

A CONTRIBUTION TOWARDS THE DEVELOPMENTAL GYNOECIUM MORPHOLOGY OF *ENGELHARDIA SPICATA* LECHEN. EX BLUME (JUGLANDACEAE)

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SUMMARY

The interpretative gynoecial morphology of the Juglandaceae and the terminology applied to their pistillar structures are critically discussed. A study of the histogenesis in the pistil of *Engelhardia spicata* Lechen. ex Bl. shows that the intralocular parenchyma is of dual origin and is mainly derived from the inner dermal cells of the pistil wall, the remainder, a thin layer of cells in the lower portion of the ovarial cavity, being formed by the superficial cells of the structure referred to as "septum-2" in the text. The anatomy and the vascularisation pattern of the pistil of *E. spicata* can not be satisfactorily explained by means of the conventional foliar carpel theory.

1. INTRODUCTION

Publications treating the gynoecial morphology of Juglandaceae usually deal only with the genera *Juglans* and *Carya*. The most important ones are the contributions by VAN TIEGHEM (1869: *Juglans regia*); A. BRAUN (1872: *Juglans* and *Carya*); KARSTEN (1902: Species of *Juglans*, *Pterocarya fraxinifolia*, *Carya amara* and *C. tomentosa*); BENSON & WELSFORD (1909: *Juglans regia*); WOODROOF & WOODROOF (1926, 1927: "*Hicoria pecan*" = *Carya olivaeformis*); SHUHART (1932: "*Hicoria pecan*"); LANGDON (1939: *Juglans mandchurica* and *Carya glabra*), and the extensive surveys by HJELMQVIST (1948: p. 30-63) and by LEROY (1955). The latter author reviewed the various genera, gave definitions of the terms he employed and attempted a comprehensive theoretical explanation of his and of the previously accumulated, observational data.

In the older literature one is often confronted with inconsistencies in the terminology, so that, on account of the resulting semantic confusion, Leroy decided to start all over again and to re-examine as many cases as possible. He was also the first to discuss the gynoecial anatomy of *Engelhardia spicata* in greater detail, concluding: "un rapide examen des fleurs de *Eng. spicata* nous a convaincu que l'étude anatomique de cette espèce ne serait pas pour nous d'un intérêt fondamental". However, this did not keep MEEUSE & HOUTHUESSEN (1964) from studying the ovarial structure of *Engelhardia spicata*. They pointed out the possible phylogenetic importance of this structure.

Both Leroy and Meeuse c.s. tried a different approach to the gynoecial morphology of the Juglandaceae by querying the universal applicability of the foliar carpel theory. CROIZAT (1966) even goes considerably farther and rejects the carpel theory altogether, whilst criticising Leroy and Meeuse c.s. in several points, the latter especially on account of their putative interpretations of

the gynoecial morphology of *Engelhardia spicata*. Considering that Meeuse and Houthuesen had only a few female flowers of this species at their disposal, it was thought desirable to re-investigate *E. spicata*, taking into account the general structure, the vascularisation pattern, the orientation of the "septum" and the development of the intralocular parenchyma of the pistil.

2. MATERIAL AND METHOD

The available material, received from the Botanical Survey of India, was collected by H. Deka in the Botanical Garden at Shillong in Oktober, 1966, and fixed in FPA. It consisted of a relatively large number of female flowers with a completely differentiated embryo sac and a few flowers in a much more immature stage showing the initial phases of integument development, apart from numerous male and some bisexual ones. Only female flowers were used in the investigation. The intermediate stages of floral development not being represented in the material, no conclusive evidence could be obtained regarding the presence of an apical tubular extension of the integument (= tubillus).

A number of flowers were microtome-sectioned by means of the standard paraffin wax technique, the average thickness of the serial sections made being about 10 micra, and the slides were stained with Saffranin-Fast Green. Nineteen of the older flowers were used for longitudinal sections through the plane of the stigmatic lobes (*i.e.*, transversely in the floral diagram), seven for longitudinal sectioning in the median plane perpendicular to the direction of the stigmatic lobes, and six for transverse sections. Of the young developmental stages, seventeen flowers were used for longitudinal and six for transversely cut serial sections.

In addition, the larger female flowers were cleared in order to study the pattern of vascularisation. The procedure recommended by SPORNE (1948, 1958) proved to be inferior to the method used by VAN LEEUWEN (1963) for pistils of *Nelumbo*. About ten flowers were treated according to the latter method

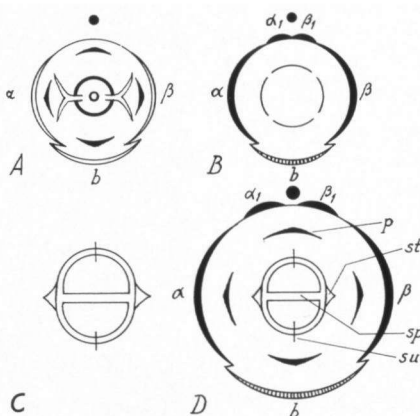


Fig. 1. Various interpretations of the floral morphology of *Engelhardia spicata*
 A. EICHLER's floral diagram
 B. NAGEL's interpretation
 C. LEROY's diagram of the pistil
 D. A combination of (B) and (C)
 p: "perianth", st: stigma, su: suture ("midrib of carpel"), sp: septum.

