Russellites, New Genus a Problematical Plant From the Lower Permian of Texas

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By SERGIUS H. MAMAY

CONTRIBUTIONS TO PALEONTOLOGY

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A discussion of the taxonomic relationships and paleogeographic significance of a potentially important guide fossil

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By Sergius H. Mamay

ABSTRACT

Fossil plants previously reported as two species of *Tingia* Halle provide the basis for description of the new genus *Russellites,* typified by *R. taeniata* (Darrah) Mamay, new combination. The material is from the Lower Permian Belle Plains Formation, Baylor County, Tex.

Russellites is distinct from *Tingia* in lacking anisophylly and in having uniquely truncated laminar apices. The foliar organs of *Russellites* are interpreted as pinnate leaves (fronds) rather than plagiotropic shoots, as in *Tingia.* Affinities of *Russellites* most probably lie within the Noeggerathiales.

Russellites promises to be valuable as a guide fossil, and possibly as a facies indicator. It constitutes an important element of contrast between the Permian floras of North America and Asia, and adds to the evidence for rapid botanical evolution during Permian time.

INTRODUCTION

In 1938, Darrah reported an occurrence of the supposed noeggerathialean genus *Tingia* Halle in the Lower Permian Belle Plains Formation of Baylor County, Tex. He described two new species, *T. taeniata* and *T. kempiae* on the basis of nine fragmentary specimens, all apparently the gift of Mrs. J. F. Kemp of Seymour, Tex. Source of the material was an outcrop on the "Emily Irish" land grant—now the property of Mr. Roland Howe of Fort Worth, Tex.—approximately 16 miles south-southeast of Seymour.

C. B. Read, U.S. Geological Survey, visited the Howe property in 1940 and made a large collection of plant fossils, some of which closely resemble the figures published by Darrah as *Tingia.* A rich and varied flora, including *Gigantopteris americana* White, is associated with these plants.

In 1955, Read conducted me to the same site, and we collected additional material. I supplemented the collections in 1957, 1961, and 1963. The site was cleared by bulldozer in 1961 to remove overburden and to expose more of the fossiliferous deposit. As a result of these collecting trips a bulk of interesting fossil material has been accumulated. Items thus far described include the noeggerathialean cone *Discinites* (Mamay, 1954), a complete acanthodian fish (Dunkle and Mamay, 1956), and the insect *Actinohymen russelli* (Carpenter, 1962); the major part of the collection, however, is undescribed.

The collection includes a large number of specimens of a taxon that I believe to be generically distinct from Halle's *Tingia* but identical with the material described by Darrah. This opinion is based largely on my examination of the specimens described by Darrah. In 1955, I visited Harvard University to study the Permian plant material there; Professor E. S. Barghoorn kindly granted me access to the collections. I was particularly interested in a reappraisal of Darrah's identification of *Tingia*, because (1) *Tingia* is morphologically a peculiar form that is difficult to interpret in terms of other groups of vascular plants, and (2) aside from Darrah's report, *Tingia* has been recorded only in Eastern Asia.

As a result of this study I conclude that Darrah's generic identification was in error, possibly because of misinterpretation of limited and incompletely preserved material. The large suite of U.S. Geological Survey specimens provides consistent evidence of morphological details that convincingly distinguish the Texas material from *Tingia* and warrant the recognition of a new genus.

ACKNOWLEDGMENTS

Thanks are due to C. B. Read, who acquainted me with the fossil locality discussed here, and with many aspects of the paleobotany of north-central Texas and adjacent areas. Arthur D. Watt, U.S. Geological Survey, assisted me in 1957, 1961, and 1963. Permission to collect at the "Emily Irish" locality was kindly granted by Messrs. Mart Russell and Ralph Howe of Seymour, lessees of

that part of the Howe property on which the plant-bearing beds occur.

LOCALITY

Despite slight discrepancies between previously published accounts of the geographic location of the "Emily Irish" deposit (according to Darrah, 1938, p. 180, it is "15 miles southeast of Seymour"; Read's locality labels say "16 to 16½ miles scaled due southeast of Seymour"; Dunkle and Mamay, 1956, p. 308, say "approximately 18 miles south-southeast of Seymour"), there is no doubt that the same rock exposure is referred to in each instance. The differences in the distances given may have resulted from the use of different starting points in Seymour. The fossil beds are well known to many of the local citizens and are the only deposit known on the "Emily Irish" land. Mr. Russell informed me (oral commun., 1957) that Mrs. Kemp, who donated the original specimens to Darrah, had collected at this site several times; moreover, Mrs. Kemp stated (oral commun., 1961) that she knew of only one plant locality on the "Emily Irish" land. From the foregoing, one must conclude that the source of Darrah's specimens and of the material described herein is the same outcrop.

The locality is reached by following U.S. Highway 183–283 south from Seymour. At a distance of 10.2 miles south of the bridge crossing the Salt Fork of the Brazos River the highway is intersected from the east by an unpaved road, which is entered by crossing a cattle guard. Six miles east of this intersection a northbound fork departs in the direction of the farm of Mrs. John Bess Fancher. A short distance north of this fork the road again branches and a narrow unimproved side road extends to the northeast through mesquite pasture. Within half a mile of the beginning of the latter road, the fossiliferous outcrop is seen as a low south-facing bluff along the bed of an intermittent stream. This site is recorded as USGS fossil plant locality 8959.

The fossiliferous bluff is one of the erosional features of a shallowly gullied, minor drainage system less than a mile south of the Salt Fork of the Brazos River. Plant-bearing beds are exposed in the face of this bluff for about 30 yards, thinning out toward both the east and west. The bluff is the south face of a ridgelike westerly extension of a group of low hills. The ridge terminates at its west end in a sharp spur, and forms part of the southern margin of a roughly circular eroded depression that occupies an area of approximately 2 acres. Fossil plants occur in several small shale exposures around the sides of this bowl; these are all remnants of the same deposit. In this area, plant remains are nowhere as abundant or well preserved as those found at the main bluff exposure.

When the site was visited in 1955 the main plant-bearing shale unit was nearly 5 feet thick. Excellent concentrations of plant fossils occurred throughout the thickness of the shale, for a lateral distance of about 30 feet. Subsequent to the 1961 bulldozing and the 1963 collecting trip, however, the fossiliferous shale face had receded 8–10 feet from the originally exposed face. At the conclusion of collecting in 1963 it appeared that the plant beds were thinning significantly in all directions; they did not exceed 4 feet in thickness, and there was a definite decrease in incidence of fossil specimens. It thus seems likely that the shale deposit represents a slow eddy in the current of a sluggish watercourse, plant material concentrating at the site of the eddy. The richest part of this plant deposit has been virtually depleted, and extensive exploration may be necessary for investigations of this flora beyond the limitations of materials already collected.

STRATIGRAPHY

The fossilferous section was measured in 1957 to preserve the limited record of the lithologic relationships of this valuable paleobotanical deposit. At that time, a maximum relatively undisturbed exposure was still available for examination. The section consisted of the following lithologic units:

Measured section, "Emily Irish" plant locality

	Feet
Recent alluvium.	
Belle Plains Formation:	
Silty mudstone, massive with irregular to conchoidal fracture; gray on fresh surface, weathers buff, having scattered light-green mottles; unfossiliferous except for rare pelecypods near top of unit	8.0
Clay-shale, jointed; variable fissility most pronounced in lowermost 12 in.; dark gray to bluish gray on fresh surface, weathers light gray; conspicuous orange-yellow limonitic layers as much as ½ in. thick, occur at intervals of 3–5 in.; fossil plants abundant, most concentrated in lowermost 12–15 in	4.5
Silty mudstone, massive; fracturing irregularly or breaking into large conchoidal lumps; mottled red green on fresh surface, weathers dark gray; locally channeled to depths of 12 in.; unfossiliferous	3.0
Intermittent streambed	
Total thickess measured	15.5

The scarcity of extensive or continuous rock exposures makes it difficult to place the above sedimentary section accurately within the Permian sequence in Baylor County, Tex. According to Romer's (1958, facing p. 178) large-scale map of the geology of north-central Texas, the "Emily Irish" locality lies roughly at the middle of the width of the outcrop belt of the

Belle Plains Formation. This location would indicate a questionable Leonard age, or a position at approximately the middle of the Lower Permian.

