ON THE STRUCTURE OF *CORDAITES FELICIS* BENSON FROM THE LOWER PENNSYLVANIAN OF NORTH AMERICA

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ABSTRACT. New material of *Cordaites felicis* Benson is described from lower Pennsylvanian petrifactions collected in eastern Kentucky. Additional information about the anatomy and epidermal pattern is provided and an emended diagnosis is presented together with a discussion of other structurally preserved cordaitean leaves.

IN 1912 Margaret Benson described a new anatomical species of cordaite leaf, *Cordaites felicis*, from British petrifaction material equivalent to lower Pennsylvanian in age. Of petrified cordaitean leaf forms, *C. felicis* is similar to three species which had been distinguished as *C. loculosus* Felix (1886), *C. robustus* Felix (1886), and *C. wedekindi* Felix (1886). Subsequent to Benson's work, Koopmans (1928) made a comparative study of Felix's species from material collected from the Netherlands and regards them as synonyms of *C. felicis*. Seward (1917) considered *C. felicis* as probably being equivalent to petrified specimens of *C. principalis* (Germar) Geinitz (Germar 1848, Geinitz 1855, Renault 1879, Stopes 1903, Harms and Leisman 1961). Harms and Leisman (1961) have suggested that another cordaite leaf which they studied, *C. crassus* Renault (Renault 1879, Seward and Sahni 1920, Darrah 1940), might also be equivalent to *C. felicis* because the vascular bundles are sometimes completely separated by fibrous tissue, a characteristic that has been generally used to delimit *C. felicis*. Darrah (1940) has also mentioned a similarity between *C. crassus* and *C. felicis*, and has reported the presence of *C. felicis* in a check list of an Iowa coal ball flora (Darrah 1941).

SYSTEMATIC DESCRIPTION

Order CORDAITALES

Genus CORDAITES Unger 1850

Cordaites felicis Benson 1912

Emended diagnosis. Leaves 0·1–1·0 mm. thick with irregular surfaces and rounded margins. Vein frequency of 10–25 per cm. determined by distance from point of attachment; veins separated by longitudinally directed fibrous partitions (primary ribs) that are continuous from abaxial to adaxial surfaces. Identical thick-walled fibres in longitudinal bands above and below veins (primary ribs) and similar hypodermal fibrous masses occasionally between vein and intervein partitions (secondary ribs), dichotomizing veins in basal sections, decreasing in frequency toward tip. Mesophyll constructed of parenchyma plates of laterally elongate cells, vertically attached to lower and upper epidermis, laterally to vein and intervein partitions; vein surrounded by outer sheath 2–7 cells thick and continuous with mesophyll plates. Mesarch xylem of 1–10 larger centripetal metaxylem tracheids (20–57 μ diam.) with secondary wall thickenings of closely spaced

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scalariform bars and multiseriate circular bordered pits, and smaller (7–12 μ diam.) less well-developed centrifugal metaxylem tracheids that partially surround centripetal elements, protoxylem tracheids 3–6 μ in diam. and difficult to delimit in all veins, presumed phloem elements typically crushed; inner sheath tracheids present on flanks and abaxial side of bundle. Stomata sunken and longitudinally oriented in rows, 1–2 rows between vein and intervein partition on the adaxial epidermis and up to 8 rows on the abaxial epidermis.

Type locality. The Colliery at Shore-Littleborough, Lancashire.

Stratigraphic position and age. Westphalian A.

Type material. (Lectotype) Specimen designated 365.2 (fig. 2 of Benson 1912), Palaeontological Collection, British Museum (Natural History).

MATERIALS AND METHODS

New material of *C. felicis*, which forms the basis of this study, provides additional information about the structure and phylogenetic relationships of this species. The specimens were collected from the Lewis Creek and Shack Branch localities in eastern Kentucky (Schopf 1961).

Anatomical features of the leaves were determined by the use of cellulose acetate peels. Additional foliage fragments were macerated from coal balls with dilute HCl and provided information on the three-dimensional structure and the surface ribbing patterns of the individual leaves. Surface configurations of the leaves were also observed by chipping coal away from leaves near the surface of the coal balls. Following the technique of Florin (1931), Ledran (1960), and Harms and Leisman (1961), small pieces of coal ball containing only cordaite leaves were completely macerated in Schulze's solution. Cuticles obtained by this process were examined to determine epidermal features. Because of the nature of the material no additional clearing or staining was necessary.

Material used in this study includes slides 3460–3745, cellulose acetate peels, and macerated cuticles from Coal Balls 121, 144, 145, 493, 1460, and 1744, all of which are included in the Paleobotanical Collection, Department of Biological Sciences, University of Illinois at Chicago Circle. Specific designations of figured specimens in this paper are included with plate explanations.

