ART. XLV.—A Study of Some American Fossil Cycads.*
Part III. *The Female Fructification of Cycadeoidea*; by
G. R. WIELAND. (With Plates VIII–X.)

Introduction.

FEMALE fruits of fossil Cycads from America have not been hitherto described. European specimens, however, have furnished two nearly perfect examples which have been made the objects of careful research and discussion during the past thirty years. In fact, the study of *Bennettites Gibsonianus* by Carruthers,³ and Solms-Laubach,^{8,9} together with Lignier's¹² investigation of *Bennettites Morière*, may well be considered one of the triumphs of modern paleobotany. As a result, the structure of the cycadeoidean seed-bearing organs is nearly as well known as that of the existing cycads.

The subject of female fructification, as far as treated before the announcement of the discovery of the corresponding male flower in Part I of these contributions, has been amply reviewed by Seward. Hence it is only necessary to state briefly that the object of this preliminary paper is to deal with several quite perfect cycadeoidean fruits as observed in certain trunks from the Jurassic of the Black Hills. These, it will be seen, are in all essential characters similar to the English, French, and Italian examples of *Cycadeoidea*, of which the best known are *Cycadeoidea* (*Williamsonia*) *gigas*, Carruthers, and *C.* (*Bennettites*) *Gibsonianus*, Carr., both from the lower Greensand of the Isle of Wight, *C.* (*Bennettites* and *Williamsonia*) *Morière*, Saporta, from the Oxfordian of Normandy, and *C. etrusca*, Capellini and Solms-Laubach, from the Etruscan Necropolis at Marzabotto, the original locality of which is unknown. The American forms are so analogous to the several foregoing species as to preclude more than specific difference, and thus add one more argument in favor of the approximately synchronous existence of these highly specialized forms on both continents. Whether or not final study will permit their retention in a single genus is, however, a doubtful question that need not now be taken up; nor can the subject of the bracts and peduncles be treated in the present paper, although recent studies by Scott²⁰ make it quite certain that their investigation will furnish valuable data.

* Part I of these studies appeared in this Journal for March of this year, and Part II in the April number following. The numbers refer to the list of papers given at the end of Part I.

The Fruit of Cycadeoidea Wielandi, Ward (MS.). ♀

General Features.—Cycadean trunk No. 77 of the Yale collection, illustrated on Plate VIII, figure 1, is the female type of the foregoing species. It is a finely preserved example, bearing laterally, in addition to ten apparently fresh scars left by the shedding of ripened fruits, forty more or less complete seed-covered fruits, which were mature or nearly so when fossilization began. The shape of these fruits is ovoid, and their average size is from 3.5 to 4^{cm} in length by 2 to 2.5^{cm} in diameter. In both size and form, they resemble the fruit of *Cycadeoidea* (*Bennettites*) *Gibsonianus*, Carr., though the seeds are less elongate in the latter species.

The embryos of the seeds of this trunk prove to be the only important structures not present in unusual clearness of detail. Moreover, this was the first seed-bearing cycad to be described as such from American formations, as well as the one upon which these studies were begun. Hence it is made the first type of female fructification in American cycads, although other more perfect supplementary material has since been studied.

A close examination of the specimens represented in the plate affords interesting facts concerning the fruit-bearing habit of *Cycadeoidea*. In their various stages of growth, maturity, and dehiscence, the fruits are borne on short peduncles approximately of the same length, thus indicating that the mature fruit was not protruded farther from the trunk by subsequent growth. Nor does there seem to be any order of maturity from the base to summit of the trunk in either direction.

In several other related trunks most of the fruits have been shed, being represented by scars only; while a few floral axes remain undeveloped or in an atrophied condition. Still other trunks of this and associated species are barren or bear embryonic fruits. The latter condition is of considerable importance, as it will permit a developmental study of the organs. The only general conclusion to be drawn at present, however, is that there was no sharply limited period when these cycads matured their flowers. Apparently there was a progressive maturity of fruits through an entire season, which was followed by several seasons of unfruitfulness.

From the characteristic form and sculpturing of the scars representing the position of the matured fruits, it would seem that the latter were shed by the parent plant with their parts intact and often with few or no accompanying bracts.

Following fructification and the shedding of ripened fruit, there was a closing up of bracts about the receptacle, with

more or less obliteration. The appearance of the fruits as apparently mature on the trunk, and of the scars mentioned above, are fairly well represented in figures 1 and 2, Plate VIII. In all cases where the seeds are exposed the tips of the bracts are necessarily more or less worn or broken away.

