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Morphology and anatomy of the developing fruit and seed of *Dalechampia stipulacea* Müll. Arg. (Euphorbiaceae)

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ABSTRACT. In forest remnants of Maringá, Paraná, Brazil, there is abundance of the liana species, with little studied reproductive structures, morphologically and anatomically. Among these species occurs *Dalechampia stipulacea* Müll. Arg., which is the object of the present study. It is a Euphorbiaceae with pseudanthium and trichomes that cause irritation of the skin. The fruits and seeds were fixed and cut freehand and in a rotation microtome, according to the usual techniques. The fruit is a schizocarp tricocca with loculicidal and septicidal dehiscence. The mature pericarp presents sclerenchymatous middle mesocarp and endocarp that originate from meristems installed in the ovary mesophyll and epidermis. The inner mesocarp is constituted by a layer of macrosclereids of subepidermic origin. The seed originates from anatropous, bitegmic and crassinucelate ovule; it is exotegmic and albuminous. The seed presents structural characteristics verified in Acalyphoideae, except for the mesotegmen vascularization.

Key words: *Dalechampia*, Euphorbiaceae, fruit, seed, ontogenesis.

RESUMO. Morfologia e anatomia do fruto e semente em desenvolvimento de *Dalechampia stipulacea* Müll. Arg. (Euphorbiaceae). Em remanescentes florestais de Maringá, Paraná, Brasil, há abundância de espécies de lianas, com estruturas reprodutivas pouco estudadas morfoanatomicamente. Dentre as espécies, *Dalechampia stipulacea* Müll. Arg., objeto deste estudo, é uma Euphorbiaceae que se destaca pelos pseudantos e tricomas urticantes. Os frutos e sementes foram fixados e secionados à mão livre e em micrótomo de rotação, segundo técnicas usuais. O fruto é esquizocarpo tricoca, com deiscência loculicida e septicida. O pericarpo maduro apresenta mesocarpo mediano e endocarpo esclerenquimático, originados de meristemas instalados no mesofilo e na epiderme do ovário. O mesocarpo interno é constituído por camada de macrosclereídes de origem subepidérmica. A semente, que provém de óvulo anátropo, bitegumentado e crassinucelado, é exotégmica e albuminosa; apresenta caracteres estruturais verificados em Acalyphoideae, exceto pela vascularização do mesotégmen.

Palavras-chave: *Dalechampia*, Euphorbiaceae, fruto, semente, ontogênese.

Introduction

The structural investigations of fruits and seeds have great usefulness in biology, preservation research, taxonomy and ecological study of plants. In Paraná, especially in the Northwest region, the original forests have been decimated, being preserved less than 1% of the forest remnants whose fruits and seeds were little studied. Studies of forest remnants of Maringá, Paraná have shown that anthropic action may cause the abundance of lianas that frequently spread their canopies over those of the trees and shrubs. The exaggerating development of the lianas may interfere in the growth of the trees and shrubs, but may also serve as food for birds and others animals.

Dalechampia stipulacea Müll. Arg. is a liana, belonging to the Euphorbiaceae family, and it stands out for their pseudantha and trichomes that cause irritation of the skin. This family presents ovules and seeds which were studied widely by Tokuoka and Tobe (1998; 2002; 2003) with systematic implications. These authors showed that five following characters are likely to be useful for comparison between and within subfamilies: a) whether the inner integument is thick or thin; b) the presence or absence of vascular bundles in the inner integument; c) whether ovules or seeds are pachychalazal or not; d) whether seeds are arillate or not; and e) whether an exotegmen is fibrous or not. Tokuoka and Tobe (2003) examined ovules and seeds of *Dalechampia caperonioides* Baill., *Dalechampia scandens* L. e *Dalechampia tiliifolia* Lam. showing that the ovules are bitegmic, the inner integument has no vascular bundles, and the seeds are exotegmic. Review of morphological and anatomical studies about Euphorbiaceae seeds on base of a literature survey showed the following investigations: *Acalypha rhomboidea* Raf. (LANDES, 1946), *Ricinus communis* L. (SINGH, 1954), *Manihot utilissima* Pohl. (TOLEDO, 1963b), *Croton bonplandianum* Baill. (SINGH; CHOPRA, 1970), *Micrantheum* species (BERG, 1975), *Croton floribundus* Spreng. and *Croton urucurana* Baill. (PAOLI et al., 1995), *Jatropha elliptica* Müll. Arg. (AÑES et al., 2005), *Manihot caerulescens* Pohl., and *Manihot tripartita* Müll. Arg. (OLIVEIRA, 2007).

