



Fig. 71.



Fig. 72.

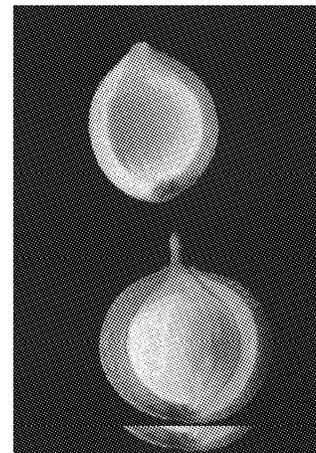


Fig. 73.

**Drupe.** Fruit with a hard endocarp (figs. 67 and 71-73); e.g., Anacardiaceae (*Spondias purpurea*, *S. mombin*, *Mangifera indica*, *Tapirira*), Caryocaraceae (*Caryocar costaricense*), Chrysobalanaceae (*Licania*), Euphorbiaceae (*Hyeronima*), Malpighiaceae (*Byrsonima crispata*), Olacaceae (*Minquartia guianensis*), Sapindaceae (*Melicoccus bijugatus*), and Verbenaceae (*Vitex cooperi*).

**Hesperidium.** Septicidal berry with a thick pericarp (fig. 67). Most of the fruit is derived from glandular trichomes. It is typical of the Rutaceae (*Citrus*).

### Aggregate Fruits

Several types of aggregate fruits exist (fig. 74):

**Achenacetum.** Cluster of achenia; e.g., the strawberry (*Fragaria vesca*).

**Baccacetum or etaerio.** Aggregate of berries; e.g., Annonaceae (*Asimina triloba*, *Cananga odorata*, *Uvaria*). The berries can be aggregate and syncarpic as in *Annona reticulata*, *A. muricata*, *A. pittieri* and other species.

**Drupacetum.** Aggregate of drupelets; e.g., *Bursera simaruba* (Burseraceae).

**Folliacetum.** Aggregate of follicles; e.g., Annonaceae (*Anaxagorea crassipetala*, *A. phaecarpa*, *Xylopia aromatica*, *X. frutescens*, *Cymbopetalum costaricense*, *C. torulosum*, *Guatteria*), Illiciaceae (*Illicium verum*, *I. anisatum*), Apocynaceae (*Aspidosperma*, *Prestonia surinamensis*, *Stemmadenia*, *Tabernaemontana*), Magnoliaceae (*Magnolia poasana*, *Talauma gloriensis*),

and Sterculiaceae (*Helicteres guazumaefolia*, *Sterculia*). *Desmopsis bibracteata* (Annonaceae) has aggregate follicles with constrictions between successive seeds, similar to those found in loment.

**Samaracetum.** Aggregate of samaras (fig. 74); e.g., Aceraceae (*Acer pseudoplatanus*), Magnoliaceae (*Liriodendron tulipifera* L.), Sapindaceae (*Thouinidium dodecandrum*), and Tiliaceae (*Goethalsia meiantha*).

### Multiple Fruits

Multiple fruits are found along a single axis and are usually coalescent. The most common types follow:

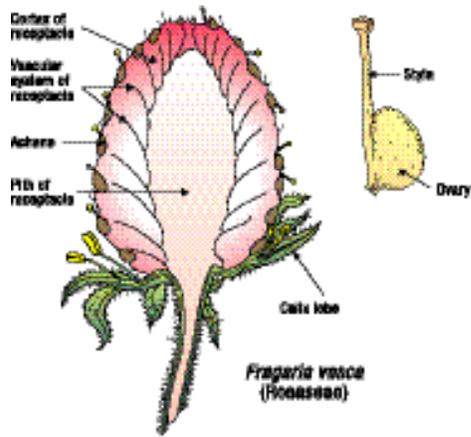
**Bibacca.** Double fused berry; e.g., *Lonicera*.

**Sorosis.** Fruits usually coalescent on a central axis; they derive from the ovaries of several flowers; e.g., Moraceae (*Artocarpus altilis*).

**Syconium.** Syncarp with many achenia in the inner wall of a hollow receptacle (fig. 74); e.g., *Ficus*.

## THE GYMNOSPERM FRUIT

Fertilization stimulates the growth of young gynostrobiles which in species such as *Pinus* are more than 1 year old. Many genera have woody gynostrobiles (*Pinus*, *Picea*, *Pseudotsuga*); others have fused scales forming a berry-like structure around the seeds (*Juniperus*). In some species, such as *Taxus* and *Torreya*, the seeds develop inside fleshy arils (Foster and Gifford 1974, Krugman and others 1974, Sporne 1965). In *Podocarpus*



*Fragaria vesca*  
(Rosaceae)

**Achenacetum**

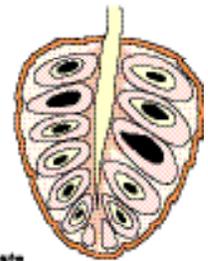


*Cananga odorata*  
(Annonaceae)

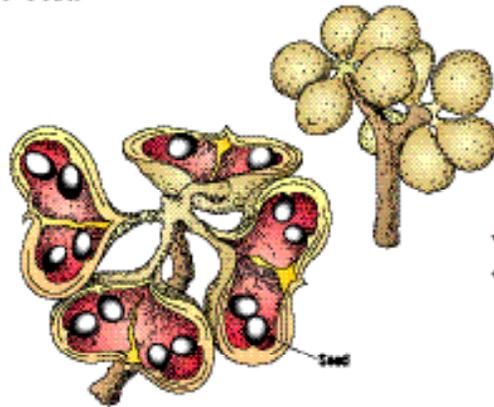
**Baccacetum**



*Annona reticulata*  
(Annonaceae)



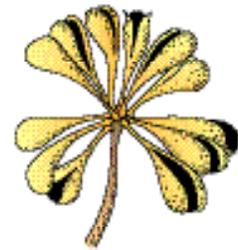
*Helicteres guazumaefolia*  
(Sterculiaceae)



*Sterculia* sp.  
(Sterculiaceae)



*Guatteria*  
(Annonaceae)



*Anaxagore*  
(Annonaceae)

**Follicacetum**

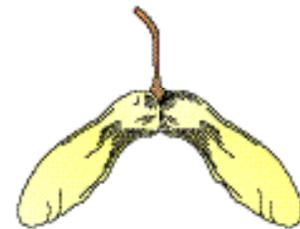


*Bursera simaruba*  
(Burseraceae)

**Drupecetum**



*Gonolobus melantha*  
(Tillaceae)



*Acer plantanoides*  
(Aceraceae)

**Samaracetum**

Fig. 74. Aggregate and accessory fruit types.

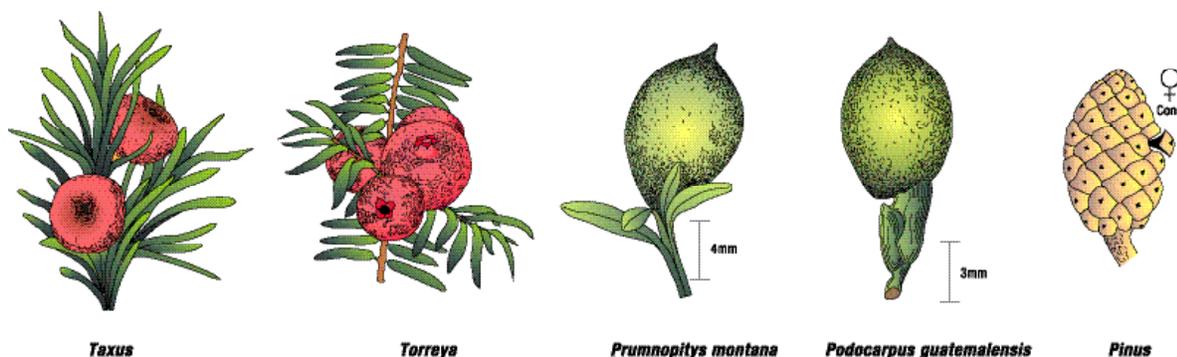


Fig. 75. Fruits of several gymnosperms.

and *Prumnopitys*, the ovuliferous scale forms a fleshy covering called epimatium, which surrounds the seed (fig. 75). This structure can be partially or totally fused to the ovule integument and even to the bract subtending the ovuliferous scale (Sporne 1965).