STRATIGRAPHY

Benson's specimens of *C. felicis* were obtained from the mine at Shore Littleborough, Lancashire. The stratigraphic position of this coal, according to Hoskins and Cross (1943) is in the Gannister beds, and is equivalent to deposits of lower Westphalian A, while the material of *C. felicis* described by Koopmans (1928) is from the Finefrau and Katharina horizons which are regarded as being equivalent to lower and upper Westphalian A respectively. Darrah (1941) has recorded *C. felicis* in a check-list of species of coal ball plants from Iowa which he indicates are equivalent to deposits of Westphalian C. An examination of the correlation chart prepared by Moore *et al.* (1940), however, shows these deposits equivalent to Westphalian D. The specimens of *C. felicis* used as the basis of this paper were collected at the Lewis Creek and Shack Branch localities in

Leslie County, Kentucky (Schopf 1961). According to Schopf, the coal balls occupy the position of the Copland Coal, immediately below the Magoffin marine zone, and are considered the oldest coal balls known in North America, intermediate in age between petrifactions recovered from the Lower Coal Measures of Britain and the Eastern Interior Basin deposits of North America. Moore *et al.* (1940) include the Copland Coa as equivalent to upper Westphalian B deposits. Huddle, Lyons, Smith, and Ferm (1963) regard the stratigraphic position of the Copland Coal as equivalent to rocks of middle Pennsylvanian age, while Prostka (1965) indicates that the Copland Coal is in strata of either lower or middle Pennsylvanian age, but makes no precise distinction.

One approach to determining the exact stratigraphic position of the Kentucky coal balls is to examine the floral components contained in these petrifactions. To date the described members of the flora from the Lewis Creek and Shack Branch localities include *Mitrospermum compressum* (Taylor and Stewart 1964), *Calamostachys binneyana* (Taylor 1967), *Bowmanites dawsoni* (Taylor 1969), and *Cordaites felicis*. All of these taxa, in addition to several studies currently in progress (e.g. *Conostoma anglo-germanicum*, *Medullosa* cf. *anglica*, *Pachytesta* cf. *olivaeformis*), are known from the Lower Coal Measures or equivalent strata. *Mitrospermum compressum* and *Cordaites felicis* have been reported but not described from Iowa coal balls of middle Pennsylvanian age (Darrah 1941). While the precise stratigraphic position of the beds containing the eastern Kentucky petrifactions is known, the application of the time stratigraphic terms lower and middle Pennsylvanian to these deposits is in dispute. On the basis of the floristics, however, it is our opinion that the floral components which are so unlike the well-known middle and upper Pennsylvanian age coal ball floras of North America, and so similar to the floras of Westphalian A in Europe, should be regarded as representing time equivalent strata of Westphalian A (= lower Pennsylvanian) in eastern Kentucky.

DESCRIPTION

External morphology. All of the specimens examined were leaf fragments; therefore no complete transverse sections of entire leaves were available. Leaf length, width, and shape are still incompletely known. In transverse section, the most complete leaf measures 32·0 mm. wide and is twice the maximum width reported by Benson in her description of *C. felicis*. According to the magnifications accompanying Benson's photographs of *C. felicis* (1912), the leaves illustrated agree in size with the specimens reported here. The data in the text portion of Benson's paper, however, appear to be $\frac{1}{10}$ of the size indicated by the photographs. It is therefore assumed that Benson's data must be multiplied by a factor of ten in order to correlate with the photographs. Leaf thickness in the Kentucky specimens ranges from 0·1 to 1·0 mm. Toward the margins the leaves gradually become thinner, but are not as thin as Benson's reported margin thickness of 19 microns (taken now as 190 μ).

Leaf margins are bluntly rounded (Pl. 10, fig. 2) and do not agree with the drawing of a supposedly young leaf similar to *C. felicis* which shows pointed margins (Scott 1924). The leaf epidermis, as exposed on the coal ball surfaces and by maceration with HCl, typically exhibits straight, axially oriented rows of ribs of uniform breadth (Pl. 10, fig. 1). According to the terminology of earlier workers, these structures are referred to as primary ribs, because they are the most prominent surface feature, and account for

raised areas on the left surface (Pl. 9, fig. 2). Macerated leaves indicate that the primary ribs are the result of longitudinally disposed fibrous hypodermal tissue associated with the veins and partitions between veins. From the surface it is impossible to tell whether a primary rib is associated with a vein or an intervein partition. Thinner secondary ribs are occasionally seen between these primary ribs (Pl. 10, fig. 1) and consist of smaller masses of fibrous hypodermal tissue often situated between the veins and intervein partitions (Pl. 9, fig. 2).

The leaves show a considerable variation in degree of surface relief in transverse section. Some have almost smooth external surfaces (Pl. 10, fig. 3), while others show an undulating surface, apparently due to crushing thinner walled cells except where the veins and intervein partitions give additional support (Pl. 9, fig. 1). Since many of the leaves have a smooth external surface in transverse section, it seems probable that originally there was little or no surface relief.

Internal anatomy. The most conspicuous characteristic of the internal anatomy of *Cordaites felicis* is the presence of complete epidermis-to-epidermis partitions between most of the veins (Pl. 9, figs. 1, 2). In transverse section these partitions resemble 'I' beams (Pl. 9, fig. 1); the top and bottom consisting of hypodermal masses of fibres which are 5–15 cell layers deep and 3–10 cells wide. Individual fibres are axially elongate (Pl. 9, fig. 5) and have small lumens. Fibre diameters range from 35 to 124 μ. In thicker fragments the partition consists entirely of these fibre-like cells, although the lumina of those cells in the centre of the partition are broader than the lumina of cells near an epidermis (Pl. 9, figs. 1, 2). In transverse sections that measure no more than about 0·75 mm. thick the fibres only extend about $\frac{1}{4}$ of the distance across the leaf from both the upper and lower epidermis (Pl. 10, fig. 3). The remaining central portion of the partition is made up of thin-walled rectangular cells with somewhat thickened corners and diameters that range between 23 and 46 μ. In paradermal section these cells measure 105–240 μ in length and 20–35 μ in width. Individual partitions extend uninterrupted throughout the length of the leaf fragments studied.

