end and measures 1.7 cm long (incompletely preserved) and 1.1 cm in diameter. The maximum diameter of the largest specimen is 2.3 cm.

Microsporophylls (leaves) are attached broadly at their bases and are spirally arranged around the central axis (Fig. 1A). They decrease in thickness rapidly toward the margin of the cone, and their upturned distal portion extends several centimeters toward the cone apex forming a tightly enclosed unit. Attached to the lower surface of each sporophyll are eight to ten radially elongate microsporangia (pollen sacs) that are arranged in a single row (Fig. 1B). Individual sporangia are approximately 0.6 by 1.8 mm and possess a multilayered wall (Fig. 1C); dehiscence occurs as a longitudinal slit in the wall along the lower surface, dividing the sporangium in half. Pollen grains (Fig. 1D) are radially symmetrical and typically compressed. In polar view they are circular and about 26 μ in diameter. The wall is thick and ornamented by projections that extend out from a tectate exine.

Internally the cone axis consists of an irregularly shaped central pith containing abundant material suggestive of mucilage. This is surrounded by a two-parted cortex of thin-walled cells (Fig. 1B). The vascular system consists of six abaxially curved primary xylem strands, the elements of which have closely spaced scalariform secondary wall thickenings. Two traces supply each sporophyll and arise from the repeated fusion and dichotomy of the axile vascular strands. Secondary tissues do not appear to be present.

There is little doubt that this cone represents a true cycadalean staminate strobilus. These strobili most closely resemble those of *Stangeria* among living cycads (*5*). Whereas the genus *Cycas* is generally regarded as the most primitive living cycad principally on the basis of seed sporophyll morphology, *Stangeria* shows the largest number of primitive and fernlike features of any member of the Cycadales (*6*).

Thus, seed plants having staminate cones essentially like those of the Cycadales existed in the Pennsylvanian, which suggests that the order Cycadales existed then. Moreover, the essentially modern aspect of the fossil cones implies that if the Cycadales descended from noncone-bearing seed ferns, the establishment of both groups must have occurred early in the Carboniferous. Furthermore, the large number of isolated Paleozoic seeds, that in some instances are identical in morphology and anatomy to those of living cycads, may ultimately be attributed to plants of the type that produced the staminate cone described here. The same may hold true for some of the stem genera placed in the order Pteridospermales at present.

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30 December 1968; revised 26 February 1969

Cycads: Fossil Evidence of Late Paleozoic Origin

Abstract. *Plant fossils from Lower Permian strata of the southwestern United States have been interpreted as cycadalean megasporophylls. They are evidently descended from spermopterid elements of the Pennsylvanian* Taeniopteris *complex; thus the known fossil history of the cycads is extended from the Late Triassic into the late Paleozoic. Possible implications of the Permian fossils toward evolution of the angiosperm carpel are considered.*

The Cycadales or true cycads—not to be confused with the Mesozoic cycadeoids—comprise a small and ancient order of gymnospermous plants. According to most authorities they are represented in the modern flora by only nine genera. They are mostly of palmlike appearance with pinnately compound leaves and large monosporangiate cones. Prior to this report, the fossil record of cycads extended only to the Late Triassic, although there has been some agreement that cycads probably arose from some group of seed-ferns during the late Paleozoic. A long history for the group is suggested by the facts that the cycads were of substantially modern aspect in their earliest geologic appearances and that they were common in Jurassic floras.

This report deals with fossil material that adds substance to the heretofore hypothetical Paleozoic origins of the cycads, and provides some insight into questions of evolution of the cycadalean megasporophyll—probably the most diagnostic and phyletically significant part of a cycad. Some of this material may also have significant bearing on the evolutionary processes leading to the origin of the angiospermous carpel.

In 1960 Cridland and Morris (*1*) described *Spermopteris*, a new genus of Late Pennsylvanian plants from the Virgil Series in Douglas County, Kansas. *Spermopteris* has ovuliferous leaves which, in the sterile state, are indistinguishable from *Taeniopteris*. One of the commonest of Upper Paleozoic form-genera, *Taeniopteris* has large, simple, linear leaves with entire margins and open dichotomous venation. *Spermopteris* was described as the fertile form of *Taeniopteris coriacea* Goeppert; it bore a row of small gymnospermous seeds on either side of the foliar midrib on the presumably lower, or abaxial surface of the leaf.

