

Fruit ontogenesis in *Clusia parviflora* Humb. & Bonpl. ex Willd. (Clusiaceae)

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RESUMO – (Ontogênese do fruto de *Clusia parviflora* Humb. & Bonpl. ex Willd. (Clusiaceae)). Aspectos morfo-anatômicos dos frutos e sementes em desenvolvimento de *Clusia parviflora* são apresentados e discutidos, visando dar continuidade aos estudos com estes órgãos em Clusiaceae. O fruto é cápsula septifraga; o exocarpo suberificado deriva da epiderme externa do ovário. O mesocarpo, originado do mesofilo ovariano, permanece parenquimático. O endocarpo é derivado da epiderme interna do ovário e de três a quatro camadas subepidérmicas, cujas células tangencialmente alongadas tornam-se lignificadas, contribuindo para a deiscência do fruto. Os óvulos são anátropos, bitegmentados, com endotélio, e originam sementes também anátropas, bitegmentadas e exalbuminosas. A exotesta apresenta células de conteúdo fenólico. O exotégmen consta inteiramente de esclereídes com paredes anticlinais onduladas. O restante do tégmen torna-se colapsado. O embrião é levemente curvado e apresenta um eixo hipocótilo-radicular cilíndrico e muito desenvolvido, com dois cotilédones muito pequenos. Parece haver uniformidade em *Clusia* com relação ao número de camadas no tegumento seminal maduro, mas o número de camadas no tegumento ovulífero pode ser um caráter diagnóstico em nível específico.

Palavras-chave: anatomia, *Clusia parviflora*, Clusiaceae, fruto, semente

ABSTRACT – (Fruit ontogenesis in *Clusia parviflora* Humb. & Bonpl. ex Willd. (Clusiaceae)). Aspects of the morpho-anatomy of developing fruits and seeds of *Clusia parviflora* are presented and discussed as a continuation of the study of these organs in Clusiaceae. The fruit is a septifrage capsule; the suberized exocarpe is derived from the external epidermis of the ovary. The mesocarpe originates from the ovarian mesophyll and remains parenchymal in nature. The endocarpe is derived from the internal epidermis of the ovary and the endocarpe is derived from the inner ovary epidermis as well as from three to four adjacent subepidermal layers, with tangentially elongated cells which become lignified and contribute to fruit dehiscence. The ovules are anatropous, bitegmatic, with an endothelium, and give rise to equally anatropous seeds. The exotesta has cells containing phenolic compounds. The exotegmen consists entirely of sclerids with anticlinal and undulating cell walls, while the rest of the tegmen collapses during maturation. The embryo is slightly curved and the hypocotyl-radicle axis is well developed, with two very small cotyledons. There seems to be uniformity in the genus *Clusia* as regards the final number of layers in the mature seed coat, being evident the continuous lignified exotegmen and the hypocotylar embryo. It should be pointed out that the number of layers in the ovule integument can be used for diagnosis at the species level

Key words: anatomy, *Clusia parviflora*, Clusiaceae, fruit, seed

Introduction

Clusia parviflora Humb. & Bonpl. ex Willd (Clusiaceae) is a dioecious shrub or tree species occurring in the Atlantic Forest of Rio de Janeiro, São Paulo, Minas Gerais, and Santa Catarina states in Brazil (Engler 1888; Engler & Keller 1925; Mariz 1974; Cronquist 1981; Heywood 1985; Gustafsson *et al.* 2002).

In addition to floral diversity, fruit and seed characteristics have been used to delimit the subfamilies and tribes of Clusiaceae (Engler 1888; Brandza 1908; Engler & Keller 1925; Melchior 1964; Heywood 1985). However, the reduced number of ontogenetic studies of these organs in this family generates doubts concerning the relationships and positions of the species in the subfamilies and tribes. This question was addressed by Mourão & Beltrati (1995a; b; 2000; 2001) who described in great detail the morphology, anatomy, and ontogeny of the fruits and seeds of *Platonia insignis* (Clusioideae-Symphonieae), *Vismia guianensis* (Hypericoideae-Vismieae), and *Mammea americana* (Kielmeyeroideae-Calophylleae), elucidating doubts in the literature about the dispersal structures and fruit types of these species.

The present work examined the morphology and anatomy of developing fruits and seeds of *C. parviflora* (Clusioideae-Clusiaceae) as a contribution to the study of these organs in Clusiaceae, with the intent to describe their structure comparing with the literature on this subject.

Materials and methods

The present study examined the flowers and fruits of *Clusia parviflora* Humb. & Bonpl. ex Willd. at different development stages, collected in the Núcleo Picinguaba area (São Paulo, Brazil). Reference plant material was prepared and deposited in the HRCB Herbarium under the numbers 9.806, 13.397, 9.470, 9.984.

All material used for morphological and anatomical studies was fixed in FAA 50 (Johansen 1940) and conserved in 70% ethanol (Jensen 1962). Anatomical descriptions were based on the analysis of semi-permanent and permanent slides of transversal and longitudinal sections of developing fruits and seeds. The slides were prepared using standard procedures and according to the methodology described by Mourão & Beltrati (1995a). The plant material was embedded in historesin according to the specifications of the manufacturer, stained with Toluidine Blue O (O'Brien *et al.* 1965), and mounted in Permount.

