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CONTRIBUTIONS TO PALEONTOLOGY

GEOLOGICAL SURVEY PROFESSIONAL PAPER 523-E

Tinsleya texana, *the first known example of seed-bearing foliage in the family Callipterideae, is described; biotic relationships and evolutionary implications are discussed*

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ABSTRACT

Tinsleya texana, n. gen. and sp., is described on the basis of a large suite of plant fossils from the upper part of the Lueders Limestone of the Wichita Group (Lower Permian) near Lake Kemp in Baylor County, Tex.

In general aspect, *Tinsleya* is similar to the genus *Callipteris* but differs in details of venation and polymorphism of the frond. *Tinsleya* is further unique in having seeds attached either apically or marginally on a few pinnules. This occurrence is the first known of seeds of any member of the Callipterideae and establishes the group as truly pteridospermous. This type of fruiting habit may eventually lend important fossil support to the classical theory of derivation of the angiospermous carpel.

INTRODUCTION

Permian plant assemblages have been recorded from many geographic localities in both the Northern and Southern Hemispheres but principally from the southern areas constituting Gondwana land. The southern floras are generally very limited in numbers of species and have commonly been regarded as depauperate as the result of having existed under postglacial conditions. They are largely dominated by the ubiquitous genus *Glossopteris*, whose problematical fructifications have attracted considerable interest during the past 15 years. (See Plumstead, 1952.)

In contrast with the southern floras, the northern contemporary assemblages show considerably more taxonomic diversity and are generally in greater need of intensive investigation. Important among the northern Permian floras are the callipterids (Callipterideae of Doubinger, 1956, p. 98), a highly variable and presumably artificial complex of pteridophyllous plants that are stratigraphically restricted to rocks of late Paleozoic age but which are broadly distributed geographically. The species *Callipteris conferta* (Sternberg) Brongniart has attracted more interest than any other single entity in this group, inasmuch as it makes its first appearance in rocks of earliest Permian age and, consequently, has been accepted as an important index fossil.

Callipteris and related taxa are generally regarded as members of the pteridosperm complex, but prior to the present paper no factual evidence has been presented to substantiate an ovuliferous reproductive habit. Indeed, the evidence bearing on the reproduction of *Callipteris* has been limited until now to Remy's (1953) description of *Thuringia callipteroides* from the Permian (Lower Rotliegende) coal-bearing strata near Crock, Thuringia, in Eastern Germany, and to Roselt's (1962) more recent discovery, also from the Lower Rotliegende of Thuringia, of organically connected male fructifications to which he applied the name *Callipterianthus arnhardti*. *Thuringia* was described as a synangial fructification at least 28 mm long and about 3.5 mm broad. It consists of several sporangia embedded in a solid groundmass of sterile tissue and contains winged spores about 50μ in diameter. Preservation of the material permitted investigation of epidermal features, and, on the basis of epidermal similarities and association, Remy suggested that *Thuringia* is in fact the male fructification of *Callipteris conferta*. Although Remy's interpretation seems reasonable, the organic connection between fructification and foliage remains to be demonstrated.

Roselt's material, *Callipterianthus*, consists of a single frond fragment bearing both sterile and fertile penultimate pinnules, so there is no doubt as to their relationship. The sterile parts are of the deeply dissected sphenopterid type, similar to *Callipteris scheibei* Gothan, *C. oxydata* (Göppert) Zeiller, or *C. naumanni* (Gutbier) Sterzel. As no epidermal comparisons were possible because of incomplete preservation, positive identification was precluded, but Roselt speculated that *Callipterianthus* was ascribable to *Callipteris nau-*

manni. The penultimate fertile pinnae are somewhat longer than the sterile ones and have rather flexuose axes bearing undivided to twice-divided fertile "trusses." The fructifications consist usually of five, or in some six or seven, terminal groups of microsporangia, 2–2.5 mm long, which apparently dehisced by slits along the inner surfaces of the sporangial walls. The microspores are round to oval, having dimensions of 20μ–24μ by 16μ–18μ.

The present paper is based on a large assemblage of fragmentary foliar compressions and impressions of a *Callipteris*-like plant having extremely variable foliar characteristics. Most of the fragments are sterile, but a few specimens demonstrate the attachment of large fertile-appearing structures that are interpreted here as evidence of the female reproductive organs. These plants occur with a few other taxa, principally walchian conifers. A brief announcement of the discovery of this material was published in 1963 (U.S. Geol. Survey, 1963), while the study of *Tinsleya* was in a very preliminary stage. The most significant specimens were found subsequently, during the fall field season of 1963. In view of its apparent dominance in this florule and its significant bearing on the matter of reproductive habits among the Callipterideae, however, this plant—*Tinsleya*, new genus—is regarded as of sufficient importance to warrant separate description at this time.

ACKNOWLEDGMENTS

I was assisted in the field during the 1957, 1961, and 1963 seasons by Arthur D. Watt, U.S. Geological Survey. Our thanks are due to Mr. Fred Parkey, general manager of Wichita County Water Improvement District No. 2, who granted permission to collect on Lake Kemp grounds, where the material discussed in this paper was found.

SOURCE OF MATERIAL

The *Tinsleya* material was accumulated during four collecting trips—in 1955, 1957, 1961, and 1963. It has been found at only one locality thus far and represents at least 75 percent of the specimens obtained from this particular site, where it occurs in association with a sparse assemblage of walchian conifers, a gigantopterid and a few other pteridophylls. The productive outcrop is approximately 6 miles north of Mabelle, in Baylor County, Tex. It is reached by following U.S. Highway 183–283 north from Mabelle to a point 0.4 mile south of the highway bridge under which the Wichita River flows eastward from the spillway of Lake Kemp. At this point one sees a conspicuous exposure of predominantly tan sedimentary rocks in a low east-facing bluff about 125 yards west of the highway; this is the plant-bearing site. As exposed at this outcrop, the

sequence consists of approximately 20 feet of siltstone and sandstone, mostly thin bedded with variable fissility, ranging in color from white to gray, bluish gray, or tan and having considerable limonitic streaking. The section is capped by a limestone bed that is light gray in color, ranges from 2 to 3½ feet in thickness, and contains minor amounts of sand. This bed is the only conspicuous limestone in the vicinity of the plant beds and doubtless is the unit mapped by Garrett, Lloyd, and Laskey (1930) as the Mabelle Limestone of Romer (1928). This fossiliferous site will be referred to here as the Lake Kemp locality (USGS paleobotany loc. 10,000).

The exposure was originally created by a roadcut, and the old roadbed itself is still evident at the bottom of the bluff. Although finely comminuted plant debris is scattered sparsely through the entire sequence below the limestone unit, the best preserved plant material was found in a 1-foot unit of tan and bluish-gray siltstone, the base of which is about 5 feet above the old roadbed. The beds in approximately the lower half of the section show minor angular unconformities and discordant bedding planes that suggest a channel-fill type of deposition. Associated with and above the main plant-bearing strata are a number of thin bone beds that contain fragmentary remains of a fresh-water fauna of small amphibians and paleoniscoid fishes. These beds and the presence of land-plant fossils indicate that the rock sequence at this locality represents a deltaic depositional environment in keeping with the generally accepted interpretations of the Permian rocks of this area.

AGE OF MATERIAL

The geology of Baylor County has not been mapped recently, or in detail. The only county geologic map available (Garrett, Lloyd, and Laskey, 1930) is based exclusively on surface exposures of a few limestone units, most of which are not named. The stratigraphic position of the Lake Kemp strata relative to Romer's Mabelle Limestone, however, places the plant beds at a level slightly above the middle of the Lueders Formation (usage of Garrett, Lloyd, and Laskey, 1930). Romer's geologic map of north-central Texas (1958, facing p. 178) does not differentiate between the Lueders and the underlying Clyde Formation, but nonetheless it substantiates a high position in the Lueders for the Lake Kemp plant beds. Thus the plants occur near the middle of the lower Permian which, according to Kummel (1961, p. 570–571) and Dutro (1961), is equivalent to the Artinskian interval of the Ural section. In terms of the mid-European section, the Lueders Limestone (of Leonard? age) would fall within the limits of the Tholey beds (Kummel, 1961, p. 572–573).

