PERMINERALIZED OVULATE CONES OF *LEBACHIA* FROM LATE PALAEOZOIC LIMESTONES OF KANSAS

by G. MAPES *and* G. W. ROTHWELL

ABSTRACT. A diverse assemblage of permineralized conifer remains has been discovered in late Palaeozoic limestones from the mid-continent of North America, near Hamilton, Kansas. Ovulate cones described as *Lebachia lockardii* sp. nov., support the structural homologies among cordaites, primitive conifers, and modern conifers proposed by Florin, and reveal anatomical features that are remarkably similar to those of many extant conifers. Features not recognized from previously described cones of *Lebachia* are dorsiventral, bilaterally symmetrical fertile shoots, inverted orientation of the ovules, and the true bilateral symmetry of the ovules. In both morphological structure and cuticular features the specimens show more variability than has previously been documented for a single conifer species, and this calls to question the reliability of features previously employed for generic separation of *Lebachia* from *Ernestiodendron*. The specimens also provide the first histological evidence for ovule abscission in Palaeozoic gymnosperms, and allow for the interpretation of several aspects of ovule ontogeny and early conifer reproductive biology.

UPPER PALAEOZOIC conifers are a relatively common component of some northern Hemisphere compression floras. Remains assignable to several genera, including *Walchia*, *Lebachia*, *Ernestiodendron*, *Lecrosia*, and *Paleotaxites*, have been described from Westphalian B (Scott 1974) and more recent strata of Europe and North America. Much of our current understanding of the earliest conifers is derived from the detailed studies and interpretations of Florin (1938–1945, 1950, 1951). However, until recently our knowledge of these forms has been limited by an almost total absence of permineralized specimens. Notable exceptions are a single leafy twig from the Pennsylvanian of Kansas (Elias 1948), a Permian ovulate cone tip (*Moyliostrobus* Miller and Brown 1973), and various wood fragments described by Florin (1938–1945) and others.

Numerous compressed Pennsylvanian and basal Permian conifer remains have been described or reported from North America. Where preservation reveals pertinent morphology and epidermal detail, some of these have been recognized as species of *Lebachia* (Florin 1938–1945; Cridland *et al.* 1963; Cridland and Morris 1964; Mapes 1981). These include *L. americana*, *L. garnettensis*, *L. parvifolia*, *L. stricta*, *L. geoppertiana*, *L. schlotheimii*, and *L. stephanensis*. In addition, *Lecrosia gouldii*, *Paleotaxites praecursor*, and several species of *Walchia* have been reported (e.g. White 1912; White 1929; Darrah 1936; Elias 1936; Arnold 1941; Read and Mamay 1964; Darrah 1969; Leisman 1971; Tidwell and Ash 1980; Kues and Kietzke 1981). Though some poorly preserved cones have also been reported, the studies have dealt primarily with isolated leafy branches or sterile foliage shoots.

As the result of extensive collecting in sediments that contain plant fragments not known from contemporaneous coal-forming peats (viz. not from coal balls), permineralized conifer remains have recently been discovered in mid-continental deposits of Oklahoma and Kansas (Mapes 1981; Rothwell 1982*b*). Permineralized specimens from these deposits range in age from middle Pennsylvanian to late Pennsylvanian or perhaps early Permian. The most diverse flora thus far encountered is near Hamilton, Kansas (text-fig. 1), and contains a wide variety of conifer remains. Included are large numbers of plagiotropic branch systems bearing forked leaves on penultimate and more basal branch orders and either long-needled or short-needled simple leaves on the ultimate branches. Both compound cones bearing ovules and simple pollen cones with *Potonieisporites*

[Palaeontology, Vol. 27, Part 1, 1984, pp. 69–94, pls. 9–16.]

are present in the conifer assemblage (Mapes 1981). A large number of the specimens display morphological and cuticular features that allow for their assignment to *Lebachia* as circumscribed by Florin (1938–1945), and provide the first opportunity to describe internal anatomy and to interpret development and reproductive biology in one of the most widely reported of all Palaeozoic conifers. The material also allows us to evaluate, from anatomical evidence, the accuracy of the structural homologies proposed by Florin for cordaites and conifers. Moreover, we can for the first time examine the isolated parts of a single *Lebachia* based on both external and internal features, and ultimately reconstruct the entire plant.

In the present study we describe and interpret several aspects of cone organization, ovule structure, ovule development, and reproductive biology in a new species of *Lebachia*. Pollen cones and vegetative organs will be addressed in subsequent studies.

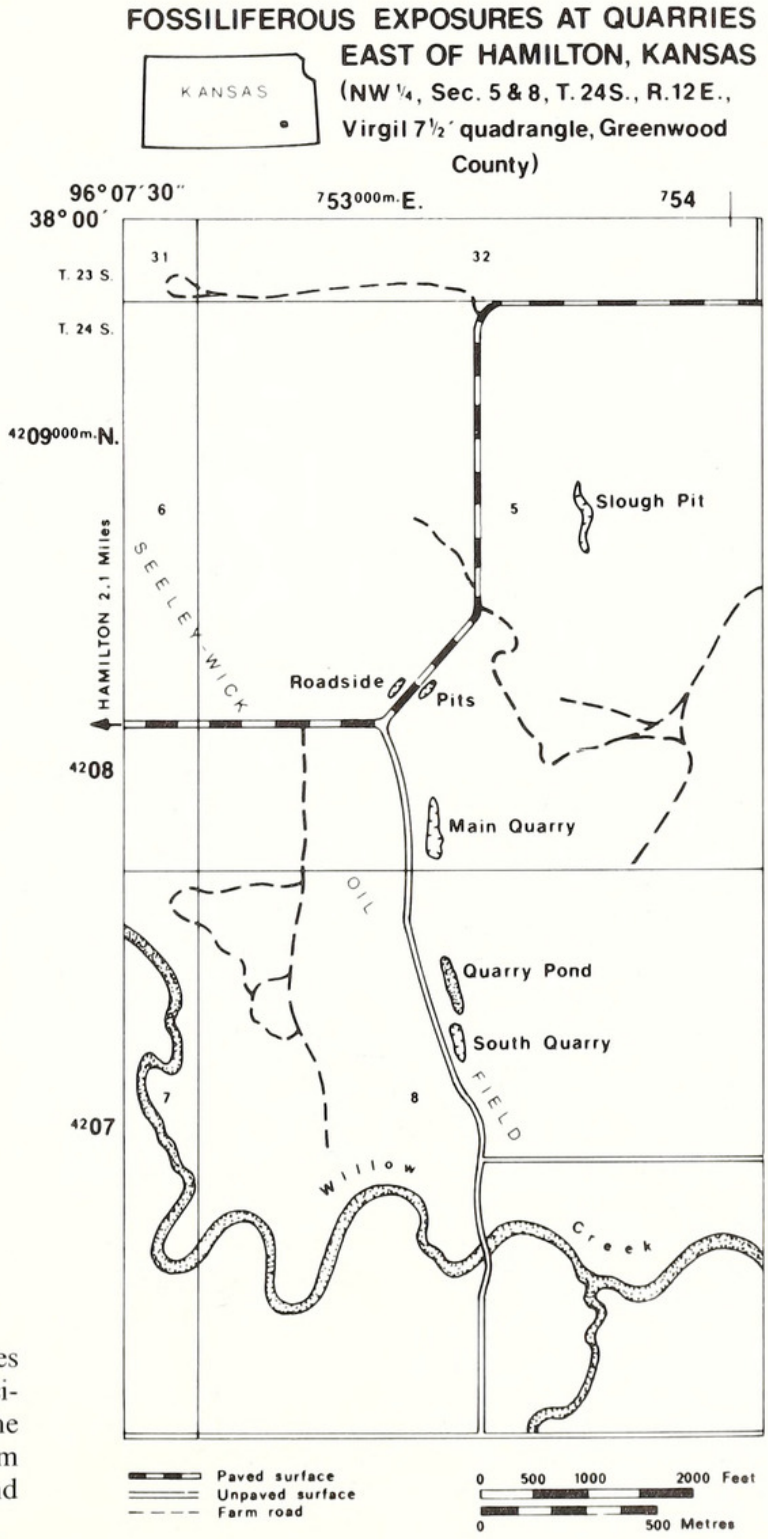
MATERIALS AND METHODS

Specimens of *Lebachia* are from an abandoned limestone quarry located east of Hamilton, Kansas (text-fig. 1). Conifer debris is common throughout the quarry (Leisman 1971), and ranges from finely disaggregated cuticles and wood fragments through compressed and/or permineralized cones and woody branching systems. The fossil flora at Hamilton is primarily gymnospermous, with conifers dominating in number and in diversity. Numerous animal remains also occur in this deposit, including insects (Hanson 1973), eurypterids (Anderson 1974), acanthodians (Zidek 1976), amphibians, foraminifera, and ostracods. Brachiopods and clams from the fossiliferous matrix have been identified as *Hystriculina wabashensis*, *Reticulatia heucoensis*, and possibly *Derbyia*, *Edmondia*, and *Myalina* spp. While these particular animal remains are sometimes poorly preserved, their occurrence in these sediments suggests strongly that the strata are of Pennsylvanian age (R. D. Hoare, Bowling Green State University, Ohio, pers. comm.).

The fossil-bearing unit at Hamilton quarry is a channel deposit, and consists of a basal conglomerate which grades into fine-grained laminated limestone. Although miscellaneous fossil remains are present in some of the clasts in the conglomerate, the permineralized plants and the majority of the animal fossils are in the limestone. While underlying and surrounding rocks have been recognized as the Hartford Limestone of the Topeka Limestone Formation, Shawnee Group, Virgilian (Andersen 1974: Zidek 1976), the age of the conifer-rich horizon *per se* has not been determined with certainty. In addition to the conifers, the Hamilton flora contains various cordaitean, fern, and seed fern remains. Certain highly dissected foliage was originally reported as the pre-ginkgophyte *Dichophyllum* (Andrews 1941), but has since been interpreted as *Callipteris flabellifera* (Remy *et al.* 1980). If this is correct, several alternatives are possible stratigraphically. The Hamilton beds could be equivalent to one of the Permian zones 11 to 14 (Remy 1975) of Read and Mamay (1964) or to the European Autunian (Remy and Havlena 1960, 1962; Remy *et al.* 1966), or *C. flabellifera* may have entered the flora earlier in the eastern and mid-continent U.S.A. than in the European section. While *Callipteris* spp. have been recognized as earliest Permian indicators, there are also reports of their occurrence world-wide in lower (older) strata (Barlow 1975; Gillespie *et al.* 1978). Assignment of these beds to either the upper Pennsylvanian or lower Permian awaits additional work with the more stratigraphically diagnostic forms of the biota.

Specimens were generally revealed by splitting the limestone matrix along the bedding plain. Morphological features were examined on the surfaces. The part and counterpart of some permineralized specimens were glued back together and serial sectioned in transverse or longitudinal plane. One part of other permineralized specimens was covered with liquid plastic then sectioned, while the counterpart was macerated in 2·5% HCl for cuticular preparations. Serial sections were prepared by the well-known cellulose acetate peel technique (Joy *et al.* 1956). Pertinent sections were mounted on standard microscope slides for transmitted light study and photography. Since the matrix was often nearly transparent while a peel was still attached, three-dimensional perspective could often be seen. Some of these surfaces were photographed with polarized reflected light (e.g. Pl. 16, figs. 1, 2). Photography was also with unpolarized reflected light, transmitted bright-field,

and Nomarski differential interference contrast (DIC) optics. Some macerated cuticle, tissue fragments, and prepollen grains were mounted on microscope slides for light optical study, while others were rinsed in distilled water, mounted on stubs with double-sided tape, and coated with gold for scanning electron microscopy. Specimens examined in this study are M26, M83, M144, M145, M147–152, and bear acquisition numbers 3834 to 4268 in the Paleobotanical Herbarium, Department of Botany, Ohio University, Athens, Ohio, U.S.A.



TEXT-FIG. 1. Fossiliferous exposures at quarries east of Hamilton, Kansas. *Lebachia lockardii* specimens have been recovered from all of the pits. The majority of the permineralized cones are from excavations directly west of the Main Quarry and the Quarry Pond.

SYSTEMATIC DESCRIPTION

Order CONIFERALES
Family LEBACHIACEAE
Genus LEBACHIA Florin 1938
Lebachia lockardii sp. nov.

Plates 9–16

Diagnosis. Ovulate cones, averaging 5·0 cm long × 1·5 cm wide, borne as single terminal units on vegetative axes with helically arranged simple or bifid leaves. Cones comprised of primary axis with helically arranged bifid bracts and axillary fertile shoots. Fertile shoots bearing twenty-five to thirty sterile scales and one to two fertile scales (rarely three to five) positioned adjacent to primary axis. One terminal inverted ovule per fertile scale. Ovules bilaterally symmetrical and winged, with rounded or cordate base and attenuated micropyle. Nucellus free from integument distal to chalaza. Simple pollen chamber with nucellar beak; often containing *Potonieisporites* grains. Stomata with five to nine unipapillate subsidiary cells. Adaxial leaf structure with stomata in two parallel bands, each four to eight stomata wide with some shared subsidiary cells; single bands or isolated rows of stomata occurring on some leaves. Abaxial cuticles papillate and less stomatiferous. Unicellular hairs common at margins of leaves and bracts.

Holotype. Slides, peels, and remaining portions of specimen M26; reposited in the Palaeobotanical Herbarium, Ohio University, as numbers: 3834–3851; 3867–3912; 3968–4092; 4267, and represented herein as Plate 9, fig. 5; Plate 10, figs. 1–3, 5, 6; Plate 11, figs. 1, 3–6; Plate 12, fig. 4; Plate 13, figs. 1, 3, 5; Plate 14, figs. 1–8.

Paratypes. Specimens M147 and M148 reposited as above, as numbers 4093–4147; 4234–4251, and 3855–3865; 4160–4218; 4260–4262; 4268, respectively, and figured herein as (M147) Plate 9, figs. 1, 4, and (M148) Plate 11, figs. 2, 5, 7; Plate 12, figs. 5, 7, 8; Plate 13, figs. 1, 4, 6; Plate 15, figs. 1–3, 5–7; Plate 16, figs. 1–3.

