A study of the leaf cuticles

FROM CARBONIFEROUS DEPOSITS OF NORTH AMERICA

By Rev. Gustavus Huertas G., C. M. F. (*)

RESUMEN.—Investigación sobre cutículas de hojas de los yacimientos carboníferos de Norte América. Este trabajo es parte de un estudio presentado como tesis de grado en la Universidad de Washington, Saint Louis, Mo., U. S. A. (1956), en el que se estudia la anatomía interna foliar en mancomún con los caracteres cuticulares e indirectamente se hace notar la importancia de los fósiles descritos como ayuda para los estudios estratigráficos. Se empleó un método en cierto modo original para aislar y esclarecer las muestras de cutículas que juzgamos ser de notable utilidad para los paleobotánicos que realizan estudios similares. Se describen en él dos CORDAITALES: *Cordaites kansanus* Huertas sp. nov. y *C. pyramidalis* Huertas sp. nov. y dos FILICALES: *Neuropteris reflexa* Huertas sp. nov. y *Neuropteris siphonopilosa* Huertas sp. nov. Muy pocos estudios se han realizado sobre el particular. De ellos se hace un recuento en la sección histórica. En la taxonomía la descripción se ha hecho de propósito quizá muy minuciosa, a fin de relievar la riqueza de los caracteres estables y justos que acreditan la clasificación de especies nuevas. Finalmente se agradece muy sinceramente al Presidente de tesis, decano doctor Henry N. Andrews y a todos los que en una u otra forma cooperaron en el feliz éxito de la presente investigación paleobotánica.

RESUME.—Il s'agit de l'étude des cuticules de quelques feuilles du carbonifère (U. S. A.), thèse presenté à l'Université de Washington, Saint Louis, Mo., pour le Master of Arts. On étudie l'anatomie interne des feuilles et aussi les caractères cuticulaires. La méthode employée pour préparer les cuticules est en partie nouvelle. Deux CORDAITALES son décrits: *Cordaites kansanus* Huertas n. sp. et *C. pyramidalis* Huertas n. sp. et deux FILICALES: *Neuropteris reflexa* Huertas n. sp. et *Neuropteris siphonopilosa* Huertas n. sp. Un recueil des études realisés á ce sujet montre qu'ils sont très peu nombreux. La description taxonomique est tres poussée pour mettre en evidence la richesse des caractères donant lieu à la création des nouvelles spèces. On remercie à tous ceux qui ont aidé à la realisation de cet étude specialement à Mr. le Doyen Henry N. Andrews qui l'a dirigé.

(*) Master of Arts from Washington University, Saint Louis. Mo., Paleobotanist, National University of Colombia.

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INTRODUCTION

The extensive Pennsylvanian Coal Measures of the United States contain abundant compressions and petrifications of cordaitean and fern-like foliage which, in general, have attracted very little attention from paleobotanists. Arnold (1949) points this out when he states: "The difficulties attending the identification of cordaitean foliage are mainly responsible for the widespread neglect of them on the part of paleobotanists".

The venation features and other external characteristics permit the classification of only a few species. The size, form of the lamina, shape of the apex and the venation have been used to distinguish Subgenera such as: Poa-Cordaites and Dory-Cordaites by Grand' Eury (1877, a) but these features do not present reliable criteria for delimiting species.

It was not until the careful anatomical studies of Renault (1897) that the generic limits of the leaves assigned to *Cordaites* were clearly defined. Other studies followed which dealt particularly with the structure of the cordaitean leaves; among the more noteworthy are those of Stopes "On the leaf-structure of Cordaites" (1903, a), Lignier on *Cordaites lingulatus* (1913) and Benson on *Cordaites felicis* (1912).

For the most part, cordaitean and fern-like fossil foliage is found in a poor state of preservation. Hence, it is often difficult to make a complete diagnosis of the anatomical characters. On occasion, well-preserved specimens are encountered, such as *Cordaites affinis* described by Reed and Sandoe (1951). This study is also significant as the first one dealing with both epidermal structure and internal anatomy.

Florin (1931), the foremost investigator of coniferophyte foliage, holds that a study of the stomatal apparatus together with that of other epidermal cells contribute a more exact and critical knowledge of the species.

It seems desirable that we should have a better understanding of the cuticular structure of the leaves found in coal-ball petrifications of their own sake but particularly as a means of correlating these petrification fossils with the leaf compressions found in the shales overling the coal seams. Cuticle structure has also proved its worth in the study of other groups, including the cycadophytes and angiosperms. With reference to the latter group, Edwards (1935) in a brief resumé on the subject, comes to this conclusion: "The available evidence summarized in this review all indicates that given careful and critical work on the well-preserved material together with a detailed comparison with a wide range of living forms, results obtained from a study of angiosperm cuticles will be as valuable as those derived from any other fossil remains and certainly far more reliable than those founded on leaf compressions alone".

The present study deals with the cuticle structure of certain species of *Cordaites* and fern-like foliage which were obtained from three different localities: West Mineral, Kansas; Urbandale, Iowa; and Pinckneyville, Illinois. This had been collected by Dean H. N. Andrews and his students and was placed at the disposal of the writer for study.

It may be noted that the generic identification of a fossil leaf, on the sole basis of an anatomical study using thin sections, is very difficult and sometimes impossible. The cross-sections of the pinnule not infrequently show such unexpected variability that one would easily be induced to false interpretations concerning the determination of the species. In view of this problem, we resolved to split mechanically some coal-ball petrifications and from the exposed surfaces whole pinnules were obtained which could be assigned to *Neuropteris*.

We will describe two new species of *Neuropteris* foliage under the names of:

Neuropteris reflexa Huertas, sp. nov.
Neuropteris siphonopilosa Huertas, sp. nov.

Also two new species of *Cordaites* are described:

Cordaites kansanus Huertas, sp. nov.
Cordaites pyramidalis Huertas, sp. nov.

Very few anatomical studies have been made of Carboniferous leaves in the United States or, indeed, in other countries where such fossils are found. May this small contribution call the attention of paleobotanists to this field since every research can bring to light a clearer picture of the Carboniferous Flora.

HISTORICAL BACKGROUND

Zeiller appears to have initiated the study of Carboniferous cuticles with an investigation of *Alethopteris* in 1890 followed by a study of *Glossopteris* in 1896. In 1912 Huth first investigated the cuticle structure of *Mariopteris muricata* and in 1914 he provided additional information. In 1913 R. Potonie described *Mariopteris muricata* and in 1915 he described the cuticle of *Alethopteris* and *Paleoweichselia* followed by a study of *Callipteris conferta* in 1921. More recently (1953) he has dealt with *Paleoweichselia defrances*, *Sphenopteris*

nummularia, Mariopteris muricata and *Neuropteris schewchzeri.* Wills in 1914 studied *Neuropteris, Cyclopteris, Alethopteris* and *Pecopteris.*

Gothan contributed important studies of neuropterid cuticles as well as the first investigation of *Callipteris conferta* in 1915, and later in collaboration with Nagalhard (Gothan and Nagalhard, 1922) he present additional information on *Sphenopteris* and *Callipteris* from India. Sahni (1923) has described the cuticle of *Glossopteris* also from India.

Walton has dealt with *Mariopteris muricata* cuticles from England (1923) and Kidston in his epochmaking work on the Carboniferous fossil plants of Great Britain (1923-1925), contributed detailed description of the cuticles of *Mariopteris muricata* and *M. nervosa.*

In a series of papers Florin (1925, 1926, 1931, 1933) has contributed to our knowledge of the leaf structure of: *Dolerophyllum goldenbergii, Cyclopteris felix, C. crassinervis, C. hirta, C. cyclopteroides, C. rarinervis, Calymmatotheca hoeninghausi, Pecopteris pluckenetii, Lesleya delafrondi, Mepalopteris soutlinellii, M. fasciculata* and *M. whitei.*

Bode in 1928 described *Mariopteris muricata* and other species of *Neuropteris* of England, closely related, he says, with the group: *Neuropteris flexousa, N. gigantea, N. tenuifolia, N. rarinervis,* and *N. obliqua,* all which show, in his opinion the same general type of cuticle. A year later (1929) Bolton studied another of the same genus. Sahabi described a cuticle of an Indian *Callipteris* in 1936 and again in 1937. Finally, Remy (1953) has described the cuticle structure of *Callipteris conferta.*

Cordaites

The genus *Cordaites,* named in honor of the paleobotanist Corda has been found to have a wide-spread distribution in the Coal Measures of the world; the internal structure of the leaves is known for relatively few species and even less is known about the stomatal and epidermal characteristics.

