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CELLULAR AND MOLECULAR BIOLOGY

Anatomy and development of the edible fruits of *Cordiera concolor* (Rubiaceae)

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Abstract: A comprehensive study on the fruit anatomy and development of *Cordiera concolor* was carried out to establish the origin of the gelatinous tissue surrounding the seeds at maturity. *Cordiera* currently belongs to tribe Cordiereae, forming part of the species-rich lineage called Gardenieae complex. Most genera of Gardenieae complex has many-seeded fleshy fruits, with seeds usually imbedded in a pulp, which historically was considered of a placental nature. For the histological analyses, fruits at different stages of development were fixed in formalin-acetic acid-alcohol and examined with light microscopy. The endocarp has no woody consistency, it is what classifies a fruit as berry. The pericarp is differentiated into three histological zones: 1) the exocarp, formed of the epidermis and the sub-epidermal tannin cells, 2) the mesocarp, consisting of parenchyma with tannins and druses, and 3) the endocarp, derived from the internal epidermis of the ovary. The placental tissue has little development during the formation of the pericarp. We concluded that the gelatinous tissue surrounding the seeds in the ripe fruit is formed of the mesocarp and endocarp. The present results disagree with the widely accepted conception of the placental origin of the gelatinous pulp surrounding the seeds in Gardenieae Complex species.

Key words: berry, endocarp, exocarp, gelatinous pulp, mesocarp, placental pulp.

INTRODUCTION

The fruit is a unique structure of angiosperms that develops from the gynoecium of the flower as the result of pollination, and it has the function of protecting the seed and providing constant conditions and nutrition, and also to guarantee successful dissemination (Roth 1977, Bobrov & Romanov 2019).

In Rubiaceae the fruits are derived from an inferior, bilocular ovary, with one or many ovules in each locule. The fruits have simple forms, e.g. spherical, ellipsoid, ovoid or obovoid, the most common colors being red, yellow, orange or blackish (Robbrecht 1988). They are usually small with fruits of more than 5 cm in length being rare and mainly found in Gardenieae complex. (subfamily Ixoroideae; Bremer & Eriksson 2009, Mouly et al. 2014). In this group, the African genus *Rothmannia* Thunb. stands out with fruits that reach 15-20 cm in length (Hallé 1967). There is a great variability of fruits in the family, ranging from dry to fleshy, in which the nature of the mesocarp and endocarp determine different types: capsules, nuts, drupes or berries (Robbrecht 1988, Bremer & Eriksson 1992). The type of fruit is of great taxonomic importance, Robbrecht (1988) used carpological characters to establish classifications within the Rubiaceae. In particular, some tribes in subfamily Ixoroideae were partially delimited on the basis of fruit characteristics, e.g. distinguishing between drupes and berries (Robbrecht & Puff 1986, Bremer & Eriksson 1992).

Cordiera genus belong to the Gardenieae complex, which is a morphologically very diverse group (ca. 100 genera). In this complex are included genera historically related to the former tribe Gardenieae and other morphological similar taxa. Bremer & Eriksson (2009) have demonstrated the polyphyletic nature of the tribe Gardenieae (sensu Candolle 1830, Robbrecht & Puff 1986). As delimited by Mouly et al. (2014), Gardenieae complex is a monophyletic group, which comprises several morphological and molecular well resolved clades. One of these clades, the *Alibertia* group, was recognized at the tribal level resurrecting the old Candolle's name Cordiereae.

Some groups in Gardenieae complex have berries of different colors (Hallé 1967). Also, there is a particular type called "*Gardenia* fruits" (Robbrecht & Puff 1986), which presents coriaceous, fibrous or woody endocarp, and mesocarp with the seeds embedded in a juicy or fleshy pulp of placental origin at maturity. Later authors described the Gardenia type fruit following mostly the same principles (Eriksson & Bremer 1991, Persson 1995, 2000, Bremer & Eriksson 1992, 2009, Sonké et al. 2005, Andreasen & Bremer 2000). The exocarp may be gray or brown at maturity, sometimes with lenticels; or it may be yellow, orange, or purplish red, which attracts birds and small mammals (Hallé 1967).

