

SEEDLING VASCULAR ANATOMY OF NELUMBO
LUTEA

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This investigation was begun in 1913 in the hope of throwing further light on the origin of the monocotyls and dicotyls. During the progress of the work the development of the megasporangium, the megaspore, the female gametophyte (embryo sac), the proembryo and the embryo has been retraced. My preparations seem to be in agreement with the work of Lyon (6), York (7), Cook (2), and Conard (1). The only addition that I make to what is already known is the seedling vascular anatomy.

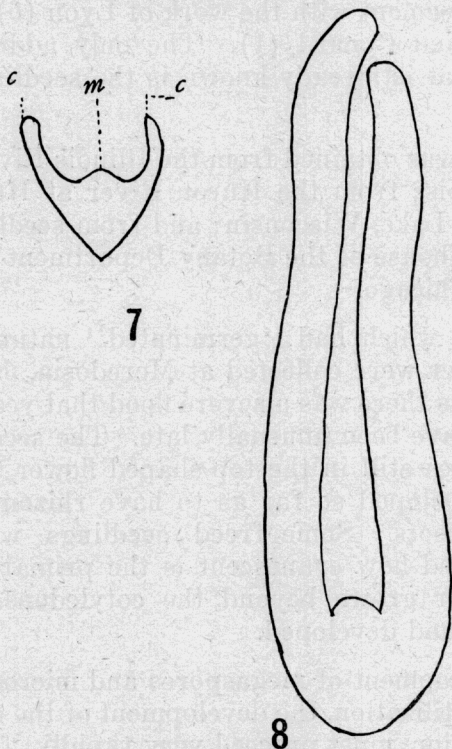
Material was obtained from the Illinois River at Meredosia, Illinois; from the Huron River at Huron, Ohio; from Grass Lake, Wisconsin; and from seedlings grown in the greenhouse of the Botany Department of the University of Chicago.

Seedlings which had "germinated" naturally in the Illinois River were collected at Meredosia, June 3, 1913 (Fig. 1). As there was a severe flood that year germination must have been unusually late. The seedlings were in some cases still in the top-shaped flower receptacles, but had developed so far as to have rhizomes and adventitious roots. Some freed seedlings were found. These showed how evanescent is the primary root; for it had never grown beyond the cotyledons. Adventitious roots had developed.

The development of megaspores and microspores, pollination, fertilization, the development of the embryo and seed formation, must proceed very rapidly; for all these stages were obtained from flowers and fruits collected on a single day, August 25, 1914, at the mouth of the Huron River. The seeds of course were not mature, the cotyledons were green and the seed coat had not been formed; but they were normal in size. In the fall the receptacles drop to the bottom of the stream, lie dormant during the winter, and the seeds "germinate" probably the succeeding spring.

FORMATION OF THE COTYLEDONS

The proembryo is spherical. I find no suspensor. My preparations seem to conform to those of Lyon (6) and York (7). However, in the light of later ideas of plant phylogeny I should place new interpretations upon them. The spherical embryo at first slightly elongates in the line of the long diameter of the embryo sac, (Figs. 2, 3). Soon it widens at right angles to the preceding elongation (Fig. 4), showing two actively growing points on



Figs. 7 and 8.

opposite sides of the periphery and a meristematic tip in the center. One of the peripheral growing points is much more active than the other, producing a single cotyledon (Fig. 5). Shortly after this the second growing point increases its activity and a second cotyledon appears (Fig. 6). The region between the two cotyledons grows very slowly. So rapid is the growth of the second

