macrophylla, *S. mahogani*), Spanish cedar (*Cedrela odorata*), and other Meliaceae with economic value illustrates this risk.

Pollination

Climatic factors such as wind, rain, moisture, temperature, light intensity, and spectral quality are the stimuli that determine the floral anthesis and the activity of the pollination vectors (Frankel and Galun 1977). The constancy or continuous change of these factors, the graduation or abruptness of any change, and the diurnal or seasonal periodicity of changes can delay or impede pollination. The covering of the pollen and the stigma are involved in the intercellular recognition of signals and stimuli.

The first interaction of pollen and stigma is the capture of pollen by the stigmatic surface, usually 30 to 60 seconds after the initial contact (fig. 34). The epicuticular waxes of the stigmatic surface and the unsteady oils of the exine are placed strategically to function as the initial lipophilic intercellular bond between the matrices of the exine (pollen) and the cutin (stigma). Selective capture of compatible pollen is not apparent in this initial interaction (Ferrari and others 1985).

The second cellular interaction is slower and takes place between pollen and stigma compatibles. When the pollen and the papillae or stigmatic surface come into contact, they form rigid convex surfaces tangentially between them (fig. 34); the macromolecular distances are long and varied. The hydrolysis and polysterification of the substances (oils and waxes) that made the initial contact connect the pollen exine with the cutin matrix. The enzymes of the cuticle (cutinase, estearase) catalyze the process. Usually 15 to 30 minutes after pollination, a tubular connection is established between the pollen and the stigmatic surface. This connection has a diameter double the size of the orifice left by the pollen tube when it crossed the cuticle. The pollen tube develops between the connection, tube, or ocreatine and goes through the cuticle of the stigma (Ferrari and others 1985). Pollen hydration and ocreatine formation may be inhibited when the pollen is incompatible. The pollen tubes of a species show strong phenotypic differences during their growth through the styles of different species. The apical end shows cytological anomalies when there are specific incompatibilities in the stigma, style, or embryo sac.

Fertilization

Fertilization in angiosperms is a two-part process: one sperm fuses with the egg cell, giving rise to the zygote, a process called syngamy by Strasburger and others (1908); another fuses with the two polar nuclei of the central cell, creating the endosperm (triple fusion).

Usually the pollen tube enters the ovule through the micropyle (porogamy), through the chalaza (chalazogamy), or through the integuments (pleurogamy). The sperm fertilizing the egg cell first penetrates through the filiform apparatus. The sperm is then transferred to a synergid cell and later to the egg cell. The fusion between the sperm and the egg cell plasmalemma results in a bridge through which the sperm enters the egg cell. The fusion of one sperm nucleus with the egg produces a diploid zygote; the fusion of another sperm nucleus with the nuclei of the central cell produces the triploid endosperm, typical in 60 to 70 percent of the dicotyledons (monosporic embryo sac of the *Polygonum* type) (fig. 21). In the other embryo sac types, the endosperm varies from 2n (*Oenothera* type) to 3n in the *Allium* and *Adoxa* types. The remaining embryo sac types develop a polyploid endosperm (Flores 1999, Maheshwari 1950). The double fertilization transforms the ovule into the seed.

Fertilization can occur within the same flower (autogamy), between two flowers on the same tree (geitonogamy), or between flowers of different individuals (allogamy or xenogamy). Some species can have autogamy and allogamy on the same tree; this phenomenon is called alautogamy (Radford and others 1974).

SEXUAL STRUCTURE IN GYMNOSPERMS

The gymnosperm, which means naked seed, is a group of superior vascular plants in which the ovules and seeds are not enclosed within a carpel. They are exposed on *scales* or similar structures, equivalent to sporophylls (Foster and Gifford 1974).

Among the gymnosperms, the Coniferales are the dominant group. Coniferales are a primarily perennial, woody species, many of which have economic value. In the Neotropics, species of frequent use and economic value are numerous, including *Pinus oocarpa* Schiede ex Schltdl., *P. montezumae* Lamb., *P. caribaea* Morelet, *P. maximinoi* H.E. Moore, *P. patula* Schiede & Schltdl. & Cham., *P. ayacahuite* C. Ehrenb. ex Schltdl., *Abies guatemalensis* Rehder, *A. religiosa* (Kunth) Schltr. & Cham. (Pinaceae), and the ciprecillos (*Podocarpus guatemalensis*, *P. costaricensis*, *P. macrostachyus*, *Prumnopitys standleyi* (Buchholz & Gray) de Laub., Podocarpaceae).
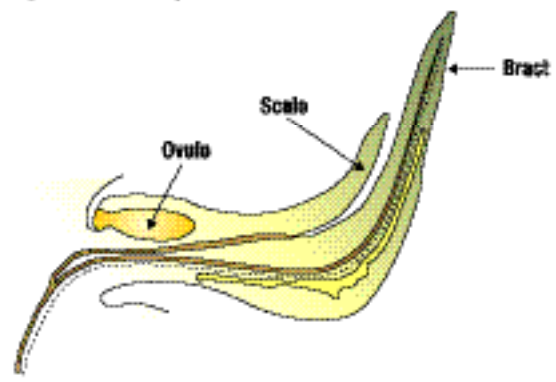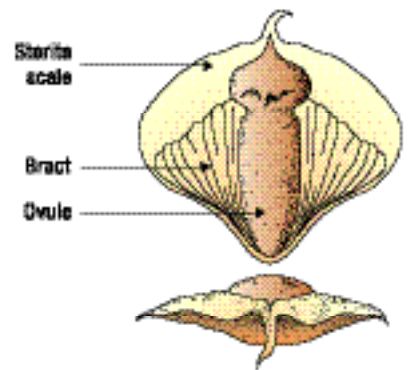
Coniferales are predominantly monoecious and have ovules and pollen grains clustered in strobiles or cones of different shapes and sizes. All the species of Pinaceae are monoecious, but some families, such as Cupressaceae and Podocarpaceae, have both dioecious and monoecious species (Bierhorst 1971, Foster and Gifford 1974, Sporne 1965). The strobile has a central axis with numerous imbricate sporophylls (2n), called scales or bracts, distributed in a closed spi-
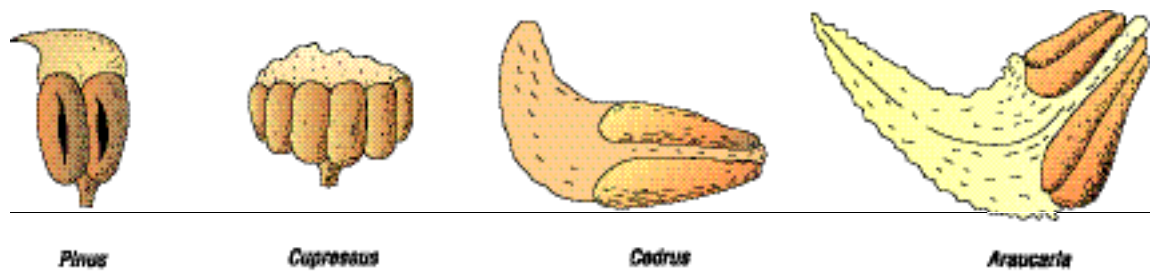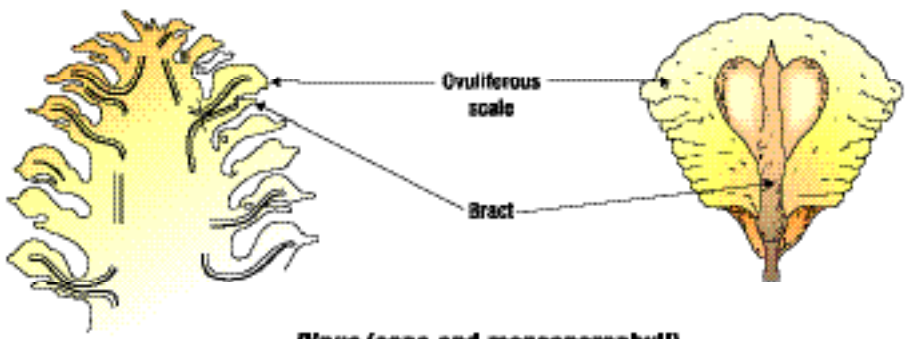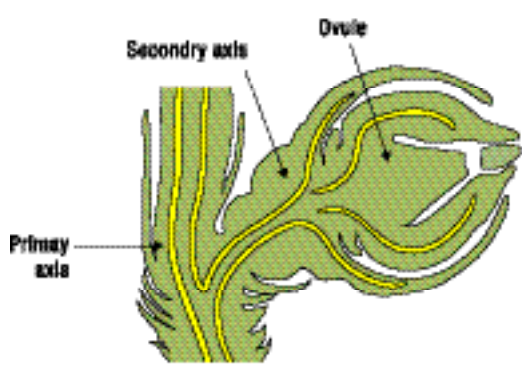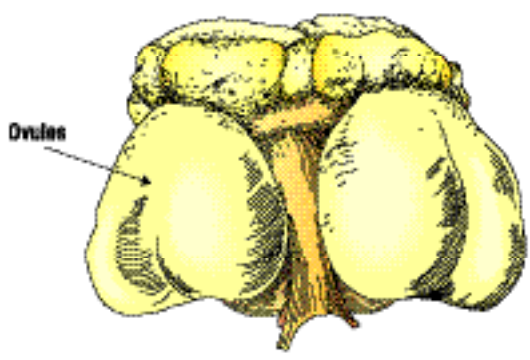
Fig. 35. Micro and megasporophylls in several gymnosperms.

ral (fig. 35). The male strobile (androstrobile) has microsporophylls; usually each microsporophyll has two pollen sacs (microsporangia) in the abaxial (lower) surface. However, *Cycas media* may produce more than 1,000 sacs, *Zamia floridana* several dozen, the Taxodiaceae 2 to 9, the Cupressaceae 3 to 6 (sometimes more), the Taxaceae 2 to 8, and the Araucariaceae 5 to 20 (Foster and Gifford 1974).

