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Fruit and seed evolution in angiosperms

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Abstract

Angiosperm fruit originates from the ovary of the flower or it develops from the ovary, besides of the carpels, other inflorescence or floral parts may be involved in fruit formation; seed originates from the ovule. Four major classes of fruits are distinguished in angiosperms, viz. multiple fruits, aggregate fruits, schizocarps and simple fruits. Multiple fruits originate from inflorescences; the aggregate fruit comes from a single flower with apocarpous, pluricarpellate and pluripistillate gynoecium; schizocarps originate only from the ovary of a single flower, when ripe can separate into fragments called mericarps; and the simple fruits either are commonly originated from the ovary of a single unipistillate unicarpellate flower or syncarpic pluricarpellate flower. The diversity of seeds is also great among angiosperms, with bitegmic or unitegmic seeds, and alate, arillate, operculate, endothelial, pachychalazal, hairy or sarcotestal seeds. Reflections on fruit evolution are, in fact, very general, selecting a few examples that are restricted to families and genera. Fruit evolution is fundamentally based on changes of gynoecium types and differentiation of the pericarp. Among the hypotheses formulated in the literature, one predicts two main lines of evolution: in the first, there must have been a progressive reduction in the number of carpels that led to monocarpy, thus giving rise to the simple follicle; the second line must have led to a syncarpy, initially a loose adnation, which may have given rise to the capsule. The literature dealing with seed evolution in angiosperm taxa is very vast, but almost always not conclusive.

Keywords: Embryo; Endosperm; Fruit classes; Gynoecium types; Pericarp tissues; Seed coat

1 Introduction

The development, structure and dispersion of fruits and seeds constitute a primordial chapter in the knowledge of the reproductive process of angiosperms. The study of fruits and seeds is essential in the preservation of species, colonization of new environments by native or exotic species, weed control, reforestation, forestry and in the investigation of medicinal and toxic plants [1].

Enormous interest and effort have been invested in reconstructing the evolutionary process of the great diversity of fruits and seeds of angiosperms since the last century. Various hypotheses about the evolution of fruits and seeds have been formulated by different researchers that take into account the phylogenetic relationships of different groups of angiosperms, the various types of diaspore dispersal, the structural analysis of fruits and seeds, and the knowledge of fossils.

Reflections on fruit evolution are, in fact, very general, selecting a few examples that are restricted to families and genera. Fruit evolution is fundamentally based on changes of gynoecium types and differentiation of the pericarp. The evolution of seeds in angiosperms must also be analyzed very carefully. The literature dealing with seed evolution in

angiosperm taxa is very vast, but almost always not conclusive. There is some more general evidence on the evolution of angiosperm seeds and others that are more specific to particular groups of angiosperms.

The paper presented here is an attempt to gather knowledge about the fruit and seed features, which shows some general evolutionary trends in angiosperms. The paper consists of the divergent concept of fruit defined by the literature, of general considerations on the ontogeny and structure of fruits and seeds, and of the evolutionary trends of fruits and seeds that have been reported by botanists, ecologists and phylogeneticists. Concepts, evolutionary trends and structure of fruits and seeds of classical and modern works are considered here.

2   Material and methods

A survey of the literature on evolution of fruits and seeds of angiosperms, from the last century to the present time, has been used to prepare this paper. Many works published on this subject are our authorship, especially those that refer to the ontogeny or structure of fruits and seeds of different families of angiosperms.

In research on ontogeny and structure of fruits and seeds, the plant material used (floral buds, flowers and fruits and seeds at different stages of development) was collected in forests, riparian forests, plant crops, natural pasture (weeds), rupestrian fields and river all located in Brazil. This material was fixed in FAA (formaldehyde, acetic acid and ethyl alcohol) or glutaraldehyde, embedded in paraffin or *Leica historesin*, sectioned in a rotation microtome and stained in Safranin, Astra blue or Toluidine blue, according to the usual techniques in plant anatomy. The illustration of the fruits and seeds was made in light microscopy with digital image capture. The terminology used in the description of fruits and seeds was based on Corner [2], Roth [3] and Souza [1,4,5].

3   Results and discussion

3.1   Definition of the fruit

The fruit has received various interpretations since the 18th century, which was classically regarded as "mature ovary" ("sensu" Roth [3]). According to Roth [3] many authors have accepted the definition of the fruit in wide sense, proposed by Knoll [6] as "flower in the state of seed maturation". The definition of fruit by Spjut [7] is quite complex, considering "fruit as a propagative unit developing from one or more fertilized egg cells (or rarely by parthenocarpy) enclosed by integuments and attached to megasporophylls, or megasporophyll-scale complex, in a strobilus, cone, gynoecium, concrescent gynoecia, or gynoecia that disseminate together at the time it or its seed(s) are dispersed from the plant, or just prior to germination on the plant, and it may also include any other attached scales, bracts, modified branches, perianth, or inflorescence parts". Barroso et al. [8] define "fruit as the structure that represents the last stage of development of the fertilized or parthenocarpic gynoecium, and it consists of pericarp(s) and seed(s)". Bobrov and Romanov [9] consider the fruit as "the reproductive structure of angiosperms which develops from the gynoecium of one flower after its pollination and fertilization (or as the result of parthenocarpy) and secures seed development, protection and dissemination; fruit itself is a transformed gynoecium, free or fused with other flower organs".

We adopted the definition of fruit proposed by Souza [1,4,10], which considers the fruit as the ovary or ovaries developed and in a state of maturation, and other parts of the flower or even the inflorescence may be added to it.

3.1.1   Fruit and seed ontogeny

Fruit (pericarp) - The fruit develops from the ovary and it may also include pedicel, bracts, bracteoles, perianth, floral receptacle, hypanthium, stigma/style and inflorescence parts. The stigma and style usually fall off during fruit development, but there are cases in which they can persist, as in the fruitlets of multiple fruit of *Maclura tinctoria* (L.) D. Don ex G. Don, Moraceae, and fruits of some species of Berberidaceae [11]. Four classes of fruits can be distinguished in angiosperms, namely multiple, aggregate, schizocarp and simple fruits [4,5].

The multiple fruits are derived from inflorescences, e.g. fruits of Bromeliaceae (*Ananas comosus* (L.) Merr.) and Moraceae (*Ficus carica L.*, Figure 1A). The multiple fruit of *Maclura tinctoria, Moraceae*, originates from a subglobulose inflorescence, which consists of small female flowers [12]. Each flower presents 6-8 green tepals and a pistil with uniloculate ovary and long style/stigma; the ovary has only one ovule with apical placentation. The ripe multiple fruit is made up of persistent perigone and stigma/style, and small drupes. The persistent perigone has succulent consistence and presents uniseriate epidermis and parenchymatous mesophyll with laticifers. The drupes consist of epidermal exocarp, collenchymatous and parenchymatous mesocarp, and endocarp composed of a layer of macrosclereids.

The aggregate fruit comes from a single flower with apocarpous, pluricarpellate and pluripistillate gynoecium; the ripe fruit is composed of several fruitlets which originate from pistils attached to the receptacle. Aggregate fruits of *Magnolia champaca* (L.) Baill. ex Pierre (Magnoliaceae) (Figure 1B) and Apocynaceae such as *Aspidosperma polyneuron* Müll. Arg. [13] and *Asclepias curassavica Griseb.* [14] originate from apocarpous bicarpellate ovary, and the ripe fruits consist of two follicle fruitlets. The fruits fleshy and indehiscent of *Victoria amazonica* (Poepp.) J. C. Sowerby can be considered as an aggregate type that typically arise by differentiation of pseudo-syncarpous ovary [15]. According to authors [15] the fruit of *Victoria amazonica* develops inside the water and it emerges when ripe; it is fleshy, indehiscent, globose, pluricarpellate, and covered abundantly by thorns.

