



FRUIT FEATURES IN SOME SPECIES OF ASTEREAE AND HELIANTHEAE ALLIANCE

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ABSTRACT

Theoretical framework: Astereae is the second largest tribe of Asteraceae, with 170 genera with a worldwide distribution. The Alliance Heliantheae clade consists of about 160 genera from various tribes, including Eupatorieae and Heliantheae. Both taxa, especially Alliance Heliantheae, have taxonomic problems, and the structure of the fruits can reveal useful characters in their taxonomy.

Objective: The fruits of *Baccharis uncinella* DC., *Inulopsis scaposa* (DC.) O. Hoffm. (Tribe Astereae), *Campovassouria cruciata* (Vell.) R. M. King & H. Rob. (Tribe Eupatorieae) and *Ichthyothere mollis* Baker (Tribe Heliantheae) were ontogenically analyzed and compared with results obtained in studies of species from these three tribes.

Method: Flowers and fruits at different stages of development were collected in Vila Velha State Park, Paraná, Brazil. The botanical material was investigated according to usual techniques in plant anatomy.

Results: The fruits of the two species of Astereae are structurally very similar, being devoid of mesocarp and phytomelanin, unlike the species of Eupatorieae and Heliantheae, which have parenchymatic and sclerenchymatic mesocarp and phytomelanin.

Conclusion: Characters that may be relevant in the taxonomy of both groups of Asteraceae are the absence or presence of mesocarp; presence or absence of phytomelanin, laminar or filamentous pappus, and occurrence/type of twin hairs.

Keywords: Mesocarp, Ontogeny, Pappus, Phytomelanin, Twin Hairs.

CARACTERES DOS FRUTOS EM ALGUMAS ESPÉCIES DE ASTEREAE E ALIANÇA HELIANTHEAE

RESUMO

Referencial teórico: Astereae é a segunda maior tribo de Asteraceae, com 170 gêneros com distribuição mundial. O clado Alliance Heliantheae consiste em cerca de 160 gêneros de várias tribos, incluindo Eupatorieae e Heliantheae. Ambos os táxons, especialmente Alliance Heliantheae, apresentam problemas taxonômicos, e a estrutura dos frutos pode revelar caracteres úteis em sua taxonomia.

Objetivo: Os frutos de *Baccharis uncinella* DC., *Inulopsis scaposa* (DC.) O. Hoffm. (Tribo Astereae), *Campovassouria cruciata* (Vell.) R. M. King & H. Rob. (Tribo Eupatorieae) e *Ichthyothere mollis* Baker (Tribo Heliantheae) foram analisados ontogenicamente e comparados com resultados obtidos em estudos de espécies destas três tribos.

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Método: Flores e frutos em diferentes estágios de desenvolvimento foram coletados no Parque Estadual de Vila Velha, Paraná, Brasil. O material botânico foi investigado de acordo com técnicas usuais em anatomia vegetal.

Resultados: Os frutos das duas espécies de Astereae são estruturalmente muito semelhantes, sendo desprovidos de mesocarpo e fitomelanina, diferentemente das espécies de Eupatorieae e Heliantheae, que possuem mesocarpo parenquimático e esclerenquimático e fitomelanina.

Conclusão: Os caracteres que podem ser relevantes na taxonomia de ambos os grupos de Asteraceae são a ausência ou presença de mesocarpo; presença ou ausência de fitomelanina, papus laminares ou filamentosos e ocorrência/tipo de pêlos gêmeos.

Palavras-chave: Fitomelanina, Mesocarpo, Ontogenia, Papus, Tricoma Bisseriado.

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1 INTRODUCTION

Astereae is a tribe of worldwide distribution of about 3000 species, and is considered the second largest tribe of Asteraceae (Funk et al., 2009). Heliantheae Alliance is made up of several tribes, but studies have shown that there is a need to rearrange the groups; Eupatorieae and Heliantheae tribes are nested in this alliance (Funk et al., 2009).

The morphology of the pappus and the structure of the cypselae can reveal characters that are important in the taxonomy of Asteraceae tribes (Judd et al., 2009). Marques et al. (2021) also recognized the high taxonomic value of cypselae in different groups of Asteraceae. Structural characters of pappus, cypselae and seeds have demonstrated significant taxonomic potential in the separation of species and genera, and in the characterization of different hierarchical groups of Asteraceae (Pandey & Singh, 1984; King, 1989; Mukherjee & Sarkar, 2001; Julio & Oliveira, 2009; Marzinek & Oliveira, 2010; Pallone & Souza, 2014; Franca et al., 2015; Batista & Souza, 2017a,b; Akhlaq et al., 2022).

