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PEABODY MUSEUM

YALE UNIVERSITY

NUMBER 150 22 JANUARY 1971

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POSTILLA

Published by the Peabody Museum of Natural History, Yale University

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A NEW TRIASSIC CYCAD AND ITS PHYLETIC IMPLICATIONS

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ABSTRACT

Upper Triassic beds in North Carolina yield excellently preserved compressions of ferns, cycadophytes and conifers. Among the cycadophyte remains are leaves comparable to those of the genus *Pseudoctenis* attached to a slender, elongated stem fragment. Other stem remains show bases of petioles with a similar arrangement. Cuticular analysis of laminae, rachises and stem surfaces suggests the existence of a member of the Cycadales with loosely arranged pinnately compound fronds on a slender stem, with cataphylls and terminal cones. Although Cycadales probably originated before the Triassic, the growth habit of only a very small number of Triassic members is known. This discovery is significant in allowing the reconstruction of one of the oldest members of the order and presents evidence that its growth habit is unlike that of later Cycadales. The slender stem and loosely spaced compound leaves point to a pteridosperm ancestry.

Dedicated to Professor Chester A. Arnold in the year of his official retirement as Professor of Botany at the University of Michigan, and in honor of his distinguished service to the fields of morphology and paleobotany.

POSTILLA 150: 21 p. 22 JANUARY 1971.

INTRODUCTION

The Cycadales represent an order of vascular plants with a number of unsolved evolutionary problems. The group is an old one and has been extensively studied; yet questions concerning its origin and subsequent evolution remain unanswered. Recent papers (Taylor, 1969; Mamay, 1969) suggest that the order first appeared during late Paleozoic times. Taylor presents as evidence a Pennsylvanian pollen cone that has certain cycadalean features; however, just as noteworthy are structures more characteristic of conifers (Taylor, 1970). Mamay described two types of fragmentary megasporophylls from the Permian, one of which resembles *Spermopteris* Cridland and Morris (1960). Although fossil remains of possible Cycadales in the upper Paleozoic are scanty, the existence in the Triassic Period of members of the order with structural features identical with those of modern genera would tend to support the suggestion that the order had become established before the onset of the Mesozoic.

As is so frequently the case, many of our efforts to understand the morphology and evolution of fossil plant groups are hampered by the fragmentary nature of the fossil remains with no accurate means of understanding how the pieces had fit together in life. With continuing paleobotanical investigations, however, it is becoming increasingly possible to present reconstructions of extinct plants. With this new knowledge of the whole plant, we are in a progressively better position to discuss biological problems involving these plants and some aspects of evolution of the plants in question.

Recently discovered Upper Triassic deposits (Hope and Patterson, 1969) with well-preserved plant remains in Chatham County, North Carolina, have yielded an abundance of cycadophyte fossils. In fact, cycadophytes are the single most important element in the flora, with ferns second and conifers next. Occurrence of persistent cuticular remains on foliar and cauline structures is inconsistent, but fortunately the fronds of cycadophytes typically have well-preserved cuticle. Thus it is possible to recognize the existence of both principal orders of cycadophytes, the Cycadales (Nilssoniales) and Cycadeoidales (Bennettitales). Of the cycadophyte fronds, *Otozamites* (Cycadeoidales) is the most abundant. The next most commonly occurring leaves are comparable to those of the genus *Pseudoctenis* (Cycadales). The latter are commonly found in association with stem fragments, and in one instance actual attachment was observed.

By cuticular analysis it is possible to correlate the separate leaf and stem fragments and to determine that the same kind of plant was involved. Attached to the stem fragment with a leaf is a structure resembling a pollen cone.

Whereas these leaves, if they had been found isolated, would have been included within the genus *Pseudoctenis,* they resemble no known species of the genus. Furthermore, demonstration of attachment of leaves, stems and cones as parts of a plant in the Cycadales warrants the establishment of a new genus for all of these parts, reserving *Pseudoctenis* for isolated leaves only. It is conceivable that the various species of *Pseudoctenis* could belong to different genera of plants.

Systematic Description

CLASS CYCADOPHYTA

Order Cycadales

FAMILY CYCADACEAE

Leptocycas, gen. nov.

