

Cambridge University Press  
978-0-521-11605-3 - The Seeds of Dicotyledons, Volume 1  
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Excerpt  
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## PART ONE

## I. Material and method

It is impossible to over-emphasize the desirability of the simplest approach, which is to study living ovules and seeds by means of free-hand sections mounted in water, cleared in lactophenol, and stained for lignin. Practice improves until sections can be cut with precise orientation under the binocular microscope. The lengthy procedure of embedding for the microtome is avoided with much saving in time, cost and result. Ovules and seeds are often oblique to the axis of ovary and fruit. The microtome supplies a large number of exasperatingly oblique sections, to which one correctly orientated free-hand section is preferable. Then, as the seed matures, its tissues become too hard for the microtome; they fracture under the blade, and the final and most characteristic features must be studied with free-hand shavings. This was the method of the early investigators, though unsupplied with modern binocular dissecting microscopes, by means of which they drew up and illustrated some of the best descriptions of seeds, e.g. Meunier on Papaveraceae. In modern research the structure of the seed-coat is often an adjunct to embryological details which require the microtome, and the results have seldom been outstanding. The microtome may seem more suitable for immature seeds because it allows microphotography, but extremely few photographs have been published which are so clear and convincing as drawings; background opacity, out of focus, blurs essentials. Moreover until structures have been followed cell by cell with the pencil, they are not appreciated. Then, a great advantage of the free-hand method is the thick, unstained but cleared, section which enables one to observe in depth and to follow oblique surfaces or strands. The advantages of studying living tissues are many; chlorenchyma, aerenchyma and mucilage-spaces are as clear as vascular bundles and lignified layers; integuments are separable when fixation causes them to adhere; and critical stages are quickly obtained. Colour, translucency

and texture reveal at once important points and remind one that the seed is a growing photosynthetic structure. Few botanists realize that ligneous tissues pass through a highly aqueous phase and that water is the medium for lignification.

The best place to work is in a botanical garden in the tropics where so many seeds require investigation. For most genera and species, however, there will be only preserved material gathered on outings. It rarely supplies a full series from ovule to ripe seed, unless it has been gathered for this purpose. Nevertheless, botanists who visit the tropics and subtropics must be urged to preserve flowers and fruits in alcohol or other fixative, in addition to the usual and, now, often unnecessary dried material. My own researches have been helped in this way by students, though their gatherings may represent only one stage in seed-development. Dried material can be used when one is sufficiently acquainted with the general structure in a family or genus but it often does not enable one to distinguish the precise layering of the tissues into their derivation from one or other integument, which is important. The distinction between the products of the inner epidermis of the outer integument and those of the outer epidermis of the inner integument is usually decisive.

For the preliminary examination of a seed, the first command is to hunt the micropyle. It may be seen externally or it may be found internally from the direction of the radicle, though this is not infallible as the seed of *Sterculia* will show. The seed must be sectioned longitudinally and transversely so as to include micropyle and chalaza, because at these places, even in mature seeds, the separation of the integuments may still be discerned. Then tangential or paradermal sections must be made to determine the shapes of the cells; a layer of fibres cut transversely may give the appearance of a palisade of columnar cells; alternatively, a palisade of cells may have elongate facets or the facets may have the stellate lobing of the epidermal cells of

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many leaves. The need for such sections is often overlooked, but becomes a first consideration with the free-hand method. If the seed is embedded in thick woody endocarp, this may be cut cleanly as with a sharp blow on a knife or it may be sawn with a fine band-saw; in either case it is usually possible to extract parts of the seed and to study them in the normal way. Whatever method is employed, the later stages of hardening seeds must not be overlooked because definitive characters are frequently the last to appear.

For illustration I have preferred line-drawing made with the *camera lucida*. In cases of low magnification without cell-details, I have indicated endosperm with stippling, sclerenchyma with coarse stippling or speckling, palisade-layers with striation, and vascular bundles with broken lines. In high-power drawings I have often exaggerated slightly by means of heavy black lines the separation of the integuments and nucellus. Air-spaces have been shown in black.

