Structural diversity of fruits: conceptual reflexions and taxonomic implications

Diversidade estrutural de frutos: reflexões conceituais e implicações taxonômicas

DOI:10.34117/bjdv7n7-218

Recebimento dos originais: 07/06/2021
Aceitação para publicação: 02/07/2021

Luiz Antonio de Souza
Doutor em Botânica pela Universidade de São Paulo (USP), São Paulo
Universidade Estadual de Maringá Av. Colombo, 5790, 87020-900, Maringá, Paraná, Brasil.
E-mail: lasouza@uem.br

ABSTRACT

Fruit either originates solely from the ovary or ovary and other floral parts and inflorescence. Besides the ovary itself, the pedicle, bracteoles, receptacle, hypanthium, sepals, petals and inflorescence axis are included in the fruit development. Analysis was made in embedded historesin/paraffin material and sectioned in microtome. In the fruit ontogeny the pericarp either may be non-multiplicative or multiplicative. In the first case, the ovary wall differentiates in pericarp without the installation of meristem. Adaxial, middle or abaxial meristems can be installed in the multiplicative pericarp fruits from the periclinal cell divisions that occur in both the epidermis and the ovary mesophyll. Separation tissue takes place in the carpel margins and midrib in dehiscent fruits or it can remain as residual tissue in indehiscent fruits. Fruit classification is complex, and it may show divergence in nomenclature among fruit specialists. Structural fruit ontogeny can be a useful tool for its classification. Fruit structure has been used as diagnostic character of species, genera and tribes of angiosperms. Hypothesis about fruit evolution indicates that apocarpic fruit with follicles can be a basic evolutionary condition, at least among the *sensu lato* dicots. The *Araucaria angustifolia* pine seed is considered here as a fruit with protocarps/spermatocarps.

Keywords: Accessory fruit parts; Dehiscence; Diagnostic feature; Fruit ontogeny; Pericarp; Protocarp

RESUMO

O fruto se origina somente do ovário, ovário e outras partes florais ou da inflorescência. Além do ovário, o pedicelo, bractéolas, receptáculo, hipanto, sépalas, pétalas e eixo da inflorescência podem participar do desenvolvimento do fruto. A análise foi feita em material emblocado em historresina/parafina e secionado em micrótomo. Na ontogenia do fruto, o pericarpo pode ser multiplicativo ou não-multiplicativo. No primeiro caso, a parede do ovário se diferencia em pericarpo sem a instalação de meristema. Meristemas adaxial, médio e abaxial podem ser instalados nos frutos de pericarpo multiplicativos, a partir de divisões celulares periclinais que ocorrem em ambas as faces da epiderme e mesofilo do ovário. O tecido de separação ocorre nas margens carpelares e na nervura central em frutos deiscentes ou ele pode permanecer como tecido residual nos frutos indeiscentes. A classificação de frutos é complexa e pode mostrar divergência de nomenclatura entre os especialistas de frutos. A ontogenia estrutural de frutos pode ser uma ferramenta útil para sua classificação. A estrutura de frutos tem sido usada como caractere diagnóstico de espécies, gêneros e tribos de angiospermas. Hipótese sobre evolução de frutos indica que o fruto apocárpico com folículos pode ser uma condição básica evolutiva, pelo menos entre as dicotiledôneas *sensu lato*. A pinha (estróbilo) de *Araucaria angustifolia* é considerada aqui como fruto com protocarpos/espermatocarpos.

Palavras-chave: Deiscência; Caractere diagnóstico; Ontogenia do fruto; Partes acessórias do fruto; Pericarpo; Protocarpo.