PREVIOUS STUDIES

A short list of fossil-plant species from a lower Lueders locality approximately 3 miles south of the Lake Kemp locality was published by Read (1943, p. 484), but inasmuch as Read's paper was primarily an analysis of the depositional environments of the outcrops involved in his study, the paleobotanical aspects were touched upon only cursorily. Otherwise, the plant content of the Lueders Limestone has not been treated in publication.

Fossil plants from other nearby exposures in Baylor County have, however, been more completely described. The Belle Plains Formation, slightly older than the Clyde Formation, provided the material on which White's (1912) important paper on *Gigantopteris* was based. The same strata yielded the first known Permian specimens of *Discinites* (Mamay, .1954). Farther to the southeast in Young County, the Moran Formation of Wolfcamp (Sakmarian equivalent) age produced a novel form of ovuliferous neuropteroid foliage described by Mamay (1960) as *Padgettia readi*.

DESCRIPTION

GENERAL

Most of the *Tinsleya* specimens consist of detached incomplete penultimate pinnae. The collection, however, contains a few larger more complete specimens which demonstrate that *Tinsleya* produced large compound fronds of at least bipinnate architecture; it is likely that the fronds were, in fact, tripinnate. The largest fertile specimen (pl. 1, fig. 4) obviously represents the terminal part of a frond and consists of a terminal pinna and four laterals; although the two basal laterals at the lower left cannot be shown to be connected to the main rachis, their positions relative to the latter are strongly suggestive of an original connection. This specimen measures 19.5 cm from the tip of the terminal pinnules to the broken base of the rachis. A larger but sterile specimen is shown on plate 3; this specimen is nearly 24 cm long and consists of a penultimate rachis with parts of 14 pinnae attached.

Penultimate rachises are relatively stout, reaching an observed maximum of 1 cm in width and averaging about 0.5 cm in most specimens. Ultimate rachises depart decurrently at angles ranging from about 30° (pl. 1, fig. 4) to 60° (pl. 2, fig. 3); none, however, approach a right angle of departure from the penultimate rachis. The rachises lack any distinguishing features such as glands or ornamentation.

FOLIAR LAMINAE

The pinnules vary considerably in size, shape, and margination, as shown on plates 1–3. Observation of many specimens showing transitional pinnule form,

however, shows that these pinnules all represent the same plant and that a fairly high degree of foliar polymorphism is present in *Tinsleya*. Some pinnules, for example, show a length-width ratio of only 2:1, whereas others, such as those shown on plate 1, figure 4, are much narrower and have length-width ratios of 4:1 or 5:1. The broadest pinnules in the collection are 12 mm broad and 24 mm long; others reach lengths of as much as 40 mm, and the narrowest specimens are only 2.5 mm wide. Notwithstanding this variability, all the pinnules observed thus far demonstrate the relatively broad basal attachment to the rachis, the gracefully decurrent departure (generally at an angle of about 45°), and the proximally directed curvature of the lamina that contribute toward morphological characterization of the *jutieri*-type of the *Callipteris* complex. The specimens shown on plate 2, figure 3, are particularly reminiscent of *C. jutieri*, as illustrated by Doubinger (1956, pl. 6, figs. 1, 1a).

Most of the pinnules are entire margined and obovate in outline (pl. 2, fig. 3), but marginal lobation and incision occur in varying degrees. All the pinnules of the specimens shown on plate 2, figure 3, are entire margined with rounded or nearly rounded tips. On plate 2, figure 2, the basal pinnule at the left is entire margined whereas the succeeding pinnule has a definite sinus at the median part of the tip, as though marginal growth had been arrested abruptly during ontogeny. (See also fig. 1B.)

A slightly more pronounced degree of marginal lobation is shown on plate 2, figure 4, where pinnules at the left side of the illustrated pinna bear shallow apical sinuses that divide the tips of the lamina into three or four bluntly rounded lobes. Much deeper incisions, resulting in long, relatively narrow linear lobes that arise usually from the basal-proximal areas of the pinnules are shown on plate 1, figure 4, a part of which is shown enlarged on plate 1, figure 2. This trend toward pinnatifid margination of *Tinsleya* pinnules seems to be expressed most acutely by the specimen shown on plate 1, figure 5. Here several pinnules are generally irregularly pinnatifid along the whole of their margins; thus some pinnules have as many as seven or eight lobes. This advanced degree of lobation approaches the condition characteristic of such species as *C. bibractensis* Zeiller and *C. lyratifolia* Goeppert (compare pl. 1, fig. 5 with Doubinger, 1956, figs. 9 and 10). These species, known principally from European deposits, have deeply and generally regularly pinnatifid pinnules that seem to separate them as a group from forms such as *C. conferta*, where the margins are entire. Doubinger (1956, p. 100) has presented a phylogenetic scheme in which depth of foliar incision or lobation apparently reflects proportionate degrees of evolutionary advancement. If the

lobate type is to be considered as having been derived from the entire-margined type, then one would expect to find forms in which transitional marginations are combined; *Tinsleya* might logically be construed as representing such a form.

A foliar feature of primary importance in distinguishing the Callipterideae from other pteridophyllous forms is found in the presence of subsidiary or rachial pinnules that arise directly from the penultimate rachises in the spaces intermediate between the successive pinna rachises. Although much of the *Tinsleya* material available for this study consists only of detached pinnae, the collection contains a fairly large number of specimens consisting of penultimate rachises with pinnae attached. Several of these rachises clearly show the attachment of rachial pinnules, and the callipteroid nature of *Tinsleya* is thus established.

Rachial pinnules are illustrated on plate 1, figure 1, and plate 2, figures 1 and 3. The specimen shown on plate 1, figure 1, consists of a fragment of a very stout penultimate rachis, to which two pinnae are attached, one at either side; the basal part of a third pinna departs to the left side of the specimen at about the middle of the upper margin of the photograph. Directly below this pinna fragment is shown the greater part of a rachial pinnule, the upper (distal) edge of which is partly confluent with the base of the pinna rachis. Three additional rachial pinnules are attached to this specimen.

The fertile specimen shown on plate 2, figure 1, has several rachial pinnules attached, which are somewhat larger than those shown on plate 1, figure 1; these, however, are rather fragmentary and do not show spatial relations satisfactorily. On plate 2, figure 3, however, the larger of the two frond fragments (trending toward the upper right of the photograph) bears several rachial pinnules; the one most clearly shown appears near the basal end of the penultimate rachis and extends toward the top of the photograph.

Rachial pinnules are opposite to alternate, depending on the relative positions of insertion of the ultimate pinnules between which they arise. Most commonly they arise singly and are approximately the same size and shape as the pinnules of the ultimate pinnae above and below. Examples are present where two discrete rachials originate from the space between two successive ultimate pinna rachises, but in such places proximity to the apical end of a penultimate rachis is usually accompanied by increasing confluence of multiple rachials. This confluence may be so marked that the penultimate rachis is virtually completely winged in its apical region, and laminar tissue extends without interruption from one pinna to the next. This feature is well illustrated on plate 3.

The strong tendency toward formation of subsidiary laminar outgrowths in *Tinsleya* apparently extends to the ultimate possible level of development; this point is illustrated by the pinna shown on plate 1, figure 5. Here are seen several pinnulets, or secondary pinnules, arising from the ultimate pinna rachis between successive pinnules. These, of course, are to be regarded as the morphological homologs of the rachial pinnules discussed in the preceding paragraphs; furthermore, their presence implies a need for caution in interpreting the rank of foliar appendages among the callipterids.

VENATION

Callipterid foliar venation is typically pinnate, with a usually pronounced midrib giving off secondary veins that may or may not divide dichotomously before reaching the pinnule margin. A few accessory veins that arise directly from the ultimate rachis may also enter the base of the pinnule. These features are particularly characteristic of callipterid forms having large relatively undissected "alethopteroid" pinnules, such as occur in *Callipteris conferta*. (See Doubinger, 1956, fig. 6.)

