

THE INNER INTEGUMENT – ITS PROBABLE ORIGIN AND HOMOLOGY

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SUMMARY

Typological and ecological considerations point to the homology of the outer integument of the bitegmic chlamydospermous and angiospermous ovules with the single integument of the “lower” cycadophytic Gymnosperms. The inner integument either originated *de novo* or developed out of an accessory organ of the ovule (for which the membranous extension of the macrosporangial = nucellar wall already forming the primary pollen chamber in pteridospermous preseminal cones comes to mind). Arguments are adduced in favour of the second alternative, but either interpretation implies that the outer and the inner integuments are inhomologous.

1. INTRODUCTION

The morphological identity and the phylogenetic history of the ovular integuments have provided the subject matter for a large number of papers (DE BOER & BOUMAN 1972, BOUMAN 1971a, 1971b). The ever increasing number of contributions clearly demonstrates that there is anything but a consensus of opinion concerning the origin and the nature of ovular coverings; compare, e.g., the most recent compilations by SMITH (1964), LONG (1966), KRASILOV (1970) and PURI (1971). The present paper is an attempt to clarify the situation by starting from a number of clear-cut and well-established morphological data, and by subsequently fitting this evidence in with a few plausible and rather generally accepted semophyletic relationships, an approach which requires only a few, likewise current or at least defensible, assumptions. The older publications, with few exceptions, will not be discussed and the reader is referred to the above-mentioned digests; most of the papers on the subject are in fact rather irrelevant, and it is often difficult to separate the chaff from the corn. Interpretations of ovular structures based on the hypothesis that an ovule is a kind of emergence on a foliar organ (“megasporephyll”) and may be surrounded by lobes of that phyllomic organ are rejected here categorically. The totally absurd idea that the ovule (and, by inference, the whole megagametophytic generation) of the Angiosperms developed *de novo* as an outgrowth of a “carpel”, so that it is not necessarily homologous with a gymnospermous ovule (EAMES 1961, PURI 1971), is not regarded as worthy of consideration either (see also KRASILOV 1970).

2. SOME GENERALITIES

The initial postulates needed as prerequisites for the discussion of ovular morphology are the following: (1) all spermatophytic ovules are essentially homolo-

gous, at least as far as their central core or nucellus (the megasporangium homologue) is concerned, and (2) Angiosperms are descendants of one or more groups of cycadophytic Gymnosperms — “*Cycadophyta*” to be taken in a broad sense, i.e., inclusive of all pteridospermous, cycadopsid, cycadeoid (bennettitalean), and chlamydospermous (gnetate) taxa.

The obvious preliminary conclusion is that of the individual nucellar coverings of the bitegmic angiospermous ovule at least one is a derivative of the single integument of the normally unitegmic gymnospermous ovule (and the same applies to the bitegmic ovules of some advanced cycadophytic gymnosperms, see SCHNARF 1973). In other words, one integument at least is present throughout, from the early Seed Ferns to the Flowering Plants, owing to an evolutionary continuity. However, the plurality of ovular “coats” in chlamydospermous, cycadeoid, and many angiospermous forms renders the recognition of the homology relations rather difficult.

In a purely phyto-graphical sense, a type of organ tightly enclosing the nucellus except at the distal end is called an integument. A similar organ enveloping an ovule already provided with an integument is also called an integument, but, in order to distinguish it from other ovular coats, it is usually called the outer integument (OI), thus, in bitegmic ovules, making the other one the inner integument (II). This circumscription should not be considered as implying that the II is phylogenetically older than the OI; in point of fact, as we shall see, the OI is the older functional integument. The terms OI and II are, as a rule, only applied to cycadophytic ovules: the outer coat of the *Taxus* ovule is called “aril” when mature, and a somewhat similar organ in the *Podocarpaceae* an epimatium, but such structures are only functionally comparable with an angiospermous aril or OI, and it is indeed advisable to retain the terms OI and II strictly for cycadophytic ovules only.

The question of the homology and, hence, semophyletic origin of the two ovular integuments of the most advanced cycadophytic forms (including the Angiosperms) is one of the essential aspects of the phylogenetic connections between the megasporangiate organs of the Lower Cycadophyta and those of the Flowering Plants. As will be discussed presently, the occurrence of bitegmic crassinucellate ovules in, by consensus of opinion, primitive Angiosperms, as against unitegmic ones in the majority of the Gymnosperms, in fact used to be a somewhat moot point.