Locality. Hamilton quarries; NW quarter, sec. 5 and 8, T.24S., R.12E., Virgil seven and a half foot quadrangle, Greenwood County, Kansas, U.S.A.

Etymology. This species is named for Walter Lockard, who recognized the potential of the unique Hamilton fossil assemblage over twenty years ago, and has diligently obtained and generously shared his extensive field collections for palaeontological studies.

Description. Fifteen whole and partial permineralized cones, and numerous compressed specimens were examined. These ovulate cones are cylindrical-ellipsoidal and quite compact (Pl. 9, figs. 1–4). Complete cones are generally 4·0 to 5·5 cm long with a maximum diameter of 1·5 cm in their mid-regions. While large branching systems with attached ovulate cones of *L. lockardii* have not been recovered, all known *Lebachia* cones are terminal, and some of the *L. lockardii* cones retain up to 4 cm of vegetative axis below the cone base (Pl. 9, fig. 1). Leaves on the subtending axes are either bifid or simple, and provide a clue to the original positions of the cones on the branch systems.

Because the ovulate cones represent compound shoots, by definition they occur on penultimate or antepenultimate branches (= ultimate and penultimate branches of Florin 1951). The primary cone axis represents the penultimate branch and the fertile, secondary shoot is homologous with the ultimate vegetative branch. Each primary cone axis bears many helically arranged fertile complexes, comprised of a bifid bract

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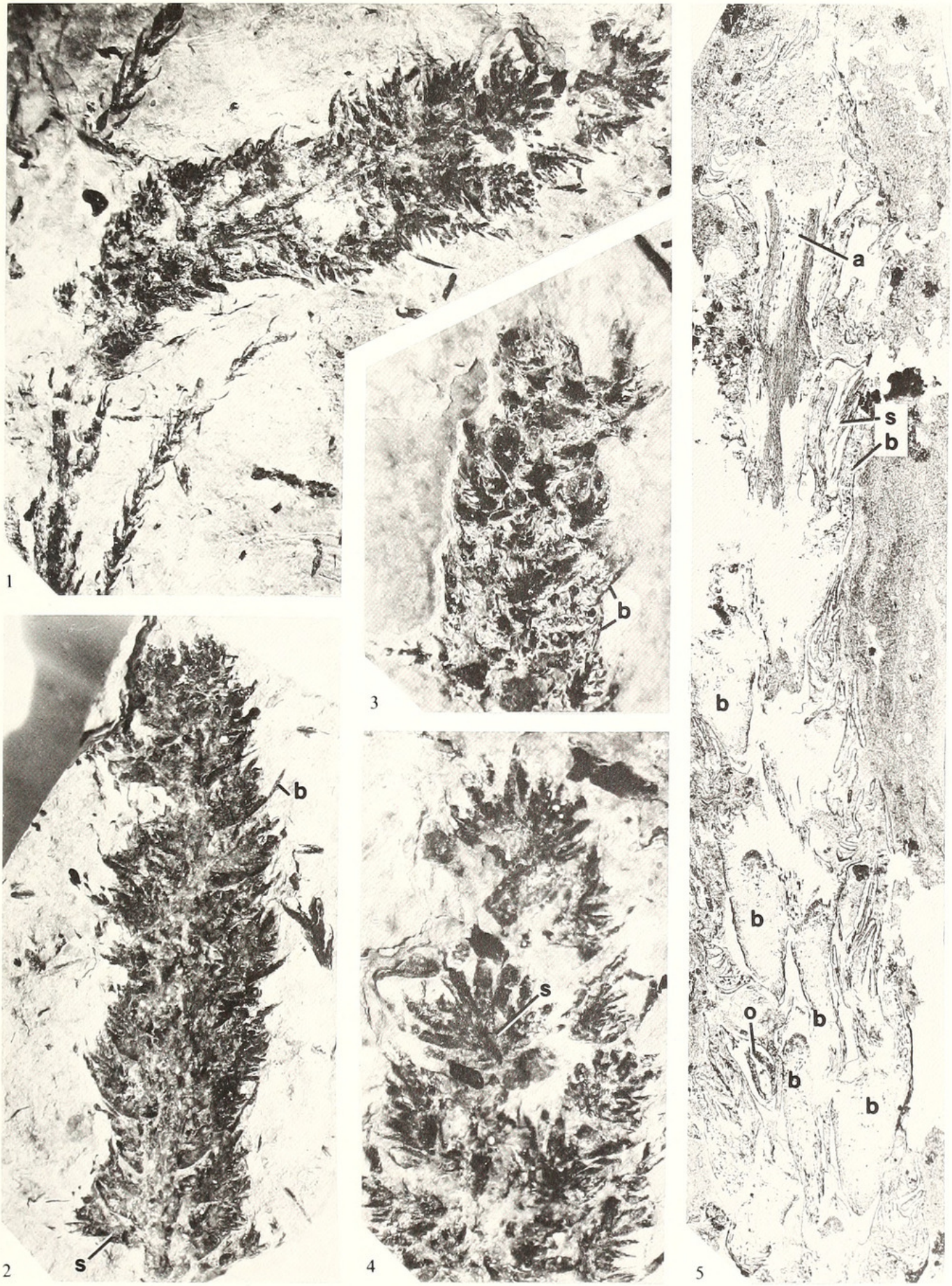
EXPLANATION OF PLATE 9

Figs. 1–5. *Lebachia lockardii* sp. nov., ovulate conifer cones from Hamilton, Kansas. a, primary cone axis; b, bract; o, ovule; s, secondary shoot. 1, cone attached to vegetative shoot, M147, × 2. 2, cone split longitudinally, note attachment of secondary shoots to cone axis, M150, × 2. 3, abraded cone surface with prominent sterile scales of secondary shoots, M146, × 2·5. 4, apex of cone in fig. 1, note sterile scales of flattened secondary shoots, M147, × 3. 5, holotype, oblique longitudinal section, showing helical arrangement of bracts and the relative positions of bracts to axillary secondary shoots, M26 No. 1, × 5.



MAPES and ROTHWELL, *Lebachia* cones

and an axillary shoot with several sterile and fertile scales. Florin (1938, 1951) called the fertile shoots 'flowers' and characterized the fertile shoot axes of *Lebachia* ovulate cones as radially symmetrical. The often excellently preserved and undistorted fertile shoots (= secondary shoots) of *L. lockardii* are clearly bilaterally symmetrical; their flatness is biologic, not taphonomic. The stele of the secondary shoot (= cone scale trace of more recent conifers) is crescent-shaped in transverse section, not radial as are the secondary shoot steles of cordaitean strobili (Rothwell 1977; Daghlian and Taylor 1979). While unabraded external surfaces of *L. lockardii* cones often retain the bifid bracts, the axillary shoots with their numerous scales are more easily recognized (Pl. 9, figs. 1–4). In the apical region of the cone, the bracts have no secondary shoots in their axils (Pl. 10, fig. 4).

The primary cone axis has a eustele with the endarch xylem maturation that is characteristic of more recent conifers. Pith and cortical cells are typically 15 to 25 μm in diameter and always thin-walled (Pl. 10, figs. 2, 3, 5). Some of these cells are elongate, have dark contents, and are up to 70 μm in diameter; cells of this type may have had secretory or storage functions. Primary xylem tracheids are narrow, average 7·5 μm in diameter, and have angular-spiral and scalariform wall thickenings (Pl. 11, fig. 1). The secondary xylem is compact, basically pycnoxylic, and forms a cylinder averaging 1·3 mm in diameter (Pl. 10, figs. 1, 5, 6). In transverse sections, tracheids are ovoid-polygonal (Pl. 11, fig. 3). Throughout most of the wood the tracheids have uniseriate pitting (Pl. 11, fig. 6), but the tracheids adjacent to the primary xylem sometimes show uniseriate oval pits and/or biseriate opposite circular bordered pits (Pl. 11, figs. 4, 6). Rays are uniseriate to biseriate, one to five cells high, and composed of poorly preserved parenchyma with no evidence of ray tracheids (Pl. 11, figs. 1, 3).

The bifid bracts have deeply heeled bases (Pl. 9, fig. 5; Pl. 10, fig. 3). Distal forking can be recognized in transverse sections near the bract apex (Pl. 14, fig. 1 at top). Similar forked leaves occur on penultimate and antepenultimate vegetative axes, and at the cone base/vegetative branch transition zone on lateral shoots bearing otherwise simple leaves (Florin 1951). Such bifid leaves and bracts are sometimes referred to *Gomphostrobus* Marion (1890) and are vascularized by a single trace which bifurcates below the bifid apex. The tracheids are usually poorly preserved, but scalariform wall thickenings have been observed. Ground tissue consists of isodiametric, loosely packed parenchyma cells (Pl. 10, fig. 3), many of which contain dark contents which may be secretory. An abaxial hypodermis occurs throughout the length of the bract, but diminishes in prominence distally. The hypodermis consists of two to four cell layers of elongate, closely packed cortical cells directly beneath the epidermis (Pl. 10, figs. 3, 5).

Lebachia leaf cuticle has been characterized by Florin (1938–1945) as thick, papillate, and amphistomatic, with each leaf commonly bearing two broad parallel bands of haplocheilic stomata. The stomata have two guard cells surrounded by four to eleven subsidiary cells with overarching papillae. Cuticles of *L. lockardii* have these features, and contribute additional information regarding variations of the cuticular features in a single species.

The stomatal bands of *L. lockardii* vary in width, length, and composition. There may be single bands or parallel bands, and stomata occur both on abaxial and adaxial leaf surfaces. Within individual ovulate cones of *L. lockardii*, there is a wide range of variation. Parallel bands, generally four to eight stomata wide, are present only on adaxial leaf surfaces. Single bands of comparable width are sometimes seen on sterile scales. Stomatal arrangement within a band is also variable. Generally, stomata are irregularly disposed, though longitudinally oriented, with some shared subsidiary cells (Pl. 12, fig. 1). In other areas there are more widely separated or even single rows of longitudinally oriented stomata (Pl. 12, figs. 3, 6) or isolated stomatal apparatuses. The least stomatiferous cuticles are those of the smallest sterile scales, the cone axes, and the abaxial surfaces of bracts. The ovulate cone cuticles of *L. lockardii* are certainly amphistomatic, but the majority of the stomata are adaxial. While comparable to the species of *Lebachia* characterized by Florin

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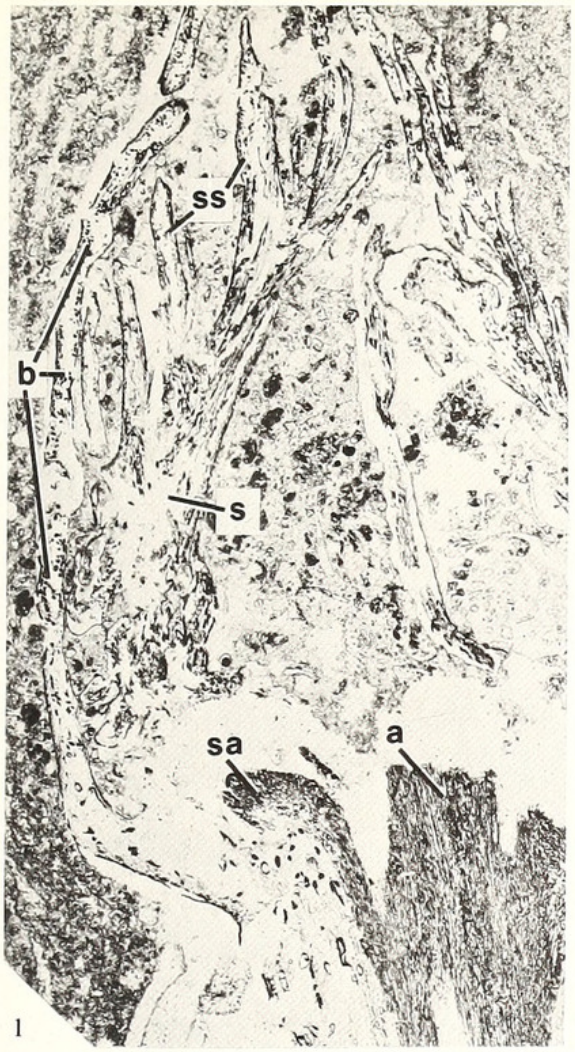
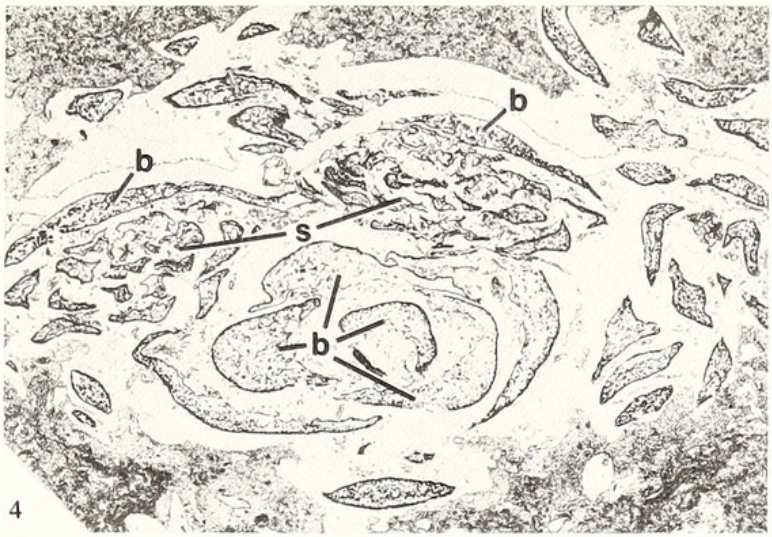
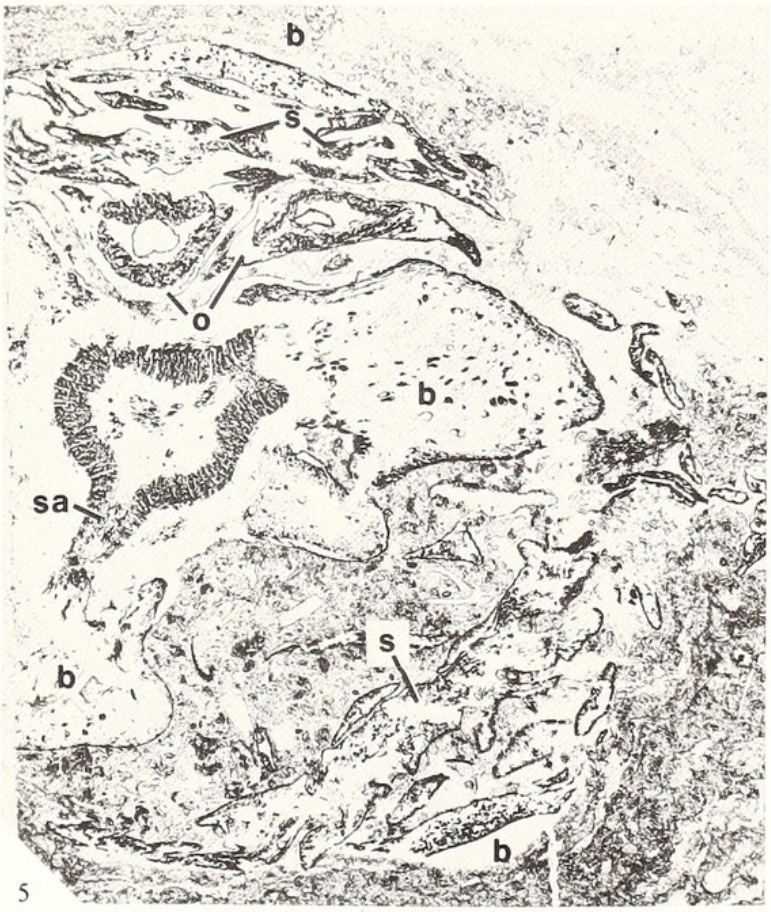
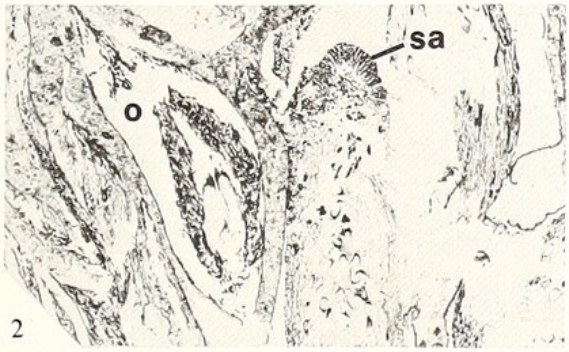
EXPLANATION OF PLATE 10

