The Seeds of Dicotyledons

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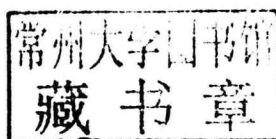
VOLUME 1

THE SEEDS OF
DICOTYLEDONS

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PREFACE

Open a book on flowering plants and find how little there is about their seeds! The subject is abstruse with little to commend it unless for the identification of the seeds of commerce but, pursued botanically, it is absorbing, penetrating and illuminating. From seeds came the plants which made fruits (angiosperms) and those which added flowers (anthophytes). Modern theories of the origin of these plants dwell on flowers. The fruit was the subject of the durian-theory. I turn now to their source in seeds.

When the late Professor Kwan Koriba came from Kyoto to Singapore in 1942 to direct the Botanical Gardens during the war, we turned in our confinement to the botany of trees. In 1945 when lies, starvation and chaos were around, we discovered this interest. We did not know of Netolitzky's book, which I have since studied and re-studied. I have pondered why such genius has passed unrecognized. His book on the seed-structure of angiosperms summarizes knowledge up till the end of 1923; no detail has escaped; the erudition is profound; and he came to the brink of the discovery that seed-structure should be the basis of the natural classification of flowering plants. Perhaps the terse descriptions and the sketchy illustrations failed to convey the message. Probably the weight of authority overwhelmed him. Engler, Wettstein, Warming, Lotsy, Hallier and other great exponents of classification failed to perceive the importance of the researches into seed-structure which French, German and Italian schools had begun to explore last century.

How to follow, for there is still an enormous amount of research to be undertaken, I have contemplated. A modern encyclopedia might be planned but parts exist, knowledge is inadequate, and patience would be unrewarded. It is possible to continue, however, where Netolitzky left off. I have built, then, on his text and borne in mind

five considerations. (1) There is great pleasure in discovering how a seed is made; it is the most elaborate part of the plant. (2) Families have characteristic seeds by which they may be related in orders. (3) Compared with monocotyledons, the orders of dicotyledons are unsatisfactory, but they have the greater variety of seed-structure. (4) Conviction calls for ample illustration. (5) A prototype must have existed for this variety if, as the intricacy of their seeds seems to prove, angiosperms were monophyletic.

The outcome is an account of the seed in those families of dicotyledons for which there is something known about the microscopic structure; the pocket-lens description is totally inadequate. It is illustrated mainly from my researches on tropical seeds, these being the less known. There is an attempt to prove the importance of microscopic structure in the ordinal classification of families, a consideration of the prototype, and a general introduction. The presentation has largely been reversed for the very reason that, in all systems of dicotyledonous classification, on which the botany of flowering plants depends, the grouping of families into orders is uncertain, even arbitrary and artificial, and for the most part unsatisfactory; most orders do not fit the precision in seed-structure which Netolitzky exposed. The family becomes of necessity the unit of description though some families are at fault. Descriptions have been assembled, therefore, in the last but major section of the work where the arrangement is alphabetical. To have assembled them by similarity in seed-structure, though ideal, would have been bewildering because there would be constant distraction through reference to an index; Vitaceae would come near Magnoliaceae with Winteraceae as far away as alphabetically; Convolvulaceae would follow Paeoniaceae; Proteaceae would accompany Papaveraceae; Cruciferae would not go with Capparidaceae, nor

Geraniaceae with Linaceae; thus one can appreciate Netolitzky's desistence. Moreover the time is not ripe. The seeds of many families are too little known or too problematic, e.g. Droseraceae. Before this main section there comes, therefore, the criticism of the customary orders. Here, with so much detail under review, it is necessary to pass continually to and fro between the orders and the families which they are supposed to embrace. I tried various methods to facilitate this perpetual motion and found none more satisfactory than the alphabetical; it does not burden the mind.

Lack of knowledge and of space have forced me to forgo an attempt to define generic differences. Even in such well-studied families as Rosaceae and Scrophulariaceae too few species have been examined, and where, as with Cruciferae, there is more certainty, the modern text can be cited.

Seed-studies begin with the ovule and end with germination. Flower and fruit pass in review. Ovary and pericarp must be sectioned. Vascular bundles must be traced. Lignification, suberization, cutinization and mucilaginization must be investigated, as well as cell-contents; all contribute to the hardening of the seed-coat which becomes its character. It is easy to stray into a multitude of problems from floral to physiological and biochemical evolution. I have left these in other hands and concentrated on the gross form of the seed, its cellular construction, vascular supply, and general lignification. The chemical characters may be as important but it soon becomes clear that, for the moribund tissues of the seed-coat, no ordinary stains or reagents are discriminatory enough in the common round of anatomy. A palisade so characteristic as the outer epidermis of the Leguminous seed or the hypodermis of the Convolvulaceous seed may or may not be lignified, and yet it is the family character. Probably the seed-coat of *Eucalyptus* has been examined in greatest detail but it affords no chemical satisfaction.

