RECONSTRUCTIONS OF SELECTED SEED FERNS[1]

Greg J. Retallack[2] and David L. Dilcher[3]

This Paper is Dedicated to the Memory of
Sergei V. Meyen

ABSTRACT

Seed ferns (pteridosperms) make up a heterogeneous group of broadleaf gymnosperms. Our attempts to reconstruct these extinct plants here summarize research over many years on the best-known seed ferns. We have named each reconstructed plant after its best-preserved ovulate fructifications, because these are the most reliable parts for identification of seed plants. We envisage Early Carboniferous (about 352 million years ago) Stamnostoma huttonense as a large tree, foresting elevated terraces and other well-drained areas of coastal plains. Swampy lagoon margins of the same coast probably were wooded with lycopods and small shrubby seed ferns such as Lyrasperma scotica. Of comparable age, but on well-drained ashy soils flanking inland volcanoes, was the early successional Calathospermum fimbriatum. Unlike these other plants, which were probably pollinated and dispersed by wind and water, arthropods may have played a role in the reproduction of C. fimbriatum. Earliest Late Carboniferous (about 320 million years old) Lagenostoma lomaxii is reconstructed as a bushy understory shrub in swamps of arborescent lycopods. Latest Late Carboniferous (about 296 million years old) Pachytesta illinoensis was a tree probably growing on elevated and nutrient-rich areas in and around permanently waterlogged swamps of marattiaceous tree ferns. Pachytesta illinoensis had large prepollen probably dispersed by insects. Its fleshy ovules may have been dispersed by large amphibians, reptiles, or fish. Another seed fern of these latest Carboniferous swamps, Callospermarion pusillum, is reconstructed as an early successional scrambling vine. Its pollen probably was dispersed by wind, and its numerous small seeds scattered widely by wind and water. In contrast to these Euramerican plants of tropical and subtropical climates, Late Permian (about 245 to 253 million years old) Dictyopteridium sporiferum was a dominant tree of cool temperate swamp woodlands of intermontane valleys in the southern hemisphere. Large air chambers in its roots enabled it to grow in waterlogged soils. Woodlands of southern hemisphere mid-continental lowlands during Late Triassic time (225 to 230 million years ago) included abundant trees of Umkomasia granulata, and a shrubby understory including Peltaspermum thomasii. Middle Jurassic (175 to 183 million years old) Caytonia nathorstii is reconstructed as a tree of lowland mixed conifer–broadleaf forest in a subtropical, seasonally wet paleoclimate. Its ovules were enclosed in berrylike cupules, which may have been pollinated and dispersed by small animals. From these examples, it is apparent that seed ferns were exceptionally diverse broadleaf plants which occupied a variety of niches now occupied by angiosperms.

Reconstructions of extinct plants from dispersed fossil organs have not been attempted to the same extent as restoration of vertebrate fossils. Presumably this is because of the modular construction of plants, because of their various deciduous organs, and because of the variety of ways and places in which fossil plants are preserved. Nevertheless, many hypotheses have been published concerning which parts of fossil plants belong together. The drawings presented here are visual expressions of some of these hypotheses for especially well-known seed ferns. We intend these drawings to be working hypotheses of reconstruction in the same way as the written accounts on which they are based. Hypotheses expressed in this way are understood more readily than pages of scientific text. By the same token, however, such drawings also make mistakes of interpretation more obvious. A further

difference between written and illustrated reconstructions of fossil plants is the difficulty of expressing uncertainty and presenting detail in a drawing. With special regard to this problem, the poses of various organs have been selected carefully, and enlargements and insets have been used liberally both to reveal detail and obscure uncertainties.

The plants reconstructed here are those regarded traditionally as "seed ferns," a group of plants being increasingly recognized as an evolutionary grade rather than a clade. This is not to say that the terms "seed fern" or "pteridosperm" should be abandoned, any more than the term "dinosaur," another often loosely defined assemblage, should be discontinued. The discovery that these fernlike fossil leaves belonged to seed-bearing plants reshaped understanding of the evolutionary relationships between seed plants and pteridophytes (Potonié, 1899; Oliver & Scott, 1904), and their importance to understanding vascular plant evolution has remained undiminished. The first seed plant and the ancestors of many other gymnosperms were probably seed ferns (Rothwell, 1982). Seed ferns or allied plants remain most likely ancestors of angiosperms (Dilcher, 1979; Retallack & Dilcher, 1981; Doyle & Donoghue, 1986).

The various organs and preservational styles of each of these fossils have separate botanical names, following accepted paleobotanical nomenclature. Our gathering together of various organs and names for different parts of the same plant should not be construed to mean that each part is equally definitive of the whole plant. A fossil species of root, for example, may have belonged to several different species distinguishable among reproductive structures. It is likely that different organs of plants have evolved at different rates. In gathering together these names we merely imply that there once existed a plant for which each of these names is appropriate for its various fossilized parts.

Our choice of a single name for each reconstructed plant does not follow the *International Code of Botanical Nomenclature* (Stafleu, 1978) in its rules of priority, because there are indications in the code that these do not apply between form genera for different kinds of plant parts. In the case of the present compilation, strict adherence to priority would result in naming eight of the plants reconstructed here from leaves, one from wood, and one from a root. Instead, we use the name of the best-preserved ovular fructifications consistently as the name for these reconstructed seed plants (following Retallack, 1980a, and Anderson & Anderson, 1985). Modern seed plants are clas-

sified mostly according to their ovulate fructifications, and a new suprageneric classification of seed plants based on ovular fructifications has recently been proposed by Meyen (1984). We do not agree with all of the criteria for his classification, but it is a welcome replacement for the preexisting miscellany of suprageneric taxa based on wood for Carboniferous groups, leaves for Permian groups, and ovular fructifications for Mesozoic groups.

Meyen (1984) outlined a new botanical nomenclature for seed plants, but here we use well-established terms such as sporophyll (phyllosperm of Meyen), sporoclad (branching polysperm), head (ultimate segment of cladosperm), and cupule (also used by Meyen). The word ovule is used here in the strict sense for unfertilized integumented megasporangia. In most gymnosperms, seeds represent dispersed propagules, whereas ovules are found in place in reproductive organs. Thus the word ovule appears in this account of reproductive organs more frequently than the word seed. In much paleobotanical writing, the latter term being understood more easily in general English usage, is used loosely for ovule or seed. We have also used the term prepollen for the microspores of very early seed ferns. Prepollen look more like spores of pteridophytes than pollen of seed plants, and, like spores, prepollen germinate from the side of the grain originally oriented within the parent tetrad (Chaloner, 1976).

We have examined type material of all the seed ferns reconstructed here and a good deal of additional material. One of us (G.J.R.) also has visited the type or comparable localities of these fossil plants in order to assess and obtain new evidence for their geological occurrence. In addition to the drawings, we have written an interpretive summary as an introduction to each plant. The remainder of each account details both evidence and arguments for and against various aspects of our reconstruction. The plants are discussed in order of geological age.

STAMNOSTOMA HUTTONENSE

Hypothetical reconstruction. We envisage this plant as a tall forest tree (Fig. 1) with coniferlike wood (*Pitus primaeva* Witham, 1833). It was a prominent tree of well-drained soils of elevated river terraces surrounding lagoons of a broad coastal plain to the south of a hilly and volcanic region now forming the Southern Uplands of Scotland. During the Early Carboniferous (late Tournaisian or about 352 million years ago) the climate of this region probably was subtropical, with a
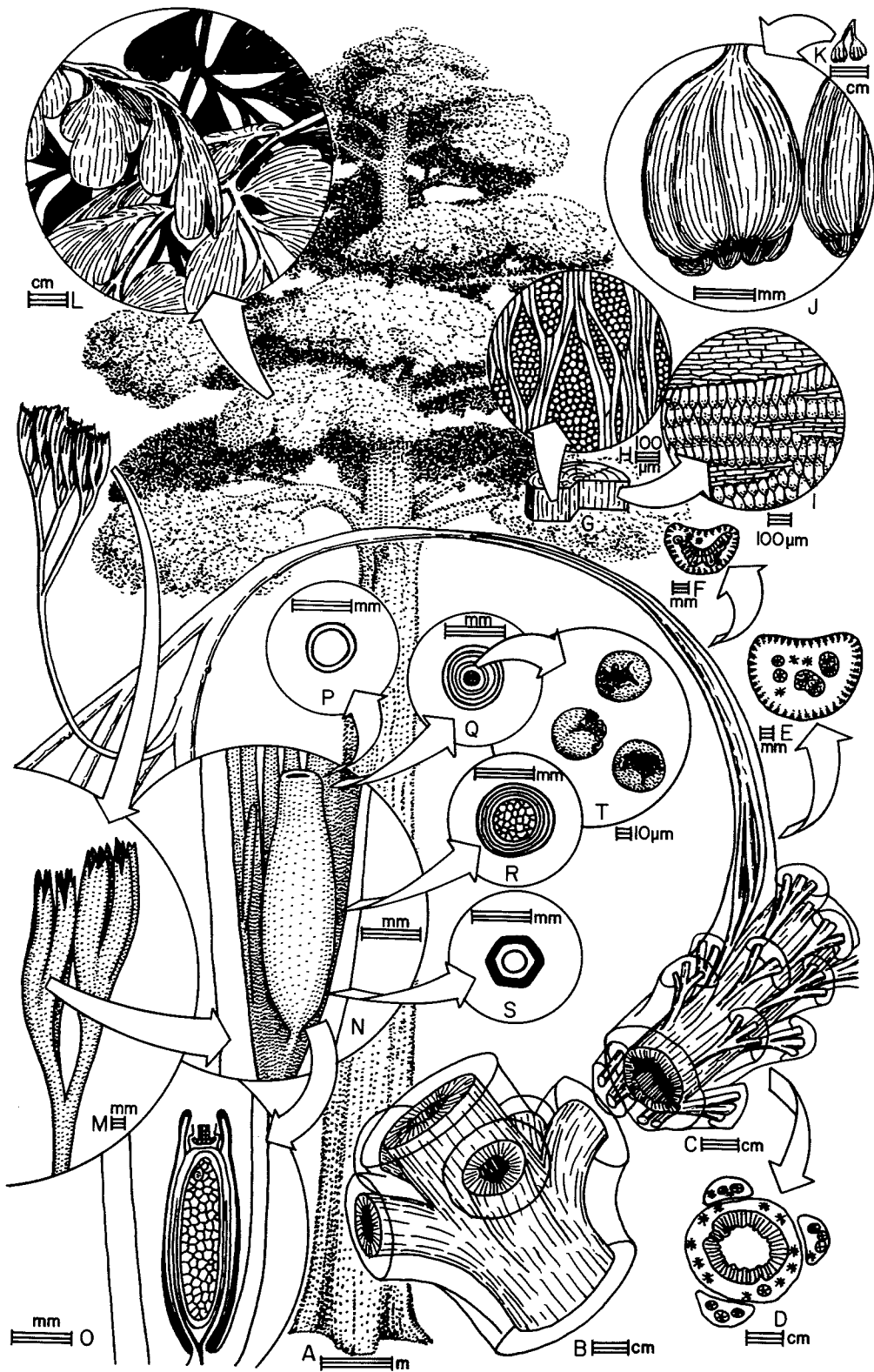
pronounced dry season. During this season, the pinnules of its large fronds (*Aneimites acadica* Dawson, 1860) may have been deciduous. In some ways these fronds resembled the plagiotropic short shoot systems of progymnosperms, but the petiole of the plant (*Lyginorachis papilio* Kidston, 1923) was dorsiventrally differentiated and its vascular structure like that of true leaves. Stalks arising from within the dichotomy of the rachis of the frond terminated in cupules (*Calathiops* sp.) bearing ovules (*Stamnostoma huttonense* Long, 1960a). The prepollen organ (*Telangium* sp. when petrified and *Telangiopsis* sp. in compression) probably was borne in a similar manner. It consisted of a copiously branched aggregate of clusters of elongate pollen sacs. The fernlike prepollen grains (*Colatisporites decorus* (Bharadwaj & Venkatachala) Williams in Neves et al., 1973) were released through an elongate dehiscence slit. These plants may have been wind pollinated at a stage when the ovules were immature. The prepollen was sealed in an apical chamber of the ovule (lagenostome) at the base of a trumpetlike opening (salpinx) by the upward and outward growth of a central plug of tissue. There it waited as the multicellular gametophyte and archegonia developed. Once fertilization was achieved, perhaps after shedding and wind dispersal of the ovule, there appears to have been little interruption in the rotting of the seed integuments and germination of the embryo.

Evidence for reconstruction. The main locality for our reconstruction is the quarries in the steep eastern banks of the Crooked Burn west of Newton Farm, near Foulden, Berwickshire, southern Scotland (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). This is in the lower Cementstone Group of the Calciferous Sandstone Series, of Early Carboniferous age (late Tournaisian, or late Courceyan in the regional stratigraphic scheme; Scott et al., 1984; Clayton, 1985) or 352 million years old (following Palmer, 1983). The attribution of these various remains to a single plant is based on anatomical similarity of petrified petioles and small branches; on attachment of petrified stalks within the dichotomy of petioles as in other fertile

seed ferns; on the similarity of pollen found in pollen sacs, in ovules, and dispersed; and on the association of both petrified and compressed remains at the same localities, often with few other associated plants (Long, 1960a, 1962, 1963, 1979a; Neves et al., 1973; Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985).

Most of this evidence has been presented by Long (1979a), but we doubt that the leaf type, *Sphenopteris affinis*, or petrified stem, *Tristichia ovensii*, belonged to this plant, for the following reasons. *Aneimites acadica* is a very common leaf at the main locality for this plant (Newton Farm), where it is represented by abundant isolated pinnules, which were probably deciduous. The overall frond morphology thus remains poorly known, and Long's (1979a) objections on this basis against this being the foliage of the petrified petioles have little substance. There are several problems with Long's view that *Sphenopteris affinis* was the leaf of the plant in question. *Sphenopteris affinis* was probably a shrubby plant growing in quite different waterlogged soils (of the Oil Shales: Andrews, 1948). Only one very poorly preserved fragment (British Museum of Natural History specimen 16865) of *S. affinis* has been found at the main locality for our reconstruction (Newton Farm) of *Stamnostoma huttonense*, and this equally could be a badly lacerated specimen of *Aneimites acadica* or a ragged specimen of *Sphenopteridium pachyrrachis*, also reconstructed here as part of *Lyrasperma scotica*. In addition, the prepollen of *Telangium affine* found in association and attached to *Sphenopteris affinis* in the Oil Shales has a clear ornament and trilete mark (Kidston, 1924), quite different from the almost featureless prepollen found in the prepollen chambers of ovules and in prepollen organs attributed to *Stamnostoma huttonense* (Long, 1962, 1979a). Further, the prepollen of *Sphenopteris affinis* is somewhat smaller (52 μm according to Kidston, 1923) than that of the reconstructed plant (54–69 μm according to Long, 1979a). This would have been a more substantial difference if the prepollen grains of *Stamnostoma huttonense* are lacking their outer wall, as Long suspected.

←

FIGURE 1. *A reconstruction of* Stamnostoma huttonense *of Early Carboniferous (Tournaisian) age, from Newton Farm, near Foulden, Berwickshire, Scotland.—A. Habit as a large tree of well-drained soils.—B, C. Xylem model of branches, petiole, and cupule.—D–F. Schematic cross sections of branches and petioles, showing primary xylem (black dots), secondary xylem (surrounding areas), sclerotic nests (asterisks), and mechanical cortex (radial shading).—G–I. Cellular structure in tangential and radial (respectively) sections of wood.— J, K. Prepollen organ.—L. Detail of leaf.—M. Ovulate cupule.—N. Ovule.—O–S. Sections of ovule, revealing multicellular megagametophyte and an archegonium.—T. Prepollen.*

Scott & Meyer-Berthaud (1985) reinterpreted *Tristichia ovensii* from the main locality for our reconstruction (Newton Farm) as a separate small seed fern with *Rhodea*-like leaves, "small uncupulate seeds," and "small, lateral, pedunculate male organs." They also questioned whether the specimens of *Tristichia ovensii* between the fork of *Lyginorachis papilio* and aligned with *Stamnostoma huttonense* (Long, 1963) are really attached. We accept their reconstruction of this other plant but see little reason to question the attachments described by Long, especially in view of the very generalized anatomy of *T. ovensii*. Very small axes of several species of seed ferns may have been comparably anatomically simple.

Habit. *Stamnostoma huttonense* was a large tree, with trunks up to 25 m long and 1.4 m in diameter (Long, 1979a). On some of the petrified trunks, branches and petioles have been found attached in a closely spaced helix, whereas other axes lack branches for considerable lengths. This is a common branching pattern in modern forest trees (Rauh's model of Hallé et al., 1978). This plant also had the long and short shoot organization found in many modern conifers, such as Scots pine (*Pinus sylvestris*).

Unlike the leaves of most conifers, its leaves were fernlike. These fossil trees were superficially similar to extinct progymnosperms such as *Archaeopteris ovata* (see Beck, 1981). These had leaves similar to the pinnules of *Aneimites acadica*, although these were arranged in large dorsoventrally planated shoot systems quite different from the true leaves of *A. acadica* (Kidston, 1924).

Ovules were attached on stalklike structures which formed the central axis of a trichotomy of the rachis of the frond. A petrified terete stalk with a triarch stele has been found in the dichotomy of a petrified petiole (Long, 1962). This was a common mode of attachment of ovular and pollen-bearing structures, seen in other Early Carboniferous compression fossils, such as *Sphenopteris affinis* (Kidston, 1924), *Sphenopteris bifida* (Long, 1979a), and *Diplopteridium teilianum* (Walton, 1926, 1931). Compared with modern gymnosperms in which axillary branching and clear differentiation of stem and leaf are the rule, this epiphyllous sporoclad is peculiar. Presumably this arrangement was inherited from progymnosperm ancestors that lacked consistently axillary branching (as shown by Scheckler, 1976, 1978).

The sporoclads of *Stamnostoma huttonense* may have been erect. Their stalks are terete and gently curved, rather than the dorsiventrally planated and flexuous as in pendent fructifications. Niklas (1981) has shown that an erect orientation would have been more effective for pollination, because the rachides of the fronds would have remained in the way of pendent ovules even if all the pinnules were abscised at the time of pollination. Long (1965) and Walton (1964) argued that cupules of other species were pendent because this would protect the pollination drop from rain. However, the open form of this particular cupule would have been a rain guide, rather than protection.

Reproduction. The life cycle of this plant was probably similar in general outline to that of a number of associated Early Carboniferous seed ferns (Rothwell, 1986). Irregularly branching cupulate structures of other species sometimes are found with poorly developed ovules or prepollen sacs (Long, 1969, 1975, 1977a, 1979b). We interpret these as fructifications at the stage of pollination or earlier, analogous to modern fructifications of cycads (*Dioon edule*) and maidenhair trees (*Ginkgo biloba*) at this stage in their development (Chamberlain, 1935). The smooth prepollen were produced in great quantity. These are features of modern wind-pollinated plants (Faegri & van der Pijl, 1966; Whitehead, 1969). The size of the prepollen (54–69 μm in diameter) approaches that of modern insect-dispersed pollen, but their aid in pollination is unlikely in view of other features of the prepollen. At pollination stage the funnellike nucellar apex (salpinx) may have retained a pollination drop for entrapment and withdrawal of prepollen (Walton, 1964) as in some modern conifers.

The best-preserved fossils of mature ovules have a central column filling much of the salpinx and a multicellular megagametophyte, occasionally with one to three apical archegonia (Long, 1960a). These may have been ovules during the long period after pollination and before or shortly after fertilization. Judging from the abundance of remains of this stage, this was a long period in the life cycle, perhaps taking several months, as in modern cycads and *Ginkgo* (Chamberlain, 1935). Even mature ovules have three small cutinized megaspore remnants at the apical end, representing aborted spores of the parent tetrad (Long, 1975). This feature, presumably a legacy of heterosporous progymnosperm ancestors, is no longer seen in modern seed plants.

Mature seeds were small (up to 3.75 mm long by 1.5 mm wide) and had a thin, dense seed coat. Compared with modern seeds (Van der Pijl, 1972), they were unspecialized and possibly scattered by
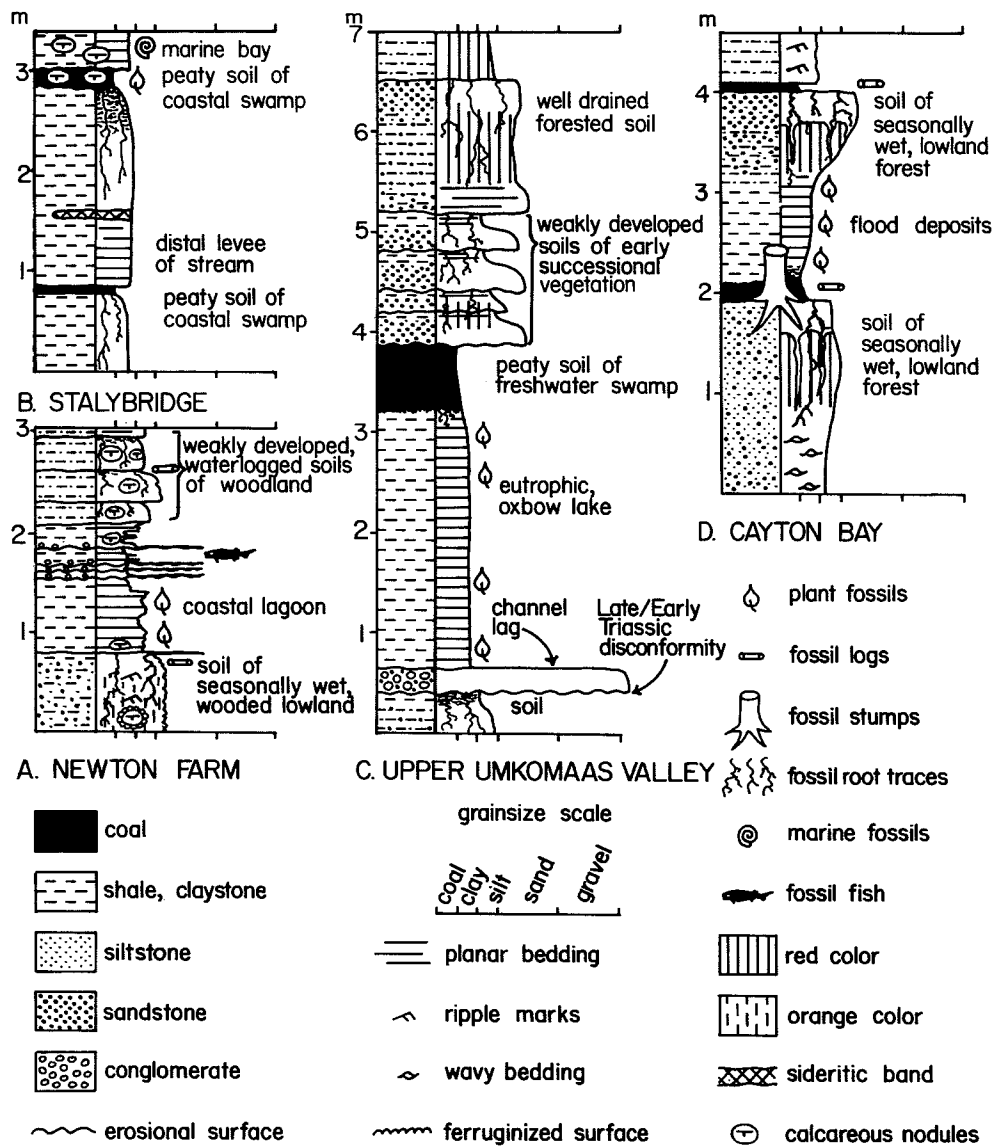
FIGURE 2. *Stratigraphic sections and interpreted paleoenvironments of fossil localities at:—A. Newton Farm, near Foulden, Scotland (for* Stamnostoma huttonense *and* Lyrasperma scotica*).—B. Hough Hill Colliery, near Stalybridge, Cheshire, England (for* Lagenostoma lomaxii*).—C. Near Vergelegen Nature Reserve, upper Umkomaas Valley, Natal, South Africa (for* Peltaspermum thomasii *and* Umkomasia granulata*).—D. Southern Cayton Bay, Yorkshire, England (for* Caytonia nathorstii*). Sections were measured in the field by G.J.R., except for B, which was compiled from sections described by Stopes & Watson (1909) and Tonks et al. (1931).*

shaking from the cupules, followed by wind and water dispersal.

No seeds with embryos have been found among many examined in Early Carboniferous rocks. Those few possible seed fern embryos found have two seed leaves and are free of their seed integuments (Long, 1975). It is likely that germination followed rapidly after fertilization, again as in modern cy-

cads and *Ginkgo* (Chamberlain, 1935). If most embryos grew without pause into small seedlings, this would explain their rarity.

Habitat. The gray shales at Newton Farm (Fig. 2A) have yielded a variety of fossil sharks, palaeoniscid and acanthodian fish, crustaceans, bivalves, and plants (White, 1927; Long, 1960a,

1962, 1964; Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). Apart from arborescent lycopods and rare sphenopsids, the best-known plants from here are the seed ferns reconstructed as *Stamnostoma huttonense* and *Lyrasperma scotica*, and a small plant with *Rhodea*-like foliage. Remains of all these plants have been found mixed together in shales of what was once a large brackish-to-freshwater coastal lagoonal system (Clarkson, 1985).

Several fossil soils (paleosols) in this sequence allow more precise understanding of where *Stamnostoma huttonense* grew. Overlying the lagoonal shales are sequential, thin, waterlogged paleosols (gleyed Inceptisols of Soil Survey Staff, 1975). The size and nonanastomosing cortical striations of fossil root traces in these are most like those of *Lyrasperma scotica*, also reconstructed here. A better-drained paleosol containing larger and more deeply penetrating root traces underlies the lagoonal shales. *Stamnostoma huttonense* probably grew in such well-drained soils, considering the deeply penetrating roots under its fossil stumps, its well-cuticularized seeds, and the growth rings in its wood, not seen in coeval arborescent lycopods of swamps (Gordon, 1935).

The well-drained paleosol thought to have supported *Stamnostoma huttonense* has a carbonaceous surface horizon: an indication that it was not always entirely dry. Its subsurface zone of iron-staining and deep (60 cm) horizon of calcareous nodules (caliche) mark the minimum usual depth of the water table. It was a young soil (probably formed in only hundreds of years before covered), because development did not proceed to the extent that the original bedding was entirely destroyed. It probably formed on an alluvial terrace, a meter or so above the level of the nearby lagoonal system.