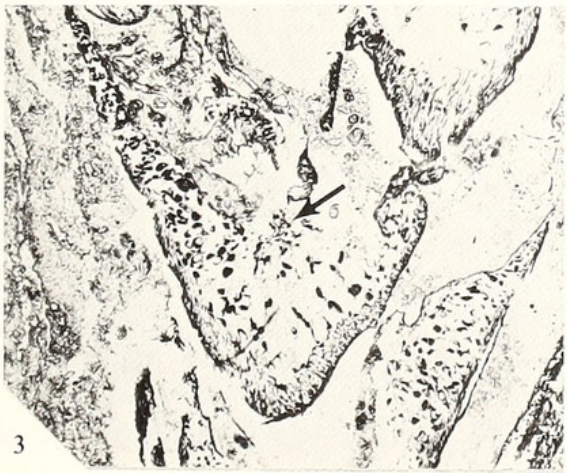
Figs. 1–6. *Lebachia lockardii* sp. nov. a, primary cone axis; b, bract; o, ovule; s, secondary shoot; sa, secondary shoot axis, ss, sterile scales. 1, longitudinal section of cone near apex. Note arrangement of vascular tissues, bract, and axillary secondary shoot, M26 B side No. 5, × 14. 2, tangential section of detached ovule and crescentic vascular trace of fertile secondary shoot, M26 No. 1, × 13. 3, bract bases in tangential section. Note abaxial hypodermis, cortical cells with dark contents, and vascular trace at arrow, M26 A side No. 4, × 16. 4, transverse section near cone apex, M83 Top No. 25, × 14. 5, transverse section of cone, note two ovules of one secondary shoot, M26 B Top No. 58, × 12. 6, transverse section of primary cone axis below fertile zone, M26 A Top No. 33, × 14.

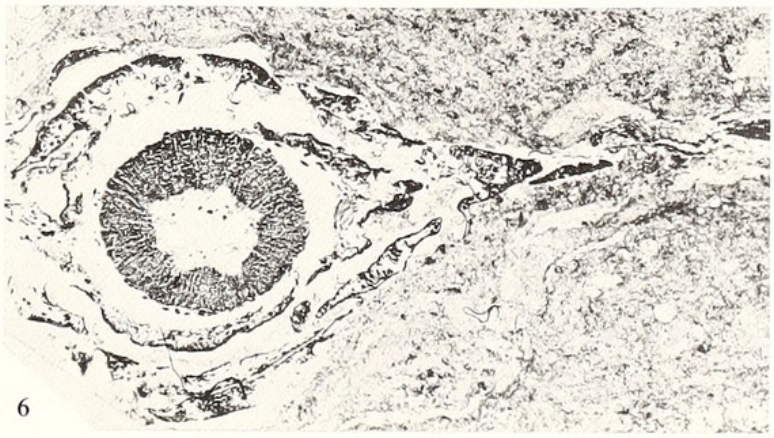












MAPES and ROTHWELL, *Lebachia* cones

(1938–1945), each stoma of *L. lockardii* has five to nine subsidiary cells, each with a single papilla overarching the stomatal opening (Pl. 12, fig. 6). In bands of closely spaced stomata, subsidiary cells are sometimes shared by adjacent stomata, but papillae are usually single. More commonly, small epidermal cells intervene, separating the subsidiary cells of adjacent stomata (Pl. 12, fig. 6 at arrow). The guard cells are generally not preserved.

Epidermal cells within and between stomatal bands vary in shape and size, and in the presence or absence of papillae and hairs. Papillate epidermal cells are sometimes present on both abaxial and adaxial surfaces (Pl. 12, figs. 2, 7), but are most common on abaxial cuticles. In addition, they occur both in and between the bands of stomata. Although exceptions have been noted, there is usually only one papilla per epidermal cell. Papillae are most often on small, rather isodiametric cells, but they also occur on the tabular and the broadly polygonal epidermal cells (Pl. 12, figs. 2, 7). Uniseriate hairs are common on the margins (Pl. 12, figs. 1, 8) and can be seen on both surfaces of *L. lockardii* leaves. The longest hairs (up to 0·6 mm long) are often twisted and some may be multicellular.

A feature of considerable interest characterizes certain small epidermal cells. These cells are rounded rather than angular, and display a central circular area, av. 8–12 μm diameter, with raised rim and often dislodged cuticular surface (Pl. 12, figs. 4, 5). These areas resemble closely the waxy plugs or cuticular flaps which cover sunken stomata of certain species of fossil and modern *Araucaria* (Stockey and Taylor 1978*a*, *b*). However, these cells are not associated with the stomata of *L. lockardii*. Rather, they are often surrounded by larger epidermal cells and can be easily recognized in surface view or optical section by their coronas (Pl. 12, figs. 4, 5). We interpret the corona to represent the area between the rim of the circular area and the widest lateral extent of the walls of the small isodiametric cell, where the cell wall margin subtends that of the adjacent surrounding epidermal cells. The surface flap or plug of cuticle probably resulted from the collapse of a small hair or a broad low papilla. These cells resemble some of those Florin called hair bases (e.g. *L. americana*, text-abb. 20A, Florin 1938–1945).

In *L. lockardii* numerous irregularly arranged sterile scales and one or more fertile scales are typically present on each secondary shoot (Pl. 10, figs. 1, 5). This deviation from the helical arrangement of leaves on vegetative stems of *Lebachia* results from the combination of flatness of the secondary shoot axis (Pl. 10, fig. 5) and the smaller number of scales present on the side of the shoot that lies adjacent to the primary cone axis. Where the bracts are not preserved, fertile shoots often display a fan of nine to twelve sterile scales (Pl. 9, figs. 2–4). In some transverse sections, twenty to twenty-five scales can be seen at a single level, and serial sections indicate that more than thirty scales may be present on individual fertile shoots.

Within cones, the fertile secondary shoots are attached to the primary axis at intervals of approximately 5 mm, and average 2·0–2·5 mm long. In transverse sections below scale attachment, individual secondary shoot axes are 0·2–1·0 mm in diameter, expanding up to 3 mm wide in the zone of scale attachment (Pl. 10, fig. 5). On some bedding planes isolated shoots from disaggregated cones can be recognized among the coniferous debris. The isolated shoots are comparable to those within the ovulate cones, but never have mature ovules attached.

The sterile scales most distally attached to each secondary shoot are usually fused at their bases (Pl. 9, fig. 4; Pl. 13, figs. 4, 6), and can sometimes be macerated loose as dentate units of two to five scales. Most of the macerated sterile scales taper to an acutely pointed apex, but a small number of scales have an abruptly truncated tip with a central cleft and subapical protruberance (Pl. 13, fig. 5). The latter scales are remarkably similar to certain fertile scales of ovulate *Cordaianthus* strobili, where the ovules are either extremely immature

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EXPLANATION OF PLATE 11

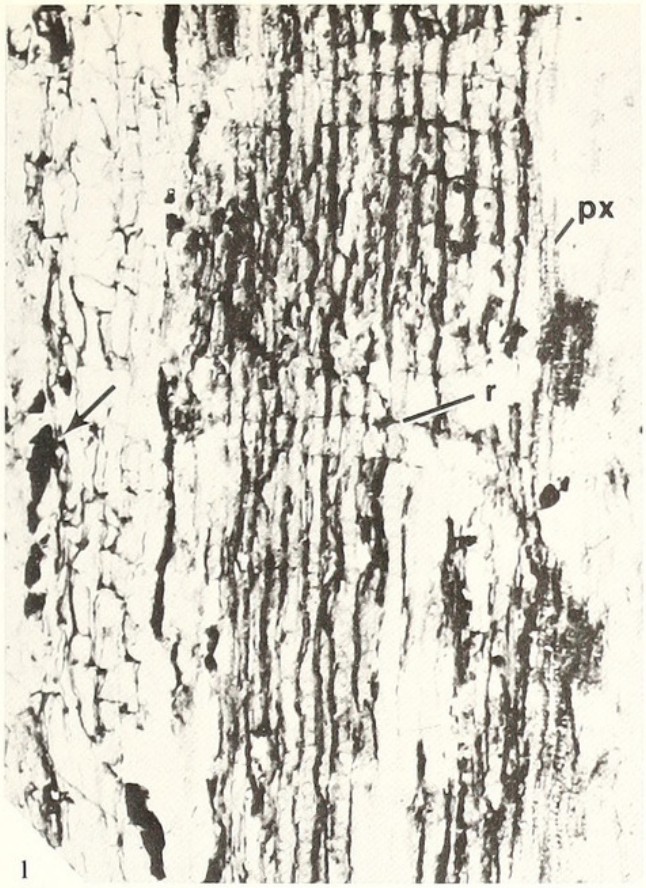
Lebachia lockardii sp. nov. Wood and leaf anatomy. bs, bundle sheath; px, primary xylem; r, ray.

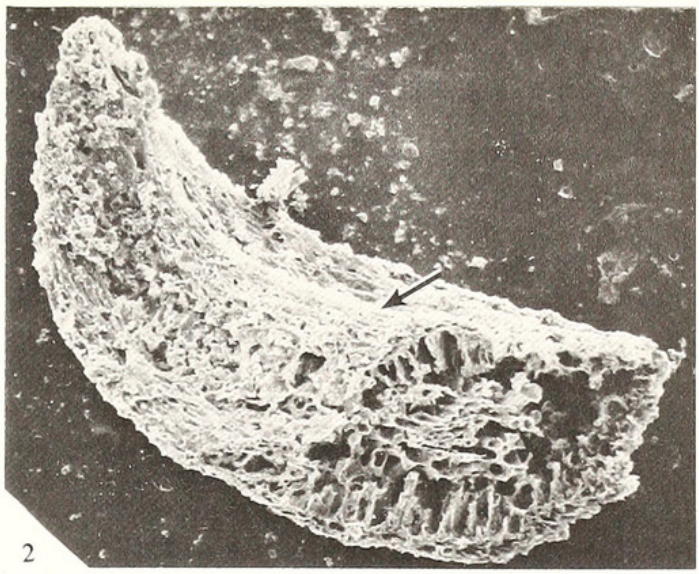
Fig. 1. Radial section of wood of primary cone axis, arrow indicates secretory cells, M26 B side No. 1, × 130.

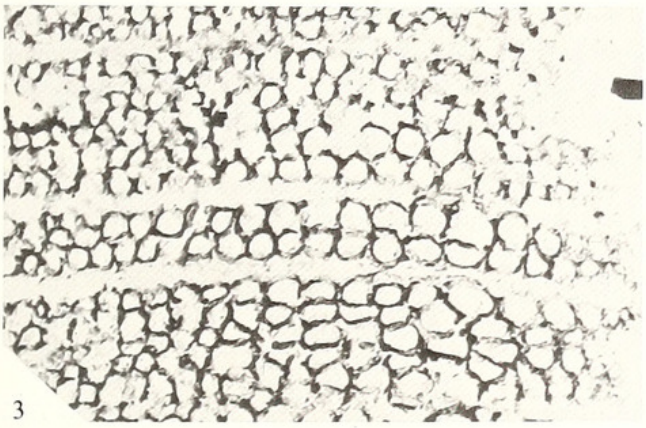
Figs. 2, 5, 7. Scanning electron micrographs of coalified sterile scales from ovulate cone maceration. 2, note adaxial ridge at arrow, and upcurved leaf tip, M148 Mac Leaf A, × 80. 5, epidermis, palisade, and vascular trace with bundle sheath, M148 Mac Leaf A, × 250. 7, spongy mesophyll tissue and vascular trace with bundle sheath, M148 Mac Leaf B, × 250.