Among the living cycads the primitive megasporophyll, as exemplified by that of the genus *Cycas*, is a leaflike structure with bilaterally arranged, basal ovules; a foliar origin of *Cycas* megasporophylls is further indicated by the fact that they are not borne in a compact cone but are part of a loose, leaflike terminal crown. Thus *Spermopteris*, with its bilaterally arranged seeds, meets the morphological requirements of a precursive cycadalean megasporophyll. The essence of this concept was published in 1968 (*2*).

The material [some mine and some from the collections made in the 1910's by White (*3*)] originated from seven outcrops in the Lower Permian of Texas, Oklahoma and Kansas. Four genera are recognized—*Cycadospadix* Schimper, *Spermopteris* Cridland and Morris, and two new genera which, for the purpose of this account, will be referred to as new genus A and new genus B.

New genus A, from the Elmo Limestone Member of Dunbar (*4*) of the Wellington Formation near Elmo, Kansas, consists of a stout, elaminar axis with small seeds attached in two lateral rows along its entire length. The well-preserved seed cuticles have cycadlike organization. Alternating with the seeds are small resinoid globules, interpreted as the remains of glands. Similar globules are found on taeniopterid leaves associated with new genus A in the same beds; these bodies are not present on any of the several other associated foliar types. On the basis of similarity of the glandular bodies, the known seed-bearing habit of *Taeniopteris*, and other substantial indirect evidence, new genus A is interpreted as the fertile basal part of a cycadean megasporophyll possessing a taeniopterid distal lamina; a reconstruction of this structure is presented in Fig. 1A. New genus A is envisioned as having evolved from a *Spermopteris*-like Pennsylvanian ancestor by a phylogenetic restriction of the fertile function to the base of the sporophyll and reduction of the lamina in that area so as to produce two basal, lateral rows of sessile ovules, such as are developed by the modern genus *Cycas*. Aside from its presumably taeniopterid, entire-margined digital lamina, new genus A is of fundamentally modern cycadean aspect.

New genus B, from the Belle Plains Formation, is based on several specimens from two localities in Baylor County, Texas. It consists of small megasporophylls with four to six basal pairs of tightly appressed ovules and a sterile, distally expanded lamina. Unlike new genus A, the fertile basal area of new genus B is laminar, with a slightly modified, foliar blade partly enveloping the ovules like the marginal indusia of some ferns. The ovules are attached to the presumably abaxial surface of the "indusium" a short distance from the midrib, similarly to the seeds of *Spermopteris* (Fig. 1B). The lower surface of a sporophyll has not been seen, and the actual extent of envelopment of the ovules by the basal indusium is unknown. It is presumed, however, to have been incomplete (Fig. 1B′). In having retained a prominent laminar tissue in the fertile base, new genus B represents an important form; it is morphologically intermediate between *Spermopteris*, with its undifferentiated lamina, and the modern *Cycas* megasporophyll, with its elaminar fertile base. A hypothetical reduction series, involving elimination of the basal lamina of new genus B and resulting in an essentially modern cycadean megasporophyll, is shown (Fig. 1, B′–E). An alternative possibility must be considered, although it is not necessarily preferred by the writer. It is conceivable that the indusium of new genus B, instead of undergoing reduction and eventual elimination, became proliferated in such a way that the opposing edges met, fused, and eventually effected complete enclosure of the ovules (Fig. 1, B′–H). The resultant ovuliferous structure would entail some of the fundamental morphological characteristics of an angiospermous carpel and, accordingly, might suggest either derivation of the angiosperms from the cycads, or a common pteridospermous ancestry for the two groups.

