CHAPTER 1

Seed Biology

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Seeds have been associated with human development since prehistoric times. In the post-glacial gathering era, Paleolithic people depended upon seed plants for their existence. They collected wild berries, nuts, and many edible seeds capable of providing nutrients and useful products (Baker 1965, Schery 1952). Since ancient times, seeds have been symbolic in the religious creeds of human groups. In ancient Egypt, for example, seeds symbolized the mysteries of death, resurrection, and life after death. Mummies were buried with a vessel of viable seeds to fill the food requirements in a new life (Evenari 1980/1981). Seed symbolism continues to be a part of religious rituals and ceremonies practiced by numerous people. The Bribri Indians of Costa Rica believe that grave-diggers and women are responsible for maintaining a basic seed stock because the Bribri are born as cocoa trees and a dead Indian is comparable to a dead tree since both of them leave seed (Bozzoli 1979). Because the Bribri god Sibö gave rise to the trees when Earth was created, Bribris believe they are immortal, everlasting, and perpetuated through the fruits and seeds they produce (Bozzoli 1979).

With the birth of agriculture, this symbol of resurrection and life became a necessity for the development of civilization. Gathering, storing, selecting, and sowing seeds capable of producing good crops became an art and an obligation: human food security was dependent on seeds. Throughout the centuries, seeds have been a means to reproduce species and a source of nutrients upon which all developing civilizations have been built. Seeds have ultimately produced fibers, carbohydrates, proteins, essential oils, insecticides, beverages, alkaloids, phytoestrogens, animal fodder, and other less important products (Hughes 1988).

Agricultural development and the recognition that seeds are the primary base for obtaining good crops promoted the study of seed biology in crops. Traditionally, this study focused on cereal, grain, and other seeds basic to the human diet such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), corn (*Zea mays*), barley (*Hordeum vulgare*), rye (*Secale cereale*), beans (*Phaseolus vulgaris*), peanuts (*Arachis hypogaea*), and soybeans (*Glycine max*). The study and research of these basic seeds continues to grow, especially when demographic explosion and climatic global change undermine our confidence that we have the capacity to feed present and future human populations.

Widely studied seeds include those of plants that produce commercial trichomes such as cotton (*Gossypium hirsutum, G. arboreum*); fibers such as flax (*Linum usitatissimum*) or ramie (*Boehmeria nivea*); oil such as the coconut (*Cocos nucifera L.*) or the oil palm (*Elaeis guianeensis, E. oleifera*); nuts such as the cashew (*Anacardium occidentale*), the Brazilian (*Bertholletia excelsa*), the American hazel (*Corylus americana*), the pecan (*Carya illinoinensis*), and the Queensland or Australian (*Macadamia ternifolia*); beverages such as coffee (*Coffea arabica*) and cocoa (*Theobroma cacao*); and spices and condiments such as nutmeg, mace (*Myristica fragrans*), and pepper (*Pimenta dioica*). Among the drug-producing plant seeds studied are some species of the genus *Strychnos*, which produce strychnine

and brucine; the quinas (*Cinchona*), which produce quinine; and the coca (*Erythroxylum coca*), which produces cocaine.

Because of the importance of biodiversity conservation, natural forest management, reforestation, agroforestry, and agro-silvo-pasture systems, our study of forest tree seeds in the Tropics is only the beginning.

FOREST TREE SEEDS INTEREST AND STUDY

The systematic study of tropical forest tree seeds is becoming increasingly important as we realize that the forest and forest trees are not a boundless resource, and as we realize the value of treating the forest as a crop. The exhaustive, indiscriminate, and haphazard use of forest resources gradually limits the supply of traditional woods and other forest products important in national and international markets. Resource reduction also hastens the loss of a multiple use resource that beneficially affects soils, hydric regimes, biodiversity, landscapes, and microclimates. Additionally, the forest mass fixes CO_2, diminishes atmospheric contamination and deterioration, and contributes to sustaining human survival (Reynolds and Thomson 1988).

Today, increasing the existing knowledge about forest dynamics, trees as basic and essential units, and seeds and seedlings as indisputable factors of regeneration has become important. Challenging issues include generating new knowledge; developing effective techniques that promote conservation, management, and rational use of remaining forests; and implementing successful reforestation programs.

Most tropical tree pioneers, that is those typical of early forest succession, have small orthodox and dormant seeds. Easily dispersed, these seeds may form seed banks on the forest floor and may be photoblastic or thermoblastic. Germination of most of these seeds is stimulated by environmental alterations or disturbances, such as natural or artificial clearings in the canopy, on different spatial or chronological scales. Changes in the rates of red/far-red light or temperature fluctuations produced by vegetation removal may increase the germination rate (Bazzaz 1991). In contrast, a large number of climax species have big recalcitrant or intermediate seeds. Recalcitrant seeds germinate quickly, an advantage in terms of avoiding insect predation and preventing lipid degradation from diverse microorganism action (Whitmore 1990). A recalcitrant seed lacks maturation drying and its development is uninterrupted; however, the speed of embryo development (growth and differentiation) varies greatly among species. Diaspore permanence on the forest litter or substrate before root protrusion may vary from days to months. For example, root protrusion in *Dipteryx panamensis* (Pittier) Record & Mell and *Pentaclethra macroloba* (Willd.) Kuntze occurs 8 to 10 days after sowing; in *Virola koschnyi* Warb., 11 to 14 days; in *Carapa guianensis* Aubl., 14 to 16; in *Calophyllum brasiliense* Cambess., 15 to 18; in *Lecythis ampla* Miers, 45 to 48; in *Ocotea austinii* C.K. Allen, 50 to 55; and in *Minquartia guianensis* Aubl., 150 to 160 (5 months or more) (Flores 1992a, 1992c, 1994a, 1994b, 1994d, 1994e, 1994f). While pioneer species such as *Cecropia*, *Goethalsia meiantha* (Donn. Sm.) Burret, *Hampea platanifolia*, *Heliocarpus appendiculatus*, and *H. americanus* form seed banks on the forest floor, the species with recalcitrant seeds form seedling banks. The seedlings that remain until advanced stages of forest regeneration are, in many species, more important than the seed banks as a source of regeneration (Bazzaz 1991).

Regeneration includes dormancy types and germination times and types that are all obviously related to the morphology, physiology, and ecology of seeds (Grübb 1977). Consequently, the study of these aspects is becoming increasingly important to understanding seed behavior and predicting the regeneration capacity of the trees and the forest. The completion of a life cycle or the regeneration of a plant community depends on the production of physiologically independent individuals, which happens through seed or vegetative reproduction. Establishment of the species reproduced by seeds is dominant in communities in early succession after strong disturbances, and in forests of intermittent regeneration, throughout a vegetation mosaic (Ashton 1984, 1989; Bazzaz and Ackerly 1991; Hall and others 1994; Harris and Silva-López 1992; Hilty 1980).

The genotype of a tree seed is the result of the evolutionary forces operating on the species for centuries. It is adapted to the present environmental conditions but not to those of the future, especially when environmental conditions are being drastically modified by accelerated global change. Even if scientific and technological knowledge could be increased, the forests of the past and those of today cannot be replicated tomorrow. The natural processes that gave rise to the species, communities, and ecosystems we want to preserve have been built over a long period of time and in large spaces (Pickett and others 1992). To preserve and reproduce tree species by seed, we must know the limits imposed on the ecophysiology of seeds by nature through the evolutionary process. The genetic combinations able to survive through environmental changes have intrinsic value and must be carefully selected.

Seed germination is also influenced by the environmental conditions during seed development and maturation while

on the parent tree. Day length, temperature, parental photothermic environment, light quality, and elevation are factors that significantly influence germination capacity (Dorne 1981; Fenner 1991, 1992; Foster 1986; Grime and Jeffrey 1965; Gütterman 1991; Kigel and others 1977). Additional factors include the inflorescence position on the parent tree, seed position in the fruit or infrutescence, and parent tree age during floral induction (Gütterman 1991).

These factors, plus others, explain the strong variation found in seed parameters (weight, color, water content, germinability) among seed groups and among seeds in the same group.

To most people, the concept of "seed" is deceptively simple. It is compared to a pill, isolated from the environmental impact, replicated many times, and capable of producing a plant (Janzen and Vásquez-Yáñez 1991). However, a seed is attached to a long and complex evolutionary and physiological history, and it is also conditioned to the variations of a long and complex future. The study of seeds has many facets and should not be limited to collection, storage, and sowing.

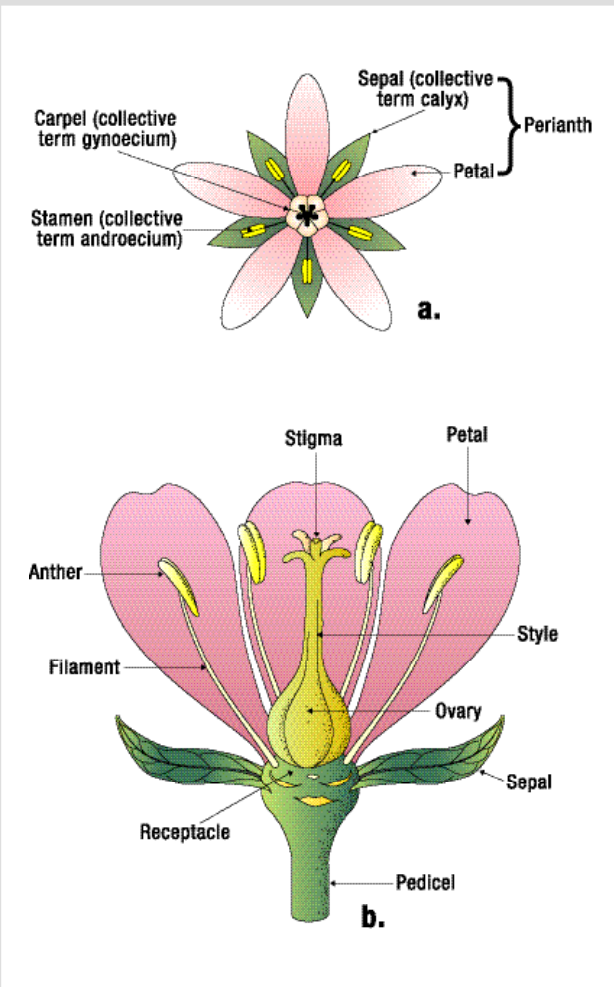

Fig. 1. Perfect flower. a, viewed from above; b, longitudinal section.

REPRODUCTIVE BIOLOGY IN TROPICAL TREES

SEXUAL STRUCTURES IN ANGIOSPERMS

The flower is the reproductive structure in angiosperms. The classic flower has a pedicel, floral receptacle, calyx (group of sepals), corolla (group of petals), androecium (ensemble of stamens), and gynoecium (ensemble of carpels) (fig. 1). The androecium and the gynoecium are the fertile organs; the remaining organs are sterile (vegetative structures).

Most flowers have a specific numeric arrangement of organs. In monocotyledons, the flowers generally have three pieces: three sepals, three petals, and usually three stamens or a multiple of three stamens; these flowers are called trimerous. The dicotyledons have flowers built in an array of four or five pieces and are called tetramerous or pentamerous. The flower plan is more evident in petals and sepals, and to some degree in the stamens; the plan is not applied to carpels. In the flower, the sepals alternate with the petals and the petals frequently alternate with the stamens. Groups of inner stamens may alternate with groups of outer stamens; sometimes the carpels are opposite to the sepals.

When all of the typical organs—petals, sepals, stamens and carpels—are present in a flower, it is complete; if one or more organs are missing, the flower is incomplete. A nude flower lacks a perianth; a flower is apetalous if it lacks a corolla (e.g., *Roupala montana*, *Macadamia integrifolia*, *Oreomunnea pterocarpa*, *Sterculia apetala*, *Alfaroa costaricensis*, *Hyeronima alchorneoides*).

The terms regular and irregular are commonly used in reference to flowers. These terms generally involve the perianth (corolla + calyx); the reproductive organs are occasionally included. A regular, or actinomorphic, flower (e.g., *Coccoloba tuerckheimii*, *Terminalia amazonia* (J.F. Gmel.) Exell, *Ocotea austinii*, *Magnolia poasana*, *Gustavia hexapetala*) has perianth pieces of similar shape and size. The flower can be divided into equal halves by a vertical plane in several directions. This flower has radial symmetry (polysymmetric) (fig. 1). Bisymmetric flowers have two planes of symmetry (bilateral flowers; typical in Brassicaceae) (Strasburger and others 1908, Weberling 1989). The irregular, or zygomorphic, flowers are dor-

Fig. 2.

siventral or monosymmetric (e.g., *Andira, Diphysa americana* (Mill.) M. Sousa, *Dipteryx panamensis, Erythrina, Gliricidia, Hymenolobium mesoamericanum, Theobroma cacao, Bertholletia, Cariniana, Couratari, Lecythis, Eschweilera, Qualea paraensis* [figs. 2 and 3]) (Strasburger and others 1908, Weberling 1989). The irregularity usually involves the petals, but the sepals and the perianth as a whole could be included. There are also asymmetric flowers. This asymmetry must be produced by organ reduction, multiplication, or modification (e.g., *Vochysia,* and typical in *Canna* and *Maranta*) (Strasburger and others 1908, Weberling 1989).

Floral reduction can occur in one or several organs simultaneously. By reduction, organs may change their shape, structure, and function. The transformation of petals and stamens in glands, or of stamens in staminoids or petals, is the most common change. Stamen reduction may occur in different degrees, from anther abortion to organ disappearance. Carpel reduction usually refers to reduction in size and ovule number; for example, the achene is a fruit with only one ovule. Ovule reduction and loss is usually gradual; it may take place in acropetal direction, retaining only the distal ovule(s), or proceed in basipetal direction; in this case only the basal (proximal) ovule(s) remain (Eames 1961, Flores 1999).

The receptacle resembles a shoot in ontogeny and structure. It has nodes, internodes, and appendages; the nodes are crowded due to internode reduction or suppression. The fertile and sterile floral organs arise at the receptacle nodes and are grouped in spirals or verticils.

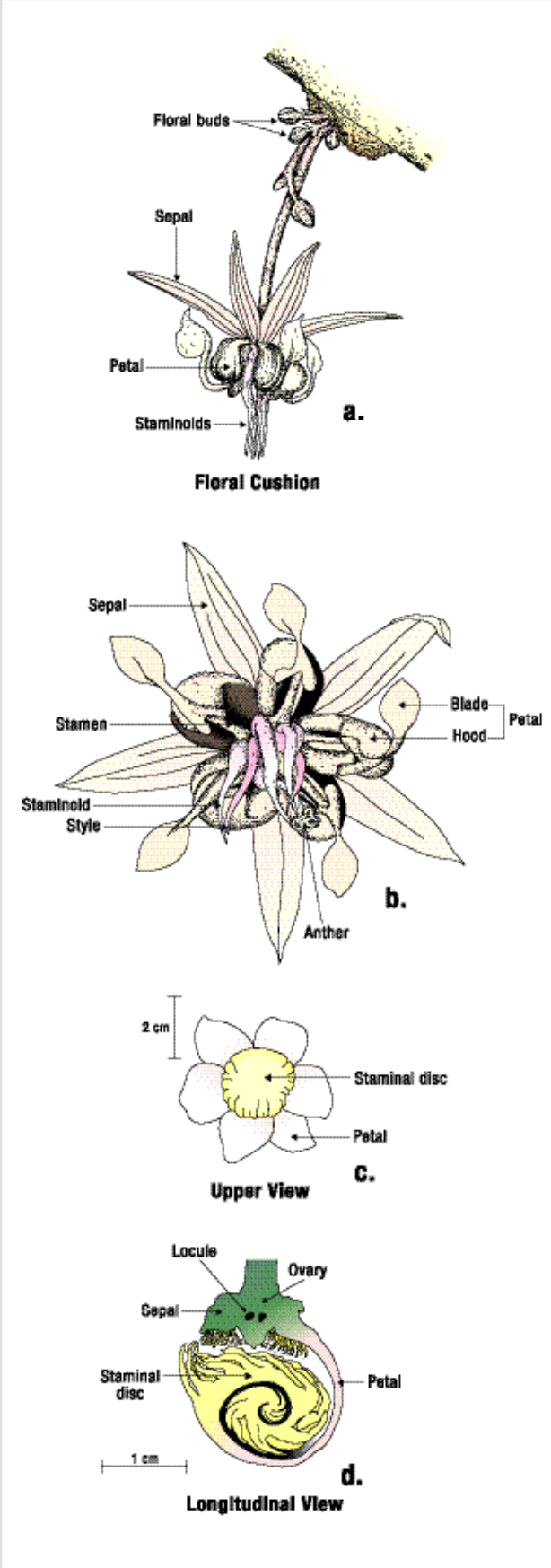

Fig. 3. Zygomorphic flower. a,b, *Theobromoa cacao* (Sterculiaceae); c,d, *Eschweilera sp.* (Lecythidaceae).

The calyx and corolla are vegetative structures and collectively constitute the perianth (fig. 4). They are easily distinguished in many flowers (e.g., *Xylopia sericophylla*, *Cananga odorata*, *Annona*, *Drimys granadensis*, *Guajacum sanctum L.*); in other flowers the perianth parts are indistinguishable and are named *tepals* (e.g., *Cecropia*, staminate flowers; *Allocasuarina*, staminate flowers; *Hernandia didymantha*, *Magnolia poasana*, *Gyrocarpus*). In many flowers, the sepals and petals are modified leaves.