The lateral, or proliferous, inflorescence here exhibited is noteworthy. In this respect these specialized culminant fossil types vary from all the higher existing forms which are sympodial, and partially agree with the genus *Cycas*. The latter is the most primitive living form, and has its peduncles distributed between the petioles for some distance below the apex of the trunk. Among the various species represented in the Yale collection there are none showing the sympodial type and but few flower-bearing examples which have no flowers on the lower half of the trunk, though the male trunks incline to bear the most of their flowers near the summit.

Special Organs.—As stated above, these fruits are ovoid bodies borne on short peduncles. The latter take their origin on the trunk after the manner of the petioles and terminate in an elongated receptacle. This bears laterally an involucre of slender enveloping bracts, and terminates in a "parenchymatous cushion," as termed by Carruthers.³ The face of this cushion, or secondary receptacle, is flatly convex and bears two series of densely set organs, much modified according to their central or more peripheral position. The first of these are the seed-bearing stems, or essential organs, while the second are merely interstitial and quite analogous to chaff. They are termed "interseminal scales" by Lignier.

The disposition of these parts is illustrated in the longitudinal sections, figures 10 and 12, Plate IX, and in the corresponding transverse sections, figures 9 and 11 of the same plate, as well as in the several transverse sections on Plate X.

In this arrangement of densely set seed-bearing stems and surrounding scales borne on a fleshy bract-enveloped receptacle, there is a certain simulation of the flowers of *Compositæ*.

Histological Structure.

The Parenchymatous Cushion.—This is composed of soft parenchyma centrally, but becomes more dense peripherally. Though no well-marked bundles have been noted, sparse and irregularly branching strands of scalariform cells apparently supply the seed stems. As there is usually a cleavage line, or zone of imperfect preservation, just at their origin, this could not be readily determined. The strands may scatter and end in the cushion. They are illustrated by Carruthers in his description of *Bennettites Gibsonianus*.

Seed Stems.—These are very closely set on the cushion, and as it is difficult to separate their elements from those of the interseminal scales in the longitudinal sections, they may be best studied in transverse sections. Such a section from the middle of the fruit is shown in figures 14 and 16, Plate X, where the stem is seen to consist of a central vascular bundle enclosed in an endodermis which is surrounded by a broad woody outer layer, or xylem zone, the "enveloppe tubuleuse" of Lignier.

Each seed stem is uniformly surrounded by from 5 to 6 interseminal scales. A series of transverse sections from the base to the summit shows no variation from this general arrangement, although there is a slow diminution in the diameter of the stems, accompanied by marked changes in the cell conformation of the xylem zone. In this and other species, there is often at the base a strong compression of the surrounding scales, while the xylem areas are more or less polygonal and composed of cells quite regularly sub-rhombic in section. Of these, from 30 to 40 may be counted radially, as shown in figure 4, Plate VIII. Towards the summit there is a constant increase in the size and regularity of these cells, which finally become quite round, accompanied by a decrease in the width of the xylem band, until at the base of the seeds it consists of but two layers of cells surrounding the central bundle, which remains constant in character.

This bundle is well illustrated in the enlarged view given in figure 15, Plate X. Centrally there are from 3 to 10 small woody elements. These are enveloped in soft parenchyma, not preserved in all specimens, and the bundle terminates in a well-marked endodermis. Such concentric bundles recall the somewhat similar structures seen in many ferns. The atrophied peduncles, or those lacking a well-marked central bundle, described by Lignier in *C. (Bennettites) Morière*, have not been observed thus far. The interesting case of bifid seed stems, or those with two central bundles within the same tubular, or xylem zone, however, rarely repeats itself in the present specimens.

It may be mentioned that while the figure of the transverse section of the seed stems, "vascular cords," given by Carruthers is a faithful one, its being cut too near the base, where there is much compression of the several elements, prevented a true conception of their significance. Only at some distance above the base does the clear differentiation of parts seen in figure 14, Plate X, appear. Judging from the transverse section by Carruthers, just mentioned, and the additional one given by Solms-Laubach, the tubular layer, or xylem zone, of *C. (Bennettites) Gibsonianus* was composed of more angular cells than in the case of the present specimen.

Lignier gives a section of a seed stem from near a seed base (peduncle, figure 27, Plate II),¹² in which the tracheidal cord is followed by fundamental tissue, and this by a layer of cells (*assise colorée*), which is in turn surrounded by a single row of cells laterally dovetailing. This alteration at the seed bases has not been observed as yet by the writer, and no doubt must stand as one of the specific variations between the foregoing species.