In families such as Pinaceae, the female strobile (gynostrobile) has megasporophylls and each has two ovules inverted in the adaxial (upper) surface. Other families have more or fewer ovules per megasporophyll; for example, the Taxodiaceae have two to nine and the Cupressaceae two to many, while Araucariaceae, Podocarpaceae, and Taxaceae have a single ovule (Foster and Gifford 1974, Sporne 1965).

The numerous male strobiles have a short life span;

when mature they may have a yellowish, purplish, or reddish coloration. The less numerous female strobiles also show variations in color. The color is genetically determined and can vary with elevation; for example, the white fir (*Abies concolor*) has light green or dark purple cones. The morph with green cones is more common in low elevations, while the morph with dark purple cones becomes more numerous with increases in elevation (Sturgeon and Milton 1980).

Reproductive Cycle

Figure 36 illustrates the reproductive cycle in a gymnosperm. Anther dehiscence permits pollen release, and scale opening in the cone permits pollen entrance. The period of postpollination-prefertilization may last from weeks to years. In the
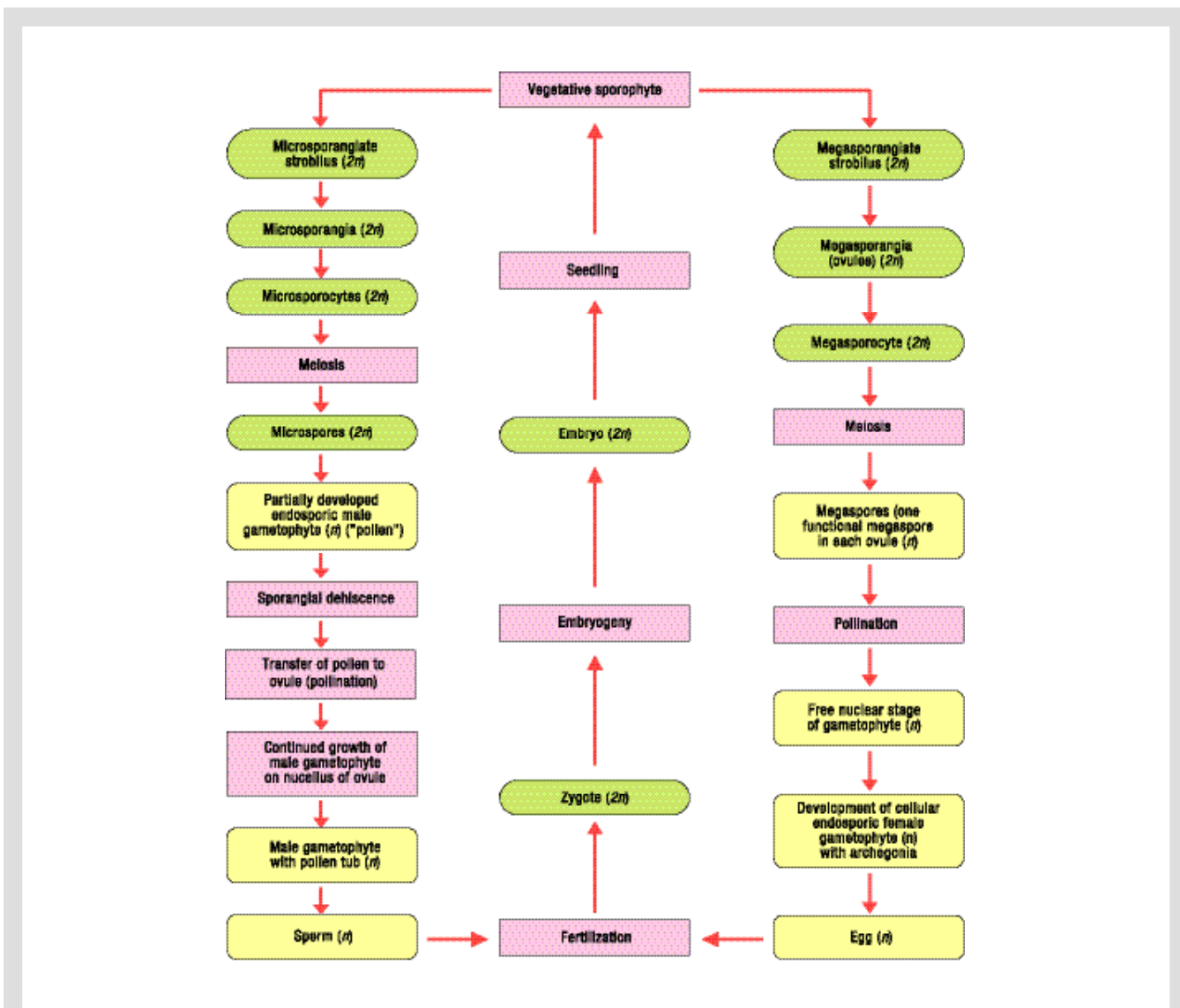

Fig. 36. The reproductive cycle in gymnosperms.

species *Pinus*, the period from ovule inception to seed dispersal can last 2.25 years (Krugman and others 1974, Bonner and others 1994) (fig. 37). This period includes pollen germination, pollen tube growth, and penetration of the nucellus, as well as archegonium and gamete development (Owens and Morris 1990).

Pollen

The microsporangium (2n) or pollen sac has wall, tapetum (in many species), and sporogenous cells. The latter give rise to the microspore mother cells or microsporocytes, each producing four microspores (n) by meiosis. The microspores remain inside the microsporocyte wall for variable periods of time depending on the species (figs. 36-38). During this period, the microspore divides three times and forms the microgametophyte or partially developed pollen grain. The latter has two prothallic cells (they die early), a generative cell, and a tube cell. Pollen sac opening and pollen grain release usually occur in this stage. After pollination, the pollen grain germinates and develops the pollen tube, which penetrates through the nucellus to the archegonium, absorbing nutrients from nucellar origin. Usually, the generative cell divides during pollen tube penetration, giving rise to two or sometimes more sperm. In the cycads and *Ginkgo*, the sperm are multiflagellate; the conifers lack flagella and are steady (Bold 1967, Foster and Gifford 1974, Jensen and Salisbury 1972, Sporne 1965).

In genera such as *Pinus*, *Podocarpus guatemalensis*, and *Prumnopitys standleyi*, the pollen has air vesicles or wings (Torres-Romero 1988); in others, such as *Pseudotsuga*, the pollen grains are spherical or oval with a smooth wall and lack wings. The pollen is yellow and abundant (Bierhorst 1971, Foster and Gifford 1974, Krugman and others 1974).

Ovule

The ovule has one integument fused to a multicellular body called the nucellus (functionally equivalent to the megasporangium). In the apex (distal end) the integument forms the micropyle (figs. 36-39). The proximal end, opposite the micropyle, is the chalaza. In the micropylar end of the megasporangium, a megasporocyte or megaspore mother cell (2n)
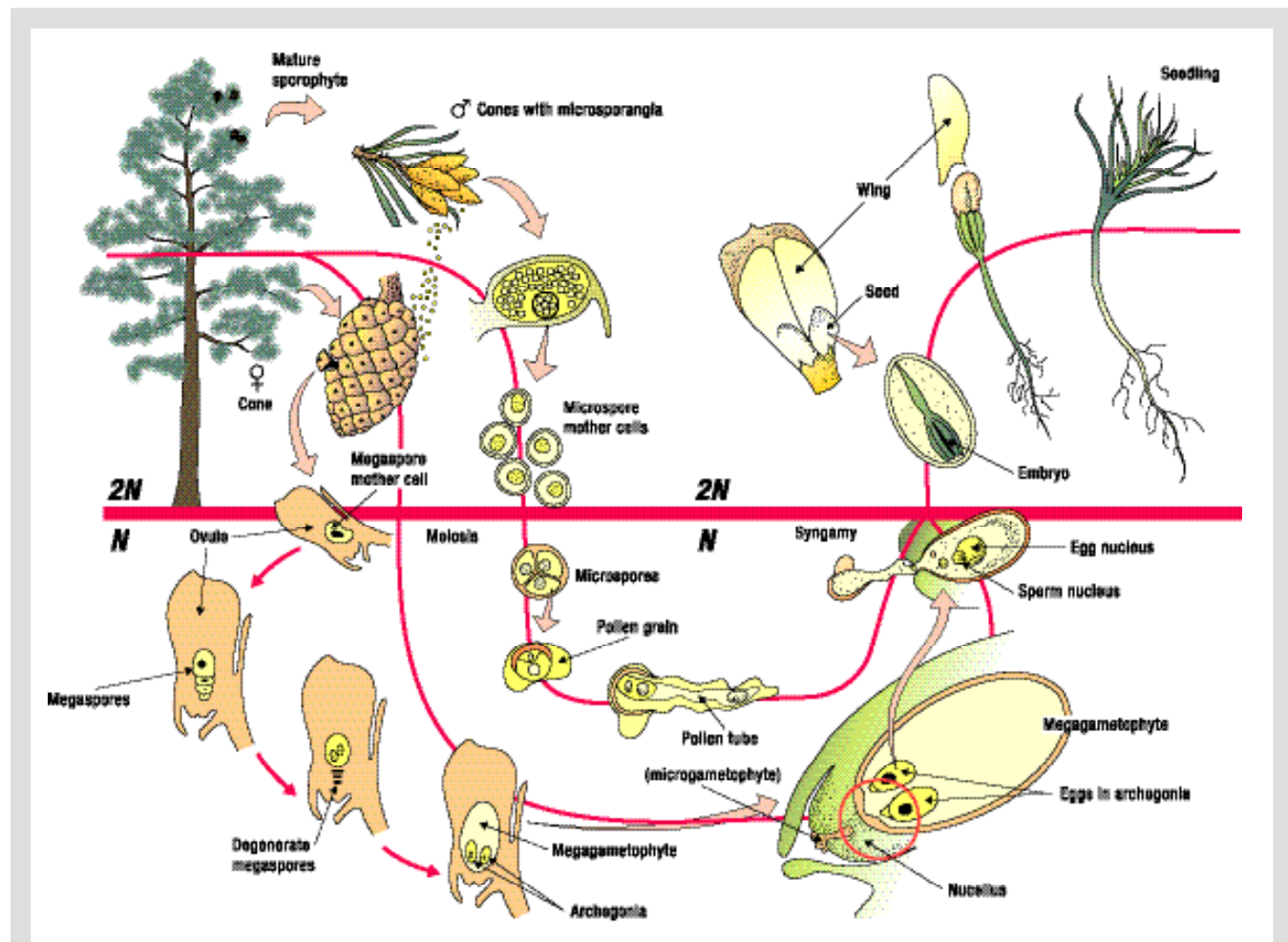