At flowering stage, often completely envelop the ovules. They continue to grow during the development of the fruit, immersing the seeds in a juicy or fleshy pulp (Hallé 1967). These fruits, characterized by a pulp of placental origin surrounding the seeds, have been widely mentioned in different genera of the tribe, but exclusively in a taxonomic context, as is the case for *Agouticarpa* C.H. Perss. (Persson 2003), *Amaioua macrosepala* C.H.Perss. & E.Méndez-Varg. (Persson & Méndez 2015), *Duroia* L.f. (Hallé 1967), *Euclinia* Salisb (Hallé 1967), *Gardenia* J. Ellis (Puttock 1988, Wong & Low 2011, Low 2013), *Polycoryne* Keay (Hallé 1967), and *Randia* L. (distinguishable from other species because the pulp turns dark when dry; Hallé 1967, Gustafsson 2000, Gustafsson & Persson 2002), among others. Rodriguez (1976) mentioned that in species of *Genipa* L. the fruits present the coriaceous and lignified endocarp and many seeds embedded in a fleshy mass, but he does not mention the origin of this mass nor makes histological studies of it.

However, in many genera of the Gardenieae complex, it is difficult to differentiate the pulp of the placenta from the wall of the fruit because they have almost the same structure, and the endocarp in between is almost indistinguishable (Robbrecht & Puff 1986, Sonké et al. 2005). The fruits of this group stand out because they have many uses (Hallé 1967), the pericarp can be consumed (*Atractogyne* Pierre, *Euclinia*, *Gardenia*, *Genipa*, *Posoqueria* Aubl., *Rothmannia*, *Sherbournia* G. Don, etc.), the placental tissue is used as a dark blue (*Genipa*, in America) or black dye (*Rothmannia*, in Tropical Africa). In West Africa the woody endocarp of *Gardenia imperialis* K.Schum. is used as a spoon (Hallé 1967). According to Persson & Delprete (2017), the most, or perhaps all fruits of *Cordiera* A. Rich. are edible by humans.

Cordiera, type genus of the tribe Cordiereae, has ca. 25 species distributed from Panama to Bolivia, southern Brazil and northern Argentina (Delprete 2010, Persson & Delprete 2010). Commonly, *Cordiera* species have small fleshy fruits (Delprete & Persson 2004, Persson et al. 2004, Persson & Delprete 2010). Until now, the fruits have only been studied in a few species of *Cordiera*, the only anatomical work being that of Matsuoka (2008) who classified them as berries. *Cordiera concolor* (Cham.) Kuntze is a typical tree of the dense, shady forest of the Atlantic coast, from Brazil to Argentina and Paraguay (Delprete et al. 2004). The species is dioecious (Delprete et al. 2004, Judkevich in press) and it is widely known as "Marmeladinha" in Brazil for its sweet, edible fruits (Persson & Delprete 2017).

The present study aims to describe the morphology and structure of the fruit of *Cordiera concolor* in different stages of development, and to establish the origin of the pulp surrounding the seeds in the mature fruit.

MATERIALS AND METHODS

Mature flowers and fruits at successive developmental stages were photographed in the field and preserved in FAA 70 (5 ml formalin, 5 ml acetic acid, and 90 ml 70% ethanol). Voucher are deposited in the "Carmen L. Cristobal" Herbarium (CTES): *Cordiera concolor*. ARGENTINA. PROV. MISIONES: Dpto. San Ignacio, Teyú Cuaré, 01 Mar 2013, flowers and fruits (from female plant), M. D. Judkevich & R. M. Salas 11. Idem, 23 Apr 2016, flowers and fruits (from female plant), M. D. Judkevich & R. M. Salas 74.

For anatomical observations, fixed flowers and fruits were dehydrated and embedded in paraffin (Johansen 1940, modified by Gonzalez & Cristóbal 1997) and then cut into 12-15 μm sections using a Microm HM350 rotary microtome (Microm International, Walldorf, Germany). Cross sections were stained with safranin and astra blue (Luque et al. 1996) and mounted in synthetic Canada balsam. Observations and digital images were acquired using a Leica DM LB2 (Leica Microsystems) light microscope (LM) equipped with a Leica DATA digital camera. The presence of lignin and crystals was confirmed by observation with polarized filters.

Samples of cross-sectioned fruits in different developmental stages also were subjected to the following reagents: Lugol for detection of starch, ferric chloride for tannins, and Sudan III for lipids (Johansen 1940).

RESULTS

Cordiera concolor has plants with male flowers (Fig. 1a) and plants with female flowers (Fig. 1b) which are distinguished at first sight by the larger diameter of the ovarian region. The fleshy fruits (Fig. 1c) are of the berry type of an inferior ovary, globose, 7.0 to 12.0 mm in diameter, violet-black at maturity, glabrous to puberulent (Fig. 1d). The fruits have 1-8 seeds, which are embedded in a gelatinous pulp of blackish-brown color (Fig. 1e).