Interseminal Scales.—Five or six of these commonly surround each seed stem, and rise beyond the seeds, their tips expanding to form the rounded summit of the fruit. Figure 13, Plate X, displays a transverse section of one of these organs cut near its middle height. In the case of cycad No. 77, figure 14, Plate X, the parenchyma surrounding the central vascular strand is not preserved; but the central strand, the large subepidermal cells (much less continuous in this species than in *C. Morièrie*), and the epidermis, are so uniformly present as to differentiate these tissues as absolutely as any staining. From the base toward the summit, as the seed stems decrease in diameter, the scales increase in size by the enlargement of the cross area of the parenchyma cells, which are usually rounded in section and quite elongate. Beyond the seeds, the cells composing the expanded summits are entirely lignified. In the seed zone, the scales are also more or less lignified and often very thin and flat as they pass between the seeds, where it is sometimes difficult to differentiate them from the seed coats. Exterior to the outer seed stems there is a flattened overlapping series of scales, forming a kind of lateral wall of the fruit several scales in depth. The distal portions of these modified scales are elongate, tetrangular, and lignified, as they appear on the fruit surface.

It is difficult to detect the several elements of the scales in longitudinal section. That some of the xylem cells are spirally marked is certain, and that there is an occasional scalariform marking is also certain. The woody elements of these scales regularly take their origin below that of the cells of the xylem zone of the seed stems, and in figure 5, Plate VIII, are seen extending down into the parenchymatous cushion as small projecting brushlike groups.

It need scarcely be pointed out that there is an analogy between these scales and the central bundle of the seed stems, the variation being in a uniformly large central strand, the addition of a broken subepidermal layer with apical sclerotization, and the presence of occasional ducts in the case of the scales.

The Seeds.—The seeds thus far observed in the present and other species show much variety of preservation. Their study is therefore a difficult one, requiring time, especially for the

purpose of comparing a large number of the same and different species, and determining how far the structures supplement each other. Hence no detailed account of seed structure will be now attempted, although the appended figures, which in reality are but little diagrammatic, are introduced.

FIGURE 1.—*Cycadeoidea* (*Bennettites*) *Morièrei*, Saporta ♀: longitudinal section of seed. (After Lignier.)

a, micropylar tube; *b*, prismatic layer; *c*, pulpy tissue; *d*, corpuscular mass; *e*, interseminal scales; *f*, embryo space; *g*, remains of nucellus; *h*, chalaza; *i*, tubular layer (= xylem zone); *k*, micropylar canal; *l*, nucellar beak; *m*, pollen chamber; *n*, fibrous stratum; *o*, basal expansion of *n*; *p*, parenchyma of seed stem.

FIGURE 2.—*C. Wielandi*, Ward ♀: longitudinal section of seed. $\times 12$

a, micropylar tube; *b*, interseminal scale; *c*, the same; *d*, cotyledons; *e*, fibrous layer ending below the chalaza in an expanded base of scalariform tissue; *f*, a structureless zone; *g*, stringy remains of cells lignified and slightly expanded below; *h*, chalaza; *i*, woody scalariform tissue; *k*, prismatic outer layer of seed ending in xylem zone; *l*, parenchyma.

General Considerations.

Owing to the large number of male and female examples of *Cycadeoidea* in the Yale collection, their proper correlation will require considerable time. Nevertheless, several facts of im-

portance present themselves for mention. A number of species bear fruits of the type represented in the well-known figure of *C. etrusca* given by Capellini and Solms-Laubach (Plate IV).¹⁰ These heart-shaped fruits have very closely set, rodlike seeds arranged prismatically on a short, fleshy axis, traversed by numerous gum ducts and usually devoid of the regularly arranged seed stems and interseminal scales characterizing *C. (Bennettites) Gibsonianus*, *C. Morière*, and *C. Wielandi*. Should there prove to be no intervening forms and no connection during developmental stages, this must be finally regarded as a strong generic difference. One of the Yale specimens not yet fully studied, but nearly related to *C. etrusca*, as far as may be judged from general features, displays seeds with well-marked cotyledons, as represented in figure 7, Plate IX. Another closely related trunk, of which the female form also is known, shows well-preserved male cones of essentially the same character as those described in Part I of these contributions. Pollen grains, both distended and dessicated, and represented in figures 9–16, are present in rare preservation. They are so like the dissociated pollen figured by Capellini and Solms-Laubach¹⁰ in their description of *C. etrusca* that figures 17–20 in the text are introduced for comparison, as well as pollen from the living cycad *Ceratozamia*, figures 3–8. That these fossil bodies represent characteristic cycad pollen is beyond all question. Sections of the cycadeoidean cone from which the pollen of figures 9–16 was derived are given in figures 17 and 18, Plate X.

FIGURES 3-8.—*Ceratozamia longifolia*, Miquel; pollen grains. (After Juranyi.)
× 610.

3, mature pollen in dry condition; 4, 5, the same swollen in water; 6-8, the respective transverse sections, or end views.

FIGURES 9-16.—*Cycadeoidea*, sp., Black Hills; pollen grains. × 250.

9, 10, 13-15, more or less dessicated grains; 11, 12, 16, normal forms.

