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Original article

On the true identity of *Mendoncia* "stellate" trichomes

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ABSTRACT

The present survey of leaf-blade trichomes of *Mendoncia* used SEM and light microscopy to investigate the diversity of trichome types in Neotropical and Paleotropical species of the genus. The eglandular trichomes are filiform, uniseriate, with asymmetric epidermal cells arranged radially around the trichome, these epidermal cells may be short or elongated, oriented in two groups. These cells, when elongated, are covered with epicuticular wax, forming smooth thick plates. African species have dendritic but not stellate trichomes. Character states such as number and length of basal cells were shown to overlap within the same species and therefore their use in isolation is not recommended for subgeneric classification of *Mendoncia*. Neotropical *Mendoncia* trichomes with well-developed epidermal cells arranged radially around the trichome appear to be unique to this group, without parallel in other plant families.

Keywords: Acanthaceae, anatomy, hair types, indumentum, micromorphology, SEM, taxonomy, Thunbergioideae.

Introduction

Acanthaceae Juss. is a large, pantropical family with 191 genera and c. 4900 species, displaying notable habit and habitat diversity (Manzitto-Tripp *et al.* 2022). Among the varied characters of the family, reproductive features such as corolla aestivation, and pollen (Scotland & Vollesen 2000) and seed morphology (Manzitto-Tripp *et al.* 2022) have featured often in studies, however leaf indumentum has been less studied at the family level. Ahmad (1978) performed the only family-wide study of Acanthaceae leaf indumentum; he examined 109 species in 38 genera and recorded both glandular and eglandular trichomes.

Only a few groups in subfamily Acanthoideae Eaton are reported as having stellate trichomes, such as a section of *Barleria* L. (Darbyshire 2008) and some species of *Whitfieldia* Hook. (Grall & Darbyshire 2021). The taxonomic revision of 26 species of *Duosperma* Dayton (Acanthoideae) (Vollesen 2006) recorded stellate trichomes in four taxa, and this indumentum was used as a distinctive taxonomic feature. In Thunbergioideae T.Anderson, this type of trichome is present in a few species of *Thunbergia* Retz., and *Mendoncia* Velloso ex Vand. (Breteler & Wieringa 2018), while only in *Pseudocalyx* Radlk. the stellate trichomes are found in all species (Manzitto-Tripp *et al.* 2022). Oersted (1854) described stellate hairs in *Mendoncia costaricana* Oerst. Ahmad (1978) sampled only two Neotropical species of

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Mendoncia, reporting eglandular uni- or multicellular uniseriate trichomes with stellate bases, and glandular trichomes with globular or disc-shaped heads that may frequently appear quadrangular or triangular in surface view.

Basally branched trichomes in *Mendoncia* were first noticed by Turrill (1919), who stated that these were "*pilis simplicibus vel e basi stellata orientibus*" (simple trichomes with stellate base, somehow oriented, perhaps referring to the fact that the "arms" of the stars are not radially symmetric). The leaf-indumentum of *Mendoncia* was studied in detail by Bremekamp (1938), who described "hairs anchored in the epidermis with a kind of stolons (sic.)" and urged that they not be called stellate hairs, as these trichomes have a base that is imbedded in the epidermis and are not free. Bremekamp (1938) recognized three species of *Mendoncia* for Suriname using the basal cells of the trichomes as a taxonomic character. Leaf-blade trichomes were given special importance by Rizzini (1948), who used two trichome types (basally branched and glandular) to segregate 18 species of *Mendoncia* into 4 subgenera (*Dialyactinocithus* Rizz. with separate ray cells; *Gamoactinocithus* Rizz., with fused ray cells; *Anactinocithus* Rizz., without ray cells and *Bremekampia* Rizz. with separate ray cells above and cells with smaller rays beneath), and 9 sections. Profice (1988) roughly followed Rizzini´s subgenera, repositioning several species from one subgenus into another (Tab. 1). After concluding that the density of glandular trichomes was very variable even within species, Profice (1988) decided to abandon the sectional classification proposed by Rizzini (1948). Finally, Breteler and Wieringa (2018) have observed stellate to dendritic trichomes in African *Mendoncia*. We studied leaf-blade trichomes throughout *Mendoncia* under SEM and light microscopy in order to understand their morphology, specifically ascertaining whether they can be considered stellate or not, and also to investigate their taxonomic value as part of an ongoing revision of the Neotropical species of the genus.

