Ontogeny and structure of the pericarp and the seed coat of *Miconia albicans* (Sw.) Triana (Melastomataceae) from "cerrado", Brazil

PRISCILA ANDRESSA CORTEZ[1] and SANDRA MARIA CARMELLO-GUERREIRO[1,2]

ABSTRACT – (Ontogeny and structure of the pericarp and the seed coat of *Miconia albicans* (Sw.) Triana (Melastomataceae) from "cerrado", Brazil). *Miconia albicans* fruit and seed coat ontogeny were described under light microscope. The samples were fixed in formalin-aceto-alcohol (FAA), neutral-buffered formaldehyde solution (NBF) and formalin-ferrous sulphate (FFS) solutions, embedded in plastic resin, sectioned at 10 μm and stained with Toluidine Blue. Specific dyes and/or reagents were used for the microchemical tests. The ovary is semi-inferior and the indehiscent, fleshy globose berries are originated mainly from the development of the inferior portion of the ovary. The immature pericarp is mainly parenchymatous with some sclereids, druse crystal and phenolic-like compounds idioblasts widespread in the mesocarp. In the mature pericarp, the endocarp cells are often collapsed, the mesocarp is thick with cells more or less turgid, and the sclereids, the druses and the phenolic-like compound idioblasts are almost absent. The ovules are anatropous, bitegmic and crassinucellate, and the zig-zag micropyle is formed by both the exostome and the endostome. The mature seed is pyramidal-elongated in shape, exalbuminous and testal. The raphal part occupies about 40% of the seed coat total length and had the mechanical layer derived from its inner layer. The antiraphal side is non-multiplicative and the exotesta, mesotesta and endotesta are differentiated into a sclerotic layer, with the exotesta being the mechanical one. The tegmen is absent.

Key words - anatomy, fruits, Melastomataceae, *Miconia*, ontogeny

RESUMO – (Ontogenia e estrutura do pericarpo e do envoltório da semente de *Miconia albicans* (Sw.) Triana (Melastomataceae) do cerrado, Brasil). A ontogenia dos frutos e das sementes de *M. albicans* foi descrita sob microscopia de luz. Os materiais foram fixados em soluções de formalina – ácido acético – álcool etílico 50% (FAA), formalina neutra tamponada (FNT) e sulfato ferroso em formalina (SFF), embebidos em resina plástica, seccionados a 10 μm de espessura e corados com Azul de Toluidina. Corantes e/ou reagentes específicos foram usados para os testes microquímicos. O ovário é semi-ínfero, e os frutos são bagas indeiscentes, originadas em sua maior parte a partir do desenvolvimento da porção ínfera do ovário. O pericarpo imaturo é principalmente parenquimático, com esclereídes, idioblastos cristalíferos e com compostos fenólicos no mesocarpo. No pericarpo maduro as células do endocarpo estão freqüentemente colapsadas, o mesocarpo é espesso, com células túrgidas, e as esclereídes e os idioblastos cristalíferos e com compostos fenólicos estão em pequena quantidade. Os óvulos são anátropos, bitegumentados e crassinucelados, e a micrópica, em zig-zag, é formada pelo exóstoma e pelo endóstoma. A semente madura é piramidal-alongada, exalbuminosa e testal. A porção rafeal ocupa aproximadamente 40% do comprimento total da semente e possui a camada mecânica derivada de suas camadas internas. A porção anti-rafeal é não-multiplicativa e possui a exotesta, a mesotesta e a endotesta diferenciadas em camada mecânica (esclerótica). O tégmen é ausente.

Palavras-chave - anatomia, frutos, Melastomataceae, *Miconia*, ontogenia

Introduction

Melastomataceae Juss. is one of the richest and most abundant families among Angiospermae with nearly 4,570 species and 150-166 genera [excluding Memecylaceae, a sister group according to Renner (1993) and APG II (2003)]. Flowers are bisexual, radially symmetric, and diplostemonous, and stamens often have enlarged and/or appendaged connectives.