Corda first described the form and cellular structure of cordaitean leaves in 1845. Grand'Eury (1877, b) when describing some French species noted certain epidermal and stomatal characters. Renault in 1879 studied and figured the arrangement of the stomata and epidermal structure of *Cordaites crassus* and included incidental notes on the descriptions of other species. Probably the first figured formal description of *Cordaites* cuticle was made by Wills in 1914 from the coal seams of England. Florin described and illustrated the cuticle of *Cordaites* sp. cf. *lingulatus,* and an undetermined species in 1931. Darrah gave the first anatomical study of a North American species, *Cordaites* cf. *crassus,* from Iowa coal balls in 1940 and this was followed by the detailed study of Reed and Sandoe in 1951 (1).

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(1) Since the ending of this study some new contributions have been made on the subject such as the entitled "Sur la nervation de quelques feuilles de *Cordaites*" by Christiane Ledran, 1956 Sorbonne, Paris.

WORKING-METHOD AND MACERATION TECHNIQUE

The material used in the present study has been prepared by the customary methods of colloidon peels and thin section. The entire series of preparations include 130 peels and 120 thin sections and cuticles. For the preparation of the latter, however, we have used a special treatment, simple, fast and successful. The samples were treated as follows:

(1) Cut with a diamond-saw in small slabs of half inch squares as thin as possible, or split with a geologist hammer into thin small portions. When it is possible, remove only the epidermis from the matrix with the help of a scalpel.

(2) Place the samples of the epidermis in glass dishes and treat with strong HCl for five minutes (No water).

(3) When the reaction is over, wash the material with water and remove the detritus with a dropper, being careful not to lose the smallest pieces which commonly are the best for the study.

(4) Add to the samples or epidermis HNO_3 + $KClO_3$ and leave to settle two or three hours according to the hardness or softness of the material.

(5) Wash with water, remove the coarse oxidized detritus and leave the material in water, adding some drops of ammonia.

(6) When the process is applied to the material without intrusions of pyrite or when the pyrite is present in small proportions, the method can be accomplished without the above mentioned intervals of time. In this case it would be necessary to leave the isolated structures in the water with some drops of ammonia, at least half an hour, so that the material begins to soften and does not break. The same procedure has been applied in the case of removing the epidermis by the scalpel.

(7) If the material contains a large quantity of pyrite as is the usual condition in the coal balls, it would be necessary to treat the sample again with the mixture of HNO_3 + $KClO_3$ for another hour and occasionally to clean the samples, placed into a drop a water, with a needle, operating with much care in order not to break them. By means of repeated knocks with the needle, clear samples are finally obtained. It is time-consuming but let us remember the latin axiom: *Labor omnia vincit.*

Following this method of transfer-preparation, we may be almost sure that if the cuticle is present in the sample the results will be successful. In general, the petrifications which are rich in carbonates contain the best-preserved fossils. Many ferns, because the outer and radial walls of the epidermal cells are slightly cutinized, if at all, preserve as very fine amorphous epidermal tissue and, therefore, we fail to find the cuticle-structure in many cases.

TAXONOMY

Neuropteris siphonopilosa sp. nov.

The study of *N. siphonopilosa* and *N. reflexa,* described below, is based upon only the small portions of the frond exposed when pieces of the sample were broken, so we were unable to identify the fern-like foliage with any previously-described species of *Neuropteris.*

The pinnules are 18 mm. long and 12 mm. wide and often plicate; in general outline they are tongue-shaped and entire with faintly-curved margins; the base is distinctly cordate, slightly inequilateral and the pinnules are attached by a short pedicel. The midrib, almost effaced at the base, is quite visible at the central part of the lamina, and effaced again when it approaches the apex, resembling the so-called "neuroalethopterid" type of foliage. On the lower surface, the midrib is scarcely more projecting than on the upper surface preserving, as to the rest, the same pattern. The lateral veins are raised and dichotomize some distance from their attachment-point and occasionally forked again near the tip of the pinnule.

The epidermal cells of the ventral surface about 45 microns in diameter and their shape differs from those of the dorsal surface. The former exhibit a wide variety of forms, but always preserve the undulate or sinuous feature of their cell walls. Almost every individual cell of the ventral surface bears approximately on the center a single or rarely two papillae each 15 to 22 microns long and 15 microns wide. They are globose in shape and are attached by a small rounded foot cell. Their distribution is entirely uniform throughout the length of the ventral epidermis, including the stomatal region and even the subsidiary cells.

The cells of the upper surface are polygonal with very thick walls and they measure nearly 45 microns in diameter. These cells are not variable in shape as are those of the ventral surface. They resemble hairs that have been reported by previous workers on *Callipteris.*

The tubiform hairs (Fig. 7) which are present on both surfaces of the lamina have an ovulate expanded annulated base. These hairs are unicellular, ovate, and measure 90 microns long by 60 microns wide, tapering in the direction of the tip. The base of the hair covers the whole surface portion of the foot cell (Fig. 8). Their function may be glandular. The hairs, although irregularly arranged, tend to be equidistant.

The stomata (Fig. 10) are 30 microns long by 26 microns wide, slightly sunken below superficial epidermis. They have an ovate shape with seven or eight subsidiary cells with undulate margins, the size of the latter being nearly the same as that of the stomata. The elliptical aperture is 28 microns long and the lower chamber seems to be of rather great size in comparison to the whole stomatal apparatus. Some of the stomata permit us to see clearly the stellated sulcate rays of the stomatal, almost elliptical guard-cells.

The upper epidermis is very thin, succeeded by a layer of hypodermis of almost rounded cells of rather small size, 70 microns in diameter and thick walls, arranged in one row. The mesophyll is made up of two rows of palisade cells of thin walls measuring 45 microns long and 13 microns wide. The spongy tissue is abundant but usually poorly preserved.

A distinctive ring of parenchyma cells surrounds the midvein; these cells measure 105 microns to 120 microns in diameter and appear somewhat rectangular in a section parallel to the midrib. Each lateral vascular bundle shows a sheath of one, or occasionally two rows of cells surrounding the xylem which seems to be centrifugal.

Xylem cells measure about 30 microns in diameter and in longitudinal section show spiral walls. Protoxylem was not distinguished in the lateral veins. Small patches of phloem consisting of nearly rectangular cells about 22 microns in diameter are seen on the outside of the xylem strand. The sclerenchyma occupies almost one-half part of the leaf thickness in cross-section and has from four to five rows of rounded cells of very heavy walls, arranged in girdle-fashion and connected to the sheath.

Diagnosis: *Neuropteris siphonopilosa* sp. nov.

Pinnule 18 mm. long by 12 mm. wide; edged-tongue-shaped, entire; slightly-curved margins; base faintly inequilateral; pedicel short. On the lower surface midrib slightly projected. Lateral veins dichotomized far from their departure. Dorsal epidermal cells average 45 microns; waved or nearly straigh-elongated; papillose. Papilla size 15 to 22 microns long and 15 microns wide, globose; present even on the subsidiary cells. The upper epidermal cells usually polygonal, thickened, 45 microns in diameter. Tubiform scattered hairs present on both surfaces; expanded base. The hair body of a single ovate cell 90 microns long and 60 microns wide tapering to the tip. Stomatal 30 microns long and 26 microns wide, sunken, ovate, with seven or eight subsidiary wavy cells. Elliptical aperture 28 microns. Epidermis very thin. Hypodermis with rounded walled cells 70 microns in diameter. Two palisade cell rows of thin walls of 45 microns long and 13 microns wide. Spongy tissue abundant. Parenchyma well-developed with cells from 105 to 120 microns in diameter. Vascular bundles with sheath of usually a single cell row. Spiral cells of 30 microns on the xylem. Small patches of phloem of cells of 22 microns in diameter, outside of the xylem strand. Sclerenchyma of four to five rows of very heavy rounded cells forming girdles, connected to the sheath.

