

THE GYNOCECIUM OF *ENGELHARDIA SPICATA*
(JUGLANDACEAE) AND ITS PHYLOGENETIC
SIGNIFICANCE

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ABSTRACT

1. After a concise survey of a neomorphological approach of the evolution of the one-ovuled gynoecia of several angiospermous groups the homology of certain pistils with one-ovuled pteridospermous cupules is postulated.

2. The morphology of the pistil of *Engelhardia spicata* is discussed in terms of this new interpretation, and seen in this light the so-called "female flowers" of the *Juglandaceae* may be expected to consist of a bitegmic ovule enveloped by the homologue of the cupule (the gnetalean "chlamys").

3. The close semophyletic relationship between the juglandaceous "female flowers" and the chlamydote ovules (one-ovuled cupules) of the gnetalean Cycadopsids is strongly suggested by the presence of a distal extension of the inner integument in *E. spicata* which is manifestly the homologue of the micropylar tube or tubillus of chlamydospermous forms, so that apparently in all *Juglandaceae* the outer integument must be represented by the "ovary wall" (conventionally of carpellary derivation), and the cupule by the third covering (traditionally the "perianth" or "calyx") which is partially adnate to the second integument.

4. The gynoecia of *Engelhardia* and of several, or all, other genera of the *Juglandaceae* are technically still "gymnospermous", their primary micropyles being exposed, and they provide a series of transitional stages between the primitive gnetalean condition and an almost complete state of "angiospermy" by showing the gradual coalescence of the distal regions of the integuments and the cupule homologue.

5. The advent of "angiospermy" or, probably more correctly, pseudo-angiospermy in the *Juglandales* initiated as the lateral adnation of the distal region of the outer integument to the terminal portion of the micropylar tube of the inner integument (the exostomium formed by the tubillus remaining exposed), conceivably after the differentiation of the distal end of the tubillus into an infundibuliform stigmatic area, followed by the severance of the connection between the perinucellar portion of the integument and its narrow tubular extension (*i.e.*, the stylar canal or conductive stylar tissue in a more conventional terminology) that coalesced with the outer integument by the reduction of the proximal part of the integumentary tube.

6. A singular characteristic of the *Juglandales*, *viz.*, the presence of a cavity ("ovary chamber") between the outer and the inner integument is associated with the formation of parenchymatous tissue and of "false" partitions between the integuments: the intertegumentary "packing (or filling) tissue" most probably originated as a lateral rim-like extension of the basal portion of the tubillus as found in some gnetalean forms, and during the evolution of the pistil subsequently proliferated basipetally.

7. In other angiospermous forms the lateral and basipetal outgrowths of the collar of the micropylar tube became extended peripherally (over the outside) of the outer integument, so that the angiospermy or pseudo-angiospermy in these taxa can only have been attained by a coalescence of the cupule homologue (chlamys) with the micropylar region of the tubillus without the participation of the outer integument in the formation of the "stylar" and "stigmatic" area

of the "pistil"; derivatives and remnants of basipetally developed outgrowths of the micropylar tube overarching the outer integument are frequently met with in the form of arillodes, obturators and caruncles.

8. Not only has the fundamental significance of the gynoeceal morphology of *E. spicata* in the reconstruction of the evolutionary history of the Angiosperms thus been demonstrated, but the structure of the juglandaceous pistil is also particularly instructive in showing at least two alternative ways of the gradual change-over from "gymnospermy" to "angiospermy" leading to primarily one-ovuled pistils which are perhaps only pseudo-angiospermous in that the exostomium of the original micropyle, *i.e.*, the distal end of the "stylar canal" (a derivative of the tubillus!), is still exposed.

INTRODUCTION

In some recent publications (CAMP & HUBBARD, 1963a, 1963b, MEEUSE, 1963, 1964) the first importance of the evolutionary history of the ovule in the interpretative morphology of the female genitalia of the higher *Cycadopsida* has been pointed out. In fact, the neomorphological inquiry into the phylogeny of the whole reproductive region pivots on the semophylysis of the megasporangium and its protective coverings.

One of the most striking features of some angiospermous ovules is the presence of a distal extension of the inner integument which is so strongly reminiscent of the micropylar tube or "tubillus" of the Chlamydosperms that it must represent its homologue. A tubular outgrowth of the integument was also a feature of the protocycadopsid *Corytospermaceae*, which is suggestive of a phylogenetic relation between gnetalean and at least some angiospermous forms and these rather primitive Mesozoic fossils. The importance of the tubillus in the evolution of the ovuliferous organs was recognised as early as 1947 by CROIZAT after FAGERLIND (1944) had described its presence in the ovary of *Leucosyke*. Later, LEROY (1950) independently discovered its occurrence in *Canacomyrica* and (1950, 1957) pointed out the resemblance to the prolonged inner integument of the gnetalean ovule. However, the tegumentary tube had already been observed as early as 1924 or 1925 in the juglandaceous *Engelhardia spicata* by E. W. MANNING (priv. comm.).

