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## Diversity of non-glandular trichomes in subtribe *Lychnophorinae* (Asteraceae: *Vernonieae*) and taxonomic implications

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**Abstract** *Vernonieae* is one of the major tribes in Asteraceae (subfamily Cichorioideae) with ca. 1,100 species placed into 129 genera. Currently, 21 subtribes are recognized in *Vernonieae* and one of them is *Lychnophorinae*, almost entirely endemic to Brazil, containing 11 genera and ca. 100 species. About 42 % of *Lychnophorinae* genera are monophyletic, reflecting the poorly understood relationships among the members of the group. Trichomes are one of the most useful anatomical characters to be used in angiosperm taxonomy; they are diverse, exist in many taxa and are not difficult to study. This work intends to illustrate non-glandular leaf trichome diversity in *Lychnophorinae* and discuss this diversity in the light of the subtribe's taxonomy. Sampled material included 67 species of 11 genera. Macerations and free hand sections were performed to be analyzed in the light microscope and photographed. A phenogram was generated using a matrix with 67 terminals (species) and 18 characters coded as binary. The subtribe *Lychnophorinae* displays a great diversity of non-glandular trichomes (5 types and 18 subtypes). The present study reveals the great diversity of non-glandular trichomes in *Lychnophorinae*. While trichome complement is of little use to distinguish genera, it appears to be a valuable characteristic at a lower taxonomic level to identify closely morphologically related species.

**Keywords** Leaf anatomy · Hair morphology · Systematics · Compositae

### Introduction

*Vernonieae* is one of the major tribes of Asteraceae (subfamily Cichorioideae) with ca. 1,100 species placed into 129 genera (Keeley and Robinson 2009), which are distributed into two main diversity centers, Brazil and Africa. *Vernonieae* are very variable in habit, from small herbs to large trees; bearing generally alternate leaves and discoid capitula with white, blue or purple florets, rarely red or yellow. The most distinctive feature of the *Vernonieae* is given by the styles, which are slender with filiform, pilose style branches with inner surface completely covered with stigmatic papillae, and a pilose upper shaft. The pollen is highly ornamented, lophate, sublophate, echinate or psilate (Keeley and Jones 1979; Keeley and Robinson 2009). The tribe is rich in genera with only one or two species (about 60 %), clearly reflecting how poorly the relationships between *Vernonieae* genera and subtribes are understood (Keeley et al. 2007; Keeley and Robinson 2009).

Among the 21 subtribes currently recognized in *Vernonieae*, the subtribe *Lychnophorinae* is nearly endemic to Brazil (only one species occurs in Bolivia) and contains 11 genera and ca. 100 species (Dematteis 2007; Keeley and Robinson 2009). Most species are restricted to *campo rupestre* (literally rocky fields) in the highlands of southeastern and northeastern Brazil and to the *Cerrado* (Brazilian savanna), a region that represents also one of the diversity centers of *Vernonieae*. Established by Bentham (1873), the subtribe *Lychnophorinae* initially contained taxa with one- to few-flowered capitula, these densely aggregated into glomerules or syncephalia and possessing

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simple biseriate, paleaceous, rarely setose, pappus setae (Hind 2000a). However, this traditional definition has been completely abandoned by Robinson (1999) in his review of American Vernoniae, through the inclusion of genera with separate heads (*Anteremanthus*, *Minasia*, *Piptolepis*, *Proteopsis*) in Lychnophorinae (Robinson 1992, 1999; Keeley and Robinson 2009) and the proposal of a set of alternative characteristics (not necessarily restricted to Lychnophorinae, but rather consistent within the group) to define the subtribe: lack of enlarged nodes or sclerified cells at the bases of the styles, usually extensive presence of a pubescence of T-shaped trichomes, presence of sclerified cells and lack of glands in the anther appendages and presence of type A pollen (Robinson 1992).

Trichomes are some of the most helpful anatomical characters to be used in angiosperm taxonomy. They are diverse, exist in a variety of taxa, and are not difficult to handle for study (Carlquist 1961). Certain trichome types can be consistent in all taxa of a taxonomic group, helping taxonomists to circumscribe it (Heintzelman and Howard 1948). Also, trichome morphology has already been used to clarify tribal or sectional classifications (Webster et al. 1996; Al-Shehbaz et al. 2006) and, more recently, has been used as data in phylogenetic studies (e.g. Belstein et al. 2006, 2008; Caruzo et al. 2011; van Ee and Berry 2011).

As well as with tribe Vernoniae, subtribe Lychnophorinae holds a high proportion of monotypic genera (42 %) reflecting how poorly relationships among the members of the group are understood. Also, the generic limits of *Eremanthus* and *Lychnophora* are controversial: *Haplostephium* (Coile and Jones 1983; Semir 1991, 2011), *Lychnophoriopsis* (Semir 1991, 2011; Robinson 1992) and *Paralychnophora* (MacLeish 1987; Semir 1991, 2011; Robinson 1997; Hind 2000a) have been variously recognized at generic level. Several species of Lychnophorinae have also an uncertain generic position (in *Eremanthus*, *Lychnophora* or *Piptolepis*) (Coile and Jones 1981; Hind 1993). Some authors have placed several Lychnophorinae in *Vernonia* s.l. (MacLeish 1984; Hind 1995, 2003), whereas Robinson (1999) considered most of them as members of the subtribe. As a consequence, Coile and Jones (1981) recognized 11 species of *Lychnophora* whereas Semir (1991) acknowledged 41 species (not including in these 41 the 27 unpublished new species).

The first molecular phylogeny of Vernoniae (Keeley et al. 2007) does not solve issues regarding Lychnophorinae, due to the poor sampling of Brazilian taxa. The genera currently recognized in subtribe Lychnophorinae are: *Anteremanthus*, *Chronopappus*, *Eremanthus* (including *Vanillostephium*), *Lychnophora* (including *Haplostephium*), *Lychnophoriopsis*, *Minasia*, *Paralychnophora*, *Piptolepis*, *Prestelia*, *Proteopsis* and *Vinicia*.

Trichomes have only epidermis-originated cells (Werker 2000) and it has been found that more than 40 genes take part in the regulation of trichome development (Schwab et al. 2000). They may exist on any part of the plant, and their type and proportion may vary among the whole plant and among different taxonomic levels (Werker 2000). Classifying trichomes is difficult due to their diversity in form, origin, size, location, ability to secrete, secretion types, and function. The principal categories used are glandular and non-glandular trichomes (Werker 2000).

The role of non-glandular trichomes relies on their form, location in the plant and direction or orientation. Usually they provide leaf protection, help dispersal units in epizoochory, help reduce mechanical abrasion, reduce leaf wetness, help in pollen dispersion and collection and serve as trapping mechanism. The role of protection may encompass that against herbivores, pathogens, extreme temperatures, excessive light, water loss, and allelopathy by competitors (Theobald et al. 1979; Werker 2000; Wagner et al. 2004).

Robinson (2009) stresses the importance of micro-characters in Asteraceae systematics, with trichome morphology being informative at different taxonomic levels. For example, the subfamily Barnadesioideae presents a characteristic trichome called “barnadesioid” (Cabrera 1959). Drury and Watson (1966) used data from trichome types to infer subtribal classification in tribe Inuleae. Krak and Mráz (2008) surveyed trichomes of 135 species of tribe Lactuceae and proposed a new circumscription of subtribe Hieraciinae characterized by a unique combination of two trichome types. The genera *Dresslerothamnus* H. Rob. and *Urostemon* B. Nord. of Senecioneae present multi-tiered T-shaped trichomes not found in any other tribe (Robinson 1989). At specific level, data about leaf and cypsela trichomes of 45 species of *Senecio* L. were used by Drury and Watson (1965), along with other morphological characters, to propose a new classification for the genus.