The pre- and postfertilization development of the strobile shows many facets similar to those of angiosperm fruits. Parameters such as size and moisture content show daily fluctuations as a consequence of variations in the moisture level, increasing dry weight, high respiratory rates, and storage of carbohydrates and minerals. However, in the last stages of maturation the moisture content decreases. Weight may be lower, respiration is lower, and nutrients are mobilized to the seed. The metabolic activity declines with strobile dehydration and the scales become open (Krugman and others 1974, Singh and Johri 1972).

and organs) influences, at different ontogenetic stages, the nature and efficiency of the functional activities.

## THE ANGIOSPERM SEED

### Seed Development

The ovule, whose embryo sac was fertilized twice, is the starting point for seed development (Bhatnagar and Johri 1972). In some cases, the process is long and complicated; in others, it is short and simple.

In seed development, three functional phases can be identified:

(1) Cell divisions produce the tissues that will form the seed-coat, the endosperm, and the embryo (early embryogenesis); this stage is characterized by a fast increase in fresh weight.

(2) Ontogenetic changes guarantee the success of the offspring as an independent unit, through the storage of reserves. They lead to an increase in dry weight.

(3) Maturation drying leads to a stage of metabolic quiescence, interpolated between the end of seed development and the beginning of germination. In this stage, fresh weight decreases. Many studies suggest that this period of dehydration is important to the transition of activities from seed development (especially embryo) to germination-seedling development (Bewley and Black 1982, 1994; Kermode 1990, 1995, 1997; Kermode and Bewley 1985a, 1985b, 1986; Kermode and Jiang 1994; Kermode and others 1989).

## THE SEED

The seed is the site of a partial development of the sporophyte (*embryo*) and the linkage between successive generations. It is a critical intermediate stage in the life cycle of angiosperms and gymnosperms, which guarantees the propagation and survival of the species.

Seeds are dynamic and tridimensional entities, and their morphology is the result of the physiological and environmental processes involved in their development. The physical configuration (size, shape, distribution, and structure of tissues

Maturation drying guarantees the permanent inactivation of seed metabolism during seed dispersal and the period before germination. The reduction of water content in the tissues, the impermeability of the seedcoat, and the presence of inhibitors cause seed inactivity. The influence of these factors varies from one species to another, but many seeds do not germinate if they are removed from the maternal plant before this stage. However, a precocious germination may be induced through a desiccation-rehydration period (Bewley and Black 1994, Kermode and others 1989). The maturation drying stops seed development and irreversibly stunts the germination-seedling development. A dramatic reduction in the synthesis of storage proteins occurs. Synthesis of reserves stops and synthesis of proteins related to germination-seedling development is introduced (e.g., enzymes related to reserve mobilization). The change in genetic expression seems to act at the transcription and post-transcription (mRNA) levels. The drying suppresses the production of messages to synthesize proteins for development. When the seeds rehydrate, the messages to synthesize proteins used in development and growth increase (Kermode and Jiang 1994, Kermode and others 1989).

Growth regulators present in the tissues of developing seeds (indol acetic acid, IAA), gibberellins (GAs), cytokinins, and abscisic acid (ABA) seem to be involved in several processes. These processes are development of the seed (growth: cell division and elongation) and cellular differentiation (qualitative differences between cells, tissues, and organs), including the arrest of growth prior to seed germination; accumulation of the storage reserves; development of the extraseminal tissues (growth and cell differentiation); and several physiological effects on tissues and organs close to the developing fruit (Bewley and Black 1994).

The biologically active gibberellins show high concentrations during the growth (mainly cell division) of the embryo and the endosperm. Abscissic acid plays an important role in the development and maturation of seeds. It is associated more with the reduction of embryo growth than with its promotion; in many cases, it can be present in the normal embryogenesis but not in the germination and longitudinal extension of the embryo axis. Abscissic acid concentration also appears to influence the deposition of proteins and other reserves and, in many species, the highest content of ABA is coincident with the highest rate of reserve synthesis (Bewley and Black 1994). It also induces dehydrin expression (LEA), which is the accumulation of proteins during the last stages of seed maturation (late embryogenesis). However, the entire role of ABA is not yet well comprehended. Dehydrin expression finishes when germination starts (Farrant and others 1993). Water loss during the process of maturation is common to many seeds, which may diminish to less than 5 to 10 percent of their fresh weight.

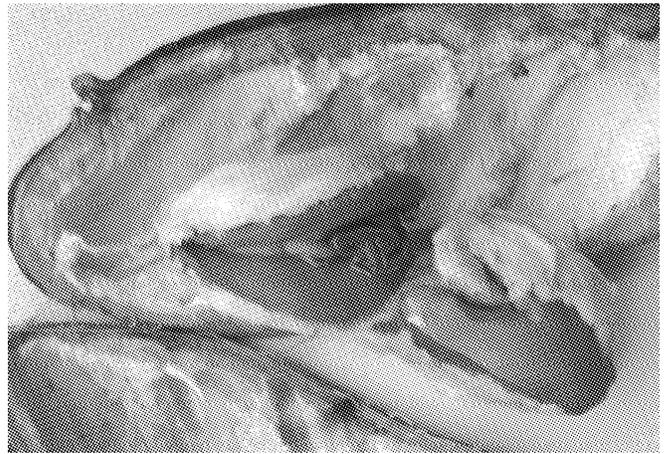


Fig. 76.



Fig. 77.

In temperate zones, and especially in the tropics, many seeds do not undergo drying, do not experience reduced cellular metabolism, and do not exhibit a clear end to seed development (Côme and Corbineau 1996a, 1996b; Corbineau and Côme 1988; Finch-Savage 1992a, 1992b, 1996; Finch-Savage and Blake 1994; Kermode 1997). During fruit dehiscence and dispersal, seed development is followed by germination-seed development without interruption. In some species, the seedling develops when the seed is still inside the fruit and is attached to the parent tree. These seeds are called *viviparous*, and it has been demonstrated experimentally that the inhibition of their development requires high concentrations of ABA (Bewley and Black 1994). Mangroves growing on protected tropical coasts are the best-known examples of viviparous seeds. Common on the American coasts are *Rhizophora racemosa* (Rhizophoraceae), *Pelliciera rhizophorae* (Theaceae), *Avicennia germinans* (L.) L., *A. bicolor* (Verbenaceae), and *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae). *Inga pater-no* Harms (Fabaceae-Mimosoideae) also has a viviparous seed (fig. 76). *Cojoba arborea* and *C. costaricensis* (Fabaceae-Mimosoideae) show an incipient viviparity (fig. 77). The overgrown seeds described by Corner (1951, 1953), which have a

continuous embryo development limited by a hard and indehiscent pericarp or a late dehiscence pericarp (*Dipteryx panamensis*, *D. odorata*, *Prioria copaifera*), seem to be an intermediate type. In these seeds, the cotyledons fold and become disfigured because space is inadequate. The plumule, which is well developed, usually has an incipient epicotyl and several foliar primordia in different stages of development.

## Embryogenesis

Embryo development includes two fundamental processes: the establishment of a precise spatial organization of the cells derived from the zygote (pattern of formation), and the generation of cell diversity inside the developing embryo (cytodifferentiation). These processes are coordinated to develop a recognizable morphological structure, regulated by the embryogenic pattern of the species. Although in plants most organogenesis occurs in the postembryonic stage, the embryonic pattern reveals coordinated growth and development during the process of development (Flores 1999, Lindsey and Topping 1993).