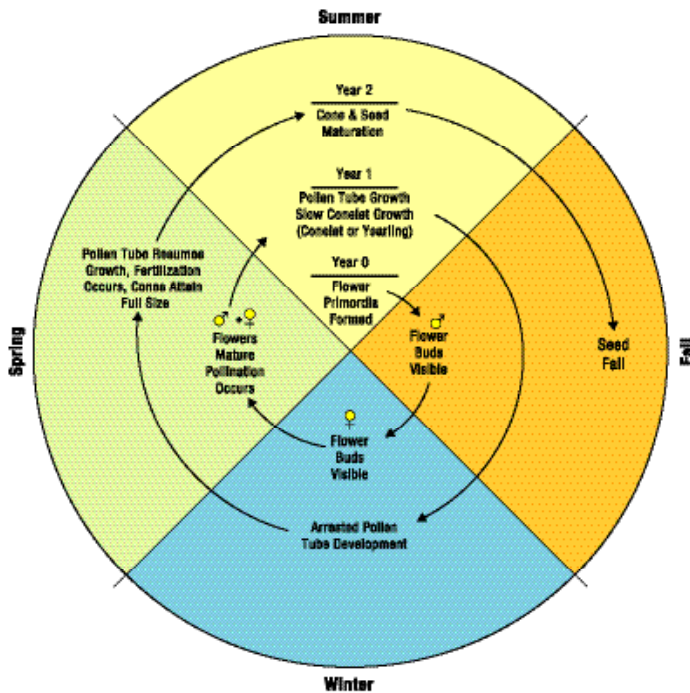**Fig. 37.** The reproductive cycle of *Pinus*. (Redrawn from Jensen & Salisbury. 1972).

Fig. 38. Life cycle of a gymnosperm (*Pinus* sp.).

(Redrawn from Bonner, Vozzo, Elam & Land. 1994).

develops. Through meiosis, this cell originates a linear tetrad of megaspores (n); only the innermost megaspore is functional. Inside the functional megaspore, numerous free nuclear divisions occur (e.g., up to 2,000 nuclei in the Pinaceae); cell wall formation occurs later. It begins in the periphery and proceeds centripetally. A cellular megagametophyte forms and is surrounded by the megaspore wall, which frequently increases in thickness (Sporne 1965). The megagametophyte cells are rich in nutrients. During or after cell wall deposition, some surface cells in the megagametophyte, usually placed at the micropylar end, form varying numbers of archegonia (e.g., 2 to 6 in *Pinus*, 2 in *Ginkgo*, up to 60 in *Sequoia*). A jacket of sterile cells enclosing and protecting an egg cell placed at the canal base forms each archegonium.

Pollination and Fertilization

Pollination is the transport of the partially developed endosporic microgametophyte (pollen grain) from the pollen sac to the micropyle. The developmental stage in which polli-
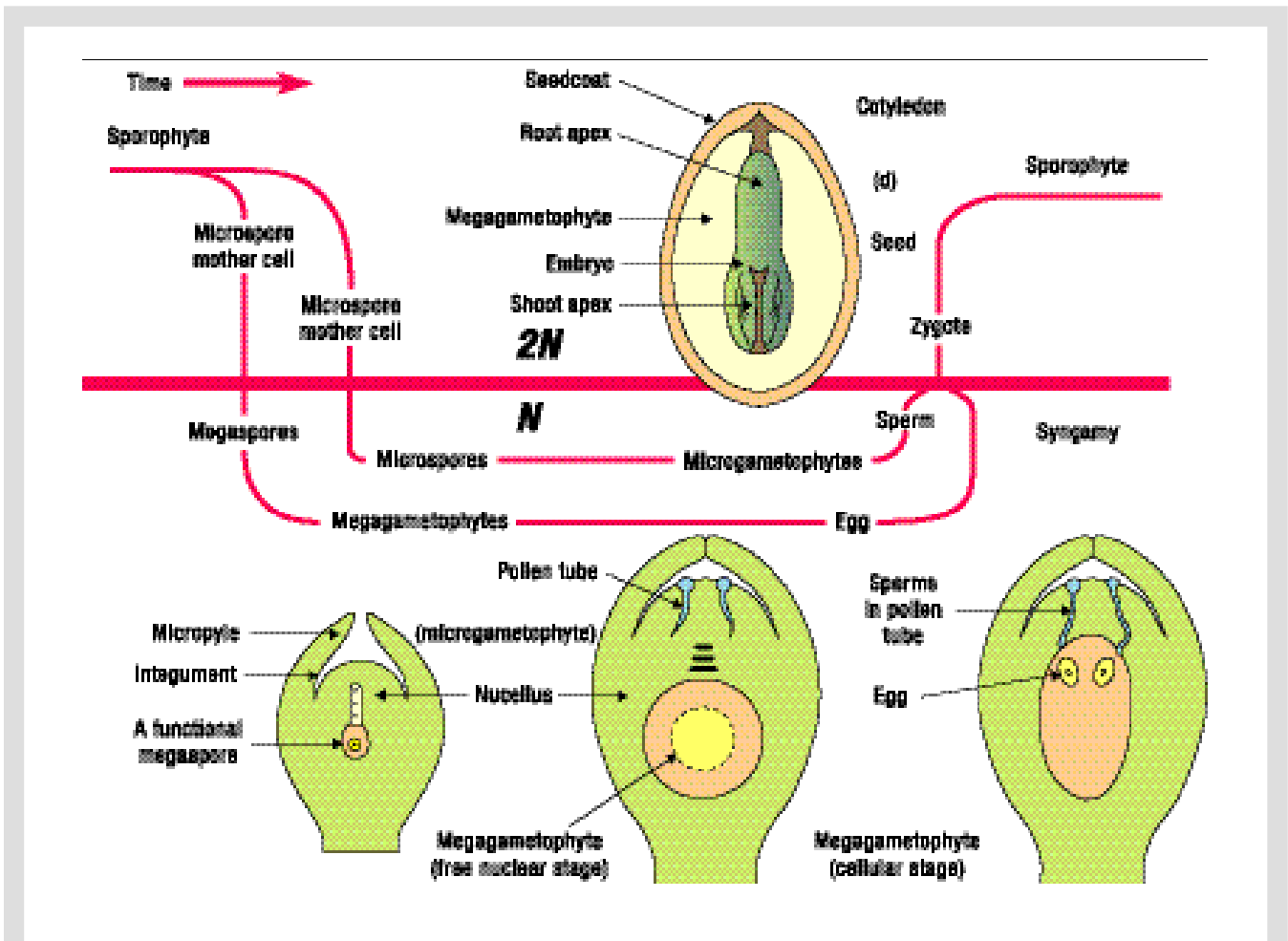

Fig. 39. The development of the megagametophyte and the seed of the gymnosperms. (Redrawn from Jensen & Salisbury. 1972).

nation occurs in gymnosperms varies. In most conifers, taxads, and *Ginkgo* it occurs when the ovule has only sporogenous cells or megaspore mother cells (Singh and Johri 1972). During the prepollination phase the micropyle is open and many cell divisions occur in the ovule. In many species, a pollen chamber is formed at the micropilar end through degeneration of nucellar cells (Singh and Johri 1972).

The wind is the main pollination vector, although several species are entomophilous. Coleopterans and hymenopterans are the most frequent agents. Examples of entomophily include *Zamia pumila* (Tang 1987), *Macrozamia communis* (Chadwick 1993), and *M. riedlei* (Connell and Ladd 1993). The angiostrobiles of some cycads release a strong odor, which helps to attract the insects (Chamberlain 1935). Many conifers, such as *Pinus*, have pollen adhering to the integument and floating later in the liquid exuded by the ovule (pollination drop). While the drop evaporates, the pollen is mobilized to the base of the micropylar canal where it finds the egg cell (Owens and Blake 1985, Singh and Johri 1972). In other species, such as *Larix occidentalis* and *Pseudotsuga menziesii* (Mirb.) Franco, the pollen is captured and detained by a stigmatic extension with many trichomes. The trichomes produce a small secretion that contributes to the initial development of the pollen tube (Owens and Molder 1979, Owens and Morris 1990). The pollen tube enters the megaspore wall and elongates to reach the archegonium where it establishes (Foster and Gifford 1974, Owens and Morris 1990). Usually, a long period of time elapses between pollination and fertilization. In this period the ovule undergoes several changes: the closing of the micropylar canal and the increasing in size, through cell division and activation, of the spongy tissue or tapetum. The latter originates from sporogenous cells not functioning as spore mother cells or from nuclear cells surrounding the sporogenous tissue. Later, this tissue degenerates and collapses (Singh and Johri 1972).