Approximately 10 % of the veins have neither hypodermal fibrous tissue nor thin-walled cells between them, although they are surrounded by a common sheath. This absence of partitions varies considerably with leaf thickness; leaf fragments thicker than 0·6 mm. have approximately 17 % of their veins unpartitioned. Leaves between 0·3 and 0·6 mm. thick have approximately 7 % unpartitioned veins. Specimens less than 0·3 mm. thick have about 4 % unpartitioned veins. It is assumed that the thicker leaf fragments represent the basal portion of the leaf, as has been suggested by Benson

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EXPLANATION OF PLATE 9

Figs. 1–5. *Cordaites felicis*. 1, Transverse section of portion of leaf showing fibrous ribs, disposition of veins, and intervein partitions (IP); arrow indicates position of inner sheath; C.B. 145A bot, # 39, ×60. 2, Transverse section of portion of leaf showing hypodermal fibrous masses responsible for primary (PR) and secondary (SR) surface ribs; C.B. 145A bot, # 31, ×115. 3, Oblique section of leaf showing mesophyll plates (MP); C.B. 145A bot, # 31, ×120. 4, Transverse section of vein and position of outer sheath (OS); C.B. 145F (2) top, # 67, ×130. 5, Longitudinal section of leaf showing thick-walled fibres of hypodermal masses and secondary wall thickenings of centripetal xylem elements; C.B. 145F (1) bot, # 9, ×155.

(1912), Harms and Leisman (1961), and other authors who have described various structurally preserved cordaite leaf species. The frequency of unpartitioned veins further supports the conclusion that divisions occur most frequently at the basal region of the leaf (Pl. 10, fig. 3). This feature of vein frequency is consistent with Benson's description of *Cordaites felicis*, and agrees with the presumed pattern of vein dichotomy in other structurally preserved cordaite leaf species (Harms and Leisman 1961) as well as those known only from compression specimens. Successive transverse sections indicate that when vein dichotomy occurs it is at a very acute angle.

Incomplete partitions that do not extend from epidermis to epidermis occur between less than 0·1 % of the veins. This frequency of incomplete partitions is not the case with *C. crassus* and *C. principalis* (Harms and Leisman 1961) which are otherwise described as being very similar to *C. felicis* in their internal organization.

The distribution of the veins of *C. felicis* is typical of most cordaite leaf species. The number of veins and associated tissues (vascular bundle sheath) ranges from 10 to 25 per cm. and in transverse section occupies 50–75 % of the leaf thickness. Masses of fibrous hypodermal tissue are located above and below the veins (Pl. 9, figs. 1, 2) and have the same general dimensions as those which form part of the intervein partitions (Pl. 9, figs. 1, 2). Vascular elements are surrounded by a sheath of thin-walled cells 4–7 cell layers thick that thins laterally to 2–3 cells in thickness (Pl. 9, fig. 4). In transverse section sheath cells are approximately circular in outline and have diameters that range from 20 to 40 μ while in paradermal section they are rectangular and measure 115–305 μ long and appear identical to those cells found in the centre of the intervein partitions.

The xylem in *C. felicis* is mesarch. One to ten broad (20–57 μ) thick-walled metaxylem elements are situated on the adaxial side of the bundle (Pl. 10, fig. 5). Protoxylem elements (3–6 μ diam.) occur as a small strand immediately below these cells (Pl. 10, fig. 5) but are not identifiable in all of the bundles. Centrifugal metaxylem elements, of smaller diameters than the centripetal metaxylem cells and larger diameters than the protoxylem tracheids, radiate out to the side of the centripetal cells from below the protoxylem (Pl. 10, fig. 5). Radial sections of veins show the centripetal elements to be very long and characterized by secondary wall thickenings that range from closely spaced scalariform bars to multiseriate circular bordered pits (Pl. 11, fig. 3). Centrifugal elements are smaller and more circular in outline than the centripetal elements and have diameters that range from 7 to 12 μ. These cells occasionally form an arc that laterally encloses the centripetal xylem. Often, small areas of centrifugal xylem are present only on the lateral sides of the centripetal elements (Pl. 10, fig. 5).

Additional xylem elements often occur just inside the thin-walled vein sheath (Pl. 9, fig. 1; Pl. 10, fig. 5). These cells, that range in diameter between 9 and 23 μ, have been referred to as the 'inner sheath' by early workers (Renault 1879, Stopes 1903). They intermittently occur below and to the side of the centripetal and centrifugal metaxylem elements (Pl. 10, fig. 5) and often merge with the centrifugal xylem present laterally and adjacent to the centripetal tracheids (Pl. 10, fig. 5). Cells presumed to be phloem can occasionally be distinguished between the inner sheath and the central portion of the centrifugal xylem (Pl. 10, fig. 5), but their general poor preservation precludes a detailed description.

Hypodermal masses of fibrous tissue sometimes occur between the veins and intervein partitions associated with both surfaces of the leaf (Pl. 10, fig. 1). These masses are usually

smaller groups of fibres than those associated with the veins or partitions. They are sometimes attached to the outer sheath of veins and may be associated with a new intervein partition that has arisen just distal to the point of a vein dichotomy. No constant relationship exists between vein division and these masses of fibres. These small fibrous masses usually occur in the thicker leaf fragments, and are responsible for the so-called secondary ribs sometimes seen in surface and sectional views (Pl. 9, fig. 2).