Material and methods

Taxon sampling.—*Mendoncia* is represented by c. 90 species, with the greatest diversity in Central and South America, where about 80 species are distributed. The remaining species are native to Africa or Madagascar (Magnaghi & Daniel 2017). In the present study, 31 Neotropical and 10 Paleotropical species were analysed (Tab. 1).

Light microscope examination.—Fully expanded leaf tissue was sampled for herbarium specimens (about 2 cm^2) were rehydrated (Smith & Smith 1942) and stored in 70% ethanol. Fragments from the middle and basal portion of the leaf blade (including midrib and margin) were cleared with 5% sodium hydroxide and 20% hypochlorite solutions, stained with 50% ethanol-diluted fuchsin (Shobe & Lersten 1967) and mounted in glycerinated gelatin (Kaiser 1880). Three reagents were used to detect cell wall composition. 1) Toluidine blue (O'Brien *et al.* 1964) is a metachromatic dye that exhibits different colours according to the substrate it reacts to. Mucilage and walls rich in pectin stain purple, cellulosic walls stain blue, and lignified walls and non-structural phenolic contents stain green. 2) Sudan Black B stains suberin blue to black (Pearse 1972). 3) Phloroglucinol-HCl stains lignin pink to red (Johansen 1940). Observations and photographic documentation were performed with a light microscope (Axio Scope. A1, ©Carl Zeiss) equipped with a digital camera (AxioCam HRc, ©Carl Zeiss). Macro images were obtained using a stereomicroscope (SteREO Discovery. V8, ©Carl Zeiss) with a coupled digital camera (AxioCam ICc5, ©Carl Zeiss).

Scanning Electron Microscopy.—Samples were obtained from herbarium specimens and placed onto stubs with the adaxial side up using double-sided stick carbono tape. The stubs were sputter-coated with gold in an Emitech K550 sputter coater and were then examined and photographed at different magnifications in a TESCAN MIRA3 scanning electron microscope at 15 kV acceleration voltage.

Description and analysis of anatomical characters.—Anatomical descriptions were based on terms from a set of diagnostic parameters for the classification of trichomes drawn from relevant plant anatomy literature (Metcalfe & Chalk 1975; 1979; Evert 2006), as well as studies including trichome micromorphology (Ahmad 1978; Wurdack 1986; Pinto-Silva *et al.* in press).

Results

The eglandular trichomes are filiform, uniseriate, and can be uni- to tricellular, with asymmetric epidermal cells arranged radially around the trichome. The epidermal cells may be short or elongated, and are often oriented in two groups. These radially asymmetric epidermal cells, when elongated, are covered with epicuticular wax, forming smooth thick plates, evidenced by scanning electron microscopy (Fig. 1). The epidermal cells can also be conical or rosulated (Fig. 1A-E). In some cases the epidermal cells are free and not organized symmetrically, and are oriented in roughly two groups, bilaterally rather than radially disposed (Fig. 1F-K). Dendritic trichomes without thickened epidermal cells were observed in African species (Fig. 1L). Optical microscope observations of cleared leaf fragments were used to ascertain the epidermal origin of those cells (Fig. 2). The pectic composition of the cell wall of the epidermic cells, together with the absence of suberin and lignin were made evident in our analyses (Fig. 2J-L).

Table 1. Neotropical and Paleotropical species of *Mendoncia* samples analysed under Scanning Electron Microscopy (SEM) and Light Microscopy (LM). Subgeneric classification follows *Rizzini (1948) and + Profice (1988); vouchers for SEM and LM are noted.

