widespread genus (Plate I, 1), but *Gangamopteris* is generally the earliest leaf type to appear and is found in sedimentary rocks directly above glacial deposits in many areas of Gondwana (Plate I, 2).

Reproductive organs were first described by Plumstead (1952), followed by various interpretations of the morphology of these organs, resulting in a proliferation of generic names [>30 ovulate genera at present; see McLoughlin (1993) for a recent summary of genera]. The total range of reproductive organs includes not only those attached to *Glossopteris* leaves, but also ovule-bearing axes that occur at the same localities as leaves (e.g. *Arberia*, *Rigbya*). These unattached reproductive organs will not be considered here (but see McLoughlin, 1993).

The majority of glossopterid reproductive organs are poorly preserved impressions and it was not until 1977 that Gould and Delevoryas, utilizing permineralized material, established that the seeds were borne on leaves and that the group should be classified as a type of seed fern. However, the group continues to be considered enigmatic for several reasons: the origins of the group remain unclear and glossopterid fossils appear in the fossil record rapidly in a geologic sense. The paleoecology of the glossopterids has been variously interpreted, but the widespread distribution and abundance of these plants is somewhat puzzling. The reproductive structures (both ovulate and pollen-bearing) are complex, poorly understood, and morphologically diverse. Surange and Chandra (1975), among others, have suggested that there are two basic types of ovulate reproductive organs, but the leaves in these two groups are virtually indistinguishable. Pigg (1990a; Pigg and Taylor, 1990) has shown that even though glossopterid leaves may have similar external morphologies, they contain very different internal anat-

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PLATE I

Glossopteridales.

1. Numerous *Glossopteris* leaves from Skaar Ridge, central Transantarctic Mountains (Buckley Formation, probably Late Permian). ×0.3.
2. *Gangamopteris* leaf from eastern side of Aztec Mountain (Beacon Heights area, southern Victoria Land, Antarctica). ×0.8.
3. Transverse section of ovulate organ originally described by Gould and Delevoryas (1977) from the Bowen Basin, Queensland, Australia. Arrows point to overlapping margins of megasporophyll. 15,281. ×9.
4. Transverse section of ovulate organ described by Gould and Delevoryas (1977) from the Bowen Basin, Queensland, Australia. Note the large number of seeds borne on a single megasporophyll. 15,292. ×7.
5. Longitudinal section of Bowen Basin seed showing delicate meshwork (arrow) extending from micropylar region. Note attachment of ovule to megasporophyll below. 15,290. ×48.
6. Longitudinal section of seed from reproductive organ described by Taylor and Taylor (1992) from Skaar Ridge, Antarctica. 451 E-1, T-47a. ×50.

omies. This has led some authors to speculate as to what features have made the glossopterid leaf morphotype so adaptable.

Perhaps the most important reason the Glossopteridales continue to be regarded as taxonomically enigmatic is that the reproductive structures are complex and, due in large part to the poorly preserved nature of many of these structures, have been variously interpreted (see, e.g. Plumstead, 1952, 1956; Surange and Chandra, 1975; Schopf, 1976; Pant, 1977; Rigby, 1978; McLoughlin, 1990a). These interpretations range from three-dimensional cones to flattened, dorsiventral structures, although several authors have discounted the three-dimensional cone interpretation (e.g. McLoughlin, 1990a). Surange and Chandra (1975) divided the glossopterids into two large groups, based on the morphology of the ovulate structures. These authors considered one type to have affinities with the seed ferns (Pteridospermales of Surange and Chandra), because of the cupulate morphology of the ovulate organs. This group includes taxa such as *Lidgettonia*, *Denkania* and *Partha*, in which small, cupule-like structures are attached by stalks to the surface of, or in the axil of a *Glossopteris* leaf. The second group was not considered to be closely related to any other gymnosperms. According to Surange and Chandra, this group is characterized by multiovulate fructifications, such as *Scutum*, *Dictyopteridium*, *Senotheca* and *Jambadostrobus* (Glossopteridales of Surange and Chandra). In this morphological type, ovules are borne on the surface of a flattened structure, which has been variously described, but is now known to represent a megasporophyll, based on Gould and Delevoryas' work (1977). The megasporophyll is borne either on the adaxial surface of a *Glossopteris* leaf (e.g. *Jambadostrobus*), or in an axillary position. Because anatomically preserved specimens have not been found that include this attachment, the exact relation to the leaf and axis is currently uncertain.

Based on currently available evidence, the simplest interpretation of all the attached glossopterid reproductive organs is that there are at least two different morphological types, both of which may be classified as seed ferns. The anatomical evidence assembled thus far supports this interpretation. One type consists of a single, flattened, multiovulate megasporophyll (e.g. *Scutum*), while the other consists of what appear to be ovule-bearing cupules borne in various arrangements on *Glossopteris* leaves (e.g. *Lidgettonia*). These two types will be termed multiovulate and cupulate types, respectively.