Although *Tinsleya* resembles a typical "alethopteroid" form of *Callipteris* in most of its foliar features, it shows a marked tendency toward the *Odontopteris* type of open venation. The vascular system of *Odontopteris* pinnules characteristically lacks a pronounced midvein; instead, in most species it has several independent veins entering the lamina directly from the ultimate rachis. These veins usually divide dichotomously from one to three times before reaching the pinnule margin. In *Odontopteris minor* Brongniárt there is a tendency toward formation of a midrib, but species referable to *Odontopteris* predominantly lack this character.

The ultimate venation in *Tinsleya* is generally not well preserved, but its features are shown remarkably well in several specimens (fig. 1), and thus there is no reason for hesitancy in presenting its description on the basis of the material on hand.

From four to eight thin veins arise from the ultimate rachis and enter the base of the pinnule. These veins depart from the rachis with a gentle decurrence equal to that of the lamina and usually are evenly spaced and approximately equal in strength. The veins extend entirely to the margins of the pinnules; most terminate in the rounded pinnule apices, but some end in either the adrachial or abrachial margins of the lamina.[1] The veins are either simple or forked; some

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[1] The terms "adrachial" and "abrachial" are introduced here in a sense analogous to the commonly used terms "adaxial" and "abaxial" because of the absence here of a midrib that would separate the pinnules into two well-defined virtually equal linear divisions. "Adrachial," then, refers to the approximate linear half of the pinnule that creates an acute angle with the rachis, whereas "abrachial" refers to the opposite half.
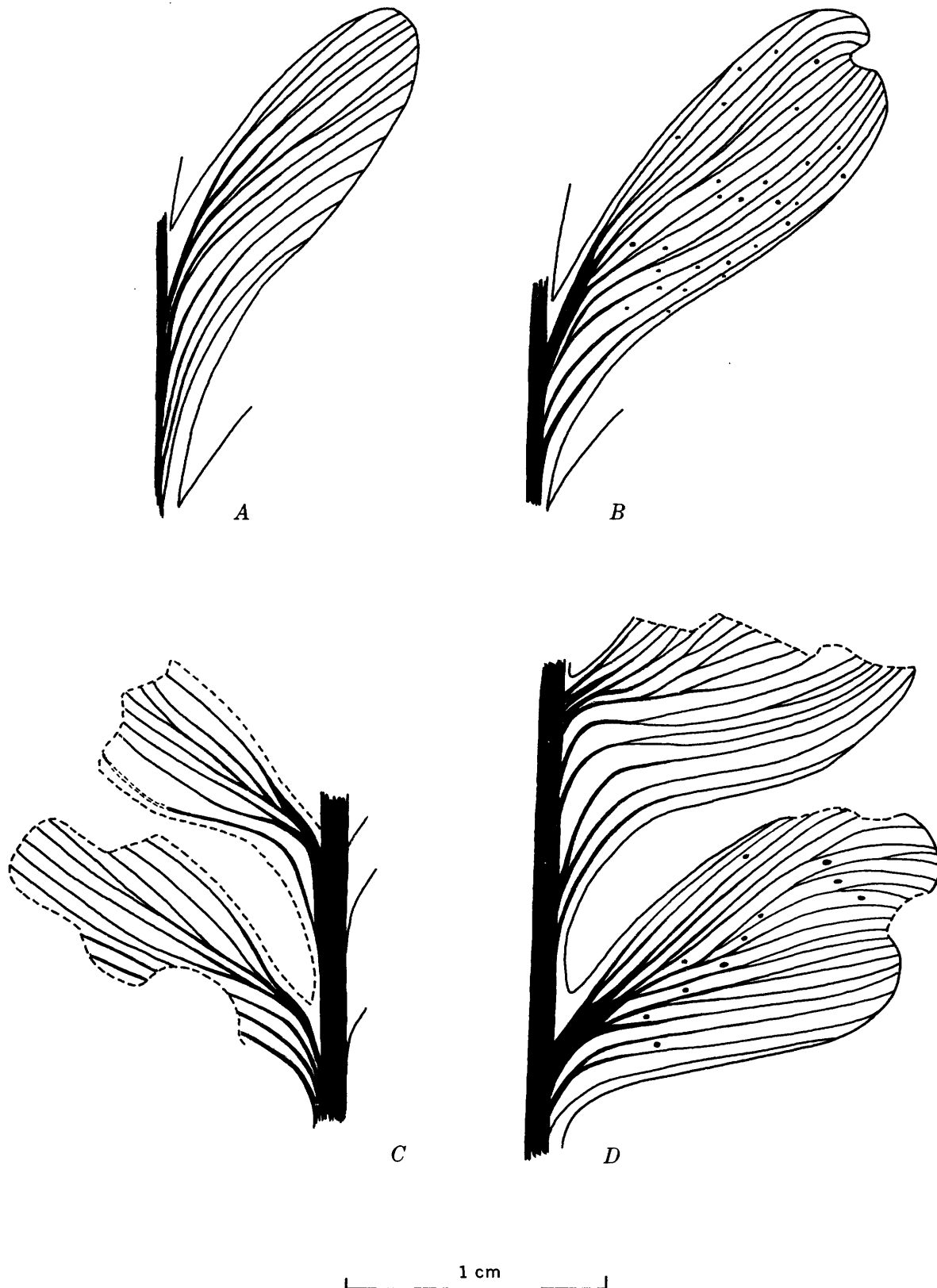
1 cm

FIGURE 1.—Variation in venation of *Tinsleya* pinnules, showing tendency toward unequal development of the veins. Drawings adapted from USNM specimens as follows: *A*, 42565; *B*, 42559b; *C*, 42564; *D*, 42563. Black dots on *B* and *D* represent probable remains of glandular structures.

individuals divide three or four times during their extent. Thus a pinnule that receives only four or five veins from the rachis may produce as many as 18 or 20 vein termini at its tip.

All the veins of a given pinnule do not necessarily divide at equal intervals or rates. Rather, it is more usual for the basalmost one or two veins not to divide at all; dichotomies occur mostly among the veins that enter the lamina toward the adrachial margin. Thus, even though there is a virtually equal spacing of veins at the pinnule bases, the concentration of veins becomes greater adrachially than abrachially, as the tip of the pinnule is approached. This feature of the venation is shown in figure 1.

The drawings in figure 1 also illustrate a striking degree of variability in the character of the ultimate venation. In some pinnules one or more of the veins are slightly more robust than the others as they enter the base of the lamina (fig. 1A; upper pinnule in fig. 1D). Other pinnules show a more pronounced differential in relative thickness of the veins (figs. 1B, C), and in a few specimens one of the veins is approximately equivalent in thickness to the vascular strand of the ultimate rachis from which it originates (lower pinnule in fig. 1D). The thicker veins persist as such for only a relatively short distance into the lamina, beyond which they divide into several less robust strands, which in turn dichotomize one to three times to provide the greater part of the vascularization of the pinnule. Because the thicker veins invariably enter the pinnule well toward the adrachial edge at its base, pinnules with uneven development of basal venation always have the greatest concentration of veins in their adrachial areas.

Unequal development of the veins has not been observed in the rachial pinnules.

REPRODUCTIVE STRUCTURES

Three specimens of *Tinsleya* (fig. 2; pl. 1, figs. 2, 4, 6; pl. 2, fig. 1) are of considerable morphologic interest in that they bear on their pinnules large specialized structures of apparently reproductive nature; a fourth specimen (pl. 2, fig. 4) has certain characteristics that are suggestive of immature forms of the same structures.

Near the apex of one of the distal pinnae of the holotype (pl. 1, fig. 4), one of the pinnules at the right is seen to bear a single urn-shaped structure, which is imbedded basally in the lamina of the tip of the pinnule but extends out beyond it; this structure is shown enlarged on plate 1, figure 2. As a matter of convenience and with no morphological implications intended at this point, this and other similar structures to be discussed here will be referred to as the "seeds."

This particular seed is 15 mm long and 8 mm wide at its broadest point, about one-third of the distance away from its rounded base. Apically the specimen gently tapers, diminishing to a width of only 3 mm. Its apical end terminates in three lobate projections, each about 1.0 mm long and slightly less than 0.5 mm wide at the tip. The overall attitude of the seed coincides with the graceful decurrence of the parent pinnule, which on its lower margin bears two long, narrow foliar lobes; one of the latter originates near the base of and seems to "subtend" the seed.