TYPE SPECIES. **Leptocycas gracilis,** sp. nov.

GENERIC DIAGNOSIS. Same as for the type species, see below.

Leptocycas gracilis, gen. et sp. nov.
(Figs. 1–12)

DIAGNOSIS. Stems slender, 3 to 5 cm wide, bearing terminal crown of loosely arranged, pinnately compound leaves of the *Pseudoctenis* type, with persistent bases of petioles a little farther down, and devoid of foliar structures at lower levels. Cataphylls intermixed with leaves, cones borne terminally.

Cuticle of pinnae, rachises and stems with straight epidermal cell walls and haplocheilic stomata tending to be oriented parallel with veins; dorsal wall of guard cell thickened into a flangelike structure; pole of guard cell extending beyond the dorsal thickening.

Pinnae decurrent, with parallel venation, attached to rachis laterally and broadly, but the base of pinna tilted with respect to rachis axis; distal edge of pinna closer to the ventral surface of the leaf than proximal edge.

STRATIGRAPHIC OCCURRENCE. Pekin Formation, Upper Newark Group, Upper Triassic.

HOLOTYPE. YPM Paleobot. 1148.

DESCRIPTION. *Leaves*. The fronds, comparable to those usually assigned to the genus *Pseudoctenis,* are petiolate, with pinnately arranged, linear leaflets (Figs. 1, 4, 5). An entire frond has not been found, but one fragment measured 21 cm long (Fig. 4). This fragment has no petiole, but the fact that other pieces of fronds with proximal portions preserved indicate that the petiole may be as long as 10 cm (Fig. 5) is evidence that the entire frond may have exceeded 30 cm in length. Pinnae average about 4.5 cm long and about 3.5 mm wide. Venation is only barely discernible, and no anastomoses were observed. Attachment of the pinna base to the rachis is not parallel with the rachial axis, but rather, the pinna is slightly tilted, with the distal edge of the pinna closer to the ventral surface of the leaf than the proximal edge. As a result, pinnae are not parallel with bedding planes, and splitting of the shale often does not expose the entire pinna, but only a thin strip of it, and the width of the pinna appears narrower than it actually is. Pinnae are decurrent along the rachis. There seems to be no relationship of pinna position on both sides of the rachis; pinnae generally appear to be alternate, although in some instances they are opposite.

Epidermis. Cuticle was removed from the shale matrix mechanically, either with a needle or a brush, placed in Schulze's reagent until it became translucent, washed, and then placed in a very dilute solution of ammonium hydroxide for a short time. After another washing, the cuticle fragments were carried through an alcohol-xylene series and mounted in one of a number of synthetic resins. Epidermal cells have smooth walls, with stomata arranged parallel to the pinna veins and only on the lower side. Stomata are characteristically cycadalean (see Greguss, 1968) with haplocheilic guard cell ontogeny (Figs. 6–11). The guard cells are sunken, elongated and somewhat boat-shaped, with the poles bent toward the surface of the leaf. The dorsal thickening on each guard cell flares outward (away from the stomatal opening), and the thickening on the two adjacent guard cells are such that two pairs of projections overlap the guard cells, with the poles of the guard cells extending beyond. This configuration is identical to that in a number of cycad genera (Greguss, 1968); Pant and Nautiyal, 1963).

Stems. Consistently frequent association of compressed stem fragments (Fig. 3) with the *Pseudoctenis*-like leaves suggests that leaves and stems are parts of the same kinds of plants. More definite evidence, however, is the one stem fragment with an attached leaf (Fig. 1). These stem fragments are slender (3 to 5 cm wide) and, instead of closely spaced persistent leaf bases so characteristic of many cycads, the stems bear loosely spaced, slender leaf bases (Fig. 3). The stem surface has coarse wrinkles, but the epidermis itself appears fairly smooth. Stomata are present in the cuticle of stems (Figs. 7, 9) and petiole bases (Fig. 11) as well as on parts of laminae of the leaves (Figs. 6, 8, 10). In fact, the precise correspondence of stomatal and epidermal configurations on pinnae, petioles and stem fragments makes it convincing that all of these parts, even though connection is not always evident, are portions of the same kind of plant.

