THE PETRIFACTION FLORA OF THE DEVONIAN-MISSISSIPPIAN BLACK SHALE[1]

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GENERAL ASPECTS OF THE BLACK SHALE FLORA OF UNITED STATES

THERE is an extensive series of fissile black shale exposed in several areas of eastern United States. These range in age from Middle Devonian to Lower Mississippian. Similar sequences of near-comparable age are known from a number of regions of western North America. Contemporaneity of all of these is not indicated. For example, the earliest of mid-Palaeozoic black shales in New York are of Middle Devonian age. Westward development of this or a similar facies in Ohio are of Middle and Upper Devonian, and the same strata transgress the Devonian-Mississippian time boundary in Kentucky, Tennessee and Indiana.

Recognizable organic remains are usually restricted or concentrated to certain geographic areas and/or geologic zones. Much of the black shale sequence is essentially devoid of fossils of stratigraphic value. This has led to considerable uncertainty about the age from place to place. Much of the dating has been done by inference drawn from study of associated and occasionally intercalated strata. The difficulty of recognizing unconformities, diastems and rate of accumulation of these sediments makes precise dating of some of the thicker black shales by this procedure difficult.

The principal recognizable floral remains are divisible into three categories : (1) spores, thalloid plant bodies, and dissociated resistant fragments of higher plants ; (2) occasional silicified drift logs ; and (3) isolated phosphatized or pyritized stems or phosphatic and pyritic concretions containing miscellaneous plant and animal debris. In addition, occasional pockets or fragments of generically unidentifiable coalified plant tissue occur throughout the black shales. Rarely are leaf compressions or impressions found, at least in the Interior Region.

The most notable of the black shale plants occur in, or associated with, phosphatic concretions. Near the top of the New Albany shale concentration zones of these are found. The nodules are abundant throughout one thin widespread zone called the Falling Run member of the Sanderson formation ; fairly abundant in layers near the top of the Henryville and Sanderson formations ; and scattered through the general matrix of the Sanderson (TEXT-FIG. 4). The nodules weather out of these concretion bands in great quantities. In places where the topography is relatively level, the phosphatic nodules form regular pebble flats (TEXT-FIG. 1). Where streams of low gradient cross these flat-lying concretion zones (TEXT-FIG. 3), good collections have been made. In such places the isolated wood and bone fragments (TEXT-FIG. 3a) are often exposed among the nodules. The nodules themselves must be split open and examined for wood fragments. In a few places relatively large isolated stem slabs or segments are found (TEXT-FIG. 5). Some of these are considerably water-worn, some are split by the secondary accretionary growth of siliceous material (TEXT-FIG. 5a) which first penetrated the centre, and many had decayed considerably before burial. Portions of some of the larger specimens exposed on steep banks by erosion may break off periodically and the fragments become distributed for great distances down the slopes. In such an instance searching may yield a number of pieces which fit together to form a large specimen. The fossils range in size from minute fragments and whole stem segments no more than 2 mm. in diameter, up to several inches in diameter

1. This is the tenth paper in a series of joint palaeobotanical contributions which we have co-authored. The order of listing of names is not significant here or on any of the previous papers of the series as we are equally responsible for the research leading to the contents of each contribution, and the preparation of the manuscripts.

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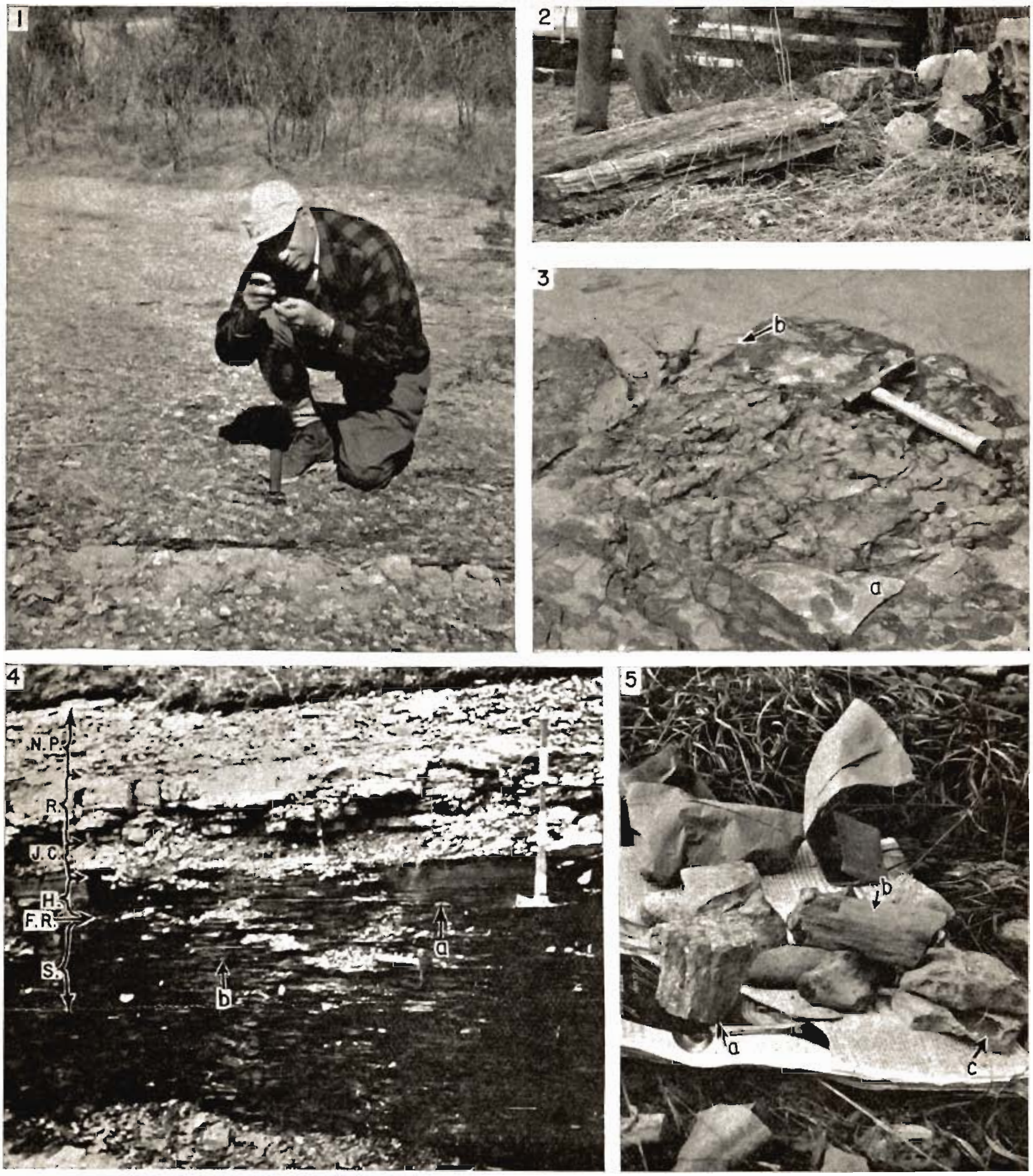
and several feet in length. It is often necessary to scrutinize every nodule or fragment with a hand lens in order to distinguish the wood from the matrix which has a similar colour, texture and general appearance.

The larger logs (*Callixylon*, TEXT-FIGS. 2 & 12 A) of the Upper Devonian portion of the black shales have not been found in the Mississippian part. These are generally silicified and are found as isolated sunken drift logs or as segments forming the nuclei in large calcareous or ironstone concretions.

Many of these fossils, especially the *Callixylon*, give the appearance of having drifted in a quiet sea for some time before



TEXT-FIGS. 1-5

finally becoming water-logged and sinking to the black organic mud at the bottom. The smaller plant fragments in some concretions are often found incorporated as constituents of a coprolitic nucleus composed of bone, teeth, wood and spores. The general nature of the enveloping concretions is often constituted largely of spores but as often of similar appearing porous phosphate rock.

The perplexing problem of the origin of these plants must be considered in this investigation. They are certainly carried for some distance from their native habitat. The water-worn character of rounded or pebble-like pieces, the occurrence of attached crinoids on the bottom and rarely the sides of some of the *Callixylon* logs as embedded in the shale and probably as they floated in the sea, the total lack of soils, the foul black sea type of sedimentation and the absence of leaf materials or, in fact, any of such delicate plant fragments, are evidences in favour of the postulation of long transportation. The presence of numerous well-preserved minute stems and good preservation of many larger pieces are against the theory that they could have come from great distances. Their greater abundance in the vicinity of the Cincinnati Arch and the numerical decrease of them to the east, south and west would suggest that they had been derived from the vegetation of an island in the New Albany sea such as the oft-postulated Cincinnatia. The numerous geologic evidences against the existence of such an island are difficult to disprove. The several hundred miles separating the bulk of these plant fossils from the known land mass of Appalachia to the east and south or Ozarkia to the west make such sources difficult to envision from the palaeobotanical viewpoint.

A number of associated faunas have been used in an attempt to date these strata as of Devonian or Mississippian age. *Lingula, Barroisella, Orbiculoidea, Tornoceras, Manticoceras, Spathiocaris*, and *Rhadinichthys* are typical. A great number of conodonts occur throughout the black shales and major breaks are indicated by sweeping changes from one group of these to another, such as from the *Ancyrodella* group of the Devonian to the *Siphonognathus* group of Mississippian portions of the New Albany shale. There is still considerable controversy over the age of some of the black shale sequences based on faunal evidence.

STRATIGRAPHY

The geologic age of the flora of the upper part of the New Albany is carefully and extensively treated in the excellent work of

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TEXT-FIG. 1 — The late Professor Birbal Sahni at the classic Linietta Springs locality near Junction City, Kentucky, at the time of his visit there on February 27, 1948. The pebbles or concretions and isolated pieces of fossil wood weather out of the one-foot layer of phosphate nodules (Falling Run member of the Sanderson formation) and inter-mixed grey shale (Bedford) at the edge of the shrub-grass line. The New Providence (Waverly) shale forms the bare slope visible through the brush in the upper left corner of the picture.

TEXT-FIG. 2 — Large log of *Callixylon Newberryi* and several smaller pieces from the Devonian part of the New Albany black shale near Henryville, Indiana. The large log shows the joint-like segmentation originating from pre-burial shrinkage and the upright block to the right shows the same jointing in a recently weathered condition.

TEXT-FIG. 3 — Phosphate nodules in six-inch layer of the Falling Run horizon (Sanderson f.) at the top of the fissile, black New Albany shale. Well-developed joint systems occur throughout the shales (b). Large fragments of the head shield of a Placoderm (cf. *Dinichthys*) are noted at (a).