Although the preservation of the pinnule and its seed is insufficiently good for observation of minute details, there can be no doubt as to the original organic continuity between the two, or that the base of the seed was indeed imbedded in the tip of the lamina. Further, even though some of the fusinized film representing the original organic constituency of the plant was removed from the surface of the specimen when the matrix was split, ample evidence still remains, in the form of a much thicker coaly film, that the seed itself was originally thicker and bulkier than the lamina of the parent pinnule. There is also a distinct suggestion in the specimen that the seed received a substantially concentrated vascular supply from the pinna rachis. Careful examination of the pinnule, as shown on plate 1, figure 2, shows a dark—albeit not sharply delineated—fairly broad line of coalification extending from the pinna rachis, traversing the length of the pinnule, and entering the base of the seed; there it flares out to attain a breadth of approximately half that of the seed. Individual veins are difficult to discern in this pinnule, but the presence of this median area of apparently increased coalification is indicative of an increased concentration of vascular strands, as would be necessary to supply the additional physiological demands of a terminal seed or other type of propagule.

A second fertile specimen is illustrated on plate 2, figure 1. This specimen is noteworthy in that it shows evidence of attachment of at least seven seeds. This number of seeds borne on a relatively small frond fragment suggests a foliar dimorphism in *Tinsleya*, the fertile function being ordinarily restricted to a limited proportion of the foliage.

So far as can be seen, all the seeds present on this specimen are imbedded in the adrachial areas of the pinnules and protrude in the direction of the apex of the frond. Apical extensions are quite prominent in some of the seeds, particularly those at the lower left and upper left of the specimen. These further demonstrate a roughly urnlike shape and a constricted neck, whereas the seeds at the lower left and upper right of the photograph show lobate apices similar to that seen in plate 1, figure 2. (See also fig. 2.) The largest seeds
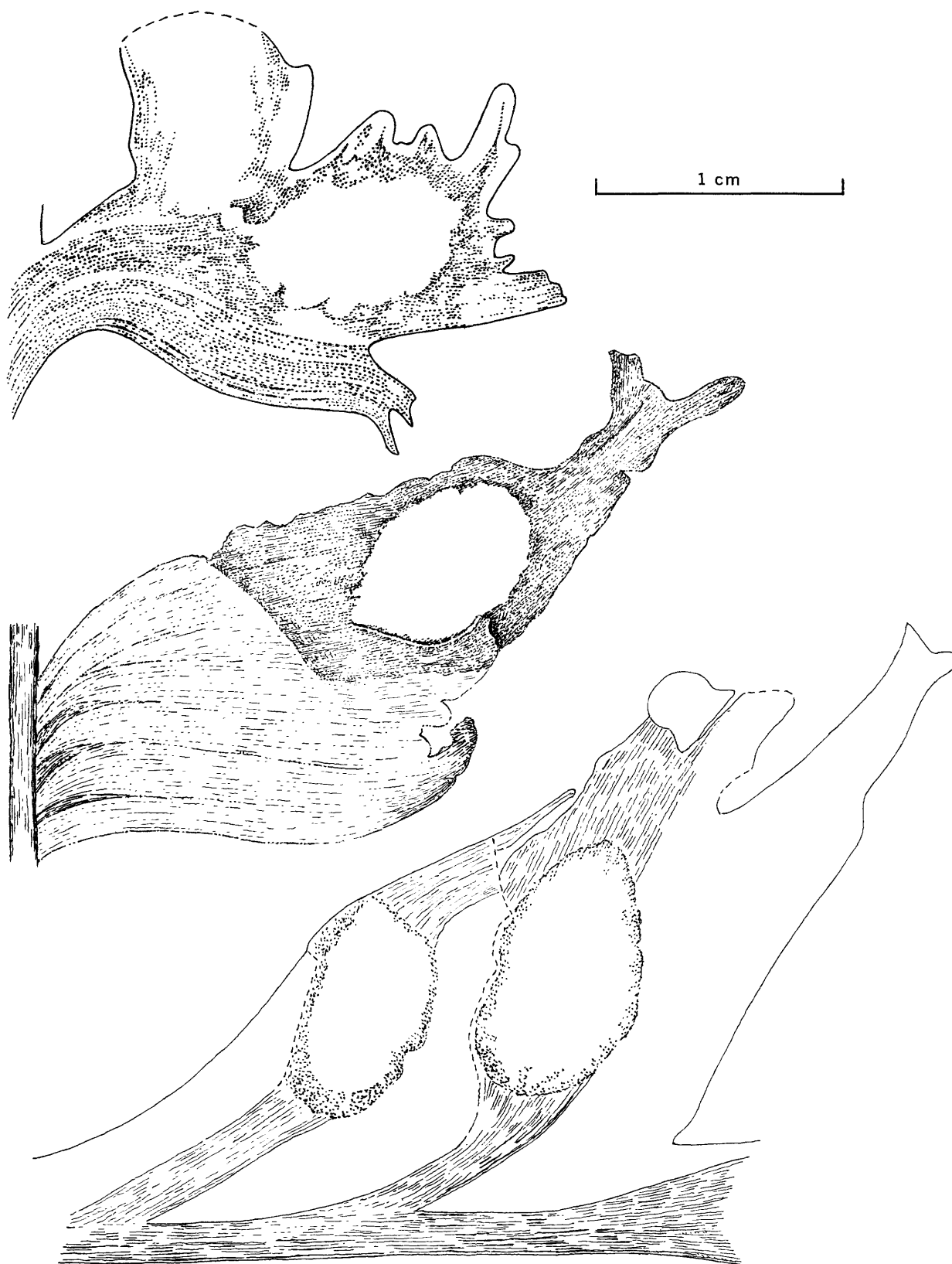
1 cm

FIGURE 2.—Seeds of *Tinsleya*, showing relationship to pinnules and apical lobation of investitures. Unshaded ovoid
areas apparently represent the originally bulky central parts of the seeds comparable to the specimen shown on
plate 1, figure 6. Urnlike shape of the investiture is best shown in drawing in center. Specimens depicted in
bottom and top drawings apparently bore two seeds each, but details are poorly preserved. All drawings adapted
from parts of USNM 42558. (See pl. 2, fig. 1.)

on this specimen are nearly 2.0 cm long and approximately 0.8 cm wide.

A third fertile specimen is shown twice actual size on plate 1, figure 6. It consists of only one detached pinnule bearing a single apical seed which, like that shown on plate 1, figure 2, is "subtended" by a narrow extension of the lamina. The ovoid seed is 8 mm long and 5 mm wide at its broadest point. Its apex is rather sharply truncated. This shape may represent the original form of the seed or it may be due to faulty preservation, inasmuch as careful excavation of both counterparts revealed no apical lobations such as are present in other seed specimens. Even though it may be an incomplete specimen, this seed is important in that it demonstrates a considerable thickness relative to that of the lamina. The coalified residue of the seed is nearly 1.0 mm thick in places, whereas the thickness of that of the supporting lamina is negligible. These relative amounts of coalification of parts (lamina versus seed) strengthen the interpretation suggested by the holotype (pl. 1, fig. 2), that is, that the structures discussed here were originally of much more substance than the supporting foliar laminae and in all likelihood were of a propagative nature.

One other specimen is available that may be interpreted as an ovuliferous frond part; it is shown on plate 2, figure 4. Even though the physical evidence of organic differentiation in this specimen is vaguely preserved and limited to small surface depressions and small patches of slightly heavier carbonaceous films, the positions of these features are such that they lend a certain amount of support to an interpretation of *Tinsleya* as a plant with ovuliferous fronds.