About 2,150-2,350 melastome species of 38 genera have berries, and 2,000-2,200 species of 112 genera have capsules as fruit type (Clausing & Renner 2001). This family is well represented in "Cerrado", and several species are specially important in the recovery of degraded areas due to their pioneer character, presence in the local flora and resistance to pollutants (Pompéia *et al.* 1989). Moreover, zoocory, specially ornithocory, are common dispersal syndromes in the "Cerrado" biome (Pinheiro & Ribeiro 2001), and the fruits and seeds of some species of Melastomataceae, such as *Miconia*, are often mentioned as important diet items of birds (Stiles & Rosselli 1993, Gridi-Papp *et al.* 2004), rodents (Magnusson & Sanaiotti 1987) and primate (Galetti & Pedroni 1994).

1. Universidade Estadual de Campinas, Instituto de Biologia, Departamento de Botânica, Caixa Postal 6109, 13083-970 Campinas, SP, Brasil.
2. Corresponding author: smcg@unicamp.br

Lack of detailed ontogenetical studies of flowers, fruits, and seeds of angiosperms has generated difficulty in fruit classification and in the correct description of the structures that cover the seeds (Spjut 1994). Anatomical studies about reproductive organs of melastome are scarce mainly when we consider the remarkable diversity and distribution of their species. Examples from close relatives of Melastomataceae suggest that critical morphological homology assessments are needed if fruit characters are to be used in phylogenetic analyses of this family (Clausing *et al.* 2000). For Melastomataceae, a study carried out by Clausing *et al.* (2000) about fruit anatomy and morphology of 85 species, mainly from palaeotropical tribes, showed a notable heterogeneity of capsules and berries. The morpho-anatomical survey together with the evidence from combined *rbc*L, *ndh*F, and *rpl*16 sequence data suggests that both fruit types may have evolved several times within the family, so the use of berries as a supposed synapomorphy of Blakeeae, Dissochaeteae, and Miconieae, for example, resulted in the unnatural grouping of a large number of palaeotropical and neotropical genera (Clausing & Renner 2001).

The study of seed morphology and anatomy has provided taxonomic, evolutionary and ecological insights in a number of angiosperms groups. In Melastomataceae, the size and the external surface of the small seeds are considered important features in tribal and in general distinctions (Whiffin & Tomb 1972, Corner 1976, Michelangeli 2000).

In the present study, the fruit and the seed coat ontogeny of *M. albicans* were described. This shrubby species occurs in nearly all Brazilian states, and it is specially abundant in "Cerrado" areas; its individuals have pentamerous and diplostemonous flowers aggregated in terminal scorpioid panicles, semi-inferior and trilocular ovary with axilar placentation, and many seeded berry fruits with a jade-green color when ripened (Goldenberg 2004).

Material and methods

This study was carried out in the "Fazenda Palmeira da Serra", a Private Reserve of "cerrado" located in Pratânia municipality, and in the "cerrado" area of the "Laboratório Nacional de Luz Síncrotron" (LNLS), located in Campinas municipality, both in the State of São Paulo, Southeastern Brazil. *Miconia albicans* flowers, fruits and seeds, in several stages of development, were collected from at least five distinct individuals in each area. Voucher specimens were deposited in Herbarium UEC ("Universidade Estadual de Campinas") (UEC 130.141 and 130.114), as representative of the two populations. A morphological-anatomical study was carried out from longitudinal and cross-sections from

fresh and fixed materials. Formalin-aceto-alcohol (FAA) (Johansen 1940), neutral-buffered formaldehyde solution (NBF) (Lillie 1954) and formalin-ferrous sulphate (FFS) (Johansen 1940) were used as fixing solutions.

Morphological characteristics were described and illustrated from ripe fruits and seeds, 100 unities each, sampled from all individuals collected. The unities were individually measured by using a digital caliper and weighed in analytical balance. Both mean and standard deviations were recorded. Illustrations were made with stereomicroscope and the scales were obtained in the same optical conditions.

