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ORIGINAL ARTICLE

Leaf Secretory Structures in Asteraceae: A Synthesis of Their Diversity and Evolution

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Abstract

This study presents the first comparative analysis of the leaf secretory structures across Asteraceae. In this work, the leaf secretory structures of more than 500 species of 35 of the 40 tribes and 11 of the 13 subfamilies of Asteraceae are described and compared to evaluate their diversity at the tribe level and to identify evolutionary patterns. Leaf secretory structures are present in 28 of the 35 analyzed tribes and correspond to canals (recorded in 17 tribes), secretory cavities (1 tribe), hydathodes (19 tribes), laticifers (4 tribes) and glandular trichomes (24 tribes). Canals are mostly associated with vascular bundles and predominate in Asteroideae, while cavities were only present within Tageteae. Hydathodes occur in leaves without divisions and with well-developed teeth. Laticifers were observed only in the tribes of Cichorioideae. Seven glandular trichome morphotypes were differentiated by their cellular composition and shape. These observations together with the available information showed that secretory structures are found in 80% of the Asteraceae tribes. Four of the 40 tribes did not present any type of secretory structure. Our study reveals that almost all of the tribes possess one to three types of secretory structures, and are absent in some early-diverging clades. Character evolution analyses show that glandular trichomes are plesiomorphic in Asteraceae. This study found that secretory structures prevail in late-diverging lineages and were taxonomically informative at different levels. Our comparative study of the secretory structures in Asteraceae is essential for the standardization of its terminology and will provide a frame of reference for future studies.

Keywords Glandular trichomes · Canals · Secretory cavities · Laticifers · Hydathodes

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Introduction

In plants, secretions account for the isolation or elimination of all types of substances not stored for their remobilization or incorporation into other metabolic processes; these substances are generally products of secondary metabolism or substances not modified by the action of cell metabolism (Fahn 1979). These compounds can be retained in subcellular compartments or released from the cells without compromising their integrity (Fahn 1982; Beck 2010). Individual cells or multicellular structures that are responsible for carrying out secretory functions are called secretory structures, and their classification has represented a great challenge because of their physiological, anatomical or topographic (its location on the plant body) aspects (Fahn 1979; Mauseth 1988). However, the topographic criterion, e.g., internal or external secretory structures, seems to be the most widely used by many authors. The first corresponds to secretory cells (also named secretory idioblasts), cavities, canals, and laticifers, while the latter includes glandular trichomes, papillae, colleters, nectaries, hydathodes, and the stigmatic tissue of the gynoecium (Esau 1977; Dickison 2000; Evert 2006; Beck 2010). Secretory structures can be found in all plant organs, although their major diversity is concentrated in the leaves (Fahn 1979).

The study of secretory structures has focused on highly diverse angiosperm families, such as Apiaceae, Fabaceae, Lamiaceae, Malvaceae, Rosaceae, Rutaceae, and Solanaceae, in which a large number of phytochemicals have been identified (Moerman et al. 1999; Evans 2009; Gras et al. 2021). These compounds are not only relevant from a pharmacological perspective but also very important in the field of chemical ecology. Because Asteraceae is the most diverse family within angiosperms and has a large number of medicinal species that have been the subject of numerous phytochemical studies (Pérez-Castorena et al. 2000, 2001; Arciniegas et al. 2011, 2018; Heinrich et al. 2012; Cilia-López et al. 2021), this family is an interesting case study for studying the diversity of secretory structures. Most of the published studies are focused on the general leaf anatomy or the epidermal appendages in some punctual genera of certain tribes of the Asteraceae, such as Anthemideae (Dere & Aytas Akcin 2017), Cardueae (Ozcan et al. 2015), Heliantheae (Bombo et al. 2012; Silva et al. 2015; Bezerra et al. 2018), Madieae (Carlquist 1958; Carlquist 1959a, b, c), Senecioneae (Rojas-Leal et al. 2017), Tageteae (García-Sánchez et al. 2012) and Vernonieae (Redonda-Martínez et al. 2012, 2016). Past works that investigated leaf anatomy and epidermal appendages were not focused on secretory structures; therefore, the descriptions are often vague or unspecific and use different terms to refer to similar structures.

Several studies have comprised and compared the different tribes of Asteraceae, including the work of Lersten & Curtis (1985), who analyzed the presence of hydathodes in 88 species of 80 genera in 10 tribes; and Castro et al. (1997), who analyzed the leaf secretory structures in 72 species of 21 genera in 6 tribes. In 2009, Robinson presented a revision of the most important microcharacters of the family, while in 2019, Liesenfeld et al. analyzed the leaf trichomes of 34 species of 24 genera in 11 tribes. However, if we consider that Asteraceae includes approximately 40 tribes in 13 subfamilies (Panero & Crozier 2016), a descriptive comparative study that analyzes most of the tribes within the family based on the most recent phylogenetic

hypothesis is essential. Comparative studies allow us to establish homology hypotheses (De Pinna 1991) and are fundamental for developing a reference scheme in highly diverse taxa, such as Asteraceae. In this work, the leaf secretory structures occurring in members of 35 of the 40 recognized tribes are compared and described. This sampling included 11 of the 13 subfamilies of Asteraceae. Our aim was to recognize the diversity along the family, identify which secretory structures are found in each tribe, determine the variations of each structure, and discern the evolutionary patterns of the main types of secretory structures in the family.

Material and Methods

Taxonomic Sample

A total of 542 species from 35 tribes and 11 subfamilies of Asteraceae were selected, representing 87.5% of the tribes and 84% of the subfamilies according to Panero & Crozier (2016; ESM 1). For each species, at least one individual was selected from field collections or specimens deposited in the National Herbarium of Mexico, Universidad Nacional Autónoma de México (MEXU) and in the University of Texas at Austin Herbarium (TEX). One to two leaves per individual were sampled. The selection criteria were fully developed leaves without apparent damage and leaves not associated with inflorescences.

Microtechnique

The middle third of the leaf blade (including the intercostal area from the middle vein to the margin) of the fresh samples was fixed with FAA (37% formaldehyde, glacial acetic acid, 95% ethanol, and distilled water, Ruzin 1999). The samples obtained from the herbarium specimens were previously rehydrated in boiling water and subsequently treated with a 20% NaOH solution to restore both the shape and size of the cells. An entire leaf or part of it (depending on the size of the leaf) was removed from the herbarium specimens and processed using the leaf clearing technique (Martínez-Cabrera et al. 2007). All samples were dehydrated with ethanol (10–100%) in a Leica TP1020 automatic changer (Leica, Wetzlar, Germany), with the samples maintained at each concentration for 24 h. The tissues were infiltrated and embedded with Paraplast®, and 12–16 μm sections were made in the transverse and paradermal planes with a rotary microtome (Leica RM2125RT, Leica, Wetzlar, Germany). The sections were stained with safranin-fast green (Johansen 1940) and mounted with synthetic resin. Photographs of secretory structures were taken with an EvolutionTM LC color digital camera coupled to an Olympus Bx51 microscope (Olympus, Tokyo, Japan). The terms used to describe secretory structures are based on Fahn (1979), Mauseth (1988), Castro et al. (1997), Evert (2006) and Funk et al. (2009). According to the microscopic observations and information from the literature, a synthesis of the types of secretory structures in each of the Asteraceae tribes was carried out.

Phylogenetic Analyses

The chloroplast DNA matrix generated by Rivera et al. (2020), including eleven molecular markers (*atpB*, *matK*, *ndhD*, *ndhF*, *ndhI*, *rbcL*, *ndhJ*, *ndhK*, *ndhC*, *trnL-trnF*, *23 S-trnA*) was used. Because not all the species included in the original molecular matrix were analyzed in this study, taxa for which no anatomical information was available were eliminated. To represent the four tribes included in Cichorioideae, sequences of *matK*, *ndhF*, and *trnL-trnF* of *Sinclairia ismaelis* (Funk et al. 2012; JN837476.1, JN837373.1, JN837283.1) from GenBank (Sayers et al. 2020) were incorporated into the matrix. Thus, the reduced matrix with 171 species of most of the tribes of Asteraceae and its sister groups (members of Calyceraceae and Goodeniaceae) was aligned using the default parameters in MAFFT v.7 (Katoh et al. 2002).

Phylogenetic analysis was carried out through Bayesian inference using MrBayes 3.2.7a (Ronquist & Huelsenbeck 2003). The nucleotide substitution model for the plastid dataset was selected using jModelTest2 (Darriba et al. 2012) with eleven substitution schemes, and the model fit was evaluated using the Akaike information criterion to select the best model. Analyses were performed using two runs with four Markov Monte Carlo chains of 10,000,000 generations, saving one tree every 1000 generations, starting with a random tree. The burn-in was set after the first 25% of the generations, and the remaining trees were summarized in a majority-rule consensus tree. Both model selection and phylogenetic inference were carried out at the CIPRES Science Gateway (Miller et al. 2010).