Schizocarps (schizo, splitting) develop from the pluricarpellate ovary of a single flower. The ripe fruit separates into mericarps that can be dehiscent or indehiscent, each composed of one carpel with a single seed. Schizocarps may be found in Euphorbiaceae, Rutaceae and Malvaceae. *Euphorbia heterophylla* L. schizocarp (Figure 1C) presents two dehiscent regions, a dorsal region and another region along the carpel sutures, and it is composed of three mericarps [16]. The schizocarps of the rutaceous *Pilocarpus pennatifolius* Lem. [17] and *Metrodorea nigra* A. St.-Hil. [18] originate from ovary that exhibits carpels united at the base and small splits along the line of separation between the carpels; the mature dry fruit became woody and split inside out down the dorsal sutures, liberating the seeds and the respective rigid endocarp. Fruits of the Malvaceae weedy species *Sida rhombifolia L., S. urens L.* and *S. regnellii* R. E. Fr. are schizocarps that dehisce along sutures between carpel walls, separation close to the central column and rupture of the carpel wall itself (dorsal region) [19].
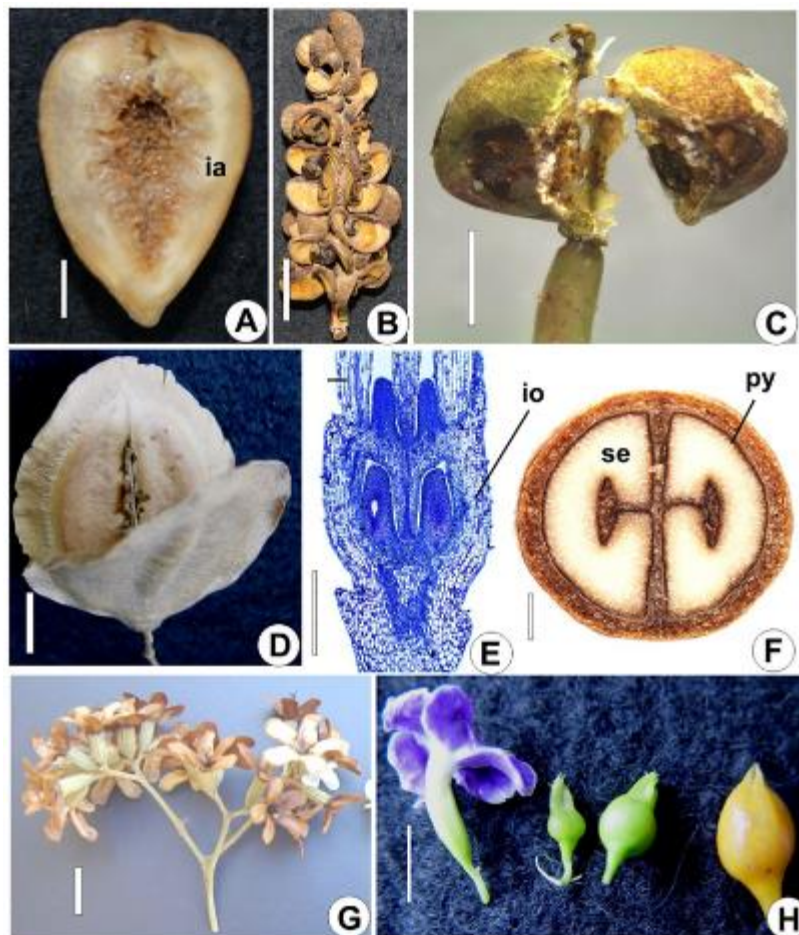

Figure 1 Fruit morphology. A – Multiple fruit of *Ficus carica* (Moraceae). B – Aggregate fruit of *Magnolia champaca* (Magnoliaceae) with fruitlets type follicle. C – Schizocarp of *Euphorbia heterophylla* with two mericarps. D – Capsule of *Jacaranda mimosifolia* D. Don (Bignoniaceae). E – Flower in longitudinal section of *Rudgea jasminoides* (Cham.) Müll. Arg. (Rubiaceae) evidencing the inferior ovary. F – Fruit type pomaceous drupoid nuculanium of *Rudgea jasminoides* in cross-section. G – Fruit of *Cordia trichotoma* (Cordiaceae) with calyx and corolla persistent. H – Development of anthocarp of *Duranta repens* L. (Verbenaceae). (ia=inflorescence axis; io=inferior ovary; py=pyrene; se=seed). Scale bars: 1 mm (E,F), 6 mm (H), 1 cm (A,C,D), 2 cm (B,G). Figures by Aline Rosado (C) and Anderson F. Santos (E,F).

Simple fruits exhibit a wide variety of morphological types that originate from the unicarpellate ovary or syncarpous pluricarpellate ovary, superior, inferior or semi-inferior. Structures beyond the pericarp, such as hypanthium, receptacle, placentae, calyx and corolla, may be part of the simple fruit. The simple fruit terminology employed by Souza [5] appears to be most satisfactory. The author distinguishes the simple fruits that originate from the superior (Figure 1D) or semi-inferior ovary from those called pomaceous, which derive from the inferior ovary (Figure 1E,F). Hitherto the various types of simple fruits have been studied from different families, such as Amaranthaceae [20,21], Asteraceae [22,23,24,25,26,27], Bignoniaceae [28,29,30], Cactaceae [31,32], Cordiaceae [33], Euphorbiaceae [34,35,36,37], Fabaceae [38,39,40], Lauraceae [41], Meliaceae [42], Moraceae [43], Myrtaceae [44], Nyctaginaceae [45,46]; Piperaceae [47,48], Rubiaceae [49] (Figure 1E,F), and Santalaceae [50].

The calyx and corolla may persist in the ripe fruit, as in the fruit of *Cordia trichotoma* (Vell.) Arráb. ex Steud. (Cordiaceae) (Figure 1G). Perigone that participates in fruit formation of Nyctaginaceae deserves some consideration. Roth [3] has reported a special case of perigone in this family which is known as anthocarp, "consisting of the lower part of the perigone tube, completely substitutes the real pericarp which is rather obliterated during the development". The anthocarp of *Pisonia aculeata* L. [1,45] originates from the thick and lobed tubular-campanulate perigone, which closes and loses its lobes during fruit development. The mature anthocarp that replaces the pericarp in this species has large secretory emergences in the epidermis that release a sticky substance with dispersal function by animals. Another Nyctaginaceae species investigated with anthocarp was *Boerhaavia diffusa* var*. hirsuta* Kuntze which consists of perigone with glandular trichomes with zoophilic dispersion [1]. The anthocarp concept formulated for fruits of Nyctaginaceae was used for the fruit of *Duranta repens* L., Verbenaceae [1] (Figure 1H). In this case the persistent floral calyx replaces the pericarp; it is thick, juicy, yellow-orange and is sought after by birds. The Nyctaginaceae anthocarp deserved the attention of Sukhorukov et al. [51] who anatomically analyzed this structure in 159 species from 28 genera representing 6 of 7 tribes, and phylogenetic character state reconstructions.

Souza [5] proposed a classification of angiosperm fruits based on ontogeny studies and literature consisting of classes, types and subtypes of fruits. It is detailed below:

- Class: Multiple fruits - They originate from inflorescences and occur in Bromeliaceae and Moraceae.
- Class: Aggregate fruits – They originate from a single flower with apocarpous, pluricarpellate and pluripistillate gynoecium, and occur in Apocynaceae and Rosaceae.
- Class: Schizocarps – They develop from pluricarpellate ovary of a single flower, and the ripe fruit separates into mericarps. They consist of the types:
  - Regmoid schizocarp - It has persistent carpophore and occurs in Simaroubaceae and Geraniaceae;
  - Coccoid schizocarp - Carpophore may or may not be persistent; it occurs in Euphorbiaceae, Malpighiaceae, Sapindaceae and Tropaeolaceae.
  - Cremocarp schizocarp – Carpophore is persistent, bicarpellate. It occurs in Apiaceae.
  - Rutaceous schizocarp – The schizocarp has a sclerenchymatic endocarp enveloping each seed, attached to the hardened funicle, separates from the rest of the pericarp, and it is ejected some distance away. It occurs typically in Rutaceae.
  - Samaridian schizocarp – It is a schizocarp with wing. It is registered in Sapindaceae, Malpighiaceae, Rhamnaceae, Rutaceae and Zygophyllaceae.
  - Malvaceous schizocarp – It is devoid of carpophore, and occurs typically in Malvaceae.
- Class: Simple fruits - They originate from the superior or inferior ovary of a single flower.
  - Unicarpellate dehiscent dry fruits
    - ❖ Follicle – Dehiscence by one longitudinal slit in ventral suture, rarely dorsal. Examples: *Sterculia chicha* (Malvaceae) and *Consolida ajacis (L.)* Schur (Ranunculaceae).
    - ❖ Legume – Dehiscence by two longitudinal slits (ventral and dorsal sutures). It occurs typically in Fabaceae.
    - ❖ Utricle – Dehiscence by irregular slit, transversal or longitudinal. Example: *Amaranthus blitum* L. (Amaranthaceae).
  - Bicarpellate or pluricarpellate dehiscent dry fruits
    - ❖ Siliqua – Bicarpellate, dehiscence by two longitudinal slits, with replum. Examples: fruits of Brassicaceae and Papaveraceae.
    - ❖ Capsule – Two or more carpels, dehiscence by longitudinal slits (subtypes loculicidal, septicidal, septifragal, mixed or biscidal). Examples: Liliaceae, Malvaceae, Aristolochiaceae, Meliaceae.
    - ❖ Opecarp - Dehiscence by pores. Example: *Papaver orientale* L. (Papaveraceae).
    - ❖ Pyxidium – Dehiscence by transversal slit (releases an operculum). Examples: *Plantago major* L. (Plantaginaceae), *Lecythis pisonis* Cambess. (Lecythidaceae).

