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NOTES ON THE LEPIDOCARPACEAE

BY

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James M. Schopf

Introduction

Members of the Lepidocarpaceae are characteristic of the Eur-American floral province and are known to be present in both the Lower and Upper Carboniferous. Both in western Europe and in America recent records have added to our knowledge of this plant family, and it is now possible to present a discusison of the classification and evolution of the groups included in the lepidocarp alliance. It is the purpose of this paper to call attention to some of the bio-characters[2] which appear to be important in distinguishing lepidocarp genera but which have not been given equal consideration by different authors, thereby leading to some ambiguities and conflicting conclusions. It is hoped that this review will lead to greater consistency of treatment and to more rapid progress in understanding the geological and biological history of this group of plants.

The writer wishes to acknowledge the help of Dr. J. Marvin Weller and thank him for critically reading the manuscript.

The Lepidocarp Family

The Lepidocarpaceae, like many other families of fossil plants, represent a group of indefinite taxonomic status. This family seems never to have been formally diagnosed, and hence its taxonomic validity has not been established beyond question — rather it has been a name defined through implications lent by the genera included in it. In the writer's opinion it comprises a group having undoubted natural affinity whose scope seems to be comparable to certain families of modern plants. The Lepidocarpaceae can be defined briefly as follows:

Ligulate lycopsid plants, of arboreous or arborescent habit, producing male and female fructifications separately (probably never in the same cone, nor in juxtaposition on fertile branches equivalent to cones). Female fructifications specialized so that individual sporophylls or parts of them have assumed the essential characters of seeds in each of which only one megaspore normally matures. Sporangium indehiscent in the sense that the seed megaspore is not expelled; seed megaspore exceedingly large and lacking the thick impervious type of spore coat that characterizes the megaspores of free-sporing lycopsids.

A rather sharp distinction should be made between the lepidocarp family

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2 A bio-character is considered to be a definable unitary feature that has hereditary significance.

(Lepidocarpaceae) and the other groups of Paleozoic lycopsids because the differences between lepidocarp fructifications and fructifications of all the free-sporing lycopsids appear to be valid criteria for at least family differentiation. The foregoing diagnosis of this family is, nevertheless, incomplete because definite knowledge of the vegetative characters is still lacking. It is hardly conceivable that the vegetative organs are wholly unrecognized in the fossil flora, but they are probably classified erroneously at present in some other family.

The writer suspects that plants classified as *Lepidophloios* Sternberg[3] may be vegetative correlatives of genera belonging in the Lepidocarpaceae. *Lepidophloios scoticus* Kidston is the only species of this genus whose fructification characters have been even partially ascertained. Its cones are borne on specialized branches, an advanced mode of fructification *not* characteristic of *Lepidostrobus* or lepidodendrids in general. Nothing whatever is known, however, of the spores produced by these cones. *L. scoticus* is restricted to the Lower Carboniferous, the cones being known from oil shales of the Calciferous Sandstone series in Scotland. At other localities and horizons the only evidence as to *Lepidophloios* fructifications still has to be deduced from association of disconnected fruiting structures. The lepidocarps, although they generally have passed unrecognized, appear to be among these associated types. In America *Lepidophloios* seems to be the only well represented group of lycopsids whose mode of fructification is so obscure. The lepidocarps, on the other hand, do not seem to have as plausible affinities with any other group based on vegetative characters.

The fact that the Lepidocarpaceae and *Lepidophloios* coincide in their time range, both being limited to the Carboniferous and both being reasonably well represented throughout these beds, is perhaps as definite a point of evidence as can be cited now. *Lepidophloios* aff. *L. laricinus* (Sternb.) Sternberg is a characteristic species found in roof shales over the Herrin (No. 6) coal which, in addition to the Mazon horizon, has also provided specimens assigned to *Lepidocarpon mazonense* Schopf. A form identified by Lesquereux as *Lepidophyllum auriculatum* (probably *Lepidocarpon*), was found at St. John (Perry County, Illinois, above No. 6 coal) closely associated with a species of *Lepidophloios* which Lesquereux (1870, p. 432, 439; 1880, p. 422, 450) identified by the same specific name. He considered that the two species probably were correlated. *Lepidophloios* ranges through the English Lanarkian (which includes the "Lower Coal Measures") and is characteristic of the Lower Carboniferous where it is associated with *Lepidocarpon* (Walton 1935; Walton, Wier & Leitsch 1938). Other occurrences need not be cited here but the apparent association of these fossils may be significant.

Correspondence that passed between the late Professor A. C. Noé and W. Hemingway of Derbyshire, England, concerning a shipment of sections sent

[3] Sternberg's original spelling of this name was "Lepidofloyos." There is a question whether the original spelling, or the now accepted "correction" of it should be used. I am indebted to Dr. F. C. MacKnight for calling this to my attention.