The primary difference between gymnosperms and angiosperms is that fertilization in the former is not a two-part process. A single fertilization occurs in which one sperm fuses with the egg cell and the zygote (2n) develops. The remaining sperms degenerate and no true endosperm is formed. Usually, the egg cells of several archegonia are fertilized; however, only a single embryo develops. The reserve materials stored in the female gametophyte nourish the embryo. The ovule is usually the same size as the mature seed. *Ginkgo* and the cycads have an haustorial pollen tube (Sporne 1965). Double fertilization has reportedly occurred in several gymnosperms such as *Ephedra*, *Gnetum*, *Pseudotsuga*, *Thuja,* and *Welwitschia*; nevertheless, double fertilization has been corroborated only in *Ephedra nevadensis* (Friedman 1986, 1987, 1990).

THE FRUIT

THE ANGIOSPERM FRUIT

Structure, development, and ripening

The fruit is the structure containing the seed. It develops from the gynoecium of the flower, which is frequently associated with other floral organs. The process of fruit development has four stages:

(1) Initiation and development of the floral bud leading to the formation of the mature flower, with one or several ovules in the gynoecium (Nitsch 1965).

(2) Cessation of cellular division and elongation during pollination, pollen tube development, and ovule fertilization (Nitsch 1965). After pollination, many flowers close the corolla or undergo a fast collapse of the corolla and the other floral organs. Floral collapse is correlated to increasing respiration and ethylene production (Flores 1999, Leopold and Kriedemann 1975).

(3) Postfertilization events:

Growth of the ovary wall and associated tissues, by cell elongation and ovary wall transformation into the fruit wall or pericarp.

Seed development from the fertilized ovule; however, some fruits may develop without fertilization or seed development (parthenocarpy). In general, seed development and perianth and stamen withering and abscission are simultaneous (Flores 1999, Leopold and Kriedemann 1975, Nitsch 1965).

(4) Fruit ripening followed by senescence and, sometimes, dehiscence and abscission.

The pericarp can be more or less differentiated and frequently shows two or more different layers. If the layers are distinguishable, they are called (from the outside to the inside): exocarp (epicarp), mesocarp, and endocarp. These terms are used for descriptive purposes and do not relate to the ontogenetic origin of the layers.

Numerous fruits have sigmoid growth patterns, which start with an exponential increase in size, diminishing later to

adjust to a sigmoid pattern. Other fruits have more complex growth patterns involving periods of growth with an interval of reduction or detention of growth. The fruits of many tropical trees have the latter type, as well as some crops with edible drupes (Leopold and Kriedemann 1975).

Fruit growth requires cell division and cell elongation. The range of cell division differs from one fruit to another. Some complete division during pollination while others extend it into the postpollination period (Leopold and Kriedemann 1975). The reserves stored by fruits are synthesized in the leaves and transported by the phloem. The existence of haploid, diploid, and triploid tissues (sporophyte 2n, embryo 2n, but differing from the sporophyte genome; the endosperm usually 3n, and the perisperm 2n) complicates the growth pattern. During fruit development, the differential growth follows different directions in the distinct parts and tissues of the fruit.

Normally, fruit development depends on and is controlled by growth regulators synthesized in the developing seeds. The seeds produce auxins, gibberellins, cytokinins, abscissic acid, and ethylene. The relationships between these substances are very complex but the most important fact is the balance of regulators at the different stages of development (Kozlowski 1971, Leopold and Kriedemann 1975, Nitsch 1965). In many species a fruit lacking seeds can develop well; for example, the empty and filled fruits (samaras) of *Terminalia amazonia* and *T. oblonga* (Ruiz & Pav.) Steud. are indistinguishable externally (Flores 1999, 1994h). Generally, the extraction of fertilized ovules from a developing fruit stops development.

Fruit shape usually reflects the internal distribution of the seeds (e.g., *Cojoba arborea*), and seed shape frequently reflects the number of seeds inside the fruit (e.g., *Carapa guianensis* (Flores 1994a), *Eschweilera panamensis*, *E. costaricensis*). Seed number inside the fruit and final fruit and seed size are correlated. In many cases, the fruit shape reflects the internal pressures exerted by the overgrown seed(s) developing inside it; in this case, embryo growth is limited by the pericarp (e.g., *Prioria copaifera* Griseb., *Dipteryx panamensis*). Fruit maturation is the ensemble of processes associated with the attainment of maximal size and the qualitative transformation of the tissues. The latter involves tissue softening as a product of hydrolytic conversions of stored reserves, as well as changes in pigmentation, production of tastes, and disappearance of astringent substances (e.g., *Achras*, *Elaeoluma*, *Manilkara*, *Micropholis*, *Pouteria*, Sapotaceae).

The hydrolytic changes in the reserve materials result in the production of sugars by starch and lipid chemical transformation. Proteins follow an opposite tendency; their synthesis intensifies during the process of ripening (Biale 1950, 1964; Sacher 1973). Enzymes present in the tissues soften the fruit

tissues and the process requires that pectic substances present in the cell walls become soluble.

Fruit ripening promotes drastic changes in the respiratory rate. The increase in respiration known as climacteric respiration is related to ethylene concentration. Other events associated with fruit ripening include the increase in ribonucleic acid (RNA) and the change in cellular permeability. Climatery is the developmental period of certain fruits (especially fleshy fruits) in which many biochemical changes occur that determine the transition from growth to senescence and ripening. These changes are promoted by the autocatalytic production of ethylene (Smith and Parker 1966).

Fruit Abscission

Abscission is the organized separation of cells resulting in tissue separations; this occurs in leaves, flowers, fruits, and stems (Leopold and Kriedemann 1975). Abscission occurs during the opening of many types of fruits (fruit dehiscence). The actions of growth regulators cause abscission at different stages of fruit development. When it occurs at maturity, the fruits may contain seeds (indehiscent fruits; e.g., *Minquartia guianensis*, *Prioria copaifera*). The fruit usually lacks seeds if the dehiscence precedes abscission (e.g. *Cedrela*).

The abscission zone varies in the different fruits and a fruit may have more than one zone. For example, apples abscise at the base of the pedicel, while *Prunus* (prunes), *Calophyllum brasiliense*, and *Minquartia guianensis* first separate at the fruit base and then at the pedicel base.

The degree of cell differentiation in the abscission zone also varies from one fruit to another. Abscission is an active process involving the separation of the middle layers of the cell walls in the abscission line, under enzymatic action. Usually a cellulase and a polygalacturonase are involved. The abscission process requires the synthesis of proteins; e.g., the ethylene stimulates the abscission and induces the synthesis of enzymes in the cell wall (Biale 1950, Leopold and Kriedemann 1975, Sacher 1973, Wilson and Hendershott 1982).

Dehiscence

The spontaneous breaking of the pericarp allowing seed dispersal is known as dehiscence. Methods of dehiscence are diverse (fig. 40). If the ovary derives from a single carpel, the pericarp may break longitudinally along the ventral suture (suture joining the carpel margins), along the dorsal suture (midvein line), or along both sutures. In ovaries with two or more carpels, tissue separation takes place along the lines (septa) joining contiguous carpels; this type of dehiscence is called septicidal. Rupture along the carpel backs (middle of the
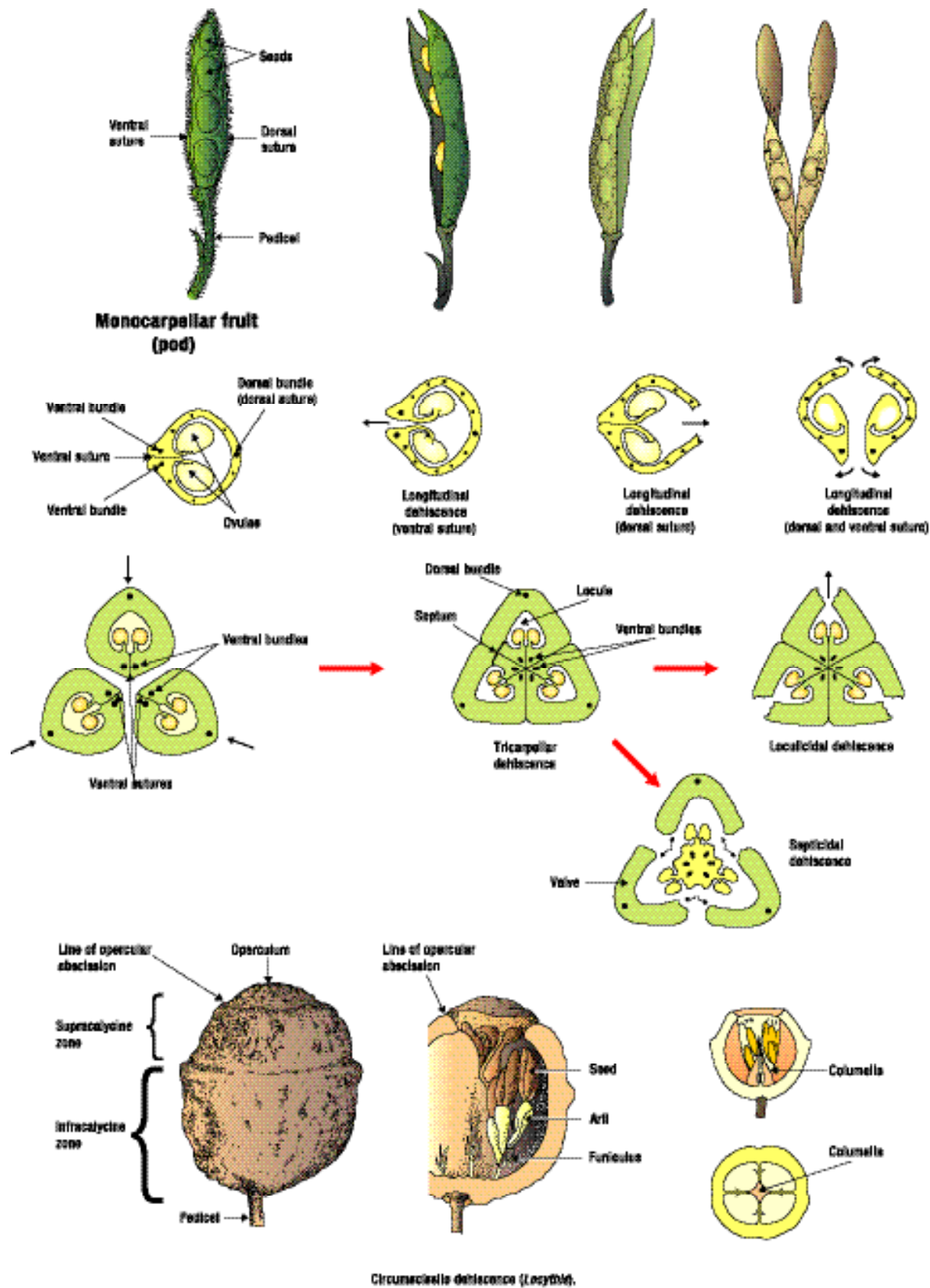
Fig. 40. Types of fruit dehiscence.

loculus) where the dorsal bundles are located is loculicidal dehiscence. In some fruits the dehiscence that occurs along a horizontal ring involving all carpels is known as circumscissile dehiscence. Dehiscence can also take place along one or several pores (poricide dehiscence) which sometimes have an operculum (poricidal-operculate dehiscence).