In the present work, four species were selected to study the pappus and the developing fruit, two from the Astereae tribe and two from the Heliantheae Alliance. The data obtained were compared with other species already studied belonging to the same groups (Table 1). Our objective was to show whether these characters can be diagnostic in the separation of species and tribes, and can also be useful in the phylogeny of both groups.

2 MATERIAL AND METHODS

Plant samples – Branches with floral buds, flowers and fruits at different stages of development of *Baccharis uncinella* DC., *Inulopsis scaposa* (DC.) O. Hoffm. (Tribe Astereae), *Campovassouria cruciata* (Vell.) R. M. King & H. Rob. (Tribe Eupatorieae) and *Ichthyothere mollis* Baker (Tribe Heliantheae) were collected in Vila Velha State Park, located in the municipality of Ponta Grossa, Brazil. Vouchers were deposited in the Herbarium of the State University of Maringá, Brazil, under registration numbers 29611, 24551, 24608 and 24588, and 24597, respectively.

Analysis in light microscope – Buds, flowers and fruits were fixed in FAA 50 (Formaldehyde, Acetic Acid and 50% Ethyl Alcohol), embedded in Leica® historresin as recommended by the manufacturer, sectioned transversally and longitudinally in a rotation microtome and stained in toluidine blue (O'Brien et al., 1964). Photomicrographs were taken



using a Leica EZ4D light microscope and subsequently processed using Leica Application Suite version 1.8 software.

Analysis in scanning electron microscope (SEM) – The micromorphological analysis (Bozzola & Russel, 1999) of the pappus and surface of the fruit of the four species was carried out on material fixed in FAA 50, dehydrated in an ethyl series and dried at the critical point of CO₂ (Horridge & Tamm, 1969). Then, the samples were mounted on aluminum supports and covered with a layer of 30 to 40 nm gold. The analysis was carried out using a scanning electron microscope (SEM) model Shimadzu SS 550, with the scales of the electron micrographs directly printed on them.

3 RESULTS AND DISCUSSION

Our results on the analyzes of the ovaries and fruits (pappus and pericarp) of the four species investigated here are shown in Tables 2 and 3. The ovaries of the two species of Astereae have significant differences, with the glabrous external epidermis and homogeneous mesophyll in *Baccharis uncinella*, and with twin hairs in formation and mesophyll with two differentiable histological regions in *Inulopsis scaposa* (Figure 1B). Both species of Eupatorieae and Heliantheae, *Campovassouria cruciata* and *Ichthyothere mollis*, exhibit more similarities between them, in which the mesophyll of both species has three tissue regions (Figure 1C,D). Twin hairs were found only in *Ichthyothere mollis* (Figure 1D).