Free-hand sections of fresh material were stained for histochemical analysis using Sudan III and Sudan IV for lipids; ferric chloride for phenolic compounds; phloroglucinol and sulfuric acid for lignins (Johansen 1940), and IKI (Jensen 1962) for starch.

Fruit descriptions were based on Barroso *et al.* (1999). The terminology adopted to define the pericarp layers is in agreement with Roth (1977), and the nomenclature used for seed coats was based on Corner (1976) as modified by Schmid (1986).

Results

Fruit development – After fertilization, the petals and sepals close over and cover the ovary. The petals then fall away while the sepals and sessile stigma remain until fruit

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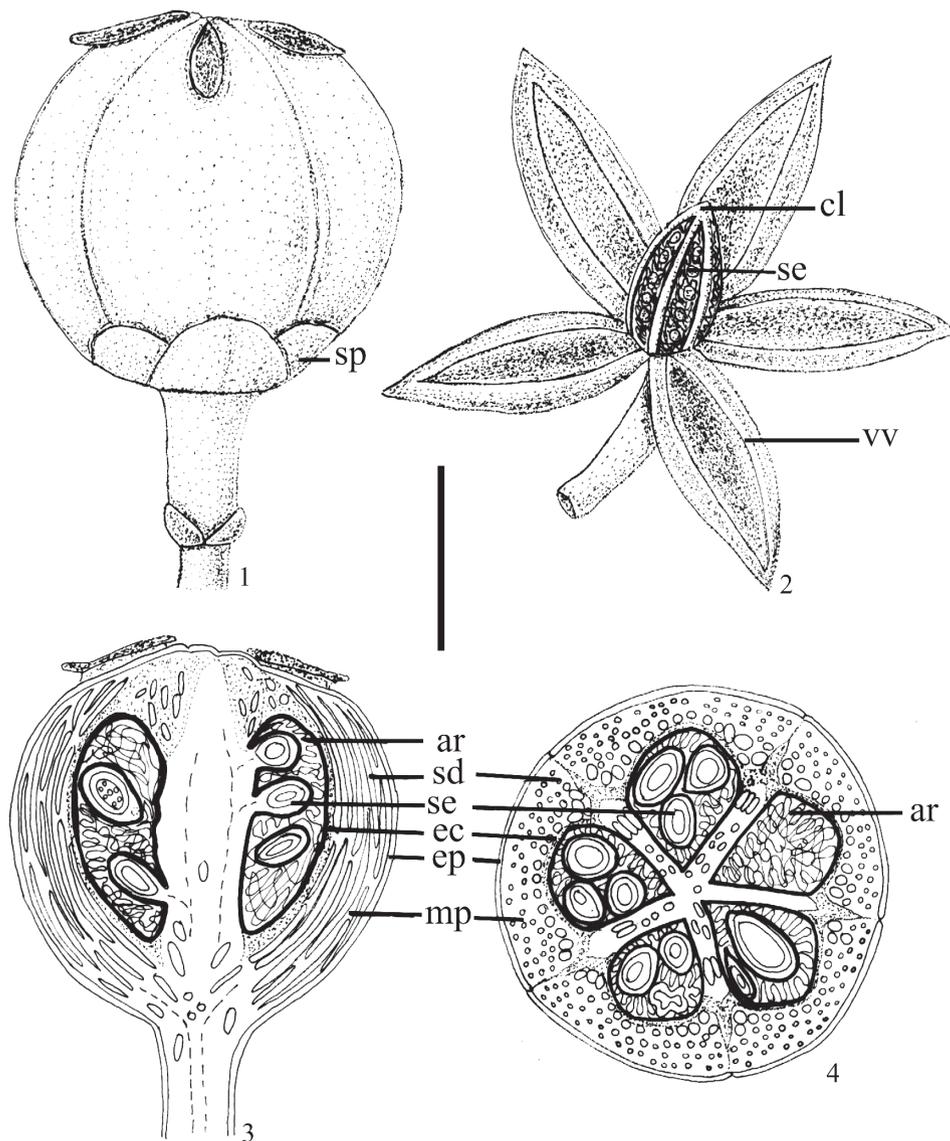
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maturation (Fig. 1). The fruits of *C. parviflora* are greenish-yellow spherical capsules approximately 25 mm in diameter. The seeds and aborted ovules, both covered by a sugar-rich pulp, are either attached to the central column or to the inner cavity of the fruit valves and become exposed when the fruit dehisces (Fig. 2).

The 5-carpellary and 5-locular ovary of *C. parviflora* is superior and has sessile stigmas. The ovules have axial placentation. The outer epidermis of the ovary is uniseriate and is composed of cubic to slightly elongated cells covered by a thin cuticle (Fig. 12). Five to six tangentially elongated cells layers define the locule (Fig. 9). The ovarian mesophyll is composed of fundamental parenchyma, where a number of branched secretory ducts and vascular bundles can be observed. These ramified secretory ducts have a

longitudinal orientation, and are also observed in the septum (Fig. 5-6).