In many flowers, the calyx and corolla may be reduced, vestigial, or missing. Reduced sepals may be toothed, scaly, bristled, or ribbed. Petals are usually laminar and bigger than sepals. They vary widely in size and shape. Flowers with large and elaborate petals can be found in families such as Fabaceae-Caesalpinioideae (*Cassia grandis* L.f.), Hippocastanaceae (*Billia*), Lecythidaceae (*Lecythis*, *Eschweilera*, *Grias cauliflora*), Fabaceae-Papilionoideae (*Dipteryx oleifera*, *D. panamensis*, *Hymenolobium mesoamericanum*, *Hymenaea courbaril* L.), and Vochysiaceae (*Vochysia*, *Qualea paraensis*). Those with small, reduced, vestigial, or no petals are in families such as Betulaceae (*Alnus acuminata* Kunth in H.B.K.), Casuarinaceae (*Allocasuarina*), Euphorbiaceae (*Hyeronima*), Fagaceae (*Quer-*

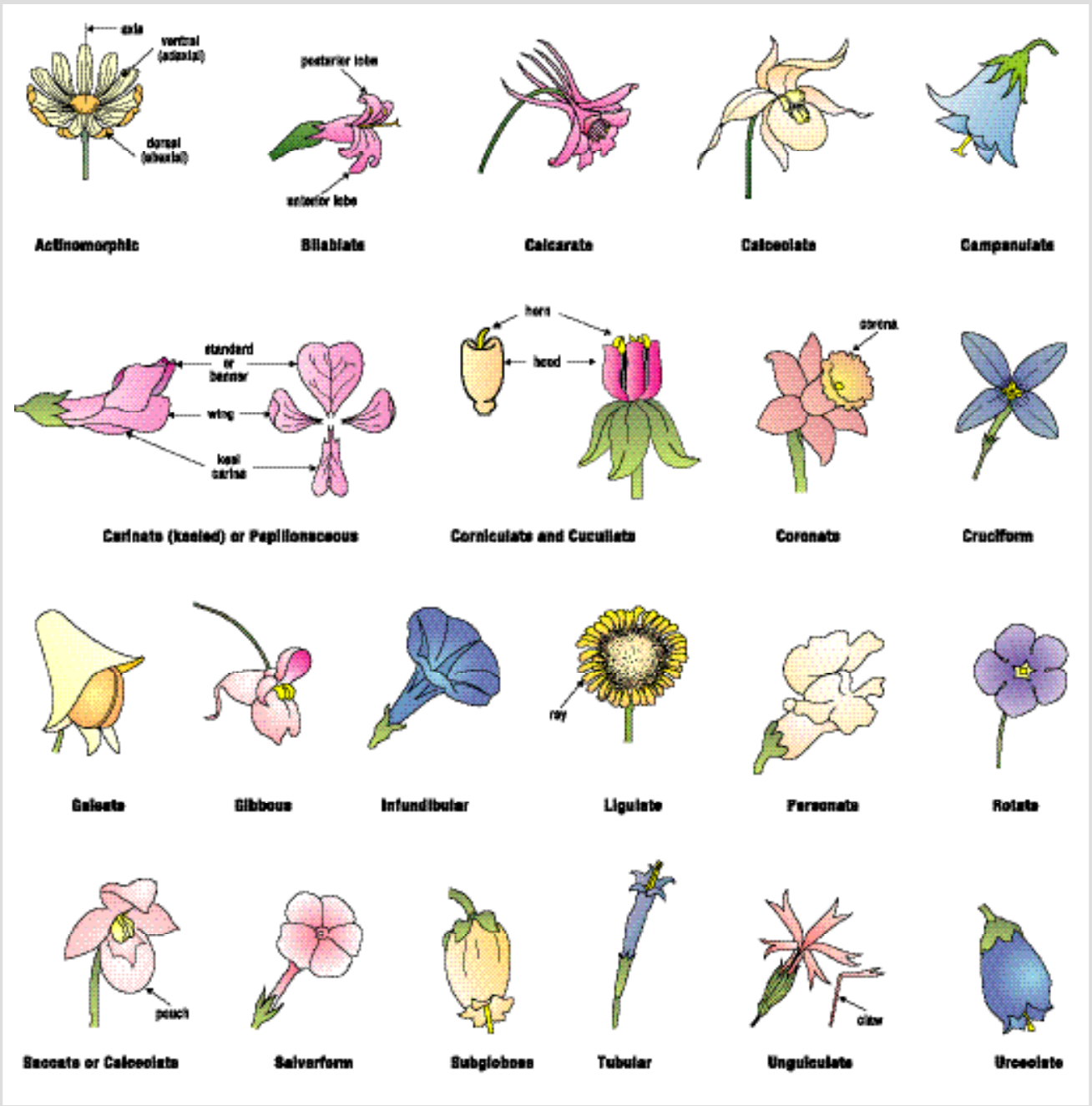

Fig. 4. Perianth structural types.

cus), Juglandaceae (*Alfaroa costaricensis* Standl.), Moraceae (*Brosimum*, *Maclura tinctoria* [syn. *Chlorophora tinctoria*], *Castilla elastica*, *Naucleopsis naga*), Myristicaceae (*Virola*, *Myristica fragrans*, *Otoba novogranatensis* Moldenke), Salicaceae (*Salix*), and Ticodendraceae (*Ticodendron incognitum*). When reduced, the petals may form scales, bristles, or glands of varied size and shape.

The position of the calyx and corolla pieces in the floral bud (aestivation) sometimes persists in the mature flower. There are several aestivation types (fig. 5); the following classification follows that of Radford and others (1974):

Alternate. Two rows or series of organs or structures where the margins of the inner group are overlapped by a margin from each adjacent outer piece.

Cochleate. A hollow or helmet-shaped structure encloses or surrounds the other pieces.

Contorted or regular. Several structures or organs in a whorl or close spiral have one margin covering the margin of the adjacent structure.

Convolute. A leaf or perianth piece partly rolled in another, commonly twisted distally.

Imbricate or irregular. Piece margins overlap.

Induplicate. Piece margins fold inward, touching the margins of the adjacent structures.

Quincuncial. Five pieces: two are interior and two exterior; the fifth piece has one margin covering the interior pieces while the other margin is covered or surrounded by one margin of the exterior pieces.

Valvate. Margins of the adjacent structures touch at edges without overlapping.

Vexillate. Large piece surrounds other minor pieces, parallel-oriented with respect to the outer piece semilimbs.

Perianth aestivation has taxonomic value; for example, the corolla aestivation is a feature distinguishing Caesalpinioideae from Papilionoideae.

The androecium is the ensemble of stamens. The typical stamen has the anther and the filament, which connects the anther to the floral axis or another organ (fig. 6). The anther comprises four elongated microsporangia (pollen sacs), where pollen develops. The androecium is outside the gynoecium and inside the corolla; the stamens are sometimes attached to or inserted upon the petals, the corolla (epipetalous), or the gynoecium (gynandrous). The stamens may be united through coherent or connate filaments in a single group (monadelphous), in two groups (diadelphous), or more (polydelphous) or by union of their anthers into a ring (syngenesious; fig. 6); (Porter 1967).

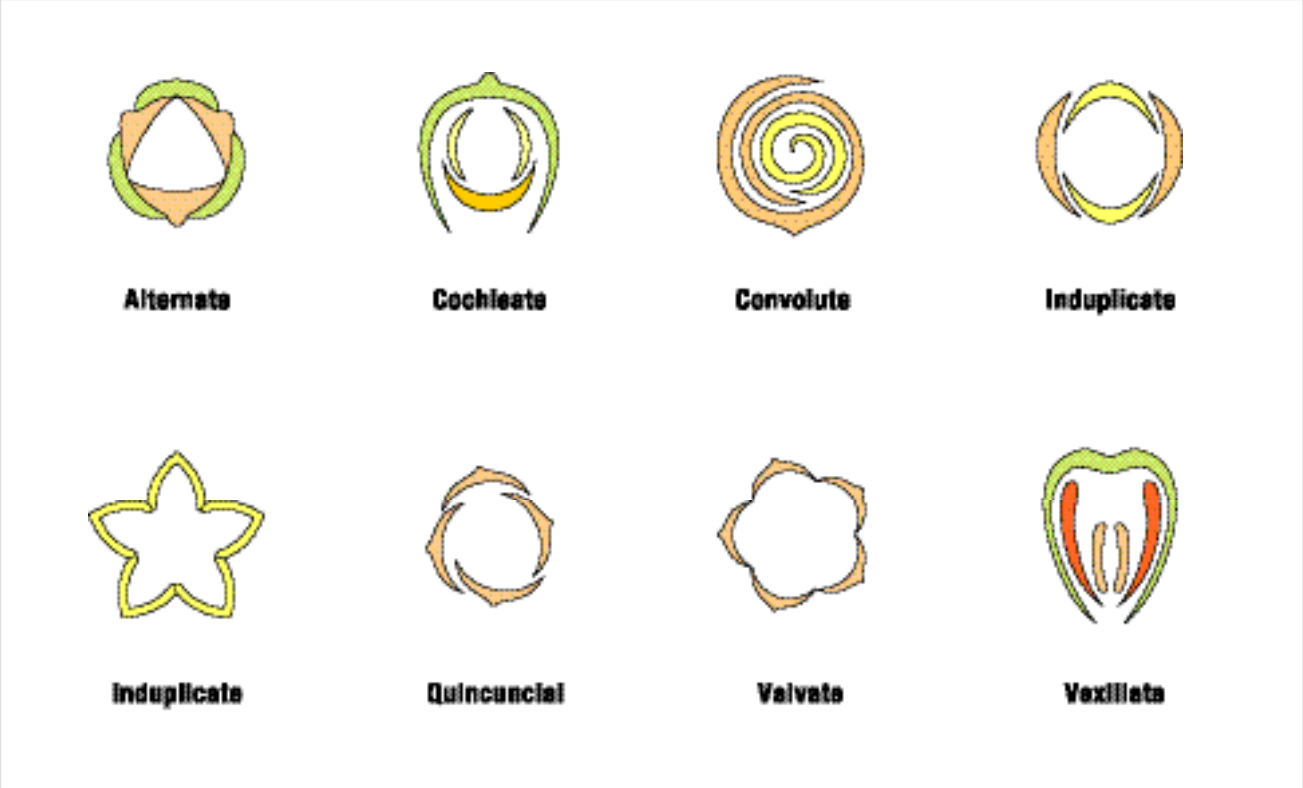

Fig. 5. Perianth aestivation types.

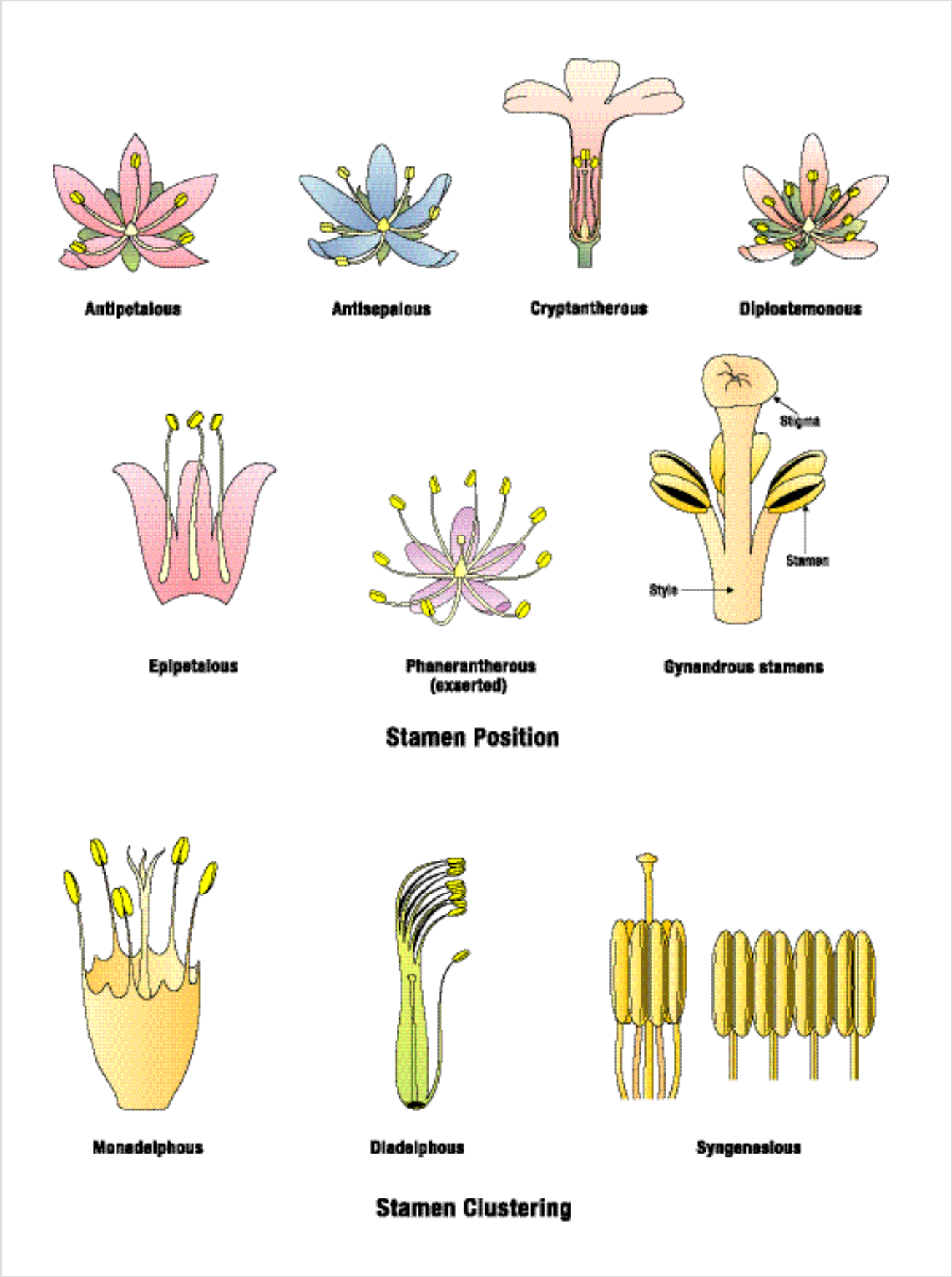

Fig. 6. Stamen position and clustering.

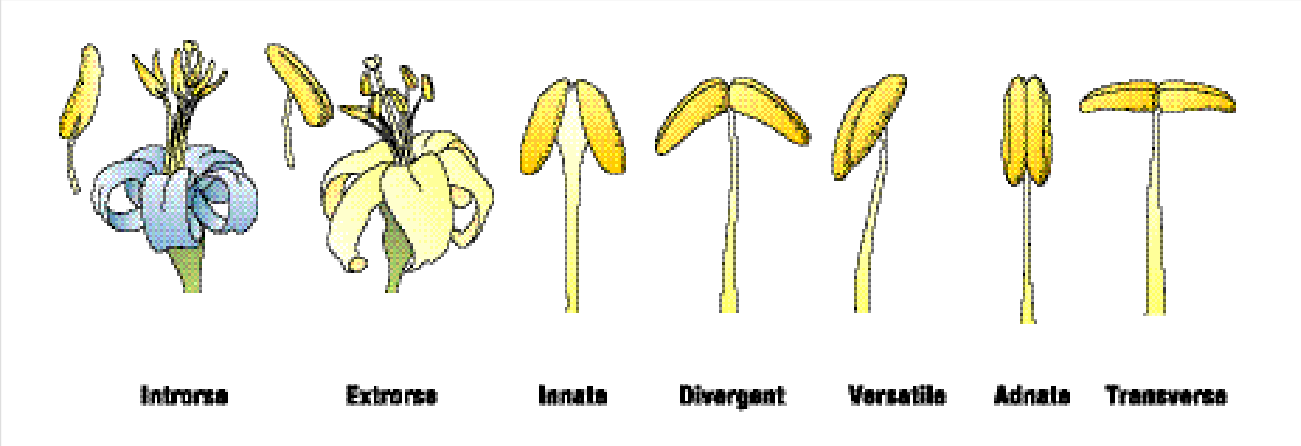

Fig. 7. Anther Attachment.

The attachment of the anther to the filament (fig. 7) is innate when the microsporangia are terminal and the filament is continuous between the microsporangia. It is adnate when the microsporangia are elongated and attached lengthwise to the filament. When the anther is attached by its middle, with both ends free, it is versatile. Dorsifixed anthers are attached dorsally and medially to the filament tip, while basifixed anthers are attached distally to the filament. In some species the microsporangia are in a transverse position.

The number of stamen in a flower ranges from one to many, and from an indefinite number to a defined one (Eames 1961). The arrangement on the receptacle could be spiral (helical), whorled (verticillated), or fasciculate (clustered); the fascicles are commonly in whorls. The spirally arranged stamens represent a primitive condition from which the whorled and fasciculate types developed (Eames 1961). The fascicles have various numbers of stamens and are formed by aggregation and conation of individual stamens to different degrees. When the stamens are in one whorl the androecium is haplostemonous. When the stamens are distributed in two whorls and the members of the outer verticil alternate with the petals, the androecium is diplostemonous; if the members of the outer whorl are opposite the petals, the androecium is obdiplostemonous. An androecium with more than two stamen whorls is polystemonous (Eames 1961).