Near the apex of the stem fragment with the attached leaf are some cataphylls, about 3 cm long, 5 mm wide at the base, and tapering to a point. These appear to have been coriaceous and thick, and must have dropped off, along with the expanded leaves, lower down on the stem.

Attached to the stem apex is a structure resembling a cycad pollen cone (Figs. 1, 2). It is bent downward, measures about 6 cm long and 1.5 cm thick, and has only fair preservation. Neither cuticular remains nor pollen grains could be retrieved from it.

Reconstruction. The various parts of this cycad suggest a plant such as that figured in the reconstruction (Fig. 12). The stem was slender, devoid of leaf bases below, with a surface that was somewhat wrinkled but that had a smooth epidermis, at least in the upper portion. At higher levels there were persistent leaf bases rather loosely arranged. A crown of leaves was borne at the apex, and cones, when present, were borne terminally. It cannot be ascertained whether the cone actually terminated the stem, or whether it represented a branch produced close to the stem apex. It is not possible, either, to determine whether these plants were dioecious, as are all living cycads, or monoecious.

Discussion

This discovery of cycad remains is of interest for a number of reasons. First, even though parts of cycads are abundant in Mesozoic deposits and the group was an extremely important one in Mesozoic floras, stem remains are rare. Florin's (1933) familiar reconstruction of *Bjuvia simplex* showing a rather massive, erect stem was not based on actual stem remains. Similarly, Harris' (1961) reconstruction of the Jurassic plant bearing leaves of *Nilssonia tenuinervis,* pollen cones of *Androstrobus wonnacotti* and seed cones of *Beania mamayi* was not based on any stem fossils. Harris admitted, however, that there were other, indirect pieces of evidence for assuming a stem of that kind. Archangelsky and Brett (1963) reported a new genus, *Michelilloa,* from the Triassic of Argentina. They compared this plant with the modern *Dioon spinulosum* on the basis of anatomical structures. Jain (1962) described a stem fragment, *Fascisvarioxylon mehtae,* that he considered to be a cycad. However, even with these reports of fossil material purported to belong to the Cycadales, there exists no accurate reconstruction of a Mesozoic cycad with parts known from the actual fossil record. In restorations of Mesozoic dioramas that include plant communities, members of the Cycadales are shown looking like modern genera, with no basis for this type of habit.

One of us (Delevoryas, 1968) presented a survey of all known cycadeoids in an attempt to detect the most commonly occurring body form among members of the Cycadeoidales. The usual picture of cycadeoids is of a plant with a squat, fleshy stem with closely spaced persistent leaf bases which, along with thick ramental scales, formed a dense armor on the trunk surface. It appears, however, that this concept has arisen primarily because the genus *Cycadeoidea,* which this description best fits, is the best known. In reality, most cycadeoids seem to have had slender stems, often branched, and leaf bases did not necessarily persist over the entire stem surface.

A paper by Harris (1969) adds further evidence that cycadeoids were often slender, branched plants. In that work he presents a partial restoration of a plant, *Bucklandia pustulosa,* that was previously known from stem remains assigned to that taxon, leaves called *Ptilophyllum pecten,* and cones known as *Williamsonia leckenbyi.* This restoration fits precisely into the concept of the body form postulated by Delevoryas as the typical one for Mesozoic cycadeoids.

Bucklandia dichotoma, recently described by Sharma (1969) from the Middle Jurassic of India, is another example of a cycadeoidalean stem from the Mesozoic that is slender and branched.

Although fewer members of the Cycadales are preserved as fossils, on the basis of what is known about the stems of fossil members of the order, as well as other pieces of indirect evidence, we would suggest the same kind of habit for most Mesozoic members of the order. Harris, when he presented his tentative reconstruction of *Beania,* apparently felt the same way, at least about that plant. The remains of *Leptocycas* from North Carolina are good evidence to reinforce the idea that early Cycadales had slender stems, and that the more "typical" form, with squat, fleshy stems is most likely a derivative and not the primitive form.