Gould and Delevoryas (1977) described the first anatomically preserved, multiovulate type of fructification from the Bowen Basin of Queensland, Australia. It consists of a leaf-like megasporophyll, approximately 3–11 mm wide by 10–42 mm long, that bears several ovules on one surface (Plate I, 3, 4). The sporophyll is partially enrolled and, in some cases, overlaps to cover the ovules (Plate I, 3). The ovules are surrounded by a meshwork of filaments that appear to extend from the micropyle of each ovule (Plate I, 5); many of the ovules include megagametophyte tissue. The megasporophylls occur in permineralized peat with numerous *Glossopteris* leaves. Due to poor preservation, it was impossible for Gould and Delevoryas (1977) to determine whether the seeds were borne on the abaxial or adaxial side of the megasporophyll. The megasporophyll apparently opened at maturity, because they also decribed specimens that were not enrolled.

Taylor and Taylor (1992) described an ovulate structure of similar morphology from permineralized peat collected on Skaar Ridge, Antarctica. This megasporophyll was considerably smaller (1 × 6 mm) and bore fewer (5–6), smaller seeds (Plate I, 6) than that from the Bowen Basin. In addition, it was not enrolled to cover the ovules in any way (Plate II, 1). Based on the orientation of the vascular bundles, it was clear for the first time that the ovules were attached on the adaxial surface of the megasporophyll (Plate II, 1). Reexamination of Gould and Delevoryas' (1977) material indicates that the ovules were also borne on the adaxial surface of this megasporophyll. Although these two taxa are generically distinct, they both provide evidence that the multiovulate glossopterids were seed ferns that bore their ovules on the adaxial surface of a megasporophyll. These contributions can be combined with an analysis of impression/compression fossils to reinterpret earlier reconstructions of some of these reproductive organs. Unfortunately, neither of these studies provides information about the relationship of the megasporophyll to the plant axis. However, investigations of impression/compression fossils have suggested that the reproductive structures were axillary (Pant and Singh, 1974; Holmes, 1990; McLoughlin, 1990b) or partially fused to the underlying *Glossopteris* leaf (e.g. *Jambadostrobus*; Chandra and Surange, 1977).

Additionally, considerations of pollination biology can be clarified by the information obtained from anatomically preserved fructifications (Taylor and Taylor, 1992). Early interpretations of the multiovulate impression fossils (e.g. Plumstead, 1952; Surange and Chandra, 1975) suggested a megasporophyll (fertile scale or other terms of earlier authors), which was covered by a "sterile scale". Subsequent authors (e.g. Schopf, 1976) discounted the sterile scale, but reconstructed the ovules on the abaxial surface of the sporophyll; that is, facing the subtending *Glossopteris* leaf. Either of these interpretations would necessitate pollination by specialized means, i.e. organisms capable of reaching the ovules while they were sandwiched between the two scales, or pollination after abscission from the plant. It is unlikely that the megasporophylls abscised, however, because they are commonly found in close association with the subtending leaf, even after the ovules have been shed (e.g. McLoughlin, 1990a). The reinterpretation of these megasporophylls based on anatomical evidence, however, suggests that the ovules were exposed at some point in their development. Gould and Delevoryas' (1977) material includes megasporophylls which were partially unrolled, thereby exposing the ovules, while the megasporophyll described by Taylor and Taylor (1992) was clearly open. In this position, pollination could have been effected by wind, or, if necessary, by other, possibly biotic means. The glossopterids have traditionally been assumed to be wind-pollinated, due to the occurrence of bisaccate pollen in the group.

Until now, the only two anatomically preserved fructifications that have been described are both representative of the multiovulate type of glossopterids (Glossopteridales of Surange and Chandra, 1975). Zhao et al. (1994) recently reported a new permineralized fructification from the Skaar Ridge locality in Antarctica which appears to represent the first example of an anatomically preserved cupulate type of fructification. It consists of groups of four, uniovulate cupules borne on a common stalk, and morphologically could be compared to impression genera such as *Denkania* or *Partha*.

In summary, anatomical studies have provided excellent evidence on several aspects of the glossopterids that have traditionally made the group taxonomically enigmatic. Permineralized specimens clearly show that there are two groups, based on the morphology of the ovulate reproductive organs. These structurally preserved forms also show that the multiovulate types bear their ovules on the adaxial surface of a flattened, leaf-like megasporophyll. Unfortunately, permineralized specimens have not yet been found that clearly demonstrate the attachment of either the cupulate or the multiovulate types to the underlying *Glossopteris* leaf. However, the best-preserved impression/compression material indicates that the reproductive structure is axillary and may be partially fused to the midrib region of the underlying leaf. With a clearer picture of the exact morphological nature of these plants, based on anatomically preserved specimens, perhaps the other taxonomically enigmatic aspect of the glossopterids (i.e. no apparent close relationship to ancestors or descendants) can now be addressed more accurately in a cladistic analysis.

The other enigma relative to the glossopterids is their distribution in time and space. The group appears relatively suddenly in the Late Carboniferous/Early Permian and, by the Late Permian, is so widespread that paleobiogeographic classifications often equate the Gondwana flora with the *Glossopteris* flora (e.g. Plumstead, 1973; Meyen, 1987). When compared to other coeval assemblages of plants, the *Glossopteris* flora has traditionally been considered rather homogeneous. This apparent consistency, however, may actually be due, in part, to a lack of understanding of the components of the flora. For example, good reconstructions of the *Glossopteris* plants are still lacking and little is known about their reproductive biology. More recent detailed floristic studies (e.g.

