

Chapter **15**

**Seed and Fruit  
Structure:**

*significance in seed conservation  
operations*



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### Summary

The purpose of this contribution is to draw seed conservationists' attention to the value of a basic appreciation of seed and fruit structure in their work. By way of revision for some, and introduction for others, it reviews the main morphological and structural features of seeds and fruits, their diversity and developmental origins. It then attempts to emphasise the significance of some of the features in seed conservation operations, by reference to their functions. For example, procedures aimed at removing physical dormancy imposed by the seed-coat, frequently involving some kind of disruption of the coat, may compromise its protective functions, with detrimental effects on subsequent germinability.

### Introduction

Packaging and dispersing their resting (in the great majority of cases) young sporophytes as seeds is the defining characteristic of Spermatophytes. The purpose of seeds is to ensure the dispersal and survival of embryos in more or less stressful environments, so as to maximise the chances of establishing at least one and hopefully many viable, reproducing offspring. In general, these functions are reflected in the major structural components of seeds. These consist of: an embryo, i.e., the next generation; food storage tissue, to provide nutrients for the growing embryo or seedling until it is fully autotrophic; and covering structures, which are mostly adapted to provide protection for the embryo and its food store and/or aid dispersal. Species vary enormously in the sizes and shapes (e.g., Harper *et al.*, 1970) and in the internal morphologies (Martin, 1946) of their 'seeds' (*sensu lato* – see later). This variation presumably results from diverse evolutionary pressures operating on a suite of seed developmental possibilities, which themselves may be phylogenetically constrained to a greater or lesser degree in different groups of plants. While the properties of the seeds of most species make it possible to conserve representative samples of plant populations effectively *ex situ* in seed (gene) banks, they have not evolved to suit the convenience of people wishing to store seeds in such banks! Indeed, it is possible to imagine and to cite actual instances (see later) where seed structural features may affect the efficiency of seed banking operations, especially where wild species are concerned. The authors believe strongly that a sound working knowledge of seed and fruit structure, its great diversity and relation to function is a valuable tool for seed bank personnel. It will help them to predict and overcome problems they may encounter in obtaining, processing and managing their collections, including:

- species' identification, and also of contaminants;
- estimation of maturity and optimal collecting time for maximum longevity;

- devising seed cleaning techniques that minimise potential damage to the valuable seeds; and
- the use of scarification and surgical techniques to remove certain types of dormancy.

At the very least, relatively routine and even tedious tasks are potentially more intellectually profitable, and thus enjoyable, by being set in the context of such knowledge.

In preparing this review, the authors acknowledge the good number of general and comparative accounts of seed and fruit structure already available in the literature; and refer readers to them, when more detail or clarity is required. These range from the appropriate chapters in general plant science (e.g., Raven *et al.*, 1999), or plant anatomy textbooks (e.g., Fahn, 1990; Rudall, 1992), to works wholly devoted to seed (Werker, 1997; Netolitzky, 1926; Corner, 1976) or fruit (Roth, 1977) anatomy. Jensen (1998) has compiled an extensive bibliography of pre-1990 published work containing information on seed (and indehiscent fruit) morphology, arranged by family. Due to the wealth of suitable, well illustrated published literature, and in order to save space, extensive illustrations are not provided in this chapter. Of the works on seed anatomy, Corner is concerned primarily with systematics; while Werker pays particular attention to functional aspects, perhaps more relevant in the present context. Boesewinkel and Bouman (1995) have also described seed structure from a functional viewpoint; and both this and their earlier review (Boesewinkel and Bouman, 1984) are excellent introductions to the subject. Ellis *et al.* (1985) gave an introduction to seed morphology and development, aimed specifically at seed conservationists, together with a useful glossary. Despite the existence of these and other works, for the sake of completeness we begin with an overview of the main features of seed and fruit structure and development.

## Seed and Fruit Structures/Developmental Origins

In the strict botanical sense, a true seed develops from a **fertilised ovule**, in both Gymnosperms and Angiosperms, which together make up the Spermatophytes, or seed plants. The word ‘seed’ is frequently used in scientific, and almost universally in popular communication in its broad, functional sense. That includes also those sexual ‘propagules’ or ‘dispersules’ that include some tissues or structures derived from the post-fertilisation development of the **ovary** (part of the carpel), as opposed to just the ovule, and sometimes even other floral structures; i.e., they are actually fruits, or so-called false fruits (see below). Gymnosperm (literally ‘naked seed’) ovules are

not borne within carpels, rather they are borne on ovuliferous scales within the female (ovulate) cone. So, their seeds cannot have fruit tissue associated with them, though a few, such as *Taxus* have appendages (**aril** in this case - see later) that mimic fleshy fruit, thus a 'false' fruit; and in *Juniperus* the scales themselves become fleshy, almost completely enveloping the seeds at maturity.

A typical ovule consists of a fleshy megasporangium, known as the **nucellus**, retaining a single functional megaspore (haploid, usually designated female), surrounded by one or two layers of tissue, the **integuments**. These envelop the megasporangium completely, except for an opening at its apex, the **micropyle**, which allows the entry of microspores, or pollen grains – see Figure 15.1.

### 1. Gymnosperms

In gymnosperms, such as *Pinus*, the scales of the female cone grow together following pollination in the spring, to help protect the developing ovules. Meanwhile, on contact with the nucellus, the pollen grain (shed from the male cones and spread on the wind) germinates to form a pollen tube. It is not until about one month after this that meiosis actually takes place in the megasporangium, to give four megaspores, only one of which (the functional megaspore) survives. Development of the megagametophyte (female gametophyte, haploid) is slow, until about fifteen months after pollination, when two or three archegonia (typical female sex organ of most gymnosperms and lower plants, producing female gametes) are formed at its micropylar end and it is ready for fertilisation. Meanwhile, growth and maturation of the germinating pollen grain (male gametophyte) has been equally slow. Before fertilisation it produces two sperm, and when the pollen tube reaches the egg cell of an archegonium, one sperm nucleus joins with the egg nucleus and the other degenerates. Usually the eggs of all archegonia are fertilised, but only one develops fully; however, 3–4 percent of pine seeds can be polyembryonic, giving rise to multiple seedlings on germination. At the same time as the embryo develops, the integument develops into a **seed coat**, its middle layer becoming sclerified. While *Pinus* seeds in particular take a long time to develop, and are not mature until the autumn of the second year following pollination, other conifers are quicker and complete their seed development within one year. At maturity, the conifer seed is a genetic mixture of two different diploid sporophyte generations and one haploid gametophyte. The seed coat and the papery remains of the nucellus represent the maternal sporophyte, surrounding the female gametophyte (megagametophyte), which has developed to take on the role of food storage tissue. More or less embedded in the female gametophyte is the diploid **embryo**, which has a number, frequently as many as eight, **cotyledons** (first leaves). Other gymnosperms have broadly similar life cycles, with variations on the same basic theme. For example, in *Ginkgo*, whose ovules ripen to produce fleshy-coated, evil-smelling seeds, fertilisation may not occur in the ovules until they have

been shed from the parent tree. In *Ephedra* and *Gnetum* (Gnetophytes), among several angiosperm-like features, both the sperms are involved in fertilisation ('double fertilisation'), but in this case they form extra embryos, rather than endosperm (see below).