FIGURES 17-20.—*Cycadeoidea etrusca*, Capellini and Solms-Laubach; isolated and dried pollen grains. (After Capellini and Solms-Laubach).

But one interpretation of these facts is possible—*Cycadeoidea etrusca* represents a fertilized dioecious plant, the male flower of which has now been definitely recognized in an allied species. The so-called "antheriferous tissue" noted by Capellini and Solms-Laubach hence remains an unexplained structure, possibly of much significance. Should this tissue represent a developmental stage instead of permanent structure, as certain sections made by the writer suggest, it nevertheless merits the closest examination, and may have some connection with a "corona" such as that of *Williamsonia gigas*.

Another close resemblance between the American and European species having prismatic seeds is the characteristic surface sculpturing. Figure 2, Plate VIII, is introduced here for comparison with a Bennettitean specimen illustrated by Seward (Fossil Plants of the Wealden, Plate XV, figures 5 and 6).*

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EXPLANATION OF PLATES.

PLATE VIII.

- FIGURE 1.—*Cycadeoidea Wielandi*, Ward ♀; type specimen. $\times \frac{1}{2}$.
 FIGURE 2.—*Cycadeoidea* (sp.) ♀; surface sculpturing of a fruit. $\times 10$.
 FIGURE 3.—*Cycadeoidea Wielandi*, Ward ♀; portion of a trunk, showing scars left by the shedding of fruits. $\times \frac{1}{2}$.
 FIGURE 4.—*Cycadeoidea turrita*, Ward ♀; transverse section of a seed stem (from near the parenchymatous cushion) surrounded by an unusual number of interseminal scales. $\times 30$.
 FIGURE 5.—*Cycadeoidea Wielandi*, Ward ♀; longitudinal section through seed stems, showing their origin on the parenchymatous cushion. $\times 24$.
 FIGURE 6.—Same fruit as figure 5; transverse section of seed stems near periphery of fruit. $\times 30$. (Compare with figure 14.)

PLATE IX.

- FIGURE 7.—*Cycadeoidea* (sp.) ♀; nearly transverse section through the periphery of a fruit, cutting 5 seeds, in several of which the cotyledons may be seen. $\times 16$.
 FIGURE 8.—*Cycadeoidea Wielandi*, Ward ♀; longitudinal section through a fruit near the summit, cutting superimposed seeds. $\times 12$.
 FIGURE 9.—*Cycadeoidea Wielandi*, Ward ♀; type specimen; transverse section through fruit; showing seeds, seed stems, and interseminal scales. $\times 4$.
 FIGURE 10.—Same fruit as preceding; longitudinal section through seed stems and parenchymatous cushion. $\times 4$.
 FIGURE 11.—*Cycadeoidea turrita*, Ward ♀; transverse section through fruit, cutting a single seed obliquely. $\times 25$.
 FIGURE 12.—Same fruit as preceding; longitudinal section. $\times 4$.
 a, seed; *b*, densely set interseminal scales and aborted seed stems (?); *c*, the parenchymatous cushion; *d*, involucre bracts; *e*, line of dehiscence (?).

* In the case of generic and specific names, the writer has followed Prof. Lester F. Ward of the U. S. National Museum, as the recognized authority on American cycads. Fortunately for scientific uniformity, Prof. Ward has described practically all the cycads discovered in this country.

PLATE X.

FIGURE 13.—*Cycadeoidea Wielandi*, Ward ♀; transverse section of an interseminal scale. × 185.

a, xylem zone of a bordering seed stem; *b*, epidermis of the interseminal scale; *c*, xylem; *d*, parenchyma; *e*, heavy and much broken subepidermal layer.

NOTE.—Where two scales border there is a double layer of *b*.

FIGURE 14.—*Cycadeoidea Wielandi*, Ward ♀; type specimen; transverse section through seed stem and surrounding interseminal scales, no parenchyma of either of these organs being preserved. × 22.

FIGURE 15.—Same fruit as figure 13; transverse section through the central bundle of a seed stem. × 185.

a, xylem zone; *b*, endodermis; *c*, parenchyma; *d*, xylem; *e*, cellular interspace.

FIGURE 16.—Same fruit as preceding; transverse section of seed stems and interseminal scales, all elements being preserved. × 22.

FIGURE 17.—*Cycadeoidea* (sp.) ♂; transverse section through the pendent sori of a sporophyll. × 18.

a, epidermis of prismatic cells which entirely invests each sorus, the latter consisting of two parallel rows of sporangia; *b*, one of the sporangia containing pollen grains as illustrated in text, figures 7-14, page 389.

FIGURE 18.—Same as preceding, but showing a larger area. The arrow points towards the floral axis. × 3.

CYCADEOIDEA INGENS, Ward (type); leaf structure

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