Additional evidence of Early Carboniferous forests of *Stamnostoma huttonense* can be seen at other British localities. Along the King Water between Spadeadam and Gilsland in Cumbria, northern England, there are ten petrified stumps of *Pitus primaeva* preserved in growth position within 200 m of outcrop (Long, 1979a). Considering the likely canopy of these trees and the size of the stumps, they would have dominated a forest with closed canopy.

In addition to forests of *Stamnostoma huttonense* and swamp woodlands of *Lepidodendron* and shrubby *Lyrasperma scotica*, documented at Newton Farm, seed ferns lived in a variety of other habitats in southern Scotland during Early Carboniferous time. The oil shale north of Cove Harbour (Craig, 1975) contains abundant *Sphenop-*

teris affinis, as well as narrow, shallowly penetrating root traces. This was a weakly developed, waterlogged paleosol (Aquent of Soil Survey Staff, 1975), supporting scrubby vegetation similar to modern fen carr. Other seed ferns are now preserved in calcareous nodules (caliche) of paleosols (Inceptisols of Soil Survey Staff, 1975) flanking deposits of a small (about 10 m wide) creek in the Cementstone Group deposits exposed in the southern sea cliffs of Oxroad Bay, south of Tantallon Castle, East Lothian (Long, 1976, 1979b; Barnard & Long, 1973, 1975; Matten et al., 1980; Scott et al., 1984). This fossil assemblage, including *Calathospermum fimbriatum* reconstructed here, appears to have been in large part scrubby, early successional vegetation on the well-drained, ashy soils of a nearby volcano. Even at this early time in the geological history of seed ferns, they appear to have been varied in habit and habitat, and included stately forest trees such as *Stamnostoma huttonense*.

Paleogeographic setting. This plant and its various parts are widely distributed in the lower Cementstone Group of Early Carboniferous age southern Scotland. At this time, the Cementstone Group accumulated in a coastal plain south of a hilly region including basaltic and rhyolitic volcanoes, and north of a shallow marine shelf, a few large islands, and open equatorial ocean (Anderton et al., 1979). Southern Scotland enjoyed a warm tropical climate, in which corals and large fusuline foraminifera flourished. Statistical analysis of palynological data provides evidence of dry climate at this time (van der Zwan et al., 1985). Calcareous nodules in paleosols of the Cementstone Group (Fig. 2A) are evidence of a climate at least as dry as subhumid, and probably seasonally dry. A dry season is also apparent from growth rings in fossil wood of this sequence (Long, 1979a; Creber & Chaloner, 1984) and the development of marine evaporites in tropical seas to the south (Ramsbottom, 1973). Although close to the equator, this area was in the rain shadow of large mountain ranges to the west (Bambach et al., 1980).

LYRASPERMA SCOTICA

Hypothesized reconstruction. *Lyrasperma scotica* is reconstructed as a small bush, with stiff, coriaceous, fernlike leaves (Fig. 3). It probably formed a shrubby understory to swamp woodland of arborescent lycopods around coastal lagoons of the same age and areas already described for *Stamnostoma huttonense*. Its leaves (*Sphenopteridium pachyrrachis* (Goeppert) Potonié, 1899) were

strengthened by a thick cuticle and, in the rachis and petiole, by a cortical mechanical tissue (dictyoxylon cortex), formed by radially arranged blades of sclerenchyma. Their petioles (*Kalymma tuediana* Calder, 1938) had a pulvinus and numerous vascular strands. They were borne stiffly and horizontally, in a well-spaced helix on slender erect stems (*Stenomyelon tuedianum* Kidston in Scott, 1909). The stems were smooth and barkless, with an outer dictyoxylon cortex and an inner parenchymatous cortex, and a soft, mixed pith within the central cylinder of secondary xylem. The prepollen organs of this plant are not known, but some ovules were found containing prepollen (*Colatisporites denticulatus* Neville in Neves et al., 1973). The ovules (*Lyrasperma scotica* (Calder) Long, 1960b, when petrified, and *Samaropsis bicaudata* (Kidston) Kidston, 1902, in compression) were lenticular and had two prominent horns on either side of the apex. Ovules only have been found isolated. They may have been enclosed within epiphyllous cupules (*Alcicornopteris convoluta* Kidston, 1887). Like other Early Carboniferous seed ferns, pollination was presumably by wind, and dispersal by wind and water. The distinctive large horns of the ovule may have aided dispersal over water.

Evidence for reconstruction. Our reconstruction of this plant is based on the same Early Carboniferous (Tournaisian) locality near Newton Farm, southeastern Scotland, already discussed for *Stamnostoma huttonense* (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). The attribution of these various remains to one plant is based on the similarity of dispersed prepollen to that found in the ovule; attachment of petrified petioles to petrified stems; the similar size, shape, stelar arrangement, long internodes, evidence of sclerotic nests, and nonanastomosing woody cortex in petrified and compressed petiole-bearing stems; the similar size and shape of petrified and compressed ovules; and consistent association at the same localities (Long, 1960b, 1964). A most important specimen for our reconstruction is the large compressed trunk with attached leaves excavated by Long (1964). Although pinnae associated with this compressed trunk agree with *Sphenopteridium pachyrrachis*, the petioles of the specimen lack the pinnae below the fork and the rough transverse bars usually found in that species (Long, 1964). Comparably anomalous compression fossil leaves were referred to the same species by Walton (1931), and it is uncertain whether this is part of the natural variation of this species or represents a distinct new form.
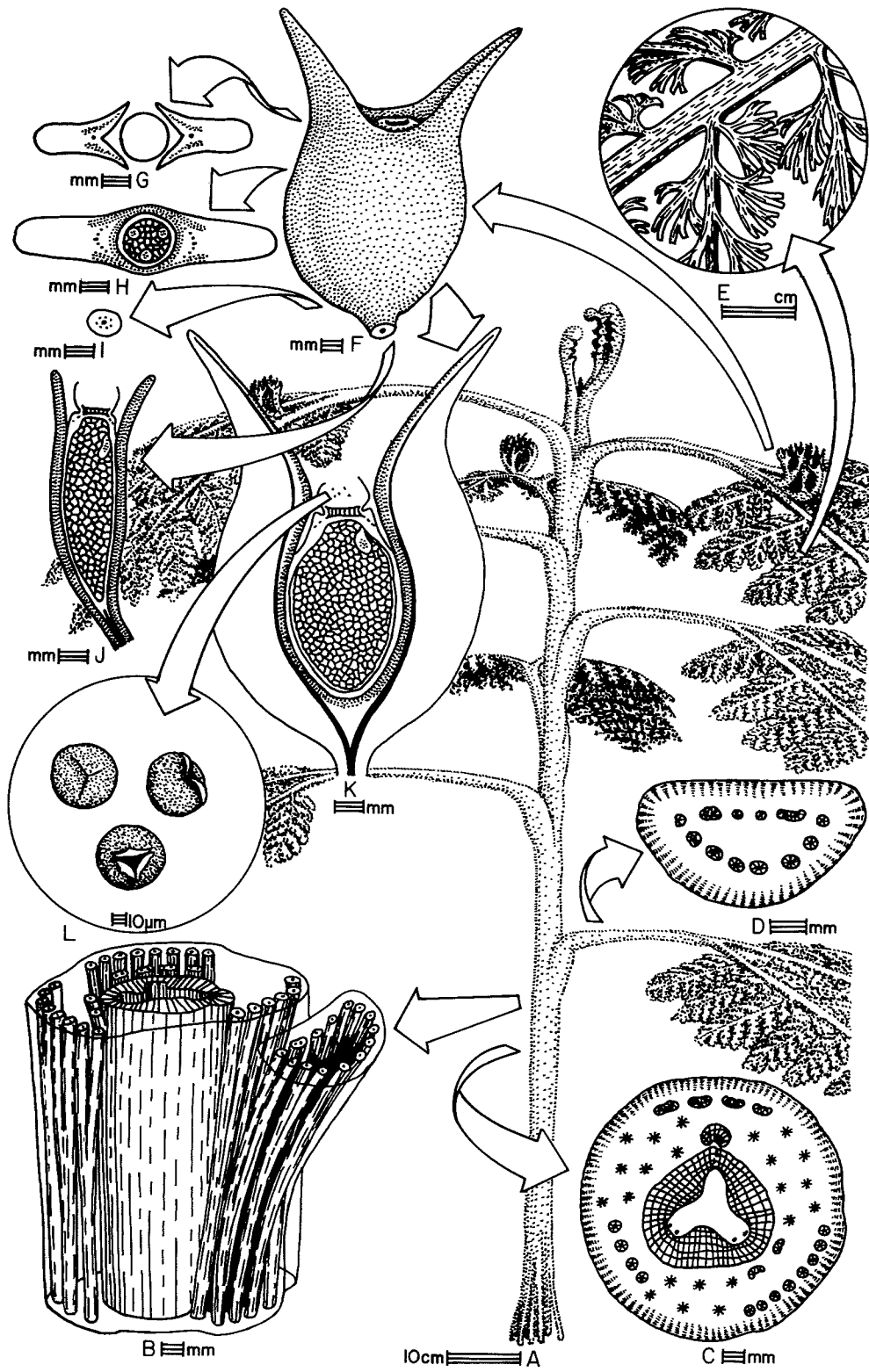
Habit. This plant had an unbranched erect

trunk (Corner's architectural model of Hallé et al., 1978). Its stems were quite succulent, as they had a wide parenchymatous cortex, a mixed pith, and inflated petiole bases (Seward, 1917: 184). Compression of soft tissues in some specimens has given the misleading appearance of "multicellular projections" (Taylor, 1981: 363). These slender stems were strengthened by an outer zone of woody mechanical tissue—bands of sclerenchyma forming a dictyoxylon cortex, which in this plant was not anastomosing. There is no indication of bark, and the stem probably was smooth.

The leaves were coriaceous and strengthened by sclerenchyma within their petioles. The base of the petiole was expanded into a broad, fleshy, pulvinuslike structure. Attached leaves were arranged stiffly and horizontally on the stem.

The arrangement of ovules in this plant is uncertain because they only are known isolated. In similar Late Carboniferous plants described by Delevoryas & Taylor (1969) and Corsin (1928), synangia and ovules were borne bipinnately on what appears to be a fertile frond, in a similar fashion to our reconstruction of *Lagenostoma lomaxii*. In contrast, Long (1977a) has argued that the ovules of *Lyrasperma scotica* were borne in complexly branched cupules, similar to our reconstruction of *Stamnostoma huttonense*. Long's argument is based mainly on the widespread association of ovules (*Samaropsis bicaudata*) and cupules (*Alcicornopteris convoluta*), the very similar anatomy (especially of the lagenostome) of other ovules (*Eurystoma angulare*, *E. burnense*, and *Hydrasperma longii*) known to be borne in cupules (Long, 1965, 1969, 1975, 1979b; Matten et al., 1980), and the existence of compressed fronds (of *Sphenopteridium pachyrrachis*) showing a trichotomy of the rachis (Kidston, 1923, pl. 39, fig. 5; Long, 1960b). It is most likely that the ovules, and perhaps also sporangia, of this plant were borne within infolded cupules as in *Alcicornopteris*. We regard many of Long's *Alcicornopteris*-like specimens of *Hydrasperma longii* (Matten et al., 1980) as immature and have modeled our reconstruction of the cupule after that of *Eurystoma angulare* (Long, 1969). As in the generalized reconstruction of similar plants by Camp & Hubbard (1963), the cupule is shown erect on the frond for reasons similar to those given for our reconstruction of *Stamnostoma huttonense*.

Reproduction. The early development and pollination of *Lyrasperma scotica* was probably similar to that of *Stamnostoma huttonense*. *Lyrasperma scotica* had a wide, shallow salpinx, un-

like many other Early Carboniferous seed ferns. The mechanism of sealing the pollen chamber after pollination could not have been by upward growth of a plug of tissue, as envisaged for *Stamnostoma huttonense* or *Lagenostoma lomaxii*. It may have been by lateral growth of the central column or buckling of the central column by growth of the tent pole.

The prominent horns of the ovule are somewhat reminiscent of those in the living water chestnut (*Trapa natans*), in which barbed spines may serve as floats during dispersal over water and deter consumption by fish or other aquatic vertebrates. The fossil ovule does not have an especially woody or fleshy integument of the kind found in modern fish-dispersed seeds (Gottsberger, 1978).

Habitat. A lowland habitat is indicated by the occurrence of *Lyrasperma scotica* at the same locality on Newton Farm (Fig. 2A) already discussed for *Stamnostoma huttonense* (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). Here seed fern roots with nonanastomosing striations, like those of this plant, as well as poorly preserved lycopod cones, have been found in paleosols overlying the lagoonal shale. These paleosols lack coal, and fossil root traces penetrate them more deeply than usual for permanently waterlogged soils. Nor do they have the reddish oxidized minerals of well-drained soils or the prominent relict bedding of very young soils. They were weakly developed, periodically waterlogged, clayey lowland soils (gleyed Inceptisols of Soil Survey Staff, 1975), probably marginal to the lagoon. Fossil fish and shrimp in the underlying lagoonal deposits (Clarkson, 1985) are evidence that this was a brackish-to-freshwater inland part of a large coastal lagoonal system, connected to the ocean. *Lyrasperma scotica* may have formed a shrubby understory to this lagoon-margin woodland.

The suggested succulence and thick leaf cuticles of this fossil plant could be considered indications of a locally or regionally arid climate, but considering geological evidence for its habitat, these features more likely allowed its growth in salty or nutrient-poor, stagnant groundwater. This interpretation is also compatible with the elaborate, fleshy, open-mouthed seeds of this plant, which would have required moist but not necessarily nutrient-rich conditions for germination and early seedling growth.

Paleogeographic setting. This plant is found at several localities in the Cementstone Group of Early Carboniferous age in southern Scotland, in the same region and time as *Stamnostoma huttonense* (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985).

CALATHOSPERMUM FIMBRIATUM

Hypothesized reconstruction. Also of Early Carboniferous age (Tournaisian or 352 million years old), this small herbaceous-to-shrubby plant was possibly an early successional colonizer of the banks of gullies and ephemeral creeks in ash at the foot of volcanoes within a large rift valley, now the Midland Valley of Scotland (Fig. 4). Its leaves (*Sphenopteridium capillare* Walton, 1931) were dichotomously forked, and the pinnae copiously divided into terete and filiform segments. The stem (*Calathopteris heterophylla* Long, 1976) had a wide cortex with narrow medullated rings of secondary xylem. Ovules were borne within large cupulate structures (*Calathospermum fimbriatum* Barnard, 1960), which had a series of pinnae on the petiole like those of ordinary foliage leaves. Within the cupule were about 16 erect-growing, elongate ovules (*Salpingostoma dasu* Gordon, 1941). The prepollen organ (not yet known) may have been attached to the central stalk of a trichotomously divided leaf rachis. It may have been a copiously branched structure with numerous elongate sporangia, as in allied seed ferns. The prepollen of this plant (*Perotriletes tessellatus* (Staplin) Neville in Neves et al., 1973) were so large (104 μm in diameter) that this plant may have been pollinated by small animals. The long integumented ovules may have been shaken from the cupules by wind.

←

FIGURE 3. *A reconstruction of* Lyrasperma scotica *of Early Carboniferous (Tournaisian) age, from Newton Farm, near Foulden, Berwickshire, Scotland.—A. Habit as a shrub of coastal swampland.—B. Xylem model of stem and petioles.—C, D. Schematic cross section of stem and petiole (respectively), showing primary xylem (black points), secondary xylem (surrounding cellular pattern), sclerotic nests (asterisks), and mechanical cortex (radial shading).—E. Detail of leaf.—F. Ovule.—G–K. Transverse and longitudinal sections of ovule, showing vascularization (heavy lines), woody integumentary layer (stipple), megagametophyte (cellular pattern), and archegonium (circle with stippled center).—L. Prepollen.*
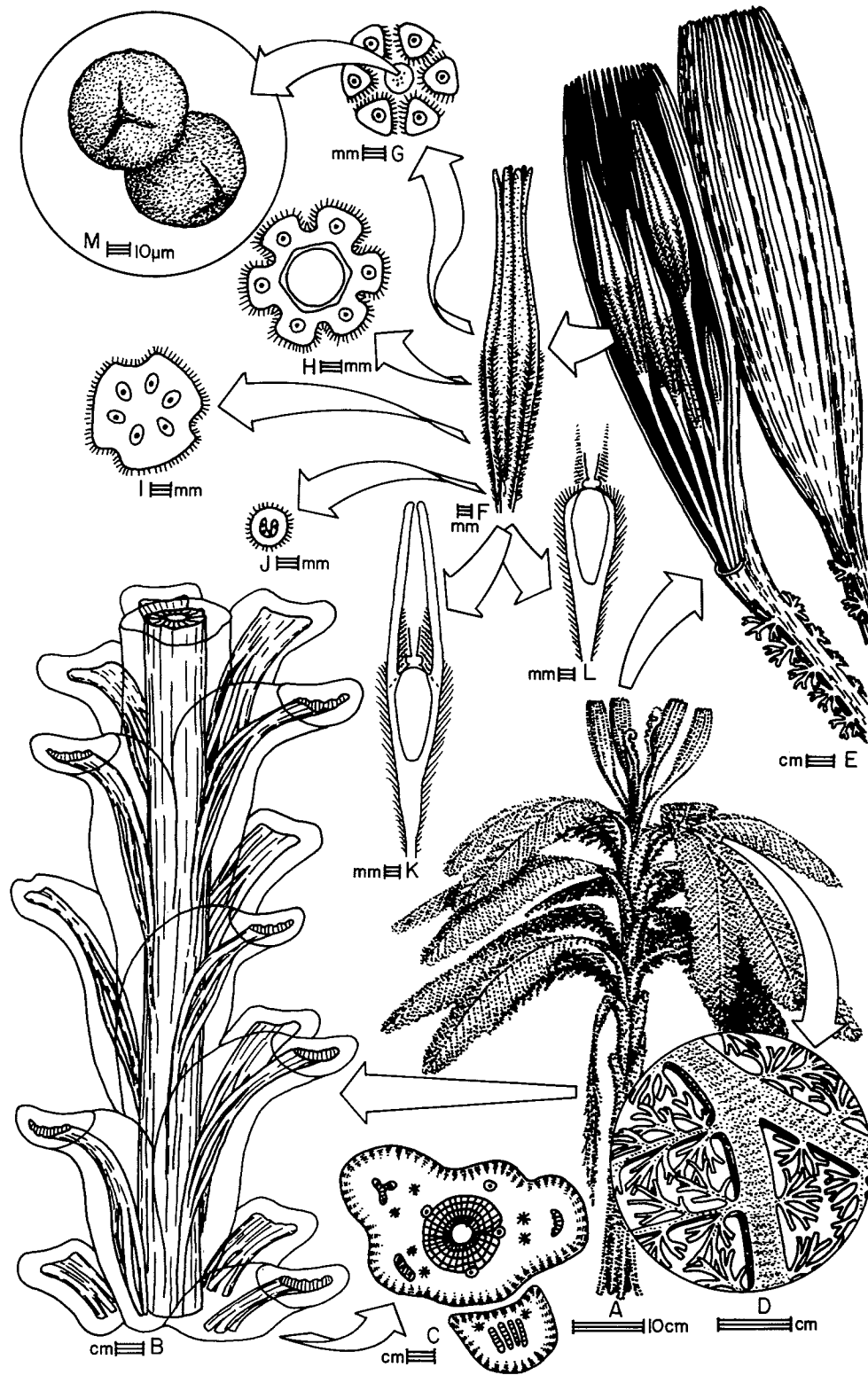
Evidence for reconstruction. The various parts of *Calathospermum fimbriatum* have been put together from similarities in anatomy and hairs between isolated ovules and cupules; from the similar anatomy of petioles of petrified cupules and petioles of petrified stems; and from close association at one especially well-studied locality (Barnard, 1960; Long, 1976; Scott et al., 1984). These are the calcareous, nodular layers of a buried creeklike feature in sea cliffs south of Tantallon Castle, in Oxroad Bay, East Lothian, Scotland (Long, 1976). This is part of the Cementstone Group, Calciferous Sandstone Series, of Early Carboniferous age (late Tournaisian or Courceyan of Scott et al., 1984), or 352 million years ago (following Palmer, 1983).

The prepollen of this plant have been found in petrified ovules (Long, 1976) and are similar to a common type of dispersed grain (Neves et al., 1973). Similar prepollen are found in a fructification of another closely allied species (*Staphylotheca kilpatrickensis* Smith, 1962) from another Scottish locality of comparable age (Loch Humphrey Burn). The prepollen organ of *Calathospermum fimbriatum* may have been similar in some respects but remains unknown. Only the petioles likely to have borne the prepollen organ of *Calathospermum fimbriatum* are known.

No compression fossils have been found in association with the petrified remains, but the petrified pinnae below the fork of the cupule agree in all respects with *Sphenopteridium capillare* (G.J.R., pers. obs.), a leaf known from other localities in Fife, Scotland (Walton's, 1931, material from Burntisland; British Museum (Natural History) specimen v31831 from Ardross). Unlike Oxroad Bay, these Fife localities are within the Oil Shale Group or its equivalents (MacGregor, 1968) and are slightly younger (Visean) within Early Carboniferous time (equivalent or older than Pettycur fossils from this area; Scott et al., 1984).

Other kinds of fronds are unlikely to have belonged to this plant, as they are thought to have had quite different fructifications (*Stamnostoma huttonense* and *Lyrasperma scotica*, as reconstructed here, and fertile *Sphenopteris bifida* of Long, 1979b), or they differ in having few (*Sphe-*nopteris affinis: see Kidston, 1924, pl. 100, fig. 1) or no pinnae below the fork (*Adiantites machanekii, Diplotmema bermudensiforme* and *Spathulopteris ettingshausenii* of Walton, 1931). The other common kind of leaves of this age (*Rhacopteris* spp.) were unforked, although their microsporangiate axes were forked (Walton, 1926). Compression fossils showing these leaves attached to stems (Walton, 1926) are very similar in size, phyllotaxy, angle of attachment of petioles, and spacing of pinnules to petrified plant remains (referred to Buteoxylaceae by Barnard & Long, 1973, 1975), different from the plant reconstructed here.

Habit. From a distance these plants probably looked like umbelliferous weeds, such as hemlock (*Conium maculatum*) and anise (*Pimpinella anisum*). The stem of *Calathospermum fimbriatum* was weak, with medullated secondary wood (Long, 1976). No growth rings were seen. The single stem found was densely clothed in leaves and showed no branches within its 17 cm length (Long, 1976). It was not a copiously branched plant and had much weaker wood than seed ferns such as *Stamnostoma huttonense*. We have reconstructed it as a small shrub, but the available specimen may have been a young plant of a species usually more complex in architecture (G. W. Rothwell, pers. comm., 1985).

Reproduction. The enlargement and differentiation of the megagametophyte between the time of pollination and fertilization was not synchronous. There are small, poorly developed ovules on short stalks near the base of the cupule, as well as large, mature ovules on long stalks near the mouth of the cupule (Barnard, 1960). Such variation in development is not nearly so marked in other Early Carboniferous seed ferns, although these do include occasional "aborted" ovules (Long, 1960a). "Continuous flowering" of this kind is commonly found in modern plants of disturbed habitats, where opportunities for seedling establishment are unpredictable (Heinrich, 1976).

Several features of this plant suggest a syndrome now associated with pollination by animals (Faegri & van der Pijl, 1966). These features are especially striking in comparison with co-existing wind-polli-

←

FIGURE 4.   *A reconstruction of* Calathospermum fimbriatum *of Early Carboniferous (Tournaisian) age, in Oxroad Bay, East Lothian, Scotland.—A. Habit as a weedy shrub of inland streamsides.—B. Xylem model of stem and petioles.—C. Schematic cross section showing primary xylem (black points), secondary xylem (surrounding cellular pattern), sclerotic nests (asterisks), and mechanical cortex (radial shading).—D. Detail of leaf.—E. Ovulate cupules.—F. Ovule.—G–L. Transverse and longitudinal sections of ovule.—M. Prepollen.*

nated seed ferns such as *Stamnostoma huttonense* and *Lyrasperma scotica*. The cupules were large and almost radially symmetrical, and so might have been easily recognized by animals. They were borne erect, as can be seen from the kink where the cupule was bent farther upwards (adaxially) on the attached petiole (Barnard, 1960; Long, 1975). The prepollen of this plant were large (104 μm), much larger and heavier than is effective for wind-pollinated plants today (Whitehead, 1969). Finally, the ovules and the interior of the cupule were covered with numerous glandular hairs (Gordon, 1941; Barnard, 1960) of unknown function. They may have offered a nutritional reward to animals or protected the ovules from them.

It is difficult to be certain what kinds of creatures could have been pollinators—few likely terrestrial animal fossils are known from this geological time. There is a poor Late Devonian and Early Carboniferous fossil record of canopy-dwelling spiders and mites. Winged insects are not found as fossils in rocks older than earliest Late Carboniferous (Namurian: Rolfe, 1980).

The propagules of this plant appear to have been individual ovules, because only a few mature ovules are found in any particular cupule, and in some cases cupules contain none. Mature ovules were elongate and of moderate size (6 mm diameter and 5 cm long including nucellar extensions). There were zones of resinous hairs on the inside of the nucellar extensions and between the ribs of the body of the ovule, which was enveloped in a hard sclerotesta. The whole structure is larger, heavier, and more elaborate than propagules usually dispersed by wind or water alone, such as the pappus of modern Compositae which Walton (1964) thought comparable. They were probably shaken loose from the cupule by wind (a "wind ballist" of van der Pijl, 1972). Also possible is dispersal by ground-dwelling spiny millipedes and similar large arthropods (Rolfe, 1980).

Habitat. This fossil plant at Oxroad Bay is found encased in calcareous nodules (caliche) of weakly developed paleosols (Inceptisols of Soil Survey Staff, 1975) on the aggrading banks of a small (10 m wide) creek deposit (Gordon, 1941, pl. 1, fig. 1; Scott et al., 1984). The stabilized banks (rooted calcareous nodules) can be seen to be laterally impersistent, eroded on top, and covered alternately on each side of the creek. The area was well drained and quite near the volcano, as can be seen from the nature of these paleosols and associated bouldery volcanic mudflows. In such well-drained, frequently disturbed soil one would

expect small, xeromorphic, and early successional plants.