Concerning the Euphorbiaceae pericarp that is scarcely investigated (TOLEDO, 1963b; BERG, 1975; OLIVEIRA, 2007), the formation of sclerenchymatous tissue may be considered as one of the most important events in the ontogeny of dehiscent dry fruits.

In that way, the main purpose of this investigation was the morphological and anatomical analysis of the developing fruit and seed of *Dalechampia stipulacea*. This study still includes: a) the discussion about the origin and differentiation of the sclerenchymatous tissue that occurs in dry fruits of Euphorbiaceae; and b) to evaluate whether the ovule and seed of this species present the basic characters of Acalyphoideae and Plukenetieae that were formulated by Tokuoka and Tobe (2003).

Material and methods

The floral buds, flowers and fruits of different developmental stages of fruit were collected at the "Bosque dos Pioneiros" which is a forest remnant situated in the city of Maringá, Paraná State, Brazil. Voucher materials were deposited at the UEM Herbarium, collection number: *Dalechampia stipulacea* Müll. Arg. – Brasil. Paraná: Maringá, Bosque dos Pioneiros, 08-VIII-2005, K. S. M. Mourão 11720 (HUEM); 01-VII-2005, L. A. Souza 11746 (HUEM).

The morphological analysis of the fruits and seeds was made in stereoscope microscope. The seed study was made in longitudinal and cross-sections. The morphological description of the developing fruits and seeds was based on Corner (1976) and Roth (1977).

The collected material was fixed in FAA 50, dehydrated using an ethyl alcohol series, and embedded in historesin (GERRITS, 1991). Longitudinal and cross-sections were made in rotation microtome and stained in toluidine blue 0.05% (O'BRIEN et al., 1964) and mounted in Permount resin. Freehand sections of developing pericarp and seed were also made, and stained with the astra blue and safranin (SOUZA et al., 2005). Specific microchemical test was done for lignin (phloroglucin test) (JOHANSEN, 1940).

Illustrations were prepared using an optical microscope (Wild M20) equipped with a reflex camera. Photographs were taken with optical microscope (Olympus BX50) and the digital camera (Canon Power Shot A95) and subsequently using the software Zoom Browser EX 4.6. All samples were prepared on the same micrometric scale.

Results

Pericarp structure

Ovary

The ovary wall of the floral bud (Figure 1A) is formed by uniseriate outer and inner epidermis. The outer epidermis consists of cuboid cells larger than those of the inner epidermis. The mesophyll is parenchymatous with 4-5 cell-layers. In floral bud relatively of large size the outer epidermis presents trichomes (Figure 1B) and stomata.