PLATE II


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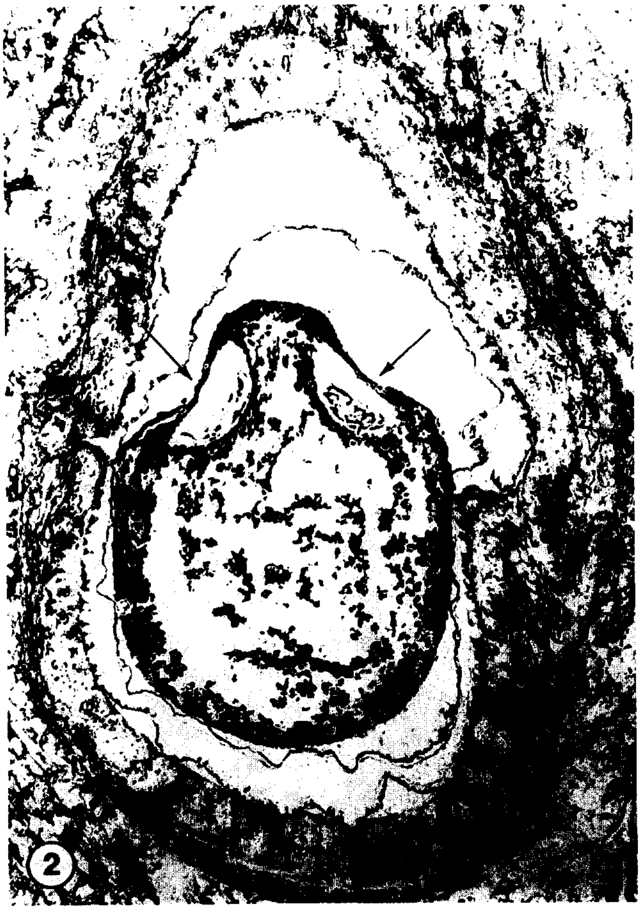
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Archangelsky, 1984, 1986, 1990; Archangelsky and Cúneo, 1991) now show that there are considerable geographic and stratigraphic variations among the various *Glossopteris* floras. In addition, until recently modern paleoecological methods had not been widely applied to understanding the depositional environments and distribution of the elements of the flora. This problem has been addressed in recent studies of the paleoecology of *Glossopteris* floras, both in Antarctica and South America (e.g. Archangelsky and Cúneo, 1991; Cúneo et al., 1993).

Part of the apparent enigma can be resolved by examining the geologic origin and biologic nature of these plants. I suggest that part of the widespread distribution and geologically sudden appearance of the glossopterids can be explained by their biological strategies. When glossopterids first appear in the Early Permian, they possess many of the characteristics of *r*-selected plants (i.e. they are colonizers). The group, first recognized in the fossil record by the occurrence of *Gangamopteris* leaves, appeared soon after the retreat of glacial ice in Gondwana (Late Carboniferous/Early Permian, depending upon the location) and rapidly became widespread. Many of these early types produced small seeds in large numbers (i.e. the multiovulate types), which is a trait common to *r*-selected plants (Pianka, 1970). A stratigraphic examination of the distribution of multiovulate vs. cupulate reproductive organs throughout Gondwana indicates that the multiovulate types appear earlier in the Permian than the cupulate types. Vegetatively, these plants bore relatively large, strap-shaped leaves, at least some of which were probably produced in a low helix, often resulting in dense clusters of leaves that mimicked whorls (Pigg and Taylor, 1993). They thus possessed great potential to shade out competitors, and this feature, combined with the production of large numbers of small seeds, ensured their success in colonizing situations. Once the multivoulate types had colonized the landscape following glacial retreat, there was little opportunity for other groups to move in, and they were able to maintain their dominance position throughout the Permian.

Perhaps as the ecosystem further developed and the climate warmed later in the Permian, cupulate reproductive types became more widespread. Compared to multiovulate types, they produced fewer seeds per individual, and these were partially enclosed by leaflike cupules. MacArthur and Wilson (1967) suggested that *r*-selection may be more common in high latitudes, where climates are strongly seasonal. It has also been hypothesized that polyembryony arose in gymnosperms inhabiting high latitudes as an evolutionary advantage in a colonizing environment (Durzan, 1993). The earliest evidence of polyembryony in the fossil record was described in ovules of *Plectilospermum* from the Permian peat in Antarctica (Smoot and Taylor, 1986). *Plectilospermum* was distinguished by the high percentage of seeds that contained either embryos or multicellular megagametophytes (Taylor and Taylor, 1987; Plate II, 2–5).