The stamens may vary in size and shape, but before dehiscence all anthers have two pairs of microsporangia in the anther lobules. The microsporangia are separated by a zone of sterile tissue called intervenal connective. In some species only one microsporangia develops; however, many bisporangiate anthers are truly tetrasporangiate. At maturity the two contiguous sporangia of each side flow together because the partition separating them breaks down.

All stamen parts can be modified in the evolutionary process. The filament length is variable and may be missing. The microsporangia may be reduced and sterile, and the stamens become staminodia. The zygomorphic flowers have only modified stamens or a reduced number of them.

The gynoecium has a central position and may have one to several free or connate carpels (fig. 8). Each free carpel or gynoecium formed by several carpels has a stigma (structure receiving the pollen), a style (narrow portion below the stigma), and an ovary (wide base containing one or more ovules) (figs. 1 and 8). Some gynoecia lack styles (e.g., *Clusia*, Clusiaceae), but ovaries and stigmas are always present. In the gynoecium, the ovules develop from the placenta. When the gynoecium has individual carpels, the flower is apocarpous (e.g., *Magnolia*); if carpels are connate, the flower is syncarpous (e.g., *Oreomunnea*).

Ovaries have at least two zones: the wall and the locule(s). Multilocular ovaries have a third zone: the septa or partitions (fig. 8). Each carpel has two placentas on the adaxial surface near the margins. When reduction of the carpelar margins is accentuated, the contiguous placentas join and sometimes fuse.

Placentation is the type of ovule distribution in the carpels forming the gynoecium (fig. 9). Carpels are located in the ovary. The primitive, free, laminar carpel has submarginal placentation because ovules develop in the placenta between the dorsal and ventral bundles. The closed carpel usually has laminar placentation such as in Mimosoideae, Caesalpinioideae, and Papilionoideae. When the ovule develops close to the ovary base it is basal even when it is morphologically pseudobasal (e.g., *Calophyllum brasiliense*, *Virola koschnyi*). The suspended ovules are near the distal end of the ovary (e.g., *Allocasuarina*, *Roupala montana* Aubl., *Terminalia amazonia*). When the carpels

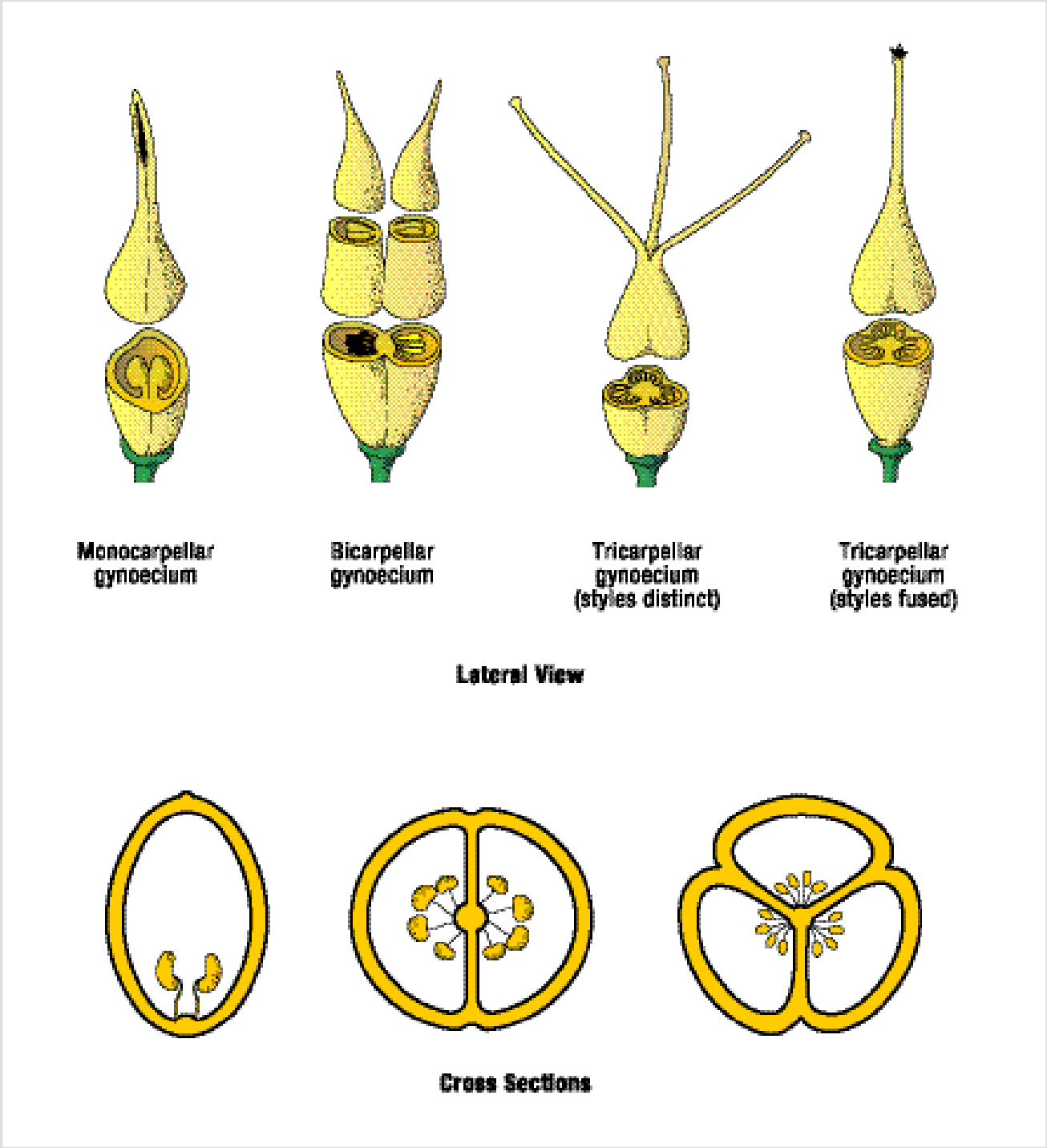

Fig. 8. Different gynoecium types.

are open and connate (syncarpous), placentation is parietal (e.g., *Bixa orellana*, *Escallonia myrtilloides*, *Hasseltia floribunda*, *Homalium racemosum*, *Casearia arborea*); if the carpels are closed and connation occurred after closing, placentation is axilar (e.g., *Lecythis ampla*, *Vochysia*, *Luehea seemannii* Triana & Planch., *Pseudobombax septenatum*, *Swietenia macrophylla* King, *Cedrela odorata* L.). In some cases, the carpel walls or septa dividing the ovary in locules are destroyed during development. A central column appears in the ovary, and the ovules appear attached to it. This placentation is free-central (e.g., *Theobroma cacao)*. If the carpels forming a syncarpous gynoecium were open before connation, usually only a central locule forms. Generally, a carpel has three vascular bundles: a dorsal (median) vein and two ventral (lateral, marginal) veins. Many

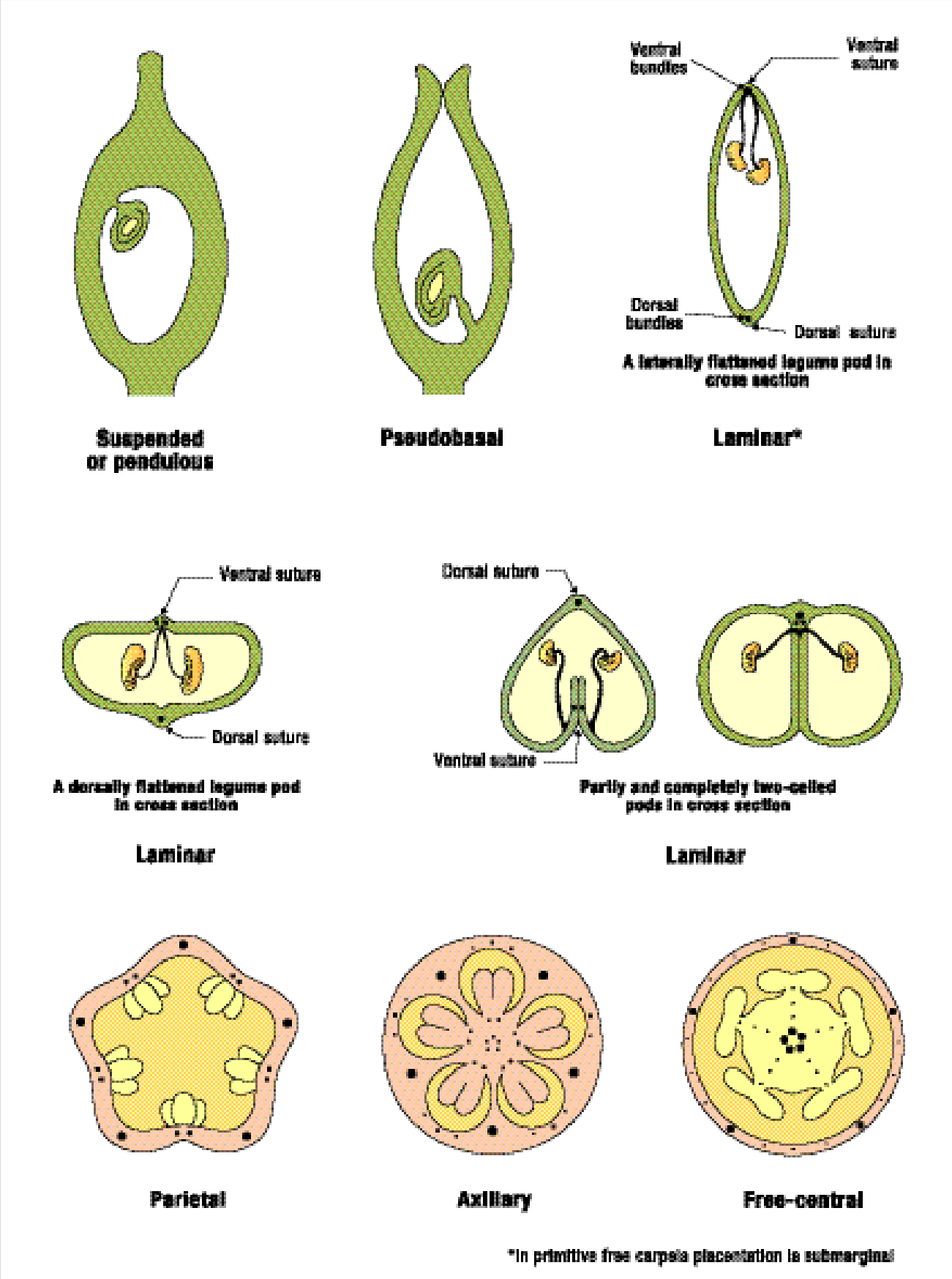

Fig. 9. Placentation types.

carpels have additional veins while others have lost veins by reduction and have fewer than the basic three.

When the gynoecium is in the distal end of the floral axis, the ovary is superior and the flower hypogynous (fig. 10). When the gynoecium occupies the lowest level in the floral axis and its wall is adnate to the floral tube or hypanthium to which the other floral organs (perianth and androecium) are attached, the ovary is inferior and the flower is epigynous. Some flowers have the perianth and androecium attached to the floral tube or hypanthium surrounding the ovary without fusing to it. These flowers are perigynous and the ovaries are semi-inferior. They are transitional forms to epigyny. More complicated classifications include several subtypes (see Radford and others 1974).

The style is the narrow carpel zone located between the ovary and the stigma. In the syncarpic gynoecia that bear a single style, tissues of the carpels integrating the gynoecium form the style. The carpels may be partially fused distally, where the style is a single structure at the base and a compound one at the top. The style may have stylar branches (stylodes); usually, one stylode per carpel (e.g., *Hibiscus*), and the styles or stylodes can be solid or have a central canal (hollow).

The stigma is the receptive surface that captures the pollen grains. It is formed by specialized surface cells that connect to the stylar tissues. Style and stigma morphology is diverse; it depends on flower structure and pollination type (fig. 10). The stigma captures and accepts the pollen and provides a suitable environment for pollen germination. The stigma can provide nutrients to the pollen and orient pollen tube growth; it also helps regulate flower metabolism (Van Went and Willemse 1984). The stigmatic surface must provide balanced osmolarity and the necessary water supply to promote pollen germination. Frequently, changing environmental conditions delay pollination, and the style and stigma must maintain the vitality to continue functioning.

The pollen wall and the stigmatic surface are involved in the cellular reception and recognition of signals or stimuli. Some of the macromolecules involved in this mechanism are allergic substances, stigmatic antigens, carbohydrates, proteins, gycoproteins, and glycosphingolipids (Ferrari and others 1985, Flores 1999, Shivanna and Sastri 1981).

Stigmas are divided into two categories: wet stigmas, with a copious fluid secretion; and dry stigmas, with a slight fluid secretion. The dry stigmas have receptive cells dispersed in multiseriate stylodes or concentrated in ridges, zones, or heads. Those with specialized reception areas may be separated into papillate and nonpapillate stigmas (Van Went and Willemse 1984). Wet stigmas have a receptive surface with small or medium-sized papillae. The binucleate pollen grains seem correlated to wet and dry stigmas, while trinucleate pollen grains are associated more with dry stigmas (Van Went and Willemse 1984).

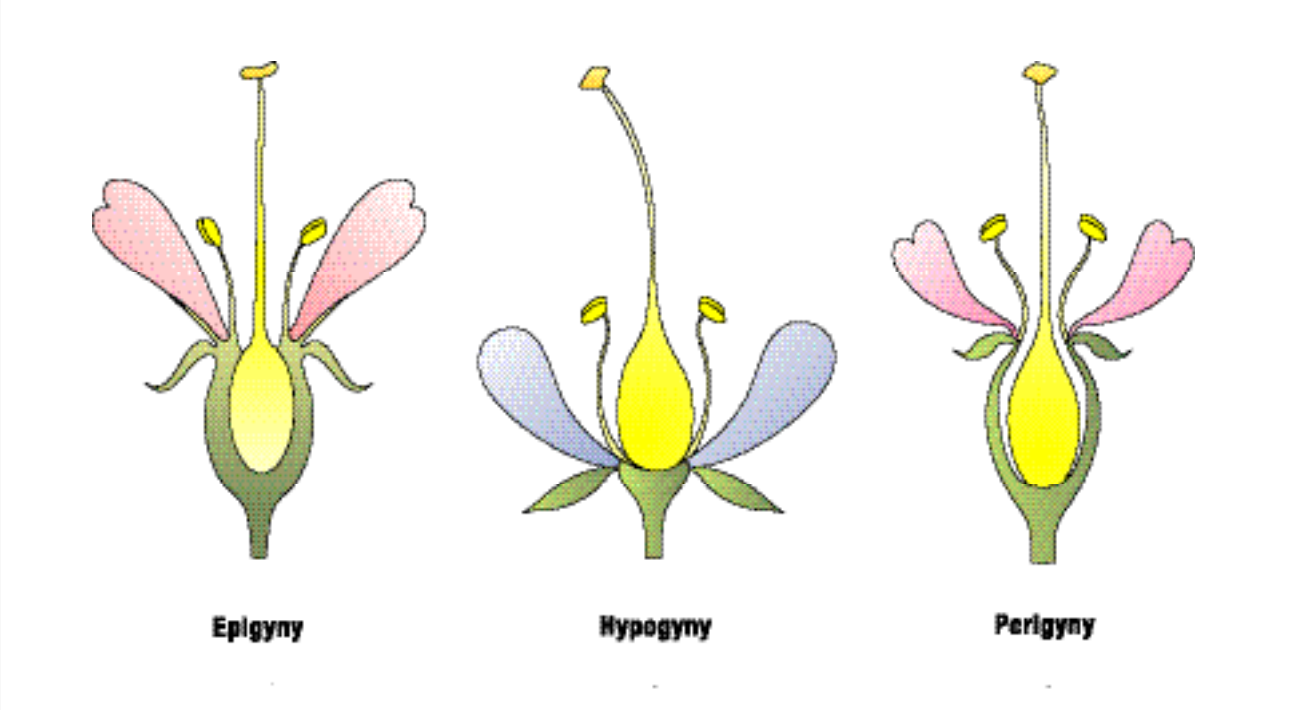

Fig. 10. Ovary position and flower types.

Sexual Expression in the Flower, the Inflorescence, and the Sporophyte

The morphology and physiology of the flower in tropical trees are varied and are associated with pollination and the sexual systems of the species. Plants can be either self- or cross-pollinated; however, sex separation in space or time, as well as self-sterility (homogamy) are frequent mechanisms used to favor cross-pollination. In the individual flower the separation of sexes in space has three modalities (fig. 11a):

Perfect, bisexual, or hermaphrodite. Flowers with pistillate (gynoecium) and staminate (androecium) organs. Examples include: *Persea americana* Mill., *Dipteryx panamensis, D. oleifera, Samanea saman, Stryphnodendron microstachyum, Vochysia guatemalensis* Donn. Sm., *Pentaclethra macroloba, Terminalia amazonia, Lecythis ampla,* and *Sideroxylon persimile*.