Trichomes have been shown to be a valuable source of characters in the taxonomy of the tribe Vernoniae for Old and New World groups. Only simple and T-shaped trichomes occur in Eastern hemisphere Vernoniae, the more complex types (stellate, globular, goblet shaped) are found exclusively in the New World groups (Robinson pers. comm.). Within the American subtribe Piptocarphinae, stellate, diversely spurred to branched or goblet-shaped trichomes support the DNA evidence to distinguish *Critoniopsis* Sch. Bip. from *Tephrothamnus* Sch. Bip. and *Eremosis* (DC.) Gleason, previously synonymized by Robinson (1993). These two latter genera have, respectively, T-shaped and simple trichomes (Keeley et al. 2007; Robinson 2009). Differences in trichome type in Old World Vernoniae genera also assisted the separation of *Acilepis* D. Don, which has simple trichomes, from the

*Cyanthillium* Blume group, with T-shaped trichomes (Adejeji and Jewoola 2008; Robinson 2009). Detailed surveys of Vernoniae trichomes are limited to North American taxa of *Vernonia* Schreb. (Faust and Jones 1973) and Mexican *Vernonia* and *Vernonanthura* H. Rob. (Redonda-Martínez et al. 2012).

Information on trichome diversity in subtribe Lychnophorinae is quite limited. Handro et al. (1970) studied the leaf anatomy of some Asteraceae species from Brazilian *campo rupestre*, including seven species from two Lychnophorinae genera, which present common leaf features of xeric conditions: *Lychnophora* Mart. (five spp.), and *Prestelia eriopus* Sch. Bip. [as *Eremanthus eriopus* (Sch. Bip.) Baker]. In these genera, the trichomes are pluricellular, in most cases, branched and display small basal cells. Luque et al. (1999) studied the leaf anatomy of 34 species of the genera *Lychnophora*, *Lychnophoriopsis* H. Rob. and *Paralychnophora* MacLeish, emphasizing the xerophytic characteristics of the leaves including pubescence and trichome types.

This work intends to illustrate trichome diversity in Lychnophorinae and evaluate the relevance of this diversity for the subtribe's taxonomy.

## Materials and methods

### Plant material

The present study is based on an almost complete set of the entire subtribe Lychnophorinae: 67 species were studied, belonging to 11 genera. One individual of each species was chosen for anatomical studies, with two of its leaves sampled for study. Two other herbarium specimens of each species were used for confirmation of trichome type, except when less than two specimens were available. This sampling is similar to the one employed in the simultaneous phylogenetic study of the subtribe (Loeuille 2011). The plant material was obtained from the herbaria ESA, SPF and UEC. A list of studied specimens vouchers is provided in Appendix 1.

### Light microscopy

Macerations were prepared according to the modified Franklin method (Franklin 1945), stained with safranin and mounted in glycerin. Dried leaves of herbarium specimens were rehydrated with water and glycerin, and freehand horizontal and longitudinal sections were made. The sections were stained with safranin and astra blue and mounted with glycerin. Trichome type was determined by analysis in light microscope Leica LMDB. Photographs were obtained with Leica software and camera assembled

with a light microscope Leica DM4000B. Visual confirmation of trichome type was performed with herbarium specimens, using a stereomicroscope (Olympus SZ60; zoom range of 6.3:1). Two leaves of each specimen were fully analyzed and their trichome types were then compared to those obtained in anatomical studies. In case of doubts, new anatomical studies were performed. Simple techniques were preferred to allow a large number of observations, always an important feature in taxonomic studies, and essential in comparisons amongst taxa. Due to the high-density indumentum, scanning electron microscopy did not present suitable results to understand trichome morphology.

### Trichome classification

Trichomes were classified according to their general morphology. Terminology from Theobald et al. (1979) was used, and when needed terms from other works were used, such as 'auriculate' which was used by Luque et al. (1999); the terms 'curly', 'bladder-like', and 'middle-cells' were all taken from the glossary from Payne (1978), the trichome type 'one-armed' was described by Ramayya (1962) and the term 'spurred' was used by Robinson (2009).

We generated a phenogram using a matrix with 67 terminals (species) and 18 characters (corresponding to each trichome type) coded as binary (absence and presence). A distance matrix was computed through the use of the Jaccard index and a phenogram was obtained using the NJ method with PAST 2.17b (Hammer et al. 2001). *Eremanthus crotonoides* was chosen as an outgroup based on preliminary phylogenetic analyses (Loeuille 2011).

