ART. XIV.—*A Study of Some American Fossil Cycads.*
Part V. Further Notes on Seed Structures*; by G. R.
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MAINLY in recent years through the continued study of the wealth of fossil plants in the remarkable calcareous nodules or "coal balls" of the Coal measures of England by the English group of Paleobotanists, has the list of ancient seeds illustrated in detail become a long one. In fact, material has so augmented as to make the investigation of fossil seeds a subject of considerable scope and even unique fascination and promise.

So far, however, the best known old seed types are chiefly gymnospermous and Paleozoic with the notable exception of the Mesozoic Cycadeoideas. But fortunately whatever the latter lack by reason of isolation they more than make up by abundance and exquisite preservation in a half dozen different species. Not only is the structural representation ample, but the number of mature strobili now runs into the thousands. In fact the subject of Cycadeoidean seeds has assumed a continuous interest. For in addition to the mature seeds we have the seeds well outlined in many young strobili varying in size all the way from a pea to a small pear, as well as a proembryonic stage, considered present in one form (*Cycadeoidea Macbridei*? Y. S. 131); while the fully developed dicotyledonous embryos are finely conserved and have now been seen by thousands!

Yet for a number of years following Carruthers' (1) description of *Bennettites Gibsonianus* such material seemed exceedingly rare, and it was not until 1894 that the isolated fruit *Bennettites* (Williamsonia) *Morièrei* (found by Morière in 1865) was finally described by Lignier (3) in a memoir which still retains its place as the most accurate detailed account of the Cycadeoidean seeds so far given. Five years later the first observation of seed cones on American trunks was announced by Ward (5) and Wieland (6), while in the latter's volume on American Fossil Cycads (8) a glimpse was had for the first time of the great extent and variety of ovulate fructification in the American species.

And now, as if nature designed for the student of gymnospermous seeds "a beauty beyond compare," there has recently been found near Hermosa in the eastern Black Hills Rim, by Doctor Darton of the U. S. Geological Survey, half of a truly monocarpic trunk now in the collections of the U. S. National

* Parts I-III of these studies appeared serially in this Journal for March, April, and May, 1899, and Part IV in June, 1901.

Museum. Even as illustrated by Professors Coulter and Chamberlain in their new book on the Morphology of Gymnosperms, in only a single small text figure this specimen shows something of its extraordinary characters. But on inspecting the original, one can have but the single first thought—that the fossil record can become rich indeed!

From the sections of the Boulder (Colorado) trunk *Cycadeoidea nigra*, made some years ago, it was determined that a peduncle was present in every leaf-base axil, but the fruits had protruded beyond the zone of silicification. The general resemblance of this form to the Italian *Cycadeoidea Masseiana* was pointed out in my American Fossil Cycads; and more recently we have been enabled, through the interest of Capellini, to cut sections from this Italian type proving that it belongs to the series with fruits in every leaf-base axil, except that these fruits are very young. So, too, it was pointed out that in *Cycadeoidea Stantonii* axillary buds complement the entire leaf-base series. But though it was thus observed that in Italy, in the Black Hills, in California trunks of monocarpic habit were characteristic members of the *Cycadeoideæ* and doubtless could be conserved with all their fruits, none of the known localities gave much promise of yielding such an unique and marvellous fossil.

However only a casual examination of the Darton specimen showed it to have small-sized but evidently quite mature seed cones but little different from those of *C. Wielandi*, in the axil of most leaf-bases far up towards the apex of the trunk, and apparently occupying all of the lateral trunk surface that ever would be available for the production of fruits. At least no trunks are known with old peduncles in the basal region and a clearly young series of fruits above, while the trunk *C. turrita*, illustrated in American Fossil Cycads, Plate V, fig. 5, with the regularity of its leaf-base spirals disturbed by but a single ovulate cone was at once recalled.

On plotting the lateral surface of the Hermosa specimen it at once became evident that even the half trunk as collected bears from 500 to 600 ovulate cones, thus exceeding all records in fossil plants; and on cutting sections from a portion of the armor, which I was kindly permitted to break away for examination, so far as bearing on my comparative studies, the conclusion from the microscopic examination was fully confirmed.

That the armor portion selected, though completely coated over with lime, must contain concealed fruits was confidently expected. None the less the surpassing beauty of the sections obtained was scarcely anticipated. The first section cut, a transverse one, showed the entire lateral surface to be occupied

by strobili, as it revealed three entire and two nearly entire axillary ovulate strobili, with but two of the five complementary leaf-bases; and with the cones thus located an equatorial armor section was at once cut through the summits of three adjacent ovulate cones. In all the cones the mineralization is, after the manner of silicification, not so distinct as calcification, but yet excellent, and nearly every seed contains a mature embryo, not so well conserved as those of Yale trunk 131,* but yet showing quite satisfactorily the character of the embryonic tissues. Especially valuable for purposes of comparison are these embryos, because little shrunken, and with the epidermal cells nearly always more or less distinct. Other sections of *Cycadeoidea* embryos showing more of detail we have in abundance, but none more beautiful than these.

In continuing the elaboration of material for the volume on the Taxonomy of the American Fossil Cycads, now in course of preparation under the auspices of the Carnegie Institution of Washington, many new strobili have been cut during the past year. Also, in addition to the strobili cut from the new Black Hills trunk, I have made seed sections of *Bennettites Gibsonianus* of the Isle of Wight, and already had at hand the sections of *Bennettites Morièrei* obtained from Professor Lignier as related in my American Fossil Cycads. In short, there has thus been brought together a representation of all the forms so far known; and on the basis of this complete representation it has been found very desirable to simplify ideas of the structure of the testa in the *Cycadeoidea*, not alone for the purpose of forwarding present studies, but of making the paleobotanic text on this subject short and satisfactory.