Anatomy and development of the fruit

The ovary (Fig. 2a-c) is inferior, bicarpellar, and surrounded by the remaining floral pieces welded into a floral tube. It has diffused axillary placentation with two placentas occupying the entire volume of the locules (Fig. 2b). In this type of placentation, the growth of the placenta is continuous and occurs at the same time as the differentiation of the ovules (personal observation). There are 5-7 ovules immersed in each placenta (Fig. 2b). The septum is formed of parenchymatic cells of circular contour and contains idioblasts with calcium oxalate druses (Fig. 2c) and idioblasts with tannins (Fig. 2e-h).

Anatomically, the wall of the ovary is formed of an epidermis of quadrangular to rectangular cells, interspaced with stomata, and sparse, small lignified unicellular trichomes (Fig. 2d). In the mesophyll there are two zones, an external vascularized zone, which occupies practically the entire thickness of the mesophyll and is formed of polygonal cells; and an internal zone with fewer vascular bundles formed of a few layers of elongated cells, arranged periclinally around the locules (Fig. 2e). The external vascular bundles correspond to the floral tube and the internal bundles correspond to the carpels. A large number of the cells in the mesophyll has tannins and druses. The internal epidermis (Fig. 2e) is formed of rectangular cells smaller than

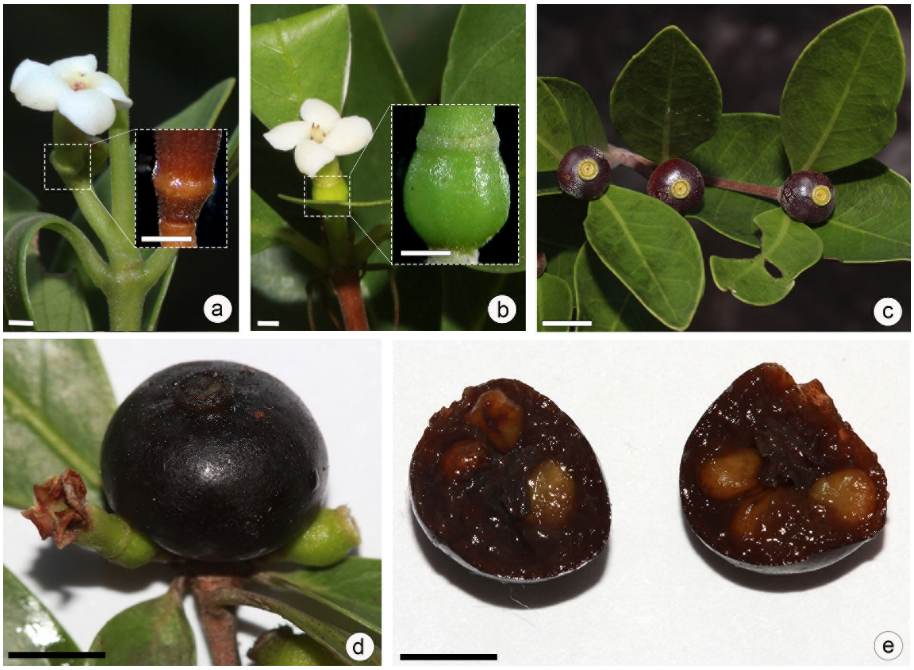

Figure 1. **Flowers and mature fruits of *C. concolor*. a. Branch with male flower and detail of the ovary (fixed material). b. Branch with female flower and detail of the ovary. c. Branch with fruits. d. Fruit flanked by faded flower and undeveloped fruit. e. Cross section of the fruit showing the pulp between the seeds. Scales: a-b= 1 mm; c= 1 cm; d-e= 5 mm.**

those of the external epidermis and is without any stomata or trichomes.

When young, the fruits have a yellowish-green color (Fig. 2f-h). In the first stages of fruit development the external epidermal cells increase in volume anticlinally and the cytoplasm becomes dense. Anatomically, in the immature fruit, the two zones described in the mesophyll of the ovary and corresponding to the mesocarp are well defined (Fig. 2h). The main change is observed in the internal zone of the mesophyll, where the cells increase in size and grow radially. Protuberances (Fig. 2h) are formed, occupying the space between the developing seeds and the placentas. No formation of new vascular bundles occurs and there are few cells with tannin compared with the external layer (Fig. 2h). At this stage a slight growth of the placenta is observed. As the seeds grow, they emerge from the placental tissue (Fig. 2g).

At an older stage, the fruit becomes yellow to reddish (Fig. 3a). Morphologically it is globular and of firm consistency (Fig. 3a). Anatomically, in the mesocarp, both the cells in the external and internal regions increase in volume which leads to an increase in the size of the fruit (Fig. 3b-c). The epidermal cells have thicker walls than in the previous stage and the cuticle is more notable (Fig. 3d).