Anatomical characteristics were described from the samples which were fixed and embedded in plastic resin (Gerrits & Smid 1983). The blocks were sectioned at 10 μm on a rotary microtome with steel knives type C. The sections were stained with Toluidine Blue 0.05% in acetate buffer with pH 4.7 (O'Brien *et al.* 1964). For the microchemical tests, the non-stained sections were submitted to specific dyes and/or reagents, such as Lugol solution (Jensen 1962) for starch; potassium dichromate (Gabe 1968) and aqueous solution of ferric chloride (Johansen 1940) for phenolic compounds; Phloroglucinol-HCl (Johansen 1940) for lignified walls; Ruthenium Red (Johansen 1940) for pectins; and Sudan IV (Pearse 1980) for lipids. The anatomical descriptions were taken from temporary slides assembled with distilled water and cover glass, which were examined under light microscope (Olympus BX 51). The anatomical records consisted of photomicrographs, with the scales obtained in the same optical conditions.

Results

The fusion point of the hypanthium with the ovary wall delimits the free and the inferior portion of the ovary, and the apex of the superior portion of the ovary is projected around the basis of the style in a circular structure (figures 1 to 4). The indehiscent, fleshy globose berries are originated mainly from the development of the inferior portion of the ovary (figure 5). Early in the development, the fruits are brown to green, with the color often masked by dense indumentum. During the ripping, the fruit color changes to the characteristic jade-green. Ripped fruits do not have indumentum, they are thick and succulent 8.14 ± 0.52 mm of width, 6.23 ± 0.87 mm of height and 0.248 ± 0.043 g.

Both longitudinal and cross sections of ovary and fruits showed similar anatomical characteristics, thus the anatomical descriptions are of middle cross-sections. We recognize three stages of development from ovary to mature pericarp, Immature-I, Immature-II and Mature, according with the anatomical structure of the pericarp. The pericarp is clearly differentiated, in all developmental stages, in exocarp, mesocarp and endocarp; the exocarp is developed from the outer epidermis of the hypanthium,
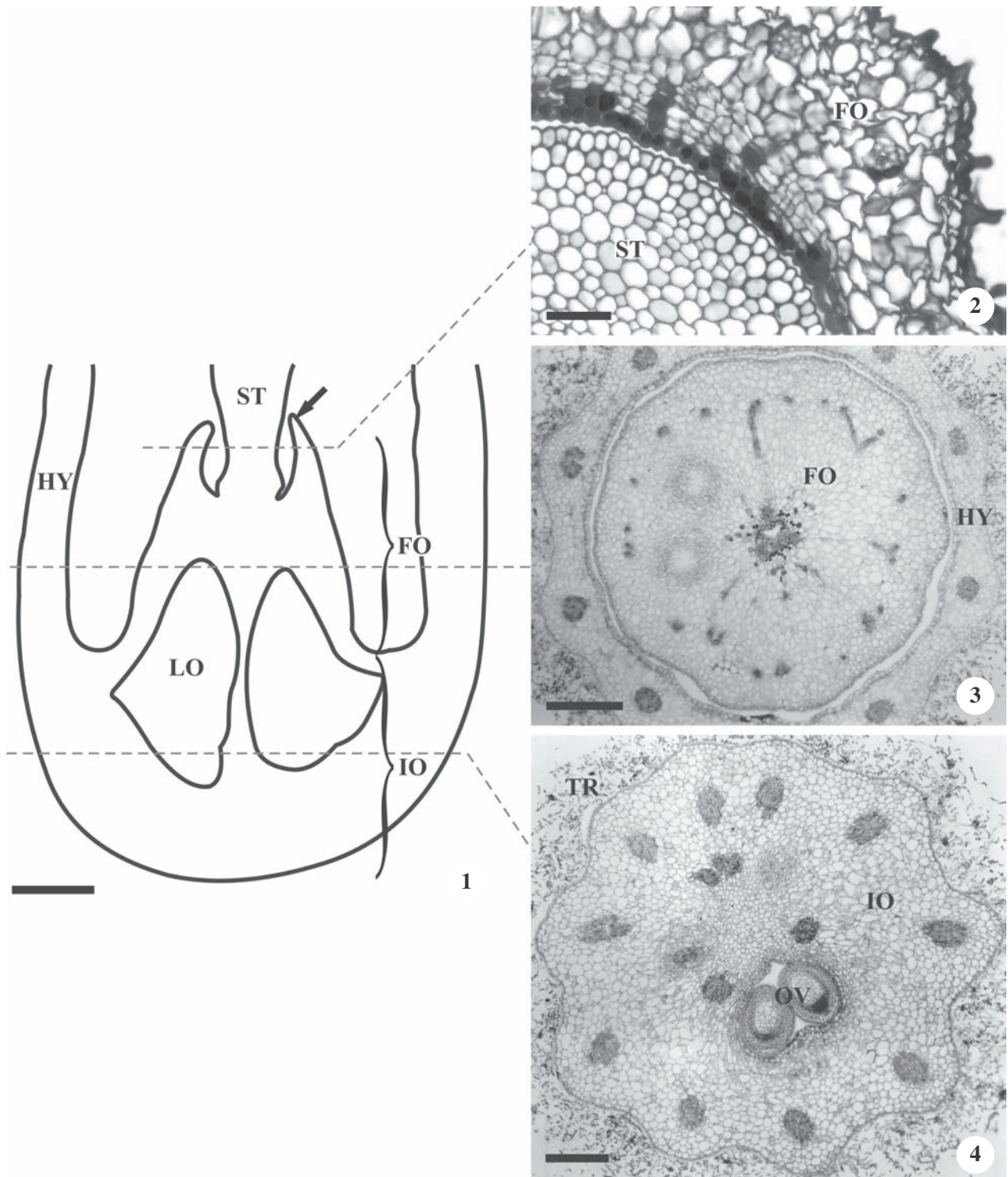
Figures 1-4. *Miconia albicans* semi-inferior ovary. 1. Median longitudinal section of ovary showing its free and inferior portions and the apical projection (arrow) around the basis of the style. 2-3. Cross-section of the ovary free portion. 4. Cross-section of the inferior portion. (FO = Ovary free portion; HY = Hypanthium; IO = Ovary Inferior portion; LO = Locule; OV = ovule; ST = Style; TR = Trichomes). Bars = 40 μm (2), 270 μm (4), 330 μm (1,3).