In the ovary after fertilization (Fig. 7), cell divisions occur in all planes. Pericarp structure of immature fruits (Fig. 1) is basically the same as in the ovary both before and after fertilization (Fig. 3-4, 7). The exocarp, which is derived from the outer epidermis of the ovary, becomes suberized in the immature fruit. The mesocarp, which is derived from the ovarian mesophyll, remains parenchymatic (Fig. 7). The endocarp is derived from the inner ovary epidermis as well as from three to four adjacent subepidermal layers. The tangentially elongated cells of these adjacent layers become lignified during fruit development (Fig. 7, 10-11). The dehiscence line occurs along the carpelar suture and consists of small parenchymatic cells, visible in the ovarian mesophyll, that divides into two near



Figures 1-4. *Clusia parviflora* (Sald.) Engler. 1-2. General aspect of the mature fruit before and after dehiscence, respectively, showing the sessile stigma and seeds covered by the aril attached to the central column. 3-4. Medium longitudinal and transversal sections, respectively, showing tissue zonation in the pericarp. ar: aril, cl: columella, ec: endocarp, ep: exocarp, mp: mesocarp, sd: secretory duct, se: seed, sp: sepal, vv: valve (Bar scale = 1.5 cm).

the locule (Fig. 5, 7-8, 13); the fruit is a septifrage capsule (Fig. 2). Most of ovules develop into seeds (Fig. 3-4).

Seed development – The ovules (Fig. 14-15, 19) are anatropous and bitegmic; the outer integument is composed of four to five cell layers, while the inner integument is composed of three to four layers. The inner epidermis of the inner integument has radially elongated cells, which form the endothelium. The micropyle channel is formed by the endostome and by the exostome, although these openings are not aligned forming a “zigzag” micropyle. The embryo sac is longitudinally elongated. A group of elongated nucellar cells in the chalazal region with large nuclei constitute hypostasis. A provascular strand penetrates through the funicle, extending to the chalaza. Arilar lobes with two cell layers have developed within the ovule and occupy the entire locule. The aril has a funicular and exostomal origin (Fig. 14), with a circular shape in the apical region of the ovule.

Ovule structure is basically maintained during development (Fig. 18); however, a layer of cells with sinuous anticlinal walls differentiates in the outer epidermis of inner integument. This differentiation begins in the chalazal and endostomal region (Fig. 16-17) and continues

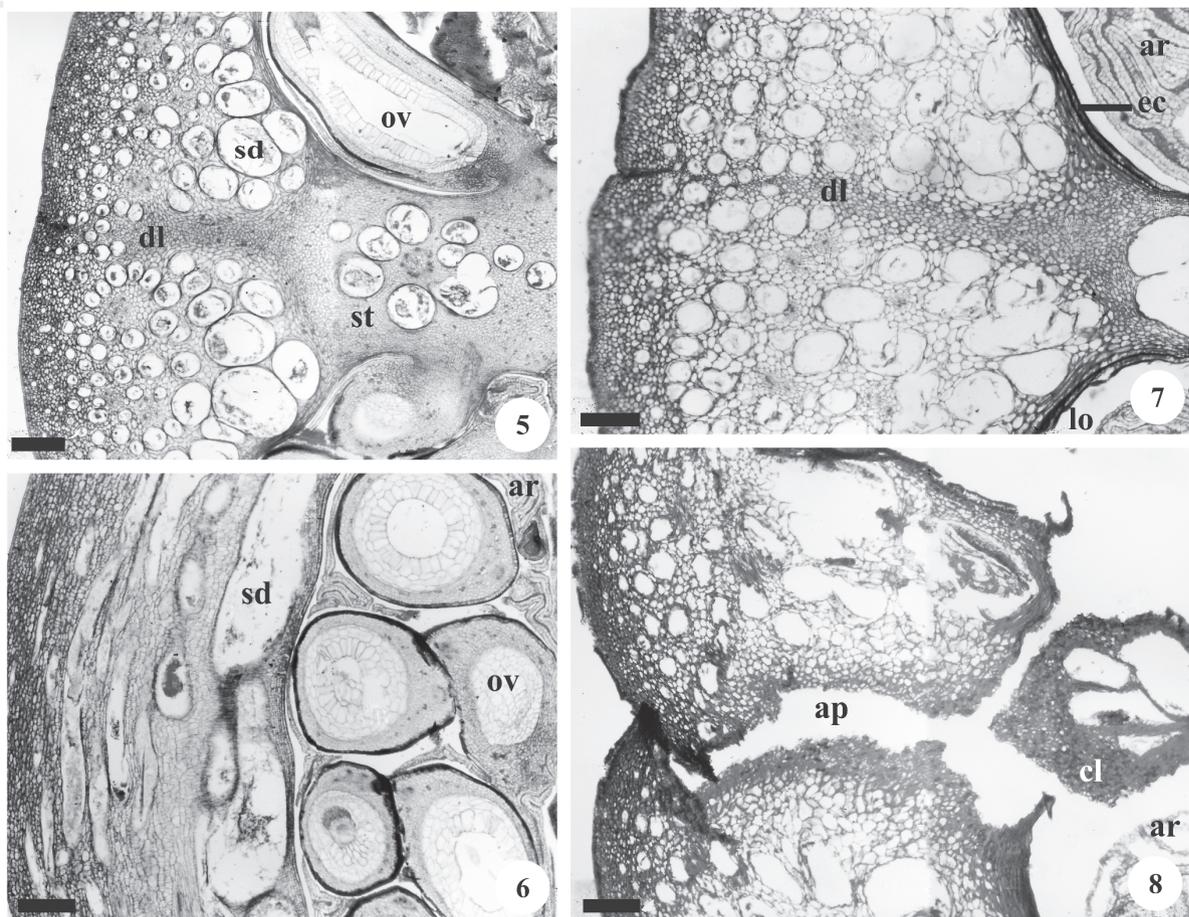
throughout the sides of the seed in development, with the cells walls of all exotegmen becoming lignified at maturity (Fig. 20-22).

