

A STUDY OF THE STRUCTURE OF THE
GYNOECIUM OF NELUMBO LUTEA
(WILLD.) PERS.

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INTRODUCTION

In the course of time the genus *Nelumbo* has repeatedly been given a different taxonomic status. DUMORTIER (1829) and LINDLEY (1836) raised *Nelumbo*, previously included in the *Nymphaeaceae*, to the rank of a separate family *Nelumbonaceae*. Their views have only recently found recognition. LI (1955) considered *Nelumbo* to be so aberrant that he proposed a separate order *Nelumbonales* for this genus, which, according to TAKHTAJAN (1959), is also accepted by Snigirewskaya. As the principal differences between *Nelumbo* and the *Nymphaeales* Takhtajan mentions the tricolpate pollen grains, the morphology of the gynoecium, the absence of a suspensor and of perisperm, the large, massive embryo with semiglobose cotyledons, the presence of a special "respiration pore", the green plumule, the lack of ideoblasts and the different basic chromosome number. In Takhtajan's classification the *Polycarpicae* are treated as a super-order, consisting of the orders *Magnoliales*, *Laurales*, *Piperales*, *Aristolochiales*, *Nymphaeales*, *Nelumbonales*, *Illiciales*, *Ranales*, *Papaverales* en *Sarraceniales*. HUTCHINSON (1958), on the other hand, includes *Nelumbo* in *Nymphaeaceae*.

The first ontogenetic studies were made by BAILLON (1871) who described the emergence of what he called "la feuille carpellaire" and already mentioned the occasional occurrence of petaloid stamens of which I have also found some striking examples. STRASBURGER (1887) considered the gynoecium of *Nelumbo* to consist of monocarpellate apocarpous carpels which during their ontogeny sink into the hypanthium. TROLL (1933, 1934a, 1934b) examined *Nelumbo nucifera* (*sub speciosum*) in connection with his theory of the peltate carpel and called the placentation "laminar-median".

The first description of the vascular anatomy was given by WIGAND (1888) in his extensive monograph of *Nelumbo nucifera* (*sub speciosum*) in which he states, among other things, "... das ellipsoidische Pistill hat eine trichterförmige Narbe" and, furthermore, "... auch sieht man in diesem Cambialgewebe (*i.e.*, of the pistil) *hie und da* Gefässe, deutlich ist, dass eine Gefässbündel von der Basis eindringt, welche seitliche Aeste abgiebt". TROLL (1934a) reports the occurrence of a "dorsal" vascular strand of and one "ventral" and many laterals, but he does not mention the vascular innervation of the ovule. SAUNDERS (1939) studied *Nelumbo lutea* and concluded that the carpel contains a

dorsal strand which does not extend as far as the apex, two ventral bundles from which branches to the ovule split off, and two accessory bundles. In her opinion the vascularisation of the carpel is palmate. This interpretation is adopted by EAMES (1961, fig. 85, d.). Recently SASTRI (1957, 1959) investigated the floral morphology of several Ranales including *Nelumbo nucifera* (*sub speciosum*). Unfortunately the illustrations of his publication (1957) could not be consulted, but he reported (1959) in contradistinction to Troll, Saunders and Eames, that he could not find structural or functional differences among the various vascular strands in the pistil wall. The innervation of the ovule is accomplished by numerous branches of the ascending vascular strands. He considers this type of carpellar vascularisation to be a primitive condition and the basic type of the various types of vascularisation in the Ranales. The vascular anatomy of the carpel in this group is supposed to be palmate.

SIMPSON's (1937) claim that tricolpate sporomorphs with two large and one small lobe occurring in the Jurassic Brora coal of Scotland are pollen grains of *Nelumbo* has been the subject of several discussions. WALTON (1940, 1958) considers it to be most unlikely that such a highly specialised type of pollen would have developed so early in more than one group of plants and he concludes that it must indeed be assigned to *Nelumbo*. ERDTMAN (1948) also agreed with this interpretation which has been followed in several text books. GOTHAN & WEYLAND (1954), for instance, state that the fossil pollen-grains under discussion cannot be distinguished from those of *Nelumbo*. DARRAH (1960) reports that Simpson's sporomorphs are undoubtedly referable to *Nelumbo*. HUGHES & COUPER (1958) also studied Brora pollen and re-examined Simpson's specimens. Their conclusion is that the sporomorphs ascribed to *Nelumbo* are those of a gymnospermous plant and must be referred to *Zonalapollenites*. SCOTT *et al.* (1960) adopt this view in their argumentation that fossil remains of angiospermous plants are not likely to occur in pre-Cretaceous strata.

The purpose of the investigation reported in this paper was a study of the vascular anatomy of the gynoecium of *Nelumbo lutea* in order to attempt a morphological interpretation of this singular structure. The terminology used is that of Jackson (1949).

MATERIAL AND METHODS

Material (young flower buds) of *Nelumbo lutea* (Willd.) Pers. fixed in FAA was upon request kindly made available by Dr. F. W. Went of the Missouri Botanic Garden and his staff and by Dr. R. H. Godfrey of Florida University, Tallahassee. Apart from longitudinal and transverse microtome sections 8 to 12 μ in thickness and stained with Safranin and Fast Green (JOHANSEN 1940), cleared bleached preparations of whole young pistils were studied. MOSELEY (1958) also used a clearing technique when he studied the gynoecia of *Nymphaeaceae* but reported that the usual methods were not effective when tried on the gynoecium of *Nelumbo* (he, therefore, only discussed the

vascularisation of the stamen). It seems worth while to describe the method I used which yielded very satisfactory results. The procedure is as follows:—

(1) After removal of the perianth lobes and stamens the buds are bleached for about 24 hours in a commercial hypochlorite solution diluted with an equal amount of water.