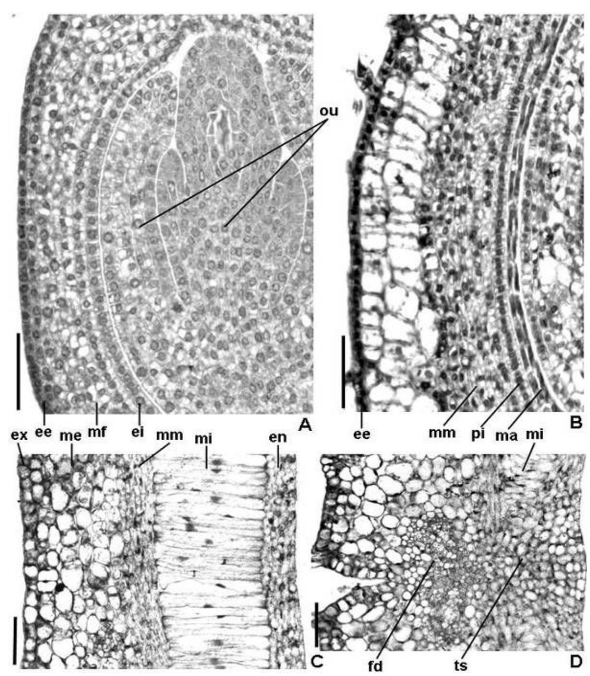

Figure 1. Anatomical details of the developing pericarp of *Dalechampia stipulacea*. A – Longitudinal section of bud floral showing wall ovary and ovule. B – Longitudinal section of the wall ovary of floral bud. C – Immature pericarp in cross-section. D – Dorsal region of immature fruit in cross-section. (ee = outer epidermis; ei = inner epidermis; en = endocarp; fd = dorsal vascular bundle; ma = adaxial meristem; me = outer mesocarp; mf = mesophyll; mi = inner mesocarp; mm = middle meristem; ou = ovule; pi = precursor of inner mesocarp; ts = separation tissue) Bars = 50 μm.

The trichomes are unicellular tector with thick-walled. The glandular trichomes are constituted by a central cell armed with a sharppointed, surrounded by several epidermal jacket-cells. In pre-anthesis, the middle portion and the inner epidermis of the ovary differentiate in two meristems (Figura 1B) (middle meristem and adaxial or ventral meristem).

After anthesis, the ovary presents uniseriate outer epidermis and mesophyll with three tissue regions: 1) An outer parenchymatous region, with thin-walled cells that vary in size and shape, and may present druses; 2) A middle region that originates from the middle meristem and consists of elongated cells that are oriented obliquely or transversely to the longitudinal axis of the ovary; and 3) An inner region that is uniseriate and has short palisade-like cells. The inner epidermis is constituted by a tissue that originates from the adaxial meristem, and it shows cells elongated tangentially.

Developing pericarp

The immature pericarp (Figure 1C) maintains the same number of cell layers of the ovary. The exocarp is uniseriate and presents stomata and pluricellular glandular trichomes. The mesocarp consists of three tissue regions: the outer parenchymatous mesocarp with druse idioblasts; the middle mesocarp with elongated and thin-walled cells; and the inner mesocarp (originated from middle meristem) with palisade-like cells. The endocarp (originated from adaxial meristem) is similar to the middle mesocarp. In the dorsal region of the pericarp (Figure 1D) occur a small reentrance, a collateral vascular bundle and the abscission (separation) tissue.

As the pericarp nears ripening (Figures 2A, B and C), the exocarp is uniseriate and consists of polyhedral cells with straight anticlinal walls, and thick outer periclinal walls. The exocarp presents tector and glandular trichomes, and paracytic stomata.

The outer mesocarp is formed of spongy parenchyma with druses and collateral vascular bundles. The middle mesocarp is sclerenchymatous with fibers oriented longitudinally or obliquely to the longitudinal axis of the fruit. The inner mesocarp consists of macrosclereids with lignified thick-walled; the macrosclereids are arranged more or less perpendicular to middle mesocarp and endocarp cells. The endocarp is also sclerenchymatous with fibers oriented similar to the middle mesocarp.