The seeds increase in size due to the formation of abundant endosperm (Fig. 3b, e). Unlike what happens at anthesis, where the placenta is found enveloping the ovules, at this stage, where there is no increase in the size or number of cells in the placenta, it becomes restricted to the base of the seeds. The cells of the septum decrease in volume (Fig. 3b, e).

The mature fruit (Fig. 4a-f) is blackish and has a globular shape (Fig. 4a). The skin of the fruit or exocarp (in the broad sense) is made up of the epidermis and 2-4 subepidermal layers of cells with thickened walls and containing tannins in the cell lumina (Fig. 4c-d). The epidermis is covered by a conspicuously thickened cuticle, and some simple unicellular trichomes remain (Fig. 4e).

The mesocarp is fleshy. The inner and outer regions of the mesocarp, distinguishable in

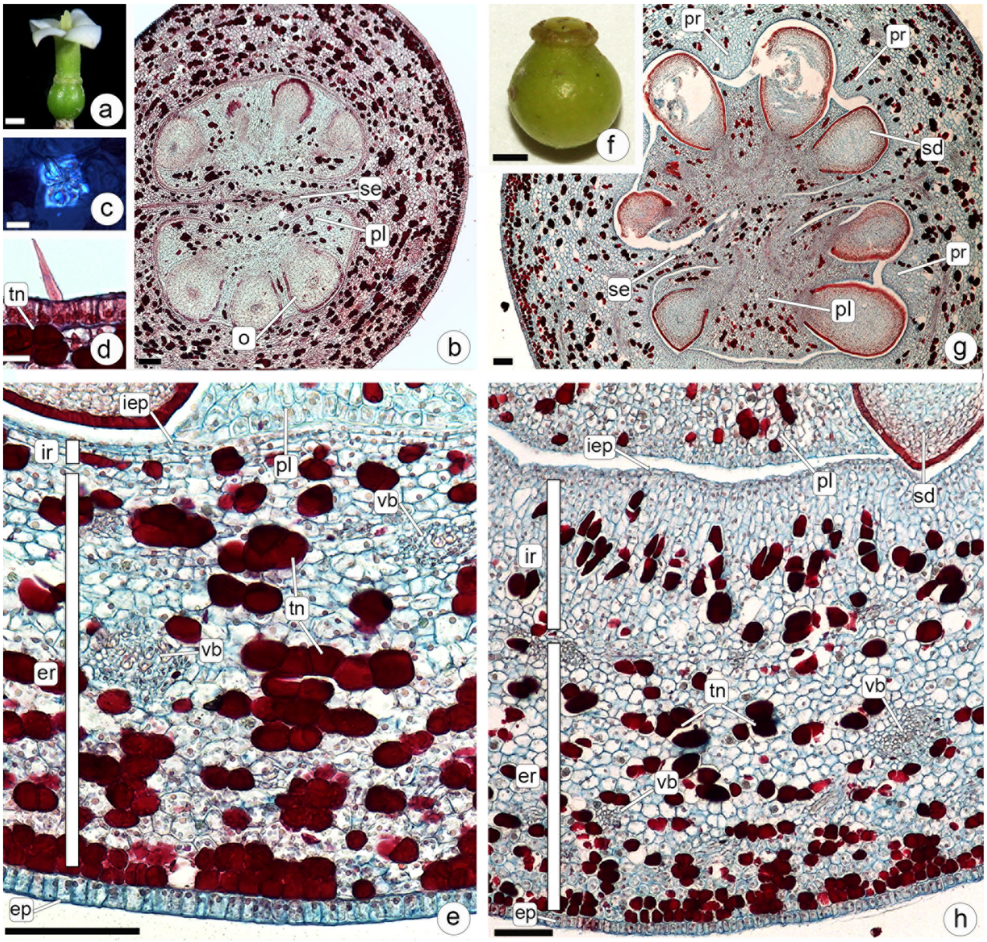

Figure 2. Anthetical flower (a-e) and young fruit (f-h). A. Female flower. b. Cross section of the ovary. c. Druse observed with polarized light. d. Detail of a trichome. e. Ovary. f. Young fruit. g. Cross section of the young fruit. h. Detail of the pericarp. Abbreviations: ep= external epidermis; er= external region of mesocarp; iep= internal epidermis; ir= inner region of mesocarp; o= ovule; pl= placenta; pr= mesocarp protrusions; sd= seed; se= septum; tn= tannin cell; vb= vascular bundle. Scale: a, f= 1 mm; b, e, g-h= 100 µm; C-D= 10 µm.

the young fruit, are no longer discernible; the cells of the mesocarp remain thin-walled and acquire greater volume. The same applies to the mesocarp cells in the protrusions penetrating the gaps between the seeds (Fig. 4b-c). The endocarp is formed of the cells of the internal epidermis, some of these cells may be crushed (Fig. 4c).

