Rodriguésia 67(3): 649-659. 2016
http://rodriguesia.jbrj.gov.br
DOI: 10.1590/2175-7860201667309

Structural development of the fruits and seeds in three mistletoe species of *Phoradendron* (Visceae: Santalaceae)

Anderson Polli[1], *Luiz Antonio de Souza*[1,2,4] & *Odair José Garcia de Almeida*[2,3]

Abstract

Phoradendron is a New World genus of chlorophyllous hemiparasite plants with the distribution extending from the United States to Argentina, including the West Indies. The names given to the fruits within the Visceae are variable and include a viscous berry or pseudoberry bearing a single seed lacking the testa. Here, it was performed an anatomical study about the development of fruit and seed of three species of *Phoradendron.* During the fruit development the structure of the mesocarp undergoes intense activity of cell division, and it differentiates onto two new mesocarpic regions: the parenchyma and the viscid layer. In its maturity, the seed is ategmic, presenting the embryo entirely embedded within a chlorophyllous endosperm. The occurrence of chlorophyll in the endosperm may be associated to absence of integuments on the seed, which allows the light to reach the seminal tissues throughout the somewhat transparent pericarp. In addition, the Pomaceous fruit, "viscidio" type is proposed as an alternative classification for *Phoradendron* fruits.

Key words: anatomy, chlorophyllous endosperm, fruit classification, semiparasite plant.

Resumo

Phoradendron é um gênero de plantas hemiparasitas clorofiladas do Novo Mundo, que tem distribuição desde os Estados Unidos até a Argentina, incluindo o leste da Índia. Os nomes dados aos frutos de representantes de Visceae são variáveis, incluindo baga viscosa ou pseudobaga, apresentando uma única semente sem testa. Nesse trabalho, foi realizado um estudo anatômico para investigar o desenvolvimento do fruto e da semente de três espécies de *Phorodendron.* Durante o desenvolvimento do fruto, a estrutura do mesocarpo sofre intensa atividade de divisão celular; diferenciando-se em duas novas regiões mesocárpicas: uma camada parenquimática e outra de viscina. Quando o fruto amadurece, a semente atégmica, apresenta embrião inteiramente embebido em um endosperma clorofiliano. A ocorrência de clorofila no endosperma pode estar associada à ausência de tegumentos seminais, permitindo que a luz alcance os tecidos da semente, através do um pericarpo relativamente transparente. Em adição, fruto Pomaceo do tipo *viscidio* é proposto como uma alternativa para a classificação de frutos para o gênero *Phoradendron*.

Palavras-chave: anatomia, endosperma clorofiliano, classificação de frutos, planta hemiparasita.

Introduction

Phoradendron Nutt. is a New World genus of chlorophyllous branch parasites with a distribution extending from the United States to Argentina and including the West Indies (Ashworth 2000). The genus has 55 species in Brazil (BFG 2015) and more than 230 in the World (Stevens 2001). Kuijt (2003) made important considerations about *Phoradendron*, such as: the forests of the neotropics are vanishing at a terrifying rate, dragging vast ecosystems into permanent oblivion; the mistletoes, being parasites upon woody plants, are perhaps more vulnerable, and their disappearance will be less bemoaned than that of nearly any other group

---

[1] Universidade Estadual de Maringá - UEM, Programa de Pós-graduação em Biologia Comparada - PGB, Av. Colombo 5790, 87020-900, Maringá, PR, Brazil.
[2] Universidade Estadual de Maringá - UEM, Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais - PEA, Av. Colombo 5790, 87020-900, Maringá, PR, Brazil.
[3] Universidade Estadual Paulista - UNESP, Programa de Pós-Graduação em Biodiversidade Aquática, Praça Infante Don Henrique s/n, Pq Bitarú, 11330-900, São Vicente, SP, Brazil.
[4] Autor para correspondência: lasouza@uem.br

of plants; their seeds live only for brief periods and, not having a seed coat, probably cannot be stored except for short periods and; the seed dispersal itself is obligately dependent on the action of frugivorous birds, who themselves are in similar threat. Thus, if it is increasingly difficult to convince people and governments to protect trees and forests, who will speak for the mistletoes parasitic on them?

The names given to the fruits within the Visceae (Santalaceae) (Stevens 2001) are variable and include a viscous berry (bacca) or pseudoberry (pseudobacca) with a single seed lacking testa (Richardson 1993; Spjut 1994; Barroso *et al.* 1999; Judd *et al.* 2002; Kuijt 2003).

In fact, Kuijt (2003) stated that unfortunately, detailed anatomical accounts of the *Phoradendron* fruit are not abundant, and some examples are the studies of Cannon (1901), Billings (1933), Calvin (1966), Roth (1977), Gedalovich *et al.* (1988), Kuijt (2003), Rigon & Cervi (2013), and Gomes-Sánchez *et al.* (2011). The present paper, therefore, deals with the comparative development and structure of seeds and fruits in *Phoradendron quadrangulare* (Kunth) Grisebach, *P. dipterum* Eichler and *P. piperoides* (Kunth) Trel. In addition, an alternative classification of the fruit is proposed.

Material & Methods

Flowers and fruits of various ages from at least three individuals of each species were collected at Maringá, Brazil (23°24'S e 51°56'W), in order to have samples of the different phases of their development. Voucher material was deposited in the State University of Maringá Herbarium (HUEM): *P. piperoides* - A. Polli *w.n.* HUEM 22.574; *P. quadrangulare* - A. Polli *w.n.* HUEM 22.575; and *P. dipterum* - A. Polli *w.n.* HUEM 23.381. These three species were chosen due to their abundance on the site of study. The material collected was fixed in glutaraldehyde (1% in 0.1M phosphate buffer, pH 7.2, maintained at 4°C), transferred into 70% alcohol, following the protocol of Johansen (1940), dehydrated through alcohol series, embedded in hydroxymethacrylate (Gerrits 1991), sectioned with a rotary microtome (cross and longitudinal sections), thickness from 8 to 10μm, and stained with 0,05% toluidine blue in a phosphate buffer at pH 4.7 (O'Brien *et al.* 1964). Photomicrographs were prepared using a Leica microscope with digital camera - ICC50, and subsequently processed using the software Leica Application Suite version 1.8.1.

Specific microchemical tests were carried out for lignin with phloroglucinol and hydrochloric acid (Berlyn & Miksche 1976), lipid substances with Sudan IV (Rawlins & Takahashi 1952; Ruzin 1999), starch with lugol (Berlyn & Miksche 1976), pectin with ruthenium red (Johansen 1940; Jensen 1962), and calcium crystal with sulphuric acid (Sass 1951).