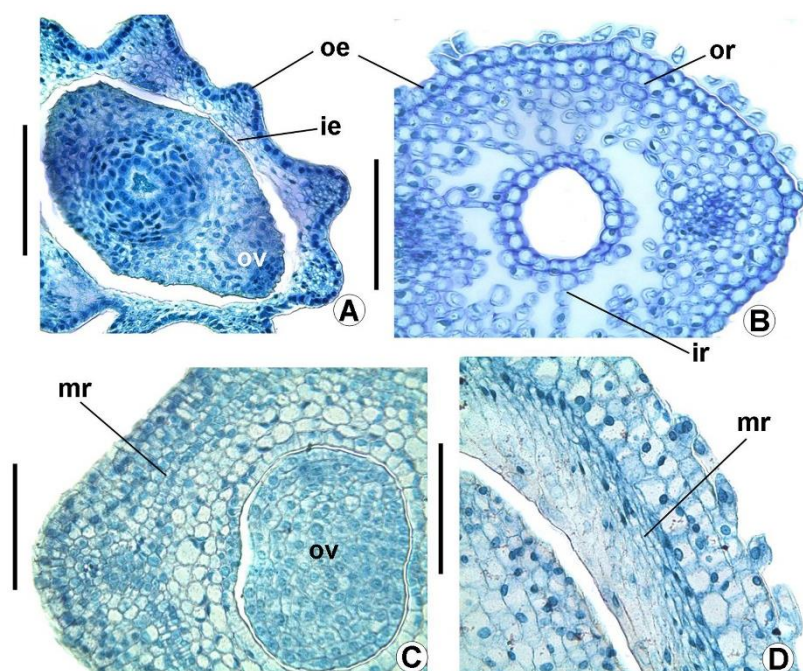


Figure 1 – Ovary structure of *Baccharis uncinella* (A), *Inulopsis scaposa* (B), *Campovassouria cruciata* (C) e *Ichthyothere mollis* (D), in cross-sections. (ie=inner epidermis; ir= inner region of the mesophyll; mr=middle region of the mesophyll; oe=outer epidermis; or=outer region of the mesophyll; ov=ovule). Scale bars: 30µm (A,B,D), 100µm (C).

Source: Produced by the author Fabiana Regina Gallo.

The literature on Astereae reveals analysis of ovary tissues from only the species *Conyza bonariensis*, which consists of an outer epidermis with twin hairs and a parenchymatic mesophyll with two regions, one with radially elongated cells and the other with three to four cell layers. The cypselsae of other Astereae species have been structurally investigated, but Mukherjee & Sarkarj (2001) did not analyze the anatomy of the ovary wall (Table 1).



The Eupatorieae species *Campovassouria cruciata* (Table 2) revealed ovary mesophyll with three different tissue regions (Fig. 1C), but mesophyll with two tissue regions has also been reported by Marzinek & Oliveira (2010), and Batista & Souza (2017a,b) in other species of the tribe (Table 1). It has been observed the outer mesophyll with two or more cell layers, and inner mesophyll that varies from three to six cell layers (Table 1) (Marzinek & Oliveira, 2010; Batista & Souza, 2017a,b).

The number of three tissue regions found in the ovary mesophyll of *Ichthyothere mollis* is ordinarily the same as the number found in other species of Heliantheae (Table 1). Both species of *Bidens* (Julio & Oliveira, 2009), *Tridax procumbens* (Pallone & Souza (2014), and *Eclipta alba* and *Parthenium hysterophorus* (Batista & Souza, 2017a,b) exhibit mesophyll with three types of parenchyma (Table 1).

Table 1 - Structural characters of the ovaries and cypselae of species belonging to the tribes Astereae, Eupatorieae and Heliantheae, according to different authors.

Tribes	Species	Ovary mesophyll	Cypsel mesocarp	Trichomes	Pappus	References
Astereae	<i>Aster amellus</i> L.	Not described	Sclerenchymatous bundles at the lateral lobes or rib regions only	Twin hairs, glandular trichomes	Bristly	Mukherjee & Sarkarj (2001)
Astereae	<i>Aster peduncularis</i> Wall, ex Nees (= <i>A. asperulus</i> (DC.) Hook f.)	Not described	Sclerenchymatous bundles at the lateral lobes or rib regions only	Twin hairs, glandular trichomes	Bristly	Mukherjee & Sarkarj (2001)
Astereae	<i>Aster thomsonii</i> C.B. Clarke	Not described	Sclerenchymatous bundles at the lateral lobes or rib regions only	Not described	Bristly	Mukherjee and Sarkarj (2001)
Astereae	<i>Baccharis halimifolia</i> L.	Not described	Sclerenchymatous bundles at the lateral lobes or rib regions only	Absent	Bristly	Mukherjee & Sarkarj (2001)
Astereae	<i>Brachycome campylocarpa</i> J. M. Black	Not described	Sclerenchymatous multilayered (lateral sides); parenchymatous with thick-walled cells (anterioposterior sides)	Terminally coiled or hooked hairs	Uniseriate, twin type pappus hairs or coronate	Mukherjee and Sarkarj (2001)
Astereae	<i>Brachycome ciliaris</i> (Labill.) Less. var. <i>ciliaris</i>	Not described	Sclerenchymatous unilayered mesocarp; sclerenchymatous multilayered (lateral sides)	Twin hairs, glandular trichomes	Uniseriate, twin type pappus hairs or coronate	Mukherjee & Sarkarj (2001)
Astereae	<i>Brachycome curvicarpa</i> G.L. Davis	Not described	Sclerenchymatous mesocarp (two rows); sclerenchymatous multilayered (lateral sides)	Terminally coiled or hooked hairs, glandular trichomes	Uniseriate, twin type pappus hairs or coronate	Mukherjee & Sarkarj (2001)
Astereae	<i>Brachycome heterodonta</i> DC. var. <i>heterodonta</i>	Not described	Sclerenchymatous mesocarp (two or three rows);	Twin hairs, glandular trichomes	Uniseriate, twin type pappus	Mukherjee & Sarkarj (2001)