## 2. Angiosperms

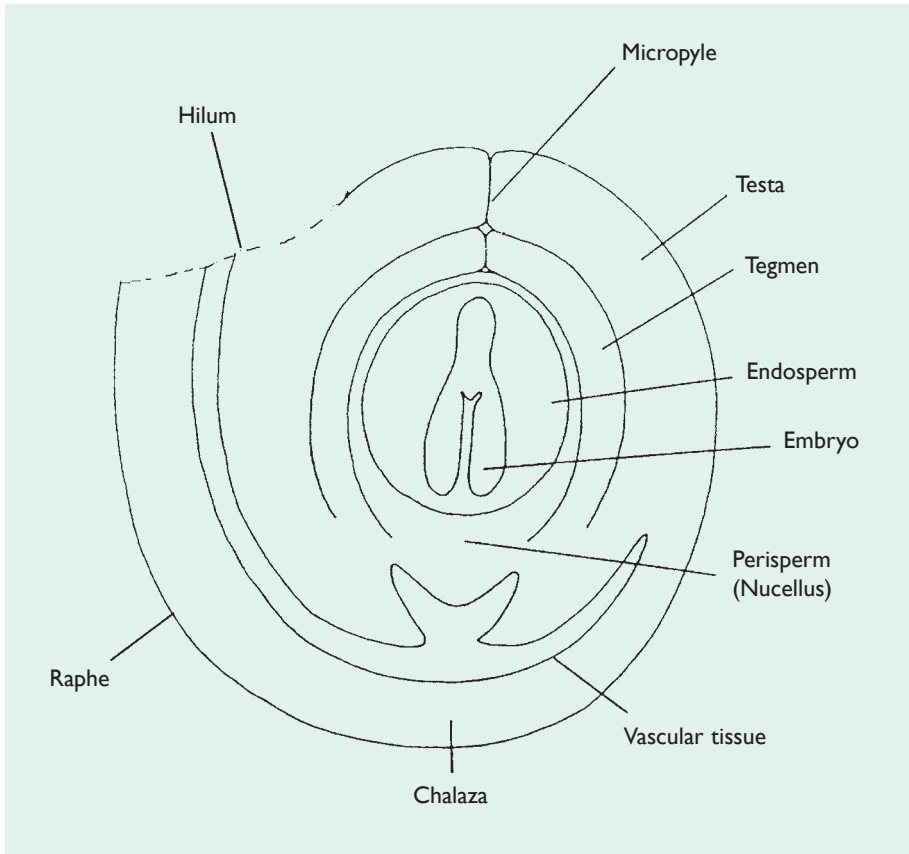
In angiosperms, the ovules are borne within **ovaries** (c.f. the naked ovules of gymnosperms), which form part of the specialised female floral structures, the **carpels**. Ovaries have one or more **locules** (cavities), where the ovules are borne. The ovule-bearing regions of the ovary wall, or **placentae** may give rise to one to many ovules, depending on species. An ovule is borne on a stalk known as a **funiculus**, and consists of a nucellus (megasporeangium), like the gymnosperms, completely enveloped, except at the micropyle, by one or two integuments. Again like gymnosperms, meiosis gives rise to four haploid megaspores, only one of which usually survives – the functional megaspore. This grows at the expense of the nucellus and undergoes three rounds of mitosis. After wall formation the typical mature female gametophyte, or **embryo sac** consists of eight nuclei in seven cells. At the micropylar end three cells comprise the egg apparatus – one large **egg cell** and two **synergids**. At the opposite, or **chalazal** end are the three **antipodals**; and in between is a single cell containing the two **polar nuclei**.

Pollination in angiosperms results in pollen grains being deposited on the stigma, the receptive organ of the carpel. Each grain germinates to produce a pollen tube, which grows through the tissue of the style to the ovary, and then via the micropyle into the embryo sac, into which the two sperm nuclei are discharged. The synergid nuclei may have a role, not yet properly understood, in that discharge. One of the sperm nuclei fuses with the egg nucleus to form the diploid ( $2n$ ) **zygote**, which divides and develops to form the new **embryo**. The whole process of pollen tube growth and fertilisation takes just a few minutes or hours in angiosperms, compared with weeks in Gymnosperms (except *Ephedra*, where it is only a few hours). Rather than degenerating, as it does in all gymnosperms except *Ephedra* and *Gnetum*, the second nucleus migrates to the central cell, where it unites with the two polar nuclei there, to form a triploid ( $3n$ ) (with a few exceptions, e.g., *Lilium*, where it is  $5n$ ) primary **endosperm** nucleus. This '**double fertilisation**' is characteristic of the angiosperms; though a rudimentary double fertilisation occurs in *Ephedra* and *Gnetum*, resulting in a diploid product in those cases (an extra embryo – see above).

Following double fertilisation, the processes leading to the development of the seed and fruit begin:

- the primary endosperm nucleus divides to form the endosperm - triploid tissue, with genetic contributions in the ratio 2:1, maternal to paternal;

- the zygote develops into an embryo, or young sporophyte - diploid, with maternal and paternal genetic contributions equal (though plastid and mitochondrial inheritance is maternal);
- the seed coat develops from the integument(s); while the ovary wall and other related structures develop into the fruit – both seed coat and fruit wall tissues are genetically wholly maternal.



**Figure 15.1** Diagrammatic representation of the main features of a dicotyledonous seed in longitudinal section – derived from an anatropous ovule in this case. Re-drawn after Boesewinkel and Bouman (1984).

### 3. Fruits and their Diversity

The colossal diversity of fruit size, shape, consistency, anatomy and method of opening has led botanists to try to classify them into a certain number of types. Most of these classifications are at least somewhat artificial, depending on whether the author has approached the task from a standpoint of developmental purity (homology – for which good data are often lacking), from one of function, or a blend of the two. Difficulty arises because the classifications attempt to deal with variation that is not only great, but also frequently continuous in reality. Moreover, the results of convergent evolution often mean that functionally similar fruit structures may be derived from either similar or different floral structures in different angiosperm lineages. An additional complication is that post-fertilisation development often includes non-carpel tissue, floral or vegetative, in which case the resulting organs are commonly described as ‘false’ or ‘accessory’ fruits, as mentioned above. These factors have led to an ever more complex and potentially confusing nomenclature, in which synonymy abounds. Spjut (1994) surveyed the existing schemes and applied a valuable, botanically rigorous and logical synthesis that describes no less than ninety-five distinct types. Regrettably, that complexity is probably the reason for the apparently slow take-up of his classification, and is likely to remain a barrier among applied users, including seed bank personnel. There is a need for a ‘read-across’ between Spjut’s rigorous and botanically correct system, and one of the simpler, mainly functional, general-purpose schemes.

The great diversity of fruit morphology and its underlying anatomy results from the many possible ways in which the ovary wall or **pericarp** can develop after fertilisation in different species. The ovary wall usually consists of three distinct layers, with the innermost **endocarp** surrounded successively by the **mesocarp** and **exocarp**; and it is the growth or atrophy of any or all of these tissue layers (especially the first two) that give mature fruits their particular characteristics.

In a basic general-purpose classification, mature fruits belong to one of four main types – fleshy or dry, dehiscent or indehiscent. Put simply, dry fruits usually result from the limited development or atrophy of the mesocarp, which eventually dries out, along with the rest of the pericarp. If, by contrast, the mesocarp cells divide more or less extensively, frequently swelling to contain (usually) sugary juice or sap, the result is a fleshy fruit. Whether a fruit is dehiscent or not usually depends on the development of one or more dehiscence zones with specialised anatomy in the pericarp tissue. These are activated by drying, during late fruit maturation; and the overwhelming majority of dehiscent fruits are regarded as dry. Roth (1977) regards both pomegranate (*Punica granatum* L.) and nutmeg (*Myristica fragrans* Houtt.) to be examples of dehiscent fleshy fruits (capsules). However, in *Punica* at least, the fruit tissue is rather more pithy, becoming sclerotic and the well known juicy material is actually composed of the sarcotestas (fleshy seedcoats, see later) of the many seeds. The dehiscent capsule of *Aesculus hippocastanum* Linn. is similarly fleshy, though pithy rather than juicy.

The simplest type of indehiscent fleshy fruit is the **berry** (or *bacca*), derived from a single carpel and containing one or many seeds. Classic examples include the grape (*Vitis vinifera* L.) and the tomato (*Lycopersicon esculentum* Mill.). Variations on this basic type include the **hesperidium**, typical of the citrus fruits (*Rutaceae*), where the exocarp forms a tough, oily rind, with a pithy mesocarp and the endocarp cells enlarged to form juice vesicles. Although the **pepo** of the *Cucurbitaceae* is regarded as a kind of berry, again with a thick rind, it is strictly an accessory fruit, because it is from an inferior ovary and includes a small proportion of the extra-carpellary tissue. Exocarps are frequently brightly coloured when ripe, to attract animal dispersers; and the associated colour changes may be indicators of the maturity of the seeds inside.