If the habit of Mesozoic Cycadales was, indeed, in the form of a slender, probably branched, plant, with leaves not arranged in a crowded fashion, it would be easier to visualize the late Paleozoic pteridosperms as the likely ancestors. Stem structure and anatomy, as well as compound leaves and seed features are all held in common between the seed ferns and the Cycadales. Furthermore, the occurrence of reproductive structures on leaves tends to hold the two groups together. Mamay (1969) believes that the primitive Cycadales had entire leaves, and that the divided leaf came later. He points out that in all of the known fossil sporophylls the lamina is undivided. Although we have no evidence to dispute this suggestion, and admit that it could be correct, we feel that there is really little difference between an entire cycadophyte leaf and a pinnately compound one, and that it may be premature to conclude that the primitive megasporophyll was consistently entire. We await discovery of additional late Paleozoic and early Mesozoic cycads to provide the definitive answer.

ACKNOWLEDGMENTS

Thanks are extended to Carl Wester for his elegant reconstruction in Figure 12. This paper profited from discussions with R. E. Gould concerning fossil Cycadales. We are grateful to the authorities of the Boren Clay Products Company, especially to E. L. Rummage, for their cooperation in making it possible to collect material from their quarry. Russ Patterson, Sanford, North Carolina, was extremely helpful with his enthusiasm in the field. Research for this project was supported by National Science Foundation Grant GB 20999X to T. D. and by a research grant from Campbell College to R. C. H.

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FIG. 1. *Leptocycas gracilis*. Holotype, consisting of a stem fragment, one attached leaf, cataphylls and a cone. YPM Paleobot. 1148.

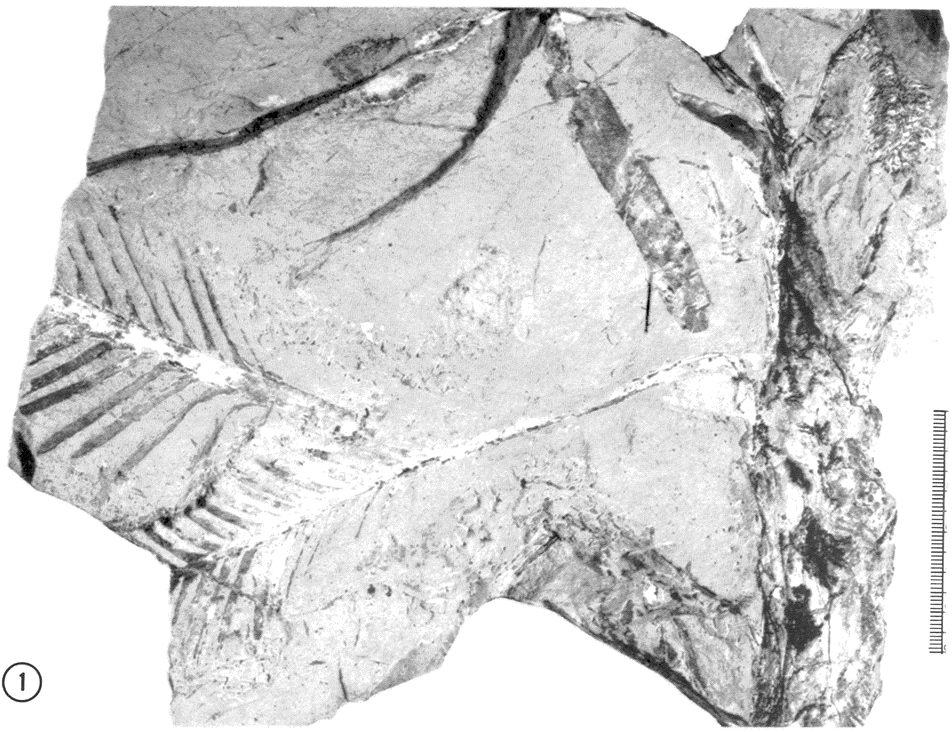

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FIG. 2. *Leptocycas gracilis*. Distal part of holotype with details of petiole base (lower left), cataphylls and terminal cone. YPM Paleobot. 1148.