The mature seeds are elongated ellipsoids about 5.0 mm long and 3.0 mm in diameter, and have a brown color. The rounded hilum is completely surrounded by arilar lobes that cover about two thirds of the seed. The dispersal unit is composed of all developed seeds and aborted ovules in each locule, covered by their respective arils.

The mature seed is anatropous and exalbuminous. The embryo is slightly curved and has a well developed, cylindrical hypocotyl-radicle axis, with two small cotyledons (Fig. 24-25).

The exotesta cells of the mature seed contain phenolic compounds. The exotegmen is entirely composed of sclerids and its lignified anticlinal walls appear sinuous in surface view. The other layers of the testa and the tegmen have collapsed by this phase (Fig. 21-22).

The protoderm of the embryonic axis is composed of cubic cells with thick cell walls and cuticles. The fundamental meristem, which is more evident in the cortex, is composed of rounded cells with lipidic contents, thin cell walls and secretory ducts with longitudinal orientation (Fig. 22-23). A



Figures 5-8. *Clusia parviflora* (Sald.) Engler. 5-6. Young fruit in transversal and longitudinal section, respectively, evidencing the seeds and ramified secretory ducts with a longitudinal orientation, which occur also in the septum. 7. Transversal section of the immature fruit (note the lignified cells of the endocarp with tangential orientation and the cells of the dehiscent line and mesocarp with thin walls). 8. Mature fruit in dehiscent (note that all pericarp cells lost water). ap: aperture, ar: aril, cl: columella, ec: endocarp, dl: dehiscent line, lo:locule, ov: ovule, sd: secretory duct, st: septum (Bar scale = 250 μ m).

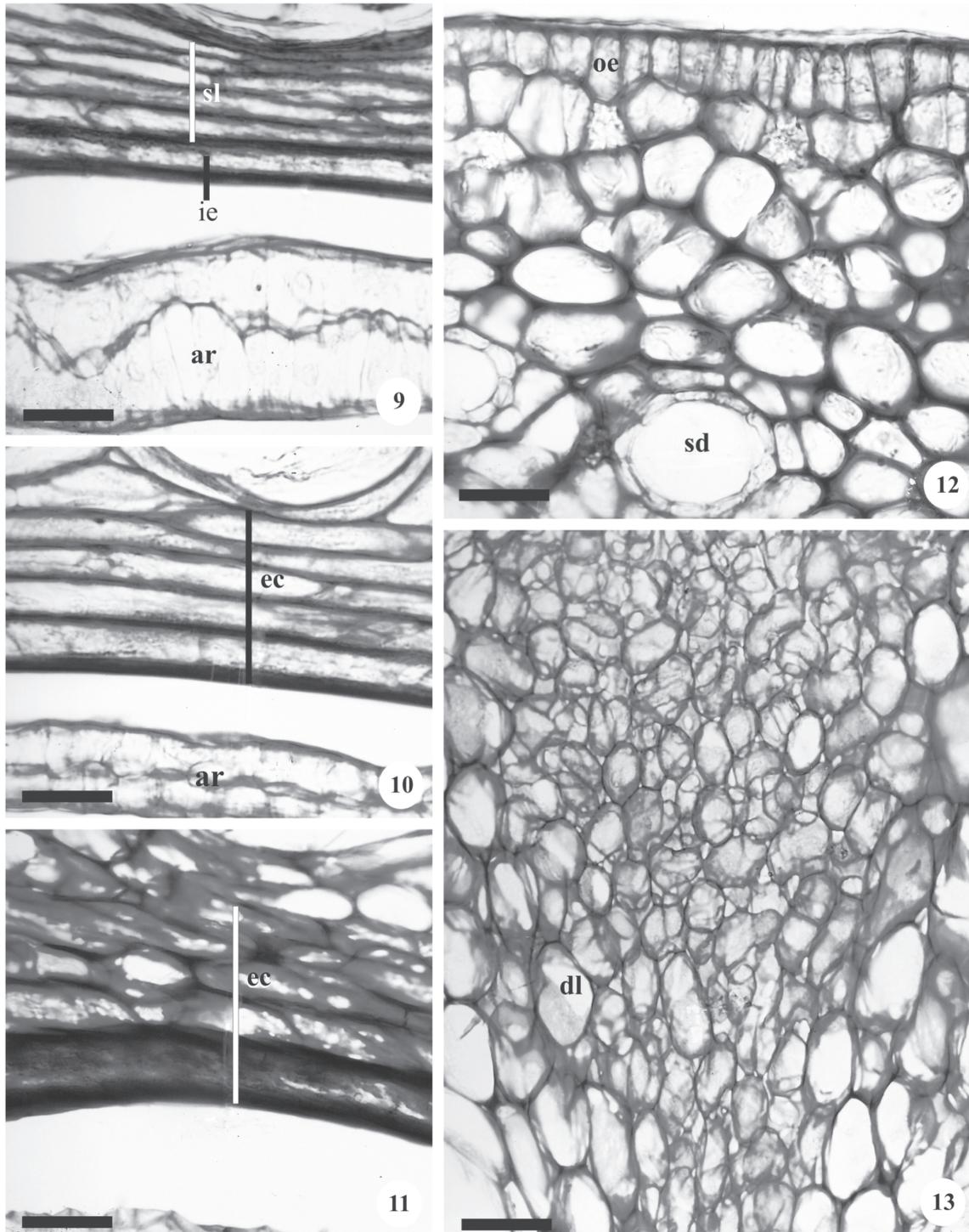
procambial cylinder extends the length of the embryonic axis (Fig. 24).