Unisexual. Single-sex flowers with androecium or gynoecium. Examples include *Brosimum alicastrum* Sw., *Diospyros nicaraguensis, Hura crepitans* L., *Hyeronima alchorneoides* Allemao., and *Virola koschnyi*. In species such as *Carapa guianensis* Aubl., the flowers are unisexual (male or female) but maintain vestiges of the other sex. There are two subtypes of unisexual flowers:

(1) **Staminate or male**—Flowers with an androecium but no gynoecium. For example: *Batocarpus, Casuarina, Hyeronima, Otoba novogranatensis,* and *Virola*.

(2) **Pistillate, carpellate, or female**—Flowers with a gynoecium but no androecium. For example: *Batocarpus, Casuarina, Hyeronima, Otoba novogranatensis, and Virola*.

Neutral or agamic. Sterile flowers with abortive or no sexual organs.

In the inflorescence, the spatial separation of sexes may have numerous variations and combinations (fig. 11b). In the individual tree, the sexual expression must be as follows:

Hermaphrodite or monoclinous. Tree with only hermaphrodite flowers (bisexual). For example: *Pentaclethra macroloba, Stryphnodendron microstachyum,* and *Terminalia amazonia.*

Monoecious or diclinous. Tree with both staminate and pistillate flowers. For example: *Artocarpus, Carapa guianensis, Hernandia didymantha, Poulsenia armata,* and *Ricinus communis.*

Dioecious. Tree with only one type of unisexual (imperfect) flowers. For example: *Virola, Hyeronima,* and *Batocarpus*. There are two subtypes:

(1) **Gynoecious, pistillate, or female**—Trees with only pistillate flowers. For example: *Guarea rhopalocarpa, Hampea, Virola,* and *Hyeronima*.

(2) **Androecious, staminate, or male**—Trees with only staminate flowers. For example: *Ilex, Myristica fragrans, Siparuna grandiflora, Virola koschnyi,* and *Hyeronima alchorneoides.*

Androdioecious. Some trees with hermaphrodite flowers and others with staminate or male flowers.

Andromonoecious. Tree with both hermaphrodite and staminate flowers. For example: *Calophyllum brasiliense, Parkia bicolor,* and *Schefflera*.

Gynodioecious. Some trees with hermaphrodite flowers and others with pistillate or female flowers. For example: *Ocotea tenera*.

Gynomonoecious. Tree with both hermaphrodite and pistillate flowers.

Polygamous or trimonoecious. Tree with hermaphrodite, pistillate, and staminate flowers. For example: *Aesculus hippocastanum* and *Gyrocarpus jatrophifolius.*

Polygamo-dioecious. Staminate, pistillate, and hermaphrodite trees in the same species. For example: *Coccoloba uvifera* (L.) L.

In many plants, a mechanism under genetic control prevents the ovules being fertilized by pollen from the same tree. In these species, the pollen may reach the stigma of its own flower but fertilization does not occur. In dioecious species, cross-pollination is the only alternative; in monoecious species, the separation of sexes into different flowers promotes but does not guarantee cross-pollination.

The separation of sexes by time prevents self-pollination in hermaphrodite flowers; the stamens and stigmas mature at different times, diminishing the possibility of self-pollination. The separation of sexes by time is known as dichogamy. There are two modalities of dichogamy:

Protandry (protandrous flowers). Stamens mature first and pollen release occurs before stigmas are receptive.

Protogyny. Stigmas mature first and are receptive and functional before anther dehiscence and pollen release.

Protandry is common in legumes (Fabaceae) and Malvaceae; protogyny is frequent in many families including

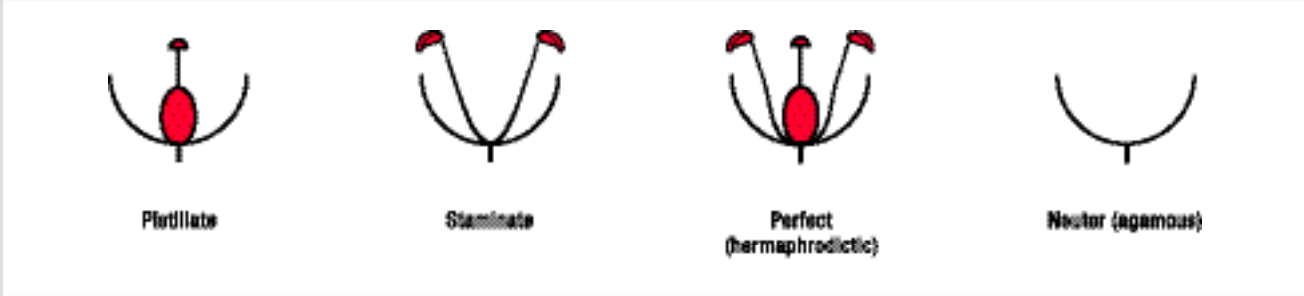

Fig. 11a.

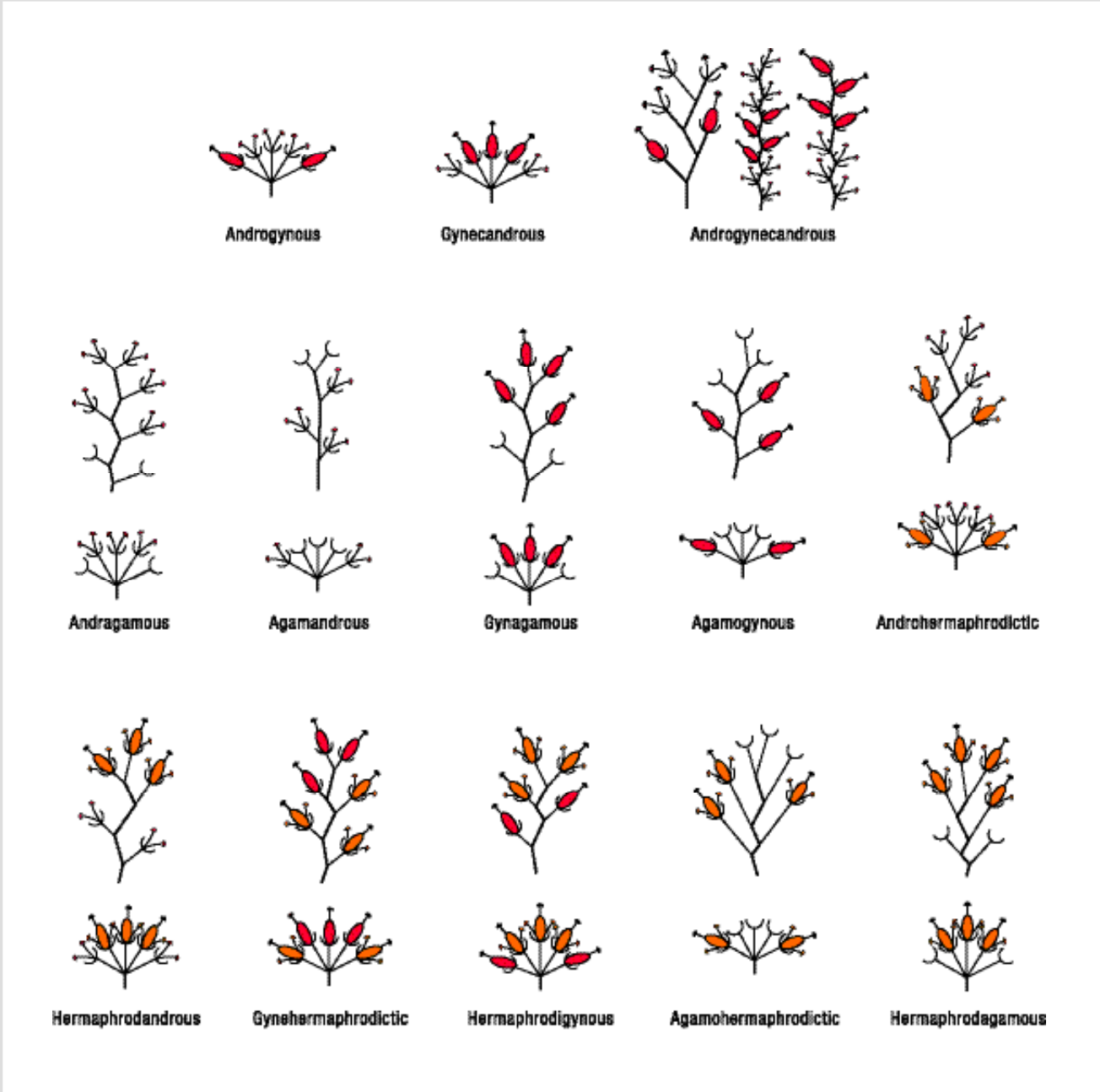

Fig. 11b. Inflorescence sex. (Redrawn from Radford *et al.* 1974).

Moraceae (*Ficus*), Rosaceae, Annonaceae (some *Annona*), Chrysobalanaceae, Combretaceae, and Lauraceae.

In Lauraceae, the flowers are protogynous (proterogynous) and the floral mechanism in the family is the synchronized dichogamy (Frankel and Galun 1977, Kubitzki and Kurz 1984). In the family, the species have two types of flowering in different individuals. In some, the flowers have receptive stigmas (opening of the female phase) in the early morning, ceasing activity at noon (closing of the female phase). In the afternoon of the same day or the following day, the stamens release pollen (opening of the male phase), ceasing activity at dusk (closing of the male phase). In other trees, the flowers have receptive stigmas in the afternoon and cease activity at dusk. The following morning, the stamens release pollen. This mechanism preventing self-pollination and cross-pollination becomes obligatory (Frankel and Galun 1977, Kubitzki and Kurz 1984). If the rhythm is disturbed by changing climatic conditions, the flower could be pollinated and fertilized by pollen coming from another flower in the same tree (geitonogamy), but the fruits undergo an early abscission. A postzygotic mechanism of incompatibility has been suspected (Kubitzki and Kurz 1984). Dichogamy has also been documented in Annonaceae [*Annona squamosa*, *A. cherimolia*, *A. reticulata*, *Cananga odorata*, *Rollinia membranacea* (syn. *R. jimenezii*), Betulaceae (*Alnus acuminata*) and Combretaceae (*Terminalia amazonia*)] (Deroin 1988; Flores 1994g; Flores and Sandí 1995; Gottsberger 1989a, 1989b, 1993; Kubitzki 1993). *Terminalia amazonia* has protogynous flowers. It is believed that the flowers are pollinated by pollen coming from the flowers of other trees (xenogamy); however, sporadic geitonogamy appears to occur. In this species, a postzygotic mechanism of incompatibility has also been suggested (Flores 1994g, Flores and Sandí 1995).

In numerous species, the dichogamy is partial and the second sexual phase begins before the first sexual phase is over. The flowers are functionally unisexual in the initial phase and bisexual (hermaphrodite) in their terminal phase (Faegri and Van der Pijl 1971, Frankel and Galun 1977). For example, the flowers of *Symphonia globulifera* L.f. are protandrous, with a bisexual phase in which the stigma is receptive and the anthers release pollen (Pascarella 1992).

The homogamous (self-sterile) hermaphrodite flowers release and accept pollen at the same time; nevertheless, they are not always autogamous. Both morphological (heteromorphic autoincompatibility) and physiological (homomorphic autoincompatibility) mechanisms may prevent self-pollination, self-fertilization, or seed development, thus promoting self-sterility (Faegri and Van der Pijl 1971, Frankel and Galun 1977).

Heteromorphic self-incompatibility is characterized by intraspecific differences in floral structure, reinforcing cross-pollination and cross-fertilization. Floral heterostyly is the most typical mechanism. In this case, two or three floral morphs exist. A distylous species has two floral morphs; in some flowers the styles are long, in others they are short. In the flowers with long styles, the stamens are found below the stigma level while in those with short styles, the stamens are above the stigma level. Other features are usually associated with style length. Morphs with long styles and short stamens have small pollen grains and long stigmatic papillae; morphs with short styles and long stamens have big pollen grains and small stigmatic papillae (Boshier 1995). These features favor cross-pollination between the two floral morphs. However, some species have a diallelic mechanism of incompatibility, lacking stylar and staminal polymorphism, and others have a polymorphism that is reduced to the style (Ganders 1979).

The homostyly of neotropical laurel [*Cordia alliodora* (Ruiz & Pav.), Boraginaceae] flowers has been described repeatedly (Johnston 1950, Miller 1985, Opler and others 1975); however, the species has a kind of heteromorphy restricted to stylar variation, and the small flower size may hinder differentiation between style and stigma (Boshier 1995). Additionally, two tree groups exist in which intercrossing is possible but intracrossing is not. The low variation in stylar length must be associated with a diallelic incompatibility system in the sporophyte (Boshier 1995).

Heterostyly is a type of genetically controlled polymorphism shared by at least 25 families of angiosperms (Ganders 1979), e.g., *Byrsocarpus*, *Rudgea*, *Psychotria*, *Turnera ulmifolia*, *Erythroxylum coca*, and *Cratoxylum* (Barrett and Richards 1990, Bawa 1992, Bawa and Beach 1983, Bawa and others 1985a, Bawa and others 1990). In distylous species, the polymorphism acts in conjunction with a diallelic incompatibility system to prevent self- and intramorphic fertilization (Boshier 1995).

Homomorphic autoincompatibility can be divided into two subtypes (Radford and others 1974):

Gametophytic. Fertilization is inhibited as a result of genetic action in the pollen grain (male gametophyte) when the pollen tube protrudes through the stigmatic-stylar tissues (e.g., *Tectona grandis* L.f.).

Sporophytic. Inhibition of pollen germination or pollen tube growth is imposed by genetic action of the sporophytic tissues such as the stigma, the style, and sometimes the embryo sac; e.g., *Dalbergia retusa* Hemsl., *Dalbergia miscolobium*, *Dipteryx panamensis*, *Myrospermum frutescens* and probably *Terminalia amazonia* (Barrett and Richards 1990, Bawa and Beach 1983, Flores and Sandí 1995).

The incompatibility systems share a common factor: both maintain a high degree of genetic heterozygocity in the species population. With a few exceptions, the incompatibility system operates at the stigma or style level. Because both structures have diploid tissues and a sporophyte genome (parent tree), the incompatibility reaction is controlled by the genome of the parent tree. The male gametophyte (pollen grain) has in part the genome of the sporophyte in which it develops and some sporophytic components. Thus, the incompatibility reaction of the pollen can be controlled by the gametophyte itself or by the sporophytic components carried with it. In the gametophytic incompatibility the haploid genome of the pollen and the diploid genome of the stigma/style genetically control the pollen-stigma/style interaction. Incompatibility that occurs in the embryo sac is haploid-haploid (Frankel and Galun 1977). The sporophytic incompatibility is determined by the genome reaction of the paternal sporophyte from which the pollen grain originated.

In some species, homogamous flowers can be cleistogamous. In these flowers, pollen release and stigma receptivity are synchronized before floral perianth opening. Species with this type of flower include *Annona muricata*, *Cyathocalyx*, *Dasymaschalon*, *Goniothalamus* sp. in Annonaceae (Kessler 1993), *Lithospermum caroliniense* (Levin 1972), and *Coffea arabica* (Rubiaceae). If the maturation and functioning of the unisexual flowers (staminate and pistillate) in a monoecious tree are not synchronized, cross-pollination is obligatory. In dioecious species, cross-pollination and cross-fertilization are obligatory. The forests in the lowlands of the Atlantic coast in Costa Rica show dominance of species with hermaphrodite flowers in the canopy and subcanopy; dioecious species have a lower representation and monoecious species are scarce (Bawa and others 1985a, b).

Inflorescence Types

Because the traditional nomenclature used to describe inflorescences, which shows morphological inconsistencies, is widely used, descriptions and definitions follow. The stem bearing the inflorescence is the peduncle, while that bearing the flower is the pedicel. The flowers develop in the bract axil; if the inflorescence lacks bracts it is ecbracteate. The groups or whorls of bracts form an involucre; secondary involucres, as in the compound umbels, are involucels of bractlets. When a single conspicuous bract subtends a floral group (usually a fleshy spike or spadix), it is called a spathe.

The most common types of traditional inflorescences are the following (see fig. 12):

Dichasium. Peduncle with a terminal flower and a pair of branches, each producing a single flower. The central flower matures first. The simple dichasium can be repeated as a unit several times giving rise to a compound dichasium. The dichasium has been named cyme, but the term is used indiscriminately and its use is inappropriate.

Monochasium. Peduncle with a terminal flower and a basal lateral branch bearing a single flower. The simple monochasium can be replicated several times giving rise to a compound monochasium, which may form the following subtypes:

(1) **Bostryx (helical monochasium)**—Flower distribution spirally coiled around the main axis.

(2) **Cincinnus**—Flowering alternately to one side and then the other along one side of the axis, the whole inflorescence often coiling downward.

(3) **Rhipidium**—A bostryx is extended in one plane, and the inflorescence is sometimes fan-shaped.

(4) **Drepanium**—A cincinnus bears all the branches on one side. The inflorescence extends in one plane and coils downward to one side.

Panicle. Inflorescence with a central axis giving rise to lateral branches that are themselves branched. The minor ramifications can be dichasial. A crowded, nearly cylindrical panicle is called a thyrse.

Raceme. Inflorescence with a central axis, along which simple pedicels of similar length are located. The blooming usually proceeds upwards, although it may be irregular.

Spike. Elongated inflorescence with an unbranched central axis with sessile or subsessile flowers. The blooming usually proceeds upwards. The spikelet or locusta is the basic unit of the inflorescence in grasses and sedges.

