THE ANATOMY AND MORPHOLOGY OF CERTAIN CORDAITES LEAVES

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INTRODUCTION

Plants of the extinct gymnosperm genus _Cordaites_ were very prominent constituents of most Carboniferous Age floras. They are of interest as one of the oldest known seed plants, with a fossil history extending back to the latter Devonian Period, dating them contemporary with the seed ferns. The genus _Cordaites_ represents one of the earliest known off-shoots of the great cordaitean-ginkgophyton-conifer line, to which most of the present day gymnosperms belong. _Cordaites_ became extremely abundant and widely distributed over the world during the Upper Carboniferous Period, then gradually diminished in importance but persisted through most of the Permian Period. The various Mesozoic claims once made for _Cordaites_ have been disputed by recent investigators (Florin, 1951), and very likely the genus became extinct toward the end of the Paleozoic Era.

Cordaites plants were tall forest trees frequently reaching a height of 30 meters, with slender trunks rising upward for a considerable distance before giving rise to a crown of branches bearing spirally arranged, sessile leaves. The root system consisted of branching, horizontally extending arms. The plants were monoecious with the staminate and ovulate strobili borne laterally on separate short branches.

The leaves of _Cordaites_ are found abundantly as fossilized impressions, compressions, and petrifactions especially in Pennsylvanian Age strata. Most of the early taxonomic work attempted the speciation of the impression and compression leaf material on the basis of external form and ribbing patterns, and a vast number of specific names were instituted. Relatively few cordaitean leaf species have been described in terms of their internal structure, a situation which Reed and Sandoe (1951) ascribed to an apparent anatomical uniformity of the leaves in petrifactions. Only a very small number of cordaitean leaf species have had their epidermal structure determined. Both the external morphology and internal anatomy of some species, such as C. principalis, C. lingulatus, and C. angulosostriatus, have been determined, but to the author's knowledge only the study by Reed and Sandoe (1951) on C. affinis has previously attempted to actually correlate the external ribbing and epidermal pattern of a species with the internal anatomy.

There is considerable uncertainty at present regarding the validity of many of the described cordaitean leaf species recorded in the literature. Many compression species, especially those from America described by Lesquereux and Dawson, were established upon very fragmentary or poorly preserved material. The slight variations in leaf shape and ribbing which sometimes have been used as distinguishing speciation features may frequently be merely a reflection of foliar polymorphism or of varying states of fossil preservation. There is a need to relate the anatomically described species from petrifactions with the form species described from impression and compression material. A broader combination of speciation criteria appears to be necessary to eliminate the present confusion and delimit the truly valid species.

The present study was an attempt to gain further insight into the taxonomic problems of cordaitean leaf speciation, by ascertaining and correlating the internal anatomy, the external morphology, and the epidermal structure of certain cordaitean leaf species found in Kansas and Iowa coal balls.

REVIEW OF LITERATURE

Generic Nomenclature and Classification

Leaves now referred to Cordaites were originally placed in the genus Flabellaria by Sternberg in 1823, who considered them related to the palms. Corda disproved this supposed relationship to the monocotyledons, and in 1850 Unger instituted the new generic name of Cordaites, honoring Corda's work. Subsequent investigators, notably Grand'Eury (1877) and Renault (1879), confirmed the gymnosperm nature of Cordaites.

The generic name of Cordaites is primarily applied as the form genus of the leaves, with the other plant parts designated under a variety of organ generic names. However, in its broad sense as the original generic name, Cordaites should include the whole plant once the various parts have been correctly associated.

Present day classification schemes place the genus Cordaites in the family Cordaitaceae, of the fossil order Cordaitales, whose exact relationship to other gymnosperms is still rather obscure, but contemporary and perhaps of common origin with the pteridosperms

(Haupt, 1953), and rather closely related to the Ginkgoales and Coniferales (Darrah, 1940).

General External Morphology of Cordaitean Leaves

Cordaitean leaves were simple, entire, and quite coriaceous. They were characterized by close parallel venation from base to apex, with the veins dichotomizing inconspicuously at intervals to adjust to different lamina widths. The distance between adjacent veins varied from species to species.

There was a great variation in the size and shape of cordaitean leaves, although most commonly they were long and broadly linear, often reaching a meter in length. Others were lanceolate, spatulate, or obovate in form, with acute, acuminate, or obtuse apexes (Arnold, 1947). Often they were inrolled, possibly accounting for the common imbricated condition found in fossils. Occasionally the apex was shredded. According to Dawson (1871) and Lesquereux (1878) the leaves were generally attached to the stem by a broad, inflated, semi-clasping base.

The subgeneric names of Eu-Cordaites, Dory-Cordaites, and Poa-Cordaites, instituted by Grand'Eury (1877) and based upon external leaf forms and ribbing patterns, are often used in classifying cordaitean leaf species of impression and compression material. These sub-generic names serve a useful descriptive purpose, even though it is recognized that they may have only limited taxonomic meaning (Seward, 1917). Eu-Cordaites, or the typical Cordaites in its more limited usage, referred to generally large and relatively broad leaves of varied shapes, with obtuse or rounded apexes, and fairly widely spaced equal or unequal ribs. Dory-Cordaites referred to variously sized, narrowly lanceolate, non-fleshy leaves, with pointed apexes and fine equal ribs. Poa-Cordaites referred to very narrow, fleshy leaves, never exceeding 1 cm. in width, with obtuse apexes and equal unbranched ribs.

Renault and Zeiller (1885) instituted another subgeneric name, Scuto-Cordaites, to refer to some leaves with unequal ribs, round contracted bases, and narrowly shredded distal portions. The additional subgeneric name of Dictyo-Cordaites was originated by Dawson (1890) to refer to some ribbon-like leaves with broad bases, unevenly truncate apexes, and distinct acutely forked veins.

General Epidermal Structure of Cordaitean Leaves

Although the form and ribbing patterns of cordaitean leaf species have received much attention in impressions and compressions, a knowledge of their epidermal characteristics is rather meager. The leaf epidermis was covered with a moderately thick cuticle. The epidermal cells were rectangularly shaped, usually being several times longer than broad, with rather thick straight walls, as seen in superficial view. The cells were arranged lengthwise in regular rows parallel to the veins, and sometimes bore hairs or papillae.

On the lower epidermis the stomata usually appeared in definite stomatiferous bands, whose relative width varied in different species. The stomatal distribution within a stomatiferous band varied, but frequently they were borne in regular stomatal rows.

The stomata were oval-shaped and elongated in a direction parallel to the veins. The somewhat submerged guard cells were surrounded by 4-6 subsidiary cells, 2 of them polar and attached to the ends of the guard cells. Florin (1931) stated that the stomatal apparatus of Cordaites was haplocheilic of the monocyclic type, with the stomal mother cells having divided once to form the 2 guard cells, and the perigene epidermal cells functioning directly as subsidiary cells without dividing to form radial rows of encircling cells. The subsidiary cells sometimes bore papillae or cuticular ridges which were useful in specific diagnosis.

Only Wills (1914) has reported stomata as being present on the upper epidermis, indicating that they are few in number, smaller than on the lower epidermis, arranged in rows parallel to the venation, and frequently surrounded by 4 subsidiary cells forming a thickened ring around the sunken guard cells. Wills stated that the upper epidermal cells were thicker walled than the lower, and that circular structures of unknown significance were sometimes present. Whiteford (1916) also reported these circular openings to be present in a supposed Cordaites leaf from Nebraska and suggested the possibility of their having been hydathodes.

General Internal Anatomy of Cordaitean Leaves

Although most cordaitean leaf species were basically rather similar in their internal structure they differed somewhat in various anatomical features. Some species had well-differentiated palisade and spongy mesophyll regions, while in others the mesophyll was more uniform. In most species there was considerable lacunar tissue.

Well developed hypodermal masses of sclerotic tissue were almost invariably present, but their position and extent varied considerably in different species. Sometimes the hypodermal fiber strands were present only above and below the veins, at other times between the veins in various arrangements and amounts, and occasionally in bands reaching from one epidermis to the other between the veins.

The veins were usually enclosed by a well defined outer sheath of thin walled cells. Early workers often interpreted a layer of tracheid-like cells just within the outer sheath in many species as an "inner sheath of primitive transfusion tissue". Stopes (1903) considered this "inner sheath" as developed from the centripetal xylem, while Benson (1912) regarded it as probably a part of, or derived from, the centrifugal xylem. Seward (1917) questioned that this "inner sheath" could really be distinguished from the true xylem elements.

The xylem has generally been reported to be mesarch, with the central protoxylem elements giving rise to a prominent strand of large centripetal tracheids above, and an irregular crescent of narrower centrifugal tracheids below. In some leaves, or parts of leaves, the centrifugal xylem remained undeveloped, hindering the detection of the mesarch protoxylem condition. The phloem, not often well preserved, was located below the centrifugal xylem.

The vascular arrangement varied somewhat in the different cordaitean leaf species that have been anatomically described, although in many of the specimens studied, the preservation was too poor to allow for a very accurate determination of the xylem and phloem condition.

Criteria for Species Determination

Paleobotanical speciation at best is rather arbitrary, being of necessity based entirely upon morphological criteria, and complicated by such special problems as fragmentary plant parts and fossilization changes. These difficulties inherent in fossil speciation have led to the paleobotanical practice of maintaining as distinct form species each morphological variant encountered, until organic connections have verified their identity as the same species.

The specific determination of cordaitean foliage in impression and compression material has been based traditionally upon leaf shape and the arrangement of the course and fine ribs on the leaf exterior. Species have been distinguished upon differences in rib frequency, the number and distinctness of intermediate striae between the main ribs, and differences between the upper and lower surfaces. However, it is realized that leaf shape and ribbing are rather variable characters upon which to base speciation, since foliar polymorphism was probably not uncommon, and the rib frequency was known to vary in different leaf parts, and in leaves of different sizes and ages. The presence of intermediate striae marking the location of internal sclerotic bands was probably too dependent upon fossilization conditions to be a very reliable taxonomic feature. Although leaf width had been considered rather important, Reed and Sandoe

(1951) showed that the width of a cordaitean leaf as it appeared on a rock surface may be only a fraction of the width of an originally inrolled or imbricated leaf.

The use of internal anatomy as revealed in petrifactions is an important additional taxonomic aid. Anatomical features used in cordaitean leaf speciation include leaf thickness, vein frequency, the position and extent of the hypodermal sclerotic bands, the degree of palisade and spongy mesophyll differentiation, and the vascular bundle arrangement. Darrah (1940) has pointed out that anatomical studies do have taxonomic limitations since different leaf portions may have varied considerably in their degree of tissue development, making it necessary to know from which leaf part a section was made. This danger was illustrated when Benson (1912) concluded that 3 separate cordaitean leaf species established by Felix (1886) upon anatomical characteristics, were in reality different parts of the same leaf form. Another taxonomic limitation results from anatomical differences between leaves of different ages. This latter problem was approached by Lignier (1913) who made histological studies upon a C. lingulatus bud showing the tissue ontogeny from very young to adult leaves of the same species. In using anatomical criteria, it must be realized that vertical compression during the fossilization process may have considerably distorted the leaf thickness, the distance between the bundle if the leaf were not in a horizontal plane in the matrix (Reed and Sandoe, 1951), and perhaps even the original cell shapes (Walton, 1936).

The use of epidermal characters, especially of the stomatal structure and arrangement, has opened another valuable taxonomic approach. Florin (1931), after a study of the cuticles of both fossil and living gymnosperms, concluded that epidermal and stomatal features in combination with the usual morphological approach constitute a complex of features valuable in generic and specific determination. Florin (1931) examined the epidermal structure of 3 cordaitean leaf species, and noted that they differed in their stomatal patterns, but unfortunately he failed to publish the identity of these 3 species.

Epidermal features which have been considered of taxonomic value with reference to cordaitean leaves were the relative width of the stomatiferous and nonstomatiferous bands, the shape of the epidermal cells in both bands, the stomatal arrangement within a band, the arrangement and size of the subsidiary cells surrounding the guard cells, the stomatal frequency, and the presence of special epidermal structures such as hairs, papillae, or cuticular ridges.

It is recognized that each of the criteria which have been previously used to delimit cordaitean leaf species possess individual limitations, causing considerable taxonomic confusion. This problem was reflected by Arnold (1941) when he stated that "the difficulties attending the identification of cordaitean foliage are mainly responsible for the widespread neglect of them on the part of paleobotanists".

The most reliable approach in the systematics of cordaitean leaves would appear to be the simultaneous use of as many different speciation criteria as possible. This has been attempted in the present study through the use of coal ball petrifactions which can reveal the external ribbing pattern, the internal anatomy, and the epidermal structure of the same Cordaites leaf. Coal balls are limited, however, in seldom revealing the over-all length of the long cordaitean leaves.

Cordaitean Compression Species

Some of the cordaitean leaf species which have been described from their general shape and ribbing patterns in impression and compression material are listed below, with very brief descriptive accounts of several of the more significant ones. It is unfortunate that many of these compression species were either established upon very fragmentary or poorly preserved material, or were imperfectly described and figured in the literature, with even the location of the early type specimens frequently unknown.

C. borassifolius (Stbg.) Ung. (fig. 1-A) was a widely distributed species of large ovate-lanceolate leaves with obtuse and sometimes slit apexes, reaching 60 cm. in length by 4-10 cm. in width and having alternately thick and thin ribs at a frequency of 50-70/cm. (Lesquereux, 1878). The American species of C. robbii Daws. (fig. 2-A,B,C), was referred to C. borassifolius by Stopes (1914).

C. (Dory-Cordaites) palmaeformis (Goepp.) Weiss (fig. 1-B) was a common European species of long lanceolate leaves measuring about 10 x 80 cm., which tapered gradually from broad middle portions to acute apexes, and had 30-50 fine equal ribs/cm. (Seward, 1917).

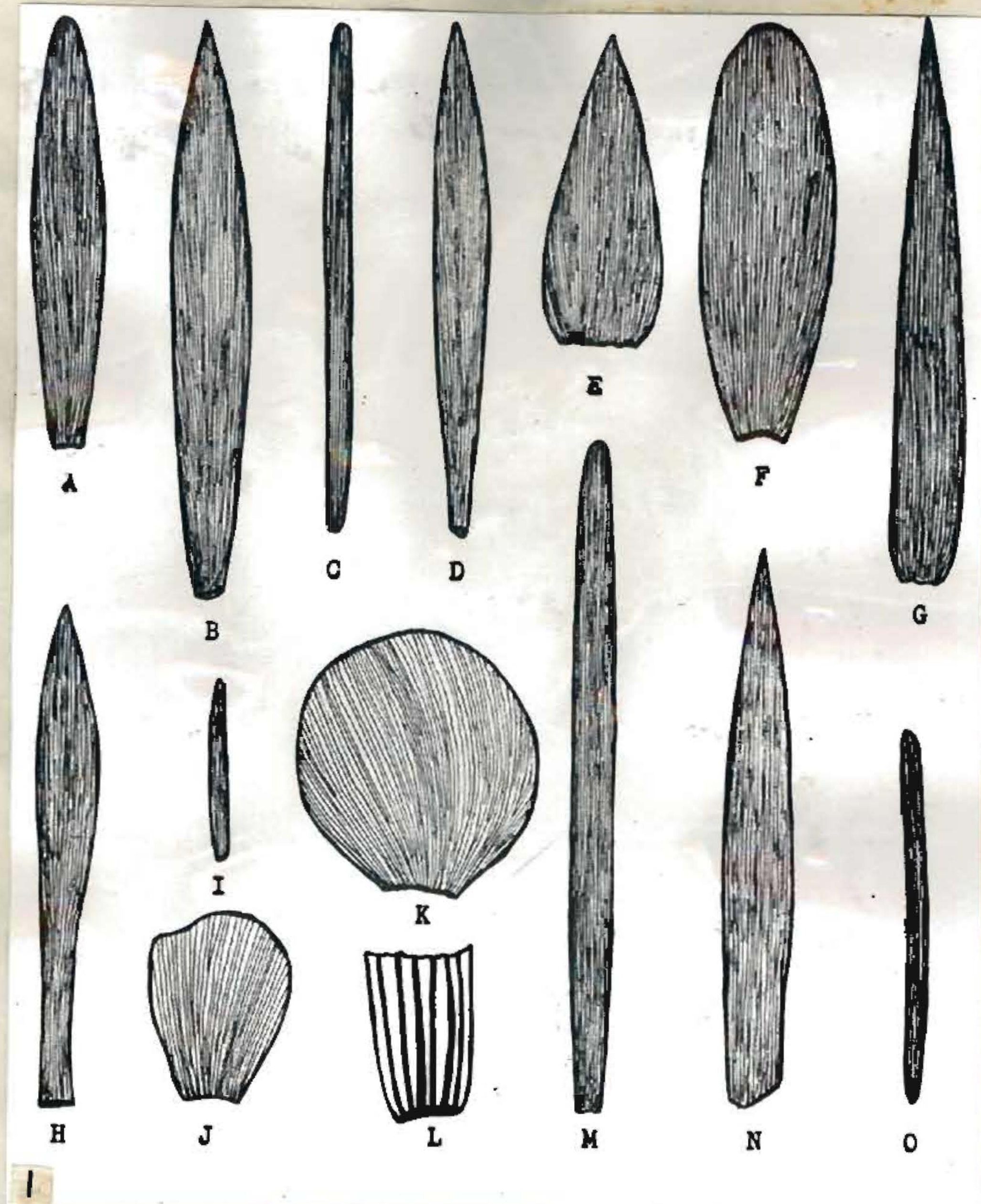


Fig. 1. Some cordaitean compression leaf forms.
A--*C. borassifolius* (Stbg.) Ung. X 0.1 (after Dawson, 1892).
B--*C. palmaeformis* (Goepp.) Weiss X 0.1. C--*C. microstachys* Gold. X 1 (after Kidston, 1902). D--*C. intermedius* Gr.'Eury X 0.2.
E--*C. acutus* Gr.'Eury. F--*C. foliolatus* Gr.'Eury X 1. G--*C. alloidius* Gr.'Eury. H--*C. affinis* Gr.'Eury (after Moret, 1943).
I--*C. oxyphyllous* Gr.'Eury X 1. J--*C. quadratus* Gr.'Eury. K--*C. circularis* Gr.'Eury (after Seward, 1917). L--*C. crassinervis* Heer, leaf base X 1 (after Arnold, 1949). M--*C. linearis* Gr.'Eury X 0.5.
N--*C. lancifolius* Schmalh. X 1 (after Schmalhausen, 1887). O--*C. tenuifolius* Schmalh. X 0.25 (after Schmalhausen, 1887). (B, D-G, I, J, and M after Grand'Eury, 1877).

C. (Poa-Cordaites) microstachys Gold. (fig. 1-C) consisted of very narrow linear leaves of less than 1 cm. width but 4-30 cm. in length, with obtuse apexes, and about 30 equal ribs/cm. (Weiss, 1872). Seward (1917) considered the species of C. linearis Gr'Eury (fig. 1-M) and C. tenuifolius Schmal. (fig. 1-O) probably identical with C. microstachys.

C. crassinervis Heer (fig. 1-L) was a widespread leaf species reported from both Europe and North America, characterized by extremely coarse ribs that were 1 mm. broad and about 2 mm. apart with no finer striae between them (Arnold, 1949).