			sclerenchymatous multilayered (lateral sides)		hairs or coronate	
Astereae	<i>Brachycome parvula</i> Hook. f. var. <i>lissocarpa</i> (J.M. Black) G.L. Davis	Not described	Sclerenchymatous mesocarp (one row); sclerenchymatous multilayered (lateral sides)	Terminally coiled or hooked hairs	Uniseriate, twin type pappus hairs or coronate	Mukherjee & Sarkarj (2001)
Astereae	<i>Conyza bonariensis</i> (L.) Cronquist	Two parenchymatous regions: an outermost layer of radially elongated cells, innermost region with 3–4 layers	Two regions: sclerenchymatous unilayered outer mesocarp; collapsed parenchymatous inner mesocarp	Twin hairs	Pappus with thick-walled cells	Batista & Souza (2017a,b)
Astereae	<i>Erigeron acer</i> L.	Not described	Sclerenchymatous bundles at the lateral lobes or rib regions only	Twin hairs, glandular trichomes	Bristly	Mukherjee & Sarkarj (2001)
Astereae	<i>Erigeron villarsii</i> Bell. (<i>E. atticus</i> Vill.)	Not described	Sclerenchymatous bundles at the lateral lobes or rib regions only	Twin hairs, glandular trichomes	Bristly	Mukherjee & Sarkarj (2001)
Astereae	<i>Myriacalis humilis</i> Merrill	Not described	Sclerenchymatous bundles at the lateral lobes or rib regions only	Twin hairs, glandular trichomes	Uniseriate, twin type pappus hairs or coronate	Mukherjee & Sarkarj (2001)
Astereae	<i>Vittadinia gracilis</i> (Hook, f.) Burbidge	Not described	Multilayered sclerenchyma in furrow regions of cypselae	Twin hairs, glandular trichomes	Bristly	Mukherjee & Sarkarj (2001)
Eupatorieae	<i>Campuloclinium macrocephalum</i> (Less.) DC.	Outer mesophyll (2 layers), with elongated cells; inner mesophyll (4,5 layers), small cells	Mature pericarp with most cells collapsed, fibers and phytomelanin layer remaining	Biseriate tector, biseriate glandular	Bristly, bristles lignified and vascularized (the most)	Marzinek & Oliveira (2010)
Eupatorieae	<i>Campuloclinium</i> DC. (11 species)	Not described	Outer parenchymatous mesocarp; phytomelanin layer; inner mesocarp with sclereid layer and parenchyma (absent in 4 species)	Biseriate tector, biseriate glandular	Bristly, lignified	Marques et al. (2022)
Eupatorieae	<i>Chromolaena stachyophylla</i> (Spreng.) R. King and H. Robinson	Outer mesophyll (2 layers), with elongated cells; inner mesophyll (4,5 layers), small cells	Mature pericarp with most cells collapsed, fibers and phytomelanin layer remaining	Biseriate tector, biseriate glandular	Bristly, bristles lignified and vascularized (the most)	Marzinek & Oliveira (2010)



