Article

Hoehnea 46(3): e752018, 2 tab., 4 fig., 2019 http://dx.doi.org/10.1590/2236-8906-75/2018

Morphological diversity of foliar trichomes in Asteraceae from Sand-fields of the Pampa biome, Rio Grande do Sul State, Brazil

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Received: 10 August 2018; accepted: 19 August 2019

How to cite: Liesenfeld, V., Gentz, P., Freitas, E.M. & Martins, S.M. 2019. Morphological diversity of foliar trichomes in Asteraceae from Sand-fields of the Pampa biome, Rio Grande do Sul State, Brazil. Hoehnea 46: e752018. http://dx.doi.org/10.1590/2236-8906-75/2018.

ABSTRACT - (Morphological diversity of foliar trichomes in Asteraceae from Sand-fields of the Pampa biome, Rio Grande do Sul State, Brazil). Asteraceae is the largest family of angiosperms and occurs predominantly in grassland areas. This study aimed to identify and characterize the foliar trichomes of 34 Asteraceae species from Sand-fields of the Pampa biome, by means of epidermal analyzes (front and transverse view) under light and scanning electron microscopy. Eleven types of trichomes were identified and characterized: three glandular (recurved on the epidermis, erect-capitate and uniseriate to multiseriate vesicular-capitate) and eight non-glandular (simple conical, flagellate-filiform, aseptate-flagellate, whip-like, oblique-flagellate, branched with one arm, branched with two T-shaped arms, branched with three or more arms). The most representative glandular type was the uniseriate to multiseriate vesicular-capitate (58%) and the non-glandular type was the simple conical (35%). A large number of trichomes is an adaptive strategy to the adverse conditions of the Pampa biome and its morphological diversity can be useful in the family systematics.
Keywords: anatomical adaptations, glandular trichomes, leaf anatomy, non-glandular trichomes, taxonomy

RESUMO - (Diversidade morfológica de tricomas foliares em Asteraceae dos Campos de Areais do bioma Pampa, Estado do Rio Grande do Sul, Brasil). Asteraceae é a maior família das angiospermas e ocorre predominante em áreas campestres. Este estudo buscou identificar e caracterizar os tricomas foliares de 34 espécies de Asteraceae dos Campos de Areais do bioma Pampa por meio de análises da epiderme (vista frontal e transversal) em microscopia de luz e eletrônica de varredura. Foram identificados e caracterizados 11 tipos de tricomas: três glandulares (recurvado, capitado ereto e capitado vesicular unisseriado a multisseriado) e oito tectores (cônico simples, filiforme-flagelado, asseptado-flagelado, forma de chicote, oblíquo-flagelado, ramificado com um braço, ramificado com dois braços em forma de T, ramificado com três ou mais braços). O tipo de tricoma glandular mais representativo foi o capitado vesicular unisseriado a multisseriado (58%) e o tipo não glandular (tector) foi o cônico simples (35%). A grande quantidade de tricomas é uma estratégia adaptativa às condições adversas do bioma Pampa e a sua diversidade morfológica pode ser útil na sistemática da família.
Palavras-chave: adaptações anatômicas, anatomia foliar, taxonomia, tricomas glandulares, tricomas tectores

Introduction

Asteraceae is the largest of the angiosperm families, with approximately 23,000 species distributed in over 1,600 genera, 13 subfamilies and 44 tribes (Funk *et al*. 2009, Panero *et al*. 2014). Its representatives are predominantly herbaceous, with simple and usually lobed leaves, inflorescence of the capitulum type and fruit of the cypsela type, which, along with the pappus, characterize its unit of dispersion (Roque & Bautista 2008, Funk *et al*. 2009). In Brazil there are 2,100 species, 290 genera and 28 tribes of the family (Flora do Brasil 2020), with Vernonieae, Eupatorieae, Heliantheae, Astereae,

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and Gnaphalieae being the richest tribes according to floristic surveys of the family in some localities (Nakajima & Semir 2001, Almeida *et al*. 2005, Ritter & Baptista 2005, Heiden *et al*. 2007, Beretta *et al*. 2008, Fernandes & Ritter 2009, Borges *et al*. 2010).

Asteraceae is one of the most successful plant families, because of the great diversity of secretory structures, the specialized methods of pollination and dispersion and phenotypic plasticity that contribute to the high number of species and their distribution in almost all habitats and vegetation formations (Smiljanic 2005, Beretta *et al*. 2008). However, a greater occurrence of the family is observed in open and arid areas (grasslands and savannas) and of high altitude and, less commonly, in forest environments (Barroso *et al*. 1991, Anderberg *et al*. 2007).

In Brazil, Asteraceae is distributed predominantly in the grassland formations of the Pampa biome (Ritter & Baptista 2005, Cancelli *et al*. 2007), which in the country is restricted to the State of Rio Grande do Sul and presents mixed vegetation of grassland formations and forests, with a predominance of grasslands (Overbeck *et al*. 2007). In addition, the Pampa biome presents different phytophysiognomic units (Seasonal Forest, Central Fields, *Barba-de-bode* Fields, Deep-soil Fields, Savannoid Vegetation, Coastal Fields, Sand-fields, Parkland Vegetation, Shallow Soils and other formations) (Boldrini *et al*. 2010), among which the Sand-fields (southwest of the State) are distinguished by the high species richness of Asteraceae (77 spp.) in relation to the other families, being Astereae (17), Eupatorieae (12), Gnaphalieae (10) and Vernonieae (nine) the most representative tribes (Freitas *et al.* 2010).

The high representativeness of Asteraceae in the Sand-fields is possibly a result of the morpho-anatomical adaptations of these plants, which allow their survival under extreme and limiting local environmental conditions such as sandy and low-fertility soils, water deficit, strong winds, high temperatures and high luminosity (Azevedo & Kaminski 1995, Klamt & Schneider 1995, Marchiori 1995, Freitas *et al*. 2009, 2010, Overbeck *et al*. 2015). These adaptations, usually xeromorphic, involve the presence of narrow leaves to reduce the surface area exposed to sunlight, presence of xylopodia and/or thick subterranean organs, presence of secondary metabolites to protect against predation, and a large number of trichomes on the vegetative organs (Lindman & Ferri 1974, Boldrini 2009).

Trichomes have a fundamental role in protection against high temperatures, excessive light, pathogens and herbivores (Werker 2000, Wagner *et al*. 2014). In addition, they are one of the most useful characters used in taxonomic studies of many angiosperms due to their almost universal presence among taxa, easy observation and morphological diversity (Faust & Jones 1973, Payne 1978, Adedeji & Jewoola 2008, Krak & Mráz 2008).

Trichomes can occur on vegetative and reproductive organs, varying in type and density over all parts of the plant and across different taxonomic levels (Werker 2000, Adedeji & Jewoola 2008). Due to the high diversity of forms, sizes, functions, modes, and types of secretion, the classification of trichomes is wide, and the distinction between glandular (secretory) and non-glandular trichomes (non-secretory) is one of the most widely used categorizations (Werker 2000, Evert 2007, Krak & Mráz 2008, Wagner *et al*. 2014).

Studies of trichomes began with Solereder (1908) and continued under other researchers in different families of angiosperms (Hemenway & Allen 1936, Heintzelman & Howard 1948, Metcalfe & Chalk 1950, Metcalfe 1960, Ramayya 1962, Aleykutty & Inamdar 1980). In the family Asteraceae, although the number of species and variety of trichomes is great, few studies have been carried out to know about these structures (Saha & Mukherjee 2012, Arunprakash *et al*. 2014, Perveen *et al*. 2016).