C. (Noeggerathiopsis) hislopi (Bunb.) Sew. (fig. 3, 4-A-D) was the common cordaitean form of the southern hemisphere, consisting of coarsely ribbed, thick, cuneate leaves measuring about 5 x 50 cm., which widened upward from narrow truncate bases to broadly rounded, slightly oblique apexes. The uniform, slightly forked ribs radiated gradually from the basal area. The proximal regions had a rib frequency of 10/cm. compared with 20/cm. in the distal portions. The abaxial epidermal pattern, as reported by Seward and Sahni (1920), consisted of a regular alternation of nonstomatiferous bands composed of elongated epidermal cells bearing hairs, with stomatiferous bands composed of nearly isodiametrical epidermal cells without hairs. There was a stomatal frequency of 140/mm^2, with 6-8 encountered across the width of a band, although the stomata were not strictly arranged in lengthwise rows. C. (Noeggerathia) aequalis (Goepp.) Sew. (fig. 4-E) and C. (Rhiptozamites) goepparti (Schmalh.) Sew. (fig. 4-F,G), although referring to smaller spatulate leaves, have been identified

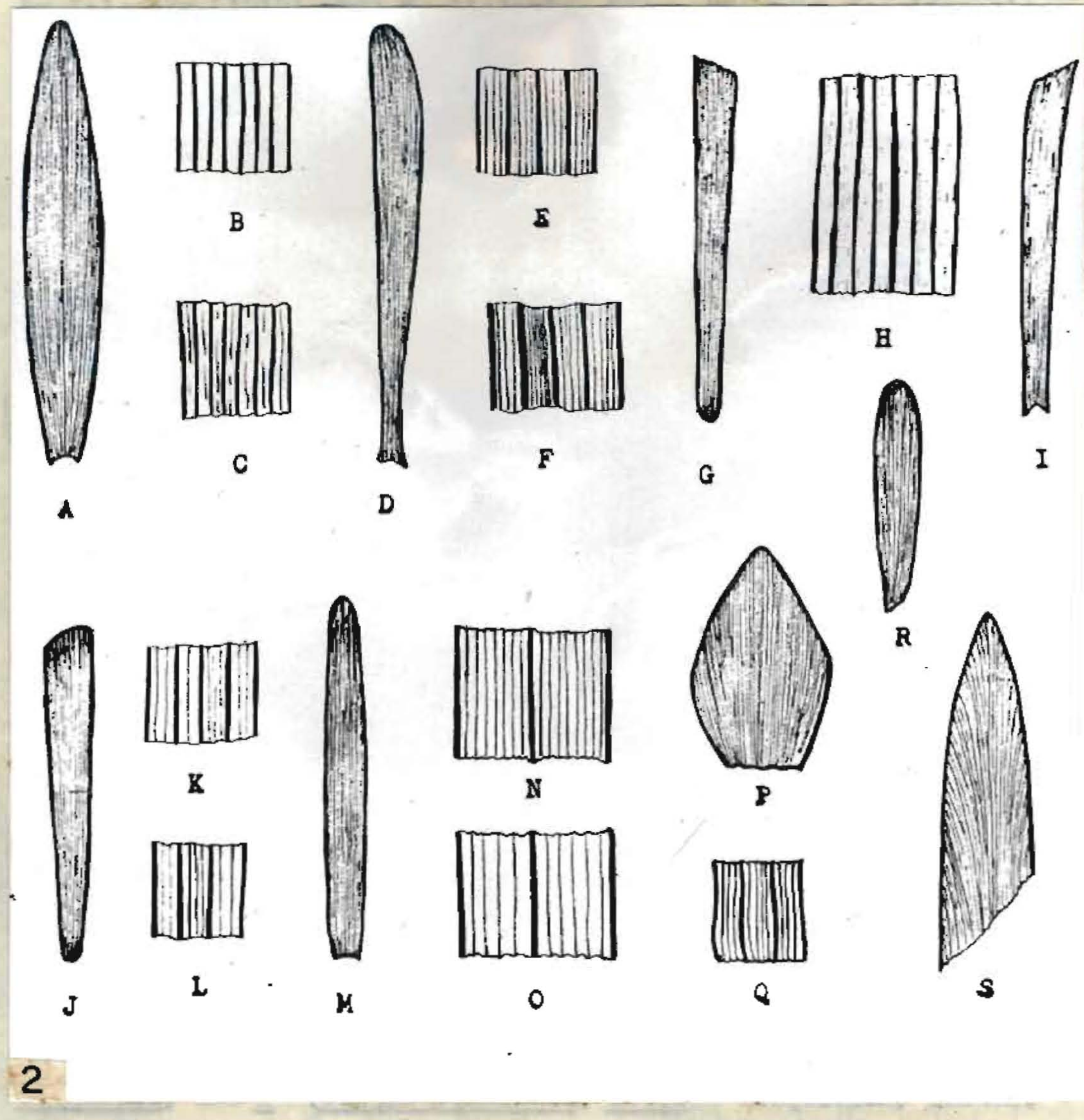


Fig. 2. Some cordaitean compression leaf forms and ribbing patterns. A--*C*. *robbii* Daws. X 0.2 (after Dawson, 1871). B--*C*. *robbii* X 4 (after Dawson, 1871). C--*C*. *robbii* X 4 (after Stopes, 1914). D--*C*. *communis* Lesq. X 0.2 (after White, 1899). E--*C*. *communis* X 6. F--*C*. *costatus* Lesq. X 8. G--*C*. *costatus* X 0.5. H--*C*. *diversifolius* Lesq. X 10. I--*C*. *diversifolius* X 0.4. J--*C*. *gracilis* Lesq. X 0.5. K--*C*. *gracilis* X 5. L--*C*. *mansfieldi* Lesq. X 4. M--*C*. *mansfieldi* X 0.33. N--*C*. *validus* Lesq. upper leaf surface X 10. O--*C*. *validus* lower leaf surface X 10. P--*C*. *lacoei* Lesq. X 1 (after Seward, 1917). Q--*C*. *serpens* Lesq. X 4. R--*C*. *clerci* Zal. X 0.5 (after Seward, 1917). S--*C*. *comptus* Zal. X 0.5 (after Zalessky, 1934). (E,K,N, and O after Lesquereux, 1878. F-J,L,M, and Q after Lesquereux, 1879).

by Zalessky (1912) with C. hislopi. There has been considerable hesitation on the part of many paleobotanists to identify this species as Cordaites, rather maintaining Feistmantel's (1880) generic name of Noeggerathiopsis, mainly because this species was a representative of the Glossopteris type flora of the southern hemisphere.

Among the compression species established by Grand'Eury (1877) were C. intermedius (fig. 1-D), C. acutus (fig. 1-E), C. foliolatus (fig. 1-F), C. cuneatus, C. alloidius (fig. 1-G), C. quadratus (fig. 1-J), C. (Poa-Cordaites) oxyphyllous (fig. 1-I), and C. (Dory-Cordaites) affinis (fig. 1-H). Grand'Eury (1890) also established the species C. circularis (fig. 1-K) and C. sub-germarianus.

C. huttoni House, C. (Scuto-Cordaites) grand'euryi Ren. and Zeill., C. lancifolius Schmalh. (fig. 1-N), C. clerci Zal. (fig. 2-R) and C. comptus Zal. (fig. 2-S) were some additional species described from European compressions.

Dawson, the pioneer American paleobotanist, established a number of cordaitean leaf species including C. angustifolius, C. flexuosis, and C. (Dictyo-Cordaites) lacoi. Lesquereux, another pioneer American paleobotanist, instituted a large number of specific epithets including C. costatus (fig. 2-F,G), C. diversifolius (fig. 2-H,I), C. lacoei (fig. 2-P), C. serpens (fig. 2-Q), C. grandifolius, and C. radiatus. Unfortunately, a large percentage of the species described by Dawson and Lesquereux were based upon very fragmentary and rather poorly preserved material.

C. communis Lesq. (fig. 2-D,E) was a species of spatulate leaves with somewhat oblique, broadly truncate or rounded apexes,

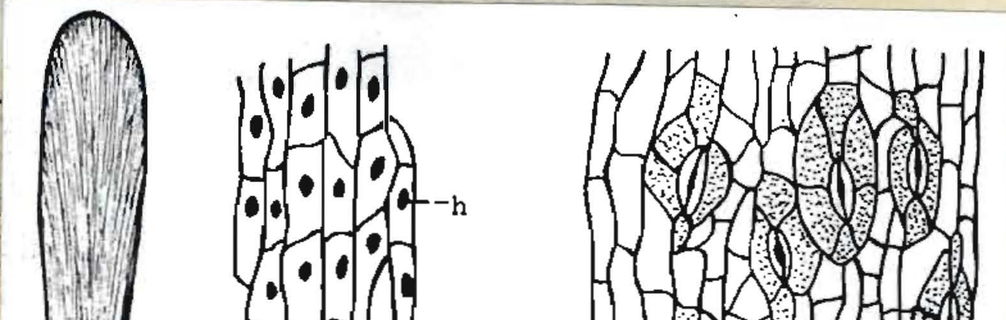


Fig. 3. C. (Noeggerathiopsis) hislopi (Bunb.) Sew. X 0.5 (after Seward and Sahni, 1920). Fig. 4. A-D--C. (Noeggerathiopsis) hislopi (Bunb.) Sew. (after Seward and Sahni, 1920). A--Leaf form X 0.1. B--Abaxial epidermal cells of nonstomatiferous bands X 200; h, hair base. C--Stomal apparatus X 370; p, polar subsidiary cell; l, lateral subsidiary cell; g, guard cell. D--Stomatal arrangement in stomatiferous bands X 217. E--C. aequalis Goepp. X 0.25 (after Seward, 1917). F-G--C. (Rhiptozamites) goepperti (Schmalh.) Sew. X 0.2 (after Schmalhausen, 1879).

measuring about 2-6 x 30 cm., and having 15 primary ribs/cm. with 2-6 intermediate fine striae (Lesquereux, 1878).

C. gracilis Lesq. (fig. 2-J,K) referred to some sublinear leaves about 9 cm. long, which gradually enlarged from a basal width of 0.5 cm. to 1 cm. at the obliquely truncate apexes. There were 10-20 distinct primary ribs/cm. on the lower surface with 1-4 intermediate fine striae (Lesquereux, 1878).

C. validus Lesq. (fig. 2-N,O) denoted some thick leaves measuring about 5-8 x 55 cm., whose upper surface was obscurely striated by 7-8 ribs/mm. and lower surface more distinctly marked by 3-5 irregular obtuse primary ribs/mm. separated by prominent furrows (Lesquereux, 1878).

The 3 common compression species of C. principalis (Germ.) Gein. (fig. 32), C. lingulatus Gr.'Eury (fig. 15), and C. anguloso-striatus Gr.'Eury (fig. 22), to be discussed more fully later, are of special interest because they represent well known compression species whose internal anatomy has also been ascertained. Seward (1917) stated that the compression species of C. ottonis Gein. and C. mansfieldi Lesq. (fig. 2-L,M) were probably identical with C. principalis.

Cordaitean Anatomical Species

C. rotundinervis Gr.'Eury (fig. 5-7) was a species of uniformly veined leaves anatomically described by Grand'Eury (1877) from French silicified specimens. The hypodermal sclerotic tissue apparently was limited to the regions above and below the veins. No differentiation of the mesophyll into definite palisade and spongy layers was evident, although the cellular tissue was somewhat denser toward the adaxial side. The mesophyll adjacent to the lower surface was composed of somewhat elongated small cells with open regions associated with each stoma. The middle mesophyll between the veins consisted of a mass of large and small cells, which in sagittal sections (fig. 6) revealed strands of cells and lacunar chambers oriented perpendicularly to the veins. The veins had a central xylem strand of reticulate tracheids, surrounded by an inferior arch of other reticulate elements. According to Grand'Eury's (1877) illustration (fig. 7) and Seward and Sahni (1920), the stomata on the lower epidermis were not aligned in definite rows, but scattered within the stomatiferous bands, where about 6 might be encountered across a band width.

C. rhombinervis Gr.'Eury (fig. 8, 9) was a species of leaves anatomically described by Grand'Eury (1877) and Renault (1879) from French siliceous petrifactions. The superficial ribbing of this species resembled that of C. rotundinervis, being caused by internal triangular sclerotic masses restricted to the regions above and below the veins. The veins, and therefore the external ribs, were evenly spaced at distances of about 0.4 mm., resulting in a vein frequency of approximately 25/cm. The mesophyll was differentiated into an upper palisade region of evenly arranged isodiametrical parenchyma cells and a lower spongy region. A sheath of elongated, somewhat porous cells surrounded the vascular bundle. Located in the superior part of the bundle was a triangular xylem strand consisting of

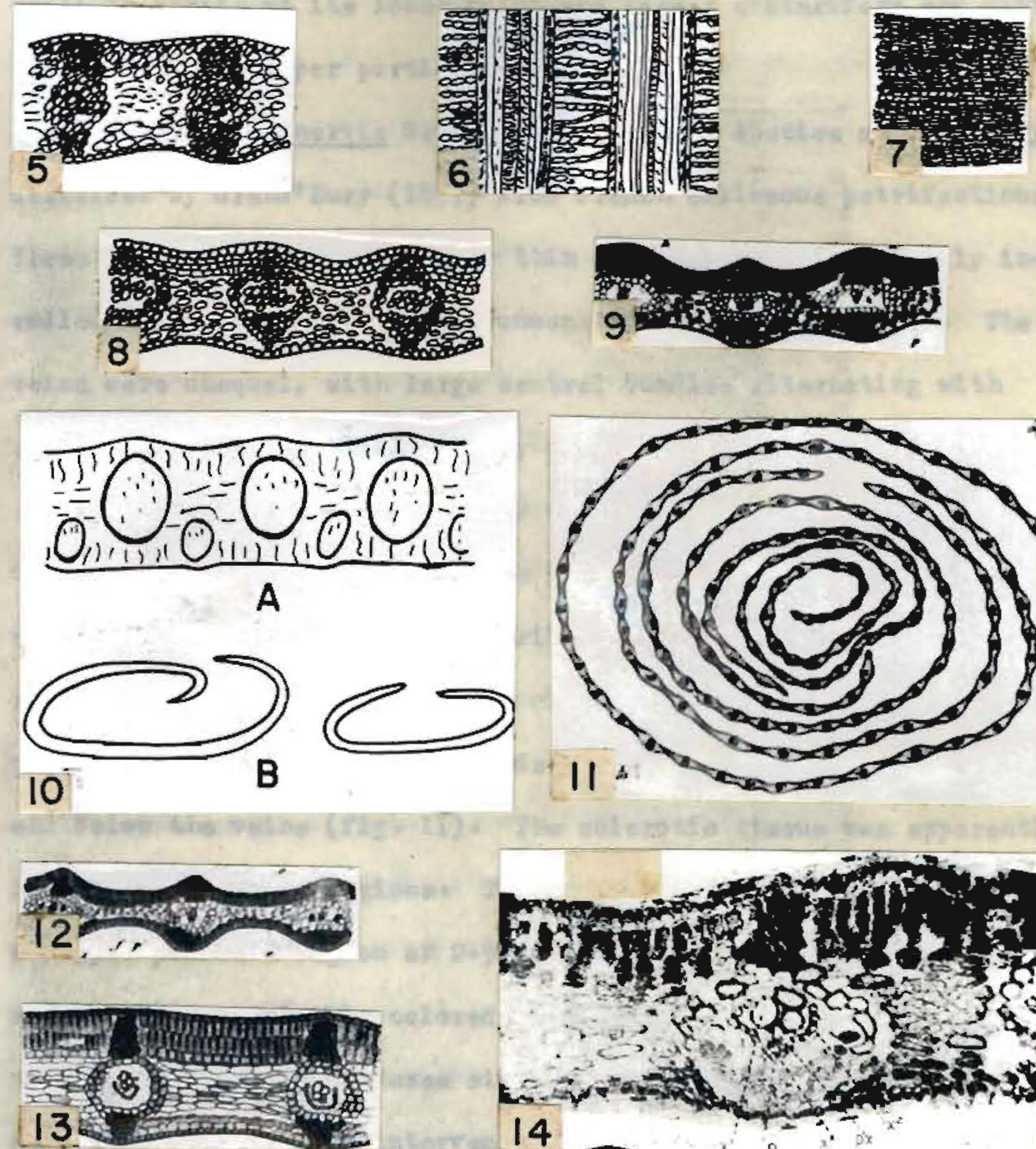


Fig. 5-7. C. rotundinervis Gr.'Eury (after Grand'Eury, 1877). Fig. 5. Transverse section. Fig. 6. Sagittal section. Fig. 7. Lower epidermis. Fig. 8. C. rhombinervis Gr.'Eury transverse section (after Grand'Eury, 1877). Fig. 9. C. rhombinervis transverse section X 40 (after Renault, 1879). Fig. 10. C. duplicinervis Gr.'Eury (after Grand'Eury, 1877). A--Transverse section. B--Inrolled leaf appearance. Fig. 11-12. C. tenuistriatus Gr.'Eury (after Renault, 1879). Fig. 11. Transverse section of bud X 8. Fig. 12. Transverse leaf section X 40. Fig. 13-14. C. lingulatus Gr.'Eury. Fig. 13. Transverse section X 45 (after Renault, 1879). Fig. 14. Transverse section X 130; px, protoxylem; x^1, centripetal xylem; x^2, centrifugal xylem; p, phloem (after Stopes, 1903).

small tracheids at its lower point and larger scalariform and pitted elements in the upper portion.

C. duplicinervis Gr.'Eury was another species anatomically described by Grand'Eury (1877) from French siliceous petrifactions. These delicate leaves were very thin and narrow, with markedly inrolled borders often forming pronounced spirals (fig. 10-B). The veins were unequal, with large central bundles alternating with smaller bundles appearing on only one side (fig. 10-A).

C. tenuistriatus Gr.'Eury was a leaf species anatomically described by Renault (1879). The leaves were characterized externally by narrow, equally spaced ribs about 0.6 mm. apart, representing an approximate frequency of 17 ribs/cm. These superficial ribs were caused by internal bands of sclerotic tissue located above and below the veins (fig. 11). The sclerotic tissue was apparently limited to the vein regions. The mesophyll was differentiated into an upper palisade region of 2-3 rows of evenly arranged isodiametrical cells with darkly colored interiors. Adjacent to the lower epidermis was a rather dense single layer of spherical, darkly colored, parenchyma cells. The intervening region of the mesophyll between the veins was composed of a fairly compact parenchymatous tissue composed of transversely elongated cells and lacunae directed perpendicularly to the veins. This lacunar central portion was often rather crushed by external compression resulting in a more pronounced superficial relief than originally existed. A bundle sheath composed of very large, sometimes darkly colored, porous cells surrounded the veins. The tissue between the sheath and the xylem elements was seldom preserved. A triangular xylem wedge, located in the central part of the bundle, consisted of 1-2 small protoxylem tracheids at its lower point, and larger scalariform and pitted tracheids radiating out above them. The upper epidermal cells of this species were characterized by having borne papillae. Renault (1879) described and illustrated (fig. 12) a large bud of this species which was 4-5 cm. in length and 6-7 mm. in diameter.

C. lingulatus Gr.'Eury (fig. 13-21) represents a well known compression species whose internal anatomy was studied by Renault (1879), Lignier (1913), and to some extent by Stopes (1903). The leaves were obovate in shape with bluntly rounded, almost truncate apexes, reaching 11 x 35 cm., but decreasing to a 4 cm. basal width (fig. 15). The superficial ribs of the basal portion were unequally prominent with 1-3 fine striations between the main ribs, but the ribs of the middle and apical portions appeared equal at intervals of 0.6 mm., with a frequency of 17/cm. These superficial ribs were caused by the internal hypodermal sclerotic bands which were limited to the regions above and below the veins.

The mesophyll was clearly differentiated into a distinct upper palisade region and a lower spongy region with considerable lacunar tissue (fig. 13, 14). The veins were enclosed by an outer bundle sheath composed of cells with irregular bordered pits. A centripetal xylem strand of large scalariform, reticulate, and pitted tracheids was located in the center of the vein with the spiral protoxylem tracheids at its lower point. A centrifugal xylem crescent of small reticulate or pitted tracheids was located below, separated from the centripetal strand above by a row of parenchyma cells (fig. 18). Lignier (1913) indicated that certain centrifugal elements, representing an anterior extension of the centrifugal arc, were found around and above the centripetal xylem mass. Isolated thick walled lateral tracheids just within the outer sheath, have been interpreted by Lignier (1913) as an inner sheath of transfusion elements which he termed "bois diaphragmatique" because of the closely pitted diaphragmed nature of these cells. A darkly colored cell located within the "inner sheath" on either side of the bundle, was interpreted by Lignier as a secretory cell (fig. 16, 21). The phloem was located in the region below the centrifugal xylem arc.

Lignier (1913) studied the sequence of tissue development from young to adult leaves of this species, thus providing a valuable aid to the identification of leaves of different ages, and undoubtedly providing an indication of the order of tissue differentiation in other species as well. In general the tissues of the lower vein region developed first. The phloem appeared early, preceding the metaxylem. The very small protoxylem annular elements were the first definitely differentiated cells of the xylem, successively followed by the spiral, scalariform, and finally the pitted centripetal tracheids. Concurrently the outer bundle sheath was differentiated, and the hypodermal sclerenchyma cells became lignified. The last xylem elements to differentiate were the centrifugal tracheids, with their development paralleled by the formation of the lateral "inner sheath" elements. Lastly the palisade mesophyll region was differentiated by the division of a single layer forming 2-3 tiers of cells.

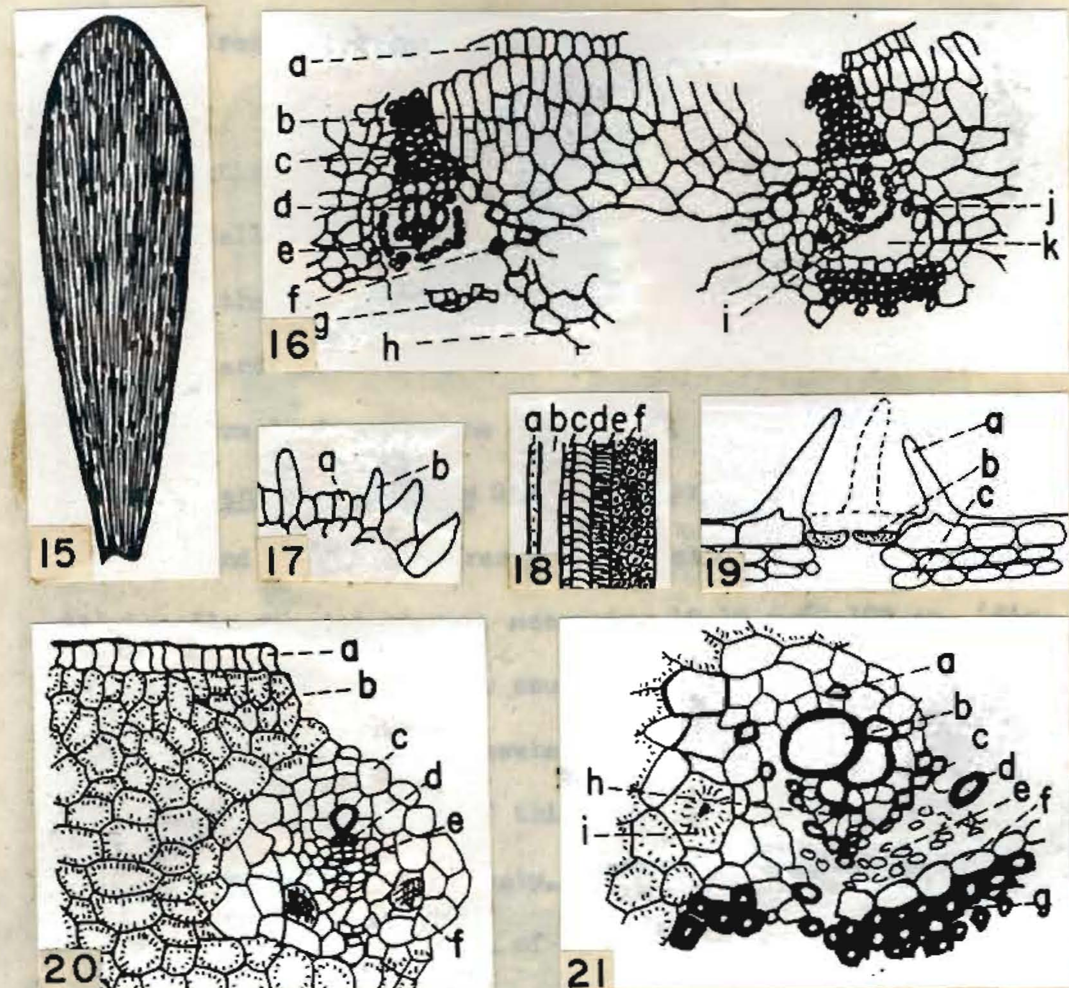


Fig. 15-21. C. linguletus Gr.'Eury. Fig. 15. Leaf shape X .2 (after Moret, 1943). Fig. 16. Transverse section X 235; a, upper epidermis; b, palisade parenchyma; c, adaxial hypodermal strand; d, centripetal xylem; e, protoxylem; f, secretory cell in inner sheath; g, outer bundle sheath; h, lacunar parenchyma; i, centrifugal xylem; j, inner sheath element; k, phloem region. Fig. 17. Transverse section of lower epidermis X 235; a, epidermal cell; b, papilla. Fig. 18. Radial section of vein; a, centrifugal pitted tracheid; b, parenchyma cell; c, protoxylem annular element; d, centripetal spiral tracheid; e, centripetal scalariform tracheid; f, centripetal pitted tracheid. Fig. 19. Transverse section of stomal region; a, cuticular papilla on subsidiary cell; b, guard cell; c, spongy mesophyll (after Florin, 1931). Fig. 20. Transverse section of very young leaf in bud X 235; a, adaxial epidermis; b, mesophyll only slightly differentiated; c, bundle sheath; d, protoxylem; e, phloem; f, secretory cell. Fig. 21. Transverse section through vein X 235; a, anterior centrifugal tracheid; b, centripetal xylem; c, centrifugal xylem; d, inner sheath element; e, phloem; f, bundle sheath; g, abaxial hypodermal strand; h, protoxylem; i, secretory cell. (Fig. 16-18, 20, and 21 after Lignier, 1913).