Such a habitat agrees with several adaptive features of this plant: small size (Long, 1976), dissected pinnae (Walton, 1931; Barnard, 1960), cupular protection of ovules (Barnard, 1960), long extensions of the ovular integument, and hairy coat and woody integument of the ovule (Gordon, 1941). This also is compatible with what is known about the other fossil plants found there (listed by Scott et al., 1984). Lycopods and remains of arborescent plants such as *Stamnostoma huttonense* are rare and fragmentary. Most common are small seed ferns and enigmatic plants (family Buteoxylaceae).

Paleogeographic setting. This reconstruction is based mostly on petrified fossils of Early Carboniferous (late Tournaisian) age, from Oxroad Bay, East Lothian, Scotland (Long, 1976; Scott et al., 1984). Only the basal parts of pinnae are known from Oxroad Bay, and the remainder of the frond is modeled after compressions from Ardross and Burntisland, Fife, Scotland (Walton, 1931; British Museum specimen v31831).

All of these localities were in a large rift valley, now occupied by the Midland Valley of Scotland. This was flanked by the Grampian Highlands to the north and the Southern Uplands to the south, and opened out to the sea toward the southwest (Anderton et al., 1979). It was a volcanic landscape with extensive flows from fissure eruptions and some imposing alkali-basaltic volcanoes (Francis, 1983).

Calathospermum fimbriatum may have lived more inland and at higher elevation than the coastal lagoons colonized by *Stamnostoma huttonense* and *Lyrasperma scotica*, and probably in a similar subtropical and seasonally dry climate. As Gordon (1941) argued, it may have lived in a drier climate than these other plants. It was within the rain shadow of rift valley walls, volcanoes, and the mountain ranges of the Grampian Highlands and contiguous ranges now in North America (Bambach et al., 1980).

LAGENOSTOMA LOMAXII

Hypothesized reconstruction. We envisage *Lagenostoma lomaxii* as a shrub with an irregular crown of large leaves (Fig. 5). It grew in extensive, permanently waterlogged swamps, dominated by arborescent lycopods, on deep peaty soils. During the early part of the Late Carboniferous (early Westphalian A or about 320 million years ago)

this area was in the subhumid tropics. The trunk (*Lyginopteris oldhamia* (Binney) Potonié, 1899) was slender (3–4.5 cm diameter) and strengthened by a thick outer zone of sclerenchyma forming an anastomosing system of radially arranged plates (dictyoxylon cortex). The lower part of the stem was anchored by numerous slender prop roots (*Kaloxylon hookeri* Williamson, 1875), which ran directly down from the stem and branches but did not sheath the stem as they do in many modern tree ferns and palms. Its petioles (*Rachiopteris aspera* Williamson, 1874) were flattened and had two vascular strands near the base. The leaves (*Sphenopteris hoeninghausii* Brongniart, 1828) were large and spreading, with a dichotomously forked rachis and numerous small, orbicular, third-order pinnules. The frond rachis and the stems were clothed in prominent stalked glands. Cupulate ovules (*Lagenostoma lomaxii* Williamson in Oliver & Scott, 1903, when petrified, and *Calymmatotheca hoeninghausii* (Brongniart) Stur, 1877, in compression) were borne pinnately, in modified apical parts of fronds. Prepollen organs are not certainly known, and prepollen are represented only by badly corroded specimens within the pollen chamber of the ovules. The cupulate cover to the ovules was liberally studded with stalked glands like those on the stem and leaves.

Evidence for reconstruction. Our reconstruction of *Lagenostoma lomaxii* is based principally on structurally preserved fossils in coal balls from the Hough Hill Colliery, presently abandoned on the south face of the hill 1 km south of Stalybridge, near Manchester, in Cheshire, England (Stopes & Watson, 1909). They come from the "Six Inch Mine Coal" of the uppermost Millstone Grit, of early Late Carboniferous age (early Westphalian A; Tonks et al., 1931; Phillips, 1980) or about 320 million years ago (in time scale of Palmer, 1983). The distinctive stalked glands on these fossil leaves, petioles, stems, and cupules were the main evidence used by Oliver & Scott (1903, 1904) in their reconstruction of this plant, which was the first indication that some gymnosperms included plants with fernlike leaves. There are additional anatomical similarities between the various parts, which are closely associated in coal balls and shales (Benson, 1904; Oliver & Scott, 1903, 1904; Seward, 1917; Jongmans, 1952; van Amerom, 1968).

There has been considerable debate about the likely prepollen organ of this plant. Benson (1904) argued that it was *Telangium scottii*, but *T. scottii* is nonglandular, and so more likely to have belonged with *Lagenostoma ovoides*. Kidston (1905,

1906) thought the prepollen organ was the fossil now known as *Crossotheca kidstonii* (Hemingway) Jongmans (1952) found attached to leaves in siderite nodules of slightly younger geological age (Westphalian B) in the Lancashire Coalfield. However, Jongmans (1952) pointed out that the attached foliage belongs to another species of *Sphenopteris*, lacking the characteristic stalked glands. A third possibility figured by Seward (1917) is a fragment of a petrified pinnule with an attached sporangium on the abaxial side, and a nearby emergence where it appears that another sporangium may have fallen off. A similar specimen with glands and stalks was figured by Kidston (1906, fig. 2). Until this material is studied further, the prepollen also remain poorly known, because those found in the ovules are too badly corroded to be identified with dispersed species.

Habit. Because of the small size of these stems (up to 4.5 cm diameter), this plant has been considered a vine (Phillips, 1981). This was a common habit for some Carboniferous seed ferns such as *Callospermarion pusillum* (reconstructed here). By comparison *Lagenostoma lomaxii* has a much more prominent zone of mechanical tissue in the cortex and a lesser development of secondary xylem, and lacks asymmetric wood. This plant is also very abundant locally (it may comprise up to 38% by volume of some coal balls: Phillips, 1981). It may have grown in waterlogged soils, because there are lacunae within the cortex of the stems (Blanc-Louvel, 1966). It was branched copiously, with some very slender branchlets (Blanc-Louvel, 1966). Both axillary and nonaxillary lateral branching have been observed. For all these reasons we do not think that *Lagenostoma lomaxii* was a vine. Nor do we follow the reconstruction of Scott (1900), showing the plant leaning for support on adjacent trees. Instead, it was probably a shrubby plant with a tangle of prop roots (Attim's model of Hallé et al., 1978).

Reproduction. Judging from compression fossils (Jongmans, 1952) and the anatomy of cupule stalks (Oliver & Scott, 1904), the cupulate ovules were borne pinnately on fertile fronds or parts of fronds. After pollination, the prepollen chamber was occluded by growth of the central column against the overarching sclerotesta of the ovule.

A considerable delay between pollination and fertilization is likely. This would account for the abundance of either ovules or of pollen organs of allied species, but not both, in association with compressed foliage. Jongmans (1952) has argued
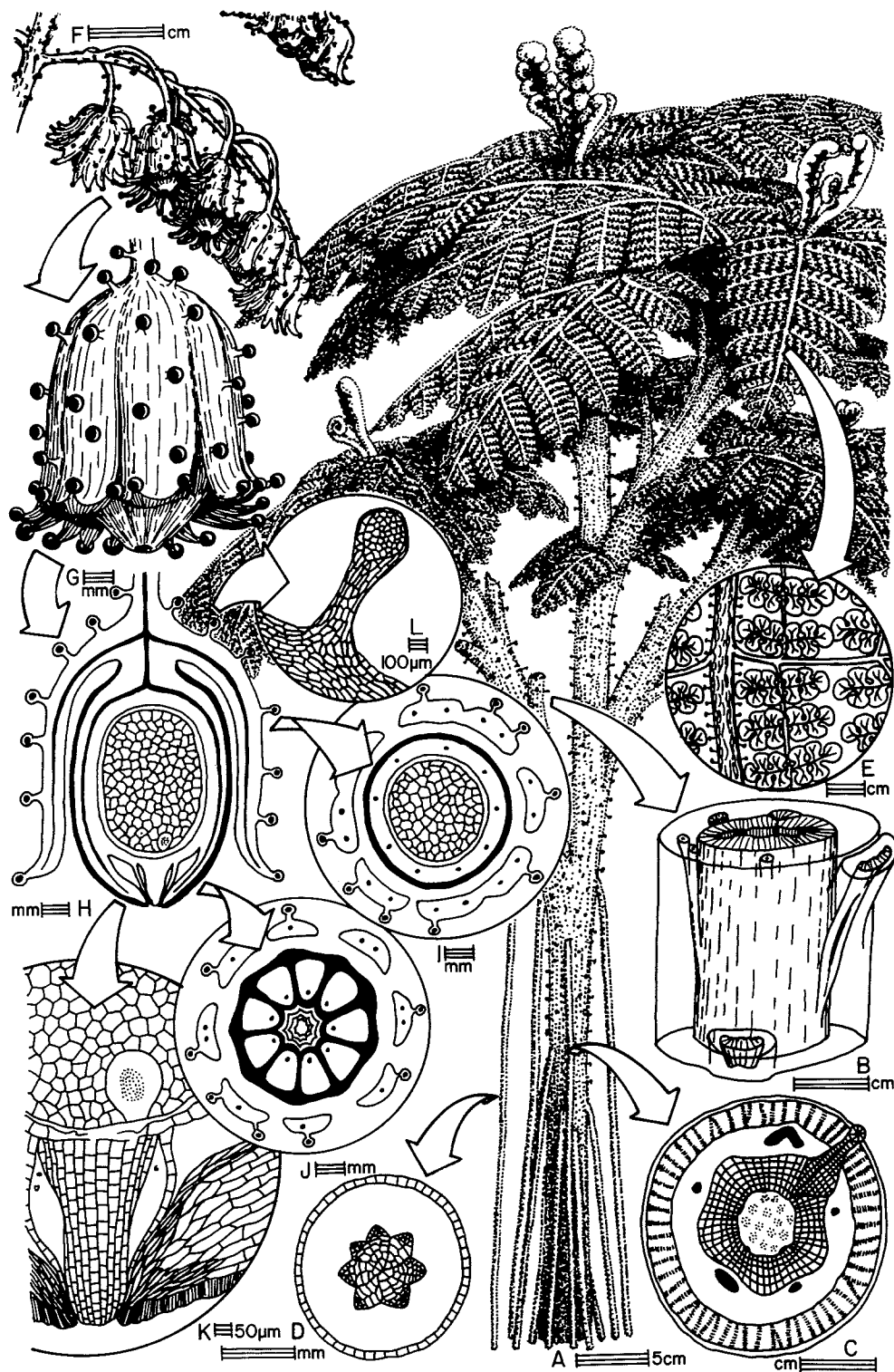
FIGURE 5.   *A reconstruction of* Lagenostoma lomaxii *of earliest Late Carboniferous (Westphalian A) age, from Hough Hill Colliery, near Stalybridge, Cheshire, England.—A. Habit as a swampland shrub.—B. Xylem model of stem and petioles.—C, D. Schematic cross sections of stem and of root (respectively), showing mixed pith*

that pollen organs and mature ovules were produced, abscised, and then decayed during different parts of the year. Compressions of conical cupules lacking prominent ovules (Jongmans, 1952; van Amerom, 1968) may have been fertile fronds with immature ovules at or close to the time of pollination. Petrified ovules containing megagametophytes and archegonia are a good deal larger than these remains and set within a bell-shaped cupule with flaring lobes (Oliver & Scott, 1904).

Lagenostoma lomaxii may have been pollinated by insects, considering the large size (averaging 55 by 70 μm) and coarse ornament of the prepollen (Oliver & Scott, 1904), within the range found in modern insect-pollinated plants (Whitehead, 1969). A case also could be made that the capitate glands were insect attractants, but we find this unlikely. The distribution of glands over almost all known parts of the plant is most compatible with interpretation as organs to deter insect herbivory. Winged insects were around in some diversity and abundance by this geological period (Rolfe, 1980).

By the time the ovule was ready for dispersal, it was about 5.5 by 4.5 mm in size (Oliver & Scott, 1904). The cupule appears to have spread open and the capitate glands withered, judging from compression specimens (Benson, 1904; Seward, 1917). Since many of these lacked attached ovules, it is doubtful that the cupule played a role in dispersal.

Habitat. This fossil plant is best known in coal balls from Hough Hill Colliery near Stalybridge, England (Stopes & Watson, 1909). Coal balls are calcareous or dolomitic nodules found within coal seams (Scott & Rex, 1985). Although modified somewhat during burial (Rao, 1985), coal balls developed as the peat accumulated, as a kind of caliche nodule in peaty soils (Retallack, 1986). In most swamps the development of such nodules is limited by acidity. Coals containing coal balls form under fen or carr vegetation of neutral to alkaline wetlands, where acidity is buffered by a subhumid, seasonally dry climate and nearby limestone bedrock.

The coal containing coal balls in Hough Hill Colliery is interpreted here as the less decayed (mor) humus layer of the organic horizon of a peaty

paleosol (Histosol) of permanently waterlogged ground (Fig. 2B). It is underlain by a thick zone of carbonaceous claystone (Tonks et al., 1931) representing a more decayed (mull) humus, which may have formed at a time during the development of this soil when it was periodically better drained. Below this dark clay is gray, leached clay with root traces ("fireclay"). A thin zone of siderite ("ironstone") represents a deep gley horizon of this older paleosol (comparable to cases discussed by Retallack, 1976).

This paleosol changes character along strike, and in places the organic horizon (Six Inch Mine Coal) directly overlies levee (Rough Rock Flags) and channel deposits ("massive current bedded grit" of Rough Rocks; Tonks et al., 1931) of a former stream. Clayey soils (Entisols of Soil Survey Staff, 1975) of the stream levee supported vegetation dominated by seed ferns, such as *Alethopteris lonchitica* and *Mariopteris muricata* (Stopes & Watson, 1909, discussed this "flora in shales"), quite different from vegetation of the swamp (the flora in coal balls).

The former stream may have flowed into a lagoon or bay, which ultimately inundated the swamp. The shale overlying the coal contains marine fossils such as goniatites (*Gastrioceras* sp. aff. *G. listeri*) and scallops (*Pterinopecten papyraceus*, ?*Posidonomya insignis* and *Posidoniella* sp.: Tonks et al., 1931) as well as plant fragments (*Lepidodendron lycopodioides*: Stopes & Watson, 1909).

In general, *Lagenostoma lomaxii* is found in coal balls dominated by the remains of arborescent lycopods (more than 90% by volume of the coal ball assemblage: Phillips, 1981) and a variety of understory ferns (Phillips, 1980). We envisage it as a small bush of these lycopod-dominated wetlands. Vegetation of these permanently waterlogged woodlands was distinct from that of streamsides, which were dominated by other seed ferns. There was not any detectable marine influence in these lycopod woodlands, although coastal lagoons may not have been far away.

Paleogeographic setting. *Lagenostoma lomaxii* is best known from coal balls in the uppermost Millstone Grit (Stopes & Watson, 1909; Tonks et al., 1931; Phillips, 1980). The same species is

---

←

(clumped stipple), primary xylem (black), secondary xylem (cellular pattern), and mechanical cortex (radial shading).—E. Detail of leaf.—F, G. Cupules with ovules.—H–K. Longitudinal and transverse sections of cupulate ovules, showing vascularization (heavy lines), multicellular megagametophyte (cellular pattern) and archegonium (circle with central stipple).—L. Longitudinal section of capitate gland.
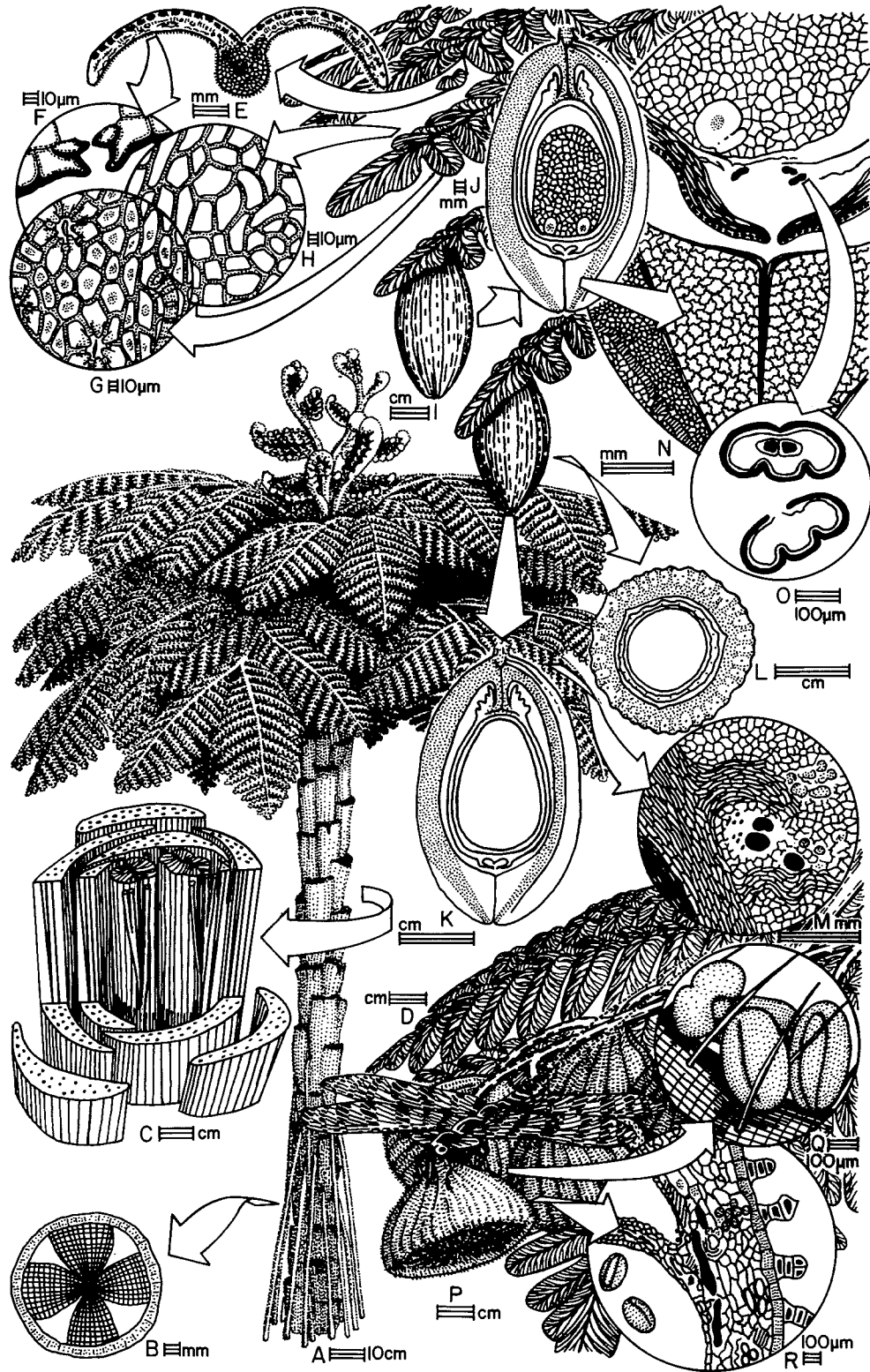
found also in shales of about the same age elsewhere in the British Isles and western Europe (Jongmans, 1952).

In Cheshire, the coal accumulated as peat in a coastal swamp on the northern margin of the Wales–Brabant landmass (Anderton et al., 1979), which was a promontory extending west into the mountains of eastern North America (Ziegler et al., 1979). During most of the Late Carboniferous this was a subhumid part of the tropics, in the rain shadow of mountains to the west (Bambach et al., 1980). There were dry periods (perhaps seasonal) and forest fires, which left charcoal in the swamps (Scott, 1979).

PACHYTESTA ILLINOENSIS

Hypothesized reconstruction. Pachytesta illinoensis was similar to modern tree ferns in overall appearance (Fig. 6). It probably grew on river and deltaic levees and other open and slightly elevated or disturbed areas of midcontinental North American coastal swamps of late Pennsylvanian (Stephanian) age, about 296 million years ago. By this time the dominant swampland plants were no longer arborescent lycopods but marattiaceous tree ferns. By comparison with these and modern tree ferns, this plant had less copiously divided and more leathery leaves (*Alethopteris lesquereuxii* Wagner, 1964). Its trunk (*Medullosa noei* Steidtmann, 1944) was formed largely of closely adpressed leaf bases. It had a wide fleshy cortex and little woody tissue. Large ovules of this plant (*Pachytesta illinoensis* (Arnold & Steidtmann) Stewart, 1954) hung pendulously from beneath terminal pinnules. Synangiate prepollen organs (*Bernaultia formosa* (Schopf) Rothwell & Eggert, 1986) containing large prepollen (*Schopfipollenites ovatus* (Schopf) Potonié & Kremp, 1954) dangled in pinnate structures replacing parts of fronds. These fructifications were among the largest and most conspicuous of Carboniferous swamps, and the prepollen grains

so unusually large and heavy that insect pollination is likely. Among the great variety of Late Carboniferous insects known, Paleodictyoptera such as *Homaloneura dabasinkasi* Carpenter (1964), shown in our reconstruction, were the most likely pollinators of these plants. After pollination, the megagametophyte differentiated and the pollen chamber was sealed by continued growth of the outer integument. The large (2.5 by 4.5 cm) ovules had well-developed fleshy layers of the kind attractive to animal dispersers. Their sclerotesta could have protected them from crushing and acids of the digestive tract. Animals of that time sufficiently large to swallow such ovules included reptiles, amphibians, fish, and sharks. With large food reserves, the young seedlings could grow in the shade and tolerate other adverse influences of competing vegetation. Although this plant is associated with disturbed, nutrient-rich parts of swamps, it was probably not the earliest successional colonizer, but a later species in plant succession.

Evidence for reconstruction. Our reconstruction is based on remains preserved in coal balls from the bed of Sugar Creek 3.7 km northwest of Berryville, Lawrence County, Illinois. Another well-known locality is a tributary of Bonpas Creek 4.5 km east of Calhoun, in nearby Richland County, Illinois. These are both from the Calhoun Coal of the Mattoon Formation in the McLeansboro Group, of Late Pennsylvanian (Stephanian) age (Phillips, 1980), or about 296 million years ago (in time scale of Palmer, 1983). Our reconstruction may also be valid for fossils from coal balls of the Herrin No. 6 coal of slightly older (Westphalian D) Pennsylvanian age, where many of the species gathered together here have been found in association (Phillips & DiMichele, 1981). Because of the probability of mosaic evolution, we do not mean to imply that the whole plant existed in every locality where some small part of it has been found. The attribution of these various remains to one plant is based on the

←

FIGURE 6. *A reconstruction of* Pachytesta illinoensis *of Late Pennsylvanian (Late Carboniferous or Stephanian) age, from Berryville, Illinois, U.S.A.—A. Habit as a palmlike tree of well-drained parts of swampland.—B. Schematic cross section of adventitious root, showing secondary xylem (cellular pattern).—C. Cutaway model of xylem and petiole traces of stem.—D. Detail of leaf.—E. Cross section of leaf.—F. Cross section of stomate.— G, H. Lower and upper (respectively) cuticles.—I. Attached ovules.—J–L. Schematic longitudinal and transverse sections of ovule, showing sclerotesta (stipple and rectilinear cellular pattern) and vascular strands (black).— M. Detail of secretory gland, with black resinous contents in transverse section.—N. Detail of prepollen chamber, apical end of megagametophyte and archegonium in longitudinal section. O. Cross section of prepollen, with supposed sperm (black and subtriangular, above).—P. Prepollen organs and a palaeodictyopteran insect.— Q. Prepollen on hairy leg of insect.—R. Cross section of prepollen organ, showing glandular hairs (outer margin) and internal secretory glands (black).*

anatomical similarity of petioles attached to leaves, stems, and prepollen organs (Ramanujam et al., 1974); the similar pollen found in prepollen organs and ovules (Taylor, 1965); and close association of different organs in coal balls (Schopf, 1948; Taylor, 1965; Phillips, 1981).

Although preserved as petrifactions, splitting and degaging of coal balls has revealed the nature of the leaf, which conforms in shape and venation to *Alethopteris lesquereuxii* var. *cerverae* Wagner, 1968 (Stidd, 1981), and has a cuticle (Ramanujam et al., 1974; Oestry-Stidd & Stidd, 1976; Reihmann & Schabilion, 1976, 1978) generally similar to that of the compression species *A. davreuxii* (Barthel, 1962). There are other alethopterid leaves in coal balls at the main locality for this plant (Berryville, Illinois), and these have blunter, shorter, and straighter pinnules, more like the impression species *A. bohemica* and *A. grandinoides* var. *subzeilleri* (Mickle & Rothwell, 1982). Similar impression fossils have been found in nearby Indiana with numerous small ovules attached (Taylor, 1981, figs. 13–18A, B), and it is likely that this second type of frond is the foliage of other small fructifications, such as *Pachytesta berryvillensis* and *Dolerotheca villosa*, also found in Berryville coal balls (Schopf, 1948; Taylor, 1965; Phillips, 1980). There is only one other allied species in these coal balls (*Pachytesta hexangulata*), and this is much rarer than the other two (known from only one specimen: Taylor, 1965).

Habit. Our reconstruction of *Pachytesta illinoensis* follows that of Stewart & Delevoryas (1956), which is drawn as if it were a young plant. Fossil stems of this plant range from 10 to 50 cm in diameter. They probably were about 5 m high and occasionally attained heights of 10 m (Wnuk & Pfefferkorn, 1984). It is a common plant, yet branches have not been found on long stem compressions (Pfefferkorn et al., 1984), so it probably conformed to Corner's architectural model (of Hallé et al., 1978), as do modern tree ferns such as mamaku (*Cyathea medullaris*) of New Zealand. As in modern tree ferns, *Pachytesta illinoensis* probably had a crown of about ten large leaves, oriented so that a good deal of the trunk was visible from the side (Wnuk & Pfefferkorn, 1984). Like these modern plants also, it was perennial, growing slowly by the development of new leaves above the leaf bases of the old crown. The trunks were strengthened somewhat by several bundles of wood. These were not separate steles, but rather a single eustele with secondary xylem and phloem developed in several separate bundles (Basinger et al.,

1974; Stewart, 1983; Smoot, 1984b). The base of the plant was invested in adventitious roots, although these did not cover the stem to the same extent as in associated fossil tree ferns, and it was more like New Zealand mamaku in this respect. Like this modern plant also, the fossil trees lacked lacunar spaces in their roots (Phillips, 1981).