The placenta retracts due to the collapse of its cells and the increase in the size of the seeds (Fig. 4f). The cells of the septum lose their shape and idioblasts with fragmented tannins are observed.

Histochemistry of the fruit

In the anatomical preparations stained with Astra blue, no mucilage was discerned. Lugol was positive in the cells of both regions of the mesocarp (Fig. 5a-f), with a higher content of starch grains in the cells belonging to the outer region of the mesocarp (Fig. 5d-f). As the fruit develops, the amount of starch in the mesophyll is maintained in the form of single grains (Fig. 5f). Ferric chloride was positive for cells with tannins at all stages of fruit development (Fig. 5a, d, g-i). Sudan III was only positive in the cuticle (Fig. 5g-i).

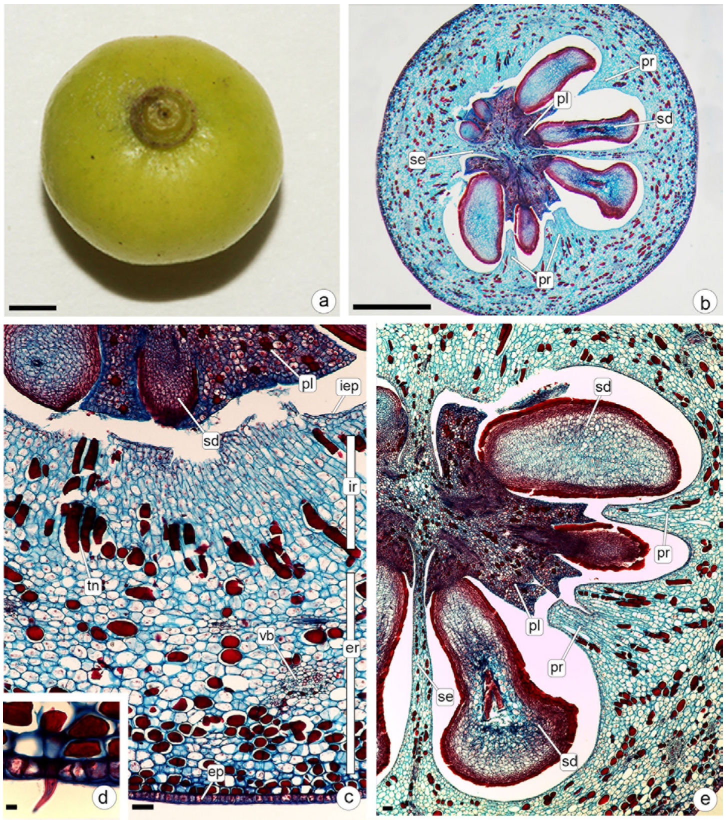

Figure 3. Fruit at older stage. a. Apical view of fruit. b. Cross-section of fruit. c. Transection of pericarp. d. Detail of the external epidermis. e. Detail of one locule, showing seeds, remains of placenta and protrusions from mesocarp. Abbreviations: ep= external epidermis; er= external region of mesocarp; iep= internal epidermis; ir= inner region of mesocarp; pl= placenta; pr= mesocarp protrusions; sd= seed; se= septum; tn= tannin cell; vb= vascular bundle. Scale: a, b = 1 mm; c, e= 50 µm; d= 10 µm.