### Early Embryogenesis

The pattern of embryogenic formation has three levels: pattern of cellular organization, pattern of protein accumulation, and pattern of gene expression (Lindsey and Topping 1993).

The unicellular zygote evolves into a multicellular embryo with differentiated organs and the potentialities of the adult plant. This occurs through a programmed sequence of events (pattern of embryogenesis). In angiosperms, the embryo is located at the micropylar end of the embryo sac. Its basal end is attached to the embryo sac wall and its apical end faces the central cell. After fertilization the zygotic cell polarizes (establishes structural and physiological differences). The endoplasmic reticulum and the cellular organelles reorganize around the nucleus. During mitosis, the polarized zygote divides, forming two daughter cells that have cytoplasmic elements differentially distributed. This fact has a strong effect on the embryogenesis. In most angiosperms the zygote divides transversely, producing a chalazal or apical cell (ac) and a basal cell (bc); in several exceptional cases, cell division is longitudinal or oblique as in Piperaceae and Dipsacaceae (Flores 1999, Natesh and Rau 1984). The cells derived from the apical cell contribute to form most of the proembryo and embryo (usually the plumule and the cotyledons); the basal cell and its derivatives commonly form the hypocotyl and the suspensor.

The variations in cell wall orientation and the sequence of cell divisions in the embryo are the basis for classification of embryonic types (fig. 78). The separation of types, except the piperad, is based on the destiny of the proembryo apical cell

during the second and subsequent cell divisions, and in the contribution of the basal cell to the embryo organs.

In the onagrad type, a vertical division in the apical cell (ac) and a transversal division in the basal cell (bc) result in a tetrad of cells forming a "T". The ac and its derivatives form most of the embryo (cotyledonar zone, apical meristem, hypocotylar zone). The bc forms the radical cortex, the root cap, and the suspensor. The proembryo in the asterad type is formed through a vertical division in ac and a transverse division in bc. In some taxa, the ac divides obliquely and when the quadrant is formed, one of the cells forms the epiphysis. Through further growth, the epiphysis produces the epicotyl. The remaining cells in the quadrant develop into the cotyledons. In this type, bc contributes to form a considerable portion of the embryo (hypocotylar region, radical cortex, root cap, suspensor). The solanad type forms a linear tetrad of cells. The two cells derived from ac form most of the embryo; bc does not take part in embryo organization but forms the root cap and the suspensor. The chenopodiad type also has a linear tetrad; ac produces the cotyledonar region, the apical meristem, and a hypocotyl half, while bc provides the other hypocotyl half, the radical cortex, the root cap, and the suspensor. The caryophyllad type differs from the other types. Here, the bc does not divide and the ac originates the embryo. The piperad type includes those cases in which the zygote divides in a longitudinal plane (Natesh and Rau 1984).

The time and the fixation mechanism of the polar axis in the zygote are very important in morphogenesis. The establishment of the polarity, and the zygote and proembryo histodifferentiation occur in the absence of cell movement due to the rate and planes of cell division and subsequent cellular elongation. As a result, the regions giving rise to the apical and radical meristems are formed (Flores 1999, Steward 1970, Steward and others 1970). These changes mark the beginning of mRNA synthesis in the zygote during early embryogenesis (Flores 1999).

During the zygotic, proembryonic and embryonic stages, coordination exists at the biochemical level. A specific pattern also exists for the synthesis of proteins, lipids, and carbohydrates in the embryo and other seed structures. The three types of protein involved in this synthesis are as follows: enzymes involved in reserve mobilization, structural proteins associated with the membranes and the ribosomes, and storage proteins in which the LEA or dehydrins are critical.

The activation and expression of genes during embryogenesis, especially those regulating specific aspects of development, are the subject of increasing research. Lindsey and Topping (1993) identified a gene in *Arabidopsis* that expresses in the basal region of the proembryo when the latter is in the heart stage, and in the radical meristem when in the adult

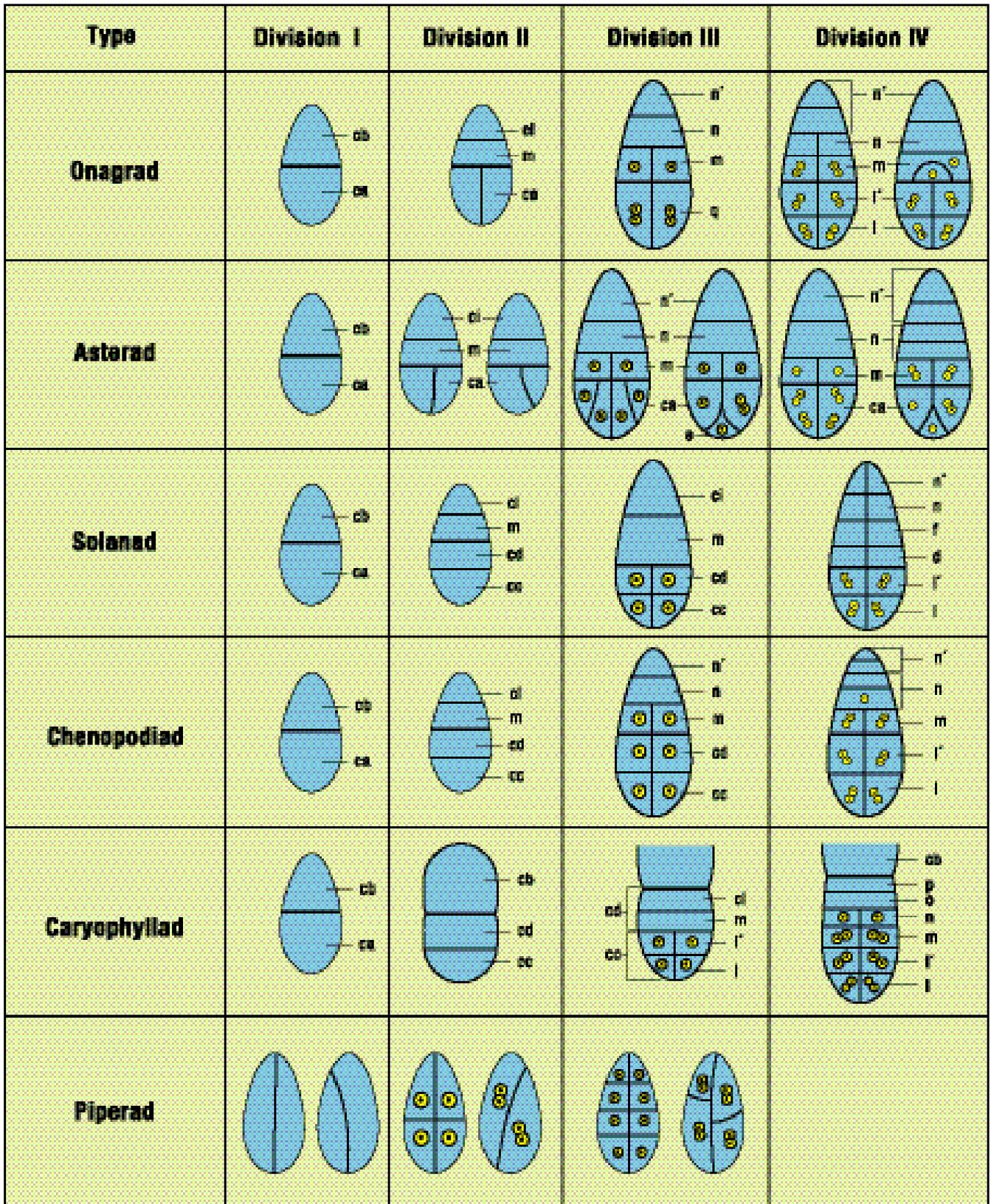


Fig. 78. Main types of embryogeny. (Redrawn from Natesh & Rau, 1984).