Corymb. Flat-topped inflorescence with a central axis giving rise to branches of unequal length. The lateral branches may branch further or be simple pedicels. Blooming usually begins in the external flowers and proceeds centripetally, but can also be irregular.

Head (capitulum). A determinate or indeterminate, rounded or flat-topped cluster of flowers placed at the same level. The flowers can be sessile or subsessile and are placed on a wide receptacle. Blooming usually begins at the periphery and proceeds centripetally. Heads may be solitary or form diverse aggregates. Each bract of the involucre is a phyllary.

Umbel. Inflorescence with several branches arising from a common point, in the distal end of the peduncle. If each branch ends in a single terminal flower, the umbel is simple; if

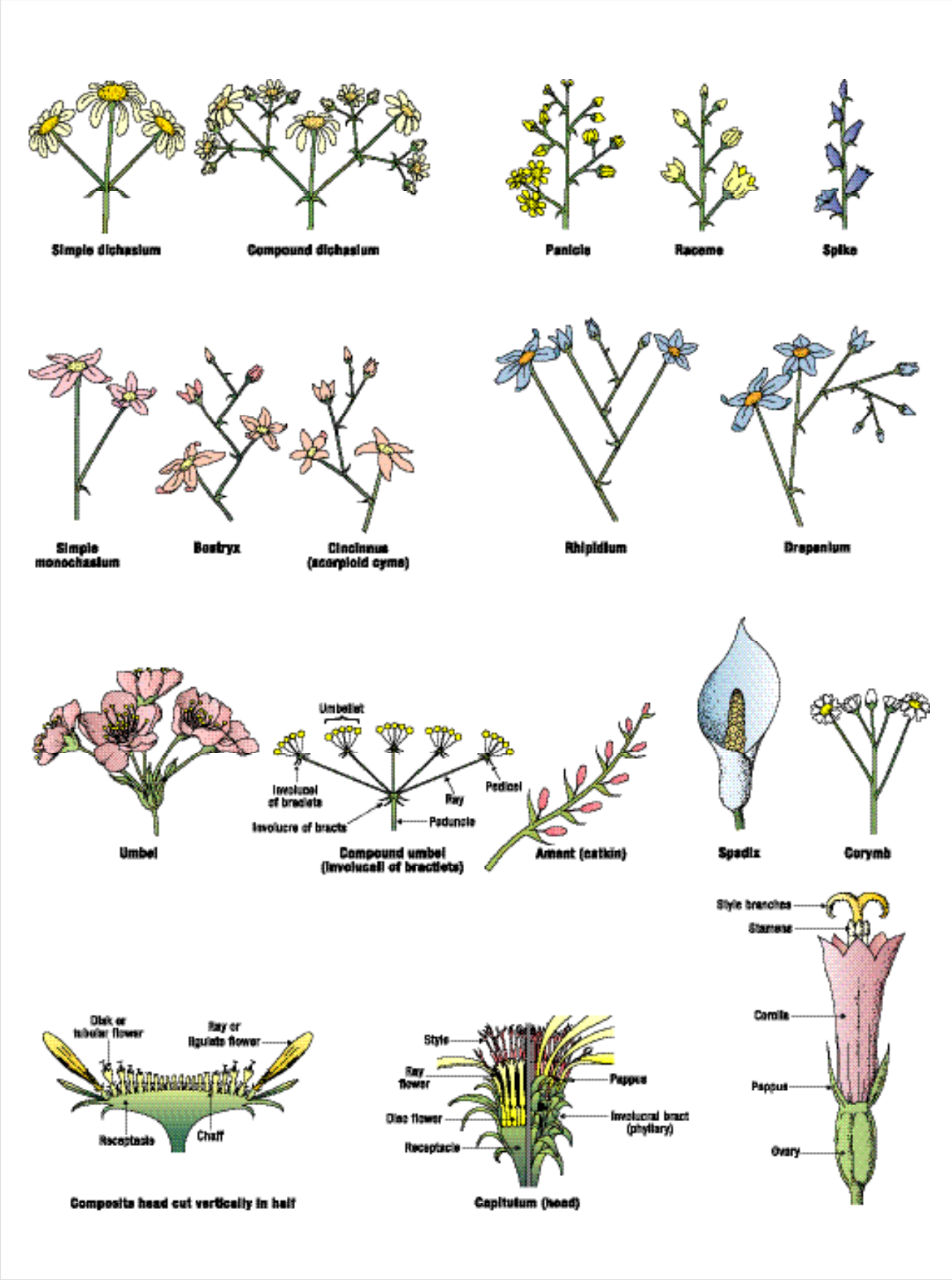

Fig. 12. Morphological inflorescence types

it ends in a secondary umbellate, the umbel is compound. Flowering usually begins in the peripheral flowers and proceeds centripetally. The umbel may have an involucre at the peduncle distal end. If the umbellates have similar whorls of bracts, they are involucels and each bract is a bractlet. The main branches of a compound umbel are rays, and the corresponding members of the umbellate are pedicels.

Ament (catkin). Spike, raceme, or dichasium of apetalous unisexual flowers. It can be long or short, erect or hanging. The flowers are usually very small and subtended by a scaly, small bract.

Spadix. Spike with a thick, fleshy apex, surrounded by a large, usually colored bract (spathe). Frequently, the flowers are very small and unisexual.

Siconium (hypanthodium). Inflorescence with small flowers on the wall of a concave head.

Other inflorescence types include:

Glomerule. Inflorescence formed by an indeterminate cluster of sessile or subsessile flowers.

Verticillaster. A group of whorled dichasia at the nodes of an elongated axis.

Pseudanthium. Inflorescence with several flowers simulating a single flower but composed of more than a single axis bearing subsidiary flowers. The pseudanthium is subtended by an involucre: scapose, with a single flower or inflorescence on a leafless peduncle; or scape, usually arising from a basal rosette.

Reproductive Cycle

During the flowering period of angiosperms, the tree or sporophyte produces microspores forming microgametophytes or pollen grains, and megaspores producing megagametophytes or embryo sacs inside the ovules (Flores 1999). In most angiosperms the entire reproductive cycle, from floral inception to fruit and seed maturation, occurs in one season (fig. 13); however, there are exceptions such as the red oak (*Quercus* subg. *Quercus*) (Bonner and others 1994) and *Allocasuarina* (Flores 1976, Flores and Moseley 1982).

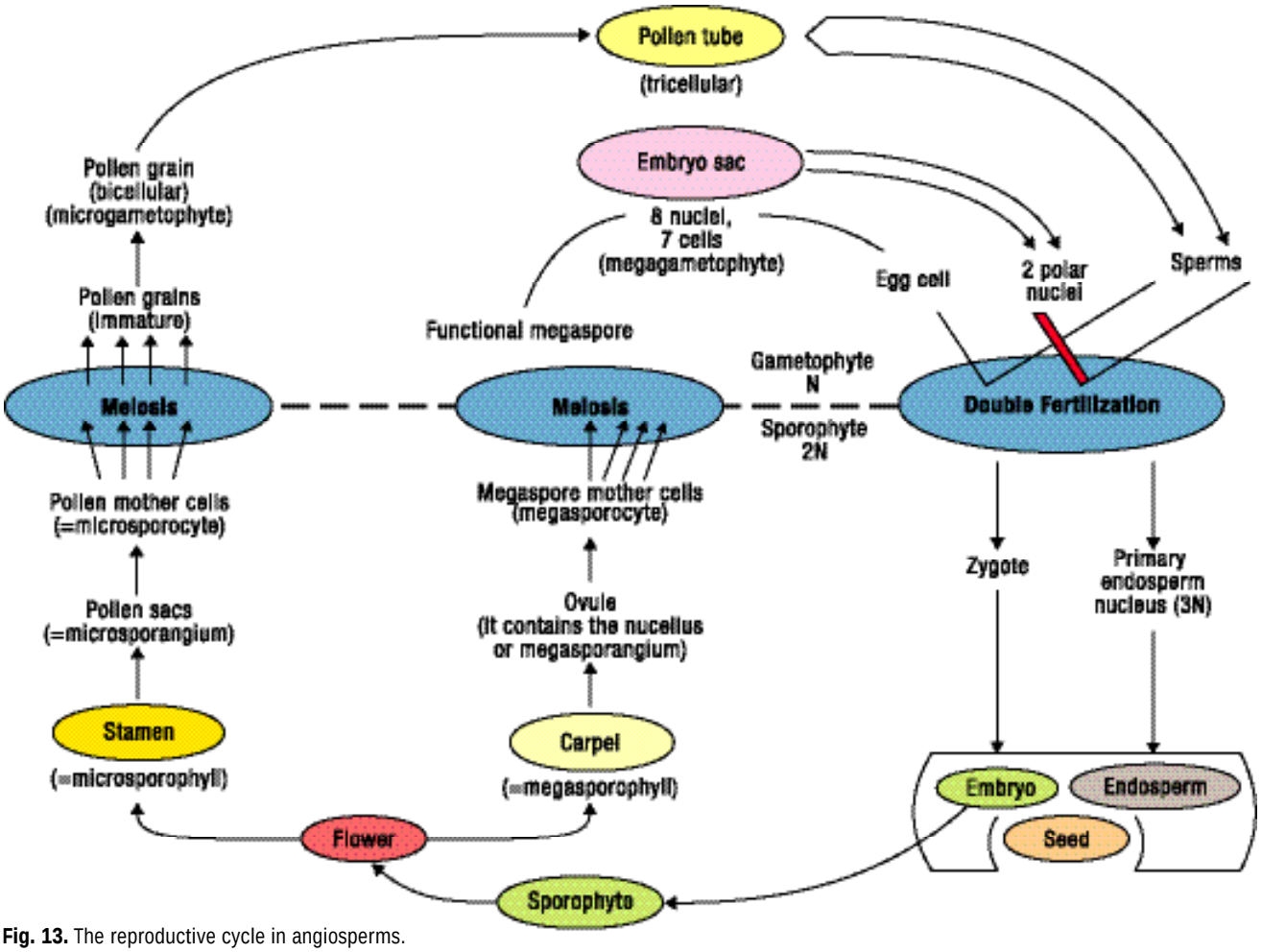

Fig. 13. The reproductive cycle in angiosperms.

Pollen

The embryonic anther has a mass of fundamental tissue surrounded by a protodermis. This layer forms the epidermis of the anther. In the four corners of the developing anther, two to four hypodermal cells are formed; each group divides periclinally forming a series of primary parietal cells and primary sporogenous cells (internal layer). Figure 14 shows the histogenesis of a typical anther; figure 15 illustrates the structure of a mature anther. In the mature anther the outer layer or epidermis covering the microsporangium wall may remain intact in families such as Lauraceae, Magnoliaceae, and Winteraceae. In others, such as Moraceae and Ulmaceae, the epidermal cells restrain or fall down during anther maturation. In some species, the epidermis has trichomes; in others, it develops fibrillar bands and is called an endothecium. If the epidermis falls down, the underlying layer substitutes for it. This layer is commonly called the endothecium or fibrous layer because it has cell wall thickenings; these thickenings are absent in the stomium.

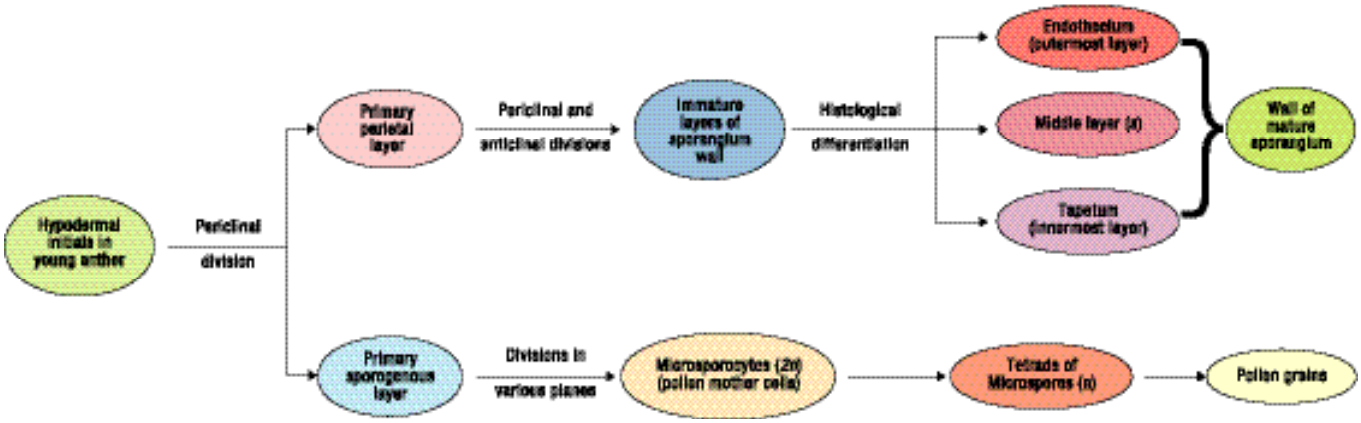

Fig. 14. General pattern of development of the microsporangium in the angiosperms.

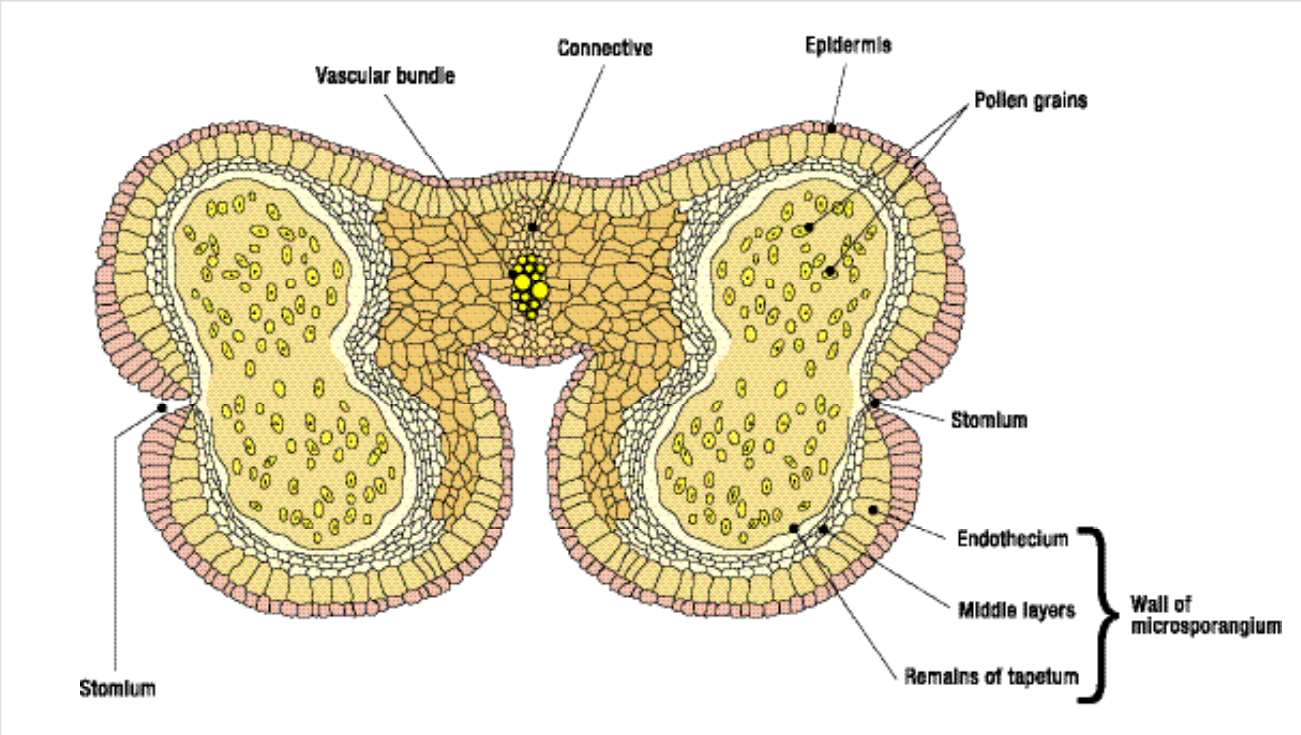

Fig. 15. Mature anther.

Middle layers consist of one or several layers of tubular cells with thin walls beneath the endothecium. These layers are compressed or crushed during microspore formation. The inner layer of the microsporangium wall is the tapetum. It seems to accomplish three functions: microspore nutrition, exine formation, and synthesis of some materials contributing to pollen grain wall formation (tryphine and pollenkitt). In angiosperms the tapetum can be glandular (secretory) or periplasmodial (amoeboid). In the first case, the cells remain intact and persist in situ; in the second, the cell walls break down and the protoplasts mingle. The protoplasmic mass forms a multinucleate periplasmodium, which becomes mixed with the pollen mother cells.

The cells in the primary sporogenous layer can divide before microsporogenesis, or directly become the microsporocytes or pollen mother cells. These, through meiosis, produce haploid microspores (n) which later differentiate as pollen grains. The cells in the primary parietal layer form, through periclinal and anticlinal divisions, a variable number of layers concentrically placed, which differentiate and become the several layers of the mature sporangium wall (Flores 1999).