Not even Croizat fully appreciated the significance of the occurrence of a micropylar tube in angiospermous taxa, although he accepted the fundamental correspondence between the gnetalean chlamydotate ovule and the angiospermous one-ovuled pistils with a tegumentary tubillus. The more elaborate discussion of the subject in his "Principia Botanica" (CROIZAT, 1960, especially Chapter 5, p. 391-399) does not add much to his previous brief account and the way in which he exploits the established relation is considerably hampered by his outspoken disdain for conventional morphological dicta, so that his subsequent deductions confuse rather than clarify the semophyletic connections between the female reproductive organs of cycadopsid gymnosperms and those of the Flowering Plants.

The far-reaching consequences of the homology of chlamydotate (*i.e.*, cupulate) gnetalean ovules and the one-ovuled "pistils" of certain groups of the Angiosperms have already been explained

elsewhere (MEEUSE, 1961, 1963, 1964), but the family Juglandaceae is particularly instructive in this connection because it shows various traditional stages from a condition which is essentially still gymnospermous to a more or less complete state of angiospermy or, perhaps, rather pseudo-angiospermy as will be shown presently. The so-called "female flowers" or "pistils" of a few species of *Engelhardia* (such as *E. spicata*) are of special interest, so that a description and an interpretation of their singular morphology appears to be worth while.

THE IDENTITIES OF THE VARIOUS PROTECTIVE OVULAR COVERINGS

If it is postulated that the ovules of the gymnosperms are basically bitegmic (CAMP & HUBBARD, 1963b, MEEUSE, 1964), the two integuments of the Angiosperms can be supposed to represent the direct semophyletic derivatives (the full homologues) of the inner two ovular coats of their gymnospermous ancestors. A characteristic organ of the *Cycadopsida* is the cupule which occurs among advanced but still gymnospermous groups in various modifications such as the chlamys of *Gnetum*. It is, accordingly, plausible to assume that also in the Angiosperms a cupule homologue is sometimes retained.

In the higher *Cycadopsida* the cupule or its derivative almost invariably contains only a single (bitegmic) ovule and this provides a fairly reliable criterion to identify a homologue of a cupule, because the cupule forms a third protective envelope of the ovule immediately adjacent to the outer integument. The gnetalean cupulate ovule is technically still gymnospermous, because, of the three covering organs, the distally extended inner integument is usually the longest, so that the micropyle is completely exposed. In some species of *Gnetum* the outer integument or the cupule homologue (the chlamys) is, or both are, about as long as the inner ovular coat, but this does not change the "gymnospermous" character, the tip of the micropylar tube (the exostomium) remaining exposed. The pistils of the Flowering Plants are conventionally defined as "angiospermous" because the ovules are encased by the ovary wall which is fairly generally supposed to represent sterile carpellary tissue, so that the pollen grains cannot gain immediate access to the micropyle, *i.e.*, to the distal orifice of the inner integument. This traditionally "unbridgeable" gap between Gymnosperms and Angiosperms was an inevitable consequence of the classical carpel concept which implies that all angiospermous gynoecia ("pistils" or "ovaries") represent one to many carpels, so that a gnetalean ovule and a reputedly carpellate angiospermous "pistil" were thought to belong to two morphologically different and hence uncomparable categories of organs. There are, accordingly, two alternative approaches of the morphology of the angiospermous gynoecium, the one based on the neomorphological (*i.e.*, phylogenetically deduced) supposition that primitive angiospermous taxa have bitegmic ovules surrounded by a homologue of the cycadopsid cupule, and the other on the classical postulate that all angiosperms have carpellate gynoecia.

The most current interpretation of the pistil, based on the ranalian or euanthium theory, presupposes primitive carpels with several marginal ovules, so that one-ovuled pistils can only be imagined to have evolved from pluri-ovulate prototypes representing at least one whole carpel by oligomerisations and reductions, and must of necessity be derived ("pseudo-monomerous"). On these grounds, all taxa with monovulate ovaries such as several orders of the Monochlamydeae, nearly all the *Piperales*, and the *Cyperales* became reputed to be "advanced". However, there are cogent indications that *Monochlamydeae* and *Piperales* cannot possibly be so very much derived, because they have some unmistakably primitive features (see, e.g., MEEUSE, 1963, p. 73, Additional Note no. 2). The assumption that their gynoecia are extremely modified carpellate structures requires a long semophyletic history of their female genitalia, which is incongruous with the simultaneous occurrence of primitive characters. Accordingly, the alternative supposition that the one-ovuled pistils of, e.g., *Juglandales*, *Urticales*, *Piperales* and *Cyperales* are primitive gynoecial structures is at least equally probable and agrees with the postulated origin of the Angiosperms from chlamydospermous-bennettitalean prototypes with, typically, one-ovuled cupules. In other words, the most primitive form of an angiospermous pistil must be one-ovuled and possess at least three protective coverings corresponding with those of a cupulate (chlamydote) gymnospermous ovule, of which the inner two are the integuments, so that the third, usually (but not, as we shall see presently, in Juglandaceae) forming the "ovary wall", must represent the cupule. On this basis, also the juglandaceous gynoecium may be expected to consist of a single bitegmic ovule enveloped by a derivative of the cupule and its morphological interpretation can be aligned with the fundamental gnetalean pattern.