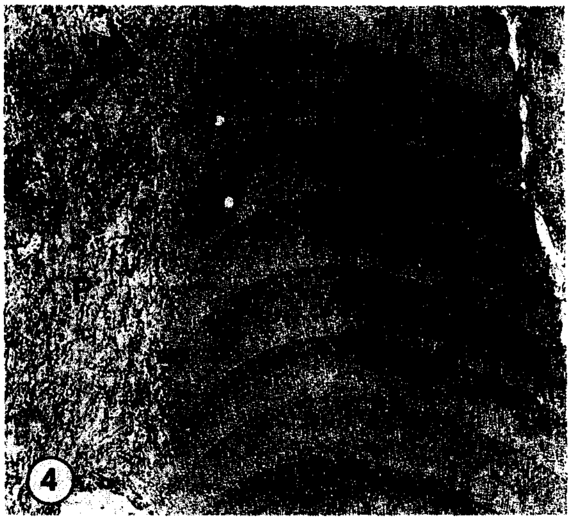
Evidence to support the suggestion that glossopterids were colonizers comes from several floras and an in-situ forest in Antarctica (Taylor et al., 1992a; Cúneo et al., 1993). At these high-latitude sites there is evidence for little, if any, understory in *Glossopteris* forests, and even the young trees grew in dense stands (Taylor et al., 1992a). Moreover, Cúneo et al. (1993) noted a high concentration of *Vertebraria* roots in both levees and point bar deposits, habitats typical of colonizers.

PLATE II

Glossopteridales.

1. Transverse section of Skaar Ridge ovulate organ. Arrow indicates abaxial surface of megasporophyll. Note vascular bundle (*V*) and attachment of seeds on adaxial surface. 451 D-2 (B-59a). ×31.
2. Oblique longitudinal section of *Plectilospermum* with megagametophyte and two archegonia (arrows). 451 D (B-29ß). ×31.
3. Transverse section through apex of *Plectilospermum* with megagametophyte. Arrows indicate two embryos. Upper embryo magnified in 4. 451 D (B-103ß). ×31.
4. Embryo from *Plectilospermum* seed showing differentiation of embryo and coiled suspensor (arrow). 451 D (B-103ß). ×160.
5. Archegonial chamber of *Plectilospermum* with remnant of embryo (arrow). 451 D (B-29ß). ×125.

PLATE III



These authors note that the glossopterids do not appear to have been restricted to one particular kind of habitat, since fossil leaves are found in floodplain, abandoned channel, and lacustrine deposits. Root fossils were also found in fluvial rocks where leaves were rarely preserved. Because glossopterid fossils appear in many types of environments, we cannot explain the widespread distribution of the group as being well-adapted to only a single type of enviroment, as some authors have suggested.

4. Corystospermales

Although they have probably been studied less, the corystosperms show many parallels with the glossopterids. They too appear rather suddenly at the beginning of the Triassic in Gondwana (although there are Early Triassic floras in India that include both *Glossopteris* and *Dicroidium* leaves). In general, Gondwana Triassic floras are more diverse than those from the Permian. Nevertheless, the *Dicroidium* leaf type (Plate III, 1), with its distinctive forking frond (Fig. 1B), still dominates many Triassic floras and is widespread, having been collected on all Gondwana continents. Various foliage types have been considered to be produced by the corystosperms, including *Johnstonia* and *Xylopteris* (see e.g. Petriella, 1981), but some authors include these as synonyms of *Dicroidium*. [It is believed the group includes some Northern Hemisphere representatives, such as the foliage genus *Pachypteris* (Taylor and Taylor, 1993), but these will not be discussed here.]

The reproductive organs of the corystosperms are somewhat better known than those of the glossopterids, since the group was initially described from well-preserved compression fossils (e.g. Thomas, 1933; Townrow, 1957, 1962). Nevertheless, there are still a number of questions that remain to be answered about their organization and reproductive biology. The group includes foliage of *Dicroidium*, stems of *Rhexoxylon* and *Kykyloxylon* (Fig. 1E), ovulate organs assigned to *Umkomasia* (Fig. 1A), and pollen organs of *Pteruchus* (Fig. 1F,G). All of these taxa are known from compression material and, with the exception of *Umkomasia*, have now been described from permineralized specimens as well.

Petriella (1978, 1981), based in part on earlier work by Archangelsky (1968), reconstructed the "*Dicroidium*" plant as a medium-sized tree bearing frond-like foliage. His reconstruction resembles a modern tree fern in that there is no branching and the fronds are attached in a group at the crown of the plant. This reconstruction correlates with the unusual anatomy found in *Rhexoxylon*, which is similar to many lianes (Walton, 1923). Although Walton (1923) reported what he described as a single branch trace in *R. africanum*, this was not sectioned and could represent either a bifurcating axis or a branch trace. Other than this one report, branching has not been described in *Rhexoxylon* specimens. *Rhexoxylon* apparently reached very large diameters (e.g. Herbst and Lutz, 1987), but this alone may not contradict the liane-like morphology, since the basal stem diameter of some modern lianes can also be quite large. Petriella's (1978) reconstruction was based on the constant association of compressed *Dicroidium* fronds with permineralized stems of *Rhexoxylon*, especially in

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PLATE III

Corystospermales.

1. *Dicroidium* from Gordon Valley, central Transantarctic Mountains (upper Fremouw Formation, Middle Triassic). T-4-31. × 1.2.
2. Transverse section of *Kykloxylon* stem from permineralized peat at Fremouw Peak, Antarctica (upper Fremouw Formation, early Middle Triassic). Note numerous secretory cavities in pith and cortex. 568 B (T2-d). × 16.
3. Portion of *Rhexoxylon* stem (transverse section) from col at Fremouw Peak (upper Fremouw Formation, early Middle Triassic), showing two bands of secondary xylem separated by bands of parenchymatous tissue. 11,314 A bot. × 0.65.
4. Detail (rotated 90°) of *Rhexoxylon* stem in 3, showing wood with growth rings (right) and parenchymatous zone (*P*). 11,314 A bot #3δ. × 7.
5. Transverse section of *Dicroidium* rachis showing complex organization of vascular strands and conspicuous secretory cavities (arrows). 10,109 B2a side B #10. × 20.