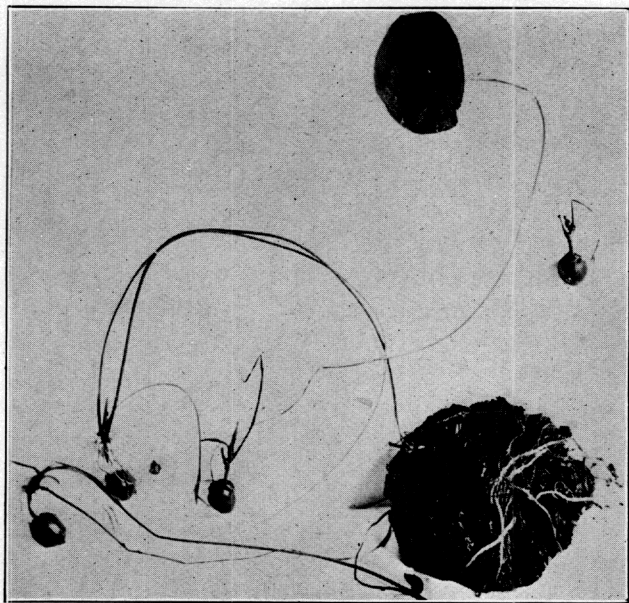
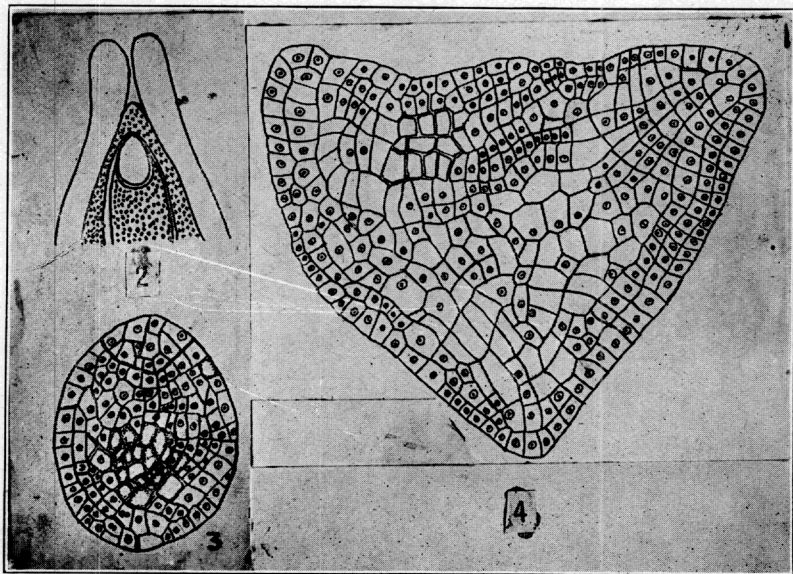


Fig. 1.



Figs. 2, 3, 4.

cotyledons that both are soon practically of the same size (Figs. 7, 8).

Desmogen strands show distinctly in a seedling having cotyledons 15 mm. in length with an epicotyl 4 mm. in length (Fig. 9). Phloem and xylem are not distinctly differentiated in the strands; but they can be traced easily. There are four root strands and one strand to each cotyledon. The latter forms three desmogen

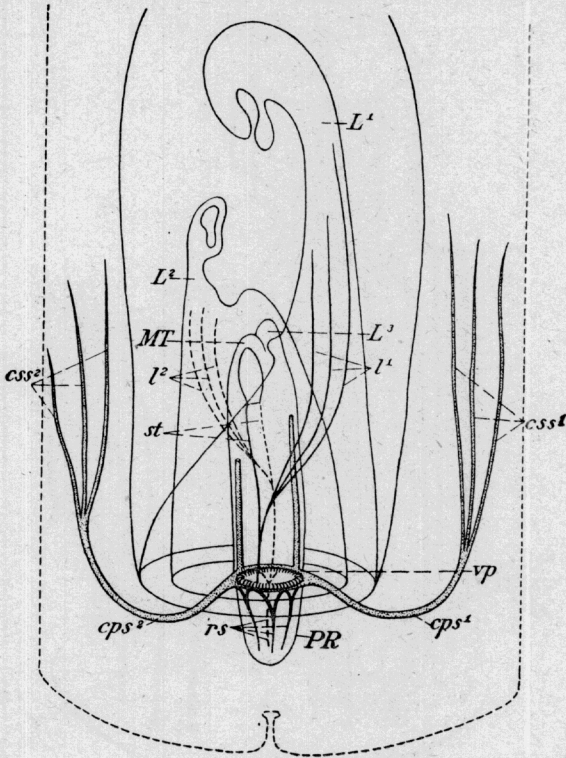


Fig. 9.

strands. The first and second leaves show early traces of similar strands. A single strand shows on each side of the epicotyl. The primary root is present, but no adventitious roots.