Prof. Noé in 1925 contains a significant statement regarding the relations between *Lepidophloios* and *Lepidocarpon*. Mr. Hemingway wrote:

> *Lepidocarpon "Lomaxi"* represents quite a group of seed-like bodies and cannot yet be separated in sections. *Lepidocarpon majus* [n. comb.!] has been found attached to stems of *Lepidophloios laricinus* and *Lepidocarpon lanceolatum* [n. comb.] to *Lepidophloios acerosus*. They are therefore the megasporocarps of *Lepidophloios*.

Mr. Hemingway also stated:

> *Lepidocarpon Lomaxi* represents the "seed" of *Lepidophloios*—they have been found attached. The so-called species probably represents the seeds of several species of *Lepidophloios*. *Lepidostrobus Oldhamius* also represents the microspore cones of *Lepidophloios* and embraces several species.

It may be that Mr. Hemingway had reference to the leaves at the tip of a vegetative branch of *L. acerosus* (L. & H.) Kidston (instead of *"L. laricinus"*) that Kidston (1893, pp. 553, 559) illusttated and compared with *Lepidophyllum majus* Brongniart, and to the lanceolate leaves Macfarlane (1883) associated with *Lepidophloios laricinus* (=*scoticus* Kidston). If so, these associations perhaps have value only as analogies. Mr. Hemingway, however, has evidently also noted the lepidocarp characters commonly associated with the *majus* type sporophyll, and others which supported an identification with *Lepidocarpon lomaxi*.

A few obvious lines of investigation suggest themselves for obtaining additional evidence. To judge by the earlier papers of Kidston and others the cones of *Lepidophloios scoticus* are not rare. Even though they all may be immature when intact, evidence of the spores should be obtainable from them upon maceration. An attempt should be made to obtain compression specimens of *Lepidocarpon* from the Calciferous Sandstone series where they are to be expected because of their common occurrence as petrifactions. Mr. Hemingway's suggestion that *Lepidocarpon lomaxi* is separable into more definite species deserves consideration, and if the *lomaxi* group is reinvestigated, evidence bearing on the relationship of *Lepidophloios* also should be sought. It is particularly important that the geological longevity of respective diagnostic biocharacters distinguishing the various intimately related species be investigated.

If the suggested correlation of the genus *Lepidophloios* with several lepidocarpaceous genera be eventually substantiated it need occasion no great surprise. In the main it may be taken to indicate that in this Carboniferous group, as in modern plant groups, reproductive organs in general are more responsive to evolutionary change than are the vegetative ones.

The oldest members of the lepidocarp family have been reported from the Calciferous Sandstone series of the Lower Carboniferous (Scott, 1900, 1901; also reported from Arran by Walton 1935, p. 318), and *Cystosporites* appears among the youngest members reported in Stephanian beds of Lower Silesia and the Saar district (recorded as *Triletes giganteus;* Zerndt, 1937, 1940). The family is well represented in America both in beds of Pottsville and Allegheny age. *Lepidocarpon* also has been reported from Calhoun coal balls (Fisher and Noé, 1939) of probable upper Conemaugh age (cf. Schopf, 1941). Diversification seems more apparent within this family in America than in the old

world. This may be explained, in part at least, by the fact that the best fossiliferous (coal ball) deposits in America are younger than those most studied in Europe, and these younger beds may contain representatives of the family at the apex of its geologic history.

The Genus Lepidocarpon

Lepidocarpon Scott, first recognized and defined about forty years ago, is the type genus of the Lepidocarpaceae. Scott's original diagnosis (Scott 1900, p. 309) is as follows:

> *Lepidocarpon*, gen. nov.—
>
> Strobilus, with the character of *Lepidostrobus*, but microsporangia and megasporangia each surrounded by an integument, growing up from the upper surface of the sporophyll. Megasporangium completely enclosed in the integument, except for a slit-like micropyle along the top. A single functional megaspore developed in each megasporangium. Sporophyll, together with the integumented megasporangium, detached entire from the strobilus, the whole forming a closed, seed-like, reproductive body.
>
> It is proposed to name the coal measures form *Lepidocarpon Lomaxi* and that from Burntisland *L. Wildianum*. Both were included by Williamson under his *Cardiocarpon anomalum*, which however, is quite different from the seed so named by Carruthers.

Scott also noted on page 307 that "the outer layer of the sporangial wall has the columnar or palisade-like structure characteristic of *Lepidostrobus;* it is lined by a more delicate inner layer which may be several cells thick."

In the diagnosis published with his more complete treatment of *Lepidocarpon* (1901), Scott omitted mention of the microsporangiate structures because he was more doubtful of their relationship than he had been previously. The main points of his later diagnosis are as follows:

(1) Strobilar habit—like *Lepidostrobus;*
(2) Integuments present when mature;
(3) Megasporangium entirely enclosed except for micropylar slit;
(4) A single functional seed megaspore nearly fills the sporangial cavity;
(5) Sporophyll became detached from the cone axis as a unit.

To these an additional point may be added from p. 304 of Scott's detailed description.