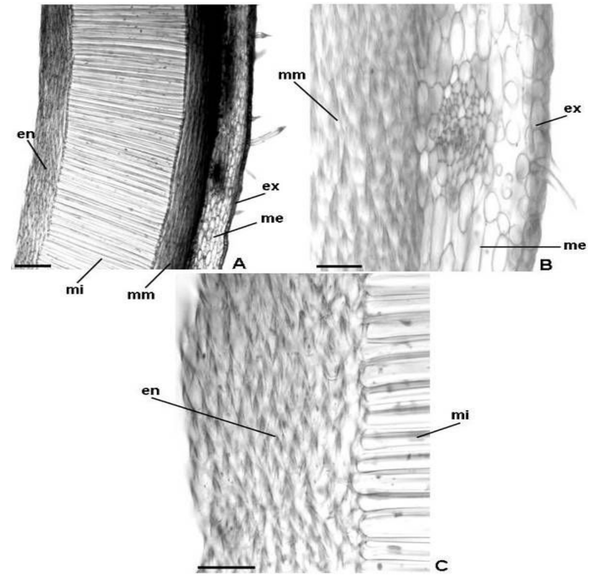

Figure 2. Anatomical details of mature pericarp of *Dalechampia stipulacea*, in cross-sections. A – Pericarp. B – Exocarp, outer mesocarp and middle mesocarp. C – Inner mesocarp and endocarp. (en = endocarp; ex = exocarp; me = outer mesocarp; mi = inner mesocarp; mm = middle mesocarp) Bars = 150 μm (A) and 50 μm (B, C).

Septum and carpophore

The septum originates from cohesion of the carpel walls. Most of the septum presents similar structure to the remaining of the carpel, except for the presence of spongy parenchyma located middling in the septum (Figures 3A and C; 4A and B).

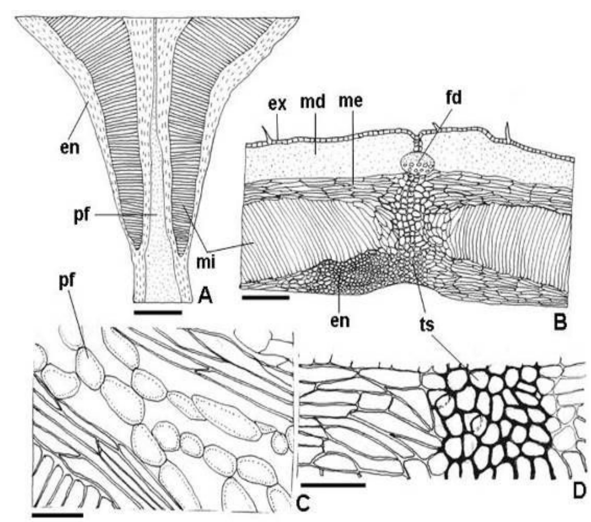

Figure 3. Cross-sections of the septum and abscission region of *Dalechampia stipulacea*. A – Septum diagram. B – Abscission region (dorsal) diagram. C – Anatomical detail of the septum showing spongy parenchyma and endocarp. D – Detail of the dorsal carpel region showing abscission tissue. (en = endocarp; ex = exocarp; fd = dorsal vascular bundle; me = outer mesocarp; mi = inner mesocarp; mm = middle mesocarp; pf = spongy parenchyma; ts = abscission tissue) Bars = 300 μm (A), 150 μm (B), 50 μm (C, D).

In the central region of the septum or carpophore occur ventral vascular bundles, parenchyma and sclerenchyma. The carpophore is separate from the septum for the abscission tissue (Figure 4B).