Among the studies with trichomes in Asteraceae, we highlight those performed for the family as a whole developed by Carlquist (1961), Ramayya (1962), Saha & Mukherjee (2012), Arunprakash *et al*. (2014) and Perveen *et al*. (2016). On the other hand, some studies with a focus on taxonomic levels below family stand out: Carlquist (1958) for the subtribe Madinae; Narayana (1979) for the genus *Vernonia*; Krak & Mráz (2008) for the tribe Lactuceae; Hayat *et al*. (2009) for the genus *Artemisia*; Redonda-Martínez *et al*. (2012) for the genera *Vernonanthura* and *Vernonia*; Sulborska (2013) for the species *Inula helenium* L.; Trindade *et al*. (2014) for the species *Lomatozona artemisiifolia* Baker; Wagner *et al*. (2014) for the subtribe Lychnophorinae; Fernandes *et al*. (2016) for the species *Trichogonia cinerea* (Gardner) R.M. King & H. Rob.; Redonda-Martínez *et al*. (2016) for the subtribe Leiboldiinae and Rojas-Leal *et al*. (2017) for the genus *Senecio* section *Mulgediifolii*.

Considering the ecological importance of trichomes and representativeness of Asteraceae in the

Sand-fields of Rio Grande do Sul (important area for conservation of native vegetation), this study aimed to identify and characterize the foliar trichomes observed in the species of the family occurring in this place, contributing to the knowledge of these structures and supporting taxonomic work in the Asteraceae family.

Material and methods

The 34 Asteraceae species studied (table 1) were collected in the southwestern region of Rio Grande do Sul - Brazil, in the municipalities of Alegrete, Manoel Viana and São Francisco de Assis (between latitudes 29°00'S and 31°00'S and longitudes 54°30'W and 58°45'W), in areas of natural grasslands of sandy soils susceptible to the sandy patch process, with or without influence of livestock activity (Freitas *et al.* 2010).

In this region the climate is humid subtropical (Moreno 1961) with an average annual rainfall of 1400 mm (Nimer 1979); however, rains are poorly distributed, with periods of reduced rainfall interspersed with heavy rains that can concentrate rain in just one day (Freitas *et al*. 2009). Due to high evaporation, periods of water deficit can occur (Berlato *et al*. 2006). The mean annual temperature is 14.3 °C in winter and 26.3 °C in summer (Nimer 1979), although absolute minima and maxima are -4 °C and 40 °C, respectively (Cordeiro & Soares 1977).

The relief, originating from the Botucatu sandstone formation, is gently undulating punctuated with flat areas. The soil is Ortic Quartzarenic Neosol (Streck *et al*. 2008), with arenous and silty-arenous texture, high acidity, phosphorus and potassium deficiency, an excess of aluminum and difficulty in water retention (Azevedo & Kaminski 1995, Klamt & Schneider 1995, Verdum 2004). These characteristics reduce its fertility, making it highly susceptible to erosion and water scarcity in periods of drought (Azevedo & Kaminski 1995, Klamt & Schneider 1995).

The collections were carried out in the months of May, October and December 2016 and in February and May 2017. Fertile individuals were herborized and deposited in the collection of the UNOP Herbarium of the Universidade Estadual do Oeste do Paraná - Cascavel campus (table 1). The specimens were identified through comparison with the samples deposited in the herbarium ICN of the Universidade Federal do Rio Grande do Sul and herbarium of the Universidade do Vale do Taquari and by specialists (Gustavo Heiden, Mara Angelina Galvão Magenta, Eduardo Pasini and Roberto Lourenço Esteves).

For the analysis of leaf epidermis in frontal view in scanning electron microscopy (SEM), portions of the median region of fully expanded leaves were fixed in 2.5% glutaraldehyde, washed in phosphate buffer (0.1 mol L^{-1} and pH 7.3), dehydrated in ethanol series and metalized in gold. The images were captured with

Table 1. Asteraceae species studied, their respective vouchers and the collecting municipality, in Sand-fields areas, southwest Rio Grande do Sul State, Brazil.

Tribes/ Species	Voucher	Municipality of collection
Tribe Astereae		
Noticastrum acuminatum (DC.) Cuatrec.	UNOP 8759	Alegrete
Tribe Cichorieae		
Hieracium commersonii Monnier	UNOP 8761	São Francisco de Assis
Tribe Eupatorieae		
Chromolaena squarrulosa (Hook. & Arn.) R.M. King & H. Rob.	UNOP 8763	Manoel Viana
Eupatorium subhastatum Hook. & Arn.	UNOP 8764	Manoel Viana
Gyptis crassipes (Hieron.) R.M. King & H.Rob.	UNOP 8861	Manoel Viana
Gyptis tanacetifolia (Gillies *ex* Hook. & Arn.) D.J.N. Hind & Flann	UNOP 8750	Manoel Viana
Mikania thapsoides DC.	UNOP 8762	Manoel Viana
Praxelis diffusa (Rich.) Pruski	UNOP 8730	Manoel Viana
Tribe Gnaphalieae		
Achyrocline satureioides (Lam.) DC.	UNOP 8720	São Francisco de Assis

continue

Table 1 (continuation)

Tribes/ Species	Voucher	Municipality of collection
Facelis retusa (Lam.) Sch.Bip.	UNOP 8753	São Francisco de Assis
Gamochaeta americana (Mill.) Wedd.	UNOP 8755	São Francisco de Assis
Gamochaeta falcata (Lam.) Cabrera	UNOP 8751	São Francisco de Assis
Lucilia acutifolia (Poir.) Cass.	UNOP 8721	Manoel Viana
Lucilia nitens Less.	UNOP 8736, 8735	São Francisco de Assis
Tribe Heliantheae		
Aspilia montevidensis (Spreng.) Kuntze	UNOP 8727, 8728	São Francisco de Assis
Dimerostemma grisebachii (Baker) M.D.Moraes	UNOP 8739	Manoel Viana
Tribe Inuleae		
Pterocaulon alopecuroides (Lam.) DC.	UNOP 8745	Manoel Viana
Pterocaulon angustifolium DC.	UNOP 8722, 8723	São Francisco de Assis
Pterocaulon polystachyum DC.	UNOP 8760	Manoel Viana
Stenachaenium riedelli Baker	UNOP 8744, 8743	São Francisco de Assis
Tribe Millerieae		
Acanthospermum australe (Loefl.) Kuntze	UNOP 8741	São Francisco de Assis
Tribe Mutisieae		
Chaptalia integerrima (Vell.) Burkart	UNOP 8748	Manoel Viana
Tribe Neurolaeneae		
Calea uniflora Less.	UNOP 8738, 8737	São Francisco de Assis
Tribe Senecioneae		
Senecio leptolobus DC.	UNOP 8752	São Francisco de Assis
Senecio oxyphyllus DC.	UNOP 8754	São Francisco de Assis
Senecio selloi (Spreng.) DC.	UNOP 8746	Alegrete
Tribe Vernonieae		
Centratherum camporum (Hassl.) Malme	UNOP 8758	Alegrete
Chrysolaena cognata (Less.) Dematt.	UNOP 8757, 8756	São Francisco de Assis
Chrysolaena flexuosa (Sims) H.Rob.	UNOP 8860, 8859	São Francisco de Assis
Lessingianthus brevifolius (Less.) H.Rob.	UNOP 8726, 8725, 8724	São Francisco de Assis
Lessingianthus macrocephalus (Less.) H.Rob.	UNOP 8734	São Francisco de Assis
Orthopappus angustifolius (Sw.) Gleason	UNOP 8742	Manoel Viana
Vernonanthura chamaedrys (Less.) H.Rob.	UNOP 8858	São Francisco de Assis
Vernonanthura nudiflora (Less.) H.Rob.	UNOP 8733, 8732, 8731	Alegrete

the aid of an EVO LS-10 scanning electron microscope and SmartSEM software. This analysis was performed at the Laboratory of Scanning Electron Microscopy of the Science and Technology Park - Tecnovates of the Universidade do Vale do Taquari - Univates, Lajeado, RS.