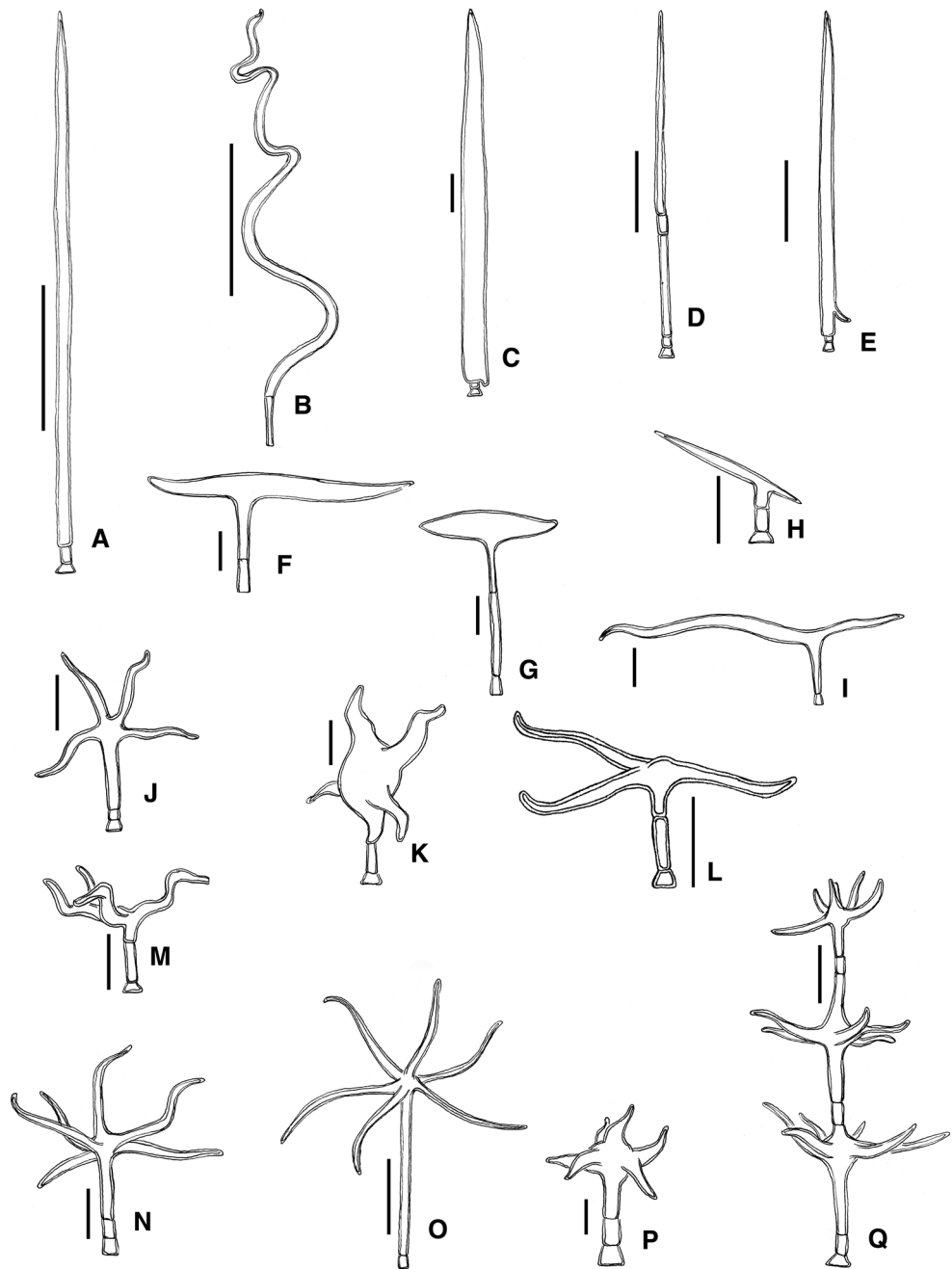
## Results

Some features were observed in all studied trichomes, such as the presence of a stalk, with either one or more cells, therefore sessile trichomes were absent; all trichomes were multicellular, presenting the stalk cells and the top main cell; top cells were always unicellular, even if composed of many arms, the exception being those that present 'middle cells', cells with similar shape and wall thickness as the stalk cells interspersed between two trichome top cells.

According to Theobald et al. (1979), stellate trichomes can be either rotate, with all arms spreading in one plane, or multiangulate, with arms spreading in diverse planes. All stellate trichomes observed here were multiangulate.

In order to better illustrate the relationships between species and their trichome types, and to simplify comparisons, trichome types were assigned letters (from A to F) and the subtypes were assigned the correspondent letter and a number:

**Fig. 1** Trichomes in Lychnophorinae. Unbranched: **a** unbranched, long, thin, *Chronopappus bifrons*; **b** unbranched, curly—*Lychnophora markgravii*; **c** unbranched, auriculate, *Piptolepis monticola*; **d** unbranched, middle-cells, *Chronopappus bifrons*. **e** Branched, spurred, *Lychnophora sellowii*. Branched, 2-armed: **f** branched, 2-armed, T-shaped, *Vinicia tomentosa*; **g** branched, 2-armed, T-shaped, bladder-like, *Minasia alpestris*; **h** branched, 2-armed, arms diagonal to stalk, *Lychnophora humillima*; **i** branched, 2-armed, T-shaped, curly arms, *Lychnophora markgravii*. Branched, 3- to 5-armed: **j** branched, 3- to 5-armed, *Paralychnophora harleyi*; **k** branched, 3- to 5-armed, bladder-like, *Eremanthus elaeagnus*; **l** branched, 3- to 5-armed, arms long and thin, *Lychnophora diamantinana*; **m** branched, 3- to 5-armed, arms curly, *Lychnophora pinaster*. Stellate: **n** stellate, *Eremanthus auriculatus*; **o** stellate, *Eremanthus crotonoides*; **p** stellate, bladder-like, *Piptolepis martiana*; **q** stellate, geminate, *Chronopappus bifrons*. **a, b, d, e, 200**  $\mu\text{m}$ ; **c, j, l, n, o, q 100**  $\mu\text{m}$ ; **f, g, h, k, m, p, 50**  $\mu\text{m}$ ; **i, 25**  $\mu\text{m}$



**A.** *Unbranched trichomes*—these do not present branching, usually needle-like.

**A1.** *Unbranched, long, thin trichomes* (Figs. 1a, 2a)—presenting a one- to many-celled stalk and a long thin arm that is composed of one cell, usually needle shaped.

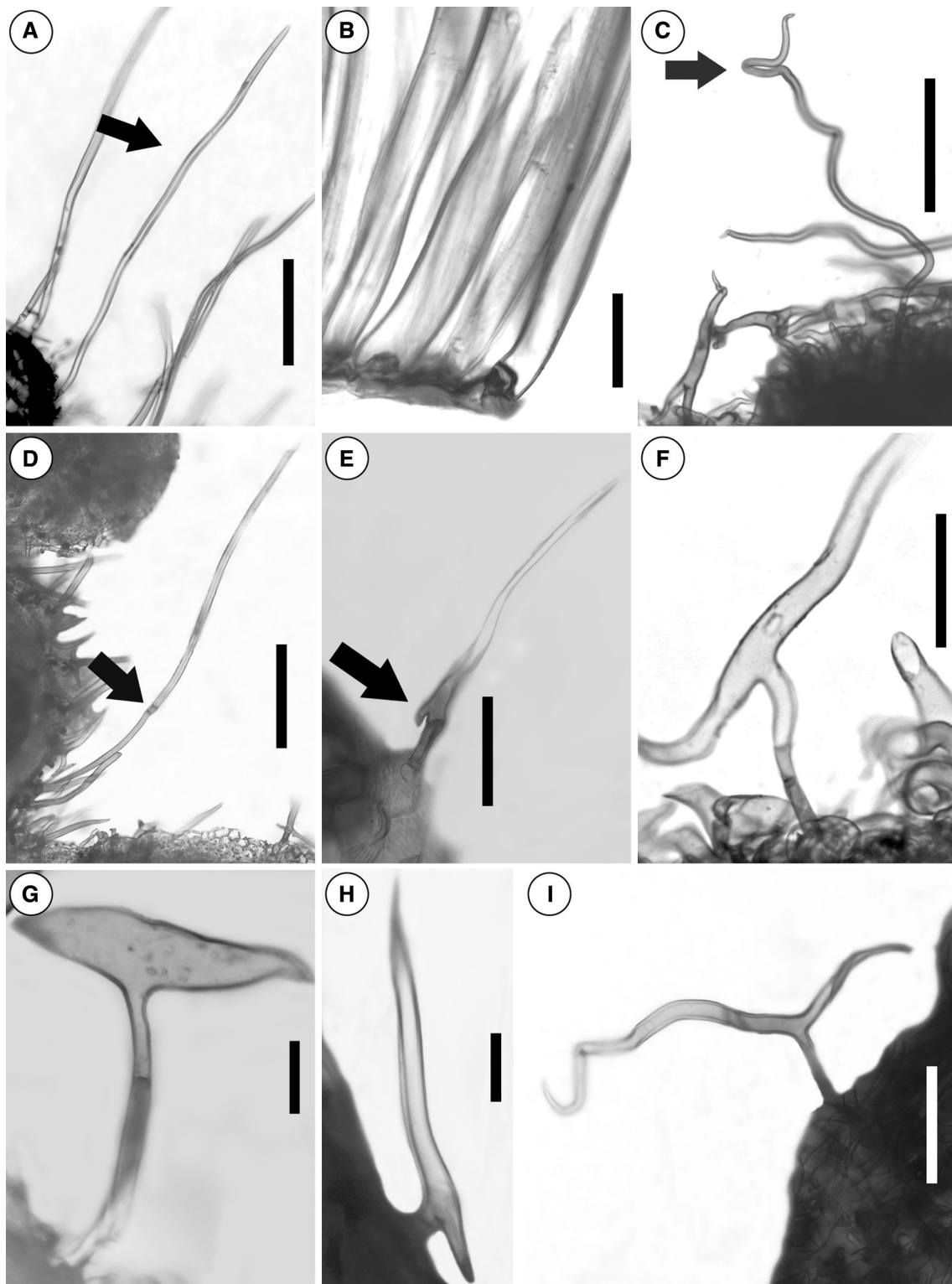
**A2.** *Unbranched, long, thin, curly* (Figs. 1b, 2c)—presenting coiled arms, having a curly appearance.