The fourth specimen consists of an incomplete ultimate pinna, 7 cm long, having parts of seven pinnules on the right side and an equal number on the left. Of the pinnules on the right, the three basal ones are incomplete and show no notable characteristics that might be interpreted as evidence of fruiting structures, but the two next higher pinnules each have in the medial areas of their apices a small ovoid depression, partly covered with a fusinized film of carbon, suggesting as in other specimens, the original presence of a bulky ovoid body embedded in the apex of the pinnules. Counting next from the bottom of the left side of the specimen, pinnules 2, 3, 4, and 6 each have in approximately the medial part of the pinnule apex a small dark area, elongate parallel to the length of the pinnule and created by a slightly thickened film of fusinized carbon. The consistent placement of these coalified areas and ovoid depressions—both in relation to the pinnule apices and to the positions of the larger structures described on the three previously discussed specimens—suggests that in

this specimen we may be dealing with an early ontogenetic phase of development of the seeds of *Tinsleya*.

The matrix from the Lake Kemp fossil locality contains no cuticularized material such as leaf epidermis or spore coats. Spore analyses showed samples of this matrix to be barren (R. A. Scott, written commun., 1963) as are most plant-bearing sedimentary rocks from the Permian of north Texas. Had megaspore membranes been preserved and observable in the structures described as seeds in the preceding paragraphs, there would be little doubt as to their true morphologic nature. However, the absence of megaspore membranes in this material need not necessarily invalidate the interpretation of these large bulky bodies on the foliage of *Tinsleya* as ovuliferous structures. Certain aspects of these fossils that weigh heavily in favor of such an interpretation in spite of the incomplete preservation are discussed in succeeding pages.

MORPHOLOGICAL INTERPRETATIONS

An interpretation of the obviously specialized foliage-borne reproductive structures of *Tinsleya* as evidence of bona fide seeds may not meet with universal acceptance among botanists—particularly those who adhere strictly to morphological definitions—because it is not possible to demonstrate the presence in these structures of either megaspore membranes or embryos. The evidence discussed here is partly circumstantial, but in presenting my views it should be stated at the outset that the entire concept of the existence of true seeds in the Paleozoic phanerogamous assemblages is likewise based partly on circumstantial evidence.

A seed is defined by plant morphologists as a "matured ovule," and consequently the presence of an embryo is a technical requisite to the classification of an organ as a seed. It is a well-known, broadly discussed, and perennially enigmatic fact, however, that until now not one indisputable embryo has been recognized in a Paleozoic "seed." This circumstance has given rise to the often debated concept of the "prephanerogams" (Emberger, 1944, p. 269), in which the existence of seeds in the Paleozoic is denied. Paleozoic seeds commonly contain megaspore membranes, so they at least fulfill the basic requirements for classification as ovules. Furthermore, many of the Paleozoic seeds are extremely well preserved as petrifactions, such as those found in the abundant coal balls from Carboniferous coal seams in Europe, Great Britain, the United States, and the Soviet Union. These seeds have been investigated in detail, and some (*Physostoma, Conostoma, Lagenostoma,* and *Pachytesta*, as examples) are known to have had extremely complex and specialized anatomical devices, such as micropyles, pollen chambers, and plinths, in the apical regions. Such characteristics are doubt-

less structural adaptations for the phanerogamous process of pollination, and, but for the absence of demonstrable embryos, they eminently distinguish the organs as true seeds.

The literature dealing with Paleozoic seeds is extensive, and the notion that seed-bearing plants (the cordaiteans and pteridosperms) were conspicuous elements in the Paleozoic flora is generally accepted; it is reflected in all modern classifications of fossil woody plants except that of Emberger. Arnold (1948) thoroughly discussed the subject of Paleozoic seeds and the absence of visible embryos, giving particular attention to the times of fertilization and shedding of the seeds. He arrived at the well-taken conclusion (p. 463) that "It therefore seems unduly dogmatic and arbitrary to exclude from the seed category these ripened ovules that occur in such copious quantities in the rocks."

A brief review, based on acceptance of Arnold's philosophy regarding the phanerogamous nature of Paleozoic seeds, of the various positions and modes in which they were borne on the parent plant seems appropriate at this point, apropos of interpretation of *Tinsleya* and its fructifications.

The seed-bearing organs of the Paleozoic cordaiteans and early conifers were all generally conelike structures that need not be considered here. The pteridosperms, however, showed a variety of seed-bearing habits that appears to entail more than one evolutionary trend and suggests a complex set of evolutionary relationships.

Halle (1929, p. 18–22) reviewed the seed-bearing habits of certain Paleozoic plants in which organic connection of seeds to foliage was known. He demonstrated a striking series of modification of seed position in which lower Upper Carboniferous seeds were terminal on reduced foliar segments (*Lyginopteris oldhamia* Binney; *Aneimites fertilis* White), whereas some seeds were terminal on ordinary pinnules in the middle Upper Carboniferous (*Neuropteris heterophylla* Brongniart; *N. obliqua* Brongniart). The trend toward decreased heterophylly and increased proximity of seed to lamina was continued by the upper Upper Carboniferous *Pecopteris pluckeneti* Schlotheim, in which the seeds were borne marginally on nearly normal pinnules. The migration of seed position was culminated during the Permian in such plants as *Alethopteris norinii* Halle, *Sphenopteris tenuis* Schenk, and *Emplectopteris triangularis* Halle, in which the seeds were attached directly to the surfaces of unreduced foliar segments or, as in *Alethopteris norinii*, to the rachis.

Subsequent to Halle's important publication, other examples of seed-bearing foliage have been described from upper Paleozoic rocks. On the basis of one large specimen from the upper Stephanian near Decazeville, France, Doubinger and Vetter (1950) described a seed-bearing odontopterid plant; they named it *Odontopteris Bourranensis*. The plant bore small seeds, 5–7 mm long and 2–3 mm wide, which were attached by short pedicels to the bases of the pinnules in "axillary" positions.

Kon'no (1950) erected the genus *Shirakiopteris* on the basis of seed-bearing foliage from the middle Permian beds of the Pen-hsi-hu coal fields of Manchuria. The fronds bore small cupulate seeds on the lower surfaces of slightly reduced pinnules. The cupules are shallow structures with pointed marginal lobes.

The upper Paleozoic rocks of the United States have yielded two additional examples of seed-bearing pteridospermous foliage—*Spermopteris* Cridland and Morris (1960) and *Padgettia* Mamay (1960). The *Spermopteris* material [type species *S. coriacea* (Goeppert) Cridland and Morris] was collected from the Ireland Sandstone Member of the Upper Pennsylvania (Virgil) Lawrence Formation in Douglas County, Kans. It consists of fertile leaves that would be referable to the form genus *Taeniopteris* in the sterile condition. The leaves bear a row of apparently platyspermic seeds on each side of the midvein, the seeds being oriented perpendicularly to the midvein. The seeds are apically notched and seem to resemble isolated seeds known as *Diceratosperma carpenteriana* Andrews.

Padgettia readi Mamay was found in the material in the Lower Permian (Wolfcamp) Moran Formation of Young County, Tex. It consists of many neuropterid pinnules, some of which contain one to several seeds arranged parallel to the midribs and apparently embedded within the tissues of the pinnules; the apices of the seeds were truncated exactly at the pinnule margins.

In spite of the unconventional morphological aspects of the various seed-bearing habits briefly discussed above, significant evidence continues to accumulate in support of Halle's ideas on the evolution of the pteridospermous seed position in the late Paleozoic. The fact that seeds were produced directly on the foliar lamina has been established by recorded fossil occurrences and has lost much of its original bizarreness in the eyes of the paleobotanist. In view of this and other evidence, then, I have no hesitation in regarding the foliar inclusions of *Tinsleya* as seeds. In further support of this interpretation the following points are set forth:

1. The previously discovered evidence of fructifications among plants of the *Callipteris* alliance is distinctly indicative of pteridospermous microsporangiate structures rather than fern sporangia.
2. The structures on *Tinsleya* are too large for fern sporangia and totally unlike any organs known to be pteridospermous microsporangiate fructifications. Rather, they are of a size and shape comparable to any number of Paleozoic seeds.

3. No evidence has been found in the Paleozoic of vegetative propagules among the ferns with which the *Tinsleya* seeds might be compared.