> The structure of the sporangium is however the same, as in its naked condition [e.g., in *Lepidostrobus*]. The wall has a superficial columnar layer, with a more delicate lining tissue within it. The cells of the columnar layer are often shorter and broader than in the non-integumented sporangium [of *Lepidoacrpon lomaxi*] owing no doubt to superficial extension of the wall; at other places, however, and especially at the apex where the narrow ridge of the sporangium fits into the micropylar opening, the structure is quite unchanged.

In defining *Lepidocarpon* the writer considers it advisable to follow Scott's generic interpretation rather carefully. The diagnosis provided by Scott in 1900 and slightly emended in 1901 may well be altered, however, so that it will reflect some of the additional observations made by various workers during the last forty years of sporadic study of this group of plants. It is now possible to refer compression and impression specimens to this genus and with the progressive elimination of non-biologic differences (resulting from differences of pres-

ervation) the classification of these fossil plants becomes more truly phyletic. Lack of diagnostic information due to vagaries of preservation will probably always make it necessary to recognize non-biological distinctions to some extent in scientific classification. *Lepidocarpon,* however, appears to be an example where these differences can be relegated to less than generic importance.

LEPIDOCARPON Scott (1900)

(Revised diagnosis)

A genus of ligulate lycopsid plants characterized by,

(1) *Strobilar habit of fructification;*
(2) *Sporophylls attached to cone axis as in Lepidostrobus;*
(3) *Sporophylls shed entire by disintegration of the cone axis;*
(4) *Seeds provided with a distinct integumentary organ;*
(5) *Integument, attached lateral to sporangium along pedicel, invests the sporangium closely and its two edges project ventrally above the seed body as a micropylar crest;*
(6) *Slit between the two membranes of the crest corresponding morphologically to a micropyle;*
(7) *Megasporangium large, indehiscent (fertile spore not shed), attached for the greater part of its length to the ventral midline of the pedicel;*
(8) *Outer wall of sporangium of prismatic or columnar cells, similar in structure to the sporangium wall of free-sporing lycopods;*
(9) *Intrasporangial tissue more persistent than in most free-sporing lycopsids;*
(10) *Seed megaspore relatively enormous (for lycopsids), spore coat with more or less fibrous texture and trilete apparatus at its proximal end (usually turned toward the anterior or distal end of the seed);*
(11) *Maturation of only one seed megaspore per sporophyll, derived from a single tetrad; abortive megaspores also evident.*

English Species of Lepidocarpon

The cone of the genotype species, *Lepidocarpon lomaxi* Scott, is medium sized (20-30 mm. diameter), of compact structure with sporophyll laminae long and strongly reflexed upwards. Toward the tip of each lamina the blade seems to have been membranous and impersistent but near the seed it was rather fleshy and is commonly well preserved. Mature seeds are fully integumented but the integument is frequently incomplete on immature specimens, and in this condition it is represented by fleshy cushions along both sides of the pedicel. The integument is presumed to have been formed last, late in ontogeny. A simple layer of columnar or prismatic cells, very similar to the prismatic layer of *Lepidostrobus,* covers the sporangium. Radial length of fruit is 8-14 mm., — tangential height through seed body 5-11 mm., — width at distal end of seed body 5-12 mm. This species occurs in the English "Lower Coal Measures." It has been reported in most coal seams of this age that have provided coal balls, and thus it must be considered a rather widespread and characteristic element of the upper Lanarkian flora.

Scott also described a second much older species, *L. wildianum,* from the Calciferous Sandstone at Pettycur that is somewhat smaller than *L. lomaxi,* but otherwise not readily distinguishable. The seed megaspore shows an "irregular reticulation" (Scott, 1901, p. 315) which in all likelihood is similar to the fibrous network composing the *Cystosporites* membrane. *L. wildianum* is doubtless a distinct species, and future studies will probably make known biological

characters by which it can be recognized, but at present its true distinguishing characters are not known. More thorough examination of Lanarkian forms will probably also result in additional species being recognized, as suggested by Scott and others who have examined many "Lower Coal Measures" specimens.

For convenience *L. lomaxi, L. wildianum,* and closely related but as yet undistinguished forms of Lower Carboniferous and Lanarkian age will be referred to as the *lomaxi group.* Because they possess certain characteristics reminiscent of those of free-sporing lycopsids and, in addition, because of their antecedent stratigraphic position relative to the American species, they are regarded as examples of the more primitive lepidocarp stock.