A slightly older embryo proved most helpful. Both longitudinal and transverse sections were made. A reconstruction of the arrangement of the vascular bundles was made from the transverse serial sections by means

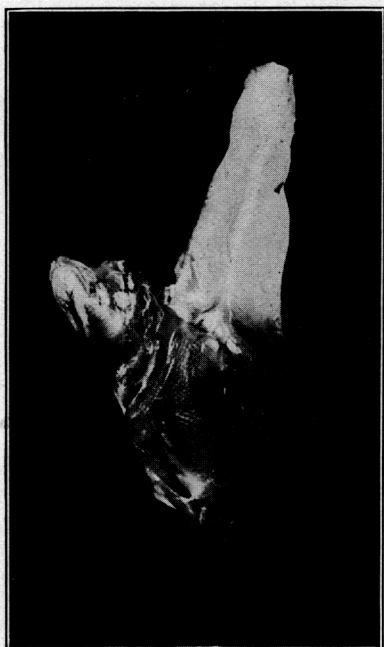


Fig. 5.

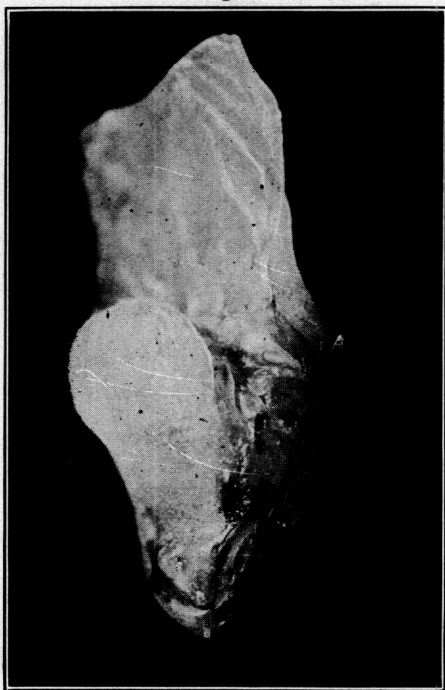


Fig. 6.

EPICOTYL ANATOMY (FIG. 13)

The following is the arrangement of the fibro-vascular bundles in the lower part of the epicotyl. In the center are four very prominent central bundles. Surrounding these are twelve smaller bundles, roughly describing a circle. The cotyledons were cut off between these bundles and the peripheral bundles. The latter are of course cotyledonary bundles, not epicotyl bundles. This arrangement continues for a considerable distance, but is disturbed at the level where the adventitious roots are given off. Six were formed in the seedling from which the model was made. They are the first permanent roots, and arise from an almost complete ring formed by the central bundles. The first leaf is supplied by strands

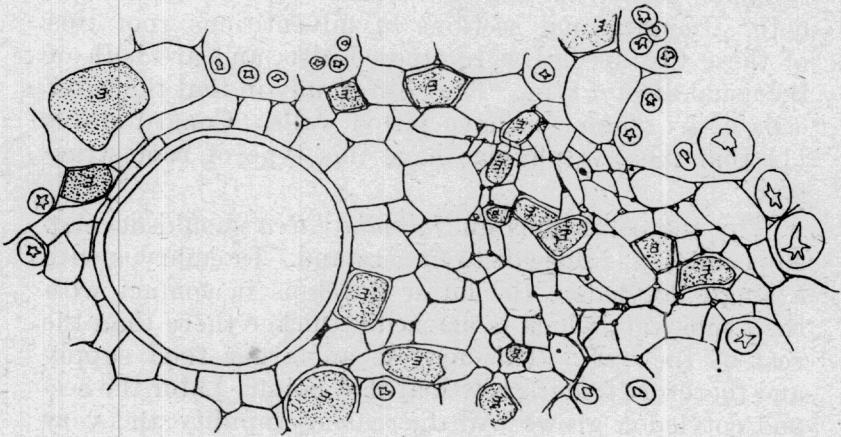


Fig. 14.

which connect with one of the four central bundles, by peripheral strands, and by fusion strands connected with these two types. However, the succeeding leaves are supplied by fusion strands from all the epicotyl bundles. The arrangement of three desmogen strands to a leaf shown so clearly in the younger seedling has given place to a fusion type of structure. At this stage the petiole of the first leaf does not show fusion of strands. The adult leaf of *Nelumbo lutea* was cleared by immersion in equal parts of hot absolute alcohol and glacial acetic acid followed by immersion in clove oil and later by immersion in xylol.