Age: Fleming coal, Cherokee shale.
Location: West Mineral, Kansas.
Type: slide Nos.: 120, 128, 175, 176, 182, 202, 266, 287, 288.

Neuropteris reflexa sp. nov.

The pinnules of this species are 10 mm. long and 3 mm. wide near the base; in general outline they are oblong-lanceolate with a pointed apex, subcordate base (Fig. 1) and are attached by a short pedicel. The pinnule margins are strongly curved downward (Fig. 2).

From the midvein, which is conspicuous on the ventral side, numerous lateral veins depart at almost right angles; these lateral veins dichotomize shortly after their departure and occasionally do so again near the margin.

The epidermal cells of the adaxial surface differ from the abaxial ones. The abaxial ones (Fig. 8) show an almost translucent striate texture with very thin walls, more or less isodiametric, and strongly sinuous in the stomatal region. These cells become abruptly enlarged with oblique end walls in the zone adjacent to the veins. They may be rectangular with straight walls but for the most part the walls are sinuous. They attain a length of approximately 60 microns. The cells immediately parallel to the veins appear to have thinner walls than those of the furrows of the stomatal zone and frequently have brown contents.

The adaxial epidermal cells are more or less rectangular with thin walls measuring from 45 to 75 microns in diameter.

The stomata, with guard-cells of 22 microns long by 15 microns wide, are confined to the grooves but are occasionally present in proximity to the veins (Fig. 8, 9). They are deeply sunken in the epidermal layer and the subsidiary cells usually number from five to six (Fig. 9). The ovate pore is nearly 13 microns long. When the cells approach the stomata they join in a characteristic polygonal aperture (Fig. 3, 9). This front cavity aperture of approximately 25 microns in diameter is surmounted by a group of cells or rings, the cells of which appear clearly to be different from the subsidiary cells but inserted on the outer edge. The ring-cells are a little protruded towards the center of the front cavity (Fig. 9). That they are entirely different is shown by their thicker walls and dark contents and mainly by the fact that we have found intact the subsidiary cells without the presence of the ring-cells (Fig. 3). Each cell of the ring measures about 9 microns to 13 microns and its shape is nearly ovate.

Multicellular unbranched glandular hairs are abundant on the abaxial epidermal cells and usually they are confined to the raised papillose ribs being arranged in rows (Fig. 1, 2, 8), but they are absent from the adaxial surface. They are equally distributed over the veins as well as in the stomatal zone and average about 350 microns long and 60 microns wide at the foot which has usually a more or less pyramidal shape (Fig. 4). The cuticle of these epidermal hairs is very thin with a reticulate-striate texture (Fig. 3). Each hair consists of two to six nearly rectangular cells which taper gradually to the tip ending in a lanceolate-obtuse apex (Fig. 5). Each hair is attached to one specialized epidermal cell which is usually ovate, measuring 160 microns long by 60 microns wide (Fig. 6). The largest foot-cells measure 190 microns long.

The ring-cells (Fig. 9) are not directly connected, their shape varies from round to ovate and they have brown contents.

The subsidiary cells of about 30 to 35 microns in diameter have undulate walls.

Immediately below the epidermis extends a layer of thick-walled, irregular cells which vary in shape from bulbous to square to rectangular (Fig. 2). The palisade tissues of compact walled cells lies below and it is arranged in two rows with rather thick walls.

The midvein structure has one small vascular bundle composed of small xylem elements (Fig. 2). The parenchyma and the lacunar tissue have nearly isodiametric cells and is well-developed. On the parenchyma of the midrib two or three rounded cells of approximately 65 microns appear very often which probably are of resin canal nature judging from their contents and rounded heavy-walled shape. The longitudinal section of the blade parallel to the midrib shows the lateral ribs to be distant each from another about 20 microns.

Diagnosis: *Neuropteris reflexa* sp. nov.

Pinnule 10 mm. long by 3 mm. wide. Pedicel short. Pinnule margins strongly curved. Midrib sunk almost effaced. Lateral veins dichotomized next to the basal portion. Adaxial epidermal cells different from abaxial; the former with sinuous margins and hyaline texture; the latter polygonal and thickned. Stomata confined to the furrows, deeply sunk. Subsidiary cells from five to six. Characteristic stomatal outer ledge. Presence of ring-cells on the stomata. Guard-cells ovate in shape. Hairs multicellular, segmented, abundant on the ventral surface and confined to the raised papillose ribs. Absent on the dorsal surface, never branched, semicupuliferous hair-foot. Cuticle rather thin; hypodermal cells large, frequently bulbiform; from nearly square to rectangular. Compact palisade of two rows of cells. The ribs have one small vascular bundle. Parenchyma and spongy tissues well-developed.

Age: Fleming coal, Cherokee shale.

Location: West Mineral, Kansas.

Type: slide Nos.: 121, 122, 127, 129, 131, 139, 171, 178, 180, 188, 189, 190, 191, 192, 193, 203, 204, 228, 283, 284, 285, 286.

CORDAITEAN LEAF STRUCTURE.—INTRODUCTION

It is of some significance to comment on the most striking characteristics of cordaitean leaf structure summarized from the descriptions of previous writers and from the results of the present investigation.

The anatomy in general suggests a xeromorphic habit of the plant (Seward, 1917, a) as shown by the rather heavy cuticle, the thickness of the epidermal cell walls and hypodermal structure of both surfaces. It is also indicated by the presence of few stomata and their predominance on the ventral surface (Huertas).

The sunken stomata are usually arranged in long rows (Arnold, 1947) although occasionally they are irregularly distributed. The kidney-shape and difference in size of the two lateral subsidiary cells appear to be characteristic features (Huertas) (Fig. 12). The cells from the nonstomatiferous bands are longitudinally elongated and rather thick-walled; they are essentially the same in both surfaces (Huertas).

The vascular bundles are mesarch or exarch (Arnold, 1947), probably never endarch as in *Cordaites* stems. The bundles are usually surrounded by a sheath of tissues, an inner one of thick-walled cells and an outer sheath composed of thin-walled cells (Stopes, 1903, b;

Seward, 1917, b). The well-developed sclerenchyma from ribs of thick-walled cells usually connected to the veins above and below (Stopes, 1903, b).

Certain other characters seem to be of some use in delimiting species, such as the extent and distribution of the palisade spongy tissue, the presence of ribs alternating with the vascular strands, width of stomatiferous and non-stomatiferous bands and the presence of transfusion tissue.

Cordaites pyramidalis sp. nov.

The leaves of this species measure 2.5 to 3 cm. wide and approximately 540 microns thick in the middle.

The epidermal cells of the upper surface are almost rectangular, being 60 to 75 microns long and 18 microns wide; the walls of these cells are rather thin, becoming thicker where they adjoin guard-cells. Cells in the non-stomatiferous areas are larger, reaching a length of 90 microns and 16 microns wide (Fig. 13).

The lower epidermal cells are 75 to 90 microns long and 18 microns wide and are intermixed with small groups of 2 to 4 specialized cells with thicker walls which are ovate to round and about 30 to 45 microns in diamater.

As is usual in cordaitean leaves, a hypodermal layer of cells is present; these are very thick-walled and 15 microns in diameter (Fig. 17).

Stomata are present in both surfaces but in the upper epidermis (Fig. 14) they are widely-spaced and few in number and appear to be arranged in just one row. In the ventral surface, on the contrary, they form two or three rows in each rib and are always absent from the inter-rib areas (Fig. 13, 15).

The subsidiary lateral cells of the ventral surface measure 75 microns long by 16 microns wide and the polar subsidiary cells are 16 microns in diameter. The sunken guard-cells are ovate, measuring 37 microns in length and 22 microns wide (Fig. 15).