In 1914 Kidston described *Lepidocarpon westphalicum* from the Yorkian age ironstone deposits near Dudley. The type consists of an axis with scars of sporophylls previously shed and a central portion on which parts of about twenty attached sporophylls are visible. The cone is of compact construction and is preserved without crushing, but only surface features were observed and these are not all that might be desired The laminae may be of moderate length and appressed to the cone, judging from Kidston's Figs. 1, 3, 4, and 5, where they seem to appear in lengthwise fracture on both sides of the specimen. Kidston states that the "whole of the bracts have disappeared" and so the laminae, apparently seen, may be illusory. The laminae, however, may have been membranaceous distally, similar to those of *L. lomaxi* described by Scott. The particular feature that decided Kidston on the generic identification of this species was the sporangial integument, but he did not note a micropylar slit. So far as known the integument appears generally similar to that of *L. lomaxi.* Most of the sporangia have their disal ends exposed, and on many of these a small terminal irregularity appears which should be opposite the trilete apparatus of the seed megaspores inside them.[4] No remnants of the seed megaspores have been reported in *Lepidocarpon westphalicum* although they may be present. There are no very definite biological characters distinguishing *L. westphalicum* from members of the *lomaxi* group except for differences in size. The cone is about 15 mm. in diameter in contrast to 20-30 mm. for *L. lomaxi;* the sporangia are smaller and have a height-breadth ratio of 2½ to 1 whereas in *L. lomaxi* the ratio is slightly less than 2 to 1.

Records of American Lepidocarpaceae

Lepidocarpon was first reported in America by Noé (1931) in a list compiled from investigations by certain of his students. A discussion of this material was included in Miss Krick's (1932) report on seed-like fructifications from the Harrisburg (No.5) coal in Illinois. Later Fredda Reed (1936) described other isolated Lepidocarp sporophylls from the same source. The presumptive evidence that these specimens belong to *Lepidocarpon* is good, but it can not be considered entirely conclusive because the manner of pedicel

4 These may be the "smooth pits at the basal end" which Darrah (1941, p. 87) refers to as sporangial attachment marks but this interpretation is not indicated by Kidston's discussion.

attachment was not demonstrated in either case. The importance of such attachment was not then realized, and it is probable that the specimens studied by both of these authors were attached to a cone axis in the true *Lepidocarpon* fashion. Miss Reed has recently demonstrated such attachment for other Harrisburg specimens by means of an adequate series of tangential slices described at the 1939 meeting of the Paleobotanical Section. The importance of pedicel attachment in the lepidocarps is emphasized below in connection with the discussion of *Illiniocarpon*.

Both Noé and Krick identified their lepidocarp material as *Lepidocarpon lomaxi* Scott. This specific identification is doubtful, however, because the similarities mentioned by Krick concern chiefly the size of the seed body. Without supporting evidence this cannot be regarded as positive proof of specific identity. The histological details particularly must also be carefully considered. The Harrisburg material appears to be significantly younger than the "Lower Coal Measures" specimens studied by Scott.

The sporophylls described by Fredda Reed (1936) were not specifically identified. They appear to correspond with immature and abortive megasporangia such as Scott reported for *L. lomaxi*. However, the sporangium wall had a sclerotic rather than a prismatic external layer of cells. This may be a feature of considerable significance in lepidocarp evolution, inasmuch as it indicates the loss of a primitive character well represented in the lomaxi group.

The writer described two new species belonging to the Lepidocarpaceae in 1938 (Schopf, 1938a). One *(L. mazonense)* is a form common in the Mazon concretions above the Colchester (No. 2) coal in Grundy and Will counties which resembles in many respects the generalized type traditionally known as *Lepidophyllum majus*. Its reference to *Lepidocarpon* was definitely established although it is not certain that this species is distinct from earlier described but less adequately understood forms. *Lepidophyllum majus* itself is confused taxonomically because the type is a poor specimen with the seed body missing; it was originally designated *Filicites (Glossopteris) dubius* by Brongniart (1822), and its name was later changed in the Prodrome (1828, p. 87). It would probably be impossible to prove that the Mazon form is cospecific with the type, even if such were actually the case. Certainly some of the specimens referred to *L. majus* are *not* cospecific with *Lepidocarpon mazonense*, although there is no reason for believing them to be generically distinct. Probably Brongniart's species will pass into disuse because of the inconclusive nature of its type and the consequent doubt as to its accurate specific definition.

A brief description of a new type of lepidocarp seed was presented in the same publication (Schopf, 1938a). This differs significantly from the genus *Lepidocarpon* and a new generic name, *Illiniocarpon*, was given it. In transverse sections through certain parts of the seed body it closely resembles *Lepidocarpon*, but a qualitative and diagnostic difference appears in the manner of sporophyll attachment to the fertile branch. This distinction is commonly shown in longitudinal sections, and single transverse sections of either *Lepidocarpon* or *Illiniocarpon* cannot be counted on to provide conclusive evidence of

the distinction between the two genera. The individual sporophylls (not cones) of *Illiniocarpon* are properly described as *pedunculate,* and by modification of the pedicel and other changes these plants have lost the strobilar habit of fructification to a significant degree. The integumentary organ (which, as Scott emphasized, is *not* merely the upturned margin of sporophyll lamina) is more specialized, and the actual lamina is extended, broad, and doubtless served as a wing for dispersal of the fruit after it had been shed as a unit from the fertile branch. The laminae of some *Lepidocarpon* species also probably served this same function [e.g., *L. mazonense,* (?) *L. linearifolium* (Bassler)] and this may perhaps be regarded as a minor example of evolutionary parallelism in the two groups.