Fig. 20 represents a transverse section of a very young inner leaf of the bud.

Lignier (1913) reported the presence of papillae on the lower epidermal cells of *C. lingulatus* (fig. 17). Florin (1931) described papilla on the subsidiary cells surrounding the stomatal guard cells (fig. 19), and undoubtedly this species must have been 1 of the 3 whose epidermal structure he determined, but failed to identify.

C. angulosostriatus Gr.'Eury represents a well known Pennsylvanian and Permian compression species of thick spatulate leaves with broadly rounded apexes, measuring 10-15 x 60-100 cm. (fig. 22), with about 17 uneven, rather course ribs/cm., or 0.6 mm. apart, which tended to converge somewhat at the base. Renault (1879) figured the internal anatomy of this species (fig. 23). The leaves were extremely thick and fleshy, and despite considerable crushing indicated by the obliqueness of the bundles, Renault's specimen was still 1 mm. in thickness. The angular veins were completely embedded in the leaf tissue. Well developed hypodermal sclerotic bands accompanied the veins and were attached to the bundle sheath. There were also 3 additional, more-or-less equal, intermediate, hypodermal, sclerotic strands between the bundles on both the abaxial and adaxial sides. These intermediate strands did not appear to cause external striations to the extent that could be expected, probably because of their being buried in the thick mesophyll.

The mesophyll of *C. angulosostriatus* was not differentiated into palisade and spongy regions, although the parenchymatous tissue near the adaxial side was composed of a more compact layer of thicker,

Fig. 22-24. C. angulosostriatus Gr.'Eury. Fig. 22. Leaf shape X 0.1 (after Grand'Eury, 1877). Fig. 23. Transverse section X 50; h, adaxial hypodermal strand; p, parenchyma; a, scalariform centripetal tracheids; t, spiral protoxylem tracheids; b, centrifugal xylem tracheids; c, phloem; d, bundle sheath; h, abaxial hypodermal strand (after Renault, 1879). Fig. 24. Lower epidermis X 30 (after Seward and Sahni, 1920). Fig. 25. C. felicis Bens. transverse section X 55; l, lacuna; g, inner sheath; bs, intermediate sclerotic bands; ms, sclerotic masses associated with veins; Bcp, centripetal xylem; Bct, centrifugal xylem (after Leclerq, 1927).

darkly colored, polyhedral cells. Lacunar tissue was found between the bundles, but often not well preserved. Scott (1909, 1923) indicated that the bundle sheaths were seemingly connected laterally by transverse bridles of thickened cells, which he interpreted as being lateral transfusion tissue such as Worsdell (1897) originally described in the cycads. The large veins were enclosed by a strong bundle sheath composed of several layers of porous fibers. The xylem was mesarch in structure with the small spiral protoxylem elements in the center having given rise to a mass of large scalariform and pitted centripetal tracheids above, and a group of small pitted centrifugal tracheids below them. The phloem was located below the centrifugal xylem but usually was poorly preserved.

Seward and Sahni (1920) studied the epidermal structure of C. angulosostriatus (fig. 24), and reported that the epidermal cells were rectilinear with no cuticular appendages. The stomata of the lower epidermis were invariably arranged in regular single file rows separated by alternately wide and narrow nonstomatiferous bands. The narrow nonstomatiferous bands were only 0.25-0.33 as broad as the wider bands, and their alternation resulted in the characteristically paired nature of the stomatal rows of this species. Seward and Sahni speculated, without actual proof, that the broader stomatiferous bands probably corresponded to the large superficial leaf ribs, while the 2 paired rows lay respectively on the right and left slopes of an intervening groove.

C. felicis Bens. (fig. 25-27) was a specific epithet proposed by Benson (1912) to replace the names of C. robustus, C.

loculosus, and C. wedekindi, 3 anatomical species previously established by Felix (1886). Benson showed that C. robustus and C. loculosus were basal forms, and C. wedekindi was an upper portion of the same leaf type, a conclusion also supported by the study of Koopmans (1928). At first consideration, Benson's recorded measurements of this form seemed incongruously minute, but the difficulty was clarified by Scott's (1923) statement that Benson's measurements were in error and each required multiplication by a factor of 10. The leaves reached a thickness of over 1 mm. in basal portions, but decreased in thickness upward and toward the margins which measured not less than 0.19 mm. Seward (1917) stated that there were 15 veins/cm., but Benson's report would indicate a range of 16-21 veins/cm.

There was an almost continuous hypodermal sclerotic layer beneath each surface of the thicker leaf parts, but this layer was interrupted in thinner leaf portions. The most outstanding characteristic of C. felicis leaves was the extension of the intermediate hypodermal sclerotic ribs completely across from the abaxial to the adaxial side forming strong I-shaped girders between the veins. The intervening hypodermal sclerotic masses between these main partitions on both surfaces varied in number and size, but usually consisted of 3 smaller ribs between each pair of main sclerotic partitions on the lower surface, and a more-or-less uniformly thick layer along the upper surface, except where a more pronounced rib was often attached to the vascular bundles (fig. 26).

The mesophyll showed little differentiation into palisade and spongy layers although the upper region was somewhat more compact (fig. 26). This species was less lacunar than most, although radial sections usually, and sagittal sections always, revealed narrow lacunar crevices between transversely running strands of cells. The parenchyma cells in these strands were slightly elongated perpendicular to the veins.

The circular veins (fig. 27) were surrounded by a thick, well developed sheath of longitudinally disposed, occasionally pitted elements, except in the proximal leaf regions. The bundle sheath was attached to the hypodermal sclerotic masses above and below. The well developed upper centripetal xylem consisted of large pitted tracheids radiating from a small lower protoxylem group, decreasing in number as the leaf was reduced in thickness distally. The protoxylem group also gave rise below to narrow centrifugal tracheids which in well developed portions of a leaf formed a distinct crescent attached to the sides of the upper centripetal xylem. The centrifugal xylem was more abundant in the basal leaf portions, and entirely absent toward the margins and the apical regions. A layer of parenchyma usually separated the centrifugal xylem from the centripetal xylem and also from the phloem below. Elements similar to the centrifugal tracheids partially lined the lower part of the bundle sheath (fig. 27-d), and were considered an "inner sheath of primary transfusion tissue" by Benson (1912), who believed them to be derived from the centrifugal xylem.

Seward (1917), despite the anatomical work of Renault (1879) and Stopes (1903), suggested that C. felicis and C. principalis were identical, because the former was the dominant anatomical form

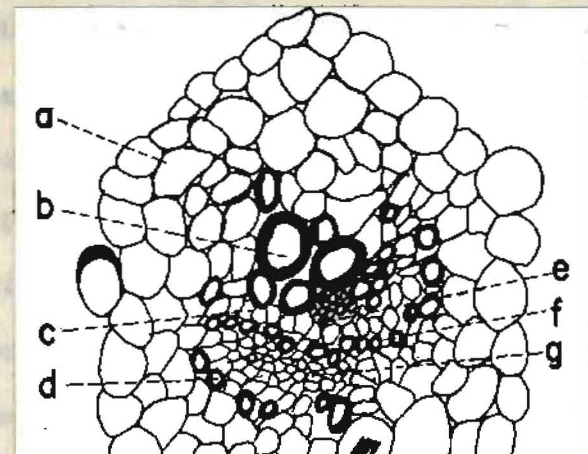


Fig. 26. C. felicis Bens. transverse section; cp, centripetal xylem; px, protoxylem; ph, phloem (after Seward, 1917). Fig. 27. C. felicis Bens. transverse section of vein; a, bundle sheath b, centripetal xylem; c, parenchyma layer; d, inner sheath; e, protoxylem; f, centrifugal xylem; g, phloem (after Benson, 1912).

and the latter was the dominant compression form in the lower coal measures of Great Britain, a premise seemingly also supported by Leclercq (1927). However, neither actually correlated the compression and anatomical forms. This contention results in considerable confusion since the anatomical description of C. principalis by Renault and Stopes differs markedly from Benson's (1912) species of C. felicis. The possibility remains that perhaps these species, which are quite different anatomically, may present rather similar compression forms, and it is known that the ribbing frequency is nearly identical.

C. weristeri Leclercq (fig. 28-31) was a leaf species anatomically described by Leclercq (1927). The leaf was 0.5-1.4 mm. thick. The sclerotic tissue consisted of almost equal, hypodermal masses lining both surfaces, but somewhat more developed on the abaxial side, with none of them crossing the leaf width or jutting very far inward. The number of these fiber masses varied, but they were always opposite in position on the 2 surfaces.

The mesophyll was only slightly differentiated, with no upper palisade layer formed. In distal leaf portions (fig. 30) the central part of the mesophyll between the veins was composed of highly developed, complex, lacunar tissue, with the lacunae appearing as superimposed planks bound together by parenchymatous tissue (fig. 29, 31). However, Leclercq's description regarding the exact orientation of these lacunae in reference to the veins seems rather confusing and her photographs (fig. 29, 31) lack clarity. Lacunar tissue was absent near the proximal leaf portions (fig. 28), where instead the

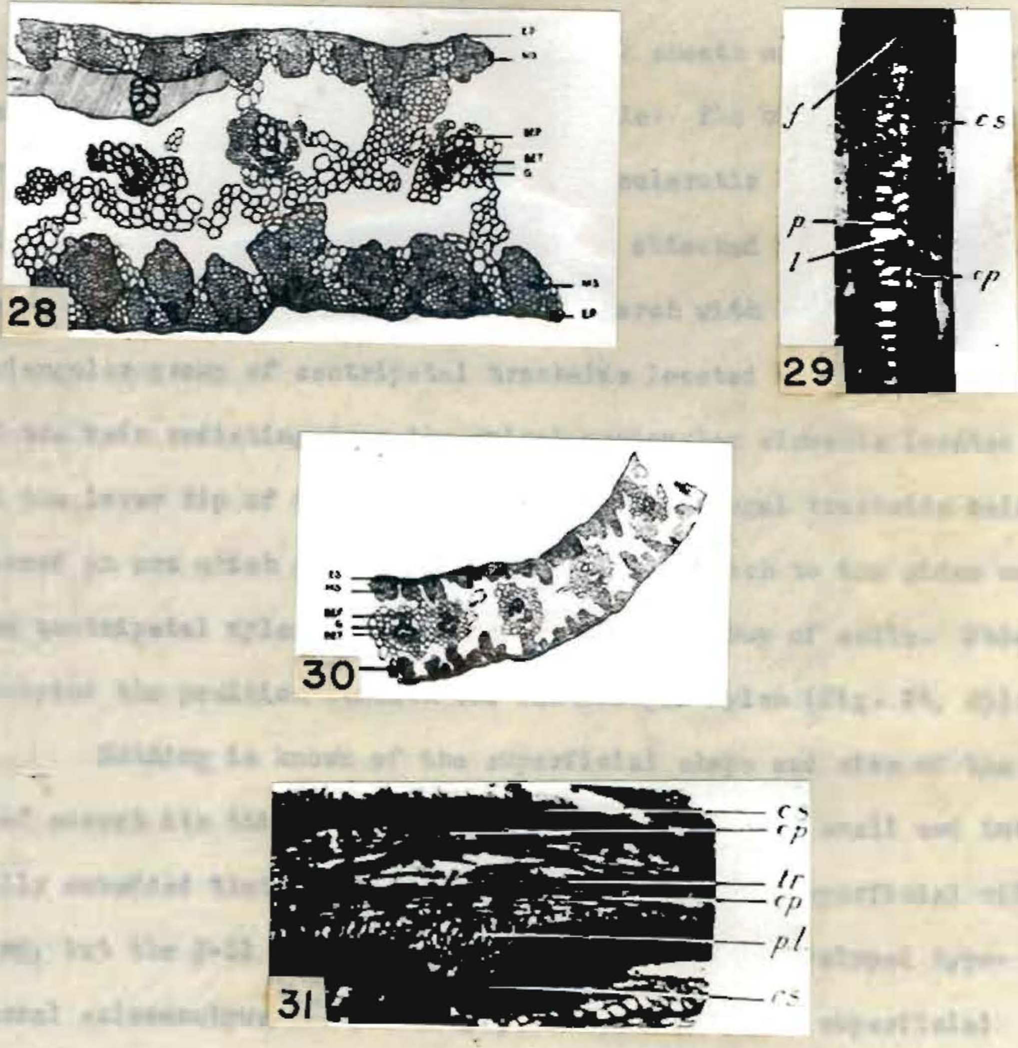


Fig. 28-31. C. weristeri Leclerq (after Leclerq, 1928). Fig. 28. Transverse section of proximal leaf portion X 25; ep, epidermis; ms, sclerotic masses; bep, centripetal xylem; bet, centrifugal xylem; g, bundle sheath. Fig. 29. Radial section through the mesophyll X 30; f, vein; p, parenchyma as superimposed planks; l, lacuna; cs, sclerotic tissue; cp, prismatic bundle sheath cells. Fig. 30. Transverse section of distal leaf portions X 25; labels as in fig. 28-29. Fig. 31. Radial section through a vein X 30; tr, scalariform centripetal tracheids; pl, lacunar parenchyma.

spongy mesophyll was quite compact.

The veins were encased by a thick sheath of 2-3 rows of prismatic cells only slightly longer than wide. The bundle sheath was often completely free of the hypodermal sclerotic bands, frequently attached only on one side, and sometimes attached both above and below to these bands. The xylem was mesarch with a well developed triangular group of centripetal tracheids located in the upper part of the vein radiating from the spiral protoxylem elements located at the lower tip of this triangle. The centrifugal tracheids below formed an arc which either curved upward to attach to the sides of the centripetal xylem, or else formed a free group of cells. Phloem occupied the position beneath the centrifugal xylem (fig. 24, 25).

Nothing is known of the superficial shape and size of the leaf except its thickness. The 26 veins/cm. were so small and internally embedded that they may not have affected the superficial ribbing, but the 7-11 masses of more-or-less equally developed hypodermal sclerenchyma/mm. probably produced fine equal superficial ribs. On this basis, and because of compression material believed present, Leclercq theorized, with no direct evidence, that C. weristeri might represent the anatomical form of the compression species of C. borassifolius. Because of its close association and resemblance to some of Felix's (1886) leaf forms included by Benson (1912) in her species, Koopmans (1928) has suggested the possibility that C. weristeri might belong to C. felicis.

C. principalis (Germ.) Gein. (fig. 32-38) was a well known compression species found commonly in both European and North American

Carboniferous and Permian strata. The leaves were long and narrowly lanceolate, with blunt apexes sometimes split into segments (fig. 32). The leaf's broadest portion was at about 2/3 of its distance from the base, with the width gradually tapering both toward the base and the apex. According to Kidston (1893), the basal leaf portion gradually narrowed but immediately at its attachment to the stem it expanded slightly. The smaller leaves, which were most often complete in compression material, measured about 4 x 50 cm., but many exceeded this size (Arnold, 1949). Stopes (1903) reported that the leaf thickness was about 0.4 mm., in agreement with Renault's (1879) figure. The superficial ribbing was strong and distinct throughout the leaf length, with the primary ribs about 0.45 mm. apart according to Stopes and Renault, but as far apart as 0.67 mm. in Lesquereux's (1878) description of *C. mansfieldi* Lesq., an American compression species later referred to *C. principalis* by Seward (1917). The primary rib frequency was therefore 14-22/cm. There were 1-5 fine intermediate striae between each pair of main ribs on the adaxial superficial surface, and a regular alternation of more distinct secondary intermediate ribs with the primary ribs on the abaxial leaf surface.

Renault (1879) first figured the internal anatomy of *C. principalis* and Stopes (1903) investigated it more thoroughly. Well developed hypodermal sclerotic strands were located above and below the veins and were attached to the bundle sheath. A fairly prominent intermediate sclerotic strand was located midway between the veins against the abaxial side, and 2-4 smaller, irregular sclerotic

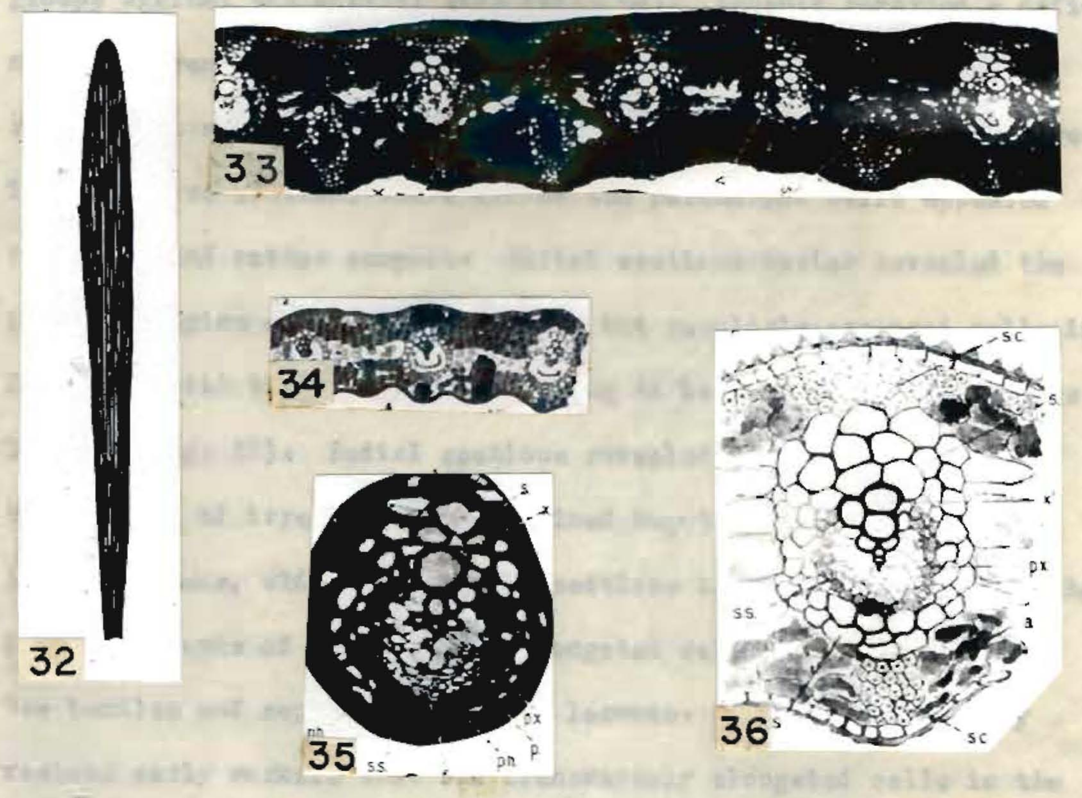
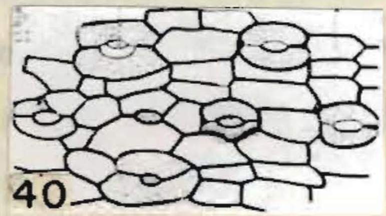


Fig. 32-38. C. principalis (Germ.) Gein. Fig. 32. Leaf shape X 0.1 (after Kidston, 1902). Fig. 33. Transverse section X 55. Fig. 34. Transverse section X 45 (after Renault, 1879). Fig. 35. Transverse section of vein X 150; px, protoxylem; x, centripetal xylem; p, xylem parenchyma; ph, phloem; ss, inner pitted sheath of "primitive transfusion tissue"; s, outer pitted sheath of "peridesmic transfusion tissue"; f, crushed phloem cells. Fig. 36. Transverse section X 135; sc, sclerotic strands; s, spongy mesophyll; other labeling as in fig. 35. Fig. 37. Radial section through a vein X 225; si, large superior sheath cells adjacent to the centripetal xylem; other lettering as above. Fig. 38. Radial section through the mesophyll X 100; sc, abaxial sclerotic strand; s, spongy tissue; p, palisade tissue. (Fig. 33,35-38 after Stopes, 1903).

groups against the adaxial side (fig. 34). Renault reported a definite differentiation of the mesophyll into a palisade and spongy region, but according to Stopes this distinction was rather obscure in transverse sections where all of the parenchyma cells appeared hexagonal and rather compact. Radial sections better revealed the palisade region as composed of broad but regularly arranged cells in 2-4 rows, with the lower row beginning to be separated by slit-like lacunae (fig. 38). Radial sections revealed the spongy tissue to be composed of irregular cells chained together to form a highly lacunar tissue, while in sagittal sections the parenchyma was in the form of strands of transversely elongated cells extending between the bundles and separated by large lacunae. It was suggested by various early workers that the transversely elongated cells in the middle portion of the mesophyll extending from bundle to bundle in this and other species might be considered a type of "lateral transfusion tissue", but even Stopes admits that these cells were hardly specialized enough to warrant this designation.