- o Indehiscent dry fruits
- ❖ Achene - Fruit originates from a superior ovary, unilocular, with a seed attached to the pericarp. Examples: Plumbaginaceae, Amaranthaceae.
- ❖ Cypsela - Fruit originates from an inferior ovary, unilocular, with a seed not coalescing to the pericarp. It is regarded as the name for a fruit of the Asteraceae.
- ❖ Caryopsis - Fruit originates from the superior ovary, uni to tricarpelar, unilocular, unispermic, pericarp adnate to the seed. It is a fruit of the Poaceae.
- ❖ Samara - Fruit originates from the superior ovary, and it is wing. Examples: Fabaceae, Petivariaceae, Rutaceae.
- ❖ Arthrocarp – It is an articulated fruit, which can form dispersion units or diaspores that are originated by carpel division (subtypes carcerulide, lomentum, craspedium). Examples: Fabaceae, Lamiaceae.
- ❖ Indehiscent legume and follicle – They are unicarpellate fruits that do not open when ripe. Example: Fabaceae.
- o Fleshy or semi-fleshy fruits
- ❖ Drupoid fruits – They have endocarp of leathery or rigid texture that receives the name of pyrene (subtypes drupe, nuculanium, drupamilde). Examples: Lauraceae, Cardiaceae, Arecaceae.
- ❖ Bacca – It has membranous or leathery epicarp, succulent mesocarp, membranous or cartilaginous endocarp. Examples: Caricaceae, Passifloraceae, Solanaceae, Vitaceae.
- ❖ Hesperidium – It is a typical fruit of citrus plants (Rutaceae).
- ❖ Anthocarp – It is a fruit with perigone or perianth replacing the pericarp. Examples: Nyctaginaceae, Verbenaceae.
- o Fleshy legume and follicle – They are dehiscent or indehiscent fruits that have a fleshy pericarp. Example: *Inga* Mill. (Fabaceae).
- ❖ Fleshy capsule – Capsule-like fruit with fleshy pericarp that opens when ripe. Example: Meliaceae.
- ❖ Pomaceous fruits – They are simple fleshy, semi-flesh or dry fruits, which originate from an inferior ovary.
- ❖ Balausta – Fruit of *Punica granatum* L. (Lythraceae), with endocarp divided into a lower and upper region by a transverse diaphragm, and into numerous cavities bordered by dissepiments.
- ❖ Cactidium – Fruit of Cactaceae with accessory structures of pericarpellar (receptacular) origin; pericarpel may produce scale-leaves, bristles, spines, or even other fruit.
- ❖ Capsulidium – It occurs in *Eucalyptus* L'Hér., Melastomataceae, Rubiaceae, which are characterized by opening by longitudinal splits.
- ❖ Melonidium – It is an unilocular fruit without placental advancement; it occurs in Cucurbitaceae.
- ❖ Peponidium - It is a fruit in which there is advancement of the placenta forming false septa; example: *Cucumis sativus* L. (Cucurbitaceae).
- ❖ Myrtidium – It is a fruit derived from inferior ovary, with 2-5 carpels, fleshy, many seeds; it occurs typically in Myrtaceae.
- ❖ Musidium – It is a fruit derived from tricarpellate inferior ovary, fleshy, usually with a separable leathery pericarp; it occurs typically in Musaceae.
- ❖ Pomidium – It is a fruit of Rosaceae (*Malus sylvestris* Mill., *Pyrus communis* L.).
- ❖ Viscidium – It is a fleshy fruit from the inferior ovary that has a mesocarp that produces viscin, a sticky mucilaginous substance; it occurs in hemiparasitic species of Loranthaceae and Viscaceae.

It is important to emphasize that some fruits, such as cypsela and pyxidium, must be considered pomaceous because they originate from the inferior ovary.

During the ontogenetic process, some simple fruits (follicles, legumes, capsules), schizocarps and fruitlets of aggregated fruits can have multiplicative pericarp (Figure 2A,B). These fruits are characterized by having a meristem that develops on the ovary wall in pre-anthesis or post-anthesis phases. Special meristems can be installed on these developing fruits, either on the adaxial or ventral surface (Figure 2A,B) or on the abaxial or dorsal surface of the ovary wall. Adaxial and abaxial meristems have been reported in various fruit types [1]. In certain species of the Bignoniaceae the fruits develop a middle meristem in the pericarp [29,30]. It has been pointed out that some fruits of Amaranthaceae (Figure 2C-E), Bromeliaceae, Cordiaceae and Melastomataceae have non-multiplicative pericarp [4].
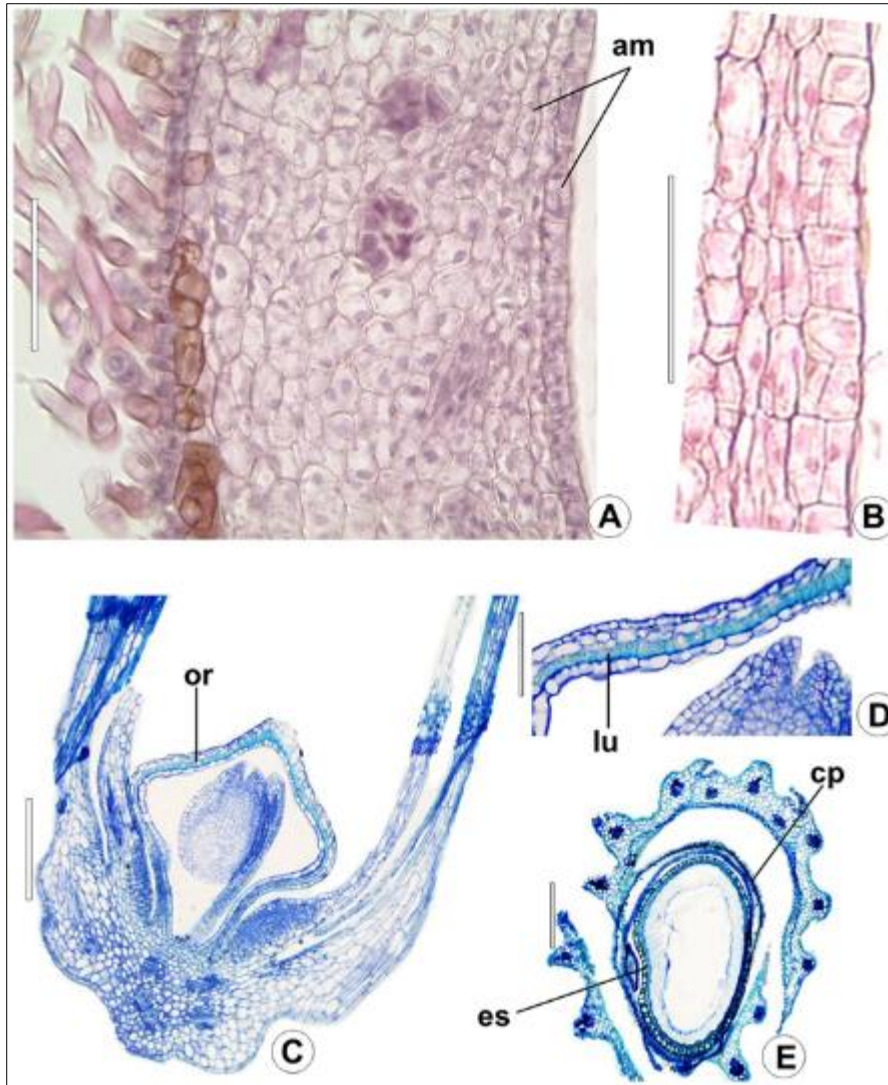
Figure 2 Multiplicative and non-multiplicative fruits of *Lonchocarpus muehlbergianus* (Fabaceae) (A,B) and *Alternanthera tenella* Colla (Amaranthaceae) (C-E). A,B. Anatomical details of the wall of the young fruit showing the installation of an adaxial or ventral meristem. C-E. Fruit devoid of meristem (non-multiplicative pericarp). (am=adaxial meristem; cp=collapsed pericarp; es=exotestal seed; lu=cell layer with U-shaped parietal thickening; or=ovary). Scale bars: 60μm (A,B), 70μm (D), 200μm (C,E). (Figures A,B provided by Souza (2022); C-E figures by Vanessa C. Harthman).

Seed - "Seed-studies begin with the ovule and end with germination" wrote Corner [2] in his classic work on dicot "sensu lato" seeds. Angiosperm seeds show great structural complexity and can originate from ovules without curvature (orthotropous) or curved (anatropous, campylotropous, hemitropous, amphitropous and circinotropous (Figure 3A)), tegmic (bitegmic or unitegmic) (Figure 3A,B) or ategmic, and crassinucellate (Figure 3A), pseudocrassinucellate (term employed by Davis [52]) or tenuinucellate (Figure 3B). The botanical literature consists of several classical treatises on seed studies [2,53,54].