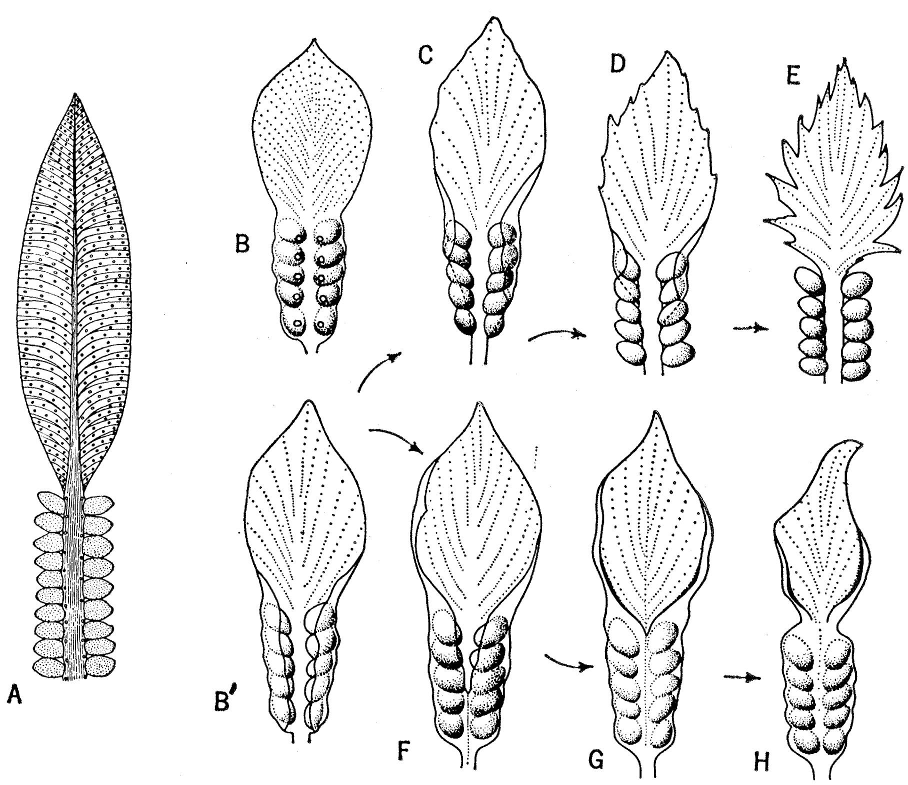

Fig. 1. Semidiagrammatic reconstructions of Permian cycad megasporophylls and possible phylogenetic derivatives. (A) Reconstruction of new genus A, showing two lateral rows of basal seeds and a taeniopterid distal lamina. Small glands appear between veins on the lamina and singly between adjacent seed bases. Size of lamina reduced (approximately 50 percent) relative to the size of the ovuliferous petiole. (B and B′) Reconstructions of megasporophylls of new genus B, showing paired, basal ovules, partly enclosed by inrolled margins of the lamina; extent and margination of the distal lamina conjectural. (B) New genus B shown in presumed adaxial view, with basal lamina rendered transparent in order to show seed positions; small circles on seeds represent points of attachment to the lamina; (B′) same, shown in presumed abaxial view, with ovules partly enclosed. (B′, C–E) Proposed evolutionary series, beginning with new genus B, and resulting in a modern *Cycas*-type of megasporophyll (E) by reduction of the lamina in the basal, ovuliferous part of the sporophyll; C and D are hypothetical intermediate forms. (B′, F–H) An alternative evolutionary series involving proliferation and marginal fusion of the basal part of the lamina, resulting in a carpel-like structure (H) with completely enclosed ovules; F, G, and H are hypothetical forms.

Relationships between new genera A and B are debatable, although new genus A is probably the more advanced of the two because of its reduced lamina in the ovuliferous area. Direct derivation of new genus A from B is unlikely because the two are essentially contemporaneous; more probably they represent early cycadean divergences from a common Pennsylvanian spermopterid ancestral stock. The fact that *Taeniopteris* is the only foliar element common to all the Permian floras containing cycadalean fossils strongly suggests derivation of most, if not all, cycads from a taeniopteroid complex.

The summary effect of this study is to confirm long-standing suspicions that the cycadean lineage arose from the Paleozoic pteridosperms. It seems clear that much of the basic evolution of the megasporophyll occurred during the Wolfcampian time interval of the Early Permian. This is strong evidence in support of Harris' opinion (*5*) that "by Jurassic times the family had probably completed its evolution."

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20 January 1969