Numerous large fibrous sack-like bodies (seed megaspores) with trilete appartus at one end similar to those Zerndt (1930) described as *Triletes giganteus* have been obtained by the writer from maceration residues of coal. These seed megaspores are closely related to *Lepidocarpon mazonense* but because essential diagnostic characters can not be established and because these isolated seed megaspores appeared to be moderately generalized, it has seemed unwarranted to identify them with either of the two genera that had been previously recognized in the Lepidocarpaceae. Their characters, however, fully supported their reference to this family, and the genus *Cystosporites* was proposed for their reception (Schopf, 1938b). This genus may be entirely or only in part equivalent to the Lepidocarpaceae but it clearly exceeds the scope of other genera more adequately diagnosed on the basis of their sporophyll structure. Biologically it appears to overlap both of the established genera, and the isolated spores are thus classifiable with less precision than is possible where complete fruits are available, but for scientific reporting a name is none the less essential for them. It is incorrect to assume that *Cystoporites* is only the seed megaspore of *Lepidocarpon* (Darrah 1941, p. 89), because its relationship is definitely broader. The significant contribution afforded by the recognition of *Cystosporites* is that it shows best how geologically long lived and widespread the Lepidocarpaceae were in Carboniferous times (cf. Schopf 1938b; Zerndt, 1937, p. 68; 1940, p. 142). Not only is *Cystoporites* a practical generic designation of use in classification of these isolated seed megaspores, but it also indicates a group of natural affinity and certain biological significance. The delimitation of its natural affinity is in fact far more precise than a great many other generic groups commonly used in the classification of fossil plants. It should be recognized that the introduction of such a genus is not a "purely artificial method of classification" and that plants which have been classified as *Cystosporites* do not already possess any other properly assignable generic names.

In 1938 the writer discovered that the holotype of *Carpolithes corticosus* Lesquereux is clearly cospecific with a form previously discovered in the Mazon shale which he had interpreted as a variant of *L. mazonense.* Further study showed conclusively that Lesquereux' species was quite distinct from *L. mazonense.* Later, when Janssen's treatise on certain of the Lesquereux types was in preparation, the writer was invited to contribute a revision of this form,

and the species was transferred to the genus *Lepidocarpon* (Schopf, in Janssen, 1940). *Lepidocarpon corticosum* (Lesq.) Schopf is most closely related to *L. novaculeatum* and *L. robustum* both of which were transferred from Bassler's genus *Cantheliophorus*[5] which is discussed on a later page. An abortive megaspore from the original tetrad is present in its normal position near the anterior of the seed body in the holotype of *L. corticosum* in addition to the large fertile one. *L. mazonense* and *L. corticosum* furnish substantial proof that histological features are not essential for recognition of this genus, and in this respect Kidston's generic identification of *L. westphalicum* is confirmed.

Darrah has recently described a new species under the name of *Lepidocarpon glabrum* (1941). Although cellular detail is preserved in his specimen few characters were available for distinguishing this species and consequently its generic classification deserves more critical examination. This plant has seeds which consist (so far as the types at least are concerned) of a sporangium with well developed internal tissue surrounding the seed megaspore. No information as to the pedicel, lamina, or axial attachment of the complete sporophyll is provided nor is there any evidence of the integuments that characterize mature seeds of all other members of the genus.[6]

Illiniocarpon was distinguished from *Lepidocarpon* (1) because the sporophyll was pedunculate in one and normally situated on a strobilar axis in the other; (2) because in *Illiniocarpon* the integuments are separately vascularized posterior from the peduncle and are developed differently, being far more evaginate; (3) the sporophyll lamina in *Illiniocarpon* is straight and not reflexed as in *Lepidocarpon*. (4) Apparently correlated with this last character is a further specialization of the sporangium wall near the ligular region at the anterior end of the seed which has not yet been found in *Lepidocarpon*.

Lepidocarpon glabrum is inadequately known regarding (1) strobilar (compact, lax) or non-strobilar habit, (2) presence, absence, or nature of the true lepidocarp integument, and (3) character of the lamina. It cannot be positively identified with *Lepidocarpon* because these important diagnostic characters

5 The writer is not quite certain, that Bassler's *L. robustum* and *L. novaculeatum* are specifically distinct from each other or from *L. corticosum*. The relationship in any case is evidently very close. However there seems to be ample basis for specific discrimination between the other forms Bassler described. Nevertheless, the arrangement of plates and descriptive data is such that careful study of Bassler's paper is required in order to clearly establish the specific differences.

6 Darrah has described the external layer of the sporangial wall as the "integument." From a purely descriptive standpoint the term may be so used, but it is inadvisable because all other Lepidocarps have a distinct organ, called the *integument* by most writers, that is entirely separate from the megasporangium. Specimens of *Lepidocarpon glabrum*, do not now possess any integument of this sort. Whether the sporangia were originally integumented when the sporophyll was complete is unknown, although from Darrah's account it seems unlikely that they were.