but the time of hydrolysis in N/1 HCl at 60°C was cut down to 10 min and the duration of the bleaching in commercial hypochlorite (1:3) reduced to at most four days to prevent desintegration of the flowers. The flowers treated in this way were examined under a binocular dissecting microscope with oblique incident illumination at an angle of about 45°C. Some bleached flowers were stained with safranin and differentiated again in hypochlorite. An appropriate intensity of staining enables the recognition of the vascular bundles as red strands against a paler and more transparent background. The outer wall layer of the flower contains crystal cells which obscure the observation, so that this layer must carefully be scraped off under the dissecting microscope without damaging the vascular strands.

3. GENERAL GYNOECIAL STRUCTURE

The outer envelope of what is usually called the female juglandaceous "flowers" has received various names as the knowledge of this outer structure increased. EICHLER'S (1878) interpretation is reproduced in *fig. 1A*: the outer envelope is interpreted as a lateral concrescence of the floral bract (*b*) and two prophylls (α and β). The diagram shows cleft stigmatic lobes, but not the bifid lobe $\alpha^1\beta^1$ opposite *b* as represented in NAGEL'S (1914) diagram (*fig. 1B*). Leroy has given a diagram of the structure of the "fruit" (see *fig. 1C*) which shows two carpels in the median position and commissural stigmas. A combination of the last two diagrams (*fig. 1D*) is used as a starting point for a discussion of the morphology. The definitions and the terminology of Leroy are followed here, the most important circumscriptions being:

Suture – midrib of each carpel, the sutural plane being the (median) plane bisecting both carpels and also the principal "bract" (*b*).

Commissure – the coalesced lateral edges of the two carpels which lie in the *intercarpellary* (i.e., transverse) plane, in which plane also lies the dissipated or septum so that it is sometimes called the *septal plane* of symmetry.

These terms are here used in a purely descriptive or typological sense and only intended as topographical indications, irrespective of any possible phylogenetic or morphogenetic interpretation. In my opinion, one can not accept the presence, in the Juglandaceae, of carpels and of a perianth in the conventional morphological sense. It appears to be of essential importance to distinguish between the two different meanings. If one tends to consider the Juglandales to be very primitive Angiosperms or advanced cycadopsid gymnosperms, one avoids such terms as "flowers", "perianth", "carpels", etc. for semantic reasons. Meeuse *et al.* adhere to this principle as much as possible and refer to the traditional carpels (ovary wall) as outer integument and to the "perianth" as a homologue of a pteridospermous cupule (or gnetalean chlamys). The "5-lobed persistent bract" is not discussed in detail, but in order to avoid possible confusion, it should be mentioned that this bract is called a "cupule" by Benson and by Shuhart (*N.B.*: this is presumably a semantically different "cupule", viz., the so-called cupule of the "Cupuliferae" among the Amentiferae), and a

"cupular involucre" by Langdon. Manifestly, the theoretical background and the personal views of the various workers determine the terminology they employ, so that I have shied of mentioning morphological interpretations unless they proved to be elucidating. The use of such terms as "flowers", "perianth" and "carpels" does not imply that I have made a definite choice in favour of the foliar carpel theory (or any other theory, for that matter) and are only intended for descriptive purposes.

A floral diagram being only a simplified representation of a flower, the floral morphology of *Engelhardia spicata* is considerably more complicated than the diagram (fig. 1D) suggests and a more detailed description of some parts is indicated.

The septum: – The classical carpel theory does not provide a straightforward interpretation of the septum and the explanation thus becomes decidedly forced, which results in dissenting opinions among the older workers and also in a number of inconsistencies. Eichler stated: "Ganz regelmässig sind 2 Scheidewandbildungen von den Verwachsungslinien der Fruchtblätter ausgehende vorhanden, die somit unter den Begriff der ächten oder primären Scheidewände fallen; diese vereinigen sich stets im unteren Teile der Frucht bis zu variabler Höhe und bilden durch das zusammenstossen eine Art Mittelsäulchen, auf dessen Gipfel der Same befestigt ist".

Accordingly, most subsequent authors refer to it as a *primary* septum, even Langdon who (in accordance with the views of C. DE CANDOLLE, 1862; Karsten, NICOLOFF, 1904–1905; NAWASHIN, 1895; and Shuhart) is of the opinion that the ovule of the Juglandaceae is a derivative of the floral apex and that the carpels do not "contribute" towards the formation of the ovule. This interpretation of the ovule as a "terminal" structure implies that the septum is not an outgrowth of the fused margins of the carpels and consequently should not be called a primary septum. Nevertheless Langdon speaks of "carpels" and "in-turned margins" of carpels, and of a "primary" septum.