For the anatomical analyses in light microscopy (LM), three fertile individuals of each species were collected, and fully expanded leaf blades were fixed in FAA 50 (37% formaldehyde, glacial acetic acid and 50% alcohol in a ratio of 1:1:18) (Johansen 1940) and preserved in 70% alcohol. For leaf blade observation in frontal view (FV), fragments of the leaf medial region were dissociated with hydrogen peroxide and acetic acid at a concentration of 1:1 (Franklin 1945, modified) and then stained with basic fuchsin in 50% alcohol. The trichomes were also analyzed in transverse view of the leaf blade, and cross-sections (CS) were performed by hand, with the aid of a razor blade, in the median region of the leaf blades of the species under study. Cross-sections were clarified with 50% sodium hypochlorite, stained with alcian blue and basic fuchsin (Kraus *et al*. 1998) and then mounted on semi-permanent, glycerinated gelatin (Kaiser 1880).

All FV and CS images were captured using a DP041 digital camera coupled to an Olympus Bx70 photomicroscope, using the DP Controller program, at the Photomicroscopy Laboratory of the Center for Biological Sciences and Health of the Universidade Estadual do Oeste do Paraná - Unioeste, Cascavel, PR.

The trichomes were identified and characterized based on the system proposed by Ramayya (1962) and complementary literature (Castro *et al*. 1997, Martins 2003, Budel *et al*. 2006, Duarte *et al*. 2011, Trindade *et al*. 2014, Wagner *et al*. 2014).

Results and Discussion

Based on the proposal of Ramayya (1962) and complementary literature, 11 types of trichomes were identified and characterized, of which three were glandular and eight non-glandular. Most of the analyzed species present both glandular and non-glandular trichomes on the same leaf blade, except for *Senecio leptolobus* DC. and *Senecio selloi* (Spreng.) DC., which presented only glandular trichomes and *Vernonanthura chamaedrys* (Less.) H.Rob. that had only non-glandular trichomes (table 2). As for distribution, the trichomes (glandular and non-glandular) occur generally on both surfaces of the leaf blade and, when restricted to one side, this is predominantly the abaxial (table 2).

The variety of trichome types observed in the species of this study corroborates with other studies already done in the family that highlight the diversity of trichomes in Asteraceae (Solereder 1908, Ramayya 1962, Castro *et al*. 1997, Amrehn *et al*. 2013). Faced with this morphological diversity, studies on trichomes in the family have resulted in a variety of terminologies that often overlap in meanings and make it difficult to compare the types of trichomes found in the various family representatives (Wagner *et al*. 2014). Another factor that hinders these comparisons is the use of the same terminology for different types of trichomes (Wagner *et al*. 2014). In this way, the identification and characterization of trichomes in the family is not an easy task. The types of trichomes identified in this study are characterized and discussed below.

Glandular trichomes - In most species they occur on both surfaces of the leaf blade (table 2, figures 1-2), generally in depressions in the epidermis (figures 1g-h, 2b-l), corroborating with other studies that reveal glandular trichomes of Asteraceae in this position (Solereder 1908, Metcalfe & Chalk 1950, Trindade 2013).

Three types of glandular trichomes were identified and characterized in the species studied here: recurved on the epidermis, erect-capitate and uniseriate to multiseriate vesicular-capitate.

Recurved on the epidermis (G1) - multicellular, uniseriate, filamentous, recurved on the epidermis; foot and stalk with 3-4 cells; head unicellular, varying from globoid to spatulated (figure 1a-c). They have been observed on both leaf surfaces of the species of tribe Eupatorieae (figure 1a-c), except for *Mikania thapsoides* DC., in *Aspilia montevidensis* (Spreng.) Kuntze and *Dimerostemma grisebachii* (Baker) M.D.Moraes (Heliantheae tribe) (table 2). Studies with other representatives of the Eupatorieae (Amorin *et al*. 2014, Trindade *et al*. 2014, Fernandes *et al*. 2016) and Heliantheae tribes (Empinotti 2005, Oliveira *et al*. 2013) also indicate the occurrence of this type of trichome, which can be interpreted as a probable affinity between these tribes (Castro *et al*. 1997, Fernandes *et al*. 2016).

Erect-capitate (G2) - multicellular, uniseriate or biseriate, filamentous, erect and capitate (figure 1d-l). The number of foot and stalk cells, as well as the morphology (semigloboid, globoid, oblong-ovate or ovate) and the number of head cells (unicellular, bicellular or multicellular) may vary. The foot and stalk are uniseriate with 2-4 cells in *Calea uniflora*

Table 2. Tribes and species of Asteraceae studied with their respective types of trichomes. G1: recurved on the epidermis glandular trichome. G2: erect-capitate glandular trichome. G3: uniseriate to multiseriate vesicular-capitate glandular trichome. N1: simple conical non-glandular trichome. N2: flagellate-filiform non-glandular trichome. N3: aseptate-flagellate non-glandular trichome. N4: whip-like non-glandular trichome. N5: oblique-flagellate non-glandular trichome. N6: branched with one arm non-glandular trichome. N7: branched with two T-shaped arms non-glandular trichome. N8: branched with three or more arms non-glandular trichome. Ab: abaxial. Ad: adaxial. [-]: absent.

Tribes/ Species	G1	G2	G3	N1	N2	N3	N4	N5	N6	N7	N8
Tribe Astereae											
Noticastrum acuminatum	-	Ab,Ad	-	-	-	Ab,Ad	-	-	-	-	-
Tribe Cichorieae											
Hieracium commersonii	-	Ab,Ad	-	-	-	-	-	-	-	-	Ab,Ad
Tribe Eupatorieae											
Chromolaena squarrulosa	Ab,Ad	-	Ab,Ad	Ab,Ad	-	-	-	-	-	-	-
Eupatorium subhastatum	Ab,Ad	-	Ab	Ab,Ad	-	-	-	-	-	-	-
Gyptis crassipes	Ab,Ad	Ab,Ad	Ab,Ad	Ab,Ad	-	-	-	-	-	-	-
Gyptis tanacetifolia	Ab,Ad	Ab,Ad	-	Ab,Ad	-	-	-	-	-	-	-
Mikania thapsoides	-	-	Ab,Ad	Ab,Ad	-	-	-	-	-	-	-
Praxelis diffusa	Ab,Ad	-	Ab	Ab,Ad	-	-	-	-	-	-	-
Tribe Gnaphalieae											
Achyrocline satureioides	-	-	Ab,Ad	-	Ab,Ad	-	-	-	-	-	-
Facelis retusa	-	Ab	-	-	Ab,Ad	-	-	-	-	-	-
Gamochaeta americana	-	Ab,Ad	-	-	Ab,Ad	-	-	-	-	-	-
Gamochaeta falcata	-	Ab,Ad	-	-	Ab,Ad	-	-	-	-	-	-
Lucilia acutifolia	-	Ab,Ad	-	-	-	-	Ab,Ad	-	-	-	-
Lucilia nitens	-	Ab,Ad	-	-	Ab,Ad	-	-	-	-	-	-
Tribe Heliantheae											
Aspilia montevidensis	Ab,Ad	Ab	-	Ab,Ad	-	-	-	-	-	-	-
Dimerostemma grisebachii	Ab,Ad	-	Ab,Ad	Ab,Ad	-	-	-	-	-	-	-
Tribe Inuleae											
Pterocaulon alopecuroides	-	-	Ab	-	Ab	-	-	-	-	-	-
Pterocaulon angustifolium	-	-	Ab	-	-	-	-	Ab,Ad	-	-	-
Pterocaulon polystachyum	-	-	Ab,Ad	-	-	-	-	Ab,Ad	-	-	-
Stenachaenium riedelli	-	-	Ab	Ab,Ad	-	-	-	-	-	-	-
Tribe Millerieae											
Acanthospermum australe	-	-	Ab,Ad	Ab,Ad	-	-	-	-	-	-	-

continue

Table 2 (continuation)