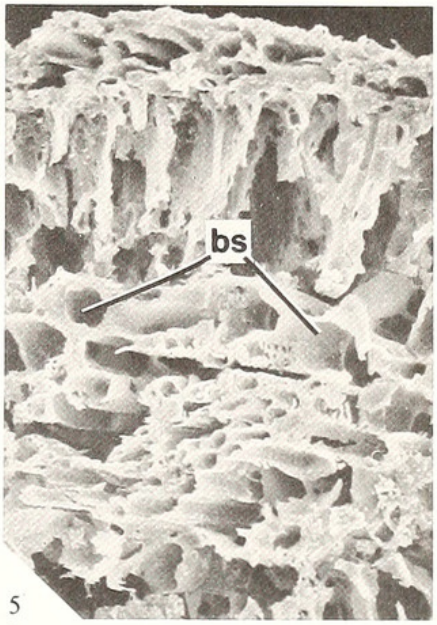
Fig. 3. Transverse section of wood from primary cone axis. Note poorly preserved rays, M26 B Top No. 33, × 185.

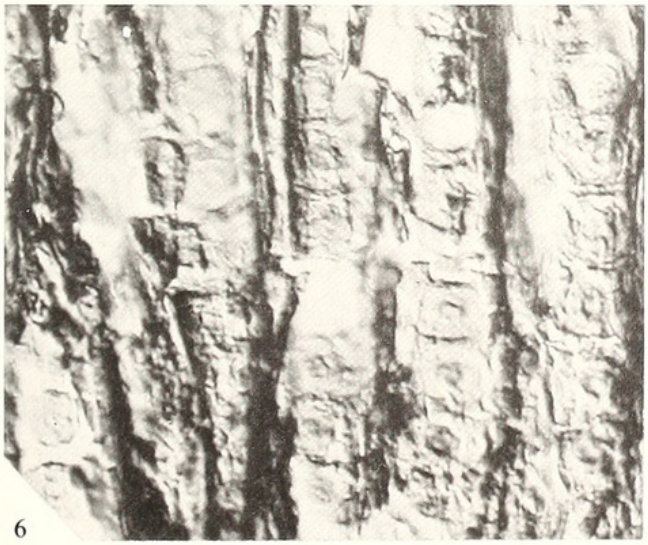
Figs. 4, 6. Bordered pits (Nomarski DIC). 4, single tracheid with uniseriate to biseriate oval pits, M26 A side No. 1, × 820. 6, tracheids with uniserate circular pits, M26 A side No. 1, × 820.

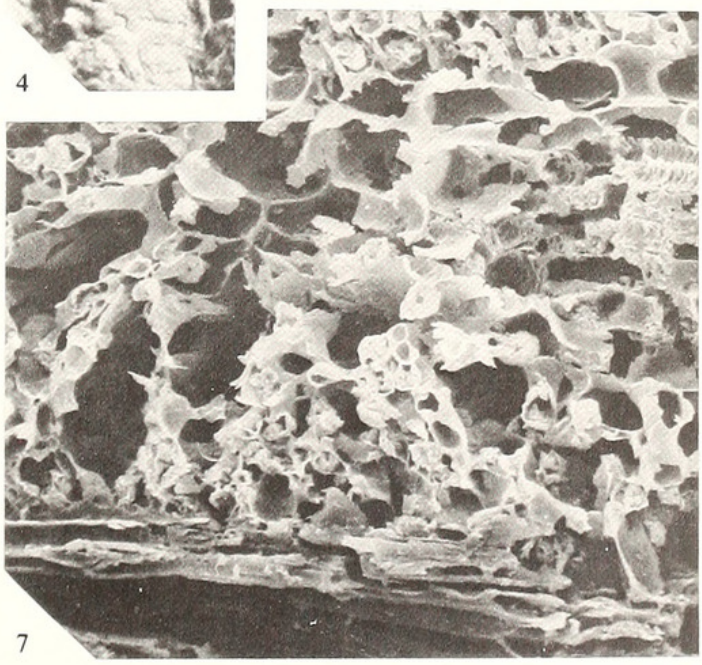












MAPES and ROTHWELL, *Lebachia* cones

or abortive (Florin 1951, fig. 21; Rothwell 1982*a*). Specimens of this type suggest that there was potentially a larger number of fertile scales on *Lebachia* fertile shoots than is reflected by the number of well-formed ovules.

Papillae are common on all surfaces and prominent hairs are sometimes preserved at the scale margins. Ground tissue of the scales is comprised of loosely packed spongy mesophyll (Pl. 11, fig. 7) comparable to the cortex of the bifid bracts, and a weakly developed palisade can sometimes be recognized (Pl. 11, figs. 2, 5).

The fertile scales, or sporophylls, are comparable to the sterile scales in both anatomical and morphological features. They are sometimes rounder in cross-section, averaging 0·3 to 0·8 mm (Pl. 13, fig. 4), and are from 0·5 to 2·0 mm long (Pl. 13, fig. 1). Fertile scales are always located adjacent to the primary axis, and are either abruptly truncated, with no epidermis at the apex, or terminate in a single ovule. Some fertile shoots bear one or two ovules, but many have none, possibly because the ovules had already dropped off, or because none had formed.

Of particular interest are ovulate scales with histological features like those of extant plants in which organs have been sectioned at various stages of abscission (e.g. Barnell 1939). Some specimens show good cellular continuity between the scale tip and the chalaza of the ovule (Pl. 13, fig. 2), but the width of the attachment is noticeably reduced by a prominent groove extending around the periphery of the constricted attachment area (Pl. 13, fig. 3). In other specimens the ground tissue at the level of the groove is poorly preserved with only the darker, apparently thicker-walled, cells at the centre of the zone connecting the ovule to the scale (Pl. 13, fig. 3). In still other instances, the cellular continuity between scale and ovule is completely disrupted (Pl. 13, fig. 4). Upon closer examination of the groove region, most of the cells of the ground tissue appear thin-walled, relatively isodiametric, and randomly disposed (Pl. 13, fig. 2). In specimens with partly or completely disassociated ovules (Pl. 13, figs. 2–4), cells in the groove region are like those in the separation layer of abscising organs, after the cell walls have undergone enzymatic gelatinization and dissolution. Two or three cell layers proximal to the separation layer of some fertile *Lebachia* scales there exists a small number of cells that are rectangular in section view and aligned both parallel to and at right angles to the line of abscission. Cells of this latter type conform closely to those of the protection layer often formed proximal to the separation layer in the abscission zones of extant plants (Esau 1965). Prominent cell walls containing lignin and/or suberin have not been observed in these *Lebachia* specimens.

Perhaps the most surprising feature of *L. lockardii* is the mode of ovule attachment. While the ovules are terminal on the scales of the secondary shoots, they are inverted, rather than erect as interpreted by Florin for all previously known species of *Lebachia* (Florin 1938–1945, 1951). The basipetal serial sequence of transverse sections illustrated in Plate 4 clearly demonstrates the relationship of two ovules with the secondary shoot upon which they were borne. Figure 1 is closest to the cone apex and shows the bases of both ovules. The left ovule is sectioned just below the level of attachment to its fertile scale, while the right ovule is sectioned above the level of attachment, and is represented only by its two basal lobes. Several sterile scale tips can be seen at this level and the distal portion of the bract subtending the secondary shoot is at the top of the figure. The central constriction marks the position where the bract apex forks distally. The helical arrangement of the cone parts is indicated by the broad bract base and the secondary shoot stele diverging from the primary cone axis at the lower left.

Progression basipetally shows the basal lobes of the right ovule join (Pl. 14, fig. 2) and the ovule becomes attached to its fertile scale. Note the cuticle in the area of the abscission zone is continuous (Pl. 14, fig. 3) except for a small mechanical break at far right. By the level represented at fig. 4, the right ovule has separated from its fertile scale and the seed cavities of both ovules are evident. The nucellar beaks of the left ovule and right ovule are seen in figs. 5 and 6 respectively, and the remaining sections proceed through the

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EXPLANATION OF PLATE 12

Figs. 1–8. Cuticular features, *Lebachia lockardii* sp. nov. 1, bract cuticle, adaxial surface with band of stomata and prominent marginal hair, M149 Mac No. 6, ×100. 2, abaxial cuticle with many coronate and/or papillate cells, M149 Mac No. 1, ×210. 3, longitudinally oriented rows of stomata, M145 Mac No. 9, ×110. 4, portion of cuticle viewed from inside. Note coronate, circular rimmed cells (Nomarski DIC), M26 A side No. 1, ×740. 5, cuticle surface with apparent cuticular flaps or plugs, M148 SEM-13, ×600. 6, stomata with overarching papillae. Arrow notes epidermal cells between adjacent stomata, M145 Mac No. 9, ×260. 7, papillate epidermal cells, M148 SEM-9, ×1200. 8, hairs at bract margin, M148 Mac No. 3, ×290.

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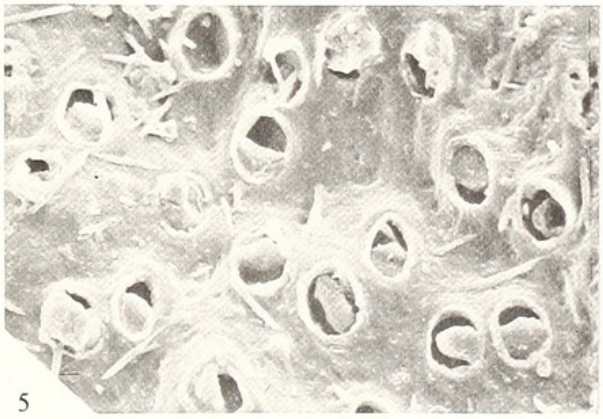
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MAPES and ROTHWELL, *Lebachia* cones

narrowing, attenuated micropyles (Pl. 14, figs. 6–8). The longitudinal section in Plate 13, fig. 1, and text-fig. 2, also demonstrate the relative positions within a fertile complex. Although ovules are often found dislodged laterally within the cones of *L. lockardii*, when attached they are always in an inverted orientation with micropyle located between the primary cone axis and the base of the secondary shoot (Pl. 13, fig. 1).

Approximately seventeen ovules remain within the cones of *L. lockardii*. Several of these are poorly preserved, incomplete, and/or possibly abortive, but others are more complete. All of the ovules are clearly bilaterally symmetrical (Rothwell 1982*b*) and have an attenuated micropyle. In transverse sections the micropylar canal tapers gradually toward the apex of the ovule (Pl. 14, figs. 6–8) and may be reduced to as little as 0·1 mm in maximum diameter. However, none of the specimens is well preserved at the apex. The base of the ovules is either cordate (Pl. 14, fig. 1) or rounded (text-fig. 2). Individual ovules measured in transverse sections average 2·3 mm in the major plane and 0·6 mm in the minor plane.

The integument consists of several zones of thin-walled cells (Pl. 15, figs. 1–3) and is free from the nucellus except at the chalaza. Clearly defined sarcotesta, sclerotesta, and endotesta that characterize most mature gymnosperm ovules are not present. This may be due in part to incomplete tissue differentiation. The outer margin of the integument is delimited by a uniseriate epidermis covered by a conspicuous dark line that represents the cuticle (Pl. 15, figs. 1, 2). The epidermal cells are uniformly thin-walled and usually have empty lumina.

Individual epidermal cells are rectangular-polygonal and many are papillate. There are also conspicuous uniseriate epidermal hairs preserved on many ovules (Pl. 15, figs. 2, 6). Inside the epidermis there is a zone of variable thickness where many of the thin-walled cells contain prominent dark contents. Cells of this type are preserved only at the margins of the wings in the ovules figured on Plate 14 (Pl. 14, fig. 4), but are more uniformly preserved in other specimens (Pl. 15, figs. 1–3). Immediately to the inside of this zone is another zone of thin-walled cells which typically lack internal contents (Pl. 15, figs. 1–3). The inner margin of the integument is delimited by a conspicuous epidermis; the cells typically have dark contents (Pl. 15, figs. 1, 2). In some specimens the thin-walled cells are separated from the inner epidermis either by an empty space or by the inconspicuous remnants of extremely thin-walled cells (Pl. 15, fig. 2 at arrow). These remnants resemble the undifferentiated sclerotesta of immature Palaeozoic ovules assignable to cordaites (Stidd and Cosentino 1976) and pteridosperms (Rothwell 1971, 1980). In two specimens there are two patches each of poorly preserved, thick-walled cells at the level of the pollen chamber (Pl. 16, figs. 1, 2 at arrows). These are preserved in the minor plane and resemble the first differentiated areas of sclerotesta in previously described Carboniferous cardiocarpalean ovules.

Vascular tissue has been difficult to identify within the ovules of *L. lockardii*, but in one speciman poorly preserved tracheids have been located (Pl. 15, fig. 7). These were observed near the base of the ovule in a position which is comparable to that occupied by the integumentary bundles of cardiocarpalean ovules (e.g. *Mitrospermum vinculum* Grove and Rothwell 1980).

As is also characteristic of Palaeozoic cordaitean ovules, the nucellus of *L. lockardii* is attached to the integument at the chalaza and free distally (Pl. 15, figs. 1, 2). It surrounds the megaspore membrane of the megagametophyte, and forms a prominent pollen chamber distally (Pl. 16, figs. 1, 2). In the midregion the nucellus is several cell layers thick (Pl. 15, fig. 2). Nucellar cells are usually small and thin-walled, and many contain dark substances (Pl. 15, figs. 1, 2, 4). A cuticle is present at the outer margin of the nucellus, and in surface view reveals the size, shape, and orientation of the nucellar epidermal cells (Pl. 15, figs. 4, 5).