1 INTRODUCTION

The concept of fruit has varied among different authors (Roth, 1977). The fruit definition as "flower in the state of seed maturation" (Knoll, 1939) was adopted in the classic book on fruits (Roth, 1977), in which the fruit develops from the flower as a complex unity (carpels and other floral parts). There is a concept employed in the literature that is broader and more complex, which it was formulated by Spjut (1994): "a fruit is a propagative unit developing from one or more fertilized egg cells (or rarely by parthenocarpy) enclosed by integuments and attached to megasporophylls, or a megasporophyll scale complex, in a strobilus, cone, gynoecium, concrescent gynoecia, or gynoecia that disseminate together at the time it or its seed(s) are dispersed from the plant or just prior to germinate on the plant, and it may also include any other attached scales, bracts, modified branches, perianth, or inflorescence parts". In the Barroso et al.' (1999) book on fruit and seed morphology applied to the systematic of dicots, "the fruit is considered as the structure that represents the last stage of the development of fertilized or parthenocarpic gynoecium". Our conception of fruit may be less complete, but we consider it easier and simpler to be used in scientific studies of fruits, especially in angiosperms. Fruit for us is the ovary or ovaries developed and in a state of maturity, and other parts of the flower or even the inflorescence can be added to it.

Hitherto the various types of fruits have been defined and distinguished by different authors, fruit specialists or taxonomists, that have revealed controversies and interpretations that generate confusion in works that deal with fruits or use fruit features to characterize taxa. The literature has registered some classifications of fruits that show divergences in the denomination of fruits, which are reported by some authors (Spjut, 1999; Barroso et al., 1999; Souza, 2021). In view of these considerations, it is desirable that we have our fruit classification based on ontogeny (Souza, 2006; Souza, 2021).

This paper is a terminological reflection on structural diversity of fruits, based on its ontogeny, which can be useful in investigations that have taxonomic implications.

2 MATERIAL AND METHODS

Several types of fruits are included here, which result from our research carried out over four decades, in partnership with other fruit specialists and graduate/post-graduate students. The ovaries and fruits in developing were fixed in FAA 50 (formalin, acetic acid and ethanol) or glutaraldehyde, dehydrated through alcohol series, embedded in paraffin (Johansen, 1944) or hydroxymethacrylate (Guerrits, 1991), sectioned (cross- and longitudinal sections) with a rotary microtome, and stained with Safranin (Souza et al., 2016) or Toluidine Blue (O'Brien et al., 1964). Light microscope photographs were taken on Olympus BX50 and Leica EZ4D digital camera, and subsequently processed using the software a Zoom Browser EX 4.6 and Leica Application Suite version 1.8, respectively.

3 RESULTS AND DISCUSSION

3.1 ORIGIN AND TYPES OF FRUIT

Fruit develops from the ovary and accessory parts (perianth, floral receptacle, hypanthium, inflorescence axis) can participate in its formation. We can distinguish four classes of fruits, namely multiple, aggregate, schizocarp and simple fruits. Multiple fruits originate from inflorescences. *Maclura tinctoria* (L.) D. Don ex Steudel, Moraceae, has multiple fruit, in which it consists of fleshy perigone, inflorescence axis and achenes (Oyama and Souza, 2011).

The aggregate fruit comes from a single flower with apocarpous, pluricarpellary and pluripistillary gynoecium. Thus, the aggregate fruit is composed of several fruitlets which originate from pistils attached to the receptacle. *Aspidosperma polyneuron* Müll. Arg. (Souza and Moscheta, 1992) and *Asclepias curassavica* Griseb. (Souza et al., 2004) (Apocynaceae) have aggregate fruits with two follicle fruitlets. The pseudo-syncarpic fruit of *Victoria amazonica* (Poepp.) J. C. Sowerby also is aggregate fruit (Rosa-Osman et al., 2011).

Schizocarps (schizo, splitting) originate only from the ovary of a single flower. They are bicarpellar or pluricarpellar fruits that, when ripe, can separate into fragments called mericarps (meri, part or piece) usually unicarpellar. Mericarps can be dehiscent or indehiscent at maturity, each composed of one carpel with a single seed. Examples of schizocarpic fruits are those belonging to the family Rutaceae, as *Metrodorea nigra* A. St.-Hil. (Souza et al., 2008) and *Pilocarpus pennatifolius* Lem. (Souza et al., 2005), and Malvaceae, seen in *Sida* L. (Muneratto and Souza, 2013).