Ovule-encasing organs referred to by the names of chlamys, aril, false aril, arilloid, arillode, etc., are known from a number of mostly specialised taxa (see VAN DER PIJL 1955, 1972). The “chlamys” of some *Gnetatae* is also referred to by the name of “perianth”, e.g., even by the latest monographer (MARTENS 1971), but this is most confusing because it implies that the ovuliferous chlamys (= cupule) of the Chlamydosperms is a “flower”. This semantically most deplorable nomenclature should be dropped altogether and is disregarded in the present paper. Such structures as arils and pseudo-arils need only concern us here if they can possibly be confounded with an integument (or its mature derivative), and they will, therefore, not be discussed in great detail. Such

accessory organs can almost always easily be distinguished from integuments ontogenetically, even if they do not surround or encase two or more ovules (as cupules and “carpels” often do), but only a single one. Their mode of development – not directly, and early, from the ovule primordium like the integuments, but as an outgrowth of, e.g., the funicle, the raphe, the placenta, or an integument (!) and often becoming initiated rather late – and their topology are sufficiently distinct as a rule. An additional clue, apart from the histogenetic origin and place of insertion, is that (at least before and during anthesis) the micropyle is formed by one of the integuments or by both without the participation of any other accessory organ of the ovule (the obturator, which can not be confounded with an integument in any case, excepted).

3. THE BASIS OF HOMOLOGY RELATIONS BETWEEN INTEGUMENTS

As stated before, the Gymnosperms, barring the most advanced cycadophytic forms, are supposed to have unitegmic ovules, whereas the ovules of the basic groups of the Angiosperms are bitegmic. (Unitegmy in Flowering Plants is generally considered to be of a secondary nature, and this view is also held by the present authors.) This means that advanced cycadophytes, including the earliest Angiosperms (whose ovular morphology must have been very similar to that of extant, primitive Flowering Plants) must somehow have “acquired” the bitegmic condition, which in turn requires a plausible explanation of the origin and the nature of the additional integument if, as we have postulated, the Flowering Plants are indeed advanced members of evolutionary lineages rooting in cycadopsid Gymnosperms.

The “single” gymnospermous integument will be referred to as the “primary”, or the “first” integument, which qualification does not necessarily infer a phylogenetic primarity of this integument (the precursor of the “second”, or future inner integument may be as old as the outer one). This “primary” integument is ubiquitous in its occurrence, and the conclusion that one of the integuments of the bitegmic ovules of cycadeoid (bennettitalean), gnetoid, and magnoliophytic plants is the direct semophyletic derivative of the single ovular casing of a prototypic, unitegmic cycadopsid ovule is so obvious to be inevitable, simply because there must have been an uninterrupted phylogenetic (or hologenetic *sensu* ZIMMERMANN 1959) sequence from pteridospermous to angiospermous plants, apart from the manifest homotopy of tegumentary ovular coats. A plausible answer to the question which of the two angiospermous integuments, the OI or the II, represents that homologue of the “early” (primary) integument will also narrow down the possible alternative origins of the remaining (= “secondary”) integument of bitegmic ovules.

The present authors do not endorse the opinion expressed by some older phytomorphologists (and maintained in a different, but not fundamentally different form by a number of authors such as ZIMMERMANN 1959, 1965, CAMP & HUBBARD 1963, and KRASILOV 1970) that the two integuments are twin organs formed by the “splitting” or “duplication” of an originally single one (the more

archaic viewpoint), or arose by the repetition (or simultaneous occurrence: KRASILOV) of a semophyletic organogenesis of integuments out of groups of telomes ("Kragensyntelome" of ZIMMERMANN, see also LONG 1966, p. 357–361 and his text-figures 4 and 5). CAMP & HUBBARD held the view that the pteridosperms have adnate integuments both derived from a lobed assembly of telomic elements by a process of webbing, but LONG (1966: p. 362) has pointed out that in the interpretation of these two American authors the second integument is the thin, unvascularised membrane surrounding the (primary) pollen chamber which does not show any signs of vestigial lobing and can hardly be comparable with the vascularised and originally lobed, primary integument. According to the senior present author (M.), the two integuments had a different phylogenetic history (see MEEUSE 1963b, 1964a, 1964c), which supposition is maintained in the present paper (although not all previous conclusions are necessarily endorsed).