TEXT-FIG. 4 — Upper part of the New Albany shale and lower part of the New Providence (N.P.) formation at Henryville, Indiana. The Sanderson (S.) contains scattered phosphate nodules (b) in the fissile shale, and a thin layer of nodules (a) of the Falling Run horizon at the top (F.R.). The overlying Henryville (H.) marks the final recurrence of the black shale of the New Albany. It is intermingled with the Falling Run nodules in the absence of the Underwood grey shale which is missing here. The Jacobs Chapel grey shale (J.C.), a weak, fossiliferous zone, and the more resistant Rockford limestone above, are Kinderhook (Mississippian), as are the Henryville and Sanderson formations at the top of the New Albany shale. The principal fossil wood horizon is at (a) with scattered pieces found throughout the Sanderson.

TEXT-FIG. 5 — Several pieces of phosphatic wood and concretions from the top of the New Albany shale at Pine Lick, Kentucky. One piece of wood (a) is considerably enlarged and split apart by intercalated silica. The isolated piece (b) is considered to be very large for these collections. The nodules at the upper left and at (c) show the water-worn character of some nodules and the enclosed wood fragments (partially lost here). The amount of material shown constituted the entire lot collected in four hours' searching by Mr. Guy Campbell and us and yet was considered to be an unusually good collection for that length of time.

Guy Campbell (1946). Text-fig. 6 is a general correlation chart of the Middle and Upper Devonian of eastern United States showing the principal horizons of petrified plants. The stratigraphic sections of the east-central Interior Region have been derived principally from Campbell (1946) and the New York-Pennsylvania section is taken from several sources, especially the National Research Council's correlation chart of the Devonian (COOPER *et al.*, 1942). Discrepancies or differences of opinion in the correlation of the New Albany shale with the Ohio shale noted by Hass (1947), as based on conodont studies, need not be considered here.

The New Albany shale of Indiana is divided into five formations of unequal thickness by Campbell (1946). The principal thickness is made up of fissile black shale of the Blocher and the Blackiston which are considered Devonian in age. The lowest of the three Mississippian formations of the sequence, the Sanderson, is a black fissile shale containing scattered phosphate nodules throughout (TEXT-FIG. 4, S. b) with a concentration zone of nodules called the Falling Run member at the top (TEXT-FIGS. 3, 4a and F.R.). This member is usually only a few inches thick though occasionally it is as much as 18 in. It is in this zone that the main aggregation of petrified wood is found. Another similar nodule zone which also contains a concentration of plants occurs about a foot below the Falling Run member in southern Indiana. Occasional isolated pieces of wood of the same floral group occur in the matrix throughout the remainder of the Sanderson formation.

The overlying Underwood is a 6 in. thick grey-green shale, bearing a good brachiopod fauna but virtually no conodonts. One specimen of wood (*Periastron*) has been found in this shale. The uppermost formation of the New Albany shale is the Henryville, a black fissile shale which has yielded no petrified wood. In some places the Underwood is missing and the Henryville lies directly on the Falling Run nodule zone as shown in Text-fig. 4 at " H." and " F.R.".

Above the New Albany shale in the area north of the Ohio river, the Jacobs Chapel shale and Rockford limestone (TEXT-FIG. 4, J.C. and R.) are easily distinguished on the basis of lithology and characteristic Mississippian invertebrates. South of the Ohio river and west of the Cincinnati Arch in Kentucky, the New Providence siltstone and shale lies nearly in contact with the Falling Run zone, but on the crest of the Cincinnati Arch, near Junction City and east of it, traces of the eastward thickening wedge of Lower Mississippian Bedford formation inter-fingers with the Falling Run and in fact may furnish the matrix for the Falling Run nodules at these localities.

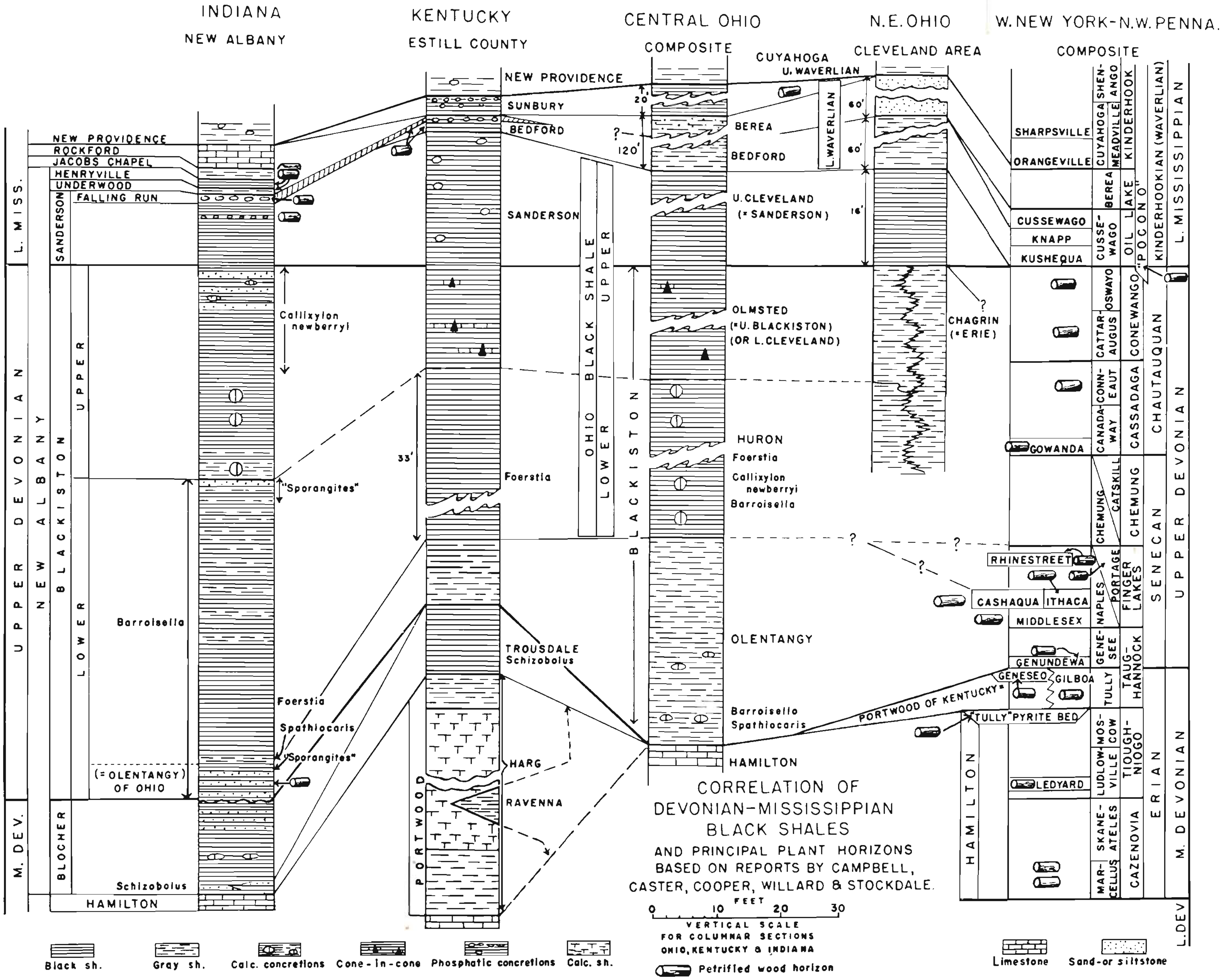
DISTRIBUTION

The Devonian-Mississippian black shales of the east-central Interior Region outcrop in a narrow belt through central Ohio, across north-central Kentucky and south through south-central Kentucky into Tennessee. From central Kentucky the outcrop also extends northward into southern Indiana. The arrows pointing to the collection localities (TEXT-FIG. 7) show this distribution rather clearly. The circumscription of the Cincinnati Arch by the black shale is easily discernible in this figure. The collections around the north end of the Nashville Dome are less complete and the outcrop there is less well indicated by Text-fig. 7.

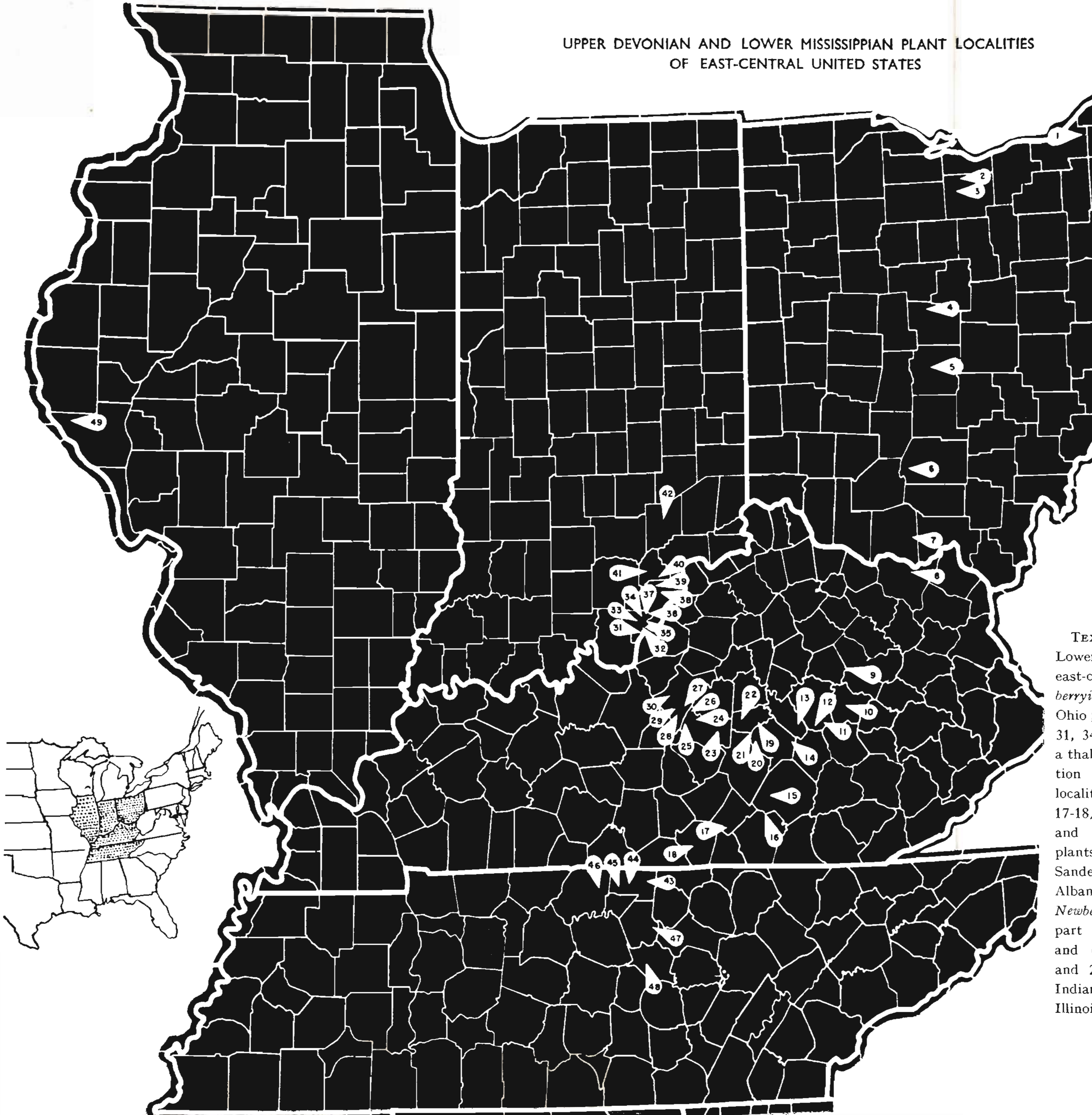
In addition to the outcrops in this area narrow bands of outcrop of the Chattanooga shale occur in eastern Kentucky and Tennessee. Beneath the glacial mantle in north-western Ohio and northern Indiana a considerable area of New Albany shale outcrops. Near-comparable stratigraphic zones of black shale occur in north-eastern Michigan, the Antrim formation, Text-fig. 13 (3) and in south-western Ontario, the Kettle Point, Text-fig. 13 (2). Throughout these areas the black shales bear abundant *Tasmanites* spores ("sporangites") and occasional specimens of *Callixylon*. Upper Devonian black shales of western New York have yielded several species of *Callixylon*.