The best available geological detail for this area is that shown in the geologic map of Baylor County by Garrett, Lloyd, and Laskey (1930). This map is at a much smaller scale than Romer's and shows a number of prominent limestone beds, some of them unnamed. The mapped unit geographically nearest the "Emily Irish" locality is an unnamed limestone ("Ad_1"), which crops out approximately 2½ miles north and northwest of the fossil locality. This unit apparently lies stratigraphically about halfway between the Beaverburk Limestone of Udden and Phillips (1912), which marks the top of the Belle Plains Formation, and the Valera Shale Member, which occupies approximately the middle one-third of the Belle Plains Formation. The Valera Shale Member is lithologically similar to the "Emily Irish" plant beds, but because it is unfossiliferous (see Keroher and others, 1966, p. 4044), paleontological comparisons between the two cannot be made. Nonetheless, whereas the "Emily Irish" plant beds and the Valera Shale Member both occur at approximately the same distance below the Beaverburk Limestone of Udden and Phillips, the two may tentatively be regarded as correlative units.

HISTORY OF *TINGIA*

The genus *Tingia* was established by Halle in 1925 to accommodate some Permian plants from China. These plants had originally been assigned to *Pterophyllum* by Schenk (1883). Schenk described the plant as having pinnate fronds, the pinnae of which had truncate, entire apices; Schenk designated this a new species, *Pterophyllum carbonicum*. Halle, however, later found that the apices of the type specimen were dentate, and subsequent collections of similar material confirmed the presence of this morphological feature. Halle also found that the "fronds" were dorsiventral axes bearing four rows of appendages, two on the upper side and two on the lower side of the axes. He concluded that these structures were not true fronds, morphologically, but were dorsiventral shoots with pronounced anisophylly. The leaves were oblong to linear, with parallel dichotomizing veins. As specified in a slightly modified generic diagnosis given by Halle in 1927, the leaves of the upper two rows of leaves are larger and directed forward at broader angles than those of the lower two rows. Halle recognized three species: *T. carbonica* (Schenk) Halle, *T. crassinervis* Halle, and *T. partita* Halle, all from the Lower Permian Shihhotse Series of Central Shansi, China. Although he acknowledged a possible relationship between *Tingia* and the genera *Noeggerathia* and *Plagiozamites*, Halle was reluctant to present conclusions regarding natural affinities of *Tingia*. He merely considered a remote comparison with the Cordaitales and Ginkgoales and tentatively proposed the monotypic family Tingiaceae (Halle, 1927, p. 239).

Subsequent to Halle's studies, six additional Asiatic species of *Tingia* were described, all from the Permian or Carboniferous of China and Korea. The strobiloid fructification *Tingiostachya* Kon'no (1929) was described from the Korean Permian and was reported later from the Stephanian of China (Stockmans and Mathieu, 1939). Various authors have discussed the possible systematic relationships of these and supposedly allied plants. The complex was discussed most recently by Boureau (1964) in his extensive review of the Sphenophyta. Boureau established the orders Noeggerathiales, Discinitales, and Tingiales as coordinate subdivisions of the class Noeggerathiopsida. Although he discussed all but one of the Asiatic species of *Tingia* to some extent, Boureau merely listed Darrah's two taxa without further comment. These remain as the only extra-Asiatic occurrences of *Tingia* recorded in the literature, although other representatives of the Noeggerathiopsida are known in the Paleozoic of North America (Arnold, 1949; Mamay, 1954).

THE TEXAS MATERIAL—BASIS FOR REDEFINITION

The Chinese material described by Halle is generically distinct by virtue of the following unique combination of morphological features:

1. Foliation anisophyllous, with appendages borne in four lateral rows, two upper and two lower; upper rows differing from the lower in size, outline, and angle of insertion of appendages.
2. Appendages more or less linear, with parallel dichotomizing venation and more or less deeply lobed or digitate apices.

The arrangement of lateral appendages in four orthostichies creates difficulties in examining this material because the upper two rows of appendages lie on different bedding planes from the lower two rows, and one pair is invariably obscured by the layer of matrix separating the paired rows. Halle (1927, p. 233) pointed this out and described a technique for preparation of specimens to demonstrate the anisophyllous nature of the plants. Halle's preparations were excellent, and his illustrations convincingly show this feature, as well as the digitate lobation of the apices of the ultimate appendages.

Darrah's specific diagnoses of the Texas material (1938, p. 180–181) contain little quantitative or specific information, and mainly consist of repetition of the salient qualitative points given in Halle's generic diagnosis of *Tingia* (1927, p. 231). Darrah's diagnoses are quoted as follows:

> *Tingia taeniata* Darrah sp. nov. 2 figures.
>
> Shoot dorsiventral, frond-like, anisophyllous, with stout axis. Leaves arranged in four rows, two on the lower side of the axis and two on the upper side, the latter forming an angle of 30–45° with the axis. Leaves of the rows on the upper side large and spreading in one plane, gradually diminishing in size terminad. Apex of the leaves slightly dissected and lobed. Veins broad and conspicuous, bifurcating several times near the base of the leaf and running in parallel directions to the apex of the leaf.
>
> *Tingia kempiae* Darrah sp. nov. 2 figures.
>
> Shoot dorsiventral, frond-like, anisophyllous, with a very thick axis and four rows of leaves. Leaves of the two rows of the upper surface spread in one plane and forming an angle of 60–80° with the axis. Leaves with a broad base, oblong-oblanceolate, three to four times as long as the greatest width. Veins numerous (more than ten), bifurcating several times near the base, and passing out into the leaf in parallel paths.
>
> No details concerning the leaves of the two lower rows are known except their departure from the axis, which is similar to the departure of the leaves of the upper rows.

Comparisons of the foregoing diagnosis with each other and with Halle's diagnosis of *Tingia* cast doubt on the tenability of the segregation of the two species, and also on the generic assignment itself. Darrah's diagnoses are inconsistent with each other, inasmuch as similar characters are not compared to provide a sound basis for delimitation of the species. Whereas a dissected leaf apex is specified for *T. taeniata*, the apex is not mentioned in the diagnosis of *T. kempiae;* dimensions of leaves are not given, nor are differences in leaf shape or density of venation noted; a length-width ratio is given for leaves of *T. kempiae* but not for those of *T. taeniata.* The only described feature of utility in distinguishing species is found in the angles of departure of the large upper leaves; they are given as 30°–45° in *T. taeniata* and 60°–80° in *T. kempiae.*

Furthermore, no comparision is given of size, shape, or attitude of the leaves of the lower two rows, either to their specific counterparts or to conspecific upper leaves. The lower leaves are simply said to be small, with "typical arangement" (Darrah, 1938, p. 179) and no mention of species is involved; in the diagnosis of *T. kempiae*, departure of the lower leaves is said to resemble that of the leaves of the upper rows (Darrah, 1938, p. 181).

Although textual comparisons between these two species are omitted, cursory comparisons are made with the Chinese species *T. carbonica* and *T. crassinervis.* The only common points of comparison are the shapes of leaves and number of veins. Leaves of *T. taeniata* are said to be "more linear" than those of either *T. carbonica* or *T. crassinervis*, and those of *T. kempiae* are broader than leaves of *T. crassinervis;* in both of the Texas species the veins are said to be more numerous than in *T. crassinervis.* Thus, by indirect comparison, *T. kempiae* and *T. taeniata* are equated in the matter of relative density of venation, but may be deduced to differ in leaf shape. The discussions and diagnoses therefore present insufficient grounds for sound, differential specific circumscription. The single quantitative feature in which the diagnoses of the two putative species differ is the angle of departure of the upper leaves (30°–45° as compared with 60°–80°). My observations of the large array of specimens in the U.S. Geological Survey collection however, prompt the conclusion that appendicular shape and angulation of decurrence are sufficiently variable as to warrant the inclusion of all of Darrah's material with the circumscriptive limits of one species.