Discussion

Engler (1888) and Mariz (1974) have classified the fruits of *Clusia* as septicide capsules. However, Barroso *et al.*

(1999) and Stevens (2007a) described the fruits of this genus as septicidal or septifragal capsules. In *C. parviflora* the ontogeny elucidated that the fruit is a septifragal capsule, but to affirm that is a condition to the genus studies with more species are necessary.

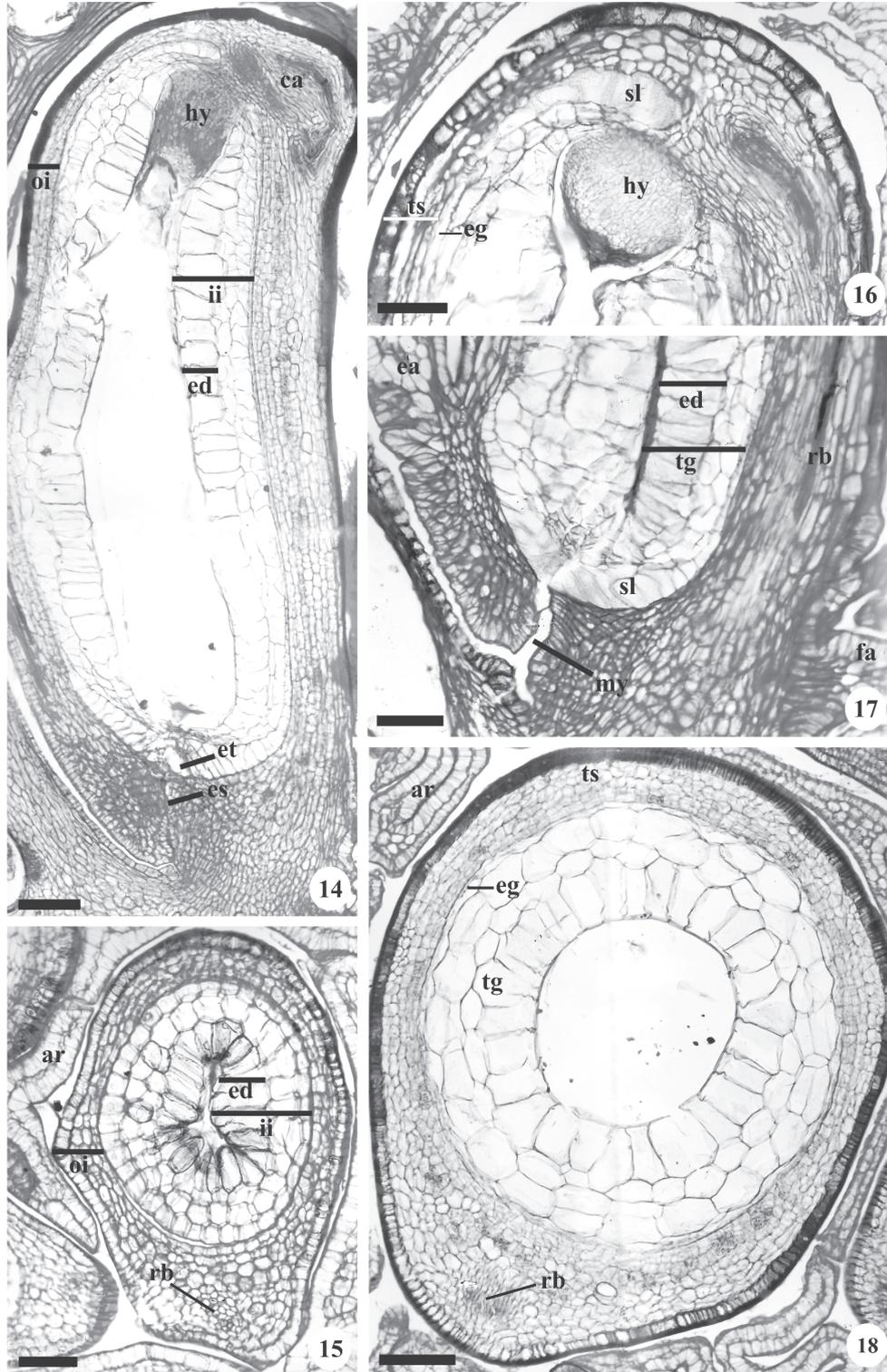
In terms of fruit development, the ovarian structure of *C. parviflora* resembles that of other species of Clusiaceae,