4. One specimen of *Tinsleya* (pl. 1, fig. 2) clearly shows apical lobations that resemble apical structures in other Paleozoic seeds. Leisman (1964) has demonstrated a fine example of apical tentaculation in *Physostoma calcaratum*, a seed from the Middle Pennsylvanian of Kansas. In compressed form, such a seed apex could bear a significant resemblance to the apex of this *Tinsleya* seed. It cannot be stated, of course, whether the urnlike, apically lobate investiture of the seed of *Tinsleya* was actually homologous with the integument of *Physostoma* or other seeds. One must admit the possibility that it is a cupulelike or indusiumlike covering within which the true seed was contained. Whatever the true morphological nature of this covering may have been, however, it is apparent that the apical aperture was sufficiently broad to permit an easy avenue of access for the pollen.

TAXONOMY

The generic segregation of *Tinsleya* is amply justified by its fructifications and by some of its vegetative features as well. Attention has already been directed to some vegetative similarities between *Tinsleya* and *Callipteris jutieri* Zeiller. However, the absence of a midrib in pinnules of *Tinsleya*, its strong tendency toward odontopterid venation and unequal development of the veins, and the polymorphism of its foliage are features that combine to distinguish *Tinsleya* from *Callipteris jutieri*. The differences between *Tinsleya* and other species of *Callipteris*, particularly the sphenopterid types such as *C. strigosa* Zeiller, are even more obvious and need no discussion here. It appears that the primary vegetative feature of importance shared by *Tinsleya* and members of the callipterid complex is the rachial or subsidiary pinnule, but this feature in itself must be regarded as subordinate to the reproductive mechanisms demonstrable on *Tinsleya*.

Tinsleya is therefore proposed here as a new genus because retention of the material within the genus *Callipteris* would necessitate expansion of the generic diagnosis of *Callipteris* to include the reproductive habit described here; this taxonomic retention would imply possession of seeds by all presently known species of *Callipteris* and would thus involve a completely unwarranted set of assumptions regarding the fruiting habits of a large number of species. Although meager, the evidence bearing on the male fructifications of the callipterids suggests that the callipterid complex consists of possibly several natural genera, and it is likely that additional discoveries of the female parts will ultimately corroborate polygeneric intrafamilial relationships.

The genus *Tinsleya* is named for Mr. T. R. Tinsley of Stamford, Tex., who conducted me to important fossiliferous exposures. Because the genus is yet monotypic, a combined generic-specific diagnosis is given.

Class **GYMNOSPERMAE**
Order **PTERIDOSPERMAE**
Family **CALLIPTERIDEAE**
Genus **TINSLEYA** Mamay, n. gen.

Type species: **Tinsleya texana** Mamay, n. sp.

Figures 1, 2; plates 1–3

COMBINED DIAGNOSIS

Fronds of generally callipteroid aspect, with laminally borne seeds.

Fronds large, bipinnate, possibly tripinnate. Penultimate rachises stout, as much as 1.0 cm wide; ultimate rachises opposite to alternate, decurrent at angles of 30°–60°. Pinnae as much as 15 cm or more in length, with 18 or more pinnules, usually closely spaced. Pinnules polymorphic but mostly obovate with broad basal attachment, gently decurrent, opposite to alternate, mostly entire margined with rounded apices; some pinnules lobed, shallowly or deeply, apically or marginally. Pinnules as much as 4.0 cm long and 12 mm wide, with length-width ratios of 2:1–5:1. One or two rachial pinnules arising from penultimate rachises between successive pinnae; rachial pinnules relatively long and narrow, approximately equal in size to nearest normal pinnules, or short and broad, roughly triangular in shape; some small rachial pinnulets produced from ultimate rachises between pinnules; rachial pinnules confluent toward frond apices, producing winged rachises.

Venation open, mostly odontopteroid. Four to eight decurrent evenly spaced veins entering pinnule bases directly from ultimate rachises, mostly terminating at apical margins of pinnules; veins simple or forking two to four times; dichotomies occurring mostly in veins of adrachial parts of the pinnules. Some veins unequally developed, one or more being dominant; stronger veins entering adrachial part of pinnule and dividing several times; venation usually most concentrated in adrachial half of pinnule. Venation of rachial pinnules always equally developed.

Seeds urn shaped, as much as 2.0 cm long and 0.8 cm wide, consisting each of an oval thickened inner body invested by a cupuliform sheath, possibly integumentary; sheath terminating in a usually narrowed neck with several digitate apical projections. Seeds borne one or two to a fertile pinnule, deeply or only slightly

imbedded in pinnules, either apically or marginally on adrachial side of lamina.

Male parts unknown.

Holotype: USNM 42554.

Paratypes: USNM 42553, 42555–42562.

Stratigraphic occurrence: Upper part of Lueders Limestone, Wichita Group, Lower Permian (Leonard?) Series.

Geographic occurrence: Lake Kemp roadcut, Baylor County, Tex.; USGS paleobotany loc. 10,000.

BIOTIC RELATIONSHIPS OF *TINSLEYA*

A surprisingly diverse representation of several groups of both plants and animals is recognizable in association with *Tinsleya* in the Lake Kemp deposit, in spite of the very limited extent of the fossiliferous exposure and the generally poor quality of preservation of the fossils. Most of these organisms still must be identified below the generic level; in some, however, this incomplete taxonomy is due not to poor quality of preservation but to the presence of distinctive morphologic features that will eventually lead to establishment of new taxa. A provisional list of the plants associated with *Tinsleya* follows:

> ?Cordaitean leaf, apparently a new taxon.
> *Gigantopteris* n. sp. A. (See Read and Mamay, 1964, pl. 19, fig. 1.)
> *Gomphostrobus bifidus* Geinitz.
> *G.* sp.
> *Neuropteris* spp.
> ?*Odontopteris* sp.
> *Samaropsis* spp.
> Other similar seeds, generically undetermined.
> ?*Saportaea* sp.
> *Taeniopteris* sp.
> *Walchia piniformis* (Schlotheim) Sternberg.
> *W.* n. spp. (possibly two).
> *Walchiostrobus* sp.

The composition of this florule is not unusual; all the previously established genera are well known in Permian assemblages from widely scattered localities in the Northern Hemisphere.

The fossil-plant assemblage seems to reflect an association of the walchian complex, with an undergrowth of pteridophylls. The walchians are conspicuously represented by handsome foliar remains, including two large slabs approximately 12 by 14 inches in dimension, completely covered by leafy branches derived from a single plant; some specimens are distinctly different from the *piniformis* type of walchians and warrant further study. Also representing the walchian conifers are several large specimens of male cones reaching 8 inches in length and more than an inch in diameter.

The presumptive cordaitean leaf indicated in the preceding floral list may not really represent the cordaites inasmuch as the venation pattern is distinctly asymmetrical, the veins predominantly bending toward one margin of the leaf in a manner somewhat reminiscent of an insect wing. This element is rare in the flora.

The neuropterids and generalized seed types found in the flora are commonplace in late Paleozoic floras. The gigantopterid (*Gigantopteris* n. sp. A), however, is of more than usual interest, inasmuch as it contains a complicated vascular system featuring four orders of venation. One complete frond and several smaller fragments have been found thus far, only at the Lake Kemp locality. The complete frond demonstrates a bifurcative mode of laminar division which, along with the unique venation pattern, sets this entity apart from any gigantopterid described thus far from America or the Eastern Hemisphere.

Animal remains recognized thus far include representatives of the following groups: polychaete worms, pelecypods, myriapods, estherids, fishes, and amphibians.

The polychaetes are represented by abundant specimens of the coiled tubes of *Spirorbis*, mostly attached to foliage of *Tinsleya*. Pelecypods are found as rare molds and casts that are neither identifiable taxonomically nor significant in terms of ecologic implications (John Pojeta, Jr., oral commun., 1965). The faint impression of one myriapod specimen, probably referable to the genus *Xylobius*, has been noted, and poorly preserved estherid valves are fairly common.

Teeth and small disarticulated skeletal fragments of both fish and amphibian origin are found throughout the exposure and are particularly concentrated in two or three conspicuous and fairly continuous bone beds that reach thicknesses of as much as 6 inches. The vertebrate genera have not yet been identified, but according to Walter Dalquest (written commun., 1964) the fishes are paleoniscoid and, together with the amphibians, definitely constitute a fresh-water fauna. The concentrations of bone in this exposure indicate a rich vertebrate population, in terms of numbers of individuals, if not of species, fairly close to the site of ultimate deposition.