It was then evident that although most of the vascular strands were closed, some of the small strands had blind endings. This would mean a dicotyl leaf venation, which was very close to monocotyledony. Immersion in a saturated chloral hydrate solution for twenty-four hours was tried for the same purpose, but with poorer success.

The fusion of bundle strands to form partial rings is a prominent feature. In some of these, leaf gaps may be seen.

The rhizome of *Nelumbo lutea* was studied. It is polystelic and shows collateral bundles without cambium, a monocotyl character (Fig. 14). However a few dicotyls are polystelic. Comparison of this rhizome with that of *Nelumbo albiflorum* shows the same type of bundle for both. Longitudinal sections of adventitious root tips of these two species were studied also, and are both of the usual dicotyl type. They differ only in that the outer cells of *N. albiflorum* have pitted walls. Conard states (1) that the Nymphaeaceae have this type of root structure.

Why the cotyledons of *Nelumbo lutea* should develop so peculiarly is difficult to understand. In embryos with a single cotyledon, the latter develops in contact with the ovule wall, which is markedly thicker there than the rest of the wall. This may mean larger food supply and therefore faster growth at that point. Later the second cotyledon grows with increasing rapidity and very soon overtakes the first. At the same time the meristem in the center grows slowly, the tissues between the cotyledons very slowly, and we have an apparent dicotyl plant. Before the second cotyledon has grown to any size, the thickening of the ovary wall has disappeared.

The researches of Coulter, Land, and Farrell show that monocotyledony and dicotyledony mean little and are very easily interchangeable. Farrell (5) found four growing points on the cotyledonary zone of *Cyrtanthus*. All except one slowed up and a single cotyledon was formed. Coulter and Land (4) found in *Agapanthus* one completely dicotyledonous seedling, while all the oth-

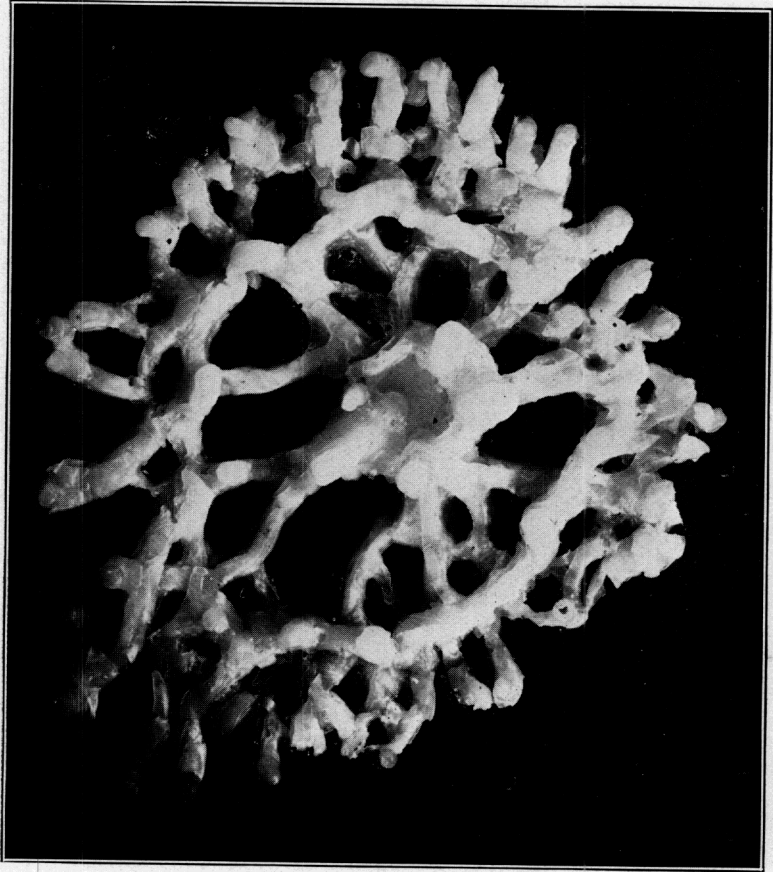


Fig. 12.

ers were monocotyledonous. The same authors show that even the grasses have in many cases a suppressed cotyledon (3).