(2) Hydrolysis in N/I HCl for 20 minutes at 60 °C, for 5 minutes at room temperature and again 20 minutes at 60 °C (the HCl solution to be changed after the first two periods).

(3) A sulphite rinse in a solution containing per 180 ml tap water 1 g Na HSO₂ and 10 ml HCl (36 per cent) for two minutes, to be repeated twice (*i.e.*, three rinses in all).

(4) Passing of the objects through an alcohol series to 96 % ethanol in which the pieces are subsequently boiled for some time.

(5) Bleaching for 8 days in a mixture of commercial hypochlorite and water 1:3.

(6) Treatment in an alcohol series and transfer via ethanol 96 % and absolute alcohol to toluene.

The cleared pieces were examined in toluene under a binocular dissecting microscope and could be peeled off with needles. Staining was not necessary.

Various developmental stages were studied from both microtome sections and cleared preparations.

OBSERVATIONS

It is generally known that the gynoecium of *Nelumbo* consists of an obconical “hypanthium” which bears the individual “pistils” in cavities. The pistils sink into the hypanthium during the early developmental stages, as already reported by BAILLON (1871–1873) and by TROLL (1933), whose observations I could confirm. Photos I

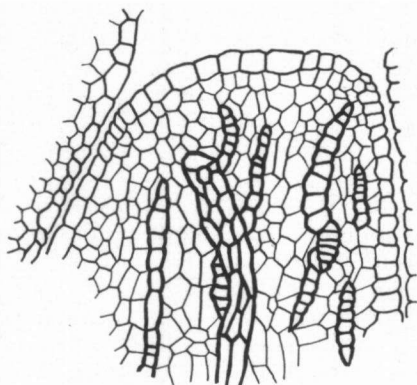


Fig. 1. Intercalary growth of the hypanthial tissue between the pistils. Some of the “cell families” derived from a single mother cell are indicated by means of a heavier outline.

and II show a portion of the gynoeceium of a young flower bud in longitudinal section; in II the pistil on the right has been cut through the median plane and the one on the left tangentially. The formation of a raised part of the hypanthium around the pistils through intercalary growth can be clearly seen (see also Fig. 1). Photo III was made of a somewhat older stage in which the pistil was already "sunk" into the hypanthium, only the rotate "stigma" still protruding. The full-grown immersed ellipsoidal pistil is basally attached to the hypanthium by means of a short stalk and has, apart from the flattened circular stigmatic apex, an abaxial protuberance or "hump" (which Takhtajan interprets as a respiration organ for the developing seed.) On the flank opposite this hump, *i.e.*, adaxially, the ovule is suspended. From the anatomical investigation it has become clear that a plane of symmetry exists which goes through the hump and the place of attachment of the ovule. The planes of symmetry of all pistils are radially placed and pass through the centre of the hypanthium (Photo IV). For the sake of convenience the conspicuous vascular bundle which lies on the abaxial side (*i.e.*, at the same side as the hump) will be referred to as D.

The vascular anatomy of the whole gynoeceium was studied. After staminal traces have split off from the vascular complex of the floral axis, a complicated system of bundles continues distally of the stamen traces, which system is conical in longitudinal section. From this conical structure two types of vascular bundles enter the hypanthium, *viz.*, (1) vascular bundles that ascend into the pistillum directly, and (2) bundles that enter the hypanthium tissue between the immersed pistils, and branch chiefly in the apical region of the hypanthium. This vasculature will be discussed in more detail presently. From the cleared preparations of developmental stages in which the pistils had already become immersed and attained a length of 6 to 8 mm, the vascular pattern of Fig. 2 was reconstructed. In the 39 pistils studied no important variation was noticed, apart from secondary changes during the later developmental stages. As the pistils grow older supernumerary branches (not drawn!) are formed between the ascending traces drawn in Fig. 2.

Fig. 3 represents diagrammatic transverse sections of the vascular structure made at the levels indicated in Fig. 2 and verified by the examination of transverse serial microtome sections. Some camera lucida drawings of corresponding sections are shown in Fig. 4. In these sections the secondary vascular bundles had already been formed and they are, therefore, drawn in, so that the number of bundles is higher than in the corresponding diagrams in Fig. 2.

From the hypanthium two sets of three vascular strands enter the basal stalk of the pistil (Fig. 2, 3-VIII). The three alternating central bundles arising from the hypanthium lie close together. The three peripheral ones, which form an outer ring, descend from the pistil and bend upwards again as soon as they are outside the stalk to enter the surrounding hypanthial tissue where they anastomose with the other bundles present in the hypanthium. It should be noted that the