## 2. Seed-form

The form of the seed, though neither its size nor its differentiation, is set usually by that of the ovule. As this organ is described in most books on plant-anatomy, it is necessary only to emphasize one point: the ovule is the embryonic seed. The cells of the ovule are small, thin-walled and isodiametric; they have large nuclei and few small vacuoles; vascular bundles are mainly procambial; air-spaces, if any, are slight; stomata, if present on the seed, are rudimentary or unformed. Then on fertilization the cells renew their growth; they divide, enlarge and differentiate; vascular bundles function; aerenchyma is formed; most seeds are photosynthetic. At length the tissues around the endosperm and embryo die; mechanical layers have been formed in certain parts of the seed-coats with characteristic position and construction; an elaborate vascular supply may have perfused the testa; micropyle, chalaza and hilum may be stoppered; many complicated chemical changes may be the result of this senescence. In like manner the ovary is the embryonic fruit but, with exposed surface and functional style, it is partly adult. Nevertheless most of the inner tissue, particularly towards the base of the syncarpous ovary, is embryonic; on fertilization it proliferates and differentiates, while the precocious style withers or is discarded.

There is an interesting paragraph on this matter in an article by Croizat (1947a), which begins 'It is curious that it never seems to have occurred to orthodox morphologists that the *flower itself is an embryonal structure*, and that in most cases fertilization reaches the flower in *its embryonal stage*.' The author compares the adult fruit with the embryonal ovary, as if it were branch to twig, and concludes that to understand the flower the fruit must be known. The paragraph is worth study because the germ of truth is hidden in a confusion between the adult and functional parts of the flower, which are external to the ovary, and its embryonic parts which are no twig but the curtailed core of the

reproductive bud. In his *Principia Botanica* (Croizat 1960), the message is forgotten and the author proceeds to estrange ovules from their nest, as if they were adult, and to doodle with them in outline on paper just as the orthodox morphologists of his complaint in their theories of ovular evolution without seed or fruit. The evolutionary process seems to have been the neotenic functioning in part of the reproductive bud whereby the divergent outer scales mature into the relatively small and caducous parts of the open flower around its embryonal centre; then, with sepals, petals, and stamens over, the centre grows into the massive fruit (Corner 1964). The primitive reproductive character of the flowering plant lies in the delayed expression of fruit and seed. The delay is successful because it avoids the expensive outlay in massive construction which would be forced upon the reproductive bud if pollination did not occur until fruit and seed were fully formed; little neotenic parts effect pollination in anticipation of the outlay and, if ineffective, the loss is minimal. The simplicity of the ovule is not primitive but primordial. Prime characters for the classification of flowering plants should lie therefore in the construction of fruit and seed, which are the parts so universally omitted by theorists. In the long run seeds also become neotenic, small and simple, and after fertilization merely enlarge the cells of the integuments to become, as it were, just adult ovules, e.g. *Begonia*, *Digitalis*. Alternatively, and as successfully, the number of seeds in a fruit reduces until the one-seeded fruit comes to function as a seed; the integuments may not differentiate in the seed-coat and the endocarp performs this duty. Thus, small or simple seeds are no more primitive than ovules. Primitive families, as those of Magnoliales, have fruits and seeds of great complexity; advanced sympetalous families simplify both. 'The difference cannot be capital between *Gnetum* and *Mezzettia* when the ovular structure of both genera is virtually

identical tegument by tegument' (Croizat 1960, p. 397). The fallacy is clear. The seed of *Gnetum* has no fruit, and the fruit and seed of *Mezzettia* (Annonaceae) are exceedingly different; their primordia are similar.

#### The bitegmic anatropous seed

Ordinarily this seed is merely the regular enlargement and differentiation of the ovule. The integuments cover the seed except at the small part of the chalaza round which they are attached; raphe and antiraphe are almost equally long and the sides of the seed are identical. In certain cases, however, the enlargement is unequal; parts become displaced; the shape of the seed differs from that of the ovule, and the manner of differentiation may be varied (Fig. 1). Then in other cases, even in families, these alterations appear neotenually in the ovule which, again, prepares the shape of the seed. It is commonly assumed that these distinctions, particularly of shape, arise in the ovule and are conveyed into the seed, but the study of seeds suggests that the reverse has been the evolutionary procedure, e.g. Bixaceae–Cistaceae. As these changes happen independently in different families, there are many differences in detail and, as they are often intricate, it is necessary to consult the description and illustrations of individual cases. The present account is but a general outline.