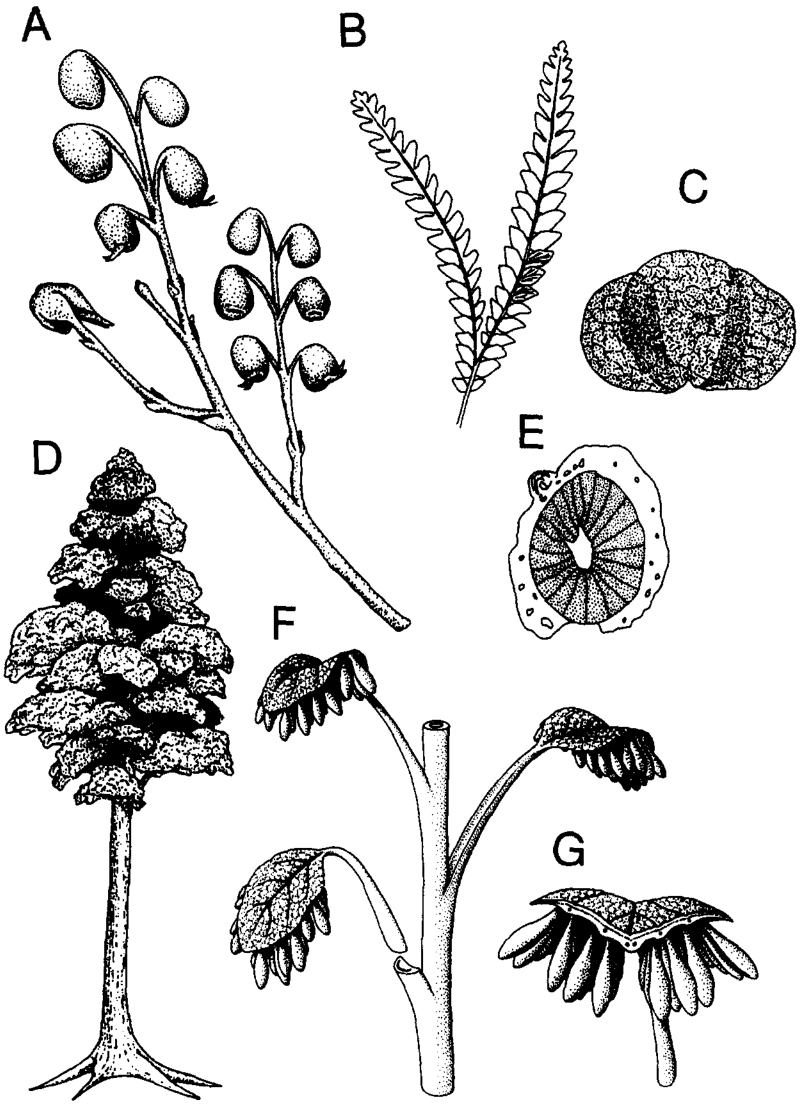


Fig. 1. Suggested reconstruction of component parts of the "*Dicroidium*" plant from Antarctica. (A) *Umkomasia* ovulate organ. (B) *Dicroidium* leaf. (C) Bisaccate pollen grain. (D) Habit of entire plant (height estimated to be 10–20 m based on diameter of Gordon Valley stumps). (E) Transverse section of *Kykloxylon* stem. (F) *Pteruchus* pollen organ. (G) Single *Pteruchus* head with pendant pollen sacs. (All drawings by David M. Dennis.)

the Ischigualasto Formation of Argentina (Archangelsky and Brett, 1961).

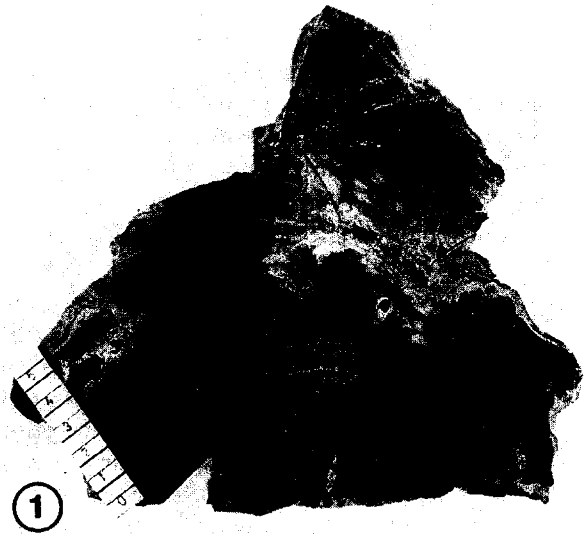
Retallack and Dilcher (1988) provided a reconstruction of the "*Dicroidium*" plant as a "woodland tree," based on a composite of fossils from South America and South Africa. However, although *Rhexoxylon* stems have been found in South Africa, they are not associated with any megafossil floras (Anderson and Anderson, 1983). Anderson and Anderson (1983, p. 69) noted that the genus has been found only in red beds which are currently considered to be Early Jurassic in age. The fact that *Rhexoxylon* is not preserved at the same sites as *Dicroidium* in South Africa, however, may simply reflect different depositional environments necessary for preservation. It is very unusual, as in the Ischigualasto Formation, to find permineralizations preserved with compression fossils. Nevertheless, a reconstruction based on specimens of different ages from different continents may not be accurate. *Rhexoxylon* has also not yet been described from Australia, and only a single specimen has been found in Antarctica (Taylor, 1992; Plate III, 3, 4). Therefore the enigma remained, if these reconstructions were generally applicable in Gondwana, where was the stem of *Dicroidium* in Australia and Antarctica?