Piperaceae seeds are derived from orthotropous, bitegmic and crassinucellate ovules; in *Piper amalago* var. *medium* seed [47] the outer integument collapses, the endotegmen is persistent, and the nucellus differentiates into copious perisperm. Fabaceae seeds of *Cassia cathartica* Mart. [55], *Lonchocarpus muehlbergianus* Hassl. [56] and *Acacia paniculata* Willd. [40] are developed from bitegmic, crassinucellate and anatropous or campylotropous ovules, and they consist of a well-developed testa with macrosclereid epidermis, generally collapsed tegmen, albuminous or not. Asteraceae seeds originate from anatropous, unitegmic and tenuinucellate ovules (Figure 3B,C), and the seed coat may be collapsed at ripe seed [57]. Seed from a hemitropous ovule is registered in the rutaceous *Pilocarpus pennatifolius* Lem. that shows sclerified mesotesta and exotegmen which is built up of tracheids with spiral or annular parietal thickenings [17]. Cactaceae seeds of *Pereskia aculeata* Miller [31] develop from an amphitropous or circinotropous,

bitegmic and crassinucelate ovules; the seeds are exotestal with epidermis composed of macrosclereids. *Phoradendron* Nutt. (Santalaceae) exhibits seeds which originate from ategmic ovules, presenting the embryo entirely embedded within a chlorophyllous endosperm [50].
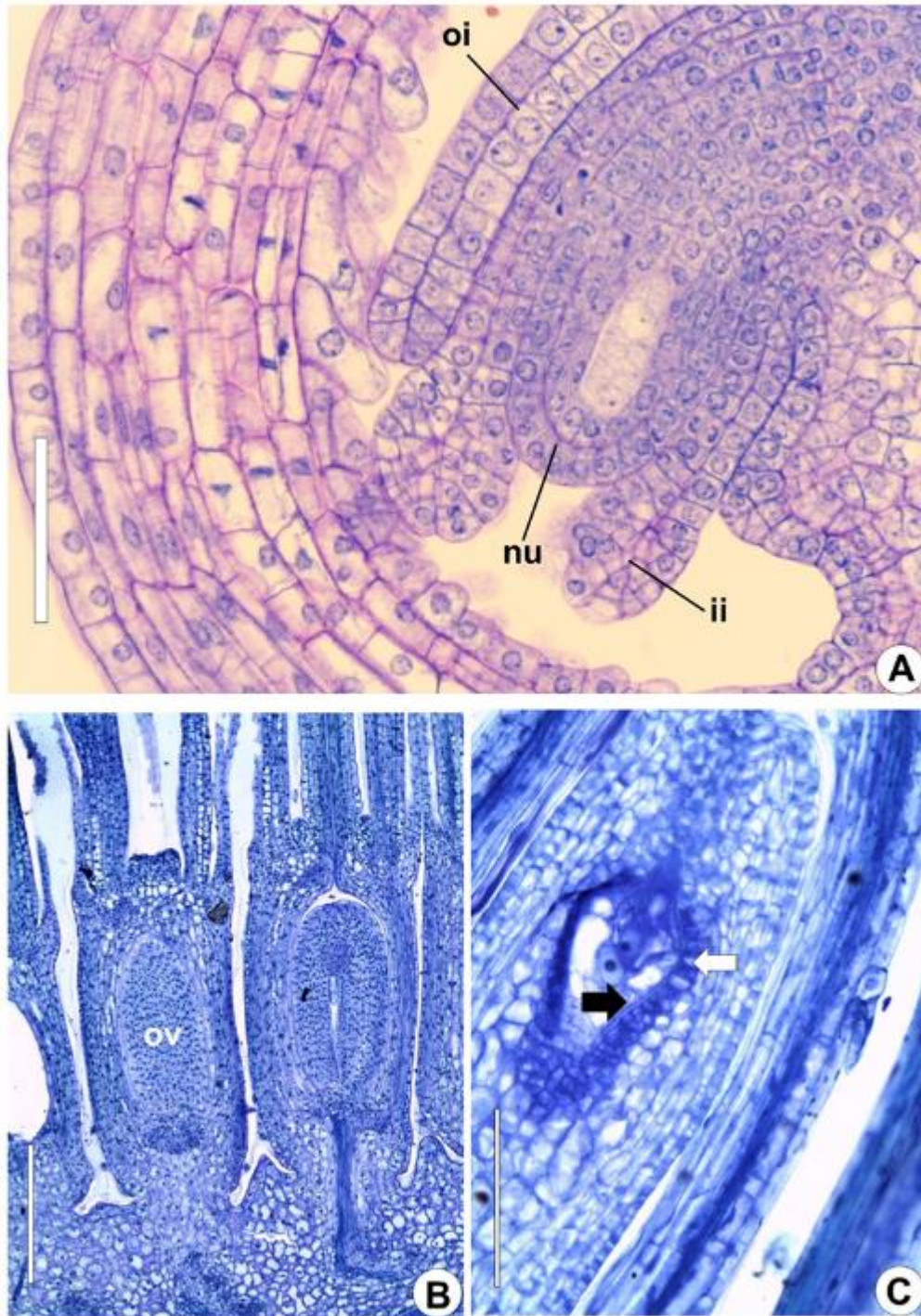

Figure 3 Ovules of extant plants *Epiphyllum phyllanthus* (L.) Haw. (Cactaceae) (A), *Emilia sonchifolia* (L.) DC. (B) and *Galinsoga quadriradiata* Ruiz & Pav. (C). A. Ovule circinotropous bitegmic and crassinucelate. B. Flowers in longitudinal evidencing the anatropous ovule. C. Detail of ovule unitegmic and tenuinucellate. (black arrow=thin nucellus; white arrow=endothelium; ii=inner integument; nu=nucellus/crassinucellate; oi=outer integument; ov=ovule). It is likely that the bitegmic crassinucelate ancestral ovule gave rise to the unitegmic tenuinucellate derived ovule. Scale bars: 60μm (A), 100μm (C), 300μm (B).

Appendages and special structures can develop on the seeds of angiosperms, such as wings, hairs, aril, operculum, endothelium (Figure 3B,C), pachychalaza and sarcotesta. Alate seeds may be found in Bignoniaceae [28,58] and Apocynaceae [13,58], as in *Handroanthus chrysotrichus* (Mart. ex A. DC.) Mattos in which the wing develops from epidermal cells of the immature integument. Arillate seeds may be seen in Amaranthaceae, Apocynaceae and Euphorbiaceae, whose arils have different origins: funicular in *Chamissoa altissima* (Jacq.) Kunth [20]; epidermal cells (coma) located between the micropyle and funiculus in *Asclepias curassavica* [14], and micropylar (caruncle) in *Croton glandulosus* L. [36]. *Commelina virginica* L. (Commelinaceae) has operculate seed, in which the operculum is a circular portion of the integument located in the micropylar region, which stands out during germination [58]. The endothelium (inner epidermis of the tegmen or the single seed coat/unitegmic seed) may remain in the mature seed of Bignoniaceae; in *Handroanthus chrysotrichus* it occurs associated with the cell layer of the endosperm, functioning as a protective envelope for the embryo [28,58]. Pachychalazal seeds (Figure 4A,B) have been found in Rubiaceae (Psychotrieae) [49], in which the chalaza forms the greatest of the seed coat; cells of the chalazal region multiply in all directions and build an intercalary growth. Seeds of *Guarea macrophylla* Vahl., Meliaceae [42], have red and shiny sarcotesta, which is composed of exotesta and mesotesta with thin-walled cells and lipid content.

3.2   Some considerations on the phylogeny of the fruit and seed

The reconstructions of ancestral states are complex and undergo changes over time, due to new studies and techniques, especially in molecular biology. Sokoloff et al. [59] are emphatic in stating that this difficulty, for example in analysis of the ancestral angiosperm flower, is related to: "a) the high structural diversity of extant lineages of basal angiosperms, and b) the inapplicability of most floral characters to the panoply of potential gymnospermous outgroups, both extant and extinct".

The origin of fruits of angiosperms is a major evolutionary innovation that greatly enhanced seed dispersal efficiency and triggered rapid diversification of flowering plants [60]. The authors emphasized, however, that little is known about the evolutionary force that drove rapid diversification of fruit types. The authors further suggest that the fruit evolution was driven at least in part by dispersal agents abundant in particular habitats.

Despite the difficulties in establishing the relationship between the different lineages of spermatophytes and the complexity of fruits in angiosperms, some recent investigations on the gynoecium seem to shed some light on the process of fruit evolution. The gynoecium, which gives rise to the fruit, consists of carpellar leaves and is composed of an ovary, style and stigma. It shows enormous variation in morphology, size, number of carpels, and number of ovules among angiosperms. At one time Pfannebecker et al. [61] also accepted the interpretation of Dilcher [62] and of Endress and Doyle [63] that the "gynoecia of the most recent common ancestor of angiosperms consisted of several ascidiate (tube-shaped) carpels that were most likely closed by secretion and fused at their apex but not among each other (apocarpous)". Takhtajan [64] also believes that the ancestral gynoecium in angiosperms was apocarpous, and that the most basal families a tendency is observed towards a greater or lesser union of carpels, which leads to the formation of the syncarpous (coenocarpous) gynoecium.