Ancestral Character States Reconstruction and Character Evolution

A tree sample was compiled from the two t.files obtained from the MrBayes run using R v.4.0 (R Core Team 2020) through RStudio v.1.1.383 (RStudio Team 2020). First, trees from all runs were concatenated, with 10% of each of the trees in each file discarded. Then, 200 trees were randomly sampled from this concatenated tree file. An ancestral character state reconstruction analysis was performed in BayesTraits V3 (Meade & Pagel 2017) using the tree sample and the presence or absence of the five main types of secretory structures. The reversible-jump Markov chain Monte Carlo (rj-MCMC) approach was used to integrate the model uncertainty. Each rj-MCMC analysis was run with an exponential hyperprior (mean on a uniform interval from 0 to 10). The chain was run for 500,000 generations, and the first 10% were discarded as burn-in. The mean values of all the posterior probabilities found were illustrated as pie chart diagrams on the majority-rule consensus tree using the package Phytools v.0.7–47 (Revell 2012) of R v.4.0 (R Core Team 2020) through RStudio v.1.1.383 (RStudio Team 2020).

Results

Secretory structures are present in 28 of the 35 analyzed tribes and correspond to canals, cavities, hydathodes, laticifers and glandular trichomes (Fig. 1). Although at least one type of secretory structure is present in most tribes, seven of the analyzed

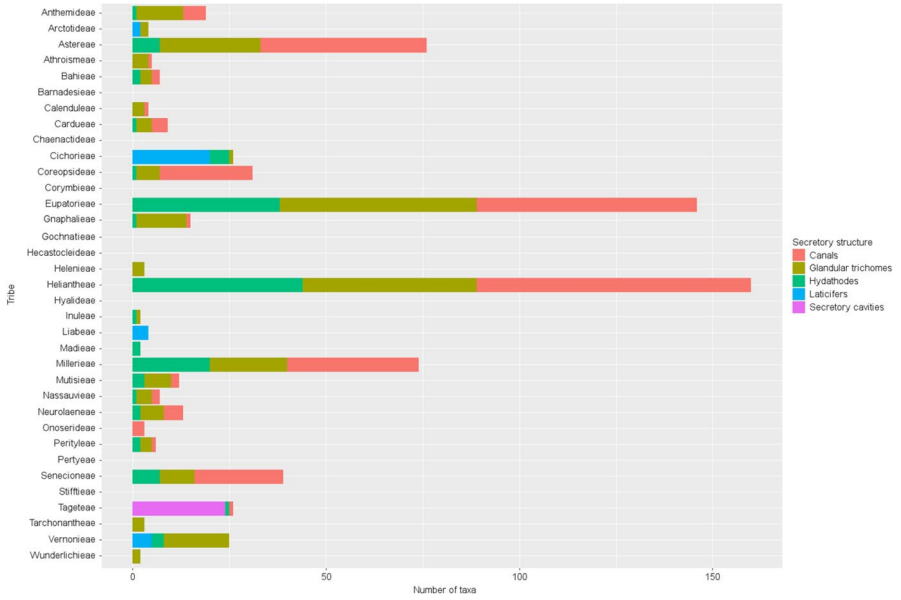

Fig. 1 Distribution of the main five types of secretory structures in the 35 tribes of Asteraceae analyzed

tribes do not present such structures: Barnadesieae, Chaenactideae, Corymbieae, Hecastocleideae, Hyalideae, Pertyeae and Stifftieae. It is important to emphasize that the simultaneous presence of glandular trichomes, hydathodes, and canals is common along the family and occurs in 11 tribes (Table 1; Fig. 1). Each of the secretory structures observed is described below.

Canals

Canals consist of intercellular spaces that are highly variable in size. Seen in paradermal sections, canals usually form a long duct (Fig. 2a, b), although in some cases, they can be solitarily short intercellular spaces that can be developed very close to each other, thus giving them the appearance of a single structure, as occurs in many species of Coreopsideae and Eupatorieae and some taxa of Astereae and Heliantheae (Fig. 2c, d). In either case, canals are always circular in transverse sections and delimited by the parenchymatous unistratified sheath with slightly thickened primary walls. Toward the canal lumen, there is a unistratified secretory epithelium that consists of small cells with thinned walls and evident nuclei, sometimes with reddish contents. In most cases, canals are associated with vascular bundles located on the xylem (Fig. 2e), phloem (Fig. 2f) or both vascular tissues (Fig. 2g). Canals can also be located laterally to the vascular bundles (Fig. 2h), mainly in representatives of Astereae and Coreopsideae. In all cases, canals are separated from the vascular tissue by the vascular bundle sheath. In some taxa of Astereae, Eupatorieae, Mutisieae, and Senecioneae, the canals are not associated with the vascular bundles. In the midrib, one to several canals are observed either toward the adaxial (Fig. 2i) or abaxial sur-

Table 1 Summary of the main types of secretory structures by tribe reported in the literature for the family Asteraceae. For each tribe the number of genera/species re-recognized sensu Funk et al. (2009) is given and in parentheses the number of genera/species studied in this work. C = Canals, SC = Secretory cavities, H = Hydathodes, L = Laticifers, GT = Glandular trichomes. +, present; −, absent. All complete references are listed in ESM 2

Subfamily	Tribe Genera/spp (genera/spp)	Secretory structures					Reference
		C	SC	H	L	GT	
Asteroideae	Anthemideae 111/1800(10/20)	+	−	+	−	+	Frey-Wyssling 1941; Vermer & Peterson 1979; Corsi & Nencioni 1995; Pagni 1995; Pagni & Masini 1999; Pagni et al. 2003; Hayat et al. 2009; Konowalik & Kreitschitz 2012; Özbek et al. 2014; Dere & Aytas Akcin 2017; this work
	Astereae 222/3100(33/55)	+	−	+	−	+	Reinke 1875; Anderson & Creech 1975; Semple et al. 1980; Lersten & Curtis 1985, 1989; Castro et al. 1997; Budel et al. 2004; Molares et al. 2009; Hulley et al. 2010; Hadad et al. 2013; Budel et al. 2017; Souza et al. 2018; this work
	Athroismeae 5/59(3/5)	+	−	−	−	+	This work
	Bahieae 20/83(4/4)	+	−	+	−	+	Rivera et al. 2019; this work
	Calenduleae 12/120(4/5)	+	−	+	−	+	Lersten & Curtis 1985; this work
	Callilepis tribe	−	−	−	−	−	**Without information**
	Chaenactideae 3/29(1/1)	−	−	−	−	+	This work
	Coreopsideae 30/550(10/25)	+	−	+	−	+	Carlquist & Grant 1963; Castro et al. 1997; Peter & Katinas 2003; Adedeji & Jewoola 2008; this work
	Eupatorieae 182/2200(37/65)	+	−	+	−	+	Ramayya 1962; Grassiolli et al. 1985; Lersten & Curtis 1985; Castro et al. 1997; Cornara et al. 2001; Monteiro et al. 2001; Budel et al. 2004; Milan et al. 2006; Freire et al. 2007; Adedeji & Jewoola 2008; Molares et al. 2009; Delbón et al. 2012; Fernandes et al. 2016; Gutiérrez et al. 2016; Pereira Sühsner et al. 2017; Budel et al. 2017; Rossi et al. 2018; Liesenfeld et al. 2019; Ornellas et al. 2019; this work

Table 1 (continued)

Subfamily	Tribe Genera/spp (genera/spp)	Secretory structures					Reference
		C	SC	H	L	GT	
	Gnaphalieae 185/1240(10/18)	+	−	+	−	+	Frey-Wyssling 1941; Liesenfeld et al. 2019; this work
	Helenieae 13/12)(5/5)	−	−	+	−	+	De Bary 1884; Beinticinco et al. 2011; this work
	Heliantheae 113/1500(48/83)	+	−	+	−	+	Carlquist 1957; Meidner & Sheriff 1976; Anderson et al. 1979; Lersten & Curtis 1985; Castro et al. 1997; Peter & Katinas 2003; Aguilera et al. 2004; Delbón et al. 2007; Bombo et al. 2012; Degen de Arrúa et al. 2012; Delbón et al. 2012; Aschenbrenner et al. 2013; Oliveira et al. 2013; Souza da Silva et al. 2014; Silva et al. 2015; Filartiga et al. 2016; Ferraro & Scremin-Dias 2017; Bezerra et al. 2018; Liesenfeld et al. 2019; this work
	Inuleae 66/687(2/2)	−	−	+	−	+	Werker & Fahn 1981; Castro et al. 1997; Aytas Akcin & Akcin 2017; Ferraro & Scremin-Dias 2017; Liesenfeld et al. 2019; this work
	Madieae 36/200(5/5)	+	−	+	−	+	Carlquist 1957, 1958, 1959a, b; this work
	Millerieae 34/400(18/34)	+	−	+	−	+	Aguilera et al. 2004; Mercado et al. 2006; Adedeji & Jewoola 2008; Degen de Arrúa et al. 2012; Delbón et al. 2012; Vitali 2017; this work
	Neurolaeneae 5/150(4/7)	+	−	+	−	+	Farago et al. 2006; Liesenfeld et al. 2019; this work
	Perityleae 7/84(3/5)	+	−	+	−	+	This work
	Senecioneae 150/3000(14/28)	+	−	+	−	+	De Bary 1884; Frey-Wyssling 1941; Hare 1941; Bercu 2014; Jianu et al. 2013; Lapp et al. 2013; Muravnik et al. 2016; Nurhan et al. 2017; Rojas-Leal et al. 2017; Liesenfeld et al. 2019; this work