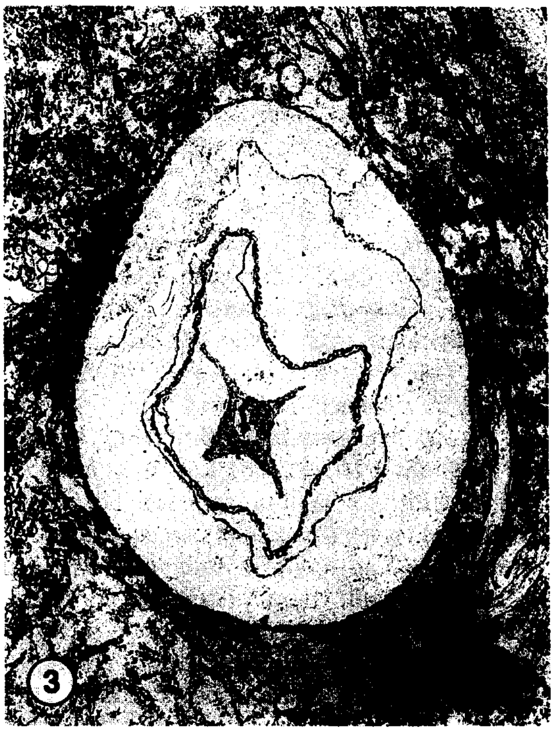
Meyer-Berthaud et al. (1992, 1993) subsequently described 1–5 year old stems of *Kykloxylon fremouwensis* in permineralized peat from Fremouw Peak, central Transantarctic Mountains (Taylor et al., 1989; Plate III, 2). The leaf bases attached to these stems are anatomically similar to the disarticulated leaves *Dicroidium fremouwensis* from the same site (Pigg, 1990b). Both stems and leaf bases contain small, characteristic secretory cavities (Plate III, 2), which are also found in leaves and rachides described by Pigg (1990b) (Plate III, 5). The stems consist of a ring of secondary xylem of the *Dadoxylon* type surrounding a pith that contains sclerotic nests. The axes bear closely spaced leaves; the presence of periderm beneath the leaf bases indicates that the plants shed their leaves following a single year of growth. This conclusion, based on anatomical characters, is supported by the presence of dense mats of *Dicroidium* leaves at several compression sites in the area (Plate III, 1). In addition, an in-situ Triassic forest from Gordon Valley in the central Transantarctic Mountains (Taylor et al., 1992b) includes large trunks (up to 60 cm in diameter) with well-developed growth rings (Plate IV, 1), rooted in shale dominated by *Dicroidium* leaves. Combined with the relatively high paleolatitude of the site (approximately 70–75°S), which would indicate some winter darkness, these data suggest that *Dicroidium* "plants, " in Antarctica at least, were seasonally deciduous.