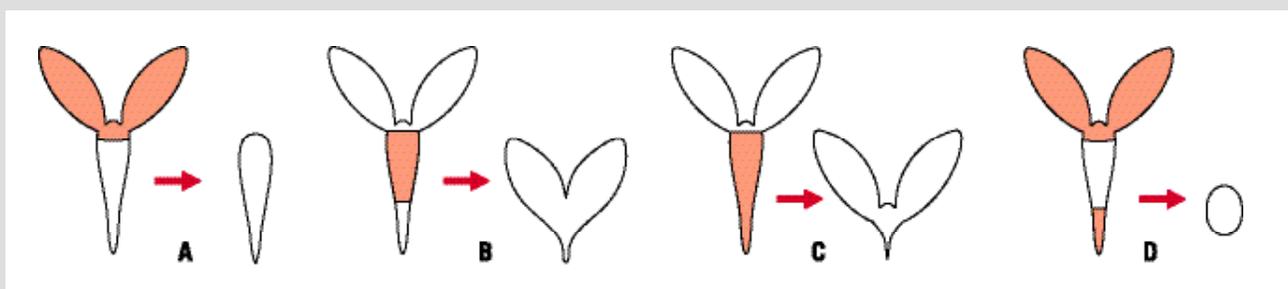


Fig. 79. Origin and final form of apical-basal pattern mutants.

(Redrawn from Lindsey & Topping, 1993).

stage. By studying mutants, researchers have proven that numerous loci control the diverse aspects of embryogenesis. Processes such as cell division and morphogenesis per se, and the establishment of polarity, embryo, and endosperm shape are determined by genes that can be recognized easily. Figure 79 depicts some mutants of the apical-basal pattern in *Arabidopsis* (Mayer and Shain 1974, Mayer and others 1991). In the mutant *a*, the apical cell does not form the plumule, and the cotyledons resemble the embryo of some Lecythidaceae such as *Lecythis ampla* (Flores 1994d, 1999). Perhaps the embryology of *L. ampla* will reveal similarities to that found in mutant *a*. Figure 80 shows the hierarchies proposed by Lindsey and Topping (1993) in the embryonic gene expression regulating cell division and cytodifferentiation during the embryogenesis.

### Embryo Differentiation

The tridimensional growth of the embryo begins with the formation of vertical walls in the derivatives of the apical cell. Further divisions in several planes produce a globular embryo. Cell differentiation begins in this stage with the establishment of the cotyledonar and epicotylar loci in the shoot pole; the hypocotyledonar region and the radical pole with the hypophysis are also distinguished. Loci organizations are not strictly related to cell lineage or row systems. The cotyledonar, epicotylar, hypocotyledonar, and hypophysial regions are identified after the growth and differentiation of the incipient organ. The hypocotyledonar region contributes to the embryo axis formation through cell division and elongation. This phase of differential growth in the embryo leads to the establishment of the meristems and accentuates the differences between shoot and root (Natesh and Rau 1984).

Embryo histogenesis in seeds without maturation drying is similar in its early stages to that of seeds with maturation drying; however, accentuated variations appear in late embryogenesis. Many seeds without maturation drying are large, with very well developed embryos such as those of *Aesculus hippocastanum* (Tompsett and Pritchard 1993), *Dipterocarpus* (Tompsett 1987), *Quercus robur* (Finch-Savage 1992a, 1992b),

*Hevea brasiliensis* (Chin and others 1981), *Calophyllum brasiliense* (Flores 1994b), *Mangifera indica* (Corbineau and Côme 1988, Corbineau and others 1987), and *Sclerocarya birrea* (Gamené 1996). Other seeds are large but have a small, rudimentary embryo such as those of *Hyeronima alchorneoides* (Flores 1993c). All these seeds increase in dry weight until fruit dehiscence, with slight or no loss in fresh weight; however, a decreasing loss in water content is characteristic of several seeds without maturation drying (Finch-Savage 1996). Embryo growth may continue (increasing in dry weight) after dehiscence in the absence of enough water to promote germination (Finch-Savage 1996); however, in the tropical forest, with very high rain regimes, the seeds or fruits (diaspores) fall down on very humid soils, sometimes inundated, and continue hydrating.

Dicotyledons and monocotyledons have similar types of embryonic development (Lakshmanan 1972). During early embryogenesis—the stages of quadrant and octant and the formation of the globular embryo—the cells in both groups are similar in lineage and configuration. The fundamental differences arise during differentiation of the globular embryo. The organization of the shoot apex follows different morphogenetic patterns. In dicotyledons, the axial cells forming the epiphysis grow slower than the circumaxial cells. In monocotyledons, one-half of the terminal cell and its derivatives grow slowly while the remaining half, which forms the cotyledonar locus, grows rapidly. The apparent lateral position of the shoot apex in late stages is due to the rapid growth of the single cotyledon in monocotyledons. The epicotyl and the cotyledon of monocotyledons develop from the same layer of terminal cells (Lakshmanan 1972). The two loci differentiate through a vertical wall in the terminal layer. The differences found in the terminal region are conspicuous during the quadrant stage (Lakshmanan 1972). In the dicotyledons, two cells opposite the terminal quadrant form the cotyledons; in the monocotyledons the number of cells forming the cotyledon in the quadrant stage is variable (Lakshmanan 1972). Despite these variations, the changes occurring in the different ontogenetic stages