Classification of Fruits

Flower organization in terms of carpel number, distribution, degree of fusion, and structure influences fruit size, shape, texture, and anatomy (Flores 1999). Fruit classifications are artificial and emphasize certain anatomical and biological characteristics, such as fruit texture (dry or fleshy) and dehiscence (dehiscent and indehiscent). Although these characteristics are valid for classification purposes they lead to juxtapositions and duplications of types in some classification systems (Flores 1999, Foster and Gifford 1974). The classification system described in this chapter is very simple and oriented to tree species; it omits the subtypes not found in tree fruits such as the caryopsis typical of grasses and the cypsela common in the Asteraceae. The fruits are separated into three categories: sim-

ple, aggregate, and multiple. A simple fruit is originated by a single gynoecium, unicarpellar or syncarpic. The aggregate fruit is derived from an apocarpic gynoecium; each carpel keeps its identity until ripening. The multiple fruit derives from an inflorescence; that is, from a combination of the gynoecia of many flowers, which are sometimes coalescent. If any of these fruits has extracarpellar tissue it is an accessory fruit (Flores 1999, Foster and Gifford 1974).

Simple Fruits
Pericarp texture is the basis used to categorize the simple fruits into dry (dehiscent and indehiscent) and fleshy fruits.

Dry Indehiscent Fruits
Those fruits that remain closed at maturity. They usually arise from ovaries in which only a single seed develops, although in some cases more seeds are present. This category includes several types of fruit (fig. 41):

Achene. Small fruit bearing one seed fused to the fruit wall at a single point; it derives from a superior ovary with only one locule; e.g., the sunflower (*Helianthus annuus*, Asteraceae).
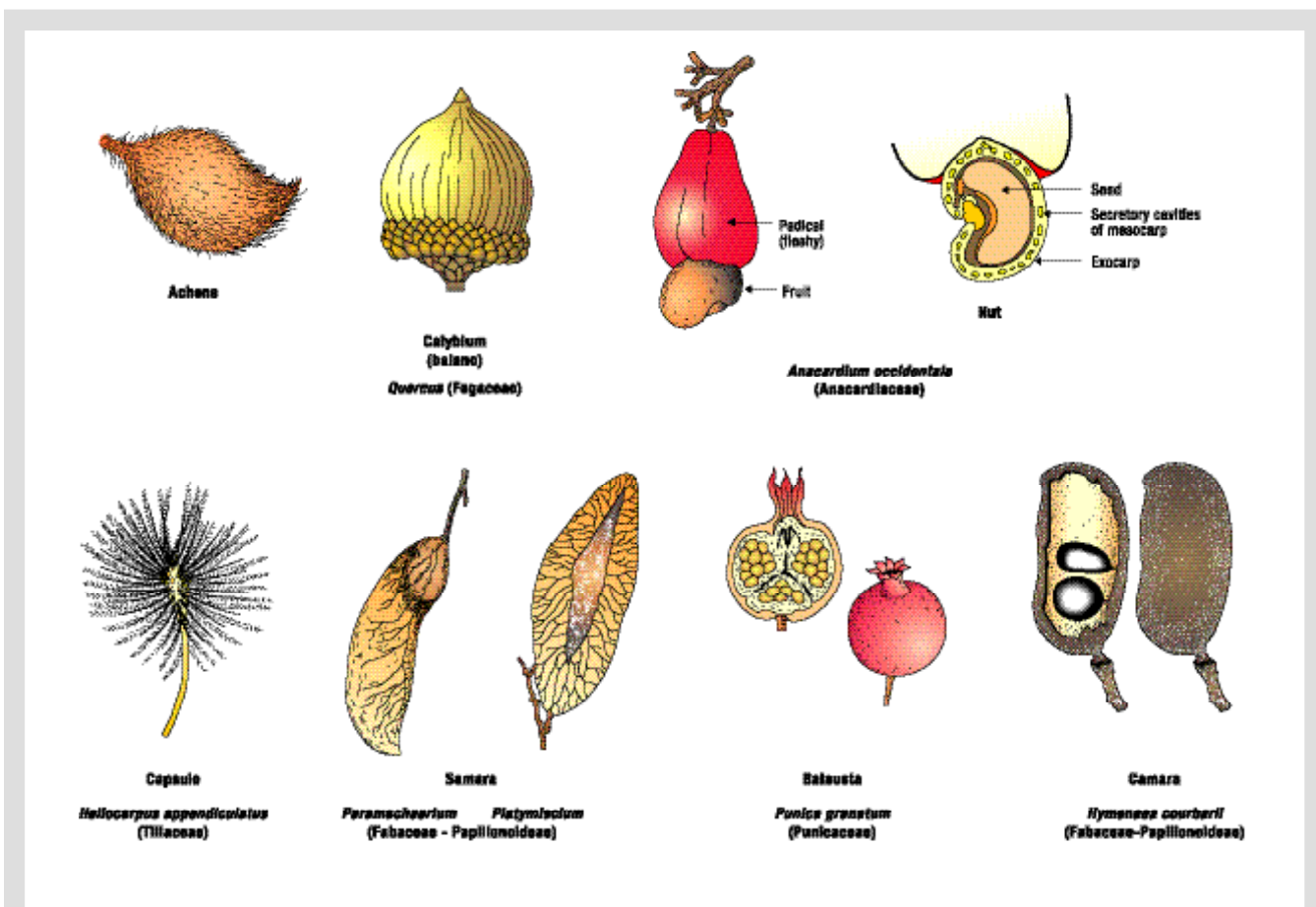

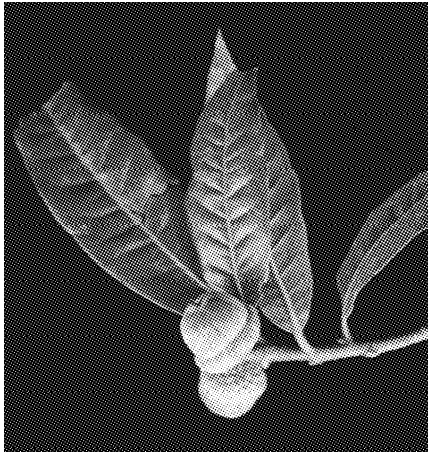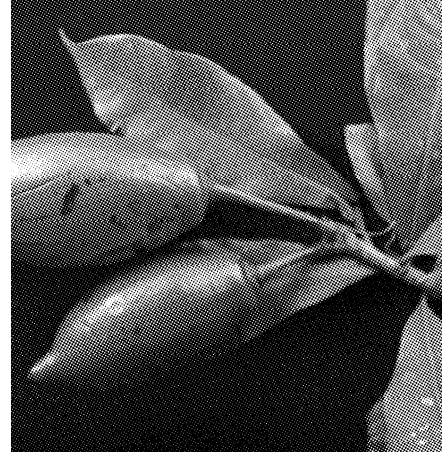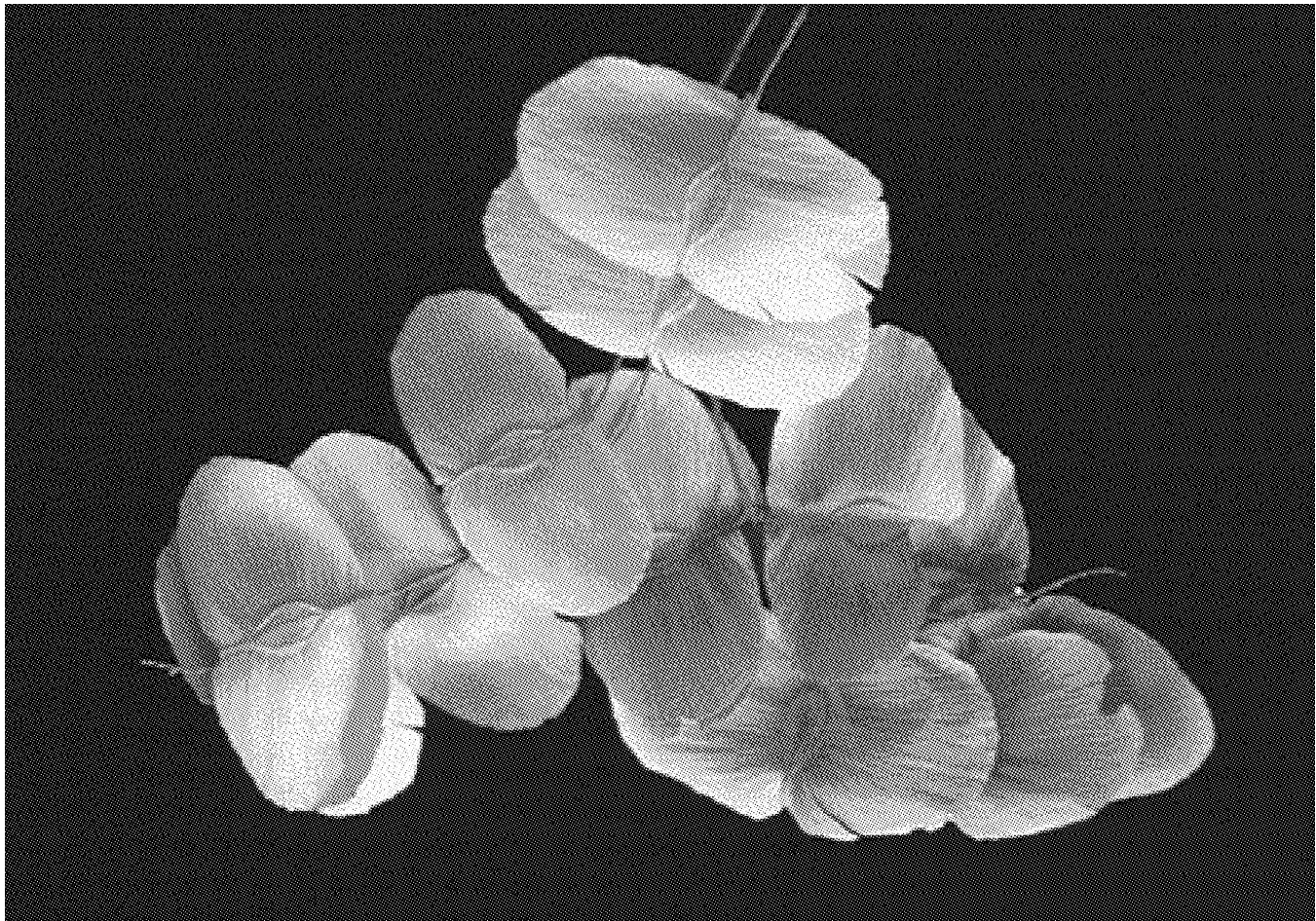**Fig. 41.** Dry indehiscent fruits.