As is always inevitable in the case of a complex fossil plant structure, the different types of mineralization, in this instance nature's own variation of her staining and imbedding methods (!), result in slightly different interpretations in the hands of different investigators. What with this factor and different modes of illustration or study of areas and features seldom taken from the same region of a seed, or showing variation of a given region in one and the same seed, it becomes all too easy to suspect greater differences in even a small group of species than actually exist; while meantime certain salient features are likewise easily overlooked. So it has proven in the case of the cycads, though of simple enough structure on closer study. In order, consequently, to bring out a fundamentally clear comparison of all the seeds, American as well as European, showing the best testal conservation, camera lucida drawings have been made of longitudinal sections at a

* Illustrated in American Fossil Cycads, Plate XXII.

point about one-third of the distance from the base to the tip as reproduced in figures 2 and 4. Before taking up these, however, it is highly desirable to briefly recall the several interpretations of the *Cycadeoidea* testa.

According to Carruthers' (1) original study given forty years ago:

"In *Bennettites Gibsonianus* . . . Two envelopes enclose the albumen and embryo. The outer envelope or testa, consists of a thin layer of delicate elongated cells; the inner is composed of a single layer of oblong cells arranged with the longest diameter at right angles to the walls, and indurated by a considerable amount of secondary deposits. . . . two coverings were produced upwards into a tubular exostome or styliform process . . . spread out like a stigma in the upper surface of the pericarp."

In this description and illustration of the general features of the seed the layer of collapsed fleshy cells immediately beneath the indurated layer is not mentioned, Carruthers then going on to say that,

"Enclosed by these envelopes is the nucleus with its membranous covering and abundant albumen . . . the subrectangular cells of which are obvious in several seeds. . . . The albumen was solid behind the embryo but was divided from top to bottom down its center, in front of the embryo."

Here we have unmistakably clear allusion to embryonic features and tissue; for the supposedly albuminous "subrectangular cells" are simply the cotyledonary epidermis and mesophyll, uniform in appearance and peculiarities of preservation, in the embryos of *Bennettites Gibsonianus*, *B. Morièrei* and several American specimens, all known in satisfactory detail.

In the next description of these cycad seeds, that of Solms-Laubach (1890), the embryos were, however, clearly recognized, and the testal structure described as follows:

"Three distinct testal regions are to be noted, a basal, middle and apical.

"In the middle region of the seed the testa is closely appressed to the nucular membrane, and wherever well conserved three distinct layers may be recognized, the middle layer of which is simply a single stratum of short prismatic palisaded thick-walled, dark-brown cells; while the inner and outer layers consist in several thicknesses of rather small thin-walled tissue.

"The tissue of the inner layer is mostly crushed and indistinct, while that of the outer layer appears as a light area following the palisade layer, and finally passes over into more or less distinctly confluent growth with the walls of the seed cavity. At least a distinct boundary appears but discontinuously. . . .

"In the apical region of the seed the testal layers were found most difficult to delimit owing to a lack of sections traversing the long and slender micropylar tube in the true median longitudinal position, and the large amount of pyrite investing the peripheral tissues of the strobilus in irregular areas."

In no form are the testal features conserved with more of diagrammatic clearness than in the French specimen *Bennettites Morièrei*, Lignier's description of which soon followed that of Solms as already mentioned. In fact the seeds of this isolated strobilus are conserved in such unrivalled perfection as to leave nothing more to be desired except the recovery of a second example, and make us anxiously ask if French collectors have really sought for further material in the original locality as diligently as they might. From the description of Lignier (1894) which enters into much detail we need not, however, quote in full in the absence of a series of photomicrographs. Though before passing on to the American seeds it should be mentioned that the limiting region between the seeds and surrounding scale-formed seed pit, which as we have just seen Solms found difficult to see in *B. Gibsonianus*, is always distinct in *B. Morièrei*. In any of the sections from the latter one may clearly see that the appearance, as of a peripheral confluent growth of the seed wall with the interseminal scales, is due to appression and the failure of the scales in places to develop their epidermal layer continuously. There thus arises a *pinching out* into a single ribbon-like layer of interseminal epidermis appressed closely to the very outermost cells of the seed. The condition does, however, show how, as the result of close growth and suppression of epidermal cells, a form of intergrowth could easily arise. Quite the only structural feature of the testal wall that Lignier leaves in doubt is the nature of the middle layer, whether stony, or, as he is inclined to believe, fleshy. On this point it is, however, reserved for the American species to throw a clear light, and to comparisons with them we may now turn.

*Comparison of testal structure in the American and European Cycadeoidean seeds.**

On comparing the descriptions of the testa already quoted, namely those of Carruthers (1), Solms (2), and Lignier (3), with each other, and with those given for the American seeds by the writer, a most substantial agreement within strict generic limits will be found and the differences due to conser-

* In these comparisons the names of testal features and seed parts proposed by Oliver and Salisbury (11) are employed, having been found convenient and usable, while a close reading of the present text will disclose one or two extensions of this necessary nomenclature of use.

FIG. 1.

FIG. 1. *Bennettites Morièrei* type (Sap. et Mar.). $\times 75$.