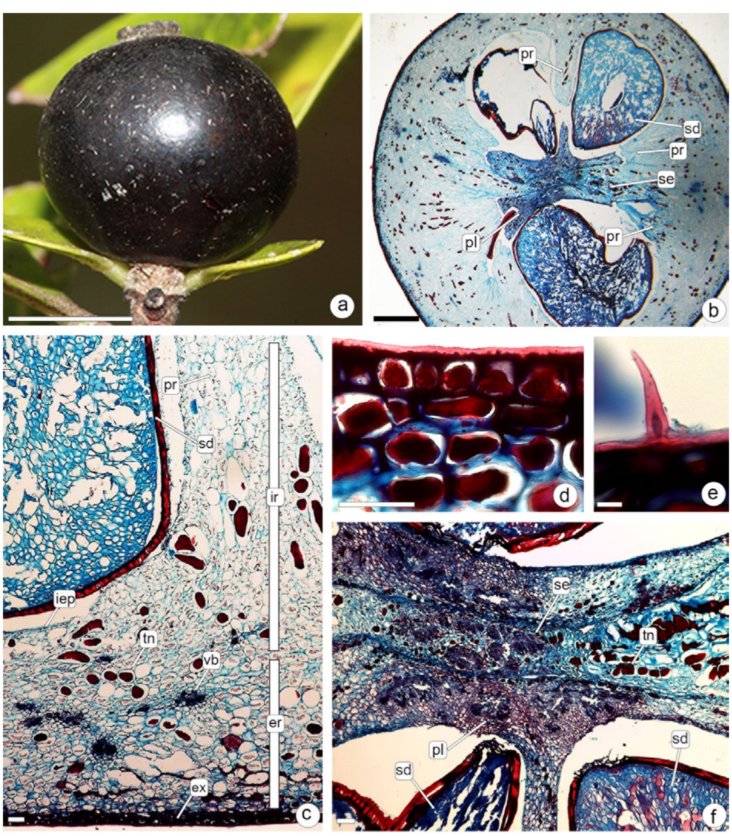

Figure 4. Mature fruit. a. Fruit. b. Cross-section of fruit. c. Fruit wall. d. External epidermis. e. Trichome. f. Septum and placenta. Abbreviations: er= external region of mesocarp; ex= exocarp; iep= internal epidermis; ir= inner region of mesocarp; pl= placent; pr= mesocarp protrusions; sd= seed; se= septum; tn= tannin cell; vb= vascular bundle. Scales: a= 5 mm; b= 1 mm; c-d= 50 µm; e= 10 µm; f= 100 µm.

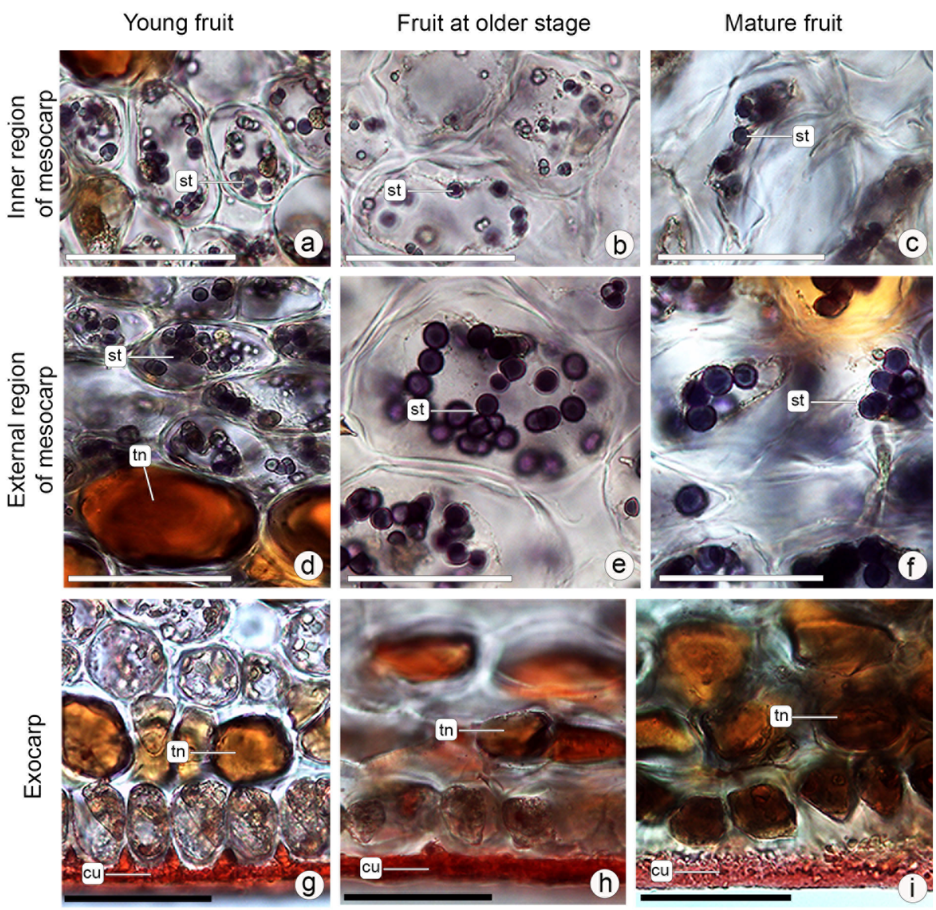

Figure 5. Histochemistry of the fruit of *C. concolor*. a-i. Ferric chloride. a-f. Lugol. g-i. Sudan III. Abbreviations: cu= cuticle; st= starch; tn= tannin. Scale: 50 µm.