Darrah also infers (op. cit. p. 95) that the sporangial wall of *Lepidocarpon* includes sclerotic "protective tissues." Scott's description of specimens of the *lomaxi* group do not support this conclusion and in only one form (aside from *L. glabrum*) has sporangial wall sclerenchyma appeared (Reed, 1936).

have not been observed. Characters other than those of the seed megaspores are shown, however, so that the species is classifiable with more precision than is possible when only isolated seed megaspores are present. Positive differences are exhibited which may have significance of more than specific value. The seeds of *L. glabrum* are mature, and the individual sporangia (evidently *not entire sporophylls*) have been shed. There is no previously described species of recognized lepidocarps in which shedding of mature sporangia apart from their integument was possible. The number of isolated sporangia which Darrah records indicates decisively that shedding of the individual sporangia was a normal occurrence in this species. The only mark reported on the mature sporangial seed (which in this species is equivalent only to a ripened ovule — without the additional sporophyll parts possessed by seeds of other lepidocarps) is at the point of its attachment to a pedicel or pedicel-equivalent. Mature megasporangia (seeds) of *Lepidocarpon* or *Illiniocarpon* were not so separated from their sclerous integuments. Abortive and immature sporophylls of *L. lomaxi* commonly lack the integument, but *functional* seeds are equipped with them. Typical *Lepidocarpon* sporangia are not sclerotic but have walls whose prismatic layer is strikingly similar to that of *Lepidostrobus*. Their preservation appears primarily to result from the efficient protection of the integumentary organ.

Darrah's illustrations and description of the wall of *L. glabrum* sporangia (seeds) thus suggest that they differ considerably from sporangia of the *lomaxi* group. The unintegumented sporophylls described by Fredda Reed also are noteworthy in their lack of a prismatic sporangial coat. Similar sporangia of the *lomaxi* group described by Scott possess a somewhat thicker sporangial wall tissue than the integumented forms, but the prismatic layer apparently is developed typically in all. *Illiniocarpon* shows a different type of modification in the sporangial wall. In the lower anterior region the wall is thick, and although the prismatic layer is easily recognized it is considerably modified and possesses larger cells with undulant walls (cf. Fig. 9; Schopf, 1938a). The anterior prongs show rather typical prismatic (columnar) structure but the posterior part of the sporangium wall is more delicate and can hardly be considered prismatic. In fact it resembles the epidermal layer of a well protected ovule. This is what would be expected if the lepidocarp sporangium were modified in accordance with the degree of exposure and protection afforded by the integument. The adaxial ("posterior") part of the seed body in *Illiniocarpon* is well enclosed and probably was somewhat better protected than in *Lepidocarpon*, but the anterior part of the seed (facing the lamina) may have been more exposed because the sporophyll lamina was not reflexed upwards around it. Evidently the character of the sporangium wall deserves more thorough study in the lepidocarps because it probably reflects the type of seminal modification.

Intrasporangial tissue within the dermal layer in *Lepidocarpon glabrum* also appears to be a significant character. In the unintegumented sporangia of the *lomaxi* group the sporangial tissue is consistently thicker than in the integumented seeds, and this was explained on physiological-ecological grounds. In

L. glabrum, however, this tissue is so much more developed that the character has probably become hereditary. Concordantly the seed megaspore of *L. glabrum* also occupies proportionally less space in the sporangium than in those of other lepidocarps. This appears to be true, at least in so far as the sections shown on Darrah's Plate II are typical of the species. In the *lomaxi* group and in *Illiniocarpon* there is no comparable development of the "nutritive" tissue.

Darrah's species therefore probably lacks diagnostic features which assuredly would place it in the genus *Lepidocarpon* and in addition shows other modifications which indicate considerable divergence from that group. Because of the lack of a prismatic palisade layer, Fredda Reed's specimens may occupy an intermediate position between *Lepidocarpon* Scott and Darrah's divergent type, *L. glabrum.* It is important that the divergent characters of the latter be recognized, and the writer regards them, in conjunction with the lack of information in other particulars, as conclusively indicating a need for *L. glabrum,* at least, being classified under a distinct generic name. However, there is no basis for doubting that its relationship is definitely with the Lepidocarpaceae.