Of considerably more moment is the fundamental matter of Darrah's generic indentification of the Texas material with Halle's *Tingia.* Careful inspection of Darrah's publication, his original material, and the material subsequently collected at the type locality reveals overwhelming evidence in refutation of Darrah's taxonomic assignment. The evidence contrarily indicates that the "Emily Irish" material represents a distinctive new genus, possibly not related to *Tingia.*

The anisophyllous differentiation of leaves, fully described and illustrated by Halle, is beyond doubt the most critical generic feature of *Tingia* and one that appears, to the best of my knowledge, in no other fossil plant. Darrah's specific diagnoses for *T. taeniata* and *T. kempiae* both include this feature, but its presence is not corroborated by the illustrations. The diagnosis of *T. taeniata* says nothing specifically about a lower pair of rows of leaves, and the illustrations give no indication of foliar differentiation. The diagnosis of *T. kempiae* comments on the mode of departure of lower leaves, but again illustrative substantiation is lacking. Darrah (1938, p. 179) states that two of the nine available specimens were "risked" for excavation to expose the small leaves: ("On both of these specimens the typical arrangement of the small leaves can be observed."). This statement finds no support in any part of the publication or in the Harvard fossil plant collection. My own preparations of "Emily Irish" specimens, which are described on the following pages, convince me that Darrah's claim of having observed anisophylly in this material is unfounded.

Digitate or lobate margination of the apices of the leaves is a second conspicuous, though possibly less critical, generic feature of *Tingia;* this margination differs slightly among species. Darrah's diagnosis of *T. taeniata* indicates that the leaf tips are slightly dissected, but neither his specimens nor his illustrations present substantiation. Apical margination is nowhere mentioned for *T. kempiae*, and the illustrations again lack evidence of this generic criterion.

Apical margins of the specimens in the U.S. Geological Survey collection, however, are consistently truncated in such a manner that the tips of the appendages show a cleanly cut margin with angular corners and slightly concave, crescentic outlines having a width of half or less than half the greatest width of the appendage. Every specimen in which the foliar tip is preserved demonstrates this distinctive feature, which is illustrated on plate 1, figures 3 and 4. Furthermore, Darrah's types and figures show suggestions of truncated apices, and there are several specimens in the Harvard collection that show this character very well. The label accompanying the latter says "Emily Irish land, south side of Salt Fork, Brazos River, 15 mi. southeast of Seymour. Coll. Witter & White, 1938." Whereas these specimens were collected in 1938 and Darrah's paper was published in April of the same year it may be presumed that they were not available to Darrah while his manuscript was in preparation; otherwise it would be difficult to compromise his generic identification. Nonetheless, the presence of the 1938 collection at Harvard, bearing locality data identical with that contained in Darrah's paper, serves to corroborate the conclusion that Darrah's material is from the same locality and is congeneric with the material described here.

In view of the evidence—to be fully elucidated in succeeding paragraphs—that the Texas material is neither anisophyllous nor digitately incised at the foliar apices, the conclusion is unavoidable that the Texas plants actually have little morphological similarity with *Tingia*. They both show pinnate, frondlike architecture and have more or less linear lateral appendages with entire lateral margins and parallel dichotomous venation. There the similarity ends, however. The Texas plants might be compared much more aptly with any of several genera of plants characterized by more "conventional" frondlike organs with isophyllous foliation. Among the entities possibly comparable with the Texas plants, however, none are known to possess their peculiar, concavely truncate foliar apices.

DESCRIPTION OF THE "EMILY IRISH" MATERIAL

This description is based on an aggregation of about 400 rachial fragments with pinnae attached; the number of pinnae ranges from 4 to 20. For reasons to be further elaborated, the Texas specimens are regarded as pinnate fronds rather than shoots with leaves arranged in flat planes; consequently the terms "rachis" and "pinnae" will be used here. The longest rachial fragment, shown on plate 3, figure 1, is 19.5 cm long, with a greatest width of 1.0 cm. This axis is extremely stout relative to the size of attached pinnae, and a similar degree of rachial development is shown consistently by all the specimens available. This fragment has 12 pinnae attached bilaterally, six on each side; apparently a seventh was originally attached slightly below the middle of the left side, but was lost in the splitting of the matrix.

Several other stout rachial fragments have been noted with widths of a centimeter or slightly more; it is assumed that these represent the basal parts of the fronds. At the opposite extreme are a few specimens, such as the one shown on plate 1, figure 1, that represent the frond tips. The specimen shown on plate 1 consists of a very slender rachis less than 2 mm wide and densely clothed with small crowded pinnae that obviously terminate the frond. Rachial fragments with widths intermediate between these two extremes are abundant, with widths of 4–6 mm most predominant. Because rachial preservation is poor, no demonstrable evidence of indument or ornamentation was found. If stipular basal appendages were present, they were not preserved; likewise there is no evidence of circinate vernation. Furthermore, none of the axial fragments show branching—a fact that lends support to the belief that these organs are true fronds, rather than shoots as in the case of *Tingia*. As none of the rachial fragments show any appreciable rate of tapering in thickness, a considerable length—perhaps as much as 2 meters—may be assumed for the fronds. They must have been handsome structures.

The pinnae vary somewhat in size, shape, and disposition on the rachis. Characters of the venation and margination are fairly consistent, however. Furthermore, intergradation of characters in the large suite of specimens available is sufficient for me to regard the variations in size and other features of the pinnae as attributable to one species.

The pinnae are attached to the rachis in two lateral rows and, in contradistinction to the anisophyllous arrangement of leaves in *Tingia*, they thus form a dorsiventral frond. To establish this point unequivocably, 15 specimens were selected for mechanical preparation; each specimen bore from 3 to 7 pinnae on either side of the rachis. The preparation was similar to the technique applied by Halle in demonstrating anisophylly in *Tingia*. The matrix of the Texas material is extremely fissile in its fossiliferous parts and splits readily along the planes of its abundant plant compressions; it thus lends itself well to mechanical excavation with the Vibro-Tool.

The Vibro-Tool was used to excavate a trench in each specimen. Every trench was approximately 1 cm wide, 5–8 mm deep, parallel to the rachis, and about halfway between the rachis and the tips of the pinnae. By careful manipulation of the Vibro-Tool it was possible to excavate across the pinnae and yet leave their bases and tips intact. A trench was dug on one side of the rachis in each specimen, but the opposite side was left undisturbed. Trenches were also dug across the rachises of some of the specimens. During this preparation, careful note was made of the plant material uncovered. Some extraneous foliar material was seen, but there was no evidence of buried pinnae that might have constituted additional rows of appendages. One specimen thus excavated is illustrated on plate 2, figure 2.

Both counterparts of one well-preserved specimen (USNM 42712) were prepared as above, with the assumption that if additional rows of appendages were attached to the rachis but obscured from sight by embedment below the surface of the matrix, these appendages should be revealed by excavation of one or the other of the counterparts. Both counterparts were excavated across the rachis and across the appendages of the same side of the rachis, but no evidence of buried appendages was found.

These prepared specimens are preserved as USNM 42706 and 42712–42725. My obeservations of these specimens confirm my conviction that only two rows of lateral appendages are attached to the rachises in these specimens and in Darrah's original material. Because of the abundant plant material contained in the matrix and the occasional superposition of several fragmentary specimens of the plant under discussion, I can only attribute Darrah's claim of having observed anisophylly to accidental superposition of unconnected plant parts.

The pinnae vary in shape from nearly linear to oblong, lanceolate, oblanceolate or, in a few examples, spatulate. Their bases are very broad and are attached to the rachises in an obliquely clasping position (pl. 1, fig. 3; pl. 3, figs. 1, 3); in some specimens it appears that the pinna bases extend entirely around to the back or buried surface of the rachis. The pinnae are generally widest at about the middle, but the ratio of length to width varies from about 8 : 1 to 2 : 1, with the most slender pinnae borne at the tips of the fronds (pl. 1, fig. 1; pl. 3, fig. 2). The shorter, relatively broader pinnae are assumed to be most characteristic of the basal ends of the fronds. Complete frond specimens have not been found, however, and this point thus remains speculative. A very broad or "stubby" pinna, 4.0 cm long and 2.0 cm wide, is shown on plate 2, figure 3.