the mesocarp is developed from the ground tissue of both the hypanthium and the ovary, and the endocarp is developed from the inner epidermis of the ovary (figures 6 to 9).

The Immature-I pericarp (figure 6) is similar to the ovary wall in structure and cell layers, except for the initial differentiation of sclereids in the mesocarp. The exocarp and the endocarp are unisseriated and the exocarp cells are covered with a thick and ornamented cuticle. Stomata and lignified trichomes are found only in the exocarp developed from the outer epidermis of the ovary inferior portion. The mesocarp is about 15-cell-layer thick, parenchymatous, with minute intercellular spaces. The vascular bundles are concentric, the 10 largest ones enveloped by a parenchymatous sheath. Druse crystal idioblasts are spread in the mesocarp, and also concentrated in the fruit apical portion and in the subepidermical inner layers. Idioblasts with phenolic-like compounds are observed mainly in carpels septa, in placental tissues, in vascular bundle, and in apical portion of the fruit.

The Immature-II exocarp cells (figure 7) become papilliform with basal nuclei. The mesocarp is about 30-layer thick. The druses are rare. A great number of isodiametric sclereids are found widespread in the mesocarp, and also forming small groups in the apical region of the fruit and close to the exocarp and endocarp. There are no significant changes in the endocarp.

The Mature exocarp (figures 8 and 9) looses the trichomes. Stomata are easily visibly prominent over this layer, and the papilliform cells have flocculate contents of phenolic-like compounds. The endocarp cells are often collapsed. The mesocarp is about 50-layer thick, with some portions showing a marked radial elongation. The parenquimatous cells are irregular in shape and size, and more or less turgid with fluids. Some of them are under protoplasm-dissolving process or even complete desintegration, with thinner and weaker cell walls and some intercellular spaces among them. The vascular bundle sheath cells develop thick and lignificated walls. The druses and phenolic-like compound idioblasts are almost absent and the sclereids are restricted to smalls groups close to the exocarp, the endocarp and the fruit apical portion.

We recognize two stages of seed coat development, from ovules to the mature seeds, Immature and Mature, based on the anatomical structure of the seed coat. The opposite of the raphal side is referred as the antiraphal side. The ovules are anatropous, bitegmic, crassinucellate, with axillary placentation and a *sensu lato* hypostase. The outer and the inner integuments are four- and two-layer thick respectively, and the zig-zag micropyle is formed by both the exostome and the endostome (figure 10).