For scanning electron microscopy (SEM) studies of developing and mature fruits/seeds, the material was fixed in 1% glutaraldehyde (Karnovsky 1965). After washing in a 0.1M sodium cacodylate buffer, the samples were dehydrated in a graded acetone series, critical point dried with CO2, mounted on aluminum stubs, and coated with gold. Fruits and seeds were analyzed through Shimadzu SS-550 Superscan at 3,0kV.

Results

Fruit structure

The fruits are originated from small, 3-petals, monochlamydeous, actinomorphic, epigynous, and unisexual flower (Fig. 1), being each flower placed in a shallow cup (receptacle) (Fig. 1b,g). The flowers of the three species have triangular aperture (Fig. 1), they are greenish in *P. quadrangulare* (Fig. 1a,e) and *P. dipterum* (Fig. 1b,f), and orange-green in *P. piperoides* (Fig. 1c-d,g-h). Immature fruit of *P. dipterum* is ovoid-globose and green (Fig. 2a). When ripen it acquires ovoid-elongated format and whitish coloration with strong pink shade in the apex (Fig. 2a-c). The young fruit of *P. quadrangulare* is ovoid and green, and in the mature stage it is globular and of orange coloration (Fig. 2d). The fruit of *P. piperoides* maintains the ovoid format during the whole development, acquiring in the maturity the yellow color on the fruit basis and orange color in the superior third (Fig. 2e-g).

Annular nectary occurs encircling the style in the ovarian superior region in the flowers of the three species studied; besides it is illustrated just for *P. dipterum* (Fig. 3a). In the pistillate flowers, the structure of the unilocular and uniovulate ovary is relatively uniform among the species. It is made up of uniseriate outer epidermis (Fig. 3b-c), with thick cuticle and flanges, and papillose epidermal cells in the ovarian superior half. The mesophyll consists of three tissue regions (Fig. 3f): a parenchymatous outer region with thin-walled cells, interspersed with crystal idioblasts and sclereids of thickened and pitted walls (Fig. 3c); the tissue in the median region contains smaller cells and larger nuclei (Fig. 3d); and the inner region is also composed of thin-walled cells, that can present periclinal cell divisions and crystals (Fig. 3e). The inner epidermis is uniseriate (Fig. 3e). The ovary vasculature (Fig. 3f) is made up of collateral bundles, which are arranged in two rings: the external ring is located in the outer mesophyll and the internal ring between the middle and inner mesophyll.

The most striking histological distinction between the ovary and fruit in development takes place in the mesocarp, mainly in the middle region, where the intensification of cell division occurs, along with the differentiation of two new mesocarpic regions: the parenchyma and the viscid layer (Fig. 4a-b). In the latter is produced viscin, a sticky mucilaginous substance. Other events of differentiation from ovary stage into developing fruit also occur, as the enlargement and collapse of parenchyma cells, vacuolization, and thickening of cell walls of the mesocarpic sclereids, but they are less significant from an ontogenetic point of view. Strands of tracheids and fibers develop from thin-walled and elongated cells located in the periphery of the viscid layer of *P. dipterum* and *P. piperoides* (Fig. 4c-d).

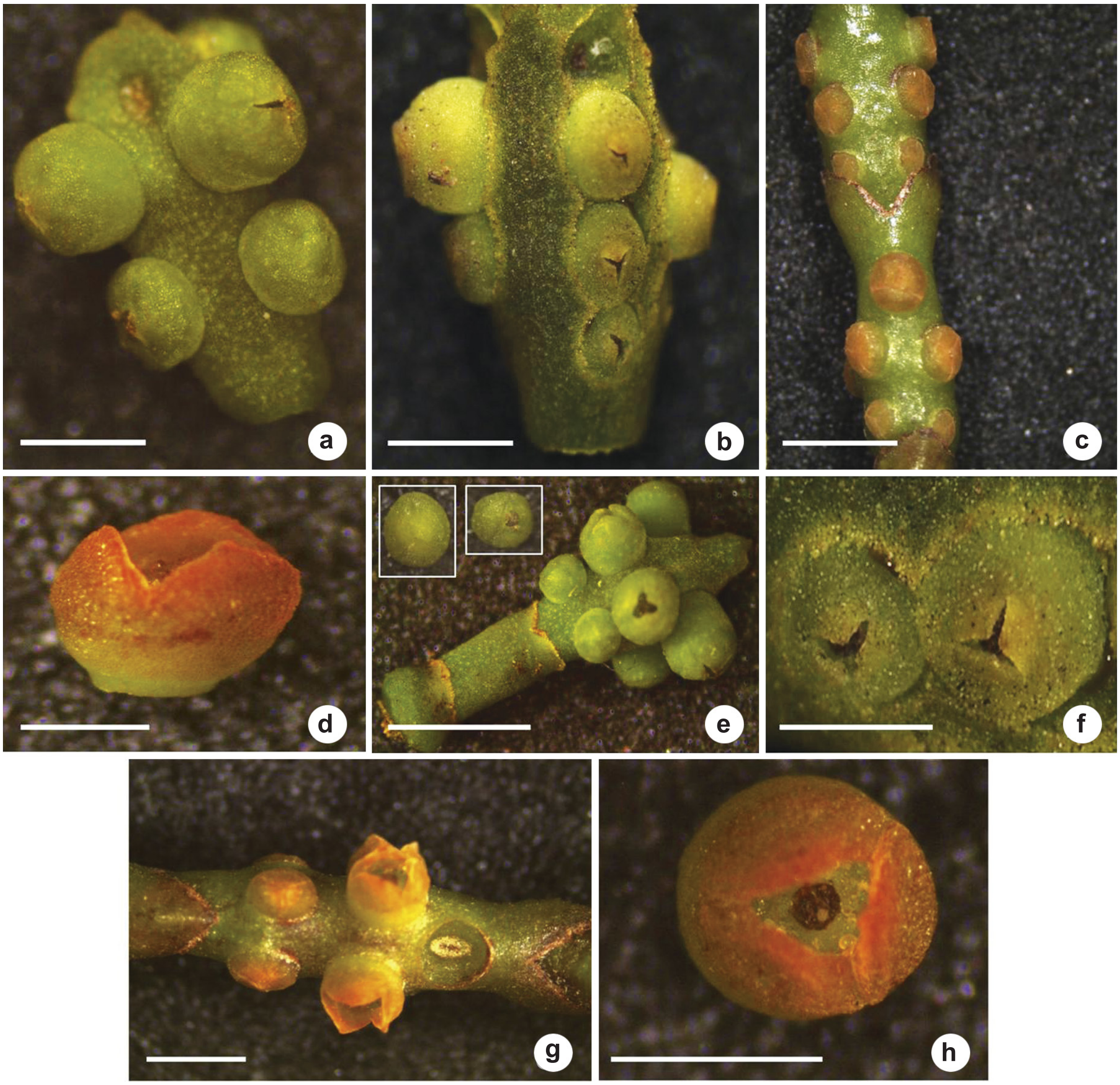

Figure 1 – Flowers of *Phoradendron* species – a,e. *Phoradendron quadrangulare*; b,f. *Phoradendron dipterum*; c-d,g-h. *Phoradendron piperoides*. Bars = 1 mm.