To the evidence of fresh-water vertebrates of parts of the fauna may be added the fact that the estherids indicate fresh to brackish aquatic environments, and the myriapod specimen certainly suggests proximity to land. Thus the overall aspect of the faunal assemblage provides grounds for the assumption that deposition of this fossiliferous unit occurred in a deltaic environment, in probably brackish but certainly not highly saline water. The physical evidence of channeling in the sediments adds support to this interpretation.

The spirorbids inject an extremely interesting ecological note into the plant-animal association observed at this locality. As previously mentioned, the coiled tubes of *Spirorbis* are found in some abundance in the

Lake Kemp biota; however, only a few isolated specimens have been seen lying free in the matrix. The great majority of *Spirorbis* specimens are attached to *Tinsleya* foliage; none has been seen attached to any of the associated plants. A few specimens of *Tinsleya* carry such dense concentrations of *Spirorbis* tubes that the entire leaf specimens present a generally rugose appearance; this condition is well demonstrated by the leaf fragment shown on plate 1, figure 1. The specimen shown on plate 3, figure 1, also carries a large number of *Spirorbis* tubes, some of which are particularly well shown on the pinnules at the right in the vicinity of the locality label. The substrate selectivity on the part of these spirorbids is so striking that coincidence may safely be discounted and an explanation sought in terms of physiological relations between *Spirorbis* and *Tinsleya*.

The attachment of spirorbids to Paleozoic plants is observed commonly, and Barrois (1904) cited numerous examples. Trueman (1942) indicated the frequent occurrence of *Spirorbis* tubes attached to plants, marine shells, and nonmarine lamellibranchs in the British fresh-water and marine Coal Measures. Malaquin (1904) presented an excellent discussion of the growth, habitat requirements, and adaptability of *Spirorbis*. He also pointed out that fossil plants were often observed as a substrate for these worms. None of the preceding authors, however, indicated examples of the degree of selectivity shown by the Lake Kemp *Spirorbis* in attaching itself only to leaves of *Tinsleya* and avoiding all associated plants.

Seward (1910, p. 102–104) described and figured a fascinating example of the *Spirorbis*-fossil plant association that may contain an explanation of the *Spirorbis-Tinsleya* relationship. He discussed a Carboniferous specimen of *Lepidodendron* in which *Spirorbis* tubes are attached to the parichnos scars of the leaf cushions. Seward's more pertinent remarks (p. 103) follow:

> The fact that with one exception all the Spirorbis shells on the specimen of *Lepidodendron*, of which two leaf cushions are shown in fig. 146, E, occur on the large parichnos scars on the cheeks of the cushions, suggests the possibility that the escape of gases from the parichnos tissue may have rendered the position attractive to the *Spirorbis*. It can hardly be accidental that the shells occur on the parichnos strands. This fact recalls the view held by Binney and accepted with favour by Darwin that *Lepidodendron* and other coal-forest trees may have lived with the lower parts of the stems in sea water.

The final statement in Seward's remarks clearly reflects the opinion that the Carboniferous *Spirorbis* was necessarily a marine organism and that the *Lepidodendron* substrate was a living plant at the time that the *Spirorbis* became attached to the parichnos scars.

According to Trueman (1942, p. 317), however, most of the Coal Measure spirorbids "lived under non-marine (probably fresh water) conditions * * *"; Haack (1923, p. 589–590) pointed out that *S. pusillus* Martin occurs in the Carboniferous of Belgium, northern France, England, and Germany in not only marine but also in brackish and fresh-water deposits and that one Triassic species, *S. zimmermanni*, may have been euryhaline. Malaquin (1904) presented evidence that the Carboniferous spirorbids were adapted to fresh as well as salt-water habitats. Weller (1957, p. 333), in his treatment of the Pennsylvanian of Illinois, discussed the pelecypod *Aviculopecten rectilaterarius* Cox:

> * * * It also occurs more sparingly in gray calcareous shale, associated with a few common marine species, and in ironstone concretions with *Spirorbis* which has never been observed as a member of a normal marine Pennsylvanian fauna. This worm appears to have been a fresh-water species with considerable tolerance for brackish conditions.

In consideration of the foregoing series of comments on the salinity tolerances of the Carboniferous spirorbids, the conclusion is inescapable that the *Lepidodendron-Spirorbis* association described by Seward need not have been produced in marine water, but that a fresh-water or brackish environment was probably a more logical setting.

Seward's inference that the *Lepidodendron* was alive at the time of attachment of the spirorbids is also open to question. The *Lepidodendron* may in fact have been alive and partly submerged in fresh or slightly brackish water and gases produced by life functions and escaping through the parichnos openings may have attracted the spirorbid larvae, but it strikes me as equally possible that the *Lepidodendron* was dead and that the escaping gases that attracted the *Spirorbis* larvae to the parichnos were actually the products of decay. Whichever alternative is correct, the strikingly preferential location of the *Spirorbis* tubes on the parichnos scars can hardly be explained in terms other than attractiveness to the young animals of some sort of gas. In my opinion this thought contains the preeminently logical explanation of the preferential attachment of *Spirorbis* to *Tinsleya* in the Lake Kemp collection.

Considering the great abundance of *Tinsleya* in this plant assemblage, it is not difficult to visualize a virtually pure, dense stand of this plant, surrounding and extending up to the edge of a pool or sluggish watercourse, with the less common associated plants growing farther away from the water on slightly higher ground. Some of the fronds of *Tinsleya* may have dangled into the water while still alive and photosynthesizing; perhaps the oxygen emitted through the stomata attracted the settling larvae of *Spirorbis*, which attached themselves to the submerged leaves. A necessary adjunct to

this set of conditions would have been protracted submersion of the substrate foliage for a period of time sufficiently long for the spirorbids to build their tubes. Whether or not a continuing supply of the originally attractive gas was necessary to the continued growth of the worms is a moot point, but it remains possible that, once attached to the *Tinsleya* pinnules, the worms continued to grow even though the leaves became detached and dropped into the water.

On the other hand, this selectivity on the part of *Spirorbis* may be hypothetically explained in terms of quality of gaseous decay products. Inasmuch as the *Spirorbis*-laden foliage of *Tinsleya* occurs not only in the same beds but on the same bedding surfaces with parts of other, unrelated plants that show no evidence of attached *Spirorbis* tubes, it may logically be assumed that detached parts of the whole floral assemblage were washed into the site of sedimentation at approximately the same time; let us assume further that none of the plant debris carried *Spirorbis* tubes until this time. If we then recognize that decay of the plant debris began soon after detachment from the parent plants, the preferential attachment of *Spirorbis* may be explained as the result of an element of attraction to the animals in the gaseous decay products of *Tinsleya* that was absent from the decay products of the other plants. Relative amounts of cutin, starch, chlorophyll, and other plant substances may have produced a complex system of subtly differing decay products, only those of *Tinsleya* offering the peculiarly attractive ones that might explain the substrate selectivity of the *Spirorbis* larvae. Acceptance of this alternative explanation must, of course, be predicated on the assumption that disintegration of the *Tinsleya* foliage was forestalled for a period of time sufficient for completion of the worm tubes; otherwise the association of plant and animal could not have been preserved as fossils.

Admittedly the alternative explanations offered here must be oversimplifications of a complicated ecosystem involving conditions and rates of growth of the spirorbids, as well as conditions for and rates of decay of the plants. The valid explanation may never be known, but it is hoped that description of this peculiar example of selective epiphytism will draw attention to similar examples that will eventually shed light on the overall problem.

EVOLUTIONARY SIGNIFICANCE

The recorded fossil occurrences are far from sufficiently complete to permit conclusions as to the systematic positions and possible derivative forms of such plants with seed-bearing foliage such as *Tinsleya*, *Padgettia*, and others. These plants nonetheless, are of sufficient interest to invite a certain amount of specula-tion as to their places in the succession of spermatophytes. The diverse types of Paleozoic seed-bearing habits strongly indicate that the interrelationships of these plants, if ever fully understood, will not prove to have been simple. It is not the intent to treat here any major part of the phylogenetic possibilities offered by that complex. Rather, I wish to discuss briefly the possible implications of the seed-bearing habit of *Tinsleya*, because it entails an intriguing element of morphological nature that eventually may contribute toward an understanding of the ultimate sources and evolutionary development of the angiospermous carpel.