The large, hemispherical, compound prepollen organ (microsynangium) included numerous elongated sporangia oriented perpendicularly to the flat side. The pattern of their open ends in this flat (lower) side is almost radial and has been interpreted to be homologous to an infolded stack of bladelike synangia (Rothwell & Eggert, 1982, 1986) and, alternatively, to a branch of pinnately arranged individual sporangia (Dufek & Stidd in Stidd, 1981). By either arrangement and considering the number of vascular strands in its petiole (Ramanujam et al., 1974), each large synangium is the morphological homolog of a primary pinna of a frond. We do not think that prepollen organs were scattered randomly among otherwise sterile fronds, an impression that could be gained from uncritical inspection of the reconstruction of Ramanujam et al. (1974). They were probably borne pinnately in special fertile fronds or parts of fronds. Such an arrangement has been demonstrated for other synangia of closely comparable structure (*Potoneia*), but containing different prepollen (Taylor, 1982, pl. 6, fig. 2).

Ovules of *Pachytesta illinoensis* have not been found attached, but their mode of attachment can be inferred from similar compressions of ovules found attached under the terminal pinnule of the leaves (Crookall, 1959). We do not think that they formed at the end of the pinna (as reconstructed by Darrah, 1939: 95). Close inspection of these specimens often reveals the terminal pinnule twisted into a less-conspicuous upright position beside the heavier and larger ovule (Crookall, 1959: 27, figs. 1–5). Other related species of ovule have been found attached farther back on the rachis of the pinna (Halle, 1929; Wagner, 1968; Zodrow & McCandlish, 1980).

Reproduction. The prepollen of *Pachytesta illinoensis* had an alveolate exine ultrastructure and was so large (300–350 μm long by 200–250 μm wide) and heavy that it would not have been dispersed far by wind. It was more likely dispersed by insects (Taylor, 1978). The glandular hairs of the microsynangium and the resinous internal glands of both the microsynangium and ovules may have produced a nutritional reward for pollinating insects or have deterred their herbivory. Both organs also

were enclosed in fleshy tissue, which may have been nutritious.

It is uncertain which among the great variety of Carboniferous insects known could have pollinated this plant, but several circumstantial lines of evidence implicate Paleodictyoptera. These were superficially like modern dragonflies, but, unlike these modern carnivorous insects, had only narrow sucking mouthparts (Kukalova, 1970). The example we have shown in our reconstruction is *Homaloneura dabasinkasi* Carpenter, 1964, known largely from wings with camouflage color-banding in siderite nodules of slightly older Late Carboniferous age (Westphalian D) near Braidwood, Illinois. Paleodictyopterans were active, flying insects, with large compound eyes and hairy legs: all features of modern insect pollinators. Their sucking mouthparts match in size and shape the fine borings seen in petrified microsynangia and ovules (Schopf, 1948). The claim of paleodictyoptera as pollinators of these plants could be regarded as diminished by the discovery of prepollen like that of *Pachytesta illinoensis* lodged in the leg joints of a large fossil millipedelike creature (Scott & Taylor, 1983), but it is unlikely that these extinct arthropods were any more adventurous in the canopy than modern litter-feeding millipedes (Rolfe, 1980). Coprolites containing these prepollen also have been found (Scott, 1977), but these cannot be attributed to any particular animal. A variety of animals probably ate these grains, both in the canopy and on the ground.

As in all the seed ferns considered here, there was a period of time between pollination and fertilization. For ovules with such large megagametophytes this was probably at least a few weeks. Fossil prepollen grains within ovules of *Pachytesta illinoensis* have been found with two large black bodies (Stewart, 1954), which have been compared to the ciliated, motile sperm of modern cycads (Chamberlain, 1935). Such opaque "spots" in petrified cells also could be remains of decayed cytoplasm, as paleobotanists have learned from painful experience in the study of other fossils (Knoll & Barghoorn, 1975). However, there is other possible cytoplasmic material in the medullosan pollen grain in question.

The ovule of *Pachytesta illinoensis* was conspicuous in its large size (about 2.5 cm in diameter and up to 4.5 cm long). Like many modern stone fruits, the fossil ovules had well-differentiated sarcotesta and sclerotesta. The sarcotesta was especially thick near the apex, which was early to decay or be eaten, judging from some specimens (Stewart, 1954). This succulent flesh may have attracted
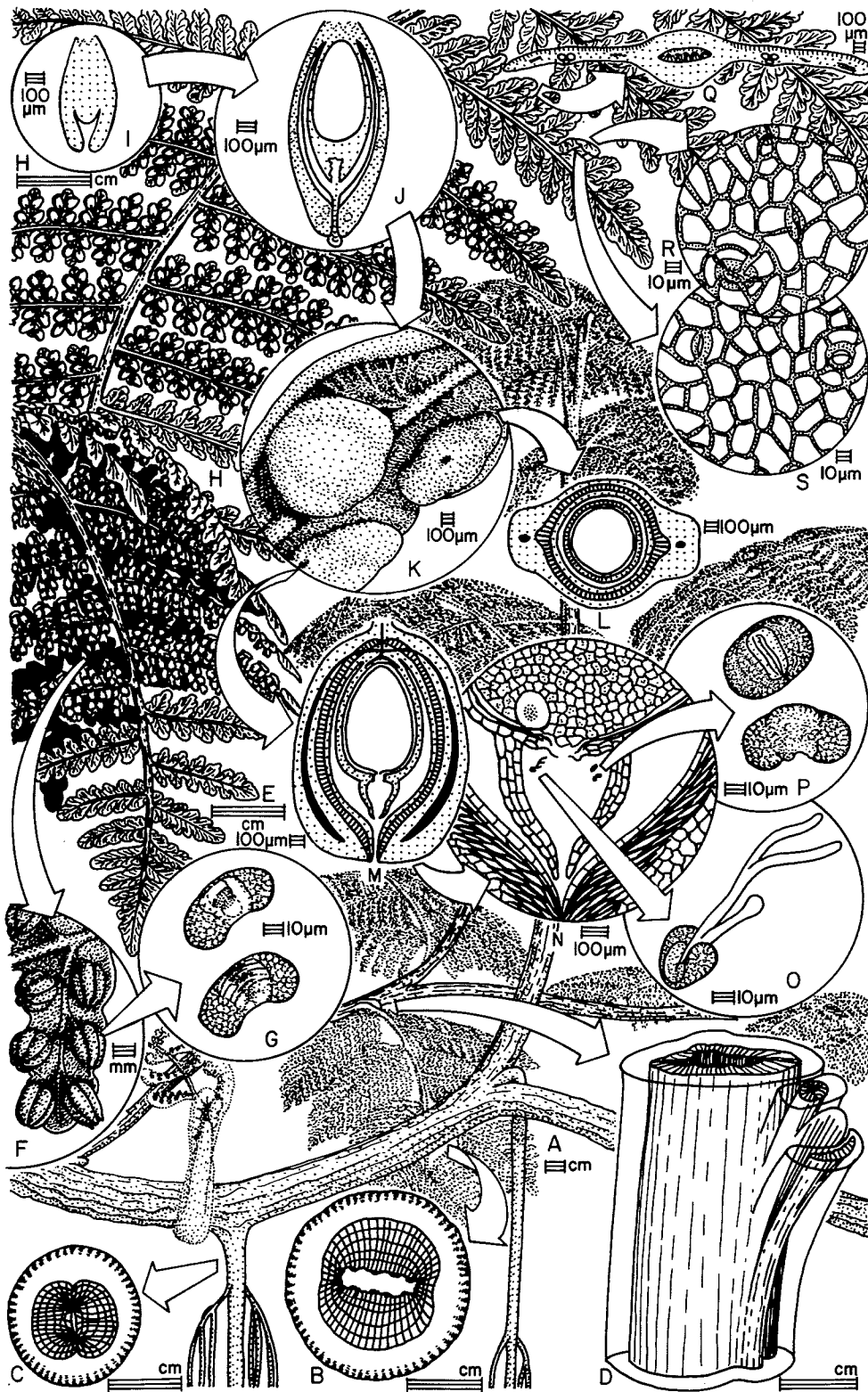
animal dispersers. The sclerotesta can be seen to seal the micropyle in some specimens (Taylor, 1965). Similar stones in modern fruits serve to withstand crushing and acidity during passage through the guts of animals (van der Pijl, 1972). Of the array of known Late Carboniferous reptiles and amphibians (Moodie, 1916; Reisz et al., 1982), edaphosaurs, temnospondyls, and microsaurs were large enough to have been able to swallow a fruit this size. Considering the likely habitat of this plant, the ovules could have been dispersed by fish, as are some modern angiosperm fruits in the varzea swamp forests of Amazonian Brazil today (Gottsberger, 1978). Large palaeoniscid fish and pleuracanth sharks were common within parts of the Late Carboniferous swamps of Illinois (Zangerl & Richardson, 1963; Zangerl & Case, 1973).

Individuals of *Pachytesta illinoensis* and related plants appear to have borne fruit in massive bursts, judging from local accumulations of petrifactions and molds-and-casts of similar large ovules (Seward, 1917, fig. 423; Tonks et al., 1931, pl. II; Taylor, 1965; Jennings, 1974). Such a reproductive effort probably was not begun until after a few years in the life of the plant. In modern angiosperms, copious production of fruit ensures that some remains unmolested by animals and is especially common in trees with large fruits (Janzen, 1978).

Habitat. This plant was preserved in coal balls in the manner already described for *Lagenostoma lomaxii*. Although *Pachytesta illinoensis* grew in and near swamps, it lacked root lacunae usually found in plants of waterlogged ground and thrived in slightly elevated and nutrient-rich parts of the swamp (Phillips, 1981). A similar habitat is indicated by the bundle sheath cells (Krantz anatomy) found around veins within petrified leaves, thought by Baxter & Willhite (1969) to indicate the C_4 photosynthetic pathway for this extinct plant. Like modern plants using this pathway (Chazdon, 1978), *Pachytesta illinoensis* may have been able to endure hotter, sunnier, and drier sites than many associated plants.

Leaves of the plant had thick cuticles, especially on the adaxial surface. Stomates and hairs were confined to the abaxial surface, and each stomate was overhung by papillae borne on the subsidiary cells (Ramanujam et al., 1974; Oestry-Stidd & Stidd, 1976; Reihmann & Schabilion, 1976, 1978). These are all features of sun leaves of plants subject to deficiency of water or nutrients (Mickle & Rothwell, 1982).

Such large ovules would have been able to main-

tain the growth of seedlings, even under the shade and other adverse influences of other plants, as in modern plants of the "competitive strategy" (of Grime, 1979). Although *Pachytesta illinoensis* is geologically associated with disturbed and more-elevated parts of the swamps, it may have been a late species in succession, growing through and then shading out the earliest successional plants. In better-drained areas outside the swamps, similar plants may have formed stable, long-term communities, but within the swamp itself these plants were less persistent than associated tree ferns and lycopods (Phillips & DiMichele, 1981).

Judging from paleobotanical and palynological studies of Calhoun coal balls (Phillips et al., 1974; Phillips, 1980), *Pachytesta illinoensis* formed a minor part of vegetation dominated by marattiaceous tree ferns (with *Psaronius* spp. trunks and *Scolecopteris* spp. and *Asterotheca* spp. fructifications). Lycopods (*Sigillaria ichthyolepis*) and horsetails (*Calamites retangularis*) were moderately common, and the rest of this diverse flora was made up of rare cordaites, other ferns, and seed ferns.

Ecologically, *Pachytesta illinoensis* probably preferred elevated, slightly dryer, nutrient-rich parts of the swamp where there was either sandy or clayey soil or exposed dry, dusty peat. It was not the earliest successional colonizer of such habitats. In shale floras of stream and lake margins (Scott, 1979), calamites and small ferns appear to have occupied that niche. In coal balls of peat swamps, successional patterns are less clear (Phillips & DiMichele, 1981), but weedy plants of erratic occurrence include other seed ferns (such as *Callospermarion pusillum* reconstructed here), and small herbaceous lycopods and horsetails. Nor were *Pachytesta illinoensis* or allied plants part of marine-influenced swamps (mangroves) at this time. This habitat was dominated by cordaites (Raymond & Phillips, 1983).

Paleogeographic setting. The principal locality for our reconstruction of *Pachytesta illinoensis* is in Sugar Creek near Berryville, Illinois, of late Pennsylvanian (Stephanian) age (Phillips, 1980). Illinois was then part of a large central lowland within North America, bordered on the west by mountains in what is now Nevada and Montana, on the north by low hills and limestone plateaus on the Canadian Shield, and on the east by the Appalachian Mountains. These mountains were much more imposing than they are today, and more like the present European Alps (Heckel, 1977). Much of the mid continent was inundated by shallow seas opening out on deep ocean in the area of modern Texas. At the time the Calhoun Coal formed, the sea extended only as far as western Illinois and Missouri. Most of central Illinois was covered by a swamp, dissected by a large stream system draining the granitic shield and carbonate plateau country to the north. This ancient river is usually called the "Michigan River" but is in some senses a forerunner of the Mississippi (Stanley, 1985). To the west in Indiana and Ohio were more swamps and riverine lowlands. The present area of Illinois was about 5° north of the equator at this time, on the margin of the tropical humid and subtropical subhumid belts (Heckel, 1977). Evaporites formed in the dry climate of the present area of the Black Hills of South Dakota. Climate became increasingly humid southeastward toward the equatorial Appalachian Mountains (Schopf, 1975).

CALLOSPERMARION PUSILLUM

Hypothesized reconstruction. We envisage *Callospermarion pusillum* as a scrambling fernlike vine (Fig. 7). It probably formed dense tangles in moist, disturbed sites within and around Late Pennsylvanian swamp forests of tree ferns. Leaves of this plant (*Dicksonites pluckenetii* (Schlotheim)

←

FIGURE 7. *A reconstruction of* Callospermarion pusillum *of Late Pennsylvanian (latest Late Carboniferous or Stephanian) age, from near Berryville, Illinois, U.S.A.—A. Habit as a swampland early successional scrambling vine.—B, C. Schematic cross sections of stem and root, showing primary xylem (black), secondary xylem (cellular pattern), and mechanical cortex (radial shading).—D. Xylem model of a node with petiole, bud, and root traces.—E. Fertile pollen-bearing leaf.—F. Pollen organ.—G. Monosaccate pollen with 2- and 4-cell microgametophytes.—H. Fertile ovulate leaf.—I. Longitudinal section of young ovule.—J. Longitudinal section of ovule at pollination time.—K–N. Overview and cross section of mature ovules, showing vascular strands (black) and sclerotesta (hachured), multicellular megagametophyte (equant cellular pattern), and archegonium (circle with central stipple).—O, P. Monosaccate pollen from pollen chamber of ovule, one showing a pollen tube.—Q. Cross section of leaf showing vascular bundles (hachured), secretory cells (open circles), and palisade layer (vertical lines).—R, S. Upper and lower cuticles, both with stomates.*

Sterzel, 1881) had stomates on both sides and little differentiation between the upper and lower surface. The clambering stem (*Callistophyton poroxyloides* Delevoryas & Morgan, 1954) was woody and perennial. In addition to horizontal runners, there were slender erect leafy stems and, at intervals, stout adventitious roots, which arose in the axils of foliage leaves or from within bifurcations of the main axis. Pollen-bearing organs (*Idanothekion callistophytoides* (Stidd & Hall) Rothwell, 1980) and ovules (*Callospermarion pusillum* Eggert & Delevoryas, 1960) were borne in zones on the abaxial surface of foliage leaves otherwise normal in appearance. The numerous pollen organs released abundant small saccate pollen (*Vesicaspora schaubergeri* (Potonié & Klaus) Jizba, 1962). Pollination may have been by wind and possibly occurred before the megagametophyte or pollen chamber was fully differentiated. After fertilization, which may have occurred on the ground, the seeds were already worn back to their sclerotesta. The numerous small seeds were probably dispersed largely by wind and water.

Evidence for reconstruction. This plant is best known at the locality near Berryville, Illinois, already discussed for *Pachytesta illinoensis,* and also is known from nearby coal-ball localities such as the one near Calhoun, Illinois. Reconstruction of *Callospermarion pusillum* was based on the similarity of secretory cavities in stems, sterile foliage, ovules, and microsporophylls; on the occurrence of similar pollen in the pollen organs, in the ovule pollen chamber, and dispersed; and on close association of its parts (Stidd & Hall, 1970a, b; Millay & Taylor, 1974; Rothwell, 1975, 1980, 1981).

Habit. The young stems have a nearly cylindrical mass of secondary xylem, a thin zone of secondary phloem, and a subsurface zone of mechanical tissue formed from anastomosing bands of sclerotic cells (dictyoxylon cortex: Rothwell, 1975; Smoot, 1984a). These were probably erect, leaf-bearing stems. Older stems do not all have such well-developed mechanical tissue, but rather a thick bark and a large central asymmetric mass of secondary xylem. These were probably horizontal runners. Stout adventitious roots arose from these runners, usually in the axils of leaves, but also within the branches of the main axis (Kidston, 1924; Rothwell, 1975). Buds, petioles, and adventitious roots often arise from within the dichotomies of stems and leaves. These are false dichotomies (Kidston, 1924) arising by development of opposite branches with suppression of the terminal meristem. This branching system is similar to Leeuwenberg's architectural model of plants proposed by Hallé et al. (1978), although the two are not strictly comparable because the leaf-borne fructifications of seed ferns are very different from those of most modern plants. A similar architecture is seen in the modern Australian and Southeast Asian fern *Gleichenia dicarpa.*

The synangiate pollen organs were attached on the underside of the leaves in a manner similar to sporangia of marattiaceous ferns (Kidston, 1924; Stidd & Hall, 1970a). They contain, however, monosaccate pollen rather than fern spores. The saccus is laterally expanded, so that it is superficially similar to bisaccate grains (Hall & Stidd, 1971; Millay & Taylor, 1974). As in modern bisaccate grains, the saccus of the fossil pollen formed by detachment and expansion of the sexine from the lamellated nexine. These fossil pollen also were similar to those of modern gymnosperms in germinating through the side of the grain opposite the point of attachment in the original tetrad, unlike the prepollen of the other Carboniferous seed ferns already considered (Eggert & Millay, 1976).

Ovules and their attachment scars are found over large areas of compressed fronds (Grand'Eury, 1905; Kidston, 1924). Ovules were attached at the ends of veins near the abaxial margin of the pinnules, and their micropyles faced inwards toward the pinnule midribs (Loubière, 1929; Rothwell, 1980).

Reproduction. *Callospermarion pusillum* was probably wind pollinated, considering the moderate size (37–54 μm long by 30–49 μm wide: Millay & Taylor, 1974) of its pollen and the large amount of it produced. Saccae sometimes have been considered the "wings" of wind-dispersed pollen, but they are now thought to have served more for orientation and flotation in an inverted pollination drop (Doyle, 1945). Microgametophytes at the two- and four-celled stage have been found in some synangia (Millay & Eggert, 1974), indicating that these were fully formed at the time of pollination.

In some coal balls, ovules have been found which vary considerably in degree of maturity (Rothwell, 1971). Large fructifications of modern weeds of disturbed habitats show comparable "continuous flowering," thus improving chances that some propagules will mature at an appropriate time (Heinrich, 1976). The youngest ovules found are small and weakly differentiated. At what is thought to have been pollination stage, the ovule was small, with an imperfectly differentiated seed coat and no indication of a megagametophyte. A fossilized pol-

lination drop has been reported in a closely related species (*Callospermarion undulatum*: Rothwell, 1977), but it appears rather more resinous than modern pollination drops (described by Doyle & O'Leary, 1935b) and contains spores known to belong to other plants (Rothwell, 1980). It may be an exudate from the micropyle of a partly decaying ovule rather than a pollination drop. Nevertheless, larger ovules than this do contain pollen grains and have a sealed micropyle, thus suggesting that ovules were at this stage of development at the time of pollination. With further growth after pollination, the micropyle was occluded by growth and differentiation of sclerotesta and sarcotesta as the megametophyte developed. In the most mature ovules, presumably already dispersed, there were several archegonia at the apical end of the megagametophyte, and the sarcotesta was abraded away.

A germinated pollen grain with a branched pollen tube has been found in the pollen chamber of an immature ovule of a related species (*C. undulatum*; Rothwell, 1972). It could be that this pollen tube merely served for nutrition and stabilization of the pollen grain during its long wait until fertilization was achieved by motile gametes. Alternatively, this pollen tube, or at least one branch of it, may have delivered nonmotile sperm nuclei to the archegonium (siphonogamy), as in living conifers such as black pine (*Pinus nigra = P. laricio* in Chamberlain, 1935). Rothwell (1980) was impressed with the coniferlike development and morphology of this plant's ovules, pollen, and pollen tubes, and thought that siphonogamy was more likely.

The small ovules were dispersed individually, as can be inferred from compressed leaves showing only the attachment scars where ovules had abscised (Kidston, 1923). The ovules were numerous, small, and somewhat flattened, with narrow wings. They were probably dispersed largely by wind and water. The ovules were made in quantity, rather than quality, thus maximizing the chance that at least a few would find places suitable for germination, as in modern weedy plants ("ruderals" of Grime, 1979).

Habitat. This reconstruction is based on specimens from coal balls found in Sugar Creek northeast of Berryville, Illinois (Rothwell, 1975, 1980), and it is known from coal balls of comparable age at several other localities in the mid-continental U.S.A. (Phillips, 1980). This species of compressed leaves (*Dicksonites pluckenetii*) has long been known from compression floras of Britain and France (Grand'Eury, 1905; Kidston, 1923), where

allied species of petrified plants have also been found (Loubière, 1929; Rothwell, 1981). Like *Pachytesta illinoensis* reconstructed here, it was locally abundant in swampy lowlands.
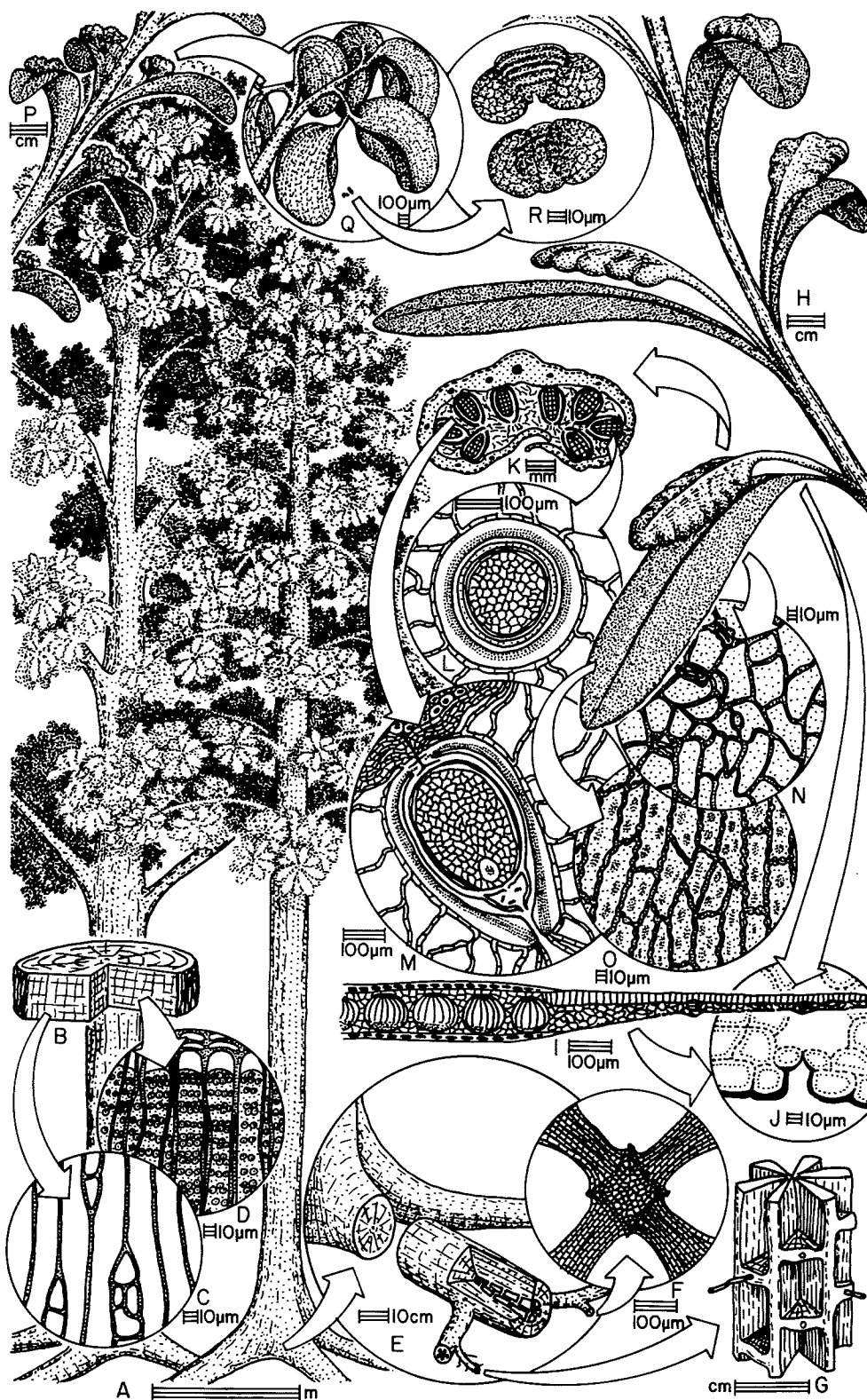
Several features of *Callospermarion pusillum* can be construed as evidence that it was a plant of moist, somewhat shady understory habitats. The pinnules are attached along the middle of the rachis of the frond (Rothwell, 1975), and there is little differentiation between the upper and lower cuticle, both of which are stomatiferous (Barthel, 1962).

Considering this and its weedy reproductive features, we hypothesize that *Callospermarion pusillum* was an early successional plant of disturbed ground. This may have included stream margins, tracts of forest devastated by hurricanes, locally well-drained peat, forest defoliated by fire, or light gaps around fallen trees. It lived among swamp forests dominated by tree ferns during the late Pennsylvanian (Stephanian: Phillips, 1980).

Paleogeographic setting. This plant is known from the locality of *Pachytesta illinoensis* already described. *Callospermarion pusillum* lived in very similar climate and general environment.