"The major functional innovation of the advent of angiospermy is pollination on the surface on the carpel (the stigma), and no longer on the surface of the ovule (the micropyle), and, concomitantly, the formation of a pollen transmitting tract" [65]. Another innovation is that the stigma and pollen transmitting tract act as sites where self-incompatibility reactions occur, complement the authors.

According to Pfannebecker et al. [61] the origin of the carpel is unknown, but many components of the gene regulatory network (GRN) governing carpel development and their genetic interactions are known from the core eudicot *Arabidopsis thaliana*. These authors complement that "the carpel GRN components are of various ages, but interestingly, they were identified especially high retention rates for carpel development genes in Brassicaceae".

It is possible, therefore, that the ancestral fruit of angiosperms originated from an apocarpous gynoecium devoid of stigma and style as in extant angiosperms. Phylogenists and systematic researchers seem to have no doubt that this fruit was follicle-like or multifollicle-like.

In the case of the seed that originates from the ovule, Rudall [66] did an extensive review of the origin of the ovule in spermatophytes, and she affirms that "most inferences on the early evolution of the ovule are drawn from Late Devonian and Carboniferous seed-fern fossils that are anatomically preserved, allowing clear identification of the various tissue regions". For the author "the origin and early evolutionary history of the ovule are commonly viewed as a series of evolutionary transitions involving traits associated with heterospory, pollen capture (e.g. elaboration of the nucellar apex into a pollen chamber) and protection (e.g. fusion of telomes to form an integument). Understanding the

evolutionary history of the ovule requires a comparative and phylogenetic approach that is problematic when comparing extant angiosperms not only with phylogenetically distant extant gymnosperms but also with taxa known only from fossils [66].

In view of these considerations, it seems convenient to consider the relationships of the various lineages of spermatophytes. Phylogenetic study on spermatophytes [67] revealed a consistent and well-resolved phylogeny of seed plants, which places Gnetales as sister to Pinaceae, Cycads plus Ginkgo is sister to the remaining gymnosperms, and that Gnetales and angiosperms have similar molecular evolutionary rates, which are much higher than those of other gymnosperms. Based on the literature, the authors [67] register that the "Gnetales includes three morphologically isolated genera (*Ephedra*, *Gnetum* and *Welwitschia*) that show some morphological characters similar to angiosperms, like net-veined leaves in *Gnetum*, vessels and reproductive organs made up of flower-like structures, and exhibit unusually high substitution rates in all three genomes". Rudall [66], citing Yamada et al. [68], reports that "it was found that the *Gnetum* gene GpANTL1, an orthologue of ANT, is expressed in developing *Gnetum* ovules as four distinct rings around the three integument primordia and around the nucellar tip, thus resembling ANT expression in *Arabidopsis*, which is implicated in early ovule development and integument initiation".

3.3 Fruit and seed evolution in angiosperms
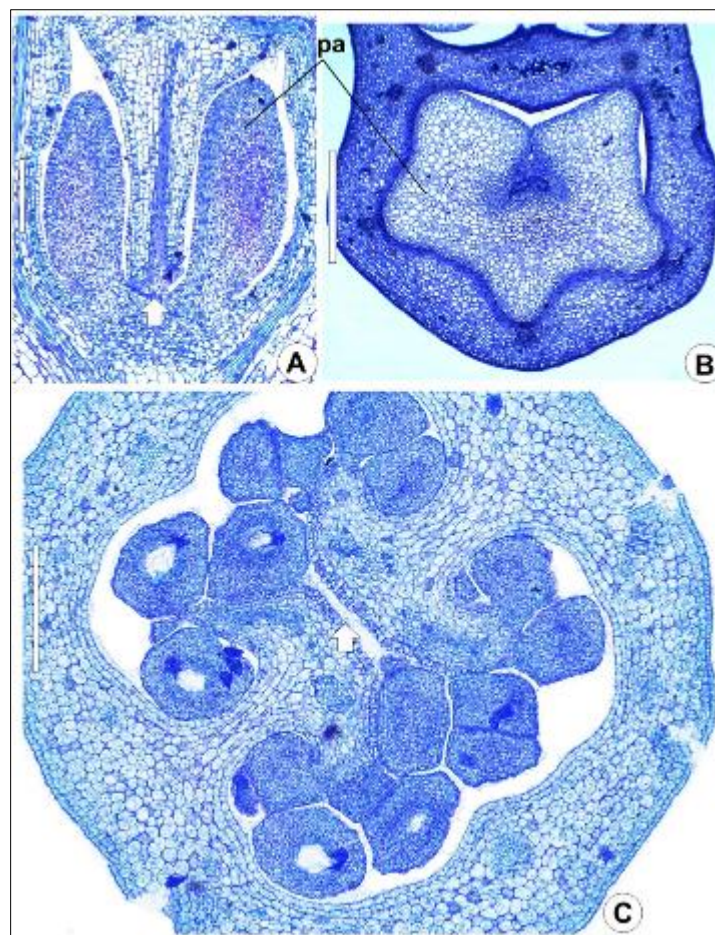
3.3.1 Fruit evolution

Figure 4 Seed development and compitum of *Rudgea jasminoides* (Cham.) Müll. Arg. (A), *Palicourea croceoides* Desv. ex Ham. (B), Rubiaceae, and *Solanum caavurana* Vell. (C), Solanaceae. A – Flower in longitudinal section evidencing ovules with pachychalaza. B. Immature fruit in cross-section showing a pachychalazal seed. C – Ovary in cross-section evidencing the compitum. (white arrow=compitum (split); pa=pachychalaza). Scale bars: 300μm (A,B), 500μm (C). Figures A,B by Anderson F. Santos and figure C by Tamara F. Santana.

Gynoecium and pericarp - Fruit evolution is fundamentally based on changes of gynoecium types and differentiation of the pericarp. With a view to explaining the peculiarities of the evolutionary process of the gynoecium in angiosperms,

Soltis et al. [65] report some important structural considerations about the development of the gynoecium. The authors recognize several variations during the gynoecium development related to the closure and sealing of the carpels attained by secretion or postgenital fusion, syncarpy or apocarpy, presence of a compitum in syncarpous gynoecia, and the inferior ovary. The advent of syncarpy from apocarpy is considered the major evolutionary trend in the angiosperm gynoecium [69]. Advantages of the syncarpy may be related to the increases in both offspring number and quality that can explain the multiple origins and the predominance of syncarpy in modern angiosperms [70].

The inferior ovaries have evolved many times and are more frequent in derived groups of angiosperms [65]. It has long been assumed that inferior ovaries are derived from superior ovaries, and that they are rare in Magnoliidae and predominant in groups such as Rubiales, Campanulales, Zingiberales and Orchidales [69]. It must be pointed out here evolutionary reversals from epigyny to hypogyny may occur, verified for example in Rubiaceae [65]. Two major theories have been proposed to explain the origin of the inferior ovary, the appendicular and receptacular ones [3,71]. The former establishes that there is extensive fusion (connation and adnation) of the outer lower portions of the surrounding floral whorls to one another and to ovary wall (epigynous flower) (Figure 1E); the latter assumes that carpels have phyletically "sunk" into tissue at the end of the cauline axis, with fusion of the receptacular tissue to the abaxial carpel wall [71]. Appendicular inferior ovaries may have occurred in ancestral Myrteae, Myrtaceae [44], and Cactaceae consists of a receptacular (pericarpel) inferior ovary [32].

The pericarp subdivided into exocarp, mesocarp and endocarp regions can vary significantly in tissue composition among angiosperm species. The exocarp is epidermal and/or peridermal in nature, which may present trichomes, emergences and stomata. The mesocarp exhibits a wide range of anatomical variations with parenchyma, collenchyma and sclerenchyma, in addition to various idioblasts, laticifers, canals and secretory cavities. The endocarp can be epidermal uniseriate or it is pluriseriate parenchymatic or sclerenchymatic. Dry, fleshy fruits can open at maturity, and the dehiscence may occur in very different ways, distinguishing the types circumscissile, poricidal, loculicidal, septicidal and septifragal. Details on the anatomy of angiosperm fruits are found in books such as those by Roth [3] and Souza [1].

A classic study on structural diversity of the pericarp was carried out by Fahn and Zohary [72] in nearly 100 species belonging to over 50 different genera of the Fabaceae. The authors choice seventeen main anatomical types of the pericarp, and it has been shown to exist a close correlation between the mode of dehiscence of the legume, the orientation of the fibers and the micellar structure of their walls. The authors suggest that a sclerenchymatous stratum consisting of two fiber layers with different orientation seems to be the basal type, while valves devoid of any sclerenchymatous stratum seem to be most derivative in Fabaceae.

Evolutionary trends in angiosperm fruits - Historically, the literature shows some evolutionary trends in fruits that deserve attention. According to Eames [73] the evidence from broad comparative studies in the angiosperms supports the view that the follicle with many seeds is the ancestral fruit (Figure 5A). Probably, characters such as reduced number of ovules and loss of dehiscence must have given rise to achene and other types of fruit [73]. The classic treatise on fruits of angiosperms [3] has reported that the "most primitive (basal) fruit was probably a follicle (Figure 1A) of woody or cartilaginous consistence, and by loss of dehiscence and reduction of seeds, nut and drupe developed".