**A3.** *Unbranched, long, thin trichomes with top cell enlarged above stalk—auriculate* (Figs. 1c, 2b, 3b)—these present an

enlargement at the base of the top cell that spreads downwards along about half or a third of the walls of the stalk.

**A4.** *Unbranched, long, thin, middle-celled trichomes* (Figs. 1d, 2d)—with a multicellular top cell, which is interspersed with middle-cells between the basal and distal cells of the arm. These middle-cells are similar in shape and wall thickness to the stalk cells.

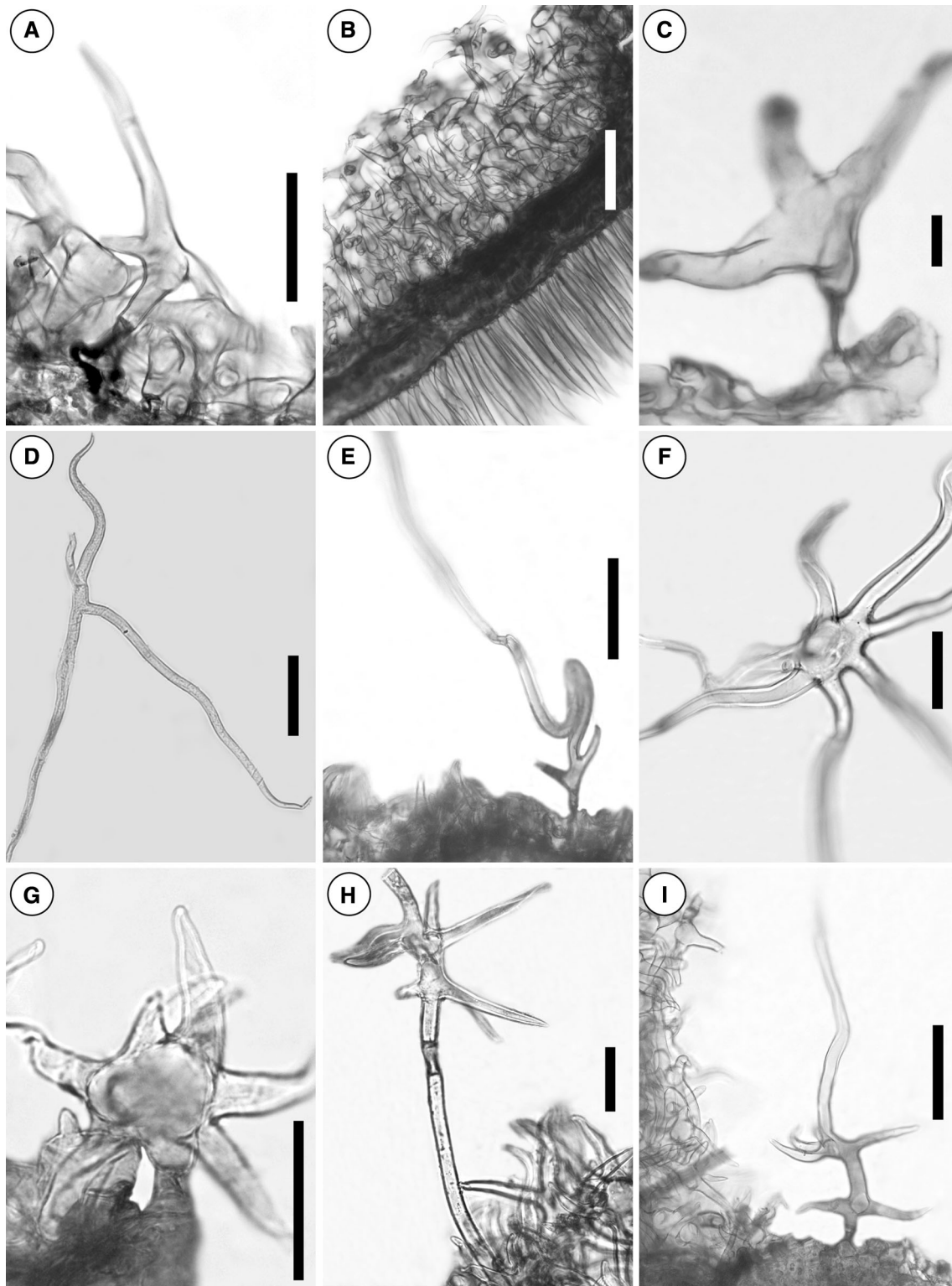
**B.** *Branched, spurred trichomes*—these bear one main arm, which is incompletely branched, usually forming a spur.



**Fig. 2** Trichomes in *Lychnophorinae*. Unbranched trichomes: **a** black arrow unbranched, long, thin trichome, *Lychnophora mellobarretoii*; **b** trichome unbranched, auriculate, *Proteopsis* sp.; **c** black arrow unbranched, long, thin, curly trichome, *Lychnophora markgravii*; **d** trichome unbranched, long, thin, with middle-cell, *Chronopappus bifrons*, black arrow middle-cell. **e** Branched, spurred

trichome, *Lychnophora sellowii*, black arrow side arm. Branched, 2-armed trichomes: **f** branched, 2-armed, T-shaped trichome, *Vinicia tomentosa*; **g** branched, 2-armed, bladder-like trichome, *Minasia alpestris*; **h** branched, 2-armed trichome, arms diagonal, *Prestelia robusta*, **i** branched, 2-armed trichome, curly arms, *Lychnophora markgravii*. **a, c, d** 200  $\mu$ m; **e, f, i** 100  $\mu$ m; **b, g, h** 50  $\mu$ m





**Fig. 3** Trichomes in Lychnophorinae. Branched, 3- to 5-arms trichomes: **a** branched, 3- to 5-armed trichome, *Eremanthus mollis*; **b** indumentum of *Piptolepis martiana* with branched, 3- to 5-arms trichomes on the top and unbranched, auriculate ones below; **c** branched, 3- to 5-trichome, bladder-like, *Eremanthus glomerulatus*; **d** branched, 3- to 5-armed trichome with long thin arms, *Lychnophora*

*diamantinana*; **e** branched, 3- to 5-armed trichome, with one long arm with middle-cell, *Chronopappus bifrons*. Stellate trichomes: **f** stellate trichome, *Eremanthus crotonoides*; **g** stellate, bladder-like trichome, *Eremanthus crotonoides*; **h** stellate, geminate trichome, *Chronopappus bifrons*; **i** stellate, geminate, porrect trichome, *Chronopappus bifrons*. **b** 200  $\mu\text{m}$ ; **a, i, d, e** 100  $\mu\text{m}$ ; **f, g, h** 50  $\mu\text{m}$ ; **c** 20  $\mu\text{m}$