Sampling	Classification	SEM	LM
Neotropical species			
Mendoncia bivalvis (L.f.) Merr.	n.a.	*W. Hahn 5781* (RB474253)	n.a.
Mendoncia blanchetiana Profice	n.a.	*R.S. Pinheiro 1212* (RB151893)	n.a.
Mendoncia caquetensis Leonard	n.a.	*R. López-C. 3981* (HUA136152)	n.a.
Mendoncia cardonae Leonard	n.a.	*V.A. Funk 6089* (RB361364)	n.a.
Mendoncia gigas Lindau	n.a.	*F.A. Silva 692* (MG241766)	*F.A. Silva 701* (MG241775)
Mendoncia glabra Poepp. & Endl.	*Bremekampia* Rizz.+	*F.A. Silva 621* (MG239746)	*F.A. Silva 707* (MG241781)
Mendoncia hitchcockii Wassh.	n.a.	*C. Kajekai 1712* (SP453926)	n.a.
Mendoncia hoffmannseggiana Nees	*Dialyactinocithus* Rizz.*, *Bremekampia* Rizz.+	*F.A. Silva 516* (MG239696)	*F.A. Silva 679* (MG241387)
Mendoncia hymenophyllacea Rizzini	*Gamoactinocithus* Rizz.*, +	*F.A. Silva 590* (MG239481)	*F.A. Silva 427* (MG239607)
Mendoncia killipii Leonard	n.a.	*E. Asplund 18838* (R125347)	n.a.
Mendoncia klugii Leonard	n.a.	*D.C. Daly 5109* (MG134634)	n.a.
Mendoncia lasiophyta Leonard	*Dialyactinocithus* Rizz.+	*A.S.L. Silva 577* (MG78137)	*A.S.L. Silva 577* (MG78137)
Mendoncia litoralis Leonard	n.a.	*E. Forero 2611* (SP183617)	n.a.
Mendoncia meyeniana Nees	*Dialyactinocithus* Rizz.*	*F.A. Silva 698* (MG241772)	*F.A. Silva 698* (MG241772)
Mendoncia mollis Lindau	*Dialyactinocithus* Rizz.*, *Gamoactinocithus* Rizz.+	*V.C. Souza 39839* (RB648951)	*W. Ganev 1539* (SP86984)
Mendoncia multiflora Poepp. & Endl.	*Dialyactinocithus* Rizz.*, *Bremekampia* Rizz.+	*A. Ducke 1127* (MG19111)	n.a.
Mendoncia pedunculata Leonard	*Anactinocithus* Rizz.+	*P. Kukle 191* (RB344133)	*M.Y. Rimachi Y. 10049* (MBM166800)
Mendoncia pilosa Mart.	*Dialyactinocithus* Rizz.*,+	*F.A. Silva 709* (MG241783)	*F.A. Silva 709* (MG241783)
Mendoncia puberula Mart.	*Gamoactinocithus* Rizz.*,+	*G. Hatschbach 41755* (MG107248)	*I.G. Martinelli 4* (SPF234934)
Mendoncia retusa Turril	n.a.	*M.R. Pace 701* (RB767536)	n.a.
Mendoncia riedeliana Nees	n.a.	*A.M. Carvalho 4552* (RB339091)	*T.S. Santos 556* (CEPEC5477)
Mendoncia rizziniana Profice	n.a.	*G.T. Prance 3005* (INPA18528)	n.a.
Mendoncia sericea Leonard ex Wassh.	n.a.	*E. Asplund 18815* (R125346)	n.a.
Mendoncia smithii Leonard	n.a.	*A. Ducke s.n.* (MG7521)	n.a.
Mendoncia sprucei Lindau	*Bremekampia* Rizz.*,+	*F.A. Silva 595* (MG239720)	*F.A. Silva 346* (MG239529)
Mendoncia squamuligera Nees	n.a.	*J.T.F. Guimarães 34* (MG232806)	*J.T.F. Guimarães 34* (MG232806)
Mendoncia tonduzii Turrill	n.a.	*C.L. Castaño-Rosalba & G.E. Muñoz 148* (HUA50941)	n.a.
Mendoncia tovarensis (Klotzsch & H. Karst. ex Nees) Leonard	n.a.	*G. Davidse 18676* (MG100749)	*G. Davidse 18676* (MG100749)
Mendoncia trichota Leonard	*Gamoactinocithus* Rizz.+	*E. Lleras P17069* (MG47008)	n.a.
Mendoncia velloziana Mart.	*Bremekampia* Rizz.*,+	*G. Hatschbach 48627* (MG117421)	*F.A. Silva 909* (MG246023)
Mendoncia sp.	n.a.	*J.S. Vigo 11690* (RB344134)	*M. Silva 974* (INPA37065)
African and Madagascan species			
Mendoncia camerounensis Breteler & Wieringa	n.a.	*X. Van der Burgt 1700* (K001061985)	n.a.
Mendoncia combretoides (A. Chev. ex Hutch. & Dalziel) Benoist	n.a.	*J.W.A Jansen 873* (K)	n.a.
Mendoncia cowanii (S. Moore) Benoist	n.a.	*M. Cheek & J. Dransfield B1383* (K)	n.a.
Mendoncia decaryi (Benoist) E. Magnaghi	n.a.	*B. Du Puy & D. Du Puy 163* (K)	n.a.
Mendoncia flagellaris (Baker) Benoist	n.a.	*N. Messmer 745* (K)	n.a.
Mendoncia gilgiana (Lindau) Benoist	n.a.	*P.M. Haba 603* (K001393687)	n.a.
Mendoncia kely E. Magnaghi	n.a.	*O. Andrianantoanina 11* (K)	n.a.
Mendoncia lindaviana (Gilg) Benoist	n.a.	*F.J. Breteler 8106* (K)	n.a.
Mendoncia phytocrenoides Benoist	n.a.	*N. Halie3358* (K)	n.a.
Mendoncia vinciflora Benoist	n.a.	*H. Humbert & R. Capuron 25353* (K)	n.a.