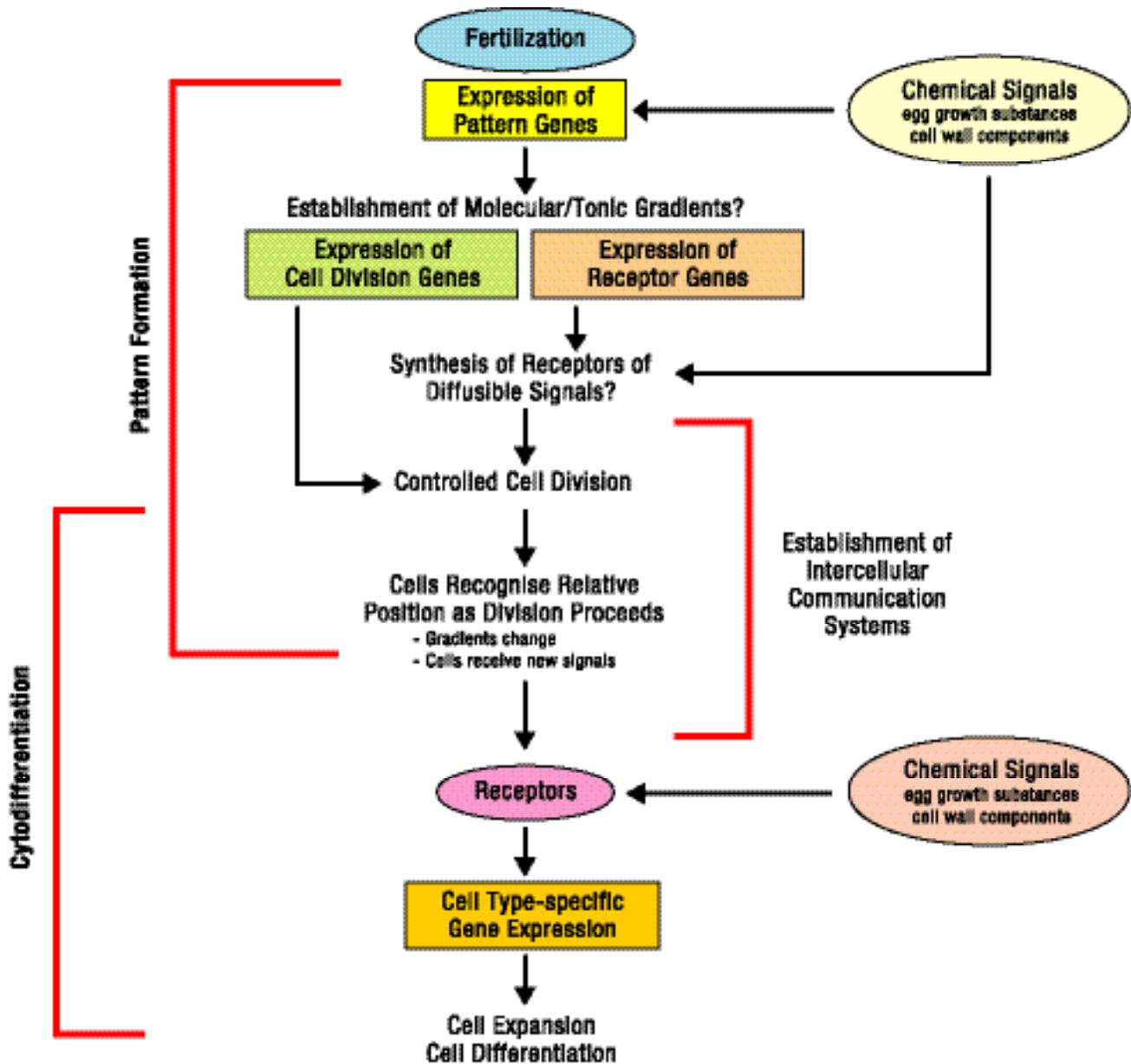


Fig. 80. Hierarchies in embryonic gene expression.

(Redrawn from Lindsey & Topping, 1993).

result in an organized morphogenetic system from which the future tree evolves (Natesh and Rau 1984).

#### Structure and Function of the Suspensor

The suspensor plays an active and dynamic role during embryogenesis (Alpi and others 1975; Natesh and Rau 1984; Newcomb 1973; Schulz and Jensen 1968a, 1968b, 1969; Singh and Dathan 1972; Yeung and Cutler 1978). The suspensor has a stable cell number and its rate of growth is higher during the early stages of embryogeny. In many species it has transfer cells, suggesting an active role in the absorption and exchange of nutrients for embryo growth. During the late stages of the embryogeny, the suspensor degenerates and seems to be

digested by the embryo (Natesh and Rau 1984).

The suspensor seems to accomplish two functions: (1) nutrient absorption from the surrounding somatic tissues and transportation to the developing embryo (Schulz and Jensen 1968a, 1968b, 1969); and (2) a source of nutrients and growth regulators for the developing embryo (Schulz and Jensen 1968a, 1968b, 1969). In vitro, gibberellic acid can partially replace the suspensor; therefore, the suspensor must be a source providing this growth regulator to the developing embryo. The suspensor also contains auxins and cytokinins; the concentrations of these substances have the same fluctuation pattern as those of gibberellic acid (Alpi and others 1975, Natesh and Rau 1984, Yeung and Cutler 1978).

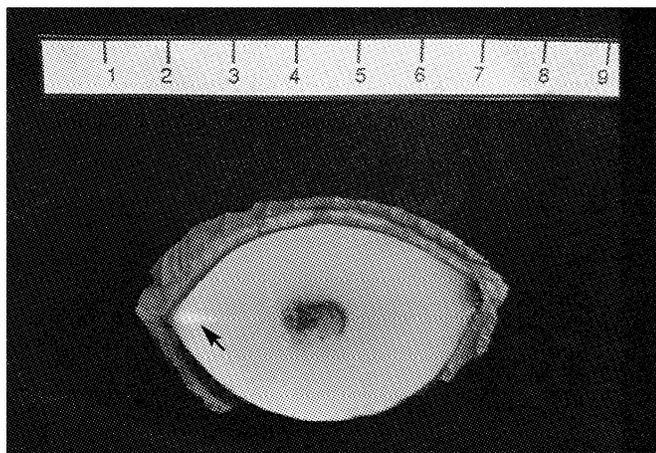


Fig. 81.

The embryo of some taxa (*Tilia*) do not have a suspensor; others have a reduced structure (*Euphorbia*, *Ruta*). Usually, the taxa with haustorial endosperm do not have a suspensor or have one that is reduced and ephemeral. Families such as Rubiaceae have a massive and haustorial suspensor (Natesh and Rau 1984). In Fabaceae, the suspensor may be missing or may form a massive structure, filamentous or tubercular.

### Embryogenic Deviations

In some parasite and saprophyte taxa, as well as in some forest trees [Olacaceae (*Minquartia guianensis*), Myristicaceae (*Virola koschnyi*, *V. sebifera*, *Otoba novogranatensis*), Icacinaceae (*Calatola costaricensis*), Piperaceae (*Piper*, *Peperomia*)] minute embryos are found (fig. 81). Frequently they are also rudimentary (Flores 1992c, 1994c, 1994e, 1996, 1999). Other embryos have deviated since their origin. Some deviations are formed by apomixis (asexual process); they may derive from the unfertilized egg cell (haploid parthenogenesis) or from another cell from the gametophyte (haploid apogamy). In many cases, there is no meiosis and a diploid gametophyte is formed, leading to diploid parthenogenesis or diploid apogamy.

### Endosperm Development

The fusion of the sperm nucleus with the central cell nuclei forms the primary endosperm cell. Through successive mitosis, this cell forms the endosperm. This tissue does not have a significant role at the proembryo stage, but it is important to embryo nutrition during embryo development and seed germination. In most dicotyledons the endosperm is reabsorbed during seed maturation and storage proteins accumulate in the tissues of the embryo. During seed development, the interactions between endosperm and embryo are essential to insure reproductive success. The formation of the endosperm, its reabsorption, and the transference of reserves to the embryo are genetically established (Lindsey and Topping 1993).

Three types of endosperm are recognized: nuclear, cel-

lular, and helobial. Many free nuclear divisions before cell wall formation characterize the nuclear type; its formation varies from one species to another. The endosperm is consumed before partial or total wall formation occurs in many species. The seeds of other species, such as *Virola koschnyi*, *V. sebifera*, *V. surinamensis*, and *Compsoeura sprucei*, have nuclear endosperm when they are dispersed (Flores 1999). Several species have haustorial endosperm (Vijayaraghavan and Prabhakar 1984).

In the cellular endosperm, each cell division is followed by cell wall formation; this type of endosperm is frequently haustorial. The helobial endosperm has a different development: the first endosperm cell divides and gives rise to a pair of unequal chambers; usually, the micropylar chamber is bigger. It undergoes free nuclear divisions before cell wall formation; in contrast, the nucleus of the chalazal chamber does not divide or undergo division before giving rise to a coenocyte. Sometimes cell wall deposition takes place later. The helobial endosperm is typical of the monocotyledons (Vijayaraghavan and Prabhakar 1984).

### The Mature Seed

The mature seed generally has a seedcoat (product of one or both ovule integuments), an endosperm, and an embryo (fig. 82). Some mature seeds retain a remnant of nucellar tissue called a perisperm. The degree to which these structures continue their development, are reduced or reabsorbed, or disappear during the late stages of seed development leads to distinct structural patterns associated with physiological differences.

### Seedcoat

In bitegmic seeds the seedcoat has a testa (former outer integument) and a tegmen (inner integument). Each integument has its own opening at the seed's distal end; the opening

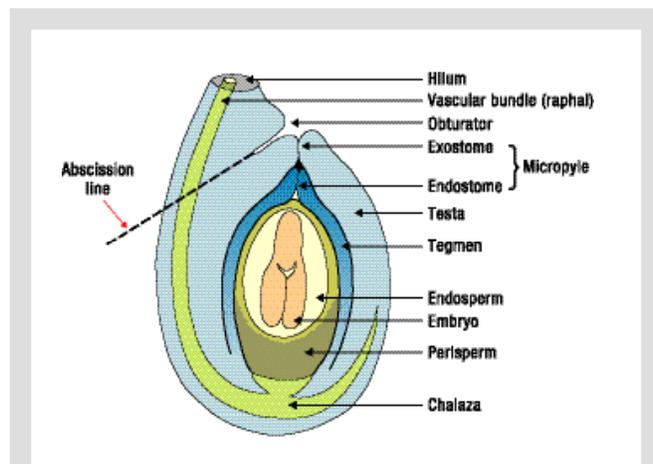


Fig. 82. Typical seed (longitudinal section).