The simple fruits either are commonly originated from the ovary of a single unipistilated unicarpellar flower or syncarpic multicarpellar flower. In some fruits, other non-pericarpic parts, such as pedicel, perianth and hypanthium, may participate in their formation. There is a huge variety of simple fruits among the angiosperms, which consist of features that are used in their classification, such as water content in the pericarp, seed number, carpel number, type of dehiscence and others. There is a wide variety of simple fruits. They may be dry or fleshy, dehiscent or indehiscent, and they may originate from a superior or inferior ovary. A detailed classification of simple fruits was recently presented (Souza, 2021; Souza et al., 2021).

There is more complex terminology employed by Spjut (1994). This author distinguished two great groups of fruits, the Spermatocarpia and Eucarpia. In the first group the author includes the Araucariaceae, Cupressaceae, Zamiaceae and other taxa. The three classes of fruit proposed by us make up Spjut (1994)' Eucarpia. In another classification of fruits (Barroso et al., 1999) are distinguished the compound fruits (multiple fruits in our classification), multiple fruits (aggregate fruit for us) and simple fruits (schizocarpic and simple fruits).

3.2 FRUIT STRUCTURAL ONTOGENY

The fruits either can have non-multiplicative or multiplicative pericarp. In the first case the ovary wall that consists of outer epidermis, mesophyll and inner epidermis differentiates in the pericarp, which is composed of exocarp (originating from the outer epidermis), mesocarp (originating from the mesophyll) and endocarp (resulting from the differentiation of the ovary inner epidermis). In a number of cases, for example, the achene of *Alternanthera tenella* Colla and the utricle of *Amaranthus blitum* Linnaeus the pericarp is composed of the same number of cell layers as the ovary which collapse during the mature phase, except for the inner mesocarp, where U-thickened cell walls and crystals remain (Harthman and Souza, 2012). It has also been pointed out that *Chaetostoma armatum* (Spreng.) Cogn., *Microlicia confertiflora* Naudin (Figures a1, a2), *M. rugosa* R. Romero & Versiane, *Trembleya parviflora* (D. Don) Cogn. (Microlicieae, Melastomataceae) (Hernandes et al., 2020), and *Cordia trichotoma* (Vell.) Arrab. ex I. M. Johnst (Boraginaceae) (Souza, 2008) have fruits with non-multiplicative pericarp.

Adaxial (ventral) (Figure b1), middle or abaxial (dorsal) meristems may be installed in multiplicative pericarp fruits. They are meristems that add new cell-layers to the pericarp, can be located in the inner epidermis or subepidermal layers (mesophyll) (Figure b1), middle mesophyll or in outer epidermal, respectively, of the fertilized wall ovary. The meristematic activity of the inner epidermis and/or subepidermal layers occurs in legume of *Acacia paniculata* Willd. (Souza, 1993), follicle of *Lonchocarpus muehlbergianus* Hassler (Souza, 1984) (Figures b1, b2), and schizocarps of *Pilocarpus pennatifolius* Lem. (Souza et al., 2005) and species of *Sida* L. (Muneratto and Souza, 2013). A meristem is formed in the middle region of the ovary mesophyll of Bignoniaceae capsules, as in *Macfadyena unguis-cati* (L.) A. H. Gentry (Souza et al., 2008). The growth in thickness of the pericarp that originates from abaxial meristem is registered in *Eclipta alba* L. Hassk. (Batista and Souza, 2017).

The condition of fruits that have two meristems in the pericarp in developing deserves some attention. Fruits of Euphorbiaceae, as *Euphorbia* L. species (Gagliardi et al., 2012) and *Dalechampia stipulacea* Müll. Arg. (Silva and Souza, 2009), develop two meristems, in the middle region of the mesophyll and inner epidermis. In certain species de Asteraceae (Batista and Souza, 2017), too, the adaxial and middle meristems are described in the unripe pericarp.

Among the structures beyond the pericarp, the inferior ovary is of special interest in the ontogeny of fruits. Two principal interpretations have been reported in the literature, concerning the morphological nature of the inferior ovary: the appendicular and receptacular theories (Roth, 1977; Dickison, 2000). In the Cactaceae it is well defined that the inferior ovary has a receptacular nature (Rosa and Souza, 2003; Almeida et al., 2018). As pointed out by various authors (Pimentel et al., 2014; Harthman, 2016; Martos et al., 2017), some considerations seem to indicate that the inferior ovary of Myrtaceae has an appendicular origin. Recent investigations on fruits of Melastomataceae (Araujo, 2020) and Psychotrieae *sensu lato* (Rubiaceae) (Santos, 2020) have also revealed that the inferior ovary may be appendicular origin.