The cuticle is rather thin on the upper surface and somewhat thicker on the lower surface.

There is no differentiation of the mesophyll into palisade and spongy tissues (Fig. 17); it consists of large rounded cells of 45 to 52 microns in diameter. The parenchyma between the ribs has an hourglass shape in cross-section and the cells measure about 37 to 45 microns (Fig. 17).

The sclerotic strands or ribs are rhomboidal in shape and composed of very thick-walled fibers (Fig. 11).

The vascular bundle consists of six to ten tracheidal elements about 22 microns in diameter of the scaleriform or pitted type. The protoxylem appears to be exarch. The bundle is surrounded by a sheath of two rows of cells more or less round in shape. These cells average 45 microns in diameter (Fig. 17).

Discussion:

C. pyramidalis has noteworthy characters which seem to warrent the description of new species. We will note now the most salient features.

Cordaites pyramidalis Huertas differs from *C. crassus* Renault in possessing a different distribution and development of the sclerenchyma ribs, absence of the transfusion tissues in the sheath region and stomata in two or at most three rows with different structure. In *C. tenuistriatus* Gr., there are no intervening sclerenchyma masses between every two vascular bundles and four rows of palisade. These two features are absent from *C. pyramidalis*. *C. angulostriatus* Gr. possesses a characteristic well-developed palisade tissue which does not occur in *C. pyramidalis*. *C. affinis* Reed and Sandoe shows four layers of palisade and the stomata are distributed from three to five rows. *C. pyramidalis* has no palisade and the stomatal structure is very different. *C. principalis* Germ. is found to have four layers of palisade.

Diagnosis: *Cordaites pyramidalis* sp. nov.

Leaf 2.5 cm. wide. Ribs number from 45 to 50 bands. Thickness of the leaf 52 to 56 microns. Epidermal cells of upper surface almost rectangular from 60 to 75 microns long and 18 microns wide. Cells of non-stomatiferous areas larger than those of the stomatiferous ones from 9 microns long to 16 microns wide. The upper epidermal cells differ from the lower ones in shape and thickness of the walls as well as in the structure of the stomata, lower thicker epidermal cells measuring about 75 to 90 microns long by 18 microns wide, usually longitudinally elongated. Stomata present on both surfaces on the dorsal surface arranged in two or three longitudinal rows, on the ventral one, scattered and arranged in one row with more specialized structure. The upper surface stomata measure 45 microns in length and 17 microns in width. Cuticle slightly thicker on the lower surface. Single row hypodermal cells of nearly rounded cells of 15 microns in diameter. Well-developed parenchyma not differentiated into palisade and spongy cells about 37 to 45 microns in diameter.

Sclerenchyma of strong fibers of almost rhomboidal shape. Sheath of two rows of cells completely surrounding the vascular bundle of 45 microns in diameter. Vascular bundles with metaxylem of 6 to 8 elements of thick walls with 22 microns in diameter and bordered pits on the radial walls. Protoxylem with small groups of very small cells provided with 6 to 9 elements of 5 microns in diameter.

Age: Herrin (Nº 6) coal. Base of Mcleansboro.

Location: Pyramid Mine, Pinckneyville, III.

Type: slide Nos.: 267, 268, 269, 270, 271, 272, 273, 275, 278, 279, 289, 290, 291, 301, 302, 303.

Cordaites kansanus sp. nov.

The leaves of this species are 15 to 30 mm. wide and fragments up to 9 cm. long have been obtained. The leaves are about 560 microns thick. The primary ribs are from 35 to 40 in number.

The cuticle of the upper surface is somewhat thicker than that of the lower surface. The upper epidermal cells usually are longitudinally elongated with an average of 60 to 75 microns and 18 microns wide, some of them constantly showing thicker walls with dark contents and in some areas measuring only 40 microns with a tendency to have an ovate shape.

The lower epidermal cells are somewhat thinner than those of the upper surface, narrower and shorter, their length reaching from 56 to 65 microns and their width being from 16 to 25 microns. They have a tendency to be longer and narrower on the stomatiferous ribs.

The stomata are relatively few in the upper surface and are rather irregularly distributed throughout the length of the epidermis. The guard-cells are 45 microns long by 30 microns wide and the aperture (stomate) is 15 microns in diameter. The lateral subsidiary cells measure from 60 to 65 microns long by 17 microns wide. The polar subsidiary cells are 45 to 55 microns long and 16 microns wide and are larger than those of the lower surface.

The lower surface has ovate stomata (Fig. 12, 16, 18) arranged in six or seven rows and they are comparable with those of the upper surface except that the polar, ovate-rounded subsidiary cells (Fig. 18) are only 17 to 20 microns in diameter. It is a very striking feature of both lower and upper epidermis that the opening between the subsidiary cells is elongate and at right angles to the stomatal opening. The subsidiary cell opening measures from 30 to 35 microns (Fig. 18).

The cuticle is a little thinner on the upper surface. In cross-section, the hypodermal cells appear to be almost square, measuring from 17 to 20 microns in diameter. Immediately below the hypodermis are alternating ribs of well-developed sclerenchyma and parenchyma (Fig. 11). The sclerenchyma covers a large area and surrounds the bundle sheath in more or less kidney-shaped form. The cells are very thick-walled, 16 to 22 microns in diameter, with an almost obliterated lumen. The mesophyll is occasionally well-preserved and consists of polygonal cells 45 microns in diameter.

A sheath consisting of two rows of cells from 30 to 40 microns in diameter surrounds the vascular bundle. No transfusion tissue has been observed. The vascular bundles are ovate and consist of 6 to 10 narrow tracheids. The protoxylem seems to be centripetal.

Discussion:

Cordaites kansanus sp. nov. is characterized by the arrangement of the stomata in usually seven rows on the lower surface and just one single row of scattered stomata on the upper surface. No dichotomy of the ribs was observed in the ribs of the epidermis. No intervening masses of sclerenchyma occur between every two vascular bundles. The phloem was not observed on the vascular bundle. The protoxylem occurs on the both lower sides of the metaxylem but never is present downwards of it.

The palisade tissue does not occur and probably the transfusion tissue also is present. All these characteristics of the leaf structure which are not found together on the species to the date described warrant the description of this specimen as a new species.

Diagnosis: *Cordaites kansanus* sp. nov.

Leaves from 15 to 30 mm. long from margin to margin. Ribs from 35 to 40 in number. Normal thickness 56 microns wide. Cuticle of the upper surface somewhat thicker. Upper epidermal cells longitudinally elongated from 60 to 75 microns long by 18 microns wide; frequently with dark contents. Lower epidermal cells thinner, measuring 56 to 65 microns long and 16 to 25 microns wide.

Stomata of the upper surface in a single row irregularly distributed. Lateral subsidiary cells from 60 to 65 microns long by 17 to 20 microns wide. Stomata of the lower surface arranged in seven rows, deeply sunken, ovate; polar subsidiary cells larger than those of the upper surface stomata. Stomata pore from 30 to 35 microns in diameter Mesophyll loosely arranged. Strongly developed sclerenchyma on the ribs of cells measuring 17 to 22 microns in diameter. Sheath of two rows. Xylem centrifugal. Metaxylem of 6 to 10 elements. Presence of tracheids.

Age: Cherokee shale.

Location: West Mineral, Kansas.

Type: slide Nos.: 132, 133, 134, 135, 137, 139, 142, 171, 174, 181, 183, 184, 186, 187, 274, 295.

BIBLIOGRAPHY

ARNOLD, C. A. 1947.—An Introduction to Paleobotany; New York. London. 298.

ARNOLD, C. A. 1949.—Flora of the Michigan Coal Basin; *Contrib. Mich. Univ. 7*: Nº 9, 222.

BENSON, M. 1912.—*Cordaites Felicis* sp. nov. a Cordaitean Leaf from the Lower Coal Measures of England; *Ann. of Bot. 26*: 201-207. London.

BOLTON, E. 1929.—On the Cuticle of Certain Species of *Neuropteris*; *Ann. Bot. Lond. 43*: 414-415. London.