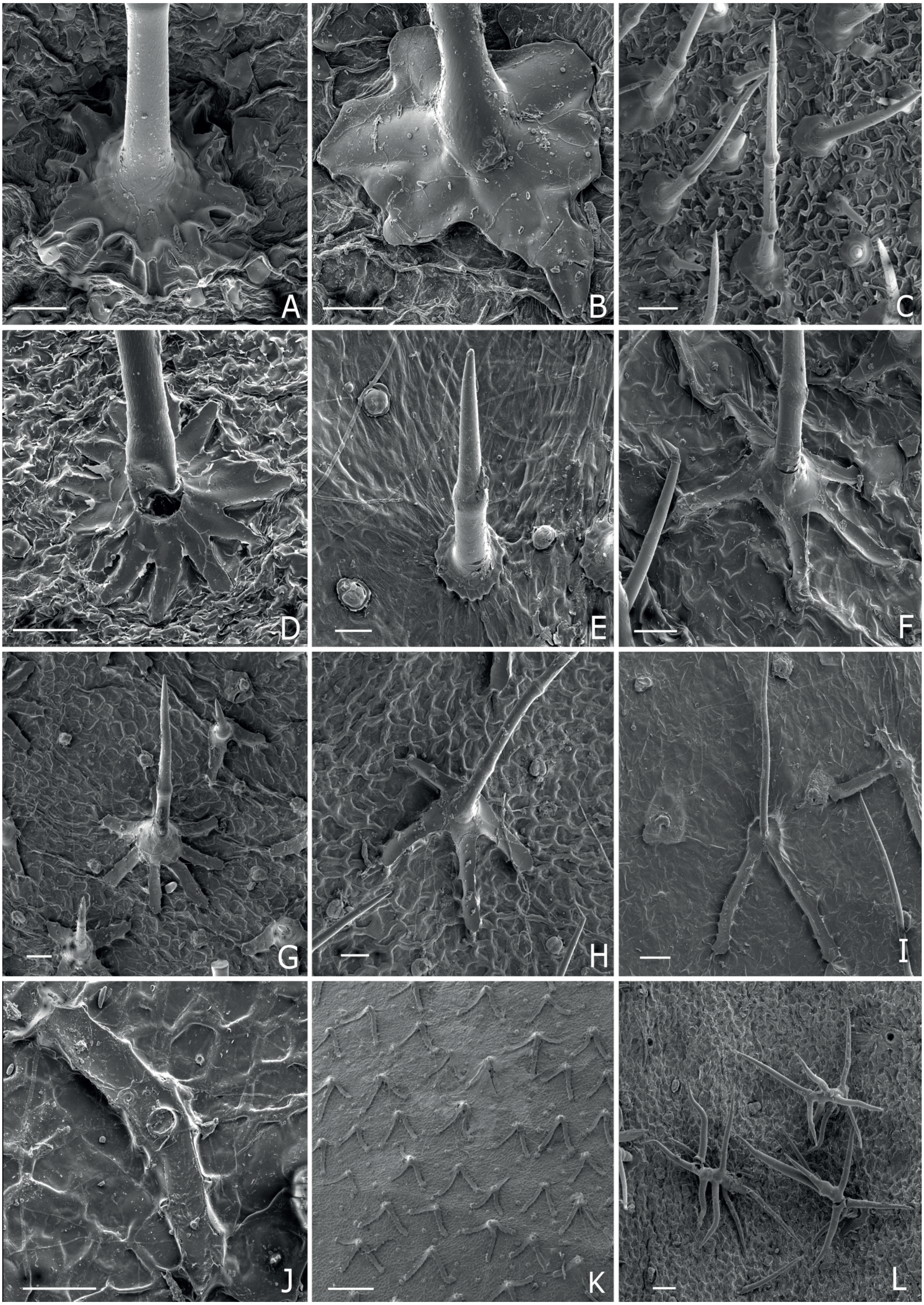

Figure 1. Types of trichomes on the adaxial surface of the leaf-blade in species sampled from *Mendoncia*. **A.** *M. bivalvis*. **B.** *M. hymenophyllacea*. **C.** *M. mollis*. **D.** *M. camerounensis*. **E.** *M. cowanii*. **F.** *M. riedeliana*. **G.** *M. pilosa*. **H.** *M. squamuligera*. **I.** *M. meyeniana*. **J.** *M. multiflora*. **K.** *M. gigas*. **L.** *M. camerounensis*. Scale bars: A–J, L= 50 µm; K= 0.5 mm (Specimens analysed in Table 1).