Palisade parenchyma is absent in *Cordaites felicis*, as has been reported in *C. principalis* and *C. crassus*; however, it is present in other petrified forms. The entire internal tissue between the veins and intervein partitions of *C. felicis* consists of spongy mesophyll making up parenchyma plates that are perpendicular to the leaf surfaces, and to the axially oriented veins and intervein partitions (Pl. 9, fig. 3; Pl. 10, fig. 1). Each plate is a single cell layer in thickness and is attached to both the upper and lower epidermis (Pl. 10, fig. 1). The plates extend laterally between a vein and adjacent intervein partition and in this direction can be seen to have 5 to 9 cells (Pl. 10, fig. 1). In some specimens these plates consist of flattened, laterally elongate cells suggestive of a flaccid condition of the mesophyll tissue (Pl. 10, fig. 1). Other plates, however, consist of apparently turgid cells that are isodiametric and measure 20–30 μ in diameter (Pl. 10, fig. 4). Between plates are conspicuous lacunar areas that approximate the width of the turgid mesophyll parenchyma cells. Toward the veins and intervein partitions these spaces become smaller, with the plates of parenchyma cells adjoining the intervein partition or outer sheath of a vein (Pl. 10, fig. 3). Similar appearing mesophyll cells that make up plates of photosynthetic tissue have been described by Cross (1940) in *Taxodium distichum* and Esau (1965) in *Pinus*. Studies of *T. distichum* indicate that the lacunar spaces are the result of cell separation brought about by a slower rate of cell enlargement in the mesophyll as compared with that of the surrounding tissues. The absence of extensive foliar specimens at this time precludes a developmental interpretation of this kind for *C. felicis*.

In transverse section, cells of the mesophyll parenchyma appear similar to the cells of the outer sheath, and in some instances the two cannot be distinguished (Pl. 10, fig. 3). The difference is only seen in paradermal view, where the sheath cells appear more axially elongated than the cells of the parenchyma plates.

Epidermal structure. The epidermis consists of longitudinal rows of stomata located above the regions where there is no hypodermal fibrous tissue, and intervening rows of rectangular accessory cells above the fibrous tissue (Pl. 11, figs. 1, 4). Accessory epidermal cells are oriented parallel to the long axis of the leaf, measure 60–150 μ long and

EXPLANATION OF PLATE 10

Figs. 1–6. *Cordaites felicis*. 1, Slightly oblique paradermal section of leaf showing position of primary ribs (PR) and mesophyll plates; arrow indicates secondary rib; C.B. 1460 bot, # 37, × 100. 2, Transverse section of leaf at margin; C.B. 145D (1) top, # 30, × 150. 3, Transverse section of leaf showing smooth adaxial surface and vein at level of dichotomy (arrows); note continuity of cells of outer sheath (OS) and those of mesophyll plates; C.B. 145F (2) top, # 67, × 120. 4, Paradermal section of leaf showing turgid nature of mesophyll plate cells; C.B. 121J top, # 20, × 200. 5, Transverse section of vascular bundle indicating position of centripetal (X) and centrifugal metaxylem (X′), protoxylem elements (PX), phloem (P), and inner sheath (IS); C.B. 145A bot, # 39, × 250. 6, Transverse section through two guard cells (G) and lateral subsidiary cells; arrow indicates cuticular extension over stoma; C.B. 145D (1), # 31, × 1000.

12–28 μ wide, and occur in easily identifiable bands across the epidermis (Pl. 11, fig. 1). Cuticles show a faint longitudinal median line associated with some of the accessory cells (Pl. 11, fig. 2). This feature occurs only on isolated cuticles and appears to be a property of the cuticle since no evidence of such a thickening can be seen in the same position on sections of the epidermis. The accessory cells have end walls that are straight, while the radial walls are irregularly thickened and exhibit primary pits (Pl. 11, fig. 2).

The epidermal cells which occur over the regions between the fibrous tissue are variable in shape (Pl. 11, fig. 5). They are usually shorter than the accessory cells over fibrous areas and tend to be more isodiametric, often having bluntly rounded end walls. These cells are associated with the stomatal apparatus.

Regions at the presumed basal (thick) part of the leaf which have narrow areas between the relatively massive zones of fibrous tissue have few stomata. At all other regions both the upper and lower epidermis contain stomata. This is not consistent with Benson's (1912) description of *C. felicis* in which stomata are reported as occurring only on the lower epidermis.

The upper epidermis has bands that contain one or two rows of stomata (Pl. 11, fig. 1). Slightly narrower bands containing only accessory cells alternate with stomatiferous bands (Pl. 11, fig. 1). Superficially, the stomata appear scattered, but upon close examination are seen to arise from the same row or rows of cells showing no sharing of terminal subsidiary cells.

The lower epidermis contains one or two rows of stomata positioned between the hypodermal fibrous masses in basal areas of the leaf. The stomata are more closely spaced than are those of the upper epidermis, often having adjacent terminal subsidiary cells. On the thinner, presumably more distal parts of the leaf, where there are few fibrous masses between the veins and intervein partitions, more rows of stomata appear (Pl. 11, fig. 4). Often 5–7, and occasionally 8 rows of stomata occur between a vein and an adjacent intervein partition (Pl. 11, fig. 4). The rows are usually staggered, all the stomata of adjacent rows are not lined up in transverse bands as in *Cordaites principalis* (Harms and Leisman 1961) and *C. affinis* (Reed and Sandoe 1951). Under these crowded conditions terminal subsidiary cells are often shared with adjacent stomata in the same cell row for several consecutive stomata. When there are fewer than 5 rows of stomata on the lower epidermis subsidiary cell sharing is not common.