DISCUSSION

During the development of the fruit, the wall of the ovary is developed into the pericarp. In fruits derived from flowers with an inferior ovary, the extracarpellar tissues also participate, either as part of the fruit in the case of a pome or berry or as part of the "skin" or "peel" as in a pseudo-berry, whose most representative example is the banana (Roth 1977, Weberling 1989). In the mature fruit of *Cordiera concolor* we described the exocarp in a broad sense formed by the epidermis with a thickened cuticle and a few layers of subepidermal tannin cells which give the skin of the fruit its characteristic dark color.

The fruit of *C. concolor* is described as a berry or bayoid in taxonomic descriptions (Delprete 2010). Berries are indehiscent fleshy fruits, composed mainly of parenchyma (Roth 1977, Bobrov & Romanov 2019). According to Roth (1977) these fruits have a pericarp formed of a pigmented exocarp, composed of the epidermis and the subepidermal tissues, a mesocarp that can be differentiated in different layers and a uni-stratified endocarp only composed of the internal epidermis. These characteristics of a berry type fruit coincide with those found in the fruits of *C. concolor*. However, given that in this species the fruit is derived from an inferior ovary, the term that should be applied to the fruit of *C. concolor* is "a berry of an inferior ovary" following Fahn (1985), to differentiate it from the typical berry derived from flowers with superior ovaries.

As for the nature of the pulp surrounding the seeds in the fruits of the Gardenieae complex, few studies describe which tissue was found. According to Hallé (1967) in the mature fruits of *Duroia* (Cordiereae), *Euclinia* (Gardenieae *s.s.*), *Polycoryne* (now known as *Pleiocoryne* Rauschert, Gardenieae *s.s.*) and *Randia* (Gardenieae *s.s.*) it is the placenta that decomposes, forming a semi liquid mucilaginous pulp of black or brown color with a scent of alcoholic fermentation. However, he did not study the ontogeny of the fruit to affirm that hypothesis. At first sight it is difficult to differentiate the pulp of the fruit wall from the placenta in the mature fruit of *C. concolor,* as mentioned in many genera of Gardenieae complex (Robbrecht & Puff 1986, Sonké et al. 2005). However, it was possible to determine in the anatomical sections that the gelatinous tissue in which the seeds are embedded mainly corresponds to the mesocarp (Fig. 6).

The presence of a gelatinous pulp in the fruit of *C. concolor* is not enough to include it among the so-called "*Gardenia* fruits" that have been described in the Gardenieae *s.l.* (Robbrecht & Puff 1986, Eriksson & Bremer 1991, Bremer & Eriksson 1992). This type of fruit is characterized by the presence of coriaceous, fibrous or woody endocarp, with the seeds embedded in a pulp of placental origin at maturity. In contrast, *C. concolor* has a fleshy endocarp and the pulp is formed by part of the pericarp.

Matsuoka (2008) described the fruits of four species of *Cordiera* and two species of the closely related genus *Alibertia* A. Rich. (Cordiereae). They have globose and succulent berries, only *Alibertia edulis* (Rich.) A. Rich. has a ligneous appearance. Although Matsuoka (2008) mentions that the seeds are immersed in a gelatinous pulp, he does not define to which tissue it corresponds, and it is not possible to determine it through an interpretation of the photographs of this work since it does not show the region of the fruit where the seeds are immersed. Therefore, only in *Cordiera concolor*