DICTYOPTERIDIUM SPORIFERUM

Hypothesized reconstruction. In our view, *Dictyopteridium sporiferum* was a swampland tree, widely distributed in cool-temperate regions of the Gondwana supercontinent during Late Permian time, some 245 to 253 million years ago (Fig. 8). In Queensland and New South Wales, it grew in an extensive system of intermontane valleys west of a volcanic mountain range like that of the modern South American Andes, and east of the plains and hill ranges of inland Australia. Its tongue-shaped leaves (*Glossopteris communis* Feistmantel, 1876) were seasonally deciduous. They had a thick adaxial cuticle and stomates sunken into the abaxial surface. Their venation was reticulate, but not organized into veins of different thickness, as in modern angiosperms. Its wood (*Araucarioxylon bengalense* (Holden) Maheshwari, 1972) was massive and coniferlike, with clear growth rings. Large roots spread out horizontally from the trunk, and the rootlets (*Vertebraria australis* McCoy, 1847) had internal chambers, which may have allowed growth in oxygen-poor, waterlogged, peaty soils. Ovule-bearing (*Dictyopteridium sporiferum* Feistmantel, 1881) and pollen-bearing structures (*Eretmonia* sp. cf. *E. hinjridaensis* Surange & Maheshwari, 1970) were borne on the midrib of leaflike structures. These were arranged helically on fertile

Scale bars: P cm, Q 100μm, R 10μm, H cm, K mm, 100μm, 10μm, L, N, M 100μm, O 10μm, I 100μm, J 10μm, B, D 10μm, C 10μm, A m, E 10cm, F 100μm, G cm

short shoots, but it is not certain whether these shoots were bisexual or unisexual. Pollen sacs (*Arberiella africana* Pant & Nautiyal, 1960) were borne at the ends of slender, copiously branched stalks. They dehisced longitudinally to release numerous bisaccate, striate pollen grains (*Protohaploxypinus limpidus* (Balme & Henelly) Balme & Playford, 1967). These plants were probably wind pollinated. Numerous ovules (*Stephanostoma crystallinum* (Pant) Pant & Nautiyal, 1960) were borne on the underside of a leaflike organ and loosely enclosed by its inrolled margins. The ovules were interconnected by a meshwork of multicellular hairs and probably also a good deal of mucilage. By the time of fertilization the leaflike structure bearing ovules probably was unfurled, shrivelled, and decayed. Seeds were numerous, small, and lightweight. They probably were scattered by wind.

Evidence for reconstruction. This reconstruction is based on petrified material from near the Homevale–Elphinstone road at the southwest property boundary of Homevale Station (or "cattle ranch"), 87 km west-southwest of Mackay, Queensland, Australia (Isbell, 1955; Gould & Delevoryas, 1977). These petrified peats are part of the Fort Cooper Coal Measures, Blackwater Group, of Late Permian age (Jensen, 1975) or about 245 to 253 million years old (in time scale of Palmer, 1983). In these petrified fossils, sterile leaves are anatomically identical to leaflike structures bearing ovules; pollen is present in pollen sacs and in ovules; the same kind of tracheids are found in leaves and trunks; and identical secondary xylem is found in trunks and around large septate roots (Gould & Delevoryas, 1977).

These petrified fossils have not been named but appear identical to several compression fossils from the same region. The petrified fructifications are the same size and elongate shape and enclose numerous wingless ovules of the same size as compression fossils of *Dictyopteridium sporiferum* Feist-

mantel (1881) from Late Permian coal measures of India (Surange & Chandra, 1975), Queensland (as "*Cistella bowenensis*" of White, 1964, and "*Plumsteadia microsacca*" of Rigby, 1971, 1978), and New South Wales (Holmes, 1974; White, 1978). The petrified material also agrees closely in size and anatomy with compression fossils of ovules and pollen sacs comparable in age from India (Pant & Nautiyal, 1960). The petrified pollen organs have up to 17 pollen sacs in a cluster (Gould & Delevoryas, 1977), more like the compression genus *Eretmonia* than *Glossotheca* (as defined by Surange & Chandra, 1975). Impressions of *Eretmonia* from New South Wales (White, 1978) and a variety of "scale fronds" from Queensland (White, 1964) have a thickened tip, most like *Eretmonia hinjridaensis* Surange & Maheshwari (1970). Most of the pollen from petrified remains (Gould & Delevoryas, 1977) is identical to the broadly defined dispersed species *Protohaploxypinus limpidus* (Balme & Henelly) Balme & Playford, 1967 (Foster, 1975; Rigby & Hekel, 1977).

Impressions of *Dictyopteridium sporiferum* from Queensland have been found attached to leaves of *Glossopteris communis* Feistmantel, 1876 (White, 1964; Rigby, 1971). *Glossopteris communis* is a common fine-meshed leaf, like *G. indica*, *G. linearis*, and *G. angustifolia*. This last-mentioned species also has been considered the leaf of *Dictyopteridium sporiferum*, although on less secure evidence of association and venation density (White, 1964; Maheshwari, 1965). The petrified ovular heads and associated leaves (Gould & Delevoryas, 1977; G.J.R., pers. obs.) were also fine-meshed (veins about 0.2 mm apart), but they have a clearly defined midrib of a size most like that in *Glossopteris communis*. Associated coarse-meshed *Glossopteris* leaves in the Late Permian coal measures of Australia belonged to quite different plants, as shown by their attachment to nearly circular ovulate fructifications bearing winged seeds (Holmes, 1974; White, 1978). The petrified leaves of the

←

FIGURE 8. *A reconstruction of* Dictyopteridium sporiferum *of Late Permian age, from near Homevale Station, Queensland, Australia.—A. Habit as a swamp woodland tree.—B–D. Cellular details of wood structure in tangential and radial sections (respectively).—E. Cutaway reconstruction of secondary wood of basal trunk and main roots.—F. Cross section of wood of small root, showing primary xylem at points between arms of secondary wood.—G. Xylem model of small chambered root.—H. Ovulate fertile leafy shoot.—I. Cross sections of leaf, showing vascular bundles of midrib (circles with curved hachure), their sheathing sclerenchyma (black ellipses), upper palisade cells (vertical lines), and spongy mesophyll (irregular pattern).—J. Cross section of stomate, showing cuticle (heavy outline) and cell walls (dotted and broken lines).—K–M. Transverse and longitudinal sections of ovulate fertile structure and ovules, showing vascular traces (black), woody integumentary layer (stipple), multicellular megagametophyte (irregular pattern), and archegonium (circle with central stipple).—N, O. Lower and upper (respectively) cuticles of leaf, with stomates on under side only.—P. Pollen-bearing organs.—Q. Dehiscent sporangia.—R. Striate bisaccate pollen.*

plant reconstructed here are hypostomatic, with low papillae on the abaxial side, similar to the cuticles of the compression species *Glossopteris waltonii* Pant & Gupta (1968), after which our cuticular restoration was modeled.

Petrified wood of this plant, both within trunks and its distinctive chambered roots, includes late wood like *Araucarioxylon arberi* (Seward, 1919) Maheshwari (1972) and early wood like *A. bengalense* (Holden, 1917) Maheshwari, 1972 (Gould, 1975). We have chosen the latter name for our reconstruction on the grounds of priority.

There have been some nomenclatural problems also with the name for the root of this plant, which Schopf (1982) decided should be *Vertebraria australis* McCoy (1847). Only one species of *Vertebraria* is recognized. This fossil species probably includes remains of what were roots of numerous species of glossopterid plants recognized from their reproductive structures.

Habit. The overall habit of the plant has been reconstructed from specimens of trunks showing alternate and whorled branching (Gould & Delevoryas, 1977). The whorled specimen conforms to Rauh's architectural model of modern trees (Hallé et al., 1978). The other trunks may represent other growth forms but also could be old or damaged trunks. Regularly whorled young trees and extensively repaired and irregular old trees are characteristic of many living conifers, of *Ginkgo biloba*, and some angiosperms (Hallé et al., 1978; Retallack & Dilcher, 1981). The wood of this plant was like that of modern softwoods, with very narrow unicellular rays and abundant pitting in the cross field. It was a kind of wood apparently conservative in gymnosperms and still found in many conifers and in *Ginkgo biloba* (Beck, 1971).

Leaves were arranged in close helices on short shoots, which in turn were arranged on long shoots (Pant & Singh, 1974). The venation of the leaves was a fine mesh, with a zone of much narrower meshes and a sclerenchyma sheath forming a midrib. There is a good deal of evidence that these plants were seasonally deciduous: the noncoriaceous nature of the leaves compared with those of associated and presumably evergreen conifers, well-developed abscission scars at the bases of the petioles, and well-marked growth rings in its fossil wood (Gould & Delevoryas, 1977; G.J.R., pers. obs.). A variety of triangular scalelike leaves have been found in association with these fossils (Walkom, 1922; White, 1964, 1978). Some of these were fertile scales, but others may have been young leaves or protective scales of dormant winter buds.

Fertile structures were attached to leaflike or-

gans arranged in a closely spaced helix (Pant & Singh, 1974). Fertile scales arranged on the same short shoot as sterile leaves would have formed distinct clusters (White, 1978). On some short shoots there were up to three kinds of scales or leaves (White, 1978), but there is no evidence that any of these shoots were bisexual.

Pollen sacs were borne at the end of copiously dichotomizing stalks arising from the midrib of a scale leaf. Although much reduced, this epiphyllous structure is similar to that found in seed ferns such as *Telangium affine* (Kidston, 1923) and *Diplopteridium teilianum* (Walton, 1926, 1931). In many of these Early Carboniferous plants, the sporangia were fused into bell-like synangia, but in *Dictyopteridium sporiferum* the sporangia were free, as in other enigmatic Early Carboniferous plants (Skog & Gensel, 1980) and Late Devonian progymnosperms (Beck, 1981). The walls of each pollen sac were only one cell thick (Gould & Delevoryas, 1977). They opened by way of a long, sinuous slit (Pant & Nautiyal, 1960), which presumably developed because of diagonal stresses arising during drying.

Ovules were borne on the underside of an infolded leaflike structure which was attached by a long stalk to the midrib of the adaxial side of what looks like an ordinary foliage leaf. This epiphyllous structure also can be compared with fructifications of Early Carboniferous seed ferns, such as *Sphenopteris bifida* (Long, 1979b). The structure of these fossils was anticipated in some studies of impression fossils (Schopf, 1976) but did not become clear until well-preserved petrified fossils were studied (Gould & Delevoryas, 1977). In earlier studies of impressions, they were thought to have been bivalved cupules (Plumstead, 1958a) or bracteate cones (Surange & Chandra, 1975). The first view is now thought incorrect, but the second interpretation has gained some support from experimental compaction of model structures (Rex, 1986) and from cuticular studies of compressed specimens (Chandra & Surange, 1976). In our view, however, the three separate cuticles can be explained as (1) a central abaxial hair-bearing cuticle with holes marking positions of ovule attachment; as (2) a peripheral abaxial stomatiferous cuticle with hair bases; and as (3) an adaxial thick non-stomatiferous cuticle. A comparison of experimentally deformed structures with compression fossils indicates that some real biological diversity may be reflected in the large number of generic names for glossopterid fructifications (reviewed by Rigby, 1978), but some of them may be merely different developmental and preservational states of the same kinds of fructifications (Gould & Delevoryas, 1977).

Reproduction. Each pollen sac contained numerous pollen grains. The combined release of pollen from a stand of trees could have produced clouds of yellow dustlike grains. Considering the amount of pollen produced and its moderate size (32–46 μm in breadth and 14–26 μm in corpus diameter: Gould & Delevoryas, 1977), this plant was probably wind pollinated. As in *Callospermarion pusillum*, the saccae may have served to orient and float the grains in a pollination drop. Stout striae on the body of the pollen grain also may have functional significance, because similar striate bisaccate grains were also produced by apparently unrelated seed ferns in Permian coal swamps of Siberia (Meyen, 1984). Mormon tea (*Ephedra* spp.) has pollen with bands that strengthen the grain against stresses arising from desiccation in a dry climate (Hughes, 1976). Striae on the pollen of *Dictyopteridium sporiferum* may have served to withstand stresses associated with moisture losses during wind pollination.

At the time of pollination the ovule-bearing head was infolded to enclose the ovules and an interovular mesh of unicellular hairs. Rigby (1978) has suggested that these filaments were fungal hyphae, from decay of the fossil. This seems unlikely considering their radiation from the micropyles of the ovules without plugging them, the apparent lack of damage tissue in petrified specimens (Gould & Delevoryas, 1977), and the cuticularized hair bases seen in macerated preparations (Pant & Nautiyal, 1960; Chandra & Surange, 1976). The filamentous meshwork may have produced or trapped fluid which bulged from the gaping lips of the underside of the ovule-bearing structure, like pollination droplets. Pollen of *Dictyopteridium sporiferum* entrapped in this material and floated and oriented by their inflated saccae would have been pulled into the micropyles of the ovules inside as the fluid dried back along the guiding filaments.

Ovule-bearing heads have been found withered and open, partly or wholly naked of ovules (Gould & Delevoryas, 1977). The seeds of this plant lacked wings or fleshy layers found in associated fossil plants (Walkom, 1922; Holmes, 1974; Plumstead, 1963). They were numerous, small (0.8–1.5 mm long: Gould & Delevoryas, 1977), and possibly were shaken from the fructifications by swaying in the wind (a "wind ballist" of van der Pijl, 1972), then dispersed widely by wind and water. The hair bases appear to have been quite persistent on dispersed seeds (Pant & Nautiyal, 1960) and may have aided dispersal.

Habitat. Leaves of this plant are abundant in roof shales and clastic partings within coal seams, and its roots riddle the drab underclays to coal seams (Jensen, 1975; Retallack, 1980b). These plants lived in waterlogged muds, silts, and sands (gleyed Entisols of Soil Survey Staff, 1975), as well as in peaty organic substrates (Histosols of Soil Survey Staff, 1975).

Trunks of this plant (Jensen, 1975, fig. 45; Gould, 1975) and of glossopterids in general (David, 1907; Plumstead, 1958b) had shallow root systems. This kind of tabular root system is commonly found in modern plants of waterlogged habitats (Jenik, 1978). Such a habitat also may explain the peculiar construction of the roots of these plants, in which xylem is restricted to narrow radial arms and transverse platforms that enclose empty spaces within the root. There has been some concern whether these spaces were filled with parenchyma, but calluslike groups of parenchyma cells on the walls of mature examples is evidence that they were originally empty (Gould, 1975). They may have served for aeration of the root in oxygen-poor ground, as in living crack willow (*Salix fragilis*: Kawase & Whitmoyer, 1980).

The texture of the leaves, with an adaxial thick cuticle and an abaxial stomatiferous and papillate cuticle (Gould & Delevoryas, 1977) is similar to sun leaves of modern angiospermous trees (Salisbury, 1927). This, together with the abundance of these leaves, is an indication that these probably were dominant canopy trees.

Modern riverside weed trees such as sycamore (*Platanus occidentalis*) and sheoak (*Casuarina cunninghamiana*) produce seeds in comparable numbers and sizes to those of *Dictyopteridium sporiferum*. Associated fossil seeds of other glossopterid plants (Walkom, 1922) are generally larger and more elaborate, thus supporting the view that *D. sporiferum* was weedy in comparison. Judging from their sedimentary context, the earliest successional plants were horsetails (*Phyllotheca* spp.) and lycopods (*Selaginella harrisii*). Other species of glossopterids were probably the dominant plants of stable swamp woodlands. Associated osmundalean tree ferns (Gould, 1970) may have formed understory shrubs and small trees. In contrast to those of *Glossopteris*, the leaves of these tree ferns were delicate, like those of shade plants. Higher land to the west, and perhaps also the volcanic highlands to the east, were forested by conifers (*Walkomiella australis*: Retallack, 1980b).

Paleogeographic setting. *Dictyopteridium sporiferum* is exquisitely preserved in Late Permian silicified peat near Homevale Station and is found as compression fossils in shales elsewhere in the northeastern Bowen Basin (Jensen, 1975). This
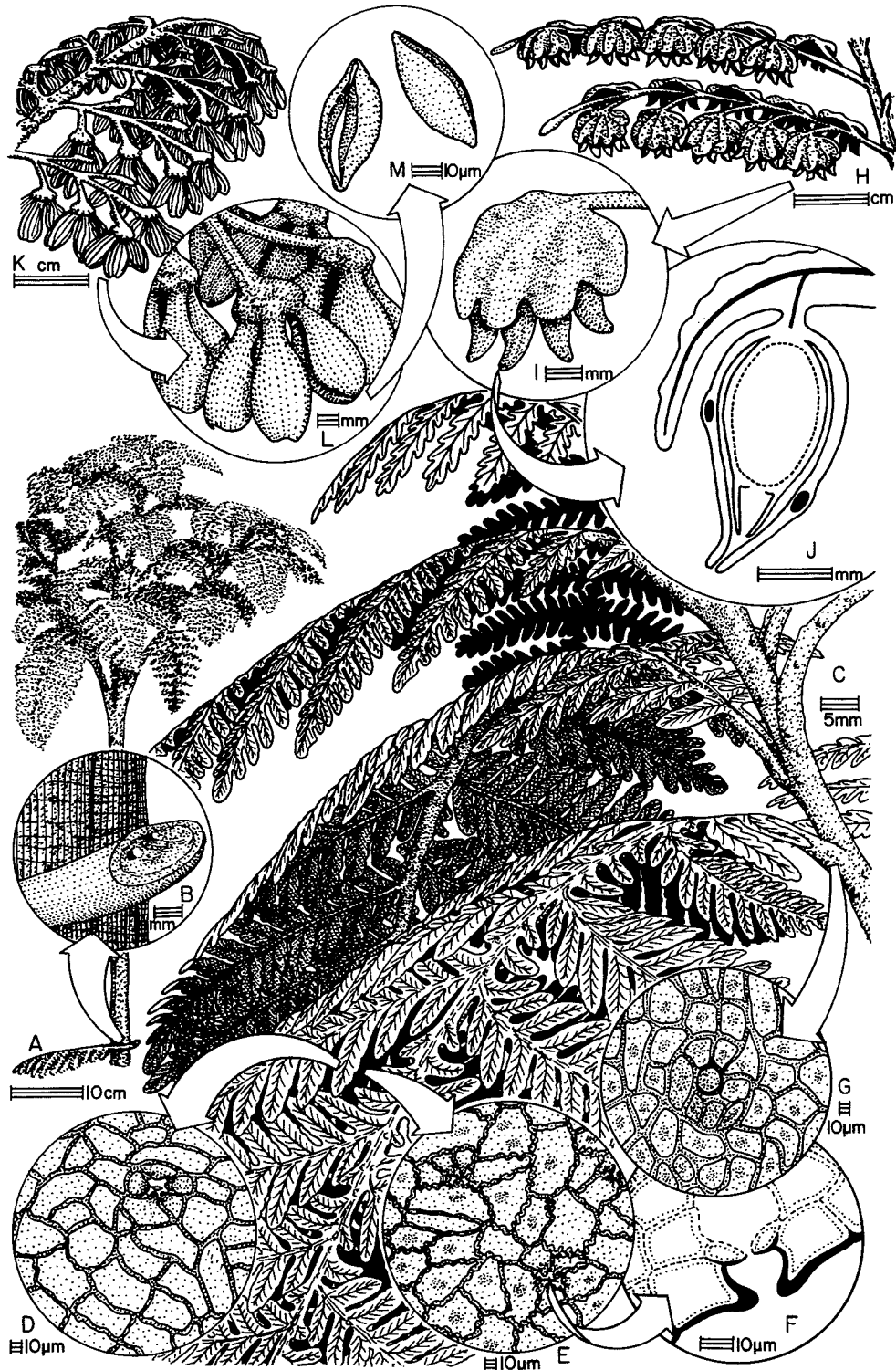
FIGURE 9. *A reconstruction of* Peltaspermum thomasii *of Late Triassic (Carnian) age, from the upper Umkomaas Valley, Natal, South Africa.—A. Habit as a shrub of seasonally wet bottomlands.—B. Abscission scar and leaf traces of petiole base.—C. Leafy shoot.—D, E. Upper and lower (respectively) leaf cuticles, with*

basin is continuous to the south with the Sydney Basin of New South Wales. Coal measures in the Sydney–Bowen Basin accumulated in a broad intermontane depression between the plains and hill ranges of inland Australia to the west and a volcanic, Andean-style mountain range to the east (Jensen, 1975).

The eastern Australian part of the Gondwana supercontinent was at very high paleolatitudes during the Late Permian (Herbert, 1980). There is no clear evidence of glaciation in the Bowen Basin at this time, but there were probably alpine glaciers on high mountains to the east. There are several lines of evidence for a seasonal, cool temperate climate throughout these lowlands. Growth rings are seen not only on fossil wood (Rigby, 1971) but also in the shells of marine shellfish, which were much less diverse in this region of the world during Late Permian time than in other formerly tropical regions (Runnegar & McClung, 1975). Varved lacustrine shales have been found with rafts of leaves at the very top of the silty layer, overlain by the thin shaley layer of the varve. This may be explained as coarse material washed out by brisk spring runoff and summer storms, followed by autumn leaf fall and slow winter accumulation of clay (Retallack, 1980b). Winters were not harsh by this time, because osmundalean tree ferns were widespread. They are represented by silicified trunks and foliage in the Bowen Basin (Gould, 1970).

PELTASPERMUM THOMASII

Hypothesized reconstruction. This plant is thought to have been a low-growing perennial shrub, vegetating stream, pond, and lake margins within temperate mesophytic woodlands and forests of South Africa and other southern continents during Late Triassic (Carnian) time, about 225 to 230 million years ago (Fig. 9). Its leaves (*Lepidopteris stormbergensis* (Seward) Townrow, 1956) were coriaceous, stiff, and fernlike. They varied from pinnatifid to bipinnatifid and in the proportion of stomates on either side of the leaf. This and the blisterlike hydathodes covering the frond rachis and the stem are features found in some modern waterside plants. Leaves had clear abscission scars, so it probably was a long-lived, perennial plant and may have been seasonally deciduous. The pollen-

bearing (*Antevsia extans* (Frenguelli) Townrow, 1960) and ovulate organs (*Peltaspermum thomasii* Harris, 1937) were pinnately arranged, and each frondlike structure formed a large paniclelike fructification. Pollen (*Monosulcites minimus* Cookson, 1947) was moderately sized (23–40 µm) and produced in great quantity: both features of modern wind-pollinated plants. The reconstructed plants may have had a pseudostigmatic kind of pollination, in which pollen adhered to the ovule or head and only pollen tubes entered the micropyle, as in modern conifers with relatively inaccessible ovules and nonsaccate pollen. Seeds of the fossil plant probably were dispersed mainly by water.

Evidence for reconstruction. This reconstruction is based largely on fossil compressions from the black shales of "Burnera Waterfall," where a tributary creek of the Umkomaas River drops over a scarp of the basal Molteno Formation, 4 km southeast of Vergelegen Nature Reserve, Natal, South Africa (our Fig. 2C; locality Umk 111 of Anderson & Anderson, 1983). These shales form the base of the Molteno Formation and are Late Triassic in age (*Yabeiella* oppel-zone of Retallack, 1977; or Carnian in the marine time scale), which is about 225 to 230 million years old (in time scale of Palmer, 1983). The various fossil organs attributed to this species have also been found in association at other localities in South Africa, South America, and New South Wales (Retallack, 1977; Anderson & Anderson, 1983). The remains discussed were attributed to one plant by Townrow (1960) for several reasons: the close similarity of the cuticles of leaves, microsporophylls, and megasporophylls; pollen found dispersed and in microsporophylls; and close association at several localities.

Habit. This plant is mainly known from coriaceous, bipinnatifid to pinnatifid leaves. Unipinnate leaves also have been included in the genus (Townrow, 1960). These have identical cuticle and may be closely allied plants but are now placed in the genus *Pachydermophyllum* (Retallack, 1981). Also variable is the distribution of stomates on both sides of the leaf in *Lepidopteris stormbergensis*. They are usually more numerous on the abaxial side but occasionally are more common on the adaxial side, which can be distinguished because

←

stomates overhung by papillae.—F. Cross section of stomate.—G. Blisterlike structure on cuticle of petiole.— H, I. Ovulate fructification.—J. Reconstructed longitudinal section of ovule, showing vascularization (heavy lines) and resinous glands (black ellipses).—K, L. Pollen-bearing organ.—M. Monocolpate pollen.

of its thicker cuticle and less-bulging venation. Such a stomatal distribution is found in leaves of understory shrubs (Salisbury, 1927) and of waterside herbs (Townrow, 1960). The peculiar blisterlike swellings under hair bases on the stem and rachis of this plant are similar to hydathodes in waterside herbs such as water dock (*Rumex hydrolapathum*: Townrow, 1960). A waterside understory habitat seems likely, but we reconstruct this plant as a small, much-branched, perennial woody shrub for the following reasons. The leaves have thick cuticles and were probably stiff and coriaceous. Leaf bases with clear abscission scars and two leaf traces have been found (Townrow, 1960). These were abscised, perhaps seasonally. Slender stems of this plant have also been found which have stomates and blisters like those of the leaves (Townrow, 1960). Such stems are unlikely to have been the main stem of a plant with a single palmlike stem. It is more likely that these were short shoots of a branched plant.

Pollen sacs and ovules were arranged radially on more or less laminar organs, which were arranged pinnately. These pinnate structures formed large, lax, paniclelike structures (Anderson & Anderson, 1983, pl. 23, and possibly also their "female cone gen. C. sp. A." of pl. 26).

Reproduction. Wind pollination of this plant may be indicated by its copious production of smooth, moderately sized (23–40 μm) pollen. However, its large (5 mm long by 2 mm wide) pollen sacs, with glandular bumps and borne in groups of four, are distinct from the more numerous, nonglandular, smaller pollen sacs of other Mesozoic seed ferns usually regarded as wind pollinated, such as *Umkomasia granulata* (also reconstructed here).

Ovulate fructifications have been found in several different stages of maturation. The least-developed examples have only bumps rather than obvious ovules underneath the ovular head (Retallack et al., 1977). These may be remains at or close to the time of pollination, when the ovules and their elongate micropyles were not as obvious as in other remains with ovules attached (Townrow, 1960).

Pollination by means of a pollination drop is unlikely, considering the nature of the pollen grains. Unlike the bisaccate pollen of related peltasperm seed ferns such as *Pteroma* (Harris, 1964) and *Townrovia* (Retallack, 1981), *Peltaspermum thomasii* had nonsaccate pollen grains. This is also true of some modern conifers such as western hemlock (*Tsuga heterophylla*) and Prince Albert's yew (*Saxegothaea conspicua*), compared with closely

allied conifers with bisaccate pollen (Doyle, 1945). These modern conifers with nonsaccate pollen have pseudostigmatic pollination, in which pollen grains adhere to parts of the plant near ovules, and long pollen tubes enter the ovules. The time between pollination and fertilization in these conifers is no less brief, compared with other conifers such as pines (Doyle & O'Leary, 1935b), because the tip of the pollen tube overwinters in the nucellus of the ovule (Doyle & O'Leary, 1935a, c).