The mature fruit consists of single-layered exocarp, covered with a well-developed cuticle with flanges (Fig. 5a), being warty with central region smooth in *P. quadrangulare* (Fig. 5b) and *P. dipterum*, and striate in *P. piperoides* (Fig. 5c). All species have exocarpic cells that form papillae, except in the inferior third of the fruit (Fig. 5a,d). The mesocarp (Fig. 5e) is distinguishable into four zones: three of them are parenchymatous and one that consists of the viscid layer, which originates between middle and inner mesocarpic layers. The outer mesocarpic layer (Fig. 5a,e) is made up of thin-walled cells,

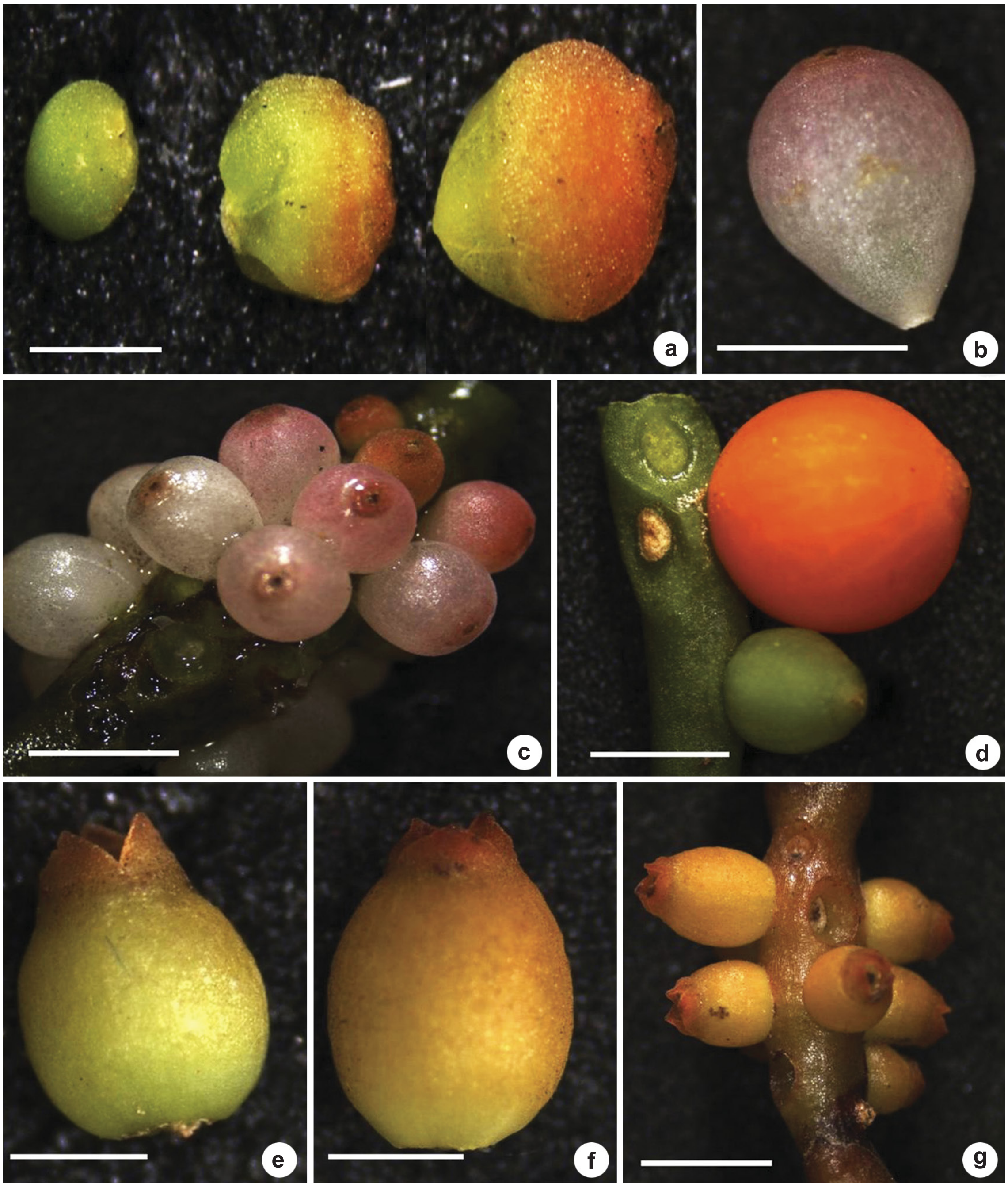

Figure 2 – Fruits in development of *Phoradendron* species – a-c. *Phoradendron dipterum*; d. *Phoradendron quadrangulare*; e-g. *Phoradendron piperoides*. Bars = 1 mm.

interspersed with druse cells and lignified sclereids with simple pits. The middle and inner mesocarpic parenchyma layers (Fig. 5e,g) are built up of thin-walled cells, which are mostly compressed during the viscid layer and seed development. The viscid layer, located between the middle and inner mesocarp, occupies most of the pericarp in all three species of *Phoradendron* (Fig. 5d,e,g). This layer is pluriseriate (Fig 5e-g) with intercellular spaces, and consists of elongated cells which are extended in radial direction with pectic substances located in the cell walls. The viscid layer in *P. quadrangulare* and