The Immature seed coat (figure 11) is parenquimatous and non-multiplicative, and the antiraphal side is differentiated in exotestal, mesotestal and endotestal layers. There are prismatic crystal idioblasts widespread in the mesotestal layer. The raphal portion is about 10 cells-thick, with a unique vascular bundle until the chalaza, where there is a hypostase *sensu lato* with phenolic-like compounds. Early in the development there is a radial elongation of some cells, in the exotesta of the antiraphal side and in the inner layer of the raphal side. The tegmen appears as a pellicle of thin cells, not lignified and, often soon crushed.

The Mature seed (figures 12 and 13) is pyramidal-elongated in shape, exalbuminous, testal 0.79 ± 0.09 mm of width, 1.10 ± 0.07 mm of height, and 0.0036 ± 0.0003 grams. The seed coat colour is brown to yellow and the raphal part is clearly visible, occupying about 40% of its total length. The seed is testal. The antiraphal side is non-multiplicative and has the exotesta, mesotesta and endotesta differentiated into sclerotic layers, with the palisade exotesta *sensu* Corner (1976) being the mechanical layer, while in the raphal side the palisade sclerotic mechanical layer is derived from its inner layer. The tegmen is absent.

Discussion

Pericarp – The fruit is usually considered as a flower in the stage of seed maturation (Spjut 1994). Since it develops as a complex unity, other floral parts besides the carpels may be involved in fruit formation, and much has been discussed about the inclusion or not of ovarian accessory tissues in the fruit concept (Pijl 1972, Roth 1977, Spjut 1994, Judd *et al.* 1999). The presence of a well-developed urn-shaped hypanthium often adnate to the gynoecium is very common in melastome (Clausing *et al.* 2000), and the fruit wall thus consists of two parts of different morphological origin. The inclusion of hypanthium tissues in the fruit definition of *M. albicans* is very consistent as the major piece of its pericarp resulted from the development of the ovary inferior portion, which is adnate to the hypanthium.