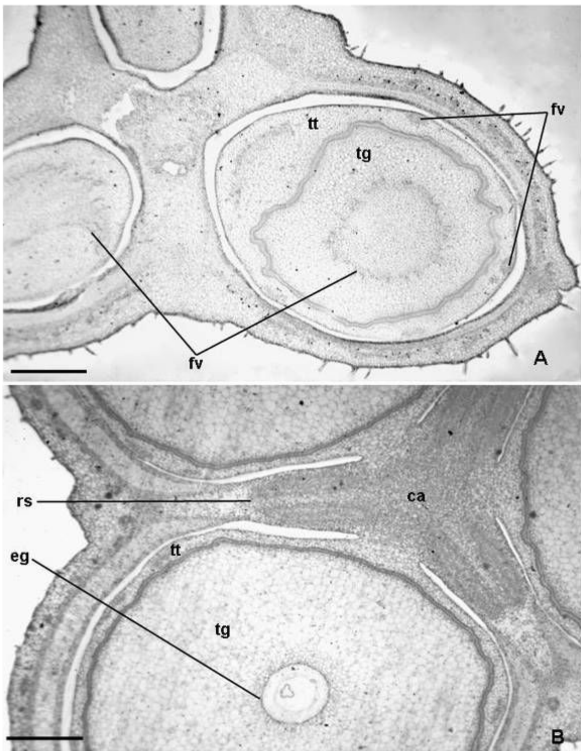

Figure 4. Cross-sections of *Dalechampia stipulacea* immature fruits showing vascularization of the inner seed integument (A), and abscission regions in the septum (B). (ca = carpophore; eg = endotegmen; fv = vascular bundles; rs = abscission region in the septum; tg = tegmen; tt = testa) Bars = 70 μm.

Dehiscence region

The fruit presents two dehiscence regions: dorsal dehiscence (Figuras 3A and B; 5A and B), and other one that occurs along the carpel sutures (Figuras 3A, 4B and 5A). The both dorsal dehiscence and suture (ventral) dehiscence may be identified in immature and mature fruits, among other structural characters, for a groove verified on the pericarp surface. In the dorsal dehiscence (Figuras 3B and D) the exocarp and outer mesocarp undergo few modifications, but the middle mesocarp and endocarp fibers, and macrosclereids are substituted gradually by isodiametric sclereids. In the dorsal dehiscence region is pointed out a large vascular bundle of each carpel. In the ventral suture dehiscence (Figures 3A and C) abscission tissue among the carpel walls occurs. Between the septum and the carpophore there is also abscission tissue (Figure 4B).

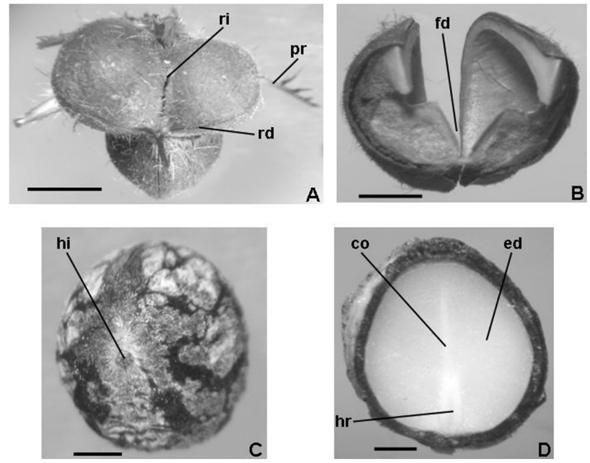

Figure 5. Mature fruit and seed of *Dalechampia stipulacea*. A – Tricocca fruit. B – Open coccum. C – General aspect of seed. D – Seed in longitudinal section. (co = cotyledons; ed = endosperm; fd = opening along mid-region of the carpel; hi = hilum; hr = hypocotyl/radicle axis; pr = perigone; rd = dorsal region of the carpel; ri = ventral suture) Bars = 2,5 mm – 1,6 mm – 1,0 mm – 1,0 mm, respectively.

Seed structure

Ovule

The seed originates from anatropous, bitegmic, crassinucellate ovule. Both ovule integuments are pluriseriate, being the inner one with larger number of cell layers (Figures 6A and B). The integuments possess outer and inner epidermis of cuboid to prismatic cells with relatively dense cytoplasm and a large nucleus. In the central region of the septum or carpophore occur ventral vascular bundles, parenchyma and sclerenchyma. The carpophore is separate from the septum for the abscission tissue (Figure 4B).