Darrah's comparison of *Lepidocarpon glabrum* with *Lepidocystis* is highly significant, and it may be that this ambiguous and poorly defined group will be clad with useful biological meaning after all. The *Lepidocarpon* described by Reed from Harrisburg coal balls, which also lacks a prismatic sporangial wall, is not integumented and may not be abnormal as Reed supposed. It also might be classified with this divergent lepidocarp group having "lepidocystoid" characters. However, there appears to be considerable disharmony among specimens which have been labeled "*Lepidocystis*" in the past. Few of them have been shown to possess spores in place, but those specimens in which spores have been recognized are clearly referable to the free-sporing lycopods, probably to the Lepidodendraceae. It is altogether possible (in fact, probable, in view of *L. glabrum*) that many specimens which do not appear to have spores, actually enclose unrecognized seed megaspores of the cystosporean type. These specimens would necessarily belong in the Lepidocarpaceae. The availability of the name *Lepidocystis* for lepidocarp species with this latter character evidently must be determined by restudy of the genotype which is *Lepidocystis pectinatus* Lesquereux.[7]

The conclusion that there are at least two divergent branches of the primitive integumented lepidocarp stock in the American Pennsylvanian is plausible. One branch shows greater specialization of the integuments and other structures and is represented by *Illiniocarpon.* The other branch is represented by *L. glabrum* in which the seeds have been subject to a different kind of specialization involving, probably, loss of the integument. Presumably the less specialized true *Lepidocarpon* type coexisted with both of the more specialized lineages, but the ancestry of the latter groups may be sought among the more primitive lepidocarps that geologically antedate them.

7 The holotype of this species is listed in Lesquereux' "Coal Flora" as No. 423 of the Lacoe collection, now in the U. S. National Museum at Washington, D.C.

Cantheliophorus and Lepidocarpon

A substantial addition to the Lepidocarpaceae was made by Harvey Bassler (1919) in his description of twelve species under the generic name of *Cantheliophorus,* although he misinterpreted the structure of his material.[8] Bassler recognized that his species were highly specialized and his statement (1919, p. 97) that "members of a group with structure as intricate and diverse as this will have high stratigraphic value if treated with great systematic refinement" seems more than ever warranted.

Lepidocarp sporophylls in shale are preserved differently, depending upon whether the plane of rest is determined by a broad lamina or by the form of the seed body itself. The seed body generally is higher than broad, and if the lamina forms too narrow an appendage, the height of the seed body is most likely to parallel the bedding. All of Basser's species seem to have been preserved in this position and those he illustrates are compressed parallel to the organic longitudinal plane. Thus they appear much different from most specimens of *Lepidostrobophyllum* in which the laminal breadth more consistently parallels the bedding planes. Although characters of size and proportion of sporophyll laminae are generally considered to be of specific importance, they probably lack generic significance.

The features Bassler considered to be unique in *Cantheliophorus* were, (1) two sac-like sporangia per sporophyll, borne on short sporangiophoric stalks; (2) a plate of sterile sporophyll tissue ascending from the ventral midline of the pedicel and to which the sporangiophores were attached laterally and distally. The structures ilustrated, however, do not support this morphologic interpretation of them. They are instead more satisfactorily explained by comparison with *Lepidocarpon,* and according to this interpretation they comply entirely with the essential diagnostic characters of that genus. Bassler has not presented evidence proving the existence of two sac-like bodies on any single sporophyll — he has not shown the "median" plate to be other than the compressed form of the *Lepidocarpon* integument.

The "sporangia" of *Cantheliophorus* agree precisely with seed megaspores of the lepidocarps, and they must be interpreted in this light. It is understandable how Bassler and others failed to note this resemblance because no lepidocarp megaspores had been isolated previously and they are remarkable objects quite different from the common free-sporing forms in general outline and size. Nevertheless the *single* fertile lepidocarp seed megaspore is clearly recognizable from Bassler's figures for most of the *Cantheliophorus* species. They agree in habit with those the writer has illustrated from *Lepidocarpon corticosum* (Schopf 1938a, 1938b, 1940) and also with seed megaspores obtained from *L. mazonense.* The agreement with seed megaspores Bocheński (1936) obtained

8 Bassler's descriptions are given in terms of his hypothetical interpretation of the sporophylls, but there is no reason for preserving this terminology because his specimens are easily described by other terms that were previously and still are in good technical usage.

from lepidocarp cones in the Lower Silesian coal field is just as striking.[9]

This striking agreement is by no means limited to the seed megaspores but continues in remarkable detail to all other portions of the lepidocarp sporophylls and is perhaps best illustrated by comparison with a larger species of *Lepidocarpon* (as yet undescribed) represented by numerous examples in the Illinois Survey collections from near Wyoming Hill (Muscatine County) Iowa. The latter specimens are compressed in a dark fissile shale and thus entirely agree with Bassler's in mode of preservation, even showing similar lengthwise folding of the sporophyll laminae. Where the shale is intact these sporophylls contain well preserved lepidocarp seed megaspores. On mild macerative treatment the fibrous megaspores of cystosporean type are easily isolated; they show the characteristic trilete commissure at the apex and are associated with abortive tetrad members. The "plate" Bassler described is represented in these specimens (just as it is shown in his illustrations of *Cantheliophorus*) by a very definite micropylar crest which is similar to that unmistakably shown in *Lepidocarpon mazonense*. The coaly and external integumentary impression surfaces of Wyoming Hill shale specimens agree absolutely with Bassler's figures and characterization (*op. cit.*, p. 79) as "usually granulose to the unaided eye and minutely rugulose-bullate under the lens." Observation under the Greenough microscope shows the surface rugosity is due to the type of sclerotic cells present on integumentary surfaces. *Lepidocarpon corticosum* (Lesq.) although preserved a little differently also is similar to Bassler's material in many respects.