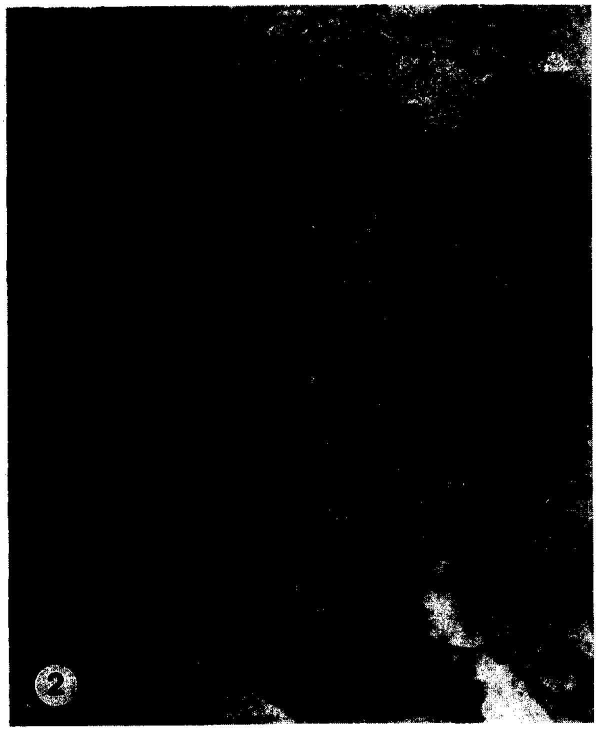
Meyer-Berthaud et al. (1993) also noted the presence of axillary buds on *Kykloxylon* stems, thus providing evidence for more typically gymnospermous branching, rather than the growth form typical of tree ferns. These authors concluded that perhaps *Dicroidium* in western Gondwana (i.e. South America and South Africa) was borne on *Rhexoxylon* stems and that *Dicroidium* in eastern Gondwana (East Antarctica and Australia) was borne on *Kykloxylon* stems (Fig. 1E) or, more generally, on *Dadoxylon*-type woody axes. Del Fueyo et al. (1994) have examined the wood of the fossil forest from Gordon Valley, Antarctica. Because no primary xylem/pith was preserved, the material could not be included in any existing Mesozoic form genera (Plate IV, 1). For this reason, they proposed to place it in a new genus. This genus exhibits so-called abietinean pitting (either one row of circular, separate pits or two rows of circular, opposite and separate pits). Meyer-Berthaud et al. (1993) described the pitting in *Kykloxylon* as variable: older specimens show crowded, biseriate pits that can be either alternate or opposite. In other specimens, the pitting is uniseriate and separate or contiguous, while several very large tracheids exhibit triseriate pitting. This pitting can neither be described as clearly abietinean or araucarioid (multiseriate, alternate and hexagonal pits). I believe the possibility that *Kykloxylon* and the Gordon Valley trees may represent the same plant cannot be ruled out; the latter representing the trunk and the former the distal twigs. Overall, this plant is a large tree with gymnospermous wood and axillary branching that bore seasonally deciduous *Dicroidium* fronds (Fig. 1D). A number of authors have discussed the difficulties of taxonomic determinations based on wood anatomy and the pitfalls involved in classifying woods as either "abietinean" or "araucarian" (e.g. Bailey, 1933; Philippe, 1992). In addition, as noted above, the fossil forest in Gordon Valley is rooted in shales that consist almost exclusively of *Dicroidium* leaves.

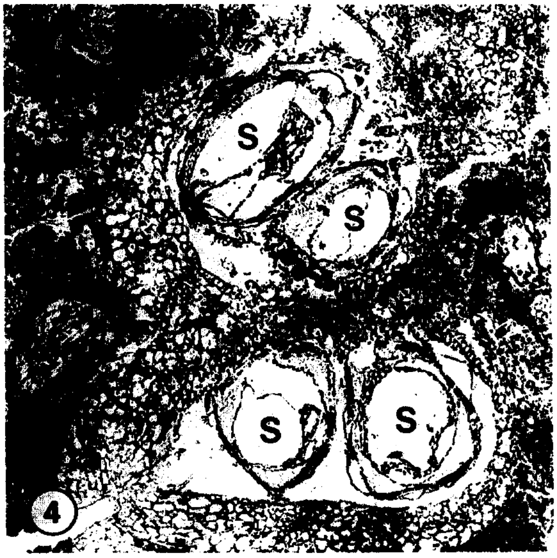
The reproductive structures of the Gondwanan corystosperms, as currently understood, are much less diverse than those of the glossopterids. Microsporangiate organs have been assigned to two genera, *Pteruchus* and *Pteroma*. Since the latter is known only from the Jurassic of Yorkshire (Harris, 1964), only *Pteruchus* will be considered here. *Pteruchus* has been described from all parts of Gondwana and is remarkably consistent from region to region. It consists of a flattened structure (variously termed a microsporophyll or a pinnule),

PLATE IV









Corystospermales.

1. Transverse section of portion of trunk from Gordon Valley forest, central Transantarctic Mountains (upper Fremouw Formation). 11,471 A. ×0.2.
2. Compressed *Umkomasia*-like reproductive organ from the Allan Hills, Antarctica (Lashly Formation). Arrows indicate uniovulate cupules. ×25.
3. Longitudinal section of *Ignotospermum* ovule from Fremouw Peak permineralized peat. 557 B bot #2δ. ×21.
4. Portion of *Petriellaea* cupule with four enclosed seeds (*S*). 10,025 B top #6α. ×251.

which bears elongate pollen sacs on the abaxial or lower surface (Fig. 1F,G). Pollen is bisaccate (Fig. 1C). Controversy has arisen over the morphological interpretation of the reproductive organ, with some authors describing it as an axis bearing microsporophylls, others as a rachis with pinnae or pinnules attached to it, or a fertile branch bearing lateral branches (see Yao et al., 1995). There has also been much discussion as to whether the laterals (i.e. microsporophylls) were borne on the main axis helically, in two ranks, or sub-oppositely (e.g. Townrow, 1962).

Yao et al. (1995) described permineralized *Pteruchus* from the Fremouw Formation, Antarctica and thus were able to determine that the pollen organ actually represents an axis bearing helically arranged microsporophylls. These authors characterized the microsporophyll as leaflike, including a basal stalk and a distal flattened head that bears pollen sacs on its abaxial surface (Fig. 1G). In addition, although *Pteruchus* is generally accepted as the microsporangiate organ of the corystosperms, it has never been found attached to stems bearing *Dicroidium* leaves. The attribution of *Pteruchus* to the corystosperms is based primarily upon its constant association at various localities. Perhaps the best method to determine affinities of disarticulated plant parts, aside from attachment, is similar anatomical features. Yao et al. (1995) detailed the presence of distinct secretory cavities in *Pteruchus* that are identical to those noted by Pigg (1990b) in leaves of *Dicroidium fremouwensis* and by Meyer-Berthaud et al. (1993) in stems of *Kykloxylon*, thus providing the most definitive evidence to date that *Pteruchus* and *Dicroidium* are parts of the same organism.