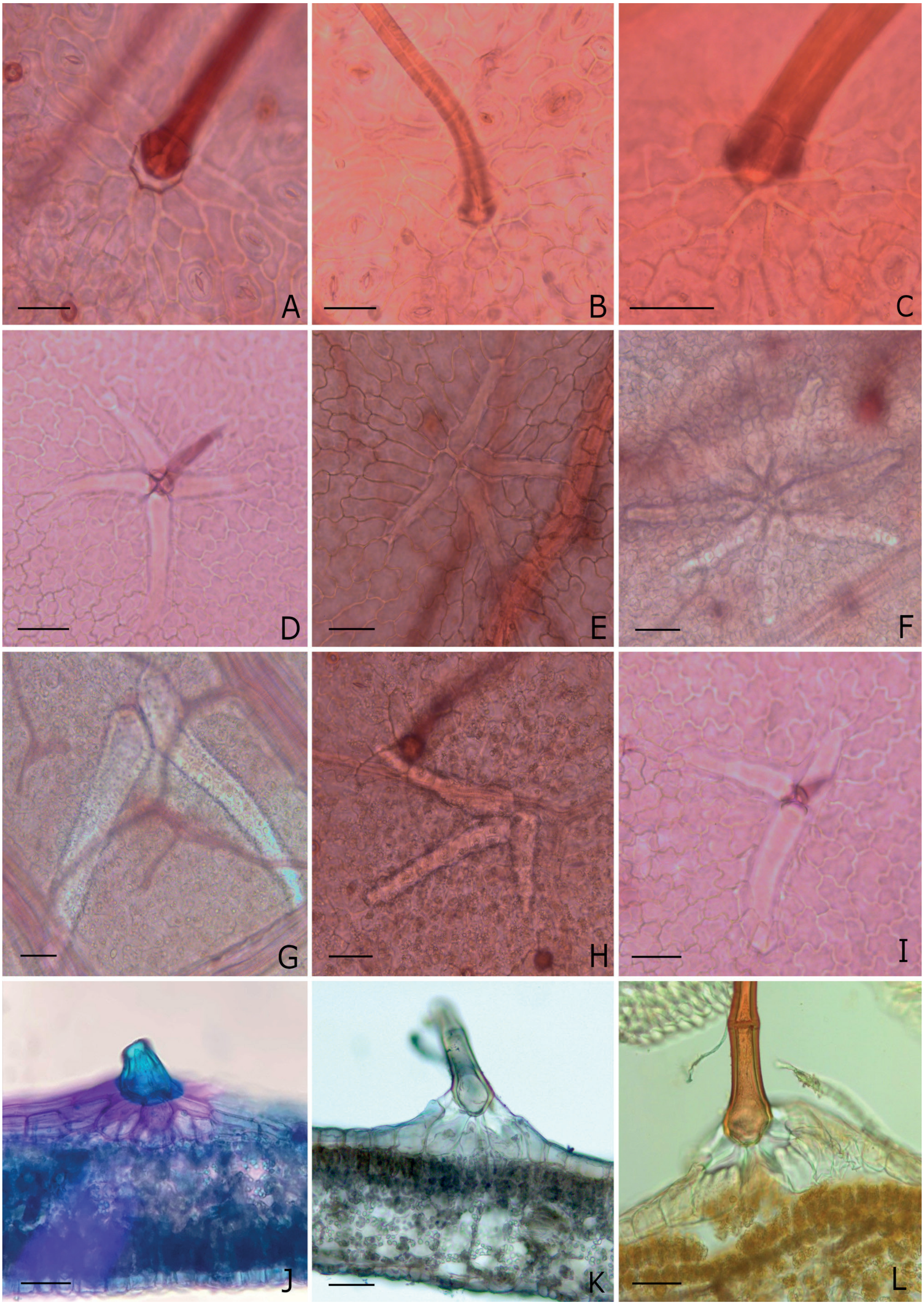

Figure 2. Types of trichomes on the adaxial surface of the leaf-blade in species sampled from *Mendoncia*. **A.** *M. hymenophyllacea*. **B.** *M. mollis*. **C.** *M. puberula*. **D.** *M. glabra*. **E.** *M. hoffmannseggiana*. **F.** *M. pilosa*. **G.** *M. meyeniana*. **H.** *M. gigas*. **I.** *M. glabra*. **J-L.** *M. hymenophyllacea*. **J.** Trichome stained with toluidine blue. **K.** Trichome with reaction to Sudan Black B. **L.** Trichome with reaction to Phloroglucinol-HCl. Scale bars: 50 μm (Specimens analyzed in Table 1).

Summarizing our findings, a total of 41 species (31 Neotropical and 10 Paleotropical) were examined and the following eglandular trichome types were detected:

Type 1. Filiform trichomes with (5–)6–18 radially disposed, united basal cells (Fig. 1A-E and Fig. 2A-C) were observed in 8 Neotropical and 7 Palaeotropical species (Tab. 2).

Type 2. Filiform trichomes with 3–8 bilaterally disposed, free basal cells (Fig. 1F-H and Fig. 2D-F) were observed in 18 Neotropical species (Tab. 2).

Type 3. Filiform trichomes with 2(–3) Y or V-shaped basal cells (Fig. 1I-K and Fig. 2G-I) were found in 19 Neotropical species (Tab. 2).

Type 4. Dendritic trichomes (Fig. 1L) were found in three Palaeotropical species; these were associated with Type 1 filiform trichomes in two species (*M. camerounensis, M. phytocrenoides*) (Table 2).

In our sample, only *M. pedunculata*, *M. flagellaris* and *M. lindaviana* lacked eglandular trichomes.

Glandular trichomes were observed in the majority of species and were generally more abundant near the midrib and the margin rather than than in the intercostal area of the leaf-blade and, in some species, they were confined to the veins and the margin. The glandular trichome type observed was capitate and peltate, with 2 to 4 secretory head cells (Fig. 3, Table 2).