An outer bundle sheath, consisting of 2-3 layers of thin-walled elongated cells, surrounded the veins. The sheath was better developed on the upper side where very large cells frequently were found between the xylem and the hypodermal fibers. Stopes indicated that the sheath cells sometimes appeared to merge with the adjacent transversely elongated middle tissue between the bundles. The xylem (fig. 35-37) consisted of a well marked protoxylem group giving rise to a wedge of centripetal xylem above, with the elements varying in size from spiral protoxylem tracheids only 10 μ in diameter to the large pitted centripetal tracheids reaching 50 μ in diameter. A striking characteristic of this species was the complete absence of centrifugal xylem in all leaf bundles. An "inner sheath" of tracheids, which Stopes interpreted as "primitive transfusion tissue", was present extending around and below the phloem just within the outer bundle sheath. It is a remnant of this "inner sheath" that Stopes believed Renault had figured as an external xylem arc below the phloem and labeled as centrifugal xylem (fig. 34). The phloem was located in the region below the protoxylem and consisted of small radially elongated elements with delicate oblique walls, upon which sieve areas were not detected.

C. crassus Ren. was a species of very thick fleshy leaves anatomically described and figured by Renault (1879) from French siliceous petrifactions (fig. 39-44), and later identified and illustrated by Darrah (1940) from Iowa coal balls (fig. 45). Darrah mistakenly attributed the authorship of this species to Grand'Eury, an error which unfortunately has been perpetuated by American paleobotanists ever since. Renault reported the veins to be 0.7 mm. apart, but Darrah illustrated them as frequently being closer and more irregularly spaced (fig. 45). Large intermediate hypodermal sclerotic strands extended far into the mesophyll from the abaxial side, alternating with single smaller strands which coincided with, but were not directly attached to the vascular bundles which were buried in the mesophyll. Renault indicated that the hypodermal sclerotic tissue on the adaxial side was limited to small strands occurring immediately above the veins (fig. 39), but Darrah reported a fairly



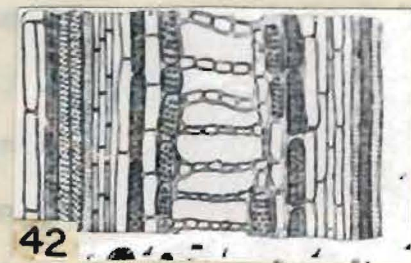


Fig. 39-45. C. crassus Ren. Fig. 39. Transverse section X 45. Fig. 40. Stomatiferous band of lower epidermis X 85. Fig. 41. Upper epidermis X 85. Fig. 42. Sagittal section X 85; a, vascular tissue; c, long thin cells; d, bundle sheath; m, mesophyll in strands; l, lacuna. Fig. 43. Radial section through a vein X 85; ep, epidermis; p, adaxial "palisade" cells; h, hypodermal sclerotic tissue; v, pitted upper tracheids; s, scalariform tracheids; tr, spiral protoxylem tracheids; b, pitted centrifugal tracheids; p', compact abaxial parenchyma. Fig. 44. Sagittal section of compact adaxial "palisade" parenchyma layer X 85. (Fig. 39-44 after Renault, 1879). Fig. 45. Transverse section X 14 (after Darrah, 1940).

extensive development of hypodermal sclerotic masses along both surfaces (fig. 45). Darrah also noted a characteristic pairing of the veins with the large intermediate abaxial strands usually occurring only between every 2 bundles.

Darrah reported the mesophyll to be rather homogeneous without distinct palisade and spongy regions, although Renault indicated that the parenchyma near the adaxial epidermis was somewhat more compact and slightly layered (fig. 39, 44). The lacunar tissue consisted of anastomosing strands of cells directed perpendicular to both the lamina surfaces and to the veins (fig. 42), with slitlike intercellular spaces between them. Renault stated that this species was less lacunar than some others he had described.

The veins (fig. 39, 43) were enclosed by a bundle sheath of doubtful origin (Darrah, 1940) composed of large, porous, radially elongated cells, often filled with dark granular substances (Renault, 1879). Renault described a delicate tissue located between the sheath and the xylem tracheids, composed of narrow, radially elongated, thin-walled cells. The xylem was mesarch, composed of upper centripetal and lower centrifugal tracheids, but no external "inner sheath" was present.

Renault and Seward and Sahni (1920) reported that the stomata were confined to the lower epidermis, where they were arranged in stomatiferous bands of 5-6 alternative rows, with a stomatal frequency of $150/mm^2$. The epidermal cells of both surfaces were rectilinear without the presence of cuticular papillae (fig. 40, 41).

<u>C. affinis</u> Reed and Sandoe (fig. 46-58) represents the only

other cordaitean leaf species besides C. crassus that has been anatomically described from American petrifactions. Unfortunately, Reed and Sandoe (1951) ascribed to this form a specific epithet previously employed by Grand'Eury (1877) for another species (fig. 1-H), causing a taxonomic problem. Nevertheless, this species represents one of the better known anatomical forms, since its internal structure has been correlated with its epidermal pattern. The length of the leaves is unknown, with the longest segment of 8 cm. being considered a mere fragment. The leaves appeared flat and narrow on the petrifaction surface, but were often actually considerably inrolled within the matrix, with the widest leaf studied being 4.5 cm. from margin to margin. The relatively smooth external surface had fine, closely-set, parallel veins which occasionally dichotomized. On the upper surface there were 2, 3 or more secondary striations between the main ribs (fig. 46), while on the lower surface there was a single distinct secondary rib alternating with the primary ribs (fig. 47).

The hypodermal sclerotic strands were composed of typical fiber cells elongated about 20 times their width, and so thick-walled that the lumen was barely visible. The arrangement of the fibrous strands agreed with the superficial ribbing pattern, with the largest bands accompanying the veins. There were 2-3 small fiber ribs located between the veins on the adaxial surface and a single fairly large rib was located about midway between the veins on the abaxial surface (fig. 53).

The mesophyll could supposedly be divided into an upper, relatively compact palisade tissue of 3-4 cell rows, and a lower lacunar spongy region. The palisade cells were best seen in radial sections (fig. 58), parallel to the veins, but in transverse sections (fig. 53) they were hardly distinguishable from the spongy tissue. The lower spongy tissue cells were smaller, more irregularly shaped, but fairly compactly arranged. In sagittal sections through the spongy mesophyll near the abaxial side these parenchyma cells were often seen as anastomosing strands separating lacunae (fig. 57). In poor, very compressed specimens the lacunae were often not seen.

Surrounding the veins was a well defined bundle sheath of 1-3 rows of thin-walled cells attached directly to the hypodermal fiber strand above and below. The sheath cells had bordered pits on their radial walls, and many of them appeared darkly stained. The xylem elements seemed to form an arc across the upper portion of the vein and down the sides of the phloem (fig. 55). The largest tracheids were located in the upper central portion and bore multiseriate bordered pits on their radial walls. The smaller, more numerous tracheids below and on either side usually had scalariform markings (fig. 56). Some xylem parenchyma was scattered among the tracheids. Reed and Sandoe did not report the position of the protoxylem, but assumed it to be mesarch. The phloem region was located below the xylem arc, but these elements were seldom preserved. The cellular detail of the actual vascular tissues was poorly preserved in the described specimens, and Reed and Sandoe stated that they could "write with less assurance of the xylem and phloem than

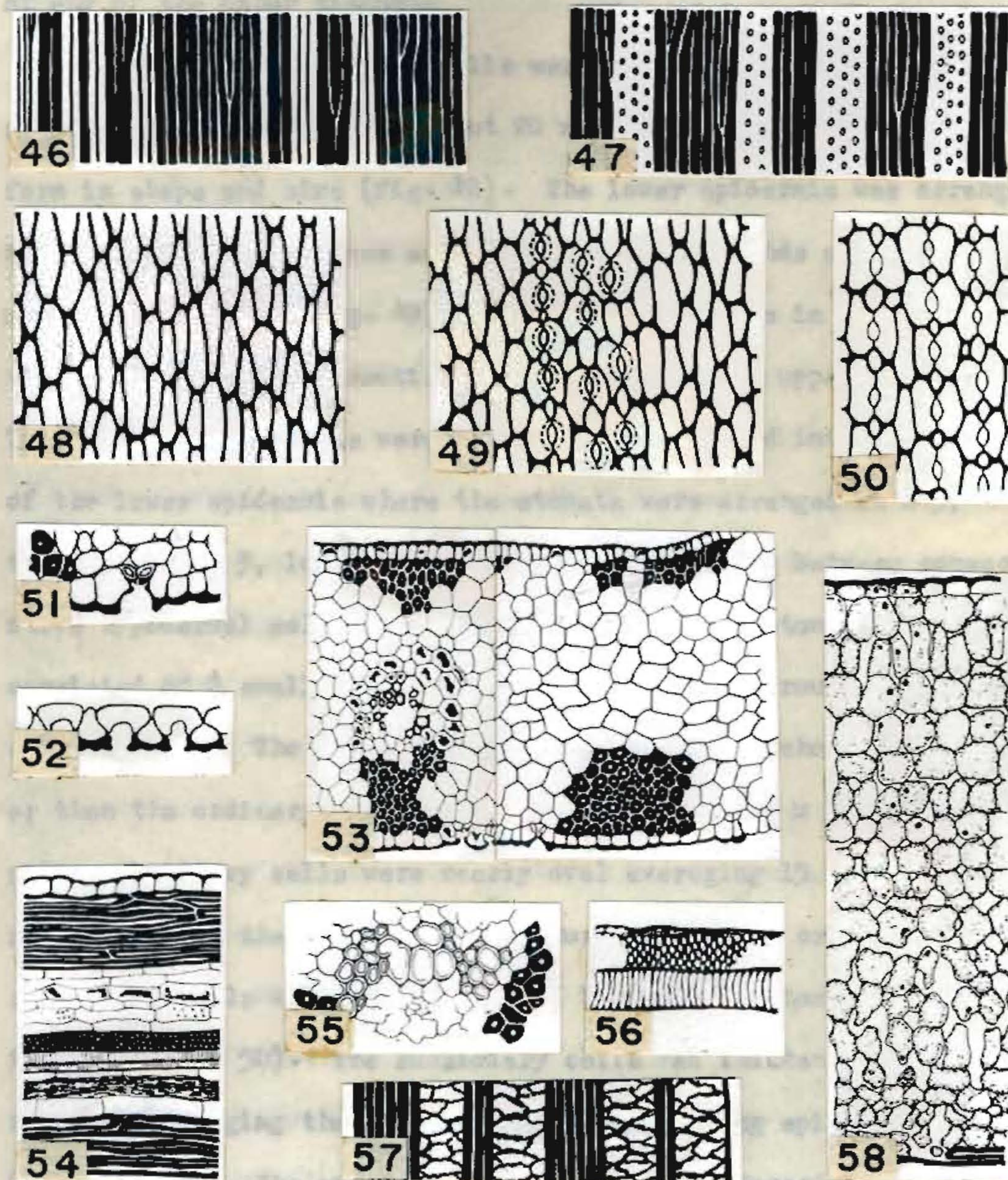


Fig. 46-58. O. *affinis* Reed and Sandoe (after Reed and Sandoe, 1951). Fig. 46. Upper superficial surface showing ribs. Fig. 47. Lower superficial surface showing ribs and stomata. Fig. 48. Upper epidermis. Fig. 49. Lower epidermis. Fig. 50. Stomatiferous band of lower epidermis. Fig. 51. Transverse section of stoma. Fig. 52. Radial section of stoma. Fig. 53. Transverse leaf section. Fig. 54. Radial section through a vein region. Fig. 55. Transverse section of vein. Fig. 56. Metaxylem tracheids. Fig. 57. Sagittal section through sclerotic strands and spongy parenchyma. Fig. 58. Radial section through the mesophyll.

of any of the other tissue".

The upper epidermal cells were thick-walled and longitudinally elongated, measuring about 20 x 60 µ and appearing fairly uniform in shape and size (fig. 48). The lower epidermis was arranged in definite stomatiferous and nonstomatiferous bands of approximately equal width (fig. 49). The epidermal cells in the nonstomatiferous bands were essentially like those of the upper epidermis. The stomatiferous bands were found in the furrowed inter-rib regions of the lower epidermis where the stomata were arranged in 2-5, though usually 3, longitudinal rows in each furrow between consecutive hypodermal sclerotic bands (fig. 47). The stomatal apparatus consisted of 2 small, oval, sunken guard cells surrounded by 4 subsidiary cells. The lateral subsidiary cells were shorter and broader than the ordinary epidermal cells, averaging 35 x 50 µ, and the polar subsidiary cells were nearly oval averaging 15 x 25 µ. The stomata within these stomatiferous furrows were so crowded that subsidiary cells were usually shared by adjacent stomata and stomatal rows (fig. 50). The subsidiary cells had thickened cuticular ridges overhanging the sunken guard cells forming epistomal chambers (fig. 51, 52). The epidermal cells of both surfaces were narrow with tapering radial walls when seen in transverse view, but those of the adaxial epidermis were somewhat deeper and narrower than those of the abaxial surface.

Reed and Sandoe differentiate their species of _C. affinis_ from the similar _C. principalis_ on the basis of leaf thickness, distance between the bundles, the absence of an inner sheath of thick-walled primitive transfusion tissue, and a lack of intervening transversely elongated cells between the bundles.

METHODS AND MATERIALS

The cordaitean leaf fossils examined in this study were obtained from Kansas and Iowa coal balls. Coal balls with K.S.T.C. collection numbers of #28, #504, #508, #510, #511, #530, #535, #648, #714, and #1373 were obtained from the strip mining area of the Pittsburg and Midway Coal Co. near West Mineral, Kansas, a locality geologically ascribed to the Fleming Coal Seam of the Cherokee Group, which occurs slightly below the middle of the Des Moines Series of the Pennsylvanian Age strata (Abernathy, 1946). Coal balls with K.S.T.C. collection numbers of #245 and #260, and University of Minnesota collection numbers of #1054 and #1288, were obtained from the strip mining area of the What Cheer Clay Products Co. near What Cheer, Iowa, a locality geologically ascribed to the lower portion of the Des Moines Series. Coal balls with U. of Minn. collection numbers of #607, #609, #858, #870, #997, #1004, #1035, #1042, #1044, #1092, #1099, #1103, #1117, and #1121 were obtained from the Carbon Hill Mine; CB #622, #767, and #1126 were obtained from the Old Atlas Mine; and CB #784 and #785 were obtained from the Ellis Mine; all of these are located in the Oskaloosa and Ottumwa, Iowa area and also geologically ascribed to the lower portion of the Des Moines Series.

During the course of this study it was necessary to determine the superficial ribbing pattern, the internal anatomy, and the epidermal structure of a single Cordaites leaf. The superficial ribbing pattern of a leaf was revealed by fragmenting the coal ball in such a way that the cleavage plane revealed the leaf surface.

Internal sections were obtained by using the cellulose acetate film technique. The coal balls were cut with a diamond-edged slabbing saw at the necessary angles to obtain desired internal sections of individual leaves. The cut surfaces were then polished, etched with dilute hydrochloric acid, flooded with acetone, and covered with a strip of cellulose acetate film. The films, when removed, retained the carbonized cell walls, and could be cleared with xylene and mounted on slides for anatomical study. For increased cell definition thin sections were also made by the well known method of attaching the rock specimen to a slide and grinding it thin. At least 3 kinds of internal sections were made of each individual leaf examined, in as many different leaf portions as possible. These included (1) transverse sections perpendicular to both the blade surface and the vein courses, (2) radial sections perpendicular to the blade surface and parallel to the vein courses, and (3) sagittal sections parallel to the blade surface. Various oblique sections were also attempted in the hope that they might shed further light on the leaf anatomy.

Whenever satisfactory internal sections of well preserved Cordaites leaves had been obtained, the maceration technique, employed extensively by Florin (1931) on other gymnosperms, was used to determine their epidermal structure. A small part of the coal ball containing a portion of the single cordaitean leaf was chipped off and placed in dilute hydrochloric acid. As the limestone matrix dissolved, the acid resistant cuticles were allowed to separate freely. By careful use of dissecting needles both the upper and lower cuticles of a leaf could often be separated simultaneously. The leaf cuticles, thus freed, usually retained the epidermal cell structure, and could then be mounted and studied to determine the epidermal pattern of the leaf.

All slides made during this investigation have been filed in the paleobotanical collection of Kansas State Teachers College, Emporia.

RESULTS AND DISCUSSION

Description of Cordaites affinis Reed and Sandoe

Occurrence.--Coal balls #28, #504, #508, #510, #511, #530, #535, #648, #714, and #1373, from West Mineral, Kansas, and CB #245, #260, #1054, and #1288 from What Cheer, Iowa, contained large numbers of leaves that could be identified as belonging to Reed and Sandoe's (1951) species of C. affinis. This species appeared to represent the most common, and in fact the only clearly recognizable form of cordaitean leaves in the West Mineral, Kansas, and What Cheer, Iowa, coal balls investigated.

A doubtful leaf form, characterized by being relatively shorter and thicker, with closer veins and extremely large sclerotic caps associated with the bundles (fig. 61), was found in association with typical C. affinis leaves in almost all coal balls from the above-mentioned localities. This leaf type, measuring

1-2 cm. in width and 5-8 mm. in thickness across the middle rib portions, had large abaxial sclerotic caps occupying nearly $\frac{1}{2}$, and adaxial caps occupying $\frac{1}{4}$ of the leaf thickness, with the vascular tissue located in the remaining space between them. The infolding of the inter-vein regions produced a very strongly ribbed superficial surface and gave this form an accordian-like appearance in transverse sections. This leaf form was undoubtedly the one mentioned and illustrated by Baxter (1959) as belonging to his new terminal stem species of *Mesoxylon birame*. Microscopic examination usually revealed that such leaves had undergone rather severe crushing of the mesophyll, bundle sheath, and most vascular tissue except for the thick-walled tracheids. Fig. 61 identifies this form with the thicker uncrushed leaf form illustrated in fig. 60, which does not give such an over-all appearance of exaggerated sclerotic bands. Despite its somewhat different general appearance, this form has been anatomically identified by means of epidermal structure, by successive peel series, and by similarity in vascular tissues, as a basal form of *C. affinis* leaves. Numerous attempts in fragmenting the coal balls to isolate such forms, resulted in superficially revealing the actual leaf bases within 1-2 cm. of these transverse sections (fig. 66).

External Morphology.--As is the case with many other anatomical species, rather little is known about the over-all size and shape of *C. affinis* leaves. The width from margin to margin of 65 recorded leaves, ranged from 0.55-4.10 cm., with the number of veins varying from as few as 12 to as many as 60 in fairly direct

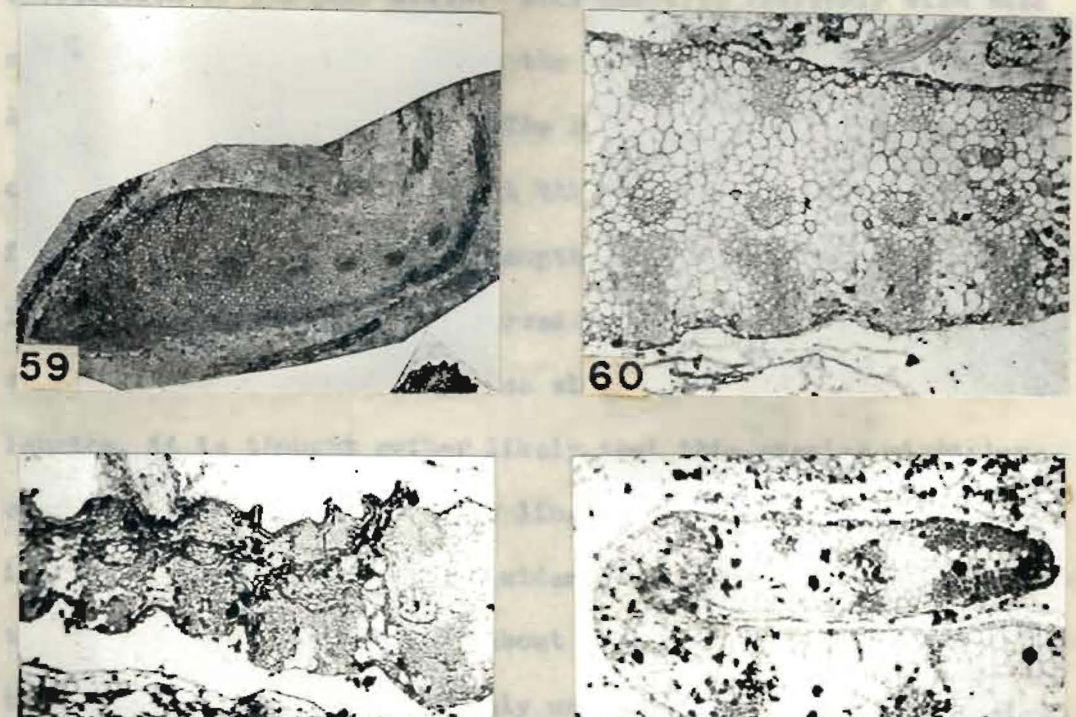


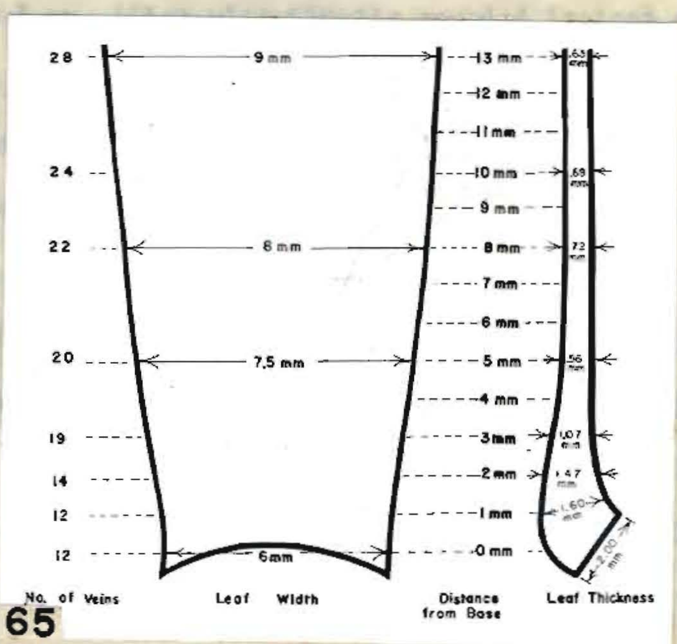
Fig. 59-64. Transverse sections of various *C. affinis* leaf forms. Fig. 59. Leaf base X 9 (SL 714-M). Fig. 60. Uncrushed proximal leaf form X 45 (SL 658-1-b). Fig. 61. The commonly encountered crushed proximal form with an uncrushed portion X 45 (SL 658-1-b). Fig. 62. Uncrushed medial or distal form showing leaf margin X 45 (SL 508-1-a). Fig. 63. Common undulating form of medial and distal portions X 45 (SL 714-B). Fig. 64. Excessively crushed form X 45 (SL 1288-1-C).

correlation to the leaf width. This compares favorably with Reed and Sandoe's (1951) report that the widest leaf found by them was 4.5 cm. with about 60 veins. The longest fragment found in the coal balls was about 10 cm., but this appeared to be only a small fraction of the original leaf length, since only slight changes in leaf width and vein number occurred in the extent revealed. Since the width and venation changed so slightly in the observed leaf lengths, it is thought rather likely that this species might have consisted of very long, broadly linear leaves, perhaps over 50 cm. in length which very gradually widened from a basal width of a centimeter or less to a width of about 4.5 cm., and then probably tapered again toward a completely unknown apex. Such a conjecture, however, is really unsubstantiated by direct evidence, since the coal balls can not give a true indication of the total length of these rather long _C. affinis_ leaves.