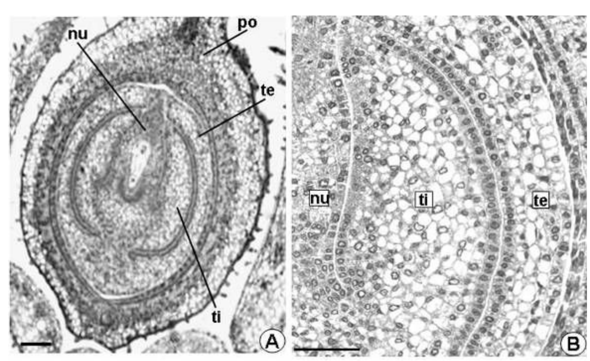

Figure 6. *Dalechampia stipulacea* ovule in longitudinal section. A – General aspect of the ovule. B – Anatomical detail of the nucellus and integument. (nu = nucellus; po = ovary wall; te = outer integument; ti = inner integument) Bars = 100 μm and 50 μm.

The nucellus (Figures 6A and B) is quite well developed and broad with polyhedral and thin-walled cells. Subepidermal and apical cells of the nucellus show evidences of periclinal division.

Through division of the cells in the micropylar end of the nucellus, a cell proliferation is developed that extends beyond the micropyle (Figure 6A). The nucellar cells that limit the embryo sac are elongated tangentially.

In the chalazal region occurs hypostase which presents strongly staining and thick-walled cells.

Developing seed

In the developing seed both integuments are multiplicative but the tegmen presents larger number of cell layers. The exotesta (Figure 7A) stays uniseriate, in which the cells become vacuolate and maintain thin-walled. The mesotesta (Figure 7A) is parenchymatous presenting collateral vascular bundles and druse idioblasts. The uniseriate endotesta (Figures 7A and B) is formed by columnar cells. The exotegmen (Figure 7A) consists of cells that undergo elongation, and a secondary thickening of the wall-cell. The mesotegmen (Figure 7B) is parenchymatous, and undergo considerable increase of the layer number and size of the cells (Figure 4B). The endotegmen (Figure 4B) presents small and tabular cells which are ultimately crushed. The endosperm is nuclear (Figure 4B). The basal part of the tegmen undergoes intercalary growth and vascularization that comes from the chalaza (Figure 4A), characterizing the formation of an endopachychalaza.

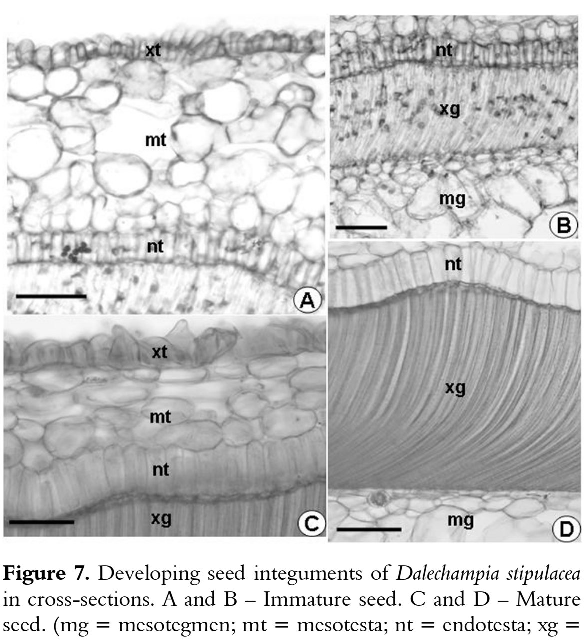

Figure 7. Developing seed integuments of *Dalechampia stipulacea* in cross-sections. A and B – Immature seed. C and D – Mature seed. (mg = mesotegmen; mt = mesotesta; nt = endotesta; xg = exotegmen; xt = exotesta) Bars = 50 μm.

The mature seed (Figures 7C and D) is bitegmic. The epidermal and uniseriate exotesta presents papillose cells. The mesotesta consists of pluriseriate parenchyma, varying the amount of cell layers. The mesotesta parenchyma is spongy with thin-walled cells. The collateral vascular bundles occur in this parenchyma. The endotesta presents inner epidermis with thin-walled palisade-like cells.