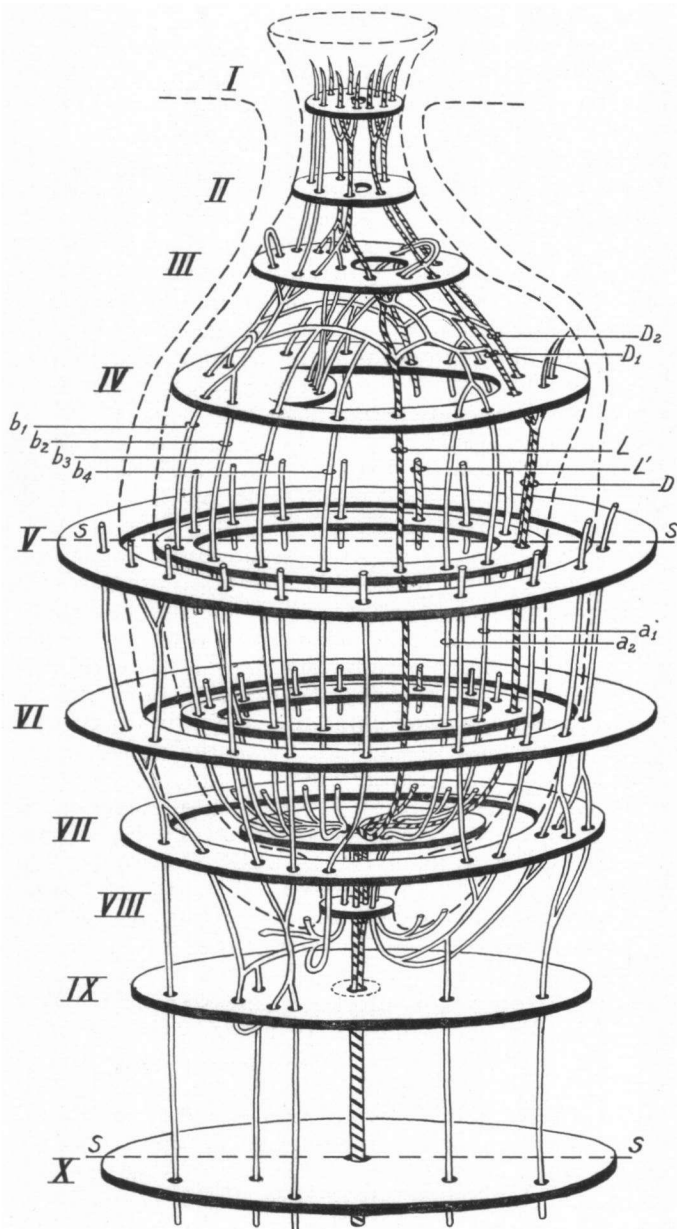


Fig. 2. Stereoscopic reconstruction of the vascularisation of a pistil of *Nelumbo lutea* from cleared preparations examined in toluene, verified by means of serial transverse sections. The secondarily formed bundles have been omitted. Of the bundles descending from a and b only those in the anterior plane of symmetry have been drawn. The Roman numerals indicate the levels discussed in the text.

The plane of symmetry is indicated at the levels V and X.

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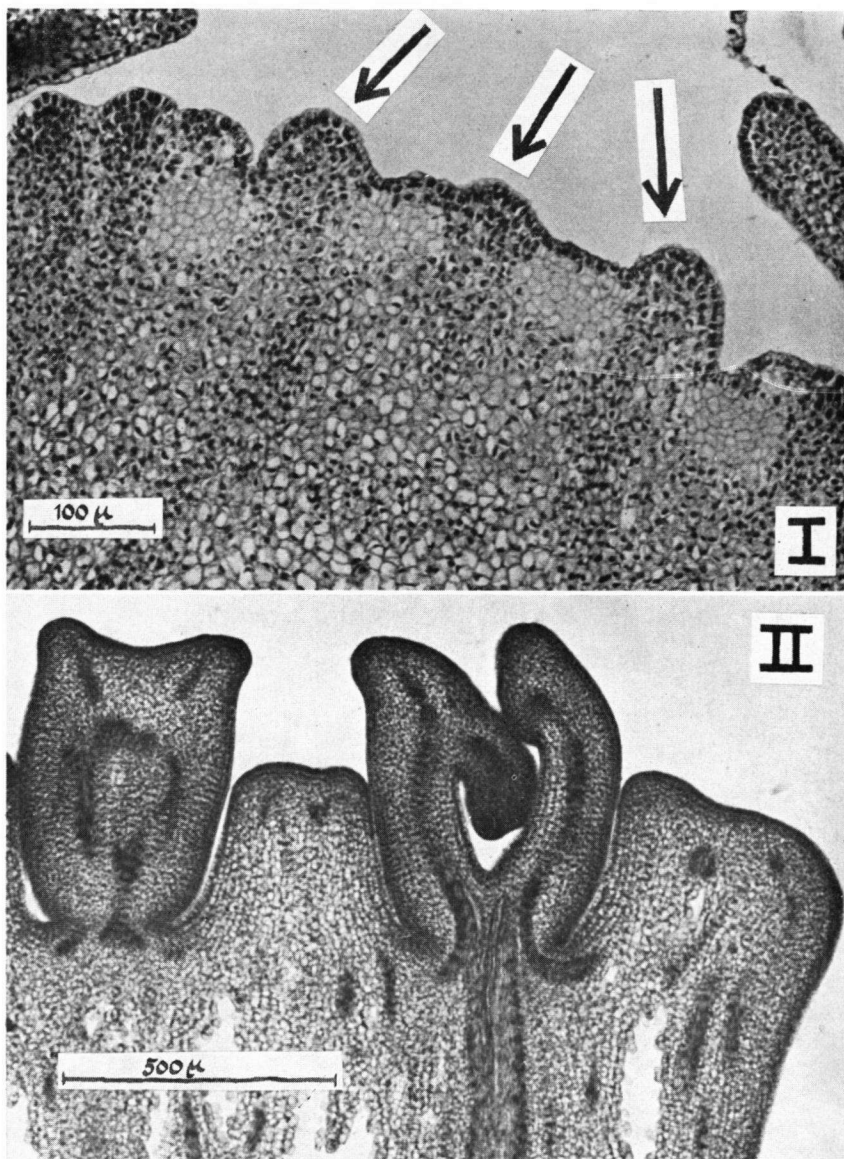


Photo I. Longitudinal section of the upper part of the hypanthium of *Nelumbo lutea*. A very young stage.