Meeuse and Houthuesen call the septum "false", because in their interpretation, it divides the space between two integuments and can not possibly be of carpellary derivation. However, as they also consider the juglandaceous gynoecium to be an ecarpellate structure, the term "false septum" had perhaps better be dropped because a "false" septum is traditionally a dividing wall in an ovary which has originated from the dorsal (median) region of a carpel and develops centripetally (*fide* Eichler). My conclusion is that we should refer to the juglandaceous ovarial dissipation simply as "the septum", at the same time indicating its plane of orientation, and thus evade all theoretical implications.

As regards the situation in *Engelhardia spicata*, Leroy speaks of a *cloison primaire* in the intracarpellary (*i.e.*, the transverse) plane. In addition, he depicts in his fig. 72 a transverse section of a fruit of a species of *Engelhardia* sect. *Psilocarpae* and draws an *excroissance septale tabulaire* supposed to be a septum-like outgrowth perpendicular to the plane of the "primary" septum.

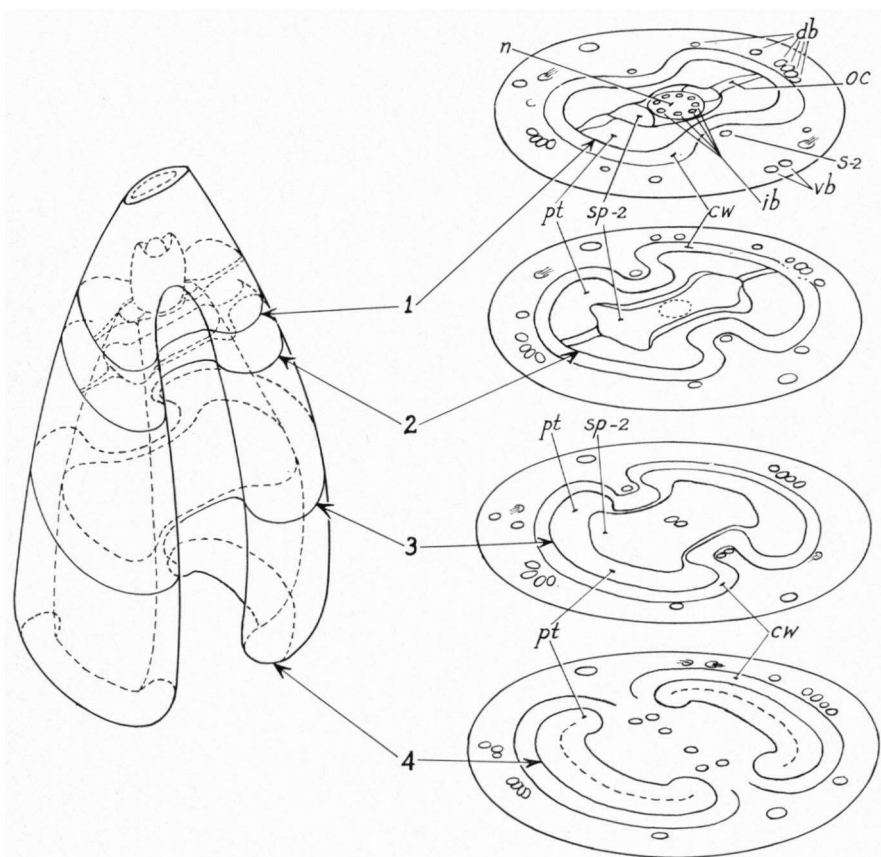


Fig. 2. Diagrammatic three-dimensional representation of the pistillar septum of *Engelhardia* and of its accrescence ("septum 2": excroissance septale tabulaire of LEROY) and (right) semidiagrammatic cross-sections at four levels, drawn in perspective.

pt: packing tissue (intralocular parenchyma), *oc*: ovarian cavity, *i*: integument, *n*: nucellus, *sp-2*: septum-2, *vs*: vascular strand, *db*: dorsal bundle, *sb*: septal bundle, *vb*: ventral bundle, *cw*: "carpel" wall, *p*: lobe of "perianth", *b*: lobe of bract, *st*: stigmatic lobe, *ib*: integument bundle, *sp*: septum, *su*: suture.

(The same symbols are used in the other figures)

From my observations of the Shillong material I finally managed to reconstruct the septum and the septum-like outgrowth (see fig. 2). This diagrammatic three-dimensional figure is more or less distorted because the transverse sections used in the reconstruction are drawn apart and actually lie much closer together, and the drawing is also somewhat drawn out in the other directions (so that the septum appears relatively broader than it actually is). A longitudinal section made perpendicular to the plane of the septum and comparable with Leroy's fig. 72 A is shown in my fig. 3. The outgrowth is not so strongly developed as in the fruit depicted by Leroy. In my fig. 3 one can clearly see that the "out-