Tribes/ Species	G1	G2	G3	N1	N2	N3	N4	N5	N6	N7	N8
Tribe Mutisieae											
Chaptalia integerrima	-	Ad	-	-	-	-	-	-	-	Ab,Ad	-
Tribe Neurolaeneae											
Calea uniflora	-	Ab,Ad	Ab,Ad	Ab,Ad	-	-	-	-	-	-	-
Tribe Senecioneae											
Senecio leptolobus	-	Ab,Ad	-	-	-	-	-	-	-	-	-
Senecio oxyphyllus	-	Ab,Ad	-	Ab,Ad	-	-	-	Ab	-	-	-
Senecio selloi	-	Ab,Ad	-	-	-	-	-	-	-	-	-
Tribe Vernonieae											
Centratherum camporum	-	-	Ab,Ad	-	-	-	-	-	-	Ab,Ad	-
Chrysolaena cognata	-	-	Ab	-	-	-	-	-	Ab,Ad	-	-
Chrysolaena flexuosa	-	-	Ab,Ad	-	-	-	-	-	Ab,Ad	-	-
Lessingianthus brevifolius	-	-	Ab,Ad	-	-	-	-	-	Ab,Ad	-	-
Lessingianthus macrocephalus	-	Ab	Ab	-	Ab,Ad	-	-	-	-	-	-
Orthopappus angustifolius	-	-	Ab,Ad	-	-	-	-	-	Ab,Ad	Ab	-
Vernonanthura chamaedrys	-	-	-	-	-	-	Ab,Ad	-	-	-	-
Vernonanthura nudiflora	-	Ab,Ad	Ab,Ad	-	-	-	-	Ab,Ad	-	-	-

Less. (figure 1h), *Lessingianthus macrocephalus* (Less.) H.Rob. (figure 1d) and *Vernonanthura nudiflora* (Less.) H.Rob. (figure 1e); are uniseriate to biseriate with 3-11 cells or pairs of cells in the studied members of the tribes Astereae, Heliantheae (except *Dimerostemma grisebachii*) (figure 1f), Mutisieae, Senecioneae (figure 1k-l), Gnaphalieae (except *Achyrocline satureioides* (Lam.) DC.) and in *Gyptis tanacetifolia* (Gillies *ex* Hook. & Arn.) D.J.N. Hind & Flann and *Gyptis crassipes* (Hieron.) R.M. King & H.Rob. (figure 1j); are biseriate with 6-8 pairs of cells in *Hieracium commersonii* Monnier (tribe Cichorieae). The head is unicellular with an oblong-ovate or ovate shape in *Lessingianthus macrocephalus* (figure 1d) and *Vernonanthura nudiflora* (figure 1e); unicellular or bicellular (in biseriate trichomes) and of a semigloboid shape (figure 1f-g) in *Aspilia montevidensis* (figure 1f), *Gyptis tanacetifolia*, *Noticastrum acuminatum* (DC.) Cuatrec. and all species of the Gnaphalieae tribe (except *Achyrocline satureioides*); unicellular to multicellular, uniseriate to multiseriate, of globoid shape, in *Calea uniflora* (figure 1h), *Chaptalia integerrima* (Vell.) Burkart (figure 1i), *Gyptis tanacetifolia*, *Gyptis crassipes* (figure 1j), *Hieracium commersonii* and all species of the Senecioneae tribe studied (figure 1k-l).

These trichomes occur on both sides of the leaf blade in most species and only on one side in some species (table 2). In *Senecio leptolobus* these trichomes are restricted to the region of midrib depression and in *Calea uniflora* they occur together with uniseriate to multiseriate vesicular-capitate glandular trichomes - G3 (figure 1h).

Erect-capitate glandular trichomes were quite representative in this study, occurring in 50% of the analyzed species. Trichomes with an oblong-ovate head similar to those observed in *Lessingianthus macrocephalus* were also described in *Lessingianthus buddleiifolius* (Mart. *ex* DC.) H. Rob. (Santos 2013), although these are indicated as structures unpublished by the author. Thus, information about these trichomes is increased for the genus *Lessingianthus*. Similar trichomes to the semigloboid head were reported by Castro *et al*. (1997), Martins (2003) and Duarte *et al*. (2011) in other species of Asteraceae. Globoid head trichomes were also reported in other representatives of the Senecioneae tribe (Martins 2003, Rojas-Leal *et al*. 2017) and trichome heads with this shape have already been described in *Calea uniflora* by

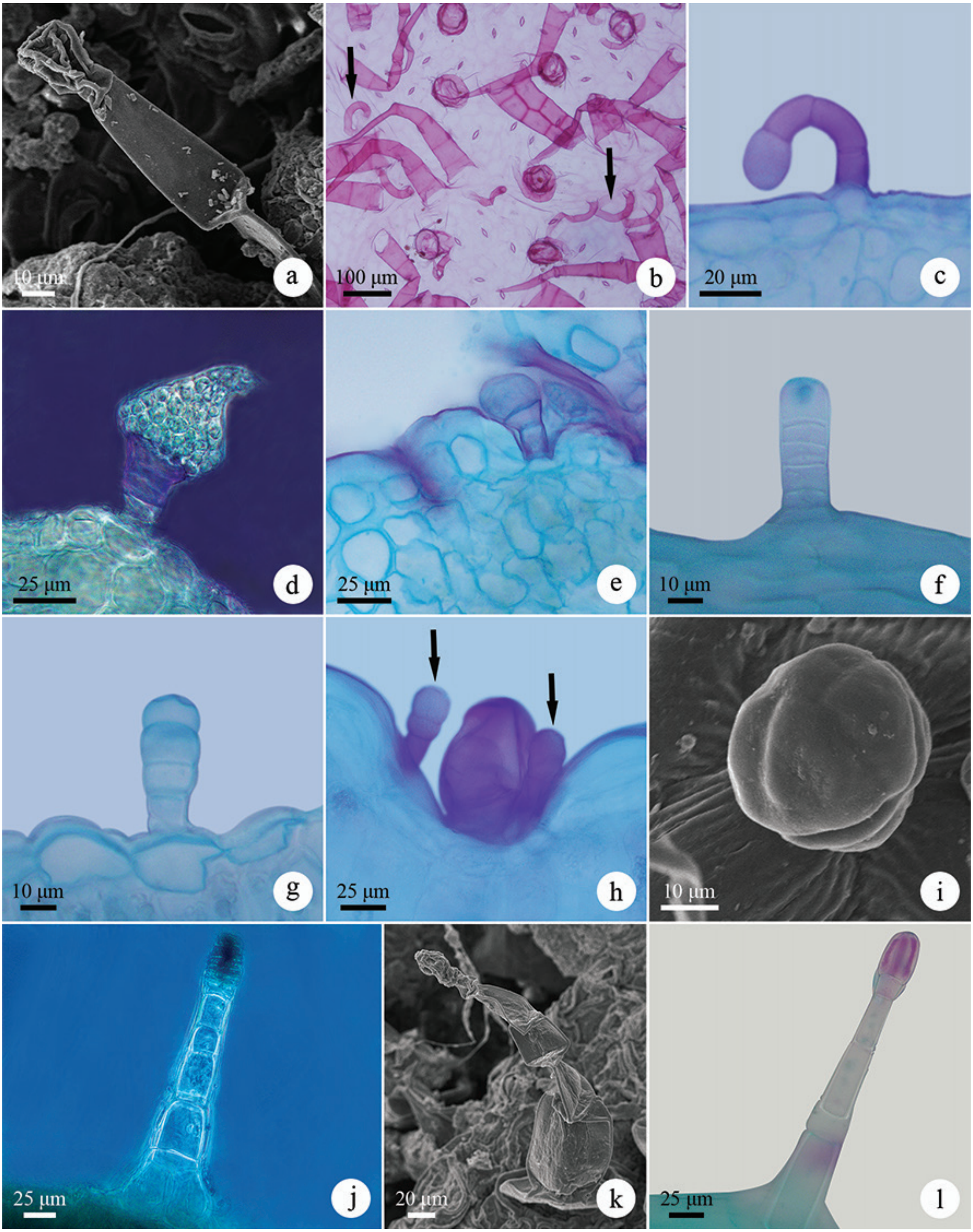

Figure 1. Glandular trichomes of Asteraceae species in light microscopy (b-h, j, l) and scanning electron microscopy (a, i, k). a-c. Recurved on the epidermis glandular trichomes (G1) in *Chromolaena squarrulosa* (Hook. & Arn) R.M. King & H. Rob., *Gyptis crassipes* and *Eupatorium subhastatum*, respectively. d-e. Erect-capitate glandular trichome (G2) with oblong-ovate head in *Lessingianthus macrocephalus* and *Vernonanthura nudiflora*, respectively. f-g. Erect-capitate glandular trichome (G2) with semigloboid head in *Aspilia montevidensis* and *Lucilia acutifolia*, respectively. h-j. Erect-capitate glandular trichome (G2) with globoid head in *Calea uniflora*, *Chaptalia integerrima* and *Gyptis crassipes*, respectively. k-l. Erect-capitate glandular trichome (G2) with globoid head in *Senecio selloi*.