The principal flora considered here, i.e. from the Mississippian portion of the upper New Albany shale, is most abundant at localities through central Kentucky and southern Indiana. A few specimens are found in southern Kentucky, and in Tennessee at locality No. 47, Text-fig. 7. None have been found in Ohio.

One additional collection of a representative of this flora has been made at Kinderhook, Illinois (TEXT-FIG. 7, locality No. 49). This will be discussed later.



TEXT-FIG. 6—Geologic correlation chart showing the principal petrified plant-bearing horizons of the black shales of the eastern Interior Region and the general correlations with the New York-Pennsylvania fossil-bearing zones.



TEXT-FIG. 7 — Upper Devonian and Lower Mississippian plant localities of the east-central United States. *Callixylon Newberryi* has been found at locality Nos. 1-7 in Ohio; 9, 16, 24, and 28 in Kentucky, and 31, 34, 38, and 40-42 in Indiana. *Foerstia*, a thalloid alga, has been found in association with *C. Newberryi* and below it at locality Nos. 5 and 31 and elsewhere at 8, 11, 17-18, and 29 in Kentucky, 41 in Indiana, and 43-46 in Tennessee. Phosphatized plants, either isolated or in nodules of the Sanderson (Mississippian) part of the New Albany shale, have been found above the *C. Newberryi* zone of the Blackiston (Devonian) part of the black shale at 28, 34 and 38 and elsewhere at 10, 12-15, 17-23, 25-27, and 29-30 in Kentucky, 32-37 and 39 in Indiana, 47 and 48 in Tennessee and 49 in Illinois.

COLLECTIONS

The first study of the plants of the upper part of the black shale sequence in the United States was contained in the report by Scott and Jeffrey (1914). This fundamental study concerned some excellent material from "the base of the Waverly shale at Linietta Springs, near Junction City, Kentucky". These specimens have not been available to us but duplicate material of most of the genera and species are in hand. A general view of a portion of this classical locality taken at the time of the late Professor Birbal Sahni's visit there with us in February 1948 is given in Text-fig. 1.

A large collection of this flora is in the United States National Museum in Washington D.C. Most of this material was accumulated by Dr. C. B. Read, both by personal collection and from Mr. Guy Campbell, of Corydon, Indiana.

The most enterprising and persistent collector of these floras is Mr. Campbell. It was he who found most of the localities which yielded a large number of the specimens in the U.S. National Museum collection. He also accompanied us on numerous trips to these localities and aided in the discovery of many new collecting sites during the past five years. He has placed in our hands a great many specimens collected at frequent intervals for more than ten years subsequent to the time of the loan of his collection to the U.S. National Museum.

Our personal collection includes large numbers of specimens of the genera and species heretofore described. There are many new forms which are being investigated.

One of the most fortunate of the recent discoveries was made by Dr. Raymond C. Gutschick of the University of Notre Dame. This is a specimen of *Callixylon* from the type locality of the Kinderhook series in Illinois [TEXT-FIG. 7 (49)], which will be discussed later.

Additional specimens have been collected from black shale sequences and other strata of near-comparable age in several states. It is not possible to state at this time how some of these collections will correspond to the extensive petrifaction flora of the Upper New Albany shale.

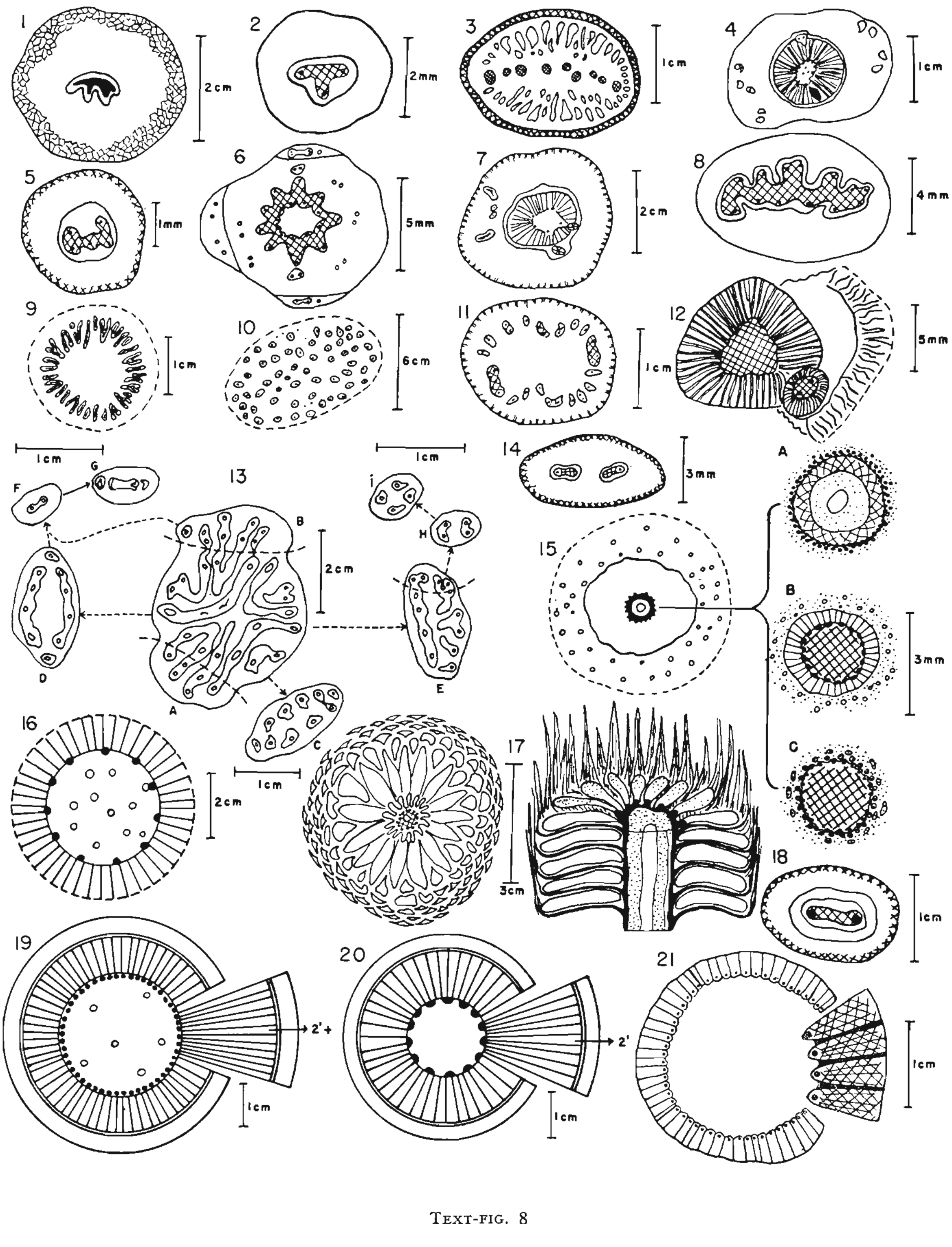
THE DESCRIBED FLORA

The vascular flora of the Upper New Albany shale of southern Indiana and Kentucky, as recorded in literature, includes forty described species in twenty-nine genera. The identification and proper assignment of a few of these will ultimately have to be checked when additional material is found. A number of new species and genera await description. We have prepared a manuscript for publication elsewhere which deals with the disposition of four species previously described, but a brief statement concerning these will be given here later. Nine monotypic genera have been described from this Upper New Albany shale, none of which have been recorded from other areas (TEXT-FIG. 14). A number of dissociated stems classified under different generic names can be considered to be different orders of branching of a single plant type.

Text-fig. 8 gives a diagrammatic representation of twenty-four recorded genera of this flora. The review or/and diagrams of these plants here is not intended to indicate that we concur in the assignment or interpretation of the genera and species given. This is simply a summation of the published information. *Polyxylon* is omitted since there is no generic description. *Protolepidodendron* and *Asteroxylon*, which were previously reported by Read (1939), are to be illustrated later in this paper. *Calamopteris* has been transferred to *Kalymma* (READ, 1937). *Arnoldella* is too poorly understood to prepare a reasonable basic diagram. *Pitys* (TEXT-FIG. 8, No. 19) is included, though the species recorded by Read (1936) has since been unofficially referred to *Callixylon* (TEXT-FIG. 8, No. 20), because of the uncertainty of the status, and possible relationship, of *Archaeopitys* (TEXT-FIG. 8, No. 16).

The centre of the axis of *Lepidodendron* (TEXT-FIG. 8, No. 15) has been enlarged in 15 A and 15 B to show the tissue arrangement of the two species, *L. boylensis* and *L. novalbaniense*, described by Read (1936 & 1939 respectively). Additional new material is being studied. The centre of a stem of *Lycopogenia*, which is possibly related, is shown in 15 C. It has distinctive generic features and has been referred to the lycopods by Read.

An explanation of some of the symbols for the diagrams in Text-fig. 8 might aid in their examination. The solid black dots or circles in Nos. 2, 5, 6, 8, 9 (solid lines in bundle outlines), 10-15, 17, 18 and 21 indicate protoxylem points or areas. The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TEXT-FIG. 8

cross-hatched areas in 2, 5, 6, 8, 11, 12, 15, 17 and 18 indicate primary wood or metaxylem. The cross-hatching in number 3 is for primary wood (complete bundles) but in number 21 it indicates secondary wood. The solid black circles, dots or areas in Nos. 1, 4, 7, 16, 19 and 20 also indicate the whole primary wood area or bundles. The radially aligned lines indicate secondary wood in 4, 7, 12, 15 B, 16, 19 and 20.