Fig. 83.

in the outer integument is the exostome while that of the inner integument is the endostome. The exostome and the endostome form the micropyle. Unitegmic seeds have only one opening (micropyle) and the seedcoat is called the testa. The seedcoat has a funicular scar called the hilum, indicating the point at which the funiculus separates from the seed. This zone has a different structure and often includes the micropyle. Frequently, a longitudinal ridge (raphe) formed by differential growth of the funiculus is found near the hilar zone. It forms as a result of a curvature of about 80 degrees that occurs during the ontogeny of the anatropous ovules. The hilar zone may extend and be a significant part of the seedcoat as observed in the Sapotaceae (*Manilkara chicle*, *M. zapota* (L.) P., *Micropholis crotonioides*, *Pouteria congestifolia*, *P. viridis*), or may combine its extension with an extension of the chalazal zone (pachychalaza) as seen in the Meliaceae (*Carapa*, *Guarea*), and Hippocastanaceae (*Aesculus*, *Billia columbiana*, *B. hippocastanum*) (figs. 83-84). Other seeds have only a chalazal extension (*Cupania glabra*). A funicular protuberance close to the chalaza is found in many seeds (numerous Cactaceae in the Subfamily Cereaneae). The vascular bundle supplying the ovule follows its course along the raphe—a characteristic easily observed in the seeds of Fabaceae-Papilionoideae (*Erythrina*).

The seedcoat is formed not only by the integument tissue(s) but also by the chalazal and raphal tissues. When the outer layer of the outer integument differentiates as a layer for mechanical protection (exotesta), the outer layer of the raphe and the chalaza undergo an equivalent differentiation. The same happens with the formation of the mesotesta (middle layers) and the endotesta (inner layer of the outer integument). In small seeds, the integument cells undergo mitosis sporadically after fertilization, and their elongation and differentiation form the seedcoat. Many large seeds have complex seedcoats as a result of many anticlinal and periclinal divisions in the integument cells. When periclinal divisions are dominant and more cell layers are formed, the integument is multiplicative



Fig. 84.

(Magnoliaceae, Myristicaceae, Annonaceae, Clusiaceae, Fabaceae, Bombacaceae). If the seedcoat extends primarily by anticlinal cell division and does not develop more cell layers, the integument is nonmultiplicative (Corner 1976). Frequently, multiplicative integuments form seedcoats with many layers (Corner 1976). The periclinal divisions may be diffused or localized in the outer integument. The testa can be soft-textured (*Cojoba arborea*, *C. costaricensis*), hard (*Enterolobium cyclocarpum*, *Samanea saman*, *Tamarindus indica*), or fleshy (*Inga*, *Guarea*, *Punica granatum*, *Carica papaya*, *Magnolia*). The fleshy testa is the sarcotesta. In general, the outer integument is the fleshy and juicy part; however, in *Magnolia* and other related species as well as in *Punica granatum*, the sarcotesta originates only from the mesotesta. In Connaraceae, Meliaceae, and Sapindaceae the fleshy pachychalaza is similar to the aril. It may have lipids, sugars, and attractive color.

The presence of a multiplicative mesotesta is common; these layers may form an aerenchyma (Bursaraceae, Bombacaceae, Meliaceae, Simaroubaceae, Fabaceae). Usually the endotesta divides anticlinally. An endotesta with multiple layers is common in the zoochorous seeds. In most species, the inner integument is thin and slightly specialized; it collapses in early stages and is then partially or totally reabsorbed. In exceptional cases, it forms multiplicative middle layers that produce the aerenchyma (e.g., many Euphorbiaceae), although in several families those layers disintegrate during seed maturation (Boesewinkel and Bouman 1984).

The seedcoat may have cell layers or cell groups with tannins, oils, crystals, mucilage, cork, sclerenchyma, or colenchyma cells. The parenchyma may serve as storage tissue, as chlorenchyma, or as aerenchyma. The tannins form in vacuoles, and are formed by polyphenoles and substances of hard metabolic transformation. The presence of tannins serves as a requisite for alkaloid deposit and probably protects the plant against herbivore predators (insects), pathogens (bacteria, fungi), and light. They also increase seed hardness and provide

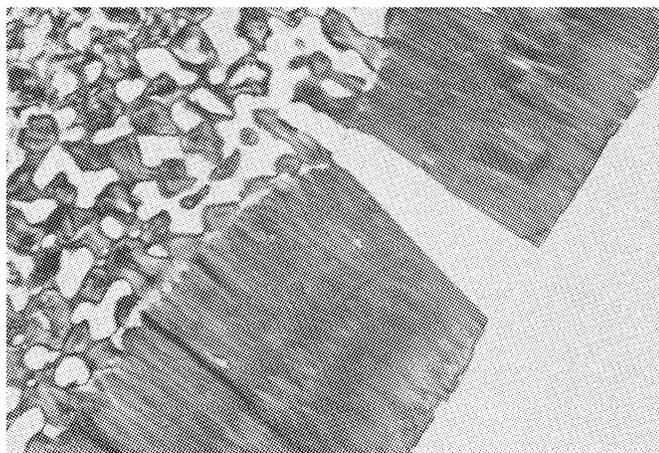


Fig. 85.

color. The crystals are variable in shape and are formed by calcium oxalate, calcium carbonate, or silica (Flores 1999). The mucilage cells are found primarily in the epidermal cells of the exotesta. They form by hydration of substances in the secondary walls of the cells. Some species in Sterculiaceae have mucilage sacs in the testa and tegmen. In Ebenaceae, these sacs are restricted to the tegmen (Boesewinkel and Bouman 1984). Mucilage secretion (myxospermy) appears to help seeds adhere to animals and fix in the soil. Other proposed functions of myxospermy include water retention, germination regulation, oxygen barrier, storage substance, and covering lens (Boesewinkel and Bouman 1984).

Sclerenchyma and collenchyma cells provide mechanical strength. In some seeds, cell walls impregnated with suberin serve as a barrier in the chalazal zone and seal the testal or tegmic layers. These cell walls are also found in the integuments of the hydrochorous seeds and in mucilaginous epidermal cells (Corner 1976). The sclerenchymatic cells (fibers or sclereids) provide hardness and rigidity to the seedcoat. Additionally, the lignin protects against herbivore and pathogen attacks. The more typical macrosclereids are the Malpighi cells of the exotesta in Fabaceae (fig. 85). These cells are elongated radially, have a linea lucida (light line), and in early stages deposit a wall of irregular thickness, which is sometimes lignified. The apical region shows suberized incrustations reinforcing the walls and influencing water permeability. The linea lucida is not involved in cell wall permeability and shows a high density of cellulose microfibrils without interfibrillar spaces. The seeds of Rhamnaceae and Elaeagnaceae have a linea lucida in the external epidermis of the testa. The structure is also present in the external epidermis of the tegmen (Boesewinkel and Bouman 1984, Corner 1976).