Figures 9-13. *Clusia parviflora* (Sald.) Engler. Transversal sections of the fruit: 9-11. Endocarp development, showing the tangentially elongated cells of the inner and subepidermal layers. 12. Ovarian outer epidermis and subepidermal layers. 13. Detail of the dehiscence line of an immature fruit, evidencing the spongy tissue before the maturation. ar: aril, dl: dehiscence line, ec: endocarp, ie: inner epidermis, oe: outer epidermis, sd: secretory duct, sl: subepidermal layers (Bar scales = 25 μ m (9), 50 μ m (10-13)).

principally due to the occurrence of secretory ducts in the ovarian mesophyll. Corner (1976) also observed ducts in the pericarp of all species of Clusiaceae. Besides this feature is evident in *Platonia insignis* (Clusioidae-

Symphonieae) and *Mammea americana* (Kielmeyeroideae-Calophylleae), which have long and well-ramified ducts with schizogenic origin (Mourão & Beltrati 1995a; 2000). In *Vismia guianensis* (Hypericoideae-Vismieae), these



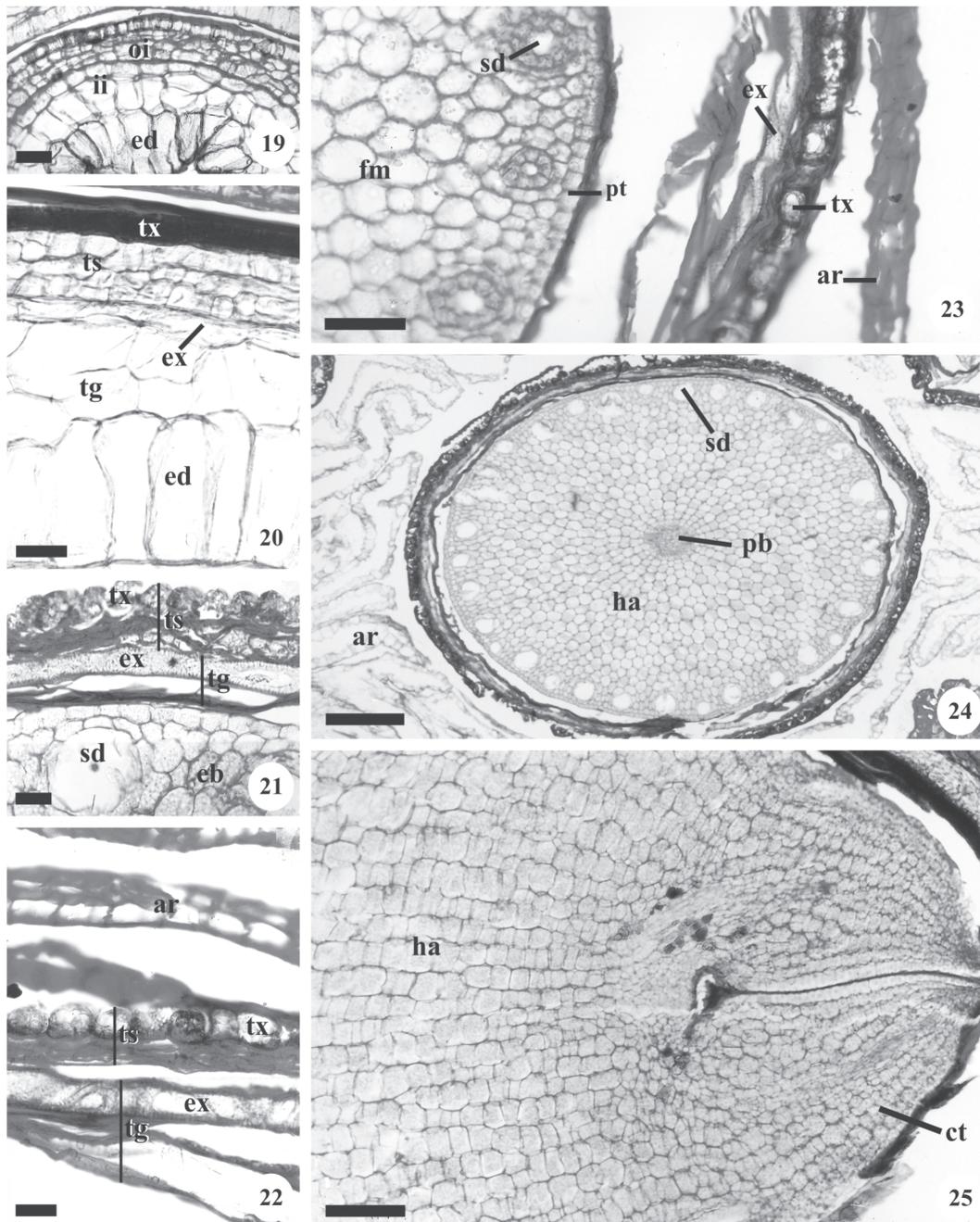
Figures 14-18. *Clusia parviflora* (Sald.) Engler. Longitudinal and transversal section, respectively, of the seed in development. 14-15. Ovule, showing the integument layers. 16-18. Young seed, showing seed coat layers and funicular and exostomal aril. ar: aril, ca: chalaza, ea: exostomal aril, ed: endothelium, eg: exotegmen, et: endostome, es: exostome, fa: funicular aril, hy: hypostasis, ii: inner integument, my: micropyle, oi: outer integument, rb: rapheal bundle, sl: sclereid, tg: tegmen, ts: testa (Bar scales = 100 μ m (14, 18), 50 μ m (15-17))