Table 1 (continued)

Subfamily	Tribe Genera/spp (genera/spp)	Secretory structures					Reference
		C	SC	H	L	GT	
	Tageteae 32/270(10/25)	−	+	+	−	+	Simon et al. 2002; Fonseca et al. 2006; Milan et al. 2006; García-Sánchez et al. 2012; Oliveira et al. 2015; Lusa et al. 2016; Ferraro & Scremin-Dias 2017; Lizarraga et al. 2017; Lusa et al. 2017; Páez et al. 2019; Younis et al. 2020; this work
Barnadesioideae	Barnadesieae 9/91(5/8)	−	−	−	−	−	Uturbey 1999; Padin et al. 2015; this work
Carduoideae	Cardueae 73/2400(9/14)	+	−	+	−	+	Frey-Wyssling 1941; Lersten & Curtis 1985; Lotocka & Geszprych 2004; Ozcan et al. 2015; this work
	Dicomae 7/97	−	−	−	−	−	**Without information**
	Oldenburgieae 1/4	−	−	−	−	−	**Without information**
	Tarchonantheae 2/13(2/3)	−	−	−	−	+	Herman 2002; this work
Cichorioideae	Arctotideae 17/215(3/3)	−	−	+	+	+	Karis 2006; this work
	Cichorieae 86/1500(20/20)	−	−	+	+	+	De Bary 1884; Stahl 1900; Curtis 1943; Frey-Wyssling 1941; Perrin 1971a, b, 1972; Banerjee & Deshpande 1973; Lersten & Curtis 1985; Pickard 2007; Hagel et al. 2008; Krak & Mráz 2008; Makbul et al. 2011; Chwil et al. 2015; Castelblanque et al. 2016; Makbul et al. 2016; Wang et al. 2018; this work
	Liabeae 18/190(3/4)	−	−	−	+	−	Robinson 1978, 1983, 1990; Bremer 1994; Funk et al. 1996; Cabrera et al. 1999; Funk & Zermoglio 1999; Moran & Funk 2006, 2007; Soejima et al. 2008; Dillon et al. 2009; Funk et al. 2012; Gutiérrez & Luján Luna 2013; this work

Table 1 (continued)

Subfamily	Tribe Genera/spp (genera/spp)	Secretory structures					Reference
		C	SC	H	L	GT	
	Vernonieae 120/1000(11/18)	−	−	+	+	+	Metcalfe 1967; Narayana 1979; Castro et al. 1997; Milan et al. 2006; Adedeji & Jewoola 2008; Favi et al. 2008; Redonda-Martínez et al. 2012; Oliveira et al. 2015; Lusa et al. 2015 2016, 2018; Liesenfeld et al. 2019; this work
Corymbioideae	Corymbieae 1/9(1/2)	−	−	−	−	+	Weitz 1989; this work
Famatinanthoideae	Famatinantheae 1/1	−	−	−	−	+	Freire et al. 2014
Gochnatioideae	Gochnatieae 4/88(4/7)	−	−	+	−	+	Castro et al. 1997; Freire et al. 2002; Melo-de-Pinna 2004; Rossatto & Kolb 2010; Youssef et al. 2013; this work
Gymnarrhenoideae	Gymnarrheneae 1/1	−	−	−	−	−	**Without information**
Hecastocleidoideae	Hecastocleideae 1/11/1	−	−	−	−	−	This work
Mutisioideae	Mutisieae 14/200(19/24)	+	−	+	−	+	Castro et al. 1997; Melo de Pinna 2004; Liesenfeld et al. 2019; this work
	Nassauvieae 25/300(12/22)	+	−	+	−	+	Katinas 1996; Castro et al. 1997; this work
	Onoserideae 6/52(4/7)	+	−	−	−	−	This work
Pertyoideae	Pertyeae 4/80(1/1)	−	−	−	−	+	Cai-Fei et al. 2020; this work
Stifftioideae	Stifftieae 6/?(3/4)	−	−	−	−	−	Ruiz et al. 2016; this work
Wunderlichioideae	Hyalideae 4/6(2/2)	−	−	−	−	−	Melo de Pinna & Menezes 2003; this work

Table 1 (continued)

Subfamily	Tribe Genera/spp (genera/spp)	Secretory structures					Reference
		C	SC	H	L	GT	
	Wunderlichieae 4/36(4/6)	−	−	−	−	+	This work

face (Fig. 2j) or surrounding the vascular bundles (Fig. 2k). In most taxa, canals do not preserve their contents; however, in some cases, they preserve yellow contents with a crystallized appearance (Fig. 2l). Such canals were present in 280 species and 17 of the analyzed tribes (Fig. 3).

Cavities

Cavities are distinguished as large elliptical to rounded intercellular spaces in paradermal sections (Fig. 2m). They are always solitary and externally delimited by the cavity sheath, which includes several strata of nonsecretory cells with thickened walls that surround the secretory region and by more than one layer of epithelial cells surrounding the cavity lumen (Fig. 2n). Given their size, they are evident to the naked eye, and in almost all taxa, they partially conserve their contents. Cavities were only present in the species analyzed from the tribe Tageteae.

Hydathodes

In the studied species, hydathodes are generally present in leaves with well-developed teeth; however, it is also possible to find hydathodes in leaf blades with entire margins or even in strongly divided leaf blades. In all cases, hydathodes are irrigated by a vein (primary, secondary or higher order) that divides into xylem strands upon reaching the tooth. The surrounding mesophyll of these strands differentiates into an epithem with large intercellular spaces (Fig. 4a, b). In the hydathode, one or more guttation pores are observed in the epidermis. They were found in 141 species and 19 tribes (Fig. 5).

Laticifers

In paradermal sections, highly branched elongated cells are observed (Fig. 4c). Laticifers fuse with each other, forming articulated laticifers; however, they are not very evident because in most species, they lose their contents with histological processing. Some taxa partially retain grayish (Fig. 4d) or reddish (Fig. 4e) contents, both of granular consistency. In all the analyzed species, laticifers are associated with vascular bundles and are more visible toward the abaxial surface of the midrib, where they can be solitary or in groups (Fig. 4f). Laticifers were only observed in species of the tribes Arctotideae, Cichorieae, Liabeae, and Vernonieae.

Glandular Trichomes

Glandular trichomes in Asteraceae share the presence of thin cuticles and cell walls, large nuclei toward the apical cells of the trichome, and generally reddish cellular contents. Here, we recognize seven morphotypes: (1) vesicular, (2) stipitate, (3) peltate, (4) uniseriate, (5) globoid, (6) capitate, and (7) spatulate. Glandular trichomes can only be found on the abaxial surface (88 species) or on the adaxial surface of the leaf blade (3 species), although the predominant condition is on both surfaces (155 species). In all cases, glandular trichomes derive from epidermal cells and are mostly

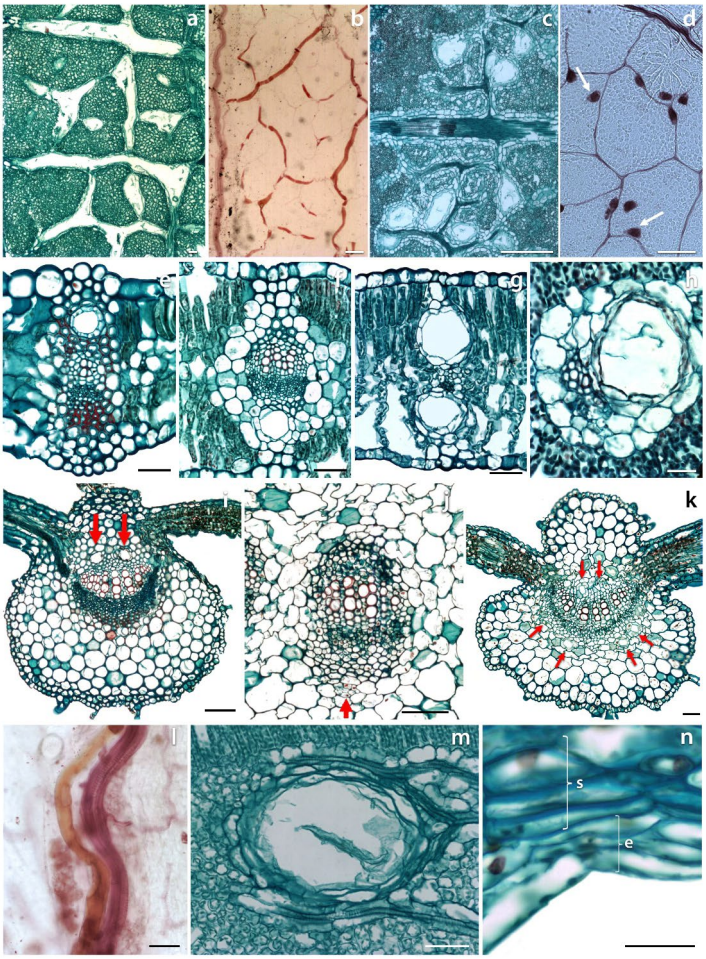

Fig. 2 Canals and cavities. (**a**) *Verbesina virgata*, canals, PS. (**b**) *Galinsoga parviflora*, canals, CL. (**c**) *Baccharis salicifolia*, canals, PS. (**d**) *Aldama dentata*, canals, CL. (**e**) *Lagascea rigida*, canal on xylem side of the vascular bundle, TS. (**f**) *Baccharis salicifolia*, canal on phloem side of the vascular bundle, TS. (**g**) *Verbesina virgata*, canals on both sides of the vascular tissue of the vascular bundle, TS. (**h**) *Cosmos parviflorus*, canal on lateral side of the vascular bundle, TS. (**i**) *Brickellia secundiflora*, canals on xylem side of the vascular bundle in the midrib, TS. (**j**) *Centaurea rothrockii*, canal on the phloem side of the vascular bundle of the midrib, TS. **k**) *Ageratina pichichensis*, canals in both sides of the vascular tissue of the midrib, TS. **l**) *Tridax rosea*, canal with contents, PS. **m**) *Dyssodia papposa*, secretory cavity, PS. **n**) *Dyssodia pinnata*, detail of the cavity sheath (s) and secretory epithelium (**e**), PS. In all cases, the red arrows indicate the position of the canals with respect to the vascular bundles. Scale bar is 50 µm in a, **e**–**g**, **k**–**n**; 100 µm in **b**, **d**, **i**, **j**; 300 µm in **c**; 25 µm in **h**. PS=paradermal section, TS=transverse section, CL=cleared leaf