When the sclerenchymatous layer forms in the external epidermis of the testa, the seedcoat is called exotestal. The mesotestal seeds have sclerenchyma in the testal middle layers;

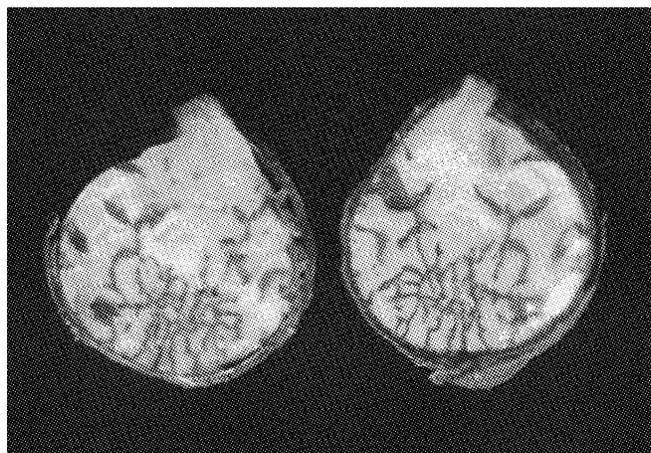


Fig. 86.

the endotestal, in the epidermis of the testa. If the sclerenchyma differentiates in the tegmen, the seeds are exotegmic, mesotegmic, and endotegmic respectively. In families with dry indehiscent fruits or drupaceous fruits (e.g., Anacardiaceae), there is a marked tendency toward seeds with a slightly differentiated testa, sometimes lacking mechanical layers. In extreme cases, the mature seed lacks a seedcoat, as in parasites, some Apocynaceae, and Rubiaceae (Boesewinkel and Bouman 1984, Corner 1976).

The seedcoat has an external cuticle on the external epidermis of the testa, a middle cuticle between testa and tegmen (if both exist), and an inner cuticle between the epidermis of the inner integument and the nucellus (Flores 1999). The cuticles contribute to the impermeability of the seedcoat (to water and gases) and may influence the metabolism and growth of the embryo.

The external surface of the seedcoat has characteristics of taxonomic value. Its morphology sometimes shows the influence exercised by the endocarp of the fruit or by arillar structures (e.g., Myristicaceae). Characteristics such as cell distribution, form, surface (conic, papillate, reticulate, striate, micropapillate, or hairy external wall), and epicuticular waxes (scarce) define the external surface of the seed. In many species, the seeds have stomata localized in the external epidermis of the testa.

Some families, such as Myristicaceae, have seeds with an irregular tegmen producing invaginations inwards; these invaginations protrude into the endosperm. This type of endosperm is ruminant (fig. 86). The seeds with a network of lobules in the endosperm are labyrinthine. The lobulation can be the result of the invagination of the tegmen and the folding of the embryo cotyledons (Vijayaraghavan and Prabhakar 1984).

The testa has special structures such as the caruncle, strophiole, and aril (figs. 54 and 62). The caruncle is a fleshy protuberance or swelling arising in the exostome (*Ricinus*,

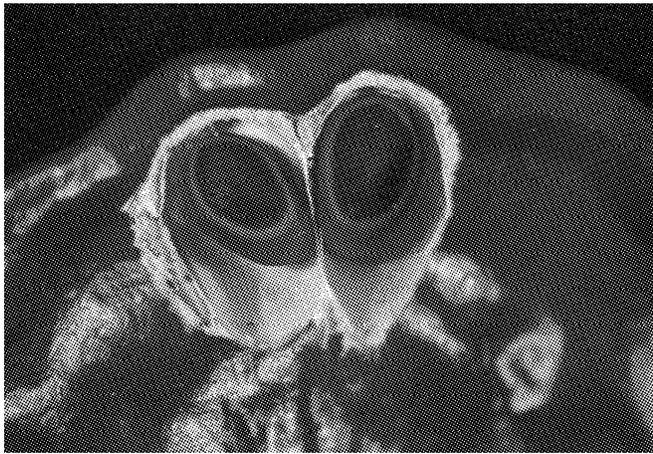


Fig. 87.



Fig. 88.

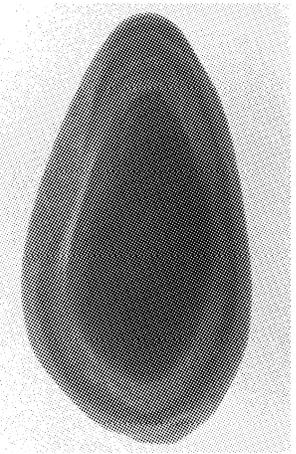


Fig. 89.

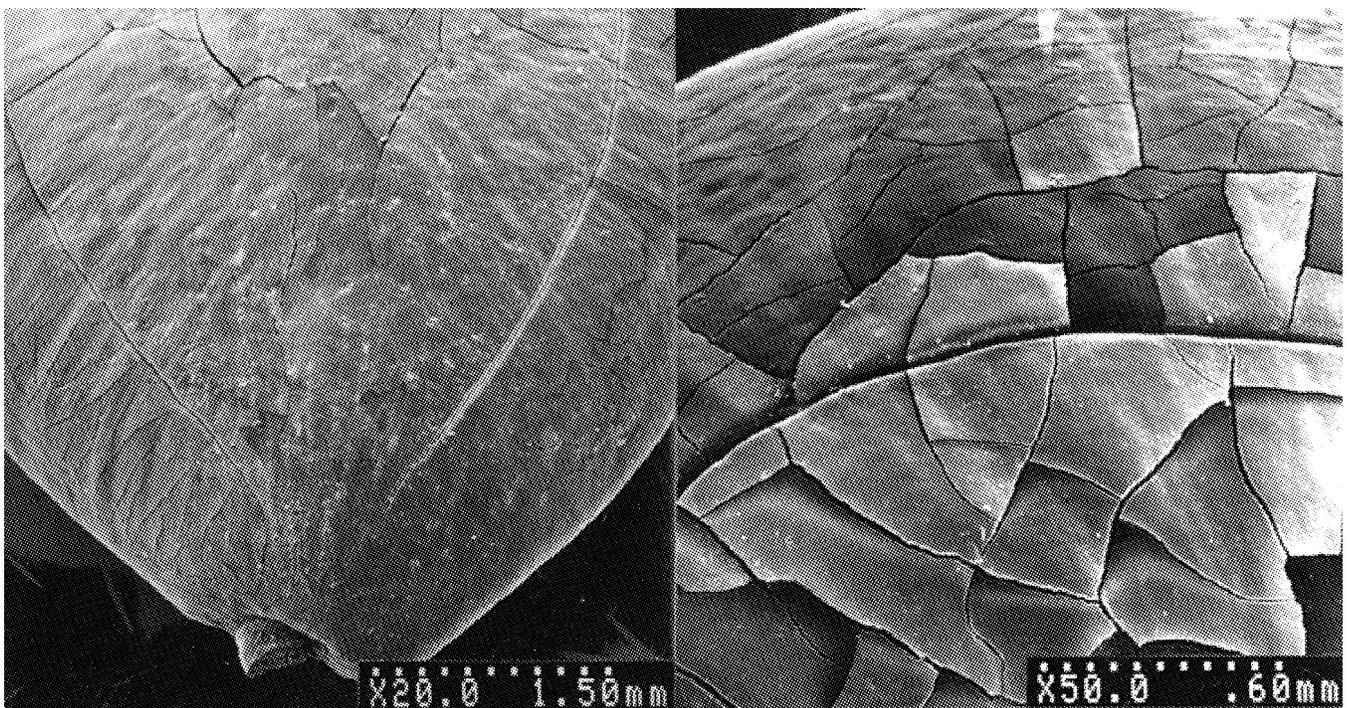


Fig. 90.

*Euphorbia*). Some caruncles (elaiosomes) are oily, or rich in ricinoleic acid (e.g., *Turnera*). These caruncles are white or yellow, fleshy, and edible and are detached, eaten, and dispersed by ants. The strophiole is an outgrowth of the raphe. The aril is a funicular or hilar outgrowth and may cover the whole testa (complete) or part of it (incomplete; e.g., *Stemmadenia*, *Lecythis ampla*, *Phitecellobium dulce*). Some arils are reticulate or have frimbriate projections (frimbriate arils; e.g., *Myristica fragrans*, *Virola*, *Otoba*). The aril develops after fertilization. When complete, the aril may cover the micropyle. Morphologically the caruncle is considered an exostomic aril and the strophiole a raphal aril (Boesewinkel and Bouman 1984; Flores

1999; Van der Pijl 1957, 1972).