DARRAH, W. 1941.—The Fossil Flora of Iowa Balls. III. Cordaianthus; *Bot. Mus. Leaflets. Harv. Univ. Cambridge, Mass. 8*: Nº 1. 12-13.

EDWARDS, W. N. 1935.— The Systematic Value of Cuticular Characters in Recent and Fossil Angiosperms; *Biol. Rev. Cambridge Philos. Soc. 10*: 442-457. London.

FLORIN, R. 1926.—Uber einige Blatterabdrucke von *Cyclopteris* Typus aus dem Carbon und Permian. *Ark. f. Bot. 20A*: 1-19. Sthlm.

FLORIN, R. 1931.—Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales; *Klg. Svenska. Ak. Hdl.* (3), Bd. *10*: Nº I. 498-501. Sthlm.

FLORIN, R. 1933.—Zur Kenntnis der palazoischen Pflanzengattungen Lesleya. Lesquereux, und Megalopteris, Dawson; *Ark. f. Bot. 25*: 1-23. Sthlm.

GOTHAN, W. 1915.—Uber die Methoden und neue Erfolge der Untersuchung Kohlig rehaltener Pflanzenreste; *S. B. Ges. Naturf. Freunde*: Nº 2. 44-48. Berlin.

GRAND'EURY, C. 1877, a.—Flore Carbonifère. Dept. Loire; *Mem. Acad. Sci. Inst. France. 24*: 214-222. Paris.

GRAND'EURY, C. 1877, b.—Ibid. 208-277.

KIDSTON, R. 1925.—Fossil Plants of the Carboniferous Rocks of Great Britain. First. Sec. 6: 529-608. London.

POTONIE, R. 1913.—Uber Blatt Epidermen einiger fossiler "Pteridospermen"; *S. B. Ges. Naturf. Freunde*: Nº 10. 453-461. Berlin.

POTONIE, R. 1915.—Uber die Diathermie einiger Carbon "Farne"; *Beih. z. Bot. Centralbl. Bd. 32*: Abt. I, 470-474. Dresden.

POTONIE, R. 1921.—Uber mazereirte Kohlige Pflanzenfossilien. 5. Uber die Minierlarrengange an Blattern von *Callipteris conferta*; *Zschr. f. Bot.* (6) Bd. *13*: 87-88. Jena.

POTONIE, R. 1953.—Zur Palaeobiologie der Karbonischen Pflanzenwelt; ***Die*** *Naturwissenschaften.* Bd. *40*: H. 4. 124-125, Berlin.

REED, F. D., and SANDOE, M. F. 1951.—*Cordaites affinis*, a New Species of Cordaitean Leaf From American Coal Fields; *Torrey Bot. Club. 68*: Nº 6, 449-457. New York.

REMY, WINDFREID. 1953.—Beitrage zur Kenntnis der Rotliegedflora Thuringens. *S. R. Deutsch Akad. Wiss. Klass. Math. & allg. Naturw.*, T. I. 5-18 Berlin.

RENAULT, M. B. 1879.—Structure Comparée de Quelques Tiges de la Flore Carbonifère; *Nouv. Arch. Mus.*: 295-304. Paris.

SEWARD, A. C 1917, a.—Fossil Plants. *3*: 225-244. Cambridge. England.

SEWARD, A. C. 1917, b.—Ibidem, pp. 230.

STOPES, M. C. 1903, a.—On the Leaf-structure of Cordaites; *New Phyt., 2*: 91-98. London.

WALTON, J. 1923.—On a New Method of Investigating Fossil Plant Impressions; *Ann. Bot. Lond., 37*: 384-386. London.

WILLS, L. 1914.—Plant Cuticles From the Coal Measures of Britain; *The Geol. Mag.*: New Ser. Nº 1, 386-388. London.

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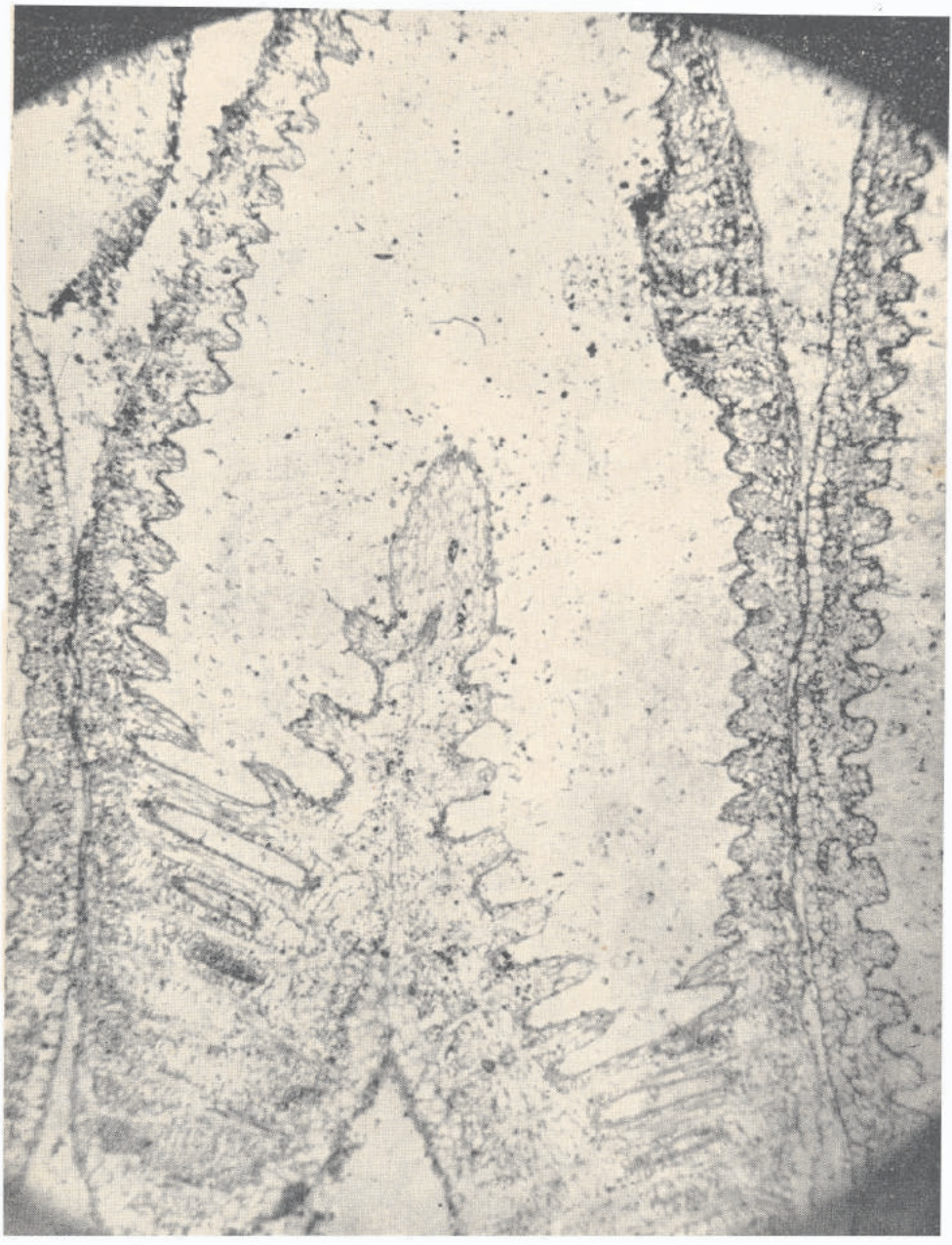

PLATE I. Fig. 1.—*Neuropteris reflexa* sp. nov. longitudinal tangential section of the pinnule showing the mid and the lateral veins structure and the attachment of the multicellular hairs.