SUMMARY

1. The massive spherical proembryo without a suspensor is considered to be a primitive characteristic.

2. The root, perhaps the most conservative organ, appears to show the prevailing dicotyl type, having a region of undifferentiated cell tissue from which calyptogen and dermatogen are ultimately derived. This arrangement corresponds to DeBary's third type of root tip.

3. The other vascular bundles of the plant are of the generally accepted monocotyledonous type as is shown by:

- (a) Three vascular strands to each leaf and cotyledon in the juvenile stages.
- (b) Polystelic bundle arrangement. However it must be remembered that while most monocotyls have this arrangement, some dicotyls also have it.
- (c) Rhizome and epicotyl bundles are collateral and without stelar cambium. However a very few of the dicotyls are without stelar cambium and some monocotyls are said to show traces of stelar cambium.
- (d) The venation of the adult leaf is dicotyledonous.
- (e) One cotyledon precedes the formation of a second cotyledon.

CONCLUSION

Nelumbo lutea is phylogenetically one of the higher angiosperms having both monocotyledonous and dicotyledonous characteristics. The fibro-vascular bundles are strongly monocotyledonous but they throw no light on the origin of the seed plants.

Finally, I wish to express my sincere thanks to Dr. J. M. Coulter, to Dr. W. J. G. Land, and to Dr. C. J. Chamberlain for kind assistance given me while making this investigation. Also to Dr. W. E. Davis of Manhattan, Kansas, to the authorities of the Missouri Botanical

Garden, and to Miss Gladys Gladfelter for helping me to secure material difficult to obtain. Also to Dr. L. C. Petry of Syracuse University for making the photograph of the vascular structure of the cotyledonary plate.

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LEGENDS FOR FIGURES.

- Fig. 1. Seedlings which had germinated naturally, in the Illinois River.
- Fig. 2. Micropylar end of young ovule.
- Fig. 3. Spherical proembryo from Fig. 2. Begins to show traces of the traces of the formation of the root and cotyledons.
- Fig. 4. Older proembryo.
- Fig. 5. Photograph of a wax model of a young embryo with a single cotyledon.
- Fig. 6. Photograph of a wax model of a slightly older embryo. The first cotyledon is large and in the background; the second cotyledon is small and is in the foreground.
- Fig. 7. Diagram giving the shape of an older embryo: c, cotyledon; m, meristemic tip.
- Fig. 8. Diagram giving shape and relative size as compared with Fig. 7, of an older embryo.
- Fig. 9. Diagram of the desmogen strands of a young seedling made from serial longitudinal sections. Actual size of embryo. Length of cotyledons 15 mm. Length of epicotyl 4 mm. PR, primary root; vp, cotyledonary ring; L¹L²L³, first, second and third leaves; MT, meristematic tip; rs, root strands; cps¹, cps², primary cotyledonary strands; st, stem traces; css¹, css², secondary cotyledonary bundle traces; l¹, l², leaf traces.
- Fig. 12. Photograph of a wax model made from serial transverse sections of the cotyledonary plate of the same seedling. The sections were 10 u thick. Four central bundles usually termed "stem bundles" are seen. Surrounding these are two concentric rows of bundles. The cotyledons were cut off from the stem between the inner and outer peripheral rows of bundles. The lattice work arrangement of the vascular strands is evident.

- Fig. 13. Diagram of bundles in the epicotyl of the same seedling. Constructed by means of a model from the serial transverse sections 10 μ thick. The base plate shows the arrangement of bundles thru the lower part of the epicotyl, from the region where the cotyledons are cut off, to the region where the adventitious root strands (AR) arise.
S¹, S², S³, S⁴,—central epicotyl bundles.
F¹, F², F³,—first, second, and third leaves.
LG¹, LG², LG³,—first, second, and third leaf gaps.
L¹, L²,—peripheral vascular strands.

- Fig. 14. Transverse section of a bundle from the rhizome of *Nelumbo lutea*.

NOTE: In the preparation of the model of the oldest seedling pictured, comparisons were made with still older seedlings to determine certain points difficult to ascertain in so young a seedling. Some of the ideas thus gained are incorporated in the model.