The leaves of this species, though sometimes rather flat, were usually incurved at the margins or inrolled to various degrees, as was reported and well illustrated by Reed and Sandoe, who indicated that the surface width visible might be misleading if ever found in compression material.

While splitting techniques quite frequently disclosed the leaf bases (fig. 66), identifiable apexes were never thus revealed. The well preserved leaf bases were 0.6-1.2 cm. wide, and 1.5-2 mm. thick in the central region, giving somewhat the appearance of a flattened ellipse in transverse sections (fig. 59). The variations noted in the width and thickness of these leaf bases appeared to be due, at least in part, to differences between young and mature leaves. The presumably young leaves found attached to the small, terminal stem attributed to Mesoxylon birame Baxter (fig. 67) were at the lowest extreme, and the older leaves in which some basal secondary tissue has been identified (fig. 79) were at the highest extreme of this variation. The thickened base was somewhat recurrent with a slightly concave or semi-clasping adaxial surface, quite similar to Seward's (1917) description of the base of Germar's type specimen of C. principalis. The leaf narrowed slightly 1-2 mm. above the base and then widened steadily to reach about 1.33 times its original width at 1 cm. above the base. Thereafter, the width seemed to gradually increase upward at a much less perceptible rate. The leaf thickness upward from the base was rather sharply reduced to about 50% of the original thickness in a 3 mm. distance, and another reduction of about 25% occurred during the next 3 mm. Thereafter, the lamina thickness tapered only very gradually to eventually reach the 0.3 to 0.5 mm. average thickness through the central rib regions that was most characteristic of the wider, non-proximal portions of the leaves. Fig. 64 represents a reconstruction of the basal region of a somewhat narrower than average C. affinis leaf. Transverse views at the leaf base revealed the characteristic form shown in fig. 59, while transverse sections of the proximal leaf regions somewhat above the base revealed the form shown in fig. 60 if relatively uncrushed, or that shown in fig. 61 if excessively crushed.

The thickness of C. affinis leaves in coal balls varied,



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66

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Fig. 65. Reconstruction of a C. affinis base X 5 (after SL 714-M). Fig. 66. Superficial view of C. affinis base X 2.2 (CB #28). Fig. 67. C. affinis leaf attachment to small stem of Mesoxylon birame Baxter X 7 (SL 504-A).

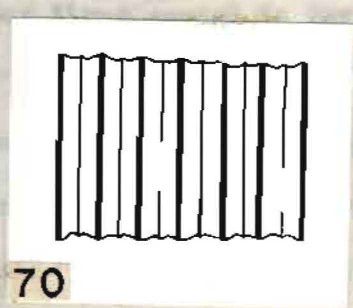
undoubtedly being quite dependent upon the degree of preservation. All leaves tapered somewhat in thickness toward the margins, which were 0.1-0.3 mm. thick with bluntly rounded instead of tapered ends (fig. 62). Although some well preserved leaves were more-or-less uniform in thickness (fig. 62), most of the leaves had the inter-rib regions crushed or pinched inward to various degrees (fig. 63). In many leaves the thickness of the inter-vein regions was only about ½ of that across the veins, while in a few the inter-vein regions were so crushed that in transverse sections the leaf resembled a series of beads on a string (fig. 64). These variations probably have little significance other than illustrating differences in compression during the preservation process. It can be readily seen that the degree of inter-vein crushing affects the degree of prominence of the external ribs.

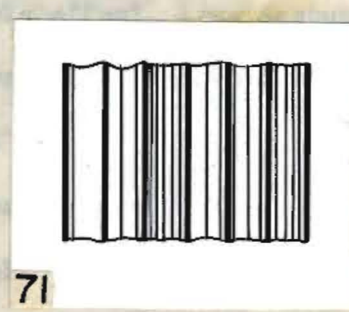
The primary superficial ribs were caused by hypodermal sclerotic tissue associated with the veins which resisted the crushing that depressed the inter-vein regions. The intermediate ribs were produced by hypodermal strands of sclerotic tissue between the veins. The 92 leaves recorded showed a considerable variation in primary rib (or vein) frequency from 13-28/cm. There proved to be a definite correlation between total leaf width and the number of primary ribs (or veins)/cm. with narrow leaf sections having closer veins and wider leaf sections having more distant veins. Leaf sections with lamina widths of 0.55-1.2 cm. averaged 22.6 veins/cm., with 0.44 mm. distance between the veins. These narrower sections were presumably near the base, as borne out by their increased thickness, and, due to the more frequent dichotomizing of the veins, the primary ribs often were somewhat associated in pairs. Leaf sections of 1.3-1.9 cm. widths averaged 18.7 veins/cm., spaced at intervals of about 0.53 mm. Leaf sections of 2.0-2.9 cm. widths had an average of 16.5 veins/cm., or about 0.61 mm. apart. Leaf sections exceeding 3 cm. widths averaged 15.1 veins/cm. with 0.66 mm. distance between the veins. It was further noted that the 2 broadest leaf specimens with widths of 3.8 and 4.1 cm. averaged only 13 and 14 veins/cm. respectively. The average figures for all C. affinis leaves observed in this study, revealed a vein or primary rib frequency of 18.6/cm., with the veins 0.53 mm. apart. Considerable variation in vein frequency and the regularity of their spacing was noted even within the same leaf specimens. Reed and Sandoe do not report the number of veins/cm. in their original description of C. affinis, but it may be inferred from their report that a leaf 4.5 cm. wide had about 60 veins. Therefore, the type specimen must have averaged about 13.3 veins/cm. with the bundles being about 0.75 mm. apart, placing it at the extreme end of the vein frequency range as determined in the present investigation. From the width correlations observed this would seem to be the expected position of a leaf as wide as 4.5 cm.

There seemed to be a tremendous variation in the degree to which intermediate ribs were evident on the superficial lamina surfaces, even on different parts of the same leaf specimen. The abaxial surface usually revealed a single, fairly distinct, but not overly prominent, intermediate rib about midway between the primary ribs (fig. 68, 70). However, this intermediate rib was not always evident, or occasionally fine striae were seen on either side of it. The greatest variation was noted on the adaxial superficial surface where either none, or 1-3, or as many as 5 fine intermediate striae were evident between the primary ribs (fig. 69, 71). The intermediate striae situated adjacent to the primary ribs seemed to be the most prominent, but none seemed continuous for any long distance. This compares exactly with the superficial ribbing pattern determined by Reed and Sandoe for this species (fig. 46, 47), and incidently also to that reported for *C. principalis* as well.

The extreme variability of the primary rib spacing and the visibility of intermediate superficial ribs as demonstrated in this study, would tend to cast serious doubts upon the reliability of the extensive traditional reliance upon superficial ribbing patterns in cordaitean leaf speciation of compression material.

Internal Anatomy.--It was possible to observe the etched transverse leaf sections and superficial ribbing patterns simultaneously under low magnification, and by such examination to clearly perceive the correlation of the superficial ribs with the hypodermal fibrous strands beneath each epidermal layer. This correlation was also revealed quite graphically by oblique sagittal sections (fig. 81). Large sclerotic strands inferior and superior to the veins abutted against the bundle sheath and the epidermis except in basal regions, with the abaxial sclerotic masses somewhat more extensively developed (fig. 76-d, j). A rather prominent hypodermal





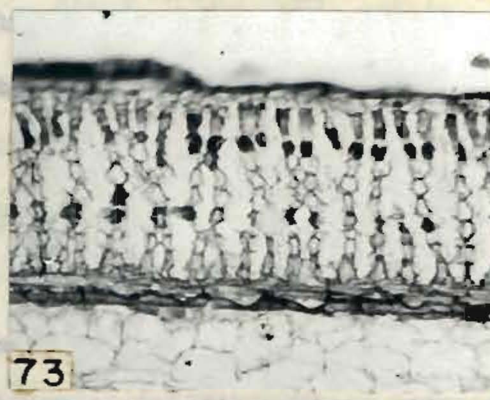


Fig. 68-70. C. *affinis* superficial ribbing patterns. Fig. 68. Abaxial surface X 7 (CB #714). Fig. 69. Adaxial surface X 7 (CB #714). Fig. 70. Abaxial surface X 10. Fig. 71. Adaxial surface X 10. Fig. 72. Transverse section of C. *affinis* mesophyll region X 85 (SL 714-3). Fig. 73. Radial section of C. *affinis* mesophyll region X 85 (SL 1288-D-a).

sclerotic strand (fig 76-n) about 0.1-0.2 mm. wide and extending about 0.10-0.15 mm. into the mesophyll was located midway between the veins on the abaxial side usually causing the regular alternation of primary and secondary superficial ribs seen on the abaxial leaf surface. Under the adaxial surface the arrangement of the hypodermal sclerotic tissue was more variable, but usually consisted of 2-5 small masses of fibers (fig. 76-a). These sometimes resulted in small superficial striae on the adaxial surface, but at other times seemed to have no observable effect, thus accounting for the variability found in the external ribbing pattern. Cuticles reveal that some fibrous material underlaid much of the epidermis, but was extremely thin in stomatal regions. The sclerotic strands were composed of true fiber cells with walls 3-4 μ thick and lumens 3-25 μ in diameter. In slightly oblique transverse sections the lumens appeared almost obscured by the thick cell walls, but in true transverse sections the walls were revealed as much thinner and the lumens often relatively large. Longitudinal sections revealed the fiber cells to be tapered, often twisted, and elongated, averaging 0.65 mm. but occasionaly reaching 2.5 mm. in length.

One of the more interesting aspects of C. affinis leaves was the mesophyll arrangement. Transverse sections with well preserved mesophyll revealed it as a rather uniform mass of fairly large, hexagonal parenchyma cells, without a palisade region being distinguishable, although the mesophyll near the adaxial side appeared slightly more compact (fig. 72). Excessive crushing often resulted in the appearance of somewhat transversely elongated cells arranged in short strands or masses in the central mesophyll region. A frequently noted lack of mesophyll preservation in transverse sections was often rather surprising, since the vascular tissues of the same sections appeared well preserved.

Radial sections revealed the mesophyll as anastomosing strands of variously shaped, but usually vertically elongated, parenchyma cells separated by large lacunae extending between the abaxial and adaxial side (fig. 73). These strands seemed to be attached to compact parenchymatous layers against either epidermis. The strands often approached each other so closely near the adaxial side that about 3-4 fairly uniform cell layers appeared to form a palisade region, but with the lower layers beginning to be separated by slit-like lacunae. However, some radial sections revealed a complete separation of these strands even in this upper region. Reed and Sandoe's radial section drawing (fig. 58) does not represent the typical mesophyll condition as was seen in most of the radial sections examined in the present study, but appeared somewhat similar to radial sections of the more basal or marginal leaf regions, which it quite likely represents.

Sagittal sections revealed the mesophyll as separate anastomosing strands of transversely elongated cells extending between the vascular bundles and attached to the bundle sheath or sclerotic masses. Fig. 81 shows an oblique sagittal section revealing a single densely arranged layer of small parenchyma cells immediately adjacent to the lower epidermis with circular lacunar openings at each stomal position. Fig. 74 represents a somewhat oblique sagittal section showing a compact layer of large hexagonal parenchyma cells located just below the upper epidermis. The intervening mesophyll region between these compact layers consisted of cell strands separated by progressively wider lacunae as one proceeded from the adaxial to the abaxial side. All oblique cuts between true radial and true sagittal sections also revealed the mesophyll as composed of apparent strands of cells, while oblique cuts between true sagittal and true transverse sections showed all variations between mesophyll strands, no mesophyll preservation, and rather compact parenchymatous tissue.

The conclusion is reached, therefore, that except at the leaf base and leaf margins, the mesophyll of *Cordaites affinis* leaves normally is composed of a series of anastomosing plates between the vascular bundles, oriented with their surfaces perpendicular to both the leaf surfaces and to the vein courses, as diagrammatically depicted in fig. 75. These plates are separated by very large lacunar spaces, especially in the middle and more abaxial portions. The similarity between the septate pith of mature cordaitean stems and the plate-like mesophyll of these *C. affinis* leaves is noteworthy. These mesophyll plates seem to be composed of about 7-10 cell rows from vein to vein, and nearly an equal number from epidermis to epidermis. The plates approached each other so closely toward the adaxial side that they formed an apparent palisade region, especially when viewed in radial sections. The individual parenchyma cells of the central region appeared to have

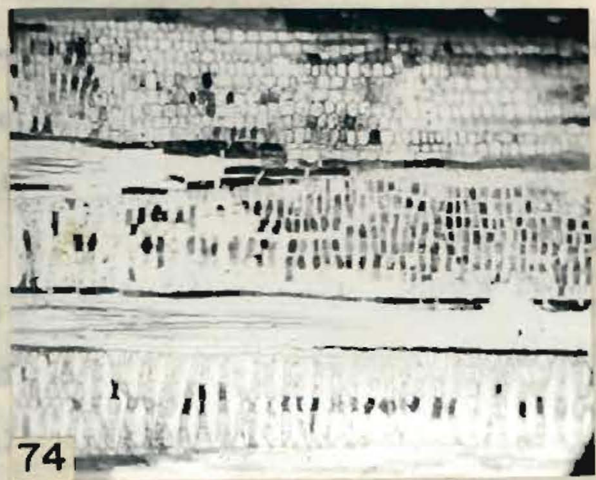


Fig. 74. C. *affinis* slightly oblique sagittal section showing compact mesophyll near adaxial side and separated plates in lower mesophyll region X 45 (SL 1288-A). Fig. 75. Interpretive diagram of cordaitean leaf mesophyll plates; a, adaxial epidermis; b, bundle sheath; c, mesophyll plate; d, abaxial epidermis.

almost isodiametrical faces as seen in transverse view (fig. 72), ranging from 20-60 μ in diameter. However, the cells were actually flattened to about 12-30 μ in thickness so that in radial views they appeared elongated vertically between the epidermal layers (fig. 73), and in sagittal sections they appeared elongated transversely between the veins (fig. 74). The cell size and shape was quite variable, but the size usually decreased slightly toward the abaxial side. Intracellular material was frequently present and gave the appearance of preserved nuclei and cytoplasmic material. The compact upper palisade layer immediately adjacent to the adaxial epidermis was usually composed of almost isodiametrical cells as seen in all views with diameters of 20-60 μ. The compact lowest layer of mesophyll immediately adjacent to the abaxial epidermis also appeared to be composed of almost isodiametrical cells as seen in all views but with diameters of only 15-35 μ. The mesophyll plates were usually separated by about 160 μ in the central and lower mesophyll regions, forming extremely large lacunar spaces, which narrowed gradually toward the adaxial surface until they became mere slits between the lower "palisade" cells. With this arrangement it is doubtful that one can interpret the mesophyll of this species as having been differentiated into anything more than a very "incipient palisade" region.

A clearly defined bundle sheath composed of 1-3 layers of large, thin-walled cells enclosed the veins, and, except near the base, abutted directly against the inferior and superior sclerotic hypodermal strands. The sheath was broadest superior to the vein, consisting here of the largest elements with diameters of 25-80 μ. The sheath narrowed to a single cell layer inferior to the vein, consisting here of smaller elements with diameters of only 18-35 μ (fig. 76-e). The sheath cells were clearly distinguished from the surrounding mesophyll by being radially elongated in the direction of the veins, and arranged in even lengthwise rows. The cells appeared rectangular with very straight end walls, ranging from 40-160 μ in length, as seen in longitudinal sections (fig. 80). The appearance of bordered pits on the walls of the sheath cells, as originally reported by Reed and Sandoe, was also verified in this study.

The protoxylem was located in the central region of the vascular bundle and consisted of 1-2 very narrow spiral tracheids measuring 4-8 μ in cross-sectional diameter (fig. 76-h). It was usually separated from the metaxylem tracheids above by a layer of small rectangular xylem parenchyma cells measuring 3-5 μ in cross-section. The main mass of centripetal metaxylem consisted of a wedge-shaped core of progressively larger tracheids upward from the protoxylem (fig. 76-f) and ranged from the smaller scalariform to the larger reticulate or pitted elements (fig. 77). The small metaxylem tracheids in the lower region of the centripetal xylem mass were 8-15 μ in diameter, while the largest tracheids located in the upper part of the bundles frequently reached diameters of 50 μ. Longitudinal sections revealed that the largest scalariform tracheids often reached 1.5-2.0 mm. in length, while the even larger reticulate or pitted tracheids sometimes exceeded a length of 3 mm.

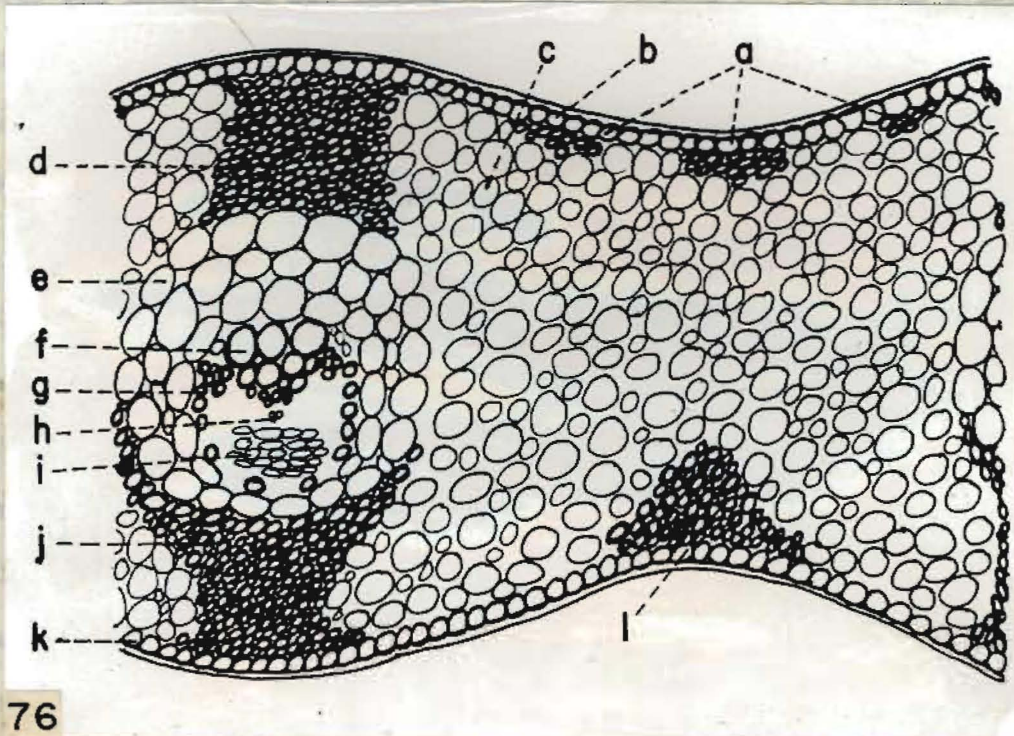


Fig. 76. Transverse section drawing of C. affinis leaf internal anatomy X 200; a, adaxial intermediate hypodermal sclerotic strands; b, adaxial epidermis; c, mesophyll; d, superior hypodermal sclerotic cap above vein; e, bundle sheath; f, centripetal metaxylem; g, side tracheid strand or inner sheath; h, protoxylem; i, phloem; j, inferior hypodermal sclerotic cap below the vein; k, abaxial epidermis; l, abaxial intermediate hypodermal sclerotic strand.