MATERIAL AND METHODS

The material used in this study was kindly supplied by Professor E. W. Manning, Bucknell University, Lewisburg (Pa.), whose generous co-operation we gratefully acknowledge. It consisted of spirit material of so-called "female-flowers" of *Engelhardia spicata*, collected from cultivated specimens in the Botanic Gardens, Bogor, many years ago but still in excellent condition.

Sections made by means of the standard paraffin technique, *n*-butyl alcohol being used as an intermediary between the alcohol series and the paraffin, were subsequently stained with Safranin-Fast Green or Tannic Acid-Ferric Chloride and Safranin, and mounted in Cedax.

Clearing of whole gynoecia was tried, but the cleared pistils became too transparent to show the inner structure. The vascular bundles stood out sharply, but the pattern of vascularisation does not supply unequivocal indications of the nature of the pistil (MEEUSE, 1964) and will not be discussed in the present paper.

The technical part of the work was carried out by the junior author (J.H.).

THE STRUCTURE OF THE PISTIL OF *ENGELHARDIA SPICATA* AND THE MORPHOLOGICAL INTERPRETATION OF THE JUGLANDACEOUS GYNOECIUM

The so-called female flower of *Engelhardia spicata*, conventionally a "pistil" partly enveloped by the "perianth" ("calyx") and containing a single reputedly unitegmic ovule, is shown in Fig. 1. In a



Fig. 1. Pistil (so-called female flower) of *Engelhardia spicata*, appr. $\times 8$. The pistil is supported and basally encased by a 5-lobed persistent bract (or compound bract) which is only partially shown. The spreading lateral appendages of the pistil represent the free apical lobes of the outer ovular coat, traditionally a "perianth" or "calyx", but in the present author's interpretation a homologue of the gnetalean chlamys and, ultimately, of a pteridospermous cupule.

longitudinal section (see Figs. 2 and 2a) the inner integument appears to possess an extension which passes into a narrow "stylar canal" of which the inner epidermal layer is continuous with the cell layer forming the inner (upper) epidermis of the stigmatic lobes of the "pistil". There can be very little doubt that this long tubular extension, which is hollow in the distal region, corresponds with the tubillus or micropylar tube of the chlamydospermous gymnosperms and, most probably, of the earlier *Corystospermaceae*. The extreme distal end, *i.e.*, the exostomium of the micropyle, is completely exposed and the tegumentary tube still forms a partly open connection between the stigmatic area and the interior of the ovule, which are both gnetalean, in other words, gymnospermous features.

As regards the second integument, this is either reduced, so that the ovule is unitegmic (the conventional point of view), or it is represented by the second envelope of the ovule which forms the almost completely closed pistil wall and has hitherto been considered to consist of carpellary tissue. There is no reason to assume that during the semophylysis of the manifestly primitive ovuliferous organ of