Photo II. Longitudinal section of an older stage. The "immersion" of the pistils, which is actually a circumvallation by hypanthial tissue, not yet completed. The pistil on the left sectioned tangentially, the one on the right through the median plane.

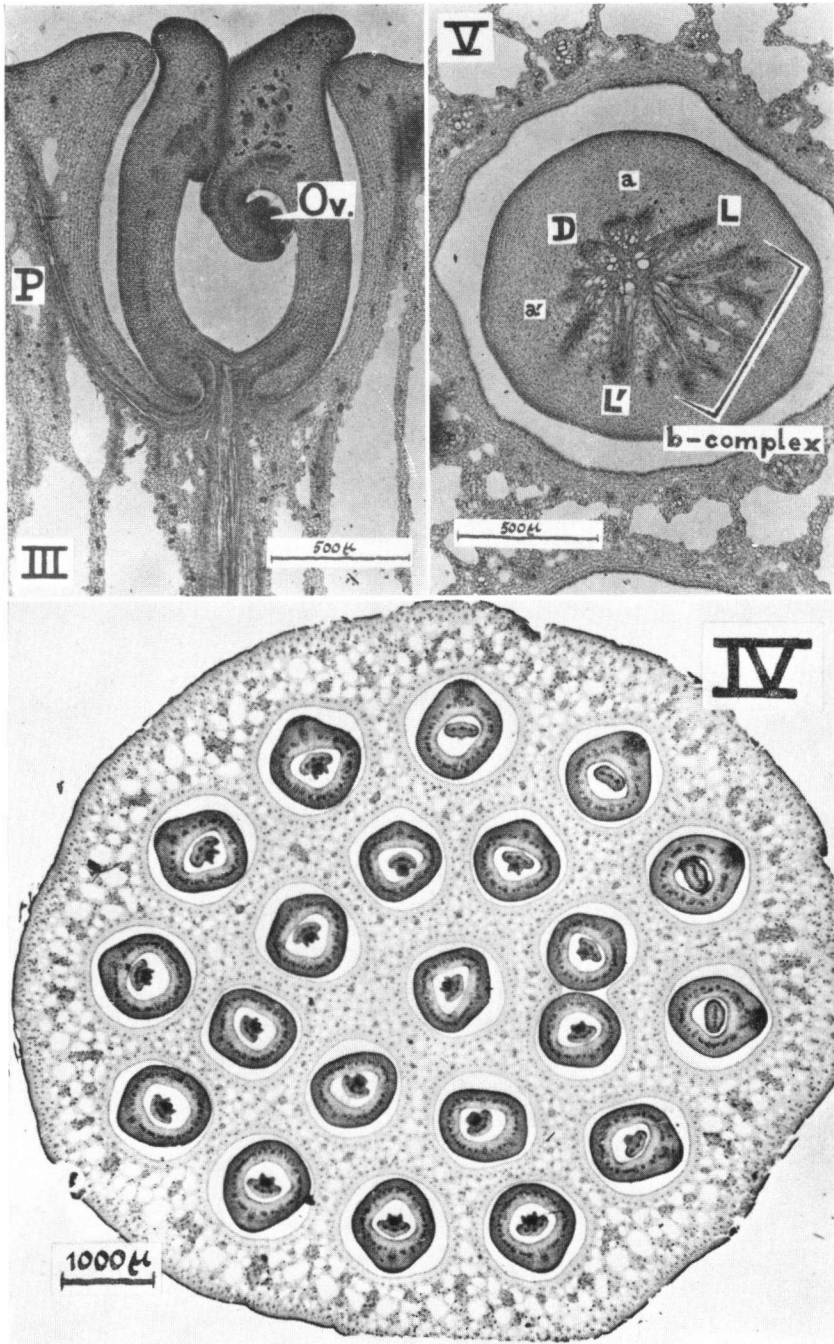


Photo III. Longitudinal section of an already "immersed" pistil, cut approximately through its plane of symmetry. At P can be seen that a vascular trace bending back from the pistil is innervated from below. Ov = ovule.

Photo IV. Transverse section of the whole hypanthium at level IV in Fig. 2. The planes of symmetry of all pistils all pass approximately through the centre of the hypanthium.

Photo V. Transverse section at level VII of Fig. 2. D = dorsal, L and L' = "laterals"; a, a' and the b-complex are indicated by letters.