Many seeds of Fabaceae-Mimosoideae (*Albizia niopoides* (Spruce ex Benth.) Burkart, *Entada*, *Enterolobium cyclocarpum*, *Pseudosamanea guachapele* (Kunth Harms, *Stryphnodendron microstachyum*, *Samanea saman*) are laterally compressed and have a special mark on each lateral surface called a pleurogram (Corner 1951) and a fissure (linea sutura or linea fissura) delimiting the pleurogram. The linea fissura is parallel to the raphe-antiraphe line and breaks to the hilar end (figs. 87-90). The linea fissura seems to be associated with the gradual dehydration of the seed during maturation and storage, and the slow imbibition of the seed during germination.



Fig. 91.

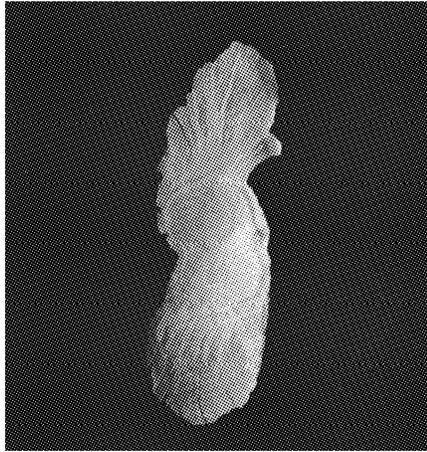


Fig. 93.



Fig. 94.



Fig. 92.

The wings or hairs found on many seeds seem to be devices for anemochorous dispersal (figs. 91-94). Some winged seeds (*Vochysia*, *Qualea*, *Cedrela*, *Swietenia*, *Bernoullia flammea*) have one to several testal extensions that form wings; in many seeds the wing is circular or oval in outline (e.g., *Tabebuia rosea*, *Jacaranda copaia*). Other seeds have a tuft of trichomes at

one end (*Macrohasseltia macroterantha*) or hairs distributed at random. The crowned seeds have a crown of hairs at one end, and the crestate seeds have one or several ridged excrescences. There are also punctate seeds covered by small excrescences or depressions, round umbonate seeds with a central or lateral umbo, and warty seeds with wart-like foldings.

## Vascular System of the Seed

The vascular system of the ovule is formed by procambial or partially differentiated vascular strands. The differentiation of the vascular system occurs during the development of the seed. The vascular system supplying the seed is formed by placental, raphal, and funicular vascular bundles. These bundles transport nutrients to the developing seed. The larger seeds have a more extensive and well-developed vascular system; the small seeds have partially differentiated or no vascular bundles. The large seeds usually have a massive or compound raphal vascular bundle, well differentiated, which ends at the chalaza. Some seeds have additional vascular bundles extending from the chalaza to the outer integument; these are called postchalazal vascular bundles. Some seeds are encircled by a postchalazal vascular bundle along the median plane (Annonaceae, Polygalaceae) and others have a chalazal vascular plexus and a network of vascular bundles. Through intercalary growth, this plexus may replace the seedcoat locally (e.g., *Guarea*). Vascular ramifications in the tegmen are common. In the seeds of species such as the Myristicaceae, the vascular branches enter the tegmen invaginations, increasing the contact with the endosperm. In *Virola koschnyi*, *Otoba novogranatensis*, and *Compsonera sprucei* the vascular branches found in the tegmen invaginations have transfer cells (Flores 1999).

## Storage of Reserves

Seeds contain many substances. Some are typical to cells and tissues and others contribute to nourishing the embryo (before and after germination) and the developing seedling (in its early stages). Seeds store energy in the form of lipids, carbohydrates, and proteins to fulfill the needs of the seed during germination. They are a source of precursors for carbon skeletons and a source of energy when assembling precursors.

The seeds are perispermous if the reserves are stored in the perisperm, endospermous or albuminous if the nutrients accumulate in the endosperm, cotyledospermous if the thick and fleshy cotyledons store the reserves, hypocotylspermous or macropodial when the hypocotyl is the storage organ, and chalazospermous if the nutrients are stored in the chalaza. The cell walls of different seed tissues may also store nutrients.

Lipids, which appear as lipidic bodies in the endosperm and the embryo, are a greater source of nourishment than the carbohydrates. The amount of lipids in a seed varies: 30 percent for the sunflower *Helianthus annuus* and 50 percent for *Ricinus communis*, *Zea mays*, and *Arachis hypogaea*. In the coconut (*Cocos nucifera*) and the African oil palm (*Elaeis guineensis*) the lipid content is higher. The seeds without maturation drying are rich in lipids. For example, the lipid content in fresh seeds of *Virola koschnyi* is approximately 41 percent, in *Calophyllum brasiliense* 38 to 39 percent, in *Minquartia guai-*

*nensis* 37 to 38 percent, and in *Lecythis ampla* 40 percent (Flores 1996). The dried cotyledons of the embryo of *Carapa guianensis* have 65 to 70 percent of unsaturated lipids in the storage parenchyma (Flores 1994g); the endosperm of *Otoba novogranatensis* has about 69 percent of lipids (dry weight) (García-Barriga 1974).

Carbohydrates are stored as starch or in thick cell walls rich in hemicelluloses. Cereals contain 70 to 80 percent starch, legumes  $\pm$  50 percent (Boesewinkel and Bouman 1984, Vijayaraghavan and Prabhakar 1984). The predominant types of carbohydrates stored in cell walls are mannans, xyloglucans, and galactans. The three types of mannans—pure mannans, glucomannans, and galactomannans—are restricted to the endosperm cell walls. The pure mannans are found in the date (*Phoenix dactylifera*), the ivory nut or tagua (*Phytalephas macrocarpa*), the coffee bean (*Coffea arabica*), and *Carum carvi*. The galactomannans are found in the endosperm of the legume seeds (Grant-Reid 1985, Higgins 1984). The mannans and glucomannans are crystalline and insoluble; they confer an extraordinary hardness to the endosperm. The xyloglucans are amiloid and are found in the endosperm or the embryo of approximately 2,600 species, among them *Tamarindus indica* and *Annona muricata*. The galactans are stored in the cotyledons of the embryo of numerous legumes (Boesewinkel and Bouman 1984, Vijayaraghavan and Prabhakar 1984).

Nearly all seeds contain proteins as reserve. Proteins supply the nitrogen needed by the plant in early stages of development (Higgins 1984). The storage proteins are found as protein bodies (aleurone). These grains are the primary source of proteins and minerals, and in addition to the homogeneous protein matrix they contain crystals of proteins and calcium oxalate. Several cations (K, Mg, Ca, Fe, Ba, Mn) are also found as globoid crystals. The protein bodies are found in the embryo as the endosperm or are restricted to a specialized layer (Poaceae, Fabaceae). This layer is active only during germination. Protein reserves are necessary to synthesize the enzymes involved in starch digestion. Nuts are about 40 percent proteins (Higgins 1984). The following species have seeds with a high protein content: *Aesculus hippocastanum*, *Billia columbiana*, *Bertholletia excelsa*, *Lecythis ampla*, *Enterolobium cyclocarpum*, *Leucaena leucocephala* (Lam.) de Wit, and *Entada scandens*.

The seeds with maturation drying accumulate disaccharides, such as the saccharose and oligosaccharides, in the form of stachyose and raffinose. Some propose that these sugars are associated with tolerance to desiccation (Leopold and Vertucci 1986, Leopold and others 1992, Leopold and others 1994); however, some seeds sensitive to desiccation also accumulate sugars and saccharose (*Avicennia marina*) or saccharose and raffinose (e.g. *Quercus robur*) (Farrant and others 1993, Finch-Savage and Blake 1994).