#### Campylotropous seeds

In some species, if not genera, the anatropous ovule develops the antiraphe more extensively than the raphe, and the seed becomes curved or campylotropous, e.g. *Psidium* (Fig. 428). In Capripidae the seed is campylotropous and the transition to the neotenually campylotropous ovule can be seen in *Capparis* and *Crataeva* (Figs. 65, 69) with suborthotropous ovule. The alteration in shape is so gradual that it becomes impossible to employ accurately the various terms that have been suggested for the intermediate stages. Other examples will be found in Papaveraceae, Cactaceae, and Leguminosae.

#### Obcampylotropous seeds

This form (Fig. 1a) is the converse in which the raphe of the anatropous ovule enlarges more than the antiraphe. It occurs in *Bauhinia* (Fig. 322) and *Barklya* (Fig. 320), the seeds of which appear campylotropous in external view like those of

Papilionaceae. Their ally *Cercis* (Fig. 334) retains the anatropous seed. Such seeds occur also in Vitaceae.

#### Hilar seeds

In these (Fig. 1c) the greater part of the circumference of the seed, which is usually flattened, is made up of the extended hilum, e.g. *Mucuna* (Papilionaceae; Corner 1951). The ovule is campylotropous and undergoes this curious deformation as it enlarges into the seed; raphe and antiraphe remain short. Again various degrees of hilar development are found in other Papilionaceous genera, such as *Canavalia* and *Erythrina*, and a peculiarity of several lies in the development of most vascular bundles for the testa from the recurrent bundles of the hilum. In Meliaceae and other families with sessile arillate seeds there is often a short expansion of the hilum, e.g. *Aesculus*.

#### Pre-raphé seeds

In these the very short distance which usually separates the beginning of the raphe from the micropyle, and which causes the micropyle of most seeds to be adjacent to the hilum, is here lengthened (Fig. 1d). In consequence the micropyle is far removed from the hilum and what appears to be the raphe is actually the pre-raphé or the part between the micropyle and the hilum. This construction is characteristic of Connaraceae (Figs. 136–155); it is more or less pre-formed in the ovule, and the pre-raphé has a longitudinal vascular bundle similar to that of the raphe which is variously shortened. Many Connaraceous seeds seem to resemble Papilionaceous seeds until, as the first requirement of seed-study, the micropyle is found. The Meliaceous *Dysoxylon cauliflorum* has a kind of adnate pre-raphé which, if free of the placenta, would make the ovule and seed Connaraceous.

This kind of seed is clearly on the way to becoming orthotropous. Thus it figures in various Urticaceae which, as Conocephaloideae, are intermediate between the anatropous Moraceae and the typically orthotropous Urticaceae. Possibly it is the construction, also, in some hemi-anatropous Proteaceae. In Euphorbiaceae–Crotonoideae there may be a short pre-raphé with the hilum central on the adaxial side of the seed, e.g. *Croton laevifolium* (Fig. 227).

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### Orthotropous seeds

These are developed from orthotropous ovules and occur in several and diverse families such as Urticaceae, Proteaceae, Flacourtiaceae, Piperaceae, and Polygonaceae (Fig. 1*e*). They have been assumed to be primitive through analogy with gymnosperms, but the evidence of angiosperms points to derivation from the anatropous, either directly (as in *Chisocheton*, Meliaceae) or through the pre-raphe seeds as suborthotropous seeds for which Urticaceae, in no way primitive, is a fair example; it is true also of Proteaceae. It seems that the simple orthotropous shape is determined by the position of the ovule and the direction in which the ovarian loculus is extended by intercalary growth; the ovule-primordium ascends or descends directly in accordance, or fails to curve. The result is a radially symmetrical seed with the micropyle at the opposite end from the hilum. Post-chalazal vascular bundles may then permeate the testa, as in *Myrica*, but this genus is unitegmic and may have a pachychalazal seed. Orthotropous ovules do not occur in families which, according to the structure of the fruit or flower, are regarded as primitive, e.g. Magnoliales, Dilleniaceae, Mimosaceae, Theales, or Clusiaceae.

### The dorsal raphe

A deceptive form of the suspended and anatropous ovule is that with a dorsal raphe that curves over the adaxial micropyle. It distinguishes certain families as Lauraceae, Monimiaceae–Monimioideae, Buxaceae, Ebenaceae, and some genera of other families as Anacardiaceae, Celastraceae, Theaceae, and Proteaceae. The seed is suspended in the same manner. The relation of this ovule to the ordinary anatropous form with abaxial micropyle is uncertain.