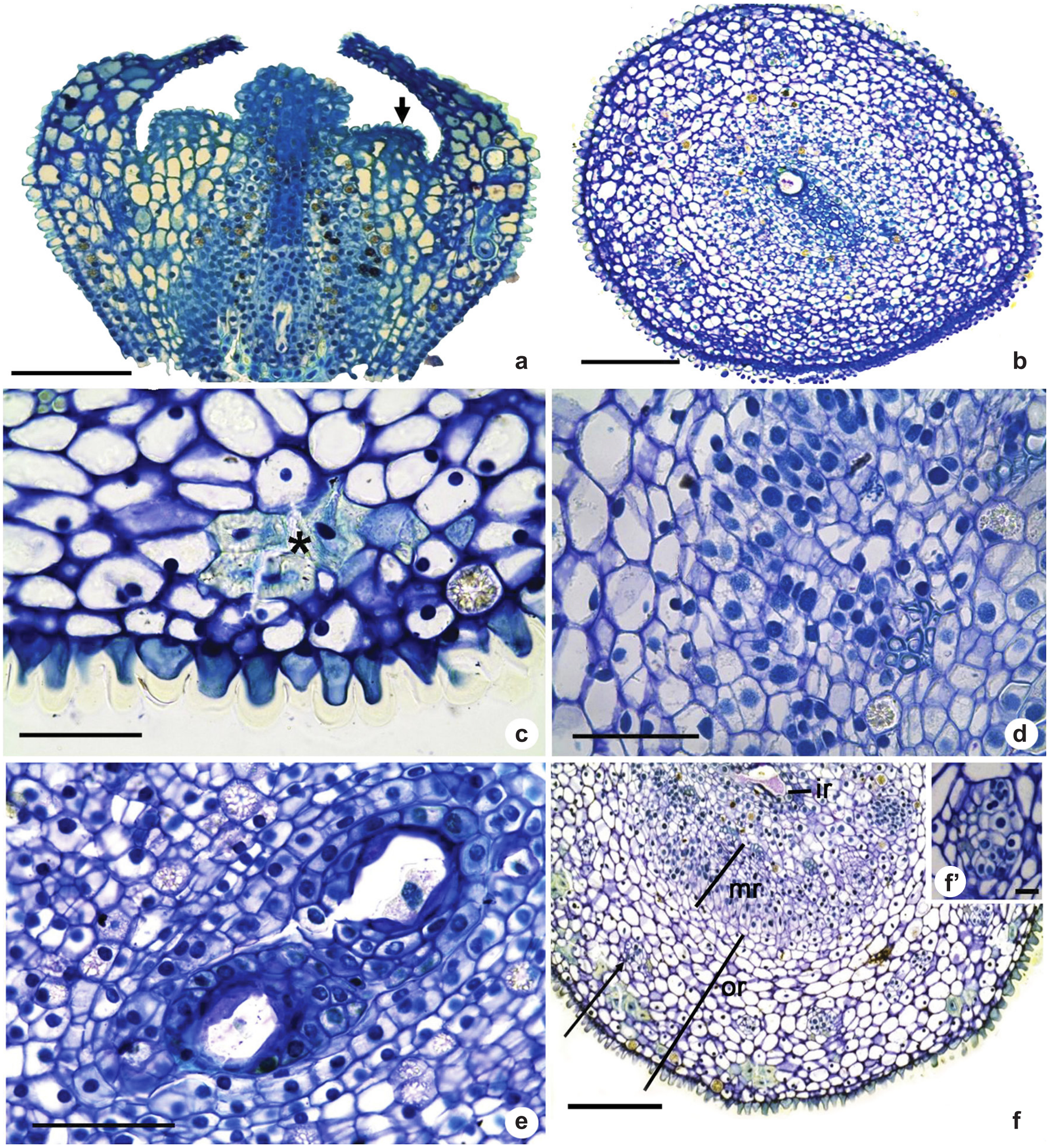

Figure 3 – Ovary anatomy of *Phoradendron dipterum* – a. longitudinal section of the ovary, note nectary at the upper region (arrow). b-f. *Phoradendron quadrangulare* – b. cross section of the ovary; c-e. details of the ovary wall – c. outer epidermis and region of the mesophyll with sclereids (asterisk) and papillae; d. middle region of the mesophyll; e. inner epidermis and region of the mesophyll; f. ovary wall showing vascular bundles (arrow), outer (or), median (mr), and inner regions (ir); f'. collateral bundle in detail (superior right corner). a. cross section; b-f. transversal sections. Bars = 50 µm (a,b,f); 10 µm (f'); 100 µm (c-e).