Transverse section of seed stem traversing point of greatest constriction exactly where expansion into the hilo-chalazal region begins (Camera lucida drawing reduced from $\times 280$).

X, xylem or central tracheid region A, imbricate to pleated layer = "assize plissée";
 P, small celled outer ground tissue; T, tubular cells of cortical region forming exterior of seed stem, and basal husk of seed;
 C, stained layer = "assize colorée";

E, outer woody layer of the enveloping interseminal scales.

As connoted the layer E is the ligneous epidermis of the five to six interseminal scales which completely enclose the seed-stem, being thus no true part of the testa, though often splitting off with the seed, and sometimes approximating a confluent growth.

The elements of the testa here appear in their simplest form, the section passing precisely through the transition region where the radio-symmetric seed-stem bundle passes over into the seed-base and testal structures. The xylem (X) is exactly on the point of expanding to form the cup-shaped base of scalariform tracheidal tissue supporting the nucellus, though still deeply enclosed by the fundamental tissue of the seed stem. In the mass of the latter, however, various resin cells characteristic of coniferous seed-base tissue (*Sequoia*, etc.) begin to appear, and peripheral groups of small cells basal to the inner flesh lie next to the conspicuous zone of resin filled cells (C). The latter gives origin to the middle zone of the testa and is strictly homologous with the gymnospermous "middle stone," though taking precisely the same mineral stain as the resinous cells scattered in the ground tissue about X. The third concentric layer, A, also a single cell in thickness, must be the continuation of the endodermis of the seed-stem bundle; it gives rise to the true outer flesh analogue, in this seed none other than the so-called "blow off" layer of the Carboniferous seed ferns. Finally the rapidly thinning and fraying zone of large, stringy tubular cells (T) is noted as the well-conserved continuation of the cortical region of the seed stems, which takes origin on the strobilar receptacle as a much thicker zone of small cells.

(From a section cut by Professor Lignier.)

vation will fully appear, if these two explanatory paragraphs be borne in mind:

Firstly.—The comparative study of all the known *Cycadeoidea* seeds and a fairly extensive list of existing gymnosperm seeds, shows that the middle layer of the seed wall is essentially a stony, rather than a merely indurated or suberous layer, and much thicker in *Bennettites Morièrei* than in any American species. Professor Lignier's description of this layer as fleshy was given with some reservation, and it is merely necessary to note that the stony layer shows varying degrees of induration in allied species, throughout the gymnospermous series.

Secondly.—In referring to the writer's own descriptions of testal structure, as given in his American Fossil Cycads with too few figures, all stress must be laid upon the fact that the seed is there spoken of as it probably appeared on splitting loose—as a shed seed—and that the form primarily dealt with is *Cycadeoidea Wielandi*, which has only traces of ribbing and now proves to have the most reduced testal structure known, being almost, or wholly, without an outer fleshy, or "blow off layer." Better sections from cones of other species show well-marked ribbing and a heavy "blow off" to be commonly present in the Black Hills Cycads. But so far there is no instance in which this structure shows the fine detail in any silicified specimens that it always exhibits in the ferrized *B. Morièrei*. In fact, the middle or indurated zone appears to have been far more susceptible to preservation by silicification, whereas the outer or "blow off" layer of the seed is infinitely better stained and conserved by iron carbonate. We think no one who sees the original preparations can fail to be struck by this complementary reaction of the outer flesh and middle stone to these two types of mineralization, as seen in the Calvados strobilus and the Black Hills fruits.

This explanation, then, entirely clears the way to a complete understanding of the similarity of testal development in the American and European fossil cycads. The seeds of the *Cycadeoideæ* containing embryos vary from one centimeter in length in *Amphibennettites Renaulti* of Fliche (†), to three or four millimeters in length in the smallest American forms, and there is a remarkable homogeneity in the testal features of the entire group. In fact, short of close study, the only differences discernible are in the ribbing and size of the seeds with some variation in the thickness of the tissue zones of the seed wall, which is normally three layered with a distinct middle stone. The outer flesh alone may, however, exhibit, aside from peculiarities due to the unusual manner in which the seed is completely encased in the solid husk of interseminal scales, marked reduction or even elimination.

FIG. 2.

FIG. 2. Longitudinal section of Cycadeoidean testas at point two-fifths of distance from base to apex. $\times 110$.

A. and B.—*Bennettites Gibsonianus* (type). Two seeds from one and the same cone. Lower Greensand, Isle of Wight.

C.—*Cycadeoidea* sp. (not *C. Wielandi*). Wealden equivalents (Lakota) of the Black Hills.

D.—*Bennettites Morièrei* (Sap. et Mar.). The type from Oxfordian or more likely Lower Cretaceous (cf. Lignier) of Calvados, Normandy. Cf. Fig. 3B.

i, indurated layer arising from *c* of fig. 1;

p, the outer fleshy or "blow off" layer arising from A of fig. 1 and expanding into five or six alæ near apex, sometimes forming horns;

f, collapsed tissue of inner flesh;

t, tubular cells forming lax or frayed husk, whence these cells may or may not appear in the longitudinal section; = *t*, fig. 1.

n, the nucellar sack tissue, always quite susceptible to silicification.*

* Between the inner flesh (*f*) in various American seeds, and the nucellar sack (*n*), as well as in the seed of *Bennettites Gibsonianus* (B) often occur loosely compacted large cells, supposed to be nucellar contents (pre-embryonal tissues). In the initial course of silicification collapse of the

Of the several species *B. Morièrei* has distinctly the heaviest walls, *B. Gibsonianus* walls of intermediate thickness, and some of the American seeds the thinnest walls of all, though there is essential agreement in testal structure extending to the cell types of the three component layers.