The stomatal apparatus consists of two bean-shaped guard cells (Pl. 11, fig. 7), two bean-shaped lateral subsidiary cells (Pl. 11, fig. 6), and two terminal subsidiary cells (Pl. 11, fig. 7). The lateral subsidiary cells of both the upper and lower epidermis range between 39–69 μ long and 11–23 μ wide. The terminal subsidiary cells of the upper epidermis measure 14–70 μ long and 11–21 μ wide; those of the lower epidermis measure 20–40 μ long and 11–18 μ wide. The terminal subsidiary cells of both the upper and lower epidermis measure approximately 20 μ in depth. In general, the terminal subsidiary cells are small when there is another stoma nearby in the same row, as is typical of the lower epidermis where the density of stomata is considerably greater. In cases where the same terminal subsidiary cell is shared by two stomata, the cell is almost circular in outline.

Guard cells measure 35–46 μ long and approximately 10–12 μ wide. In transverse section these cells appear noticeably depressed below the surrounding subsidiary cells (Pl. 10, fig. 6). The thick cuticle does not extend downward into the epistomal chamber

(Pl. 10, fig. 6). No hairs or other cuticular appendages are present on the epidermis of *C. felicis*.

DISCUSSION

Several anatomical species of cordaite leaves are similar to *C. felicis*. Of these taxa, anatomical specimens of *C. principalis* from the Carboniferous and Permian of Europe, and *C. crassus*, known from the Carboniferous of France and North America (Pennsylvanian of Iowa), have been suggested as being closely related if not equivalent to *C. felicis*. The present study indicates, however, that although these 3 species are similar in several important features including leaf thickness, vein frequency, and stomatal apparatus, *C. felicis* differs from *C. principalis* and *C. crassus* in the following important features. The maturation pattern of the primary xylem in *C. felicis* and *C. crassus* is mesarch, whereas in *C. principalis* it is exarch. Complete intervein partitions apparently run the length of the *C. felicis* leaf whereas these are infrequent and generally of limited extent in *C. crassus*, and are completely absent in *C. principalis*. In *C. felicis* a maximum of 8 rows of stomata are present between the vein and intervein partition, while in *C. crassus* only 8 rows are present between 2 veins. A maximum of 5 rows of stomata occur between hypodermal fibrous masses in *C. principalis*, with stomata aligned between adjacent rows; in *C. felicis* adjacent rows of stomata are staggered. Hypodermal fibrous masses project far into the mesophyll between the veins only in the thicker areas of the leaf in *C. felicis*, but extend from the abaxial surface through one-half of the leaf regardless of the total thickness in *C. crassus*. The outer bundle sheath in *C. crassus* is 6–7 cells wide on its adaxial or upper surface, narrowing on the sides and abaxial portion. In *C. felicis* the sheath is 4–7 cells thick; in *C. principalis* it consists of 1–3 cell layers.

The petrified foliage forms *C. rotundinervis* Grand'Eury (1877), *C. rhombinervis* Grand'Eury (1877) from the Carboniferous of France are immediately distinguished from *C. felicis* by the exarch nature of the primary xylem. In addition, *C. rhombinervis* and *C. tenuistriatus* are characterized by a mesophyll that is differentiated into a distinct palisade and spongy region, as is *C. lingulatus* Grand'Eury (1877) from the Carboniferous and Permian of Europe. The occurrence of forms designated as *C. loculosus*, *C. robustus*, and *C. wedekindi* by Felix (1886), and *C. weristeri* Leclercq (1927) from petrifaction material collected from the same stratigraphic level and in some instances occurring in the same coal ball, as well as a tendency for one species to grade into another, caused Koopmans (1928) to regard all as synonyms of *C. felicis*. Benson (1912)

EXPLANATION OF PLATE 11

Figs. 1–7. *Cordaites felicis*. 1, Cuticle of upper epidermis showing bands of rectangular cells above fibrous masses with bands of stomata between; C.B. 145F (1) Maceration slide # 18, ×130. 2, Enlargement of epidermal cells from fig. 1 showing irregular radial wall thickenings; C.B. 145F (1) Maceration slide # 18, ×400. 3, Multiseriate circular bordered pits and scalariform bars of centripetal xylem elements; C.B. 145F (1) bot, # 2, ×600. 4, Paradermal section just beneath cuticle of lower epidermis showing primary ribs (arrows) and stomatal rows between; C.B. 145F (1) side # 17, ×130. 5, Epidermal cells associated with stomatal bands from upper epidermis; C.B. 145F (1) Maceration slide # 18, ×400. 6, Stoma and subsidiary cells of upper epidermis; C.B. 145F (1) Maceration slide # 18, ×500. 7, Two stomata and shared terminal subsidiary cells from lower epidermis; C.B. 145F (1) side, # 17, ×625.

notes the general similarity of the presumed upper or distal part of *C. felicis* to *C. wedekindi*, while sections closer to the base more closely resemble material of the *C. loculosus* and *C. robustus* types.