The tegmen (Figure 7D) consists of exotegmen with lignified thick-walled macrosclereids arranged in palisade. The mesotegmen is parenchymatous with druse idioblasts, and cells that show variation in shape and size. The mesotegmen presents vascular supply in which the hilar bundle branches, it runs the mesotegmen partially, and it reaches the chalaza. The endotegmen is crushed. The hypostase is still observed in the mature seed.

Fruit and seed morphology

The mature fruit (Figures 5A and B) is simple, 3-carpellate, dry, dehiscent, of brown color, hairy, and tricocca schizocarp type. Each coccum is globose and presents a groove middling. The dehiscence occurs initially through separation of the cocca, and later each coccum opens along the dorsal suture or mid-region of the carpel. The laciniate perigone persists in the fruit.

The mature seed (Figures 5C and D) is also globose, rugose (due to the collapse of the testa tissues), brown dark and mottled with white patches. The hilum has rounded outline, and the micropylar region and raphe may be observed. The seed is albuminous with straight embryo and thin cotyledons.

Discussion

During the differentiation of the ovary in the pericarp of *Dalechampia stipulacea* the most important stage in this process was the meristematic action verified in the ovary wall still in pre-anthesis. In the developing fruits of Fabaceae (Leguminosae) and Rutaceae usually occurs the installation of ventral or adaxial meristem which originates from the ovary epidermis and/or mesophyll (ROTH, 1977; SOUZA, 2006). In *Tabebuia chrysotricha* (Mart. ex DC) Standl. (Bignoniaceae) did not occur meristem on either carpel surface, only in the middle region, among the vascular bundles of the mesophyll (SOUZA et al., 2005). Oliveira (2007) reported the occurrence of two meristems in the developing pericarp of *Manihot caerulescens* and *Manihot tripartita*, being an adaxial (epidermal) meristem and other subadaxial (subepidermal) one. In the *Dalechampia stipulacea* developing fruit are also formed two meristems in the ovary wall: an adaxial or ventral of epidermal origin, and the other, differently of the two species of *Manihot*, with origin in the middle region of the mesophyll.

The pericarp may be arbitrarily divided into layers, referred to as epicarp (outer layer), mesocarp (middle layer), and endocarp (inner layer) (EAMES; MACDANIELS, 1947; SPJUT, 1994), or may involve ontogenetic study of the fruit wall (ROTH, 1977; SOUZA, 2006). In ontogeny study on *Manihot utilissima* fruit, Toledo (1963a and b) considered that the endocarp originated from the subepidermal parenchyma, and it is composed of sclereids arranged into three regions. In the *Dalechampia stipulacea* mature pericarp in the same way occur three sclerenchymatous regions well defined ontogenetically, but with different denominations and cell composition from the established for *Manihot utilissima*. Therefore, *Dalechampia stipulacea* presents two sclerenchymatous mesocarp regions (one of fibers and another of macrosclereids) originated from the ovary mesophyll, and the sclerenchymatous endocarp (with fibers) that is originating from the inner epidermis. On the other hand, the *Manihot caerulescens* and *Manihot tripartita* fruits also present two regions in the sclerenchymatous mesocarp, being a constituted of gelatinous fiber-sclereids and another of brachysclereids; the endocarp possesses either collenchyma or fiber-sclereids (OLIVEIRA, 2007).

The dehiscence system of the dry fruits is complex could involve the pericarp structure, the tissue arrange in the pericarp, and the occurrence of abscission or separation tissue (FAHN; ZOHARY, 1955; ROTH, 1977; SOUZA, 2006). For an active dehiscence of the leguminous pod, two factors are necessary: (1) the crossing of the sclerenchymatous cells or/and the crossing of their cellulose micelles; (2) the presence of a separation tissue extending in the region of the suture from the inner to the outer epidermis (FAHN; ZOHARY, 1955). In Euphorbiaceae each mericarp separates from the adjacent mericarps as well as from the central column, when the fruit dries out, dehiscing abruptly along the dorsal suture, so that the seeds are thrown far away (ROTH, 1977). The *Dalechampia stipulacea* dry fruit dehisces by a split between the carpels, isolating a carpophore and three cocca, and later each carpel or coccum opens up for a split along the dorsal region. No doubt, the crossing apparatus that is formed by sclerenchymatous tissue of mesocarp and endocarp, and the separation tissue confined to the dorsal and ventral regions of the carpel are active factors in the dehiscence process of the *Dalechampia stipulacea* fruit.