The pollen chamber is round in transverse section (Pl. 15, figs. 1 at top, 4), and tapers distally to engage the base of the micropylar canal. The pollen chamber wall consists of one to two layers of cells that are like

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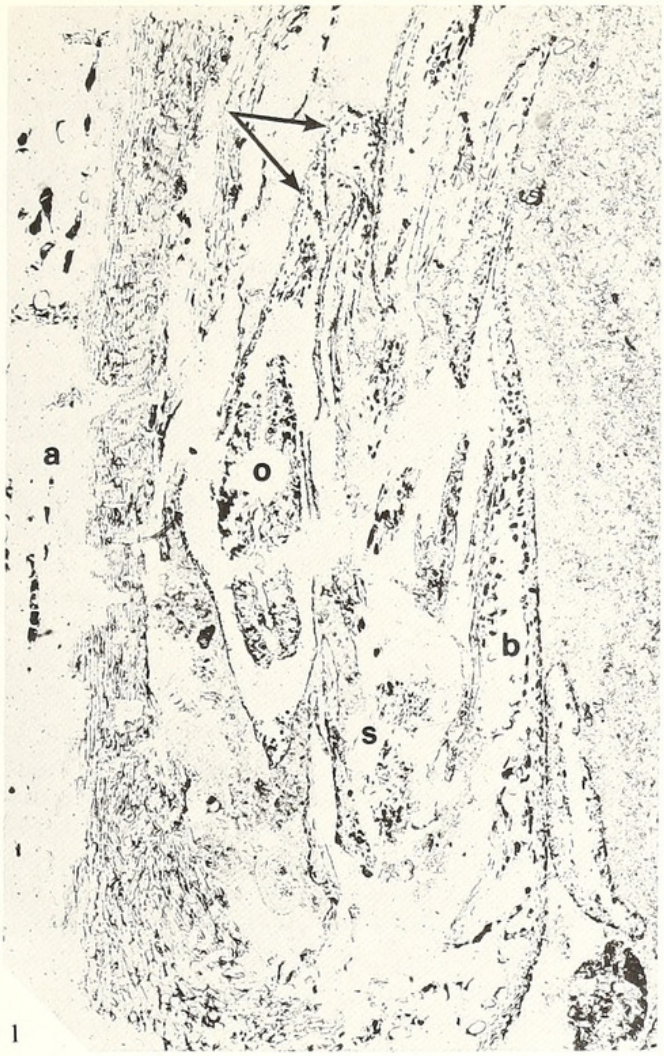
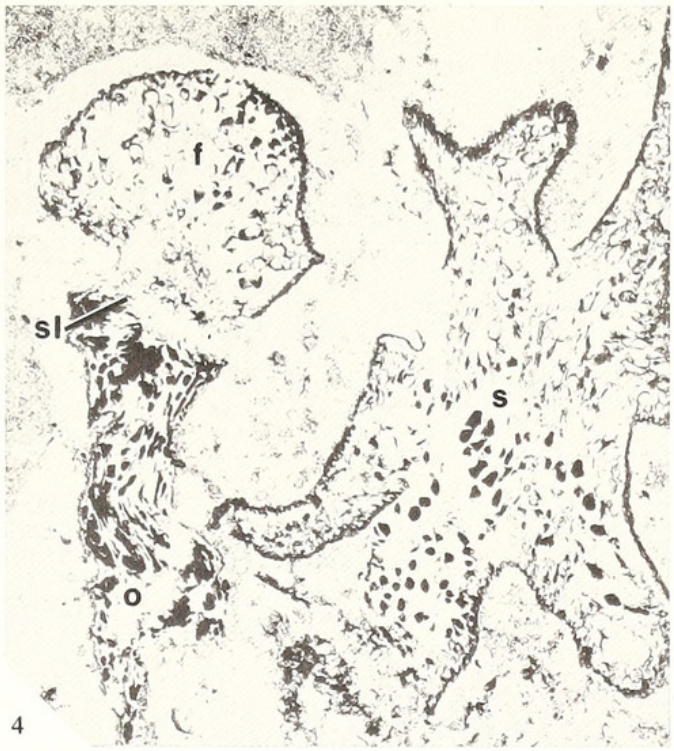
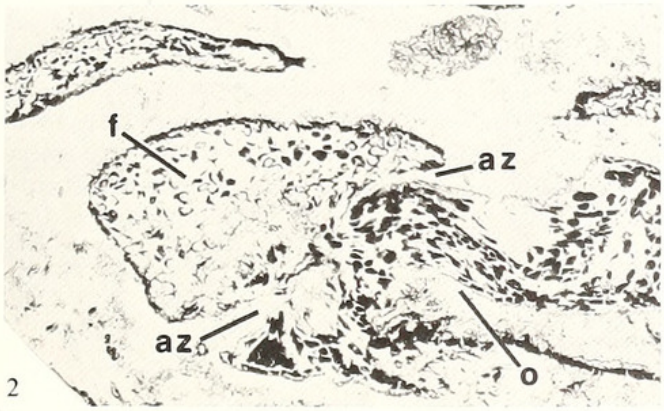
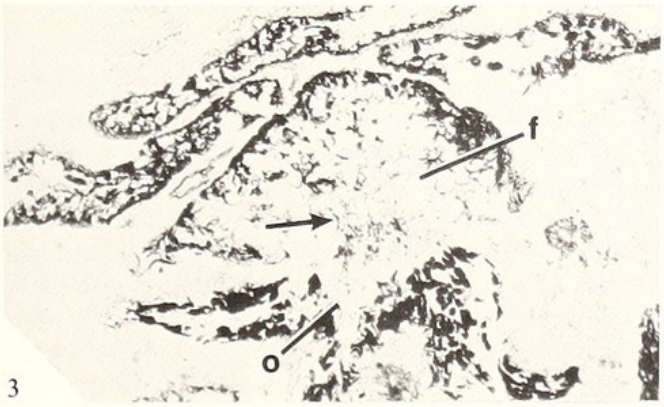
EXPLANATION OF PLATE 13

Figs. 1–6. *Lebachia lockardii* sp. nov. a, primary cone axis; az, abscission zone; b, bract; f, fertile scale; o, ovule; s, secondary shoot; sl, separation layer. 1, longitudinal section of attached secondary shoot and subtending bract. Arrows indicate area where fertile scale adjoins ovule, M26 B side No. 9, ×25. 2, fertile scale and ovule with groove at abscission zone, transverse section, M148 B Top No. 32, ×47. 3, ovule incompletely abscised from fertile scale, note protection layer at arrow, M26 B Top No. 50, ×47. .4, transverse section near tip of secondary shoot, showing ovule and scale from which it has abscised, M148 B Top No. 28, ×47. 5, lobed tip of scale with small central protrusion, M26 Mac No. 7, ×75. 6, sterile scales with mesophyll, central vascular trace (at arrow) and partial cuticle, M148 B Top No. 5, ×74.









MAPES and ROTHWELL, *Lebachia* cones

those at more proximal levels of the nucellus (Pl. 15, fig. 4). Distally, the pollen chamber wall thins to one layer of distinct cells that form a conspicuous nucellar beak like those of many Palaeozoic trigonocarpalean and cardiocarpalean ovules (Pl. 14, figs. 5, 6; Pl. 15, fig. 1; Pl. 16, figs. 1, 2). Cells of the nucellar beak are large, with conspicuous walls and empty lumina (Pl. 15, fig. 1). In some sections the cells are rectangular, and often exhibit thickened radial walls (Pl. 15, fig. 1). There is no evidence of an organized pollen chamber floor region.

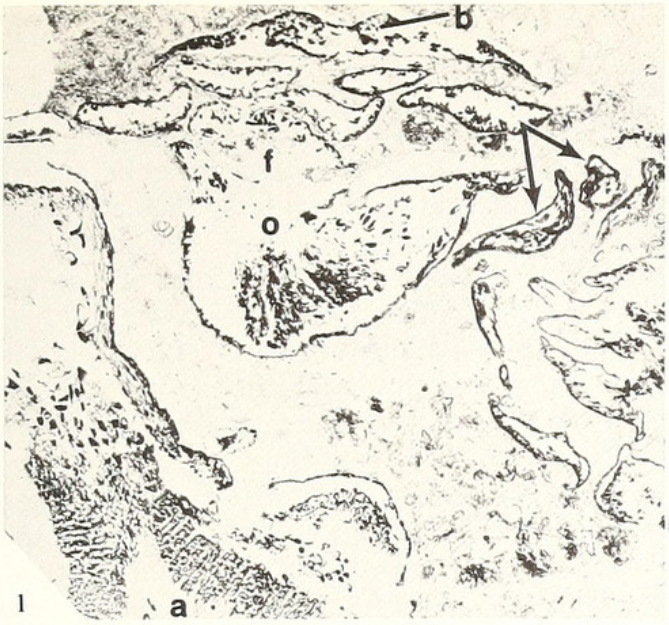
The megagametophyte in all available specimens is represented only by a megaspore membrane and the hollow it surrounds (Pl. 15, fig. 2). The megaspore membrane is golden-brown and, when viewed with light optics, is apparently homogeneous, not granular or pitted as are some (Pettit 1966; Zimmerman and Taylor 1970). Cellular megagametophyte tissue has not been observed.

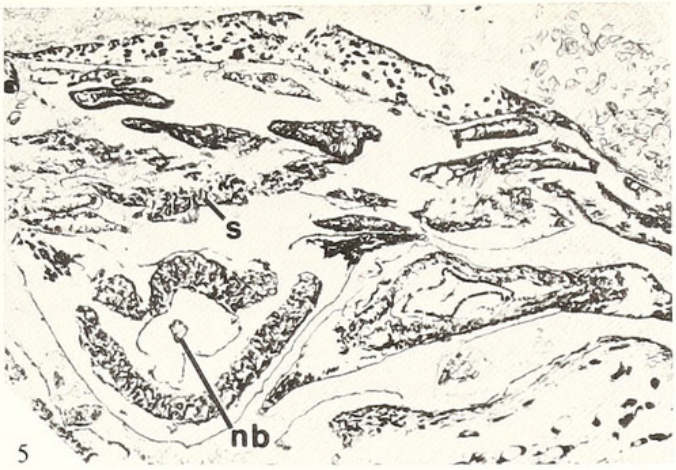
Microgametophytes are preserved within the pollen chamber and micropyle of several ovules (Pl. 14, fig. 7 at right; Pl. 15, fig. 4; Pl. 16, figs. 1–3). The grains are all of one type and assignable to *Potonieisporites* Bhardwaj (1954). Apparently identical grains are abundant in the matrix within and immediately surrounding the ovulate cones, and also within the pollen sacs of associated *Lebachia* pollen cones (Mapes 1981). *Potonieisporites* is commonly reported from upper Palaeozoic strata world-wide (Wilson and Venkatachala 1964; Nygreen and Bourn 1967; Upshaw and Hedlund 1967; Gupta 1970; Neves and Belt 1971; Bharadwaj 1972; Balme 1980). It is also known *in situ* from compressed conifer pollen cones such as *L. piniformis* and *L. hypnoides*, *Ernestiodendron filiciforme*, and *Walchianthus crassus* and *W. cylindraceus* (Florin 1938–1945; Bharadwaj 1964).

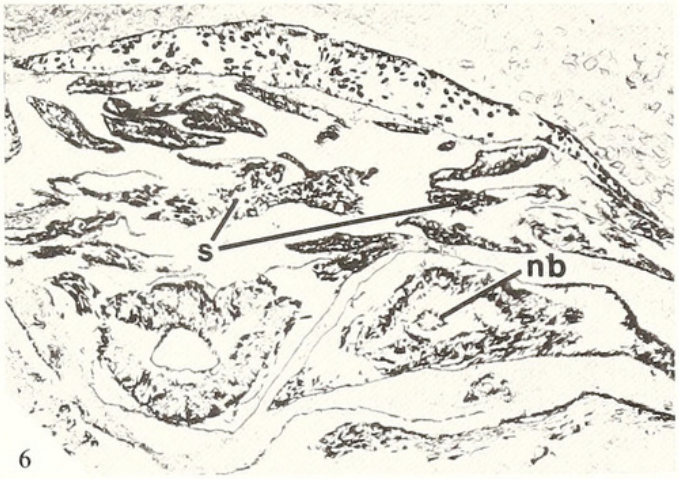
Individual grains are monosaccate with a monolete suture proximally and usually two dark, crescent-shaped areas distally (Bharadwaj 1954; Pl. 16, fig. 4). The latter areas have been interpreted by previous authors as compression folds (Bharadwaj 1956), which may delimit the germinal area on the distal surface (Potonie and Lele 1961; Clarke 1965). Maximum saccus diameter observed was 118 μm, while the corpus diameter averages 50 μm. The girdling saccus is formed by separation of the sexine from the nexine in the equatorial region, and exhibits prominent internal reticulations (Pl. 16, figs. 3, 4). The intrareticulum is generally finer than that of most *Florinites* species. In section view the intrareticulum attaches the saccus to the corpus across the distal pole (Pl. 16, fig. 4). In our specimens the nexine is more dense optically at the point where the saccus separates from the corpus at the margins of the distal surface (Pl. 16, figs. 3, 4). This produces two dark, crescent-shaped areas like those interpreted as folds by previous authors. It is also clear from our specimens that there is no thin area distally, through which germination may have occurred (Pl. 16, fig. 4). On the proximal surface the corpus and saccus are more completely fused, and form a more optically dense exine (Pl. 16, fig. 4). Previous authors have interpreted the exine on the proximal surface of *Potonieisporites* as thicker than that of the distal surface. Scanning electron microscopy reveals that the proximal surface of the corpus is ornamented by irregular crowded rugae (Pl. 16, figs. 5, 6). In areas where the outer surface of the exine has been removed from the proximal surface of the grain (e.g. Pl. 16, fig. 6 at rectangle), the inner exine layer (= nexine) shows an ornamentation of dense, irregular granula (Pl. 16, fig. 5 at bottom). Therefore, in these specimens, intrareticulations are absent from the proximal surface of the grains. In addition, the monolete suture is clearly open in all specimens (Pl. 16, figs. 4, 6). This, together with the absence of a thin area on the distal surface, indicates that germination was proximal, and that these grains fall within the concept of prepollen (Renault 1896; Schopf 1938; 1948; Rothwell and Mickle 1982).