To show this structural similarity and to further bring out minor details proving that in *Cycadeoidea* we deal with a

FIG 3.

A.—*Cycadeoidea turrita* (?). Tangential section through the sclerotesta. $\times 88$. The basal walls of these cells are far thicker than the lateral and tangential walls; the cell interior varies much in appearance, or only the solid base may appear. Again, the outer face may show a marked central concavity.

B.—*Bennettites Morièrei* (Sap. et Mar.) type. $\times 88$. Longitudinal section of testa traversing valley below the shoulder where ribs first become prominent. Compare with fig. 2D.

C.—*Cycadeoidea Wielandi*. S. 736. T. 393. $\times 50$. Longitudinal section of micropylar tube in seed type without distinctly developed "blow off." Palisaded wall in continuation from middle stone. Interior space filled with soft squarish cells, in bulk producing somewhat cancellated appearance. Dotted line shows limit of exterior surface, the thin outer layer failing of conservation.

genus of world-wide distribution and long persistence in time, I have made the series of camera lucida drawings shown in

inner flesh would favor rupture of the nucellar sack with more or less dispersion of such rounded cells, but this explanation is tentative.

The close agreement of the two European species and the American forms retaining the "blow off" layer is noteworthy, while the two seeds of *Bennettites* showing difference in the indurated layer, as seen in about the same region of the testa, suggest the character of longitudinal fluting, and completely bridge the slight structural gap between the commoner American form C. and *Bennettites Morièrei*, no more than mere specific differences appearing.

text figures 2, 4, from the equatorial region of the seed. These include all the best known forms, the seeds of *Cycadeoidea dacotensis* and of *C. excelsa* and *Jenneyana* excepted, as these have not so far been found well enough conserved to permit such drawings; though it can be seen from their general form and amount of testal development, which are well known, that they too agree within generic limits.

In comparing these drawings it must always be remembered that the seed wall is a more or less appressed one, as the result of enclosure by the five or six to as many as eight or ten interseminal scales forming the pocket in which the seed lies. Also both outer flesh and stone normally thicken markedly toward the shoulder and about the basal region of the micropylar tube to form a ribbed or even-tentacled *corona*. But while these *coronal ribs* may tend to disappear in some species, or may somewhat conform to surrounding scales, *an original and fixed number is in reality always present and representative of the species*. Furthermore the ribs may even send up a low crown of tentacle-like projections about the base of the micropylar tube, though it is only after studying the sections very attentively that one comes to see this feature, which, could one see a loose seed, would be very distinctive indeed. In short, we have to do with somewhat appressed vestigial lobes as unmistakable as those of *Physostoma*.

Lateral Testal Envelopes.—As already observed the “*enveloppe tubuleuse*” of Lignier, or cup-like husk formed by the extension of the cortex of the seed pedicels all round the seed base, tends to disappear. The really complex structure of this envelope has been conserved with diagrammatic clearness in *B. Morièrei*, where it is clearly seen to consist in an underlayer, the “*assise plissée*,” really the base of the “blow off,” and a distinctly tubular outer layer which is not found continuous all over the surface of the seed, though its cells are markedly susceptible of preservation. But in strong contrast and clearly proving reduction, fig. 4A is an accurate enough drawing of an American seed in which too few tubular cells to show appear to rest on the middle stone, while there is no appreciable preservation of the inner part or “*assise plissée*” and its apical continuation as a strongly palisaded tissue, “*assise rayonnante*” or “blow off.” This condition is, however, exceptional, but one species showing so much reduction.

Once more in examining transverse sections of American species a doubt may arise as to whether the outer layer of the seed is not actually confluent with the interseminal scales as Solms supposed it might be in places (“*Stellenweise*”) in *Bennettites Gibsonianus*. But this, it is thought, may be due in part to the fact that there are in the interseminal scales

FIG. 4.

FIG. 4. Seed walls of *Cycadeoidea* (A and B), *Lagenostoma Lomaxi* (C), and *Physostoma elegans* (D), contrasted.

A.—*Cycadeoidea Wielandi*. This seed as described is without an outer fleshy or “blow off layer,” although the inner flesh and the middle sclerenchyma have precisely the same development as in the other *Cycadeoidea* seeds.

B.—*Cycadeoidea Macbridei* (?), with thick blow off layer very poorly conserved. The sclerenchyma layer of squarish cells with their inner basal wall heavy, and the flattened inner flesh zone correspond to the outer notched and inner smooth line of A.

C.—*Lagenostoma Lomaxi*. Longitudinal section from above the cupule showing the inner flesh and mid-sclerenchyma with peg-like projections on tangential wall suggesting that an outer “blow off layer” may have failed of conservation. The structure is essentially similar to that of the most reduced of the *Cycadeoidea* seeds as shown at A, although about in proportion to the size of the seed both flesh and sclerenchyma are much thicker.

(Redrawn from Scott.)