Budel *et al*. (2006). In this way, knowledge about the occurrence and morphological variation of this representative type of trichome in the Asteraceae species is increased.

Uniseriate to multiseriate vesicular-capitate (G3) - multicellular, uniseriate, biseriate or multiseriate, capitate and vesicular (figure 2a-l). The foot and stalk vary from 3-8 cells, usually in a single series (figure 2b-d) or two series (figure 2e-g), being multiseriate only in *Mikania thapsoides* (figure 2h). The head presents 1-2 cells or pairs of cells (biseriate) (figure 2i-l) or up to three cells (multiseriate) (figure 2h). The vesicle is persistent or may collapse early (figure 2e, l). They are generally found in depressions of the epidermis (figure 2b, i-j) on the abaxial surface of seven species of distinct tribes (*Eupatorium subhastatum* Hook. & Arn., *Praxelis diffusa* (Rich.) Pruski, *Pterocaulon alopecuroides* (Lam.) DC., *Pterocaulon angustifolium* DC., *Stenachaenium riedelli* Baker, *Chrysolaena cognata* (Less.) Dematt. and *Lessingianthus macrocephalus*) or on both sides of the leaf blade of the 13 remaining species in which they occur (table 2). In *Lessingianthus brevifolius* (Less.) H.Rob. these trichomes occur restricted to regions of the midrib depression.

Among the glandular trichomes, this type of trichome was the most representative, occurring in 20 of the 34 species studied (58% of species). The occurrence of these trichomes in the uniseriate, biseriate or multiseriate format was indicated by Metcalfe & Chalk (1950) and other authors have also reported the occurrence of this type of trichome, mainly in the biseriate format, as common in the family Asteraceae (Solereder 1908, Castro *et al*. 1997, Bombo *et al*. 2012, Trindade 2013, Fernandes 2014), being this format also the most commonly found among the species studied here.

In the species studied here, these trichomes were observed in members of different tribes (Eupatorieae, Vernonieae, Inuleae, Neurolaeneae, Millerieae, Gnaphalieae and Heliantheae), as well as reported in other studies involving species of different tribes of the family: Eupatorieae (Castro *et al*. 1997, Monteiro *et al*. 2001, Del-Vecho-Vieira *et al*. 2008, Trindade 2013, Trindade *et al*. 2014, Fernandes *et al*. 2016), Heliantheae (Empinotti 2005, Martins *et al*. 2006, Bombo *et al*. 2012, Amrehn *et al*. 2013, Oliveira *et al*. 2013), Vernonieae (Narayana 1979, Castro *et al*. 1997, Empinotti 2005, Empinotti & Duarte 2008, Appezzato-da-Glória *et al*. 2012, Santos 2013, Sosa *et al*. 2014), Neurolaeneae (Castro *et al*. 1997, Budel *et al*. 2006), Millerieae (Araújo *et al*. 2013), Mutisieae (Castro *et al*. 1997, Freire *et al*. 2002, Melo-de-Pinna 2004), Astereae (Cortadi *et al*. 1999, Budel & Duarte 2007) and Inuleae (Castro *et al*. 1997). Although the literature (cited above) indicates the occurrence of uniseriate to multiseriate vesicular-capitate trichomes in representatives of the tribes Mutisieae and Astereae, these were not observed among the species of these tribes studied here, possibly due to the analysis of only one species of each of these tribes.

In addition to their wide distribution and morphological diversity in the family, glandular trichomes are responsible for the secretion of different compounds of secondary metabolism (mucilage, resinous substances, tannins, essential oils, among others), which perform important biological and pharmacological activities conferring on the family great economic importance in the production of bioactive compounds (Metcalfe & Chalk 1950, Trindade 2013, Fernandes 2014).

Non-glandular trichomes - Most species present only one type of non-glandular trichome, except *Senecio oxyphyllus* DC. and *Orthopappus angustifolius* (Sw.) Gleason, both with two types (table 2). In most species, they occur on both sides of the leaf blade (table 2) and are generally densely distributed on the leaf surface.

Eight types of non-glandular trichomes were identified and characterized: simple conical; flagellate-filiform; aseptate-flagellate; whip-like; oblique-flagellate; branched with one arm; branched with two T-shaped arms; branched with three or more arms (figures 3-4). Due to the morphological similarity of the head (long, flagellate and acute apex) of the non-glandular trichomes of the flagellate-filiform, aseptate-flagellate, whip-like and oblique-flagellate type, in the literature (Ramayya 1962, Narayana 1979, Mussury *et al*. 2007, Sancho *et al*. 2010, Redonda-Martínez *et al*. 2012, 2016), the same terminology can be used in the identification and characterization of different trichomes thus hindering comparison with the trichomes described in this study.

Simple conical (N1) - uniseriate; simple or compound foot and entire body (undifferentiated) consisting of 2-5 (figure 3a-e) or up to eight cells as in *Stenachaenium riedelli* (figure 3f); basal cells broader than long and the apical cell with a conical or pointed shape (figure 3a-e). The lateral walls are usually thick and may have adornments as in *Aspilia montevidensis* and *Dimerostemma grisebachii* (figure 3c). These

