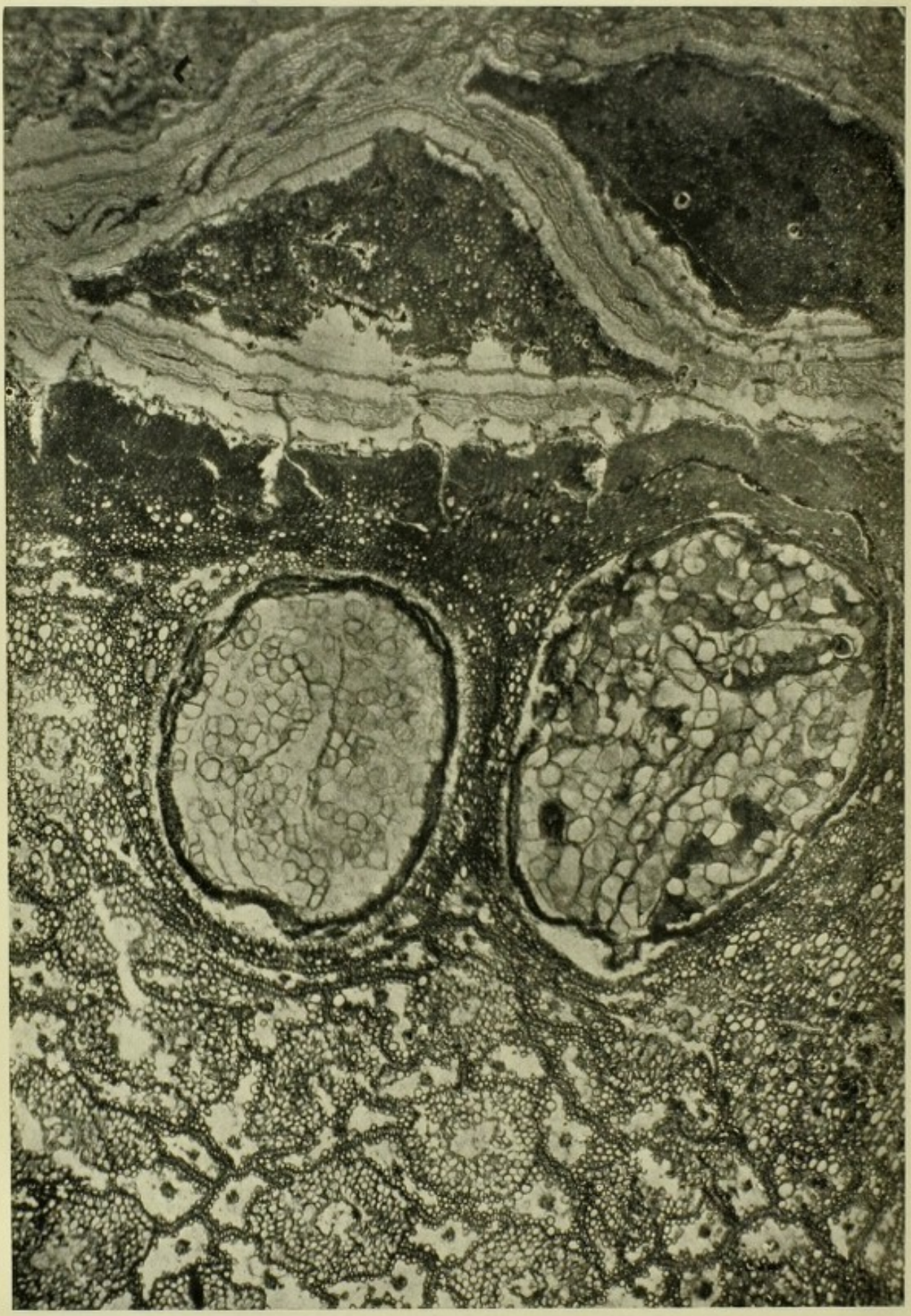
The proembryo of the Bennettiteae / by G.R. Wieland.

[From The American Journal of Science, Vol. XVIII, December, 1904.]

THE PROEMBRYO OF THE BENNETTITEÆ.

By G. R. Wieland.



Cycadeoidea Wielandi. S. 394. ×30.

Portion of a transverse section of an ovulate cone, cutting exterior bracts above and two adjacent proembryos filling the seed cavities, as surrounded by the mass of seed pedicels and interseminal scales.

Art. XLVII.—*The Proembryo of the Bennettiteæ;* by G. R. Wieland. (With Plate XX.)

During the course of the preparation and study of large numbers of sections made from many different fossil cycad trunks representing various stages of growth and fructification, no more important feature has been discovered than the *proembryos*, of which various examples have been observed in several different fruits of *Cycadeoidea* from the Black Hills. As no developmental stage, if the archegonia of *Cycadinocarpus augustodunensis* be excepted, has hitherto been observed in any extinct plant, this discovery is of extreme and novel interest. It has, therefore, been deemed appropriate to present a preliminary description, to be amplified and further illustrated in the writer's memoir on the Structure of the Fossil Cycads, now nearly ready for publication by the Carnegie Institution of Washington, under whose auspices these investigations have been pursued.