The largest ovules seen are attached singly or in pairs to fructifications with abscission scars indicating a former complement of about six ovules (Townrow, 1960). The most complete remains lack ovules, and the most common remains are of isolated ovular heads only rarely with attached ovules (Anderson & Anderson, 1983). Even at these stages, associated ovules lack differentiation of woody and fleshy integuments to the degree seen in associated seeds, such as those of *Umkomasia granulata*. Neither the ovular heads, which may have been dispersal units, nor the ovules were adapted to specialized modes of dispersal, and they probably were scattered by wind and water.

Habitat. The black shale in the Umkomaas Valley (Umk 111 of Anderson & Anderson, 1983) is the deposit of a poorly oxygenated lake. The lacustrine shale overlies a thin conglomerate, which disconformably overlies floodplain deposits of the Katberg Formation, of Early Triassic age (*Lystrosaurus* zone). Such conglomerates at the base of a shale are found often in abandoned channels (oxbow lakes) of meandering streams (McDonnell, 1974).

At the Umkomaas Valley locality the shales are overlain by a variety of paleosols in which the plants may have lived (Fig. 2C). The so-called "oil shale" overlying the black shales is a coal (du Toit, 1954) and was probably a peaty soil (Histosol of Soil Survey Staff, 1975) fringing the Oxbow Lake. Overlying this are some very weakly developed fossil soils (Entisols of Soil Survey Staff, 1975), consisting of little-modified alluvium riddled with fossil root traces. These are interpreted as early successional soils of river levees. Above these are red, clayey, noncalcareous paleosols with slightly sandier surface horizons (probably Alfisols or Ultisols). Their root traces, profile differentiation, and degree of oxidation are typical for well-drained forested soils.

Of these various possible habitats, we think that *Peltaspermum thomasii* preferred the peaty lakeside soils. Unlike other associated fossil plants, this species lived very close to the lake, because it is

equally abundant through the entire thickness of the lacustrine shales (Townrow, 1960). There also are reasons for regarding it as a waterside plant (as already discussed). *Peltaspermum thomasii* has been found in place in the organic layer and immediately overlying carbonaceous shales of waterlogged, peaty paleosols at other localities, such as Konings Kroon, South Africa (Kon 111 of Anderson & Anderson, 1983; G.J.R., pers. obs.) and in Nymboida Open Cut Mine, New South Wales, Australia (Retallack, 1977). In all of these localities *Peltaspermum thomasii* is associated with *Umkomasia granulata*.

Although a waterside and lowland plant, there are indications that it could tolerate deficiencies of water or nutrients. The stomates, for example, are overarched by papillae on the subsidiary cells. The blisters on the stems and leaves are comparable to water control structures (Townrow, 1960), such as salt glands or hydathodes (discussed by Esau, 1977). Judging from its geological occurrence, it is more likely that these peculiar features of the plant reflect growth in nutrient-deficient habitats rather than lack of water. It may have been suited to siliceous, nutrient-poor, streamside sands of point bars, or acidic swampy lowlands.

The other local habitats revealed by paleosols at the Umkomaas Valley locality seem less likely for this plant, because there is evidence from other localities that they were vegetated by other plants. Entisols of streamsides may have been colonized by broad-leaved conifers (*Heidiphyllum*) in drier, sandy, and elevated areas, and by ferns (*Cladophlebis* sterile, or *Asterotheca* when fertile) and horsetails (*Neocalamites*) in wetter places. Alfisols and Ultisols of well-drained floodplain forests and woodlands in contrast were dominated by other seed ferns (*Dicroidium elongatum* and *D. coriaceum*) and a variety of plants with ginkgolike leaves (Retallack, 1977). Within this mosaic of vegetation, *Peltaspermum thomasii* is envisaged as an understory plant of woodlands dominated by *Umkomasia granulata* in periodically waterlogged lowlands.

Paleogeographic setting. During Late Triassic time the Molteno Formation formed an extensive lowland piedmont north of the mountainous Cape Fold Belt (Turner, 1978). The lower part of the formation in the Umkomaas Valley lies disconformably on older alluvial rocks, which may have formed low hills flanking low ranges of much older (Precambrian), resistant rocks to the north, west, and east. This far north of the mountains, streams laid down sequences of sediment of a type formed in loosely sinuous modern streams transporting a mixed load of clay and sand (Turner, 1978; compare general models of Schumm, 1981).

Climate in this region was humid and cool temperate, perhaps seasonally snowy. This can be inferred from the high paleolatitude of this part of Gondwana (Anderson & Schwyzer, 1977). Late Triassic fossil wood from South Africa (Walton, 1923) has well-marked growth rings, an indication of strong seasonality. A humid climate is indicated by the quartz-rich composition of Molteno sandstones (Dingle et al., 1983) from which most of the easily weathered minerals have been lost. High rainfall probably also accounts for noncalcareous fossil soils and the dearth of vertebrate fossils in the Molteno Formation (G.J.R., pers. obs., following general models of Retallack, 1984).

UMKOMASIA GRANULATA

Hypothesized reconstruction. This was probably a woodland tree which dominated seasonally waterlogged floodplains of extensive lowlands north of mountains in the Cape region of South Africa, and of other humid regions of Gondwana during Late Triassic time, some 225–230 million years ago (Fig. 10). The leaves of this plant (*Dicroidium odontopteroides* (Morris) Gothan, 1912) had callused abscission scars, so probably were deciduous. Its wood (*Rhexoxylon tetrapteridoides* Walton, 1923) was coniferlike, but with exceptionally wide rays. Ovulate (*Umkomasia granulata* Thomas, 1933) and pollen-bearing structures (*Pteruchus johnstonii* (Feistmantel) Townrow, 1962b) of this plant were pinnately organized, and the pinnate structures were arranged helically in large paniculate fructifications. The copious production of moderately sized (corpus averaging 46 by 32 μm), bisaccate pollen (*Alisporites australis* de Jersey, 1962) is compatible with pollination by wind and possibly with a pollination drop. At ovulation, the ovules were weakly developed, and their bifid, elongate micropyles extended out below the margin of the cupulate head that enclosed their inverted bases. During subsequent development the ovule elongated well below the cupule margin and gained a sclerotesta with three broad ribs as the formerly elongate micropyle withered away. Seeds were released as their stalk abscised and the bivalved cupule spread open. The moderately-sized (3.7–7 mm × 2.2–5 mm) seeds were produced in great numbers and protected by a sclerotesta from desiccation or damage during possible ingestion. They probably were dispersed in a variety of ways, mainly by wind and water.
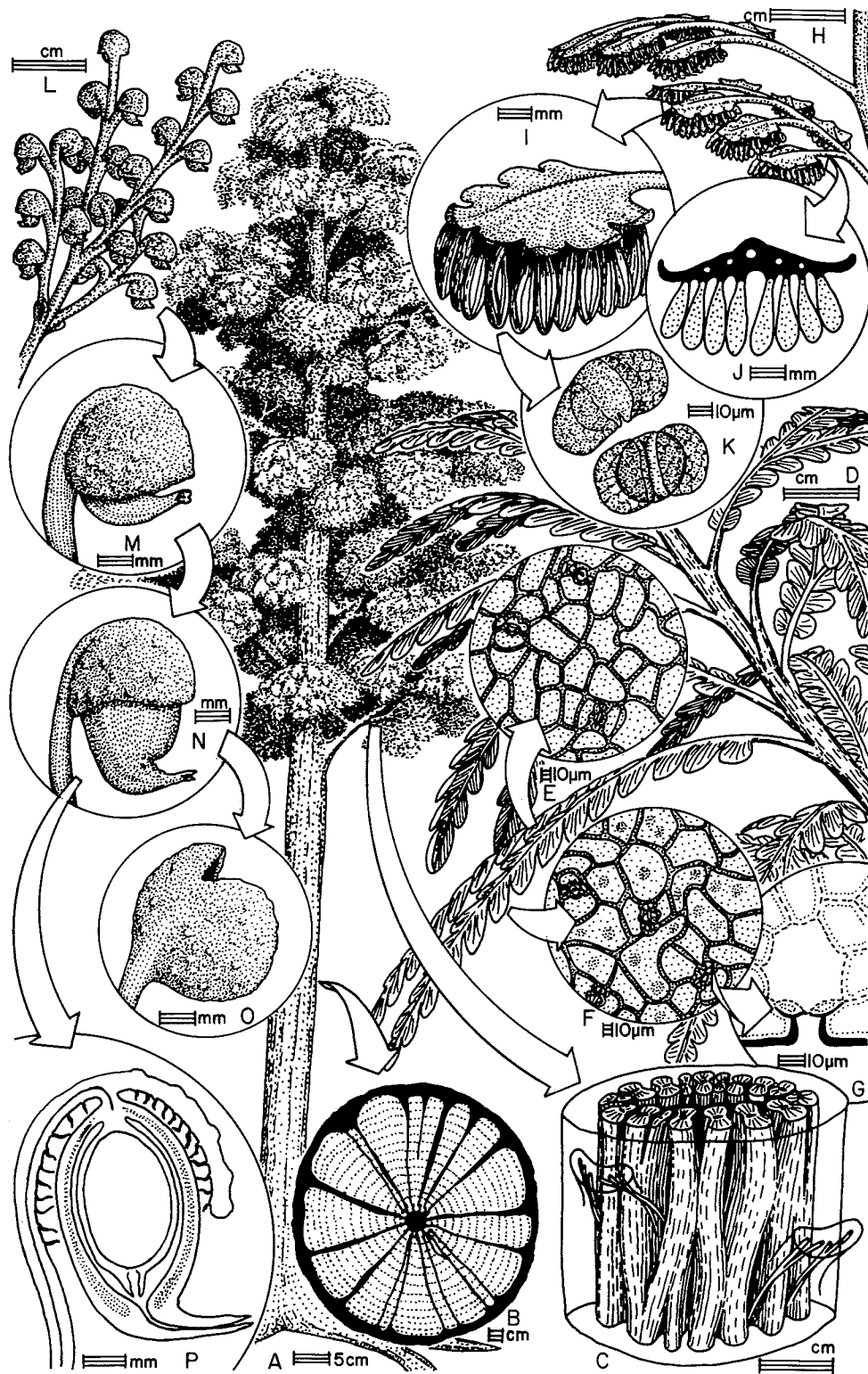
FIGURE 10.   *A reconstruction of* Umkomasia granulata *of Late Triassic (Carnian) age from the upper Umkomaas Valley, Natal, South Africa.—A. Habit as a tree of seasonally wet bottomlands.—B. Diagrammatic cross section*

Evidence for reconstruction. This plant has been put together on the basis of compressed remains of leaves, ovulate and pollen-bearing organs with similar cuticle, and similar pollen grains in pollen sacs and ovules (Thomas, 1933; Townrow, 1962a–c). These remains were first demonstrated to be closely associated in the same locality (in the Umkomaas Valley, South Africa) that also serves as a basis for our reconstruction of *Peltaspermum thomasii.* The association of these fructifications and leaves is now known at most localities where it is found in South Africa, South America, Australia, and New Zealand (Retallack, 1977, 1980c).

Evidence that this plant was a tree of deciduous woodlands and forests includes associated fossil trunks, root traces, and the callused abscission scar at the base of its leaves. Other lines of evidence have been used in support of the idea that its wood, at least in South Africa, was *Rhexoxylon tetrapteridoides* Walton (1923). There is a close association of *Dicroidium* with petrified wood of *Rhexoxylon pianitskyi* at two localities in Argentina (Archangelsky, 1968). Of the two species of *Rhexoxylon* found in South Africa, *R. tetrapteridoides* is the only one found in the Molteno Formation near, but not at, the same localities (such as the Umkomaas Valley; Walton, 1923; Anderson & Anderson, 1983) from which our reconstructions of *Umkomasia granulata* and *Peltaspermum thomasii* came. A petrified leafy shoot of *Rhexoxylon pianitskyi* from Argentina (Archangelsky & Brett, 1961) formed the basis for our reconstruction of *R. tetrapteridoides* here, which we have assumed also to have six vascular traces leading into the petioles of the leaves. Because of this, *Rhexoxylon* could not be the wood of associated conifer (such as *Rissikia* or *Heidiphyllum*) or ginkgolike foliage (such as *Sphenobaiera*), which had only one or two vascular strands in their petioles. Nor does *Rhexoxylon* show the girdling leaf traces or intimately admixed parenchyma and xylem seen in the wood of cycads and cycadeoids, which presumably produced associated foliage of *Pseudoctenis* and *Taeniopteris.* Among associated seed ferns in South Africa, *Peltaspermum thomasii* (as reconstructed here) had only two leaf traces in the petiole

(Townrow, 1960) and is here reconstructed as an understory shrub. *Glossopteris verticillata* is a rare element with multistranded petioles of this Triassic fossil flora, but it has been found attached to stems in a much closer helix than apparent for petrified *Rhexoxylon pianitskyi* or natural groups of impressions of *Dicroidium odontopteroides* leaves (du Toit, 1927; Thomas, 1952; Anderson & Anderson, 1983).

Thomas's (1933) numerous species of pollen organs have been revised and reduced in number by Townrow (1962a, b). This task has not yet been completed for ovulate organs, although most of these remains have been transferred to the genus *Umkomasia* (Holmes, 1987). From our examination of Thomas's specimens and preparations (in the British Museum of Natural History), we think that there are probably only three species. The type species of Thomas's three genera can be taken as representative of these species, which can be recognized by deeply incised cupular lobes (*Umkomasia macleanii*), weakly lobed cupule margins (*Umkomasia sewardii*), and smooth, bivalved cupule margins (*Umkomasia granulata*). These three taxa also show cuticular differences comparable to those found in the three associated species of *Pteruchus* by Townrow (1962a). Thus, the species name *Umkomasia granulata* is used broadly here to include several other named species ("*Pilophorosperma*" *costulatum*, "*P.*" *geminatum*, "*P.*" *paucipartitum*, "*P.*" *burnerense*, "*P.*" *natalense*, "*P.*" sp. type A, "*P.*" sp. type B, and "*P.*" sp. type C), which we regard as different stages of development and different parts of a large fructification. In the case of one of these species ("*P.*" *geminatum*), Thomas (1933, 1934, fig. 12F) thought that it had paired cupules, back to back. From comparison of the branching pattern of this specimen with the others, as well as our examination of its cuticular preparations, we interpret this as a dehisced, bivalved cupule. The branching pattern and small bractlike organs were regarded by Thomas (1933) as evidence that these fructifications were stalked, like the flowers of angiosperms. We prefer Townrow's (1962a) interpretation, developed for the pollen organ, that each

←

of wood showing wide parenchymatous rays (black) and secondary wood (concentric dotted lines).—C. Xylem model of a small shoot and petioles.—D. Leafy shoot.—E, F. Upper and lower (respectively) cuticles of leaf, both with stomates.—G. Cross section of stomate.—H, I. Pollen organ.—J. Cross section of head of pollen organ, showing vascular traces (white circles) and pollen sacs (stipple).—K. Bisaccate pollen.—L. Ovulate organ.— M. Cupulate ovule at time of pollination.—N. Cupulate ovule at time of fertilization.—O. Dehisced cupule.— P. Longitudinal section of cupulate ovule, showing hairy inner side of cupules (irregular extensions) and sclerotesta (stipple).

cupule is a homolog of a pinna, each "bracteole" a sterile pinna, and the whole pinnate structure homologous with a frond. This structure is in some ways similar to the ovule-bearing cupule arising from the dichotomy of a frond in early Carboniferous seed ferns such as *Sphenopteris bifida* (Long, 1979b).

Habit. Judging from the trunks of *Rhexoxylon tetrapteridoides* found (up to about 16 cm in diameter), this plant was a woodland tree (Archangelsky & Brett, 1961; Petriella, 1985). A trunk showing branch scars (Walton, 1923) provides evidence that the large branches were arranged in tiers that were not quite whorled. Like *Dictyopteridium sporiferum* reconstructed here, *Umkomasia granulata* probably had tiered branching which became more irregular with old age. This, and a long shoot and short shoot organization apparent from small petrified leafy stems and leaf groups, is very similar to our envisaged habit of *Dictyopteridium sporiferum*.

The leaves of this plant were variable in morphology, as documented in detail by Anderson & Anderson (1983). They may have belonged to a complex of hybridizing species. The Andersons have identified aberrant fossil leaves with narrow segments (*Dicroidium coriaceum* and *D. elongatum*) in some parts of the frond, and wide ones (*D. odontopteroides*) elsewhere on the same frond. These may represent hybrid leaves. Disregarding these as sports and considering variation in natural populations of these leaves (Anderson & Anderson, 1983, figs. 3, 4), *Umkomasia granulata* probably included leaves referred to *Dicroidium odontopteroides*, as well as those which have been referred to "*D. lancifolium*" and "*D. obtusifolium.*"

Stomates were distributed on both sides of the leaf but were much more abundant on the abaxial side, which had a thinner cuticle covered in papillae (Anderson & Anderson, 1983; Petriella, 1985). Fossil leaves have been found in radial groups and with asymmetric basal petioles (Anderson & Anderson, 1983).

The ovulate and pollen-bearing structures were pinnately organized and helically arranged on a larger stem (shown well in "*Umkomasia* sp. A" and "*Pteruchus* sp. B" illustrated by Anderson & Anderson, 1983, 1985). Only the ovule-bearing structure has been found in an apical position on slender shoots (Thomas, 1933; Holmes, 1987).

Reproduction. Individual laminar heads of the pollen organ bore hundreds of pendent, elongate pollen sacs (Townrow, 1962a). Pollen grains were bisaccate, nonstriate, and of moderate size (corpus averaging 46 by 32 μm in size: Townrow, 1962a). It is likely that the saccae were areas of porous exine (as indicated by Taylor et al., 1984, for a closely allied fossil species, really from the Ipswich Coal Measures near Dinmore, Queensland, according to these authors' erratum) rather than completely detached from the corpus. These are all indications that *Umkomasia granulata* probably was wind pollinated.

Only in specimens with small ovules does the elongate micropyle protruding from under the cupule appear to have been turgid and open. This was probably the stage of pollination, because in specimens with larger, more elongate ovules, the micropyle is withered and torn. The pollen chamber was narrow and tubular. It has been compared (by Thomas, 1933) to the salpinx of Paleozoic seed ferns such as *Lagenostoma lomaxii* reconstructed here. However, there is no sign of a central column, and it was not exposed like the salpinx. In these respects it was more like the pollen chamber of *Callospermarion pusillum*. Both were passive receptacles, not sealed from within by a plug of tissue, but sealed by the overarching sclerotesta of the integument. As the ovule enlarged and elongated, three broad ribs developed in the sclerotesta. This period of growth may have been when the megagametophyte and archegonia developed during the time between pollination and fertilization, as already described for *Callospermarion pusillum*.

Mature ovules and seeds were shed from the cupules by abscission from their stalk and by the cupule splitting into two lobes. Cupules at this open stage, revealing fully the degree of lobation of their margins, are the easiest of these remains to identify (Retallack, 1977). The branching fructifications found as fossils were presumably aborted or torn from the trees during storms. Much more common are isolated seeds, which were presumably the propagules. The seeds were neither exceptionally large nor small (3.5 to 7 mm long by 2.2 to 5 mm wide: Thomas, 1933), nor especially woody or fleshy, winged or spiny, even compared with the variety of associated fossilized propagules (Anderson & Anderson, 1983). They were probably dispersed by generalized methods, mainly by wind and water.

Habitat. This plant is best known from the Late Triassic locality in the Umkomaas Valley of South Africa (Fig. 2C), already described for *Peltaspermum thomasii*. Remains of these species drifted into a lake and were mixed with a variety of other plants. Fossil leaf litters preserved in paleosols at Konings Kroon, South Africa (locality Kon 111 of Anderson & Anderson, 1983) and at

Nymboida Open Cut, New South Wales, Australia (Retallack, 1977) are better evidence of its habitat and associated plants. As already discussed for *Peltaspermum thomasii*, the soils were periodically (probably seasonally) waterlogged in lowland flood-plains. High soil acidity and deeply weathered parent material of this humid region depleted nutrients in these fossil soils. Stumps and root traces penetrate deeply into these carbonaceous paleosols (Hatch & Corstorphine, 1909). This is unlike roots of modern plants in permanently waterlogged soils (Jenik, 1978). Although waterlogged for some part of the year, thus retarding decay of carbonaceous material in the soil (Retallack, 1984), these soils were moderately well drained at other times.

Also relevant to the former habitat of this plant are the distinctive wide parenchymatous rays of the wood here included in our reconstruction. This wood structure has been compared to that of modern vines, in which wide parenchymatous rays bestow flexibility (Walton, 1923). These plants are unlikely to have been vines, considering their size, but some flexibility may have been advantageous during seasonal fluctuations in water availability (Carlquist, 1975).

Judging from its abundance and likely stature, *Umkomasia granulata* was probably a dominant canopy tree of lowland mesophytic woodlands in humid, cool temperate regions of Gondwana (Retallack, 1977). Other trees included rare conifers (*Rissikia media*) and plants with ginkgolike leaves (*Sphenobaiera stormbergensis*). Among the understory plants were other seed ferns (*Peltaspermum thomasii*), cycadophytes (*Pseudoctenis* and *Taeniopteris*), ferns (*Cladophlebis*), and horsetails (*Neocalamites*). These last-mentioned pteridophytes also may have colonized disturbed parts of the forest, because they are found in other nearby localities (such as Konings Kroon localities Kon 211 and 221 of Anderson & Anderson, 1983) where they form distinctive early successional assemblages in very weakly developed paleosols (Entisols of Soil Survey Staff, 1975: G.J.R., pers. obs.).

Paleogeographic setting. Umkomasia granulata is best known from the same locality and region as *Peltaspermum thomasii*.

CAYTONIA NATHORSTII

Hypothesized reconstruction. We reconstruct this plant as a forest tree of an extensive Middle Jurassic (Bajocian or 175 to 183 million years old) coastal plain, in what is now northeastern England (Fig. 11). Climate in England at this time was subtropical, monsoonal, and seasonally dry,

with an annual rainfall within the humid range. The compound leaves (*Sagenopteris phillipsii* (Brongniart) Presl in Sternberg, 1838) of this plant had four leaflets paripinnately arranged but so close together that they appear palmately compound. Leaves developed by elaboration of the apical region of an initial scale into the four leaflets and by modification of the body of the scale into a petiole. The adaxial cuticle of the leaflets was thick and lacked stomates. The abaxial side had a thin cuticle, stomates, and papillae. Both ovulate (*Caytonia nathorstii* (Thomas) Harris, 1940) and pollen-bearing structures (*Caytonanthus arberi* (Thomas) Harris, 1941) were organized imparipinnately and arranged in a helix on slender axes. The pollen (*Vitreisporites pallidus* (Reissinger) Nilsson, 1958) were moderately sized (22–28 μm wide), bisaccate, and produced in large quantities. These are typical features of wind-pollinated plants. Pollen grains in coprolites provide evidence that these were also eaten by small animals that may have been effective as pollinators. The ovules (*Amphorispermum pullum* Harris, 1943) were borne on the inside of fleshy, berrylike cupules. At the time of pollination, ovules were small and poorly developed, and the ovulate structure consisted of cuplike inrolled flaps. Pollen were probably entrapped by a pollination drop at the opening of the ovulate structures and drawn back into the micropyles of the ovules along a series of guiding filaments as the droplet dried out. In mature cupules the ovules were completely enclosed by the overarching pressure of the turgid fleshy "fruit" and by sealing the entrance with bands of cutin and perhaps also of other substances. The fleshy, berrylike cupules have been found burst and split. They may have spilled ovules as they fell on the ground. More effective in their dispersal may have been reptiles and small mammals attracted by these fleshy fructifications. The seeds were fortified against crushing and acidity during ingestion by their sclerotesta.

Evidence for reconstruction. Caytonia nathorstii is best known from a thin (1 m) shale bed (Fig. 2D) in the rock platform south of Cayton Bay, Yorkshire, England (Harris, 1964). This is the Gristhorpe Bed of the Cloughton Formation, Ravenscar Group (Kent, 1980), and is Middle Jurassic (Bajocian) in age, or some 175 to 183 million years old (in the time scale of Palmer, 1983). This plant has been reconstructed from compression remains of leaves, buds, pollen organs, and ovule-bearing organs with similar cuticles; from the similarity of pollen in pollen sacs and ovules; and from close association at several localities (Harris, 1964).
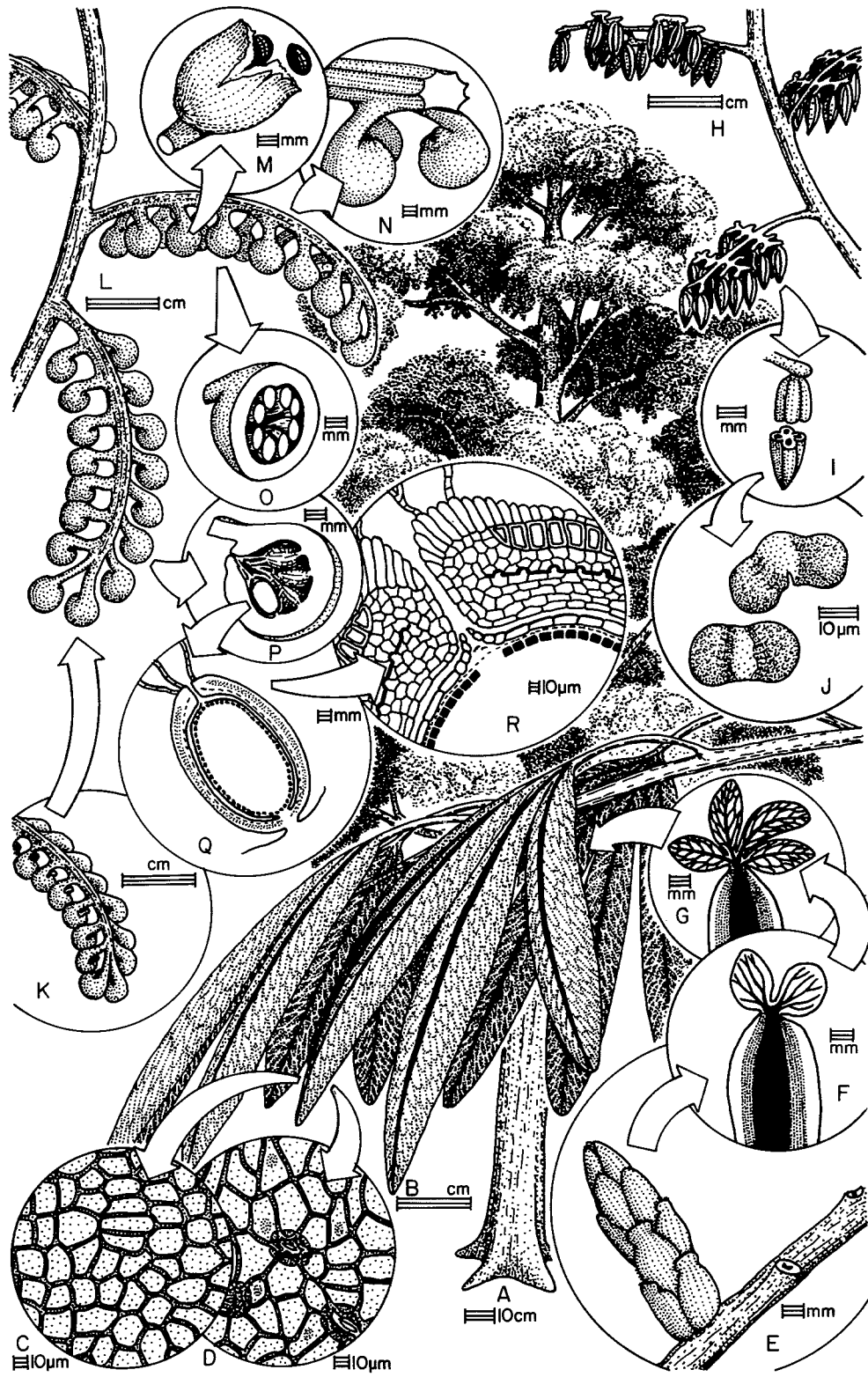
At the best-known locality, Cayton Bay, the fruc-
tifications of most of the other associated fossil
plants are known to be different (Harris, 1961,
1964, 1969, 1979; Harris et al., 1974).