- B1. *Branched, spurred trichomes, with one long arm and side arms at the base* (Figs. 1e, 2e)—these are long and thin, similar to unbranched trichomes, but present a tendency for branching, with spurred bases, diminutive side arms at the base of the top cell.
- C. *Branched, 2-armed trichomes*—presenting 2 arms, usually one opposed to the other.
- C1. *Branched, 2-armed T-shaped trichomes* (Figs. 1f, 2f)—these present a stalk with one to many cells. There are two arms that along with the stalk form a T-shape structure. In some trichomes, the top cell presents a part that extends upwards from the stalk and from which the two arms branch sideways. The arms of T-shaped trichomes can have equal or unequal sizes.
- C2. *Branched, 2-armed, T-shaped, bladder-like trichomes* (Figs. 1g, 2g)—in these, the top cell is similar to a vesicle structure.
- C3. *Branched, 2-armed trichomes with arms diagonal to stalk* (Figs. 1h, 2h)—in these, the two arms form a diagonal line in relation to the stalk.
- C4. *Branched, 2-armed, unequal-armed, arms curly trichomes* (Figs. 1i, 2i)—these bear long, curly arms, which spread sideways like a T-shape but tend to be long and coil themselves.
- D. *Branched, with 3–5 arms trichomes*—these are provided with 3–5 arms, which can be opposed to each other or spreading in different directions.
- D1. *Branched, 3- to 5-armed trichomes* (Figs. 1j, 3a, b)—these present a stalk of one to many cells and a top cell branched with 3–5-arms
- D2. *Branched, 3- to 5-armed, bladder-like trichomes* (Figs. 1k, 3c)—in these, the top cell is swollen like a vesicle structure.
- D3. *Branched, 3- to 5-armed, arms long and thin* (Figs. 1l, 3d)—here the arms spread in different angles.
- D4. *Branched, 3- to 5-armed, arms curly trichomes* (Fig. 1m).
- D5. *Branched, 3- to 5-armed trichomes, one longer arm with middle-cells* (Fig. 3e)—in these, the two short arms precede the third arm in the top of the trichome, which is much longer than the others and presents a middle-cell.
- E. *Stellate trichomes*—these present a top cell with six or more arms. In this study, all stellate trichomes are multiangulate, with arms spreading in many different directions. The stalk can be one to many celled.
- E1. *Simple stellate trichomes* (Figs. 1n, o, 3f)—with six or more arms, multiangulate.
- E2. *Stellate, bladder-like trichomes* (Figs. 1p, 3g)—here the top cell of the stellar trichome is bladder-like, or swollen like a vesicle structure.
- E3. *Stellate, geminate trichomes* (Figs. 1q, 3h)—these bear two or more groups of arms set on top of each other; these may also be called candelabra trichomes.
- E4. *Stellate, geminate, porrect trichomes* (Fig. 3i)—these present the top arm much longer than the others and directed upwards.

Table 1 lists the species of Lychnophorinae sampled in this study and their respective trichome types.

The cluster analysis (Fig. 4) produced groups with high similarity within a cluster but also with high similarity between clusters. Rarely, the high similarity groups correspond to taxonomic units, except the cluster with all the species of the genus *Minasia*. Concerning the two richest genera of Lychnophorinae (*Eremanthus* and *Lychnophora*), most species of *Eremanthus* belong to the same cluster contrasting with *Lychnophora*, species of which are scattered in the different clusters.

## Discussion

Several authors studied trichome morphological diversity, resulting in multiple terms and names, sometimes with overlapping meanings [e.g., the use of the term “stellate” in the works of Haro-Carrión and Robinson (2008) and Luque et al. (1999)]. In the present study, we choose to use a more complete classification, with categories and subcategories that thoroughly describe the trichomes, based on different authors (Ramayya 1962; Payne 1978; Theobald et al. 1979; Luque et al. 1999; Haro-Carrión and Robinson 2008), since those authors used a simpler and less specific terminology, which was combined to form the one used in the present study. It is worth noting that trichome morphology in Asteraceae is variable amongst taxa, and sometimes genera in the same tribe or subtribe can present trichomes very different from each other (Cabrera 1959; Drury and Watson 1965, 1966; Krak and Mráz 2008; Robinson 1989, 2009). This fact sometimes impairs a proper comparison among published studies, since a kind of trichome may or may not be present in a given genera, and the same name has been applied for different types in different genera.

In an early study of *Vernonia*, Faust and Jones (1973) used two different terms for the branched, 2-armed trichomes: T-shaped, for those with a many-celled stalk, and longhorn for the ones with a 1- to 2-celled stalk, similar to those found in Lychnophorinae. Redonda-Martínez et al.



**Table 1** List of Lychnophorinae species studied and their respective trichomes

| Species name                         | A1 | A2 | A3 | A4 | B1 | C1 | C2 | C3 | C4 | D1 | D2 | D3 | D4 | D5 | E1 | E2 | E3 | E4 |
|--------------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Anteremanthus hatschbachii</i>    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |    |
| <i>Chronopappus bifrons</i>          | X  | X  |    | X  |    |    |    |    |    | X  |    |    |    | X  |    | X  | X  | X  |
| <i>Eremanthus arboreus</i>           |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus argenteus</i>          |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus auriculatus</i>        | X  |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Eremanthus brevifolius</i>        |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus capitatus</i>          |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Eremanthus cinctus</i>            | X  |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus crotonoides</i>        |    |    |    |    |    |    |    |    |    |    |    |    |    |    | X  | X  |    |    |
| <i>Eremanthus elaeagnus</i>          |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus erythropappus</i>      |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    | X  |    |    |
| <i>Eremanthus glomerulatus</i>       |    |    |    |    |    |    |    |    |    |    | X  | X  |    |    |    |    |    |    |
| <i>Eremanthus goyazensis</i>         |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus incanus</i>            |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus leucodendron</i>       |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus mattogrossensis</i>    |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus mollis</i>             | X  |    |    |    | X  |    |    |    |    | X  | X  |    |    |    |    |    |    |    |
| <i>Eremanthus pabstii</i>            |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus polycephalus</i>       |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus rondoniensis</i>       |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus uniflorus</i>          |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Eremanthus veadeiroensis</i>      |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Lychnophora bishopii</i>          |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Lychnophora brunioides</i>        |    |    |    |    |    |    |    |    |    |    |    | X  |    |    | X  |    |    |    |
| <i>Lychnophora crispa</i>            |    |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophora diamantinana</i>      |    |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophora ericoides</i>         |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Lychnophora gardneri</i>          |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Lychnophora granmogolensis</i>    |    |    |    |    |    | X  |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Lychnophora humillima</i>         | X  |    |    |    |    |    |    | X  |    |    |    |    |    |    | X  |    |    |    |
| <i>Lychnophora markgravii</i>        |    | X  |    |    |    |    | X  |    | X  |    |    |    |    |    |    |    |    |    |
| <i>Lychnophora mellobarretoii</i>    | X  |    |    |    | X  |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Lychnophora passerina</i>         |    |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophora pinaster</i>          |    | X  |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |
| <i>Lychnophora ramosissima</i>       |    | X  |    |    |    | X  |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophora regis</i>             |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |
| <i>Lychnophora salicifolia</i>       |    |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophora santosii</i>          |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    | X  |    |
| <i>Lychnophora sellowii</i>          |    |    |    |    | X  |    |    |    |    | X  |    |    |    |    | X  |    |    |    |
| <i>Lychnophora syncephala</i>        |    |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophora tomentosa</i>         |    |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |    |    |
| <i>Lychnophora triflora</i>          |    |    |    |    |    | X  |    |    |    |    | X  | X  |    |    |    |    |    |    |
| <i>Lychnophora villosissima</i>      | X  |    |    |    | X  |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophoriopsis candelabrum</i>  | X  |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Lychnophoriopsis damazioi</i>     |    |    |    |    |    |    |    |    |    | X  |    |    |    |    | X  |    |    |    |
| <i>Lychnophoriopsis hatschbachii</i> |    |    |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |
| <i>Minasia alpestris</i>             |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |
| <i>Minasia cabralensis</i>           |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |

