Cycads: Evidence from the Upper Pennsylvanian

Abstract. *The fossil record of true cycads is extended from the Upper Triassic to the upper Pennsylvanian.*

Cycadophytes are a unique group of naked-seeded plants that resemble ferns more closely in foliage, anatomy, and presence of reproductive structures on megaphylls than do any other seed-producing plants. The group includes the seed ferns (Pteridospermales) that are first found in the Devonian and extend into the Upper Cretaceous, the bennettites or "fossil cycads" (Cycadeoidales) that are principally Mesozoic, and the true cycads (Cycadales) that up to this time are first found in Upper Triassic rocks (*1*). The order Cycadales is the only extant group within the Cycadophyta.

Although the order was at one time almost worldwide in distribution (*2*), the nine living genera (*Bowenia, Cycas, Zamia, Ceratozamia, Macrozamia, Dioon, Microcycas, Encephalartos,* and *Stangeria*) are now restricted for the most part to the tropical and subtropical parts of Asia, Australia, South Africa and the Americas. These plants resemble palm trees in having a stout, generally unbranched, trunk and crown of leathery frondlike leaves at the apex. Reproductive structures are produced on modified leaves that are usually arranged into compact cones in all but one genus, with male and female cones borne on separate plants. The stem has a broad pith and a ring of vascular bundles that is surrounded by a broad zone of cortical tissues with numerous mucilage canals. Secondary wood is scant and it is characterized by thin-walled tracheids and abundant ray parenchyma.

Some morphologists believe the Cycadales have evolved from some Paleozoic pteridosperm ancestor near the end of the Carboniferous. Proponents of this view (*3*) note the similarity in the loosely constructed wood, pattern of vascular system, large pith with mucilage cells, seed anatomy, pollen morphology, and extensive persistent cortical tissues present in the Cycadales and the polystelic seed ferns *Medullosa* and *Sutcliffia*. Others (*4*), however, challenge this hypothesis on the basis of the striking differences displayed by the leaves and reproductive structures in both groups and the lack of evidence of a Paleozoic origin.

Some questions about the time of evolution and ancestral stocks of this relic group of plants may now be answered in part, because of the discovery of reproductive structures that are almost identical to those of certain living cycads. These fossil staminate cones, structurally preserved in calcified petrifactions (coal balls), were recently collected from upper Pennsylvanian (Mattoon Formation) strata near Berryville, Lawrence County, Illinois. One of eight specimens discovered, the cone shown in Fig. 1A consists of the distal

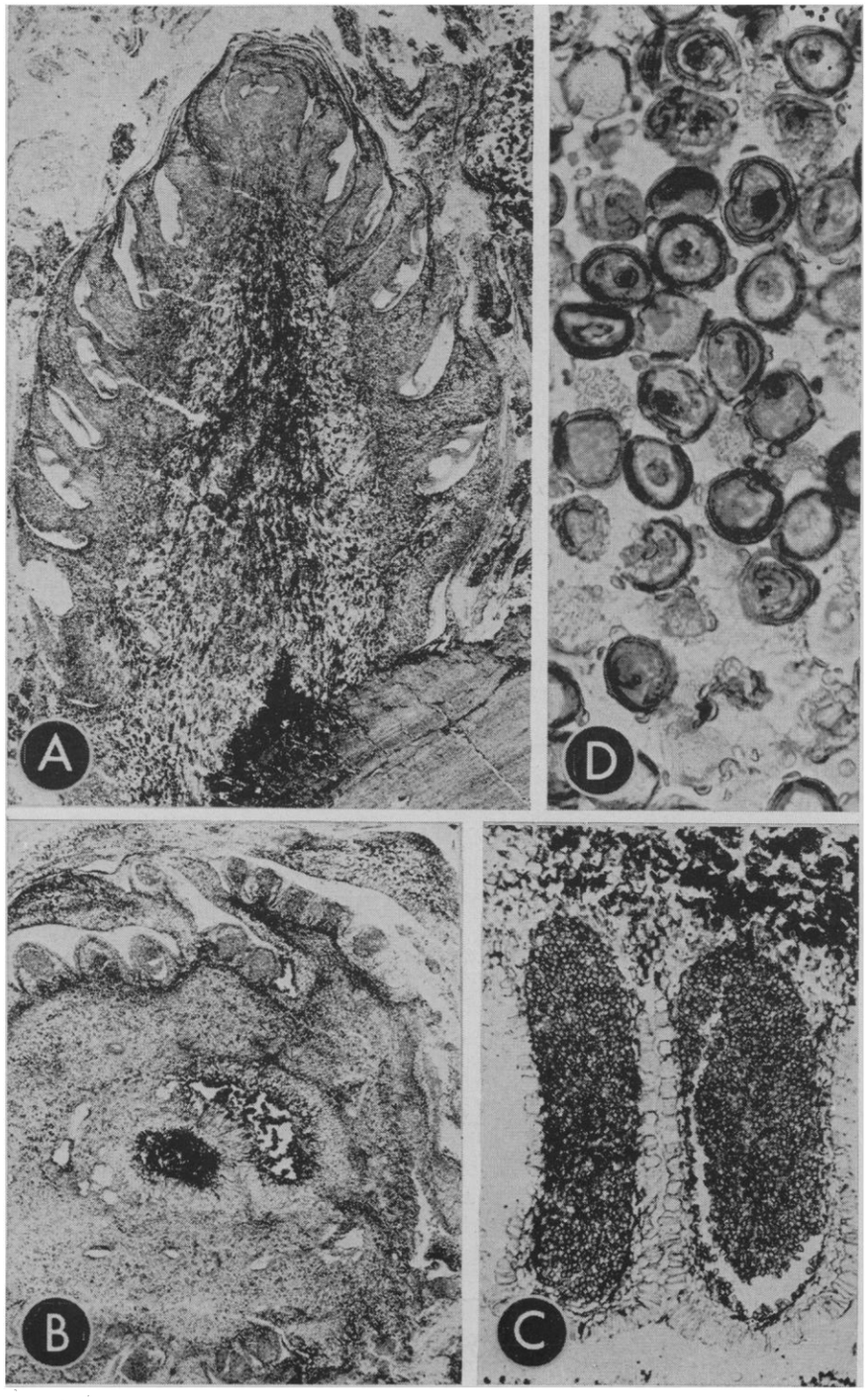

Fig. 1. Pennsylvanian staminate cone. (A) Near median longitudinal section of cone. Note the abaxial position of sporangia and upturned microsporophylls (× 6.5). (B) Transverse section of cone showing central pith, extensive cortical tissues with axile vascular strands, and sporophylls with microsporangia (× 6.5). (C) Two longitudinally sectioned microsporangia (× 5.5). (D) Spores photographed from peel preparation showing arcuate thickenings (× 400).

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.

THOMAS N. TAYLOR
Department of Biological Sciences, University of Illinois at Chicago Circle, Chicago 60680

References and Notes

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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