D.—*Physostoma elegans*. Longitudinal view of seed wall exactly showing the “blow off layer” as stippled-in cells to the right, but slightly generalizing the complex fleshy tissues between this layer and the nucellar sac which appears as a dark line to the left. Original drawing introduced to show the droop of the “blow off layer” as a peculiarity also seen in *Cycadeoidea*. In other respects interesting as a seed of ancient and complex character, between which and *Lagenostoma* there is in actuality a much greater structural gap than between this latter and the *Cycadeoidea* seed type, although the seeds of all three must be regarded as having analogous structures.

groups of sub-epidermal cells much like the tubular cells of the seed cortex or outer “enveloppe tubuleuse” and that moreover

there is often next the seed an exceedingly thin extension of the epidermal layer of the interseminal scales. There can be no final doubt as to where the seed wall ends and the enclosing scales begin.

Middle Stone.—Following interiorly to the outer flesh analogue or “blow off” layer as so much subject to variation

FIG. 5.

FIG. 5. *Cycadeoidea turrita* (?). Black Hills. $\times 25$.

Longitudinal section through ovulate cone traversing two adjacent seeds. The upper seed is cut tangentially, and the lower one in the nearly true median vertical plane. The micropylar tube is here accurately cut throughout its entire length, and the section passes through two opposite ribs. Only at the seed base is the section a little eccentric, but owing to the small size of the seeds only a few out of a great number will be found so nearly cut in the median plane as the present seed and that in the following fig. 6 A.

to form ribs and coronal appendages characteristic of the various species, the middle stone is found far more constant; yet the figures 2A and 2B from seeds of one and the same cone of *Bennettites Gibsonianus* at once show that this layer also shares in rib formation and regionally varies much in the size of its cells. Its thickness as dependent on ribbing varies from one cell in the lateral region to several or more cells as the ribs form in the upper and shoulder region of the seed and converge towards the micropylar base.

In the American species the stone layer is usually very thin, but quite distinctly indurated,—silicification in reality showing density of walls better than other types of conservation. The cells of the stone superficies appear to have had a very thin tangential wall, even subject to collapse, so as to sometimes simulate a series of flattened hexagonal cups with very heavy bottoms and sides thinning a little toward the top. In the French specimen it is the cell contents rather than the cell walls that appear to have “taken the stain,” and this produces a certain appearance as of a decidedly fleshy tissue especially in the outer cells bearing the “*blow off*.” But what the true nature of the tissue is cannot rest in any doubt; for it is as we see often highly indurated in the American specimens, and nearly as much so in the Isle of Wight specimen. While, as I fully believe, the slightly less indurated condition seen in *Bennettites Morièrei* is quite exactly paralleled by the middle layer in *Pinus resinosa*. In considering any mineralized tissues, moreover, it is occasionally necessary to note that the staining could exhibit the cell contents rather than the cell walls, which might finally fail of clear outline and be replaced by structureless mineral.

Inner Flesh.—The inner fleshy layer or tissue region lying between the stony region and the nucellar sack is of about the same breadth as the stony region in all the Cycadeoideæ, bearing in mind the reduced testa in the American *C. Wielandi* where both these coats are very thin. In no instance, however, is the inner flesh distinctly enough conserved in the lateral region of the seed to permit camera lucida drawings, or even photomicrographs showing it other than as a clearly outlined zone of soft crushed tissue. But in the Normandy seeds preservation is often diagrammatically clear near the seed base where this zone is from three to about seven cells deep, with the outer cells elongate, and flat squarish to rounded forms on the interior. The nature and succession of the testal elements is clearly illustrated in the transverse section through the radio-symmetric seed base shown in fig. 1, where the relation to the central bundle is still clear and the layers appear in their initial and simplest form. That the ancestral endosarcal bundle system is not entirely eliminated is probable, though final determination of this point still depends on favorably located rib-angle sections of exceptionally conserved seeds.

Homologies of the seed coats in Cycadeoidea.

In my American Fossil Cycads (p. 174) the view was taken that *Lagenostoma* presents the nearest known analogy to the seed wall structure of *Cycadeoidea* of any form existing or

FIG. 6. *Cycadeoidea turruta* (?). Black Hills.A.—Longitudinal section of seed. $\times 15$.

s, seed pedicel ;	pl, exterior covering or "blow off layer" ;
h, hilum ;	is, interseminal scales ;
n, nucellar sack ;	st, micropylar tube ending as a slightly flanged style.
m, megaspore membrane ;	
e, embryo ;	
il, interior layers of testa ;	

B.—Oblique section of four adjacent seeds. $\times 25$.

n, nucellar sack ; m, megaspore membrane ; e, embryo.

In A all the basal portion of the section traverses thin "blow off" tissue, which strongly thickens into a *five rib series* at the shoulder, these ribs even prolonging themselves tentacle-like into a sort of corona. The solid black line represents the middle stone or sclerenchyma, the narrow blank space between it and the nucellar sack the inner flesh, and the outer barred area the exterior soft tissue or blow off layer. In this seed a rib is cut on the upper side and a furrow is traversed on the lower side. Only in the micropyle does the diagram fail of accuracy, as the middle sclerenchyma does not give origin to all the micropylar wall.