3.3 FRUIT CLASSIFICATION

For a long time, the classification of fruits has been controversial (Spjut, 1994) not only because there is a nomenclatural disagreement between different authors, but fruit ontogeny has not been taken into account. Some conceptual reflections are made here.

3.3.1 Indehiscent follicle and legume

The fruit of *Lonchocarpus muehlbergianus* was described in the literature as indehiscent legume, but the fruit ontogeny (Souza, 1984) showed that it is an indehiscent follicle, because it consists of residue of separation or abscission tissue only in the pod sutural region. Indehiscent legume has separation tissue in both regions of the pod, in the suture (ventral region) and dorsal region.

3.3.2 Achene and cypsela

The terminology employed by Marzinek et al., 2008) for achene and cypsela appear to be most satisfactory. These authors recognize that the cypsela is a complex fruit, dry, indehiscent, unilocular, with a single seed not adnate to the pericarp, and originating from an inferior ovary; it typically occurs in Asteraceae species. Otherwise, these authors consider the achene as simple fruit, dry, indehiscent, unilocular with a single seed linked to the pericarp by the funicle, and originating from superior ovary; this condition has been observed to occur in the Plumbaginaceae. This terminology of Marzinek et al. (2008) was adopted by us. Hitherto, the several types of cypsela have been described by us in Asteraceae (Frangiote-Pallone and Souza, 2014; Batista and Souza, 2017; Pelozo, 2017; Voltolini, 2018; Elias et al., 2019).

3.3.3 Pomaceous fruits

It can be safely concluded that there is a close correlation between the ovary (inferior or superior) and the fruit type. Often simple fruits are classified in a family, tribe or genus as berries, drupes or capsules, regardless of the origin of the inferior or superior ovary. Our conception is that all fruits that originate from inferior should be classified as pomaceous, creating specific subtypes according to their features and the taxon to which they belong. This terminology was initially employed by Hertel (1959), and we have expanded it in our studies on fruit ontogeny. A brief statement of the different types of pomaceous fruits seems appropriate to mention here: I - Balaustidium (*Punica granatum* L.); II – Betulidium (Betulaceae); III – Cactidium (Cactaceae) (Almeida et al., 2018); IV – Cypsela (Asteraceae) (Frangiote-Pallone and Souza, 2014; Batista and Souza, 2017; Pelozo, 2017; Voltolini, 2018; Elias et al., 2019); V – Glandidium (*Quercus*); VI – Melonidium/Peponidium (Cucurbitaceae); VII – Myrtidium (term created by us to designate Myrtaceae fruits from the inferior ovary); VIII - Musidium (Musaceae); IX – Pomidium (Rosaceae); X – Pyxidium (*Lecythis pisonis* Cambess., *Cariniana estrellensis*

(Raddi) Kuntze, *Luffa cylindrica* M. Roem.); XI – Viscidium (term created by us to designate Santalaceae fruits) (Polli et al., 2016). Rubiaceae fruits are referred to as berry type (*sensu* Gomes et al., 2020), but recent investigations on fruit ontogeny of Melastomataceae (Araujo, 2020) and Rubiaceae (Santos, 2020) have also revealed that the fruits are pomaceous (subtypes bacca or baccoid, and nuculanium, respectively).

3.4 TAXONOMIC USE OF THE FRUIT STRUCTURE

The classic work on fruits of angiosperms (Roth, 1977) already reported the use of the pericarp structure in the taxonomy of some families. During recent years some our investigations have revealed the importance of the fruit structure as a character in taxonomy. Micromorphological characters were analyzed in cypsela of Asteraceae (Pelozo, 2017) indicating features of potential taxonomic significance in Vernonieae, Eupatorieae, Heliantheae and Gochnatieae. Uniform characters on fruit ontogeny in species of Psychotrieae *sensu lato* (Rubiaceae) (Santos, 2020) seem to indicate the maintenance of the genera *Psychotria* L. and *Palicourea* Aubl. within the tribe. In the *Miconia* Ruiz & Pavón (Melastomataceae) (Araujo, 2020) the fruit ontogeny provides some important morphological features (ovary position, fruit type and insertion of ovules/seeds into the septum), which are the taxonomic value at the specific level.