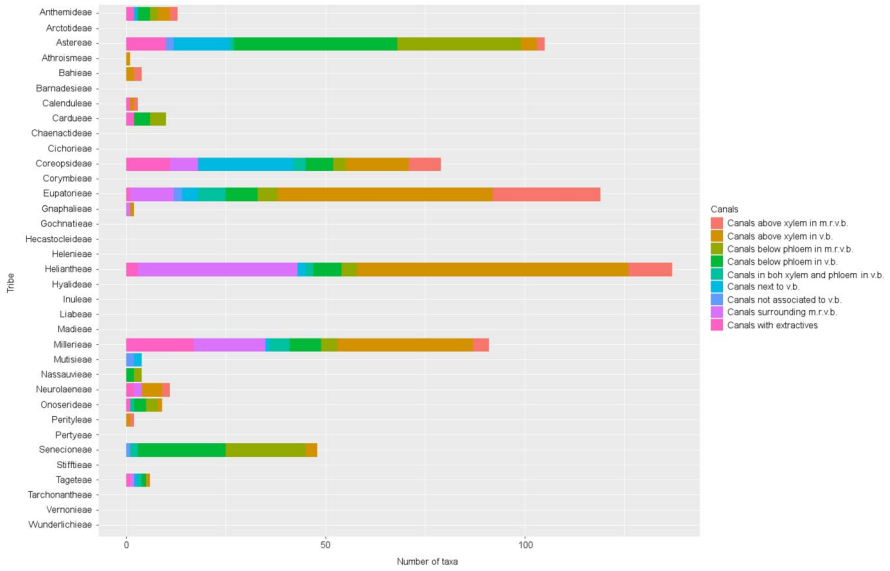

Fig. 3 Distribution of the canals in the 35 tribes of Asteraceae analyzed

multicellular at the base, body, and apex; however, the greatest variation is observed in the apical cells. Glandular trichomes occurred in 25 tribes and 247 of the analyzed species, representing 45.2% of the studied taxa (Fig. 6). Each of the morphotypes is described below.

Vesicular

In frontal view, the vesicular morphotype of glandular trichomes has both a base and short biseriate body (rarely triseriate) and the apex is bicellular (*Montanoa pteropoda*, Fig. 7a) and may or may not present an evident subcuticular space, as occurs in *Parthenium bipinnatifidum*. Vesicular glandular trichomes can sometimes be confused with uniseriate trichomes in lateral view because their position with respect to the section plane can change (Fig. 7b). Vesicular glandular trichomes can be found sunken in a depression of the epidermis or superficially. They were the predominant morphotype of glandular trichomes and occurs in 167 species and 20 of the studied tribes (Fig. 6).

Stipitate

The stipitate morphotype of glandular trichomes has a multicellular foot, the body is generally elongated, uniseriate or biseriate, and the apex can be bicellular or multicellular. At least 4 subtypes of stipitate glandular trichomes are recognized, and they differentiated by the shape of the apex and division planes of apical cells. Subtype 1 is characterized by having a conical apex with divisions in multiple planes, as in *Ageratina adenophora* (Fig. 7c). Subtype 2 is characterized by a biseriate apex that

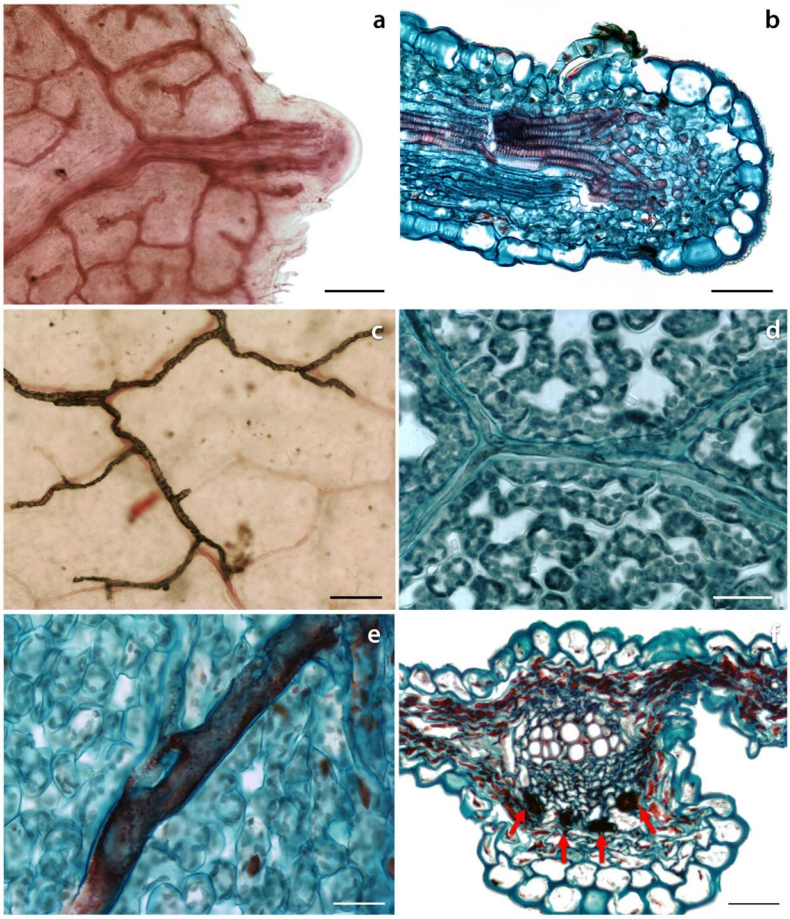

Fig. 4 Hydathodes and laticifers. (**a**) *Stevia lucida*, hydathode, CL. (**b**) *Zaluzania augusta*, hydathode, TS. (**c**) *Pyrrhopappus multicaulis*, laticifer, CL. (**d**) *Sonchus oleraceus*, laticifer with grayish contents, PS. (**e**) *Pyrrhopappus multicaulis*, laticifer with reddish contents, PS. (**f**) *Pinaropappus roseus*, laticifers toward the abaxial surface of the midrib (red arrows), TS. Scale bar is 100 µm in **a**, **c**; 50 µm in **b**, **f**; 25 µm in **d**, **e**. PS=paradermal section, TS=transverse section, CL=cleared leaf

becomes wider toward its most distal part, as in *Brickellia secundiflora* (Fig. 7d). Subtype 3 is characterized by a globose apex with divisions in multiple planes, as in *Piqueria pilosa* (Fig. 7e). Subtype 4 characterized by a bicellular apex, as observed in *Pseudognaphalium viscosum* (Fig. 7f). Stipitate glandular trichomes were observed in 15 species corresponding to 5 tribes (Fig. 6).