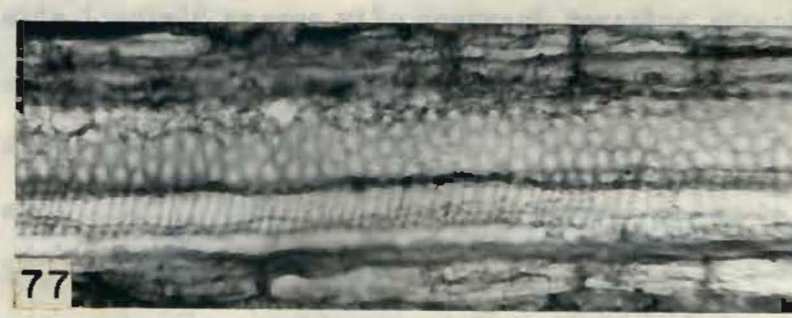
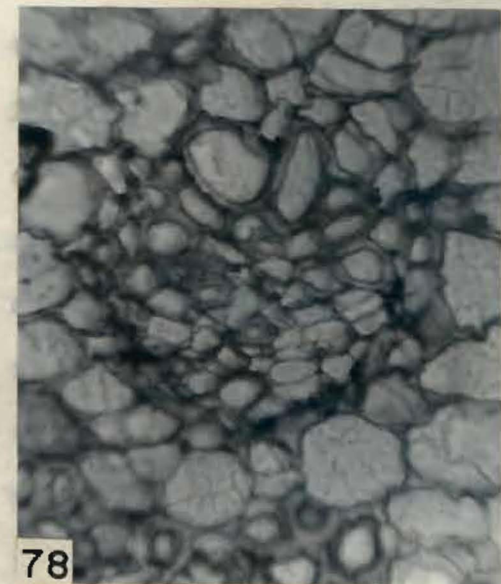


Fig. 77. Sagittal view of scalariform and reticulate centripetal tracheids of C. affinis vein X 350 (SL 1288-B).

Reed and Sandoe do not record the measurements of the xylem elements of *C. affinis* in their original report, but it is of interest to note that the measurements of the present study compare closely with those reported by Stopes (1903) for *C. principalis*.

The wedge-shaped core of metaxylem described above was flanked on either side by a clustered group of 5-6 smaller tracheids, ranging from 4-12 μ in cross-sectional diameter. Each of these groups was subtended by a strand of small thick-walled tracheids extending downward along the sides of the phloem region (fig. 76-g). These strands of tracheids usually were not continuous in the lower bundle regions but rather consisted of a few scattered tracheids around and below the phloem. Occasionally these formed a more-or-less continuous arc just within the bundle sheath enclosing the phloem region, but this was quite rare.

If the historical terminology proposed in early studies of cordaitean foliage is strictly applied to this presently determined xylem condition of *C. affinis*, it may be assumed that the superior wedge-shaped mass of tracheids represents the centripetal xylem, and the side tracheid masses with downward reaching strands around the phloem represent what was termed an "inner sheath" by Renault (1879), Stopes (1903), Benson (1912), Lignier (1913) and others. Stopes describes the inner sheath of *C. principalis* as an arc of small, thick-walled, tracheid-like cells, located just inside the outer sheath, which enclosed the phloem and attached to the flanks of the centripetal xylem where about 5-6 cells formed a group on either side. Such a description bears a striking resemblance to



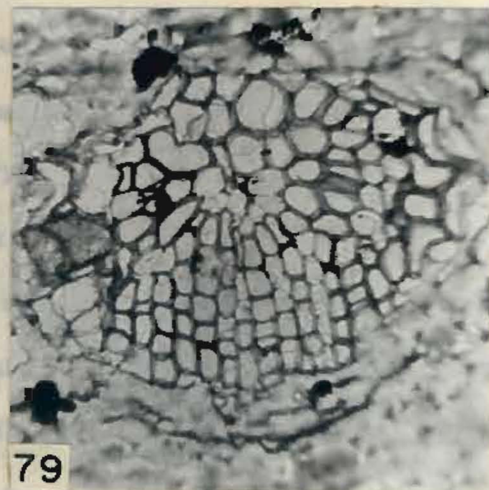


Fig. 78. Transverse section of C. affinis vein X 365 (SL 658-1). Fig. 79. Transverse section of C. affinis vein at leaf base showing secondary xylem X 180 (SL 1373-B-3, 19-4). Fig. 80. Sagittal section of C. affinis vein X 180 (SL 1288-Da-2). Fig. 81. Oblique sagittal sections of C. affinis leaf showing the correlation of the epidermal pattern with the internal structure X 45 (SL 1288-A-1).

the condition found for _C. affinis_ in the present study, except that a complete arc around the phloem was only rarely observable. It is the opinion of the writer that the earlier interpretation of these lateral tracheids as an "inner sheath of primitive transfusion tissue" was an over-zealous attempt to apply certain concepts of other gymnospermous foliage to what was then considered closely related cordaitean leaves. The terms "inner sheath" and "primitive transfusion tissue" would seem misleading, since the elements appeared to be true xylem tracheids with scalariform or pitted markings. Even Stopes admitted that these inner sheath elements appeared much more like true xylem than the transfusion tissue of recent cycads. It, therefore, might seem a more logical interpretation to view these side elements simply as a flanking development of the centripetal xylem. This would result in a somewhat amphivasal condition developing in normally collateral bundles.

A striking feature of _C. affinis_ leaves shown by this investigation was the complete absence of centrifugal xylem in all leaf regions although most other cordaitean leaf species reportedly had mesarch protoxylem giving rise to a mass of centripetal xylem above and an arc of centrifugal xylem below. Reed and Sandoe assumed that this species had mesarch protoxylem, but failed to locate any protoxylem elements, or to report the presence of any centrifugal xylem. This complete absence of centrifugal xylem in _C. affinis_ makes it similar in this respect to Stopes's (1903) description of _C. principalis_.

Secondary xylem arranged in even radiating rows between the protoxylem and the phloem was observed in basal leaf portions, attesting to the existence of some cambial activity in *C. affinis* leaves (fig. 79).

The phloem tissue was located in the region of the vascular bundle below the protoxylem, but it was only rarely preserved (fig. 76-i, 78). The phloem elements in transverse sections were small, thin-walled, rectangular cells measuring 3-6 x 5-10 μ. These phloem cells were elongated but appeared badly crushed in longitudinal sections, and no sieve areas could be clearly identified.

The anatomy of the leaf base differed only slightly from other leaf portions. Paired leaf traces from the stem divided in several steps to form the 12-16 vascular bundles found at the base. These basal bundles were buried in the thick, uniform-appearing mesophyll, and did not contact the rather uniform layers of hypodermal sclerotic tissue (fig. 59). At about 3 mm. from the base the vascular bundles began to dichotomize rather rapidly resulting in a high frequency of veins/cm. (fig. 64). The hypodermal sclerotic ribs became more prominent, and as the leaf narrowed from the margins they began to make contact with the bundles (fig. 60). A slight evidence of lacunar tissue could be observed in the mesophyll at 5 mm. from the base. If considerable crushing of the basal 3 cm. of a leaf had occurred, it often reduced the leaf thickness about 50% and obliterated the thin-walled cells composing the broad bundle sheath and compact mesophyll, resulting in the commonly found accordion-like leaf form mentioned previously and illustrated in fig. 61, which seemed to show an excessive amount of sclerotic tissue above and below the bundles.

Epidermal Structure.--The lower epidermal structure, as seen in cuticles obtained from the maceration process and also sagittal sections, revealed the presence of stomatiferous bands alternating with non-stomatiferous bands of about equal width (fig. 82). Although the width of these bands varied considerably, about 200 μ was average. The regular epidermal cells in the nonstomatiferous bands were elongated and rectilinearly arranged in a direction parallel to the veins. They were rectangular in shape, averaging 20-60 μ in surface dimensions, but showing a great size variation from leaf to leaf and even on the same leaf. Radial and transverse sections revealed these regular lower epidermal cells to average 30 μ in depth.

The stomatiferous bands were composed of stomata arranged in linear rows, typically 3 in number, but commonly 2 or 4, and occasionally only 1 or as many as 5 (fig. 82, 83). These bands were located in the inter-rib regions, 2 between each pair of veins, as diagrammatically depicted in fig. 91. Oblique sagittal sections (fig. 81) which progressively cut through the epidermal cells and then the underlying tissue, best revealed this correlation of the stomatiferous bands with the internal anatomy. The macerated cuticles themselves often gave good evidence of the position of these stomatiferous bands in relation to the internal leaf structure by the adherance of fibrous material.

Each stomatal apparatus consisted of a pair of sunken guard cells surrounded by 2 lateral and 2 polar subsidiary cells (fig. 87, 90-A). The guard cells were small and crescent-shaped in surface view, oval in transverse section (fig. 88, 90-B), and somewhat horseshoe-shaped in radial view (fig. 89, 90-C), averaging about 10-15 µ in width and depth and 40 µ in length. The guard cells frequently appeared to contain granular contents as if indicating some cytoplasmic preservation. The angular bean-shaped lateral subsidiary cells were slightly wider than the normal epidermal cells averaging 25 x 55 µ in surface view, comparing quite well with Reed and Sandoe's reported measurements of 35 x 50 µ. The polar subsidiary cells were nearly elliptical in shape, with average dimensions agreeing exactly with Reed and Sandoe's reported measurements of 15 x 25 µ. If the stomata were not consecutive in a stomatal row the polar subsidiary cells were as long as 40 µ.

Cuticular extensions overhanging the stomatal openings were noted on both lateral and polar subsidiary cells in transverse and radial sections (fig. 89, 90-g) forming the epistomal chambers previously reported and illustrated (fig. 51, 52) by Reed and Sandoe. Sometimes these cuticular extensions were pointed outward giving the appearance of papillae somewhat similar to, but considerably shorter than those pictured by Florin (1931) for C. lingulatus (fig. 19). When the cuticles were observed in surface view somewhat of a sloping depression appeared on the inner side of each lateral subsidiary cell where it was attached to the guard cell (fig. 90-A-d). This circular hollow formed by the sloping of the 2 lateral subsidiary cells and the sunken guard cells, could be readily detected by a vertical manipulation of the microscope's fine adjust-

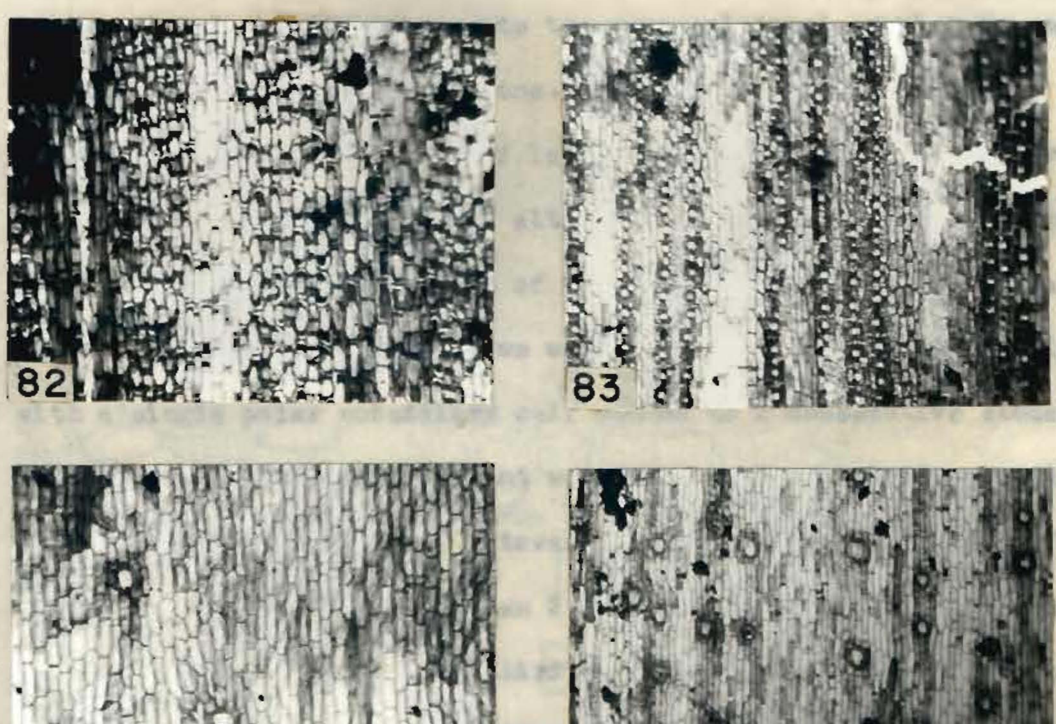


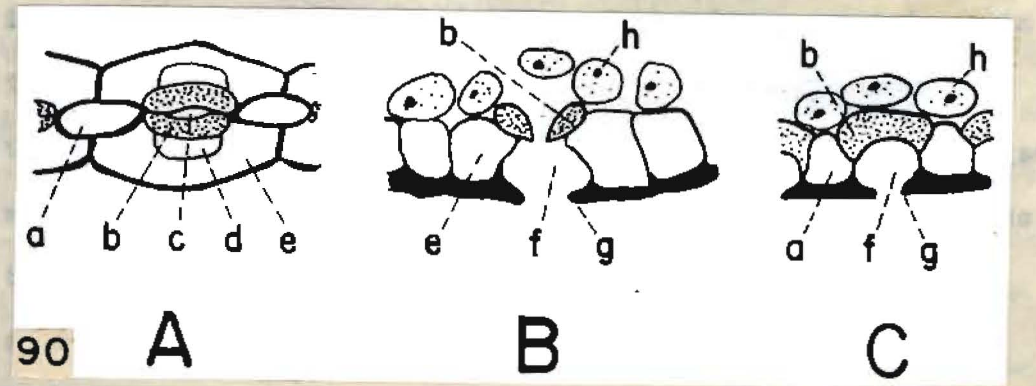
Fig. 82-87. C. *affinis* epidermis in superficial views. Fig. 82. Typical abaxial epidermal pattern with bands of 3 stomatal rows X 45 (SL 245-3). Fig. 83. A more variant abaxial epidermal pattern X 45 (SL 1288-Da). Fig. 84. Typical adaxial epidermal pattern X 90 (SL 245-1). Fig. 85. Adaxial epidermis with frequent stomata X 55 (SL 245-4). Fig. 86. Adaxial epidermis at the leaf base X 45 (SL 658-E). Fig. 87. Single stomatal apparatus of abaxial epidermis X 600 (SL 1288-A-2).

ment, and undoubtedly represents the same epistomal chamber as seen in transverse and radial sections.

Usually a single row of lateral subsidiary cells was shared by 2 parallel rows of stomata, although frequently the stomatal rows were separated by several rows of normal epidermal cells. Typically, the stomata in the stomatal rows were arranged in continuous chains with a single polar subsidiary cell common to 2 consecutive stomata, but occasionally the arrangement was less regular with the stomatal chains broken more frequently toward the basal region of the leaf, where only rarely were more than 2 stomatal rows continuous for any great distance, although the third row could frequently be detected between them. The regular epidermal cells located within the stomatiferous bands were generally somewhat shorter than those of the nonstomatiferous bands. Within several millimeters of the base the epidermal cells appeared strikingly shorter and almost isodiametrical, although still arranged in rectilinear rows (fig. 86). An average stomatal frequency of 124/mm^2 was determined for the lower epidermis of _C. affinis_.

The epidermal pattern of the upper epidermis differed from that of the lower in the apparent absence of regularly alternating stomatiferous and non-stomatiferous bands. The epidermal cells appeared rather uniform and essentially like those of the nonstomatiferous bands of the lower epidermis except that they were somewhat deeper as seen in transverse and radial sections.

Stomata were definitely present on the upper epidermis, contrary to the information reported by Reed and Sandoe (1951). These



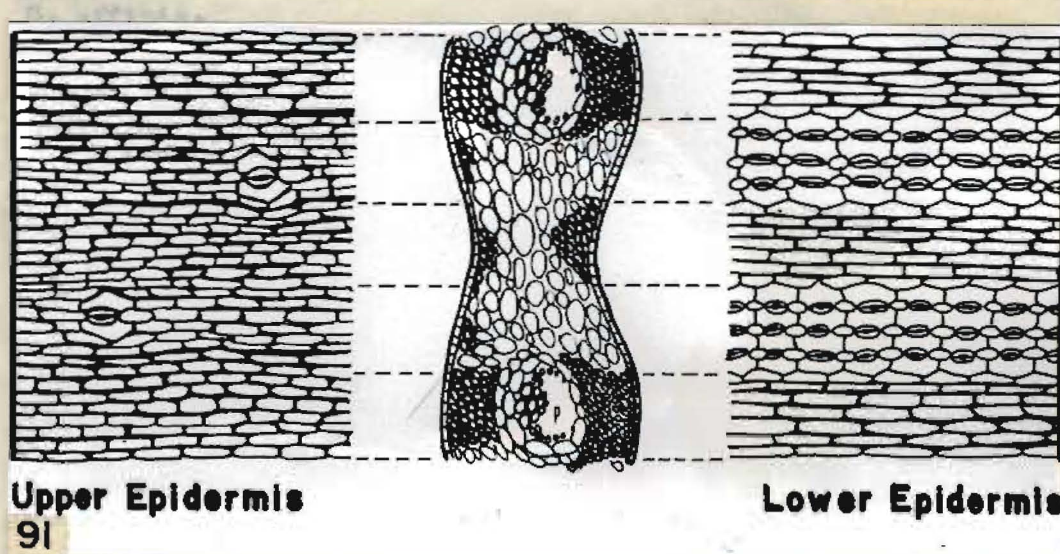


Fig. 88. C. affinis stomal apparatus in transverse section X 600 (SL 714-1-g). Fig. 89. C. affinis stomatal apparatus in radial section X 400 (SL 714-F). Fig. 90. Drawings of various views of C. affinis stomal apparatus. A--Superficial view; a, polar subsidiary cell; b, guard cell; c, stoma; d, hollowed depression; e, lateral subsidiary cell. B--Transverse view; f, epistomal chamber; g, cuticular extensions overhanging epistomal chamber h, mesophyll cell. C--Radial view. Fig. 91. A projected drawing showing the correlation of epidermal patterns with the internal anatomy of C. affinis leaves.

stomata were rather infrequent on the majority of specimens, and usually appeared quite scattered (fig. 84), and in such cases it was difficult to observe any apparent pattern except that they occurred in the inter-rib regions. However, in a considerable number of specimens, the stomata were far more numerous, and occurred in definite stomatal rows, although often quite separated within that row (fig. 85). Sometimes these stomatal rows were located within 2-5 epidermal cell rows of each other, with their arrangement strongly suggesting a basic similarity to the stomatiferous band arrangement of the lower epidermis. An average stomatal frequency of $6/mm^2$ was determined for the upper epidermis of C. affinis.

The stomatal apparatus on the upper epidermis was essentially like that of the lower epidermis except that the guard cells were more submerged, due to the greater depth of the subsidiary cells. The polar subsidiary cells, seldom connecting consecutive stomata, were not oval but elongated to about 40 µ.

Comparison of C. affinis with C. principalis.--This study has shown a striking resemblance between the leaf species of C. affinis anatomically described by Reed and Sandoe (1951) from American coal balls, with the species of C. principalis anatomically described by Renault (1879) and Stopes (1903) from European petrifactions. In view of the great similarities between these 2 anatomical forms, it is deemed worthwhile to critically review the following criteria by which Reed and Sandoe have distinguished their species from C. principalis:

(1) differences in leaf thickness,
(2) differences in the distance between the bundles,
(3) the presence in C. principalis, and absence in C. affinis, of intervening longitudinally elongated layers of cells in the central region between the bundles,
(4) the presence in C. principalis, and absence in C. affinis, of an inner sheath of thick-walled "primitive transfusion tissue".

Leaf thickness is admittedly a poor criterion for speciation as it is quite dependent upon vertical compression, but this study revealed that non-basal leaf regions of C. affinis varied from 0.3-0.5 mm. in thickness, agreeing very well with Stopes's report of 0.4 mm. as the leaf thickness of C. principalis. The distance between the bundles was not directly stated by Reed and Sandoe for C. affinis but it can be inferred from their measurements of leaf width and total number of veins, to average about 0.75 mm. The results of the present study showed that the average distance between the veins of different C. affinis leaves may vary from 0.36-0.77 mm. Since the reported distances between the veins of C. principalis vary from 0.45-0.67 mm., it is not possible to differentiate the 2 forms on this basis.

Although Reed and Sandoe stated that C. affinis differed fundamentally from C. principalis because of an absence of intervening elongated layers of cells extending between the bundles, sagittal sections (fig. 74) of the former species clearly revealed such apparent strands of cells due to the previously described mesophyll plates (fig. 75) being oriented in this direction. Even transverse sections of some considerably compressed leaves revealed apparent transversely extending cell strands, likely due to the mesophyll plates being obliquely slanted from crushing and seen in edge view. While the significance given to these transverse parenchyma chains by early workers, who sometimes interpreted them as possible "lateral transfusion tissue", was perhaps far-fetched, yet their presence in the mesophyll of C. principalis and C. affinis leaves can not be disputed.

Reed and Sandoe's contention that C. affinis leaves lacked the thick-walled inner sheath of "primitive transfusion tissue" possessed by C. principalis, appears to be partly due to a difference in the interpretation of the lateral tracheids which extended downward either partially or completely around the phloem. While Reed and Sandoe illustrated some of these side tracheids as the downward extending points of their xylem arc (fig. 53, 55), they did not identify them as part of the same tissue which Stopes perhaps misleadingly called an inner sheath of "primitive transfusion tissue" (fig. 36-ss). The present study (fig. 76-g) has revealed these side "inner sheath" tracheids somewhat better developed than did Reed and Sandoe's figures, yet a definite difference seems to exist between the 2 species in this respect, since in C. affinis bundles these lateral tracheids extending downward only rarely if ever formed a complete arc around the phloem, whereas both Renault and Stopes illustrated such a complete arc around the phloem of C. principalis (fig. 34-36).

The differences existing between the C. affinis leaves studied in the present research and the anatomical descriptions of C. principalis seem relatively minor, and it is rather questionable whether they are worthy of specific recognition. This view of the possible specific identity of these 2 species is somewhat enhanced by the fact that C. principalis represents a commonly reported compression form in North America as well as in Europe. A nomenclatural problem unfortunately exists since the specific epithet which Reed and Sandoe ascribed to C. affinis had been previously used by Grand'Eury for another species. No new specific epithet is proposed to replace it, however, because it is believed by the writer that this American anatomical form differs in no fundamental respect from the anatomical descriptions of C. principalis (Germ.) Gein.

Description of Cordaites crassus Ren.