The grouping of many of these genera into families or orders is difficult principally because of inadequate information or material. The genera appear to include root axes and leaf petioles, or their divisions, as well as stems. The few stems assigned to psilophytalean genera are insecure and, therefore, do not allow inferences or speculation on the primitive character of the flora. The specimens of familiar lycopods such as *Lepidodendron* and *Lepidostrobus* are scarce but several species of the former are indicated and two well-developed species of *Lepidostrobus* are thoroughly described and illustrated. Specimens of articulatalean affinity are rare. One species has been described as *Protocalamites* (21) and recently a specimen of peculiar but unmistakable articulate character, probably Calamitean, was placed in our hands by Guy Campbell. A number of species of fern-like plants are known from numerous specimens, one of the largest groups of these, the cladoxylalean assemblage, is a diverse group possibly containing in addition to *Cladoxylon* (13), and its form or organ genera based on different orders of branching, such genera as *Steloxylon* (10) *Stereopteris* (18) and *Pietzschia* (19). Another group which is especially well represented by a large number of specimens and several genera is the calamopityan-pityan alliance. Abundant pieces of secondary wood and quite a number of complete stems of the Cycadofilicales and Cordaitales are available. An extensive study of the distinguishing features of secondary wood will be requisite to the proper dispensation of much of this material.

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TEXT-FIG. 8—Diagrammatic cross-sections of the principal genera of fossil woods heretofore recorded occurring in the Mississippian portion of the New Albany-Ohio black shales. 1, *Microzygia* ; 2, *Reimannia* ; 3, *Periastron* ; 4, *Calamopitys* ; 5, *Mesoneuron* ; 6, *Siderella* ; 7, *Diichnia* ; 8, *Plicorachis* ; 9, *Pietzschia* ; 10, *Steloxylon* ; 11, *Kalymma*; 12, *Stenomyelon* ; 13, *Cladoxylon* and postulated related genera of its branching system ; 13 A-E, *Hierogramma* and mode of bifurcation from *Cladoxylon* ; 13 F-G, *Clepsydropsis* and origin from *Hierogramma*; 13 H-I, *Syncardia* and origin from *Hierogramma* ; 14, *Lyginorachis* ; 15, *Lepidodendron*, general tissue orientation of stem ; 15 A, *L. boylensis* type ; 15 B, *L. novalbaniense* type ; 15 C, *Lycopogenia* (centre of stem only) ; 16, *Archaeopitys* ; 17, *Lepidostrobus* (transverse and longitudinal sections of cone) ; 18, *Stereopteris* ; 19, *Pitys* ; 20, *Callixylon* ; 21, *Protocalamites*.

AN EVALUATION OF RECORDED DEVONIAN COMPONENTS

Four genera, *Protolepidodendron*, *Asteroxylon*, *Reimannia*, and *Callixylon*, which have been reported from the black shales of the east-central Interior Region of the United States, are known elsewhere only from Devonian strata. *Protolepidodendron*, Potonié & Bernard, was founded essentially on compression material and its anatomy is inadequately known. Kidston and Lang first reported *Asteroxylon* from the Rhynie Chert of Middle Devonian age. Later Kräusel and Weyland described a second species of comparable age from rocks near Elberfeld, Germany. *Reimannia* was based on a small collection of a single species described by Arnold in 1935 from the upper Middle Devonian of New York State. Several species of *Callixylon* have been described. The genus was founded by Zalessky in 1911 based on material from the Upper Devonian of the Donetz Basin in South Russia, but is perhaps best known from American species occurring in several horizons throughout the Upper Devonian.

The upper portion of the New Albany shale of Indiana and Kentucky is placed in the Mississippian as the result of recent extensive stratigraphic studies. It is pertinent, therefore, to re-examine the structural characteristics of these plant fossils occurring in the Mississippian portion of the black shales which have been assigned to the four genera mentioned above, and to evaluate the assignment of these specimens to established Devonian genera.

A. *The Genus Asteroxylon* — The two well-established species of *Asteroxylon*, *A. Mackiei* Kidston & Lang and *A. elberfeldense* Kräusel & Weyland, are not known to have occurred later than the Middle Devonian. The discovery of this genus from much younger beds is of such interest that particular attention should be given to its announcement. In their preliminary report of the New Albany shale flora, Read and

Campbell (1939) report the occurrence of a new species, *A. Setchelli*, from the black shales of the New Albany area. As has been pointed out, these plant-bearing beds are now considered to be of Lower Mississippian age.

The description of the species is quoted in full :

" 1. Stems small, the specimens seen less than 5 mm. in diameter.

" 2. Stele stellate, consisting of five radiating arms centrally united to form a relatively stocky cylinder.

" 3. Phloem and outer stelar tissues problematical but probably concentric.

" 4. Protoxylem exarch to slightly immersed.

" 5. Outer tissues parenchymatous as observed, with some traces of a thick-walled hypodermis."

A reinvestigation of the type slides of *A. Setchelli* suggests certain modifications and additions to the description given above to the extent that it appears impossible to retain this species within the genus *Asteroxylon*. Much more needs to be known from more critical sections of this species or from better material before it can be assigned with any degree of certainty to its proper systematic position.

Text-fig. 9 A illustrates the general outline and tissue arrangement of the stem. The stellate shape of the stele is probably the principal basis for the original assignment of this species to *Asteroxylon*. Actually, the stele appears to be basically four-rayed with two of the rays more prominent and slightly divided at the edge. The stelar column would appear as a deeply fluted four-angled column with two of the ridges being more prominent and slightly grooved or furrowed.

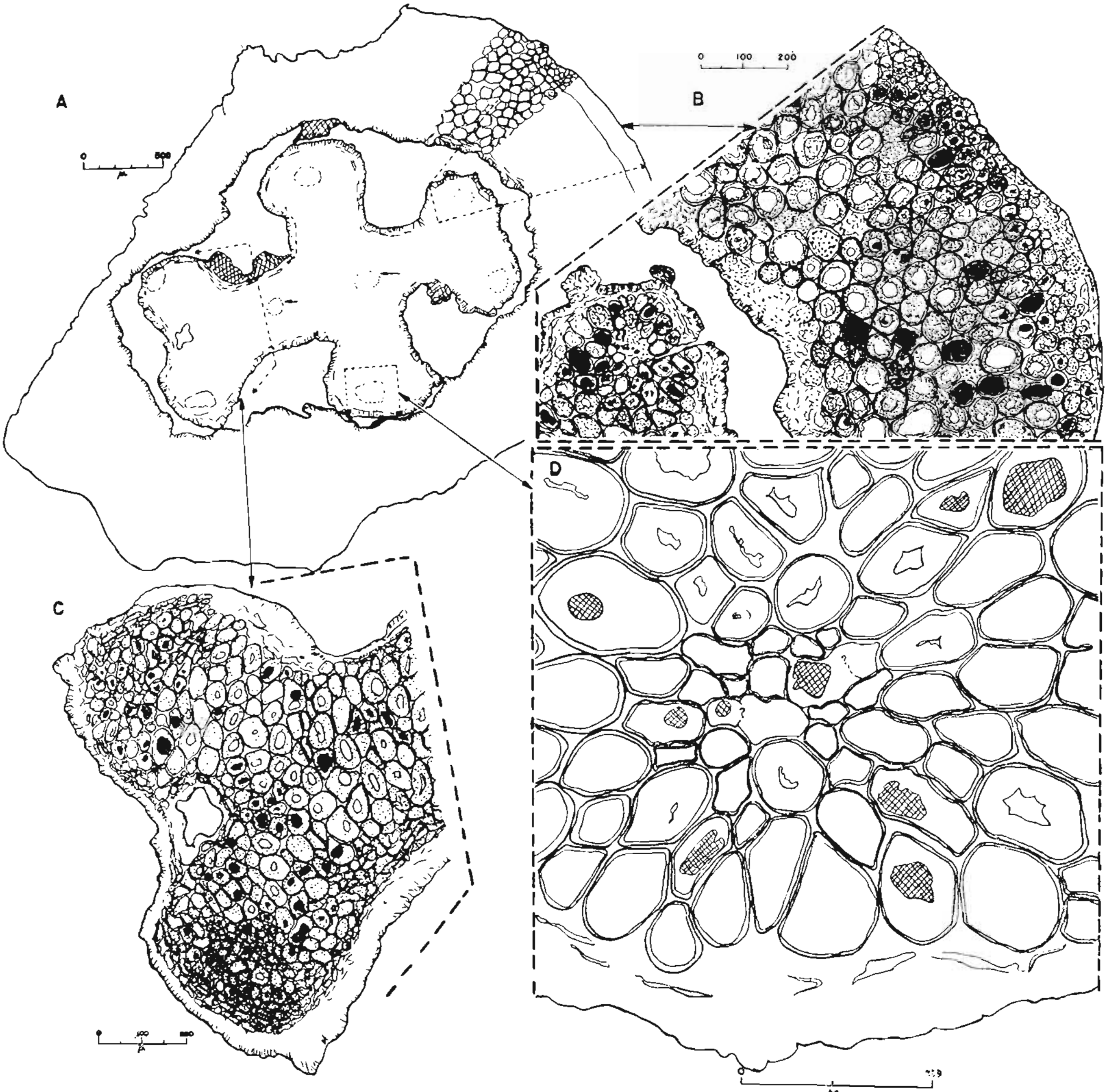
More important is the character of the protoxylem areas. They are mesarch with a number of cells between them and the outer edge of the stele (TEXT-FIGS. 9 D, lower left of 9 B, and dotted outlines in 9 A). Furthermore, there are two other protoxylem areas very deeply situated as can be seen at the centre of the stele in the positions indicated by the dotted lines and small arrows (TEXT-FIG. 9 A'). This is not a feature of the genus *Asteroxylon*. Also, the protoxylem areas are quite large, much larger than generally given for the genus.

The relatively great size of the stele to the whole stem is certainly unusual for *Asteroxylon*. There is little cortical differentiation in the New Albany species, certainly no differentiation of the main body of the cortex into an inner and outer compact zone separated by trabecular tissue. No leaf traces are found in the Indiana material. Normally *Asteroxylon* shows a number of leaf traces passing outward through the cortex. One specimen which is specifically distinct from *A. Setchelli* has a lateral branch of great size with a double bundle.

Thus the shape of the stele, the large size and mesarch position of the protoxylem, the simple and very narrow cortex without leaf traces, and features of branching furnish adequate basis for excluding the New Albany material reported by Read and Campbell from the genus. In another paper under publication elsewhere, the full description and illustration of this interesting species is given and is assigned to another genus. We are not certain of the natural affinities of this species but regardless of that, its occurrence in the New Albany shale cannot be used as evidence for either Mississippian or Devonian age.