3.5 FRUIT EVOLUTION

Reflections on fruit evolution are very general, selecting only a few examples, but through studies of a special family or genus are very rare (Roth, 1977). Hypothesis about fruit evolution indicates that apocarpic fruit with follicles can be a base evolutionary condition (Roth, 1977), at least among the *sensu lato* dicots.

Two main lines of fruit evolution must have occurred, both taking the reduction in the number of carpels and the closure of carpel edges as a starting point (Barroso et al., 1999). In the former, the progressive reduction in the number of carpels resulted in monocarpy, thus originating the simple follicle (Barroso et al., 1999). In the second line, there must have been a syncarpy, that is, the carpels approached their side walls, with gradual fusion; so, the septicidal capsule must have formed (Barroso et al., 1999).

Evolution of types of fruits is fundamentally based on changes of gynoecium types, on the one hand, and on distinct differentiation of fruit wall tissues, on the other (Roth, 1977). Fruit ontogeny on some species of Euphorbiaceae *sensu lato* reported that there are no significant features for separation of Euphorbiaceae *sensu stricto* and

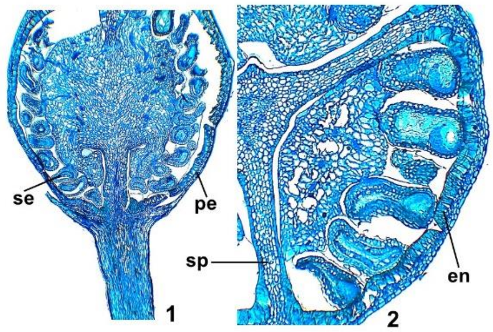
Phyllanthaceae, and it supports their close relationship (Gagliardi et al., 2014). A notable study of Myrteae (Myrtaceae) ovary was carried out by some authors (Harthman et al., 2018), which showed that the appendicular pattern of inferior ovary appears to be an ancestral state in the tribe, with mixed patter an innovation. Evolutionary trend in Cactaceae would indicate that the fruit in derived species of Cactoideae has ovary tissues deeply sunken in the receptacular cup before anthesis (Almeida et al., 2018). Psychotrieae *sensu lato* have received different proposals for reclassification involving the genera *Palicourea* and *Psychotria*; recent investigation showed that the ontogenetic features on fruits and seeds these genera are very homogeneous, which indicates that is convenient to keep both genera within the tribe (Santos, 2020).

3.6 THE SPECIAL CASE OF ARAUCARIA ANGUSTIFOLIA (BERTOL.) KUNTZE

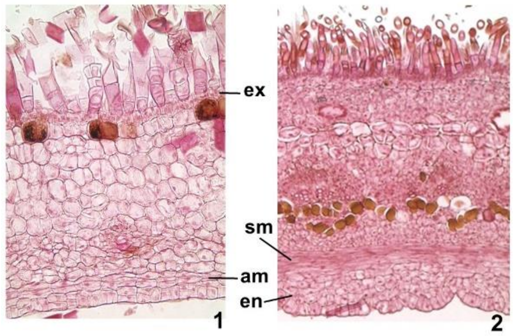
The pinion of *Araucaria angustifolia* consists of seed and envelope linked to the cone axis. We agree with the authors who consider the pinion as fruit. This special fruit is named of protocarp (Hertel, 1959; Hertel, 1980) or spermatocarp, subtype galbulus (Spjut, 1994). Further evidence in this direction has been gathered by the work of Hertel (1980) based on the vascularization of pinion; for the author the seed is not naked, but is contained within the modified leaf of the strobilus. Thus, each pinion or protocarp is considered a dry, unilocular, unispermic and indehiscent fruitlet. The situation of the pinion/cone of *Araucaria angustifolia* has been recently reviewed and studied in detail by Carmo et al. (2021); they support the view that the pinion/cone is actually a fruit.