Amongst the fossil cycads in the Yale collection closely resembling the so-called *Bennettites Gibsonianus* from the Isle of Wight, but still referred by the writer to the genus *Cycadeoidea*, the trunk numbered 393 is very completely silicified, and bears a number of fine ovulate cones. In the various longitudinal and transverse sections cut from these cones, nearly all the tissues are clearly indicated, and the seed bodies have reached approximately the size of those of the type of *C. (Bennettites) Gibsonianus*, found by Solms-Laubach to contain dicotyledonous embryos, nearly or quite filling the seed cavity, and hence exalbuminous, or nearly so. These are the only fossil embryos ever found. In the sections from trunk 393, as is usually the case in silicified plants, the seed cavity is often filled with more or less clear quartz, or by structures and traces of structure which cannot readily be interpreted. But there are in the present instance notable exceptions; a considerable number of the seeds, as one must conveniently call any stage of seed development which is not or cannot be specified, contain well preserved large angular to rounded proembryonal cells. These appear to fill the entire nucellar space in some of the transverse sections. Such an instance, where two adjacent seeds are finely conserved, is shown on Plate XX, enlarged thirty diameters. In other cases the large granular to rounded cells of the proembryo appear to have been but partially preserved, or else to have collapsed, carrying the nucellar wall inwards as if there had been a central cavity in the large-celled mass, as usually

clearly to be seen abutting on the wall of the nucellus. There are also especially to be noted in the transverse sections several irregular ribbon-like traces about the thickness of the cell walls, extending quite across the large-celled mass, filling or nearly filling the nucellus. These traces or rather surfaces occur too often to be considered wholly accidental, but are not supposed to be either suspensors, or tubular öspores, or cells such as precede embryo formation in *Ephedra*. Their fuller explanation doubtless awaits the preparation of more numerous sections and the comparisons they may permit. In some of the sections presumably cutting the upper half of the proembryo, as already hinted, there is a suggestion if not a clear indication that the mass of proembryo tissue was either less dense in its central regions, or, that there was actually present a small central cavity. This important point, which would indicate a fundamental agreement with the existing cycads, cannot be so readily settled as yet, since in no instance has a longitudinal section been cut from a proembryo as well preserved as the two shown in the plate. In one longitudinal section showing the lower two-thirds of a seed it is clear that the lower half of the nucellus was closely filled by the typical large undifferentiated cells making up the mass of the proembryo. In another longitudinal section, the superior end of the nucellus is seen to extend well into the tip of the seed, which is quite filled with the characteristic large-celled proembryo tissue. Unfortunately the middle region is in this instance not conserved.

There is nowhere a distinct indication of the presence of endosperm, or of any differentiation of the large-celled tissue filling the nucellar cavity, into an inner and outer zone. The proembryo tissue appears to be homogeneous throughout, except in one instance where some more elongate cells appear to rest against the nucellar wall. It is, however, to be constantly borne in mind that it is necessary to amplify the series of sections. Structure will be found in many instances illustrating not only all the features of the proembryo, but in all probability the other stages of development, including possibly the early stages of embryo formation; although it may be years before all the facts are learned, since it is so often the fortunate exceptional section which tells the story and yields the reward for the cutting of sections where preservation proves less clear.

Meanwhile it is possible in the light of these newly discovered proembros to make several highly interesting comparisons with existing gymnosperms. The *proembryo* was a term first used by Treub* in describing the embrogeny of *Cycas*. In

* Ann. Jard. Bot., Buitenzorg, ii, 1881, and iv, 1884.

this genus the oöspore enlarges at the expense of the adjacent tissue. Later free nuclei become very abundant in the central region, and then disorganize, all the cytoplasm massing at the base of the spore, and parietally, with a single parietal layer of equidistantly imbedded nuclei, except at the base, where there is some massing of nuclei. *Still later the sac-like cavity of this stage is partly filled up by tissue preceding suspensor development.* The proembryo of *Cycas* is, in a word, sac-like, and the endosperm large, the size of the latter in a way corresponding to the excess in size of the whole seed over that of the Bennettiteæ.

In *Gingko*, after repeated nuclear division of the oöspore, there is no parietal grouping, but instead the oöspore enlarges and comes to be compactly filled with undifferentiated cellular tissue, in which proembryo, suspensors, and embryo are all merged. This must clearly now be regarded as absolutely the most primitive condition known amongst the existing gymnosperms.

In the organization of the *Gingko* embryo, the mass of tissue just noted as filling the entire oöspore takes part, the endosperm being directly invaded without the formation of suspensors. Two cotyledons remarkably like those of the Bennettiteæ in both size and general appearance are produced; but their earliest stages have unfortunately not been figured so far as known to the writer.

Comparison with the other gymnosperms shows that the proembryo of the Bennettiteæ is unique in oocupying the entire nucellus, although this character loses not a little of its isolation from the fact that the nucellæ of the existing Cycads are almost of the same size, increase in the size of the seed having been plainly bound up with endosperm development. Again it is supposable that a progressive reduction of endosperm had taken place in the Bennettitæ and was perhaps a cause of the disappearance of the group.

The most distinct agreement of the Bennettitean proembryo is clearly with *Gingko*, long known to have much in common with some ancient Cycadean ancestry or relationship. In both these proembryos, as has been seen, large-celled homogeneous tissue fills the oöspore, and the formation of dicotyledonous embryos takes place without the intervention of suspensors. The present discovery unmistakably determines for the first time that the embryogeny of *Gingko* is the most primitive amongst existing gymnosperms.

Between the existing Cycads and the Bennettiteæ the comparison is a more general one, there doubtless having been agreement in the early history of both, and the more general facts favoring the inclusion of the Bennettiteæ within a single great group, the Cycadales.