Occurrence.--During the course of this investigation, coal balls #607, #609, #858, #870, #997, #1004, #1035, #1042, #1044, #1092, #1099, #1103, #1117, and #1121, from the Carbon Hill Mine; CB #622, #767, and #1126, from the Old Atlas Mine; and CB #784 and #785 from the Ellis Mine; all located in the vicinity of Oskaloosa and Ottumwa, Iowa, yielded large numbers of leaves that could be identified as belonging to C. crassus Ren. Darrah (1940, 1941) reported the species from this same area, as well as from the localities of Waukee, Urbandale and Williamson, Iowa. C. crassus leaves seemed conspicuously absent in all West Mineral, Kansas, and What Cheer, Iowa, coal balls where C. affinis was the dominating form. It was somewhat surprising that these two leaf species were not found associated, except for a single C. affinis leaf found in Carbon Hill CB #1092, which otherwise contained numerous C. crassus leaves. The reason for the rather sharp distinction between the cordaitean foliage found at What Cheer and that found at the other nearby Iowa localities is not known, but may have represented some local plant distribution difference, or perhaps might be better explained if the geological horizons of the coal measures involved were more exactly determined.

External Morphology.--*C. crassus*, like *C. affinis*, represents another anatomical species described only from petrifactions, with very little known of its external morphology. There was little indication of the over-all size and shape of the leaves. The leaf sections examined varied in total width from leaf bases of only 7 mm. to leaves as wide as 5.3 cm., but the majority seemed to range from 1.5-3.0 cm. in width. The longest fragment observed just slightly exceeded 9 cm., but this is considered a mere fraction of the total leaf length, since the width changed only slightly in this distance.

C. crassus leaves were comparatively very thick and fleshy, lacking the exaggerated undulating form characteristic of many cordaitean leaves. The leaf thickness varied from only 0.1 mm. in some young leaves to as much as 3.5 mm. at some leaf bases, but the majority of the leaf sections encountered were in the 0.5-1.0 mm. range of thickness. Although, neither Renault (1879) nor Darrah (1940) specifically reported the leaf thickness of this species, it may be inferred from the magnification scales of their figures that Renault's specimen from French petrifactions was about 0.5 mm. while Darrah's specimen from Iowa coal balls was about 1.5 mm. in thickness, placing both well within the range of the present findings.

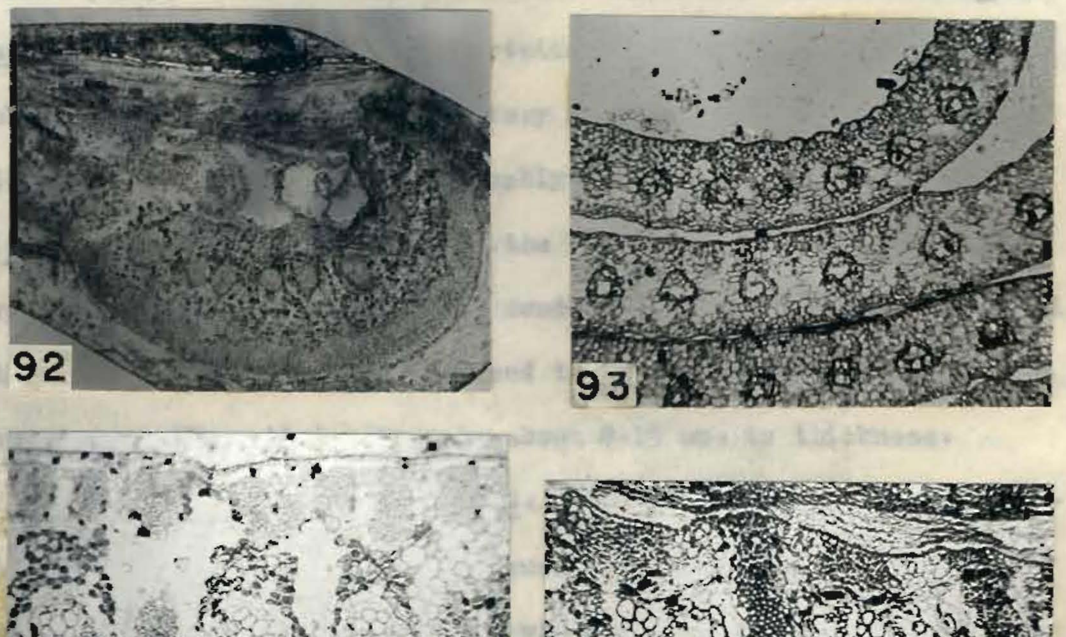


Fig. 92-97. Transverse sections of various *C. crassus* leaf forms. Fig. 92. Leaf base X 10 (SL 1121-1). Fig. 93. Young leaf form in bud X 45 (SL 1099-Bud-3). Fig. 94. Proximal leaf form with extensive abaxial and adaxial intermediate fiber ribs X 45 (SL 1099-G-1). Fig. 95. Proximal leaf form with complete intermediate fiber ribs extending across the mesophyll X 45 (SL 1121-A). Fig. 96. Leaf form intermediate between the proximal and distal forms X 45 (SL 1099-P-1). Fig. 97. Typical medial or distal leaf form with the adaxial intermediate sclerotic rib replaced by radially extending strands of large parenchyma cells X 60 (SL 1099-P-1).

Scott (1923) believed that the distinctly fleshy character of *C. crassus* leaves reflected an adaptation to xerophytic life, but it should be pointed out that the very fleshy appearance of these leaves in petrifactions may probably be due as much to a lack of inter-vein crushing hindered by the large intermediate sclerotic ribs, as to the original living condition. The leaves all appeared thicker in the central regions and tapered toward the bluntly rounded margins which were only about 0.15 mm. in thickness.

The basal morphology of *C. crassus* has been carefully studied and diagrammatically reconstructed in fig. 98. The leaf base was much thickened and recurved, with a markedly concave adaxial surface, and somewhat incurved margins. From a basal width of 7-9 mm., the leaf initially widened rather sharply to a 12-15 mm. width during the first centimeter upward from the base. Thereafter, the leaf increased in width only gradually at a scarcely observable rate. The leaf base thickness was about 2.0-3.5 mm. In the first 3 mm. upward from this much thickened base the leaf thickness was reduced markedly by about 50%. The leaves then thinned steadily at a much reduced rate for about 3 cm., and thereafter, if the leaves did become progressively thinner, the process was so gradual as to be imperceptible.

The external surfaces of these leaves were marked by the parallel ribbing characteristic of all cordaitean foliage. The ribs dichotomized frequently at very acute angles near the base, but less often upward. The surfaces were unusually smooth, with the ribbing sometimes scarcely visible without magnification, thus substantiating

Renault's (1879) suggestion that the leaves of this species should show only slight relief. The primary external ribs generally marked the position of the internal veins, and were separated by fairly prominent secondary ribs marking the position of the large intermediate sclerotic strands. A tremendous range of variation was observed in superficial ribbing patterns, largely reflecting the irregular spacing and great variability in the internal vein frequency, which ranged from only 15 to as many as 40 veins/cm. Therefore, the distance between the veins ranged from 0.25-0.66 mm., which represents a somewhat shorter distance than Renault's (1879) reported 0.7 mm. distance, but more in agreement with Darrah's (1940) illustrated (fig. 45) distances of 0.4-1.0 mm. The younger leaves (fig. 93), identified as such from a comparison with the inner leaves of a bud, possessed the greatest vein frequency, often exceeding twice that of the older leaves. The average vein, and therefore primary superficial rib, frequency was about 26/cm., with the veins 0.38 mm. apart, but discounting the young leaf forms it was only about 23/cm., with the veins averaging 0.43 mm. distance apart. The primary ribs often appeared paired due to the paired nature of the internal veins which, at least near the base, dichotomized frequently and subsequently separated very slowly, continuing long distances before the large intermediate sclerotic strands developed between them producing secondary external ribs. This frequently paired nature of the veins was noted and figured by Darrah, who listed it as one of the characteristics of this species.

The ribbing pattern of the adaxial and abaxial surfaces

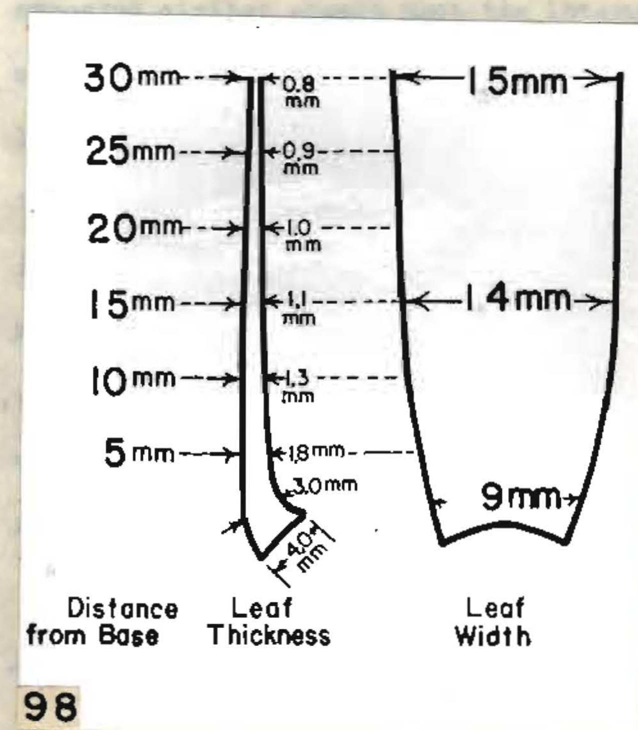


Fig. 98. Reconstruction of C. crassus leaf basal region X 2 (after SL 1121-A, 1099-K). Fig. 99. Diagram of C. crassus abaxial superficial ribbing pattern X 10. Fig. 100. Diagram of C. crassus adaxial superficial ribbing pattern X 10. Fig. 101. Superficial ribbing of C. crassus abaxial surface X 7 (CB #1099). Fig. 102. Superficial ribbing of C. crassus adaxial surface X 7 (CB #1099).

appeared similar except that the intermediate ribs were generally more prominent on the abaxial surface (fig. 99-102). Often the large intermediate sclerotic strands on the abaxial side caused external ribs just as prominent as those associated with the veins, resulting in as many as 70 equal ribs/cm. The superficial ribbing nature of this species was still further complicated by the occasional occurrence of smaller internal sclerotic masses between the veins and the main intermediate sclerotic projections, causing fine superficial striae between the primary and secondary ribs.

It is somewhat disturbing to realize that if these C. crassus leaves were to be found in impression or compression material, the same internal form might easily be relegated to at least 5, if not more, different compression species on the basis of different ribbing patterns. It is quite likely that just such situations may account for the apparent paucity of anatomical species in comparison to the relatively greater abundance of described compression species, and may point to the doubtful reliability of using external ribbing patterns in the cordaitean leaf speciation of compression material.

Internal Anatomy.--The most outstanding characteristic serving to identify C. crassus leaves was the extremely prominent abaxial hypodermal sclerotic masses projecting far into the mesophyll between the vascular bundles, often extending beyond half of the leaf thickness. Nevertheless, the extent of the hypodermal sclerotic tissue in this species was highly variable. Hypodermal sclerotic masses were located above and below the veins. Frequently these sclerotic strands did not directly contact the bundle sheath, yet, contrary to the report and illustration (fig. 39) of Renault and the illustration (fig. 45) of Darrah, it was found in this investigation that in the majority of cases these sclerotic strands actually did abut against the bundle sheath. Occasionally there were additional smaller hypodermal sclerotic masses on both surfaces between the large intermediate ribs and those associated with the veins, but those were often absent or much reduced. The very fleshy leaf base (fig. 92) had a more-or-less continuous hypodermal fiber layer, but none of the ribs projected inward as far as the veins. Beyond 3 mm. from the actual leaf base, but in the proximal region, there was considerable sclerotic development under both the abaxial and adaxial surfaces (fig. 94), and a fairly prominent intermediate sclerotic strand was located between the veins on the adaxial side opposing the larger one on the abaxial side. At times, the abaxial and adaxial sclerotic ribs joined to form a continuous fiber band from epidermis to epidermis between each pair or 2 pairs of veins (fig. 95), similar to the condition reported for _C. felicis_ (fig. 26) by Benson (1912). Darrah (1940) reported that numerous Iowa coal balls contained leaves that appeared to be much closer to _C. felicis_ than _C. crassus_, and later the same author (Darrah, 1941) more definitely listed _C. felicis_ as a form found in Iowa coal balls. However, the results of the present investigation seemed to rather clearly indicate the specific identity of this form in Iowa coal balls with the typical _C. crassus_ form, as the transition was often shown in successive sections of the same leaf.

Such a tentative conclusion in Iowa coal balls may perhaps raise somewhat of a question concerning the specific distinctness of the European forms of _C. felicis_, _C. weristeri_, and _C. crassus_, which differ only slightly except for their hypodermal sclerotic arrangement, but any such discussion is beyond the scope of this paper.

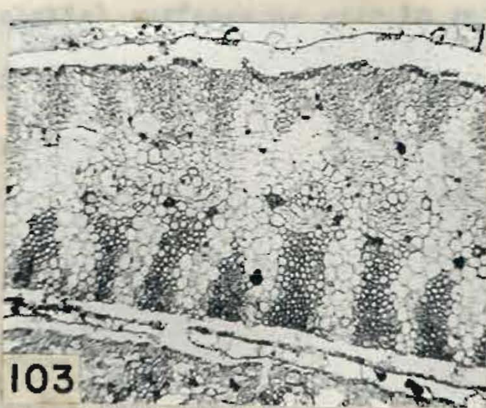
Darrah's illustration (fig. 45) appears to represent a _C. crassus_ leaf form with extensive sclerotic development near both the abaxial and adaxial surfaces, such as was found near the basal region in this study, an inference further supported by the relative thickness of the leaf and the paired nature of the veins. Renault's illustration (fig. 36) appears to represent a non-basal leaf portion lacking adaxial sclerotic development between the veins. In the present study leaves were encountered showing transitional forms (fig. 96) in which the adaxial intermediate ribs were reduced in size and then entirely supplanted by a mass of very large, dark-staining, isodiametrical parenchyma cells (fig. 97) to be discussed later in conjunction with the mesophyll of this species.

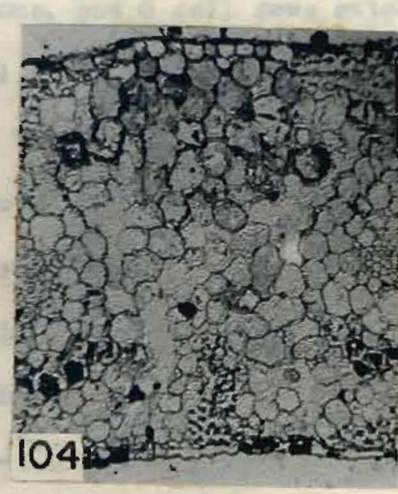
Another leaf form encountered in the same coal balls differed from the typical _C. crassus_ leaves by having excessively large sclerotic caps above and below the veins (fig. 103). This form may possibly represent another anatomical species found in these Iowa coal balls, but the personal feeling of the writer, yet unsupported by sufficient evidence, is that it may be simply a variant form of _C. crassus_. This form did not seem to differ anatomically from the typical _C. crassus_ leaves in any other respect, and the epidermal pattern appeared identical with the _C. crassus_ basal form.

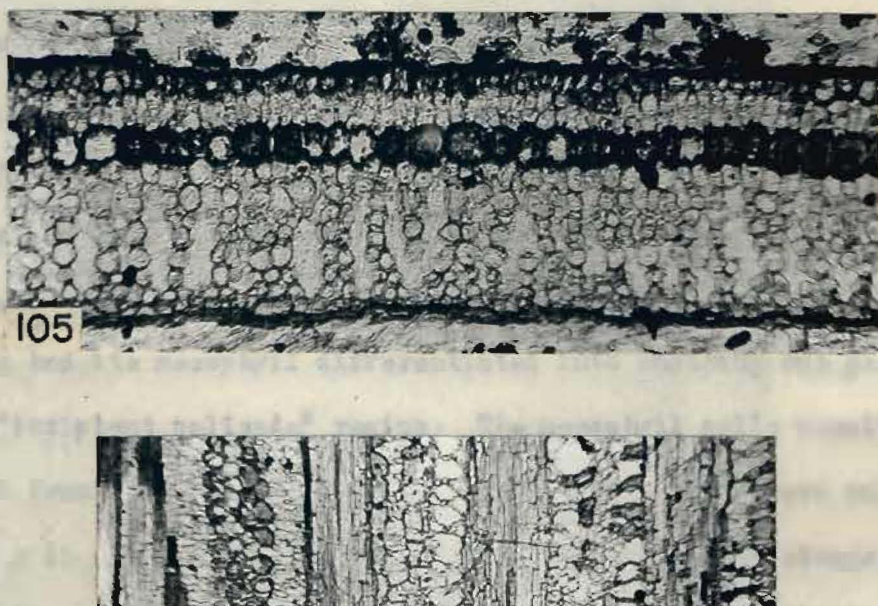
The leaf margins of *C. crassus*, as in *C. affinis*, were supported by a considerable layer of hypodermal sclerotic tissue which undoubtedly helped to maintain uncrushed the blunt rounded edges in petrifactions.

The individual elements of these sclerotic strands were typical fibers with oblique end walls tapering at about 45° angles. The cross-sectional diameter of the fibers ranged from 5-20 µ but averaged about 15 µ, while their length averaged about 0.45 mm. but occasionally reached 1.9 mm. The fiber walls were 2-5 µ in thickness.

The mesophyll of *C. crassus* leaves was basically quite similar to that of *C. affinis*, but was slightly more compact and less lacunar. In mature, non-basal, non-marginal regions of a leaf, the mesophyll tissue was in the form of plates or layers of cells separated by lacunal slits, as diagrammatically illustrated in fig. 75. These frequently anastomosing plates were oriented in a direction perpendicular to both the veins and to the laminar surfaces. Therefore, in transverse leaf sections (fig. 104) these plates were frequently revealed in face view giving a dense mesophyll appearance, while in radial sections (fig. 105) and sagittal sections (fig. 106), these plates were intersected giving the mesophyll region the appearance of anastomosing strands of parenchyma cells separated by lacunae. Renault also reported and illustrated the presence of these cell strands in sagittal sections of this and other leaf species (fig. 42). The mesophyll plates were usually composed of about 11 cell rows extending between the adaxial and







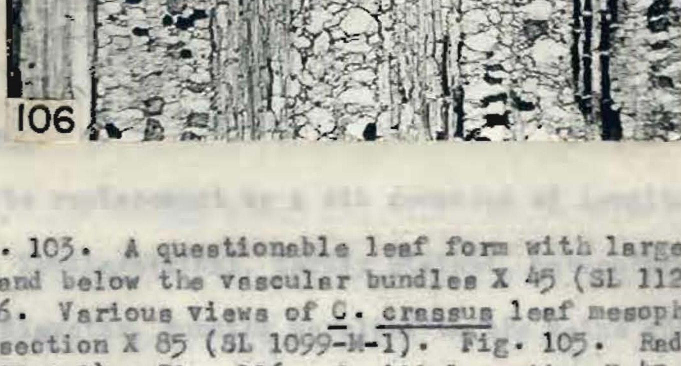


Fig. 103. A questionable leaf form with large sclerotic caps above and below the vascular bundles X 45 (SL 1126-1). Fig. 104-106. Various views of C. crassus leaf mesophyll. Fig. 104. Transverse section X 85 (SL 1099-M-1). Fig. 105. Radial section X 85 (SL 1099-A-2). Fig. 106. Sagittal section X 45 (SL 1099-A-3).

abaxial surfaces as seen in radial sections, and 6 cell rows extending from vein to vein as seen in sagittal sections, but this varied with leaf thickness and vein frequency. The mesophyll plates of this species seldom extended from vein to vein since they were interrupted by the large intermediate sclerotic strands. A rather compact layer of parenchyma cells lined the sclerotic ribs and the lower epidermis except for open spaces above each stoma. Just beneath the adaxial epidermis were found 1-2 layers of compact cells, such as illustrated (fig. 44) by Renault, representing a semi-palisade region. The lacunar slits near the adaxial surface narrowed making the upper mesophyll more compact than the lower. Radial sections of younger leaves showed the mesophyll plates approaching each other so closely as to give the appearance of a palisade layer, but in general this species could hardly be designated as having had its mesophyll differentiated into anything but perhaps a very "incipient palisade" region. The mesophyll cells usually ranged from 20-40 μ in cross-sectional diameter, but were only about 15-25 μ in depth, giving the appearance of vertically elongated cells in radial sections and transversely elongated cells in sagittal sections.

An unusual feature observed in mature, non-basal leaf regions of C. crassus, where the intermediate adaxial sclerotic rib was absent, was its replacement by a rib composed of longitudinal rows of very large, isodiametrical, darkly stained, parenchyma cells about 40-70 μ in diameter, running parallel to the veins and perpendicular to the mesophyll plates. The transverse sections of fig. 97 and

104, the radial section of fig. 105, and the sagittal sections of fig. 106 and 117, reveal these chains of large cells. The significance of this feature is not known.

The vascular bundles were quite large, usually occupying about 50%, but occasionally as much as 75%, of the leaf thickness. These veins were enclosed by a well defined sheath of thin-walled cells which were elongated in the direction of the vein courses. The cells were nearly isodiametrical in transverse view (fig. 107), but rectangular with straight end walls and arranged in even brick-like rows in longitudinal section (fig. 106, 108). The sheath was as wide as 6-7 cell layers above, narrowing to only 2-3 rows on the sides, and widening again below to 4-5 cell layers. The outer layer of the sheath was often composed of very irregularly sized cells, with occasional large cells alternating with smaller ones. The cells of this outermost sheath layer were characteristically darkly stained with opaque materials, as previously reported by Renault. The inner layers of the bundle sheath were generally composed of smaller elements. It is somewhat questionable just what Renault was referring to in his discussion of a very delicate and well preserved tissue composed of elongated thin-walled cells separating the vascular tissue from the sheath. However, his diagram (fig. 42) indicates that this tissue probably represented what has been presently interpreted as the inner layers of the bundle sheath composed of narrower elements. The sheath elements were 20-40 μ in cross-sectional diameter and 60-175 μ long. Bordered pits were noted on some of the sheath elements.