Any discussion of the morphological nature of the angiosperm carpel must ultimately hark back to the classical concept based on Goethe's (1790) interpretation of the carpel as a green leaf with marginal ovules. According to the classical view, the carpel formed by inrolling of the margins of the fertile leaf and fusion of the opposite margins; this process produced the hollow carpel, the ovules being contained within. Several other theories have been advanced and much has been written in attempts to explain the basic nature of the carpel. Eames, however, has thoroughly reviewed the various theories and expressed his summary opinion (1961, p. 218):

> * * * When evidence from all fields is considered, none of of the twentieth century concepts of the nature of the carpel can displace the classical view that the carpel is a fertile lateral appendage of a determinate stem tip. In details of position and origin on the stem, and of ontogeny and anatomy, it is like the leaf and is clearly of leaf rank.

Eames' conclusions are apparently derived primarily from evidence based on modern plants, for even though he discusses the theory of caytonialean origin of the carpel, he points out what he considers to be eminent weaknesses in that hypothesis—the palmate venation of the modern carpel as opposed to the pinnate venation of *Caytonia* fruits and the double integument of angiosperms as opposed to the single integument of *Caytonia*.

Andrews (1961) also cites the possibility of caytonialean derivation of the carpel through lateral fusion of two "carpels" of the *Pilophorosperma* or *Caytonia* types, but he admits that this concept is speculative because the later stages are unknown. He also states (p. 179) that "* * * the concept of the carpel as an enfolded leaflike structure, although long favored by many botanists, finds no supporting evidence in the form of gymnospermous plants, living or fossil, which may be regarded as ancestral." It is true that fossil evidence of conduplication or involution of megasporophylls (enfolding) is still lacking, but the beginnings of such a line of evidence become more evident, particularly in the Permian rocks, as the phenomenon of the seed-bearing leaf becomes more of a reality.

Determined attempts to uncover direct fossil evidence to support the classical theory have obviously been negligible, if one excludes the works of Zimmerman, recently summarized (1959) in a revised edition of his "Die Phylogenie der Pflanzen." As such evidence for the foliar origin of the carpel, Zimmerman (p. 510–511) cited the Pennsylvanian sporophyll *Acrangiophyllum pendulatum* Mamay, which has large monosporangia at the tips of the lobes of the pinnules. This plant is a remarkable factual facsimile of a hypothetical form proposed by Zimmerman, and even though *Acrangiophyllum* is not a megasporophyll but is either a microporophyll or isoporophyll, Zimmerman regards it as an ancestral form in the evolution of the foliar carpel. Substitution of the sporangia of *Acrangiophyllum* by seeds would result in a fertile foliar organ, a considerable step closer to approximation of the hypothetical carpel of the classical theory. (See Melville, 1964, fig. 1a). Although it retains fernlike venation and pinnulation, *Tinsleya* otherwise approximates closely the hypothetical form of primitive carpel in that it bears seeds on the margins of the lamina and thus, along with other fertile forms discussed here, suggests that continued investigations of late Paleozoic floras—with emphasis on those of the Permian—may ultimately lend undeniable support to the classical theory of carpellary evolution.

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INDEX

[Italic numbers indicate descriptions]

E15

PLATES 1–3

PLATE 1

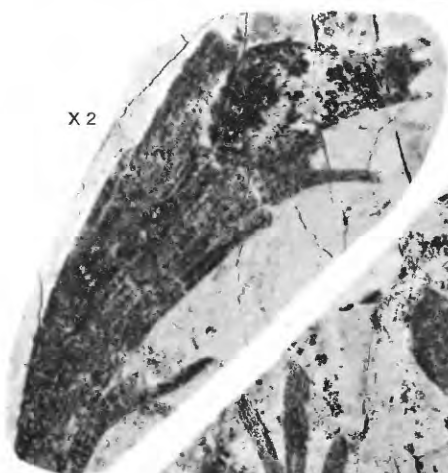FIGURES 1–5. *Tinsleya texana* Mamay, n. gen., n. sp. (p. E10).

1. Specimen showing rachial pinnules and rugose appearance of lamina, caused by numerous epiphyllous spirorbids. Paratype, USNM 42553.

2. Enlargement of fertile pinnule of holotype, showing urn-shaped seed with apical lobations and long, narrow lobations of pinnule. Holotype, USNM 42554. × 2.

3. Frond fragment showing venation. Paratype, USNM 42555.

4. Large frond fragment, with fertile pinnule near top center (enlarged in fig. 2). Holotype, USNM 42554.

5. Part of pinna, showing much-dissected pinnules and rachial pinnulets. Paratype, USNM 42556.

6. Fertile pinnule, bearing ovoid seed at apex, subtended by narrow lobe of pinnule. Paratype, USNM 42557.
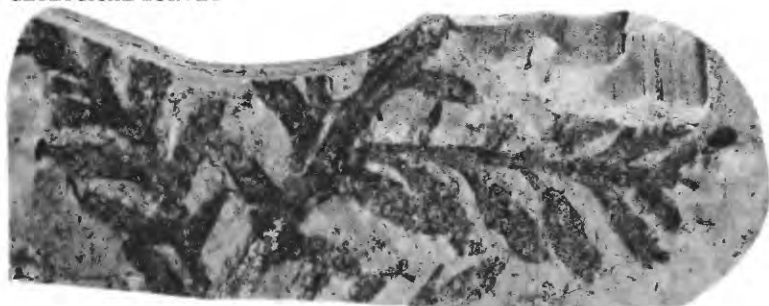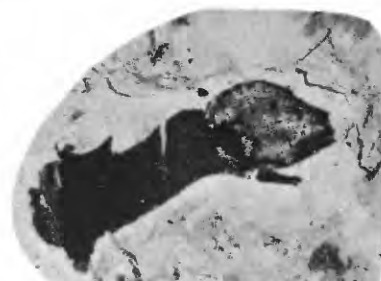
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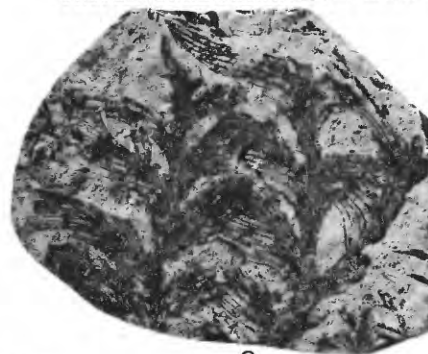
X 2

2

3

4

5

6   X 2

COMPRESSIONS OF *TINSLEYA TEXANA*

PLATE 2

FIGURES 1–4. *Tinsleya texana* Mamay, n. gen., n. sp. (p. E10).

    1. Fertile specimen with several seeds attached.   Paratype, USNM 42558.

    2. Sterile pinna showing slight degree of lobation and shallow sinuses in pinnule apices.   Paratype, USNM 42559a.   × 2.

    3. Part of large frond consisting entirely of entire-marginal pinnules and showing several rachial pinnules.   Burrow across basal part of frond excavated by unknown Recent invertebrate.   Paratype, USNM 42560.   × ½.

    4. Part of pinna with shallow apical lobations and indications of immature seeds shown by thickened apical carbonaceous areas in pinnules at left and apical depressions in pinnules at right.   Paratype, USNM 42561.   × 2.

1

2

X 2

3

X ½

4

X 2

COMPRESSIONS OF *TINSLEYA TEXANA*

PLATE 3

FIGURE 1. *Tinsleya texana* (p. E10).

Large sterile specimen showing irregular margination of lamina, confluence of rachial pinnules toward apex of frond, and attachment of numerous spirorbid tubes, particularly on right-hand parts of frond. Paratype, USNM 42562.

1

COMPRESSIONS OF *TINSLEYA TEXANA*