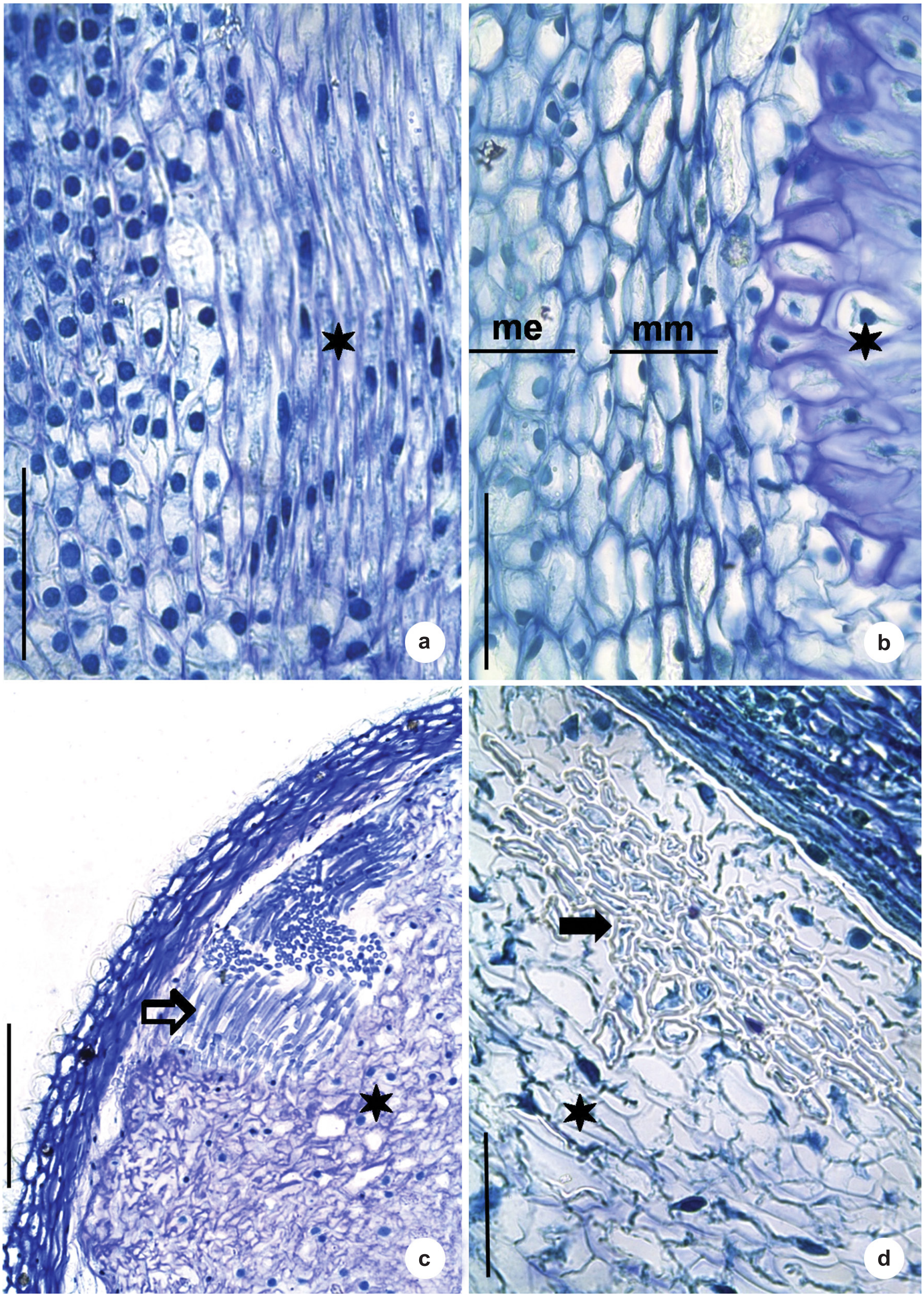

Figure 4 – Pericarp development of *Phoradendron dipterum*. a,c. *Phoradendron dipterum.* b,d. *Phoradendron piperoides* – a. mesocarp in differentiation showing the viscid layer (*); b. mesocarp evidencing the outer mesocarpic layer (me), middle mesocarpic layer (mm) and viscid layer (*); c-d. pericarp evidencing the strands of tracheids (white arrow) and fibers (black arrow) in differentiation; and the viscid layer (*). Bars = 50 µm (a,c,d), 70 µm (b). All sections are transversal.

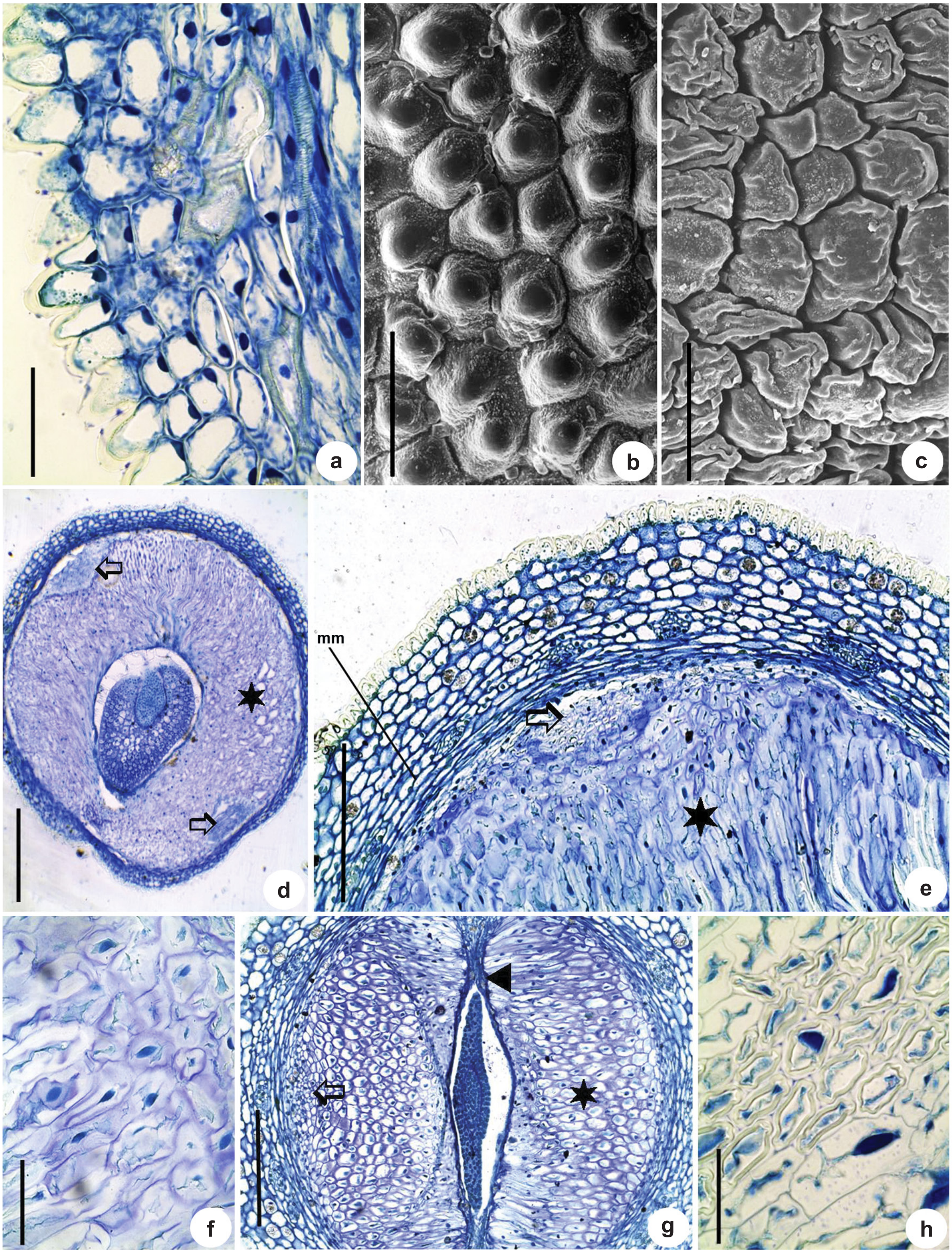

Figure 5 – Pericarp of *Phoradendron* species – a-b,f. mature pericarp structure of *Phoradendron quadrangulare*. c,e,g-h. *Phoradendron piperoides*. d. *Phoradendron dipterum* – a. exocarp, and outer mesocarpic layer evidencing the sclereids; b-c. Scanning Electron Microscopy of the exocarp surface in frontal view; d,g. fruits in longitudinal section, evidencing the single seed; e. pericarp in longitudinal section; f. detail of the viscid layer; h. detail of the strand of gelatinous fibers. (mm = middle mesocarp; arrows indicate the strands of tracheids and fibers; arrow head shows collapsed inner mesocarp and endocarp; asterisks indicate the viscid layer). Bars = 20 µm (d,g), 50 µm (c,e), 70 µm (a-b), 100 µm (f,h).