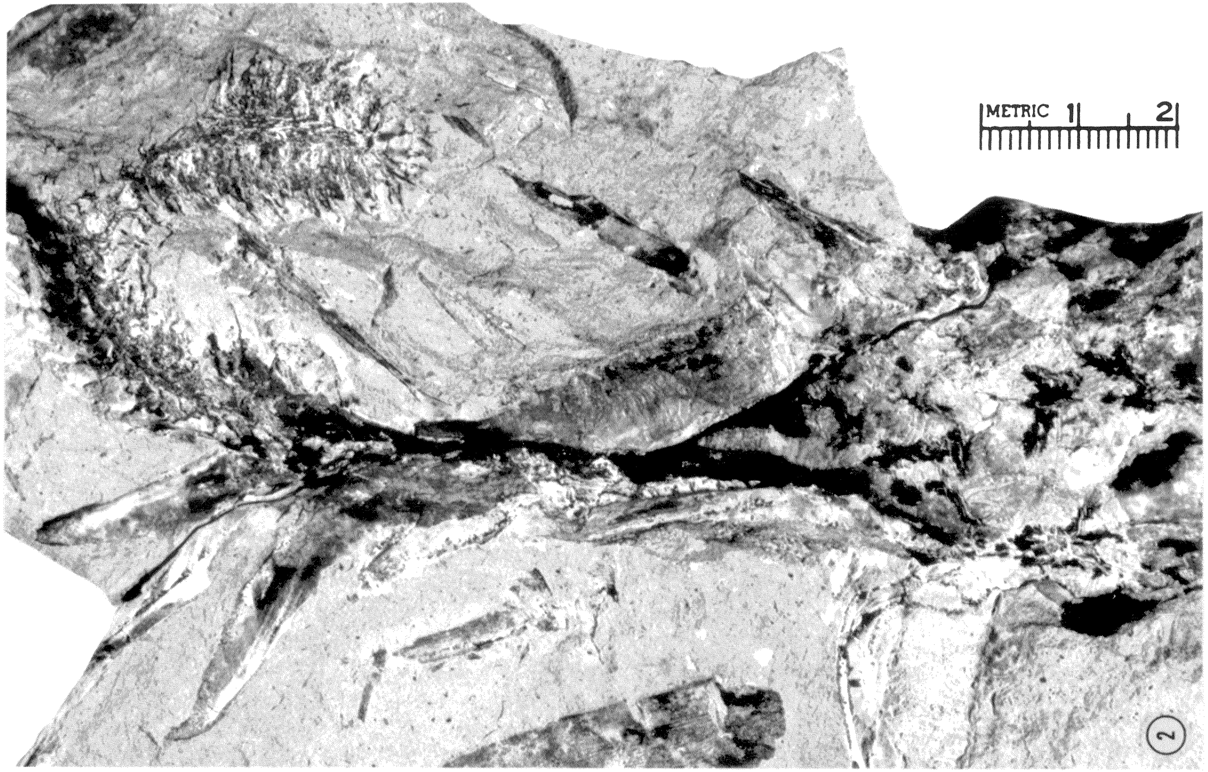
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FIG. 3. *Leptocycas gracilis*. Stem fragment with persistent petiole bases. YPM Paleobot. 1149.