**Table 1** continued

| Species name                             | A1 | A2 | A3 | A4 | B1 | C1 | C2 | C3 | C4 | D1 | D2 | D3 | D4 | D5 | E1 | E2 | E3 | E4 |
|--|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Minasia ramosa</i>                    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |
| <i>Minasia scapigera</i>                 |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |
| <i>Minasia</i> sp. ined.                 |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |
| <i>Paralychnophora atkinsiae</i>         |    |    |    |    |    |    |    |    |    |    | X  | X  |    |    |    |    |    |    |
| <i>Paralychnophora bicolor</i>           |    |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Paralychnophora glaziouana</i>        |    |    |    |    |    |    |    |    |    | X  | X  |    |    |    |    |    |    |    |
| <i>Paralychnophora harleyi</i>           | X  |    |    |    |    |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Paralychnophora patriciana</i>        |    |    |    |    |    |    |    |    |    |    | X  | X  |    |    |    |    |    |    |
| <i>Paralychnophora reflexoauriculata</i> |    |    |    |    |    |    |    |    |    |    | X  | X  |    |    |    |    |    |    |
| <i>Piptolepis ericoides</i>              |    |    |    |    |    |    |    |    |    | X  |    |    |    |    | X  |    |    |    |
| <i>Piptolepis martiana</i>               |    |    |    | X  |    |    |    |    |    | X  | X  |    |    |    |    | X  |    |    |
| <i>Piptolepis monticola</i>              |    |    |    | X  |    |    |    |    |    | X  | X  |    |    |    |    |    |    |    |
| <i>Piptolepis schultzi</i>               |    |    |    |    |    |    |    |    |    | X  |    |    |    |    | X  |    |    |    |
| <i>Piptolepis</i> sp. ined.              | X  |    |    |    |    |    |    |    |    | X  | X  |    |    |    |    |    |    |    |
| <i>Prestelia eriopus</i>                 |    |    |    |    | X  |    |    |    |    | X  |    |    |    |    |    |    |    |    |
| <i>Prestelia</i> sp. ined.               |    |    |    |    |    |    |    | X  |    | X  |    |    |    |    |    |    |    |    |
| <i>Proteopsis argentea</i>               |    |    |    | X  | X  |    |    |    |    |    |    |    |    |    |    |    |    |    |
| <i>Proteopsis</i> sp. ined.              |    |    |    | X  |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| <i>Vinicia tomentosa</i>                 |    |    |    |    |    | X  |    |    |    |    | X  |    |    |    |    |    |    |    |

(2012) used the terms “filiform” and “long-uniseriate” to define unbranched trichomes in *Vernonia* and *Vernonanthura*. Those differ from the ones found in Lychnophorinae by the lack of a stalk in the filiform kind and by the long stalk, with more than three cells, in the long-uniseriate kind. Also, the T-shaped trichomes are different, due to their long, 5- to 6-celled stalk.

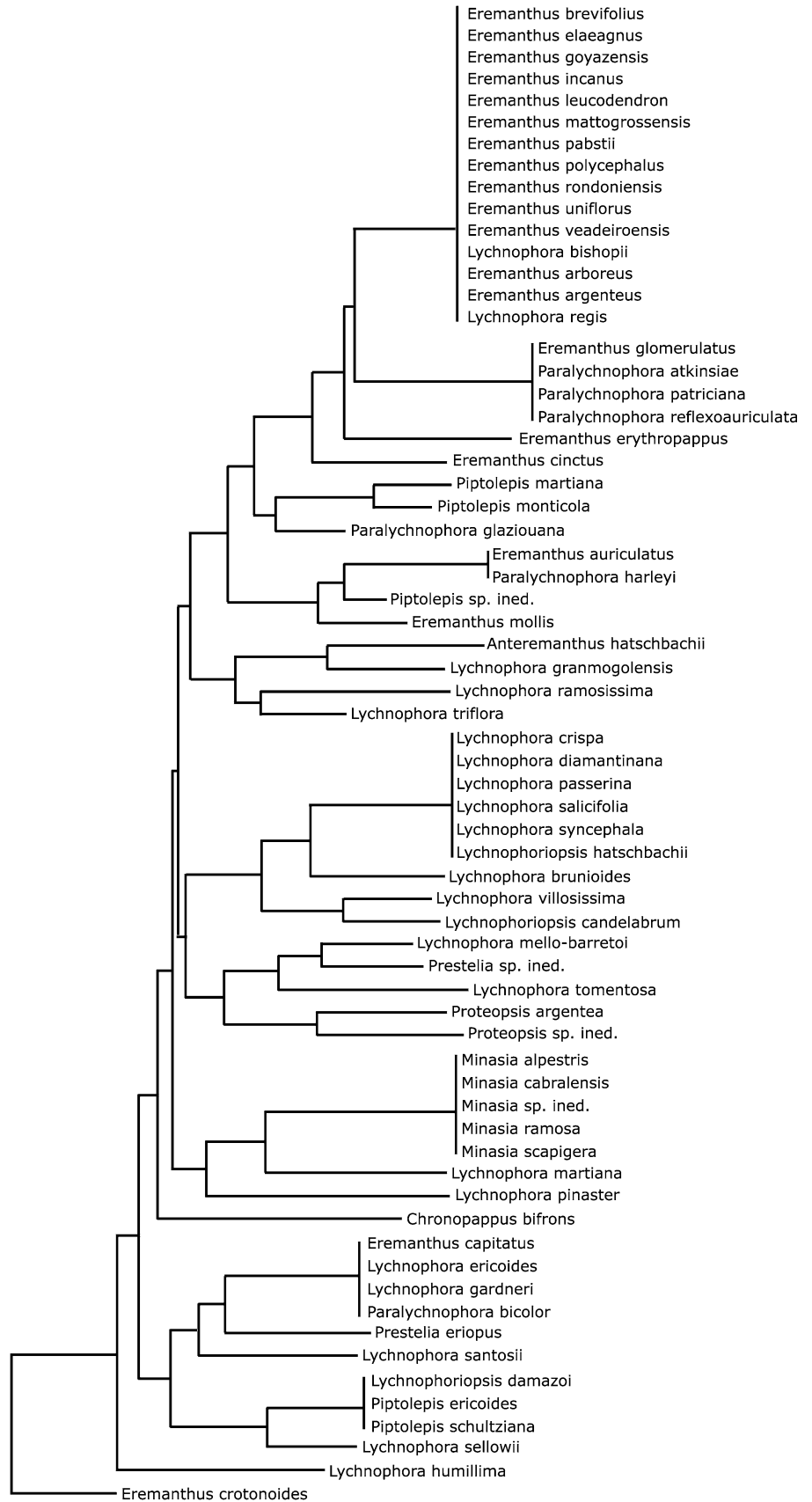
In the revision of *Critoniopsis*, Haro-Carrión and Robinson (2008) established some kinds of trichomes similar to the ones found in Lychnophorinae. The authors used two terms to define trichomes with more than two arms: scarcely branched vermiform and stellate, without making any distinction between the number of arms these kinds should have. Reviewing the figures present in their paper, it is possible to affirm that both of these kinds correspond to the 3- to 5-armed trichomes reported here for Lychnophorinae, since none of the stellate *Critoniopsis* trichomes present more than five arms. The simple and spurred kinds are also cited for this genus, the spurred kind corresponding to the branched spurred kind (type B) of Lychnophorinae; and the simple one corresponding to the unbranched kind from Lychnophorinae, except for the fact that it is not yet clear whether *Critoniopsis* trichomes present a stalk.