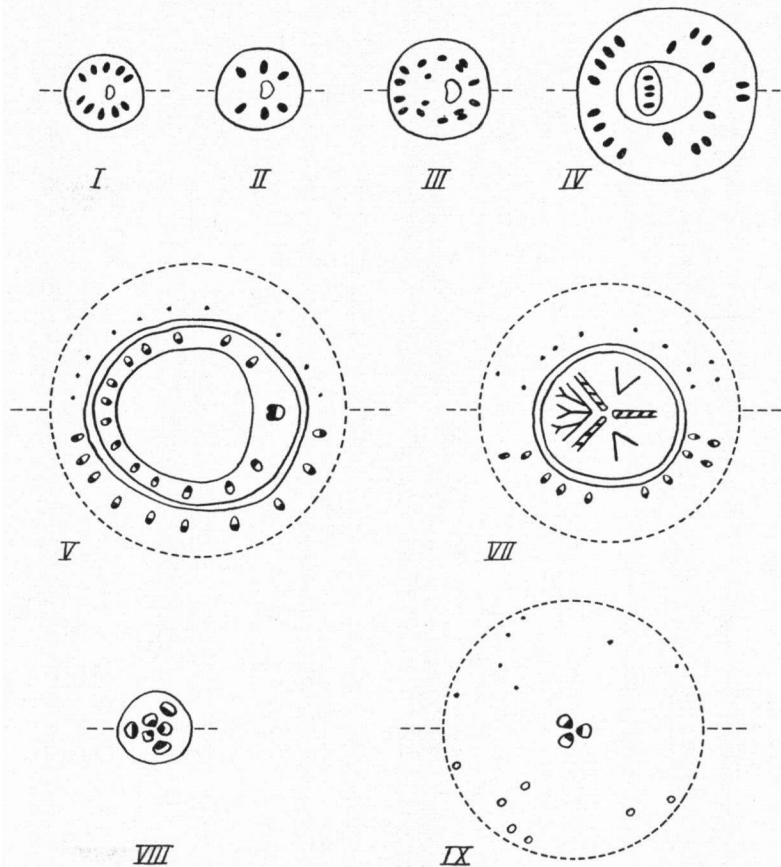


Fig. 3. Diagrammatic representation of transverse sections made at some of the levels corresponding with those indicated in Fig. 2. The plane of symmetry is indicated by a broken line.

bundle lying opposite the hump *i.e.*, the one lying on the side of the ovule, bifurcates below the stalk and forms a loop on either side of the plane of symmetry by bending back in a more or less horizontal plane towards the abaxial side of the hypanthium (Fig. 2, between the levels VIII and IX). The inner complex of three adjacent but clearly distinguishable strands is derived from a single bundle ascending directly from the central stele and splitting in three immediately below the stalk. After having entered the ellipsoidal pistil only the outer three of the two sets of three bundles branch, but they all radiate in two clearly distinguishable groups, as follows: *a* divides into *a*₁ and *a*₂ (and *a*₃), its symmetric counterpart *a'* divides in the same way; *b* separates into *b*₁, *b*₂, *b*₃ and *b*₄, and in the corresponding branches *b*₁', *b*₂', *b*₃' and *b*₄' on the other side of the plane of symmetry.

The vascular strands D-L-L' derived from the inner complex, and

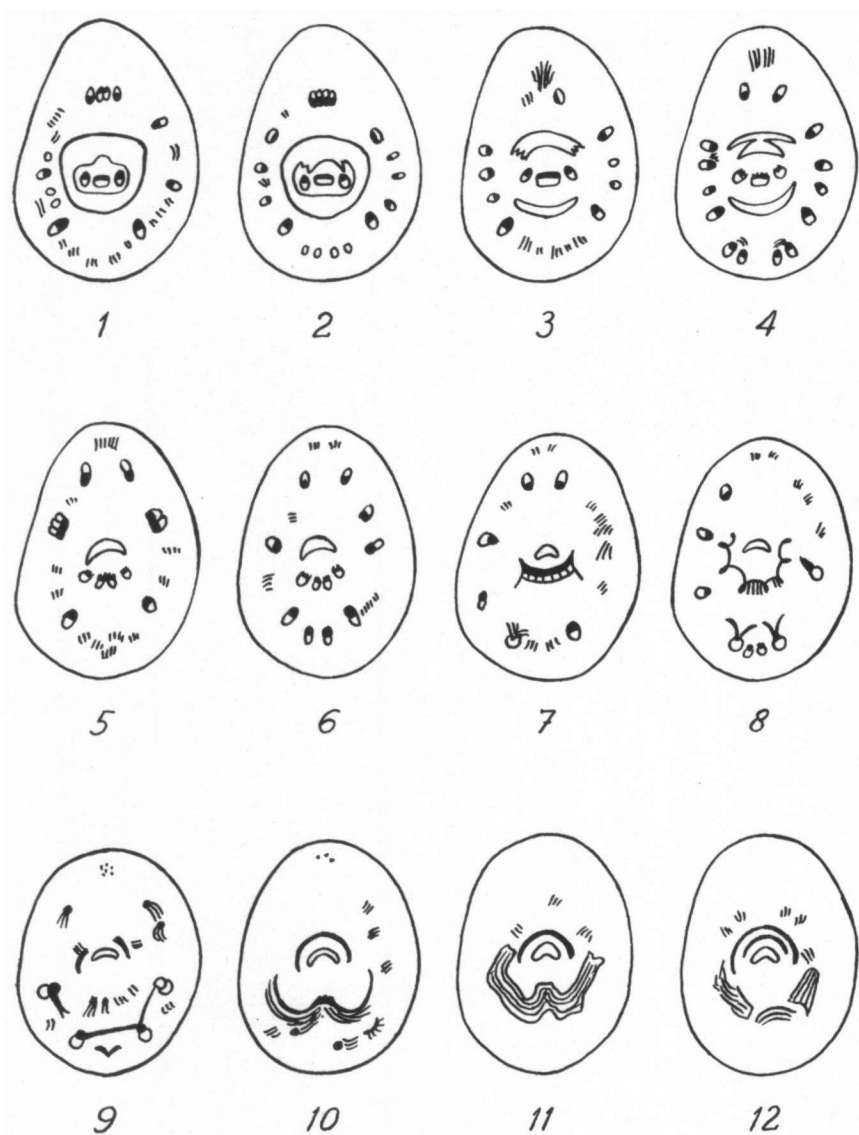


Fig. 4. Camera lucida drawings of serial section between the levels II and IV in Fig. 2. The plane of symmetry is in a vertical position. The secondarily formed bundles and/or secondarily thickened strands are drawn in. 1 is the lowest and 12 the most distal section.