The pinnae range from 2.0 to 11.5 cm in length and from 2.5 to 3.0 cm in width; the pinnae gradually decrease in size toward the frond tips. Pinnae approximately 6.0 cm long and 2.0 cm wide seem to be predominant in the collection, and lengths of more than 7.0 cm or widths of more than 2.5 cm are uncommon. Lateral margins of the pinnae curve gently and equally from base to tip; the tip is usually approximately equal to the base in width and about half as broad as the widest part of the pinna. In some of the relatively shorter, broader pinnae, however, there is a rather pronounced and abrupt constriction of the foliar outline just below the pinna apices. This constriction results in somewhat spatulate outlines (pl. 2, fig. 3). Lateral margins of the pinnae are always entire.

The most characteristic morphological feature of the pinnae is their truncated tips, clearly shown on plate 1, figures 3 and 4, and plate 2, figures 4 and 5. This character is so diagnostic and consistent, in fact, that the generic identification may be made with complete assurance on the basis of one pinna apex. The pinna apices are sharply truncated, forming apical margins virtually perpendicular to the long axes of the pinnae. The apical margin is shallowly concave, and its juncture with the two lateral margins usually forms two fairly angular corners; arcuation of the apical margins is least pronounced in the smallest pinnae. As demonstrated by comparison of plate 2, figures 4 and 5, with plate 3, figure 2, every pinna, large or small, in which the apex is preserved, demonstrates this distinguishing characteristic. Complete absence of evidence of foliar splitting is a unique circumstance which one might expect with foliar tips of this type. This is evidently due to the presence of an apparently solid strip of vascular tissue along the truncate margin. This tissue is formed by the convergence and coalescence of the veins at the pinna apex. This strip is seen as a slightly thickened carbonaceous residue in some specimens, and very possibly it served as a mechanical agent that prevented splitting of the laminae.

None of Darrah's types show incised or lobed apical margins, but there is evidence of apical truncation. The upper appendage in the specimen (Harvard University No. 19721) shown at the bottom of the plate facing page 182 in Darrah's paper (1938) shows veins converging toward a much-narrowed foliar tip, the margin of which appears to be identical with that described for the U.S. Geological Survey material. My examination of the specimen itself confirms this appearance of identity.

There is considerable variation in spacing of pinnae and angles of decurrence. In some specimens the pinnae stand out at right angles to the rachis (pl. 1, fig. 2), but in most specimens the angle of decurrence is between approximately 45° and 70°. (See pl. 1, fig. 3; pl. 3, fig. 1.) This angle decreases gently toward the frond apex, as might be expected, and in the smaller apical specimens the terminal pinnae are directed almost straight forward. The variation of this feature is so broad and subtly intergrading that, as a result of observations of the 400 odd specimens at hand, it is considered that specific differentiation is impossible on the basis of pinna decurrence. Figures 1, 2 and 3 of plate 1 show the variation in pinna decurrence.

The pinnae are inserted alternately, as is clearly shown on plate 1, figure 3. In some specimens a subopposite arangement is shown, but there is no evidence of clearly opposite foliation.

The pinnae are either widely spaced or so crowded as to overlap each other to form an imbricate arrangement. The spaces between successive pinnae on the same side of a rachis may be as much as 2 cm (pl. 3, fig. 1) or they may be so closely inserted that no intervening space is discernible (pl. 2, fig. 5). It appears that the basal pinnae are the most distantly arranged, with increasingly crowded pinnae toward the frond tips.

As shown on plate 2, figures 4 and 5, the pinnae may overlap each other to the extent that half or more of the laminar area of one is obscured by the other. In these specimens, the distal margin of one pinna is overlapped by the proximal margin of the next higher pinna; in this arrangement the pinnae approximate the succubous condition of some leafy liverworts. In other specimens the relationship is reversed, simulating the incubous condition. These arrangements are usually consistent within a given specimen and there is an approximately equal distribution of "succubous" and "incubous" specimens in the collection. In "succubous" specimens the lower, or proximal part of the obliquely clasping pinna base is visible, whereas the distal part is buried beneath the rachis; the opposite condition obtains in the "incubous" specimens. As I was not able to observe the method of attachment of these fronds to the parent plant, it was not possible to decide with certainty whether the "incubous" or "succubous" side is the ventral, or upper side of the frond.

Another noteworthy feature of these fronds is that the pinnae are nearly always preserved in unfolded or unbent conditions. They lie perfectly flat on the bedding planes of the enclosing shale, and their symmetrical arrangement is virtually undistorted. This circumstance gives one the impression that the living fronds were sturdy structures with stiff cycadlike pinnae that were sufficiently rigid to maintain their living postures after being detached and enclosed within the sediments.

The vascularization of the pinnae consists of a dense system of moderately strong, closely set parallel veins that dichotomize sparingly. Depending on the size of the pinnae, from 8 to 24 veins enter the base of the lamina, and a short distance beyond this approximately half of the veins divide equally (pl. 3, fig. 3). The area of most abundant vascular dichotomy coincides with the basal part of the pinna where the pinna width increases most abruptly. A few of the veins dichotomize a second time, but secondary dichotomies are rare relative to the incidence of primary dichotomies. The veins then continue, evenly spaced, as far as the truncated apical margin of the pinna, where they converge toward each other as the lamina decreases in width (pl. 1, fig. 4). At the margin the veins are so closely crowded that they apparently coalesce to form the previously discussed continuous band of vascular tissue across the tip. The outer veins, or the ones just inside the lateral margins of the pinnae, never terminate in the lateral margins but, as all the other veins, continue to the apical margin.

Near the broadest part of the pinna, the number of veins varies from 8 to 10 in the smallest pinnae to a maximum of 58 in the largest. Most of the pinnae (those in the 6.0- by 2.0-cm size category) have between 40 and 50 veins. The veins are as much as 0.2 mm thick, and the spacing between them at the broadest part of the pinna may be as wide as 1.0 mm; more often, however, this distance is about 0.5 mm.

Although the venation of this plant is characteristically simple and open, there is one exceptional specimen (pl. 2, fig. 1) that entails unusual morphologic interest in that it distinctly exhibits anastomosis of the venation. The veins of this specimen are unusually well preserved; they are few and are spaced widely enough to permit a comprehensive close examination. This pinna is complete except for minor breakage of the apical and disto-lateral margins. Several dichotomies are clearly shown in the basal one-quarter of this pinna; 10 veins enter the base of the lamina, but 17 are noted when counted across the middle. Within a centimeter of the apex of the pinna three distinct anastomoses—one near the distal margin and two in the proximal half of the lamina—result in a reduction from a maximum of 17 veins to 14 veins that actually extend to the pinna apex. The two anastomoses nearest the lateral margins of the pinna involve the fusion of the two members of the same basal dichotomy, the reconstituted veins then continuing undivided to the apical margin (type "A" of Arnott, 1959). The third anastomosis involves coalescence of divisions of two adjacent veins (Arnott's type "C"). Other pinnae attached to this specimen show no evidence of anastomosis; furthermore, close examination of many other well-preserved specimens revealed no other examples of vascular anastomosis. It thus seems that a decidedly anomalous situation is confronted here, and one of the rare anomalies in an otherwise simple plan of foliar venation has fortunately been preserved for observation.

Unfortunately all cuticular matter in the "Emily Irish" shale was destroyed during diagenesis. This destruction left only thin carbonaceous residues of the original plant substances. The matrix yields neither spore coats nor foliar cuticles, so that there is no information available on the epidermal characteristics of this plant. Furthermore, there is no direct evidence of the nature of its fructifications.