Acalyphoideae are the largest and most complex subfamily, comprising 116 genera and about 2150 species (includes *Dalechampia stipulacea*), and always present bitegmic ovules/seeds (TOKUOKA; TOBE, 2003). According to these authors the inner integument is multiplicative in most of the species. The inner integument of the *Dalechampia stipulacea* ovule or seed also is multiplicative producing a striking growth in thickness.

Dalechampia stipulacea registers collateral vascular bundles in the testa. According to Tokuoka and Tobe (2003), that investigated 80 genera of Acalyphoideae, 11 genera (besides *Dalechampia*) presented post-chalazal vascular branches.

The hypostase that was observed in *Dalechampia stipulacea* ovule and seed was registered for Euphorbiaceae (BOUMAN, 1984). The hypostase is situated above the chalazal vasculature and, depending on the form of the nucellar base, it may be present as cluster of cells, or a disk- or cuplike cell (BOUMAN, 1984). The literature registers many functions for the hypostase: it may act as a barrier tissue for stopping the encroachment to the embryo sac; it may connect the vascular supply with the embryo sac and, thus, facilitate transport of nutritional material; it may be responsible for the production of certain enzymes or hormones, among others (TILTON, 1980; BOUMAN, 1984).

None of the Acalyphoideae species examined has vascular bundles in the inner integument, besides in *Dalechampia caperonioides*, *Dalechampia scandens* e *Dalechampia tiliifolia* (TOKUOKA; TOBE, 2003). In fact, Tokuoka and Tobe (1998; 2002) verified that the inner integument has no vascular bundles in all the Euphorbioideae genera, and in few genera of Crotonoideae. *Dalechampia stipulacea* presents the basal part of the tegmen which develops by intercalary growth, with few vascular bundles extend from the chalaza by postchalazal branching. This observation is contrary to interpretation in which Acalyphoideae and Dalechampiinae has not vasculature on inner integument. For Werker (1997) both integuments of *Dalechampia* may be vascularized (the vascular bundles branch to the tegmen from the chalazal bundles).

The proliferation of the basal part of *Dalechampia stipulacea* tegmen may be considered strictly as pachychalaza (TOKUOKA; TOBE, 2003), and referred as tegmic pachychalaza (CORNER, 1976) or endopachychalaza (BOESEWINKEL; BOUMAN, 1984). It is stood out, however, that Tokuoka and Tobe (2003) did not register pachychalaza for ovules (seeds) of Dalechampiinae species examined.

The *Dalechampia stipulacea* seed is exotegmic following the basic structural pattern of Euphorbiaceae species (CORNER, 1976).

Exotegminal palisade occurs on many families, among the ones which Euphorbiaceae (DAHLGREN, 1991).

According to the seed characters of Acalyphoideae, *Dalechampia stipulacea* seed presents the general structural of the ovules and seeds referred by Tokuoka and Tobe (2003) for the subfamily. However, noticeable differences exist among *Dalechampia stipulacea* and Acalyphoideae species examined by these authors. Comparisons showed that *Dalechampia stipulacea* has exotegminal palisade (macrosclereids) no observed in the tribes Clutieae, Chaetocarpeae, Pereae, Dicoelieae and Galearieae. The ovule/seed outer integument of *Dalechampia stipulaceae* with vascular bundles just occurs in the subtribe Dalechampiinae (tribe Plukenetieae). With reference to the vascularization of the *Dalechampia stipulacea* inner integument there is no mention of this character in the Acalyphoideae ovules/seeds. In the same way, the endopachychalaza presence verified in *Dalechampia stipulacea*, it was not verified by Tokuoka and Tobe (2003) for species of Dalechampiinae.

Acknowledgments

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