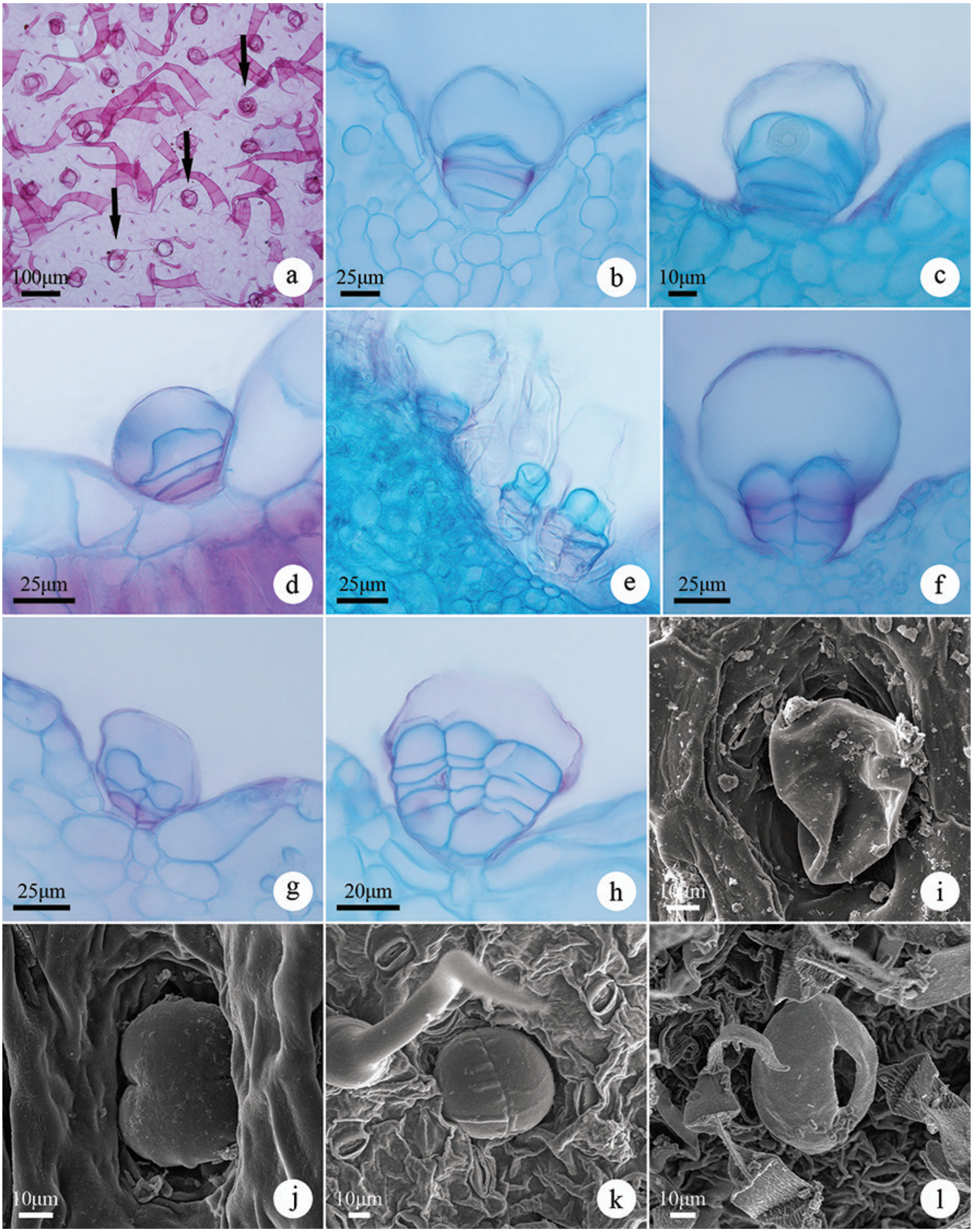

Figure 2. Uniseriate to multiseriate vesicular-capitate glandular trichomes (G3) of the species of Asteraceae in light microscopy (a-h) and scanning electron microscopy (i-l). a. Frontal view of the trichomes of *Gyptis crassipes*. b-d. Uniseriate vesicular-capitate glandular trichomes of *Gyptis crassipes*, *Vernonanthura nudiflora* and *Orthopappus angustifolius*, respectively. e-g. Biseriate vesicular-capitate glandular trichomes of *Pterocaulon angustifolium*, *Eupatorium subhastatum* and *Orthopappus angustifolius*, respectively. h. Multiseriate vesicular-capitate glandular trichomes of *Mikania thapsoides*. i-l. Uniseriate to multiseriate vesicular-capitate glandular trichomes of *Lessingianthus brevifolius*, *Vernonanthura nudiflora*, *Chrysolaena cognata* and *Mikania thapsoides*, respectively.

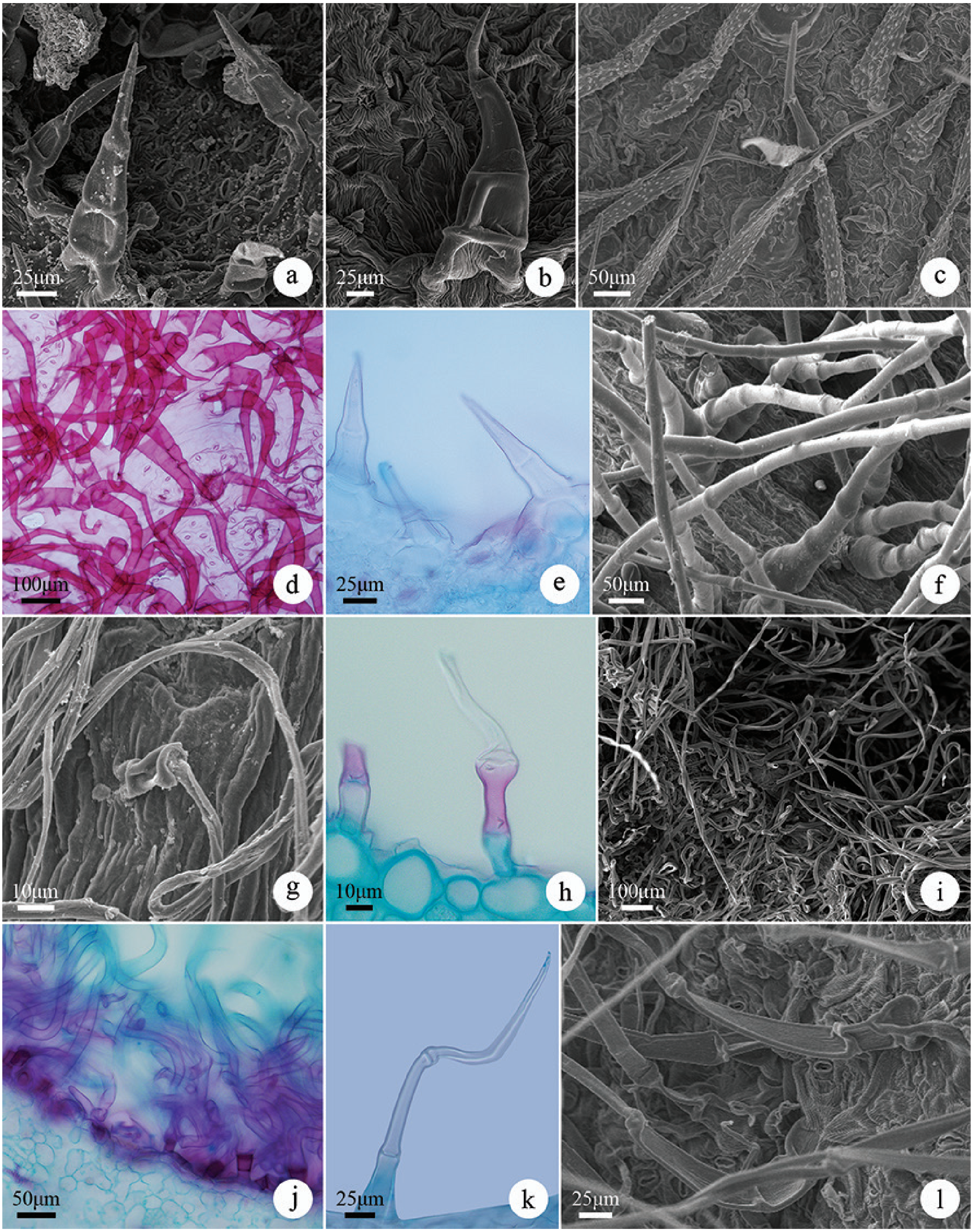

Figure 3. Non-glandular trichomes of the species of Asteraceae in light microscopy (d, e, h, j, k) and scanning electron microscopy (a-c, f, g, i, l). a-c. Simple conical trichomes (N1) in *Eupatorium subhastatum*, *Calea uniflora* and *Dimerostemma grisebachi*, respectively. d. Frontal view of the simple conical trichomes (N1) of *Gyptis crassipes*. e-f. Simple conical trichomes (N1) of *Eupatorium subhastatum* and *Stenachaenium riedelli*, respectively. g-h. Flagellate-filiform trichomes (N2) of *Facelis retusa* (Lam.) Sch.Bip. i-j. Flagellate-filiform trichomes (N2) of *Lessingianthus macrocephalus*. k-l. Aseptate-flagellate trichome (N3) of *Noticastrum acuminatum*.

trichomes occur on both sides of the leaf blade of all species of the tribe Eupatorieae, Heliantheae, Millerieae, Neurolaeneae and in *Stenachaenium riedelli* (Inuleae) and *Senecio oxyphyllus* (Senecioneae) (table 2).