Fig. 42.

Fig. 43.

Fig. 44.

Fig. 45.

Balausta. Fruit with numerous locules and numerous seeds; the pericarp is coriaceous; e.g., *Punica granatum* (Punicaceae).

Calybium (balano). Hard fruit with only one locule developed in the mature fruit (figs. 41 and 42). The calybium derives from an inferior ovary; e.g., the oaks (*Quercus*, Fagaceae). The oaks have tricarpellar, trilocular flowers with two ovules per locule, but only one locule and one seed develop (Abbe 1974).

The *Quercus* fruits have a dry, cupuliform involucre; because of that the fruit is sometimes classified as an accessory fruit under the name of cupule or glans.

Indehiscent capsule. Fruit derived from an ovary with two or more locules (figs. 41 and 43-44); e.g., *Crescentia cujete*, *Amphitecna sessilifolia* (Bignoniaceae); *Catostema fragrans* (Bombacaceae); *Apeiba tibourbou*, *Heliocarpus appendiculatus* (Tiliaceae); and *Simira maxonii* (Rubiaceae).

Fig. 46.
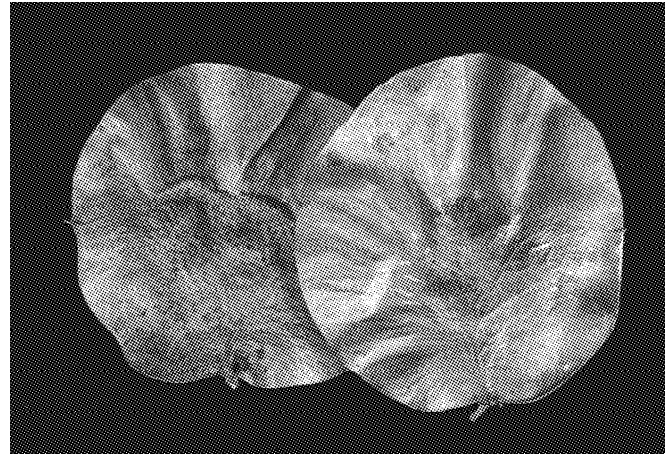
Fig. 47.

Fig. 48.

Nut. Fruit with only one seed. The pericarp is hard. Usually the nut derives from a unilocular ovary; e.g., *Anacardium excelsum* and *A. occidentale* (Anacardiaceae). In *A. occidentale* the fleshy structure corresponds to the pedicel (fig. 41).

Samara. Winged fruit or diaspore (figs. 41 and 45-48); e.g., Anacardiaceae (*Astronium graveolens*), Bombacaceae (*Cavanillesia platanifolia*), Combretaceae (*Terminalia amazonia*, *T. oblonga*), Oleaceae (*Fraxinus uhdei* (Wenz.) Lingelsh.),

Fabaceae-Caesalpinioideae (*Sclerolobium costaricense*, *Tachigali versicolor*), Fabaceae-Papilionoideae (*Dalbergia retusa*, *Hymenolobium mesoamericanum*, *Platymiscium pinnatum* (Jacq.) Dugand, *P. pleiostachyum*, *Myrospermum frutescens*, *Myroxylon balsamum* (L.) Harms, *Paramachaerium gruberi*, *Pterocarpus hayesii*), Polygonaceae (*Triplaris surinamensis*), and Ulmaceae (*Phyllostylon brasiliensis* Capan. Ex Benth. & Hook f.). Some authors call the samara of different Fabaceae samaroid pods.

Fig. 49.

Fig. 50.
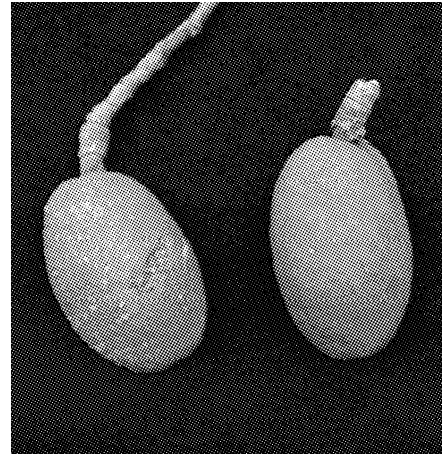
Fig. 52.
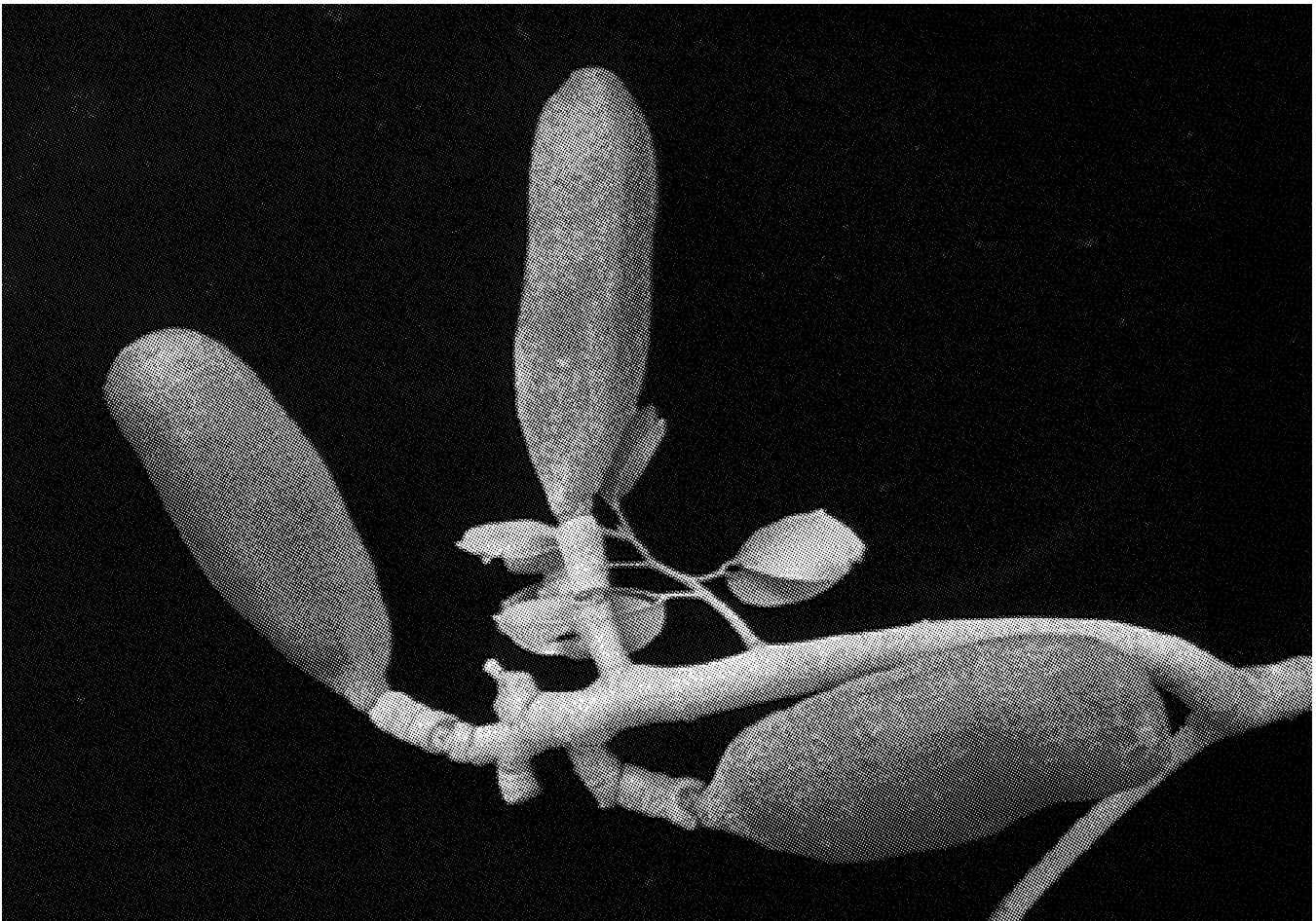
Fig. 51.