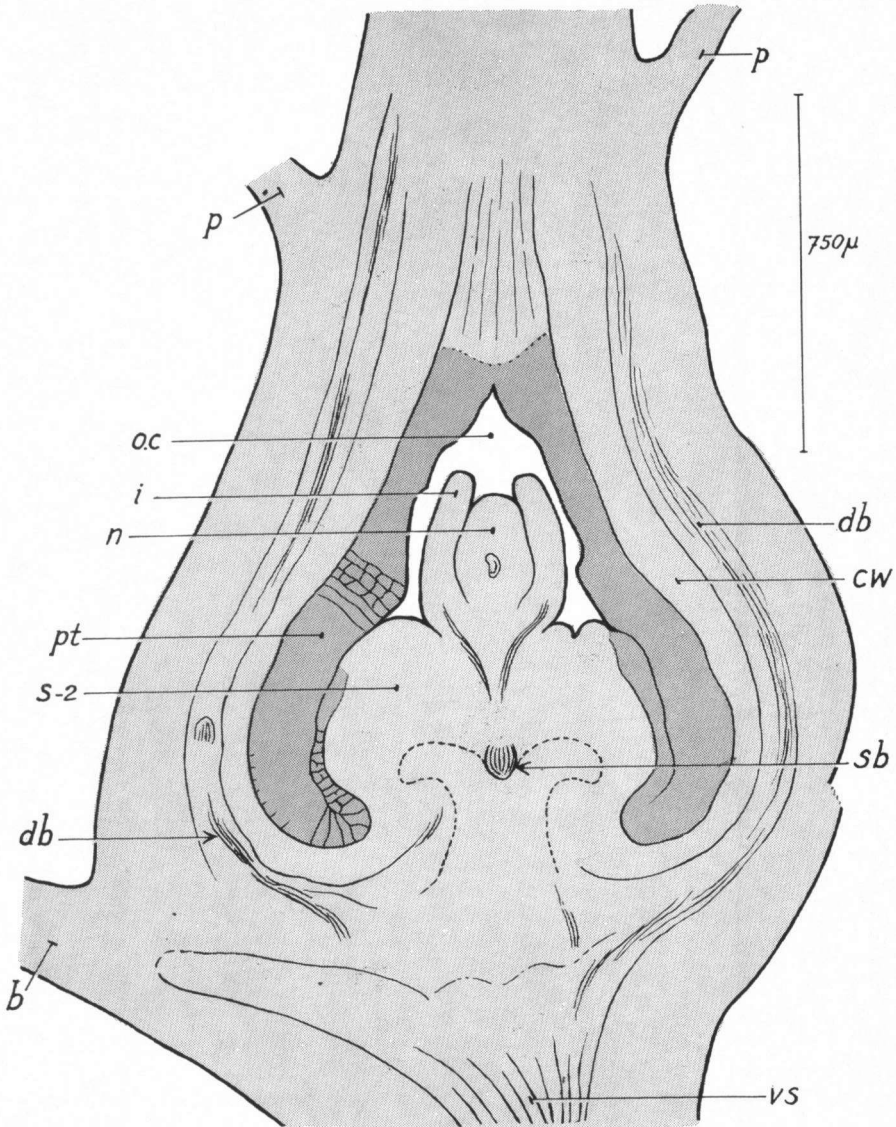


Fig. 3. Part of a longitudinal section of a "female flower" of *Engelhardia spicata*, cut as exactly as possible through the septal plane. Cellular structure partly shown in intra-locular parenchyma (pt) which is indicated by a darker shade of grey.

growth" consists of cells which were formed in more or less distinct rows and resemble the "winged evaginations" (Nawaschin), "horns" (Nicoloff) or so-called packing tissue (in the sense of Benson and others) in the pistil of *Juglans*.

However, these outgrowths are far less conspicuously developed in *Engelhardia spicata* than they are in the walnuts. The term "packing tissue" has been used by different authors in a different sense. In *Juglans*, it really is a "filling tissue", but in *Engelhardia* the homologous structure does not fill the pistillar cavity more or less completely as it does in *Juglans*, the intralocular parenchyma being equivalent to what is called the "parenchymatous endocarp" by Shuhart, a tissue originating as a centripetal proliferation of the ovarian wall. Leroy calls it *parenchyme de remplissage*, see, e.g., his fig. 73), Meeuse and Houthuesen "packing tissue" (compare their figs. 2 and 2a, which do not give an adequate idea of the gynoecial morphology because the plane of sectioning was somewhat oblique and neither exactly coinciding with the stigmatic plane nor with the commissural plane, so that not all the tissue they called "packing tissue" is of one kind and only partly represents the "parenchymatous endocarp" of Shuhart). To evade this semantic confusion I propose to call the *excroissance septale tabulaire* of Leroy "septum 2" for the time being, the more so because Leroy believes that it represents an intermediate case between the gynoecial structure of *Oreomunnea* and that of *Pterocarya*. Typologically it corresponds with the "packing tissue" (*sensu* Benson) in *Juglans*, which is a derivative of the "pedestal" on which the ovule is inserted. In the lowermost portion of the pistil the two types of septa are completely fused and histologically they seem to be contiguous. An examination of less mature flowers reveals that the "septum 2" is already present but far less extensively developed and hence not conspicuous. Their outgrowth is clearly accomplished by a differential growth of the various tissues and it appears that the classical carpel theory does not provide a satisfactory explanation of these structures. There is no question of centripetal "outgrowths" of the margins of carpels which (if the ovary is interpreted as a bicarpellate structure) are already present in the transverse plane, the septal tissues developing centrifugally from within, only ultimately to become crescent with the "carpels". As regards the orientation of the septa, there is still another problem. If one applies the definition of a primary septum, as given by Eichler, to the septal structures of *Engelhardia*, it appears that in *Engelhardia* it is "septum-2" that forms the *Mittelsäulchen auf dessen Gipfel der Same befestigt ist*. In this train of thought, the ovule is not a derivative of a primary (and assumedly carpellary) dissipation, so that, in order to save the classical interpretation, one would have to consider "septum-2" to be the primary (= carpellary) septum, and to suppose that the two carpels are not median but transversely oriented and the stigmas carinal instead of commissural. This would only add to the confusion, however. In point of fact the carpel theory requires certain interpretations which are at variance with the observations and does not explain the gynoecial morphology of the Juglandaceae unequivocally. As a general interpretation floral theory it is untenable.