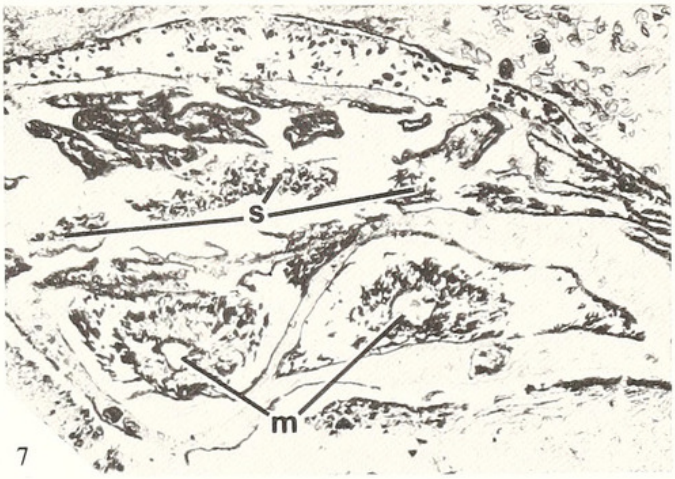
EXPLANATION OF PLATE 14

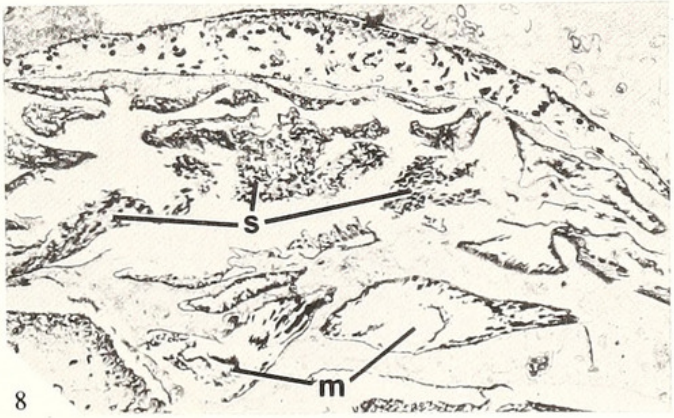
Figs. 1–8. *Lebachia lockardii* sp. nov. Holotype, basipetal series of transverse sections illustrating ovule attachment and orientation. All M26 B Top series, ×20. a, primary cone axis; b, bract; f, fertile scale; m, micropyle; nb, nucellar beak; o, ovule. 1, section near levels of ovule attachment. Note broad base of ovule at left (just below level of attachment) and bilobed segments of ovule at right (at arrows; just above level of attachment to fertile scale). Primary cone axis and secondary shoot axis at lower left, with sterile scales and subtending bract at top, No. 76. 2, lobes of right ovule joined, No. 75. 3, right ovule base attached at fertile scale with cuticle continuous at arrow. Left ovule at level of seed cavity with nucellus and megaspore membrane, No. 72. 4, right ovule flattened at level of nucellus and megaspore membrane, No. 67. 5, sterile and fertile scales at tip of flattened secondary shoot. Left ovule with nucellar beak, No. 61. 6, left ovule showing micropyle; right ovule with nucellar beak, No. 56. 7, micropyles of both ovules narrowing. Note pollen grain in ovule at right, No. 53. 8, apexes of both ovules near base of fertile shoot, No. 48.











MAPES and ROTHWELL, *Lebachia* cones

DISCUSSION

L. lockardii displays both the general morphology and the cuticular features that delimit the genus as circumscribed by Florin, and presents the first anatomical evidence upon which to characterize and interpret development and reproductive biology within the walchian conifers. The new species also provides an opportunity to clarify the nature of several features that have been interpreted as significant to the evolution of more modern conifers, and to explore the significance of variation among specimens of the Palaeozoic Lebachiaceae. As is typical of previously described *Lebachia* ovulate cones, *L. lockardii* consists of a primary axis that bears helically arranged bifid bracts with axillary fertile shoots. The fertile shoots each have a short axis that bears numerous scale-like leaves, one or two of which have terminal ovules. Fertile scales are consistently located adjacent to the primary axis.

The different expression of features preserved by compression vs. permineralization precludes detailed specific comparison and assignment to a previously described species. However, split surfaces of slabs containing fertile *L. lockardii* reveal general morphologic features, and incomplete branches are attached below some cones. Numerous isolated vegetative branches are also present in the matrix and will undoubtedly yield additional information regarding branching patterns. As described by Florin and others, the *Lebachia* compression species most comparable to *L. lockardii* are *L. parvifolia*, *L. americana*, *L. hypnoides*, and *L. piniformis*. However, until information about the internal features of these species has been obtained, serious questions regarding their specific relationships to *L. lockardii* will remain. Features of *L. lockardii* that could not have readily been determined from compression remains alone include the inverted orientation of the ovules and the bilateral symmetry of the secondary shoots. Our permineralized, uncompressed cones clearly demonstrate the bilateral symmetry of the secondary shoots. Each secondary shoot has a crescentic stele and a smaller number of scales toward the primary cone axis. While these features are useful for separation of *L. lockardii* from other species of the genus, some of the apparent differences may also be due to our less complete understanding of compression specimens.

Prior to the discovery of *L. lockardii*, *Moyliostrobus* Miller and Brown (1973) was the only Palaeozoic conifer cone known in anatomical detail. *M. texanum* is a silicified voltzialean cone apex from the lower Permian of west Texas (Miller and Brown 1973). Each flattened fertile shoot bears thirty to fifty sterile scales and one apically cleft erect ovule attached at the shoot base. Each fertile shoot is subtended by a non-bifid bract. Cuticular features are not known, but the cone morphology allows both for assignment to the Lebachiaceae and for generic separation from *Lebachia* and *Ernestiodendron*. While *Moyliostrobus*, *Ernestiodendron*, and *L. lockardii* all have flattened fertile shoots in the axils of helically arranged bracts, the bracts of *Lebachia* and *Ernestiodendron* bifurcate at the tip. Mesozoic voltzialeans all display much more reduced and modified fertile shoots, and, like *Moyliostrobus*, commonly have simple, non-bifid bracts (Miller 1977, 1982).

Florin was the first to perceive the basic homology among fructifications of cordaites, early conifers, and modern conifers. Specifically, he recognized the equivalence of the fertile secondary

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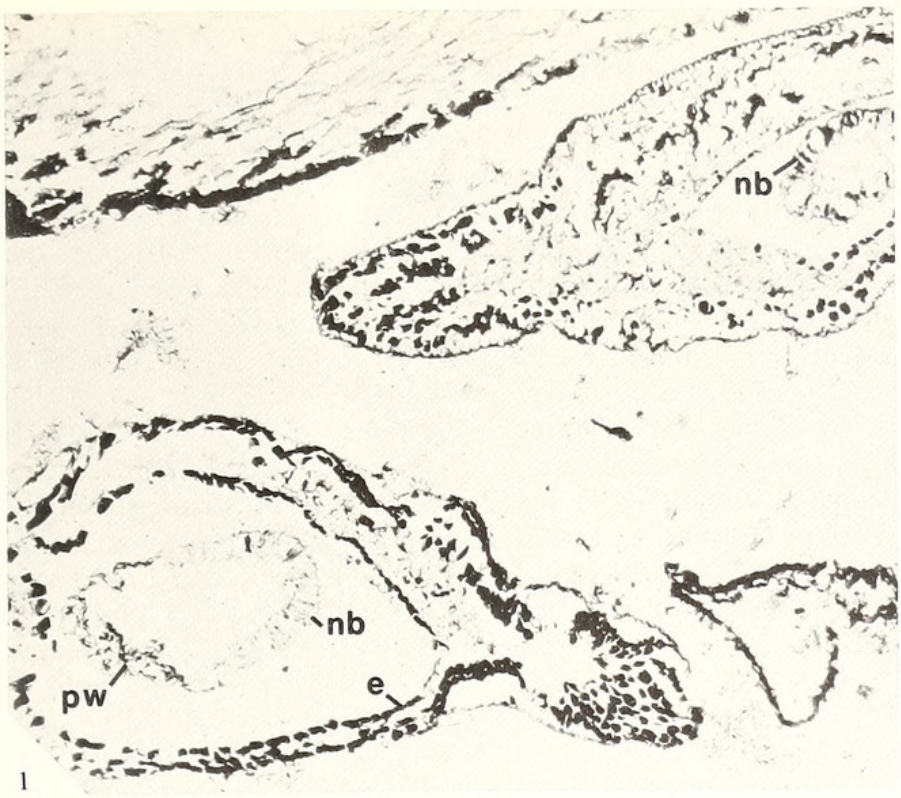
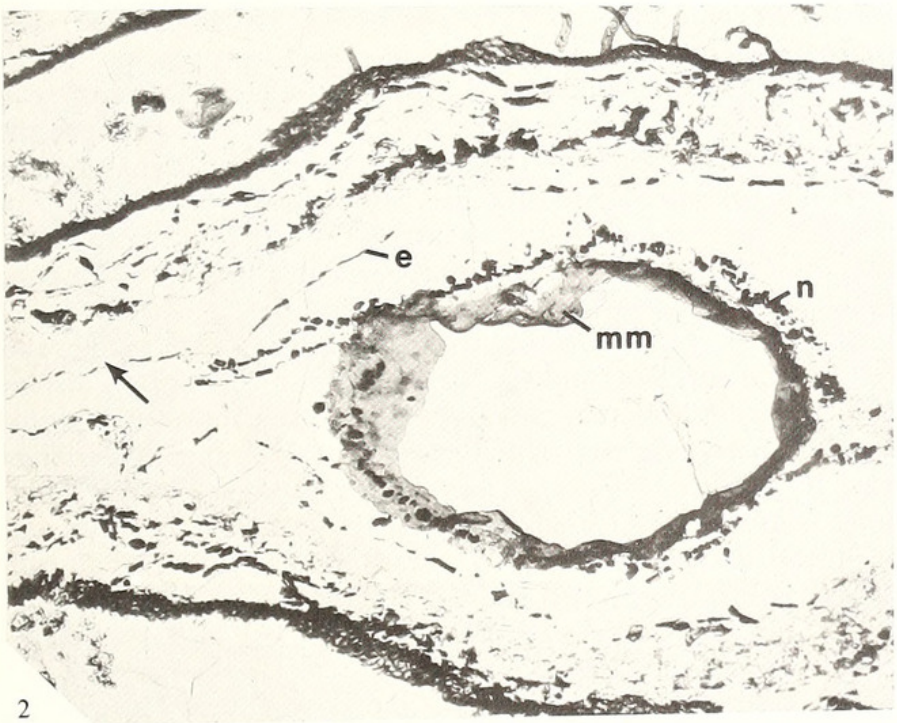
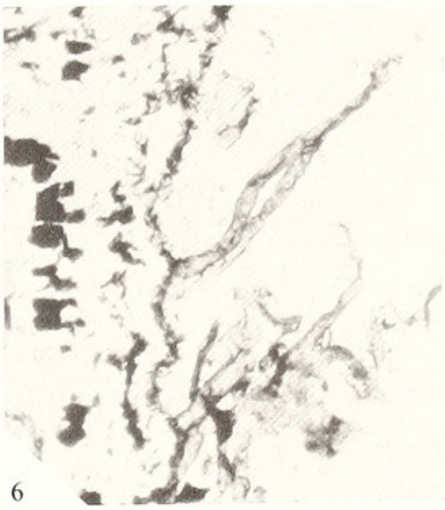
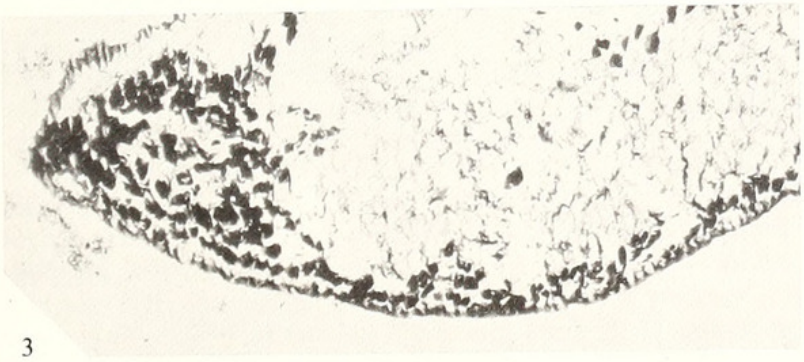
EXPLANATION OF PLATE 15

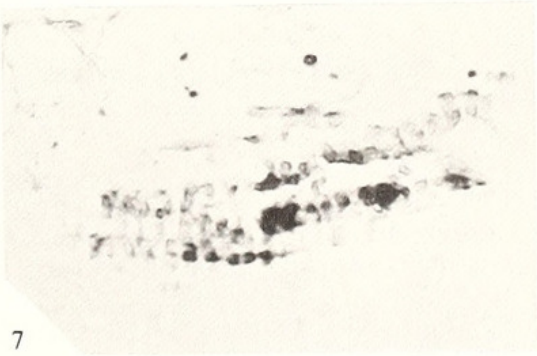
Figs. 1–7. *Lebachia lockardii* sp. nov., ovule histology. e, epidermis; mm, megaspore membrane; n, nucellus; nb, nucellar beak; pw, pollen chamber wall. 1, two ovules in transverse section. Nucellus of left ovule obliquely sectioned through pollen chamber wall and nucellar beak, M148 B Top No. 23, ×92. 2, transverse section through seed cavity. Arrow indicates position of undifferentiated sclerotesta. Note epidermal hairs at top and prominent epidermal papillae at bottom, M148 B Top No. 12, ×73. 3, two zoned 'sarcotesta', M148 A Bot No. 7, ×81. 4, *Potonieisporites* grain in pollen chamber, M145 B Top No. 4, ×71. 5, cuticle of nucellar epidermis, M148 B Top No. 13, ×105. 6, hairs on ovule integument, M148 B Top No. 19, ×170. 7, integumentary tracheids near ovule base, M148 B Top No. 7, ×670.