Barroso et al. [8] establish two main lines of fruit evolution based on the reduction in the number of carpels and the closure of the carpel margins. In the first line, the progressive reduction in the number of carpels must have led to monocarpy, thus giving rise to the simple follicle. This follicle evolved to form a special tissue in the dorsal region of the carpel ensuring regular dehiscence at fruit maturity. The increase in the opening capacity of this follicle resulted in the formation of two valves, thus constituting the legume. The second evolutionary line must have led to a still incipient syncarpy, in which the carpels in reduced number suffered loose adnation. The initially separated carpel margins close until seed maturation and then open passively, giving rise to the septicidal capsule. In an evolutionary sequence, this capsule must have given rise to the schizocarp, which must have led to the formation of the hesperidium and nuculanium. Drupoid fruits must have originated from nucoid fruits, by acquiring fleshy tissue from the pericarp. Berry-type fruits must have originated from capsules, through loss of the ability to open and acquisition of fleshy wall and pulp formation.

Lorts et al. [60] have formulated a hypothesis that fruit evolution was driven at least in part by dispersal agents abundant in particular habitats. The authors [60] surveyed 59 orders and 391 families for available fruit types, and the analyze was made in contrasting areas, an open habitat including the Indian desert and North American plains and prairies, and a closed forest habitat of Australian tropical forest. In conclusion it may stated that the majority of genera in the survey of tropical forests in Australia were fleshy fruit trees, whereas the majority of genera in the survey of prairies and plains in central North America were herbs with capsules and achenes. Both capsules and achenes are frequently dispersed by wind in the open, arid habitat, whereas fleshy fruits are generally dispersed by animals. The

authors also emphasize that the phylogenetic constraint remains weak for families with variable fruit types, and that further investigations are needed at the familial and lower levels before any generalization can be made.

Figure 5 Follicles (A) and capsule (B) of the extant plants *Sterculia chicha* A. St.-Hil. ex Turpin (Malvaceae) and *Cedrella fissilis* Vell. (Meliaceae). Follicle-like fruit is considered an ancestor of angiosperms, and capsule-like fruit may be ancestor of monocots. Scale bars: 1 cm.

Based on literature, Takhtajan [64] considers as an ancestral fruit the many-seeded distinct follicles, which have originated from a pluricarpellate apocarpous gynoecium. The multifolliculus gave rise to unifolliculus by reduction in the number of carpels (e.g. *Degeneria* I.W. Bailey & A. C. Sm., Degeneriaceae, and Ranunculaceae). From follicular fruits arose many other types of apocarpous fruits, which in their turn gave rise to numerous syncarpous fruit types.

Recent investigation on morphogenesis and types of fruits [9] has revealed interesting considerations about evolutionary trends in the fruits of angiosperms. The authors can be considered strong exponents of the view that the follicle (Figure 5A) is the ancestral fruit type of angiosperms, although they report that in monocots the most probably ancestral fruit type is the capsule (Figure 5B). The authors assume that different types of follicles were the structural basis for morphogenetic transformations in many groups of angiosperms, and they list the characters that served as modes of specialization of follicles, such as the loss of dehiscence, the reduction of seed number per carpel, the fusion of the carpels and specialization of the anatomical structure of the pericarp. The authors complement that the combination of these modes of fruit transformation in different evolutionary lines links follicles with nutlets, drupes, berries, capsules and pyrenariums of different morphogenetic types. Bobrov and Romanov [9] also believe that the drupes were the basis for further evolutionary transformations of fruits in some groups of angiosperms: the berries can evolve from drupes due to parenchymatization of the pericarp, nutlets can evolve from drupes due to sclerenchymatization of the pericarp, and pyrenariums can evolve from them due to transformation of apocarpous gynoecium into the coenocarpous gynoecium.

3.4 Evolutionary trends of fruits in some groups of angiosperms

3.4.1 Asteraceae

Some evolutionary trends using fruit characters in Asteraceae have been reported in the literature. Bonifacio et al. [74] in their embryological studies on *Stifftia* J. C. Mikan and *Wunderlichia* Riedel ex Benth. have presented some conclusive considerations that deserve some attention. According to authors the "cypsela-type fruits with a persistent calyx are character states occurring only in Asteraceae and Calyceraceae and possibly arose in a common ancestor and constitute synapomorphies for these families". The authors complement that several characters, including fruits without phytomelanin and parenchymatic pericarp, occur in Goodeniaceae, Calyceraceae and in early-divergent groups of Asteraceae, constituting plesiomorphic character states for the family. On the other hand, characters such as fruits with phytomelanin and sclerenchymatic pericarp are derived character states found only in core Asteraceae [74].

Morphological study in cypselae of the subtribe Disynaphiinae, Asteraceae [75], revealed that the number of outer mesocarp cell-layers is an important feature supporting the relationship among two of four clades studied by researchers. These authors [75] also suggest that the mesocarp with two or three layers may be the ancestral state for the subtribe. The multiplicative pericarp that was considered by the authors to be a rare feature among Asteraceae species must have evolved independently in *Symphyopappus* s.s. and *S. compressus* (Gardner) B. L. Rob.

Phytomelanin has been found in cypselae of *Lychnophora salicifolia* Mart. and compared it with *Heterocoma* DC. species [76]. Marques et al. [76] admit that phytomelanin has been considered a (syn)apomorphy to the Heliantheae alliance, but several other anatomical studies have shown that the phytomelanin in Asteraceae is more widely distributed.

3.4.2 Campanulidae clade

According to Beaulieu and Donoghue [77] this clade has about 35,000 species, and it includes Asteraceae, Apiaceae and Dipsacales. Further, the authors distinguish four categories of fruits in the clade, namely drupe, berry, capsule and achene (the latter is considered the most frequent in the clade). The present authors are inclined to believe in their analysis that the capsule-like fruit must have given rise to all other types of fruit that occur in campanulids.

3.4.3 Fabaceae

Fahn and Zohary [72], who were perhaps the first to observe the importance of pericarp structure in fruit evolution in Leguminosae, proposed some evolutionary trends in the subfamilies Mimosoideae, Caesalpinioideae and Papilionoideae. In the Mimosoideae, which is considered a basal subfamily, no species was found without any sclerenchymatous stratum, although large number of species and genera showed a two-layered sclerenchymatous stratum. In the Caesalpinioideae the number of species without a sclerenchymatous stratum is also nil, but the number of species and genera with two-layered sclerenchymatous stratum is low. In the Papilionoideae was found small number of species and genera containing a two-layered sclerenchymatous stratum and a large number of taxa with one layer of sclerenchymatous stratum. The authors concluded that legumes with two-layered sclerenchymatous stratum are more basal than those with one-layered; the investigation clearly indicates a trend leaving to reduction of this stratum; and the most derivative type seems to be legumes with no sclerenchymatous stratum.

3.4.4 Rubiaceae

Two evolutionary trends were identified in the Rubiaceae fruits. The first trend was formulated by Bremer and Eriksson [78] that believe the common ancestral of the family had capsular fruit with many seeds, which was considered as a plesiomorphic state for the family, later evolving to fleshy fruits at least twelve times during the entire evolutionary line of Rubiaceae, and at least four times in Rubioideae subfamily. The other evolutionary trend is based on molecular studies by Razafimandimbison et al. [79] who suggest that schizocarp fruits evolved independently at least twice from ancestors with fleshy and drupaceous fruits in Psychotrieae tribe.

3.4.5 Sapindaceae

Chery et al. [80] inferred that unwinged fruits represent the ancestral condition in *Paullinia* L., from which there were repeated evolutionary transitions and reversals; seven transitions are reported: five transitions from exalate to alate, one transition from exalate to echinate, and one reversal from alate to exalate. Phylogenetic studies in Serjania Mill. with emphasis on fruit evolution [81] support that the ancestral fruit type of the genus is a schizocarp, but occur at least five independent derivations to capsule and at least one transition back from capsules to schizocarps. Yet another consideration is based on the assumption that transitions from winged to wingless mericarps have occurred at least twice.

3.4.6 Solanaceae

Evolutionary trends in Solanaceae fruits were reported by Knapp [82]. According to author the capsular fruits were the plesiomorphic state in the Solanaceae, and capsules occur in most of the basal clades of the family. The occurrence of capsular fruits was registered in the *Datura* clade, and can represent a secondary derivation of the capsule from a berry-fruited ancestor. Berries are clearly derived in the family and seem to have three separate origins; "from the distribution of stone cells in berries, it is clear that they are a derived character relative to the possession of berries, and have apparently been either gained or lost several times", says the author. The author further believes that the fruit type pyxidium is a modified berry, and that it has arisen three times independently, in the *Hyoscyamus* clade, in *Oryctes* S. Watson of the *Physalis* clade and several times in the genus *Solanum* L.