COMPARISONS

The combination of linear pinnae, parallel venation, truncated tips, and obliquely clasping bases of the pinnae is unique to *Russellites*—the generic name herewith applied to the Texas material. This combination of features narrowly limits the selection of known fossils with which comparisons might be drawn. Although there are several genera of Paleozoic and Mesozoic cycadophytes (*Pterophyllum*, *Ptilophyllum*, and *Zamites*, for examples) whose pinnate fronds produced linear pinnae with parallel, open venation, they differ from *Russellites* in sufficient detail that exacting comparisons would be unwarranted. At the same time, the linear shape and parallel venation of *Russellites* pinnae suggest comparison with small leaves of *Cordaites*. However, neither the sharply truncated foliar tips nor the frondose, bilateral arrangement of laminar segments of *Russellites* are known among the cordaitaleans; the straplike leaves of the cordaitaleans have typically rounded tips and are arranged on the shoots in closely set spirals.

Another plant distantly reminiscent of *Russellites* is the late Paleozoic and early Mesozoic genus *Schizoneura*. The leaves of *Schizoneura* are shaped approximately like pinnae of *Russellites* and the venation is again parallel. The probability of identity or even affinity, however, is negated by the fact that *Schizoneura* has articulate stems with the leaves attached in whorls. From the standpoint of basal attachment and distribution of foliar laminae, the closest resemblance to *Russellites* is presented by the genus *Noeggerathia*. The leaves of *Noeggerathia* are alternate and have clasping bases, but their tips are rounded with dentate margins, and thus are readily separable from *Russellites*.

The Permian genus *Phylladoderma* Zalessky, from the Pechora basin, U.S.S.R. deserves comment at this point. Previously regarded as a cordaitean, *Phylladoderma* was recently placed in the Ginkgoales by Neuburg (1960), largely on the basis of cellular details derived from excellent cuticular preparations. The feature of primary interest in regard to *Phylladoderma* is Neuburg's (1960, fig. 7) reconstruction of a leaf of *P. arberi* Zalessky, emend. Neuburg. This drawing shows a parallel-veined leaf of approximately the same size, shape, and proportions as a large pinna of *Russellites*. The veins dichotomize sparingly near the base of the leaf, and the base contains a pair of enlarged processes that may signify a clasping habit. Particular attention is drawn to the apex of the leaf, which has a concavely truncate margin toward which the veins converge. This illustration bears the closest resemblance I know of to the apical margins of the pinnae of *Russellites*, and invites further examination of the Soviet material.

Although the laminar tips of *Russellites* and *Phylladoderma* are remarkably similar, there are also morphological disparities that merit consideration. According to Neuburg's figures 5 and 6, plate 16, figure 7, and plate 17, figures 2, 4, and 6, the leaf bases of *Phylladoderma* are attenuated into narrow petiolelike outlines totally unlike the broad bases of *Russellites* pinnae. Furthermore, the drawings in Neuburg's figures 5 and 6 indicate that the entire system of leaf venation is derived from a single vein that enters the leaf base and dichotomizes several times to produce the many parallel veins; this is in contrast to the venation of *Russellites*, in which several veins enter the base of the pinna.

In view of the foregoing contrasts and the lack of evidence of pinnate architecture in *Phylladoderma* it is concluded that *Phylladoderma* is more leaflike than pinnalike and there is no sound basis for coidentification of *Russellites* and *Phylladoderma*. The similarity between the laminar apices of the two must therefore be regarded as a remarkable case of parallelism.

TAXONOMY

It is evident from this study that (1) the U.S. Geological Survey material and Darrah's "*Tingia*" are identical, (2) the two suites of specimens are distinct from Halle's *Tingia*, and (3) they are distinct from all other fossil plants with which comparison might be suggested. In recognition of these distinctions the new generic name *Russellites* is herewith established, with Darrah's material and taxa included in the protologue. Darrah's two species, *T. taeniata* and *T. kempiae* are indistinguishable from each other except in comparison of angles of departure of the pinnae, an extremely variable feature that appears to have no infrageneric taxonomic value. The two "species" are therefore synonymized and transferred to *Russellites;* of the two names, *taeniata* is selected for the type species of *Russellites* because of its implication in regard to pinna shape.

It is a pleasure to name this genus after Mr. and Mrs. Mart Russell, of Seymour, Tex. The Russells' interests in my paleobotanical investigations have facilitated my efforts considerably, and their hospitality has contributed much to the overall enjoyment of my collecting trips to the Seymour area.

Genus RUSSELLITES Mamay, new genus

***Tingia* auct. non Halle. Darrah, 1938.**

Type species.—Russellites taeniata (Darrah) Mamay.

Generic diagnosis.—Plants with large, pinnate, bilateral cycadlike fronds. Pinnae elongate, alternate, with clasping bases; lateral margins entire, apical margins sharply truncated, with concavely crescentic outlines. Veins numerous to sparse, parallel, sparsely dichotomous, rarely anastomosing, each terminating at apical margin of pinna. Fructifications, cuticular details, and internal anatomy unknown.

Russellites taeniata (Darrah) Mamay, new combination

Plates 1–3

***Tingia taeniata* Darrah, 1938, p. 180, 2 figs. (facing p. 176); 1939, fig. 169; Boureau, 1964, p. 515.**

***Tingia kempiae* Darrah, 1938, p. 180–181, 2 figs. (facing p. 182); Boureau, 1964, p. 515.**

?*Tingia* sp., Read and Mamay, 1964, pl. 18, fig. 3.

Specific diagnosis.—Rachises unbranched, long, stout, to 1.0 cm broad, tapering gently to 2.0 mm or less in breadth. Pinnae alternate to subopposite, decurrent, with broad, obliquely clasping bases; pinna insertion on rachis distant (to 2.0 cm apart) to crowded, most crowded terminally; angles of pinna insertion varying from perpendicular to acute, typically 45°–70°, decreasing toward frond apex. Pinnae with gently and equally curving lateral margins, linear-oblong, ovate, obovate, or rarely spatulate, 2.0–11.5 cm long, 2.5 mm to 3.0 cm wide, 2–8 times as long as broad, with proportionately broadest pinnae produced toward frond bases; pinna bases and tips usually equal in width and half as wide as widest part of lamina. Pinnae overlapping, either "incubously" or "succubously." Veins slender or moderately stout, to 0.2 mm thick; 8–20 veins entering pinna bases, approximately half dichotomizing within basal one-third of lamina, some dichotomizing secondarily; anastomoses rarely formed, between members of the same dichotomy or between divisions of adjacent veins, anastomosed veins remaining undivided. Veins 8–60 per pinna, counted at broadest part of lamina, evenly spaced, converging toward pinna apices and forming narrow band of concrescent vascular tissue across truncated pinna tips.

Lectotype.—Botanical Museum of Harvard University, paleobotanical collection 19720, illustrated by Darrah (1938) as upper specimen on plate facing p. 176 (lectotype designated because of lack of holotype designation by Darrah).

Paratypes.—BMHU 19721–19723.

Stratigraphic occurrence.—Approximately the middle of the Belle Plains Formation (presumably correlative with Valera Shale Member), Leonard(?) Provincial Series, Lower Permian Series.

Geographic occurrence.—"Emily Irish" locality, Baylor County, Tex. (USGS fossil plant loc. 8959).

DISCUSSION

MORPHOLOGY OF RUSSELLITES

In order to discuss the systematic placement of *Russellites* in a completely cogent context, some reasonable morphological interpretation of these impressive structures should be attained. Are they true branches (shoots) with plagiotropically arranged appendages simulating compound leaves, or are they actually leaves? It is evident from the comparisons drawn in the foregoing pages that this fundamental morphological interpretation is not necessarily a simple one to make, particularly in the absence of knowledge of details of the gross growth habit of the plant. Leafy branch systems and pinnately compound fronds may resemble each other, and as in the specific instance of the genus *Plagiozamites*, what was thought to be a frond yesterday may be regarded as a leafy shoot today. (See Boureau, 1964, p. 493.)

Disregarding for the moment the overall frondose aspect of *Russellites*, the available evidence bearing on this important morphological question is very limited and, in fact, mostly negative. Some importance may be attached to the large number of specimens and the proportionate absence of certain features that would weigh heavily in morphological interpretations. For example, none of the axial fragments show evidence of a tendency to produce lateral branchlets, so it might reasonably be deduced that these axes were more likely leaf rachises rather than branches or shoots. The absence of stipules, aphlebiae, fructifications or other details is both unfortunate and inconclusive. A few of the specimens of *Russellites* show the terminal ends of the leafy organs, none of which give an indication of the coiling or circinate vernation that would establish beyond doubt the frondose nature of the organs, and almost as certainly would indicate affinities within the ferns or cycadophytes. It must be cautioned, however, that these may represent the tips of mature fronds in which the nature of leaf vernation cannot be established, and thus another line of possible evidence is reduced to inconclusive value.