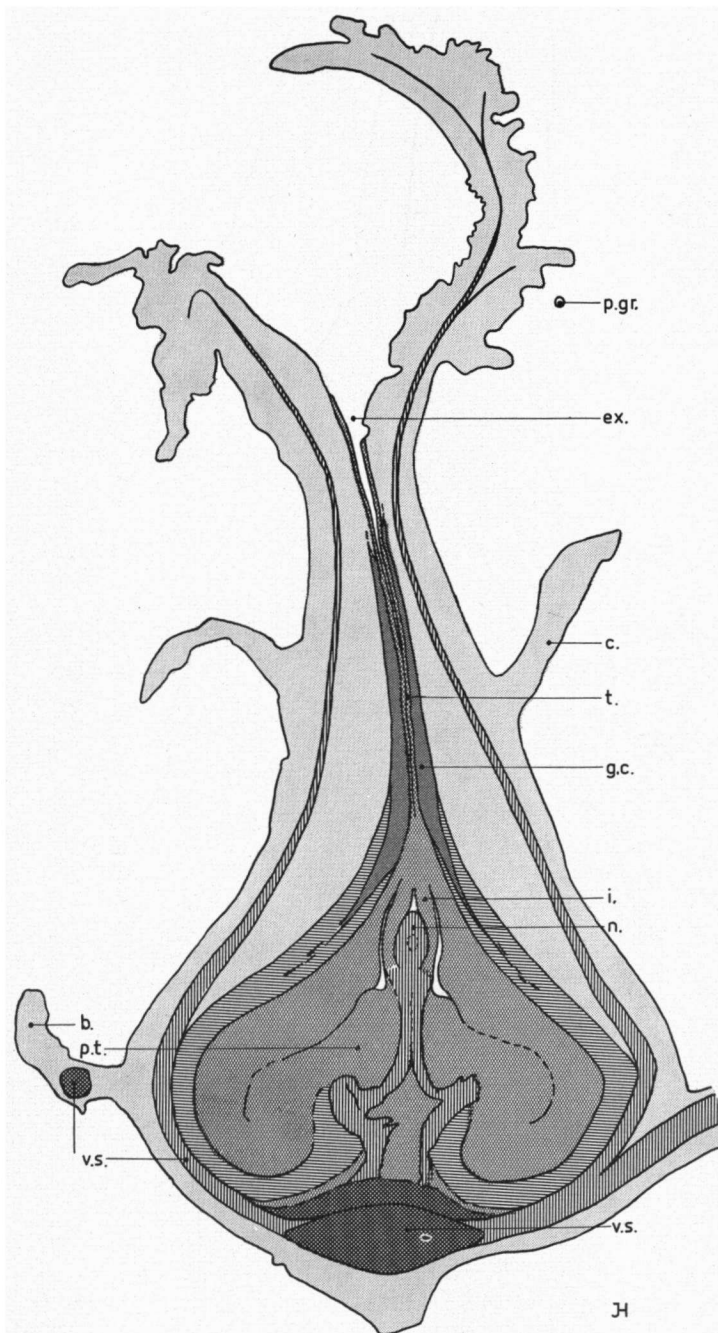


Fig. 2. Longitudinal section of the pistil of *Engelhardia spicata* appr. $\times 40$. *p.gr.*: pollen grain (as an indication of the complete stage of anthesis); *ex.*: exostomium of micropylar tube or tubillus (*t.*); *c.*: lobe of chlamys (cupule derivative) or so-called perianth (calyx); *g.c.*: zone of gum cells; *i.*: (inner) integument; *n.*: nucellus; *b.*: lobe of bract, *v.s.*: vascular strands.

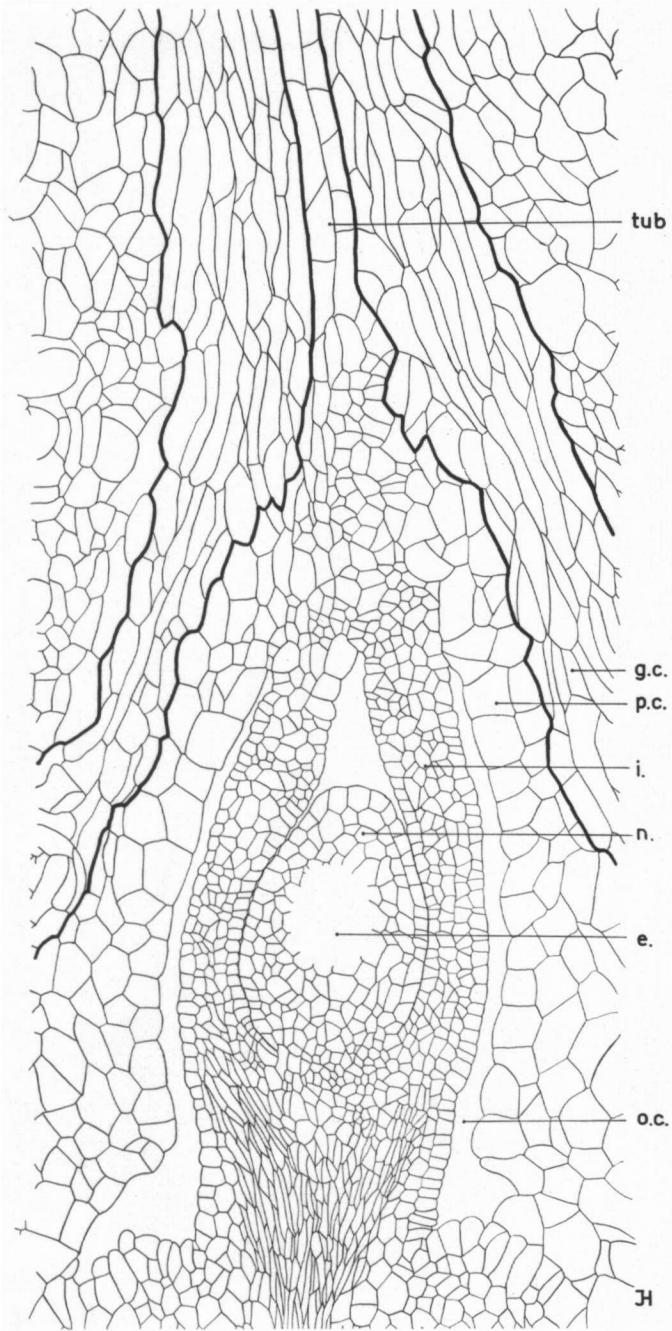


Fig. 2a. A portion of Fig. 2 (area of ovule), much enlarged. *tub*: tubillus; *g.c.*: zone of gum-containing cells (indicated by a heavier black line); *p.c.*: packing or filling tissue, continuous with the integument (*i*); *n.*: nucellus; *e.*: cavity which contained the embryo sack; *o.c.*: ovarial cavity.