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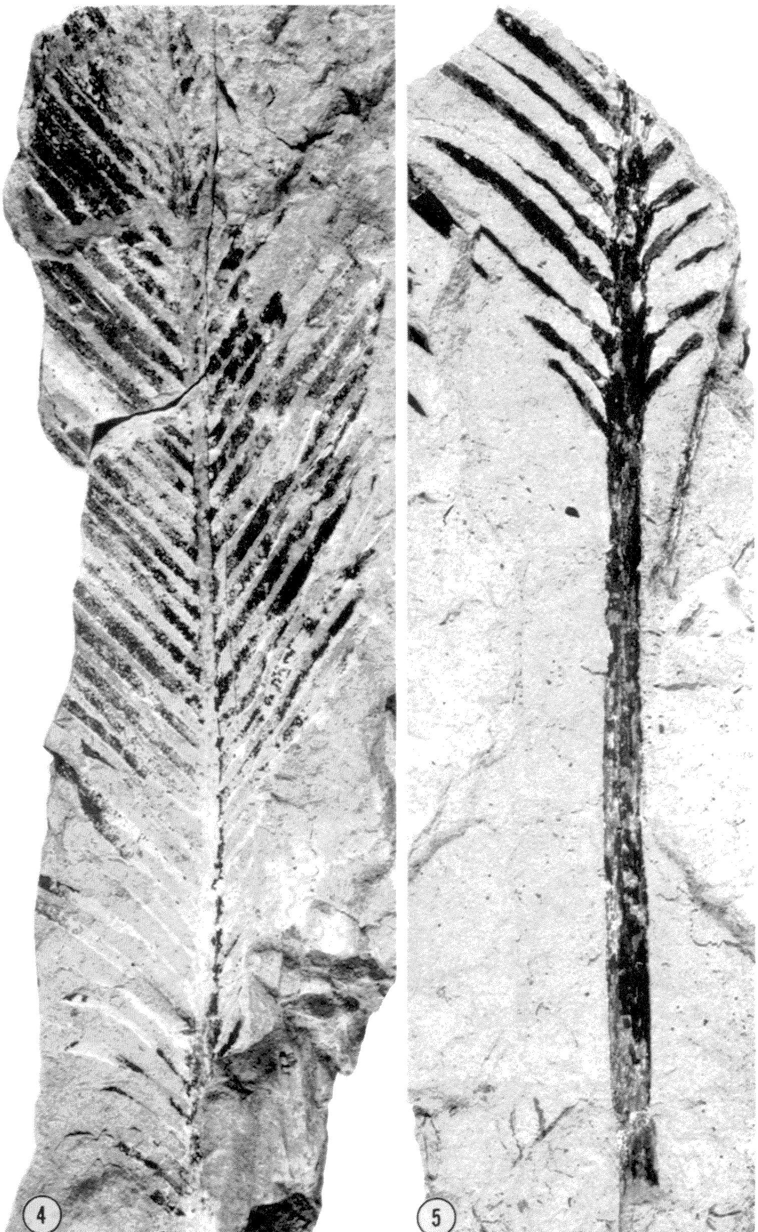
FIG. 4. *Leptocycas gracilis*. Portion of a leaf. ×0.77. YPM Paleobot. 1150.

FIG. 5. *Leptocycas gracilis*. Basal portion of a leaf. ×0.88. YPM Paleobot. 1151.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FIGS. 6–11. *Leptocycas gracilis*. Cuticular preparations from various parts of the plant. FIG. 6. From leaf epidermis of holotype. YPM Paleobot. 1148. FIG. 7. From epidermis of stem. YPM Paleobot. 1149. FIG. 8. From epidermis of isolated leaf. YPM Paleobot. 1152. FIG. 9. From epidermis of stem. YPM Paleobot. 1153. FIG. 10. From epidermis of isolated leaf. YPM Paleobot. 1154. FIG. 11. From epidermis of petiole of stem fragment with persistent leaf bases. YPM Paleobot. 1155. All figures $\times 590$.