Spjut (1994) took into account, besides ovarian characteristics, the texture, the thickness, and the stratification of the pericarp in order to establish the fruit types. As it was observed in fleshy fruits which consist in part of structures other than the carpels, *M. albicans* pericarp showed the same general histological structure of simple fleshy fruits. Based on these anatomic
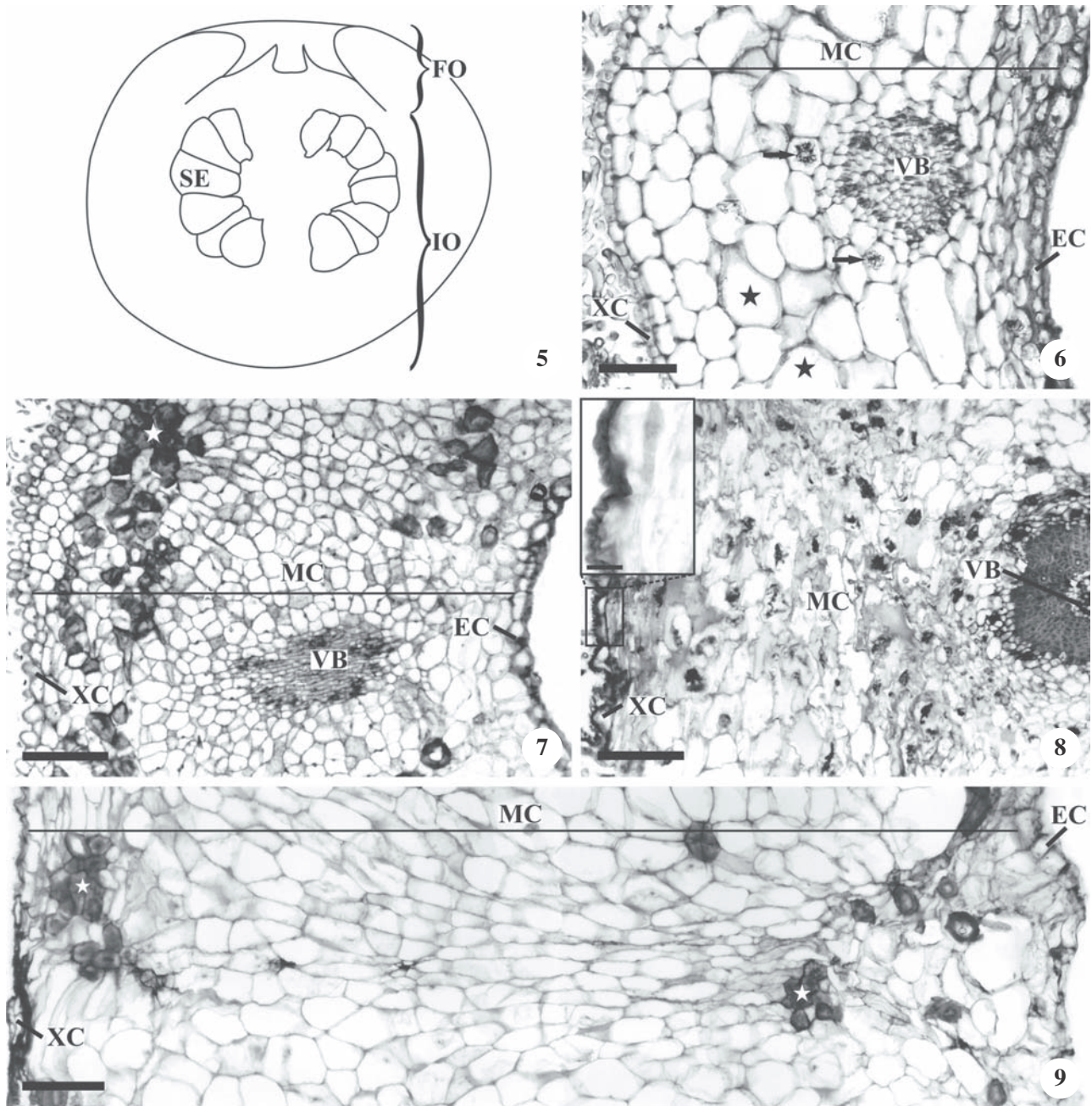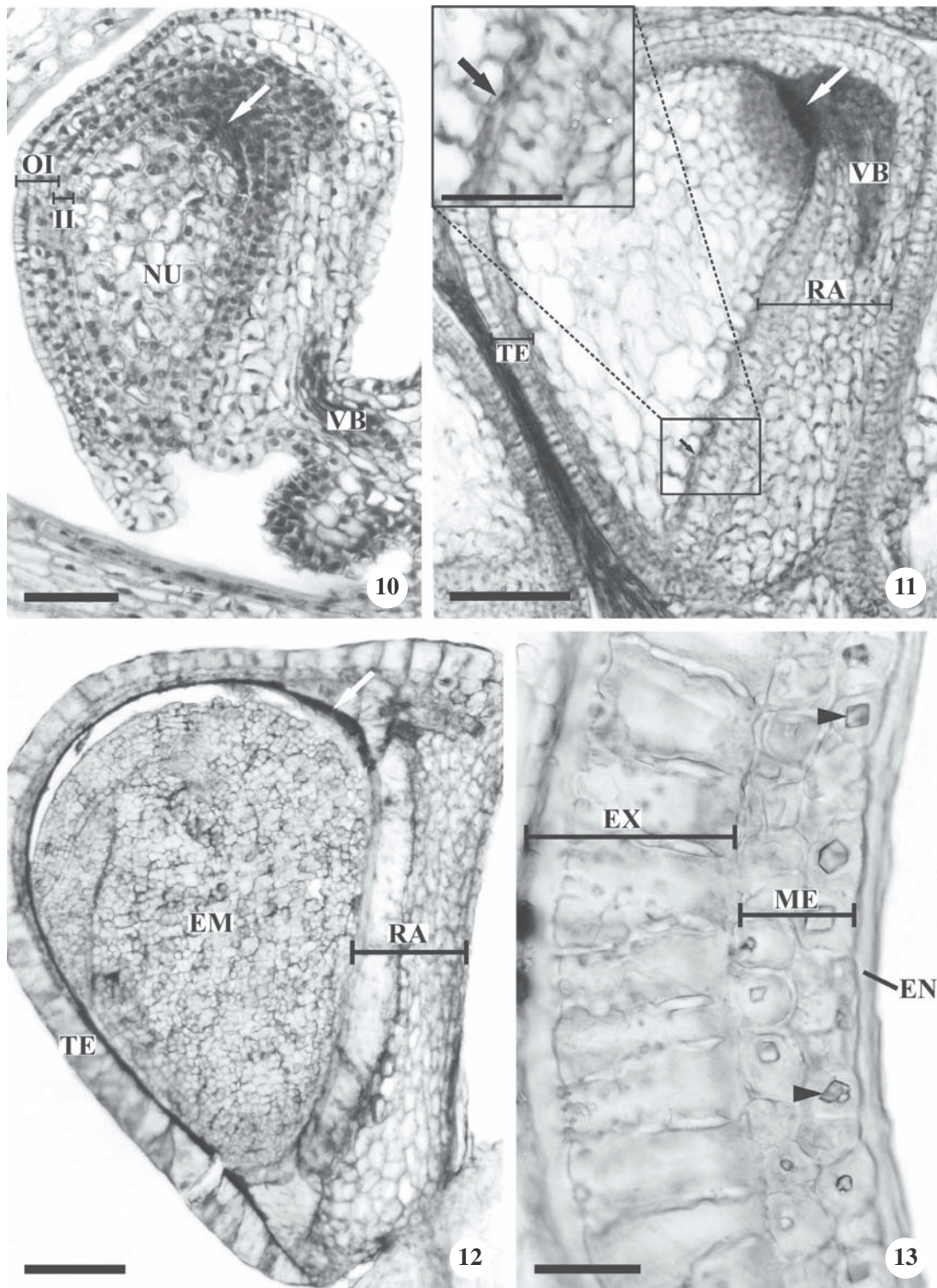
Figures 5-9. *Miconia albicans* fruit. 5. Median longitudinal section. 6. Cross section of Immature-I pericarp showing druse crystal idioblasts (arrow) and sclereids in differentiation (star). 7. Cross section of Immature-II pericarp showing sclereids (star). 8-9. Cross section of Mature pericarp showing sclereids (star) and detail of the cuticle in the exocarp (insert). (EC = Endocarp; FO = Pericarp derived from ovary free portion; IO = Pericarp derived from ovary inferior portion; MC = Mesocarp; SE = Seed; VB = Vascular bundle; XC = Exocarp). Bars = 55 μm (6), 70 μm (insert), 140 μm (8), 170 μm (9), 330 μm (7), 1 mm (5).