a-a'-b, derived from the outer ring present in the stalk of the pistil, re-group themselves into the new sets L-a-D-a-L' and the "b-complex" (see Photo V). All branches ascend independently and remain more or less parallel (Fig. 2, levels VI to IV) until at the level IV the situation changes again, L continuing into the stigma and branching dichotomously, D, after having split off a branch towards the hump, bifurcating and continuing into the stigma as the paired set D₁ and D₂, and a₁ and a₂ fusing at this level, the joint bundle (a₁ + a₂) subsequently linking up with L at level III. D₁ and D₂ branch dichotomously in the stigma and form "open" endings. At level III two subsidiary bundles from D₁ and D₂ split off and pass into the ovule to form the two lateral vascular traces of the funicle. At the same level a branch is given off by L which subsidiary bundle also enters the funicle to form with its counterpart split off from L' the central unpaired funicular trace. At level IV the funicle thus contains three strands, two lateral ones (derivatives of D₁ and D₂) and a median one (the fused branches of L and L'). The bundle b₁ also enters the stigma and establishes a connection with its counterpart b₁' at level III. At about the same level b₁ has an oblique connection with L. Immediately above level IV all ascending bundles D₁-a₂-a₁-L-b₄-b₃-b₂-b₁-b₁'-b₂'-...-D₂ are connected by a horseshoe bundle the shape of a horseshoe. The gap in the "horseshoe" lies between D₁ and D₂. A similar connection is found at level III linking L *via* D₁ and D₂ with L'. In this region there are two arcs inside one another: the one last described is the outer, the more central one establishes the connection between the two dorsal vascular bundles which form the lateral to the funicle. The strands b₂-b₃-b₄ terminate

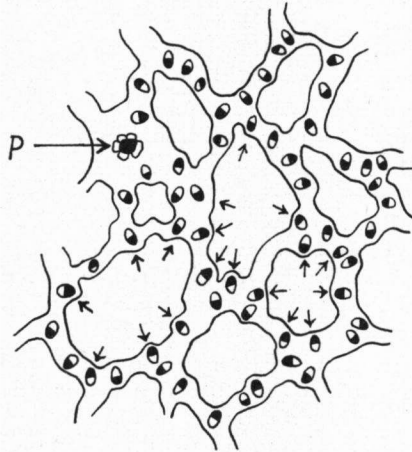


Fig. 5. In the hypanthial tissue around the canals always six vascular bundles are present, each with its xylem part facing the cavity. The arrangement of the six bundles seems to be completely at random. On the left in the upper part of the drawing a vascular bundle is seen (P) which is one of the traces innervating a pistil and is not yet divided into D-L and L'. In some of the canals the associated vascular bundles are indicated by arrows.

in the lower horseshoe-shaped arc. Apart from the traces to the pistil, other bundles ascend from the vascular complex in the basal part of the hypanthium. These bundles are situated around the vertically orientated channels already described by BAILLON (1871-1873) and arranged in groups of six around each channel with the xylem parts facing the cavity (Fig. 5). These vascular bundles branch dichotomously and form anastomoses here and there, or they link up with the bundles, descending from the outer ring of bundles of the pistil stalk and ascending in the hypanthial tissues. These latter strands show in transverse section an inversivity in respect of those in the pistil. The explanation of this inversivity will be discussed in the interpretation.

INTERPRETATION AND DISCUSSION

Vascular bundles providing, in the opinion of several phytomorphologists, important indications for the interpretation of the carpel (see EAMES 1931, 1961), it is tempting to consider the gynoeceium of *Nelumbo* as pseudo-monomerous. According to this interpretation there are two "carpels", L-a-D-a'-L' representing the fertile and the b-complex the sterile one. The ovule would thus receive its innervation from a "dorsal" and two "ventral" ("lateral") traces. The sterile carpel would have a "dorsal" bundle from the stalk upward, which bundle, like the dorsal one of the fertile carpel (D in Fig. 2), bifurcates, and two laterals which branch at a higher level (Photo V, Fig. 6), so that there would be two complete "carpels". However, this form of pseudo-monomery can be interpreted as a "stachyosporous" condition sensu LAM (1948, 1950) in the same way as PANKOW (1962) has done in the case of the gynoeceium of *Cannabis sativa*: the syncarpous gynoeceium is supposed to be formed by two (sterile) stegophylls inserted at a different level and a terminal ovule. The difficulty of this explanation is that in *Nelumbo* the ovule also receives vascular innervation from the dorsal of a stegophyll. The lateral bundles innervating the ovulum should be axial bundles. Irrespective of the fact of this gynoeceium can be interpreted as apocarpous or syncarpous, the incongruous vascular pattern might be taken as an indication of the alternative condition of phyllospory sensu Lam.