We (as well as Carmo et al., 2021) are inclined to believe that the cone of *Araucaria angustifolia* is equivalent to a multiple fruit of angiosperms, consisting of several fruitlets fertile or sterile named protocarps or spermatocarps/galbulus, linked to an axis of stem nature.

Figure 1. Fruits of *Microlicia confertiflora* Naudin (a) and *Lonchocarpus muehlbergianus* Hassler (b). (a1) Fruit in longitudinal section showing pericarp (pe) and seeds (se). (a2) Fruit in cross-section evidencing pericarp with endocarp (en), and septum (sp). (b1) Unripe pericarp in cross-section showing exocarp (ex) and adaxial meristem (am) in early cell division. (b2) Young fruit in cross-section evidencing sclerenchymatous mesocarp (sm) and endocarp (en), both originated from the adaxial meristem.



(**a**)



(**b**)

ACKNOWLEDGMENTS

The author expresses his thanks to CAPES (Coordination of Superior Level Staff Improvement) and CNPq (National Council for Scientific and Technological Development) for funding numerous researches and grants.

REFERENCES

ALMEIDA, O. J. G.; SOUZA, L. A.; PAOLI, A. A. S.; DAVIS, A. R.; COTA-SÁNCHEZ, J. H. 2018. Pericarp development in fruit of epiphytic cacti: implications for fruit classification and macro-morphology in the Cactaceae. *Botany* 96: 621-635.

ARAUJO, R. G. S. 2020. Micromorfologia e anatomia de órgãos reprodutivos de Miconieae (Melastomataceae Juss.), como contribuição para a taxonomia da tribo. Doutorado (PhD), Maringá, Universidade Estadual de Maringá.

BARROSO, G. M.; MORIM, M. P.; PEIXOTO, A. L.; ICHASO, C. L. F. 1999. *Frutos e sementes* – morfologia aplicada à sistemática de dicotiledôneas. Viçosa, Editora UFV.

BATISTA, M. F.; SOUZA, L. A. 2017. A survey of ontogeny cypsela characters contributing to the infrafamilial characterization of Asteraceae. *Journal of the Torrey Botanical Society* 144: 296-302.

CARMO, A. A. O.; GODOY, R. C. B.; SOUZA, L. A. 2021. *Caracterização morfológica de Araucaria angustifolia (Bertol.) O. Kuntze (Araucariaceae)*. Curitiba, Embrapa Florestas. (*in press*)

DICKISON, W. C. 2000. *Integrative plant anatomy*. San Diego, Harcourt Academic Press.

ELIAS, R. A.; LANDO, A. P.; VIANA, W. G.; ORTIZ, J.; COSTA, C. D.; SCHMIDT, E. C.; SOUZA, L. A.; GUERRA, M. P.; STEINER, N. 2019. Structural aspects of cypsela and seed development of *Trichocline catharinensis* (Cabrera): a Brazilian endemic species. *Protoplasma* 256: 1495-1506.

FRANGIOTE-PALLONE, S.; SOUZA, L. 2014. A. Pappus and cypsela ontogeny in Asteraceae: structural considerations of the tribal category. *Revista Mexicana de Biodiversidad* 85: 62-77.

GAGLIARDI, K. B.; ROSADO, A.; SOUZA, L. A.; MOSCHETA, I. S.; ALBIERO, A. L. M. 2012. Structure and development of fruits and seeds of weed species of Euphorbiaceae. *Acta Botanica Brasilica* 26: 38-45.

GAGLIARDI, K. B.; SOUZA, L. A.; ALBIERO, A. L. 2014. M. Comparative fruit development in some Euphorbiaceae and Phyllanthaceae. *Plant Systematic and Evolution* 300: 775-782.

GOMES, C. R. S.; PINHEIRO, L. F.; GOMES, A. R. S.; GOMES, M. R. S.; LUCENA, E. M. P. 2020. Fenofase reprodutiva da *Cordiera sessilis* (Vell.) Kuntze no Complexo Vegetacional da Zona Litorânea. *Brazilian Journal of Development* 6(8): 58793-58804.