P. dipterum is continuous, while in *P. piperoides* it is interrupted by parenchymatous mesocarp (Fig. 5g). Remarkable bundles (Fig. 5d-h) of longitudinally elongated cells occur at the periphery of the viscid layer. These bundles are made up of tracheids with helical thickenings of the cell walls in *P. dipterum*, and gelatinous fibers in *P. piperoides* (Fig. 5h); these cells are entirely lacking in *P. quadrangulare*. The endocarp is also completely collapsed (Fig. 5g) by the seed and the viscid layer, in all species analyzed here.

The vasculature of the fruit resembles the vascular system of the ovary, with two rings of collateral bundles; a ring of bundles occurs between the outer and middle regions of the mesocarp, while the other ring is located in the inner mesocarp.

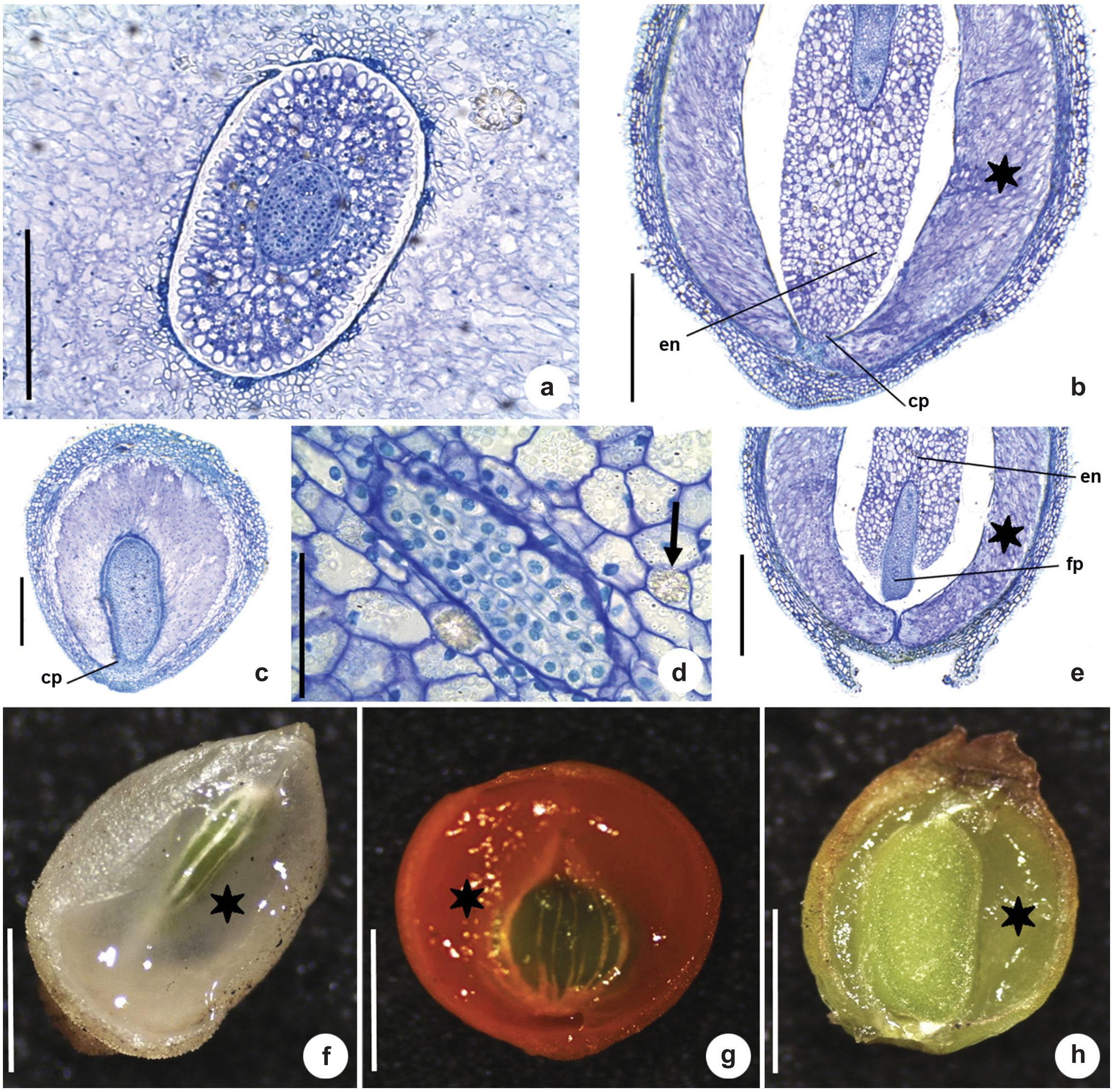

Figure 6 – Seed structure of *Phoradendron* species – a,f. mature seed structure of *Phoradendron dipterum*. b,e,g. *Phoradendron piperoides*. c,d,h. *Phoradendron quadrangulare* – a. fruit in cross section showing the seed with endosperm and embryo; b,e. fruit in longitudinal section evidencing the pericarp with the viscid layer, endosperm and embryo; c. fruit in longitudinal section evidencing the pericarp with the viscid layer and endosperm; d. detail of the endosperm with druse idioblast and embryo; d-f. sectioned fruits with seeds involved by a sticky mucilaginous substance or viscid layer. (asterisk = viscid layer; black arrow = druse idioblast; cp = endospermic portion contiguous to the pericarp; cp = endosperm; fp = free radicular pole). Bars = 50 µm (a), 100 µm (d), 300 µm (b,c,e), 1 mm (f-h).

Seed structure

The seeds are originated from ategmic ovules. The endosperm (Fig. 6a-c) is persistent, playing the tegument function. It consists of epidermis and parenchyma with starch. The endosperm (Fig. 6a) is surrounded by an uniseriate epidermis covered by cuticle; their cells are radially elongated, and just on the radicular apex they are papilous; the parenchyma is made up of cells with chlorophyll and lots of starch; idioblasts with druses occur as well (Fig. 6d). In the basal portion of the fruit (Fig. 6b,c) the endosperm has elongated cells with dense cytoplasm and large nuclei contiguously to the fruit wall.

The mature seed is chlorophyllous and ategmic; it is involved by a sticky mucilaginous substance, produced by the viscid layer (Fig. 6f-h). The embryo is erect with short hypocotyl-radicle axis, two minute cotyledons, and plumule not evident. The embryo is entirely embedded within the endosperm, except on the radicular pole (Fig. 6e).

Discussion

The fruits of *Phoradendron* are originated from epigynous flowers, i.e., they come from the inferior ovary. Concerning the morphological nature of the inferior ovary in flowering plants, two principal interpretations have been considered: the appendicular and the receptacular theories (Roth 1977). According to Smith & Smith (1942), Douglas (1944, 1957) and Fahn (1990) the former theory takes into account the result of the cohesion and adnation of the portions of all the floral organs to the gynoecium which they surround to classify the flower as having an ovary of appendicular nature. On the other hand, the later theory states that the flower which has sunken the gynoecium into a concave receptacle which has surrounded and fused with the carpels is considered having an ovary of receptacular nature.