Where the endocarp develops into a thick, hard layer around a single (usually) seed (stone, or pyrene), the fruit is a **drupe**. In this case, the true seed coat is usually much reduced or non-existent at maturity, its protective function (against crushing by dispersers/predators) having been transferred through evolution to the stony endocarp. The mesocarp is frequently fleshy, as in *Prunus* L. (peach, cherry, almond) and *Olea* L., but not always. In *Cocos* L. and other *Arecaceae* the mesocarp is fibrous rather than fleshy when ripe. Drupes are usually indehiscent, but not always so; those of some species dehisce sooner or later to expose the pyrenes, e.g., *Carya* Nutt. and some species of *Rhamnus* L. They may also occur in aggregates, e.g., *Rubus* L., where each drupelet is derived from a single distinct carpel in the same gynoeceum (the female floral parts, collectively), clustered on the receptacle. Again in the *Rosaceae*, and typified by *Malus* Mill. and *Pyrus* L., the **pome** exhibits endocarps that are leathery rather than stony, enclosing true seeds with well developed seedcoats. The greater part of the fleshy tissue actually comes from post-fertilisation development of the receptacle, which is contiguous with and barely distinguishable from the mesocarp - thus they are false fruits, being derived from inferior ovaries.

Rather than just the endocarp, the whole of the pericarp may become thickened and sclerified to protect the seed inside (kernel), in which case the dry, indehiscent fruit is a **nut** (*nux*), e.g., *Quercus* L., *Corylus* L. and *Dipterocarpus* C.F. Gaertn.

The simple case of a dry, indehiscent fruit, where the pericarp is not especially thickened or woody, but fits closely around the seed, is the **achene**. Examples include: *Carex* L.; *Ceratophyllum* L.; *Clematis* L.; *Ranunculus* L.; and *Rumex* L. Where the fruit is from an inferior ovary and includes non-carpel tissue, it is known as a **cypsela**, typical of the *Asteraceae*, such as *Lactuca* L. and *Helianthus* L.; and the more or less well-developed pappus of hairs involved in wind dispersal is derived from the calyx of each floret. In the *Rosaceae* there are a number of examples of achenes being associated with fleshy, extra-carpellary tissue in various false fruits: e.g., achenes are enclosed in a fleshy hypanthium (cup-shaped extra-carpellary tissue, usually receptacular in origin) in *Rosa* L.;

while in *Fragaria* L. they are borne on the surface of a swollen receptacle. A small, indehiscent, dry fruit with a thin wall that is loose and free from the single seed is known as an **utricle** (i.e., bladder-like), e.g., *Chenopodium* L. and *Lemna* L. Where the seed coat is so reduced as to be barely recognisable at maturity, and the pericarp is more or less fused to the seed, the special term **caryopsis** is used, typified by the *Poaceae*. It should be remembered that the natural dispersal units of many grass species include the more or less tightly attached paleas and lemmas. Thus they could be regarded as false fruits. Where the pericarp of a dry indehiscent fruit, usually containing a single seed (rarely two) develops into a wing, for wind dispersal, the fruit is known as a **samara**, e.g., *Fraxinus* L., *Ailanthus* Desf. and *Casuarina* L.

The simplest form of dehiscent fruit is the **follicle**, which is usually dry, but is fleshy or tends to fleshy in a few species. It develops from a single carpel that opens at maturity along a single, longitudinal, usually ventral suture, e.g., *Asclepias* L., *Caltha* L. and *Magnolia* L.

A dry fruit from a single carpel that dehisces (often explosively) along two longitudinal sutures (dorsal and ventral) is a **legume** (or pod), typical of many, but not all *Fabaceae*. Those having indehiscent pods include *Arachis* L. and some species of both *Cassia* L. and *Medicago* L. (*Adansonia* L. [*Bombacaceae*] and *Kigelia* DC. [*Bignoniaceae*] are examples of non-fabaceous genera regarded as having indehiscent pods). In some *Fabaceae*, the dry fruit from a single carpel breaks transversely into one-seeded segments, e.g., *Desmodium* Desv., *Sophora* L., *Ornithopus* L. and *Hippocrepis* L., and is called a **lomentum**.

Superficially like the legume, and typical of the *Brassicaceae*, is the **siliqua** (including silicle). Rather than from a single carpel, the siliqua is derived from a two-carpellate gynoecium. It dehisces on maturation drying, with the two halves of the fruit splitting away from a persistent partition or membrane (replum), from which the seeds become detached.

The general case of a dry (rarely fleshy) dehiscent fruit derived from a two- to many-carpellate gynoecium is the **capsule**. Capsules open in a variety of ways to release the seeds: longitudinal splits, e.g., *Iris* L.; a transverse or circumscissile split, releasing a cap (fruit known as a **pyxidium** in this case), e.g., *Plantago* L.; and the development of pores, e.g., *Papaver* L.

A two- to many-carpellate gynoecium may give rise to a dry, or rarely fleshy fruit that splits into one- (or few-) seeded segments at maturity and is known as a **schizocarp**. The individual segments (dispersal units) are known as **mericarps**; and they may be subdivided into 'samara-like', e.g., *Acer* L. (*Sapindaceae*), 'achene-like', e.g., most *Apiaceae*, and 'nut-like' (nutlets) or 'drupe-like' (drupelets), e.g., most *Lamiaceae*.

## Structures of the Mature Angiosperm Seed:

### *their Significance in Seed Banking Operations*

We now return to consideration of the three major structural-functional components of mature seeds, especially with respect to managing living seed collections.

#### 1. Covering Structures

To support the early stages of germination and growth of the young sporophyte, seeds are generally equipped with a large amount of nutrients. To protect its precious contents against mechanical and biological injury, a covering, consisting of a greater or lesser amount of mechanical tissue, usually covers the seed. This covering can either be derived from any layer of the integuments, or (in the case of indehiscent fruits) from the fruit wall (usually the endocarp). Where the seeds also constitute the dispersal unit, however, the primary covering structure is the **seed coat**, which is derived from the two integuments (or the single integument). The seed coat can be one or many cell layers thick with the mechanical layer potentially derived from any layer of the integument(s). According to Corner (1976), in the ripe seed, the derivatives of the outer integument form the '**testa**' and those of the inner integument form the '**tegmen**' (see Figure 15.1). The product of the single integument of unitegmic ovules is - somewhat inconsistently - also referred to as the '**testa**'. In accordance with that, seeds with a characteristic testa are called '**testal**', those with a characteristic tegmen '**tegmic**'. The most distinctive character of the seed coat lies in the position and structure of the main mechanical layer, which is composed of thick-walled, but not necessarily lignified cells. This mechanical layer can be one or more cells thick and consists of radially elongate palisades, horizontally elongate fibres or cuboid cells, with either evenly or unevenly thickened walls.

With the distinction between testal and tegmic seeds, Corner (1976) invented a simple descriptive system, based on the position of the mechanical layer, as shown in Table 15.1; e.g., exotestal seeds have the mechanical layer formed by the outer epidermis of the outer integument, and so on. The mesotegmic construction is rare and found in conjunction with either an exotegmen or an endotegmen. Most angiosperm families have one predominant mechanical layer and fall within one of these categories, but some have a double or even treble character, e.g., *Myristicaceae* and *Cucurbitaceae*, which makes it sometimes difficult to apply Corner's categories (Boesewinkel and Bouman, 1984). The Monocotyledons show much less diversity in this respect than Dicotyledons, with few exotestal and endotestal seeds, and few, if any, tegmic ones.