ducts have a schizogenic origin and their development appears to be schizolysigenous (Mourão & Beltrati 2001).

The definitions of exo-, meso- and endocarp have varied in the literature, although most modern authors prefer to use the terms exo- and endocarp in a broad sense that includes the outer and inner epidermis, respectively, as well as the subepidermal layers (Roth 1977). In *C. parviflora* as in *Vismia guianensis* (Mourão & Beltrati 2001) the exocarp is derived from the outer epidermis of the ovary. In *Mammea*

americana, however, the exocarp originates from the outer epidermis and the first subepidermal layers of the ovarian mesophyll, from which the phellogen is derived, and consequently the periderm (Mourão & Beltrati 2000).

In *C. parviflora*, as in *C. selowiana* described by Corner (1976), lignified cells in the endocarp that were derived directly from tangentially elongated cell layers that define the locule were observed to actively participate in fruit dehiscence. This event probably occurs when the pericarp loses moisture



Figures 19-25. *Clusia parviflora* (Sald.) Engler. 19-22. Integument development in transversal section, showing seed coat transformations. 19. Bitegmic ovule. 20-22. Young, immature and exotegmic mature seed, respectively. 23-24. Immature seed showing the embryo in cross section, evidencing secretory ducts of peripheral and longitudinal distribution and the central procambial cylinder. 25. Mature embryo in longitudinal section, showing the minute cotyledons. ar: aril, ct: cotyledons, eb: embryo, ed: endothelium, ex: exotegmen, fm: fundamental meristem, ha: hypocotyl-radicle axis, ii: inner integument, oi: outer integument, pb: procambium, pt: protoderm, sd: secretory duct, tg: tegmen, ts: testa, tx: exotesta (Bar scales = 25 μ m (19-22), 50 μ m (23, 25), 250 μ m (24)).

at maturation, generating opposing forces between the carpelar sections due to contraction of the endocarp cell walls.

According to Roth (1977), the mechanism of fruit dehiscence is mostly based on active movements brought about by dead or living tissues, whereby two fundamental types may be distinguished: a hygroscopic and a turgor mechanism. The hygroscopic movements generally rely on shrinkage and swelling of walls of dead cells, whereas the turgor mechanisms function with living cells which have highly elastic walls.

In hygroscopic dehiscence Roth (1977) distinguishes two types: hydrochastic and xerochastic. The acting forces of hydrochastic movements rest on water absorption, which cause a swelling of the cell walls so that a swelling pressure is developed, and in xerochastic depend on water losses, resulting in shrinkage of the cell walls. In hydrochastic mechanisms the source of energy therefore lies in the swelling power, whereas in xerochastic movements, it is developed by cohesion forces. To produce a bending of certain pericarp parts, two antagonistically acting layers are generally present which may show different structure of their composing elements, frequently fibers, that may be arranged in different directions so that the cells of one layer cross those of the other layer.

The dehiscence mechanism in *C. parviflora* seems to be a combination of hydrochastic and xerochastic movements, considering that the mostly pericarp cells don't lose water, except to the shrinkage of the lignified cells of the endocarp which have a tangential orientation and can contribute with antagonistic forces responsible for fruit aperture.

Corner (1976) described the occurrence of anatropous and bitegmic ovules in *Allanblackia*, *Calophyllum*, *Caraipa*, *Clusia*, *Garcinia*, *Havetiopsis*, *Mesua*, *Pentadesma*, *Septogarcinia*, *Symphonia*, *Tovomitopsis*, *Tsimatimia* (Clusiaceae), *Cratoxylon*, *Haronga*, *Hypericum* and *Vismia* (Hypericaceae). These characteristics were observed in *C. parviflora* in the present study and were also described in *Platonia insignis* by Mourão & Beltrati (1995a) and in *Vismia guianensis* by Mourão & Beltrati (2001). In *Mammea americana*, however, Mourão & Beltrati (2000) described anatropous and unitegmic ovules.

The ovule structure in *C. parviflora* is similar to that described for all species of *Clusia* described by Corner (1976), especially *Clusia* sp. This author was not certain if this species (which was not identified) really belonged to the genus because of the characteristics of its fruits and seeds.