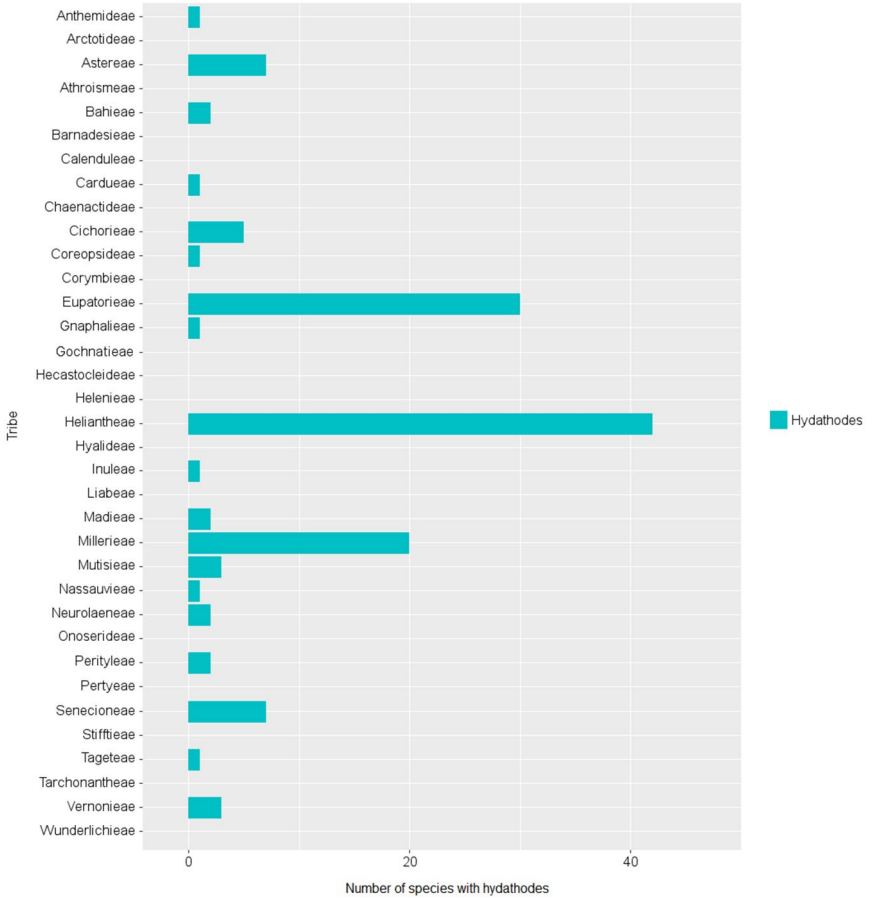

Fig. 5 Distribution of the hydathodes in the 35 tribes of Asteraceae analyzed

Peltate

The peltate morphotype of glandular trichomes are sunken in a depression of the epidermis; in surface view, they have a shield shape, while in the cross section of the leaf (longitudinal view of the trichome), they are obconic, and three different subtypes are recognized. Subtype 1 has a multicellular base and body, and the apex is not well differentiated from the body and lacks a particular cellular organization; in longitudinal sections, the terminal cells form a convex structure as observed in *Haplopappus deserticola*, *Hazardia berberidis*, and *Isocoma veneta*. (Fig. 7g, j). Subtype 2 is formed by a unicellular base and body and presents an apex that is well differentiated from the body with approximately 10 cells radially arranged, only found in *Erigeron longipes* (Fig. 7h, k). Subtype 3 is structurally similar to Subtype 1 but differs in the terminal cell form, which is flattened in longitudinal section, only in *Lophopappus tarapacanus* (Fig. 7i, l). Peltate glandular trichomes were only found in four species of Astereae and a single species of Mutisieae.

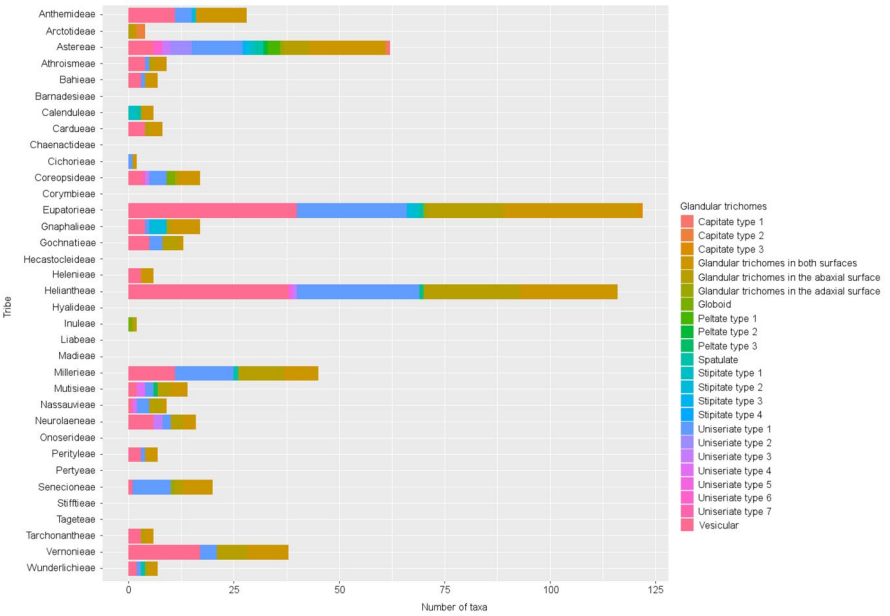

Fig. 6 Distribution of the morphotypes of glandular trichomes and their position in the leaves of 35 tribes of Asteraceae

Uniseriate

The uniseriate morphotype of glandular trichomes have a row of cells of variable number. Seven subtypes of uniseriate glandular trichomes were recognized according to the shape of the apical cell. In Subtype 1, the cells of the body are rectangular, equal in size, and the apical cell has the same shape as the rest of the trichome cells, but its distal region is rounded, as in *Chromolaena collina* (Fig. 8a). In Subtype 2, the cells of the body are more or less rounded and become larger toward the apex, ending with a flagelliform appendage derived from the cell wall, as in species of *Baccharis* and *Gutierrezia argyrocarpa* (Fig. 8b). In Subtype 3, the cells of the body are rectangular while the apical region was conical with acute distal region, as in *Chromolepis heterophylla* (Fig. 8c). In Subtype 4, the cells of the body are depressed while the apical cells were quadrangular and smaller in size, as exemplified in *Dolichlasium lagascae* (Fig. 8d). In Subtype 5, the cells of the body are rounded and have the same size while the apical cells are narrower, elongated, and sharp at its distal end, as in *Flourensia resinosa* (Fig. 8e). In Subtype 6, the cells are small and develop in an invagination of the epidermis, and they are clavate with depressed cells, except the apical cells, which are rounded, as in *Gundlachia corymbosa* (Fig. 8f). In Subtype 7, the cells are quadrangular at the base of the trichome and depressed toward the apex, and the apical cells are conical and rounded, as observed in *Cosmos bipinnatus* (Fig. 8g). Uniseriate trichomes were observed in 136 species and distributed in 15 tribes (Fig. 6).

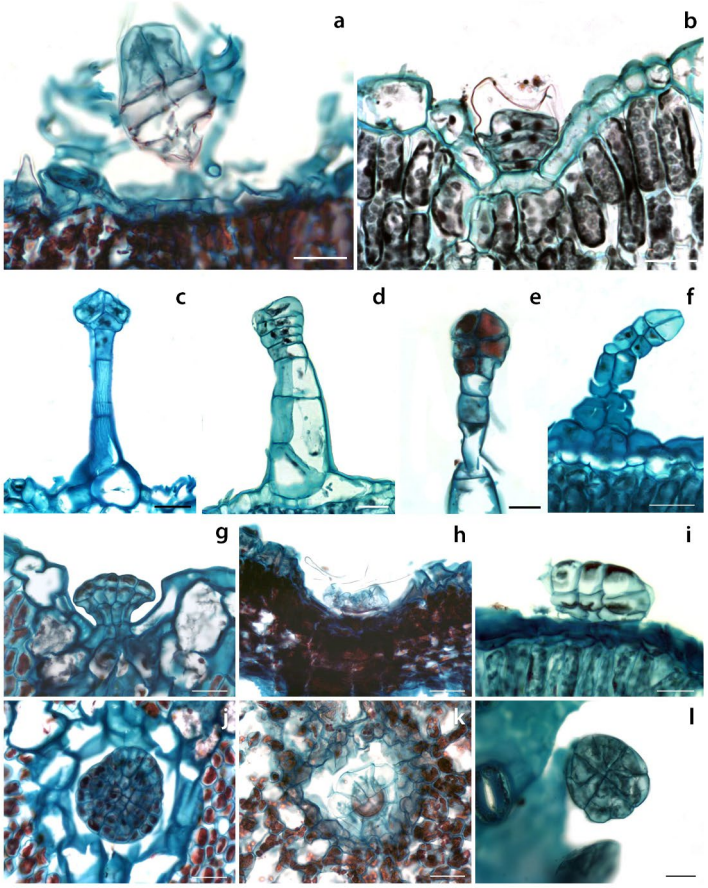

Fig. 7 Diversity of vesicular, stipitate and peltate glandular trichomes. (**a**) *Montanoa pteropoda*, vesicular glandular trichomes (frontal view), TS. (**b**) *Stevia tomentosa*, vesicular glandular trichomes (lateral view), TS. (**c**) *Ageratina adenophora*, stipitate trichome Subtype 1, TS. (**d**) *Brickellia secundiflora*, stipitate trichome Subtype 2, TS. (**e**) *Piqueria pilosa*, stipitate trichome Subtype 3, PS. (**f**) *Pseudognaphalium viscosum*, stipitate trichome Subtype 4, TS. (**g**) *Isocoma veneta*, peltate trichome Subtype 1, TS. (**h**) *Erigeron longipes*, peltate trichome Subtype 2, TS. (**i**) *Lophopappus tarapacanus*, peltate trichome Subtype 3, TS. (**j**) *Isocoma veneta*, peltate trichome Subtype 1, PS. **k**) *Erigeron longipes*, peltate trichome Subtype 2, PS. **l**) *Lophopappus tarapacanus*, peltate trichome Subtype 3, PS. Scale bar is 50 µm in **a**; 25 µm in **b**, **c**, **e**–**l**; 20 µm in **d**. PS=paradermal section, TS=transverse section