The total effect of this brief assay of the meager morphological criteria on hand is the conclusion that if

Russellites is not a conventional frond but a specialized plagiotropic shoot, there is no way of proving it without details of the internal anatomy. Pending the discovery of contradictory evidence, then, I prefer to regard *Russellites* as a frond, or pinnate leaf, simply because it looks like one.

SYSTEMATIC POSITION

In reviewing the evidence pertinent to the systematic placement of *Russellites*, its physical characteristics, geologic age, and floristic associates have all been given careful consideration. The *Russellites* material has been shown to and discussed with a number of colleagues, with the resultant emergence of several tentative ideas regarding taxonomic relationships. The pinnately compound leaf is suggestive of the ferns, pteridosperms, cycadeoids, and true cycads, and one discussant went so far as to suggest enthusiastically that it not only looks like, but is a palm, and "not even a primitive palm". The latter idea is, of course, an intriguing one and I wish I were in a position to offer incontrovertible substantiation thereof. The present state of our knowledge of the geological history of the monocotyledonous angiosperms, however, urges caution in this matter; in the absence of attached flowering parts I am not prepared to pursue this as a logical alternative.

Russellites is reminiscent of foliage of both the cycads and cycadeoids. If it could be demonstrated first that one or the other of these two groups is the proper taxonomic receptacle for *Russellites*, it would then be necessary to produce evidence of cuticular details to arrive at the ultimate decision. The concept of cycadean affinity is interesting because little is known of the early history of the cycads, and firmly authenticated reports of this group in pre-Triassic rocks are not known. To establish the presence of true cycads in the Lower Permian would constitute an exciting advance in the history of the spermatophytes, and should this be accomplished, *Russellites* could be regarded as a posible candidate for inclusion within that group. The U.S. Geological Survey collections contain several undescribed Permian specimens of seed-bearing infructescences with bilateral symmetry and other features reminiscent of the cycadalean megasporophyll. On the basis of these specimens and their association in the same beds with *Russellites* I reserve a final judgment on the taxonomic affinities of *Russellites*.

Because the cycadeoids are geologically more ancient than the cycads, it would seem more feasible to attempt to ally *Russellites* with the cycadeoids. But again, the evidence is not convincing. Petrified cycadeoids are known from the Jurassic and Cretaceous of this continent, and cycadeoid foliage was fairly common in the Triassic, but as far as I know, neither vegetative nor reproductive parts have been identified from the Permian of North America. To be sure, Bassler (1916) reported *Plagiozamites* in the Pennsylvanian Conemaugh Formation of Maryland, but according to Boureau (1964, p. 493), *Plagiozamites* is no longer regarded as cycadophytic and is treated as a member of the Noeggerathiales.

It thus strikes me that the possibility of a cycadeoidean affinity for *Russellites* is remote. Similarly, even though the ferns and pteridosperms collectively comprise the most prominent pteridophyllous element in the Paleozoic floras, I choose to discount an alliance of *Russellites* with those groups because none is known whose foliar characteristics find favorable comparison with the morphological peculiarities of *Russellites*.

Certain circumstantial evidence prompts me to terminate this discussion with an appraisal of the possibilities that *Russellites* belongs within the noeggerathiopsid complex, as recently treated by Boureau (1964). Of primary consideration is the fact that *Discinites*, perhaps the best known noeggerathiopsid fructification, appears in both the Pennsylvanian of Michigan (Arnold, 1949) and the Permian of Texas (Mamay, 1954). *Discinites* is, in fact, a conspicuous element in the "Emily Irish" flora (unpub. data), and several fine specimens have been found in the same beds with *Russellites*. By excluding from the Texas flora the taxa whose reproductive structures are substantially understood, *Russellites* stands out as one of the few entities that may eventually be proved to be part of the same plant that produced *Discinites*. The specimen illustrated by Darrah (1939, fig. 67) as a *Tingiostrobus* from the Permian of Texas might have had critical bearing on this association, had it been available for examination. The illustration shows a large strobiloid fructification attached to the terminus of a stout axis with obscurely represented foliar remains apparently attached. The cone seems to resemble closely the *Discinites* specimens in the U.S. Geological Survey collection, but the nature of the foliage cannot be determined from the photograph. Had the foliage been identical with Darrah's *Tingia* and the fructification demonstrated as *Discinites*, then the noeggerathiopsid alliance of *Russellites* would have been established. Darrah informed me (oral commun., 1967) that the specimen began to crumble soon after the illustration was published and although attempts were made to repair it, the specimen was beyond restoration and scientifically useless.

A second point of possible significance rests on similarities between *Russellites* and the various vegetative organs attributed to the noeggerathiopsids by Boureau. All these genera—*Noeggerathia*, *Tingia*, *Saaropteris*, *Plagiozamites*, and *Paleopteridium*—have more or less elongate ultimate foliar segments with parallel, sparingly dichotomous veins that terminate at or very near the laminar apices. In these genera the apices are rounded, dentate, or digitate, in sharp contrast to the truncate, entire tips of the laminae of *Russellites*. *Paleopteridium* and *Saaropteris* have bipinnate fronds, very unlike those of the other noeggerathiopsids and *Russellites*. *Tingia* is immediately distinguished from *Russellites* for reasons already delineated, but the remaining genera *Noeggerathia* and *Plagiozamites* warrant further consideration.

In *Noeggerathia* and *Plagiozamites*, the foliar segments ("leaves," according to Boureau) have broad, clasping bases that receive several veins of equal strength from the parent axis, and the bases are inserted obliquely, as in *Russellites*. In *Plagiozamites* the whole "leaf" margin is denticulate, whereas margins of the pinnae of *Russellites* are entire. *Plagiozamites* also differs from *Russellites* in the form of the tips of the "leaves," which are rounded or pointed but never truncated.

A closer comparison to *Russellites* is found in *Noeggerathia*, the "leaves" of which tend to overlap each other (Boureau, 1964, fig. 418). Thus, except for the rounded dentate-margined tips, *Noeggerathia* bears some important resemblances to *Russellites*. The foliar segments of *Noeggerathia* are commonly regarded as leaves (Halle, 1927, p. 238–239), and this viewpoint is in basic conflict with my interpretation of *Russellites*. It appears to me, however, that a final resolution of this problem must depend on knowledge of the internal vascular anatomy of these plants, and regardless of present differences of philosophical viewpoints and terminologies, it cannot be denied that *Russellites* and *Noeggerathia* share some significant physical characteristics.

Considering all the available evidence, then, it seems most plausible for the time being, to regard *Russellites* as a noeggerathiopsid, with *Noeggerathia* its putatively closest relative. Consequently, although Darrah's generic identification of the "Emily Irish" plant was incorrect, he must be accredited with an accurate evaluation of the suprageneric relationship of his material. *Russellites* might well be regarded as a rather advanced member of the noeggerathiopsid assemblage, from the standpoints of its morphologically specialized foliar apices and the clear evidence of a tendency to form an anastomosing venation pattern among a group of genera in which anastomosis is otherwise unknown.

If the association of *Russellites* and *Discinites* proves to be more than accidental and if the two represent fertile and sterile parts of the same plant, it would be well to examine the effects of such an eventuality on the systematics of the noeggerathiopsids.