In B the nearly complete occupation of the megaspore membrane by the embryo is seen to repeat itself normally. Occasionally in sections cutting many seeds a third cotyledon is indicated. In the seed to the right no embryo developed and the nucellar sack and megaspore membrane floated to the center and collapsed, whence an extra line appears as the boundary of the inner flesh.

extinct. And no reason is now seen to recede from this view. For in reality *Lagenostoma* offers in the retention of reduced inner flesh bundles, or an endovascular condition, an intermediate stage between the large thick-walled amphivascular seeds of existing cycads and the reduced or even truly monovascular *Cycadeoidea* seeds; while the archaic features in the apical region of the latter must be of far more significance than would be the retention of bundles, which were without a shadow of doubt anciently present. And the closer we study *Cycadeoidea* the clearer does it become that despite an enclosed position and despite reduction the seed apex is after all of the ancient multilobate type. Further, we think it can be accepted that the stony palisaded layer of *Lagenostoma lomaxi*, though following ripening and shedding of the seed the external one in all the lateral region of the seed, is none other than a middle stone. The small tubercles of this layer (cf. fig. 4C) were thought by Oliver and Scott (8) to have supported an outer layer of thin-walled cells, while in the *Cycadeoidea* seeds one may plainly see that the thin outer wall of the outer cells of the stone layer has to do with its function as a bearing wall for the "blow off" layer. In comparisons with *Lagenostoma* it may be remembered, too, that various species are known, and that in *L. ovoides* for instance, where both cell form and preservation suggest decided resemblance to *Cycadeoidea*, the indurated layer is several cells thick, so that this layer can vary much in thickness and development in both these genera as already known. To some the *Lagenostoma* cupule may seem to prevent comparison, but it should be recalled that this structure must have been under way of reduction, whereas the tubular layer which occupies the same region in *Cycadeoidea* and serves the same essential function as a basal cup or husk, is evidently a last remnant of some ancestral leafy structure.

So far as now recalled *Polypterosperrum* of the French Paleozoic is the only other ancient seed which has ever been suggested as offering a distinct likeness to the Cycadeoidean seed structure. Professor Lignier (3) in studying the four (occasionally five) ribbed *Bennettites Morièrei*, after pointing out marked testal resemblance to *Gnetopsis*, attached too much significance to apical appendages, reaching the conclusion that the latter seed presented no true analogy. But he went on to guardedly name an apparently related form *Polypterosperrum* as probably much nearer to *Cycadeoidea* than other ancient types, a suggestion of relationship which seems to have been little heeded. It is likely, however, that restudy of the apical region of the seeds of *Bennettites Morièrei* in conjunction with *Polypterosperrum* will be well worth while, since this region is not sufficiently known even in *Bennettites Gib-*

FIG. 7.

FIG. 7. *Cycadeoidea Macbridei* (?)

Four characteristic subtransverse to sublongitudinal sections of seeds containing embryos from as many different thin sections (Nos. 762-765) cut from one of the various strobili of the Minnekahta cycad trunk Y. S. No. 131: all $\times 15$.

A.—Subtransverse section. Passes near the "shoulder" of the seed as indicated by the apical ribs on the upper side, but below the radical since the two cotyledons with their bundles (*b*) plainly appear. In the upper cotyledon which must be cut near the cotyledonary node but four bundles are traversed, approach to the maximum number of five or six lamina bundles appearing on the lower or more basal side.

The somewhat convolute prolongation above is most readily explained as a remnant of proembryonic tissue exactly like that persisting or but slowly made over into the true embryo tissue in the very similar dicotyledonous embryo of *Ginkgo*.

sonianus, and is difficult of study in the silicified American specimens. Again, the French Paleozoic seeds are scarcely known to us in that closer detail which present methods of fossil seed study are rapidly bringing to light.

But meanwhile further interesting comparisons with ancient seeds have been made possible by the instructive interpretations of Paleozoic seed structures and noteworthy study by Oliver and Salisbury (11) of the two species *Conostoma oblongum* and *C. anglo-germanicum*.

In the species of *Conostoma* no cupule obscures the exosarcical features, but the seeds have the small size of those of *Cycadeoidea*, in consequence of which they present much difficulty of study due to dependence on chance sectional planes. Nevertheless, by plotting about a score of sections of *Conostoma anglo-germanicum* and nine sections of *Conostoma oblongum*, and then constructing models from the estimated planes of the sections, nearly concise restorations of both

B.—More nearly transverse and basal section than the preceding in which the dark staining mass clinging to the lower left cotyledon must be an endosperm remnant rather than a tissue like the convolute extension just noted in A.

C.—Sublongitudinal section. Passes through lateral hilum and emerges at the seed "shoulder," traversing nearly the entire length of the embryo with its two cotyledons (c) and their lamina bundles (b).

D.—More nearly longitudinal section than the preceding, cutting *chalazal tracheid stem* or goblet, and passing beyond the "shoulder" near to base of micropylar tube. The embryo is here especially instructive as showing the forking (b) of the cotyledonary bundles in both lamina as well as the apical proembryo folds and endosperm or albuminous remnants (a). Taking this section at W the characteristic proportion and appearance of the seed wall layers is indicated distinctly. On the inside next the embryo to which the nucellar sack clings is a considerable empty space left in part by shrinkage of the embryo, in part by collapse or failure of preservation of the spongy enclosing cells of the nucellus, and in part finally by the invariable flattening out of the cells of the inner flesh, indicated by the inside solid black line.

The inner flesh clings closely to the middle sclerenchyma, also shown in solid black but notched on the outer border, this being the artist's method of indicating the cup-shaped appearance of the component cells due to preservation of the thick inner or basal wall and thinning out of the lateral walls without easily detected conservation of the very thin tangential wall. Exteriorly comes the outer flesh, or more exactly the "blow off layer" strictly homologous to that of Carboniferous Cycadofilicinean seeds, *Physostoma*, etc. But in strobili of trunk 131 and in most American Cycadeoidean seeds the very thin cell walls of this layer are indistinct, though their characteristic palisade-droop, so pronounced in *Physostoma*, cf. figure 4 D, is plainly in evidence. Finally, the strongly lined outer basal tissue is that of the cortical husk.