There are a number of partly morphological, topological and anatomical, and partly ecological (functional) arguments pleading against a fundamental identity of the OI and the II of bitegmic ovules. Such a comparison of the two integuments is also likely to clarify the question of the identity (homology) of one of them with the single ovular envelope of the ancestral cycadophytic forms. The OI is usually better developed in respect of the II, especially after the maturation of the seed. In the dehiscent fruit types of primitive Angiosperms the OI of the exposed seeds is frequently differentiated into a juicy or pulpy and attractively coloured outer sarcotesta, and a hard or fibrous inner sclerotesta, whereas the II mostly persists only as a compressed, thin and papery layer squashed flat between the sclerotesta and the growing embryo and/or expanding endosperm. A soft sarcotesta and a tough or bony sclerotesta are highly characteristic of the seeds of various cycadopsid gymnosperms, both living and extinct, and this is clearly an adaptation to the function of these testa differentiations in the zoochorous system of dispersal of these seeds.

The sarcotesta – at maturity attractively coloured, palatable and sometimes aromatic – attracts frugivorous animals and provides a source of food for them, whereas the undigestible sclerotesta protects the vital interior of the seed. After the removal or digestion of the sarcotesta the rest of the seed, surrounded by the sclerotesta, is spat out, regurgitated, or passed through the digestive tract unharmed. Since the same functions are still fulfilled by the outer seed coat layers derived from the OI in a number of primitive Flowering Plants (compare, e.g., *Magnolia*, whose sarco- and sclerotestaceous seeds remained adapted to endozoochory, as VAN DER PIJL 1955, 1972, emphasised), the identification of the OI with the primary gymnospermous integument is almost a foregone conclusion. However, many workers mistook the *angiospermous* sarcotesta, a derivative of an integument, for an aril and confused the issue (see VAN DER PIJL 1969: p. 107–118, or 1972: p. 112–122, against, e.g., CORNER 1949a, 1949b, 1951, 1953, 1954, SPORNE 1948 et seq., TAKHTAJAN 1958). This confusion of ovular coats in a more restricted sense with accessory organs that are clearly of secondary origin (if not representing the ancient angiospermous cupule) has

resulted in several unwarranted deductions based on the false tenet of "the primitive aril" in phytomorphological (compare, e.g., MEEUSE 1963b, 1964c, 1966), in taxonomic (SPORNE) and in ecophylogenetic (CORNER 1954, 1958, TAKHTAJAN 1959, 1969) inquiry, as will be reported elsewhere (MEEUSE, in the press). Students of ovular and of seed evolution must be aware of this large-scale misinterpretation which has already led a number of botanists astray, and they are well advised to avoid this phytomorphological pitfall.

Additional anatomical arguments indicative of a morphological and semophyletic equivalence of the OI and the primary cycadophytic integument are: the lobing of the OI in early and sometimes also in later stages of development (the integument is often apically lobed in pteridospermous ovules), and the presence of vascular strands in the single integument of all more primitive cycadophytic ovules and in the OI of the bitegmic ovules of some more advanced forms (whereas the II is hardly ever vascularised in all groups with bitegmic ovules, even if the OI contains a well-developed system of vascular traces). Contrary to some previously expressed opinions (compare, e.g., PURI 1971), the inevitable corollary is that the OI represents the full homologue of the single integument of the unitegmic gymnospermous ovules.

Suggestions regarding the origin of the II vary as we have seen. The idea of a "repetition" of the formation of an integument out of an enveloping syntelome (*Kragensyntelom*) is unacceptable, because the II only became recognisable as a discrete integument very late, when primitive syntelomes did not exist any more as a starting point for organ evolution. A duplication by splitting is also most unlikely, because, among other things, the initiation of the integuments normally begins at a different stage of floral histogenesis in different places, and not by the formation of a common primordium of both integuments. If the OI and II are inhomologous, the origin of the II still needs to be explained.