Although the probability exists that several recognized cordaite foliage species represent different parts of the same leaf our studies with the Kentucky specimens of *C. felicis* do not show either a gradual or marked anatomical change taking place through many centimetres of lamina presumably representing all parts of the leaf. For example, intervein partitions, a feature used to delimit numerous anatomical species, were incomplete in only 0·1 % of all of the sections of leaves examined. The consistent absence of complete partitions in *C. weristeri* and *C. robustus* still provides a means of distinguishing them from *C. felicis*. Specimens of *C. loculosus* are described with complete intervein partitions, however, material of this type is readily recognized by the absence of a bundle sheath. General leaf thickness, extent of bundle sheath, and slender intervein partitions are features that Benson (1912) used to delimit *C. wedekindi* from *C. felicis*.

In alluding to the ultimate solution of delimiting cordaite foliage through the organic attachment of leaves to stems, Benson (1912) notes the consistent mutual occurrence of the cordaitalean seed *Mitrospermum compressum* and *C. felicis* foliage. Whereas such an association can have limited value in studies involving petrifaction material, such a correlation becomes more meaningful as identical species associations are discovered and recorded. It is, therefore, of interest that *Mitrospermum compressum* was reported and described for the first time in North America (Taylor and Stewart 1964) from the same petrifaction material that has provided the specimens of *C. felicis* used in this study.

Cuticular studies of cordaite foliage by Renault (1879), Wills (1914), Florin (1931), Reed and Sandoe (1951), and Harms and Leisman (1961) have demonstrated epidermal patterns similar to the *C. felicis* type. Patterns that are unlike this type have recently been reported in cordaitean leaves by Ledran (1958, 1960) for petrified specimens of *C. angulostriatus* Grand'Eury (1877) and *C. lingulatus*. In *C. angulostriatus* the shape and orientation of the stomata is not as consistent as it is in species such as *C. felicis*. Moreover, in *C. angulostriatus* each pair of guard cells has 4–5 subsidiary cells and the stomata are aligned in single rows. In *C. lingulatus* the stomata are randomly arranged, each with 3–8 subsidiary cells. Florin (1931) has shown prominent cuticular papillae associated with the subsidiary cells of *C. lingulatus*.

There appear to be at least two general types of cuticular patterns known for cordaitean leaves. The pattern demonstrated by *C. felicis*, *C. principalis*, *C. crassus*, *C. affinis*, and a number of described but unnamed forms by Renault (1879), Wills (1914), and Florin (1931), have guard cells and subsidiary cells oriented parallel to the long axis of the leaf. Cuticular papillae are absent and the stomatal apparatus of all of these forms are almost indistinguishable from one another.

The epidermal cell pattern characterized by *C. angulostriatus* and *C. lingulatus* shows a consistent irregular orientation of the stomata and a wide range in the number of subsidiary cells. Cuticular papillae are associated with subsidiary cells of this type.

When these two types of epidermis are considered along with internal structural features and the stratigraphic position of the leaves, a potential basis for interpreting the phylogeny of cordaitean foliage emerges. Taxa with the more regular epidermal cell

patterns tend to be characterized by prominent hypodermal fibrous masses separating veins, and are generally found in lower and middle Pennsylvanian age sediments. Cordaite leaves with less well-developed hypodermal bands between the veins and more irregular cuticular patterns extend on into Permian age rocks. It is clear that epidermal features of cordaitean leaves may not only be useful taxonomically, but may provide a means of comparison between structurally preserved leaves and the large number of presently meaningless compression species.

It is worth while here to mention the similarity between the irregular pattern of stomata disposition in some cordaite foliage species and the epidermal cell arrangements of some of the earliest coniferophyte leaves discussed by Florin (1944, 1951). In general, *Lebachia* has stomata with 4–10 subsidiary cells, each typically associated with a cuticular papilla. The orientation of the individual stoma is random within two band-like regions on each surface of the leaf. Foliage of *Ernestiodendron* has stomata in single rows. Each stoma is randomly oriented within the row and has 4–8 subsidiary cells with papillae. The epidermal cell patterns of *Lebachia* and *Ernestiodendron* more closely resemble the type of cordaite cuticles described by Ledran (1958, 1960) than the type characterized by *Cordaites felicis*. In particular the cell patterns of *C. angulostriatus* and those of *Ernestiodendron* foliage are almost identical. It is also interesting to note the similarity between the arrangement and structure of stomata on the seed scales of *Araucaria cutchensis* (Pant and Srivastava 1968), an Upper Jurassic compression from India, and the arrangement and structure of stomata in *C. angulostriatus*. A comparison of epidermal patterns may ultimately provide a clue to the group of Carboniferous cordaites from which some Permian conifers have evolved.