This type was the most representative among the non-glandular trichomes, occurring in 12 of the 34 species studied (35% of species). Trichomes of this type are considered common in the family (Smiljanic 2005) and described for members of distinct tribes, such as *Tithonia diversifolia* (Hemsl.) A.Gray (Heliantheae tribe) (Empinotti 2005), *Mikania lanuginosa* DC. (Amorin *et al*. 2014) and *Trichogonia cinerea* (Fernandes *et al*. 2016) in the tribe Eupatorieae, in some species of the subtribe Leiboldiinae (tribe Vernonieae) (Redonda-Martínez *et al*. 2016) and in species of *Podocoma* (tribe Astereae) (Sancho *et al*. 2010). In these studies, the authors reveal the occurrence of variations in the number of cells of the simple conical trichomes,

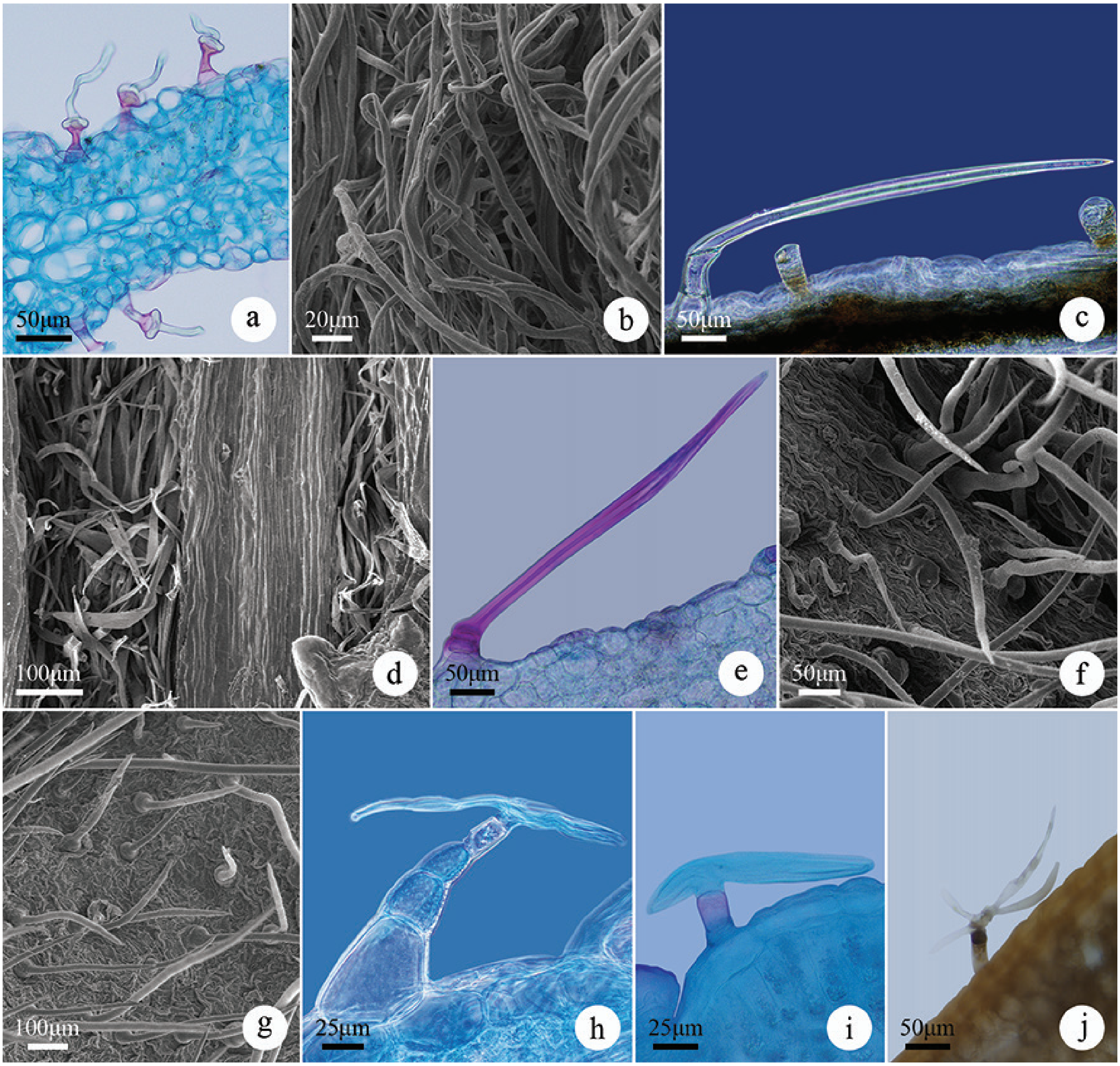

Figure 4. Non-glandular trichomes of the species of Asteraceae in light microscopy (a, c, e, h, i, j) and scanning electron microscopy (b, d, f, g). a-b. Whip-like trichome (N4) of *Lucilia acutifolia*. c-d. Oblique-flagellate trichome (N5) of *Pterocaulon polystachyum* and *Vernonanthura nudiflora*, respectively. e-f. Branched witch one arm trichome (N6) of *Orthopappus angustifolius*. g. Branched witch one arm trichome (N6) of *Chrysolaena cognata*. h-i. Branched witch two T-shaped arms trichome (N7) of *Centratherum camporum*. j. Branched witch three or more arms trichome (N8) in *Hieracium commersonii*.

corroborating with this study which found the largest number of cells in *Stenachaenium riedelli* in relation to the other species with simple conical trichomes. In addition, the description of these trichomes in *Acanthospermum australe* (Loefl.) Kuntze and *Calea uniflora* corroborates with the identification and characterization of the simple conical trichomes observed by Araújo *et al*. (2013) and Martins *et al*. (2006) in *Acanthospermum australe* and Budel *et al*. (2006) in *Calea uniflora*.

Flagellate-filiform (N2) - uniseriate, filiform; simple or compound foot and body differentiated into stalk and head; stalk with 2-4 cells generally isodiametric or with 1-2 basal cells broader than long (figure 3g-h); unicellular, flagellate and long head, tapering to a pointed apex (figure 3i-j). These trichomes occur on both surfaces of *Lessingianthus macrocephalus* and all species of the Gnaphalieae tribe (except in *Lucilia acutifolia* (Poir.) Cass.) and only on the abaxial side of *Pterocaulon alopecuroides* (table 2). As for the abaxial surface of most species, the trichomes cover the entire leaf surface of this side.

Trichomes like the flagellate-filiform observed in this study were also found in other species of the Gnaphalieae (Smiljanic 2005, Mussury *et al*. 2007) and Vernonieae (Narayana 1979, Santos 2013, Redonda-Martínez *et al*. 2016) tribes, although in these studies the authors used the term "whip" for characterization of the apical cell, whereas in our study this term describes another type of non-glandular trichome.

Aseptate-flagellate (N3) - uniseriate, flagellate; simple or compound foot and body differentiated into stalk and head; stalk consisting of 2-3 cells, one or two basal cells being broader than long and the other(s) being longer than broad; head unicellular, clearly delimited from the stalk, long and tapering upward with a pointed apex (figure 3k-l). They occur on both sides of the leaf blade only in *Noticastrum acuminatum* (table 2). Similar trichomes were observed in the leaf margin of *Calendula officinalis* L. (Calenduleae) (Ramayya 1962) and on the stem and leaves of *Gnaphalium polycaulon* Pers. (Gnaphalieae) (Jana 2014).

Whip-like (N4) - uniseriate, flagellate; simple or compound foot and body differentiated into stalk and head; stalk with two cells forming a enlarged base upwards (figure 4a); the head is composed of a generally long, whip-shaped flagellate cell whose base is broad and tapering upward to a pointed apex (figure 4a-b). These trichomes occur on both leaf surfaces of *Lucilia acutifolia* and *Vernonanthura chamaedrys* (table 2). In the first, they cover the whole leaf surface of both sides and in the second only on the abaxial surface, whereas on the adaxial surface the trichomes are sparsely distributed.

This type of trichome was described for the genus *Lucilia* by Metcalfe & Chalk (1950) and was also characterized as a peculiar trichome in *Lucilia nitens* Less. (Duarte *et al*. 2011), although in our study this species did not present this trichome, but rather the flagellate-filiform trichome (N2).