4. THE ORIGIN OF THE INTEGUMENTS

Phylogenetic arguments based on fossils from late Devonian and early Carboniferous age point to the origin of the principal (or "primary") integument (the future OI) from an aggregate of megasporangia, the formation of synangial clusters of sporangia being such a wide-spread evolutionary trend (also in the semophytesis of the microsporangiate organs). This hypothesis, first proposed by BENSON (1904) has later been revived (see MEEUSE 1963b), but does not seem to have many adherents (compare SMITH 1964, LONG 1966). The most current alternative theory, based on the assumption that a system of telomic axes surrounded a megasporangium, does not explain why female synangial clusters suddenly became reduced to a single one (as a prerequisite to this idea), whereas the synangial character of the microsporangiate organs is persistently manifest.

Presumable the origin of the pteridospermous *cupule* from aggregates of sterile axes, demonstrable by a sequence of stages in well preserved fossils (Long), has suggested a more wide-spread occurrence of phenomena of this kind, but this gradual encasing of one of more ovules took place *after* the

origin of the primary integument. As a matter of fact this idea is compatible with Benson's suggestion if one assumes that a single "whorl" of fertile (i.e., macrosporangium-tipped) telomes became laterally adnate and transformed into the integument. Other suggestions concerning the origin of the principal integument (summarised by LONG 1966) are rejected here.

The advent of the II, situated between the nucellus and what later became the OI, can only be explained by one of two alternative possibilities as we have seen, viz., either by a *de novo* development of the II, or by a modification of a part of a pre-existing organ (megasporangium, nucellus, integument) originating somewhere between the nucellus proper and the principal integument. If such a modification took place, this can be easily verified by a point-for-point comparison of the micropylar region of a typically unitegmic, cycadophytic ovule with that of bitegmic chlamydospermous, cycadeoid, and angiospermous ovules, because ultimately the II participates in the formation of the micropyle (or forms at least the endostome), and this may provide a clue.

The pteridospermous ovules (those of the earliest seed ferns perhaps excepted, but this does not concern us here) are characterised by the presence of a (primary) pollen chamber capping the apical part of the nucellus. This pollen chamber is formed by a thin collar protruding from the shoulders of the nucellus-top, a structure referred to by the name of *lagenostome* (or salpinx – see, e.g., LONG 1966, but this term is not used consistently and is apparently sometimes used for other protruding structures of seed fern preseminal). We are informed about the development of this lagenostome by the recent discovery of young ovules of *Callospermation pusillum* in different sequential stages of development (ROTHWELL 1971). The megasporangium (nucellus) primordium

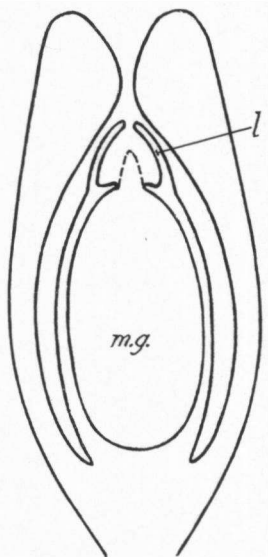


Fig. 1. Generalised diagram of a pteridospermous ovule (premen) of the *Callospermation* type at about the stage of gametophyte maturity (based on ROTHWELL 1971).

The innermost part (macrospore proper, nucellus), often with apical extension (broken line), is replaced by the megagametophyte (*m.g.*) and surrounded by the sporangium wall which forms the lagenostome (*l*) as a collar around the pollen chamber; the whole structure is enveloped by the (original) outer integument.

shows an apical depression which deepens and widens to form the lagenostome; the latter is continuous with the wall of the nucellus and may, therefore, be regarded as a derivative of the megasporangium wall (see fig. 1). The lagenostome wall must also exhibit a longitudinal growth because rows of longitudinally extended cells can be discerned in such forms as *Lagenostoma*. The possibility cannot be ruled out altogether that in such forms as *Lagenostoma* (but not in the *Callospermarion* type of ovule) the collar of tissue forming the lagenostome originated solely as a rim-like protuberance and not (partly) as a depression. The formation of the depression can be interpreted as the germination of the megaspore (i.e., the exposure of its contents by the opening of its wall), but conceivably this stage has ontogenetically dropped out in such form genera as *Lagenostoma*.