Discussion

Thus far, only filiform uniseriate trichomes with asymmetric epidermal cells arranged radially around the trichome have been found in Neotropical *Mendoncia* species, and true stellate trichomes are absent. African species have dendritic trichomes (tree-like trichomes with multiple lateral branches); these lack enlarged basal cells. However, they also lack true stellate trichomes (i.e. star-shaped trichomes with several arms arising from a common, either stalked or sessile base according to Simpson 2010). Technical limitations of magnification instruments used in the past may have led to difficulty in clearly distinguishing details of trichomes, with possible confusion between these epidermal radiate cells covered in epicuticular wax and true stellate trichomes. Our observations using different chemical reagents clearly established that the cells below the trichomes follow a distinct cellular pattern and are not associated with the trichome structure. The role of such epidermal cells remains to be researched.

Trichome type and taxonomic value

Stellate trichomes in *Mendoncia* were first referred to by Oersted (1854). Turrill (1919), possibly using better magnification tools, made a careful description of the stellate or branched base of the egladular trichomes of *Mendoncia*, and was followed by Bremekamp (1938) and Rizzini (1948). This type of trichome (types 1 to 3) was found here in Neotropical and in some Paleotropical species. Leonard (1961) mistakenly called the branched base of these trichomes cystoliths in Neotropical *Mendoncia tetragona* Leonard and *M. caquetensis* Leonard. We verified that these are actually Type 3 trichomes as seen in *M. multiflora* Poepp. & Endl. (Fig. 1J).