Eupatorieae	<i>Mikania micrantha</i> H.B.B.	Outer mesophyll (5,6 layers), with elongated cells; inner mesophyll (4,5 layers), small cells	Mature pericarp with most cells collapsed, fibers and phytomelanin layer remaining	Biseriate glandular, uniseriate glandular (secretory unicellular apex)	Bristly, bristles lignified and non-vascularized	Marzinek & Oliveira (2010)
Eupatorieae	<i>Praxelis clematidea</i> R. M. King	Outer mesophyll with radially elongated cells; inner mesophyll with 3-4 layers of parenchyma	Outer mesocarp with biseriate parenchymatous; middle mesocarp fibrous uniseriate; with phytomelanin	Twin hairs	Bristly, bristles with thick-walled cells, vascularized	Batista & Souza (2017a,b)
Eupatorieae	<i>Praxelis pauciflora</i> (H.B.K.) R. King	Outer mesophyll (2 layers), with elongated cells; inner mesophyll (4,5 layers), small cells	Mature pericarp with most cells collapsed, fibers and phytomelanin layer remaining	Biseriate tector	Bristly, bristles lignified and vascularized (the most)	Marzinek & Oliveira (2010)
Eupatorieae	<i>Symphyopappus reticulatus</i> Baker	Outer mesophyll (5,6 layers), with elongated cells; inner mesophyll (4,5 layers), small cells	Mature pericarp with most cells collapsed, fibers and phytomelanin layer remaining	Biseriate tector	Bristly, bristles lignified and vascularized (the most)	Marzinek & Oliveira (2010)
Eupatorieae	<i>Vittetia orbiculata</i> (DC.) R. King	Outer mesophyll (2 layers), with elongated cells; inner mesophyll (4,5 layers), small cells	Mature pericarp with most cells collapsed, fibers and phytomelanin layer remaining	Biseriate tector, biseriate glandular	Bristly, bristles lignified and vascularized (the most)	Marzinek & Oliveira (2010)
Heliantheae	<i>Bidens gardneri</i> Baker	Outer mesophyll with more or less isodiametric cells; parenchymatic middle mesophyll; inner mesophyll with spongy parenchyma	Parenchymatous outer mesocarp; sclerenchymatous middle mesocarp; parenchymatous inner mesocarp more or less collapsed; with phytomelanin	Multicellular non-glandular trichomes	Pappus bristly	Julio & Oliveira (2009)
Heliantheae	<i>Bidens pilosa</i> L.	Outer mesophyll with more or less isodiametric cells; parenchymatic middle mesophyll; inner mesophyll with spongy parenchyma	Parenchymatous outer mesocarp; sclerenchymatous middle mesocarp; parenchymatous inner mesocarp more or less collapsed; with phytomelanin	Multicellular non-glandular trichomes	Pappus bristly	Julio & Oliveira (2009)
Heliantheae	<i>Eclipta alba</i> (L.) Hassk.	Uniseriate outer mesophyll with large cells;	Parenchymatous outer mesocarp; fibrous middle	Absent	Absent	Batista & Souza (2017a,b)



		parenchymatous middle mesophyll; spongy parenchymatous inner mesophyll	mesocarp; Collapsed parenchymatic inner mesocarp; with phytomelanin			
Heliantheae	<i>Parthenium hysterophorus</i> L.	Uniseriate outer mesophyll with large cells; parenchymatous middle mesophyll; spongy parenchymatous inner mesophyll	Parenchymatous uniseriate outer mesocarp; middle mesocarp fibrous multilayered; Collapsed parenchymatic inner mesocarp; with phytomelanin	Absent	Absent	Batista & Souza (2017a,b)
Heliantheae	<i>Tridax procumbens</i> L.	Outer mesophyll with 1 column-like cell layer or elongated cells; middle mesophyll with tangentially elongated cells; spongy parenchymatous inner mesophyll	Thick-walled columnar cells (outer mesocarp); lignified fibrous middle mesocarp; parenchyma slightly crushed (inner mesocarp); with phytomelanin	Twin hairs	Bristly, with reduced vasculature	Pallone & Souza (2014)

Source: Own development (2023).

The cypsela of the four species investigated here have pappus (Table 3), being bristly in *Baccharis uncinella*, *Inulopsis scaposa* and *Campovassouria cruciata*, and laminar in *Ichthyothere mollis* (Fig. 2A-D). In the first three species, epidermal pappus cells have a tapered free end (Fig. 2A,C,E). The pappus (Fig. 2A,B) of the two Astereae species consists of epidermis and reduced mesophyll, mainly in *Baccharis uncinella*. Pappus vascularization is reduced in *Inulopsis scaposa* (Fig. 2D) and absent in *Baccharis uncinella* (Fig. 2B). *Campovassouria cruciata* (Eupatorieae) has a pappus similar to the two species of Astereae (Fig. 2F), but *Ichthyothere mollis* (Heliantheae) has a notably different pappus, with a laminar shape (Fig. 2G,H). The rudimentary vasculature of the pappus of these species and Astereae, associated with the reduction and sclerification of the mesophyll, reinforces the thesis that the pappus can be considered as a less differentiated form of the leaf, according to Roth (1977). Reduced vascular tissue in the pappus has been recorded in *Conyza bonariensis*, and in several species of Eupatorieae (Marzinek & Oliveira, 2010) and Heliantheae (Pallone & Souza, 2014) (Table 1).