The development of the pollen chamber exposes the apical part of the megaspore; in later stages of development very little remains of the megaspore tissue owing to the enlargement of the gametophyte. The question of the homology of the nucellus will be discussed elsewhere (MEEUSE, in preparation). In the living representatives of mesocycadophytinous forms, the Cycads, the young ovule develops a pollen chamber which originates as an apical depression of the nucellus primordium but is soon surrounded by a conspicuous nucellar beak (see, e.g., CHAMBERLAIN 1935, SWAMY 1948, RAO 1961, SINGH & JOHRI 1972). The pollen chamber is accessible to pollen grains during this stage of development but subsequently the canal in the nucellar beak closes again and the pollen chamber usually also becomes reduced in size (fig. 2, a, b, c). After the pollen has germinated the pollen tubes travel basipetally through nucellar tissue to reach an underlying cavity or archegonium chamber whose bottom is formed by the gametophyte (see fig. 2, d).

The subsequent fertilisation process will not be discussed here. It is quite clear that the formation of an apical depression and a proliferation of the surrounding rim is essentially the same process as the formation of the lagenostome and pollen chamber in pteridospermous preseminal. The nucellar beak must represent the lagenostome, but, as in seed fern preseminal, in the post-pollination phase the nucellar beak becomes inconspicuous because it can not be easily distinguished from the other tissues with which it forms the dome over the archegonium chamber.

In the more advanced group of the chlamydosperms the nucellus primordium also forms a distal differentiation which corresponds with the nucellar beak and pollen chamber of the cycadid gymnosperms. This homologue of the nucellar beak and the lagenostome, almost unanimously called "inner integument" in these and in related forms, seems to originate earlier and certainly persists much longer as a discrete entity than it does in pteridospermous and cycadaceous groups of plants. The pollen chamber remains smaller, however, and is only a slight basal enlargement of the micropylar canal. In the *Gnetatae* pollen grains reach the pollen chamber and germinate there. The archegonium chamber is vestigial or there is no trace of it left (compare fig. 3). In some cycadoid (bennettitalean) forms the pollen grains apparently did not penetrate