As well as producing a layer or layers of thick-walled cells, which might be impregnated with lignin, cutin and suberin, the protective function of the

**Table 15.1 Seed types according to Corner (1976), based on the position of the mechanical layer**

Layer with mechanical tissue	Integument	
	Inner (Tegmen)	Outer (Testa)
<b>Outer epidermis</b>	<b>EXOTEGMIC</b> e.g., <i>Malvaceae</i> , <i>Euphorbiaceae</i> , <i>Linaceae</i> , <i>Celastraceae</i> , <i>Clusiaceae</i>	<b>EXOTESTAL</b> e.g., <i>Ranunculaceae</i> , <i>Rhamnaceae</i> , <i>Fabaceae</i>
<b>Middle layer(s)</b>	<b>MESOTEGMIC</b> construction rare, found in conjunction with an exotegmen or an endotegmen	<b>MESOTESTAL</b> e.g., <i>Paeoniaceae</i> , <i>Myrtaceae</i> , <i>Rosaceae</i> , <i>Theaceae</i>
<b>Inner epidermis</b>	<b>ENDOTEGMIC</b> e.g., <i>Piperaceae</i> , <i>Saururaceae</i> , <i>Berberidaceae</i>	<b>ENDOTESTAL</b> e.g., <i>Myristicaceae</i> , <i>Dilleniaceae</i> , <i>Brassicaceae</i>

seed coat may also be achieved, or enhanced by cell layers becoming compressed and hardened. In addition, cell lumina may be filled with toxic compounds, such as phenolics, which help deter predators. A special class of these phenolic substances are the dark-coloured tannins, and their derivatives such as quinones. They are very common in seed coats, especially in the walls and/or the lumen of the innermost epidermis, which they then stain conspicuously amber-brown. However, up until the last stage of development, these substances generally appear colourless and can therefore serve as an important indicator of seed maturity (Werker, 1997). Phenolics like tannin benefit the seed through the cross-linking of polysaccharides, which leads to increased wall rigidity and resistance to microorganisms.

In the case of indehiscent fruits, especially drupaceous ones (see above) the protective function of the seed is transferred to the ovary wall or parts of it. In these cases the mechanical tissues no longer develop in the seed coats, which appear largely undifferentiated (e.g., *Anacardiaceae*, *Apiaceae*, *Cornaceae*, *Fagaceae*, *Juglandaceae*, *Sapindaceae* and *Urticaceae*). Similarly undifferentiated or degenerated seed coats may also occur in anemochorous dust seeds of dehiscent fruits, e.g., in *Orchidaceae* where the seed coat consists of a single layer of thin-walled transparent cells originating from the exotesta (Werker, 1997).

In some rare and extreme cases, the seed coat might be entirely absent. Ategmic ovules, for example, never develop any integuments in the first place, or they are much reduced. Such ovules occur in five dicotyledonous families, four of which

are parasitic (*Santalaceae*, *Viscaceae*, *Loranthaceae* and *Balanophoraceae*). A second possibility of a total loss of a seed coat is that the integuments are totally absorbed during seed development, as in some *Apocynaceae*, *Menispermaceae* and *Rubiaceae* (Werker, 1997).

Apart from its mechanical function, the seed coat can also develop structures assisting the dispersal of the seed. For example, the testa or the outer part of it can form a juicy or pulpy edible tissue called a **sarcotesta**, that is usually brightly coloured and attracts birds and other animals. Such sarcotestal seeds are found in 17 divergent families of both Dicotyledons and Monocotyledons, for example in *Magnoliaceae*, *Annonaceae*, *Cucurbitaceae*, *Euphorbiaceae*, *Flacourtiaceae*, *Meliaceae*, *Liliaceae* and *Palmae* (Werker, 1997). Sarcotestal seeds have the same function as a berry or a drupe and are usually dispersed by endozoochory. With the fleshy part on the outside, the inner layers of the seed coat will always still provide mechanical protection for the endosperm and the embryo.

In other cases, some part of the ovule or funicle proliferates after fertilisation to produce a pulpy structure, which can invest part or all of the seed. Such a structure is commonly called an **aril**. Arils or aril-like appendages may grow from specific parts of the seed surface, e.g., the raphe, the chalaza, the exostome (i.e., the micropylar opening of the outer integument), or the funicle. More often, they arise from a combination of such locations; and then they are then termed 'complex arils' (Kapil *et al.*, 1980). One well-known example of an aril is the exostome aril, also called the **caruncle**, of many members of the *Euphorbiaceae*. It is usually rich in oil, when it is known alternatively as an **elaiosome**, to attract ants for dispersal. Similar elaiosomes may be formed by the chalaza, the raphe or the funicle (Bresinsky, 1963).

While fleshy arils are indicators of zoochory, anemochorous seeds often have wings (e.g., some *Cucurbitaceae*, *Ranunculaceae*). Wings can also be formed by the fruit, i.e., the ovary and/or other parts of the flower, e.g., in *Acer* L., *Dipterocarpus* C.F.Gaertn. However, in contrast to the fruit wing, the seed wing is rarely provided with vascular bundles. Corner (1976) describes wings as follows: "The wing of the seed is a local outgrowth of the testa or, in the unitegmic seed, of the seed coat.... They may be completely peripheral as in *Bigoniaceae*, or restricted to the raphe, chalaza, antiraphe, hilum, funicle, and even along the three angles of a plump seed (*Moringa* Adans.)."

Another indicator of anemochory is the presence of hairs on seeds, although they may relate to other dispersal methods, such as the enlargement of the surface for hydrochory, or epizoochory (adhesion to animals by hooked hairs). Seeds can be entirely covered in hairs (e.g., *Gossypium* L.), or show one- or two-sided tufts (so-called 'coma', e.g., in *Apocynaceae*) and crowns of hairs (Kapil *et al.*, 1980).

### 1.1. Functional aspects of the seed coat (*sensu lato*)

Generally, seeds having only weak mechanical protection lose their viability faster in the field than those that are heavily protected. Apart from protection against mechanical and biological damage, the seed coat can also assist the dispersal of the seed (see below). Furthermore, some properties of the seed coat can strongly influence the longevity and germinability of a seed. Water impermeable seed coats, as found in many *Fabaceae* and *Malvaceae*, help to retain a low moisture content in the seeds, even against high external humidity and therefore maintain seed viability for much longer periods of time. The hard-coated seeds of *Ipomoea batatas* (L.) Lam. (*Convolvulaceae*), for example, can keep their germinability for more than 20 years. *Canna* L. seeds have proved to remain viable even after 6,000 years and seeds of the sacred lotus, *Nelumbo nucifera* Gaertn., which were about 1,000 years old, germinated only a few days after their seed coats were broken. However, the impermeability of the seed coat is not an absolute condition for seed longevity. Seeds of many *Poaceae* and *Chenopodiaceae* species, to name but two families, have high longevity, despite having permeable coats (Werker, 1997; Thompson *et al.*, 1997).

The role of the seed coat in seed longevity is diverse and changes throughout the life-span of the seed. During seed development, the integument(s), i.e., the developing seed coat, can:

- a) act as a pathway for transport and conversion of amino acids and sugars from the pericarp into the embryo sac, as well as using these compounds in its own development;
- b) accumulate reserve materials and serve as a temporary reserve tissue;
- c) assist in gas exchange;
- d) supply enzymes for digestion of the seed coat's own reserve materials;
- e) probably supply growth substances inwards to the growing embryo and outward to maternal organs;
- f) sometimes aid photosynthesis; and
- g) protect embryo and endosperm against desiccation and mechanical injury.

In the mature seed, the seed coat:

- a) provides protection of the mature embryo against desiccation and physical and biological damage;
- b) sometimes develops special structures assisting dispersal (e.g., sarcotesta, wings, etc.);

- c) acts as a regulator of water uptake - in some species it maintains seed dormancy by preventing water absorption and/or gaseous exchange (see below, and Baskin and Baskin, 2003 - Chapter 28); in other species, with permeable seed coats it may prevent rapid, uncontrolled water uptake and the risk of embryo damage or death through imbibition injury (see below); and
- d) in a few cases, serves as a storage tissue for nutrients.

### 1.2. Seed coat-imposed dormancy

Seed coat-imposed dormancy falls under the category of physical dormancy, which is discussed elsewhere in this volume (Baskin and Baskin, 2003 - Chapter 28). In the following, we therefore only briefly point out the specific role of the seed coat in dormancy. Uptake of water by the seed is a critical factor for germination, and the anatomy of the seed coat, especially the distribution of cuticles, sclerenchymatic tissue and vascular bundles, can play an important role. As well as interfering with the water uptake and gas exchange, the seed coat can inhibit germination by posing a mechanical restraint against radicle protrusion, and it can either prevent the exit of germination inhibitors from the embryo or it can supply germination inhibitors to the embryo. In many *Fabaceae* for example, interference with water uptake is probably the only factor involved. Often, however, the situation is more complex and the prevention of germination is due to more than one of these effects operating simultaneously. For example, a hard seed coat (or the endocarp) always offers mechanical resistance, which must be overcome by the embryo exerting a minimum force, or by enzymatic degradation of the restraining tissue. Both can be prevented by the presence of inhibitors held in the embryo by the impermeability of the seed coat or by inhibitors supplied by the seed coat (or endocarp) and can only be overcome in the presence of oxygen. This shows how several of the possible constraints might act at the same time to keep the seed in a dormant state (Bewley and Black, 1994).