Camara. Unicarpellar fruit, indehiscent or late dehiscent. The fruit pericarp and the seedcoat are independent (figs. 41 and 49-52). Frequent in legumes and commonly described as an indehiscent pod; e.g., Fabaceae-Caesalpinioideae (*Cassia grandis, Hymenaea courbaril, Prioria copaifera, Tamarindus indica* L.), Fabaceae-Mimosoideae (*Enterolobium cyclocarpum* (Jacq.) Griseb.), Fabaceae-Papilionoideae [*Andira inermis, A. surinamensis, Diphysa americana* (with air chambers in the pericarp), and *Dipteryx panamensis* (late dehiscence)].

Dry Dehiscent Fruits

These are fruits that open at maturity. The following types are found in this category (fig. 53):

Capsule. Fruit derived from an ovary with two or more carpels. The pericarp opens along predetermined lines as the result of tensions produced by tissue drying. Several kinds of capsules exist:
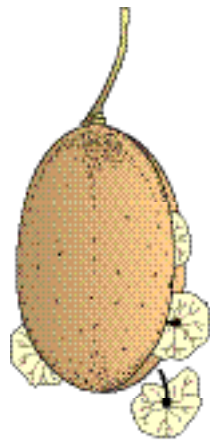
Jacaranda copaia
(Bignoniaceae)
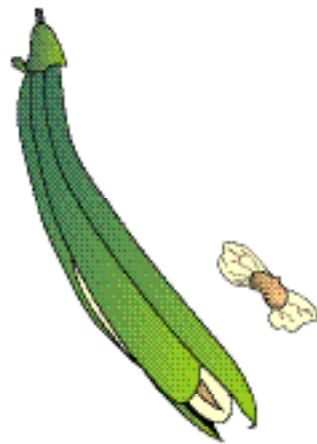
Tabebuia sp.
(Bignoniaceae)

Capsule (Loculicidal)

Muellera frutescens
(Fabaceae–Papilionoideae)

Loment

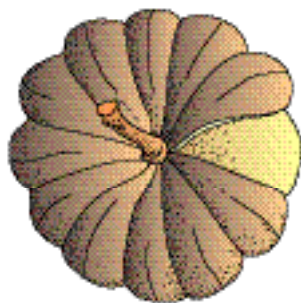**Swartzia**
(Fabaceae–Papilionoideae)

Pod or Legume

Cedrela odorata
(Meliaceae)

Capsule (Septicidal)
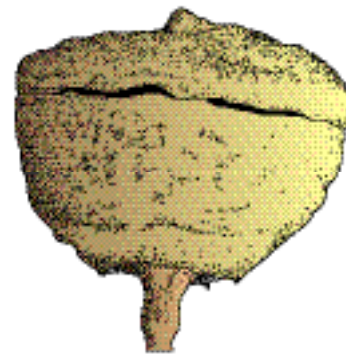
Eschweilera
(Lecythidaceae)

Capsule Circumcissile (Pyxidium)

Schizocarp
Hura crepitans
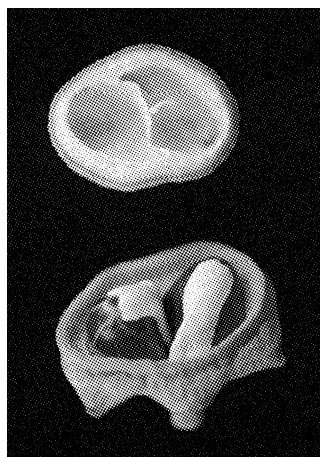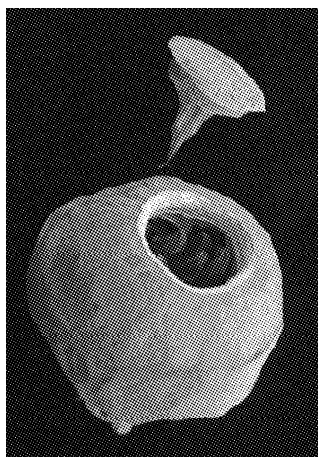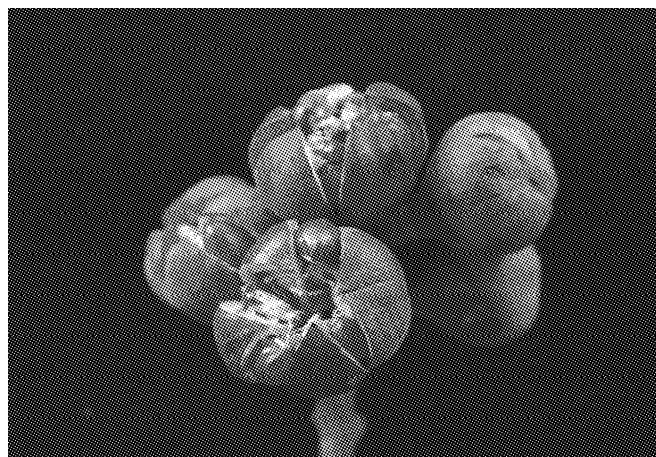(Euphorbiaceae)
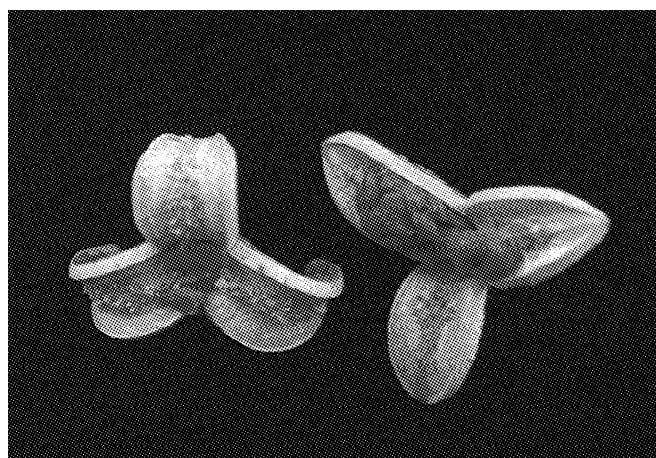
Fig. 53. Dry dehiscent fruits.

Fig. 54.
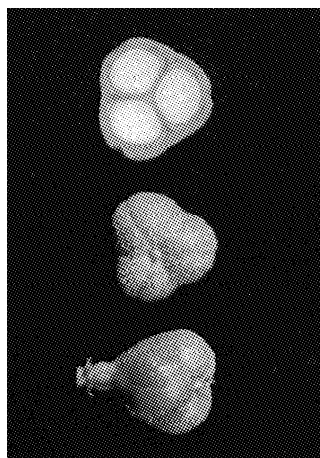
Fig. 55.

Fig. 56.

Fig.57.

Fig. 58.

Fig. 59.

Fig. 61.

Fig. 62.

Acrocidal: The capsule opens through fissures or specific openings; e.g., *Gossypium hirsutum*.

Circumscissile (pyxidium): The cover is named operculum and the dehiscence line is a well-defined circumference. It is common in Lecythidaceae (figs. 53-55); e.g., *Lecythis ampla, Eschweilera panamensis, E. costaricensis,* and *Couratari guianensis* Aubl.

Loculicidal: The capsule opens longitudinally in the locule cavity (carpel midvein region) (figs. 53 and 56-59); e.g.,

Tiliaceae (*Luehea seemannii*), Bixaceae (*Bixa orellana*), Bignoniaceae (*Jacaranda copaia* (Aubl.) D. Don, *Tabebuia rosea* (Bertol.) DC., *T. chrysantha*), Elaeocarpaceae (*Sloanea faginea, S. latifolia*), Loganiaceae (*Placospermum buxifolium*), Meliaceae (*Guarea, Trichilia*), Sapindaceae (*Cupania*), and Turneraceae (*Erblichia odorata*).

Poricidal: The capsule opens through a pore. If the pore has an operculum the capsule has poricidal-operculate dehiscence; e.g., *Triodanis*.
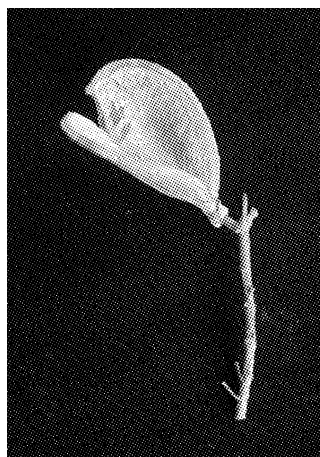
Fig. 60.

Fig. 63.

Fig. 64.