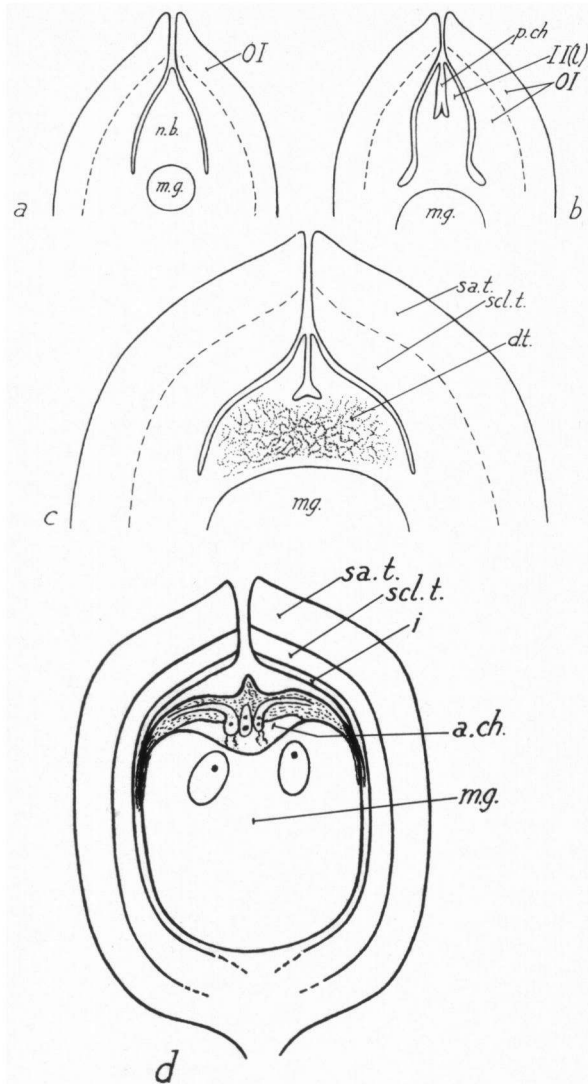


Fig. 2. *a, b, c.* Developmental stages of the apical portion of the ovule of *Cycas*. In the first stage (*a*) the nucellus (with young megagametophyte, *m.g.*) forms a nucellar beak, which (*b*) forms a depression with a wider basal part, the future pollen chamber (*p.ch.*). The part forming and surrounding the pollen chamber and its apical canal is the homologue of the pteridospermous lagenostome (= future inner integument): *I, II*. In the next phase (*c*) pollen grains can be caught by the micropyle and introduced into the pollen chamber. Below the pollen chamber the nucellar tissue disintegrates (*d.t.*) to form the later archegonium chamber (see *d*). The pollen chamber and apical canal subsequently become closed by the pressure of the surrounding tissues, especially of the (outer) integument, differentiating into a sarcotesta (*sa.t.*) and a sclerotesta (*scl.t.*). *d.* Ovule of a cycad (based on *Dioon* and *Encephalartos*) at the stage of fertilisation, semi-diagrammatic. Pollen tubes developed in nucellar tissue discharge their contents into the archegonium chamber (*a.ch.*). *m.g.*: megagametophyte with archegonia; *sa.t.* = sarcotesta, *scl.t.* = sclerotesta, *i* = innermost differentiated layer of (outer) integument or *Innenhäutchen*.

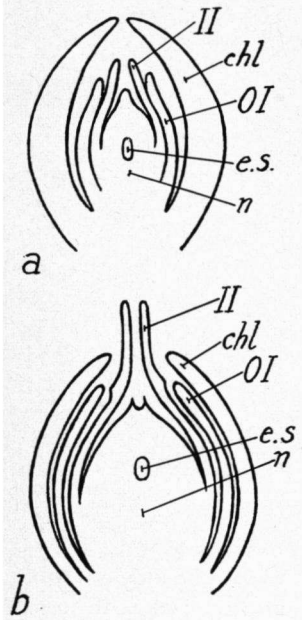


Fig. 3. *a*. Young developmental stage of ovule of *Gnetum*, semi-diagrammatic. *chl* = chlamys; *OI* = outer integument; *II*, surrounding the pollen chamber and micropylar canal = inner integument (= lagenostome collar homologue); *n* = nucellus, *e.s.* = (young) embryo sac. *b*: pollination stage, showing differential growth of *OI*, *II*, and nucellus, and vestigial archegonium chamber.

into the micropylar channel, but the function of the distal differentiation of the young nucellus remained essentially unchanged: the presence of a lagenostome or nucellar beak, and in cycadeoid and gnetate forms of their homologue now called an integument, was or is associated with the catching of pollen grains and, at least up to a point, with the protection and incubation of the pollen and of the emerging pollen tubes. During the change-over from the gymnospermous to the angiospermous level of evolution several processes and conditions became gradually altered: siphonogamy became established, seed maturation continued much longer, the ovule became more completely encased by the cupule and its derivatives ("angiovuly"), etc. There is also a proleptic acceleration and telescoping of the reproductive processes ultimately resulting in further reductions of the nucellus, the gametophyte, and ultimately of one or sometimes both of the integuments (compare *fig. 4*). One of the consequences of the neotenic (precocious) development of certain parts is a change in the relative allometric relations between the size (the extent) and the shape of the different constituting parts of the ovule and the (young) seed. We shall return to this point presently. In the more primitive Angiosperms the homologue of the lagenostome and nucellar beak is normally still present as a well-developed inner integument, as mentioned before, but it usually only persists after seed maturation as a thin layer squeezed flat between the outer testa layers and the developing seed and/or the endosperm (see, e.g., QUISUMBING 1925).

It appears that the *II* and its precursory semophyletic stages are almost as ubiquitous as the *OI* in all but the most primitive cycadophytinuous Cormophytes. Its evolution showed ups-and-downs, which is apparently associated with its

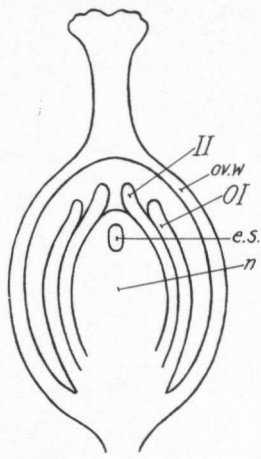


Fig. 4. Diagram of angiospermous pistil with single ovule. *ov.w.* = ovary wall, *OI* = outer, *II* inner integument. *n* = nucellus, *e.s.* = embryo sac.