Habit. There is evidence from association with
poorly preserved fossil stumps (Thomas, 1925;
Black, 1929; Harris, 1971) in a forested paleosol
(Spodosol or Inceptisol, Fig. 2D) that this plant
was part of a mixed fern–cycadophyte–conifer for-
est. Its exact habit within this vegetation is less
certain. Harris (1971) has argued that *Caytonia
nathorstii* was a tree, as shown by finds such as
leaves attached to stout woody shoots and of bud-
like short shoots of young leaves. As he argued,
few shrubby plants have such stout leafy limbs,
and those that do are often more succulent or more
completely invested with leaf bases. Buds are typ-
ical of a perennial deciduous plant.

The four leaflets of the compound leaves appear
palmately compound but are paripinnately ar-
ranged with very close points of contact (Harris,
1951). The diffuse, anastomosing venation of leaf-
lets of *Caytonia nathorstii* is superficially like that
in leaves of *Dictyopteridium sporiferum*, also re-
constructed here. *Sagenopteris* differs from *Glos-
sopteris* in having compound leaves, a true midrib
to the leaflets, and secondary venation in which
radiating and dichotomizing veins are undeviated
by confluent strut veins. These differences from
Glossopteris have been indicated also by Delevor-
yas & Person (1975) for *Mexiglossa* leaves, which
we regard as closely related to, if not congeneric
with, *Sagenopteris*.

Fossil buds (Harris, 1964) indicate that short
shoots of leaves developed synchronously, presum-
ably after a period of leaf fall, then dormancy during
a harsh season. Leaves developed from the scalelike
organs by the differentiation of two orbicular apical
leaflets, followed by a second pair on either side
behind them (Harris, 1940). Most of the scales
became differentiated into the petiole of the com-
pound leaf. The developing leaves were pilose, as

are many young organs (Esau, 1977), but mature
leaves were glabrous.

The ovules and pollen sacs were arranged pari-
pinnately on leaflike structures on either side of
an axis, which had a different adaxial and abaxial
cuticular structure, more like a petiole than a stem.
The ovulate structure was unipinnate (Harris,
1964), and the pollen-bearing structure was bi-
pinnately arranged (Harris, 1951). These fructi-
fications probably formed paniculate structures, like
those of other Mesozoic seed ferns reconstructed
here.

Pollen sacs of this plant are thought to have
been attached to the abaxial side of the leaflike
microsporophyll (Thomas, 1925; Harris, 1964),
but the orientation of the ovules is more contro-
versial. For the following reasons we believe that
they were also morphologically abaxial, as were
the openings to the cupules. The most important
evidence is a single specimen of *Caytonia na-
thorstii* attached to another axis (Thomas, 1925,
pl. 12, fig. 16). This specimen was thought lost
(Harris, 1971) but was discovered during 1980 by
us in the paleobotany teaching collection of Cam-
bridge University. We confirm that the megaspo-
rophyll at right angles to the axis is attached, as
are two berrylike cupules displayed with their oc-
cluded opening crushed on top of their stalks. From
our interpretation of the creasing at the attachment
points, clearly visible in Thomas's excellent pho-
tograph, the attachment does not appear twisted
into an unusual orientation. The occluded opening
of the fruit appears to be abaxial, and the ovules
enclosed by the fruit wall are also morphologically
abaxial. This is because, as Harris (1964) and
Reymanowna (1974) argued, the cupule is ho-
mologous with an infolded leaf. By our inter-
pretation, papillae and hair bases consistently
characterize the abaxial surface of leaves, micro-
sporophylls, and megasporophylls (Thomas, 1925;
Harris, 1940, 1964). In addition, the outer cuticles
of the cupules lack stomates and have a structure
in thinner areas (probably lenticels) very similar to

←

FIGURE 11. *A reconstruction of* Caytonia nathorstii *of Middle Jurassic (Bajocian) age from Cayton Bay,
Yorkshire, England.—A. Habit as a tree of bottomland forest.—B. Leafy shoot.—C, D. Upper and lower
(respectively) cuticles of leaf, with stomates on lower side.—E–G. Successive stages in the growth of young
leaves.—H. Pollen organ.—I. Cutaway view of quadrilocular synangium.—J. Bisaccate pollen.—K. Ovulate
organ at time of pollination.—L. Mature ovulate organ.—M. "Fruits" at time of dispersal.—N–P. Cutaway
views of mature fruits and ovules.—Q, R. Longitudinal sections of ovule, showing sclerotesta (stipple and double
wall cells), "spotted layer" (heavy dimpled line), "aleurone layer" (black rectangles), and hair bases around
micropyle.*

the adaxial cuticles of the leaves (Harris, 1940). Interpretation of the ovules as abaxial brings these plants into line with closely allied plants and with seed ferns as a whole.

We have taken pains to justify our reconstruction on this point, because it runs contrary to the opinion of the leading authority on *Caytonia nathorstii* (Harris, 1940, 1964). Since the thickest cuticle on the rachis of this fructification is on the narrow side, Harris argued that the ovules of *Caytonia* were morphologically adaxial. He interpreted this as similar to the thicker adaxial cuticle of leaves and pollen organ of this plant. We, on the other hand, have pointed out other ways of viewing cuticular homologs between different organs of this plant and regard the thick narrow cuticle of the abaxial side of the rachis as a structural thickening that prevented drooping of the heavy cupules.

Reproduction. It is difficult to determine whether fertile shoots of this plant were bisexual or unisexual. Thomas (1925) argued that individual plants were unisexual, because the best-preserved fructifications of either sex were found in different parts of the same bed. We confirmed this during our own collecting. This is compatible with the view that this plant, like modern plants that have unisexual fructifications, was wind pollinated. The fossil plant produced copious amounts of weakly sculptured, moderately sized (22–28 μm wide: van Konijnenburg-van Cittert, 1971), bisaccate pollen. Shriveling of the saccae on release, as observed in modern pine pollen by Wodehouse (1935: 254), would have greatly reduced the size of the pollen grains. The central body of the grains is only 12–18 μm long by 6–12 μm wide (van Konijnenburg-van Cittert, 1971). They could not have shrunk this much because the sacci contained an internal mesh of sporopollenin, in some ways like that found in pollen from the corystosperm microsporophyll *Pteruchus* (Pedersen & Friis, 1986). Some possible evidence for animal pollination of this fossil comes from small (4 mm diameter) coprolites full of these pollen grains. These were produced by small animals that lacked the ability to digest sporopollenin (Harris, 1964), perhaps a small arboreal mammal or lizard. Australian honey possums (*Tarsipes spencerae*), and a variety of other small animals are known to be effective pollinators, even though they are unable to fly, as is usual among the most important modern pollinators (Rourke & Wiens, 1977). Apart from dinosaur footprints (Kent, 1980), no fossil vertebrates or insects have been found in association with these plants, but from what is known of Middle Jurassic life on land elsewhere in Britain (Clemens et al., 1979; Savage, 1984), there were varied small mammals and arboreal gliding and flying reptiles. Birds had not yet appeared, and despite the diversity of insects at this time, the fossil coprolites are too large for them.

As is common in modern conifers with bisaccate pollen (Doyle, 1945), pollination may have been aided by pollination droplets. In this case it probably emerged from the mouth of the cupules at an early stage of development, when they were little more than infolded flaps (Harris, 1943, 1964). As in *Dictyopteridium sporiferum* reconstructed here, there may have been a reticulum of filaments, which guided pollen toward the micropyles of ovules inside. Filaments were observed in preparations of ovules by Thomas (1925) and Krassilov (1977) but were not noticed by Harris (1933). Pollination must have occurred when ovules were young and the cupule was open, because later in development the opening was sealed by inflation of the fleshy fruit wall and the development of cutinous bands, and perhaps also waxy or other substances (Harris, 1933, 1943). This subsequent development may have disrupted internal filaments so that they were difficult to see in mature fruits. This closure also prevented penetration of clay in the fallen mature fruits. Early ideas (Thomas, 1925) about stigmatic, angiospermlike pollination of these plants were long ago disproved by the discovery of pollen grains within the ovules inside the cupules (Harris, 1933, 1940).

At maturity the berrylike cupules were swollen and completely enclosed the ovules. Each ovule had a well-developed sclerotesta. An enigmatic layer within the ovular coat, the "spotted layer," is quite unlike a true cuticle, but nevertheless somewhat maceration-resistant (Harris, 1958a). It could be the basal layer of a zone of osteosclereids or lagenosclereids, as found in the seed coat of modern soybean (*Glycine max*: Esau, 1977). Inside the nucellus of the ovule was a layer of poorly preserved brown cell contents. Harris (1958a) called it an "aleurone layer," which is a distinctive outer enzyme-producing layer of the endosperm well known in modern angiospermous cereals, such as barley (*Hordeum vulgare*: Esau, 1977).

Dispersal of seeds may have been by bursting on impact or by rotting of the cupule. Many comparably fleshy modern fruits with stony seeds are animal dispersed. The same kinds of small reptiles and mammals already discussed as possible pollinators of this plant may also have aided in its dispersal.

Habitat. The fossiliferous shale (Gristhorpe Bed) at Cayton Bay (Fig. 2D) is a sequence of flood deposits overlying a thick (1.3 m), moderately de-

veloped sandy paleosol with a white surface (E) and orange-red subsurface (Bs) horizon (Thomas, 1925; G.J.R., pers. obs.). It was probably a base-poor, forested soil (Gley Podzol of Stace et al., 1968, or Spodosol or spodosolic Inceptisol of Soil Survey Staff, 1975) of periodically waterlogged lowlands. Stumps and large roots have been found within this paleosol (Black, 1929). These are surrounded by a layer of carbonaceous shale, which when macerated yields many fruits and seeds of *Caytonia nathorstii* and other plant debris. We interpret this as an imperfectly decayed (mor) humus layer of leaf litter in a periodically (perhaps seasonally) wet soil. Plants preserved in the overlying shales represent other leaf litter entrapped as clay and floodwaters were slowed around the trees, as in cumulic horizons of modern floodplain soils (modern examples are discussed by Birkeland, 1984). The shale layer becomes more silty and sandy higher towards the next overlying paleosol. This reflects an increase in the power and frequency of flood disturbance, which would have introduced early successional species of plants not usually found in undisturbed lowland forest.

A great variety of plants have been found in the Gristhorpe Bed (Harris, 1961, 1964, 1969, 1979; Harris et al., 1974). The commonest tree species from near the base of the bed are the seed fern *Caytonia nathorstii* and the taxodiaceous conifer *Elatides williamsonii*. Other common remains likely to have been understory plants include the osmundalean fern *Todites williamsonii*, the cycad *Nilssonia compta*, and the cycadeoid *Nissoniopteris vittata*.

Caytonia nathorstii was not common in other habitats in the coastal plains of Yorkshire. Fluvial levees were colonized largely by ginkgoes (*Ginkgo huttonii*: van Konijnenburg-van Cittert, 1971; Nami, 1976) and other nearstream, early successional environments by horsetails (*Equisetum columnare*: Harris, 1961). Near-coastal peat swamps were vegetated by cycads (*Nilssonia kendallae*), cycadeoids (*Ptilophyllum pectinoides*), and czekanowskialeans (*Sphenobaiera gyron*); and the most marine-influenced vegetation of tidal creeks was dominated by another seed fern (*Pachydermophyllum papillosum*: Thomas & Bose, 1955; Spicer & Hill, 1979). Compared with these other plants, *Caytonia nathorstii*, although a lowland plant, lived in more inland and stable sites.

Paleogeographic setting. During Middle Jurassic time Yorkshire was a flat deltaic coastal plain between moderately elevated plateaus of older rocks to the north, south, and east. To the west was a shallow sea, which connected to the south past several low islands and a broad shelf of tropical reefs to the open Tethys Ocean (Sellwood, 1978).

Yorkshire at this time was at a paleolatitude of about 35° north (Briden et al., 1974). Climatic zonation was less marked than at present, and this region enjoyed a subtropical climate (Hallam, 1975). Overall rainfall was probably in the humid range, considering the lush vegetation of pteridophytes (Harris, 1961), noncalcareous and podzolic nature of paleosols (Fig. 2D), and corrosion of the umbos of fossil unionid bivalves (Wilson, 1948). Growth zones in fossil shoots (Harris, 1971, 1979) are evidence of seasonality. The harsh season was probably dry and a time of forest fires (Harris, 1958b). As in modern continents at about this latitude and orientation, climate was probably monsoonal and winter dry (Hallam, 1975).

DISCUSSION

The reconstructions given here range from vines to stately forest trees, from plants of intertidal swamps to those of well-drained soils in locations ranging from the tropics to the high latitudes. These extinct broadleaf plants appear to have occupied many niches. In the face of such diversity it is difficult to characterize seed ferns. Certainly, they were not merely small swampland shrubs. They were a prominent component of much late Paleozoic and Mesozoic vegetation.

The seed ferns reconstructed here, representing well-understood examples of these plants, have a few features in common. They are all characterized by fernlike leaves, ovule-bearing structures which are leaflike or adnate to leaves, and gymnospermous anatomy, more or less as originally envisaged by Potonié (1899) and Oliver & Scott (1904) in proposing the terms "cycadofilicales" and "pteridosperms." However, we think it unlikely that they form a natural group or clade, because the same features distinguish other groups of plants, such as cycads. The earliest gymnosperms were probably seed ferns (Rothwell, 1982, 1986). Cycads, cycadeoids, pentoxylans, ginkgoes, czekanowskians, cordaites, conifers, and other gymnosperms all probably were derived from seed ferns (Meyen, 1984). Seed ferns were thus central to the evolutionary radiation of seed plants, and in this sense represent a grade of evolution embracing the evolutionary roots of these various other gymnosperms.

The phylogenetic relationships of gymnosperms can be expected to become clearer as lineages of seed ferns are better understood. Phylogenetic inference is beyond the scope of this article, but we

point out two quite different groups of seed ferns to underscore the artificiality of seed ferns as a taxon. The plants with fernlike prepollen (*Stamnostoma huttonense, Lyrasperma scotica, Calathospermum fimbriatum, Lagenostoma lomaxii,* and *Pachytesta illinoensis*) were different in many ways from those with true pollen (*Callospermarion pusillum, Dictyopteridium sporiferum, Peltaspermum thomasii, Umkomasia granulata,* and *Caytonia nathorstii*). The group with fernlike prepollen was similar in many ways to modern cycads, whereas the others were more like conifers. The second group includes both Paleozoic and Mesozoic plants, some of which show a number of important biological similarities (Reymanowna, 1974). The supposed morphological gap between Mesozoic and Paleozoic seed ferns, apparent in many general discussions of these plants, may be seen as a study bias. It arose from the varied experience of different investigators of these plants and from quite distinctive styles of preservation and geological settings for Paleozoic and Mesozoic plants, rather than from the plants themselves.

A variety of seed ferns have been considered as possible ancestors of angiosperms: especially forms allied to the plants here reconstructed as *Stamnostoma huttonense* (Long, 1966, 1977b), *Dictyopteridium sporiferum* (Retallack & Dilcher, 1981), and *Caytonia nathorstii* (Doyle, 1978). Another gymnospermous group thought to be ancestral to angiosperms, the cycadeoids (Arber & Parkin, 1907) were probably also derived from seed ferns. The origin of angiosperms is still a puzzle, for which more detailed understanding of seed ferns is needed.

In our role as arbitrators of conflicting views on the nature of the plants reconstructed here, we have become aware of the ease with which mistakes can be made. We do not imagine that our reconstructions will be the last word (or image) for these plants, and hope that they will serve as hypotheses that stimulate as well as instruct.

LITERATURE CITED

ANDERSON, J. M. & H. M. ANDERSON. 1983. Palaeoflora of Southern Africa. Molteno Formation (Triassic), Volume 1, Part 1. Introduction. Part 2. *Dicroidium.* A. A. Balkema, Rotterdam.
———— & ————. 1985. Palaeoflora of Southern Africa. Prodromus of South African Floras, Devonian to Lower Cretaceous. A. A. Balkema, Rotterdam.
———— & R. U. SCHWYZER. 1977. The biostratigraphy of the Permian and Triassic. Part 4. Palaeomagnetic evidence for large-scale intra-Gondwanan plate movements during the Carboniferous to Jurassic. Trans. Geol. Soc. S. Africa 80: 211–234.
ANDERTON, R., P. H. BRIDGES, M. P. LEEDER & B. W. SELLWOOD. 1979. A Dynamic Stratigraphy of the British Isles. Allen & Unwin, London.
ANDREWS, H. N. 1948. Some evolutionary trends in the pteridosperms. Bot. Gaz. (Crawfordsville) 110: 13–31.
ARBER, E. A. N. & J. PARKIN. 1907. On the origin of angiosperms. J. Linn. Soc., Bot. 38: 29–80.
ARCHANGELSKY, S. 1968. Studies on Triassic fossil plants from Argentina. IV. The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. Palaeontology 11: 500–512.
———— & D. W. BRETT. 1961. Studies on Triassic fossil plants from Argentina. I. *Rhexoxylon* from the Ischigualasto Formation. Philos. Trans. B244: 1–19.
BALME, B. E. & G. PLAYFORD. 1967. Late Permian plant microfossils from the Prince Charles Mountains, Antarctica. Rev. Micropaléont. 10: 179–192.
BAMBACH, R., C. R. SCOTESE & A. M. ZIEGLER. 1980. Before Pangaea: the geographies of the Paleozoic world. Amer. Sci. 68: 26–38.
BARNARD, P. D. W. 1960. *Calathospermum fimbriatum* sp. nov., a Lower Carboniferous pteridosperm cupule from Scotland. Palaeontology 3: 265–275.
———— & A. G. LONG. 1973. On the structure of a petrified stem and some associated seeds from the Lower Carboniferous rocks of East Lothian, Scotland. Trans. Roy. Soc. Edinburgh 69: 91–108.
———— & ————. 1975. *Triradioxylon*—a new genus of Lower Carboniferous petrified stems and petioles together with a review of the classification of early Pterophytina. Trans. Roy. Soc. Edinburgh 69: 231–249.
BARTHEL, M. 1962. Epidermis-Untersuchungen an einigen inkohlten Pteridospermenblättern des Oberkarbons und Perms. Beih. Geologie 33: 1–140.
BASINGER, J. F., G. W. ROTHWELL & W. N. STEWART. 1974. Cauline vasculature and leaf production in medullosan pteridosperms. Amer. J. Bot. 61: 1002–1015.
BAXTER, R. W. & M. R. WILLHITE. 1969. The morphology and anatomy of *Alethopteris lesquereuxii* Wagner. Univ. Kansas Sci. Bull. 48: 767–783.
BECK, C. B. 1971. Problems of generic delimitation in paleobotany. Proc. N. Amer. Paleontol. Conv. 1: 173–193.
————. 1981. *Archaeopteris* and its role in vascular plant evolution. Pp. 193–230 *in* K. J. Niklas (editor), Paleobotany, Paleoecology and Evolution. Praeger, New York.
BENSON, M. 1904. *Telangium scottii*, a new species of *Telangium* (*Calymmatotheca*) showing structure. Ann. Bot. (London) 18: 161–177.
BIRKELAND, P. W. 1984. Soils and Geomorphology. Oxford Univ. Press, New York.
BLACK, M. 1929. Drifted plant beds of the Upper Estuarine Series of Yorkshire. Quart. J. Geol. Soc. London 85: 389–437.
BLANC-LOUVEL, C. 1966. Étude anatomique comparée des tiges et des pétioles d'une Pteridospermée du Carbonifère du genre *Lyginopteris* Potonié. Mém. Mus. Natl. Hist. Nat. Ser., Sect. C, Sciences Terre 18: 1–103.
BRIDEN, J. C., G. E. DREWRY & A. G. SMITH. 1974. Phanerozoic equal-area world maps. J. Geol. 82: 555–574.
BRONGNIART, A. 1828. Histoire des Vegetaux Fossiles. Dufour & D'Ocagne, Paris.

CALDER, M. G. 1938. On some undescribed species from the Lower Carboniferous flora of Berwickshire, together with a note on the genus *Stenomyelon* Kidston. Trans. Roy. Soc. Edinburgh 59: 309–331.

CAMP, W. H. & M. M. HUBBARD. 1963. On the origins of the ovule and cupule in lyginopterid pteridosperms. Amer. J. Bot. 50: 235–243.

CARLQUIST, S. 1975. Ecological Strategies of Xylem Evolution. Univ. California Press, Berkeley, California.

CARPENTER, F. M. 1964. Studies on North American Carboniferous insects. 3. A spilapterid from the vicinity of Mazon Creek, Illinois (Palaeodictyoptera). Psyche 71: 117–124.

CHALONER, W. G. 1976. The evolution of adaptive features in fossil exines. Pp. 1–14 *in* I. K. Ferguson & J. Muller (editors), The Evolutionary Significance of the Exine. Academic Press, London.

CHAMBERLAIN, C. J. 1935. Gymnosperms. Univ. Chicago Press, Chicago, Illinois.

CHANDRA, S. & K. R. SURANGE. 1976. Cuticular studies of the reproductive organs of *Glossopteris*, Part II. *Cistella*-type fructification *Plumsteadiostrobus elliptica* gen. et sp. nov., attached on *Glossopteris taenioides* Feistmantel. Palaeobotanist 23: 161–174.

CHAZDON, R. L. 1978. Ecological aspects of the distribution of C_4 grasses in selected habitats of Costa Rica. Biotropica 10: 265–269.

CLARKSON, E. N. K. 1985. Palaeoecology of the Dinantian of Foulden, Berwickshire, Scotland. Trans. Roy. Soc. Edinburgh Earth Sci. 76: 97–100.

CLAYTON, G. 1985. Plant miospores from the Dinantian of Foulden, Berwickshire, Scotland. Trans. Roy. Soc. Edinburgh Earth Sci. 76: 21–24.

CLEMENS, W. A., J. A. LILLEGRAVEN, E. H. LINDSAY & G. G. SIMPSON. 1979. When, where and what— a survey of known Mesozoic mammal distribution. Pp. 7–58 *in* J. A. Lillegraven, Z. Kielan-Jaworowska & W. A. Clemens (editors), The First Two Thirds of Mammalian History. Univ. California Press, Berkeley, California.

COOKSON, I. C. 1947. Plant microfossils from the lignite of the Kerguelen Archipelago. Rep. British, Australian & New Zealand Antarctic Research Expedition (1929–1931) A2: 129–142.

CORSIN, P. 1928. Sur les fructifications et la position systématique de *Sphenopteris zamioides* P. Bertr. Ann. Soc. Géol. du N. 53: 222–229.

CRAIG, G. Y. 1975. Siccar Point, Cove, Catcraig. Pp. 107–177 *in* G. Y. Craig & P. McL. D. Duff (editors), The Geology of the Lothians and Southeast Scotland. Scottish Academic Press, Edinburgh.

CREBER, G. T. & W. G. CHALONER. 1984. Influence of environmental factors on the wood structure of living and fossil trees. Bot. Rev. (Lancaster) 50: 357–448.

CROOKALL, R. 1959. Fossil plants of the Carboniferous rocks of Great Britain. Mem. Geol. Surv. Great Britain, Palaeontol. 4: 85–216.

DARRAH, W. C. 1939. Principles of Paleobotany. Chronica Botanica, Leiden, Netherlands.

DAVID, T. W. E. 1907. Geology of the Hunter River Coal Measures, N.S.W. Mem. Geol. Surv. N. S. W., Geol. 4: 1–372.

DAWSON, J. W. 1860. On an undescribed fossil fern from the lower Coal Measures of Novia Scotia. Canad. Naturalist 5: 460–461.

DE JERSEY, N. J. 1962. Triassic spores and pollen grains from the Ipswich Coalfield. Publs. Geological Survey Queensland 307: 1–18.

DELEVORYAS, T. & J. MORGAN. 1954. A new pteridosperm from the upper Pennsylvanian deposits of North America. Palaeontographica B96: 12–23.

——— & C. P. PERSON. 1975. *Mexiglossa varia* gen. et sp. nov., a new genus of glossopterid leaves from the Jurassic of Mexico. Palaeontographica, Abt. B, Paläophytol. B154: 114–120.

——— & T. N. TAYLOR. 1969. A probable pteridosperm with eremopteroid foliage from the Allegheny Group of northern Pennsylvania. Postilla 133: 1–14.

DILCHER, D. L. 1979. Early angiosperm reproduction: an introductory report. Ann. Rev. Palaeobot. Palynol. 27: 291–328.

DINGLE, R. V., W. G. SESSER & A. R. NEWTON. 1983. Mesozoic and Tertiary Geology of Southern Africa. A. A. Balkema, Rotterdam.

DOYLE, J. 1945. Developmental lines in pollination mechanisms in the Coniferales. Sci. Proc. Roy. Dublin Soc. 24: 43–62.

——— & M. O'LEARY. 1935a. Pollination in *Saxegothaea*. Sci. Proc. Roy. Dublin Soc. 21: 175–179.

——— & ———. 1935b. Pollination in *Pinus*. Sci. Proc. Roy. Dublin Soc. 21: 181–190.