Engelhardia spicata an early and complete reduction of the outer integument has taken place, which implies that the second alternative is the most plausible, so that the pistil of several *Juglandaceae* is in fact technically still gymnospermous, the stigmatic regions and the exposed micropyle representing portions of the integuments. The third enveloping organ, the so-called perianth, must represent the cupule (chlamys) which is apparently not closed over the integuments — another gnetalean character.

The transverse sections of the pistil of *E. spicata* (see Figs. 3 and 4) augment the information obtained from the longitudinal ones and do not require a detailed description, except as regards the interpretation of the packing tissue of the juglandaceous gynoecea to be discussed presently.

The *Juglandaceae* exhibit several phases of the evolution of the most primitive form of an angiospermous pistil from a cupulate ovule (see Fig. 5). In *Engelhardia spicata*, as we have seen, the inner integument has a tubillus and the cupule homologue does not encase the integuments completely. In other species of *Engelhardia* and in *Juglans* the condition is essentially still the same but for the reduction of the proximal part of the micropylar tube. In species of *Carya* the cupule is relatively longer and constitutes nearly the whole outer wall of the

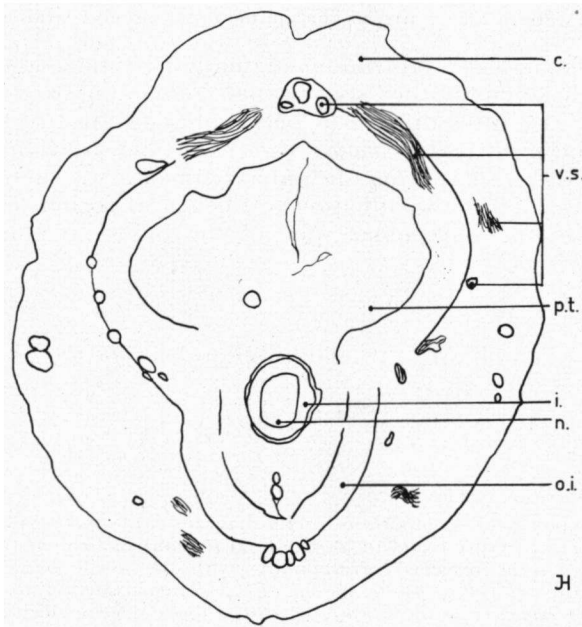


Fig. 3. Transverse section of pistil at a level which passes through the nucellus, approx. $\times 30$. *c*: outer wall (chlamys!); *v.s.*: vascular strands; *p.t.*: packing tissue; *i*: integument; *n*: nucellus; *o.i.*: part of ovary wall most probably representing the outer integument.

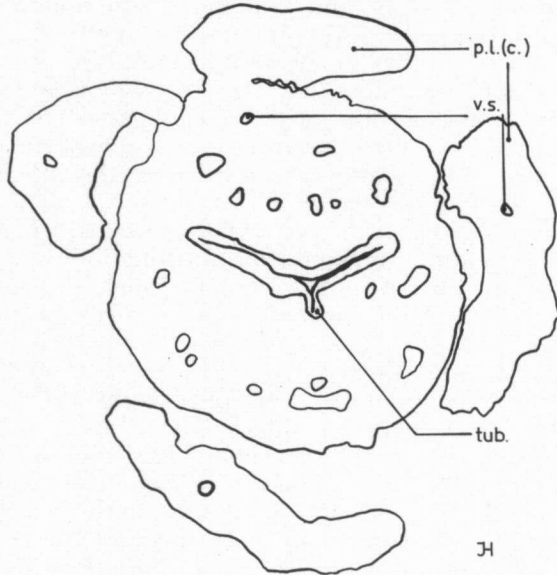


Fig. 4. Transverse section of apical part of pistil in the area of the attachment of the lobes (p.l. or c) of the longitudinal section in Fig. 2, approx. $\times 50$, tub.: tubillus; v.s.: two of the (numerous) vascular strands.

pistil, only the apically protruding stigmatic extensions and the area around the distal end of the "stylar canal" remaining exposed.