considerations, *M. albicans* is a typical berry-fruit which is characterized by a juicy and indehiscent pericarp, and by an endocarp which is not differentiated into hard or lacunous layer (Spjut 1994). With effect, according to Clausing *et al.* (2000), the indehiscence of pericarp in melastome is clearly associated with ovary/hypanthium fusion, and lack of a persistent endocarp, among other characteristics.

The globular shape of *M. albicans* fruits is observed since the early stages of development, and is attained by

Figures 10-13. *Miconia albicans* ovule and seed showing the hypostase *sensu lato* (white arrow). 10. Ovule median longitudinal section. Bar = 35 μm. 11. Median longitudinal section of Immature seed coat showing tegmen (black arrow), and detail of the endocarp (insert). Bar = 140 μm. 12. Median longitudinal section of Mature seed coat. Bar = 170 μm. 13. Median longitudinal section of Mature seed coat showing antiraphal side with prismatic crystal idioblasts (arrow head). Bar = 35 μm. (EM = Embryo; EN = Endotesta; EX = Exotesta; II = Inner Integument; ME = Mesotesta; NU = Nucellus; OI = Outer Integument; RA = Raphe; TE = Testa; VB = Vascular Bundle). Bars = 35 μm (10, 13), 70 μm (insert), 140 μm (11), 170 μm (12).

the increase in number and in size of mesocarp parenquimatous cells in a uniform way, and by some radial cell enlargement. Cell enlargement has been described in physical terms as a function of cell wall extensibility, osmotic potential of the cell, and/or turgor pressure. Flesh softening is the most conspicuous evidence of ripening in berry-like fruits, and involves progressive changes in the structure and chemical composition of the cell walls (Roth 1977). Together, these changes were responsible for the anatomical differences between the ovary ground tissue, and the matured mesocarp.