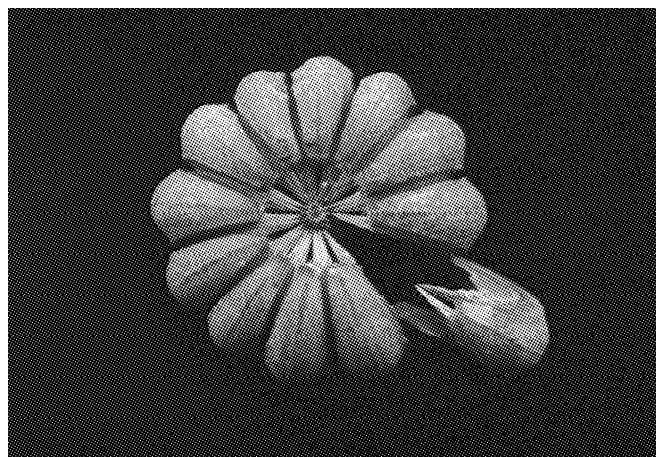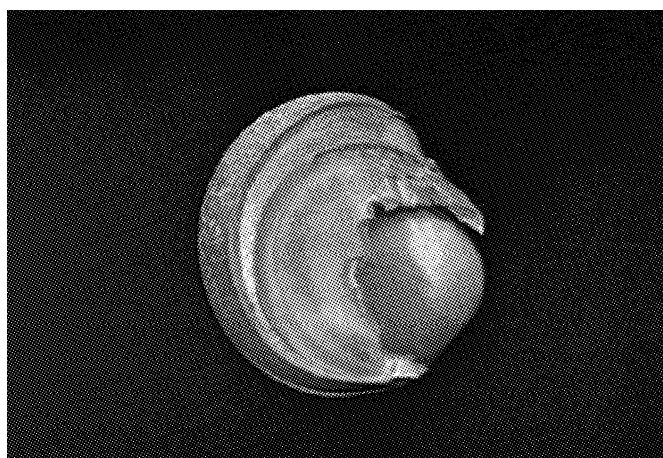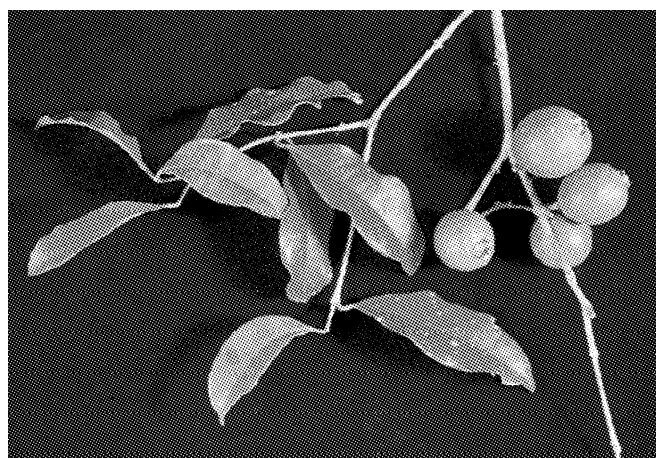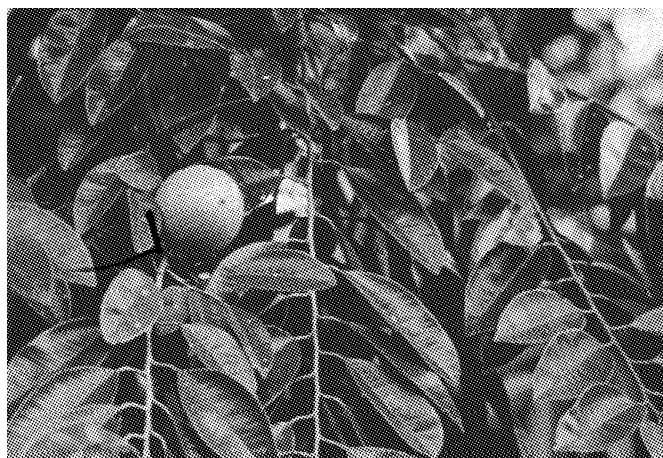

Fig. 65.

Fig.66.

Fig. 68.

Fig.69.

Fig. 70.

Septicidal: The capsule opens longitudinally through septa (figs. 53 and 60-62). It is common in Meliaceae (*Cedrela, Carapa guianensis, Swietenia*), and Myristicaceae (*Virola, Otoba, Myristica fragrans*).

Follicle. Fruit derived from a carpel opening along a suture (fig. 63); e.g., Proteaceae (*Roupala montana, Macadamia integrifolia*).

Legume or pod. Coriaceous fruit derived from a monocarpellar gynoecium. It opens along the ventral and dorsal sutures (figs. 53 and 64). Typical fruit in the Fabaceae-Caesalpinioideae (*Copaifera aromatica* Dwyer, *Peltogyne purpurea*), and Fabaceae-Mimosoideae (*Cojoba arborea, Abarema macradenia*). The dehiscence is explosive in *Pentaclethra macroloba* (Fabaceae-Mimosoideae) and *Gliricidia sepium* (Fabaceae-Papilionoideae).
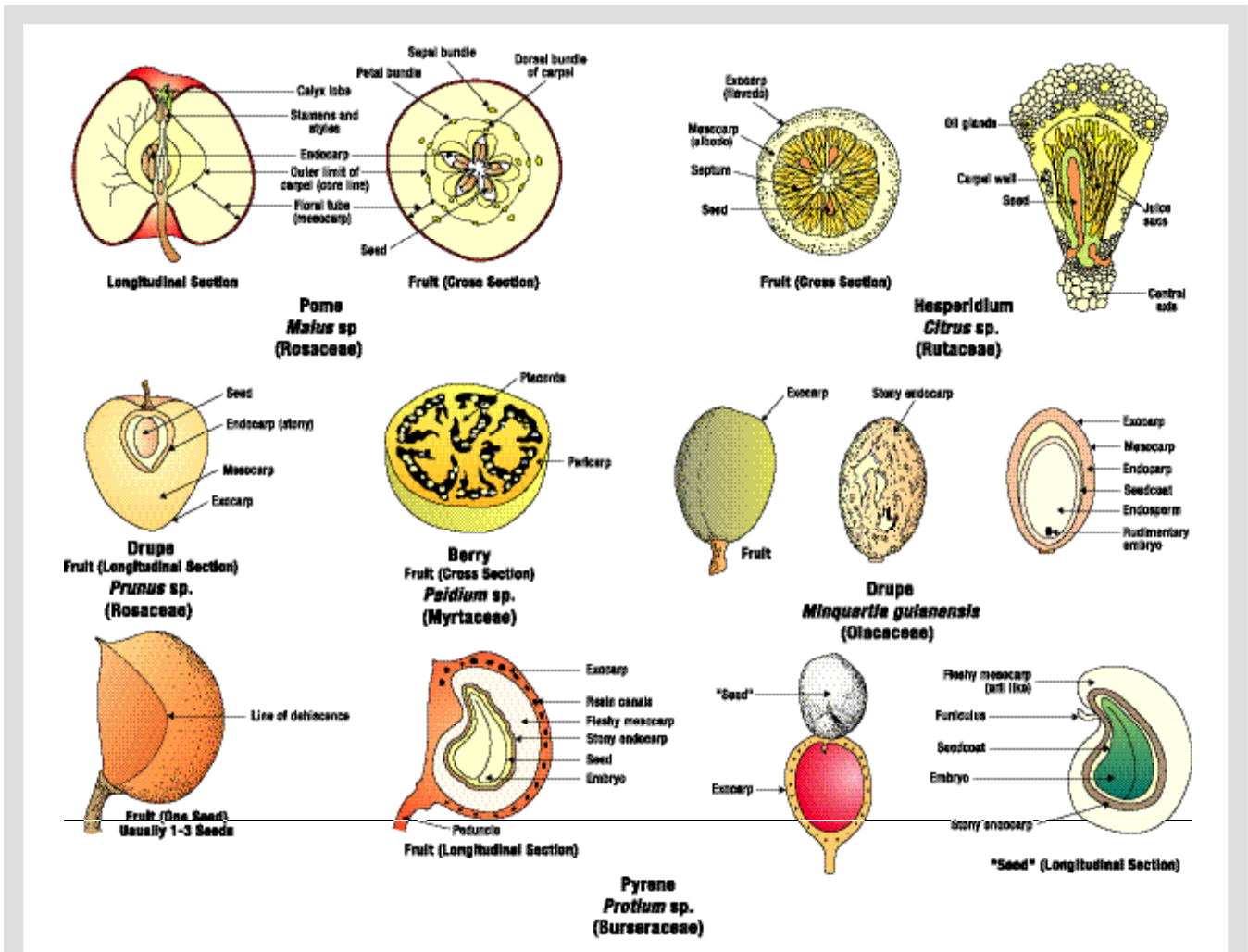
Fig. 67. Types of fleshy fruits.

Loment. Pod or legume splitting into segments each containing a seed (fig. 53); e.g., *Muellera frutescens* (Fabaceae-Papilionoideae) and *Senna skinneri* (Fabaceae-Caesalpinioideae). The last species is extremely specialized; the pod has deep constrictions in the break sites.

Schizocarp. Fruit splitting into units or fruitlets containing the seeds (figs. 53 and 65-66); e.g., *Hevea brasiliensis* Müll Arg. and *Hura crepitans* (Euphorbiaceae). The mericarp (cremocarp, carpopodium) are the units; if the unit is equivalent to half a carpel it is called a carcerule.

Fleshy Fruits

Those fruits derived from a monocarpellar or multicarpellar gynoecium (fig. 67). The pericarp has carpellar or extracarpellar tissue (hypanthium, perianth, androecium, peduncle, bracts)

(Fahn and Werker 1972). The pericarp can be fleshy in the external or internal parts; in some fruits both zones are fleshy. In some fruits the placenta and the partitions of multilocular ovaries are also fleshy. The principal fleshy fruits follow:

Pome. Fruit derived from a gynoecium with two or more carpels and an inferior ovary. The receptacle and hypanthium are adnate to the ovary and form most of the fleshy tissues. The endocarp is cartilaginous (fig. 67); e.g., Rosaceae (*Pyrus malus*, *Pyrus communis*, *Cydonia oblonga*).

Berry. Fruit with a succulent pericarp (figs. 67-70), e.g., Myrtaceae (*Psidium friederichsthalianum*, *P. guajava*, *Syzygium jambos*, *Myrcianthes fragrans*), Clusiaceae (*Calophyllum brasiliense*, *Symphonia globulifera*), Lauraceae (*Ocotea*, *Nectandra*, *Persea*), and Rubiaceae (*Posoqueria*).