There is very little difference between a gnetalean chlamydotate ovule and the pistil of *Engelhardia spicata* (see Fig. 5). The most significant advance, apart from the intertegumentary structures to be discussed presently, is the adnation of the apical region of the outer integument to the micropylar tube of the inner integument. The



Fig. 5. A typological comparison (semi-diagrammatic) of the ovuliferous reproductive organs (represented in longitudinal section) of *Gnetum* (Gn), a hypothetical case, in some respects corresponding with the sterile ovule of a male *Welwitschia* plant (H), *Engelhardia spicata* (E, packing tissue omitted, compare Fig. 2 and 2a), *Juglans* (J) and *Carya* (C). In the juglandaceous forms the cupule homologue does not participate in the formation of the stigmatic area and as a complication, the bract is adnate to the outer wall (E) or forms a substantial part of the outer layer (C). A complete tubillus is present in E, and what is apparently a remnant of a tubillus in C (the latter case is emphasised by outlining the region of the so-called stylar canal). The phenetic correspondence is thought to reflect a phylogenetic relationship.

coalescence of the apical regions of the outer integument and the tubillus was probably preceded and facilitated by a distal expansion of the latter into a funnel- or disc-shaped structure serving as a support or "container" for the pollination droplet exuded by the micropylar tube as in the sterile gynoecial elements of the functionally male reproductive structures of *Welwitschia*. A reduction of the connection between the perinucellar portion of the inner integument and that part of the tubillus which forms the "stylar canal" (and the stigmatic area including the original exostomium) renders the pistil technically angiospermous, the secondarily formed "inner" micropyle being overarched by the apical portions of the two integuments (and sometimes also by the cupule homologue as, *e.g.*, in *Carya*). However, the "outer micropyle", phylogenetically still formed by an extension of the inner integument, is still extant and it is probably more precise to call this condition pseudo-angiospermy. The gradual transition from the state of gymnospermy to more or less complete pseudo-angiospermy can thus be visualised as an adnation of the distal region of the outer integument or the cupule (chlamys), or of both, to the tubillus, followed by the reduction of the proximal portion of the micropylar tube. In other taxa than the *Juglandales* the pollen-receiving function of the inner integument may gradually have been taken over by the outer integument or by the cupule, as the case may be, but the presence of conductive tissue in the "stylar" region of many forms suggests that this tissue represents the remnant of a "stylar canal", *i.e.*, of the micropylar tube of the inner integument, which implies that the original exostomium of the micropyle is still exposed and not arched over by other protective coverings of the ovule, in other words, that these gynoecia may also be pseudo-angiospermous. The differentiation of a stigmatic and sometimes of a stylar region must have preceded the change-over to pseudo-angiospermy, at least in the phylogeny of the Juglandaceae.

The development of an "ovary chamber" (a gas-filled space) by the spatial separation of a large portion of the chlamys from the outer integument or, as in *Juglandaceae* and probably also in *Myricaceae*, of the outer integument from the perinucellar part of the inner one, seems to be only attendant and may or may not have preceded the apical closure of the pistil and the subsequent reduction of the basal part of the tubillus. The singular condition in the juglandaceous (and most probably also myricaceous) gynoecium is apparently associated with the development of parenchymatous tissue and false septa between the two integuments, so that the ovarian cavity was formed between the two integuments simply because room had to be made for the intertegumentary structures.

The semophyletic evolution of the one-ovuled cycadopsid cupule into an angiospermous pistil outlined in the preceding paragraphs does not necessarily have proceeded in exactly the same way in those lineages that acquired carpellate gynoecia. There are no cogent reasons to assume that the (arillate) ovules in a carpellate ovary always passed through a stage in which the outer integument or the

cupule (chlamys, subsequently aril) became distally adnate to the micropylar tube of the inner integument. It is not even necessary to postulate that the inner integument always had a long tubular extension in all hemiangiospermous groups. The phylogenetic history of the genitalia of the Angiosperms reflects the early divergence of several smaller evolutionary lines leading to the conventional class of the Angiosperms and is probably as varied as the ultimate floral morphology of the major taxa constituting the large assembly of Flowering Plants.

A rather singular feature of the juglandaceous gynoecia, *viz.*, the presence of soft parenchymatous tissue and "false" septa in the ovarial cavity, has already been mentioned. These two structures may be related in that the secondary septa originate from the parenchyma or at least have a common source. The spurious partitions have often been discussed in connection with the interpretation of the juglandaceous pistil, the problem being that one attempted to relate the septa with carpellary formations, *i.e.*, with the number of "carpels" and with the relative position of the carpels and their supposed stigmatic extensions (BENSON & WELSFORD, 1909, LANGDON, 1934, NAST, 1935, MANNING, 1940, HJELMQVIST, 1948, for a discussion see LEROY, 1954). The whole argument becomes inane now that the identity of the juglandaceous "pistil" with a cupulate ovule seems to be well established, because there simply are no carpels. That the partitions are "false" follows from the fact that they incompletely divide the space *between the two integuments*, so that their phylogenetic origin can only be sought in outgrowths of the inner or the outer integument or of the so-called funicle (actually the hypostase). In *Engelhardia spicata* the parenchymatous packing tissue appears to be contiguous with the extension of the integument, *i.e.*, of the proximal region of the micropylar tube and this suggests a semophyletic derivation of the integumentary parenchyma from the inner integument or its tubillus (Figs. 2 and 4). Lateral outgrowths of the basal region of the tubillus are not without counterpart in gnetalean ovules. In some species of *Gnetum*, more particularly in those in which the inner integument is longer than the outer one, the micropylar tube forms a lateral rim or collar protruding distally of the orifice of the outer integument and, in the seed stage, sealing off the apical region of the ovule by forming a cap of ultimately indurate tissue over the outer integument (PEARSON, 1929).