The acceptance of pseudo-monomery also has its disadvantages:

(1) *Nelumbo* being included in Polycarpicae, an apocarpous condition is more likely than a syncarpous one. This objection is not so cogent, however, considering that ECKARDT (1938) regards *Nandina domestica* (Berberidaceae) to be pseudo-monomerous.

(2) There is a striking resemblance between the venation of the leaf and that of the unfolded "carpel" (Fig. 6), if the "open" trace endings of the vascular strands in the pistil are left out of consideration. This second observation is important in connection with the theory of the palmate carpel. The resemblance of the vascular pattern of the unfolded pistil with that of a leaf is enhanced by the correspondence in position of the "hump" of the pistil and the apex of the leaf. In both organs one could imagine the presence of a dorsal and two

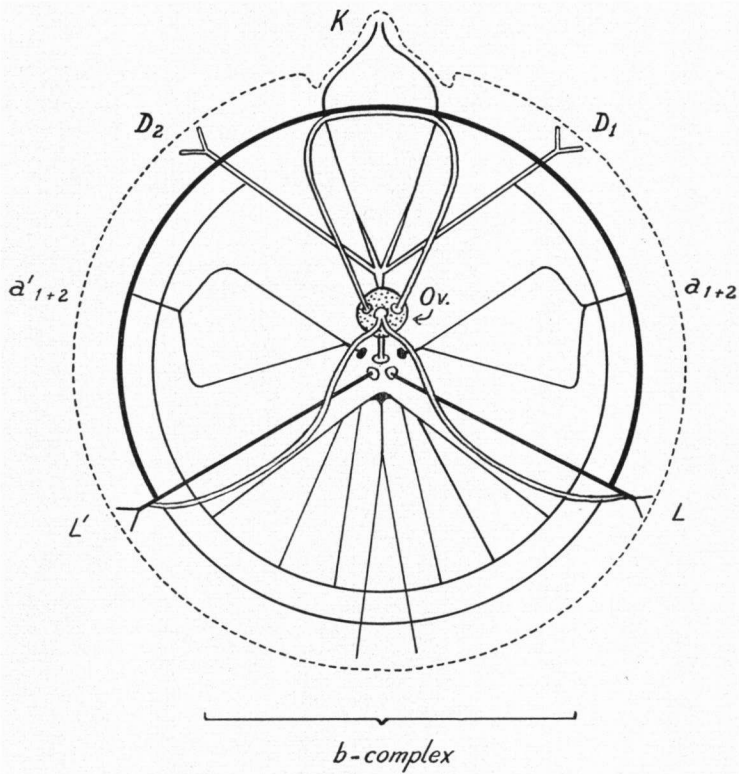


Fig. 6. The carpel unfolded and represented as if lying in a single plane of drawings. D = "dorsal", L = "lateral", Ov = ovule, K = "hump" (compare with Fig. 2).

lateral bundles, of the clearly independently innervated "b-complex" and of the arcs connecting all bundles, the vascular strands of the leaf radiating from the centre anastomosing after the third dichotomous bifurcation and thus forming a kind of ring. Outside this ring (or arc) another ring is recognisable. Seen in this light the carpel of *Nelumbo* has a palmate vascularisation. A palmate vascularisation is also postulated by SAUNDERS (1939). The interpretation would, accordingly, be as follows: the ovule is (laterally) innervated from both branches of the dichotomously bifurcating dorsal and (in the median region) from both laterals, all three vascular bundles being branches of one bundle ascending from the hypanthium. Contrary to Saunders's interpretation the dorsal bundle — dichotomously branched — continues into the stigma and in contradistinction to SASTRI's description of the gynoeceum of *Nelumbo nucifera*, in *N. lutea* a dorsal and two lateral strands can be distinguished and only these supply branches to the ovule. The remaining bundles in the carpellary wall are extensions of three traces *independently* entering the pistil (as the outer ring

in Fig. 3, level VIII). These are accessory bundles copiously branching in the pistil wall at a later ontogenetic stage of development, and must be considered to be subsidiary traces of the vascular bundles of the hypanthium. The developmental studies revealed that in very young pistils still almost completely protruding from the hypanthium the point of branching into the pistillar traces and the hypanthium traces lies below the pistil, the bundle entering the stalk of the pistil ascending obliquely (Fig. 7a). During the intercalary growth in the hypanthial

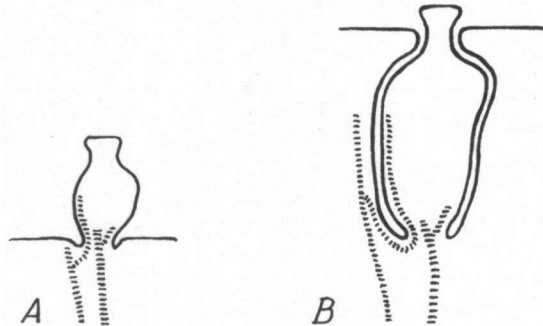


Fig. 7. During the intercalary longitudinal growth of the tissues between the pistils, the branching point of the ascending vascular trace (bifurcating into a hypanthial bundle ascending to the periphery of the hypanthium and a branch entering the stalk of the pistil) is gradually raised by the elongating hypanthial tissue. A: a pistil which is not yet immersed in the hypanthium, B: a pistil that has already been overgrown by the hypanthial tissue.