B. *The Genus Protolepidodendron* — A portion of a small stem imbedded in a phosphate nodule from the lower of the two nodule beds at the top of the Falling Run horizon of the Sanderson formation (Lower Mississippian) near the type locality of the Jacobs Chapel shale furnished the basis for the description of a new species of *Protolepidodendron*, *P. microphyllum* Read & Campbell (1939). A series of five transverse sections taken from this specimen in sequence but at unknown intervals is in the collection of the U.S. National Museum and was made available to us. The remainder of the specimen, if any, has been misplaced.

A detailed account of this specimen has been prepared for publication elsewhere, some salient features of which will be mentioned here. The exceedingly brief and scarcely diagnostic original description follows essentially as given: Stem small, about 8 mm. in diameter; stele trilobed, the three lobes united to form a central column; xylem mesarch, the protoxylem situated near the apices of the arms and forming loops; outer stelar tissues not preserved; cortex parenchymatous and limited by a sclerotic hypodermis; leaves scale-like both in aspect and in origin, parenchymatous; the leaves bifurcating a short distance



TEXT-FIG. 9 — Transverse section of a small stem from the New Albany shale originally referred to the genus *Asteroxylon*. The position of the three enlargements 9 B, 9 C and 9 D are indicated in Text-fig. 9 A. Dotted lines in the stele of 9 A indicate the position of the protoxylem areas. Note especially the two areas indicated by small arrows.

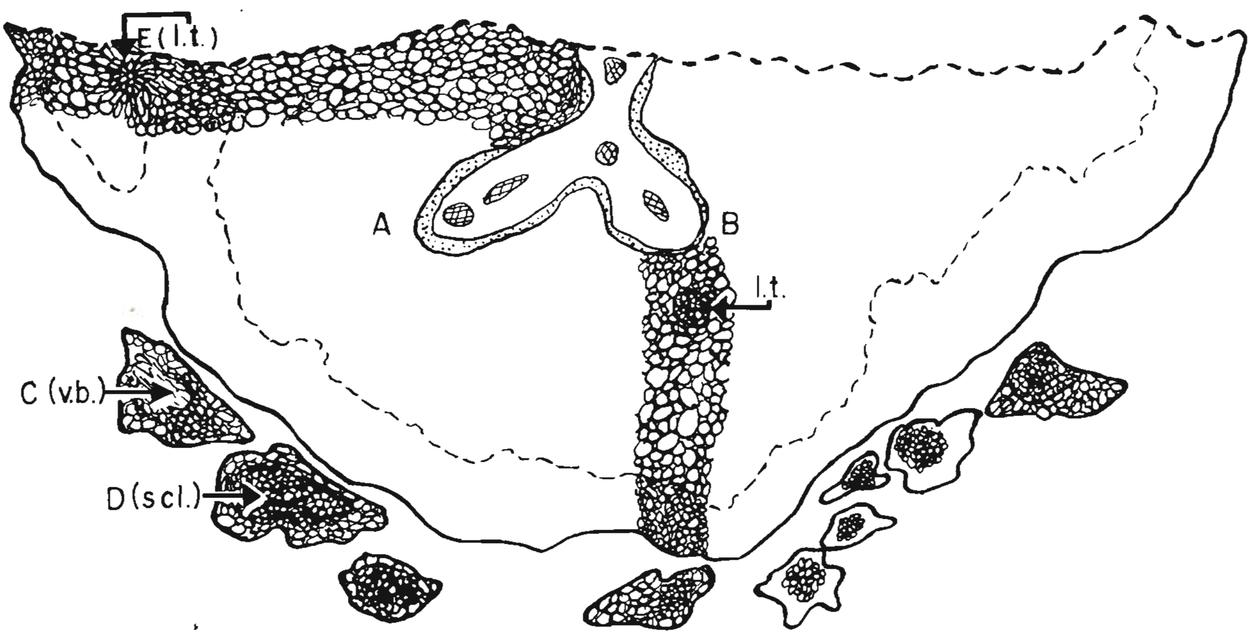
above the point of attachment, exact outline unknown, but probably linear.

There is no further discussion of the species. Its reference to *Protolepidodendron* may have been based on the reported trilobed nature of the stele and the occurrence of the apparently microphyllous leaves. Our studies of this material show certain points at variance with, and some additional features of, this description such as the position of the protoxylem areas, the nature and position of hypodermis, the character of the outer stelar tissues which are well preserved and, especially, details relative to the origin, structure and bifurcation of the leaves and the probable form of the stele.

At some level each xylem arm represented in the stele offers evidence that a leaf trace originates at its extremity. For example in Text-fig. 10 the xylem arm to the left (A) shows a double protoxylem area. At a higher level this arm becomes extended radially affording evidence of the origin of a leaf trace which then passes through the cortex into the base of a leaf. Such a trace is seen in Text-fig. 10 (l.t.) a short distance from the tip of the xylem arm (B) to the right.

When all the leaf traces are plotted throughout the range of the five sections available, together with the position of the leaves into which these traces enter, grave doubts arise as to the trilobed nature of the stele. Quite another possibility exists, namely that the preserved specimen demonstrates but a part of the entire stele, which might well have been composed of several discrete strands such as are commonly found in *Cladoxylon*, or perhaps it consisted of a single polyarch central strand. The anatomy of the available material, the position of the leaf traces and the leaves themselves may be readily interpreted on such a premise, but can be explained with difficulty, or in the case of certain leaves not at all, on the assumption of a three-lobed stele. We believe the interpretation of the stele as three-lobed cannot be maintained, and thus one of the principal bases for referring the specimen to *Protolepidodendron* is untenable.

The stem is well covered with spirally arranged, sessile, decurrent leaves. The single leaf trace present in the base of the leaf divides as the leaf itself bifurcates immediately after becoming free from the stem. Each of these divisions again divides so that each leaf has four ultimate segments. The leaves are appressed to the stem and all the bifurcations are in the same plane and at a very low angle. Following the first bifurcation the leaf rapidly becomes reduced in size and develops a conspicuous sclerotic strand near its centre (D, scl.). This is the dominant tissue of the leaf tips following the second bifurcation and the vascular strands are usually not distinguishable at this level. The bundles do not extend to the leaf tips.



TEXT-FIG. 10 — Diagram of transverse section of fragment of stem formerly attributed to *Protolepidodendron*. The two lobes of the remaining portion of the stele contain five protoxylem areas or loop structures. The leaf bases at E with its leaf trace (l.t.) is about to become free from the stem. The tips of several remaining leaves, all bifurcated twice, are seen. The sclerotic central zone (scl. at D) makes up the larger part of the tissue followed by the second bifurcation. One vascular bundle (v.b. at C) is to be seen in one leaf.

While there are certain apparent similarities between the organization of this fragment of stem and *Protolepidodendron*, which is all too little understood, in some respects it departs rather widely from our conception of that genus. The bifurcation of the leaves not once but twice, their bifurcation near their bases and their appressed character indicate marked differences. The probability is that the stele is not three-lobed at all and that only a portion of a more extensive stele is present in the preserved part. These considerations and others make its retention within the genus *Protolepidodendron* untenable, and elsewhere we have proposed another genus to include it.

C. *The Genus Reimannia* — The genus *Reimannia*, established by Arnold (1935) to accommodate a single species, *R. aldenense*, was based on several petrified specimens preserved in marcasite from the Middle Devonian Ledyard member of the Ludlowville formation of New York. The description of the species was based mainly on one small specimen which was best preserved. This specimen, most unfortunately, has entirely disintegrated and is no longer available for comparison. Thus our basis for review of this species is necessarily limited to Dr. Arnold's published description and to two fine negatives used in illustrating the type species which he kindly loaned to us.

In 1939 Read and Campbell described a second species, *R. indianensis*, from the Falling Run horizon of the Sanderson formation (Lower Mississippian) near New Albany, Indiana. Their brief description in the absence of any elaborating comment is insufficient for comparison. Three of probably four original thin sections and the specimen were loaned to us for examination by the U.S. National Museum.

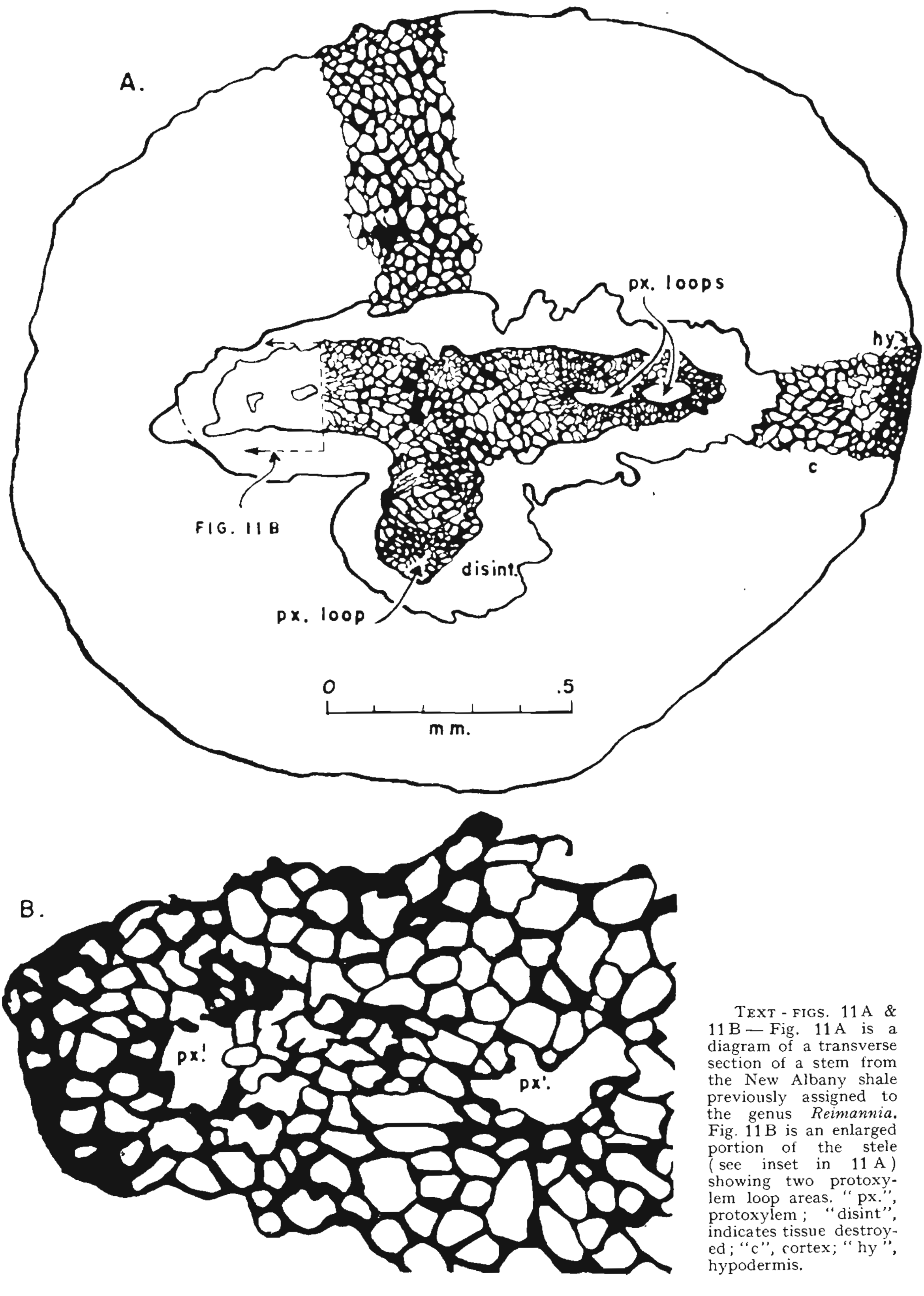
The two specimens can scarcely be retained within the same genus. *R. indianensis* (TEXT-FIG. 11A) is seen to be circular in outline, with a T-shaped stele occupying from one-half to one-third the total diameter of the axis. The cortex appears heterogeneous, with smaller cells both toward the periphery and adjacent to the stele. The stele itself is mesarch (TEXT-FIG. 11B); deep embayments occur between the arms of the "T" and the stem. In one section there is indication of the arms of the "T" being recurved back toward the stem of the "T", and evidence of a shallow depression opposite the upper end of the central arm of the "T". There is no indication of branching or leaf traces.