——— & ———. 1935c. Pollination in *Tsuga, Cedrus, Pseudotsuga* and *Larix*. Sci. Proc. Roy. Dublin Soc. 21: 191–204.

DOYLE, J. A. 1978. Origin of angiosperms. Ann. Rev. Ecol. Syst. 9: 365–392.

——— & M. J. DONOGHUE. 1986. Seed plant phylogeny and origin of angiosperms: an experimental cladistic approach. Bot. Rev. (Lancaster) 52: 321–431.

DU TOIT, A. L. 1927. The fossil flora of the upper Karroo Beds. Ann. S. African Mus. 22: 289–420.

——— (edited by S. H. Haughton). 1954. The Geology of South Africa. Oliver & Boyd, Edinburgh.

EGGERT, D. A. & T. DELEVORYAS. 1960. *Callospermarion*—a new seed genus from the upper Pennsylvanian of Illinois. Phytomorphology 10: 131–138.

——— & M. A. MILLAY. 1976. Reproduction (plant). McGraw-Hill Yearb. Sci. Technol. 15: 350–353.

ESAU, K. 1977. Anatomy of Seed Plants. Wiley, New York.

FAEGRI, K. & L. VAN DER PIJL. 1966. Principles of Pollination Biology. Pergamon, Oxford.

FEISTMANTEL, O. 1876. On some fossil plants from the Damuda Series in the Raniganj Coalfield collected by Mr. J. Wood-Mason. J. & Proc. Asiat. Soc. Bengal 45: 329–382.

———. 1881. The fossil flora of the Gondwana System, Part 2. The flora of the Damuda and Panchet Divisions. Mem. Geol. Surv. India, Palaeontol. Indica 12: 78–149.

FOSTER, C. B. 1975. Permian plant microfossils from the Blair Athol Coal Measures, central Queensland, Australia. Palaeontographica, Abt. B, Paläophytol. B154: 121–171.

FRANCIS, E. H. 1983. Carboniferous–Permian igneous activity. Pp. 297–324 *in* G. Y. Craig (editor), Geology of Scotland. Wiley, New York.

GORDON, W. T. 1935. The genus *Pitus* Witham emend. Trans. Roy. Soc. Edinburgh 58: 279–311.

———. 1941. On *Salpingostoma dasu*: a new Carboniferous seed from East Lothian. Trans. Roy. Soc. Edinburgh 60: 427–464.

GOTHAN, W. 1912. Über die Gattung *Thinnfeldia* Ettingshausen. Abh. Naturhist. Ges. Nürnberg 19: 67–80.

GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of the Humaita, Amazonia. Biotropica 10: 170–183.

GOULD, R. E. 1970. *Palaeosmunda*, a new genus of siphonostelic osmundaceous trunks from the Upper Permian of Queensland. Palaeontology 13: 10–28.

———. 1975. A preliminary report on petrified axes of *Vertebraria* from the Permian of eastern Australia. Pp. 109–123 *in* K. S. W. Campbell (editor), Gondwana Geology. Australian National Univ., Canberra.

——— & T. DELEVORYAS. 1977. The biology of *Glossopteris*: evidence from petrified seed-bearing and pollen-bearing organs. Alcheringa 1: 387–399.

GRAND'EURY, C. 1905. Sur les graines trouvées attachées au *Pecopteris Pluckeneti* Schl. Compt. Rend. Hebd. Séances Acad. Sci. 140: 920–923.

GRIME, J. P. 1979. Plant Strategies and Vegetation Processes. Wiley, New York.

HALL, J. W. & B. M. STIDD. 1971. Ontogeny of *Vesicaspora*, a late Pennsylvanian pollen grain. Palaeontology 14: 431–436.

HALLAM, A. 1975. Jurassic Environments. Cambridge Univ. Press, Cambridge.

HALLÉ, F., R. A. A. OLDEMAN & P. B. TOMLINSON. 1978. Tropical Trees and Forests. Springer, Berlin.

HALLE, T. G. 1929. Some seed-bearing pteridosperms from the Permian of China. Konigl. Svenska Vetenskapsakad. Handl. 6: 1–24.

HARRIS, T. M. 1933. A new member of the Caytoniales. New Phytol. 32: 97–114.

———. 1937. The fossil flora of Scoresby Sound, East Greenland, Part 5. Stratigraphical relation of the plant beds. Meddel. Grønland 112(2): 1–114.

———. 1940. *Caytonia*. Ann. Bot. (London) 4: 713–734.

———. 1941. *Caytonanthus*, the microsporophyll of *Caytonia*. Ann. Bot. (London) 5: 47–58.

———. 1943. Notes on the Jurassic flora of Yorkshire, 9. Ann. Mag. Nat. Hist. 10: 850–852.

———. 1951. The relationships of the Caytoniales. Phytomorphology 1: 29–39.

———. 1958a. The seed of *Caytonia*. Palaeobotanist 7: 93–106.

———. 1958b. Forest fire in the Mesozoic. J. Ecol. 46: 447–453.

———. 1961. The Yorkshire Jurassic Flora. I. Thallophyta–Pteridophyta. British Museum Natural History, London.

———. 1964. The Yorkshire Jurassic Flora. II. Caytoniales, Cycadales and Pteridosperms. British Museum Natural History, London.

———. 1969. The Yorkshire Jurassic Flora. III. Bennettitales. British Museum Natural History, London.

———. 1971. The stem of *Caytonia*. Geophytology 1: 23–29.

———. 1979. The Yorkshire Jurassic Flora. V. Coniferales. British Museum Natural History, London.

———, W. MILLINGTON & J. MILLER. 1974. The Yorkshire Jurassic Flora. IV. Ginkgoales and Czekanowskiales. British Museum Natural History, London.

HATCH, F. H. & G. S. CORSTORPHINE. 1909. The Geology of South Africa. Macmillan, London.

HECKEL, P. H. 1977. Origin of phosphatic black shale facies in Pennsylvanian cyclothems of mid-continental North America. Bull. Amer. Assoc. Petrol. Geol. 61: 1045–1068.

HEINRICH, B. 1976. Flowering phenologies: bog, woodland and disturbed habitats. Ecology 57: 890–899.

HERBERT, C. 1980. Evidence for glaciation in the Sydney Basin and Tamworth Synclinorial zone. Bull. Geol. Surv. N. S. W. 26: 274–293.

HOLDEN, R. 1917. On the anatomy of two Paleozoic stems from India. Ann. Bot. (London) 31: 315–326.

HOLMES, W. B. K. 1974. On some fructifications of the Glossopteridales from the upper Permian of N. S. W. Proc. Linn. Soc. N. S. W. 98: 131–141.

———. 1987. New corystosperm ovulate fructifications from the Middle Triassic of eastern Australia. Alcheringa 11: 165–173.

HUGHES, N. F. 1976. Palaeobiology of Angiosperm Origins. Cambridge Univ. Press, Cambridge.

ISBELL, R. F. 1955. The geology of the northern section of the Bowen Basin. Pap. Univ. Queensland, Dept. Geol. 4(11): 1–43.

JANZEN, D. H. 1978. Seeding patterns in tropical trees. Pp. 83–128 *in* P. B. Tomlinson & M. H. Zimmerman (editors), Tropical Trees as Living Systems. Cambridge Univ. Press, Cambridge.

JENIK, J. 1978. Roots and root systems in tropical trees: morphologic and ecologic aspects. Pp. 323–349 *in* P. B. Tomlinson & M. H. Zimmerman (editors), Tropical Trees as Living Systems. Cambridge Univ. Press, Cambridge.

JENNINGS, J. R. 1974. Lower Pennsylvanian plants of Illinois. I. A flora from the Pounds Sandstone Member of the Caseyville Formation. J. Paleontol. 48: 459–473.

JENSEN, A. R. 1975. Permo-Triassic stratigraphy and sedimentation in the Bowen Basin, Queensland. Bull. Bur. Mineral Resources, Geol. & Geophys., Canberra 154: 1–187.

JIZBA, K. M. M. 1962. Late Paleozoic bisaccate pollen from the United States mid-continent area. J. Paleontol. 36: 871–887.

JONGMANS, W. J. 1952. The female fructification of *Sphenopteris hoeningshausii* and the supposed relation of this species with *Crossotheca*. Paleobotanist 1: 267–274.

KAWASE, M. & R. E. WHITMOYER. 1980. Aerenchyma development in waterlogged plants. Amer. J. Bot. 67: 18–22.

KENT, P. 1980. Eastern England from the Tees to the Wash. Institute Geological Sciences, London.

KIDSTON, R. 1887. On the fructifications of some ferns from the Carboniferous formations. Trans. Roy. Soc. Edinburgh 33: 137–156.

———. 1902. The flora of the Carboniferous period, Part II. Proc. Yorkshire Geol. Soc. 14: 344–399.

———. 1905. Preliminary note on the occurrence of microsporangia in organic connection with the foliage of *Lyginodendron*. Proc. Roy. Soc. London 76: 358–360.

———. 1906. On the microsporangia of the Pteridospermeae, with remarks on their relationship to existing groups. Philos. Trans., Ser. B 198: 413–446.

———. 1923. Fossil plants of the Carboniferous rocks of Great Britain. Mem. Geol. Surv. Great Britain, Palaeontol. 2(1–3): 1–276.

———. 1924. Fossil plants of the Carboniferous rocks

of Great Britain. Mem. Geol. Surv. Great Britain,
Palaeontol. 2(5): 379–522.

KNOLL, A. H. & E. S. BARGHOORN. 1975. Precambrian
eukaryotic organisms: a reassessment of the evi-
dence. Science 190: 52–54.

KRASSILOV, V. A. 1977. Contributions to the knowledge
of the Caytoniales. Rev. Palaeobot. Palynol. 24: 155–
178.

KUKALOVA, J. 1970. Revisional study of the order Pa-
laeodictyoptera in the Upper Carboniferous shales of
Commentry, France, Part III. Psyche 77: 1–44.

LONG, A. G. 1960a. Stamnostoma huttonense gen. et
sp. nov.—a pteridosperm seed and cupule from the
Calciferous Sandstone Series of Berwickshire. Trans.
Roy. Soc. Edinburgh 64: 201–215.

————. 1960b. On the structure of Samaropsis sco-
tica (Calder) emended and Eurystoma angulare gen.
et sp. nov., petrified seeds from the Calciferous Sand-
stone Series of Berwickshire. Trans. Roy. Soc. Edin-
burgh 64: 261–280.

————. 1962. "Tristichia ovensi" gen. et sp. nov.,
a protostelic Lower Carboniferous pteridosperm from
Berwickshire and East Lothian, with an account of
some associated seeds and cupules. Trans. Roy. Soc.
Edinburgh 64: 478–492.

————. 1963. On some specimens of Lyginorachis
papilio Kidston associated with stems of Pitys. Trans.
Roy. Soc. Edinburgh 65: 211–224.

————. 1964. Some specimens of Stenomyelon and
Kalymma from the Calciferous Sandstone Series of
Berwickshire. Trans. Roy. Soc. Edinburgh 65: 435–
447.

————. 1965. On the cupule structure of Eurystoma
angulare. Trans. Roy. Soc. Edinburgh 66: 111–
128.

————. 1966. Some Lower Carboniferous fructifica-
tions from Berwickshire, together with a theoretical
account of the evolution of ovules, cupules and car-
pels. Trans. Roy. Soc. Edinburgh 66: 345–375.

————. 1969. Eurystoma trigona sp. nov., pterido-
sperm ovules borne on a frond of Alcicornopteris
Kidston. Trans. Roy. Soc. Edinburgh 68: 171–182.

————. 1975. Further observations on some Lower
Carboniferous seeds and cupules. Trans. Roy. Soc.
Edinburgh 69: 267–293.

————. 1976. Calathopteris heterophylla gen. et sp.
nov., a Lower Carboniferous pteridosperm bearing
two kinds of petioles. Trans. Roy. Soc. Edinburgh
69: 327–336.

————. 1977a. Some Lower Carboniferous pterido-
sperm cupules bearing ovules and microsporangia.
Trans. Roy. Soc. Edinburgh 70: 1–11.

————. 1977b. Lower Carboniferous pteridosperm cu-
pules and the origin of angiosperms. Trans. Roy. Soc.
Edinburgh 70: 13–35.

————. 1979a. Observations on the Lower Carbon-
iferous genus Pitus Witham. Trans. Roy. Soc. Edin-
burgh 70: 111–127.

————. 1979b. The resemblance between the Lower
Carboniferous cupules of Hydrasperma cf. tenuis
Long and Sphenopteris bifida Lindley and Hutton.
Trans. Roy. Soc. Edinburgh 70: 129–137.

LOUBIÈRE, A. 1929. Étude anatomique et comparée du
Leptotesta grand'euryi n. gen., n. sp., graine sili-
cifée du Pecopteris pluckeneti Schlot. Revue Gen-
erale Bot. 41: 593–605.

McCOY, F. 1847. On the fossil botany and zoology of

the rocks associated with the coal of Australia. Ann.
Mag. Nat. Hist. 20: 145–157.

McDONNELL, K. L. 1974. Depositional environments
of the Triassic, Gosford Formation, Sydney Basin. J.
Geol. Soc. Australia 21: 107–132.

MACGREGOR, A. R. 1968. Fife and Angus Geology.
Blackwood, Edinburgh.

MAHESHWARI, H. K. 1965. Studies on the Glossopteris
flora of India. 23. On two fructifications from the
Raniganj Stage of the Raniganj Coalfield, Bengal.
Palaeobotanist 13: 144–147.

————. 1972. Permian wood from Antarctica and
revision of some Lower Gondwana wood taxa. Pa-
laeontographica, Abt. B, Paläophytol. B138: 1–43.

MATTEN, L. C., W. S. LACEY & R. C. LUCAS. 1980.
Studies on the cupulate seed genus Hydrasperma
Long, from Berwickshire and East Lothian in Scot-
land and County Kerry in Ireland. Biol. J. Linn. Soc.
London 81: 249–273.

MEYEN, S. V. 1984. Basic features of gymnosperm
systematics and phylogeny as evidenced by the fossil
record. Bot. Rev. (Lancaster) 50: 1–111.

MICKLE, J. E. & G. W. ROTHWELL. 1982. Perminer-
alized Alethopteris from the Upper Pennsylvanian
of Ohio and Illinois. J. Paleontol. 56: 392–402.

MILLAY, M. A. & D. A. EGGERT. 1974. Microgame-
tophyte development in the Paleozoic seed fern family
Callistophytaceae. Amer. J. Bot. 61: 1064–1075.

———— & T. N. TAYLOR. 1974. Morphological studies
of Paleozoic saccate pollen. Palaeontographica, Abt.
B, Paläophytol. B147: 75–99.

MOODIE, R. L. 1916. Coal measures amphibia of North
America. Publ. Carnegie Inst. Wash. 238: 1–222.

NAMI, M. 1976. An exhumed Jurassic meander belt
from Yorkshire, England. Geol. Mag. 113: 47–52.

NEVES, R., K. J. GUEINN, G. CLAYTON, N. S. IOANNIDES,
R. S. W. NEVILLE & K. KRUSZEWSKA. 1973. Paly-
nological correlations within the Lower Carboniferous
of Scotland and northern England. Trans. Roy. Soc.
Edinburgh 69: 23–70.

NIKLAS, K. J. 1981. Simulated wind pollination and
airflow around ovules of some early seed plants. Sci-
ence 211: 275–277.

NILSSON, T. 1958. Über das Vorkommen eines meso-
zoischen Sapropelgesteins in Schonen. Acta Univ.
Lunds 54: 1–112.

OESTRY-STIDD, L. L. & B. M. STIDD. 1976. Paracytic
(syndetocheilic) stomata in Carboniferous seed ferns.
Science 193: 156–157.

OLIVER, F. W. & D. H. SCOTT. 1903. On Lagenostoma
lomaxi, the seed of Lyginodendron. Proc. Roy. Soc.
London B71: 477–481.

———— & ————. 1904. On the structure of the
Palaeozoic seed Lagenostoma lomaxi, with a state-
ment of the evidence upon which it is referred to
Lyginodendron. Philos. Trans. B197: 193–247.

PALMER, A. R. 1983. The Decade of North American
Geology, 1983 geologic time scale. Geology 11: 503–
504.

PANT, D. D. & K. L. GUPTA. 1968. Cuticular structure
of some Indian Lower Gondwana species of Glossop-
teris Brongniart, Part I. Palaeontographica, Abt. B,
Paläophytol. B124: 45–81.

———— & D. NAUTIYAL. 1960. Some seeds and spo-
rangia of the Glossopteris flora from Raniganj Coal-
field, India. Palaeontographica, Abt. B, Paläophytol.
B107: 42–64.

STANLEY, S. M. 1985. Earth and Life Through Time. Freeman, San Francisco.

STEIDTMANN, W. E. 1944. The anatomy and affinities of *Medullosa noei* Steidtmann and associated foliage, roots and seeds. Contr. Mus. Paleontol. Univ. Michigan 6: 131–166.

STERNBERG, G. K. 1838. Pp. 81–220 *in* Versuch einer geognostischen botanischen Darstellung der Flora der Vorwelt. Tentamen, Leipzig.

STERZEL, J. T. 1881. Paläontologischer Charakter der oberen Steinkohlenformation und des Rotliegenden in ergebirgischen Becken. Naturwiss. Ges. Chemnitz Ber. 7: 155–170.

STEWART, W. N. 1954. The structure and affinities of *Pachytesta illinoense* comb. nov. Amer. J. Bot. 41: 500–508.

———. 1983. Paleobotany and the Evolution of Plants. Cambridge Univ. Press, Cambridge.

——— & T. DELEVORYAS. 1956. The medullosan pteridosperms. Bot. Rev. (Lancaster) 22: 45–80.

STIDD, B. M. 1981. Current status of medullosan seed ferns. Rev. Palaeobot. Palynol. 32: 63–101.

——— & J. W. HALL. 1970a. *Callandrium callistophytoides*, gen. et sp. nov. The probable pollen-bearing organ of the seed fern *Callistophyton*. Amer. J. Bot. 57: 394–403.

——— & ———. 1970b. The natural affinity of the Carboniferous seed *Callospermarion*. Amer. J. Bot. 57: 827–836.

STOPES, M. C. & D. M. S. WATSON. 1909. On the present distribution and origin of the calcareous concretions in coal seams, known as coal balls. Philos. Trans. B200: 167–218.

STUR, D. R. J. 1877. Die Culm-Flora der Ostrauer und Waldenburger Schichten. Kgl. K. Geol. Reichsanst. Abh. 8: 1–366.

SURANGE, K. R. & S. CHANDRA. 1975. Morphology of gymnospermous fructifications of the *Glossopteris* flora and their relationships. Palaeontographica, Abt. B, Paläophyt. B149: 152–180.

——— & H. K. MAHESHWARI. 1970. Some male and female fructifications of Glossopteridales from India. Palaeontographica, Abt. B, Paläophyt. B129: 178–191.

TAYLOR, T. N. 1965. Paleozoic seed studies: a monograph of the American species of *Pachytesta*. Palaeontographica, Abt. B, Paläophyt. B117: 1–46.

———. 1978. The ultrastructure and significance of *Monoletes* (Pteridospermales) pollen. Canad. J. Bot. 56: 3105–3118.

———. 1981. Paleobotany. McGraw-Hill, New York.

———. 1982. Ultrastructural studies of Paleozoic seed fern pollen: sporoderm development. Rev. Palaeobot. Palynol. 37: 29–53.

——— & M. A. MILLAY. 1977. Structurally preserved fossil cell contents. Trans. Amer. Microscop. Soc. 96: 390–393.

———, M. A. CICHAN & A. M. BALDONI. 1984. The ultrastructure of Mesozoic pollen: *Pteruchus dubius* (Thomas) Townrow. Rev. Palaeobot. Palynol. 41: 319–327.

THOMAS, H. H. 1925. The Caytoniales, a new group of angiospermous plants from Jurassic rocks of Yorkshire. Philos. Trans. B213: 299–363.

———. 1933. On some pteridospermous plants from the Mesozoic of South Africa. Philos. Trans. B222: 193–265.

———. 1934. The nature and origin of the stigma. New Phytol. 33: 173–198.

———. 1952. A *Glossopteris* with whorled leaves. Palaeobotanist 1: 435–438.

——— & M. N. BOSE. 1955. *Pachydermophyllum papillosum* gen. et sp. nov., from the Yorkshire Jurassic. Ann. Mag. Nat. Hist. 12: 535–543.

TONKS, L. H., R. C. B. JONES, W. LLOYD & R. L. SHERLOCK. 1931. The geology of Manchester and the southeast Lancashire Coalfield. Mem. Geol. Surv. England & Wales, Explanation of Sheet 85: 1–240.

TOWNROW, J. A. 1956. The genus *Lepidopteris* and its southern hemisphere species. Avh. Norske Vidensk.-Akad., Mat.-Naturvidensk. Kl. 1: 1–28.

———. 1960. The Peltaspermaceae, a pteridosperm family of Permian and Triassic age. Palaeontology 3: 333–361.

———. 1962a. On *Pteruchus*, the microsporophyll of the Corystospermaceae. Bull. Brit. Mus. (Nat. Hist.), Geol. 6: 285–316.

———. 1962b. On the nomenclature of *Pteruchus johnstoni* (Feistmantel) comb. nov. Pap. & Proc. Roy. Soc. Tasmania 98: 113–118.

———. 1962c. On some disaccate pollen grains of Permian to Middle Jurassic age. Grana Palynol. 3: 13–44.

TURNER, B. R. 1978. Palaeohydraulics of clast transport during deposition of the Upper Triassic Molteno Formation in the main Karroo Basin of South Africa. S. African J. Sci. 74: 171–173.

VAN AMEROM, H. W. J. 1968. Die Eusphenopteridischen Pteridophyllen aus der Sammlung des Geologischen Bureaus in Heerlen, unter besonder Berücksichtigung ihrer Stratigraphie bezuglich des Sudlinberger Kohlenreviers. Meded. Rijks Geol. Dienst C3-1(7): 1–208.

VAN DER PIJL, L. 1972. Principles of Dispersal in Higher Plants. Springer, Berlin.

VAN DER ZWAN, L. J., M. C. BOULTER & R. N. L. B. HUBBARD. 1985. Climatic change during the Lower Carboniferous in Euramerica, based on multivariate statistical analysis of palynological data. Palaeogeogr. Palaeoclimatol. Palaeoecol. 52: 1–20.

VAN KONIJNENBURG-VAN CITTERT, H. H. A. 1971. In situ gymnosperm pollen from the Middle Jurassic of Yorkshire. Acta Bot. Neerl. 20: 1–96.

WAGNER, R. H. 1964. Stephanian flora in NW Spain, with special reference to the Westphalian D-Stephanian A boundary. Compt. Rend. 5° Congr. Carbonifère Paris 2: 835–851.

———. 1968. Upper Westphalian and Stephanian species of *Alethopteris* from Europe, Asia Minor and North America. Meded. Rijks Geol. Dienst C3-1(6): 1–318.

WALKOM, A. B. 1922. Palaeozoic floras of Queensland. Part I. The flora of the Lower and Upper Bowen Series. Publ. Queensland Geol. Surv. 270: 1–45.

WALTON, J. 1923. On *Rhexoxylon* Bancroft—a Triassic genus of plants exhibiting liane-type of vascular organization. Philos. Trans. B212: 79–109.

———. 1926. Contributions to the knowledge of Lower Carboniferous plants. Philos. Trans. B215: 201–224.

———. 1931. Contributions to the knowledge of the Lower Carboniferous plants (cont'd). III. On the fossil flora of the Black Limestones in Teilia Quarry, Gwaenysgor, near Prestatyn, Flintshire, with special

reference to *Diplopteridium teilianum* Kidston sp. (gen. nov.) and some other fern-like fronds. Philos. Trans. B219: 347–379.

———. 1964. The pteridosperms. Trans. Bot. Soc. Edinburgh 39: 449–459.

WHITE, E. I. 1927. The fish fauna of the Cementstones of Foulden, Berwickshire. Trans. Roy. Soc. Edinburgh 55: 255–287.

WHITE, M. E. 1964. Reproductive structures in Australian Upper Permian Glossopteridae. Proc. Linn. Soc. N. S. W. 88: 386–391.

———. 1978. Reproductive structures of the Glossopteridales in the plant fossil collection of the Australian Museum. Rec. Austral. Mus. 31: 473–505.

WHITEHEAD, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. Evolution 23: 28–35.

WILLIAMSON, W. C. 1874. On the organization of the fossil plants of the Coal Measures—Part 6, Ferns. Philos. Trans. 164: 675–703.

———. 1875. On the organization of fossil plants of the Coal Measures—Part 7. *Myelopteris, Psaronius* and *Kaloxylon*. Proc. Roy. Soc. London 23: 69–73.

WILSON, V. 1948. East Yorkshire and Lincolnshire. British Geological Survey & Museum, London.

WITHAM, H. T. M. 1833. The Internal Structure of Fossil Vegetables Found in the Carboniferous and Oolitic Deposits of Great Britain. Adam & Charles Black, Edinburgh.

WNUK, C. & H. W. PFEFFERKORN. 1984. The life habits and paleoecology of Middle Pennsylvanian medullosan pteridosperms based on an in situ assemblage from the Bernice Basin (Sullivan County, Pennsylvania, U.S.A.). Rev. Palaeobot. Palynol. 41: 329–351.

WODEHOUSE, R. P. 1935. Pollen Grains. McGraw-Hill, New York.

WOOD, S. P. & W. D. I. ROLFE. 1985. Introduction to the palaeontology of the Dinantian of Foulden, Berwickshire, Scotland. Trans. Roy. Soc. Edinburgh Earth Sci. 76: 1–6.

ZANGERL, R. & G. R. CASE. 1973. Iniopterygia, a new order of Chondrichthyan fishes from the Pennsylvanian of North America. Fieldiana Geol. Mem. 6: 1–67.

——— & E. S. RICHARDSON. 1963. The paleoecological history of two Pennsylvanian black shales. Fieldiana Geol. Mem. 4: 1–346.

ZIEGLER, A. M., C. R. SCOTESE, W. S. MCKERROW, M. E. JOHNSON & R. K. BAMBACH. 1979. Paleozoic Paleogeography. Ann. Rev. Earth Science 7: 473–502.

ZODROW, E. L. & K. MCCANDLISH. 1980. On a *Trigonocarpus* species attached to *Neuropteris (Mixoneura) flexuosa* from the Sydney Coalfield, Cape Breton Island, Nova Scotia, Canada. Rev. Palaeobot. Palynol. 30: 57–66.