MAPES and ROTHWELL, *Lebachia* cones

shoots of *Lebachia*, *Ernestiodendron*, and *Cordaianthus* to the ovuliferous scales found in cones of more modern conifers (e.g. *Pinus*). In seeking to bring order to the heterogeneous morass of compressed plant fossil fragments attributed to *Walchia*, he examined branching patterns of vegetative shoots, cuticular features, and basic cone organization.

As characterized by Florin, *L. piniformis* and *E. filiciforme* are quite distinct. In particular he draws attention to ovule orientation, fertile shoot morphology, and patterns of stomatal arrangement. While as end members these taxa are distinct, examination of Florin's illustrations clearly demonstrates these features represent morphologic continua within the walchian complex. To some extent, Florin recognized this and identified in his studies (1938–1945) several species of cones as *Walchiostrobus* and *Walchianthus*, and several species of vegetative and fertile shoots as '*Walchia* (*Ernestiodendron*?)' or '*Walchia* (*Lebachia*?)'. For example, Florin illustrates a continuum of cuticular features in his photographs. Though not emphasized by Florin, many of the cuticles show narrow bands of densely packed stomata with shared subsidiary cells in some areas, and broad internally spacious bands with no shared subsidiary cells in other areas. In still other areas, the bands are so wide that there appear to be single isolated rows of stomata. Examples of stomatal pattern variation illustrated by Florin (1938–1945) for specific taxa are as follows: *L.* piniformis, Taf. 1–2, abb. 16, 17; Taf. 5–6, abb. 1; Taf. 15–16, abb. 7, 26, 27; Taf. 21–22, abb. 1, 2; *L. hypnoides*, Taf. 103–104, abb. 9; Taf. 107–108, abb. 16; *L. parvifolia*, Taf. 31–32, abb. 5; Taf. 37–38, abb. 13; *L. laxifolia*, Taf. 53–54, abb. 12, 14, 15; Taf. 55–56, abb. 12, 19; *L. intermedia*, Taf. 77–78, abb. 6–8; *L. angustifolia*, Taf. 39–40, abb. 11–13; *L. speciosa*, Taf. 65–66, abb. 9; *L. mucronata*, Taf. 75–76, abb. 5, 6; *E. filiciforme*, Taf. 111–112, abb. 15, 16; Taf. 113–114, abb. 9; Taf. 121–122, abb. 18; Taf. 127–128, abb. 13; *Walchianthus cylindraceus*, Taf. 155–156, abb. 15; *W. crassus*, Taf. 157–158, abb. 2; and *W. papillosus*, Taf. 157–158, abb. 8, 10.

This variation is of particular interest as the arrangement of the stomata in either bands or rows is the strongest point separating cuticles of *Lebachia* from those of *Ernestiodendron*. Comparison with *L. lockardii* reveals a comparable range of variation among the cuticles of its ovulate cones (Pl. 12, figs. 1, 3, 6), with typical lebachiate parallel bands and also isolated rows of stomata. The parallel bands of irregularly diposed stomata are commonly present on the adaxial surface of bracts and large scales, while the more widely separated longitudinally oriented single rows and/or isolated stomata usually occur on the very papillate abaxial or lower leaf surfaces.

Florin has described similar cuticles from vegetative leaves of *L. parvifolia*. On these, parallel bands of stomata are present on the adaxial surfaces, and the abaxial leaf surfaces often display 'more or less disaggregated bands of separate longitudinal rows of mostly lengthwise oriented stomata' (Florin 1940). *L. lockardii* and *L. parvifolia* each exhibit a considerable range of cuticular features including those usually used to separate *Lebachia* from *Ernestiodendron*. While Florin considered the single rows of stomata characterizing *Ernestiodendron* to be present on both surfaces of its leaves, their occurrence on the abaxial surfaces of *L. parvifolia* and *L. lockardii* calls

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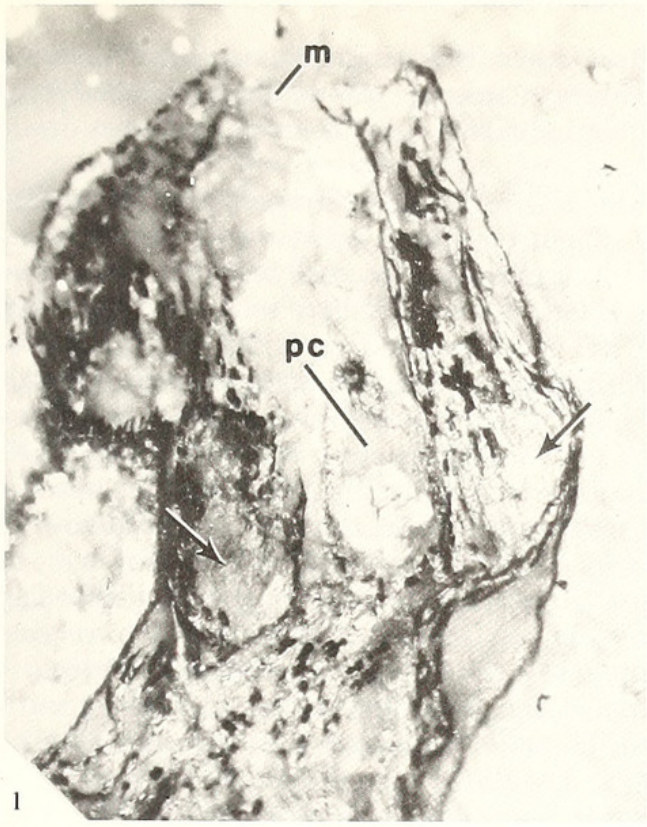
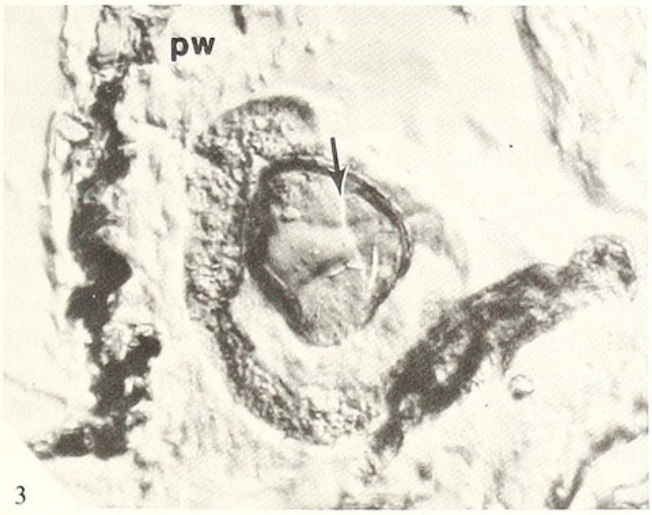
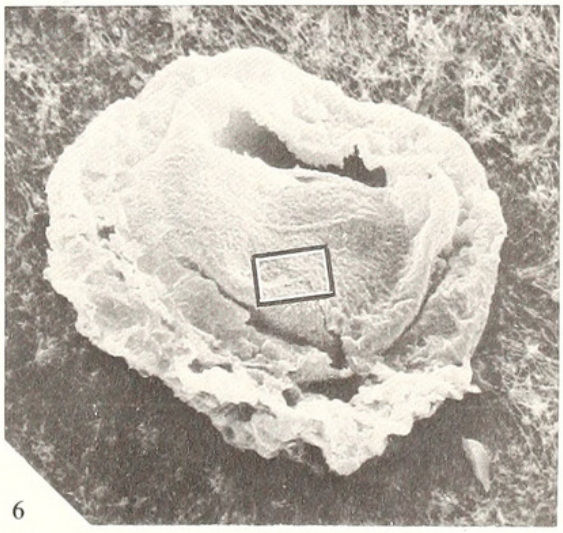
EXPLANATION OF PLATE 16

Figs. 1–6. *Lebachia lockardii* sp. nov. and *Potonieisporites*. m, micropyle; nb, nucellar beak; pc, pollen chamber; pw, pollen chamber wall. 1, oblique longitudinal section through apex of ovule showing pollen chamber, micropyle, and patches of undifferentiated sclerotesta (at arrows). Light area in pollen chamber is crystalline calcite surrounding grain shown in fig. 2 (polarized reflected light), M148 A Bot No. 7, ×89. 2, oblique longitudinal section near section in fig. 1, note nucellar beak, *Potonieisporites* grain and patches of undifferentiated sclerotesta (at arrows) (polarized reflected light), M148 A Bot No. 9, ×89. 3, grain in pollen chamber of fig. 2, arrow indicates monolete (Nomarski DIC), M148 A Bot No. 9, ×440. 4, grain in section view. Note attachment of sexine to nexine by internal reticulum on distal surface (at arrow). Also note dense exine adjacent to open monolete on proximal surface, M26 B Top No. 55, ×680. 5, proximal ornamentation. Tear reveals inner exine at bottom, M26 SEM-8, ×8000. 6, grain with collapsed saccus. Proximal view with open monolete at top. Rectangle indicates area of fig. 5, M26 SEM-3, ×800.







MAPES and ROTHWELL, *Lebachia* cones

to question the taxonomic importance of this feature. Other features that intergrade totally and therefore cannot be considered taxonomically diagnostic are cuticular papillae and epidermal hairs. The relative abundance of these probably more meaningfully reflects environmental stresses during growth.

An additional cuticular feature of *L. lockardii* can also be seen in Florin's illustrations and drawings of various *Lebachia* species (1938–1945). Small epidermal cells with a raised central circular area that is open or covered to some extent with cuticle, occur generally outside the stomatal bands (Pl. 12, figs. 2, 4, 5). Similar cells on many lebachian cuticles have been interpreted by Florin as hair bases (for examples, see Florin 1938–1945: Taf. 1–2, abb. 12, 13, 19; Taf. 31–32, abb. 10, 11, 19, 20; Taf. 49–50, abb. 13, 15, 16; Text-abb. 20A). Cells of this type somewhat resemble the podocarpalean 'Florin rings' described by Buchholz and Gray (1948) and Florin (1931, 1958) from living and fossil *Torreya*, where the surface cuticle of the subsidiary cells is fused into an optically distinct, differentially thickened, cuticular flange or ring that surrounds the stomatal opening. Certain fossil and modern *Araucaria* species display epidermal features that even more strongly resemble the distinct cuticular structures of *L. lockardii* and other *Lebachia* species. However, the araucarian epidermal features represent sunken stomata covered with waxy plugs or cuticular flaps (Stockey and Taylor 1978*a*, *b*), rather than single cells as in *L. lockardii*. Unlike those of *Aruacaria* or *Torreya*, in no instance do the distinct circular rimmed areas on *L. lockardii* cuticles appear to be associated with either abortive or regular stomata. While abortive stomata were described by Florin for cuticles of *Lebachia* (1938–1945 text and illustrations such as Taf. 1–2, abb. 20; Taf. 3–4, abb. 7; Taf. 5–6, abb. 3; Taf. 17–18, abb. 13 for *L. piniformis*, and Taf. 39–40, abb. 18 for *L. angustifolia*), especially in the middle zones between bands of regular stomata, none has been observed on *L. lockardii*. On *L. lockardii* the circular rimmed areas apparently result from collapse of a very large papilla or a very short broad, unicellular hair.

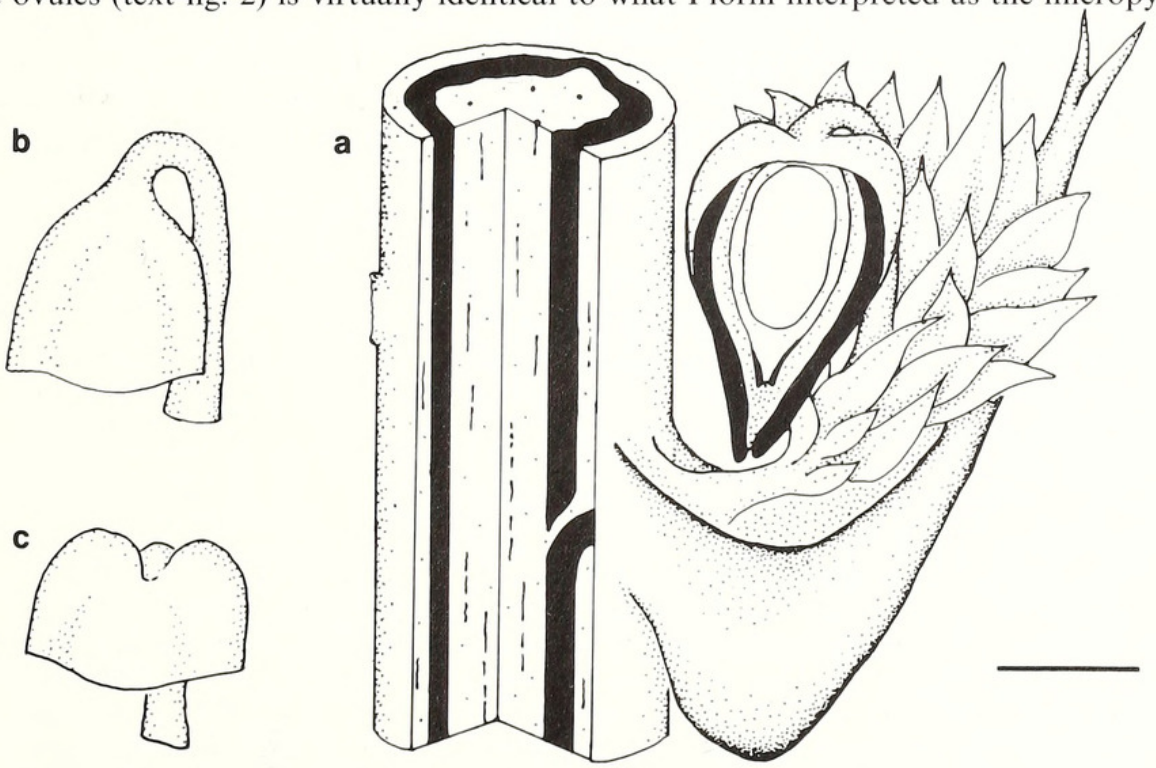
Ovulate cone morphology has been used as an important criterion for separating *Lebachia* from *Ernestiodendron*. The morphological features of *Lebachia* cones are considered by Florin to be more primitive than those of *Ernestiodendron* (Florin 1951). Though both are compound, *Ernestiodendron* cones are typically quite lax. Each fertile shoot axis is flattened with few to no sterile scales and three to seven megasporophylls, each bearing a single terminal ovule. *Ernestiodendron* ovules have been interpreted as either erect with the micropyle oriented outward, or inverted with the micropyle oriented downward and in toward the base of the fertile shoot (Florin 1951, fig. 34). Prior to the discovery of *L. lockardii*, all *Lebachia* ovules were interpreted as erect, with the micropyle oriented outward and away from the primary cone axis. Interpretive drawings of two detached fertile shoots of '*Walchiostrobus* (*Ernestiodendron*?)' sp. are figured by Florin (1951, fig. 34*e*, *f*). These are apparently drawn from specimens illustrated in his monograph (1938–1944; Taf. 163–164, abb. 3–4, Taf. 153–154, abb. 20–22), representing partially coalified impressions from the lower Permian at Thüringer Forest in Germany. The fertile shoots seem to be somewhat intermediate morphologically between those of *Lebachia* and *Ernestiodendron* as delimited by Florin, in that they each may have numerous fertile and numerous sterile scales. One shoot apparently bears four inverted ovules; the other bears four or five ovules that may be erect.