Meiosis of the pollen mother cells in the tapetum is the time of the synthesis of substances such as starch, lipids, and tryphine. The tapetum is involved in numerous activities. It keeps a delicate balance with the differentiation of the sporogenous tissue, and any alteration in it induces the degradation of pollen. Some evidence indicates that, through physical or physiological factors, the tapetum may induce the abortion of pollen. The endothecium or the vascular bundle of the filament may influence the abortion process. The carotenoids and carotenoid esters formed in the tapetal cells participate in the formation of the sporopollenin, a major component of the pollen wall. The pollenkitt (Pankow 1957) formed by lipids, glycolipids, glycoproteins, monosaccharides, flavonoids and carotenoids synthesized in the tapetum, gives adhesiveness, order, and color to the pollen grain (Heslop-Harrison 1968, 1979a, 1979b; Hesse 1979). Its probable functions are insect attraction, pollen protection against ultraviolet radiation, and adhesion to insects' bodies; the last function contributes to pollen dispersal (Heslop-Harrison 1968, 1979a, 1979b).

The pollen grain is the structure containing the male gametes. It is formed by a vegetative cell (tube cell) and a generative cell immersed in the vegetative cell cytoplasm (bicellular pollen grain or microgametophyte); both cells are haploid (Brewbaker 1967). If the generative cell divides mitotically and gives rise to the spermatic cells during pollen maturation and before pollen tube development, the pollen grain is tricellular (fig. 16). The nucleus of the vegetative cell controls the pollen tube's metabolism as well as its initial growth after germination. The spermatic cells have self-motility, are structurally different, and may have different patterns of cytoplasmic genetic transmission (Flores 1999, Knox 1984, Russell and Cass 1983).

The pollen grain covering is complex and is formed by the exine (external layer formed by sporopollenin and charac-

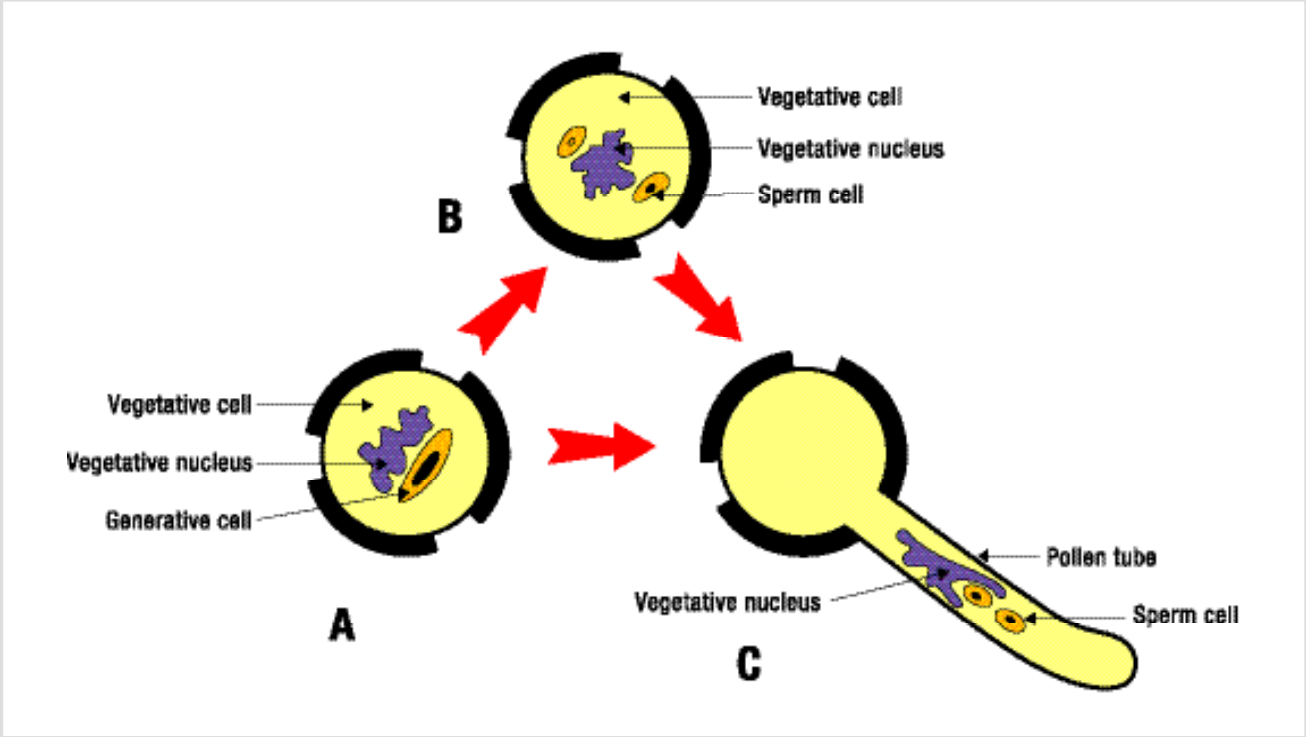

Fig. 16. Pollen grain types and pollen germination. a, Bicellular pollen grain; b, Tricellular pollen grain; c, Pollen germination and tube development.

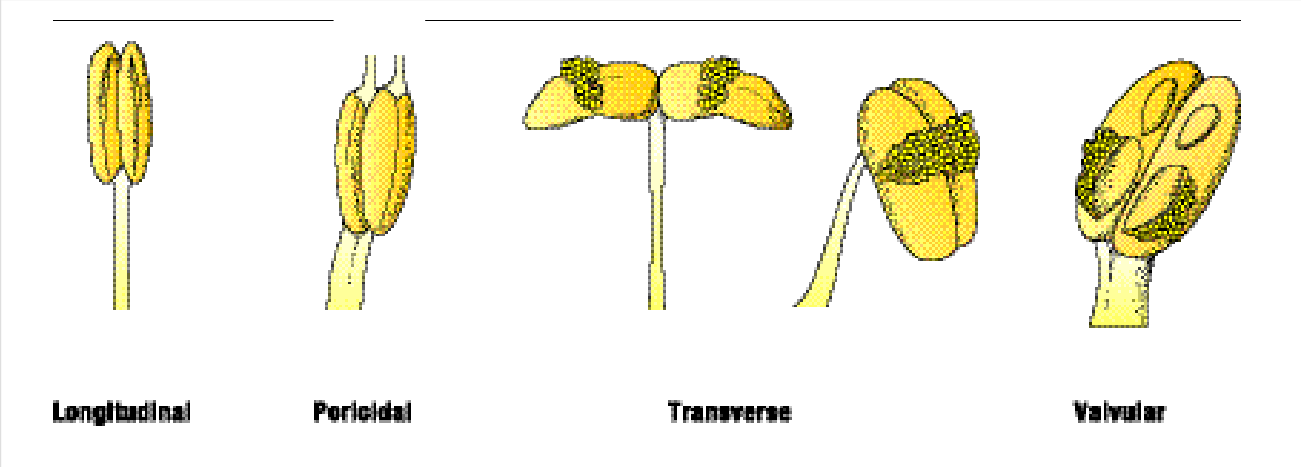

Fig. 17. Anther dehiscence.

terized by a specific ornamentation) and the intine (smooth inner layer made of polysaccharides). The layers are chemically, morphologically, and ontogenetically different (Knox 1984). Cell wall formation follows different patterns in different species, as an adaptation to various factors including cellular environment, pollination method, and potential interactions with the different pollination vectors.

The correlation between exine structure and pollination method has been corroborated in diverse families pollinated by both wind and animal vectors (Knox 1984). The transportation methods and the structures expediting pollen adhesion to the stigma are adaptations; for example, exine thickness and ornamentation, aperture type, and wall adhesives (Heslop-Harrison 1968, 1979a, 1979b; Heslop-Harrison and others 1973). Pollen-stigma recognition and the allergic reaction in humans (pollen wall proteins and glycoproteins) are also adaptations. Pollen germination and pollen tube growth throughout the style involve the action of specific enzymes and heterotrophic nutrition; these conditions represent a high degree of specialization.

The pollen of most angiosperms is a free cellular structure (monad), but in some families there are compound grains. Compound grains can be arranged in tetrads (a microsporocyte product), polyads of grains, or complex masses (pollinia). The tetrads may have zero to four fertile grains mixed with a remnant of abortive grains. Pollen shape, a genetically determined feature, is influenced by three factors: microspore position in the tetrad, number and disposition of germinal apertures, and differential cellular expansion during microspore and pollen grain development.

Anther dehiscence is the mechanism of pollen release. In some families the pollen is released through a small opening usually placed at the distal end of the anther. This type of dehiscence is poricide (e.g., *Hyeronima alchorneoides*, *Conostegia*, *Miconia*, *Gustavia*). In most species, however, the anther dehisces longitudinally along the stomium (longitudinal dehiscence; e.g., *Vochysia*, *Alnus acuminata*) (fig. 17). If the anther is oriented outward and dehisces longitudinally to the exterior, it is called extrorse; if it is oriented inward and dehisces longitudinally to the interior, it is introrse (*Lacandonia*). In other species the anther opens transversely (transverse dehiscence; e.g., *Brosimum alicastrum*). Although the force opening the stomium seems to be generated in the endothecium, this issue is still a matter of discussion. The dehiscence is not always produced by changes in the fibrous layers; in many anthers, especially those of the poricide type, this layer is missing.

Anthers with a complex shape are usually associated with special types of poricide dehiscence and have tubular projections in the pollen sac ends, through which the pollen is released. The anthers with elongated, narrow openings may have a valve. This type of dehiscence is valvular and occurs in Hernandiaceae (*Hernandia stenura*), Lauraceae (*Ocotea*, *Nectandra*), and Monimiaceae (*Mollinedia*, *Siparuna*) (fig. 17). The valve opens at the base and projects outward and backward, carrying the pollen mass outside (Flores 1999). The number and distribution of valves has taxonomic value in Lauraceae.

Ovule

The nucellus (megasporangium), integument(s), chalaza, and funiculus form the typical ovule (fig. 18). The nucellus occupies the central part of the ovule and is surrounded by the integuments. These leave a passage (micropyle) for pollen tube penetration. The integuments protect and nourish the nucellus. After fertilization, they form the seedcoat, the raphe, and the chalaza. The ovules can be bitegmic, unitegmic or ategmic. In some Annonaceae (*Cananga odorata*, *Cleistopholis patens*,

Cyathocalyx sumatranus, *Guamia mariannae*, *Mezzetia leptopoda*, *Mezzettopsis creaghi*) a third integument, placed between the testa and the tegmen, has been proposed (Corner 1976, Kubitzki 1993). The third integument in the Opuntieae (Cactaceae) is a funicular covering surrounding the seed (Flores and Engleman 1976). The funiculus is an extension, usually filamentous, that unites the ovule with the placenta. The funiculus has a vascular bundle transporting nutrients from the sporophyte to the megagametophyte (Bouman 1984, Flores 1999, Maheshwari 1950).

Frequently, the ovule has special structures:

Hypostase. Usually cupuliform, formed by differentiation of nucellar and chalazal tissues. It is located on the chalazal vascular bundle and can be a cell mass or a discoid cell plate. It is found in the ovules of the Anacardiaceae, Bixaceae, Euphorbiaceae, and Lauraceae. It is considered a physical barrier to retain embryo growth and a bridge connecting the chalazal vascular bundle with the embryo sac, which facilitates nutrient transfer to the embryo sac (Bouman 1984, Flores 1999, Tilton 1980). Other functions include producing enzymes and hormones and maintaining water balance in dormant seeds.

Podium. A nucellar remnant, resistant to the absorbing activity of the embryo sac. This structure is located at the nucellar base and is cupuliform in shape. When it is located near the micropylar end, it is epistase. After fertilization, it generally precludes the micropyle (Bouman 1984, Flores 1994a).

Obturator. Formed by funicular, placental, or funicular-placental tissues. It is a protuberance covered by secretory trichomes or epidermal papillae, functioning as transfer cells. The obturator surface extends to the micropyle or enters through it. In general, it is continuous with the ovarian, stylar, and stigmatic tissues through which the pollen tube penetrates. After pollination, the obturator degenerates (Bouman 1984, Flores 1999).

The ovules have different forms and degrees of curvature: athropous (orthotropous), anatropous, campylotropous,

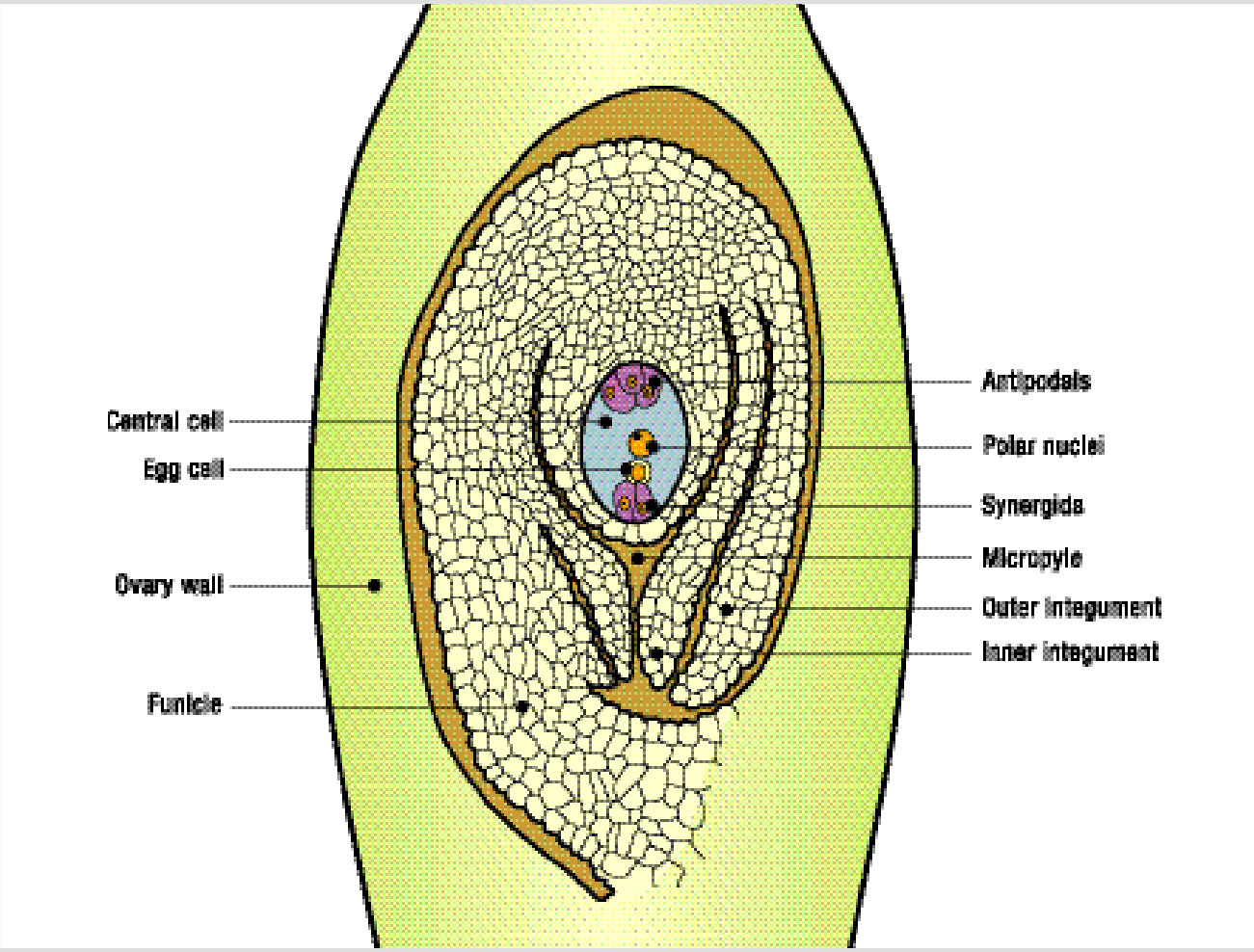

Fig. 18. Bitegmic ovule showing the common embryo sac in angiosperms (*Polygonum type*).

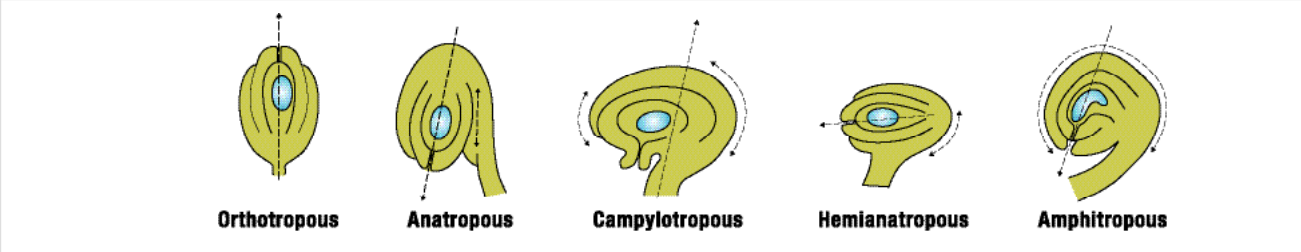

Fig. 19. Ovule types (Redrawn from Flores 1994a).