Impermeability of the seed coat to water and gas is reflected in its anatomical structure. There must be one or more layers of very tightly packed cells with no pores, intercellular spaces or stomata between them and water-repellent materials either in or on their cell walls. In a number of families of both Dicotyledons and Monocotyledons, such as *Fabaceae*, *Malvaceae*, *Convolvulaceae*, *Convallariaceae*, *Rosaceae*, *Rhamnaceae*, and *Cannaceae*, a layer of Malpighian cells is often responsible for impermeability. It can be of different origin (e.g., exotesta in *Fabaceae*, exotegmen in *Malvaceae*). Within the impermeable layer, various specific cell zones have been suggested as being responsible for impermeability of the seed coat in various species, especially in Malpighian cells (Werker, 1997):

- a) Waxy layer over the outermost cell layer.
- b) Cuticle.
- c) Pectins.

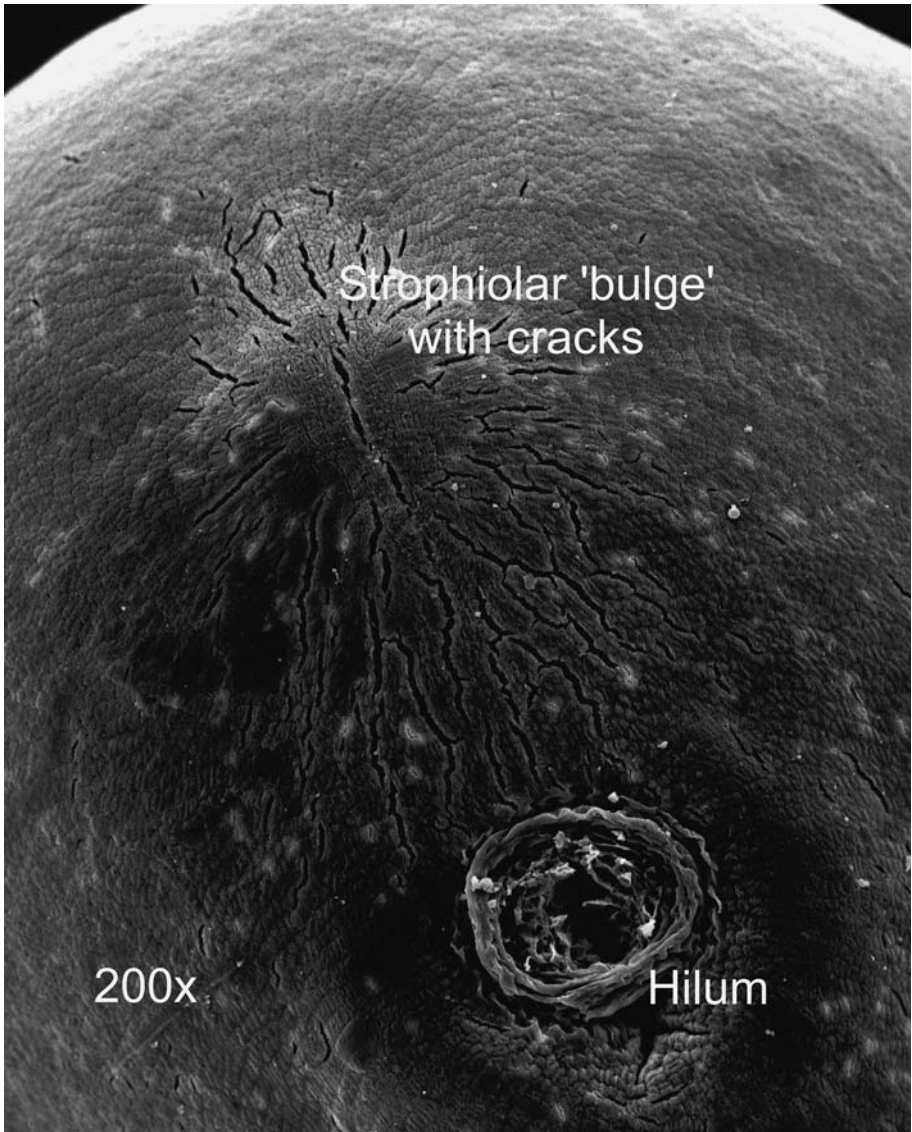
- d) The zone of light line of Malpighian cells. A light line, however, is found in the Malpighian layer of both, permeable and impermeable seeds.
- e) Changes of the micellar structure of cellulose, which occur during dehydration. This is an irreversible process manifested by a change in the swelling potential of gels.
- f) Contraction of the palisade cells as a whole on desiccation.
- g) Water repellent substances in the cell walls such as cutin, suberin, lignin, callose, phenols and quinones.

In some species of *Fabaceae* at least, it is thought that the region of the seed coat associated with the lens, or strophiole is one of comparative weakness, pre-programmed during development. It seems that physical stresses, probably caused by high temperatures or temperature fluctuations in the field, eventually cause cracks to form in the otherwise water-impermeable coat, allowing imbibition and germination. Such cracking has been induced in the laboratory by both immersion of seeds in liquid nitrogen (Pritchard *et al.*, 1988) and by high speed shaking of seeds in glass vessels to cause repeated impaction (also referred to as percussion) against the walls of the vessel (see Figure 15.2)

### 1.3. Damage to the seed coat

Whether it consists only of true seed coat, or includes mature fruit wall (achene etc), the embryo's covering envelope has a strongly protective role, and any disruption of its integrity is likely to compromise the viability and survival of the seed. Seed coat damage is possible in both seed cleaning and in germination testing. In seed cleaning, the damage is most likely to be unintentional, as the result of over-zealous rubbing etc; or, it may even result from the intentional removal of structures such as wings (to reduce collection volume, for instance), hairs, arils, paleas and lemmas, etc. As a general rule, the removal of any structure from the natural dispersal unit, especially when it is integral with it, or tightly attached to it, should be treated with caution and preferably avoided. For example, while the paleas and lemmas that form part of the dispersal unit in many grass species may sometimes have a role in dormancy, these covering structures probably also have a protective function. Any temptation to remove them during cleaning, or later should be considered carefully, depending on how firmly they are attached. In germination testing, 'damage' to the seed coat is frequently intentional, when scarification or other surgical treatments are applied, in order to break the physical dormancy due to 'hard' seed coats (see above, and Baskin and Baskin, 2003 – Chapter 28).

The work of Legesse and Powell (1992) on cultivars of cowpea (*Vigna unguiculata* (L.) Walp.) exemplifies the importance of testa integrity for the control of imbibition in this species, and presumably in others, especially in the *Fabaceae*. They found that cultivars with cream or beige coloured seed coats imbibed much



**Figure 15.2** Scanning electron micrograph (200 $\times$ ) of the strophiolar region of a seed of *Trifolium arvense* L., following an impactation treatment by shaking in a glass vessel. Note the cracks in the seedcoat confined to the strophiole. Such cracks were not seen in untreated seeds.

more quickly than those with coloured ones, and were susceptible to imbibition injury and reduced vigour as a result. When the rate of imbibition by coloured seeds was increased by scratching the testa, or piercing the micropyle, the incidence of imbibition damage also increased. This effect is likely to be magnified at the low moisture contents at which seeds are held in seed banks.

Where it has been necessary to scarify, or nick seed or fruit coats to overcome dormancy, or where physical damage may have occurred during seed cleaning, it is possible to alleviate the potential for imbibition injury. This is done by holding seeds at high relative humidity (saturated atmosphere) for 24–48 hours, before sowing on a free water-supplying substrate. Such ‘conditioning’ is thought to allow embryo cell membranes that have been temporarily disrupted by drying, to recover their normal conformation and permeability, before a rapid, uncontrolled influx of water can leach nutrients (imbibition injury), causing a focus for infection, etc. Figure 15.3 shows the results of an experiment in this laboratory on two accessions of *Lathyrus sphaericus* Retz. Seeds were dried to three different moisture contents, corresponding to laboratory ambient (highest), seed bank (15% RH at 15°C) and ultra-dry (lowest). Both seedlots were known to have high levels of physical dormancy (seed coat impermeability) and the testa of each seed was ‘chipped’ carefully with a sharp scalpel. Half the seeds in each seedlot x treatment combination were sown directly onto 1% plain water agar (control), and half were subjected to the high humidity conditioning treatment described above, before sowing. Individual points on the graph refer to replicate (6 × 25 seeds) results for each treatment combination. The results in Figure 15.3 show the clear advantage of high humidity conditioning, both in mean germination and in variability, especially at the two lower moisture levels.