One of the most notable events during the development of the *M. albicans* pericarp is the differentiation of sclereids in the mesocarp. The sclerotic cells are considered as a very important cellular type present in the pericarp of almost all fruit types, and they are related mainly to the protection of seeds from injuries, and the support of mesocarp fleshy tissues (Roth 1977). Soft berries are characterized by the absence of lignified tissues, but the pericarp may consist of mingled succulent parenchyma and sclereids in varied proportions and widespreading (Roth 1977, Clausing *et al.* 2000). This kind of cell can arise either from a belated sclerosis of parenchyma cells or directly from cells which are early individualized as sclereid primordia (Roth 1977). The first form of differentiation was observed in *M. albicans*, as there was clear thickness and sclerification of some mesocarp parenquimatous cell walls from Immature-I stage.

The number, shape and distribution of sclerotic cells appear to bear a systematic value (Roth 1977). In *M. albicans*, the sclereids are nearly isodiametric cells, the main type which can be found in fleshy fruits (Roth 1977). According to Clausing *et al.* (2000), the decrease of sclereids in melastome soft berries is associated with the indehiscence of the pericarp. Although a great decrease in sclereids cell amounts was observed along the development of *M. albicans* berries, we did not know whether it was real or simply a consequence of the increase in number and size of the mesocarp parenquimatous cells.

Further mesocarp characters concerned the presence of calcium oxalate crystals and phenolic-like compounds, which are frequently found in early stages of flesh fruit development, isolated or in small groups, mainly inside the vacuoles of idioblasts (Judd *et al.* 1999, Webb 1999). The chemical nature, the morphology, and the location of the crystals in the plant body may be specific and particularly interesting to taxonomic works, including the delimitation of some Melastomataceae subfamilies

(Baas 1981, Welle & Koek-Noorman 1981). However, some authors consider the diagnostic value of crystal types sometimes restricted, especially due to the variety and frequency found within species or even specimens (Welle & Koek-Noorman 1981).

The functional meaning of crystals is still not clear, but they may be related to tissue mechanical support, protection against herbivore, and cell level regulation and storage of calcium and oxalate, among others (Webb 1999, Molano-Flores 2001, Paiva & Machado 2005). On the other hand, phenolic-like compounds occur frequently in cells with a decreased proliferating activity, and in tissues with a high physiological activity, and possibly act as plastic materials and/or by-products of metabolism (Buvat 1989).

Seed coat – Based on seed coat morphology, Whiffin & Tomb (1972) recognized five basic seed types of neotropical capsular-fruited melastome. Although some seed types did not fit neatly into those categories, seed morphology as a taxonomic character has provided valuable information on generic relationship among the neotropical capsular-fruited genera. Corner (1976) described the seed anatomy for eleven species of eight different genera, including *Miconia*, and according to Groenendijk *et al.* (1996), the characteristics of *Miconia* seeds is typical of related genera.

The pattern of heterogeneous cell radial elongation and lignification that was observed in *M. albicans* seed coat was not mentioned by Corner (1976) for the genus, except for the presence of elongate cells in the endotesta of *Miconia magnifica*, possibly fibres, but he was unable to find such cells in his examinations. The pattern described by him to the *Blakea trinervia* seed coat is very similar to that found in *M. albicans*, although the ontogeny of the radially elongated and lignified cells was not clearly elucidated. The cylindrical construction enables the seed to whitstand pressure; due to a weak connection between the testal and the raphal sclerotic layer, the raphal part easily breaks off during germination, thus acting as an operculum, permitting the embryo to emerge (Corner 1976, Groenendijk *et al.* 1996).

The presence of calcium oxalate crystal-cells in the testa of *Miconia* species was mentioned by Corner (1976). Crystals have been found in or on the seed surface of many species, and among their possible functions, are the protection against invading microorganisms, calcium storage and seed storage protein synthesis (Webb & Arnott 1982, Ilarslan *et al.* 1997).

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