In *R. aldenense* the axis is angular, possibly related to frequency of leaf formation. The stele which is basically triarch and radial, occupies approximately one-sixth the total diameter of the axis. The cortex is bounded by a cutinized epidermis within which is a zone of sclerized cells which grade gradually into larger, thin-walled, homogeneous inner cortical tissue. The stele has the three arms rounded, with very shallow embayments between the xylem arms. Traces in the cortex may be referable to leaf traces. A more detailed study and comparison of the two species is being published elsewhere.

Thus, while both axes are of essentially the same size, both possessing a single central fluted column of primary xylem with three flanges, while both steles are mesarch and both lack secondary xylem, they are more than sufficiently different in detail to warrant the exclusion of the Indiana specimen from the genus *Reimannia*. What its true systematic position may be is uncertain. Its disposition must be delayed until additional specimens provide adequate material for study. In the meantime it is rejected from the genus *Reimannia*, and transferred to another genus. Any stratigraphic connotation suggested by this plant having been placed in the genus *Reimannia* is unwarranted.

D. *The Genus Callixylon* — *Callixylon Newberryi* (Dawson) Elkins & Wieland is the best established of the several American species of *Callixylon*. It is not uncommon in the Devonian portion of the New Albany shale (Upper Blackiston). Other species occur in various horizons of the Upper Devonian and the genus has come to be considered as an index fossil indicating the Upper Devonian age of the beds in which it occurs.

Read and Campbell in 1939, without comment other than horizon and localities, included a new species of *Callixylon* in their table of species from the upper portion of the New Albany shale (principally the Upper Sanderson formation and the Falling Run member). There is no doubt that material in the collection of the U.S. National Museum labelled *C. Brownii* was the basis not only of this report but also that of *Pitys Brownii* (READ, 1936) which was accompanied by a brief preliminary description,



TEXT - FIGS. 11A & 11B — Fig. 11A is a diagram of a transverse section of a stem from the New Albany shale previously assigned to the genus *Reimannia*. Fig. 11B is an enlarged portion of the stele (see inset in 11A) showing two protoxylem loop areas. "px.", protoxylem; "disint", indicates tissue destroyed; "c", cortex; "hy", hypodermis.

inadequate in itself for the assignment of the material either to *Pitys* or to *Callixylon*.

As several specimens in our collections show affinities to *Callixylon*, we re-examined the material labelled *C. Brownii* and have published elsewhere the detailed evidence upon which we concluded that reference of it to the genus *Callixylon* is correct. This conclusion was given weight by significant collateral evidence. In the absence of preserved pith and primary wood, several species have been referred to the genus based upon an examination of secondary wood only with special reference to the characteristic radial alignment of discontinuous pit groups. The assumption is that the occurrence of this single feature is adequate evidence for the assignment of a species to the genus *Callixylon* as no other examples of this arrangement of pits are known to occur in plants, living or fossil (ARNOLD, 1947, p. 283). When a number of pieces of secondary wood from the Mississippian portion of the black shales were split longitudinally along radial surfaces and observed under reflected light, radial banding of discontinuous pit groups was obvious. In some instances, radial thin sections confirm the observations. Text-fig. 12 A is a photomicrograph of a portion of a thin section of the silicified wood of *C. Newberryi* from the Blackiston (Upper Devonian) of Nelson County, Kentucky. This is to be compared with Text-fig. 12 B which is not a thin section, but a specimen split along a radial surface and photographed by means of reflected light. This specimen is not *C. Newberryi* but an undescribed species from the Falling Run member of the Sanderson formation (Mississippian) from Crab Orchard, Kentucky, locality No. 14, Text-fig. 7. We can demonstrate the same structural organization in specimens from Junction City, Kentucky, locality No. 19 ; New Albany, Indiana, locality No. 36 ; and elsewhere, with special reference to material from the type locality of the Kinderhook series, the lower division of the Mississippian, at Kinderhook, Illinois, locality No. 49.

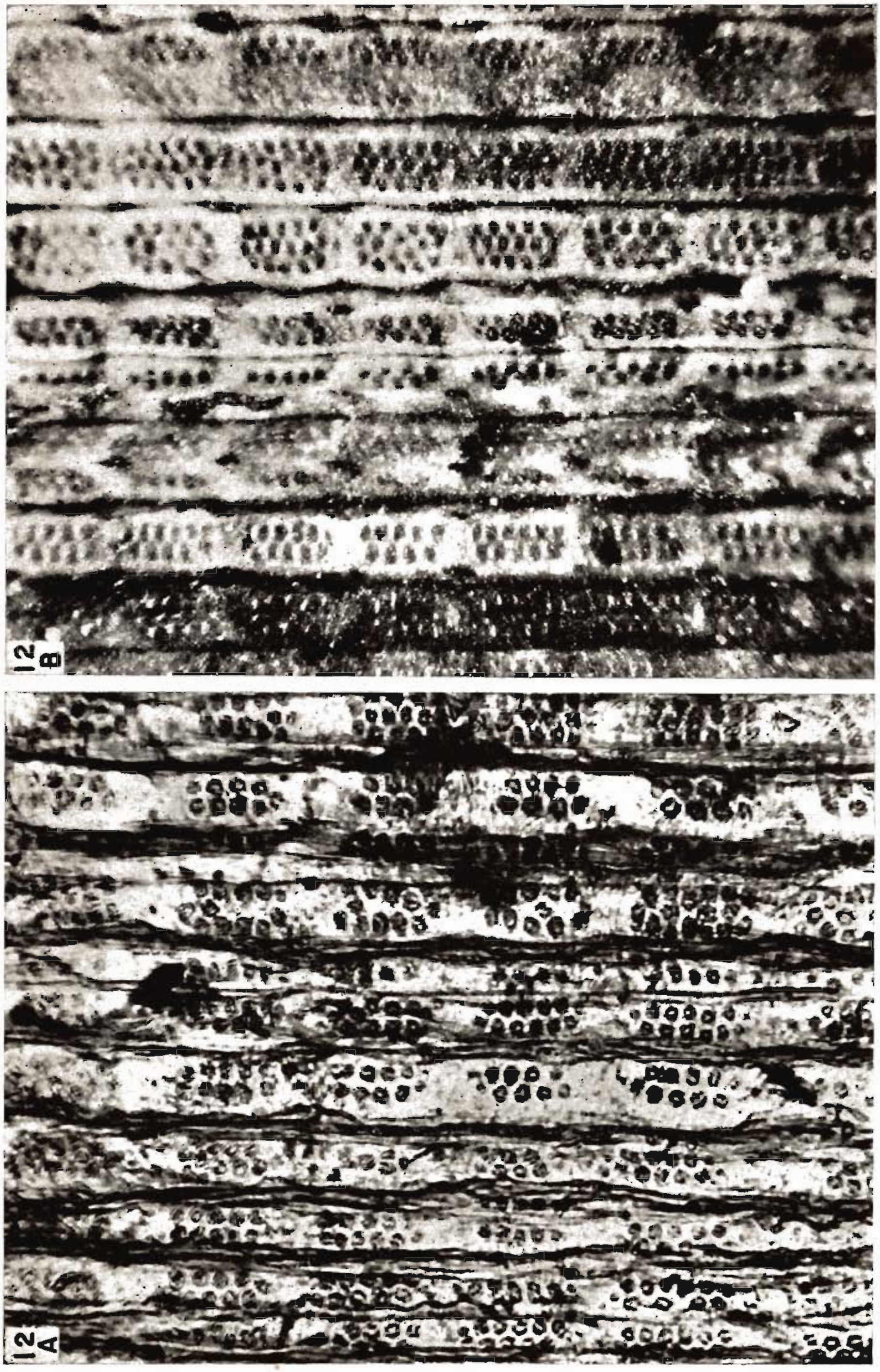
These various specimens differ among themselves in detail and all differ from *Callixylon Newberryi*. Their specific assignments are being published elsewhere.

These studies have the effect of removing the genus *Callixylon* from the rôle of an index fossil of the Upper Devonian as its range is extended into the Lower Mississippian. This does not necessarily preclude the use of certain well-established species, such as *C. Newberryi*, which may prove to have useful limits of occurrence through time. However, the recognition of the genus alone cannot be utilized as evidence of the Devonian age of the plant-bearing horizon.

E. *The Genus Cladoxylon* — One genus which has received little attention as indicating a Devonian range and which has not been recorded with certainty above the Cypridina shales in which it is abundant is *Cladoxylon*. The genus was established on some material from the Cypridina shales of Saalfeld, and has recently been restudied by Bertrand (1935). The identity of *C. Kidstoni* from the Lower Carboniferous of Berwickshire is quite uncertain. More important are two Devonian records. The earlier of these, though little noticed, was reported by Dawson (1882). Read (1935) has called attention to this specimen found by the eminent palaeontologist, John M. Clarke, in the Genundewa limestone (Upper Devonian) of New York State, and described it as a new species, *C. dawsoni* Read. Bertrand examined the only known slide of this species and agreed with Read on the identification. We have compared this slide with cladoxylalean material from the New Albany shale and are, in general, satisfied as to the general affinities exhibited by the material from the east-central Interior Region with the older species from New York. The other Devonian record, *C. scoparium*, described by Kräusel and Weyland from Elberfeld, Germany, is considered to be outside the generic limitations according to Bertrand, Sahni and others. Thus this genus, *Cladoxylon*, though principally known from beds of an age equivalent, or nearly so, to the Upper New Albany shale, has a single recognized Upper Devonian representative.