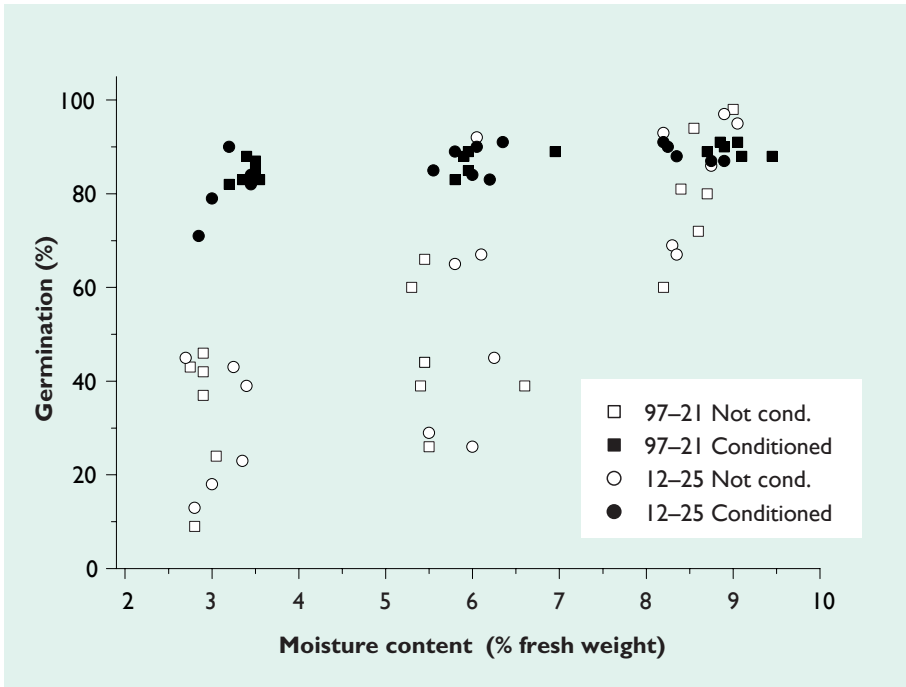
#### 1.4. Quality control of seed material

The colour and anatomy of the seed coat can give indications on whether a seed is fully ripe or not. Tannins, which are mostly responsible for the brown colouring of many seeds, are only produced at the end of the maturation process and provide some antibiotic protection for the precious contents. Therefore, a less dark colour can be an indication that a seed is not fully matured. The same is also reflected in an incomplete sclerification of the mechanical layer or layers – if there are any – in the seed coat.

Sometimes, seeds look wrinkled and therefore appear to be not fully developed (e.g., *Ipomoea* L. spp.), but are nevertheless viable.

## 2. The Internal Morphology of Seeds

The internal morphology of a seed is generally rather simple and most often involves only two components, the endosperm and the embryo. Rarely, seeds contain another type of reserve tissue derived from the (diploid) nucellus, the so-called perisperm (e.g., *Cactaceae*, *Caryophyllaceae* and *Piperaceae*). The embryo



**Figure 15.3** The effect of storage moisture content on final % germination in two seedlots (12-25 and 97-21) of *Lathyrus sphaericus* Retz., with and without high relative humidity conditioning before sowing, and after all seeds had been chipped carefully with a scalpel.

might only take up a fraction of the seed or entirely occupy it (in exalbuminous seeds, i.e., seeds without endosperm), depending on whether a nutritive tissue (i.e., endosperm or perisperm) is present apart from the embryo itself.

### 2.1. Embryo

The embryo results from growth and development of the zygote. The very first cell division results in the differentiation of the pro-embryo from its suspensor, an organ that anchors the developing embryo in maternal tissue and is involved in nutrient transport. The course of embryo development varies considerably among species and often provides valuable taxonomic characters, e.g., at the family level. This results in a wide variation in size, shape and disposition of the embryo at seed maturity. At one extreme, embryos are very well developed, occupying all or most of the seed's volume, and having an easily recognizable root (radicle) and shoot (plumule) with large cotyledons (modified first leaves packed with food storage compounds) and little or no endosperm (see below). Examples of this type are found in the *Fabaceae*. At the other extreme, the mature seeds of a number of groups have embryos that are relatively under-

developed, being small, or undifferentiated, or both, together with a relatively large amount of endosperm (e.g., *Annonaceae*, *Aquifoliaceae*, *Magnoliaceae*, *Papaveraceae* and *Ranunculaceae*). Elsewhere in this book, Baskin and Baskin (2003 - Chapter 28) describe how seeds with under-developed embryos are likely to exhibit morphological dormancy, with the embryos requiring weeks or months of slow post-dispersal development before germination can proceed normally. In contrast, the embryos of the well-developed type are usually quick to germinate under appropriate environmental conditions, being non-dormant or having only relatively weak physiological dormancy.

Relative size, shape and position of the embryo provide the most important criteria for the description of the internal morphology of seeds. Based on the examination of gross internal morphology of the seeds of 1,287 plant genera, Martin (1946) proposed a classification system, which is still widely used. His system is a quantitative one, with respect to the relative size of embryo (and reciprocally, the endosperm). It avoids applying vague terms for embryo size and does not automatically accept that a small embryo implies copious endosperm, and copious endosperm, a small embryo. Martin's quantitative classification consists of five size-designations, representing approximately quarter-unit volumetric proportions of embryo to endosperm: small (1/4 minus), quarter (1/4 plus), half (1/2 plus), dominant (3/4 plus), and total. For his principal classification of seeds according to their internal morphology, Martin (1946) selected the embryo as the principal criterion. According to differences in shape, size or position, the author distinguished twelve seed types falling into three divisions, as outlined in Table 15.2. Peripheral, bent, and sometimes also partly folded, embryos are usually the result of a curvature of the longitudinal axis of the ovule and seed. Such ovules and seeds with a curved longitudinal axis, where micropyle and chalaza don't face each other directly opposite, are called campylotropous. Embryos other than straight ones can become much longer than the actual seed and give rise to a larger seedling, presumably with an improved chance of survival (Werker, 1997).

## 2.2. Rumination

A mature seed in which the surface of any part is irregular or uneven is called 'ruminant'. Usually the term relates to the endosperm, however, similar irregularities may occur in the perisperm, seed coat or embryo, and ruminations can occur on both the inner and the outer surface of the seed. Therefore, each part of the seed (endosperm, nucellus or seed coat) can become ruminant due to uneven growth of its own cells, or by adapting to an adjacent ruminant tissue, or by both (Werker, 1997).

Ruminant seeds that show a particularly intricate network of lobes when the seed is cut in any plane are called 'labyrinth seeds' (van Heel, 1970; 1971). Such seeds, with a complicated network of interconnected lobes formed by the seed coat are found, for example, in *Annonaceae*, *Myristicaceae* and *Rubiaceae*. Whether rumination brings any advantage to the developing or germinating seed is not clear, although Boesewinkel and Bouman (1984) suggest that rumination of the

endosperm enlarges the surface between seed coat and endosperm, which might assist in the uptake of water and/or nutrients from the seed coat. Ruminant seeds have been found in 32 families of both dicotyledonous and monocotyledonous plants (Bhatnagar and Johri, 1972).

### 2.3. Food store

The storage of nutrients for the germinating embryo takes place in the embryo itself (usually in more or less well developed cotyledons, but rarely in an expanded hypocotyl, e.g., *Bertholletia excelsa* Bonpl.), the endosperm, the perisperm, or chalazosperm, or in a combination of these parts of the seed. Seeds containing endosperm or perisperm are called 'albuminous' while those without are called 'ex-albuminous'. Albuminous seeds with a small embryo and copious endosperm are generally considered to be more primitive than seeds in which the storage function has been taken over by the embryo. This transition is well illustrated, for example, in the *Fabaceae* (Smith, 1983); see also Forbis *et al.* (2002).