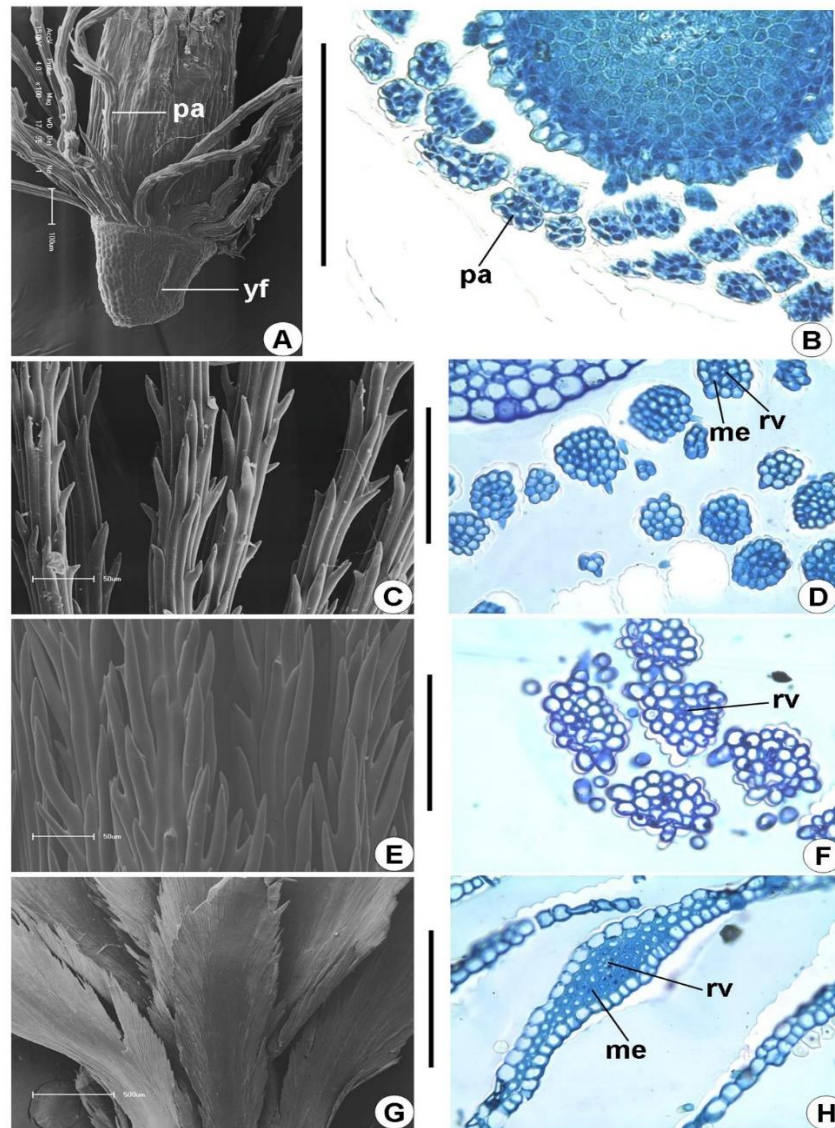


Figure 2 – Pappus structure of the cypselae of *Baccharis uncinella* (A,B), *Inulopsis scaposa* (C,D), *Campovassouria cruciata* (E,F) and *Ichthyothere mollis* (G,H). A,C,E,G – Scanning electron micrographs of the fruit (A) and pappus (C,E,G). B,D,F,H – Pappus transversely sectioned. (me=mesophyll; pa=pappus; rv=reduced vasculature; yf=young fruit). Scale bars: 40µm.

Source: Produced by the author Fabiana Regina Gallo.

Table 2 – Structural characters of ovaries of Astereae, Eupatorieae and Heliantheae species.