[These sketches of seed sections are diagrammatic in the best sense, since they are in reality the artist's excellent drawings *just as he saw them* in these particular seeds, but to be seen over and over in seeds of other strobili cut from trunk 131. This trunk was referred by Professor Ward to the species *C. Wielandi* as best represented by Yale Cycads Nos. 77 and 393, but cannot be of that species. Not only are there leaf base differences but in the seeds of 77 and 393 the "blow off layer" is virtually eliminated.]

FIG. 8.

FIG. 8. *Cycadeoidea Macbridei* (?).

Part of a somewhat oblique section through a strobilus of Y. T. 131 cutting nine seeds at angles varying from nearly transverse (*e*, *e2*) to tangential longitudinal (*e5* and *n*) and illustrating the embryos and embryo bundle system. The position of the several sections is quite obvious:—*e* with its embryo is cut high up just where the cotyledonary node gives off the two supply bundles for the cotyledons; *e2* passes lower but is still rather near the cotyledonary plate since neither radical nor sinus between the lamina appears; while in the seed *below e2* the upper part of the pedicel is cut and the forking of the bundles in the tips of the cotyledons is evident; *e5* and the seed alongside it are decidedly tangential, though in each both cotyledons appear.

In each of the seeds *e-e5* a lateral deeply stained mass of endosperm (?) appears beside the embryo. In three of the seeds the embryo fails wholly of preservation, but the nucellar sacks (*n*, *n*, *n*) are wholly distinct, collapse and folding of this sack as here so clearly to be seen being of much interest in connection with various forms of nucellar sack rupture in many *Cycadeoidea* seeds.

species have been obtained. Both are endovascular, the inner fibrous flesh being traversed by six bundles in the angles of as many simple ribs in *C. oblongum*, and four bundles in the angles of the four major or wing ribs which initially alternate with as many minor ribs in the somewhat more complex *C. anglo-germanicum*. Both species thus agree with *Cycadeoidea* in size and in being coronate radiospermic ribbed and winged forms with essentially the same wall structure, barring retention of the endosarcular bundles, traces of which are, however, yet likely to be found in the *Cycadeoideæ*.

Indeed, truly essential testal and apical differences, rather than likenesses, remain to be established now that we know *Cycadeoidea* to be a characteristically four- and five-ribbed and lobate, winged, tentacled seed which also shows some tendency to alternation of major and minor ribs.

Evidently *Cycadeoidea*, though of composite type, has, as befits its Mesozoic extinction, a clear title to admission into the great groups of Paleozoic gymnospermous seed types retaining indisputable evidence of a yet more ancient multiple integument. And this is yet more strongly indicated when we turn to the fuller lobed *Neuropteris heterophylla* seeds described as attached to their foliage by Kidston, if, indeed, these are true megaspores. Especially so, if we further consider that most remarkable six-lobed microspore-bearing fruit *Codonotheca* of quite the same size and outer aspect as the reputed *Neuropteris* seeds, and on the score of association strongly suspected to be of Neuropterid affinity when first described (7).

Reëxamination of this fossil by the writer has so far failed to establish the presence of sporangial structures on the inner surfaces of the campanular lobes where much loose and extraordinarily large-sized pollen may be seen, seemingly in quite the position in which it grew.* But while the general appearance at first seemed to preclude the drifting in from the outside of pollen attaching itself to sticky inner surfaces of free

* These *Codonotheca* or Neuropterid microspores or *prothallate pollen* grains are the largest known, even greatly exceeding *Stephanospermum*, and it remains quite probable that by some modification of Nathorst's collodion method some evidence of extensive prothallial tissue may be found.

The characteristic make up of the seed wall again appears as in the preceding figure as well as the important additional fact that breaks or gaps in the inner flesh and middle sclerenchyma quite regularly occur near the shoulder and conclusively indicate that these seeds of *Cycadeoidea* are as truly ribbed tentacular or apically lobate as any members of the *Langenostoma* group.

[It is probable that these embryos have undergone some shrinkage, though the cell structure is often clear and does not show much evidence of collapse. However, various remnants about the sides of the embryos indicate unused parenchyma. The appearance does not entirely reconcile itself with the great size of the proembryo, seen in another species.]

apical lobes of a small central seed and there undergoing prothallial growth, such an interpretation is, because of the peculiar spindle-shaped and possibly ovulate base, not easily dismissed. Should this prove to be the true interpretation of *Codonotheca*, it is the most leafy of known seeds. But any one is free to work out various alternative interpretations for himself. And certainly this singular fruit would be at once explained by many, or most, as some entirely primitive form of giant microspore case had not the ubiquitous staminate

FIG. 9.

FIG. 9. *Cycadeoidea Macbridei* (?).

Diagrammatic reconstruction of the dicotyledonous embryo showing approximate position of the bifurcation of the node (*bf*) and the probable bundle distribution in the cotyledons. The two branches leading into the cotyledons must run parallel further than here appears because the laminæ are shown as if arbitrarily flattened out.

disks of Mesozoic times led us to expect to find circular emplacements of sporophylls in process of reduction in ancient plants, and in particular taught us to see, that in such disks spores once borne ventrally may easily become falsely dorsal. In any case, however, the study of such forms must ultimately shed much light on the nature of gymnospermous testal structure, the essential and primitive elements of which already begin to appear.