Because the endosperm generally develops from the fusion of the two polar nuclei with one of the nuclei from the pollen tube, it is usually triploid, while the perisperm develops from the nucellus and is therefore diploid maternal tissue. Among the Monocotyledons, perisperm is found in many *Zingiberales* (e.g., *Marantaceae* and *Cannaceae*), but some Dicotyledons also have this type of storage tissue (e.g., *Piperaceae* and most *Caryophyllales*). The term chalazosperm refers to a nutritional tissue in the chalaza, the region in which there is no differentiation between the integuments and the nucellus (found, for example, in *Cyanastraceae*).

In the Dicotyledons and some Monocotyledons, the endosperm of the mature seed usually consists of living cells in which nuclei can be distinguished, while, for example, in the *Poaceae* only, the outermost cell layer of the endosperm (the aleurone layer) is alive and the cells containing starch are dead. Rarely, when a nuclear endosperm develops, the central part, which usually is the last to become cellular, remains fluid. One famous example of a seed with a fluid endosperm is the coconut *Cocos nucifera* L., but this phenomenon is also found in some *Poaceae*.

Chemically, the storage compounds encountered in seeds are generally lipids, carbohydrates and proteins. Lipids are found as oil bodies, often together with protein bodies (also called aleurone grains) in the cells of the endosperm and embryo, or the latter are restricted to a special layer, the so-called aleurone layer. Storage of carbohydrates takes place either in the form of starch, or as thickened cells walls composed of hemicelluloses (e.g., mannans). Such strongly thickened cells walls are found in the endosperm of some *Palmae* (e.g., the ivory nut *Phytelephas macrocarpa* Ruiz & Pav.), *Zygophyllaceae*, *Diospyros* L., *Strychnos* L. and many liliaceous families, as well as in the cotyledons of *Impatiens* L., *Lupinus* L. and *Tropaeolum* L. (Boesewinkel and Bouman, 1984). While the storage of oil and starch are usually mutually exclusive, in *Myristicaceae*, the endosperm stores both starch and oil as reserve materials.

Table 15.2 Seed internal morphology – embryo types according to Martin (1946)

Division	Subdivision	Type
<p><b>A. BASAL:</b> Embryo usually relatively small and restricted to the lower half of the seed, except in some of the Lateral type; seeds usually medium to large; endosperm abundant and generally starchy except in the Rudimentary type. The Capitata and Lateral types include only Monocotyledons, but the Rudimentary and Broad types contain both Monocotyledons and Dicotyledons.</p>	None recognised.	<p><b>1. Rudimentary:</b> Embryo small, globular to oval-oblong; seeds generally of medium size or larger; cotyledons are usually rudimentary and obscure but sometimes they are evident, making the embryos appear like miniatures of the Linear or Spatulate types. The group is not entirely clear-cut since most of the families concerned have some genera that merge into the Linear type and a few incline towards the Broad.</p> <p><b>2. Broad:</b> Embryo as wide as or wider than high, peripheral or nearly so.</p> <p><b>3. Capitata:</b> Embryo expanded above into a head-like form; Monocotyledons only.</p> <p><b>4. Lateral:</b> Embryo basal-lateral or lateral, inclined to expand in the plane of the periphery; small or half or rarely larger. This type includes only the Poaceae, but it represents much diversity in embryo size. The name Basal applies well to a majority of the grass genera though Peripheral might seem more suitable for those with expanded embryos.</p>
<p><b>B. PERIPHERAL:</b> Embryo ordinarily elongate and large, quarter to dominant, contiguous in part at least to the testa and often curved; endosperm (actually perisperm) conspicuously starchy; central or in a few instances lateral. Cotyledons narrow or expanded. Dicotyledons – but in several cases one of the cotyledons is abortive.</p>	None recognised.	<p><b>5. Peripheral:</b> The only type; characters as for the division.</p>

Table 15.2. Continued

Division	Subdivision	Type
<p><b>C. AXILE</b> (or Axial): Embryo small to total, central (axial) straight, curved, coiled, bent or folded; endosperm not starchy except in five Monocotyledon families of the Linear type. Well represented in Gymnosperms, Monocotyledons and Dicotyledons.</p>	<p><b>Linear:</b> See characters for Linear type, the only one in the subdivision.</p> <p><b>Miniature:</b> Seeds small to minute with embryos that are stocky or minute; seed covering generally delicate and often cellular-reticulate; endosperm not starchy.</p>	<p><b>6. Linear:</b> Embryo generally several times longer than broad, straight, curved or coiled; cotyledons not expanded; seeds normally not minute.</p> <p><b>7. Dwarf:</b> Embryo variable in relative size, small to total, generally stocky, usually oval to elliptic or oblong, cotyledons inclined to be poorly developed; seeds small, generally 0.3–2 mm long exclusive of testa, often nearly as broad as long.</p> <p><b>8. Micro:</b> Seeds minute, usually less than 0.2 mm long exclusive of testa, generally globular and consisting of relatively few cells, approximately 50–150 within the testa; embryo minute to total.</p>
	<p><b>Foliate:</b> Embryo large, generally quarter to total, central rather than peripheral; cotyledons expanded; seeds generally medium to large; endosperm not starchy.</p>	<p><b>9. Spatulate:</b> Embryo erect; cotyledons variable, thin to thick and slightly expanded to broad.</p> <p><b>10. Bent:</b> Embryo spatulate but bent in jackknife form; cotyledons generally thick.</p> <p><b>11. Folded:</b> Embryo with cotyledons usually thin, extensively expanded and folded in various ways.</p> <p><b>12. Investing:</b> Embryo erect and with thick cotyledons overlapping and encasing the somewhat dwarfed stalk for at least half its length; endosperm wanting or limited.</p>

### 3. Identification

Because of their tremendous diversity and the fact that the structure of the seed coat is strongly, though not exclusively genetically determined, seeds have long been known to provide an excellent tool for identification. Although seeds vary in shape, size, colour, aril-like appendages and surface patterns, even within families or genera, first clues for identification can be provided by the external morphology of seeds. Particularly important are the micromorphological patterns as they occur in certain families, especially those with exotestal (see Table 15.1) seeds (e.g., *Cactaceae*, *Caryophyllaceae*, *Crassulaceae* etc.), or otherwise thin and sculptured seed coats. Although the external seed structure is potentially influenced by conditions such as the type of fruit, or the density of the seeds in the fruit, the anatomy of the seed coat is heavily genetically determined and thus largely independent of environmental factors. The microscopic structure of the mature integument(s) can provide a lot more information than just the external morphology of the seed, especially in cases with thick and complicated seed coats. An important fact is that the overall structure of the seed coat is often quite uniform within a natural family, and its detail may often be species-specific. *Fabaceae*, for example, are characterised by an exotestal palisade and a hypodermis of hourglass cells; and *Euphorbiaceae* (*sensu* Savolainen *et al.*, 2000) are highly uniform, having an exotegmen (see Table 15.1) composed of sabre-like palisades. The possibility that the seed coat shows certain adaptations assisting dispersal has been discussed above.

### 4. Seed Heteromorphism

Although seed and fruit characters are generally rather stable and uniform, there are a few cases in which the same plant can produce two or more types of seeds or fruits. This phenomenon is called heteromorphism, or heterospermy with respect to seeds and heterocarpy with respect to fruits. It is known to be typical of certain families like the *Asteraceae*, *Brassicaceae*, *Papaveraceae* and *Valerianaceae*, although some members of other families like the *Fabaceae* might also be heterospermous (Werker, 1997; Imbert, 2002). Heteromorphic seeds or fruits can differ in external features such as shape, size, weight and colour, and internal ones, such as the anatomy and ultrastructure of the seed coat or fruit wall (e.g., thicker cells walls, higher number of cell layers) and the embryo (Werker, 1997). Such structurally different seeds often also differ in their physiological and chemical properties, which can be reflected in differences in manner of dispersal and germinability, such as morphological dormancy. The species *Ceratocarpus heterocarpus* Dur. (*Fumariaceae*), for example, produces two types of fruits and three types of seeds, which differ in morphology and germinability. Short, indehiscent fruits bear only one seed whose dormancy is imposed by the fruit coat. The long, dehiscent fruits bear two seeds. Thus, the three types of seeds produced are:

- a) the lower seed of the long fruit, which is larger and heavier than the upper one, and whose coat eventually splits dorsally along the seed;

- b) the upper seed of the long fruit, with a seed coat which rarely splits; and
- c) the short fruit seed, whose seed coat does not split (Werker, 1997).