The intralocular parenchyma. When the septal structures were discussed, the equivalence of the intralocular parenchyma of *Engelhardia* and the "parenchymatous endocarp" (as defined by Shuhart and others) was mentioned.

It develops as a more or less simultaneous centripetal proliferation of the dermal cells of almost the entire inner pistil wall. In *figs. 4* and *5* the first indication of this outgrowth is clearly visible in the form of periclinal division walls in the inner epidermal layer of the "carpels". Particularly in the basal region there is hardly any difference between the structure of the inner walls of the carpels and that of the developing septum-2. In *fig. 7* the inner carpel wall has formed centripetal rows of cells whereas the outer cell layer of septum-2 has formed only one of two layers of cells which are indistinguishable from parenchymatic cells derived from the dermal cells of the inner carpel wall. This is confirmed by the examination of transverse sections (see *fig. 2*). Only a thin layer of tissue is thus formed, but the demarcation line between the centripetally developed filling tissue and the tissue derived from "septum-2" is clearly discernible. The intralocular parenchyma is produced by the whole inner surface of the pistil wall and extends right up to the apical region of the ovarial cavity. The fact that there is no sharp demarcation line between the outer layers of septum-2 and the superficial tissue of the inner pistil wall could be adduced as an argument pleading in favour of the carpellary interpretation of the pistil, if other considerations did not render this unacceptable (see p. 59) and if no alternative interpretations (such as Leroy's "unitary" theory and Meeuse's chlamydotte ovule theory) were available.

Integuments Meeuse and Houthuesen believed to have demonstrated that the tubular connection between ovule and "stylar canal" is an apical extension

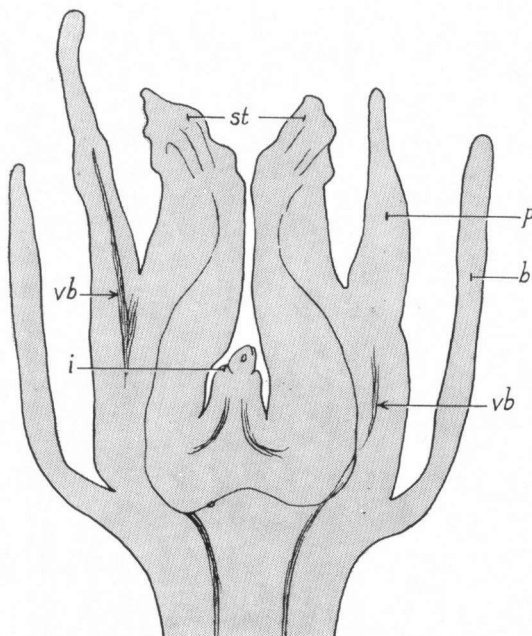


Fig. 4.

Longitudinal section made as accurately as possible through the septal plane of a young developmental stage of the gynoeceum of *Engelhardia spicata*. Integument initiation has just begun.

l: lobe of bract, *i*: (young) integument.

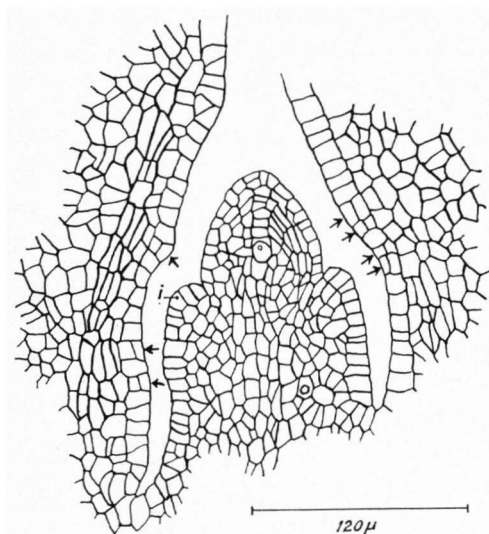


Fig. 5.