### Perichalazal seeds

The ovule in this case appears to be anatropous but, internally, the inner integument is attached to the outer along the whole course of the vascular bundle which, in ovule and seed, extends round the periphery from funicle to micropyle (Fig. 1*g*). In place of the punctiform chalaza opposed to the micropyle, a perichalaza surrounds the nucellus as a hoop or band. Instead of an extended hilum for the periphery of the seed, as in *Macuna*, there is an extended chalaza; and the complexity of the seed is rendered apparent by the manner in which

intercalary growth of the ovule is prompted. Perichalazal construction distinguishes the ovule and seed in Annonaceae (Corner 1949*b*); in a few genera it is connected with the development of a middle integument. How frequently the construction may occur in other families is uncertain, e.g. *Hortonia* in Monimiaceae (Fig. 394) and Ebenaceae, but there is a partial perichalaza at the chalazal end of the seed of *Cryptocarya* (Lauraceae, Fig. 304), along the raphe in the seed of *Swietenia* (Meliaceae, Fig. 389), in more or less complete form in some species of *Aglaiia* and *Lansium* in Meliaceae and also in some seeds of Vitaceae (Figs. 616, 622, 630); yet the ovule in these cases is not perichalazal. In the Vitaceae genera the ovule first becomes obcampylotropous and then more or less perichalazal in the developing seed. It is possible that the intrusive raphe in Convolvulaceous seeds and the intrusive hilum or placenta of Apocynaceous seeds are cognate.

### Pachychalazal seeds

The chalaza of the perichalazal seed is extended in the median plane. In the pachychalazal seed it develops in all directions and builds by intercalary growth a new container for the endosperm and embryo (Fig. 1*h*). The wall of the container is single and is constructed by the multiplication of the cells where the two integuments adjoin the nucellus and chalaza; generally it becomes highly vascular from extensions of the chalazal vascular supply. The two integuments persist at the micropylar end of the seed in a more or less vestigial state. The ovule is anatropous and the resulting seed appears normal until its structure has been followed in development.

The expression 'pachychalazal' was introduced by Periasamy (1962*b*). The construction has been found in a variety of families and, as it has certainly been overlooked, it may occur in many others. Periasamy considered that it accompanied the ruminations of the endosperm, but the instance of Annonaceae and Myristicaceae with ruminant endosperm, yet neither pachychalazal, forbids such a generalization; there are also families with pachychalazal seeds without ruminant endosperm, e.g. Meliaceae, Sapindaceae. The construction is, in fact, another instance of that intercalary growth which is so disconcerting for morphologists because it supplies in place of the growth of free parts an intercalated sheet or tube that simulates the original, cf. the

syncarpous or intercalary ovary, the leaf-sheath, the pitchers of *Nepenthes*, and indeed the lamina of entire leaves. As a basipetal growth it is the antithesis of the primitive acropetal growth of dicotyledonous organs, and the pachychalaza appears as a polyphyletic advance in seed-construction.

Pachychalazal seeds have been found in Balsaminaceae, Flacourtiaceae, Lauraceae, Meliaceae, Ochnaceae, Rosaceae, Sapindaceae, Simarubaceae, Ebenaceae and Euphorbiaceae. They may occur in Anacardiaceae, Combretaceae, Icacinaceae, Polygonaceae, Proteaceae (*Macadamia*), Rhamnaceae, Apocynaceae and, indeed, in *Nelumbo*. In some of these the characters of the testa differentiate in the single coat of the pachychalaza, e.g. *Taraktogenos* (Flacourtiaceae, Figs. 277–281). In the arillate seeds of Meliaceae and Sapindaceae, the outer part of the pachychalaza may be fleshy like the arillar tissue while the inner part may have a sclerotic layer (Figs. 374, 501). These are the sarcotestal seeds which van der Pijl has confused with the truly sarcotestal seeds of Magnoliaceae, and of course they are not primitive.