The phenomenon of heteromorphism is commonly observed in annuals of open, arid and saline habitats, where young seedlings are likely to be exposed to threats like drought and high salinity at the end of the dry season (Evenari *et al.*, 1971; Ungar, 1982; Tanowitz *et al.*, 1987; Werker, 1997; Imbert, 2002). Resistance of the seed to high salinity and differential dispersal of the seed in space and time may both confer advantages. For a detailed review of the phylogenetic distribution of seed and fruit heteromorphism and its ecological significance see Imbert (2002).

## Concluding Remarks

This review of seed and fruit morphology and anatomy has only touched the surface of a very substantial subject area. The primary literature is large and widely spread. For instance, while it is mainly concerned with vegetative anatomy, RBG Kew's Plant Micromorphology Bibliographic Database (Royal Botanic Gardens, Kew, 2001) contains well over 5,000 references covering seed or fruit anatomy. As it is searchable by family and genus, along with Jensen (1998), it is a valuable starting point for seed conservationists wishing to search the literature for information on their taxa of interest. Although much is already known and documented regarding seed and fruit structure, much remains to be discovered. The vast majority of species' seed structure has never been investigated in detail, or even at all. Inferences from genus or family level generalisations, based on just a few species, may well turn out to be inaccurate when used to predict seed structural characters in previously unstudied individual species. As a by-product of seed processing activities, seed conservationists, especially those working on diverse wild species, have a unique opportunity to make basic observations and contribute significantly to knowledge in this area. Moreover, problems arising from seed conservation operations continue to offer a number of potentially interesting structure - function research directions. For example, Adkins *et al.* (2002) have recently suggested that at least part of the dormancy breaking properties of plant derived smoke in the fruits of some grass species may have an anatomical basis in the covering structures. The Millennium Seed Bank Project recognises the basic importance of seed (and fruit) anatomical and morphological knowledge to seed conservation, by employing a full-time Seed Morphologist, not only to carry out research, but also to spread competence in the discipline among other staff of the Project and its partners.

## References

- Adkins, S.W., Bellairs, S.M., Loch, D.S. (2002). Seed dormancy mechanisms in warm season grass species. *Euphytica* **126**: 13–20.
- Baskin, J.M. and Baskin, C.C. (2003). Classification, biogeography and phylogenetic relationships of seed dormancy, pp 517–544 In: R.D. Smith, J.B. Dickie, S.H. Linington, H.W. Pritchard and R.J. Probert (eds). *Seed conservation: turning science into practice*. Royal Botanic Gardens, Kew, UK.
- Bhatnagar, S.P. and Johri, B.M. (1972). Development of angiosperm seeds, pp. 77–150. In: T.T. Kozłowski (ed), *Seed biology*, Vol. 1. Academic Press, New York, USA, London, UK.
- Boesewinkel, F.D. and Bouman, F. (1984). The seed: structure, pp. 567–610. In: B.M. Johri (ed). *Embryology of angiosperms*. Springer Verlag, Heidelberg, West Germany.
- Boesewinkel, F.D. and Bouman, F. (1995). The seed: structure and function, pp. 1–24. In: J. Kigel and G. Galili (eds). *Seed Development and Germination*. Marcel Dekker, New York, USA.
- Corner, E.J.H. (1976). *The seeds of dicotyledons*. Cambridge University Press, Cambridge, UK.
- Ellis, R.H., Hong, T.D. and Roberts, E.H. (1985). Seed morphology, pp. 34–38. In: *Handbook of Seed Technology for Genebanks*. International Board for Plant Genetic Resources, Rome, Italy.
- Evenari, M., Shanon, L. and Tadmor, N. (1971). *The Negev. The challenge of a desert*. Harvard University Press, Cambridge, Mass., USA.
- Fahn, A. (1990). *Plant anatomy*, 4<sup>th</sup> edn. Butterworth-Heinemann, Oxford, UK.
- Forbis, T.A., Floyd, S.K. and de Queiroz, A. (2002). The evolution of embryo size in angiosperms and other seed plants: implications for the evolution of seed dormancy. *Evolution* **56**: 2112–2125.
- Harper, J.L., Lovell, P.H., and Moore, K.G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics* **1**: 327–356.
- Heel, W.A. van (1970). Some unusual tropical labyrinth seeds. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam, Series C* **73**: 298–301.
- Heel, W.A. van (1971). Note on some more tropical labyrinth seeds. *Blumea* **19**: 109–111.
- Imbert, E. (2002). Ecological consequences and ontogeny of seed heteromorphism. *Perspectives in Plant Ecology, Evolution and Systematics* **5**(1): 13–36.
- Jensen, H. (1998). *Bibliography on seed morphology*. A.A. Balkema, Rotterdam, The Netherlands. 310 pp.
- Kapil, R.N., Bor, J. and Bouman, F. (1980). Seed appendages in angiosperms. I. Introduction. *Botanische Jahrbücher für Systematik* **101**: 555–573.
- Legesse, N. and Powell, A.A. (1992). Comparisons of water uptake and imbibition damage in eleven cowpea cultivars. *Seed Science and Technology* **20**: 173–180.
- Martin, A.C. (1946). The comparative internal morphology of seeds. *American Midland Naturalist* **36**: 513–660.
- Netolitzky, F. (1926). Anatomie der Angiospermen – Samen. *Handbuch der Pflanzenanatomie* Bd. X, Borntraeger, Berlin, Germany.
- Pritchard, H.W., Manger, K.R., Prendergast, F.G. (1988). Changes in *Trifolium arvense* seed quality following alternating temperature treatment using liquid nitrogen. *Annals of Botany* **62**: 1–11.

- Raven, P.H., Evert, R.F. and Eichhorn, S.E. (1999). *Biology of plants*. W.H. Freeman, New York, USA.
- Roth, I. (1977). *Fruits of angiosperms*. Gebrüder Borntraeger, Berlin and Stuttgart, West Germany. 675 pp.
- Royal Botanic Gardens, Kew (2001). Plant Micromorphology Bibliographic Database (PMBD). Published on the Internet; <http://www.rbgb.org.uk/kr/PAHome.html>
- Rudall, P.J. (1992). *Anatomy of flowering plants: an introduction to structure and development*. Cambridge University Press, Cambridge, UK.
- Savolainen, V., Fay, M.F., Albach, D.C., Backlund, A. van der Bank, M., Cameron, K.M., Johnson, S.A., Lledó, M.D., Pintaud, J.-C., Powell, M., Sheahan, M.C., Soltis, D.E., Soltis, P.S., Weston, P., Whitten, W.M., Wurdack, K.J. and Chase, M.W. (2000). Phylogeny of the eudicots: a nearly complete familial analysis based on rbcL gene sequences. *Kew Bulletin* **55**: 257–309.
- Smith, D.L. (1983). Cotyledon anatomy in the Leguminosae. *Botanical Journal of the Linnean Society* **86**: 325–355.
- Spjut, R.W. (1994). A systematic treatment of fruit types. *Memoirs of the New York Botanical Garden* **70**. 182 pp. New York Botanical Garden, Bronx, New York, USA.
- Tanowitz, B.D., Salopek, P.F. and Mahall, B.E. (1987). Differential germination of ray and disc achenes in *Hemizonia increscens* (Asteraceae). *American Journal of Botany* **74**: 303–312.
- Thompson, K., Bakker, J.P. and Bekker, R.M. (1997). *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge, UK.
- Ungar, I.A. (1982). *Atriplex patula* var. *hastata* (L.). Gray seed dimorphism. *Rhodora* **73**: 548–551.
- Werker, E. (1997). *Seed Anatomy*. Borntraeger, Berlin and Stuttgart, Germany.