The first reaction will be to suppose that I have exaggerated the importance of seed-structure. With increasing familiarity it will be realized that seed-structure is a prime inheritance. Its histological detail expresses genetic character. The many variations cannot be ascribed to environmental selection. The profoundly different seeds of crucifer, mallow, speedwell and chenopodium arrive on the same waste ground. The profoundly different seeds of *Magnolia*, *Sterculia*, *Garcinia* and *Tabernaemontana* sprout together on the floor of the tropical forest. Drupes and nuts protect seeds with thick outer lignification, yet the intrinsic details of the seed-structure may be retained, e.g. *Canarium*, *Elaeocarpus*, *Grewia*, *Scaevola* and *Terminalia*. Magnoliaceous seeds are complicated, those of Sympetalae are simplified. The main trend in seed-evolution has been simplification by reduction in complexity and size, e.g. *Myristica* compared with *Begonia* or *Bellis*, as palm to orchid. Embryologists have established the advance from the bitegmic to the unitegmic ovule and from the crassinucellate to the tenuinucellate. Simplification becomes the theme, and from the whittling away of the Magnolialean complexity there emerges the idea of a complicated prototype. Palaeobotany would not be able to recognize a primitive dicotyledonous seed. In a recent paper (Boumann 1971) phyletic emphasis has been laid not so much on the final structure of the seed-coat as on the manner in which the integuments may arise in the ovule. Both matters are important but, since the final structure of the differentiated integument is so much more explicit, it cannot be discarded.

This work is also a vindication of that part of the durian-theory which discovered a primitive factor in the arillate seed. The conclusion has been derided through prejudice and ignorance, but what is laughed at commonly comes to be taken seriously. All along the evidence accumulates in favour of the primitive envelope; it is woven into these pages in the continual effort to show that classification without seed-structure is unsound and, consequently, our knowledge of the evolution of flowering plants.

It is a pleasure to thank the many botanists who have supplied me with material, in particular H.K. Airy Shaw, J. A. R. Anderson, P. S. Ashton and F. Hallé. On two short visits to Ceylon in 1968 and 1972, I was enabled to collect a large number of critical seeds through the kindness of Professor B. A. Abeywickrama and his colleagues Dr Dassanayake and Dr Balasubramaniam of the University of Ceylon; indeed this work, begun in Singapore, has matured in Ceylon. Many slides have been prepared for me in the last three years by P. Mohana Rao, of the University of Delhi. With E. C. Bate-Smith I have had numerous discussions on the biochemical classification of flowering plants; the subject is beyond most provincial schools of botany but of increasing concern to the chemist (Bate-Smith 1972).

Dr Gh Dihoru, of the Institut de Biologie 'Tr. Savulesiu', Bucharest, has kindly supplied me with the following notes on the life of Netolitzky; they are taken from the obituary by Popovici (1947). Netolitzky was born at Zwickau, Bohemia, on 1 October 1875 and died in Vienna on 5 January 1945. He was a student in the universities of Prague, Strassburg and Vienna where, as a junior assistant from 1 January 1896 to 31 August 1899, he took his doctorate in medicine in 1899. He moved to the University of Innsbruck, 1 November 1899 to 30 April 1904, then to the University of Graz, 1 May 1904 to 31 January 1910. From 14 February 1910 to 30 September 1912 he was an assistant in the chemistry of foodstuffs at the University of Cernauți. In 1912 he became an associate professor of the University and in 1919 was made Professor of Pharmacognosy and Plant Anatomy, and Director of the Institute of Plant Anatomy and Physiology. As pensioner in 1940, he entered a professorship at the University of Iati before he retired to Vienna in the capacity of Professor of Pharmaceutical Medicine. A profound knowledge of botany illuminates his writings.

E.J.H.C.

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1. 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

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 neotenically 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 Capparidaceae the seed is campylotropous and the transition to the neotenically 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-raphe 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-raphe 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-raphe 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-raphe 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-raphe with the hilum central on the adaxial side of the seed, e.g. *Croton laevifolium* (Fig. 227).

Orthotropous seeds

These are developed from orthotropous ovules and occur in several and diverse families such as Urticaceae, Proteaceae, Flacourtiaceae, Piperaceae, and Polygonaceae (Fig. 1e). 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. 1g). 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 *Aglaia* 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 Vitaceous 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. 1h). 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 (1962b). 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 ruminate endosperm, yet neither pachychalazal, forbids such a generalization; there are also families with pachychalazal seeds without rumination, 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 Limnanthaceae 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 (Vochysiaceae), 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),