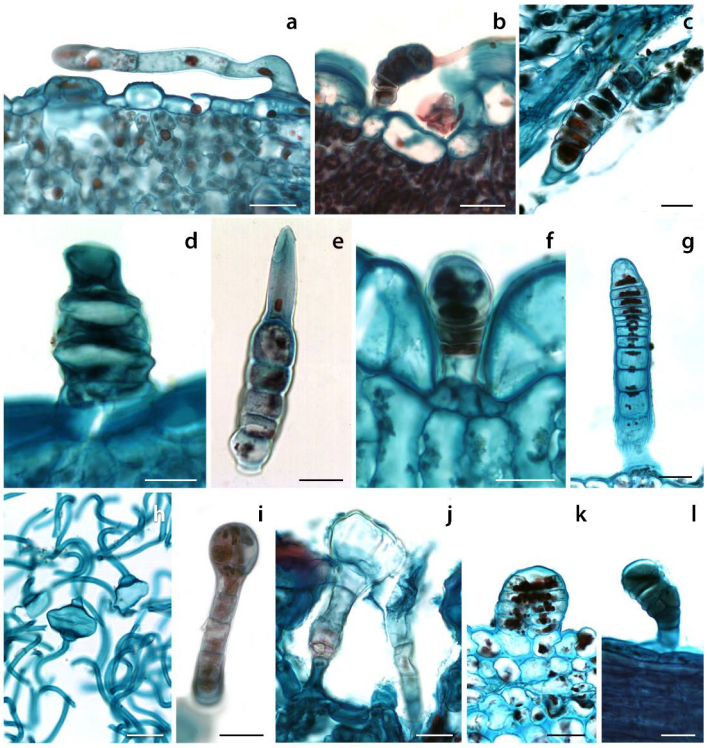

Fig. 8 Diversity of uniseriate, capitate, globoid, and spatulate glandular trichomes. (**a**) *Chromolaena collina*, uniseriate trichome Subtype 1, TS. (**b**) *Gutierrezia argyrocarpa*, uniseriate trichome Subtype 2, TS. (**c**) *Chromolepis heterophylla*, uniseriate trichome Subtype 3, PS. (**d**) *Dolichlasium lagascae*, uniseriate trichome Subtype 4, TS. (**e**) *Flourensia resinosa*, uniseriate trichome Subtype 5, PS. (**f**) *Gundlachia corymbosa*, uniseriate trichome Subtype 6, TS. (**g**) *Cosmos bipinnatus*, uniseriate trichome Subtype 7, TS. (**h**) *Arctotheca prostrata*, capitate trichome Subtype 1, PS. (**i**) *Heterothalamus alienus*, capitate trichome Subtype 2, PS. (**j**) *Campovassouria cruciata*, capitate trichome Subtype 3, TS. **k**) *Cosmos bipinnatus*, globoid trichome, TS. **l**) *Archibaccharis schiedeana*, spatulate trichome, PS. Scale bar is 25 µm in **a**, **b**, **e**, **f**, **h**, **i**, **l**; 20 µm in **c**, **d**, **g**, **j**, **k**

Capitate

The capitate morphotype of glandular trichomes present a uniseriate body and spherical apex. Three subtypes of capitate trichomes are differentiated by body length and apex characters. Subtype 1 has a unicellular base and body and a unicellular or bicellular and spherical apex, as observed in *Heterothalamus alienus* (Astereae, Fig. 8 h). Subtype 2 has a unicellular base and a unicellular and elongated body that widens abruptly in the region near the spherical apical cell (Fig. 8i), as observed in *Arctotheca prostrata* (Arctotideae). Subtype 3 has a unicellular base, a uniseriate body, and a large (2 times larger than the rest) and bicellular apex, as observed in *Campovassouria cruciate* (Eupatorieae, Fig. 8j). Capitate trichomes were present in only three species of Arctotideae, Astereae and Eupatorieae (Fig. 6).

Globoid

The globoid morphotype of glandular trichomes are constituted by a bicellular foot, bicellular body and an apical pyramidal cell; in some cases, they are bicellular (Fig. 8k). They occur in three species of Coreopsideae and Inuleae.

Spatulate

The spatulate morphotype of glandular trichomes are distinguished by being thin at the base and widening toward the apex; they have depressed cells that can show multiple divisions, but the distal portion is always rounded, as in *Archibaccharis schiedeana* (Fig. 8l). They were present in six species of the tribes Astereae, Calenduleae, Eupatorieae, Millerieae and Wunderlichieae.

The synthesis of the secretory structures in Asteraceae based on our results and the information available in the literature is given in Table 1; Fig. 9. The integration of both sources of information reveals that almost all of the tribes possess one to three types of secretory structures, although these structures predominate in the subfamily Asteroideae and are absent in some early-diverging clades. Character evolution analyses for the main five secretory structures show that glandular trichomes are the plesiomorphic secretory structure in the family (Fig. 10) recorded in the early-diverging clades, and their presence is inferred in the basal nodes of the trees. Although glandular trichomes have originated in several lineages, their occurrence appears as an ancestral state with high probability in all reconstructed nodes. Canals and hydathodes appear in three different lineages within Asteraceae: Mutisioideae, Carduoideae (Cardueae) and Asteroideae, and they predominate in Asteroideae (the most recent and diverse subfamily). Compared with trichomes, the presence of canals or hydathodes is not a common ancestral state among the three lineages in any of the reconstructed nodes. Cavities and laticifers are revealed as apomorphies within Tageteae and Cichorioideae, respectively.

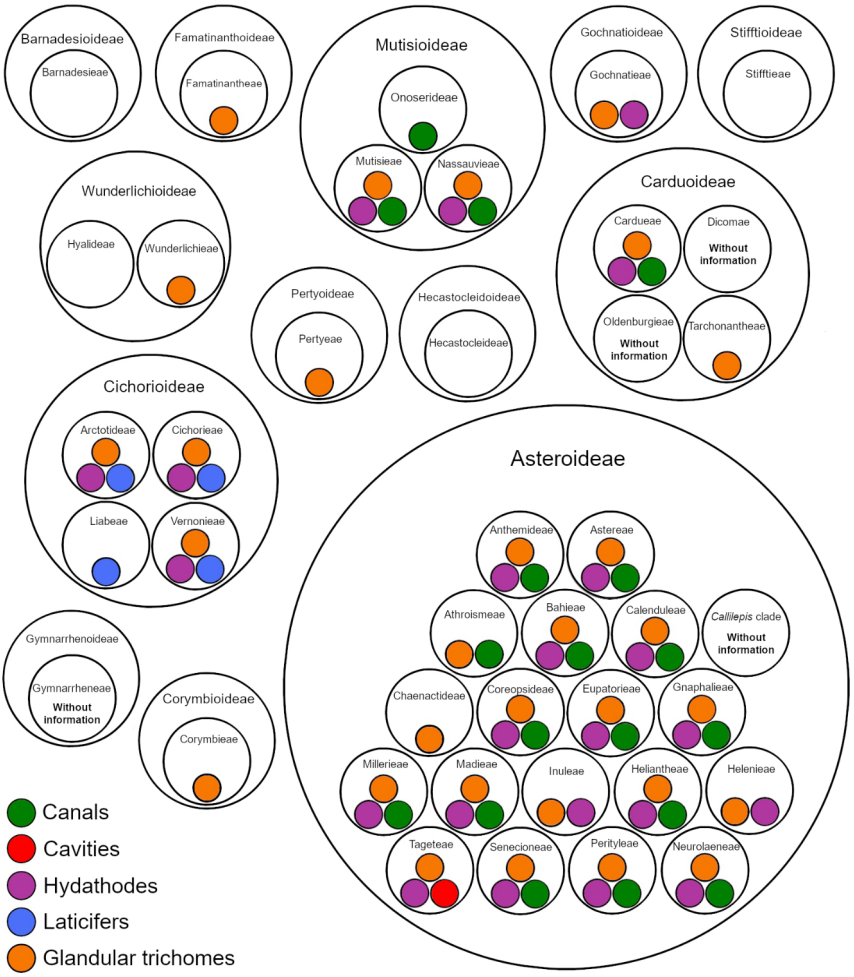

Fig. 9 Graphic summary of the distribution of the five types of secretory structures, throughout Asteraceae, reported in this work and in previous studies

Discussion

Asteraceae is the largest family among angiosperms, and it includes 23,113 to 23,600 species (Panero & Funk 2008, 2009; Villaseñor 2018). This diversity is reflected not only in its morphological variability but also in the anatomical complexity of its organs, particularly the leaves. In this study, five secretory structures occurring in the leaves were identified, which are informative at different taxonomic levels. Similarly, some tribes without secretory structures were recognized, which correspond mostly to early-diverging tribes. At the same time, some evolutionary patterns were recognized, and certain anatomical considerations of secretory structures were performed.