The ovulate reproductive organs of the corystosperms are also remarkably uniform throughout Gondwana. Several genera have been described, but *Umkomasia* is the most widespread geographically and perhaps the best-known of these. Other taxa include *Spermatocodon*, *Pilophorosperma* and *Karibacarpon*, although Holmes (1987) regarded the latter two as synonyms of *Umkomasia*. *Spermatocodon* was described on the basis of very fragmentary specimens (Thomas, 1933) and Holmes (1987) considered it a problematic taxon. There have also been ovulate organs described from the Northern Hemisphere, including a specimen of *Umkomasia* from the Jurassic of Germany (Kirchner and Müller, 1992), but these will not be addressed here.

Umkomasia consists of an axis bearing lateral branches, which in turn bear opposite pairs of uniovulate cupules (Plate IV, 2; Fig. 1A). The cupules are not enclosed and the elongate micropyle of each ovule extends beyond the cupule margin. As in *Pteruchus*, the arrangement of branches on the main axis remains unclear, and may be either helical or flattened in a single plane. An interesting feature that does not occur in *Pteruchus* is that the lateral branches are subtended by bracts (Fig. 1A). *Umkomasia* has been described from South America, South Africa, Australia, and New Zealand, but has not been found in comparable aged rocks in India. *Dicroidium* and *Pteruchus* are both known from the Indian subcontinent (Bose et al., 1990), and the floras from this area have been extensively studied, so it seems possible that the "*Dicroidium*" plant in India may have borne a different type of ovulate reproductive organ than *Umkomasia*. This may also be the case in Antarctica.

Although *Umkomasia*-like organs have been noted in several compression floras from Antarctica (e.g. Taylor and Taylor, 1988), the genus has not been found in the Triassic permineralized peat that includes *Dicroidium*, *Pteruchus*, and *Kykloxylon*. To date, only one seed and one cupulate organ have been described from this site. Perovich and Taylor (1989) characterized ovules of *Ignotospermum* as radially symmetrical, with a distinctive, bilayered nucellus and a complex integument (Plate IV, 3). A majority of the ovules examined contained a cellular megagametophyte. This is an interesting parallel to the Permian ovule, *Plectilospermum*, which also contained a high percentage of cellular megagametophytes (Smoot and Taylor, 1986; Taylor and Taylor, 1987). Perhaps the extreme shortening of the growing season, necessitated by the high latitudes at which these plants were growing, may explain the large number of ovules at one particular stage of growth in each deposit. Ovules of *Ignotospermum* (Plate IV, 3) do not exhibit the elongate, curved, and bifid micropyle so common in compressed *Umkomasia* specimens. However, as Retallack and Dilcher have noted (1988), these micropyles do not appear to be present in compression/impression specimens of mature, dispersed seeds.

The second anatomically preserved ovulate organ known from the Fremouw permineralized peat is *Petriellaea*, a cupulate structure that bears five ovules (Taylor et al., 1994). The cupule consists of a leaflike structure that completely encloses the ovules (Plate IV, 4). Based on vascular anatomy, the ovules are attached to the abaxial surface of the megasporophyll. The ovules appear triangular in cross-section, with thickened areas of the sclerotesta present in each angle of the ovule. The morphology and anatomy of this cupulate structure could not be compared directly with any known group of Mesozoic seed ferns and was placed in its own order, the Petriellales. Could this represent the ovulate organ of the Antarctic "*Dicroidium*" plant (Fig. 1)? The cupule itself does not contain the distinctive secretory cavities present in the Antarctic stems, leaves, or pollen organs of this group. However, this possibility cannot be excluded at this time, and perhaps further anatomical study of this material will resolve this intriguing question.

5. Conclusions

Anatomically preserved material can provide important details about reproductive and vegetative anatomy of so-called enigmatic fossil gymnosperms from the Southern Hemisphere. Our knowledge of the reproductive biology of the Glossopteridales and the Corystospermales, based on permineralized material, has substantially increased over the last 10 years, although there is still much to be learned about these groups. For example, anatomical studies clearly support the differentiation of the glossopterids into at least two groups, and reconstructions of corystosperms from Antarctica indicate that these plants differed from those occurring in South America at the same time. The presence of distinctive secretory cavities in stems, rachides, leaves, and pollen organs provides the opportunity to reconstruct the "*Dicroidium*" plant in Antarctica. Permineralized specimens also indicate that the *Dicroidium* leaves were deciduous.

The glossopterids and corystosperms occur at a crucial period in geologic time for the evolution of modern seed plants. In addition, they appear to be especially important in understanding the phylogeny of younger seed plants. Permineralized plants are beginning to change our conception of these groups and additional work on well-preserved material from Antarctic and elsewhere in Gondwana will no doubt further refine our concepts of these late Paleozoic and early Mesozoic "seed ferns."

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