3.4.7 Monocotyledons

Thadeo et al. [83] have discussed the anatomical development of fleshy fruits of the monocots to better understand the evolution of baccate fruits in the monocot clade. The authors studied 14 species with fleshy fruits of the taxa Alismatales, Arecales, Asparagales, Commelinales, Dioscoreales, Liliales, and Poales to determine the mechanisms through which baccate fruits attain fleshiness at maturity. The authors conclude that "fleshy fruits in the monocots do not develop through a single shared pathway, indicating that fleshiness has evolved multiple times within the clade". In the paper, the authors make some references to the evolution of fruits in monocots: a) Asparagales, Commelinales, Dioscoreales, Liliales, and Poales have probably a common ancestral fruit type, the dry and dehiscent capsule; b) the research supports the hypothesis that the follicle is the ancestral fruit type for the core Alismatales; c) it is possible that the indehiscent drupaceous fruits of Alismatales examined in the study are derived from follicles that lost dehiscence as an adaptation to aquatic life; and d) on the evolution of specialized drupes from Poales and Arecales, it is possible that the ancestral fruit type for these specialized drupes is a true berry.

3.5 Seed evolution

3.5.1 Ovule

Anatropous ovules are distributed throughout the angiosperms and are usually regarded as representing the plesiomorphic state [84]; the condition of bitegmic ovules also represents undoubtedly the plesiomorphic state in the dicots "sensu lato", say the author. According to Rudall [66] "the phylogenetic distribution of unitegmy in angiosperms indicates that it represents one or more derived conditions". Based on the literature, Rudall [66] reports that "possible means of achieving secondary unitegmy include complete suppression of an integument, or congenital synorganization ('fusion') of the inner and outer integuments". Sporne [85] considered that the ancestral type of ovule in angiosperms was crassinucellate with three envelopes (two integuments and an aril) each of which received a vascular supply. The evolution of tenuinucellate and unitegmic ovules from crassinucellate and bitegmic ones (Figure 3) is considered a major evolutionary trend in the angiosperm gynoecium [69].

A notable study of the diversity, development and evolution of angiosperm ovules was carried out by Endress [86], in which the author reports some evolutionary trends in the angiosperms. According to Endress [86] the trends that deserve to be highlighted are: "the two most salient differences between ovules of angiosperms and other seed plants are that they are basically and predominantly anatropous and bitegmic (vs. orthotropous and unitegmic); lobation of inner (and outer) integuments in angiosperms is simply a morphogenetic necessity in forming a narrow micropyle; hood-shaped and cup-shaped outer integuments co-occur within closely related clades; zig-zag micropyles in angiosperms are not basal, but rather the result of developmental overgrowth in ovules with excessive development of the antiraphal side; the evolutionary pathway to unitegmy from bitegmy in angiosperms is not uniform: in unitegmic basal angiosperms and some derived groups it probably evolved mainly by loss of the outer integument, often associated with orthotropous ovules, but in derived eudicots (asterids) it is mainly by incorporation of the outer into the inner integument, associated with anatropous ovules; ovule structure is partly shaped by locule architecture and also associated with the presence or absence of massive locular secretions; and, finally, a closer look at nucellus and integument thickness shows a clear association of some newly recognized types with larger clades in angiosperms".

3.5.2 Seed

In his book dedicated to the memory of Dr. Fritz Netolitzky, a great pioneer researcher in the study of the seed, Corner [2] devotes an entire chapter to showing the evolution of seeds of dicots "sensu lato". His phylogenetic considerations have raised controversies between systematists and phylogenists, especially when molecular studies are taken into account.

In the chapter "seed-evolution", Corner [2] idealizes a "primitive" dicot seed as having the following characters: "the seed was of medium-size (5-10 mm long); arillate; anatropous; with multiplicative integuments; mechanical layer in every epidermis (except that of the nucellus); it was at once exotestal, endotestal, exotegmic and endotegmic, perhaps even mesotestal; with elaborate chalaza; crassinucellate; albuminous, probably perispermous (starchy); and with minute embryo".

Corner's seed-progress [2] commonly has accompanied the floral evolution, as can be seen in the more advanced families of Asteraceae (Compositae) and Orchidaceae which have small simple seeds, but Corner [2] also recognizes that there are many instances (Rosaceae, for example) to show that the seed has progressed without much floral advance. The author emphasizes that each family of dicots has its own way of seed-progress, and he outlines a feature survey: (a) Specialization of the seed coat (limitation of the mechanical tissue to one cell-layer); and (b) Simplification of the seed coat (loss of aril, testa and/or tegmen; lack of tissue differentiation; loss of vascular ramification, especially the post-

chalazal, the tegmic and arillar; simplification of the chalaza; decrease in size by loss of multiplicative cell-layers; and change of the anatropous form through the campylotropous to the orthotropous).

A survey of the seed-diversity in the Cactoideae (Cactaceae) [87] was carried out to assess the potential taxonomic value of seed-characters in the subfamily. Among the analyzed characters of the seeds, those referring to the internal structure of the seed, stratification of the seed coat, gross morphology (shape and symmetry in lateral view, length/breadth ratio, size), testa appearance, testa sculpture, individual cell features, anticlinal cell-boundaries, sculpture of periclinal walls, hilum-micropylar region and appendages were emphasized. The authors [87] register some evolutionary trends in Cactoideae, such as the transference of the storage function to the massively developed hypocotyl itself, coupled with reduction of the cotyledons, and some specialized features that were considered as apomorphies restricted to individual tribes, subtribes or genera. Examples of apomorphies are undulate anticlinal walls, concavities in the periclinal walls and verrucose microrelief.

Teichman and Wyk [88] in a study of the evolution of dicotyledonous "sensu lato" seeds associated several characters, such as bitegmy and unitegmy, crassinucellate and tenuinucellate ovules, nuclear and cellular endosperm development, seed size, woody and herbaceous habit, and tropical and temperate habit, with the possible evolutionary status of the endothelium, hypostase, pachychalaza and the recalcitrant viability behaviour of seeds. The authors' conception [88] admits that "a) an endothelium is considered derived since it occurs more often in highly evolved superorders and is significantly associated with derived ovule and endosperm character states as well as with smaller seed size; b) a hypostase appears to be relatively ancestral and is significantly associated with pachychalazy and recalcitrance; and c) the pachychalazy and recalcitrance are significantly associated with ancestral ovule character states and, at the species level, with large seed size (overgrown seed), woody habit and tropical habitat". The authors finally conclude that the "presence of pachychalazy, recalcitrance and associated large seed size are therefore regarded as ancestral character states of the dicotyledons".

Takhtajan [64] agrees with Corner [2] regarding the ancestral seed type in angiosperms: this seed must be of medium-size (5-10 mm long). For the author [64] both small and large seeds are derived. The present author is inclined to follow other authors, which characterize the ancestral seed with abundant endosperm and a minute and undifferentiated embryo. On the other hand, the advanced seeds have large and well-differentiated embryo, and the endosperm is more or less reduced or even wanting.

3.5.3   Seed coats

The seed coat has been extensively studied in the characterization of different taxa of angiosperms, and it has revealed features of potential taxonomic and phylogenetic significance. A notable classic study was carried out by Corner [89] on leguminous seeds involving more than seventy species belonging to different taxa. In this work, the author makes some evolutionary considerations in Fabaceae that deserve to be highlighted, such as "the Papilionioideae (Faboideae) seed is a specialization of the Mimosoideae/Caesalpinioideae, the seed of *Swartzia* Brid. appears to be phyletically intermediate, and the seed of Amherstieae-Cynometreae is a simplification of the Mimosoideae-Caesalpiniodeae".

Regarding the phylogenetic conclusions of the seed coat in dicots "sensu lato" [2], which have raised controversy among botanical researchers, Dahlgren [84] selects three conditions which seem to be of particular phylogenetic significance: (a) Seeds with exotegmic fibers that occur in three groups of families (group consisting of taxa with multiple exotegmic fibers combined with a thick-walled exotestal layer and with crystals in the endotestal layers, e.g. Passifloraceae and Violaceae; group with nonmultiplex exotegmic fibers combined with a thick-walled exotestal layer and with crystals in the endotestal layers, e.g. Meliaceae and Proteaceae; and nonmultiplex exotegmic fibers combined with a thick-walled exotestal layer, but devoid of crystals in the endotestal layer, e.g. Celastraceae and Sapindaceae); (b) Seeds with exotegmic palisade, in which the outer layer of the tegmen comprises the mechanical tissue, for example in Malvaceae and Euphorbiaceae; and (c) Seeds with a sclerotic mesotestal layer, which may be found in Melastomataceae and Myrtaceae.