Detail of fig. 4, showing ovule and adjacent parts. The arrows indicate the first periclinal divisions of the inner "carpel wall" ultimately leading to the formation of the bulk of the intralocular parenchyma (*i*: young integument).

of the integument and they made a comparison between Juglandales and *Gnetum*. The figures they published were made from sections which were not precisely oriented in the median or transverse direction and it is doubtful whether their evidence is conclusive. The gnetalean tubillus is formed by the elongation of the rim-like apex of the young inner integument, whereas the developing integument of *Engelhardia* is bilobed at the apex (as in *Juglans* and *Pterocarya*, compare BOESEWINKEL and BOUMAN 1967). Among the specimens studied there unfortunately were no pistils of *Engelhardia* of the proper stage of development to decide this point. More material will have to be collected, also because it is of considerable importance to ascertain how the fertilisation process takes place in *Engelhardia* and if the tubular structure and the intralocular parenchyma is at all involved.

Meeuse and Houthuesen assumed that the intralocular tissue of *Engelhardia* is a derivative of the basal part of the tubillus; this is not confirmed by our study of younger pistils than they had at their disposal. CROIZAT (1966) criticises Meeuse and Houthuesen, but he did not examine any material and could not possibly know that their sections were somewhat oblique and their evidence, for that reason, not unequivocal. It is, therefore, deplorable that Croizat based certain conclusions on some of their figures and even draws an altogether imaginary line "m" in his fig. 9 (which is a reproduction of fig. 2a of Meeuse and Houthuesen) to "demonstrate" that the ovule is markedly excentric (and that the pistil has only one longitudinal plane of symmetry instead of two). My slides (and my figures!) show that there is no question of an excentrically inserted or asymmetrical ovule. Croizat also makes the peculiar suggestion that an "obturator" can originate by a shortening of the integuments. Leaving aside the question what Croizat means by an "obturator" (JACKSON 1949, gives two different definitions!), an examination of young developmental stages

of the ovule never showed that the integument ever undergoes such a decapitation, the only other tissue present in the ovarial cavity being the parenchymatous filling tissue which is not of tegumentary origin. "*Drop every theory*", Croizat writes, "*and investigate purely for facts*", but it would seem that he makes exactly the same mistake that he professes to condemn. His hypothetical female inflorescence or strobile (his fig. 5) and the "creation" of an obturator by a deliberate decapitation of integuments are not based on observational data or new "facts".

As regards integument initiation, according to F. Bouman, who examined some of my slides, this seems to begin in the same way as in *Juglans* and *Pterocarya* (see BOESEWINKEL and BOUMAN 1967) and this form of integument development may well be a characteristic feature of all representatives of the family Juglandaceae.

Vascularisation. The relatively small size of the flowers renders the accurate determination of the courses of the vascular tissues very difficult, but by examining a number of cleared specimens, and guided by transverse sections made at different levels, I managed to make a reconstruction of the pattern of vascularisation which must come pretty close to the actual situation. The reconstruction of the vascular supply to the nucellus is a particularly tedious job. The places where bundles branch off lie so closely together in the basal region of the pistil that it is almost impossible to trace the origin of the individual bundles, the more so because I have the impression that the vascularisation pattern is not constant. The differences only concern details, however.

The pistillar vascularisation was studied in other juglandaceous taxa by, e.g., Benson & Welsford, Woodroof & Woodroof, Langdon, Shuhart and Leroy. Other workers only describe the course of vascular strands but do not give illustrations. Without accompanying figures it is difficult to assess their findings because the terminology used to describe the bundles is not always unequivocal. Usually one can only decide what a certain author means by the terms "dorsal", "ventral" or "septal" bundles after a perusal of his or her illustrations.

The term "septal bundles" can be retained for those bundles which branch off in the basal gynoecial region and follow a course through the septum to the integument. It is customary to refer to the bundles which run more or less in the median plane of symmetry in the pistil wall as the "dorsal" ones, and to those which run approximately in the plane of the septum, but not in the septum itself, as "ventral" strands. In the reconstruction (see fig. 6) the dorsal bundles are drawn farther apart than they really are for clarity. In reality they form one complex vascular trace consisting of rather closely adjacent rows of tracheidal elements which can not always be individually followed along their full course. The bundles forming the vascular supply of the 5-lobed bract very soon branch off from the stelar system of the floral axis.