Tribes	Species	Shape (cross-section)	Outer epidermis	Mesophyll	Inner epidermis
Astereae	<i>Baccharis uncinella</i>	Circular with ribs	Uniseriate, glabrous, with slightly prismatic cells	Homogeneous, parenchymatous, 1-3 cell layers	Uniseriate
Astereae	<i>Inulopsis scaposa</i>	Circular	Uniseriate with twin hairs	Parenchymatous with 2 regions: outer biseriate and compact; inner spongy and multilayered	Uniseriate
Eupatorieae	<i>Campovassouria cruciata</i>	Pentagonal (5 ribs)	Uniseriate, glabrous, with quadrangular cells	Parenchymatous with 3 regions: outer biseriate,	Uniseriate



						middle biseriate, inner triseriate	
Heliantheae	<i>Ichthyothere mollis</i>	Lenticular	Uniseriate hairs	with twin		Parenchymatous with 3 regions: outer 2-3 layers, middle fiber primordia, inner biseriate	Uniseriate

Source: Own development (2023).

Table 3 – Structural characters of cypselae of Astereae, Eupatorieae and Heliantheae species.

Tribes	Species	Pappus	Exocarp	Mesocarp	Endocarp
Astereae	<i>Baccharis uncinella</i>	Circular; epidermis, mesophyll with 2 cells, without vasculature	Epidermis, thick cuticle, glabrous	Collapsed (ribs with vascular bundles surrounded by sclerenchyma)	Collapsed
Astereae	<i>Inulopsis scaposa</i>	Epidermis, mesophyll unilayered; reduced vasculature	Epidermis with twin hairs	Collapsed, persistent vascular bundles	Collapsed
Eupatorieae	<i>Campovassouria cruciata</i>	Circular/triangular; epidermis, sclerenchymatous mesophyll with few cells, reduced vasculature	Epidermis glabrous	Outer parenchymatous (3-5 layers); Middle (3 layers: outer sclerified, others with thin walls), phytomelanin between outer and middle; inner collapsed	Collapsed
Heliantheae	<i>Ichthyothere mollis</i>	Paleaceous, laminar; abaxial epidermis with thin walled-cells, adaxial one with thick walled-cells; sclerenchymatous homogeneous mesophyll; epidermal margin; reduced vasculature	Epidermis with twin hairs	Outer with two or more layers; sclerenchymatous middle; inner collapsed; phytomelanin between outer and middle mesocarp	Collapsed

Source: Own development (2023).

The cypselae of the investigated species have an epidermal, cuticularized exocarp with twin hairs (biseriate trichomes) in *Baccharis uncinella*, *Inulopsis scaposa* and *Ichthyothere mollis*. *Campovassouria cruciata* has a glabrous exocarp. These twin hairs are typical of many species of Asteraceae (Compositae) (Roth, 1977). Contrary to Roth's (1977) interpretation, Marzinek & Oliveira (2010) considered the biseriate trichomes to have taxonomic value, at least in Eupatorieae. These authors established four types of biseriate trichomes (two non-glandular and two glandular), which presented a variable number and shape of cells. Presence or absence of trichomes on the cypselar surface was considered of taxonomic value for seven *Helianthus* L. (Heliantheae) species (Basak & Mukherjee, 2001).

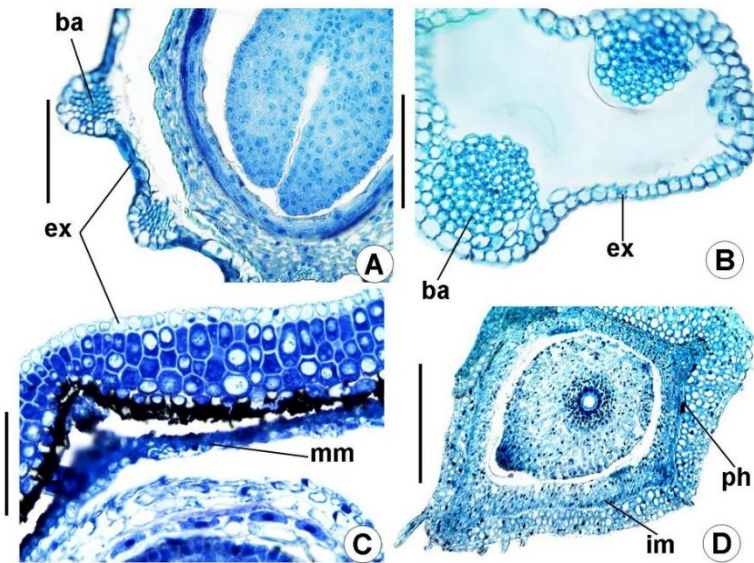


Figure 3 – Cypsel structure of *Baccharis uncinella* (A), *Inulopsis scaposa* (B), *Campovassouria cruciata* (C) and *Ichthyothere mollis* (D), in cross-sections. (ba=vascular bundle in the rib; ex=exocarp; im=immature middle mesocarp; mm=sclerenchymatous middle mesocarp; ph=phytomelanin). Scale bars: 30 μ m (A-C), 100 μ m (D).
Source: Produced by the author Fabiana Regina Gallo.