A subsequent enlargement of this collar in a basipetal direction seems to provide a fairly plausible explanation of the origin of parenchymatous tissue inside the cavity between the integuments in *Juglandaceae*, which is apparently also a feature of the pistils of some of the related *Myricaceae* such as *Canacomyrca* (see Fig. 6).

The advent of chalazogamy in the Juglandales and some other Amentiferae may be associated with the development of the packing tissue. In recent gnetalean forms the pollen grains, after having been caught by a pollination droplet, are sucked into the micropylar tube and, after they have subsequently germinated in the pollen chamber,

their pollen tubes grow downwards into the nucellar tissue. As a more advanced stage one could visualise the germination of the pollen grains on the stigmatic surfaces of the gynoecium, the pollen tubes being guided during their growth straight down to the nucellus by the tubillus which is still continuous. The gradual severance of the connection between the perinucellar portion of the inner integument and the distal portion of the micropylar tube would thus conceivably result in the development of porogamy. During the evolution of the Juglandales the development of the pistillar filling tissue may have caused a preference (or a physiological necessity) of the pollen tubes to grow through this loose parenchymatic tissue in a roundabout way rather than straight down through the proximally closed tubillus or, after the direct connection between the nucellar and stigmatic region became disrupted, through the gas-filled part of the pistillar cavity, and thus chalazogamy may have ensued. Significantly, chalazogamy is found almost exclusively in amentiferous groups (*Casuarinaceae*, *Myricaceae*, *Juglandaceae*, *Betulaceae*, *Fagaceae*), in the pistillar cavities of several of which a packing tissue or a similar parenchymatic tissue is known to occur. If there is indeed some relation between chalazogamic fertilisation and some kind of filling tissue, *i.e.*, an indirect connection between chalazogamy and a singular gynoecial anatomy, this would not only emphasise the phylogenetic and taxonomic affinity of these amentiferous groups, but also imply the homology of their gynoecia or their gynoecial elements. The two- or three-locular pistils of *Casuarinaceae*, *Betulaceae* and *Fagaceae* must, accordingly, be interpreted as di- or trimerous aggregates of units each corresponding with the monomerous gynoecia of *Gnetaceae*, *Myricaceae* and *Juglandaceae*, in other words, they represent two or three laterally coalesced (phalangiata) cupule homologues rather than carpellate structures (see also MEEUSE, 1964).

The process of fertilisation in the genus *Engelhardia* is apparently still unknown and its elucidation, especially in *E. spicata*, is highly desirable because it might provide an important indication. If typical chalazogamy does not occur in *E. spicata* or related forms, the derived character of chalazogamy and its connection with special tissues in the pistillar cavity becomes manifest. Porogamy, then, would be the general type of siphonogamic fertilisation among the Angiosperms and chalazogamy a special feature developed as a parallelism independently of porogamy, and hence, a study of the histogenetic development of the gynoecium of *Engelhardia spicata* would no doubt provide more tangible evidence of the origin of the parenchymatous-tissue in the ovarian cavity, but very young pistils in the appropriate early stages of differentiation were not available.

The occurrence of basipetal outgrowths of the inner integument is not at all restricted to the *Juglandales*. There are numerous examples of ovular structures, some of which are referred to as obturators (we only mention *Casuarina* as an illustration because it possesses an unusually massive one), and other ones as arillobes or caruncles, that represent various modifications of the basipetal tegumentary out-