The fruits of *Phoradendron* are showy (pink, orange or yellow in color) and fleshy; furthermore the viscid layer in some analyzed species of *Phoradendron* is rich in polysaccharides (neutral sugars, such as xylose and arabinose), uronic acids and proteins (Gedalovich-Shedletzky *et al.* 1989; Kuijt 2003). Thus, that layer has notable features to promote ornitocory in *Phoradendron*. The seed dispersal in *Phoradendron*, as in most mistletoe genera, takes place by birds (Kuijt 2003). Cazetta & Galetti (2007) showed that *Phoradendron quadrangulare* is almost exclusively dispersed by *Euphonia* (Fringillidae), which defecate seeds in clumps on host branches. Visceae-bird interactions are performed by birds that belong to Thraupinae and *Euphonia*/*Chlorophonia* groups (Restrepo *et al.* 2002). Guaraldo *et al.* (2013) pointed out that the dispersal systems of *Rhipsalis* Gaertn. (epiphytic cacti) and Visceae mistletoes are comparables. They have the same dispersal agents, similar fruit morphologies, and fruit chemistry, and according to the authors, it can be explained as convergent adaptive strategies that enable seeds of both groups to reach adequate microsites for establishment in host branches.

In *Phoradendron* the viscid layer occurs near the border line between the receptacle and ovary wall (Roth 1977). In fact, this study with three species of *Phoradendron* has shown the viscid layer has its origin at the middle zone of the ovary wall, resultant of meristematic activity that occurs in the cells from that region. Roth (1977) suggested that the tissue in this region seems to be part of the floral cup, since the vascular bundles which supply the perianth leaves and stamens pass through the viscid layer.

The specialized strands of tracheid-like and gelatinous fibers that occur in the viscid layer of *P. dipterum* and *P. piperoides*, respectively, are recorded in fruit of Visceae for first time. We assume that these cells are able to store water to supply the viscid layer, due to the similarity of the tracheoid idioblasts of the xeromorphic leaves reported by Mauseth (1988). The supply of the viscid layer with water is important during the swelling process and possibly for maintenance and development of the embryo. In agreement to Roth (1977; and references therein) the sticky consistence of the viscid mass enable the seeds to adhere to the host-branch on which they may fall.

Concerning the fruit classification, the literature has recorded the berry/bacca type (Roth 1977; Spjut 1994; Barroso *et al.* 1999; Judd *et al.* 2002; Gómez-Sánchez *et al.* 2011) for Visceae. Spjut (1994) recognized the bacca as a simple fruit consisting of one or more seeds embedded in a solid fleshy mass supported by an epicarp less than 2 mm thick, and pericarp not differentiated internally by a hardened endocarp. However, we consider that the concept of a bacca/berry should be restricted to fruit (pericarp) just derived from a superior ovary, and the *Phoradendron* fruits originate from inferior ovary. Thus, the fruits of *Phoradendron* have characteristics of a pomaceous fruit *sensu* Hertel (1959) and Souza (2006). Hence, we propose a new denomination of *viscidio* type, in allusion to the presence of the viscin layer, which is exclusive for this group of plants.

The Visceae ovules show extreme reduction (Eames 1961; Singh 1964; Bouman 1984), difficulting their identification inside the ovary. According to Bouman (1984) most genera of the Visceae have ategmic ovules, and the reduction may be so extreme that even the boundary between the rudimentary ovule and the placenta becomes obscure. Corner (1976) also considered the Visceae ovules ategmic. In spite of the *Phoradendron* ovules were not well defined, they were considered ategmic as well.

Obviously no testa is formed in *Phoradendron* seeds, since they result from ategmic ovules. However, the embryo is enclosed by a multi-layered endosperm. The endosperm in the *Phoradendron* seeds is chlorophyllous and contains starchy storage, which must to nourish the embryo during the germination and initial phases of the seedling establishment. Chlorophyllaceous endosperm is rare in angiosperms, but it is also known for a few genera of the families Loranthaceae, Eremolepidaceae, Misodendraceae, Santalaceae (Kuijt 2003; and references therein), and Amaryllydaceae (Meerow & Snijman 2001). The chlorophyllous endosperm, found in the species of *Phoradendron* analyzed here, can be explained due to the absence of integument on the seed and the transparence of the pericarp, so that the light can reach the endosperm layers stimulating the synthesis of chloroplasts in it, during the development of the fruit and the seed.

The special endospermic cells that maintain contact with the pericarp in the *Phoradendron* species probably function as haustorium. The haustorium that presumably transports metabolites from the circumjacent tissue to the embryo during its development (Werker 1997) has already been reported in other species of Visceae, *Arceuthobium douglasii* Engelm (Jones & Gordon 1965) and *Arceuthobium minutissimum* Hook.f (Vijayaraghavan & Prabhakar 1984).

The embryo of *Phoradendron* is also green and may play photosynthetic function. However, for Werker (1997) it is not yet clear whether the chlorophyll in embryos of undetached seeds is just a precocious development, or whether it is photosynthetically active while it remains inside the seed. The epidermal cells of the radicular end of *Phoradendron* embryo are papillose. Similar cellular projections observed in other species of parasitic plants probably enable the naked seed to secure a better hold on the host during germination (Werker 1997).

Acknowledgments

We thank CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil) and Fundação Araucária (Paraná, Brazil), for financial support. The authors are grateful to Dr. Henrique H. Tozzi, for critical review of early versions of the manuscript.

References

Ashworth, V.E.T.M. 2000. Phylogenetic relationship in Phoradendreae (Viscaceae) inferred from three regions of the nuclear ribosomal cistron. I. Major lineages and paraphyly of *Phoradendron*. Systematic Botany 25: 349-370.

Barroso, G.M.; Morim, M.P.; Peixoto, A.L. & Ichaso, C.L.F. 1999. Frutos e sementes-morfologia aplicada à sistemática de dicotiledôneas. UFV, Viçosa. 443p.

Berlyn, G.P. & Miksche, J.P. 1976. Botanical microtechnique and citochemistry. The Iowa State University Press, Ames. 326p.

BFG. 2015. Growing knowledge: an overview of Seed Plant diversity in Brazil. Rodriguésia 66: 1085-1113.

Billings, F.H. 1933. Development of the embryo-sac in *Phoradendron*. Annals of Botany 47: 261-278.