Baccharis uncinella and *Inulopsis scaposa* (Astereae) have the mature fruit devoid of mesocarp and endocarp (Fig. 3A,B), which are destroyed or collapsed during their development. In addition to the exocarp, vascular bundles located on the ribs or lobes of the pericarp remain in the mature fruit (Fig. 3A,B). The absence of mesocarp and endocarp appears to be common in many species of Astereae, as seen in *Aster amellus*, *Aster peduncularis*, *Aster thomsonii*, *Baccharis halimifolia*, *Erigeron acer*, *Erigeron villarsii*, *Myriacis humilis* and *Vittadinia gracilis* (Mukherjee & Sarkarj, 2001) (Table 1).

Considering the absence of a large part of the pericarp and phytomelanin in the ripe fruit in Astereae (Fig. 3A,B), it is likely that the protection of the embryo in species of this tribe, at least in *Baccharis uncinella* and *Inulopsis scaposa*, is provided by the seed coat. It consists of uniseriate exotesta of thick-walled cells and other inner layers that are strongly compressed. Seed coat with specialized exotesta has already been registered in several other Asteraceae species (Pandey & Singh, 1984; Pallone & Souza, 2014; Batista et al., 2015).

The fruits of *Campovassouria cruciata* and *Ichthyothere mollis*, unlike the Astereae species, have outer, middle and inner mesocarp in the youngest fruit (Fig. 3D), in which the middle mesocarp is sclerenchymatous in nature. In these fruits there is also deposition of phytomelanin between the outer and middle mesocarp (Fig. 3C,D) (Table 3). In the fully ripe fruit (Fig. 3C) of both species, the inner mesocarp and endocarp collapse. Other species of Eupatorieae (Oliveira, 1972; Pandey & Singh, 1984; Marzinek & Oliveira, 2010; Franca et al., 2015) and Heliantheae (Pallone & Souza, 2014; Batista & Souza, 2017a,b) also have mesocarp with distinct tissue regions, sclerenchyma and deposition of phytomelanin (Table 1).

Phytomelanin (Fig. 3C,D) recorded in the fruits of Eupatorieae and Heliantheae species is considered by Roth (1977) as a black or dark brown pigment that typically occurs in many cypselae, and appears to have the protective function of the pericarp and seed against excessive insolation. The presence of phytomelanin is classically associated with the Heliantheae Alliance, but recent research has reported phytomelanin in fruits of other Asteraceae taxa (Marques et al., 2021). The presence of phytomelanin in Asteraceae has long been considered a synapomorphy in the family (Panero, 2007). However, Marques et al. (2021) have shown that recent anatomical studies revealed that the phytomelanin in this family is more widely distributed.



The Astereae species analyzed here exhibit similar structural characters of the ovary and fruit, with insignificant taxonomic differences. On the other hand, Eupatorieae and Heliantheae species show differences in ovary contour and epidermis structure (Table 3). The differences in these last two tribes are still significant in relation to the fruit, mainly regarding the pappus, exocarp and mesocarp (Table 3). With reference to the three tribes, our studies (Table 3) and others carried out by different authors (Table 1) show that Astereae has significant differences when compared with Eupatorieae and Heliantheae, that is, in the former there is no mesocarp and phytomelanin in the ripe fruit, whereas in the latter the mesocarp with different histological regions and phytomelanin are present. Characters recorded in this study (Tables 2 and 3) and in similar investigations (Table 1), which may be useful in the taxonomy of the tribes are: absence or presence of mesocarp; presence or absence of phytomelanin, laminar or bristle pappus and occurrence or type of twin hairs.

4 CONCLUSION

Characters analyzed from Astereae fruits are not very significant for separating the species, showing structural uniformity in the tribe. On the other hand, the absence of mesocarp and phytomelanin is a relevant character to separate Astereae from the tribes belonging to the Heliantheae Alliance. The species investigated in this Alliance, which are part of the tribes Eupatorieae and Heliantheae, have characters related to the ovary, pappus, exocarp and mesocarp that are important for the diagnosis of the species.

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