In *C. parviflora* the inner epidermis of the inner integument has radially elongated cells, which form the endothelium. The presence of an endothelium in ovules of Clusiaceae and Hypericaceae was mentioned in *Hypericum patulum*, *H. mysorensis* (Rao 1957), *Clusia* sp. (Corner 1976), *Platonia insignis* (Mourão & Beltrati 1995a), *Vismia guianensis* (Mourão & Beltrati 2001).

Kapil & Tiwari (1978) defined the integumentary tapetum, or endothelium, as being the inner epidermis of the inner integument of bitegmic ovules, or the only integument in unitegmic ovules. In many plants it has differentiated into a specialized layer of radially elongated cells with dense cytoplasm and prominent and often polyploid nuclei. These authors have recorded the presence of an endothelium in 65 families of dicotyledons, but not in the Clusiaceae.

The presence of tanniferous cells in the chalazal region of *C. parviflora* is in agreement with the definition of hypostasis *sensu stricto* proposed by Von Teichman & Van Wyk (1991). Hypostasis also occurs in *Platonia insignis* (Mourão & Beltrati 1995a).

The seeds of *C. parviflora* are exotegmic. Corner (1976) affirms that seeds of the Hypericoideae (Hypericaceae) appear to be related to those of the Clusioideae-Clusiaceae, due to the presence of an exotegmen with star-shaped, undulating cells with thick cell walls; and the production of phanerocotyledonous embryos. Basta & Basta (1984) described an entirely lignified tegument in the seeds of *Kielmeyera coriacea* (Kielmeyeroideae-Calophylleae) without distinguishing between the testa and tegmen but, likewise, they did not undertake a detailed anatomical study of seed development in this species.

According to Corner (1976) the aril of Clusiaceae may be classified in four types. As proven in the present study in *C. parviflora* occurs the second type, exostomal and funicular aril, that is also present in *Clusia rosea* and *C. sellowiana*, *Tovomita*, *Havetia* and *Havetiopsis* (Corner 1976). This author describes for *Clusia* sp. a fourth type, an exostomal aril combined with funicular lobes but without participation of the raphe-side of the funicle. If other types of aril occur in *Clusia* only additional research with more species can provide the answer.

Stevens (2007a) comments that the seeds of arillate New World Clusiaceae are dispersed by birds, although ants subsequently affect the distribution and germination of primarily bird-dispersed seeds. Studies on dispersal in this genus are important from an ecological point of view.

Detailed chemical analyses of the seeds of *C. parviflora* have not yet been undertaken, although the present study indicated that the main reserve substances in the embryo are lipids, as was also reported by Mourão & Beltrati (1999b) for *Vismia guianensis*. Lipidic substances and phenolic compounds were detected in the embryos of *M. americana* in duct secretory cells as well as in parenchymal idioblasts, although starch was the most abundant reserve overall (Mourão & Beltrati 1999a).

The occurrence of lipidic substances in Clusiaceae seeds has often been reported in the literature (Brandza 1908; Earle & Jones 1962; Vaughan 1970; Basta & Basta 1984; Bentes *et al.* 1986/1987; Adeyeye 1991).

The genus seems to be uniform in the final number of layers in the mature seed coat, being evident the continuous lignified exotegmen and the hypocotylar embryo. In another genus of Clusiaceae, Corner (1976) described this exotegmic

contruction for *Havetiopsis flexilis* only. However, there is uniformity in Clusioideae in the hypocotylar embryo, as pointed out in the research descriptions of Brandza (1908), Guillaumin (1910) and Corner (1976), but occurring in Clusioideae - Garcinieae and Symphonieae (Stevens 2007a).

It should be pointed out that the number of layers in ovule integument, can be a diagnostic characteristic at the specific level, varying in the inner integument from 2 to 3 in the species of the present study, from 6 to 7 in *C. rosea*, from 5 to 7 in *C. selowiana* and 3 in *Clusia* sp. described by Corner (1976). In relation of the outer integument *C. parviflora* shows 3 to 4 layers, being different from *C. rosea* (4 to 5), *C. selowiana* (6 to 8) and *Clusia* sp. (2 to 3).

Considering that few studies have closely examined Clusiaceae fruits and seeds, and in light of the characteristics cited in the literature as either ancestral or derived as related to these organs, it can be concluded from the infra-familial treatment of this family (Stevens 2007a; b) that Kielmeyeroideae, Hypericoideae (Hypericaceae) and Clusioideae (Clusiaceae) demonstrate more ancestral characteristics, as they have mostly dehiscent fruits (capsule type), arilate and exotegmic seeds, and embryos with cotyledons varying from distinct to very reduced; while Clusioideae (Garcinieae and Symphonieae) have characteristics considered derived, including indehiscent fruits (berry or drupe), seeds without an aril, integuments not well differentiated or mesotestals, and hypocotylar or conferruminate embryos.

It should be pointed out that the establishment of relationships among the subfamilies of Clusiaceae using fruit and seed characteristics is extremely difficult due to a lack of developmental studies in a majority of the species.

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