Studies of Tokuoka and Tobe [90,91,92] have indicated the taxonomic and evolutionary value of seeds for Euphorbiaceae taxa. The authors reported some evolutionary trends investigating 50 genera and 111 species of Crotonoideae, 32 genera and 79 species of Euphorbioideae, and 80 genera and 172 species of Acalyphoideae. According to the authors the three subfamilies are uniovulate and have palisadal exotegmen composed of radially elongated, sclerotic, and pitted cells. The presence of palisadal exotegmen was considered a synapomorphy in the three uniovulate subfamilies, but it was later found that five tribes (Clutieae, Chaetocarpeae, Pereae, Dicoelieae and Galearieae) of Euphorbioideae do not have palisade cells, but exotegmen with longitudinally elongated cells. Compared with the Acalyphoideae and Euphorbioideae, both presence of the thin inner integument and the lack of the vascular bundles in

the inner integument of Crotonoideae are considered plesiomorphies; in contrast, the occurrence of the thick inner integument and the presence of vascular bundles in this inner integument are synapomorphies.

3.5.4 Embryo

Martin's [93] classic work deals with the internal morphology of seeds, especially the size, shape and position of the embryo. The author classifies the embryos into divisions called basal (types rudimentary, broad, capitate and lateral), peripheral and axile. The axile division is composed of subdivisions, such as linear (with the type linear), miniature (types dwarf and micro) and foliate (types spatulate, bent, folded and investing). The author regarded that smallness in embryos, as compared to size of endosperm, as representative of a basal state in seeds and, conversely, the embryos well-developed represent a higher evolutionary rank. The author, however, considers this principle "dangerously incomplete" and needs further studies. It must be pointed out that Martin [93] considers that the ancestral type of embryo can be the rudimentary embryo in its most elementary form.

With reference to seed size, Martin [93] suggests two divergent lines of progression: the first trend is related to the fact that some plants produce myriads of minute delicate seeds, while other plants produce few seeds that are large, well-developed, with food reserves, and have advanced embryo types. The author postulates that "divergent orthogenesis in these opposite directions has produced distinct forms of seeds that are particularly conspicuous in two axile subdivisions, the miniature, representing quantity production, and the foliate, quality".

The evolution of the embryo size in angiosperms was also analyzed by Forbis et al. [94] and related to seed dormancy. The authors postulated a hypothesis that the ancestral angiosperm embryo had small size reflecting the fact that the extant basal lineages (particularly within basal groups including eumagnoliids, Illiciaceae, Schisandraceae, Austrobaileyaceae, Nymphaeaceae, and Amborellaceae) have small embryos. There are cases, however, of basal angiosperms that have large embryos, as well as examples of advanced taxa with seeds provided with small embryos, complement the authors. According to authors, the Orchidaceae is a remarkable example of advanced plants that have embryo which is not large and well-differentiated as in most exalbuminous taxa; the embryos are minute and undifferentiated, consisting of only a few cells at dispersal. In the present analysis, the occurrence of reversal cases is mentioned, as the small embryo of members of Vitaceae; other cases of underdeveloped embryos among eudicot taxa that appear to represent reversals occur in, for example, Santalales, Paeoniaceae, Grossulariaceae, and Parnassiaceae.

In the relationship between embryo size and seed dormancy, Forbis et al. [94] suggest that the ancestor of extant seed plants had seeds with an underdeveloped embryo and, consequently, morphological dormancy is the ancestral dormancy type among seed plants. In the analysis, other types of dormancies are reported, physiological and physical, which are not found in basal angiosperm taxa. A fourth type of dormancy (morphophysiological: underdeveloped embryo and physiological dormancy) is recorded that can occur in basal angiosperms. In conclusion, the authors assume that "the occurrence of both morphological and morphophysiological dormancy among basal lineages makes it unclear which type of dormancy seed plant ancestors possessed, but it is likely that an underdeveloped embryo, with or without physiological dormancy, is the plesiomorphic condition for seed plants".

Chlorophyllous embryos in angiosperm seeds have been analyzed by Dahlgren [95], and the author indicates that these seeds are scattered throughout the angiosperms and have evolved in many unrelated taxa. In conclusion, the paper reports that various conditions influence the transmission of light to the embryo, and the great constancy of this character in many large groups of angiosperms suggests that this may reflect phylogenetic relationships to a certain degree within each of these complexes.

Takhtajan [64] states peremptorily that "it is almost universally accepted that the monocotyledonous embryo arose from the dicotyledonous embryo".

3.5.5 Endosperm/perisperm

Martin [93] also believes that there is an evolutionary trend for the endosperm. The author proposes that the peripheral embryo division together with three types of the basal embryo division, the capitate, lateral and broad, have close relation to conspicuously starchy endosperm. On the other hand, conspicuously starchy endosperm is not evident in any seed types previously mentioned, except for a few monocots in the linear type.

The ruminate endosperm is defined as an uneven endosperm surface that is often highly enlarged by ingrowths or infoldings of the surrounding tissue [96]. Species of *Palicourea* Aubl. and *Psychotria* L. (Rubiaceae), for example, have ruminate seeds with scanty endosperm, whose rumination originates from the folds and undulations of the pyrene [49]. Some authors of the last century have recognized the ruminate endosperm as an ancestral character among

angiosperms, but Bayer and Appel [96] argue that "there are no comparative studies of seed structure and development that prove the homology of rumination in angiosperms". These authors based on Netolitzky [53] consider it more likely that rumination evolved independently several times within the angiosperms. This assumption is supported by the scattered distribution of ruminate endosperm all over the angiosperms. Takhtajan [64] seems to agree that ruminate endosperm could be an ancestral character still occurring in present-day seeds, belonging to both basal and advanced taxa.

Takhtajan [64] makes reference to the endosperm haustoria, which may arise at the chalazal and micropylar end, or at both ends of the developing cellular endosperm. According to the author, the most archaic taxa of angiosperms, including Magnoliaceae, are devoid of endosperm haustoria. The evolutionary history of endosperm haustoria indicates that it evolved independently in various lines of angiosperms, complements the author.

Perisperm is considered as persisting nucellus which by cell division originates a nutritive tissue in the ripe seed. In dicots "sensu lato", the perisperm has been reported, for example, in seeds of Piperaceae [47] and Amaranthaceae [20,21]. Perisperm evolution in dicots may have occurred from the thin perisperm found in some basal families towards a development of a nutritive perisperm, as seen in Capparaceae [84]. In monocots, the perisperm is registered in a wide range of taxa, with different structure and origin [97]; according to author the perisperm has evolved several times in monocotyledons.

3.6 Appendages and special structures of the seed

3.6.1 *Aril and sarcotesta*

The relationship between aril and sarcotesta was discussed extensively in different taxa of dicots "sensu lato" by Corner [2], who concluded that the aril and firm exotesta were "primitive" features in the angiosperms; there was a combination of the aril with the endotestal or tegmic construction; and that on loss of the aril, the testa became partly or wholly sarcotestal. Additional noteworthy point is that the sarcotesta is polyphyletic in angiosperms and not homologous with the sarcotesta of "gymnosperms". It must be pointed out here that the aril in angiosperms is considered a derived appendage by Pijl [98].

Dahlgren [84] considers a matter of conjecture as to whether arils are basal or derived structures, but she assumes that the combination of the morphological diversity in arils and their widespread distribution indicate that arils are of polyphyletic origin and are thus not homologous in the different taxa of angiosperms.

3.6.2 *Pachychalaza (Figure 4A,B)*

The pachychalaza is considered as a polyphyletic advance in the formation of the seed, and there seems to be a relation between pachychalazy and unitegmy [2]. However, Boesewinkel and Bouman [99] did not find this relation in *Glycosmis* Corrêa (Rutaceae) ovule and seed development, because "the unitegmic condition originates ontogenetically in a much earlier stage of development than the chalazal proliferation".

The presence of pachychalaza in monocot seeds is reported by Rudall [97], especially in Cannaceae. The author, in her review of nucellus and chalaza in monocots, makes reference to "chalazosperm", which is a structure derived from chalaza and that lies outside the raphal bundle. She thinks the difference between chalazosperm and pachychalaza is not well defined.

4 Conclusion

There seems to be no doubt that the follicle-like fruit, which is characterized by having a single carpel and several seeds, must be the ancestral fruit of the angiosperms. In the specific case of the monocot clade, the ancestral fruit must be the capsule-like, with more than one carpel. When the evolutionary study is carried out within a taxon or clade, the ancestral fruit may be different from the follicle, capsule-like fruit in campanulids, Rubiaceae and Solanaceae, and schizocarp-like fruit in Sapindaceae.

It is very likely that the ancestral seed of angiosperms originated from a crassinucellate and bitegmic anatropous ovule. There seems to be no controversy that the evolution of tenuinucellate and unitegmic ovules from crassinucellate and bitegmic ones is considered a major evolutionary trend in the angiosperm gynoecium. The evolution of the seed in angiosperms is controversial and inconclusive. The literature is more conclusive when it reports the evolution of isolated parts of the seed (seed coat, reserve tissue and embryo), and appendages and special structures of the seed within a group or clade of angiosperms.

Compliance with ethical standards

Disclosure of conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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