AN EVALUATION OF RECORDED MISSISSIPPIAN COMPONENTS

A study of the ranges for the genera recorded from the Upper New Albany shale, illustrated here in Text-fig. 14, shows that four of these genera, *Lepidostrobus*, *Lepidodendron*, *Calamopitys* and *Lyginorachis*, have a continuous representation into the Upper Mississippian or higher. Another genus, *Steloxylon*, has no representation known



TEXT-FIGS. 12 A & 12 B—Comparison of radial pitting on Devonian and Mississippian *Callixylon*. 12 A, photomicrograph of thin radial section of *Callixylon Newberryi* from Nelson Co., Kentucky. 12 B, reflected light photomicrograph of radially split specimen of *Callixylon* from the Mississippian part of the New Albany shale, Crab Orchard, Kentucky.

above the transitional Devonian-Mississippian black shales except in the Permian. Two other genera, *Protocalamites* and *Stenomyelon*, range at least into later Lower Mississippian strata and possibly a little higher as evidenced by their occurrence in the Calciferous Sandstone series of Scotland. In the evaluation of the Devonian components of the Upper New Albany shale (Sanderson) flora we have shown that three of the four components previously identified are now reassigned and the fourth, *Callixylon*, is now known to have Lower Mississippian representatives. An examination of those genera with a more extensive Mississippian range or higher is, therefore, in order.

Lepidodendron is represented by a number of specimens. Two species have been described in a preliminary fashion, as already noted, and there is no reason to question the validity of the assignment to the genus. Several additional specimens that are outside the specific limits for those described are known and are to be treated in a later paper. *Lepidostrobus* specimens are quite infrequent in the collections. Two species have been described in considerable detail. The earliest known from the New Albany shale is *L. kentuckiensis* (originally *L. Fischeri*) which was found at Junction City, and completely described by Scott and Jeffrey in 1914. The other species has not been called to general attention inasmuch as it was a "weathered out" or "float" specimen. The original extensive description by Mathews (1940) indicated that it was from either the Upper Devonian Ohio shale or the Mississippian New Providence shale. It was compared with numerous other species of *Lepidostrobus* including *L. kentuckiensis* but no thought or stress was given to the fact that it might be another representative of the New Albany shale flora. However, we have examined the type material of this species, *Lepidostrobus noei*, and find that its preservation medium is not calcium carbonate as recorded (MATHEWS, 1940, p. 37) but it is calcium phosphate and is very similar, in fact indistinguishable, from other specimens of the phosphatized plant fossils from the New Albany shale. We have visited the region where the specimen was found (locality No. 13, TEXT-FIG. 7), in the vicinity of Paint Lick near Cartersville, Garrard County, Kentucky (originally misprinted as Gartersville, Gorrand Co., Kentucky, MATHEWS, 1940, p. 36), and are of the opinion that the specimen could be from an eastward extension of the Falling Run nodule zone of the Sanderson or its equivalent, possibly the Bedford formation. There is every reason to consider these two well-described species as valid early representatives of *Lepidostrobus* which ranges continuously up through the Permian.

Calamopitys, which was first described from the Cypridina shales of Saalfeld (*C. saturni*) by Unger (1856), has also been recorded from the Lydiennes horizon of France (*C. blayaci* Corsin, in BERTRAND, BOHM & CORSIN, 1935), and from the New Albany shale of Kentucky (*C. americana* Scott & Jeffrey and *C. foerstia* Read), both horizons being somewhat comparable to the Cypridina shale. It is also known from one Upper Mississippian species, *C. zonata*, of the Carboniferous Limestone of Ayrshire and an older species from the Calciferous Sandstone of Dumbartonshire, *C. radiata*. Two other closely related forms which have been transferred from *Calamopitys* to *Eristophyton* have the same general range. Two more species of close relationship to the *Eristophyton* type of Calamopityan stems are known from the Lower Carboniferous of Falkenberg, Silesia and from Balaton See, Hungary. Only one species recorded appears to be earlier than Lower Mississippian and this, from the Upper Devonian of New York, has been transferred to a new genus [*Sphenoxylon* (*C.*) *eupunctata* (Thomas) Read (1937)] which is believed to be closely related to the *Bilignea* group.

Lyginorachis is known from only two species outside the New Albany shale. The older of these, *L. Papilio* (Kidston) Scott, is from the Cement-stone group or older part of the Calciferous Sandstone series and is of near-comparable age to the New Albany. The other species, *L. Taitiana* Kidston, is somewhat younger, occurring in the lower part of the Upper Mississippian (Carboniferous Limestone).

Two more genera which possibly range stratigraphically higher than the New Albany or equivalent horizons are *Protocalamites* and *Stenomyelon*. *Protocalamites pettycurensis* (Scott) Lotsy, the genotype and the only species recorded outside the New Albany, is from the Calciferous Sandstone series of Pettycur, which is approximately the equivalent of the upper Kinderhook or lower Osage, both Lower Mississippian. *Stenomyelon* is known from two species (*C. tuedianum* Kidston and *C. tripartitum* Kidston, in Scott) from the Calciferous Sandstone series of Berwickshire, Scotland.

One species remains to be discussed of those showing range later than the New Albany shale. *Steloxylon* was originally described as a *Medullosa* by Goeppert and Stenzel but was later renamed *Steloxylon* (*M.*) *Ludwigii* by Solms in 1896. The material was found in some secondary deposits in the Permian of Siberia and thus it may be considerably older. Professor Paul Bertrand, in his study of the Cladoxylales of the Cypridina shale (1935), considered that at least one of the species of *Cladoxylon* originally described from the Cypridina shale is generically referable to the genus *Steloxylon*. Thus with three species of *Steloxylon* now known in the New Albany and Cypridina shales, and with the possible affinity of the genus to *Cladoxylon*, it is with reservation that we consider the range to extend to the Permian.

In summary, then, of the seven genera which are known to have younger representatives than those found in the Sanderson formation of the New Albany shale, two lycopods, *Lepidodendron* and *Lepidostrobus*, range through the strata at least as late as the Permian; two others, *Lyginorachis* and *Calamopitys* are known from some species in the Upper Mississippian as well as the large number from the Lower Mississippian equivalents; two more, *Protocalamites* and *Stenomyelon*, are limited to the Lower Carboniferous but may have a slightly later range than that exhibited by the New Albany; and the seventh genus, *Steloxylon* is now best known from specimens of the Upper Devonian-Lower Mississippian transition beds with one species, the genotype, of questionable Permian age.

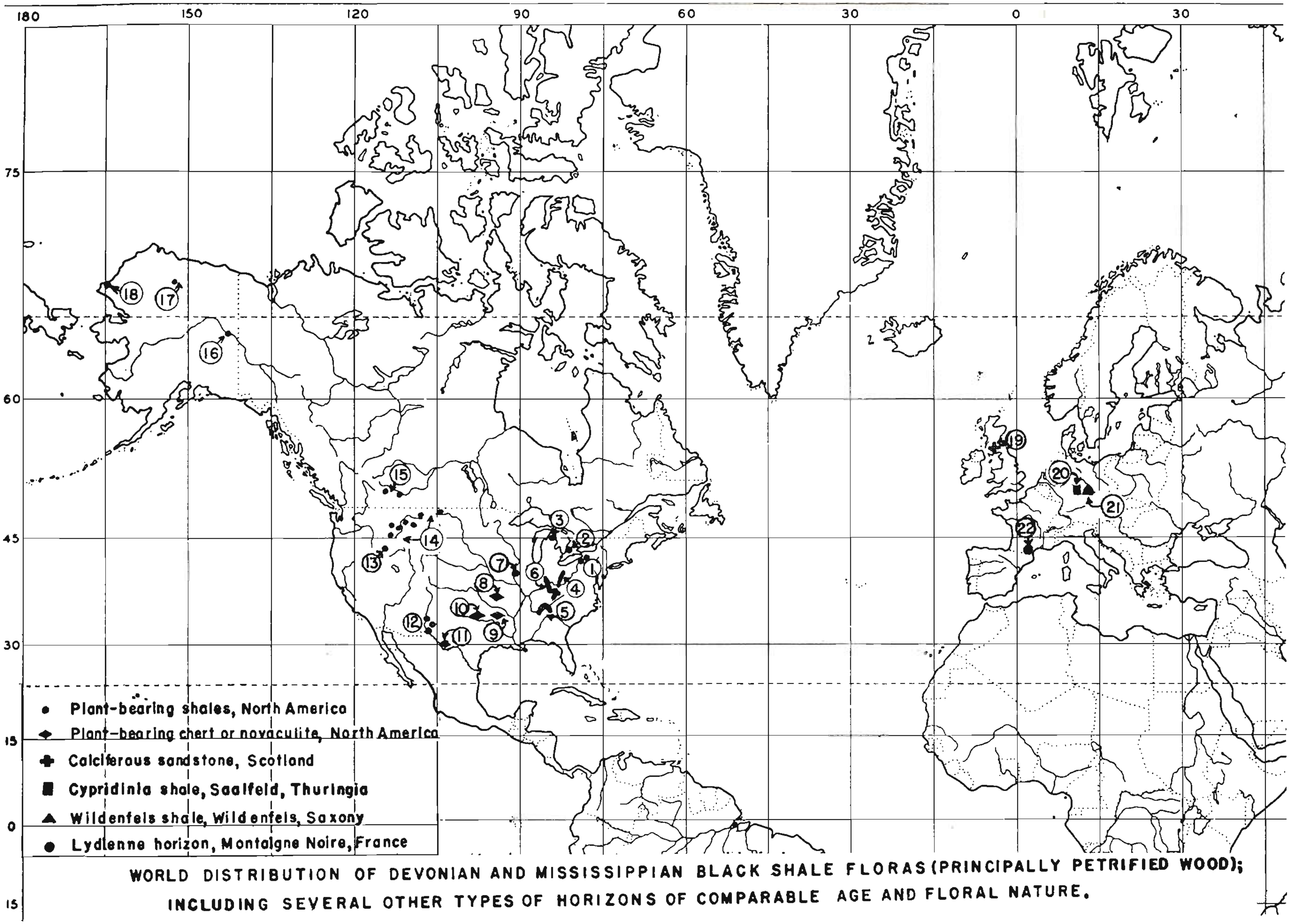
THE DISTINCTIVE NATURE OF THE UPPER NEW ALBANY SHALE FLORA

We have endeavoured to analyse the longer ranging components of the remarkable petrifaction flora which occurs in the upper part of the New Albany-Ohio black shale of the east-central Interior Region of United States in order to clarify the general character of the flora and determine the possible stratigraphic significance.