The ovulate cones of *L. lockardii* also display several morphological features which appear to be intermediate between *Lebachia* and *Ernestiodendron* as separated by Florin. There are numerous scales attached to the flattened fertile shoot axis, which often bears two megasporophylls (= fertile scales) with apparently functional terminal ovules. Some shoots also have one to three scales with poorly preserved or possibly abortive ovules (Pl. 13, figs. 2–4). In addition, attached ovules are clearly inverted, with their micropyles oriented toward the junction of the flattened fertile shoot and the primary cone axis, features generally considered restricted to *Ernestiodendron*. In general appearance, however, *L. lockardii* cones are plainly lebachiate. They are relatively compact, have numerous sterile scales per fertile shoot, and display broad stomatal bands on many leaves.

The erect ovule orientation ascribed to all previously known *Lebachia* species appears to be based primarily on cones of *L. piniformis* and *L. hypnoides*. Florin considered many of the ovules in these cones to be of *Samaropsis*-type. He also recognized two ovule types on species of

Cordaianthus, *Samaropsis* for the stratigraphically older forms (Westphalian) and *Cordaicarpus* for the more recent strobili (Stephanian). Compressed platyspermic ovules of both types are often found in sediments that yield cordaites and *Walchia*. The biological affinities of these ovules, however, are not always with only cordaites or conifers (Rothwell 1981). *Samaropsis* Goeppert (1864–1865) designates broadly winged, compressed ovules with a cleft apex forming two horns. *Cordaicarpus* or *Cordaicarpon* (Geinitz 1862) is employed for rounded, compressed ovules with a narrowed border and often a cordate base. Incomplete samaropsid impressions without the broad sarcotestal border are included in *Cordaicarpus* (Seward 1919). *Samaropsis*-like ovules have been observed on the cordaitean fructification *Cordaianthus pitcairnae* (Seward 1919), on the pteridosperm foliage *Pecopteris pluckeneti* (Schlotheim) Brongniart (Kidston 1886), and possibly on *Emplectopteris triangularis* (Andrews 1961).

As emphasized above, the ovules of *L. lockardii* are terminal and inverted, while those of *L. piniformis*, *L. hypnoides*, and other lebachias have all been interpreted as terminal and erect. It is clear that Florin considered the attached *Lebachia* ovules to be comparable to isolated ovules such as *Samaropsis delafondi* (Florin 1938–1945, Taf. 21–22, abb. 17; Taf. 161–162, abb. 20). In addition, he describes ovules in cones of *L. hypnoides* as most comparable to impressions illustrated by Goeppert (1864–1865) as '*Cardiocarpus orbicularis*'. In describing these ovule impressions (Florin 1938–1945, Taf. 109–110, abb. 23–25), Florin draws attention to the fissured coaly crack in the narrow flange beyond the seed cavity (toward the distal end of the cone), and mentions the lack of preservation at the other end of the ovule (which he considers to be the chalazal end of the ovule). Examination of the ovule-bearing fertile shoots macerated from cones of *L. piniformis* (Florin 1938–1945) also reveals the bilobed end of an ovule with a conspicuous groove and oval scar below the cleft. Although Florin interpreted this groove as the micropyle, its appearance is remarkably like the chalazal end of the isolated *Samaropsis* ovules that he also figured (Taf. 161–162, abb. 1–5, and especially abb. 20). Moreover, the distally directed, cordate chalaza of *L. lockardii* ovules (text-fig. 2) is virtually identical to what Florin interpreted as the micropylar end



TEXT-FIG. 2. *Lebachia lockardii* sp. nov. 1*a*, reconstruction of cone segment showing general features of axis, bract, and fertile shoot. Note orientation of ovule, which has been sectioned longitudinally in the major plane to reveal nucellus and megaspore membrane. Vascular tissue of axis and sectioned surface of integument represented in black. 1*b* and 1*c*, ovule bases showing range of variation in structure and attachment to fertile scales. Scale bar = 1 mm.

of his compressed *Lebachia* ovules. Similarities shared by the chalaza of Florin's *Samaropsis* and *L. lockardii* ovules, and what Florin interpreted as the apex of *L. hypnoides* ovules, include cordate shape, oval scar below the groove (attachment scar of *Samaropsis* sp. and *S. delafondi*, and *L. lockardii*), and gentle taper toward the other end of the ovule (cf. text-fig. 2; Florin 1938–1945, Taf. 161–162, abb. 20; Taf. 21–22, abb. 17; and Taf. 19–20). In all these features the ovules of *Lebachia* figured by Florin (1938–1945, 1951) are consistent with the interpretation that they may be recurved or inverted at the tips of their fertile scales.

Ovule ontogeny and reproductive biology

The attached ovules of *L. lockardii* display relatively narrow ranges of variation in size, integument structure, nucellus and pollen chamber histology, and gametophyte disposition that suggests they were all preserved at about the same developmental stage. Nevertheless, comparisons with similar features of ovules of extant conifers and other Palaeozoic gymnosperms provide an opportunity to interpret several features of development and reproductive biology (Rothwell 1971, 1980, 1982*a*). In general, development of the integument, nucellus (including pollen chamber), and gametophytes are co-ordinated with pollination, abscission, and fertilization in a sequence that is characteristic of the taxon under consideration (e.g. *Chamaecyparis nootkatensis*, Owens and Molder 1975; *Picea engelmannii*, Singh and Owens 1981; *Callistophyton*, Rothwell 1980). In *L. lockardii* the ovules show features of the integument that are like sarcotesta and endotesta of other immature gymnosperm ovules, but no lignified sclerotestal cells are present in most of our specimens. In only two *L. lockardii* ovules have possible remnants of thick-walled sclerotestal cells been identified; these are confined to two groups of cells in the minor plane of symmetry at the level of the pollen chamber. These areas appear as lighter patches to either side of the pollen chamber in the specimen figured on Plate 16 (figs. 1, 2). Their disposition is consistent with that of mature fibres at the onset of sclerotestal differentiation in other gymnosperm ovules (Rothwell 1971, 1980), where cells are lignified first in the minor plane at the level of the pollen chamber and differentiation generally proceeds basipetally (Quisumbing 1925). This interpretation is also supported by the presence of extremely thin-walled and delicate cells between the endotestal epidermis and the sarcotesta in some specimens (e.g. Pl. 15, fig. 2 at left). Cells of this type are identical to those that have been interpreted as immature sclerotesta in several other Palaeozoic gymnosperm ovules (Stidd and Cosentino 1976, fig. 14: Rothwell 1971, 1980).

Several features of the nucellus in *L. lockardii* also suggest that the ovules are immature. During differentiation the nucellus of gymnosperm ovules characteristically becomes progressively thinner, until in the mature ovules it is represented by only a thin, cuticular membrane (Singh 1961; Rothwell 1971). The several cell layers of nucellus preserved in the midregion and at the base of the pollen chamber in *L. lockardii* are characteristic of early ontogenetic stages of many gymnosperm ovules, where the integument is not fully matured. The absence of cellular megagametophytes in the *L. lockardii* ovules further suggests their immaturity. Unless the *L. lockardii* megametophytes did not exhibit the free nuclear stages that typically characterize all but the most mature of other conifer ovules (Singh 1978), or the cellular megagametophytes of *L. lockardii* were not preserved, this feature is consistent with the general developmental interpretation of the other tissues.

The histological features of integument, nucellus, and megagametophyte, interpreted above as indicators of ovule immaturity, are similar to those in Pennsylvanian gymnosperms with conifer-like reproductive biology, and also to ovules of many extant gymnosperms shortly after the stage appropriate for pollination (e.g. Rothwell 1971; Owens *et al.* 1981). The occurrence of pollen grains in the pollen chamber of several *L. lockardii* ovules (Pl. 15, fig. 4; Pl. 16, figs. 1–3) is also consistent with this interpretation. Shortly after pollination in many gymnosperm ovules, continued development of the integument leads to closure of the micropyle (Dupler 1920; Quisumbing 1925; Singh 1961; Rothwell 1971, 1980). Unless this developmental feature did not occur in *L. lockardii*, the open micropyles of all available specimens (e.g. Pl. 14, figs. 7–8; Pl. 16, figs. 1–2) suggest that they were preserved soon after pollination. If true, then ovule disposition in the specimens under investigation also provides evidence for the mode of pollination.

As stressed in the description of *L. lockardii*, the ovules are inverted with the micropyle located between the primary axis and the base of the fertile shoot (Pl. 13, fig. 1). Also, the minimum diameter of the micropyle (approx. 100 μm) is only slightly larger than the longest measurable dimension of the prepollen grains actually present within the pollen chamber of several ovules (viz., 95 μm). This combination of features makes it unlikely that the grains found their way into the pollen chambers by wind currents alone. While the occurrence of a pollination drop mechanism has been conclusively documented in only one Palaeozoic gymnosperm (Rothwell 1977), the prevalence of such a mechanism is extant conifers (Singh 1978), together with the features of ovule orientation and prepollen/micropyle size ratio, provides at least indirect evidence that a similar mode of pollination characterized *L. lockardii*.

The discovery of *L. lockardii* and associated permineralized remains provides the first extensive anatomical evidence for the reproductive organs of the earliest conifers, and also allows for the description of many morphological features not discernible from compressed specimens. Features important to our understanding of early conifer structure are the bilateral symmetry of the secondary fertile shoots and the inverted nature of the ovules. True bilateral symmetry also sets *L. lockardii* ovules apart from the cardiocarpalean ovules of Upper Carboniferous cordaites and pteridosperms (Rothwell 1982), and reveals an additional specialization among the reproductive structures of pre-Permian gymnosperms. The *L. lockardii* specimens further allow for the first correlation of epidermal features with internal anatomy of primitive conifers. The abundance of cuticular material forms the basis for evaluating the range of variability that may be expected of a single lebachian species. It is now clear that in both morphology and cuticular features walchian species may be far more variable than previously suspected.

From the viewpoint of phylogeny and evolution of the earliest conifers, *L. lockardii* allows us to test and support, with a new type of evidence, Florin's hypothesis of the structural homologies among ovulate cones of cordaiteans, Palaeozoic conifers, and modern conifers. Perhaps of greatest interest to students of fossil plant biology are the insights gained into the growth, development, and reproduction of the earliest conifers. It is now clear that *L. lockardii* had ovules that were pollinated while immature and still attached to the parental sporophyte, perhaps via a pollination drop mechanism. Likewise, the specimens support earlier interpretations of the mode of propagule dissemination in primitive gymnosperms (e.g. Emberger 1944; Rothwell 1982*a*) by providing the first histological evidence for early ovule abscission among Palaeozoic seed plants.

While *L. lockardii* and the associated walchian organs allow us to begin formulating the first whole plant biology concept for a pre-Permian conifer, the new collection and preparation techniques employed in the study are of perhaps even greater potential significance. Through these methods we are now able to investigate a far greater range of features for plants that have previously been known only from compressed or mold-cast remains. In this regard we may now expect to begin characterizing in a biological sense the plant communities that inhabited the extrabasinal lowlands ('Upland Floras' of many previous workers; Pfefferkorn 1980), and thereby dramatically enhance our understanding of late Palaeozoic tropical vegetation.

Acknowledgements. We thank H.-P. Schultze, Division of Vertebrate Paleontology, Museum of Natural History, University of Kansas; G. A. Leisman, Emporia State University, Ks.; A. Graffham and R. Cowan, Geological Enterprises, Okla.; and especially R. H. Mapes, Department of Geology, Ohio University, for field assistance and access to collections. M. J. Heaton, Erindale College, University of Toronto, Ontario, Canada; W. D. Tidwell, Department of Botany, Brigham Young University Ut.; S. H. Mamay, U.S.G.S., U.S.N.M., Washington, D.C.; Wm. C. Darrah, Gettysburg, Pa.; and T. L. Phillips and R. Winston, Department of Botany, University of Illinois, Urbana, Ill., communicated ideas and information regarding comparable *Walchia*-bearing sediments. We thank W. Lockard and A. Lyke for special permission to collect. We also appreciate comments and suggestions provided by reviewers. Acknowledgement is made to the donors of the Petroleum Research Fund, administered by the American Chemical Society, for partial support of this research (PRF No. 13329-G2 to G.M.). This work was also supported in parts by grants from the National Science Foundation (DEB80-10793 and DEB81-09682 to G.W.R.) and the Ohio University Research Committee (Grant 9644 to G.M.).

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Typescript received 29 June 1982
Revised typescript received 8 February 1983

Mapes, G and Rothwell, G W . 1984. "Permineralized ovulate cones of Lebachia from late Palaeozoic limestones of Kansas." *Palaeontology* 27, 69–94.

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