In these pachychalazal seeds of Meliaceae the fibrous exotegmen, characteristic of the family, can be found in the free tegmen round the micropyle, but is absent from the wall of the pachychalaza, e.g. *Aphanamixis* (Figs. 379, 380). In some of these, moreover, the pachychalaza is partial and affects only the dilated hilar side of the seed, e.g. *Dysoxylon*; this is the case also in the Anacardiaceous *Campnosperma* (Fig. 13). By contrast, in *Taraktogenos* there is no trace of the fibrous exotegmen, which is distinctive of Flacourtiaceae, and the affinity of this genus and its allies with the rest of the family is not certain. The condition in Euphorbiaceae is also different because the pachychalaza affects only the tegmen, e.g. *Cleidion* (Fig. 222) and *Ricinus* (Fig. 248). Such Euphorbiaceous seeds have a typical testa, and the tegmen is covered both in its free and pachychalazal part with the exotegmic palisade distinctive of the family. A further complication in Euphorbiaceae is the need to distinguish the vascular tegmen from the vascular pachychalaza.

In the preceding examples the ovule is normally bitegmic; the pachychalaza develops after fertilization. In *Ochna* (Fig. 437) the ovule is already pachychalazal and the short vestigial integuments take no part in the formation of the seed-coat. This condition was described in detail for many

Rosaceae by Péchoutre (1902). It occurs in Tropaeolaceae, some Balsaminaceae, and in *Phytocrene* (Icacinaceae). It is the intermediate state to the unitegmic ovule and seed in which, it is said or assumed, the integuments have fused. There is no fusion but a substitution of the free growth of the integuments by a basal intercalary region with the thickness of both integuments. If, as in some Rosaceae and perhaps Icacinaceae, the combination is congenital with the inception of the integuments, there results the unitegmic seed. This seems to explain the unitegmic ovule of Limnathaceae in its relation to the pachychalazal ovules of Balsaminaceae and Tropaeolaceae. The knowledge of such seeds is slender. The single seed-coat, though it is not truly integumentary, may be described as testal, as will be explained in the next chapter.

Now it is doubtful if the vascular pachychalaza of *Ochna* or *Tropaeolum* represents the original construction of the free testa in the primitive bitegmic seeds of their families. The point is important because pachychalazal ovules may signify the origin of the massively unitegmic ovule of most sympetalous families (p. 50); their seeds generally lack the complications of the polypetalous.

#### Alate seeds

The wing of the seed is a local outgrowth of the testa or, in the unitegmic seed, of the seed-coat. It displays the local morphogenetic potentialities of the ovule for it may arise from different parts. But wings are also connected with the manner in which the ovary enlarges into the fruit and the consequent change in shape of the loculus. Fruit-factors must be even more varied than those which control the development of the seed, and they remain to be analysed. Their interest for the study of seeds lies in the relation between the primitively arillate seed and the alate as an intermediate derivative (Corner 1954; Forman 1965). The generalized and extensive growth of the arillate follicle or capsule seems firstly to become constrained in a way that flattens the seed, perhaps with additional crowding through increase in number of the ovules, and then it is further narrowed to make slits into which the wings may extend. They may be completely peripheral as in Bignoniaceae, or restricted to the raphe, chalaza, antiraphe, hilum (Vochoysiaceae), funicle, and even along the three angles of a plump seed (*Moringa*); the aril itself seems not to be involved but to disappear. *Catha* (Celastraceae),

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however, has an alate aril (Fig. 83). Various genera in one family have these differences. In Theaceae *Stewartia* (Fig. 592) is peripherally alate; *Gordonia* (Fig. 587) has a raphe-wing; and *Schima* (Fig. 589) is peripherally alate except for the extended hilum and pre-raphe. These facts are seldom co-ordinated into the generic character which, at the customary level of the pocket-lens, is unable to distinguish them and to relate them into evolutionary sequence.

Some alate seeds with the wing extended from the chalazal end of the raphe carry the vascular bundle of the raphe round the periphery of the wing, e.g. *Cratoxylon* (Fig. 292), and this loop may be retained as a vestige in diminutive seeds, e.g. *Tetracentron* and *Trochodendron* (Fig. 611). Yet, it is absent from such seeds as *Ixonanthes* (Fig. 299) and *Lagerstroemia* (Fig. 352). All these details render alate seeds among the more interesting.