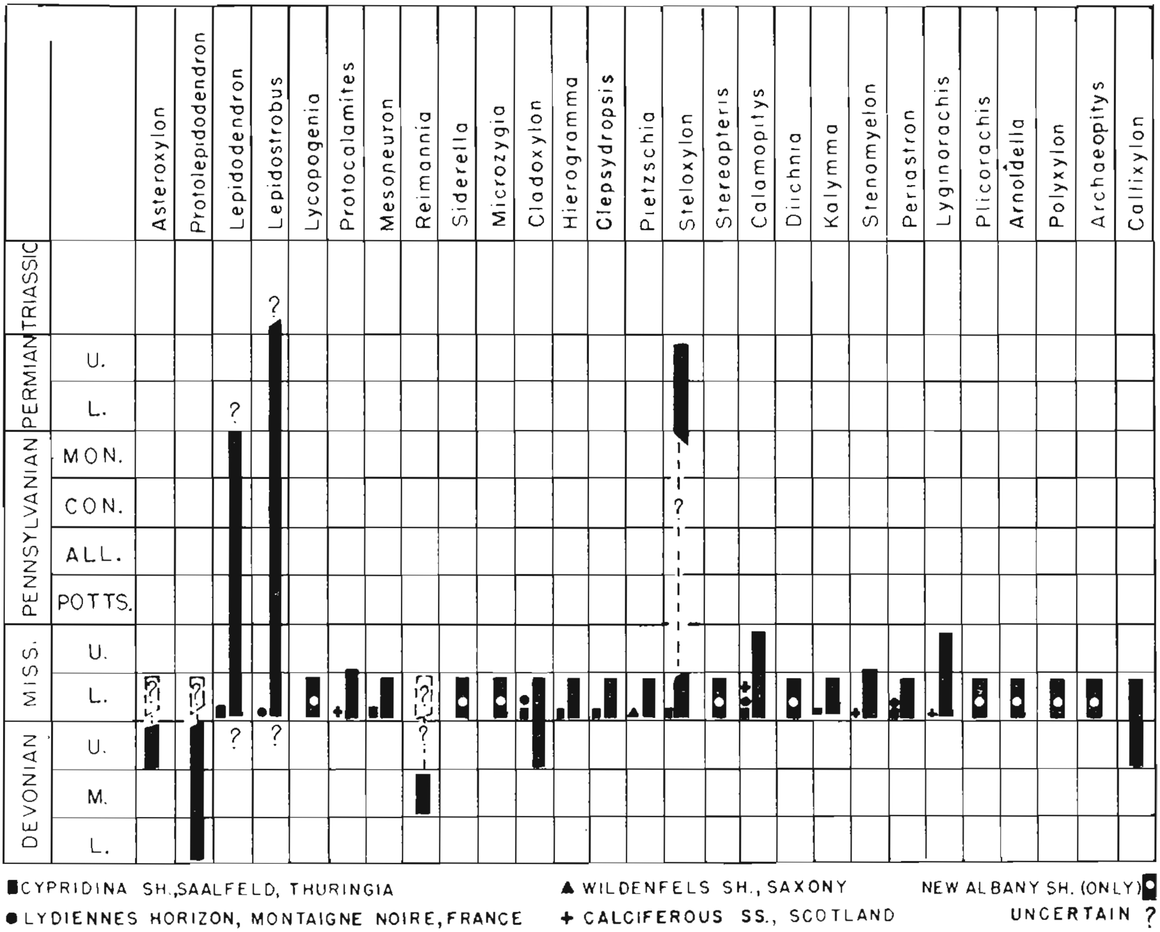
We have seen that of the five genera previously reported, which are generally known to range back into the Devonian, three of them, *Asteroxylon, Protolepidodendron*, and *Reimannia*, have been reassigned to other genera and, therefore, are not known to occur in these strata. The species which were included under these genera are for this reason of no stratigraphic significance, irrespective of their earlier presumed affinity to known Devonian genera, except in so far as their primitive characters suggest early stock. Of the two genera with proven Devonian representatives, *Cladoxylon*, which is known from the Upper Devonian by but a single specimen of a distinct species, is a representative common not only in the flora of the Mississippian portion of the black shales, but also of a number of other floras elsewhere of near-comparable or equivalent age. Only one genus, *Callixylon*, which occurs throughout the Upper Devonian, can be considered a true Devonian genus of all the 29 reported heretofore, and it includes at least several species now known also from the Lower Mississippian, including one from the type locality of one of the major divisions, the Kinderhookian series.

In a similar manner we have demonstrated that the flora is broadly differentiated from the better-known Mississippian flora though perhaps not quite so sharply. It may be useful to call attention to the fact that in every instance where the geologic range of a genus found in the New Albany shale extends on up into the later Mississippian or still higher strata, that genus is known to occur also at one or more localities of generally comparable age elsewhere (*see* TEXT-FIG. 14). Approximately two-thirds of all the genera reported are known only from the black shale flora, or in addition, from one or more of the following localities; the Cypridina shale, Saalfeld, Thuringia (locality No. 20, TEXT-FIG. 13); Wildenfels shale, Saxony (locality No. 21, TEXT-FIG. 13); Calciferous Sandstone, Scotland (locality No. 19, TEXT-FIG. 13); and the Lydiennes horizon, Montaigne-Noire, southern France (locality No. 23, TEXT-FIG. 13).

Of the four localities just mentioned, three of them, the Cypridina shale, the Wildenfels shale and the Lydiennes horizon, are quite similar in character of sediments and in overlapping of floral components. They are also comparable to the New Albany shale in these features. All of these and



TEXT-FIG. 13 — Distribution of Devonian and Mississippian black shale plant localities (principally petrified wood) including several other types of horizons of near-comparable age and flora. 1, New York-Pennsylvania ; Marcellus, *et seq.*, M. and U. Dev. 2, South-western Ontario ; Kettle Point sh., U. Dev. 3, Michigan ; Antrim sh., U. Dev.-L. Miss. 4, Ohio ; Ohio Black sh., U. Dev.-L. Miss. 5, Tennessee ; Chattanooga sh., L. Miss. 6, Indiana-Kentucky ; New Albany sh., U. Dev.-L. Miss. 7, Illinois ; Kinderhook grey sh., L. Miss. 8, Missouri ; Reeds Spring fm. (chert), L. Miss. but slightly younger (Osage) age. 9, Arkansas ; Arkansas novaculite, U. Dev. 10, Oklahoma ; Woodford chert, U. Dev. 11, Texas (Marathon district) ; Caballos chert, U. Dev. 12, New Mexico (Sacramento) and West Texas (Franklin and Hueco Mts.); Percha sh. (and upper dark sh. of Canutillo fm.), L. Miss. 13, Idaho ; Milligen sh., L. Miss. 14, Montana-North Dakota ; Three Forks sh. (Milligen and Exshaw), L. Miss. 15, Alberta ; Exshaw sh., L. Miss. 16, Yukon area, Alaska ; Nation river fm. (in part), L. Miss.-U. Dev. 17, Killik river area, Alaska ; Noatak fm., L. Miss. 18, Cape Lisburne area, Alaska ; Noatak fm., L. Miss. 19, Scotland-N.E. England ; Calciferous ss. (espec. Cement-stone Group), L. Miss. 20, Saalfeld, Thuringia ; Cypridina sh., U. Dev.-L. Miss. 21, Wildenfels, Saxony ; Wildenfels sh., U. Dev.-L. Miss. 22, Montaigne-Noire, Southern France ; Lydienne horizon, L.-M. Miss.



TEXT-FIG. 14 — Chart of the geologic range of the principal genera recorded from the upper part of the New Albany shale and the occurrence of these genera in near-comparable horizons elsewhere. *Asteroxylon*, *Protolepidodendron* and *Reimannia*, though previously reported from the black shales, have been reassigned and are not now recognized in the collections studied.

the New Albany included are of controversial age; in fact, in several instances the dating of one of these sediments has resulted in the similar dating of the others. When the Scott and Jeffrey report first appeared, and the sediments were presumed to be Mississippian in age by reason of the proximity to Mississippian strata identified on the basis of invertebrates ("at the base of the Waverley shale"), then the Saalfeld and Wildenfels beds were so identified.

Through the meritorious work of Guy Campbell, the Devonian-Mississippian transitional black shales of Indiana and Kentucky, and to a certain extent equivalent or near-equivalent black shales of Tennessee and Ohio, are now approximately dated. The principal flora is of Lower Mississippian age (Kinderhookian). Through the combined work of three French geologists, Joseph Blayac, Rodolphe Böhm and Gaston Delépine (1935) the age of the Lydiennes horizon is reasonably well established as Lower Viséan on a fauna of seven different species of goniatites, three of which are limited to the Lower Viséan and the remainder extend through more or less of the Upper Tournasien, and *Orthoceras*, phyllopodes, cirripédes and crinoids. This would be the equivalent of the Lower Meremacian strata of North

America which directly overlies the Osagean series. Therefore, the Lydiennes horizon appears to be somewhat younger than the New Albany shale. The genera of plants which are common to the New Albany and Lydiennes horizons may be quickly determined from Text-fig. 14. Because of the very close lithologic similarity of the Lydiennes horizon, with its phosphate nodules, to the Cypridina shale, and the similarity of the flora, analogies are drawn from that source for dating the floras of Thuringia and Saxony.

One horizon in America which has but three recorded species, two of which are in new genera, is the Reeds Spring formation of Lower Osagean age in south-western Missouri (locality No. 8, TEXT-FIG. 13). There is too little known of that flora to derive inter-regional or inter-continental correlations from it. The Calciferous Sandstone of Scotland is more nearly comparable to the Reeds Spring formation or other Osagean strata than to the slightly older New Albany shale, but there is considerable similarity of type of flora found in these lithologically dissimilar deposits.

This Lower Mississippian-New Albany shale flora and its counterparts elsewhere, thus, appear to constitute a flora unique in their restricted range through geologic time. It has some Devonian aspects but is not a true Devonian flora as we understand the Devonian. It is not Mississippian in the sense of being pre-Pennsylvanian. It cannot be said to inter-grade into either the earlier Devonian or the later Mississippian, for on the whole we know little of its progenitors or its progeny. It is a distinctive flora based upon diverse stems of little known plants. The nature of its leafy counterparts is virtually unknown. It is broad in its geographic distribution, restricted in its geologic range, varied in its composition, interesting in its relation to floras of somewhat comparable horizons of near-equivalent age elsewhere, and is certainly a remarkable flora requiring further exploration.

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