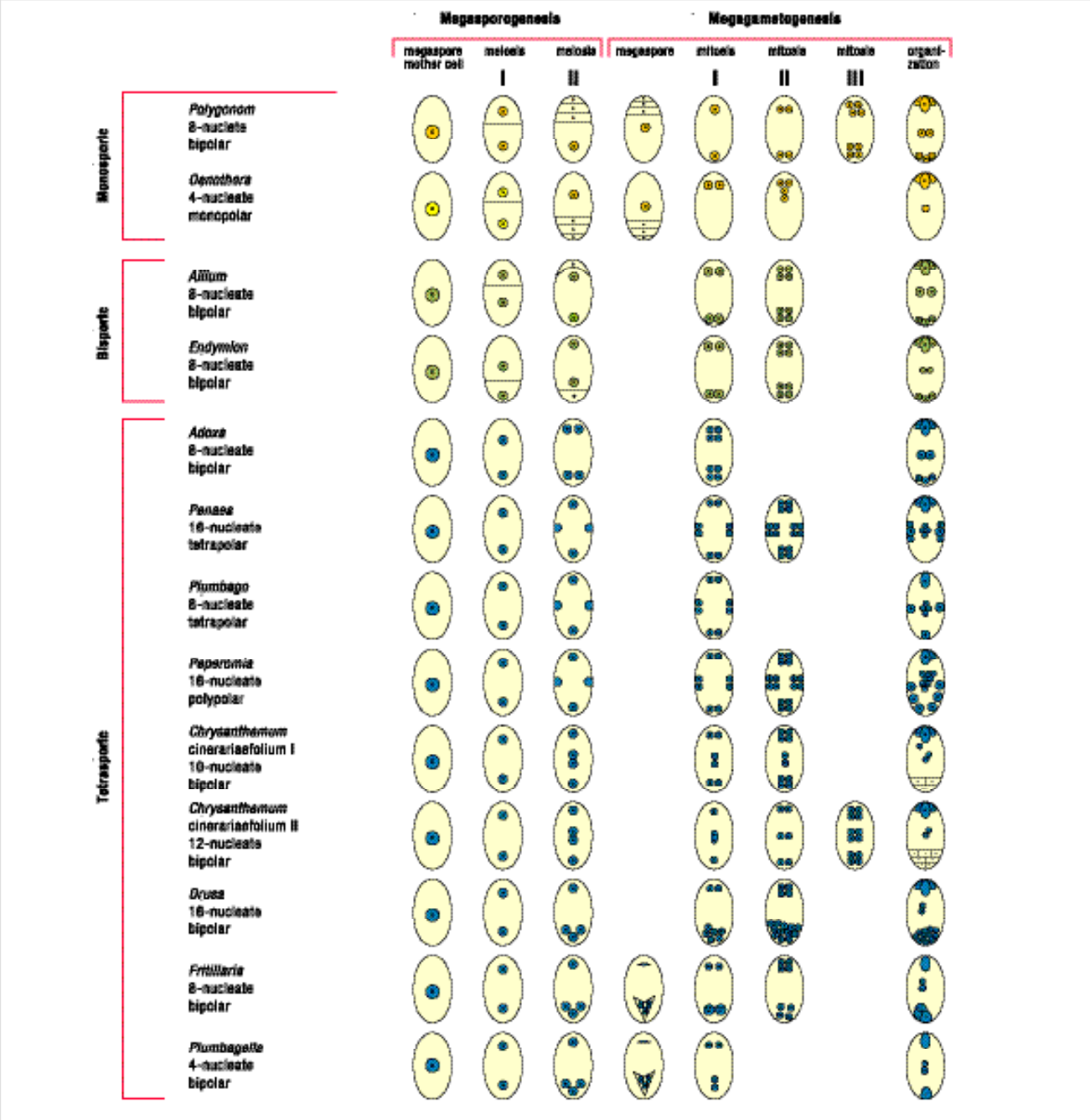

Fig. 20. Schematic representation to show the origin and development of different types of embryo sacs.

hemianatropous, or amphitropous (fig. 19). In general, the differential growth is in the funiculus-chalaza area. The integuments and the nucellus cause the differences in shape and curvature exhibited by the ovules and the mature seeds (Flores 1999, Flores and Engleman 1976). In many cases, the curvature shown by an ovule during the floral anthesis is different and usually smaller than that shown by the mature seed. After fertilization, the differential growth occurring in the different parts of the ovule may increase or diminish the ovule curvature. The seed curvature is correlated to embryo shape, micropyle position, and hilum length.

During ovule development, the archesporial cell differentiates in the nucellus. This cell originates, directly or indirectly, in the megasporocyte, meiocyte, or megaspore mother cell. The latter divides by meiosis and gives rise to four haploid megaspores. There are many variations in the megasporogenesis (fig. 20), but in most cases only the chalazal megaspore is functional. Mitotic divisions of the functional megaspore produce the monosporic megagametophyte (embryo sac). This type is common in the angiosperms. In other cases, no cell wall forms during the second mitotic division and a dyad is formed. The binucleate cell serves as a starting point for the formation of the embryo sac (bisporic). There are species in which no wall forms during the meiosis and a coenomegaspore with four nuclei is formed; it serves as the starting point for embryo sac formation (tetrasporic) (Bouman 1984, Flores 1999, Maheshwari 1950, Willemse and Van Went 1984).

Approximately 60 to 70 percent of angiosperms have an embryo sac (fig. 21) with eight nuclei and seven cells: the egg, two synergids, a central cell (binucleate), and three antipodals (Bouman 1984, Eames 1961, Flores 1999, Willemse and Van Went 1984). The egg cell and the synergids are big cells located in the micropylar end of the embryo sac and forming a structure called the egg apparatus. The synergids are partially surrounded by a wall that is thick at the micropylar end; this thickening forms the filiform apparatus. The central cell occupies the middle of the embryo sac and contains two polar nuclei or a fusion nucleus; the cell wall is partial and is restricted to the chalazal end. The cell membrane or plasmalemma has the typical invaginations of a transfer cell at the micropylar end. The antipodals are small cells with a varied structure, and may be ephemeral or persistent after fertilization. They transport nutrients from the nucellus to the central cell and store nutrients for future endosperm. These cells may also serve a secretory function including secretion of growth regulators involved in endosperm development (Bouman 1984, Flores 1999, Willemse and Van Went 1984).

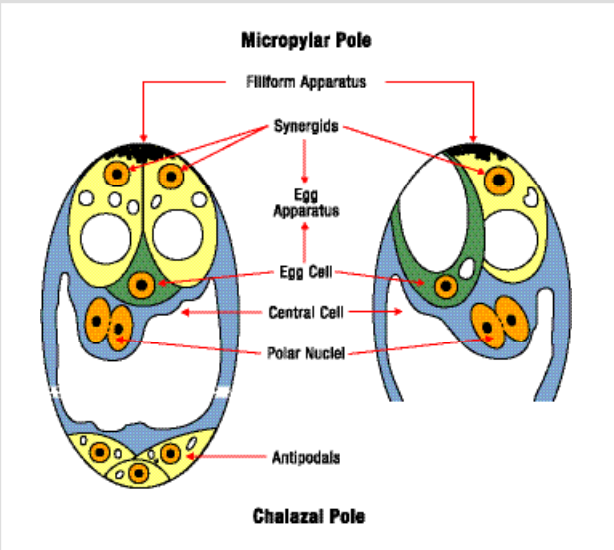

Fig. 21. Embryo sac (*Polygonum* type).

FLOWER POLLINATION AND FERTILIZATION

Pollination Vectors

In angiosperms, pollination can be biotic or abiotic; most species participate with more than a single vector. For example, in *Mabea fistulifera* (Euphorbiaceae), pollination occurs through diurnal (passerine birds, bees) and nocturnal (bats and *Didelphis marsupialis*) pollinators (Vieira and Carvalho-Okano 1996). The adaptation to pollination mechanism is controlled by numerous evolutionary principles. Floral morphology is related to the most efficient pollinator, and evolutionary adaptation is parallel between the pollination vector and the structural, spectral, and olfactory specifications of the flower (Faegri and Van der Pijl 1971, Frankel and Galun 1977, Gottsberger 1993, Kalin-Arroyo 1978).

Biotic pollination must be carried out by different vectors such as insects (entomophily), birds (ornithophily), and bats (chiropterophily). Several mammals contribute to a minor degree, including prosimians, marsupials, rodents, giraffes, reptiles such as lizards, and invertebrates such as snails and slugs (malacophily). Biotic pollination provides mutual benefits: the vector obtains a reward (nectar, fragrances, oils, or pollen) and the plant disperses the pollen (Buchman 1987, Frankel and Galun 1977, Walter 1983).

The abiotic agents are gravity, wind [air movements or air currents (anemophily)], and water [movements or currents (hydrophily)]. Pollination by gravity is unidimensional and, in general, results in species autogamy. Dispersal by wind is tridimensional; by water it can be bidimensional if it occurs on the surface or tridimensional if large water volumes or drops are involved (Frankel and Galun 1977).

The different pollination vectors are associated with floral syndromes or groups of characteristics displayed by the diversity of flowers to attract and reward them. The most common means of attraction are colors and fragrances (Brantjes 1973, 1978). For example, most hymenopterans have similar vision systems of color, with three kinds of receptors (ultraviolet, blue, and green) and only some species have tetrachromic vision (Menzel and Backhaus 1989, Menzel and Shmida 1993). Floral color is not restricted to the perianth; it may be found in bracts [*Bougainvillea* (Nyctaginaceae), *Euphorbia pulcherrima* (Euphorbiaceae)], stamens, and gynoecium. The colors can be produced by light refraction on physical structures and surfaces or by absorption of a defined light wavelength by the pigments. The carotenoids, which are aliphatic compounds, produce colors varying from light yellow to dark red. The flavonoids (anthocyanins, flavones, flavonols, aurones) produce a color scope that ranges from light yellow in the flavones to purple and blue in the anthocyanins. Most color displays and chemical mechanisms use a limited number of anthocyanins (flavonoids) and include the anthocyanin color loss and the participation of a copigment (Gottsberger 1993). The most common anthocyanins are the magenta cyanidine, the purple delphinine, and the red pelargonin. The betalains are alkaloids producing a group of colors varying from red to light ivory (Faegri and Van der Pijl 1971, Flores 1999). The color changes produced by age can be an indicator for vector visits, but the vector does not always discriminate on this basis (Gottsberger 1993).

Nectar production influences vector behavior in the pollinating process. Nectar is composed of monosaccharides (glucose, fructose) and disaccharides (maltose, melobiose), amino acids, proteins (enzymes), lipids, alkaloids, phenols, antioxidants (ascorbic acid), organic acids, saponins, dextrins, and inorganic substances (Baker and Baker 1983). The nectar can be directly ingested by the visitor (birds, bats, lepidopterans, dipterans) or carried to the nest to feed the larvae (hymenopterans). A strong correlation exists between the concentration of sugars and amino acids in the nectar and the type of pollinator (Baker and Baker 1983, Koptur 1994). In addition to pollinator reward, the nectar may have other functions. In some plants it serves as substrate for pollen grain germination; in others, inhibiting yeasts present in the nectar may inhibit pollen germination. The nectar also attracts insects to protect the plant against predators, a phenomenon present in the Neotropics (Bentley and Elias 1983, Koptur 1994, Vinson and others 1997). Flowers with elaiophores offer oils (Faegri and Van der Pijl 1971, Gottsberger 1993). The oils are formed in epithelial glands of the calyx (most New World Malpighiaceae) and released as an exudate exploited by bees such as *Centris* (e.g., *Byrsonima crassifolia* (L.) Kunth, *B. crispa*, some *Bunchosia*) and Krameriaceae. These oil-producing flowers are pollinated by oil-collecting bees (Vinson and others 1997). The plant may use mechanisms, such as inflorescence size, floral morphology, anthesis patterns, nectar production, and dichogamy, to restrict pollen remotion.

Pollinating insects can be coleopterans [beetles (cantharophily)], hymenopterans (symphytophily), wasps (vespophily), ants (phormicophily), bees (melittophily), flies (myophily), butterflies (psychophily), and moths (palaenophily) (Faegri and Van der Pijl 1971, Frankel and Galun 1977, Gottsberger 1993, White and others 1994). Some insects have mechanisms to answer the optical signals sent by the anthers, confirming that stamens and their mimetism are common signals for pollinating insects. Fragrances also attract insects; for example, the osmophores of the neotropical orchid *Stanhopea* and other genera, such as *Clowesia* and *Polycnis*, produce floral scents that attract euglossine bees (Buchman 1987, Curry 1987, Stern and others 1987, Williams 1983). These scents consist of several compounds such as monoterpenes and benzenoids (Williams and Whitten 1983). The production of heath-promoting aroma volatilization to attract pollination vectors has been corroborated in numerous tree species. For example, the flowers of *Annona muricata* and other species in the genus have thermogenic respiration which, combined with strong fragrances, attract dynastid insects (Armbruster and Berg 1994; Gottsberger 1989a, 1989b; Kessler 1993). The male euglossine bees (*Euglossa*, *Eulaema*) collect fragrances from flowers, mix them with the labial glandular secretions, and probably biochemically modify the fragrances to attract females for mating (Armbruster and Berg 1994, Knudsen and Mori 1996, Whitten and others 1989, Williams and Whitten 1983). The scent has a daily cycle, probably influenced by the thermal environment (Armbruster and Berg 1994). These variations may influence insect distribution and mating systems (Corbet 1990). Some insects can change their preference for scents with the season (Gottsberger 1993, Knudsen and Mori 1996, Walter 1983). The entomophilous species usually have large, spherical pollen grains (more than 300 ?m) and a thick, ornamented exine which facilitates the adhesion to insects and stigmatic surfaces. Many pollen grains also have an adhesive cover or lipid seal (pollenkitt) (Flores 1999, Frankel and Galun 1977, Knox 1984).

The coleoptera are a primitive group and cantharophily has been associated with the most primitive angiosperm families; nevertheless, in some families such as the Annonaceae, Calycanthaceae, Eupomatiaceae, and Magnoliaceae, the cantharophily is derived, secondary, and parallel to floral specialization (Gottsberger 1989a, 1989b, 1993). In those groups, the flowers are open, have no structural restrictions to insect access, and produce an excess of organs and tissues that are

Fig. 22.

Fig. 23.

Fig. 24.

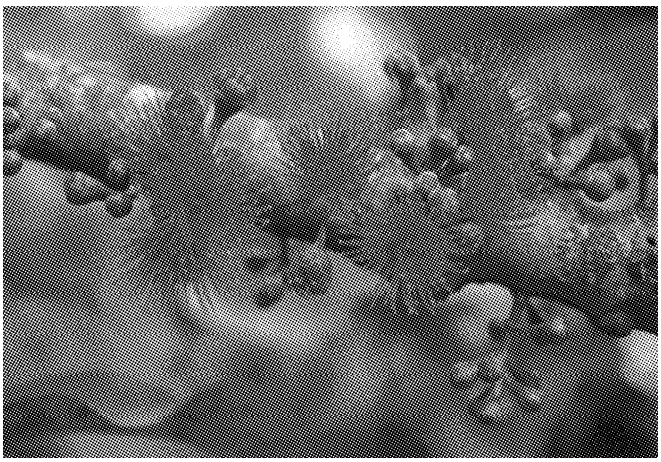

Fig. 25.

eaten by the beetles (figs. 22 and 23). Only exceptional cases have flowers with nectar (Faegri and Van der Pijl 1971, Gottsberger 1993, Knox 1984). The Myristicaceae from southeast Asia (*Myristica*, *Horsfeldia*, *Knema*, *Gymnacranthera*) also seem to be pollinated by coleoptera even when they have a floral structure that strongly differs from that of the annonaceous flowers. The flowers are whitish or creamy, have a nocturnal scent, and lack nectaries or defined secretory structures. They are unisexual and the fused perianth forms a small urn that restricts insect access; the gynoecium of the pistillate flower also has a single ovule (Armstrong and Drummond 1986). Curiously, in the Melastomataceae, with flowers having stamens with poricide dehiscence, the coleopteran squeezes the anther and extracts the pollen.

Psychophilous and palaenophilous flowers have sacarose concentrations in the nectar varying from 1 to 40 percent; the higher percentages are in the palaenophilous (Faegri and Van der Pijl 1971, Gottsberger 1993). Butterflies have diurnal activity and are usually attracted by small flowers with deep colors and soft, agreeable scents. The corolla is trumpet-shaped with a narrow base and stands in a vertical position; sometimes the flowers are not attractive but the bracts are intensely colored (*Godmania*, *Mussatia*). The anthesis is diurnal, but the flower usually does not close at night (De Vries 1985, 1988; Faegri and Van der Pijl 1971). Moths are the most important lepidopteran pollinators in the Neotropics, especially sphingids; with their elongated proboscis they easily reach pollen (Faegri and Van der Pijl 1971). The flowers are white or poorly colored, sometimes red; the tubular or lobulated corolla maintains a horizontal position or is hanging (*Leucocalantha*, *Tanaecium*). The anthesis is nocturnal, the anthers are versatile, and the scent is sweet and strong (Faegri and Van der Pijl 1971). Many species have the brush syndrome: very small flowers clustered, each with many stamens and stigma above the perianth level. These features attract large pollinators like sphingids. The species pollinated by moths include *Enterolobium cyclocarpum* (Jacq.) Griseb., *Samanea saman* (Jacq.) Merr., *Pseudosamanea guachapele* (Kunth) Harms, *Cojoba arborea* (L.) Britton & Rose., *Abarema adenophora* (Ducke) Barneby & J.W. Grimes, *Albizia niopoides* (Spruce ex Benth.) Burkart, and *Inga* (Fabaceae-Mimosoideae); *Cedrela odorata* and *Guarea* (Meliaceae); *Cordia alliodora* (Boraginaceae); and *Quararibea asterolepis* (Bombacaceae) (Bawa and others 1985a, Koptur 1994) (figs. 24-25). The *Symphonia globulifera* (Clusiaceae) species

Fig. 26.

has been considered ornithophilous and pollinated by hummingbirds, although pollination is carried out by lepidoptera. The hummingbirds remove nectar (Pascarella 1992).