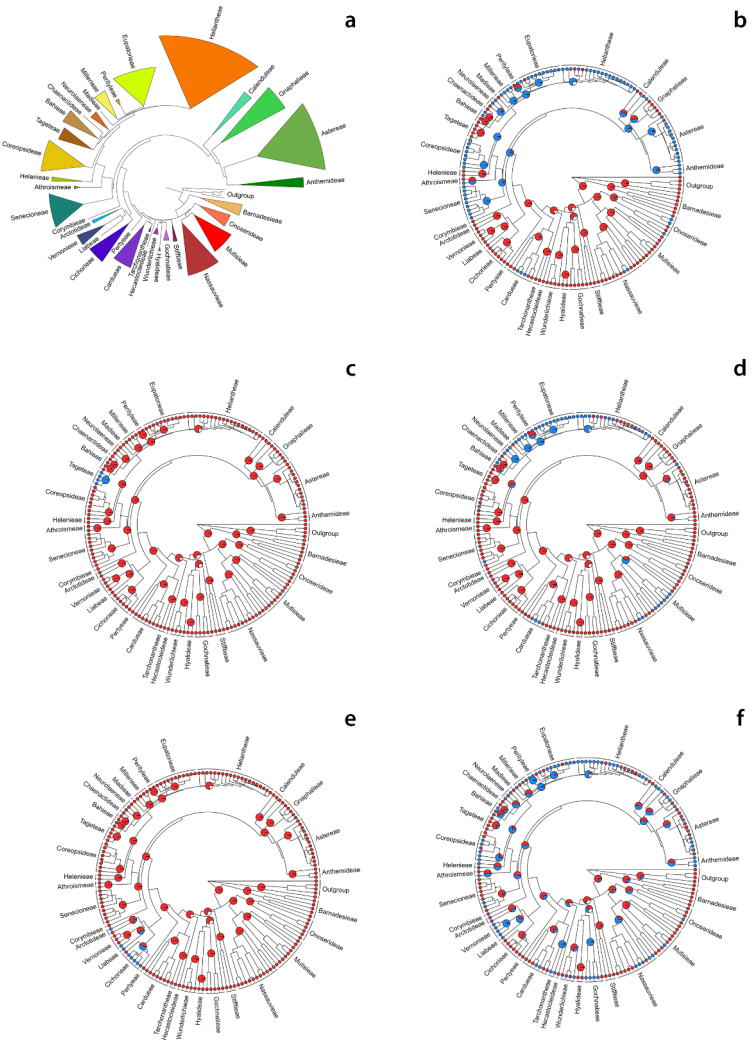

Fig. 10 Character evolution. (**a**) Summarized majority-rule consensus tree at the tribe level. (**b**) Canals. (**c**) Cavities. (**d**) Hydathodes. (**e**) Laticifers. (**f**) Glandular trichomes. Annotations: red=absence, blue=presence

Systematic Value of Leaf Secretory Structures in Asteraceae and Their Evolutionary Patterns

The observations made in 542 species of Asteraceae distributed in 35 of the 40 tribes currently recognized by Panero & Crozier (2016) along with data from the literature review (Table 1) revealed that secretory structures are present in 80% of the

tribes in Asteraceae. The representatives of these tribes have one to three types of secretory structures, with the greatest diversity of them in the tribes of the subfamily Asteroideae. Four of the 40 tribes did not show any type of secretory structures: Barnadesieae, Hecastocleideae, Hyalideae and Stifftieae. Information on the secretory structures was not available for the *Callilepis* clade (Panero & Crozier 2016) or the tribes Dicomae, Gymnarrheneae and Oldenburgieae; therefore, future studies should be focused on these taxa (Fig. 9).

The tribes of Asteraceae that did not present secretory structures belong to early-diverging subfamilies: Barnadesioideae, Hecastocleidoideae, Stifftioideae, and Wunderlichioideae (Rivera et al. 2020). An interesting aspect is that secondary metabolites of medicinal interest have been reported for some of their members, such as *Barnadesia*, *Hyalis* and *Stifftia* (Bohm & Stuessy 1995; Ybarra et al. 1997; Machado et al. 2012; Marques et al. 2012). Therefore, these compounds must be synthesized in secretory idioblasts in some regions of the mesophyll. These secretory cells could be evolutionarily important to the development of more specialized and complex structures.

Secretory structures are considered important mechanisms to avoid herbivory. However, this defensive activity in early-diverging Asteraceae lineages is oriented to the development of both mechanical and chemical barriers. For the former, there are thicker cuticles, a higher density of eglandular trichomes, and a higher proportion of sclerenchyma in their leaves (Terrazas et al. unpublished data). In this sense, the evolutionary pattern of secretory structures in Asteraceae indicates that the early-diverging lineages did not present secretory structures, whereas most of the members of the later-diverging tribes generate a high diversity of secretory structures (Fig. 10).

Glandular trichomes constitute the most diverse secretory structure in the family. These epidermal appendages (together with the hydathodes) occur in some members of some earliest-diverging clades, and they appeared and disappeared multiple times in the evolution of the tribes. However, their presence becomes more frequent toward the lately diverging lineages of the subfamily Asteroideae, which exhibit the maximum diversity. Although the morphotypes of glandular trichomes and their subtypes were not diagnostic of any of the tribes, they are an important character sources for recognizing species inside several groups (Krak & Mráz 2008; Hayat et al. 2009; Rojas-Leal et al. 2017; Vitali 2017); i.e., Subtypes 3 and 4 of stipitate trichomes are diagnostic of *Piqueria pilosa* and *Pseudognaphalium viscosum*, respectively. Trichomes are solitary in almost all the studied taxa except in the *Baccharis* species, which are grouped and generally found in a depression on the epidermis (Budel et al. 2004, 2018; Hadad et al. 2013). Compared with the rest of the morphotypes, stipitate trichomes show greater complexity, and they were previously reported for *Stevia* (Gutiérrez et al. 2016), many genera of the tribe Cichorieae such as *Stephanomeria*, *Prenanthes*, *Dubyaea*, and *Hieracium* (Krak & Mráz 2008), and *Vernonia gossypina* and *V. ramaswamii* (Narayana 1979). Even though reported trichomes did not correspond to any of the subtypes of stipitate trichomes described in this work, the seven main morphotypes proposed have characteristics that make them sufficiently robust to classify the trichomes reported as stipitate trichomes. Thus, even if another different subtype exists in other Asteraceae groups, it will be possible to group it in this category.

Canals were observed in 280 species of Asteraceae studied distributed in 17 tribes and predominated in the tribes of Asteroideae (Fig. 10). Their position with respect to vascular bundle tissues is considered to be taxonomically informative because it allows the identification of groups of species in some genera, as previously reported for *Aldama* (Bombo et al. 2012; Oliveira et al. 2013; Souza da Silva et al. 2014; Filartiga et al. 2016). In *Erigeron galeotti* and *E. janivultus* there are canals above the xylem of the vascular bundles of the leaf blade, whereas *E. karwinskianus*, *E. longipes* and *E. pubescens* have canals below the phloem of the vascular bundles. The presence of contents in the canal lumen could be important for recognizing supraspecific taxa, as observed in many species of Coreopsideae. Likewise glandular trichomes, canals are present in some of the early-diverging clades but prevail in the most diversified tribes in the family.

Hydathodes appeared in several species of different tribes and were prevalent in several tribes of Asteroideae, such as Eupatorieae, Heliantheae, and Senecioneae, although they also appeared in some early-diverging tribes, such as Mutisieae. The results of this study contributed to broadening the knowledge of the number of taxa with hydathodes for the family, now identified in 142 analyzed species distributed in 19 tribes. Lersten & Curtis (1985) mentioned the presence of hydathodes in eight of the tribes of the subfamily Asteroideae; therefore, this work expands the presence of hyathodes to twice the number of tribes, pointing out they are more common than previously considered. Hydathodes are almost never reported due to their structural simplicity, making them difficult to identify by routine anatomical analyses (because more than a single microtechnique is needed to describe them, e.g., leaf clearings); therefore, the margin of the leaf blade is not often described in detail and the presence of guttation under field conditions is rarely reported. Hydathodes are commonly present in taxa with leaves without divisions and toothed margins, but not in Cardueae, where they are absent because of the massive sclerification of the veins and the presence of a spine at the apex of the margin teeth, as occurs in *Cirsium* species. However, they are also present in several taxa with leaves whose leaf blades are strongly divided or whose leaves are not divided but have entire margins.

According to Loockerman et al. (2003), cavities correspond to a synapomorphy for the tribe Tageteae. However, these secretory structures were present only in the analyzed species of the subtribe Tagetineae, as reported in previous studies (Simon et al. 2002; Fonseca et al. 2006; Milan et al. 2006; García-Sánchez et al. 2012; Oliveira et al. 2015; Lusa et al. 2016; Ferraro & Scremin-Dias 2017; Lizárraga et al. 2017; Lusa et al. 2017; Páez et al. 2019; Younis et al. 2020); therefore, the cavities are taxonomically informative at the subtribe level.

Laticifers have only been mentioned in previous studies for the tribe Cichorieae (Fahn 1979, 1982; Evert 2006); however, the observations in this work confirm also their occurrence in Arctotideae, Liabeae and Vernonieae, as previously reported (Metcalfe 1967; Lewinsohn 1991; Karis et al. 2006; Gutiérrez & Lujan Luna 2013). These tribes belong to the subfamily Cichorioideae; therefore, although laticifers are not informative in recognizing tribes, they are informative at the subfamily level. Laticifers are commonly found toward the abaxial surface of the leaves and especially evident at the midrib, as in *Scorzonera* (Cichorieae; Makbul et al. 2011, 2016). It is possible that laticifers develop differentially in the organs of certain taxa, i.e.,

Melo-de-Pinna & Menezes (2003) reported laticifers in the adventitious roots of eleven species of *Richterago* (Mutisieae) but not in their leaves. In this work, laticifers were not observed in the leaves of *R. amplexifolia* and *R. angustifolia*. Laticifers in Asteraceae must be further studied to determine their role in the systematics of the family, such as in other angiosperm families, e.g., Sapindaceae (Medina et al. 2021).