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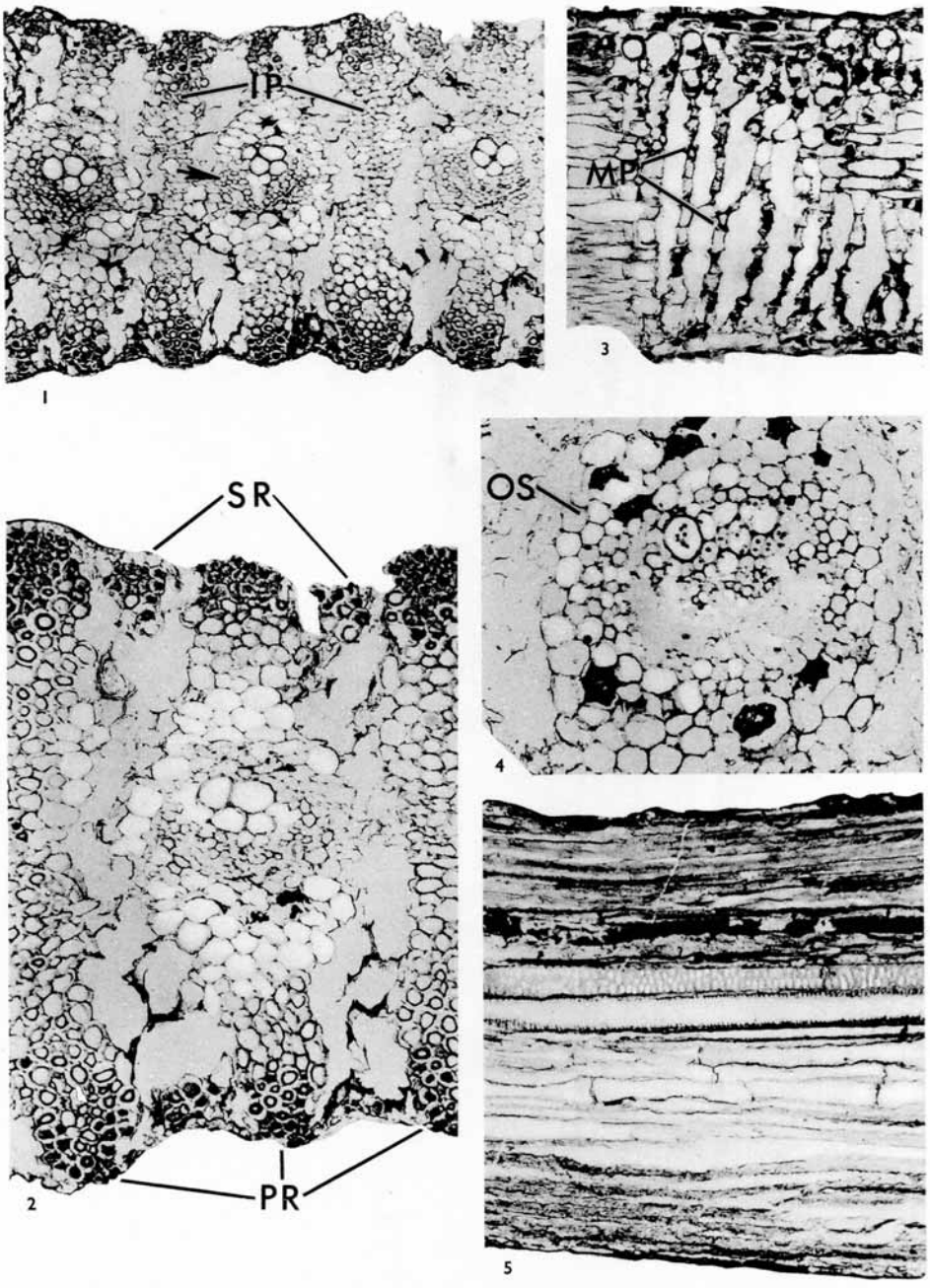

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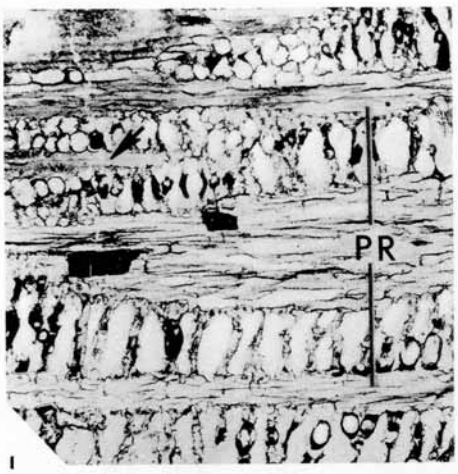

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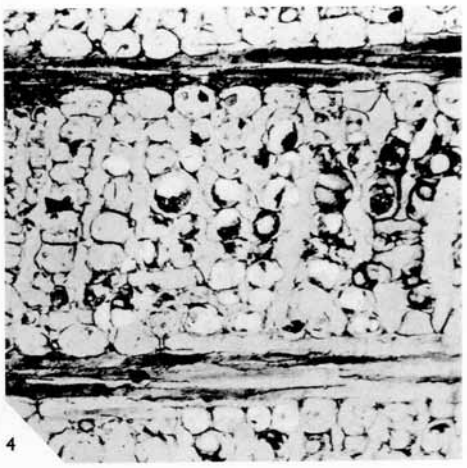

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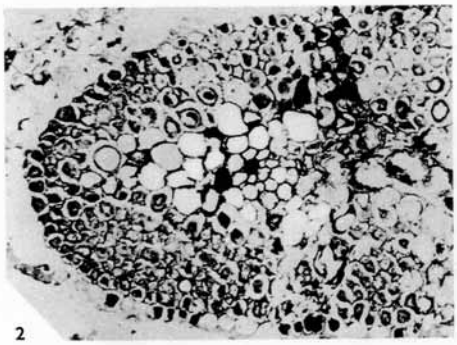

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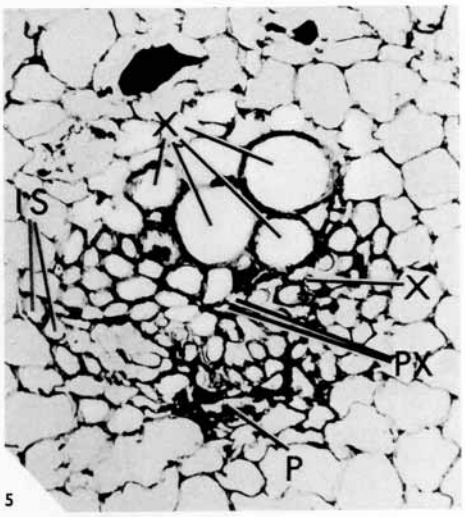