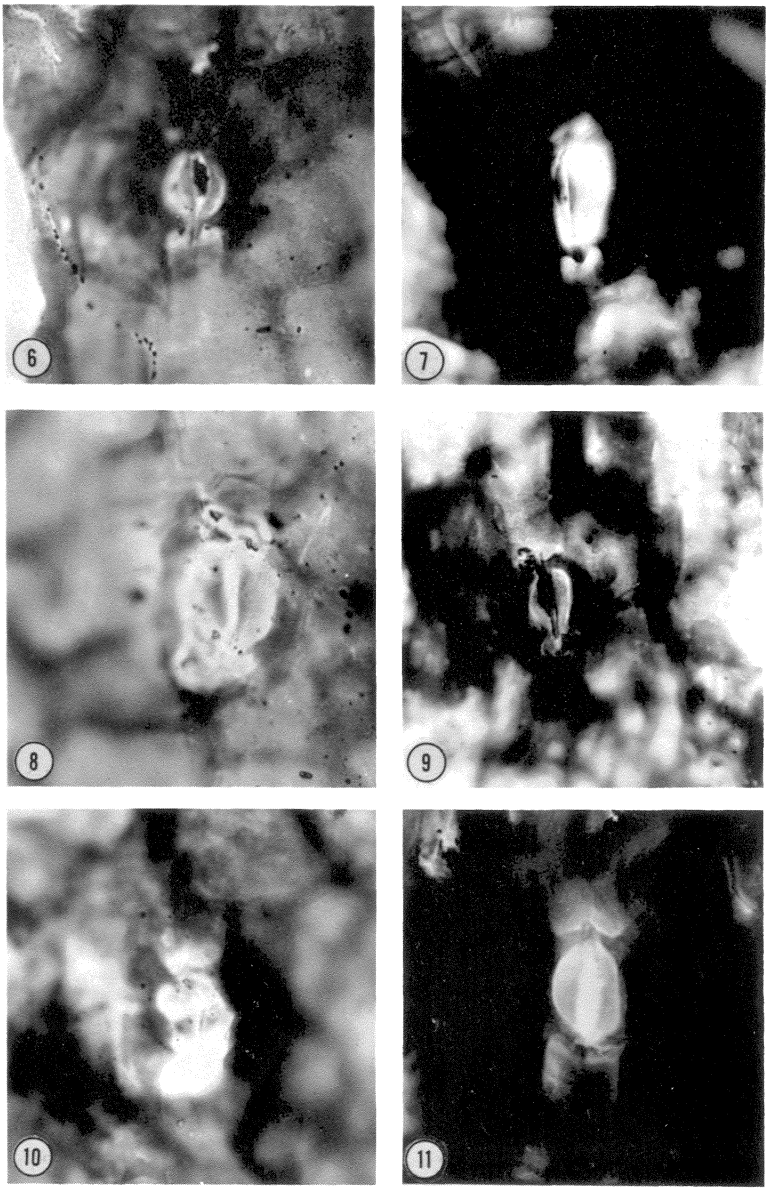
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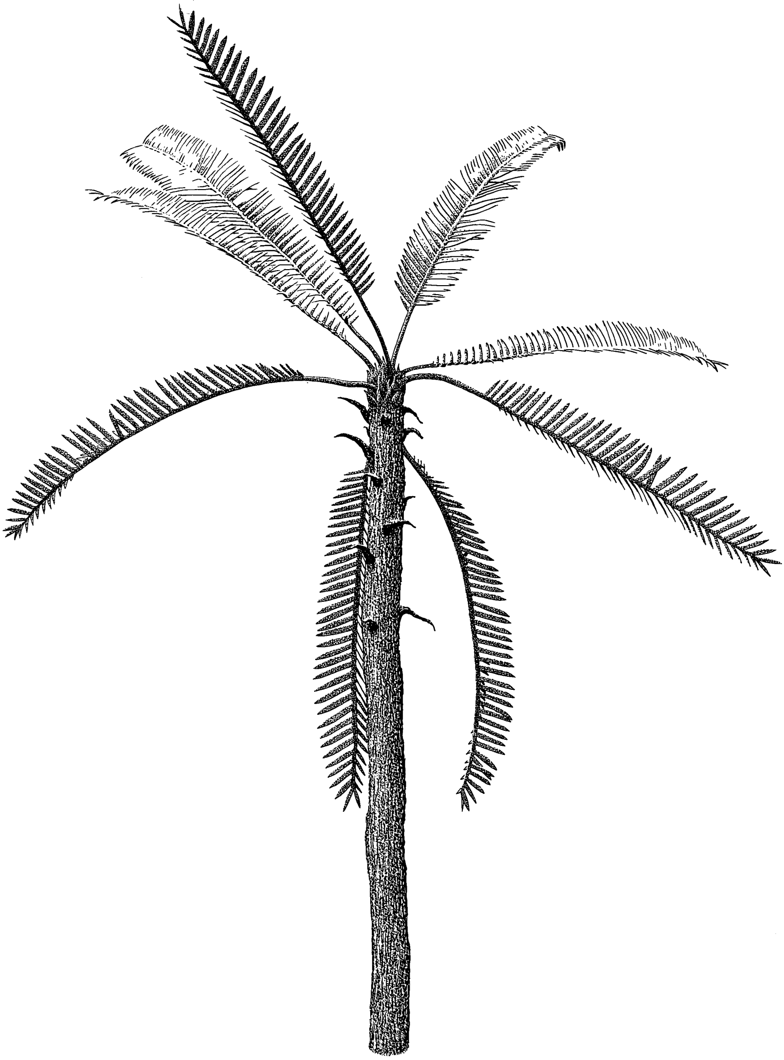
FIG. 12. *Leptocycas gracilis*. Suggested reconstruction of a plant about 1.5 m tall.



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