GUERRITS, P. O. 1991. *The application of glycol metacrylate in histotechnology* – some fundamental principles. Groningen, Department of Anatomy and Embryology State University Groningen.

HARTHMAN, V. C. 2016. Ovário ínfero de Myrtaceae e sua implicação na taxonomia e filogenia da família. Doutorado (PhD), Maringá, Universidade Estadual de Maringá.

HARTHMAN, V. C.; SOUZA, L. A. 2012. Ontogenia do fruto em desenvolvimento de *Alternanthera tenella* Colla e *Amaranthus blitum* Linnaeus (Amaranthaceae). *Acta Botanica Brasilica* 26: 642-650.

HARTHMAN, V. C.; SOUZA, L. A.; LUCAS, E. J. 2018. Characters of the inferior ovary of Myrteae (Myrtaceae) and their implication in the evolutionary history of the tribe. *Australian Systematic Botany* 31: 252-261.

HERNANDES, C. M.; MOURÃO, K. S. M.; SOUZA, L. A. 2020. Ontogenia do pericarpo em espécies de Microlicieae (Melastomataceae), como contribuição à taxonomia da tribo. 29^0 Encontro Anual de Iniciação Científica, Maringá, Brasil, 29 a 31 outubro 2020. Maringá, Universidade Estadual de Maringá.

HERTEL, R. J. G. 1959. Contribuições para a fitologia teórica II. Alguns conceitos de carpologia. *Humanitas* 4: 1-43.

HERTEL, R. J. G. 1980. Interpretação morfológica de *Araucaria angustifolia*. Thesis (professor titular), Curitiba, Universidade Federal do Paraná.

JOHANSEN, D. A. 1944. *Plant microtechnique*. Bombay, Tata McGraw-Hill Book Company.

KNOLL, F. 1939. Über den Begriff "Frucht". *Der Biologie* 8: 154-160.

MARTOS, L.; GALAN, A. T. O. F.; SOUZA, L. A.; MOURÃO, K. S. M. 2017. The flower anatomy of five species of Myrteae and its contribution to the taxonomy of Myrtaceae. *Acta Botanica Brasilica* 31: 42-50.

MARZINEK, J.; DE-PAULA, O. C.; OLIVEIRA, D. M. T. 2008. Cypsela or achene? Refining terminology by considering anatomical and historical factors. *Revista Brasileira de Botânica* 31: 549-553.

MUNERATTO, J. C.; SOUZA, L. A. 2013. Fruit (pericarp and seed) ontogeny of *Sida* species. *Gayana Botanica* 70: 44-56.

O'BRIEN, T. P.; FEDER, N.; McCULLY, M. E. 1964. Polychromatic staining of plant cell walls by toluidine blue O. *Protoplasma* 59: 368-373.

OYAMA, S. O.; SOUZA, L. A. 2011. Morphology and anatomy of the developing fruit of *Maclura tinctoria*, Moraceae. *Revista Brasileira de Botânica* 34: 187-195.

PELOZO, A. 2017. Micromorfologia de cipselas e estrutura de plântulas de Asteraceae. Doutorado (PhD), Maringá, Universidade Estadual de Maringá.

PIMENTEL, R. R.; BARREIRA, N. P.; SPALA, D. P.; CARDIM, N. B.; SOUZA, M. C.; SÁ-HAIAD, B.; MACHADO, S. R.; ROCHA, J. F.; SANTIAGO-FERNANDES, L.

D. R. 2014. Development and evolution of the gynoecium in (Myrteae Myrtaceae). *Australian Journal of Botany* 62: 335-346.

POLLI, A.; SOUZA, L. A.; ALMEIDA, O. J. G. 2016. Structural development of the fruits and seeds in three mistletoe species of *Phoradendron* (Visceae: Santalaceae). *Rodriguésia* 67: 649-659.

ROSA, S. M.; SOUZA, L. A. 2003. Morfo-anatomia do fruto (hipanto, pericarpo e semente) em desenvolvimento de *Pereskia aculeata* Miller (Cactaceae). *Acta Scientiarum, Biological Science* 25: 415-428.