The bundles running towards the "perianth" show some interesting features. A fairly regular phenomenon is that two bundles run into each of the 'perianth

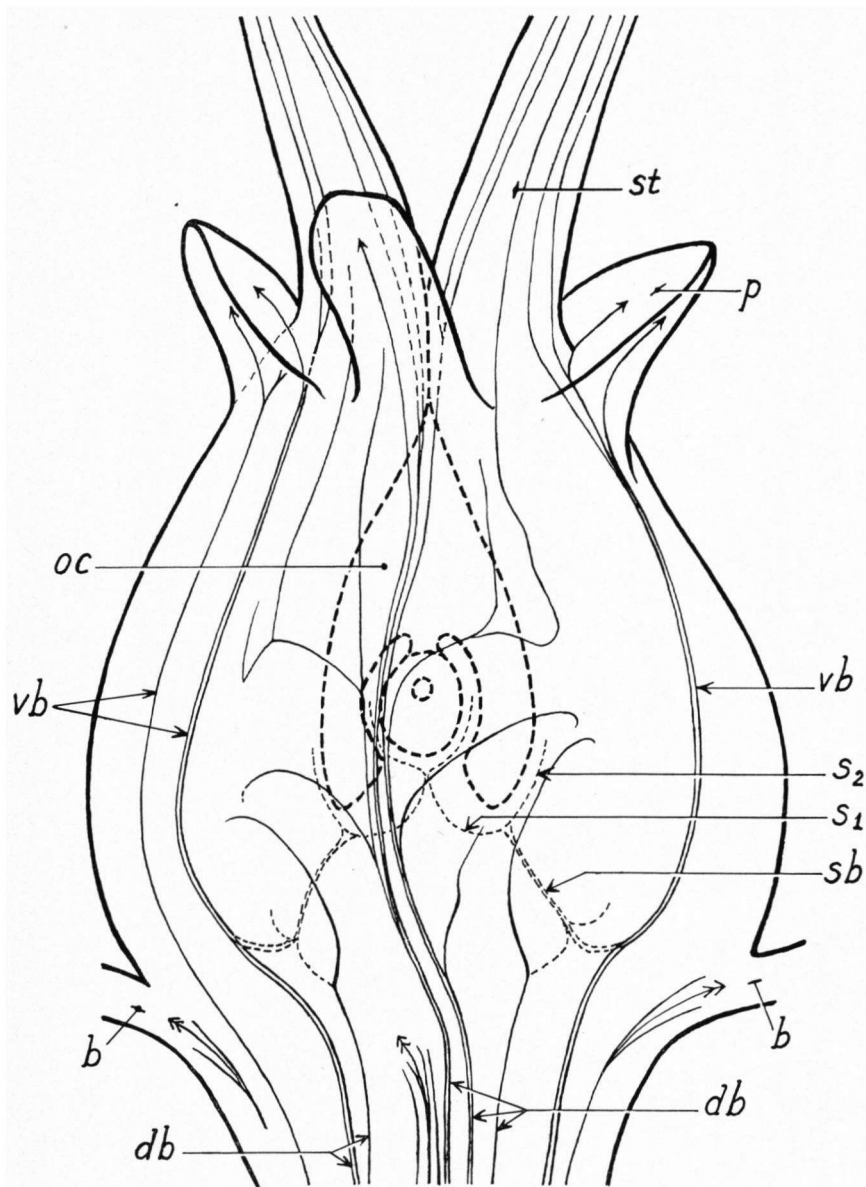


Fig. 6. Reconstruction of the vascular system of the gynoecium of *Engelhardia spicata*.
(For the meaning of the symbols S_1 , S_2 , D_1 etc.: see text)

lobes" situated in the septal plane but only one into each of the lobes placed in the median (dorsal) plane. Those running towards the dorsal lobes usually follow a more or less independent course in respect of the other dorsal strands,

i.e., they branch off at a low level, whereas those going to the ventral lobes lying in the transverse or septal plane, on the other hand, only branch off at the level of these "perianth lobes". The altogether independent trace drawn at the extreme left side in *fig. 6* is an exceptional case. The ventral traces, after having given off a branch which enters a "perianth lobe", run on in more or less the same direction to terminate in the stigmas. The dorsal bundles are much more freely ramified and their branches sometimes so strongly bend inwards that they appear as if connected with the septal bundles S2. I have very carefully tried to establish whether they indeed link up; for, if this could be substantiated, such vascular strands would be "reversely oriented bundles" (Shuhart) similar to those reported to occur in the pistils of other Juglandaceae. I managed to find only one direct connection in a transverse section, but I have the impression that this is a secondary connection and that there is no question of an originally continuous vascular strand. At the level of the 'perianth lobes' the dorsal traces usually bifurcate to form a pair of parallel bundles which continue into one of the two stigmas.

As previously mentioned, I did not manage to establish the mode of origin of the septal bundles. In young development stages the tegumentary traces have already become initiated, but there is no connection with the dorsal and ventral traces. In more advanced stages the septal bundles branching off from the ventrals seem to be "inversely oriented", but their turning point could not be located because the ventral bundles run too closely together.