But yet another comparison of the seeds of *Cycadeoidea* may be made with forms far nearer at hand that might have been thought of before. Through the great kindness of Professor R. B. Thomson, whose excellent demonstration of the megaspore membrane of the gymnosperms is well known. I have come into possession of a beautiful though limited series of longitudinal sections of existing gymnospermous seeds; and the attentive study of these shows that the smaller seeds, especially of the Abietineæ present a clear analogy to *Cycadeoidea* in all that pertains to lateral wall structure. In *Pinus resinosa*

there is, taking the lateral wall, a noteworthy parallel, and if one had before him a complete series of both transverse and longitudinal sections of the Abietineous species it is likely that traces of apical ribbing would be found and that a composite exceedingly like *Cycadeoidea* could be observed.

And this line of study promises much interest; for the Abietinean series was always regarded as a quite modern side branch rather than an old gymnosperm stem terminal, until the possession of really ancient structures was pointed out by Hollick and Jeffrey.* These writers in their admirable study of Cretaceous conifers show *Pinus* to be archaic and demonstrate a new genus *Prepinus* of more primitive structure than any other conifer living or extinct, while Jeffrey now insists without reservation that the Abietineæ are the oldest tribe of conifers.† The decided resemblances in the seed wall structure to *Cycadeoidea* lend further color to such views if any value can be assigned to present-day features of gymnosperm seeds in trying out questions of ancient relationships amongst great groups of gymnosperms, using the name in any wide sense.

Some closing remarks.—To anyone interested in the subject of fossil seeds, it will not be necessary to say that even in the case of seeds as well represented as are those of *Cycadeoidea* finality in description cannot easily be reached. To secure more exactly oriented sections, to illustrate these adequately by both photomicrographs and drawings and gain an accurate idea of the precise form and structure of the various species of seeds is a work of time and perforce the task set for further publication in connection with other features. But meanwhile, it may be stated that, regarding our view that a proembryonic tissue occupying all of the nucellar cavity is present in one species of *Cycadeoidea*, we still have no other explanation to offer. Though it can be said that whatever the nature of this tissue it seems to have been much given to bursting from the nucellar sack. Scarcely better photomicrographs showing the usual character and position of this tissue can be given than that of the transverse section Plate XXX (9), where the slight filmy tissue traversing irregularly the mass of rounded cells is none else than the much wrinkled and collapsed nucellus, though we were not at first prepared to believe that the nucellus had so frequently collapsed, ruptured and floated about in shreds amongst these cells as is now seen to be the

* Hollick, Arthur, and Jeffrey, E. C.—Studies of Cretaceous Coniferous Remains from Kreischerville, New York. Mem. N. Y. Bot. Garden, vol. III, 138 pp. with 29 plates. New York, 1909.

† Jeffrey, E. C.—A new *Prepinus* from Martha's Vineyard. Proc. Boston Soc. Nat. Hist., vol. 34, No. 10, pp. 333-338, pl. 33. Boston, 1910.

case. Others who have seen the sections are at least certain that the tissue is not endospermous; and to the objection that a proembryonic tissue would not be likely to thus occupy quite all of the nucellar cavity it is replied that such a condition is in reality only one of degree, and that it is readily conceivable as having been present in Cretaceous gymnosperms. Though it is of interest that conformably to the lesser degree to which the embryos shown in figure 7 fill up the nucellar cavity as compared with those of figure 6, far more distinct traces of endosperm are present.

The sections, which may be seen at the Yale Museum, are not only being constantly added to, but meanwhile receiving careful attention and comparison, and it is intended to give features displayed the best possible illustration. Meanwhile ink drawings of various seeds are appended in the present text figures 7 and 8 illustrating the strobili of Yale Cycad 131. This trunk is one of those referred to *C. Wielandi* by Professor Ward, but cannot be of that species as represented by trunks 77, 393, and various other specimens constituting a distinct and unmistakable group. Trunk 131, which bears strobili with not infrequent finely conserved embryos—indeed quite the best so far known—may be provisionally referred to *C. Macbridei*. The chief vegetative differences from *C. Wielandi* are exhibited by the sections through the cortical parenchyma, showing the leaf traces and the leaf bases of both to be of much larger size than in the *C. Wielandi* trunks, while the main differences in testal development are exactly noted in the legends of the respective figures, 4 C, 7, etc.

The present drawings all show the position of the young embryo bundles to agree with that seen in both *Bennettites Gibsonianus* and *B. Morièrei*, as shown by the scheme of the embryo bundle pattern, figure 9, which must closely approximate the true form. From this it is evident that a pattern a little more reduced than that of the living cycads, but not so much as that of conifers, is present. In fact, the bundle pattern is the same composite one seen in *Ginkgo biloba*, to the general form and structure of the entire embryo of which there is a very close analogy, extending to the occasional occurrence of three cotyledons instead of the normal dicotyledonous condition.

Finally, the fact that seed and embryo of these fossil cycads are of the most generalized gymnospermous type can escape no one; while the retention of pronounced cycadofilicinean features further favors inclusion in the Cycadales. Though for the present letting classifications evolve themselves as they may, it is most interesting to observe that not only were the primitive seed characters of the Cycadeoideæ little obscured by

appression in the peculiar strobilar type so much affected by the group throughout the Mesozoic, but even so much the more surely conserved as to permit the freest comparison with the ancestral singly borne multilobate leafy seeds of Paleozoic times.

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