Anatomical Considerations

In this work, five secretory structures in the vegetative leaves of the analyzed species of Asteraceae were reported: glandular trichomes, canals, cavities, hydathodes and laticifers. The number of types is greater than that of Fahn (1979), who identified four types without considering the cavities. However, it is less than that of Castro et al. (1997), who reported the presence of extrafloral nectaries and glandular appendages in addition to the secretory structures found in this work. Extrafloral nectaries and glandular appendages are only found in leaves associated with reproductive structures, such as inflorescences and involucre bracts, as Carlquist (1959a, b) and O'Dowd & Catchpole (1983) previously reported. A more exhaustive review of secretory structures can provide a new standardization of the terminology and expand the knowledge of the taxa in which these structures occur. The number of taxa with secretory structures reported in previous works, added to those here studied increased substantially their knowledge in the Asteraceae (Table 1; Fig. 10).

In taxonomic studies, trichomes viewed on the surface represents a widespread identification method; however, in this work, the transverse and paradermal sections as well as the cleared leaves allowed us to summarize the diversity of glandular trichomes in seven morphotypes according to the fine details of the cellular organization in its three regions (base, body, and apex). Performing only observations of trichomes at the surface view and their associated inferences could lead to misinterpretation by assigning the same name to glandular trichomes, which differ in their cellular conformation.

Vesicular glandular trichomes outstand as the most common morphotype in the family (present in 167 species) and have been previously reported for several genera of different tribes, such as *Aldama* (Bombo et al. 2012; Oliveira et al. 2013; Souza da Silva et al. 2014; Filartiga et al. 2016), *Dimerostemma* (Silva et al. 2015), *Flourensia* (Delbón et al. 2007, 2012), *Helianthus* (Aschenbrenner et al. 2013), *Richterago* (Melo-de-Pinna 2004), *Sigesbeckia* (Aguilera et al. 2004) and *Vernonia* (Narayana 1979; Redonda-Martínez et al. 2012; Oliveira et al. 2015; Lusa et al. 2016). However, this morphotype has frequently been described in different ways, and its variations lead to the consideration of more than one type of glandular trichome because the cells of the apex can collapse; similarly, the subcuticular storage space may or may not be visible. The position of the trichome with respect to the section plane also influences the way it is described since these structures may appear biseriate in frontal view or uniseriate in lateral view.

In general, uniseriate trichomes are thought to have no secretory function; nevertheless, uniseriate trichomes share characteristics with the rest of the morphotypes, particularly the presence of reddish contents in their cells; however, confirming whether a uniseriate trichome is glandular requires histochemical tests (Aschen-

brenner et al. 2013; Muravnik et al. 2016). These epidermal appendages are structurally very similar to each other, and the greatest variation is found in the shape of the apical cell, as previously reported (Robinson 2009; Rojas-Leal et al. 2017). In most cases, more than one type of trichome, e.g., eglandular or glandular, can be found in the leaves of Asteraceae (Redonda-Martínez et al. 2016; Liesenfeld et al. 2019). The most common pattern is Subtype I uniseriate glandular trichomes and vesicular glandular trichomes on the same leaf.

The presence of peltate glandular trichomes was reported by Favi et al. (2008) in *Vernonia galamensis* ssp. *galamensis*; according to our observations, the glandular trichomes reported by these authors actually correspond to vesicular trichomes. Peltate trichomes were only observed in the analyzed species of *Erigeron*, *Isocoma*, *Haplopappus*, and *Hazardia*, all of them members of the Astereae tribe, thus representing the first confirmed report for Asteraceae. This diversity suggests the need to perform additional anatomical studies in combination with other techniques oriented to surface observations, in order they provide an even clearer picture of the diversity of glandular trichomes in the family.

In many cases, determining what type of internal secretory structure gives rise to certain secretions can be complicated; in general, any whitish liquid is reported as latex; however, exudates can originate in laticifers, canals or cavities (Pickard 2007). In Asteraceae, the predominant inner secretory structures are canals, which have generally been described as elongated intercellular spaces that are delimited by epithelial cells; however, none of the definitions indicates their length (Mauseth 1988; Evert 2006; Beck 2010). Canals have great variability in length, from less than 100 μm to more than 800 μm. For example, in most taxa of Astereae, Coreopsideae, and Eupatorieae, there are short (< 100 μm) to very long (> 500 μm) canals in the same leaf, as in *Bidens odorata* and *Conyza bonariensis*. In some species of *Cosmos* and *Dahlia*, the short canals are more or less spherical to elliptical in paradermal sections and tend to develop very close to each other, giving the appearance of being a single structure, although they always remain independent, as previously reported for *Solidago canadensis* (Lersten & Curtis 1989). Regardless of the size, the canals in Asteraceae always show a unistratified canal sheath derived from the vascular bundle sheath, as well as epithelium made up of a single stratum of secretory cells, which is consistent with the most widely used descriptions of canals (Mauseth 1988; Evert 2006).

Although secretory cavities, such as canals, are also intercellular spaces delimited by epithelial cells, Fahn (1979) and Mauseth (1988) mentioned that this type of secretory structure is characterized by the presence of a multistratified secretory epithelium and sheath. Crang et al. (2018) highlighted other differences between canals and cavities are that the latter are generally larger, more or less spherical and isolated from each other, as occurs in Myrtaceae and Rutaceae. Structural similarities between canals and secretory cavities could lead to misinterpretation, although the characteristics of the sheath wall and secretory epithelium are consistent across taxa. For this reason, it is recommended to take them into account when making observations; in the same way, it is advisable to section the leaves in the paradermal plane in addition to the transverse plane and perform observations in cleared leaves if possible.

Laticifers in Asteraceae have been underexamined, being those of *Taraxacum* (Cichorieae; Castelblanque et al. 2016) the most studied. This is mainly because their

structural characteristics do not allow them to be easily identified, as occurs in other families of angiosperms, such as Apocynaceae or Euphorbiaceae (Hagel et al. 2008). In Asteraceae, they are generally inconspicuous because they rarely retain their cellular contents. When the latex is preserved, it can be grayish with a granular appearance, as in *Sonchus oleraceus* (Cichorieae), while in other cases, it is reddish with an oily appearance, as in *Dillandia subumbellata* (Liabeae). Such traits could provide clues about the chemical composition of the latex they produce, as has been reported in other plant families with laticifers (Bauer et al. 2014).

Rios et al. (2020) mentioned that the extrafloral nectaries and hydathodes found on leaf teeth in eudicots can be very similar in appearance. However, they emphasize that the main differences between both types of secretory structures are the presence of an epithem (absent in the extrafloral nectaries) and the vascular bundles that irrigate the leaf teeth in their terminal portion, which are formed only by xylem strands in the case of hydathodes, while in the case of nectaries, the vascular strands are formed by xylem and phloem. In the analyzed Asteraceae species, the characteristics observed in the secretory structures found in the leaf teeth were consistent with those reported by Rios et al. (2020); therefore, it was confirmed that they correspond to hydathodes, while extrafloral nectaries do not exist in the family.

Idioblasts are individual cells with secretory activity (Fahn 1979; 1982; 1988; 2000), which is why many authors consider them a category within secretory structures; however, there are several attributes that together indicate their considerable differences. First is the fact that secretory idioblasts are unicellular, whereas the rest of the categories of secretory structures are multicellular and structurally complex. These secretory cells do not have a particular morphology distinguishing them from other adjacent cells (with the exception of size in some cases), which makes their identification difficult, and specific histological techniques, such as histochemical tests, are necessary for their recognition (Fahn 1979). Another important characteristic of idioblasts is its capacity of containing a great variety of compounds of different chemical nature (e.g., tannins, starch, oils, or compounds derived from calcium; Esau 1977; Crang et al. 2018). Their secretory activity in some cases can be affected by environmental conditions (Steyn et al. 2002; Solovchenko 2010) and can originate from any parenchymatic tissue, such as the epidermis or mesophyll (Beck 2010). For these reasons, we recommend using the term "secretory systems" (Mauseth 1988) to refer to any cell or groups of cells that have secretory activity (endogenous or exogenous). Under this terminology, we treat secretory idioblasts and secretory structures as two different types of secretory systems. Secretory idioblasts have been observed in many Asteraceae taxa, and these structures should be analyzed in detail in future publications.

Conclusions

Asteraceae shows great morphological variability that is reflected in its anatomical diversity, particularly in its secretory structures. In this work, we found secretory structures in most tribes in the family but predominated in the late-diverging lineages, whereas they were absent or scarce in the early-diverging lineages. Secretory

structures allow for the recognition of taxa at different levels, and a comparative study of secretory structures in Asteraceae is essential for standardizing its terminology and thus providing a framework for future studies. The detailed descriptions presented in this work will allow us to test hypotheses through phylogenetic comparative methods and determine the evolutionary role of secretory structures in Asteraceae diversification.

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Declarations

Conflict of Interest The authors declare that have no competing interests.

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