Such precise agreement and the absence of any conflict in generic characters indicate that species of *Cantheliophorus* Bassler must be referred to the older genus *Lepidocarpon* Scott, and this has been proposed in an earlier publication by the writer (Schopf, in Janssen, 1940). The geologic time range of *Cantheliophorus* species is entirely that of *Lepidocarpon*, and there is no reason for concluding that *Cantheliophorus* is in any biological way distinct or distinguishable from Scott's genus.

Darrah (1941, p. 89) recently has stated, that "a number of sporophylls of the *Cantheliophorus* type . . . bear many megaspores of the familiar 'Triletes' type" and on this account he does not accept the synonymic reference of *Cantheliophorus* to *Lepidocarpon*. It is difficult to understand how any sporophyll bearing numerous Triletes-type megaspores can justifiably be assigned to *Cantheliophorus* or to *Lepidocarpon*. Bassler found none in the examination of a large suite of specimens, and in failing to definitely recognize spores of any sort, concluded (*op. cit.*, p. 81) that the plants probably were homosporous. It would seem that no matter what apparent similarities there may be between the superficial form of the sporophylls, no free-sporing plant can be assigned to *Lepidocarpon* (or to *Cantheliophorus* which is in complete synony-

9 Bocheński assigned these specimens to *Lepidostrobus* and compared the spores with *Triletes giganteus* Zerndt and *Sporites varius* Wicher, but his specimens also must be identified with *Lepidocarpon*. There is a great difference between the spores he isolated from these specimens and the free-sporing *Triletes* and *Sporites* genotypes, and lepidocarp megaspores now may best be compared with *Cystosporites*, a genus which, in part, was proposed for reception of Zerndt's and Wicher's species.

my with it). The presence of free-sporing megaspores is a character which not only excludes a plant from these genera but also places it beyond the family limits of the Lepidocarpaceae.

Summary

Family characteristics of the Lepidocarpaceae are given. It is suggested that *Lepidophloios* is a possible lepidocarp representative showing the vegetative features of these plants. The diagnostic characteristics of *Lepidocarpon* are reviewed, and the generic diagnosis is rephrased. The essential distinctions Scott recognized in establishing the genus are entirely valid and should be adhered to rather closely.

The genera and species discussed include *Lepidocarpon lomaxi*, the genotype of the type genus for the family, *L. wildianum*, and *L. westphalicum*, all known from English sources. Records of *Lepidocarpon* in America are reviewed with respect to the characters used in their identification. Points which distinguish *Illiniocarpon* from *Lepidocarpon* are enumerated and the relationship of these genera with the less precisely defined genus *Cystosporites* is restated. Attention is called to divergent characteristics of *Lepidocarpon glabrum* from Iowa, and possibly also represented to a lesser degree in another lepidocarp from Harrisburg coal balls, which would seem to set them apart from the genus *Lepidocarpon*. Reasons are given for referring the American forms named *Cantheliophorus* to *Lepidocarpon*.

American lepidocarps in particular are worthy of intensive study because the diversified forms present a particularly interesting problem of plant evolution. In the following tabulation of the Lepidocarpaceae each species is listed according to its approximate age. The larger number of forms occurring in post-Pottsville beds supports the conclusion that diversification was more rapid during that time.

Post-Pottsville (Post-Westphalian B)

Lepidocarpon mazonense Schopf
L. corticosum (Lesq.)
L. novaculeatum (Bassler)
L. robustum (Bassler)
L. subulatum (Bassler)
L. linearifolium (Lesq.)
L. sicatum (Bassler)—
(also in upper Pottsville)
Illiniocarpon cadyi Schopf
Cystosporites breretonensis Schopf
C. giganteus (Zerndt)
Lepidocarpon lomaxi (?)
(Noé, Krick, Fisher & Noé)
L. sp. Reed
L. (?) *glabrum* Darrah

Pottsville
(Mid-Lanarkian to Staffordian; Mid-Namurian to Westphalian C)

Lepidocarpon westphalicum Kidston
L. lomaxi Scott
L. waldenburgense (Potonié)
Cystosporites giganteus (Zerndt)
Lepidocarpon grande (Bassler)
L. ensiferum (Bassler)
L. pugiatum (Bassler)
L. iowense Hoskins & Cross
(of Pottsville age*)

* For description see Amer. Midl. Nat. **25**(3):543, 1941. (Horizon information fide Cross June 9, 1941.)

Lower Carboniferous (Mississippian, in part)

Lepidocarpon mirabile (Nathorst) *Lepidocarpon riparium* (Nathorst)
Lepidocarpon wildianum Scott—(Calciferous Sandstone).

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