Frequently, when the bundle sheath did not directly contact the inferior and superior hypodermal sclerotic masses, there occurred in the intervening region a modified type of tissue somewhat intermediate between the normal mesophyll parenchyma and the true bundle sheath elements. The cells of this tissue were somewhat elongated in the direction of the vein courses, but gradually intergraded with the normal mesophyll cells at either side. The significance of these cells is not clear, but perhaps they lend some credence to the theory that the bundle sheath, which Darrah (1940) describes as of doubtful origin, may be derived from the mesophyll.

The protoxylem, consisting of a few small spiral tracheids of about 4-7 μ in diameter, was located toward the central part of the bundle. It was mesarch, giving rise to a large wedge-shaped mass of centripetal xylem above and usually, in mature leaves, a narrow arc of centrifugal xylem below. The centripetal xylem was composed of small scalariform tracheids about 10-20 μ in diameter, and larger scalariform, reticulate, and pitted tracheids in the uppermost region of the bundle often reaching 45 μ in diameter. Some of the tracheids attained a length of 1.4 mm. as seen in longitudinal sections.

The centrifugal xylem usually consisted of a V-shaped arc of 1-2 rows of relatively small and generally reticulate-pitted tracheids of 8-20 μ in diameter. A row of small parenchyma cells separated the centrifugal xylem from the protoxylem and centripetal xylem. Often the upper ends of the centrifugal xylem arc were attached to the sides of the centripetal xylem mass. The presence or absence of centrifugal xylem was perhaps one of the most variable features of *C. crassus* leaves. It was consistently absent in the young leaves (fig. 93), and seldom present in bundles near the leaf margins, as might be expected, since Lignier (1913) reports it to have been the last vascular tissue to develop. However, even in other leaf regions, the centrifugal xylem arc was often absent in many bundles for no accountable reason.

A small mass of tracheids frequently was present on either side of the wedge-shaped mass of centripetal xylem above, somewhat similar to that described for *C. affinis*. Also a few small, scattered, thick-walled tracheids were occasionally found along the sides and beneath the phloem just within the bundle sheath, evidently representing a trace of what various early writers have termed the "inner sheath" in certain other species. However, these side tracheids were much less frequent in *C. crassus* than they were in *C. affinis*, and could almost be disregarded as a normal occurrence. Renault (1878) indicated that this absence of an external vascular arc helped to characterize this species.

Considerable secondary xylem was frequently observed at the leaf base of *C. crassus*, located between the protoxylem and the phloem, and obscuring the centrifugal metaxylem if the latter were ever present (fig. 110).

The phloem was located in the lower region of the bundle between the centrifugal xylem and the lower bundle sheath elements. Although the phloem cells usually had disintegrated prior to fossilization, in a surprising number of instances it was found remarkably

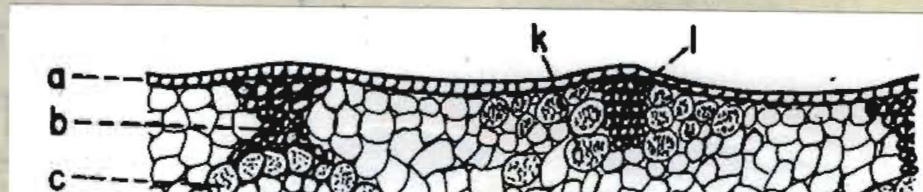


Fig. 107. Transverse section of C. crassus vein X 150 (SL 1099-F-1). Fig. 108. Sagittal section of C. crassus vein X 150 (SL 1099-G-2). Fig. 109. Transverse section drawing of C. crassus leaf internal anatomy X 100; a, adaxial epidermis; b, superior hypodermal sclerotic strand above vein; c, bundle sheath; d, centripetal metaxylem; e, lateral tracheids or "inner sheath" remnants; f, protoxylem; g, centrifugal metaxylem; h, phloem; i, inferior hypodermal sclerotic strand below vein; j, abaxial epidermis; k, large intermediate parenchyma cells on adaxial side; l, intermediate adaxial hypodermal sclerotic strand; m, mesophyll; n, large abaxial hypodermal sclerotic strand.

well preserved in leaves of this species. The phloem elements were oval-shaped with delicate, wavy-margined walls, varying from 4-10 u in cross-sectional diameter. No sieve areas could be clearly identified in longitudinal sections.

Fig. 107 and 108 represent transverse and sagittal views of C. crassus veins, and fig. 109 represents a transverse section drawing with labeled parts to help clarify the foregoing discussion.

Epidermal Structure.--The regular epidermal cells of the abaxial surface of C. crassus were rectangular in shape, averaging 18 x 16 µ in surface dimensions, and 18 µ in depth, but showing a great size variation on the same leaf as well as from leaf to leaf. The epidermal cells were aligned in regular lengthwise rows parallel to the sclerotic ribs and vein courses.

The stomata were arranged in definite stomatal rows, but the organization of these stomatal rows into stomatiferous bands differed considerably in various leaf parts. In basal leaf portions, having considerable sclerotic tissue, single or double stomatal rows were located in the regions between the veins and the intermediate ribs, as diagrammatically depicted in fig. 116. This formed a superficial epidermal pattern of rather evenly spaced stomatiferous bands consisting of single or double stomatal rows, seperated by wider, fairly equal, nonstomatiferous bands (fig. 111). However, the frequent dichotomizing of the internal veins in the basal leaf regions often caused considerable variation in the width and frequency of the stomatiferous and nonstomatiferous bands.

In non-basal leaf portions where the sclerotic tissue was

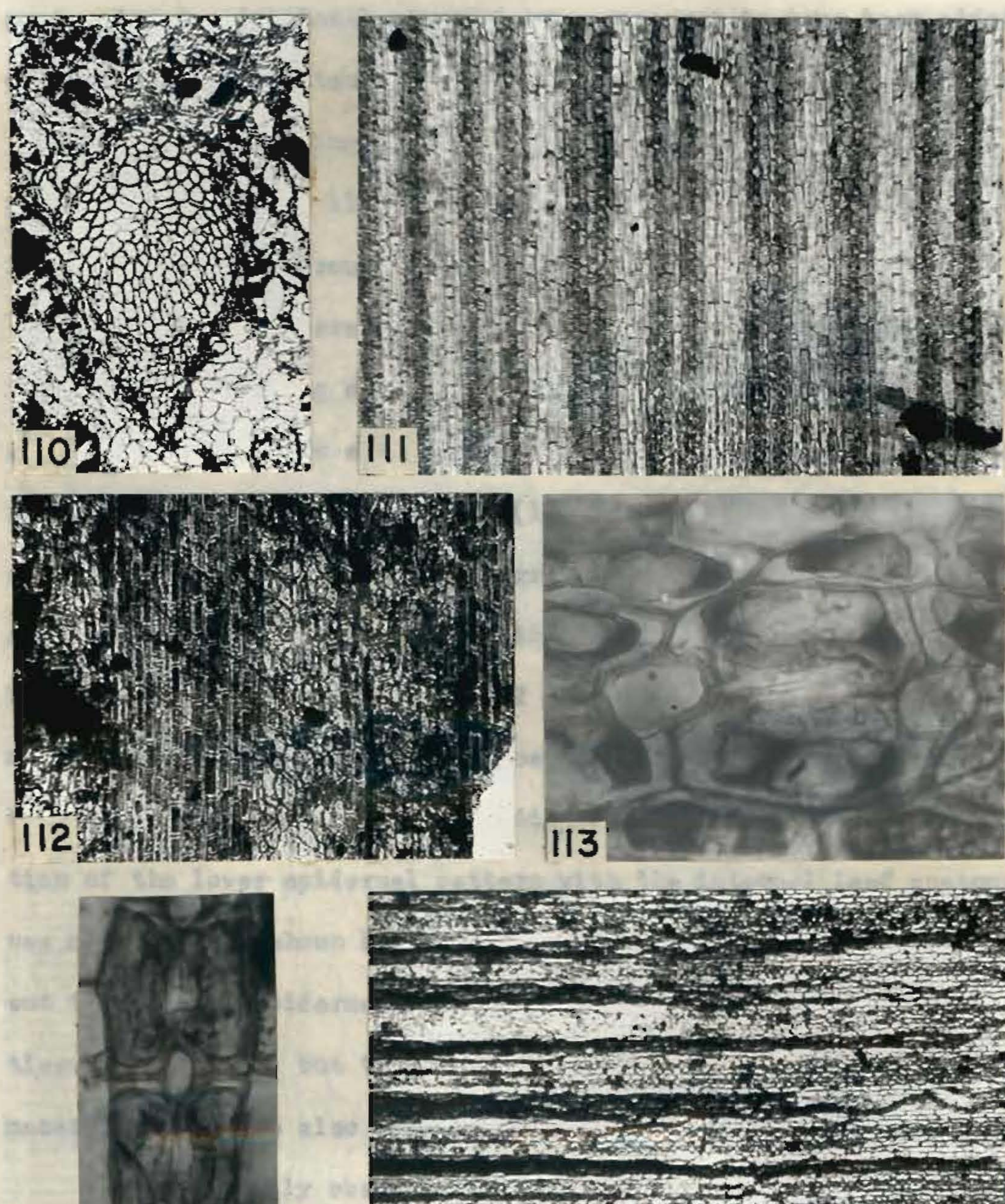
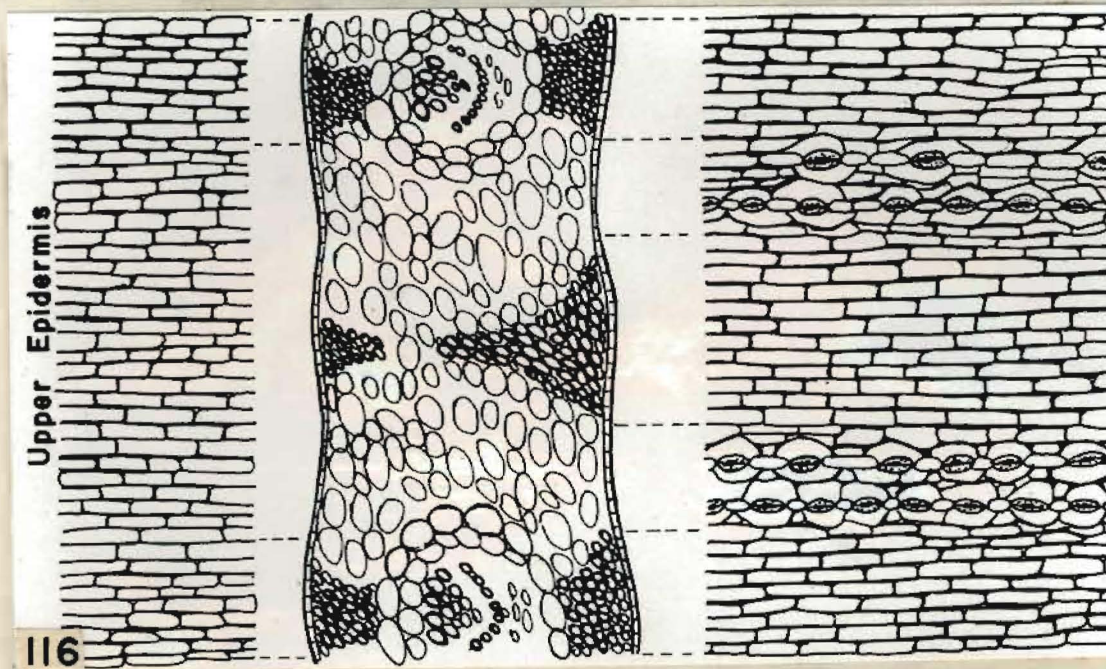


Fig. 110. Transverse section of C. crassus vein at leaf base showing secondary xylem X 85 (SL 1121-1). Fig. 111. Superficial epidermal pattern of C. crassus proximal leaf regions with extensive hypodermal sclerotic development and young leaves X 85 (SL 1099-Bu-19). Fig. 112. Superficial epidermal pattern of C. crassus medial and distal leaf regions X 85 (SL 1099-Q-5). Fig. 113-114. Superficial views of C. crassus stomatal apparatus X 640 (SL 1099-D-2; SL 1099-Q-5). Fig. 115. Oblique sagittal section correlating the lower epidermis with the internal structure of C. crassus leaves X 60 (SL 1099-L-2).

much reduced, additional stomatal rows appeared to have been added on the side of the stomatiferous bands adjacent to the intermediate rib, eventually forming a very wide band of 5-8 stomatal rows as photographed in fig. 112 and diagrammatically depicted in fig. 117. These wide stomatiferous bands occupied most of the inter-vein region, and were separated by nonstomatiferous bands of about half their width occurring at the vein regions. It was this latter epidermal pattern of the species that seems to have been described and illustrated (fig. 40) by Renault (1879), and redescribed by Seward and Sahni (1920), as a stomatal arrangement in 5-6 alternative rows. A close observation of the wide stomatiferous bands revealed that a band was actually separated into 2 parts by a very narrow nonstomatiferous strip of only about 3 cell rows width located immediately below the location of the intermediate sclerotic rib. The correlation of the lower epidermal pattern with the internal leaf anatomy was most clearly shown by oblique sagittal sections which first cut through the epidermal cells and then through the underlying tissue (fig. 115), but the adherance of fibrous material to the macerated cuticles also helped to reveal this relationship.

A frequently observed intermediate epidermal form between the basal pattern (fig. 111, 116) and the form with wide stomatiferous bands (fig. 112, 117), had equal paired bands of about 3 stomatal rows resulting from the regular alternation of the stomatiferous bands with wide nonstomatiferous bands associated with the vein regions and narrower nonstomatiferous bands associated with the intermediate rib regions.



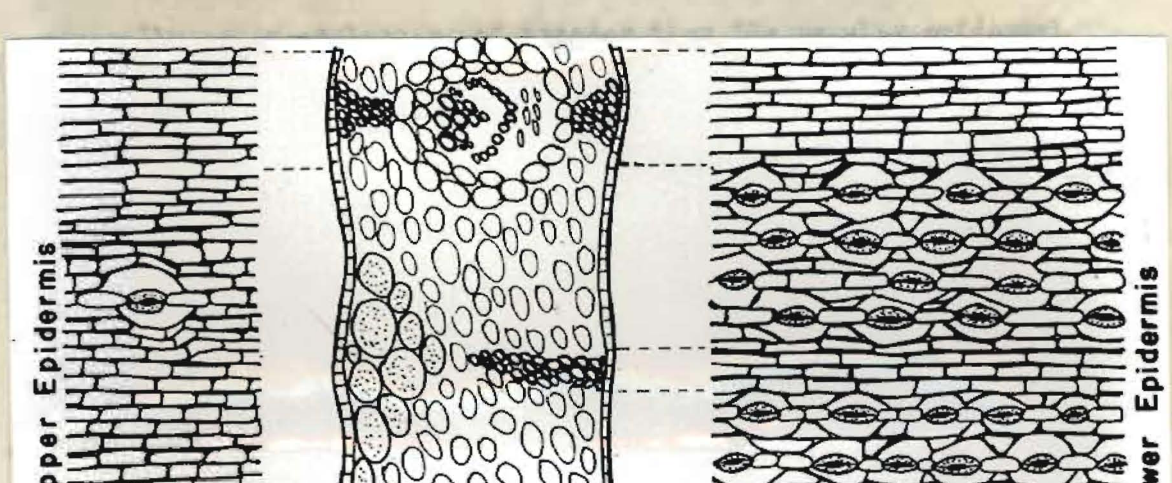


Fig. 116-117. Projected drawing showing the correlation of C. crassus epidermal patterns with the internal leaf structure. Fig. 116. Proximal leaf form with extensive hypodermal fiber ribs. Fig. 117. Medial and distal leaf form with less extensive fiber ribs.

by Renault for European C. crassus leaves was seemingly identical to that found in the present study for Iowa specimens attributed to the same species (fig. 112-114), thus lending additional support to Darrah's claim that these forms were specifically identical.

The normal epidermal cells of the upper surface were essentially similar to those of the nonstomatiferous bands of the lower epidermis, averaging 65 x 19 μ in surface view, and 21 μ in depth. An unusual banded appearance characterized some regions of the upper epidermis, which was caused by alternating strips of different cell shapes. This banded pattern was observed in those leaf forms containing the intermediate adaxial ribs of large parenchyma cells previously described and illustrated (fig. 97). The epidermal cells just above this specialized parenchymatous tissue differed markedly by being shorter, broader, and deeper (fig. 115). The correlation between the internal masses of large parenchyma cells and the difference in epidermal cell shape can be noted even in transverse sections (fig. 97), but is most clearly revealed in oblique sagittal sections which gradually cut through the epidermal cells and then the underlying tissue (fig. 117).

Contrary to the reports of Renault (1879) and Seward and Sahni (1920), stomata were definitely present on the upper epidermis of C. crassus, but were extremely rare, with an average frequency of approximately $1/mm^2$. These occasional stomata were found in the inter-vein regions usually located in the specialized bands of shorter, thicker epidermal cells, and were essentially similar in structure to those of the lower epidermis except that the guard

Fig. 118. C. crassus adaxial epidermal pattern in medial and distal leaf portions showing banded arrangement X 45 (SL 1099-M-4). Fig. 119. Oblique sagittal section showing the correlation of the adaxial epidermal bands with the internal leaf structure X 45 (SL 1099-C-2).

cells were more deeply recessed below the surface. The cuticular extensions of the subsidiary cells were also somewhat more pronounced, probably due to the presence of a thicker layer of cutin on the upper epidermis.

Bud Morphology and Anatomy.--A leafy bud of C. crassus was observed which measured 7 cm. in length extending completely through CB #1099, with neither the base nor apex visible. The bud measured 4 x 9 mm. in transverse section where it appeared as a flattened ellipse. This compares with Lignier's (1913) measurements of about 7 x 5 mm. for transverse sections of a C. lingulatus bud, and Renault's (1879) recorded measurements of a 6-7 mm. diameter and 4-5 cm. length for a C. tenuistriatus bud. This C. crassus bud was carefully studied in an attempt to correlate Lignier's (1913) work of determining the histological sequence of development from very young to mature leaves of C. lingulatus. This attempt proved rather unsuccessful as even the youngest inner leaves of the bud revealed extensive sclerotic tissue, centripetal xylem, bundle sheath elements, and some lacunar mesophyll. However, a gradual increase in lacunar mesophyll from younger to older leaves was noted, and centrifugal xylem was absent in all young leaves.

SUMMARY

Due to the taxonomic confusion surrounding cordaitean foliage a fairly extensive literature survey was deemed an essential preliminary step to any study made of Cordaites leaves. While examples of recorded compression species were only briefly mentioned because of their great number and questionable validity, the various anatomically described species were more thoroughly reviewed. The present investigation was an endeavor to help clarify some of the taxonomic confusion, by simultaneously applying as many different speciation criteria as possible to some of the common cordaitean leaf forms found in Kansas and Iowa coal balls, with an attempt to determine and correlate the external ribbing, internal anatomy, and epidermal structure of the same leaves.

Cordaites affinis Reed and Sandoe was a cordaitean leaf form extremely common in all of the West Mineral, Kansas, and What Cheer, Iowa, coal balls examined. This form was characterized externally by 13-28, but usually about 18 primary ribs/cm., alternating with a single smaller intermediate rib on the abaxial surface, and 0-5 very fine intermediate ribs on the adaxial surface. Internally, there were extensive hypodermal sclerotic strands abutting above and below the veins, a fairly prominent abaxial intermediate strand, and 1-4 small intermediate adaxial masses. The mesophyll, not differentiated into more than a very "incipient palisade" region, consisted of anastomosing plates separated by large lacunae oriented perpendicularly to both the veins and the lamina surfaces. The veins, enclosed by a 1-3 layered bundle sheath, consisted of a large upper mass of centripetal metaxylem surmounting the protoxylem, and flanked by side clusters of small tracheids which extended down along the sides of the phloem. An outstanding characteristic of this species was the apparent lack of any centrifugal xylem. The lower epidermis displayed an alternation of nearly equal stomatiferous and nonstomatiferous bands, the former being composed of about 2-4 but usually 3 stomatal rows. Stomata were also present, although infrequent, on the upper epidermis.

This American petrifaction species of C. affinis, already a taxonomic misnomer, appears to differ in no fundamental respect from the European anatomical description of C. principalis (Germ.) Gein., and its specific distinctness is questionable.

Cordaites crassus Ren. was an anatomical leaf form identified in all of the coal balls investigated from the Ottumwa-Oskaloosa, Iowa, area. The form was characterized by smooth superficial surfaces having 15-40 but usually about 23 primary ribs/cm., with a single intermediate secondary rib usually present on each surface but more distinct on the abaxial side. Internally the extent of the hypodermal sclerotic tissue varied considerably in different leaf portions, consisting of strands associated with the veins, a characteristically large abaxial intermediate mass extending far into the mesophyll, and an adaxial intermediate strand present in the proximal but not medial or distal leaf regions. In more distal leaf portions the adaxial intermediate sclerotic strand was replaced by an unusual mass of longitudinally arranged rows of large isodiametrical parenchyma cells of unknown significance. Otherwise the mesophyll was basically similar to that of C. *affinis* but slightly less lacunar. The veins, enclosed by a thick 2-5 layered sheath consisted of a small central protoxylem group, a large upper centripetal metaxylem mass, a lower centrifugal metaxylem arc, and phloem tissue inferior to the centrifugal arc. In proximal leaf portions the lower epidermis revealed single or double stomatal rows separated by wider nonstomatiferous bands, but in more distal leaf portions the stomatiferous bands widened to 5-8 stomatal rows occupying most of the inter-vein region, alternating with narrower nonstomatiferous bands. Stomata were present, but very infrequent, on the upper epidermis.

The basal morphology of both C. *affinis* and C. *crassus* leaves revealed thick, semi-clasping, recurved leaf bases which widened as well as being reduced in thickness rather rapidly initially, but later only gradually so. Secondary xylem tissue was observed in the thick basal regions of both species.

This study has pointed out the extremely variable nature of cordaitean foliage, and especially the taxonomic unreliability of using superficial ribbing patterns as speciation criteria.

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