Apart from the ventral "innervation", there are other bundles which apparently branch off from the dorsals. In the case under discussion, the term "dorsal" is a relative qualification, some bundles (such as D1) being situated in a more or less intermediate position between the dorsal bundles and of uncertain derivation. Usually it is this type of bundle from which a branch goes to the septum and continues upwards in the septum together with a branch of a ventral bundle to divide again below the nucellus – "dividing" meaning that some of the vascular bundles run towards the base of the nucellus to continue in the integument (such as S1) and other ones run through the narrow septum (S2). Bundles of the S1 type divide again at the base of the integument, so that in a cross-section 8 to 10 independent tegumentary bundles can be counted. The significance or the function of the S2 bundles is not clear, unless one interprets an S2 as the continuous principal septal bundle which sends off a branch towards the integument. However, S1 usually consists of a group of parallel traces which is considerably bulkier than the single and often tenuous strand S2, which suggests that S2 is rather an offshoot running to, *e.g.* the pistil wall, than a principal trace (*fig. 7*). An extensive comparative analysis of the vascularisation and the ontogeny of the pistils of the various genera of the Juglandaceae and related families will be necessary before any clear and consistent pattern can be recognised. Leroy briefly mentions the vascular pattern in the pistil of *Engelhardia*, but he gives a rather simplified description. The situation is much more intricate and not so constant as Leroy suggests, *e.g.*, by stating that the "cycle de faisceaux carpellaires-sépallaires" consists of 8 or 10 bundles.

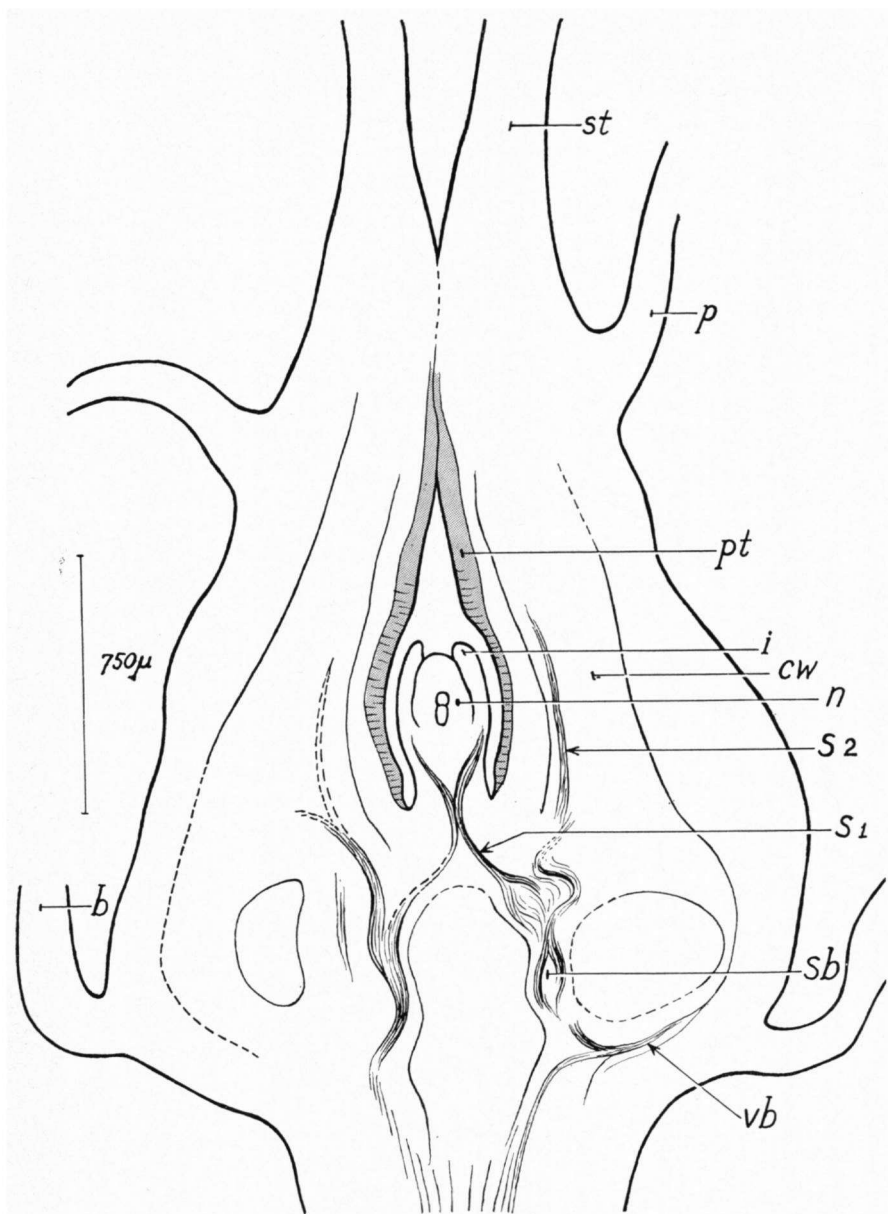


Fig. 7. Longitudinal section of the "female flower" of *Engelhardia spicata*, cut as accurately as possible through the median plane (perpendicularly to the septal plane).
(For the meaning of the symbols S_1 and S_2 : see text)

This is rather meaningless if one does not know how the vascular traces run in the various pistillar elements. The majority of the bundles situated between the

median and the septal planes of symmetry are offshoots of dorsal traces and neither the number nor the ultimate course of these branches is constant.

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