**Pleurogrammatic seeds**

Most modifications of the ovule in the course of its development into the seed affect the hilum, the chalaza or the periphery. Few affect the sides, and these I call pleurogrammatic because they leave a lateral mark of some kind. The best known is that which I called the pleurogram in the Mimosoid seed, though in this case the expression *linea fissura* or *linea sutura* has precedence (see p. 163). The mark is an alteration in the surface of the seed where, possibly, raphe-antiraphe factors impinge on others arising on the sides of the growing seed. The Mimosoid *linea fissura* is a break in the construction of the exotestal palisade. The pleurogram of *Cassia* (Figs. 329-333) is caused by a difference in the palisade-cells themselves. The complicated pleurograms of many Cucurbitaceous seeds result from differences in the layering of the complex outer part of the testa (p. 112). The feature is generally rare and, thus, helpful in seed-identification. Its physiological basis is unknown.



### 3. Seed-coats

#### Testa and tegmen

To avoid the ambiguity that arises when the integuments of the ovule and seed are called by the same names, I refer to those of the ovule as the outer integument (o.i.) and the inner (i.i.); the product of o.i. then becomes the *testa*, that of i.i. the *tegmen*. Seeds with characteristic testa can be called *testal*, those with characteristic tegmen *tegmic*. The outer and inner epidermal layers of each integument become:

o.e. (o.i.), i.e. (o.i.), o.e. (i.i.) and i.e. (i.i.)

o.e. (testa), i.e. (testa), o.e. (tegmen), i.e. (tegmen).

It is easy to confuse the first line of symbols. They cannot be applied in the same way in other languages, and in the older reports on seeds o.i. would be i.e. (*integumentum externum*).

The middle layers are referred to as mesophyll (o.i., i.i., testa, or tegmen). The outer and inner hypodermal layers, which sometimes need to be distinguished, become o.h. and i.h.

The only possible confusion may be with the words bitegmic and unitegmic which refer to ovules or seeds with two integuments or one (p. 49).

#### Multiplicative integuments and overgrown seeds

In many ovules, especially those which become large seeds, the cells of both integuments divide after fertilization and form both more cells in a layer by anticlinal division and more cell-layers by periclinal division. Both methods of growth may occur or one or other may predominate, but finally the cells enlarge, become adult, and differentiate. The second method by periclinal division I call the *multiplicative*; it results in seeds with massive and, usually, complicated seed-coats, e.g. Magnoliaceae, Myristicaceae, Annonaceae, Clusiaceae, Leguminosae, Bombacaceae. The contrast is the non-multiplicative integument which may extend by anticlinal cell-divisions, but does not develop more

cell-layers. It produces the simpler seed and, eventually, the simplified seed in which the cells of the integuments merely enlarge and differentiate without further cell-division. Such small seeds have often a few large external cells which with thickened walls give the reticulate, punctate, or verrucose surface of the testa, e.g. Caryophyllaceae, Papaveraceae, Ranunculaceae, Gesneriaceae, Scrophulariaceae. In some ovules both integuments are multiplicative; in others either the outer or the inner is more or less non-multiplicative. These distinctions are important both for the accurate description of seeds and for their theoretical consideration. Multiplicative seeds occur in families acknowledged to be primitive and show from what complexity the small seeds of advanced families have been simplified neotenually. Seed-evolution has caused in the main loss of multiplication but also, as a diversion, an excess, and such seeds with excessive multiplication are what I have called overgrown seeds (Corner 1951).

The cell-layers of the seed-coats of the overgrown seeds multiply without tissue-differentiation. The seeds come to fill the loculus of the fruit as if they were tumours. They fail to differentiate the family-character of the seed-coats which, if they are not finally crushed by the enlarging endosperm or embryo, as in *Anisophyllea*, *Barringtonia*, *Mangifera*, *Persea* or *Arachis*, remain as a more or less thin-walled jacket round the seed. Overgrown seeds occur in a variety of families, especially those with drupes or nuts. In a way they are a nuisance because they often occur in critical genera of uncertain classification for which a definite structure of the seed-coats would be decisive, e.g. various Swartziaeae (Leguminosae) and *Irvingia*. Fagaceae and most Anacardiaceae seem to have overgrown seeds. It may be the case with Ochnaceae and Simarubaceae but in these families there is also the problem of the pachychalazal seed with its overgrowth. Research is needed into all these seeds by comparison

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with related genera, e.g. *Aesculus*, *Aldina*, *Avicennia*, *Arachis*, *Persea* and *Rhizophora*. Not only the smallest seeds are the most advanced but also the largest, as shown by *Orchis* and *Cocos*.