Boureau (1964, p. 481) divided the class Noeggerathiopsida into three orders: Noeggerathiales (*Noeggerathia*, *Noeggerathiostrobus*, and *Plagiozamites*), Discinitales (*Discinites*, *Palaeopteridium*, *Saarodiscites*, and *Saaropteris*), and Tingiales (*Tingia* and *Tingiostachya*). The orders Noeggerathiales and Tingiales are characterized by plagiotropic shoots with pinnalike leaves, whereas Discinitales contains filicoid bipinnate foliage and cones of the *Discinites* type. Should the Texas *Discinites* and *Russellites* be established as parts of the same plant, and should my assumption of close relationship between *Russellites* and *Noeggerathia* be proved correct, it would become necessary to revise Boureau's concept of Noeggerathiopsida in such a way as to combine Discinitales and Noeggerathiales. It might be necessary, at the same time, to exclude *Palaeopteridium* and *Saaropteris* from the whole complex. It is evident that the noeggerathiopsids are a very specialized group and not very fernlike. The inclusion of the filicoid *Saaropteris* and *Palaeopteridium* has always struck me as far fetched, and I have previously expressed skepticism toward the supposed *Discinites-Palaeopteridium* alliance on the basis of disparities between their stratigraphic ranges (Mamay, 1954, p. 10); furthermore, Boureau (1964, p. 497) reiterates the evidence that *Palaeopteridium* is not known in association with *Discinites* where the latter has been found in Belgium and the Netherlands.

GEOLOGIC AND GEOGRAPHIC DISTRIBUTION OF RUSSELLITES

A survey of the Permian U.S. Geological Survey collections, accumulated from the southwestern United States by David White, C. B. Read, and myself, and the extensive Permian collections of the Texas Bureau of Economic Geology, has revealed no occurrences of *Russellites* from any other locality. Darrah (1937, p. 199) reported the presence of two species of *Tingia* near Geraldine, Tex.; according to Darrah (oral commun., 1967) this statement was based on field labels provided by Robert Witter and Theodore E. White. A locality near Geraldine would presumably lie somewhere within the Admiral Formation, which underlies the Belle Plains Formation. I know of no extant collections that would corroborate this occurrence.

In my study of the Harvard collection I noted one specimen of *Russellites* in a drawer of material from a locality near "3 forks of Wichita River," Archer County; the collection is indicated to be of Putnam age, significantly older than the Belle Plains material. The associated plants are predominantly walchian conifers and at least two species of *Callipteris*. Comparison of matrix and preservation gives the impression that this single specimen of *Russellites* is actually from the "Emily Irish" locality and was placed in the wrong drawer. I am very skeptical of the accuracy of its location in the collection.

The information presently available demonstrates that *Russellites* was narrowly restricted in both stratigraphic and geographic distribution. This is almost certainly partly attributable to incompleteness of the fossil record. Nevertheless, it is strange that *Russellites* has not been found at some of the several nearby localities where plants from formations adjacent to the Belle Plains occur in abundance. This circumstance may involve a facies factor. The "Emily Irish" flora, the most diversified Permian assemblage from any American locality I know of, contains a predominance of pecopterid ferns and other forms that characterized the earlier swamp floras. Other geographically and stratigraphically adjacent floras are generally much less diverse taxonomically, and they appear to reflect somewhat more rigorous environments. The restriction of *Russellites* to the lush "Emily Irish" flora may indicate a lesser degree of ecologic plasticity than most of its contemporaries, and, consequently, its occurrences in the Permian may continue to be rare. In short, the specialized morphology of *Russellites* may reflect adaptations to the type of ecologic conditions that sustained the "Emily Irish" flora, and the plant may prove valuable as a facies indicator.

The important species *Gigantopteris americana* White is abundantly associated with *Russellites* in the "Emily Irish" flora. This is not surprising, because the plant-bearing beds at Fulda, Tex., where White made the initial discovery of *Gigantopteris*, evidently lie at the same stratigraphic level as those of the "Emily Irish" deposit. This association is mentioned here in order to correct Darrah's (1938, p. 185) statement that "*Gigantopteris* in Texas is younger than *Tingia*." It is true that the stratigraphic range of the genus *Gigantopteris* extends upward into rock units younger than the "Emily Irish" deposit (see Read and Mamay, 1964, p. K13), but Darrah's statement gives the incorrect impression that the two genera might be useful as independent indices of different time units. The fact that *G. americana* and *Russellites taeniata* are intermingled in the same beds at the "Emily Irish" locality appears to distinguish this combination of species as a valuable guide to Belle Plains time. Only continued studies of the Permian plants of the southwestern United States will show which of the two species is the more critical as a guide fossil or facies indicator. Should *Russellites* prove to be stratigraphically restricted over a large geographic area, its utility as a guide fossil will be enhanced by its easily identifiable features. Thus, the same set of physical peculiarities that inject difficulties into the morphologic and systematic interpretation of *Russellites* serve conversely to emphasize its value as a stratigraphic tool.

EVOLUTIONARY AND PALEOFLORISTIC IMPLICATIONS

The "sudden" appearance of *Russellites*, with no evidence of its forebears in the form of morphologically similar plants in older rocks, presents an enigma as to the phylogenetic derivation of this plant, unless one considers the Carboniferous *Plagiozamites* as a putative progenitor. Furthermore, I know of no obvious descendants of *Russellites*. It is of no minor significance that all the forms that might be construed as having shared a common ancestry seem to be restricted to a relatively thin section of the stratigraphic column. A similar, probably parallel, situation obtains with the gigantopterids, one of the more important groups contemporary with *Russellites*. These two examples contribute to the growing accumulation of evidence that Early Permian time was an epoch of rapid plant evolution, some of the products of which may have evolved morphologically at a speed incompatible with lesser rates of physiological adaptation. The result was relatively sudden extinction of certain specialized groups such as represented by *Russellites* and *Gigantopteris*, whereas more conservative, long-established, and ecologically more adaptable lineages such as the marattiaceous ferns and subarborescent or herbaceous arthrophytes continued to persist beyond the Paleozoic.

In his paper on *Gigantopteris*, White (1912) commented on the similarities between the Permian floras of Asia and North America. Darrah (1938) reiterated and emphasized these observations, on the strength of his identification of the "Emily Irish" material as *Tingia* and its supposed congeneric identity with Halle's Chinese material. My unpublished studies of the American gigantopterids convince me that the similarities between the American and Asiatic members of that complex are more apparent than real, and therefore are misleading from the standpoint of transoceanic paleofloristic linkages. Comparisons of *Russellites* with *Tingia* permit elucidation of a case of taxonomic differences being partially masked by superficial morphological resemblances. These two instances tend to foster the opinion that thorough comparisons between the Permian floras of Asia and North America will ultimately establish a much more complex paleofloristic picture than commonly envisaged. True, the geologically long-entrenched lineages are represented in the two floras by many common elements, some even conspecific. On the other hand, taxa like *Tingia* and *Russellites* contribute to the biological individuality of their respective botanical communities.

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[Italic numbers indicate descriptions and major references]

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PLATES 1–3

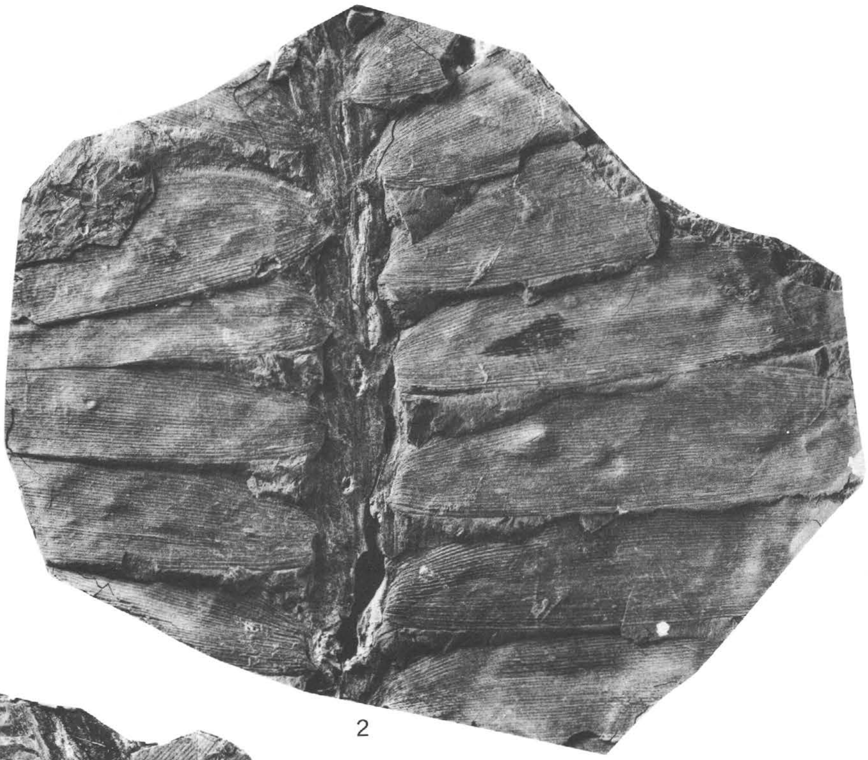
PLATE 1

[All figures natural size unless otherwise indicated]

FIGURES 1–4. *Russellites taeniata,* (Darrah) Mamay n. gen., n. comb. (p. I 9).