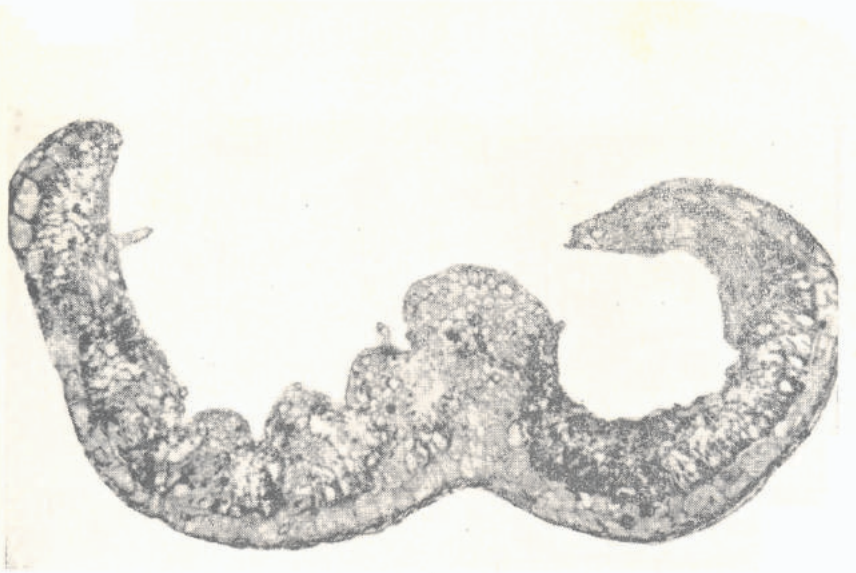

PLATE II. Fig. 2.—*Neuropteris reflexa.* Cross-section of the pinnule showing the cuticle, large hypodermal cells, papillose lower surface and hairs.

Fig. 3.—Lower epidermis of *Neuropteris reflexa* showing the cell shape and hairs under high magnification.

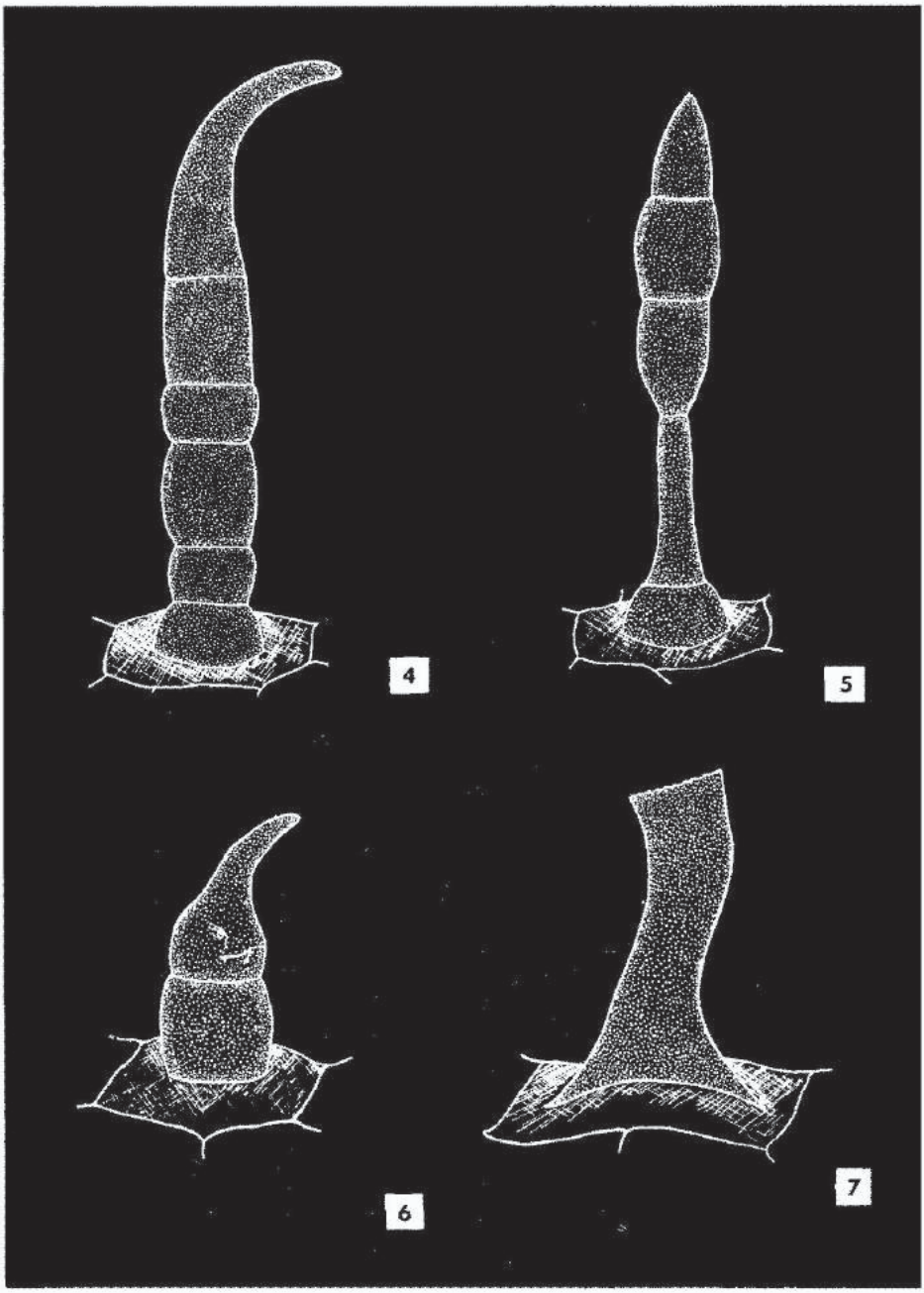

PLATE III.—Diagramatic illustration of various forms of hairs of *Neuropteris reflexa* and *Neuropteris siphonopilosa*.—Fig. 4. Multicellular hairs of *Neuropteris reflexa*. The dotted lines indicate the cellular contents which are possible of secretory nature.—Fig. 5. Hair showing a collapsed cell and different shape of the cells and head.—Fig. 6. Shape of a young hair. Fig. 7. Head and expanded attachment of the unicellular tubulous hair of *Neuropteris siphonopilosa*.

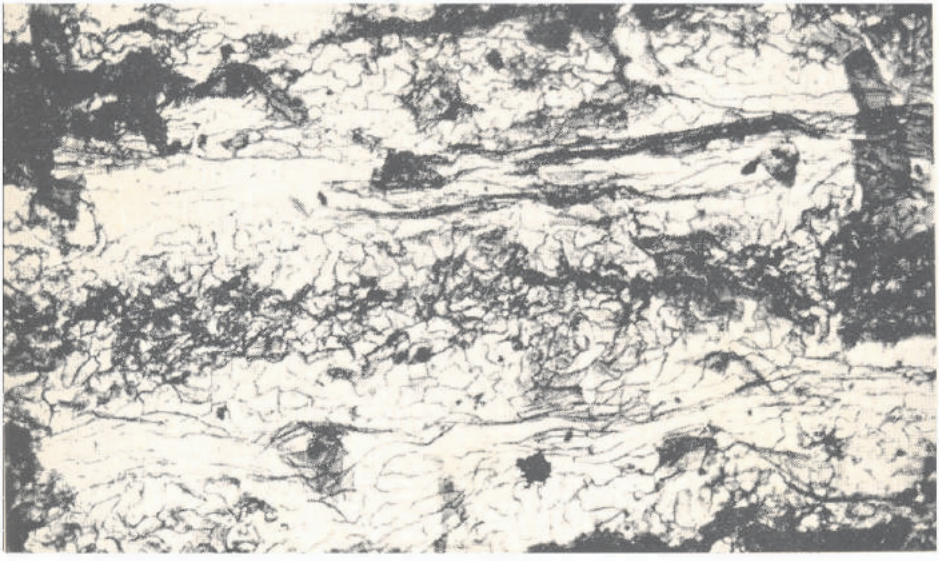

PLATE IV. Fig. 8.—This figure shows two rows of stomata and hairs from the lower epidermis of *Neuropteris reflexa*. The cells display different shapes of the stomatiferous and nonstomatiferous ribs.