tissue between the pistils (Fig. 1) the branching point is gradually lifted to a position distal of the place of insertion of the pistil and thus a loop in the vascular traces is formed (Fig. 7b, Photo II at P). This ontogenetic development is reflected in the inversivity of the hypanthial branch in respect of its counterpart ascending in the pistil wall (Fig. 8). Although it is nowadays assumed (BAILEY & SWAMY 1951, EAMES 1961) that the "two trace, one gap" innervation is primitive, SASTRI (1959) postulates for the carpel of the Ranales a primitive condition in which there is no differentiation in a dorsal and the ventrals of the numerous vascular strands all of which are supposed to supply branches to the ovule(s). From this basic condition specialisations would have occurred in the vascular bundles, viz., a reduction and a differentiation into a dorsal trace and the ventrals, and in the innervation of the ovule through a differentiation of the innervation into different directions, viz., by both dorsal and ventral traces, only by the dorsal traces, only by the ventral and "lateral" ones or only by the ventral strands. The species studied by myself (*N. lutea*) would appear to be much more differentiated than the species *N. nucifera* investigated by SASTRI (1959) and demonstrates that Sastri's postulated series of differentiations does not exhaust all possibilities — provided his observations on *N. nucifera* were accurate. Morphologically the woody Ranalians are supposed to be more primitive than *Nelumbo*, but the

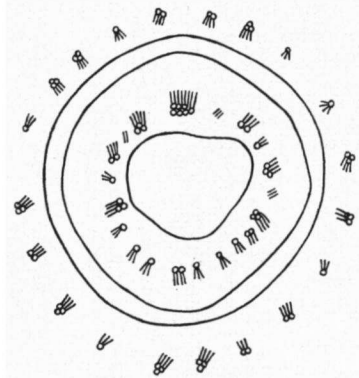


Fig. 8. The vascular bundles in the hypanthial tissue split into a component inside and a branch outside the pistils, are facing one another with their phloem parts.

innervation of the ovule in *Nelumbo* is essentially the same as in *Degeneria* and the Winteraceae (BAILEY & SWAMY 1951), viz., by both the dorsal and the ventrals (with the restriction that *Degeneria* and the Winteraceae have more than one ovule per carpel and that the ovules are not all innervated by dorsal and ventral traces). In the light of the results of the anatomical investigation of the gynoecium of *Nymphaea* by MOSELEY (1961) one could also, typologically speaking, consider the pistil of *Nelumbo* to be a mono-ovulate reduced form of the gynoecium of *Nymphaea* with laminal placentation. In comparison with *Nymphaea* there are points of resemblance (the presence of the receptacular vascular complex in the basal region of the hypanthium from which ascend bundles to each carpel; in the carpel this single bundle divides into dorsal and ventrals) and points of difference (the solitary ovule in each carpel and the presence of the b-complex).

According to the train of thought of the English school, *Nelumbo*, with its solitary ovule, must be a reduced form (EAMES 1961). However, the innervation of the ovule, combined with the finds of Jurassic "nelumboid" sporomorphs previously discussed, and the wide-spread occurrence of *Nelumbo* in three continents during the Cretaceous (ARBER 1920) are not consistent with the view that *Nelumbo* is a reduced form. This does not necessarily imply that the pistil of *Nelumbo* must be interpreted according to the theory of the peltate carpel. It could be fitted into Eames's interpretation if *Nelumbo* is supposed to be a descendant of still older, i.e., pre-Jurassic forms, but this is too conjectural through lack of more tangible evidence.

The perfect dichotomous branching of the vascular bundles in *Kingdonia uniflora* and *Circeaster agrestis* forming the "open" venation of the leaves, led FOSTER (1959, 1960) to the assumption that this form of branching is indeed a primitive character when it occurs among the Angiosperms. This view was already held by LAM (1948) and VAN DER HAMMEN (1949), but Foster adds the suggestion that because some

Angiosperms possess primitive stamens and carpels, this "open" type of venation can be expected to occur in the reproductive organ of the Angiosperms. The presence of this "open" pattern of vascularisation in the pistil of *Nelumbo* is certainly interesting in this connection.

In view of the resemblance between the "carpel" and the leaf of *Nelumbo* a study of the vegetative organs (the leaves) seems to be indicated. Possibly the interpretation of the morphology of the leaf must be changed. The "additional bundles" which are found in, e.g., *Degeneriaceae* (SWAMY 1949), *Lauraceae* (SASTRI 1952) and, as we have seen, *Nelumbo* (the "b-complex"), have been discussed by SASTRI (1959), who states "that the presence of additional bundles probably indicates that the monocarpellary gynoecium in these families has arisen from a multicarpellary condition". This is not a novel suggestion, because MEZ (1889) and COY (1928) regarded the number of bundles in the pistils of *Lauraceae* to be indicative of the number of carpels. Perhaps the leaf of *Nelumbo* may eventually prove to be an organ compounded of two phyllomes, but a more detailed study of the vegetative organs is required to substantiate such a speculation.

It still would not solve the controversy concerning the gynoecium wall — is it a "carpel", i.e., a "megasporophyll", or a sterile "bract" (stegophyll, tegophyll), or an aggregate of several such organs? The possibilities are by no means exhausted, because the gynoecium wall of some traditionally angiospermous taxa has also been interpreted as an ovular coat corresponding with the "chlamys" of the *Chlamydospermae* (MEEUSE 1961).

The limited scope of the present investigation does not permit a detailed discussion of this moot point in phylogenetic botany. The interpretation of the gynoecium of *Nelumbo* as a carpel or something else stands or falls with the solution of the problem of the origin of the Angiosperms. The advent of the Angiosperms in Cretaceous or pre-Cretaceous times is the subject of a considerable controversy.

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