ROSA-OSMAN, S. M.; RODRIGUES, R.; MENDONÇA, M. S.; SOUZA, L. A.; PIEDADE, M. T. F. 2011. Morfologia da flor, fruto e plântula de *Victoria amazonica* (Poepp.) J.C. Sowerby (Nymphaeaceae). *Acta Amazonica* 41: 21-28.

ROTH, I. 1977. Fruits of angiosperms. In: *Encyclopedia of plant anatomy,* Linsbauer, K. (ed.). Berlin, Gebrüder Borntraeger. vol. X, p. 1-675.

SANTOS, A. F. 2020. Ontogenia do fruto e sua implicação taxonômica em Psychotrieae *sensu lato* (Rubiaceae). Mestrado (Master's), Maringá, Universidade Estadual de Maringá.

SILVA, A. C.; SOUZA, L. A. 2009. Morphology and anatomy of the developing fruit and seed of *Dalechampia stipulacea* Müll. Arg. (Euphorbiaceae). *Acta Scientiarum, Biologial Science* 31: 425-432.

SOUZA, L. A. 1984. Anatomia do desenvolvimento do pericarpo de *Lonchocarpus muehlbergianus* Hassler (Leguminosae – Faboideae). *Revista Unimar* 6: 5-19.

SOUZA, L. A. 1993. Morfo-anatomia do desenvolvimento do fruto de *Acacia paniculata* Willd. (Leguminosae). *Arquivos de Biologia e Tecnologia* 36: 851-871.

SOUZA, L. A. 2006. Fruto. In *Anatomia do fruto e da semente*, Souza, L.A. (org.). Ponta Grossa, Editora UEPG. p. 10-123.

SOUZA, L. A. 2008. Morphology and anatomy of the *Cordia trichotoma* (Vell.) Arrab. ex I. M. Johnst diaspore (Boraginaceae). *Brazilian Archives of Biology and Technology* 51: 761-768.

SOUZA, L. A. 2021. *Botânica estrutural* – morfologia e anatomia de traqueófitas. Ponta Grossa, Editora UEPG. (*in press*)

SOUZA, L. A.; IWAZAKI, M. C.; OLIVEIRA, R. C. 2004. Morfo-anatomia do fruto e da semente em desenvolvimento de *Asclepias curassavica* L. (Asclepiadaceae). *Insula* 33: 39-49.

SOUZA, L. A.; MOSCHETA, I. S. 1992. Morfo-anatomia do fruto e da plântula de *Aspidosperma polyneuron* M. Arg. (Apocynaceae). *Revista Brasileira de Biologia* 52: 439-447.

SOUZA, L. A.; MOSCHETA, I. S.; MOURÃO, K. S. M.; THADEO, M. 2021. Fruto. In: *Anatomia vegetal*, Appezzato-da-Glória, B; Carmello-Guerreiro, S. M. (eds.). Viçosa, Editora UFV. (*in press*)

SOUZA, A.; MOURÃO, K. S. M.; SOUZA, L. A. 2005. Morfologia e anatomia do fruto e da semente em desenvolvimento de *Pilocarpus pennatifolius* Lem. (Rutaceae). *Revista Brasileira de Botânica* 28: 745-754.

SOUZA, L. A.; OYAMA, S. O.; MUNERATTO, J. C. 2008. Morphology and anatomy of the developing fruit of *Macfadyena unguis-cati* (L.) A. H. Gentry, Bignoniaceae. *Acta Botanica Venezuelica* 31: 1-14.

SOUZA, L. A.; ROSA, S. M.; MOSCHETA, I. S. 2008. Anatomy of the developing fruit of *Metrodorea nigra* A. St.-Hil. (Rutaceae). *Brazilian Archives of Biology and Technology* 51: 1171-1179.

SOUZA, L. A.; ROSA, S. M.; MOSCHETA, I. S.; MOURÃO, K. S. M.; RODELLA, R. A.; ROCHA, D. C. 2016. *Morfologia e anatomia vegetal* – técnicas e práticas. Ponta Grossa, Editora UEPG.

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

VOLTOLINI, C. H. 2018. Micromorfologia de cipselas e estrutura de plântulas de Asteraceae. Doutorado (PhD), Maringá, Universidade Estadual de Maringá.