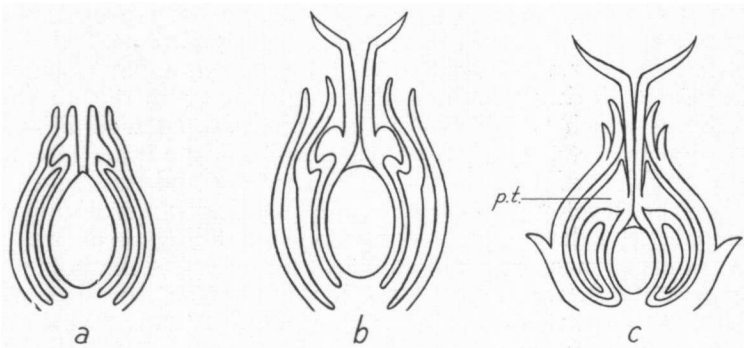


Fig. 6. Suggested semophyletic relation between the collar-like appendage of the tubillus in some species of *Gnetum* (a) and the packing tissue (*p.t.*) of the Juglandales (c, a diagrammatic representation in l.s. of the pistil of *Engelhardia*, cf. Fig. 2) by assuming (in a hypothetical intermediate stage *b*) the bypassing of the collar or rim of the inner integument by the outer integument, and the subsequent basipetal proliferation of the tissue of the rim of the tubillus which (as is shown in *c*) grows downwards to the base of the pistillar cavity and develops upwards again from the base of the cavity.

growths, which are sometimes adapted to new functions such as the conduction of the pollen tubes and seed dispersal, and in other cases have become vestigial. However, these basipetal outgrowths of the inner integument overlie the second integument and this clearly indicates that during the semophytesis of the cupule to a one-ovuled pistil usually the outer integument remained shorter than the inner one and became overgrown by the basipetal extension of the lateral collar of the tubillus (see Fig. 7), so that apparently the condition in the *Juglandales*, (*i.e.*, the presence of a packing tissue) is exceptional.

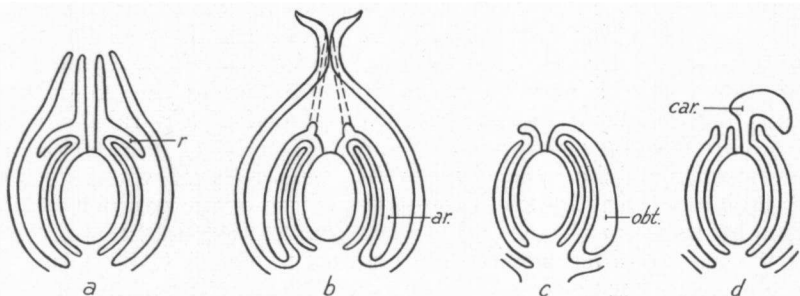


Fig. 7. Suggested semophyletic relationship between a gnetalean chlamydote ovule (a) with tegumentary rim (*r*) and an angiospermous pistil with an arillode (*ar.*) in *b*, with a form of an obturator (*obt.*) in *c*, and with a caruncle (*car.*) in *d*. Compare the text and also Fig. 6. In *c* and *d* only the ovule and its integuments are drawn.

A SUPPLEMENTARY NOTE ON THE POLLEN MORPHOLOGY OF THE JUGLANDALES

The gynoecial morphology of the *Juglandales* supports the view held by several authors—admittedly still a minority—that the Amentiferae are primitive, which implies that their other characters are not likely to be very advanced. The pollen morphology of the *Juglandaceae* and several related amentiferous families is a case in point. The evolution of the pollen grains of the Angiosperms has hardly been explored, but it can be taken for granted that the rather typical tricolpate dicotyledonous type must have evolved from some earlier cycadopsid prototype that did not possess true colpi. However, there are no compelling reasons to assume that all more or less advanced dicotyledonous forms of pollen, *i.e.*, those which are not monosulcate, zonisulcate or (primarily) acolpate, are derivatives of a tricolpate archetype as such authors as TAKHTAJAN (1959, especially Chapter VI) seem to believe. The idea that the porate grains of several amentiferous families are secondarily derived from colpate ancestral types seems to be largely inspired by the conviction that the *Monochlamydeae* are highly advanced terminal orders of angiospermous lineages primarily derived from “ranalian” archetypes. The repeatedly advocated descent of Monochlamydeae from *Hamamelidales* would indeed imply that the porate grains of *Juglandales*, etc., have evolved from the predominantly tricolpate hamamelidaceous type, but this is merely circular reasoning. Pollen grains with various kinds of pori are also found in some *Helobiae* (*Alismatales*), *Arales*, *Arecales*, *Scitamineae* and *Zingiberales*, and, considering that the Monocotyledons are hardly ever, and almost certainly not primarily, tricolpate, dicotyledonous porate types may conceivably also have originated from other than tricolpate sporomorphs. The Dicotyledons being polyrheithric rather than strictly monophyletic, the porate grains of the apparently primitive *Juglandales* and allied orders need not have evolved from colpate prototypes but may well have originated independently from some more ancient kind of pollen such as the acolpate spherical type of grain known from several *Chlamydospermae* and *Piperales*. The amentiferous panporate pollen grains most probably representing an independent (a parallel) development from acolpate ancestral sporomorphs, it is certainly not permissible to consider them to be indicative of a derived (advanced) condition in phylogenetic speculations concerning the origin and systematic position of the *Juglandales* and related forms.

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