Apart from the work of Rizzini (1948) and Profice (1988) on Neotropical species *Mendoncia*, there are no infrageneric classifications dealing with the whole genus. Some of the African species were formerly segregated into *Monachochlamys* Baker and *Afromendoncia* Gilg (Baker 1883; Lindau 1893; Moore 1906; Moore 1929), both of which were later subsummed into *Mendoncia* by Benoist (1944). Phylogenetic studies of subfamily Thunbergioideae (Borg *et al*. 2008; Borg 2012) indicate that *Mendoncia* is monophyletic, revealing a strong biogeographic segregation of species groups, suggesting two Paleotropical groups and one large Neotropical clade but with very low resolution.

The subgeneric classification proposed by Rizzini (1948) and followed by Profice (1988) for Neotropical *Mendoncia* species was based solely on their indumentum. Our analysis of this character shows that it may be variable within and between species, and thus it is not sufficient to segregate species groups. For instance, according to Profice (1988), *Mendoncia pilosa* belongs to subgenus *Dialyactinocithus* while *M. hoffmannseggiana* is placed in subgenus *Bremekampia* (Table 1). Taxonomic studies (FAdS PhD, in prep.) reveal that these taxa are very similar and often confused in herbaria, as they share subcylindric to cylindric branches, membranaceous leaf-blades with eucamptodromous venation, subfalcate bracteoles and red corollas. Moreover, the characterization offered by Profice (1988) for the subgenera overlaps in trichome basal-cell number between 2–6 in *Dialyactinocithus* and 2–4 in *Bremekampia*.

Our results show that glandular trichomes present in almost all surveyed species do not present enough discrete variation to be of taxonomic value, confirming Profice´s (1988) view, who discarded the sections defined by Rizzini (1948).

Trichome diversity in Paleotropical species

Dendritic trichomes without enlarged basal cells were observed in three of the African and Madagascan species. However, true stellate trichomes (*sensu* Wurdack 1986; Simpson 2010; Pinto-Silva *et al*. in press) are absent in the studied species. Breteler and Wieringa (2018) reported stellate to dendritic trichomes in Paleotropical *Mendoncia*, and Magnaghi and Daniel (2017) used this character in their identification key to separate *M. combretoides* and *M. phytocrenoides* from the other eight species that occur in Africa. However, their descriptions used the term “branched trichomes” rather than stellate or dendritic trichomes. Our detailed observations have not disclosed the presence of stellate trichomes, but rather a combination of stellate-based

Table 2. Types of trichomes found in sampled species of *Mendoncia*.

	Eglangular trichomes: number of basal cells in Types 1–3; presence/absence of Dendritic trichomes				Glangular trichomes
	TYPE 1 (5–)6–18 united basal cells radially disposed [number of cells]	TYPE 2 3–8 free basal cells number of cells [number of cells]	TYPE 3 2(–3) Y - and V - shaped free basal cells [number of cells]	TYPE 4 Dendritic trichomes	[number of cells]
Neotropical species					
M. bivalvis	8–14		—	—	2–4
M. blanchetiana	—	3–5	3	—	2–4
M. caquetensis	—	—	2–3	—	2–4
M. cardonae	—	4–5	—	—	2–4
M. gigas	—	3	2–3	—	2–4
M. glabra	—	3–5	3	—	2–4
M. hitchcockii	—	3	2–3	—	2–4
M. hoffmannseggiana	—	3–4	2–3	—	2–4
M. hymenophyllacea	5–6	—	—	—	2–4
M. killipii	6–8	—	—	—	–
M. klugii	6–10	—	—	—	2–4
M. lasiophyta	—	3–4	2–3	—	2–4
M. litoralis	—	3–4	3	—	2–4
M. meyeniana	—	3	2–3	—	3–4
M. mollis	6–8	—	—	—	4
M. multiflora	—	—	2	—	4
M. pedunculata	—	—	—	—	4
M. pilosa	—	3–8	3	—	2–4
M. puberula	5–6	—	—	—	2–4
M. retusa	—	—	2	—	2–4
M. riedeliana	—	3–4	—	—	3–4
M. rizziniana	8–16	—	—	—	2–4
M. sericea	—	–	2	—	4
M. smithii	—	3–4	3	—	2–4
M. sprucei	—	3–4	3	—	2–4
M. squamuligera	—	3–4	2–3	—	2–4
M. tonduzii	—	5–7	–	—	2
M. tovarensis	—	3–4	3	—	2–4
M. trichota	7–8	—	—	—	2–4
M. velloziana	—	3–4	3	—	2–4
Mendoncia sp.	—	3–4	3	—	4
African and Madagascan species					
M. camerounensis	12–14	—	—	+	2–4
M. combretoides	—	—	—	+	4
M. cowanii	14–16	—	—	—	2–4
M. decaryi	16–18	—	—	—	2–4
M. flagellaris	—	—	—	—	4
M. gilgiana	8–10	—	—	—	—
M. kely	14–16	—	—	—	4
M. lindaviana	—	—	—	—	2–4
M. phytocrenoides	6–8	—	—	+	4
M. vinciflora	6–8	—	—	—	—