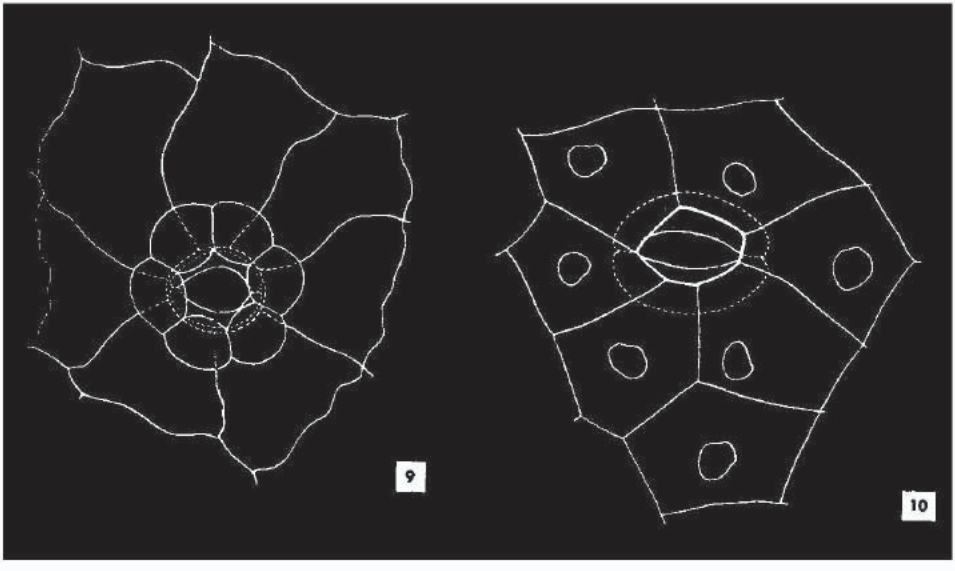

Fig. 9. Diagram of the stomatal apparatus of *Neuropteris reflexa* showing the arrangement of the subsidiary cells and typical ring-cells. The sunken guard-cells are shown by dotted lines.—Fig. 10. *Neuropteris siphonopilosa*. The diagramatic illustration shows the papilla of the subsidiary cells, the outer edge of the stomata and shape of the sunken guard-cells.

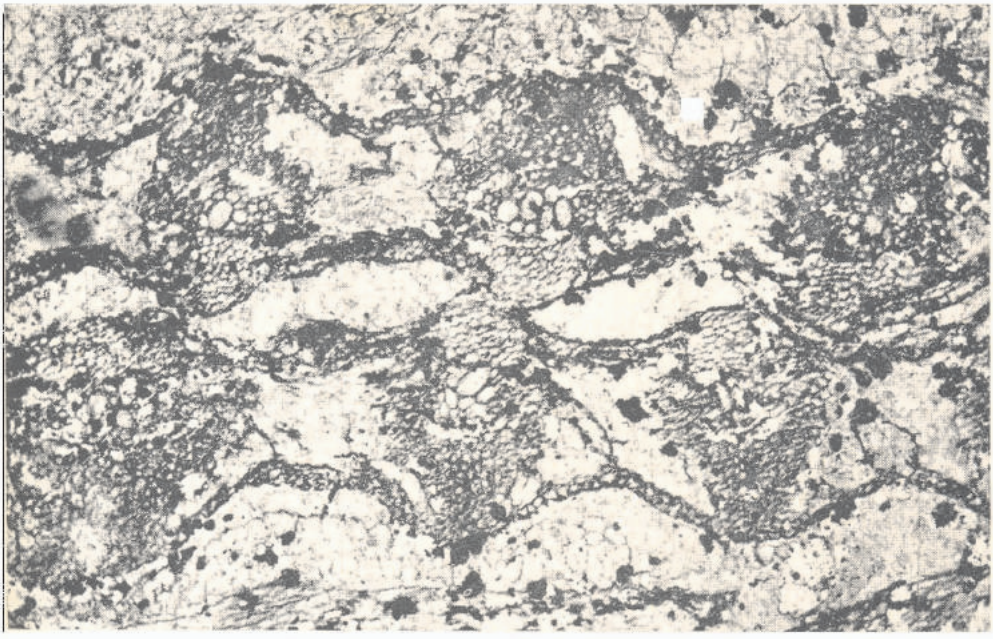

PLATE V. Fig. 11.—Oblique cross-section of the leaf of *Cordaites kansanus* showing the development of the sclerenchyma and parenchyma and the large elements of the metaxylem.

Fig. 12.—Thin section of the stomatiferous and nonstomatiferous ribs of *Cordaites kansanus*. The stomata usually are arranged in seven rows. The subsidiary lateral cells show the constant inequal size.

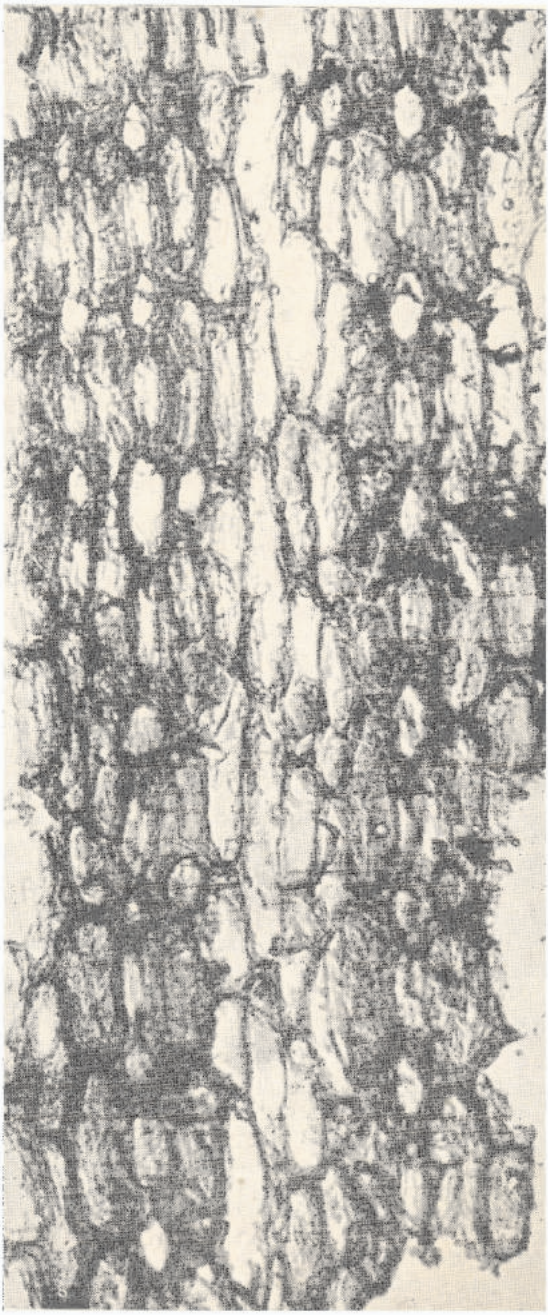

PLATE VI. Fig. 13. Lower epidermal cells and stomata of *Cordaites pyramidalis*. An intervening row of longitudinally elongated cells, two or three wide alternates the stomatal rows.