1. Apical part of frond, showing straight rachis, closely set pinnae, narrow angles of pinna insertion, and, at upper left, square-cut truncations of pinna apices. USNM 42702.
2. Frond fragment showing perpendicular insertion and "succubous" overlapping of pinnae. USNM 41773.
3. Typical frond fragment, showing distant spacing, alternate insertion, and broad angles of decurrence of pinnae. Venation and truncate apices shown well in pinnae at left. USNM 42703.
4. Distal part of pinna, showing concavely crescentic apical margin, parallel veins converging toward pinna apex, and thickened band of presumably concrescent vascular elements across pinna apex. USNM 42704. × 2.

1



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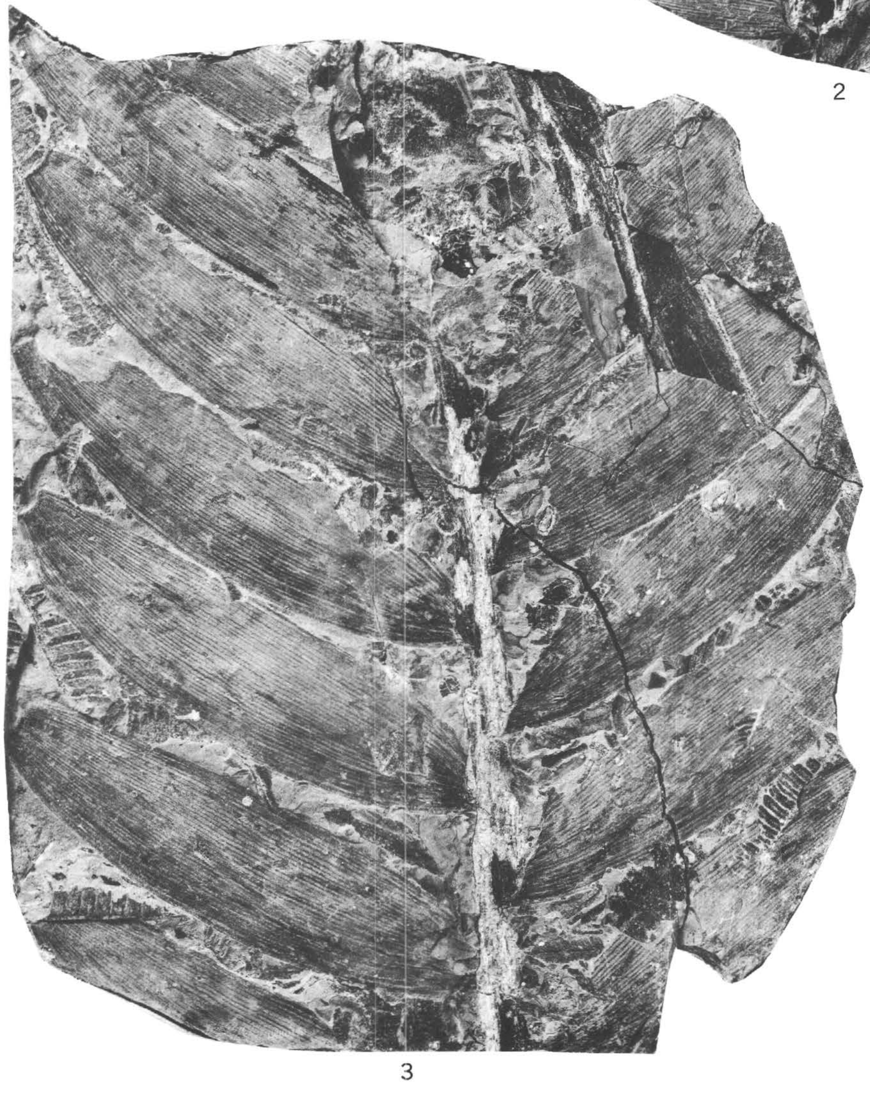

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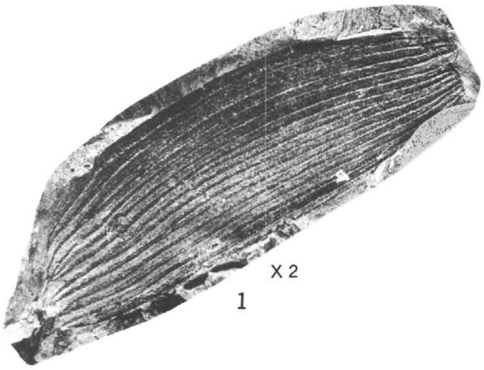
RUSSELLITES TAENIATA (DARRAH) MAMAY

PLATE 2

[All figures natural size unless otherwise indicated]

FIGURES 1–5. *Russellites taeniata* (Darrah) Mamay, n. gen., n. comb. (p. I 9).

1. Pinna showing details of venation. Basal dichotomies seen in veins toward left (proximal) end of pinna; anastomoses of veins shown toward right (apical) end of pinna. USNM 42705. × 2.
2. Specimen showing results of Vibro-tool excavation across pinnae on left and across rachis. USNM 42706.
3. Frond fragment showing relatively short, broad pinnae with abrupt narrowing of apices. USNM 42707.
4. Unusually long fragment of terminal part of frond, showing gradational spacing of pinnae, consistently truncated pinna apices, and apparent transition from "succubous" to "incubous" overlapping of pinnae. USNM 42708a.
5. Counterpart of specimen shown in fig. 4, clearly illustrating the "succubous" condition. USNM 42708b.



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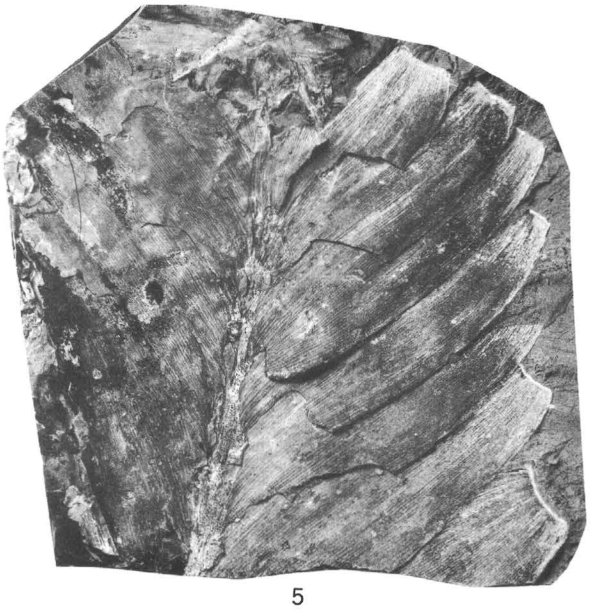

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RUSSELLITES TAENIATA (DARRAH) MAMAY

PLATE 3

[All figures natural size unless otherwise indicated]

FIGURES 1–3. *Russellites taeniata* (Darrah) Mamay, n. gen., n. comb. (p. I 9).

1. Large specimen showing thick rachis, distantly spaced pinnae, and obliquely clasping pinna bases. USNM 42709.
2. Terminal part of frond, showing small pinnae with narrow angles of insertion and nearly square apical truncations. USNM 42710.
3. Frond fragment showing details of venation and obliquely clasping pinna bases. USNM 42711. × 2.


1


2


3 X 2

RUSSELLITES TAENIATA (DARRAH) MAMAY

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