In the analysis of leaf anatomy of *Lychnophora* provided by Luque et al. (1999), a description of kinds of trichomes was made, without naming each of them; it is remarkable that all kinds are short stalked. The simple, auriculate trichome was defined by those authors as a special kind; and again, there was no differentiation between the number of

arms of the stellate and branched kinds. The distinction between both relies on how the branching occurs: stellate trichomes would show all arms to be of the same length and parallel to the leaf surface, corresponding both to 3- to 5-armed and stellate kinds as defined in the present study; and the branched trichomes bearing the top cell branches in different directions, which mostly correspond to the 3- to 5-armed type defined here.

The subtribe Lychnophorinae displays a great diversity of non-glandular trichomes (5 types and 18 subtypes). The most frequent type is the 3- to 5-armed branched trichome (bladder-like or not) (type D), present in 82 % of the studied species, being absent only from genera *Anteremanthus*, *Minasia*, *Proteopsis* and some species of *Erernanthus* and *Lychnophora* (see below for taxonomic significance). Unbranched (type A) and 2-armed (type C) trichomes are far less common than type D, while they are usually the most frequent trichome types in the rest of the tribe Vernonieae (Keeley and Robinson 2009). Branched, spurred (type B) and stellate (type E) trichomes are sporadic in Lychnophorinae. Type E is found outside of Lychnophorinae in the closely related subtribe Sipolisiinae (except *Hololepis* with type C trichome) (Loeuille et al. 2013) and Piptocarphinae, the latter sharing with Lychnophorinae also the type D trichome, especially bladder-like (subtype D2) (Haro-Carrión and Robinson 2008; Loeuille 2011). Phylogenetic analyses (Keeley et al. 2007; Loeuille 2011) indicate a close relationship between Lychnophorinae and Sipolisiinae, but a more distant one with the

**Fig. 4** Phenogram clustering 67 species of Lychnophorinae based on trichomes diversity. Jaccard index and NJ method were used to build up the phenogram



Piptocarphinae. It is worth noting that type D and E trichomes co-occur with type A in Lychnophorinae and Sipolisiinae, whereas type A has not been found in Piptocarphinae (Loeuille 2011).

As previously observed in other groups of Vernoniae (Redonda-Martínez et al. 2012), these trichome types (or subtypes) have a diagnostic value at the species level, but a lower one at the genus level. The monotypic genus *Chronopappus* presents the richest trichome complement in the subtribe with 8 trichomes types and subtypes, with subtypes A4, D5, E3 and E4 being found only in this species. This distinctive trichome complement corroborates the morphological singularity of *Chronopappus*, whose strongly muricate leaves are unique in Lychnophorinae. The genus *Minasia* has an indument composed only of bladder-like T-shaped trichomes (subtype C2), which occur, outside that genus, only in *Lychnophora markgravii*, which has also unbranched and 3- to 5-armed trichomes.

The trichome complement is useful to set apart several Lychnophorinae species that are morphologically similar. In the genus *Eremanthus*, it is fairly homogeneous and composed mostly by the D2 trichome, absent only in *E. crotonoides* and *E. mollis*, both of which present highly divergent trichome complements in comparison with the rest of the genus. *E. crotonoides* is the single species of Lychnophorinae with an indument composed entirely of stellate trichomes (subtypes E1 and E2). The uncommon spurred trichome (subtype B1) has been found in *E. mollis* along with unbranched (A1) and 3- to 5-armed trichomes (D1 and D2). The taxonomic position of both species in *Eremanthus* has been controversial; MacLeish (1984) placed them in *Vernonia* based on macromorphological characters. *Eremanthus* is of special interest due to the economic importance of *E. erythropappus* and *E. incanus* as a source of  $\alpha$ -bisabolol (Scolforo et al. 2012). These two species differ by the presence of bladder-like stellate trichome (subtype E2) in *E. erythropappus*, whereas *E. incanus* has an indument composed only of D2 trichomes. Another pair of *Eremanthus* species closely related, from northeastern Brasil (Loeuille 2011), may be distinguished by D trichome subtype (*E. arboreus* with D2 and *E. capitatus* with D1).

Most of the generic delimitation controversies concern *Lychnophora*, despite the existence of two taxonomic revisions in the last decades (Coile and Jones 1981, Semir 1991). The trichome complement of this genus is highly diverse: all the studied trichome types have been found here. Unlike *Eremanthus*, the D2 trichome is rare in *Lychnophora*, being present only in three morphologically related species from Bahia: *L. bishopii*, *L. regis* and *L. triflora*. Other macromorphological characters help distinguish this species group

from the rest of *Lychnophora*, mainly the presence of a pad-like leaf sheath and a similar habit of small dome-headed 'ericoid' profusely branched trees (Hind 2000b; Loeuille 2011). The subtype D3 is the most frequent one in *Lychnophora*. The trichome complement of *Lychnophoriopsis* is indistinguishable from the *Lychnophora* one; therefore, these data do not support recognition of two different genera.

The closely related species group formed by *L. granmogolensis*, *L. passerina* and *L. ramosissima* has been regarded as a different genus, *Haplostephium*, in the past (Duarte 1974; Coile and Jones 1983) based on the residual outer pappus. The general morphologic similarity among them led Coile and Jones (1983) to consider a single species, unlike Duarte (1974), Semir (1991) and Semir et al. (2011). The trichome complement of these species is similar to those found in other *Lychnophora* species, but it is helpful to set apart each species of the group since *L. passerina* has an indument composed only of D3 trichomes, *L. ramosissima* in addition to D3 also displays A2 and C1, whereas *L. granmogolensis*' indument is a combination of C1 and D1 trichomes.

Another species group of challenging identification is composed of *L. pinaster* and the widespread medicinal *L. ericoides*, the latter being focus of phytochemical investigations (reviewed in Keles et al. 2010) and conservation studies (Collevatti et al. 2009; Maia-Almeida et al. 2012). Leaf characters and geographical distribution are usually used to distinguish these species (Loeuille 2011; Semir et al. 2011), but differences in the trichome complement are especially helpful and straightforward: *L. ericoides*' indument is composed solely of D1 trichomes, whereas in *L. pinaster* A2 and D4 trichomes are found.

In the genus *Paralychnophora*, *P. bicolor*, *P. glaziouana* and *P. harleyi* are closely related and their identification is challenging (Loeuille 2011; Loeuille et al. 2012). These three species share the presence of 3- to 5-armed trichomes (subtype D1), which are the only kind in *P. bicolor*, while *P. glaziouana* also displays bladder-like 3- to 5-armed ones (subtype D2) and *P. harleyi* unbranched ones (subtype A1). The three other species of this genus have a combination of 3- to 5-armed trichomes with long and thin arms (subtype D3) and D2 trichomes.

One of the most striking field features of most Lychnophorinae species is the thick indument covering leaves and stems, a likely efficient protection against hydric stress (Handro et al. 1970; Wagner et al. 2004; Semir et al. 2011), fire (Coile and Jones 1981; Semir et al. 2011) and herbivory (Agrawal and Fishbein 2006). The distribution of Lychnophorinae largely mirrors the area of the Cerrado Domain, being found particularly in *campo rupestre* vegetation, where the hydric stress is intense and fires frequent (Giulietti and Pirani 1988; Harley 1988). The dense

indument might decrease water loss through reflection but also might play an important role in water absorption (Ehleringer 1984), since fog deposition is common in *campo rupestre* areas (Giulietti and Pirani 1988; Harley 1988) and it is an important water source for the vegetation. The most frequent leaf trichome type in Lychnophorinae (subtype D2) plays an active role in fog water absorption in *Eremanthus erythropappus* (Lima 2010).