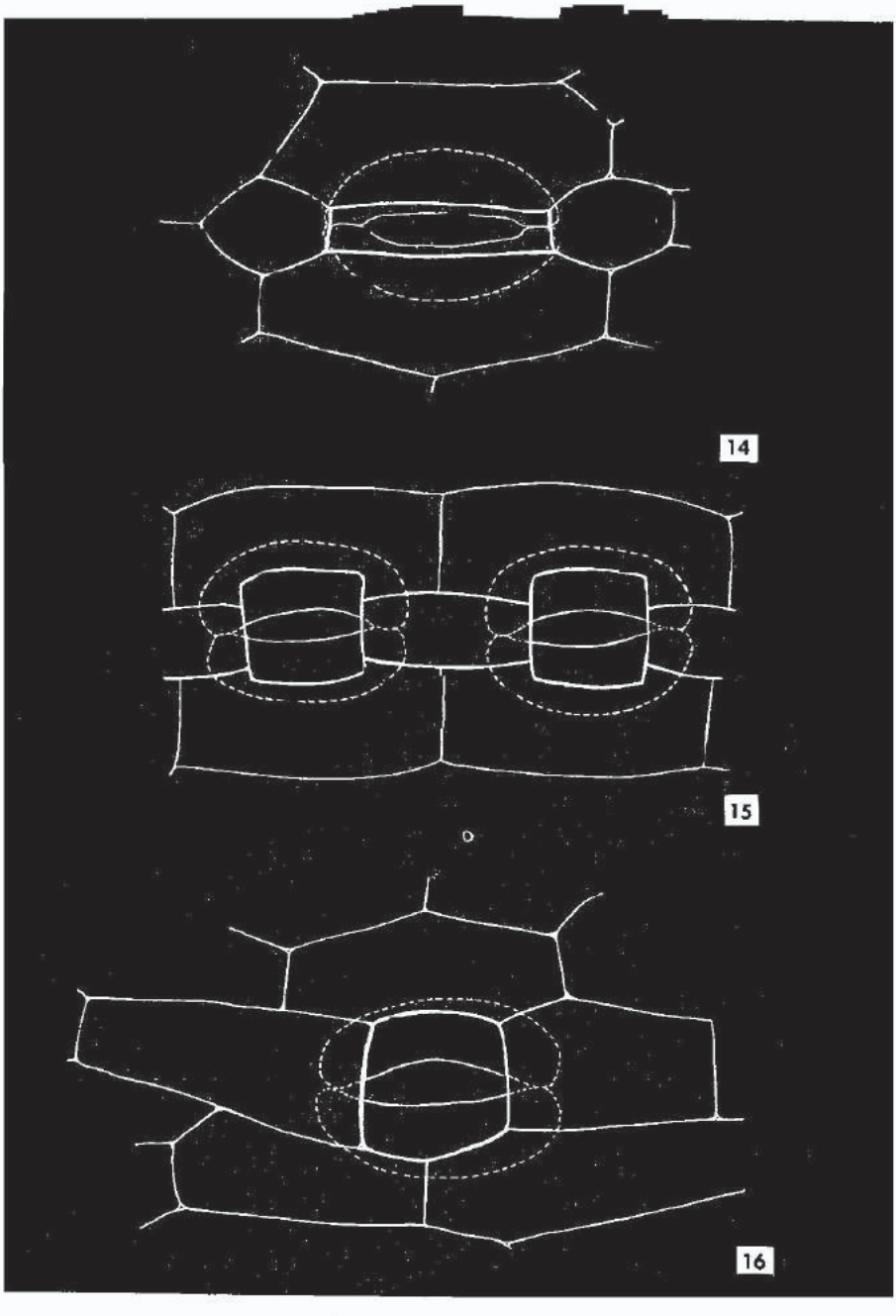

PLATE VII. Diagrams showing the surface view of the stomatal apparatus of *Cordaites pyramidalis* and *Cordaites kansanus*

Fig. 14. Stomata of the upper epidermis of *Cordaites pyramidalis* showing the arrangement and square opening of the subsidiary cells.—Fig. 15. Stomata of the lower epidermis showing the typical joint of the subsidiary cells and the sunken guard-cells.—Fig. 16. Stomata of the lower epidermis of *Cordaites kansanus* showing the shape and arrangement of the polar and lateral cells and the sunken stomata.

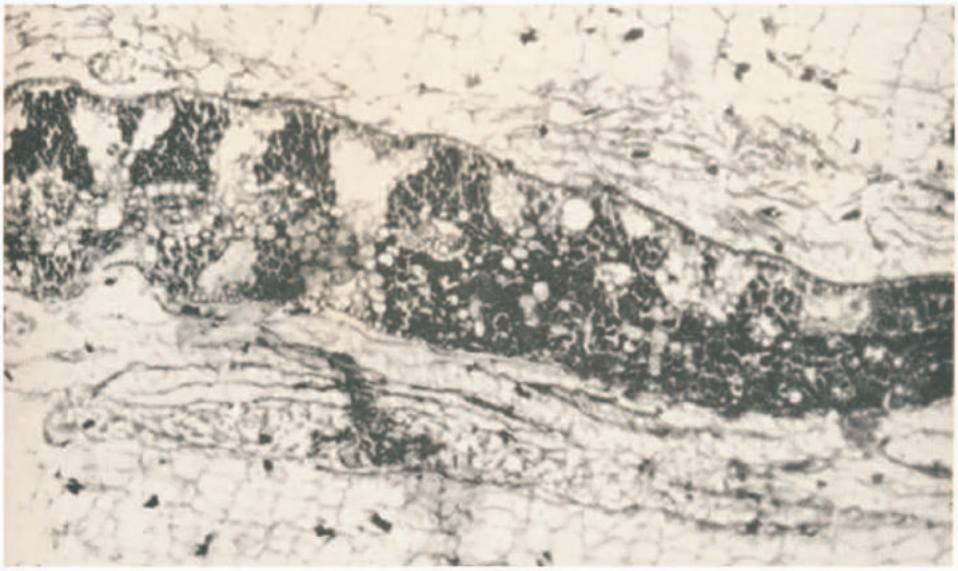

PLATE VIII. Fig. 17.—Cross-section of the leaf of *Cordaites pyramidalis* showing the general pattern and extent of sclerenchyma and parenchyma. On the right side one bundle shows the protoxylem.

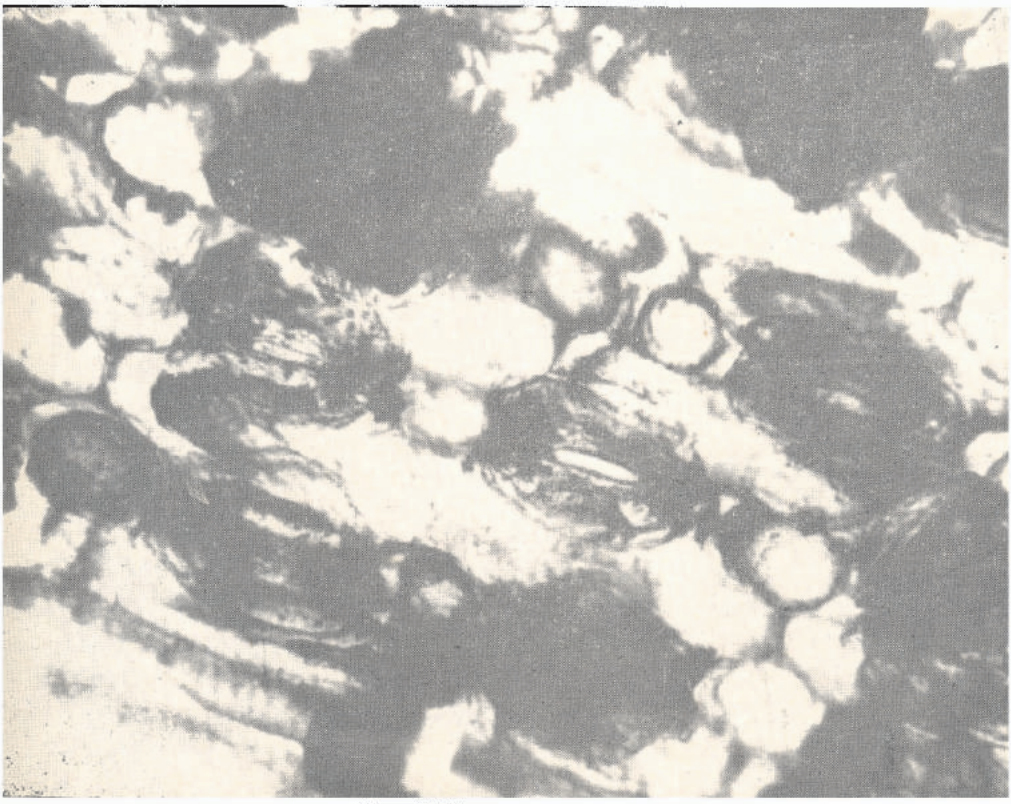

Fig. 18.—Lower epidermis of *Cordaites kansanus* showing the shape of the guard-cells and the lateral and polar subsidiary cells.