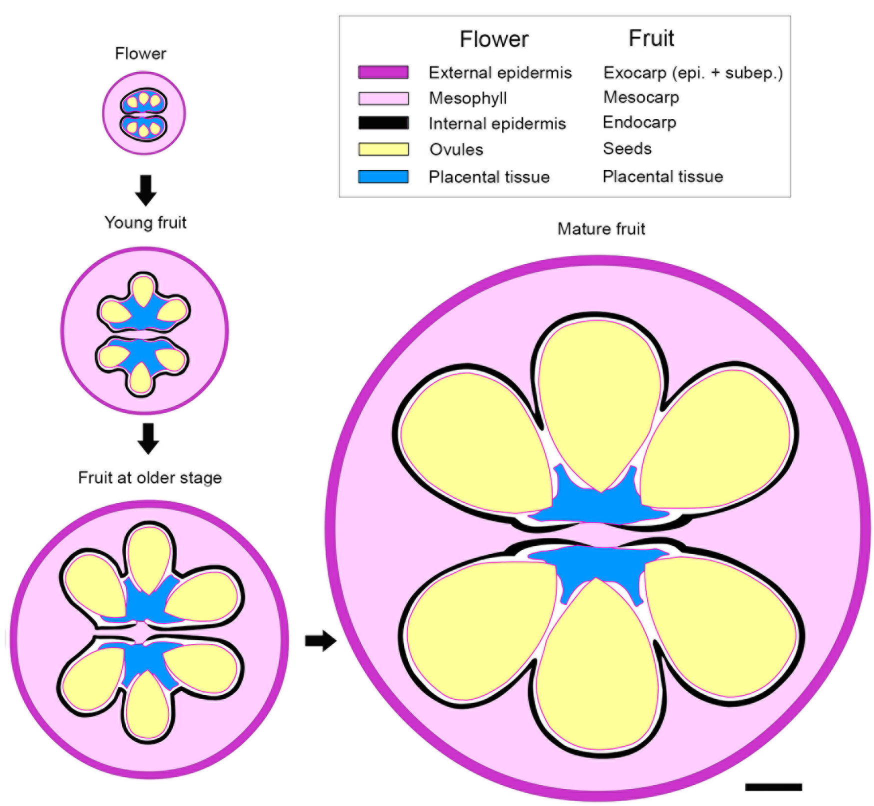

Figure 6. Diagram of the flower and the different stages of development of the fruit of *C. concolor* showing the growth of the different tissues and the retraction of the placentas. Abbreviations: epi. = external epidermis; subep.= subepidermal layers. Scale: 1 mm.

it is possible to ensure that the pulp originates from the mesocarp/endocarp and not the placenta.

In the mature fruits of *Duroia*, *Euclinia*, *Polycoryne*, and *Randia*, Hallé (1967) proposed that the decomposed placental tissue would protect the seeds from drying out and would ensure that fruit-eating animals were attracted. In *Gardenia* it has been mentioned that the fruit divides irregularly when ripe, exposing the seeds immersed in a bright orange-red flesh of placental origin, which is attractive to birds (Wong & Low 2011, Low 2013). In the case of *Cordiera concolor*, the pulp would serve to keep the seeds hydrated, and the dispersers would be attracted by the color of the exocarp. According to Eriksson & Bremer (1991), the dispersal of fleshy fruits in Rubiaceae is facilitated by birds and mammals. In *C. concolor*, the fruits are consumed by birds and bats, and are also eaten by people (Coimbra Molina 2014, Persson & Delprete 2017).

Histochemical tests confirmed the presence of starch and tannins in the fruit. Starch plays a key role in the carbon balance of most plants (MacNeill et al. 2017). On the other hand, tannins are polyphenolic substances of plant origin (Khanbabaee & van Ree 2001). They are dissolved in the vacuolar sap of some parenchymatic cells or in specialized cells like idioblasts (Montes-Ávila et al. 2018). In the fruit of *C. concolor* the starch is found in the cells of mesocarp, while tannins are distributed in the form of idioblasts in all its tissues. In the Rubiaceae, the presence of tannins is common in different plant organs (Dias Souza et al. 2013, Martínez-Cabrera et al. 2014, Judkevich et al. 2017, Jiménez Ortega et al. 2020). Both starch and tannin were also described in the fruits of *Cordiera* species analyzed by Matsuoka (2008). Some authors (Lytovchenko et al. 2011, Pattison et al. 2015, Cerri & Reale 2020) suggest that in berries the presence of starch in the parenchymal tissue surrounding the seed may play an active role in CO2 uptake and in the supply of carbon assimilates to the seed. On the other hand, given that tannins are attributed with antifungal, antioxidant, and antibacterial properties (Sofiane et al. 2015, Maisetta et al. 2019), it is important to record that the fruits in *Cordiera concolor* have a considerable amount of tannin, at least that is what is seen in the histological sections.

In conclusion, in the present study of the fruits of *Cordiera concolor*, it was possible to determine that the gelatinous mass in which the seeds are found mainly corresponds to the mesocarp and endocarp, with scarce participation of the placentas. Similar studies of fruits of other member of Gardenieae complex are needed in order to clarify whether in these fruits the pulp is of placental nature as described in historical literature or rather of mesocarp/endocarp nature as observed here in *Cordiera concolor*.

Acknowledgments

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Author contributions

MDJ and RMS collected the vegetal material. RMS provided the field photos. MDJ processed the plant material to make the histological preparations, took the microscopy photos, and prepared the figures and drawings. MDJ and AMG performed the anatomical interpretations and the discussions.