### Factors in the formation of seeds

The chief factors in the growth of the ovule-wall into the seed-coat may be summarized as follows.

- (1) Enlargement:
  - (a) By cell-division:
    - (i) periclinal, increasing the number of cell-layers,
    - (ii) anticlinal, increasing the number of cells per layer,
    - (iii) by a special meristematic layer of cells, usually epidermal or hypodermal.
  - (b) By cell-enlargement:
    - (i) uniform,
    - (ii) radial elongation to give a palisade-layer of prismatic cells with hexagonal facets,
    - (iii) tangential elongation to give tubular cells with stellate outline, or fibres parallel or transverse to the longitudinal axis of the seed.
- (2) Differentiation into tissue-layers:
  - (a) epidermal,
  - (b) chlorenchyma,
  - (c) aerenchyma,
  - (d) sclerenchyma or collenchyma, as the mechanical tissue,
  - (e) vascular bundles,
  - (f) chalazal elaboration.
- (3) Outgrowths:
  - (a) aril (in the general sense),
  - (b) wings,
  - (c) hairs.
- (4) Funicle:
  - (a) elongation,
  - (b) special developments (such as jaculators).

Multiplication of the cell-layers is often diffuse throughout the testal mesophyll, in some cases also in the tegmic, but a few families or genera are specialized in this respect and show that the process needs more careful investigation than has hitherto been given. Periclinal divisions of o.e. (o.i.) produce the firm outer layer of the sarcotesta of Magnoliaceae; those of o.e. (i.i.) make the layers of fibres in the tegmen of *Capparis*, but the fibres of Annonaceae result from diffuse divisions in the testal mesophyll. Periclinal divisions of o.h. (o.i.) make inwardly the ridges of firm tissue in the testa of Caricaceae. Similarly divisions of o.h. and i.h. (o.i.), perhaps also of i.e. (o.i.), make the massive mesophyll of *Calophyllum* (to 100 cells thick), in *Moringa* (40–50 cells thick), and in *Taraktogenos* (40–70 cells

thick). Localized periclinal divisions of i.h. (o.i.) make small ridges in the inner testal layer of *Averrhoa* (Oxalidaceae). Periclinal divisions of i.e. (o.i.) make the woody endotesta or Magnoliaceae, Rutaceae–Rutoideae, and Vitaceae. The most striking case is that of Cucurbitaceae in which, as is now well-established, the durable parts of the testa are made from fairly precise periclinal divisions of o.e. (o.i.); they result in three cell-layers which may be further multiplicative, each in its own manner (p. 113).

### Description of the seed-coats

Seeds may vary much in form, size, colour and arillar investment within a single large and manifold family, e.g. Clusiaceae, Myrtaceae, Rosaceae, Rutaceae, Sapindaceae, or Theaceae. It is the microscopic structure of the seed-coats which supplies the critical detail, and even such manifold families have a basic microscopic character. There is no *a priori* reason for this. It happens that the genera of a natural family have the same microscopic construction. Thus, the Magnoliaceous is not found in the Rosaceous or Leguminous, the Annonaceous is not Myristicaceous and the Tiliaceous is not Celastraceous. But Bombacaceae, Euphorbiaceae, Malvaceae, Sterculiaceae and Thymelaeaceae agree with Tiliaceae; Connaraceae, Flacourtiaceae, Meliaceae and Sapindaceae agree with Celastraceae; Lecythidaceae, Myrtaceae, and Rosaceae agree with Theaceae. By exploring the microscopic detail in a sample of genera from a family, one discovers this great and unexplained peculiarity of the angiosperm seed. If the structure were the same in all, the subject would not arise. Netolitzky demonstrated it but, probably for lack of conveniently brief and unambiguous notation, it has been neglected. As it is, the Magnolialean families have distinctive and complex seed-coats, of which none is so intricate as that of Myristicaceae. Advanced families with inferior ovary or sympetalous corolla have uniform and simplified seeds. Intermediate and, as it were, exploratory families display the variety that may reveal how the first turned into the advanced.

The distinctive character of the seed-coat lies in the position and structure of the main mechanical, thick-walled but not necessarily lignified, layer. It may be a palisade of radially elongate cells, a layer of fibres, or a layer of cuboid sclerotic cells. It may be one or more cells thick, but whether the