Melittophily is the most common type of entomophily in the Neotropics. Bees may be generalists or specialists and some may detect differences in the pollen availability of diverse flowers (Gottsberger 1993). The most important families are the Anthophoridae (*Xylocopa*, *Centris*) and the Apidae (social bees). *Centris* frequently pollinate flowers such as *Byrsonima crassifolia* that produce abundant lipids but lack nectar (Vinson and others 1997). In the Subfamily Meliponidae (Family Apidae) the genera *Trigona* and *Melipona* are important; in the Subfamily Bombinae (Family Apidae) the euglossine bees are the best pollinators (*Bombus*). The morphological diversity found in the group enables pollination of zygomorphic and actinomorphic flowers (Knudsen and Mori 1996). Tropical trees pollinated by bees include *Aspidosperma megalocarpon* (Apocynaceae), *Mabea fistulifera* (Euphorbiaceae), *Copaifera camibar* Poveda, Zamora & Sanchez (Fabaceae), *Andira inermis* (W. Wright) Kunth ex DC., *Dipteryx oleifera*, *D. panamensis* (Fabaceae-Papilionoideae), *Laetia procera* (Poepp.) Eichler. (Flacourtiaceae), *Couratari scottmori*, *Eschweilera*, *Grias*, *Gustavia*, *Lecythis ampla* (Lecythidaceae), *Cespedesia macrophylla* (Ochnaceae), and *Qualea paraensis* (Vochysiaceae) (figs. 26 and 27).

Because Vespidae have high nutritional requirements, especially for carbohydrates, they collect and store nectar. Almost all species of *Ficus* are pollinated by Agaonidae wasps when they oviposit the syconium. Several wasp families may pollinate the *Ficus* species (Berg 1989, Kerdelhué and others 1997). Because ants (formicophily or mirmecophily) require sugars and proteins, they collect nectar and eat anthers. They are considered nectar thieves and it is impossible to characterize the flower type with which they are associated. Presumably, ants and wasps visit the same kinds of flowers. Flies and gnats visit several types of flowers. The flowers pollinated by Vespidae are small, whitish, greenish, or yellowish, such as *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels, *Mangifera indica* L., *Tapirira guianensis*, *T. mexicana* (Anacardiaceae), *Bursera simaruba* (L.) Sarg.(Burseraceae), *Simarouba amara* Aubl. (Simaroubaceae), and *Goethalsia meiantha* (Tiliaceae) (figs. 28 and 29). The group has many pollinators. The cocoa

Fig. 27.

Fig. 28.

Fig. 29.

(*Theobroma cacao*) is pollinated by several species of Diptera, and flies pollinate *Monadera myristica* flowers (Kessler 1993).

Birds either pollinate the flowers while eating nectar or are opportunistic. Flowers are usually red, orange, or deep purple, with narrow tubes, thick texture, and no odor. Anthers are exserted or subexserted and the calyx is long and loose. The pollination of *Myrrhinium atropurpureum* (Myrtaceae) flowers illustrates an interesting case. Flowers are grouped in dichasia and placed in horizontal branches. They lack nectar and scent but the red petals are thick, fleshy, juicy, and sugary; they change in color and shape during the phases of the anthesis (pink, red, purple, black, purple). The stamens have a long filament (15 mm) and each anther contains around 8,000 pollen grains. The style is 12 to 20 mm long. Pollen presentation starts when sugar concentration in the petals is 4 ± 1 percent weight/weight and the petals are red-violaceous in color. This floral syndrome attracts passerine birds, which are the main pollinators; petal color attracts the birds, petal color variation indicates sugar variation, while the long filaments expose the anthers (Roitman and others 1997).

In the Neotropics the most specialized pollinators are the hummingbirds (Family Trochilidae), although there are other minor groups such as the Icteridae (Brosset and Erard 1986, Stiles 1985, Stiles and Skutch 1989). Bird pollination is common in epiphytes and the plants of forest clearings and secondary forests (Stiles 1985). Hummingbirds are very important pollination vectors in the upper levels of the mountain ranges (Stiles and Skutch 1989). The birds discriminate among ultraviolet radiations. Most have weak olfactory systems which are, however, sensitive enough to detect odors in the environment that can lead them to food. The anthocyanidic pigments are a typical syndrome of flowers pollinated by birds, although exceptions are found in Australia and New Zealand (Gottsberger 1993).

The flowers usually pollinated by hummingbirds may be odorless, and strongly colored, with the red, yellow, and orange colors dominant. The corolla is tubular, sometimes hanging, and lacks a lip or margin turned backward. There are nectaries at the base of the floral tube with an abundance of nectar. The filaments are rigid or fused, frequently stipitate. The position of sexual organs facilitates nectar gathering, pollen collecting, and pollen transference from one flower to another. The

Fig. 30.

anthesis is diurnal (Faegri and Van der Pijl 1971). The pollen is usually deposited in the beaks or head feathers of birds. Most pollen grains are light colored (white or pale yellow), spherical, smooth, and puverulent; sometimes the exine has spinules which expedite pollen adherence to bird feathers. In the Myrtaceae, the pollen deposited in bird beaks is smooth, spherical, or triangular and has a viscous brown, blue, or black covering (Inouye 1975, Knox 1984). Ornithophily is common in the Fabaceae-Mimosoideae (some species of *Inga*), Fabaceae-Papilionoideae (*Erythrina cochleata*, *E. crista-galli*, *E. poeppigiana* (Walp.) O.F. Cook), Rubiaceae (*Psychotria elata*, *Hamelia patens*), and Malvaceae (*Malvaviscus arboreus*). Hummingbirds pollinate these species (Bawa and others 1985a). *Vochysia* flowers, usually pollinated by bees and butterflies, are sometimes pollinated by small hummingbirds (De Vries 1988) (figs. 30 and 31). Birds are not always specific pollinators; for example, several passerine birds are diurnal pollinators of *Mabea fistulifera* (Euphorbiaceae) (Vieira and Carvalho-Okano 1996).

Nectarivorous bats are the most important group of mammalian pollination vectors. They are nocturnal, blind to color, and have a well-developed olfactory system. Because their sonar is weakly developed, bats have trouble flying in foliage. They may use their claws to hang from flowers or fly in front of the flowers like hummingbirds. The tongue is long and well adapted to extracting nectar from the flowers. The bats feed on flowers that produce abundant pollen and sticky or mucilaginous nectar. The corolla is usually wide distally and the nectar very accessible (Grünmeier 1990, Steiner 1981). The flowers pollinated by bats usually stand out in the tree crown, have a special position (cauliflory), are hanging (penduliflory), or have long pedicels. The corolla is campanulate or infundibular, whitish or creamy, greenish, purpuraceous or pinkish, and the flower has glandular tissues exuding unpleasant odors (butyric acid); the anthesis is nocturnal. They can be individual or be grouped in inflorescences. The pollen is transported from one flower to another in the bat hairs, which have scales resembling those of the bee abdomen (Eisenberg 1989, Vogel 1968).

Plant families such as Bombacaceae are pollinated primarily by bats (e.g., *Bombacopsis quinata* (Jacq.) Dugand, *Ceiba pentandra* (L.), *Pachira aquatica* Aubl., *Ochroma pyramidale* (Cav. ex Lam.) Urb. (fig. 32)). A high number of Bignoni-

Fig. 31.

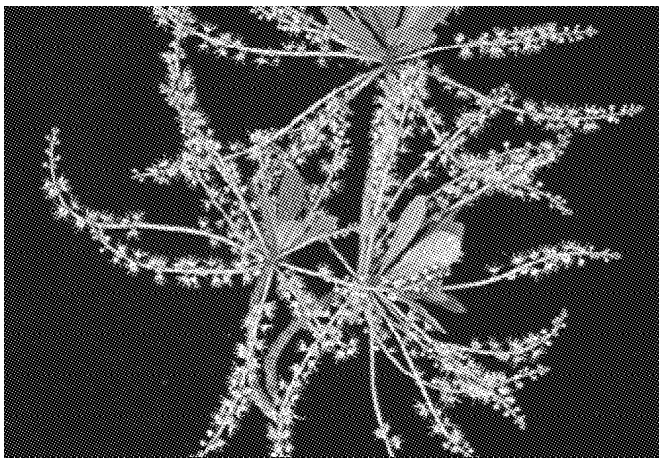

Fig. 33.

Fig. 32.

aceae (*Crescentia cujete* L., *Amphitecna sessilifolia*), Capparidaceae (*Capparis*), Caryocaraceae (*Anthodiscus chocoensis*, *Caryocar costaricense* Donn. Sm.), Euphorbiaceae (*Mabea*), Fabaceae-Mimosoideae (*Inga leiocalycina*, *Parkia pendula* (Willd.) Benth. ex Walp., and Fabaceae-Caesalpinioideae (*Peltogyne purpurea* Pittier), are also pollinated by bats. Both bats and sphingid insects pollinate some species, such as *Capparis pittieri*.

Wind pollination is difficult to detect because many flowers are also visited by diverse insects or other pollination vectors. Pollination by wind and insects (ambophily) is very common (Bullock 1994, Silberbauer-Gottsberger 1990). In general, the wind is the pollination vector of species with unisexual flowers that have reduced or no perianth and lack substances that attract birds and other animals (Faegri and Van der Pijl 1971). The anthers are exposed and have long filaments. Air-dispersed pollen grains are small (± 16 to 50 μm), light, and spherical; the exine is thin, sometimes reticulate, striate-reticulate, echinate, scabrous, psilate, sometimes rugose, geminate or discontinuous, puberulent and nonadhesive (Bullock 1994, Faegri and Van der Pijl 1971). The pollenkitt covering is restricted to the exine arcs. Pollen production is abundant in the species (Bullock 1994, Hesse 1979, Knox 1984, Rohwer 1993). Conditions that favor wind pollination include the absence of rain, low relative humidity, and good air movement (wind pollination is frequent in dry tropical forests) (Bullock 1994).

In the Neotropics, several families have species that are partially or exclusively wind-pollinated (Bullock 1994, Kubitzki 1993). These species include *Astronium graveolens* Jacq., *Tapirira guianensis*, *T. mexicana* (Anacardiaceae), *Alnus acuminata* (Betulaceae), *Terminalia amazonia* (Combretaceae), *Bernardia*, *Croton* (Euphorbiaceae), *Quercus* (Fagaceae), *Xylosma intermedia* (Flacourtiaceae), *Alfaroa costaricensis* (Juglandaceae), *Maclura tinctoria*, *Sorocea*, *Trophis racemosa* (Moraceae), *Forestiera* sp. (Oleaceae), *Agonandra racemosa* (Opiliaceae), *Zanthoxylum* (Rutaceae), *Ulmus mexicana* (Liebm.) Planch. (Ulmaceae), *Myriocarpa longipes*, and *Urera caracasana* (Urticaceae) (fig. 33). Anemophily is also present among gymnosperms such as *Podocarpus guatemalensis* (Podocarpaceae) and *Pinus* (Pinaceae).

The pollen dispersed by water has different shapes: spherical grains surrounded by mucilage; ellipsoid grains, in

linear tetrads enclosed in mucilage tubes; or filiform grains lacking exine, with an intine layer resembling that of the terrestrial pollen (Knox 1984).

The tropical trees of lowlands and coastal plains have low population densities and are pollinated primarily by animals. Pollination mechanisms, pollinators, and sexual systems vary among angiosperms. Insects are the most common pollinators and large and medium-sized bees are the most frequent vectors, followed by moths, wasps, other insects, and small bees (Bawa and others 1985a). The pollination vectors of almost one-half of the plant species forage over a wide range. The highest diversity in pollination systems occurs in the subcanopy, where hummingbirds and sphingid insects are the most active. Bats and wind are minor pollinators. Pollination systems are more uniform in the canopy, where bees and small insects dominate.

Most tropical trees have incompatible bisexual flowers (perfect or hermaphrodite). Some are dioecious (pistillate and staminate trees) and cross-pollination is obligatory; however, the strength of the incompatibility barrier varies in a population (Bawa and Krugman 1991). In forest management, the degree of individual crossing is vital to determining the genetic quality of the seed. The degree of endogamy depends not only on the genetic tendency to individual self-pollination but also on the spatial distribution of the individuals (Bawa and Krugman 1991).

Dispersal from the site of origin promotes gene displacement throughout a population or to new populations. In species with cross-pollination, the paternal genes move twice in each generation, first during pollination and second during seed dispersal. The maternal genes move only once; therefore, the paternal genes move farther in each generation (Willson 1992).

The pattern of dispersal contributes to structure population, to potential genetic drift, and to natural selection. The occasional gene transference from one population to another conspecific population is important to maintaining the genetic diversity of the recipient population (Willson 1992). The invasion and colonization of new lands permits the formation of monospecific populations. Natural or artificial monospecific populations are at high risk for diseases and infestations of parasites. The damage produced by the shootborer of the Meliaceae (*Hypsipyla grandella*) in populations of mahogany (*Swietenia*

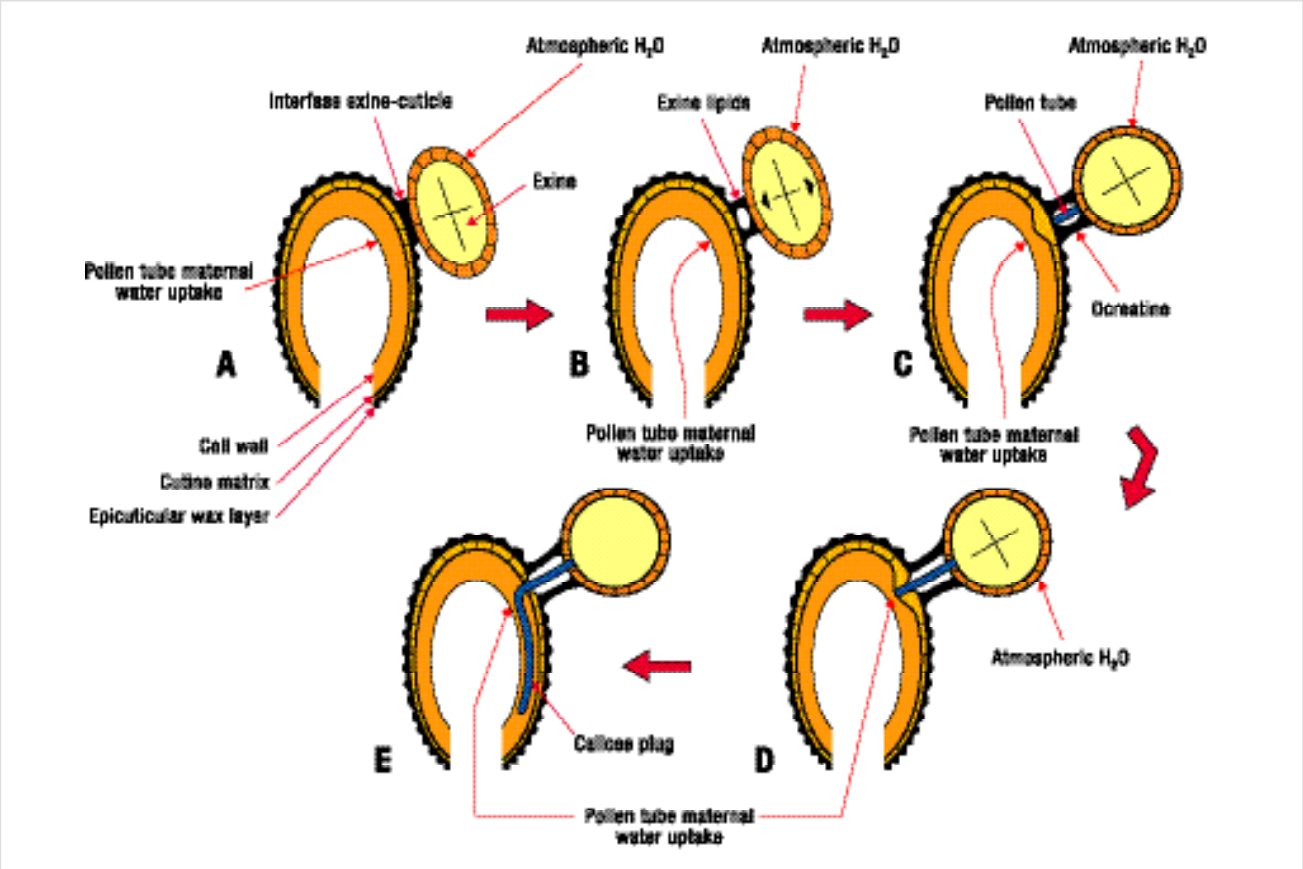

Fig. 34. Pollen-stigma interactions; a, initial contact (pollen capture); b, early stage of secondary binding reaction; c, later stage of secondary binding (pollen tube emergence); d, pollen tube penetrates the cuticle; e, pollen tube growth down. (Redrawn from Ferrari et al., 1985).