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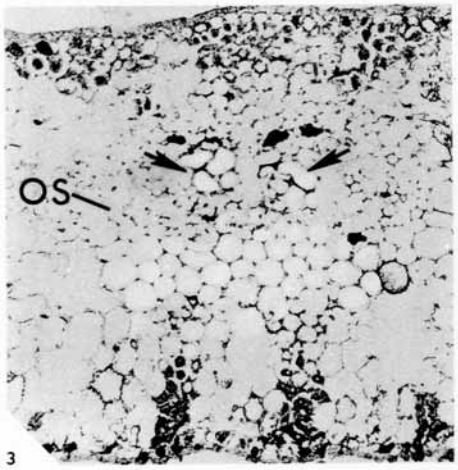

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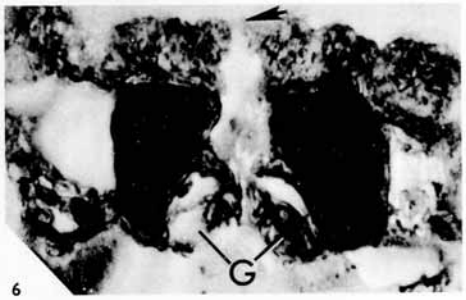

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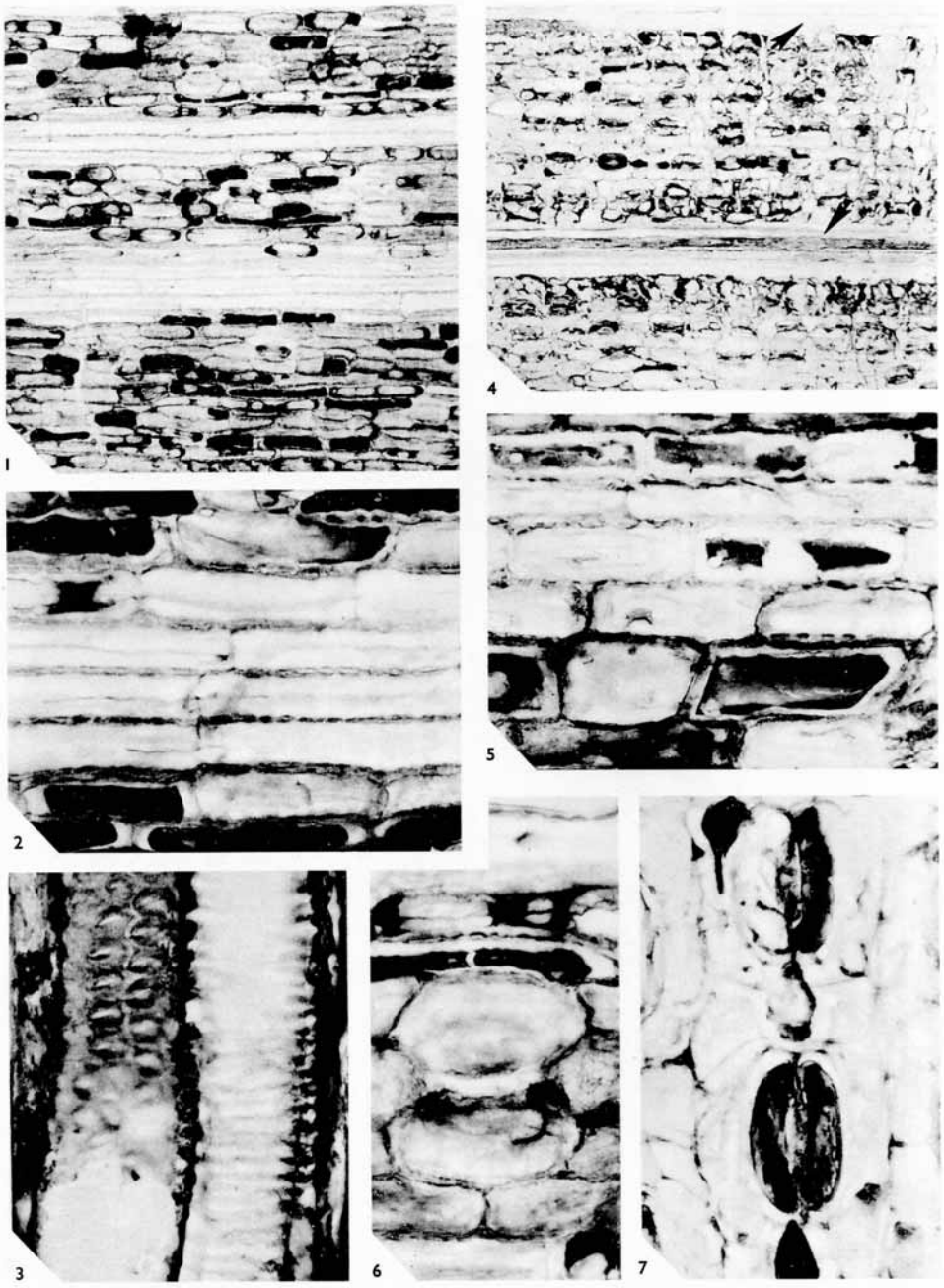

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