Oblique-flagellate (N5) - uniseriate, flagellate; simple or compound foot and body differentiated into stalk and head; stalk consisting of 2-5 cells with at least one basal cell broader than long; unicellular or multicellular head with a cell(s) longer than broad, flagellate, continuous with the stalk or clearly delimited from it by an oblique septum (figure 4c-d). They occur on both sides of the leaf blade of *Pterocaulon angustifolium*, *Pterocaulon polystachyum* DC., *Vernonanthura nudiflora* and only on the abaxial surface of *Senecio oxyphyllus* (table 2). In *Pterocaulon angustifolium* they cover the entire surface of the abaxial surface and are more sparsely distributed on the adaxial surface.

Trichomes like the oblique-flagellate type were observed by Cabrera & Ragonese (1978) in American species of the genus *Pterocaulon* (including *Pterocaulon angustifolium* and *Pterocaulon alopecuroides*, however, in our study this last species did not present this type of thichome), but these authors use the term "non-septate flagelliform" to identify this trichome. Freire *et al*. (2002) also indicated the occurrence of these trichomes in some species of the genus *Gochnatia* (Gochnatieae).

Branched witch one arm (N6) - uniseriate; simple or compound foot and body differentiated into stalk and head; stalk consisting of 1-3 cells, one or two of the basal cells being broader than long; unicellular head with a flat arm channeled into the base, forming an angle with the stalk, pointed apex (figure 4e-g) and thick lateral walls. They occur on both surfaces of the leaf blade of some representatives of the Vernonieae tribe (*Chrysolaena cognata*, *Chrysolaena flexuosa* (Sims) H.Rob., *Lessingianthus brevifolius* and *Orthopappus angustifolius*) (table 2). Similar trichomes were described for *Elepanthopus mollis* Kunth (Empinotti 2005, Empinotti & Duarte 2008) and for some species of the genus *Vernonia* (Narayana 1979).

Branched witch two T-shaped arms (N7) - uniseriate; simple or compound foot and body differentiated into stalk and head; stalk with 1-5 or more cells with at least one of the basal cells broader than long and the other cells generally cylindrical; unicellular head with two arms generally flat, channeled in the base and which may vary in shape (figure 4h-i). In the case of *Orthopappus angustifolius* (abaxial surface) and *Centratherum camporum* (Hassl.) Malme (both sides) (figure 4h-i) the two arms are short, having unequal sizes and forming a T-shaped structure together with the stalk (table 2). In *Chaptalia integerrima* (both surfaces) the arms are long and spread laterally as in the T-shaped, but tend to curl (table 2). The apex of the arms is pointed or rounded. These trichomes cover the entire leaf surface of the abaxial surface of *Chaptalia integerrima*.

Trichomes of this type are frequent in the species of the Vernonieae tribe and can be used in the taxonomy of the representatives of this tribe (Narayana 1979, Redonda-Martínez *et al*. 2012, Wagner *et al*. 2014). Similar trichomes were also observed in some species of the genus *Gochnatia* (Gochnatieae) (Freire *et al*. 2002).

Branched witch three or more arms (N8) - uniseriate; simple or compound foot and body differentiated into stalk and head; stalk composed of 1-2 cells longer than broad; branched unicellular head with 3-5 long and thin arms that spread apart at different angles (figure 4j). They occur only in *Hieracium commersonii*, on both sides of the leaf blade (table 2). Similar trichomes have been described in some species of the genus *Gochnatia* (Gochnatieae) (Freire *et al*. 2002) and the subtribe Lychnophorinae (Vernonieae tribe), where they are considered frequent (Wagner *et al*. 2014).

Due to their direct contact with the environment, glandular and non-glandular trichomes can influence many physiological and ecological aspects of plants, protecting them against stressful biotic and abiotic factors (Johnson 1975, Werker 2000, Krak & Mráz 2008, Trindade *et al*. 2014). Glandular trichomes are responsible for the secretion of different substances of secondary metabolism, which can form a continuous layer on the surface of the plant and thus act in reflecting light and in decreasing the temperature of the leaf (Wagner 1991, Perveen *et al*. 2016). In addition, the secreted substances can act in the chemical defense against pathogens and herbivores (Wagner 1991, Trindade *et al*. 2014).

Non-glandular trichomes play an important role in protecting the leaves against pathogens, herbivores, high temperatures, excessive light and excessive water loss (Johnson 1975, Werker 2000, Wagner *et al*. 2004, Trindade *et al*. 2014). The functions developed by them depend on their morphology, orientation, and density (Werker 2000, Wagner *et al*. 2004). Longer, non-glandular trichomes which cover the entire leaf surface, as observed in most of the species studied, may act as a mechanical barrier against pest attack (Levin 1973), decrease water loss through reflection (Ehleringer 1984, Wagner *et al*. 2014) and influence the wettability of the leaves making them repellent to water and thus preventing the growth of pathogenic microorganisms, the deposition of pollutants and favoring photosynthetic yield (Wang *et al*. 2015, Rojas-Leal *et al*. 2017).

Considering that the species of this study occur in Sand-fields, which are characterized by high temperatures, high light intensity, water scarcity, sandy soils and strong winds, the high frequency of glandular and non-glandular trichomes in these species can constitute an adaptive strategy to these adverse environmental conditions (Costa *et al*. 2011). From a taxonomic point of view, the morphological diversity and the distribution of trichomes in the Asteraceae family can contribute to systematics studies at different taxonomic levels of the family, since they have been shown not to be influenced by environmental and climatic factors, thus constituting reliable taxonomic characters (Narayana 1979, Wagner *et al*. 2014).

In our study, the morphological diversity of trichomes seems to be useful in the taxonomy of the family at the tribal level. Considering the tribes with the largest number of species sampled, we verified that the recurved on the epidermis glandular trichomes (G1) are more frequent in the Eupatorieae tribe (83% of the species studied) whereas erect-capitate glandular trichomes (G2) are more frequent in the Gnaphalieae (83%) and Senecioneae (all species) tribes. Uniseriate to multiseriate vesicular-capitate glandular trichomes (G3) are more frequent in the Vernonieae (87%), Eupatorieae (83%) and Inuleae (all species) tribes. Among the non-glandular trichomes, the simple conical type (N1) is more frequent in the Eupatorieae tribe, while the flagellate-filiform (N2) and the branched witch one arm type (N6) are the most frequent in the Gnaphalieae tribe (83%) and among members of the Vernonieae tribe (50%), respectively. Trichomes of the aseptate-flagellate (N3) and branched witch three or more arms (N8) type are restricted to the Astereae and Cichorieae tribes, respectively, although in each of these tribes only one species has been sampled.

These taxonomic inferences are closely related to the number of species sampled in each of the tribes studied, and the tribes with the highest frequency of some type of trichome are also the ones with the highest species richness and the highest sampling rate in our study: Vernonieae (23%), Eupatorieae and Gnaphalieae (18%). Thus, the value of trichomes as a taxonomic character at the tribal level in this study can be greatly increased by sampling more species in each tribe, especially those in which only one or two species were sampled (Astereae, Cichorieae, Heliantheae, Millerieae, Mutisieae, Neurolaeneae) and also with the joint analysis of other characters relevant to taxonomy. In addition, studies that develop a more detailed terminological analysis and, if possible, the standardization of the nomenclature used in the identification and characterization of trichomes in Asteraceae would facilitate their use in taxonomic studies of the family.

Acknowledgments

We acknowledge the team of the Scanning Electron Microscopy Laboratory of Univates - RS for providing equipment and technical support for scanning electron microscopy analysis, and Gustavo Heiden, Mara Angelina Galvão Magenta, Eduardo Pasini and Roberto Lourenço Esteves for their assistance in identification of species. We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES for the scholarship of the first author and the Araucária Foundation (51223/2017) for financial assistance of this research.

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ISSN da publicação *online* 2236-8906