function: originally, as the pteridospermous lagenostome, it formed the primary pollen chamber in which the antherozoids emerged and moved about, but subsequently the nucellar dome became more important in more advanced forms with an archegonium chamber and with pollen tubes fed by the nucellar tissue, the lagenostome becoming a part of the nucellar dome capping the archegonium chamber, and, ultimately, the level of complete siphonogamy led to a more conspicuous development in gnetate-bennettitalean forms, presumably in connection with pollen tube guidance. The homologous structure is now called the inner integument. The "catching" of the pollen grains in typically angiospermous gynoecia is the function of the stigmatic parts of the pistils and this "transference of function" was concomitant with a reduction of the II, in the first place of its tubillus (conceivably, early "angiospermy", as in *Caytonia*, was associated with an arrested development of the II which did not "acquire" a long tubillus, but this makes no difference if an angiospermous ovule is a derivative of a caytonialean precursor: the II perhaps never developed a long tubular extension in this case). In some angiospermous groups (such as the Centrospermae) the micropyle is (still?) only formed by the II, but in many other cases both integuments participate in its formation, or the II forms an endostome.

Although generally speaking the angiospermous II became progressively reduced (so that the ovules of the more advanced groups of the Angiosperms are often unitegmic), sometimes a transference of function (CORNER 1958) took place. A secondary proliferation of the II at its apical end in the form of a protrusion or a basipetal outgrowth called an arillode, a caruncle, or an elaiosome, "takes over" the function of the sarcotesta or the aril in seed dispersal (as an adaptation to endozoochory, more particularly to myrmecochory).

One must also bear in mind that the II sometimes plays a role in the feeding of the embryo and in the formation of the endosperm endothelium, and that

in exceptional cases the OI does not participate in the formation of the testa, so that the seed coat is formed by the II alone. In these instances the young II is frequently more massive than is the rule.

5. SOME COMPLICATIONS

The histogenetic origin of the II as a primordial ridge usually precedes the initiation of the primordial OI. Some theoreticists may take this as an indication of the relative phylogenetic "age" of the two integuments, so that the II must be the "older" and the OI the "younger" of the two, but this is only of academic interest. The II essentially represents a part of the outer layers of the megasporangium wall, and some of the geologically oldest pteridosperms known already had a pollen chamber, so that the fore-runner of the II or lagenostome is not much younger than the OI (and possibly even older). That the II originates ontogenetically before the OI is, therefore, not at all unexpected even if this need not be very significant in terms of the Law of Recapitulation.

The insertion of the integuments in bitegmic angiospermous ovules is usually at a low distal level, i.e., they are free from the nucellus down to nearly the chalazal end (at least on one side), whereas the nucellar lagenostome in seed ferns (and, in its young developmental stages, the II) typically emerge from the shoulders of the top of the (young) nucellus. In developing ovules of *Gnetum* the II is discernible as a separate layer at some distance acropetally of the zone of insertion of the OI. This is perhaps an intermediate phase between the early cycadophytic condition and the situation in angiospermous ovules. The development of the ovule of *Gnetum* has been studied in detail (see MAHESHWARI & VASIL 1961, MARTENS 1971), and it appears that the two integuments are formed in quick succession in rather close proximity, but subsequently their bases become gradually "shifted" in respect of one another by the differential growth of parts of the nucellus. It is assumed by the present authors that the growth of the nucellus was originally stronger in its basal part, so that the early initiated lagenostome (or II) ultimately became shifted to a subapical position by basal intercalary growth. However, such a process of differential growth does not cease when the ovule is in the phase of, say, megaspore formation, but continues until the premen or seed is shed. It all depends on the stage of pre- or post-fertilisation of the ovule whether one finds one condition or the other. In *Ricinus* (BOUMAN, in preparation) the post-fertilisation development of the ovule is mainly by basal intercalary growth whereas the whole apical part grows more in girth than in length. In some ovules the growth is not so localised, and if there is differential growth, this may start early in the presporic phase, for instance, or late (after fertilisation). A survey is given by BHATNAGAR & JOHRI (1972). The relative extent to which nucellus, integuments, and the chalazal and raphal zones develop is presumably not so important from a phylogenetic point of view.

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