The present study reveals the great diversity of nonglandular trichomes in Lychnophorinae. While trichome complement is of little use to distinguish genera, it appears to be a valuable characteristic at a lower taxonomic level to identify closely morphologically related species. The presence of a certain type of trichome is likely an adaptation against hydric stress, and such an interesting evolutionary investigation shall be further addressed to in a phylogenetic framework.

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## Appendix 1

List of specimens examined. The following abbreviations designate the states of Brazil: BA Bahia, CE Ceará, DF Distrito Federal, GO Goiás, MT Mato Grosso, MG Minas Gerais, PE Pernambuco, RO Rondônia, SP São Paulo.

*Anteremanthus hatschbachii* H. Rob., Brazil: MG, Grão Mogol, Giulietti et al. CFCR 9864 (SPF), Loeuille et al. 441 (SPF), Zappi et al. CFCR 12042 (SPF). *Chrotopappus bifrons* (DC. ex Pers.) DC., Brazil: MG, Catas Altas, Loeuille and Albergaria Pena 460 (SPF), Santo Antônio do Itambé, Loeuille et al. 465 (SPF), Souza et al. 21080 (SPF). *Eremanthus arboreus* (Gardner) MacLeish, Brazil: CE, Crato, Loeuille et al. 510 (SPF), 512 (SPF), Silva 1345 (SPF). *Eremanthus argenteus* MacLeish & H. Schumach., Brazil: GO, Alto Paraíso, Cavalcanti et al. 672 (SPF), Loeuille et al. 289 (SPF), Teresina de Goiás, Souza et al. 24698 (SPF). *Eremanthus auriculatus* MacLeish & H. Schumach., Brazil: GO, Alto Paraíso, Loeuille et al., 279 (SPF), Teresina de Goiás, Loeuille et al. 836 (SPF), Loeuille & Siniscalchi 845 (SPF). *Eremanthus brevifolius* Loeuille, Brazil: MG, Congonhas do Norte, Loeuille et al. 71 (SPF). *Eremanthus capitatus* (Spreng.) MacLeish, Brazil: BA, Abaíra, Ganév 699 (SPF), Loeuille et al. 345 (SPF), Palmeiras, Stradmann et al. PCD 451 (SPF). *Eremanthus cinctus* Baker, Brazil: MG, Uberlândia, Loeuille et al. 306 (SPF). *Eremanthus crotonoides* (DC.) Sch. Bip., Brazil: MG, Catas Altas, Pirani et al. 5336 (SPF), Loeuille et al. 9 (SPF), Santana do Riacho, Loeuille et al. 25 (SPF). *Eremanthus elaeagnus* (Mart. ex DC.) Sch. Bip., Brazil:

MG, Diamantina, Roque et al. 203 (SPF), Joaquim Felício, Loeuille et al. 430 (SPF), Santana do Riacho, Loeuille et al. 508 (SPF). *Eremanthus erythropappus* (DC.) MacLeish, Brazil: MG, Capitólio, Loeuille et al. 50 (SPF), SP, Campos do Jordão, Tamashiro et al. 556 (SPF), Jundiaí, Pirani et al. 3624 (SPF). *Eremanthus glomerulatus* Less., Brazil: DF, Brasília, Rezende, J. M. de 470 (SPF), GO, Pirenópolis, Loeuille et al. 298 (SPF), MG, Mato Verde, Pirani et al. 4255 (SPF). *Eremanthus goyazensis* (Gardner) Sch. Bip., Brazil: GO, Alto Paraíso, Uliana et al. 689 (SPF), Niquelândia, Walter et al. 2442 (SPF), Pirenópolis, Loeuille et al. 295 (SPF). *Eremanthus incanus* (Less.) Less., Brazil: BA, Abaíra, Loeuille et al. 344 (SPF), MG, Botumirim, Mello-Silva et al. 3028 (SPF), Grão-Mogol, Cordeiro & Mello-Silva CFCR 10058 (SPF). *Eremanthus leucodendron* Mattf., Brazil: BA, Abaíra, Loeuille et al. 347 (SPF), Rio de Contas, Ganév 2057 (SPF), Sano et al. CFCR 14712. *Eremanthus mattogrossensis* Kuntze, Brazil: MT, Chapada dos Guimarães, Loeuille et al. 453 (SPF), Diamantino, Loeuille et al. 457 (SPF), SP, Pedregulho, Sasaki and Junqueira 542 (SPF). *Eremanthus mollis* Sch. Bip., Brazil: GO, Pirenópolis, Loeuille et al. 305 (SPF), MG, Capitólio, Loeuille et al. 39 (SPF), Gouveia, Giulietti et al. CFCR 1740 (SPF). *Eremanthus pabstii* G.M. Barroso, Brazil: GO, Água Fria de Goiás, Hatschbach et al. 70631 (SPF), Cristalina, Hatschbach and Kummrow 46603 (SPF), Loeuille et al. 833 (SPF). *Eremanthus polycephalus* (DC.) MacLeish, Brazil: MG, Diamantina, Roque et al. 246 (SPF), Grão-Mogol, Loeuille et al. 442 (SPF), Souza et al. 25838 (SPF). *Eremanthus rondonienseis* MacLeish & H. Schumach, Brazil: MT, Poconé, Pires & Santos 16367 (SPF), RO, Vilhena, Miranda and Silva 1288 (SPF). *Eremanthus uniflorus* MacLeish & H. Schumach., Brazil: GO, Alto Paraíso, Loeuille et al. 280, 286 (SPF), Trovó et al. 448 (SPF). *Eremanthus veadeiroenseis* H. Rob., Brazil: GO, Alto Paraíso, Saavedra et al. 475 (SPF), Cavalcante, Martinelli et al. 16510 (SPF), Teresina de Goiás, Loeuille and Siniscalchi 847 (SPF). *Lychnophora bishopii* H. Rob., Brazil: BA, Abaíra, Ganév 3233 (SPF), Mucugê, Harley et al. CFCR 14267 (SPF), Rio de Contas, Sano et al. CFCR 14714 (SPF). *Lychnophora brunioides* Mart., Brazil: MG, Santo Antônio do Itambé, Loeuille et al. 466, 467 (SPF), Loeuille et al. 594 (SPF). *Lychnophora crispa* Mattf., Brazil: BA, Mucugês, Hind et al. PCD 3551 (SPF), Rio de Contas, Harley et al. PCD 4427 (SPF). *Lychnophora diamantinana* Coile & Jones, Brazil: MG, Diamantina, Forzza et al. 622 (SPF), Loeuille et al. 108 (SPF). *Lychnophora ericoides* Mart., Brazil: GO, Catalão, Arantes et al. s.n. (SPF), MG, Delfinópolis, Silva 933 (SPF), Santana do Riacho, Loeuille et al. 26 (SPF). *Lychnophora gardneri* Sch. Bip. Brazil: MG, Congonhas do Norte, Loeuille et al. 67 (SPF), Diamantina, Forzza & Mello-Silva 1500 (SPF), Serro, Pirani et al. 4070 (SPF).



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