Bouman, F. 1984. The ovule. *In*: Johri, B.M. (ed.). Embryology of angiosperms. Springer-Verlag, Berlin. Pp. 123-157.

Calvin, C.L. 1966. Anatomy of mistletoe (*Phoradendron flavescens*) seedlings grown in culture. Botanical Gazette 127: 171-183.

Cannon, W.A. 1901. The anatomy of *Phoradendron villosum* Nutt. Bulletin of the Torrey Botanical Club 28: 374-390.

Cazetta, E. & Galetti, M. 2007. Frugivoria e especifidade por hospedeiros na erva-de-passarinho *Phoradendron rubrum* (L.) Grised (Viscaceae). Revista Brasileira de Botanica 30: 345-351.

Corner, E.J.H. 1976. The seeds of dicotyledons Vol. 1. Cambridge University Press, Cambridge. 311p.

Douglas, G. 1944. The inferior ovary. Botanical Review 10: 125-186.

Douglas, G. 1957. The inferior ovary. II. Botanical Review 23: 1-46.

Eames, A.J. 1961. Morphology of angiosperms. McGraw-Hill, New York. 518p.

Fahn, A. 1990. Plant anatomy. 4th ed. Pergamon Press, Oxford. 588p.

Gedalovich, E.; Kuijt, J. & Carpita, N.C. 1988. Chemical composition of viscin, an adhesive involved in dispersal of the parasite *Phoradendron californicum* (Viscaceae). Physiological and Molecular Plant Pathology 32: 61-76.

Gedalovich-Shedletzky, E.; Delmer, D.P. & Kuijt, J. 1989. Chemical composition of viscin mucilage from three mistletoe species-a comparison. Annals of Botany 64: 249-252.

Gomes-Sánchez, M.; Sánchez-Fuentes, L.J. & Salazar-Olivo, L.J. 2011. Anatomía de especies mexicanas de los géneros *Phoradendron* y *Psittacanthus*, endémicos del Nuevo Mundo. Revista Mexicana de Biodiversidad 82: 1203-1218.

Gerrits, P.O. 1991. The application of glycol methacrylate in histotechnology; some fundamental principles. University Groningen, The Netherlands. 326p.

Guaraldo, A.C.; Boeni, B. & Pizo, M.A. 2013. Specialized seed dispersal in epiphytic cacti and convergence with mistletoes. Biotropica 45: 465-473.

Hertel, R.J.G. 1959. Contribuições para a fitologia teórica II. Algumas concepções na carpologia. Humanitas 4: 1-43.

Jensen, W.A. 1962. Botanical histochemistry (principles and practice). W.H. Freeman and Company, San Francisco. 408p.

Johansen, D.A. 1940. Plant microtechnique. McGraw-Hill, New York. 523p.

Jones, B.L. & Gordon, C.C. 1965. Embryology and development of the endosperm haustorium of *Arceuthobium douglasii*. American Journal of Botany 52: 127-132.

Judd, W.S.; Campbell C.S.; Kellogg, E.A.; Stevens, P.F. & Donoghue, M.J. 2002. Plant systematics - a phylogenetic approach. 2nd ed. Sinauer Associates, Sunderland. 576p.

Karnovsky, M.J. 1965. A formaldehyde-glutaraldehyde fixative of high osmolatily for use in electron microscopy. Journal of Cell Biolgy 27: 137-138.

Kuijt, J. 2003. Monograph of *Phoradendron* (Viscaceae). Systematic Botany Monographs 66: 1-643.

Mauseth, J.D. 1988. Plant anatomy. The Benjamin/Cummings Publishing Company, Menlo Park. 560p.

Meerow, A.W. & Snijman, D.A. 2001. Phylogeny of Amaryllidaceae tribe Amaryllideae based on *nrDNA ITS* sequences and morphology. American Journal of Botany 88: 2321-2330.

Nickrent, D.L.; Malécot, V.; Vidal-Russell, R. & Der J.P. 2010. A revised classification of Santalales. Taxon 59: 538-558.

O'Brien, T.P.; Feder, N. & McCully, M.E. 1964. Polychromatic staining of plant cell walls by toluidine blue O. Protoplasma 59: 368-373.

Rawlins, T.E. & Takahashi, W.N. 1952. Technics of plant histochemistry and virology. The National Press, Millbrae. 125p.

Restrepo, C.; Sargent, S.; Levey, D.J. & Watson, D.M. 2002. The role of vertebrates in the diversification of new world mistletoes. *In*: Levey, D.J.; Silva, W.R. & Galetti, M. (ed.). Seed dispersal and frugivory: ecology, evolution and conservation. CABI, New York. Pp. 83-98.

Richardson, I.B.K. 1993. Loranthaceae. *In*: Heywood, V.H. (ed.). Flowering plants of the world. Oxford University Press, Oxford. Pp. 174-175.

Rigon, J. & Cervi, A.C. 2013. O gênero *Phoradendron* Nutt. (Viscaceae) no estado do Paraná, Brasil. Pesquisa Botânica 64: 15-38.

Roth, I. 1977. Fruits of angiosperms. *In*: Linsbauer, K. (ed.). Encyclopedia of plant anatomy. Vol. 10. Gebrüder Borntraeger, Berlin. 522p.

Ruzin, S.E. 1999. Plant microtechnique and microscopy. Oxford University Press, New York. 322p.

Sass, J.E. 1951. Botanical microtechnique. Iowa State College Press, Iowa. 228p.

Singh, B. 1964. Development and structure of angiosperm seed-I. Review of the Indian work. Bulletin of the National Botanic Gardens 89: 1-115.

Smith, F.H. & Smith, E.C. 1942. Anatomy of the inferior ovary of *Darbya*. American Journal of Botany 29: 464-471.

Souza, L.A. 2006. Fruto. *In*: Souza, L.A. (org.). Anatomia do fruto e da semente. Editora UEPG, Ponta Grossa. Pp. 11-123.

Spujt, R.W. 1994. A systematic treatment of fruit types. Memoirs of the New York Botanical Garden 70: 1-182.

Stevens, P.F. 2001. Angiosperm phylogeny website. Version 12, July 2012 [continuously updated since]. Disponível em <http://www.mobot.org/MOBOT/research/APweb/>. Acesso em 6 abril 2015.

Vijayaraghavan, M.R. & Prabhakar, K. 1984. The endosperm. *In*: Johri, B.M. (ed.). Embryology of angiosperms. Springer, Berlin. Pp. 319-376.

Werker, E. 1997. Seed anatomy. Gebrüder Borntraeger, Berlin. 424p.

Artigo recebido em 25/06/2015. Aceito para publicação em 20/10/2015.