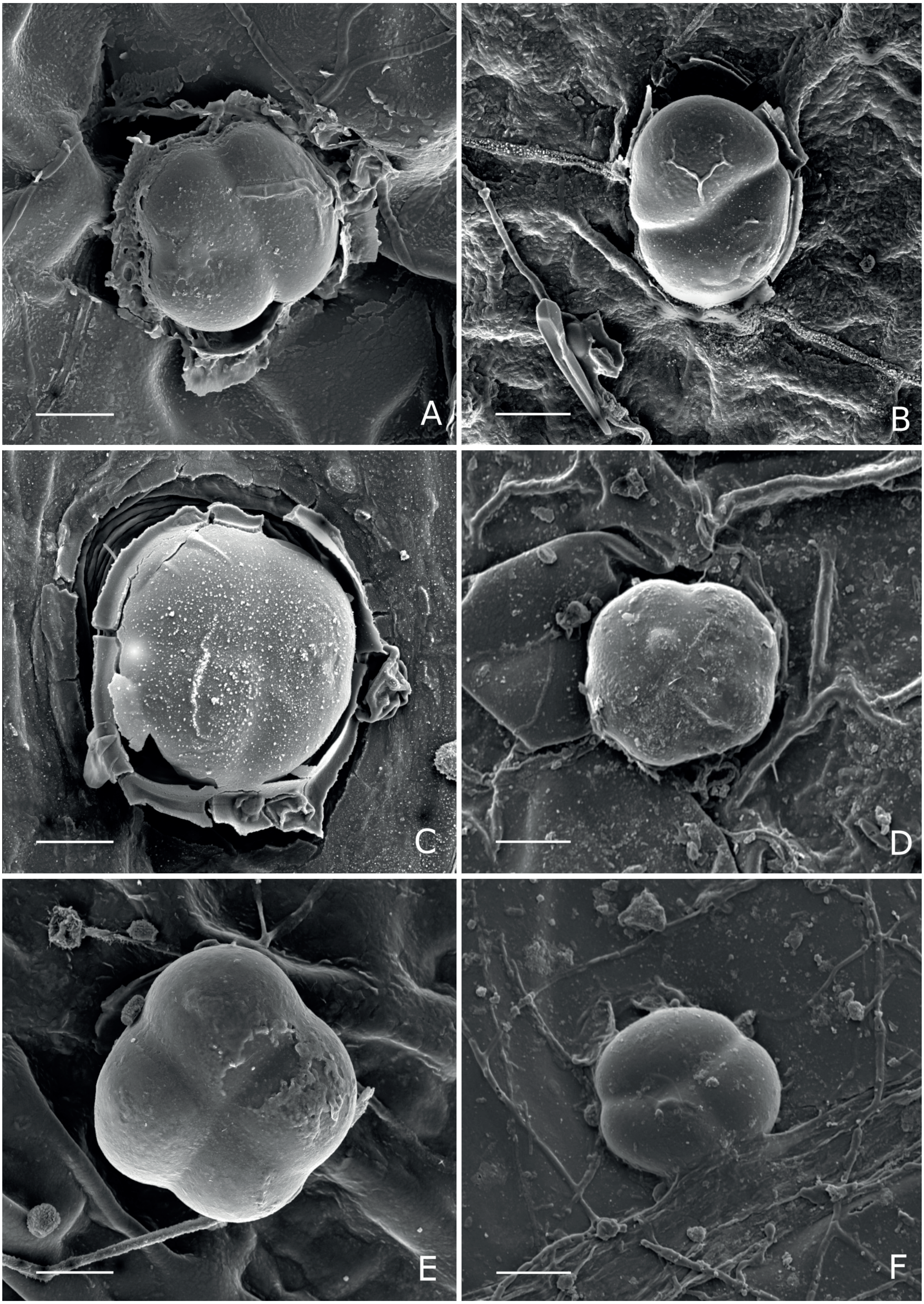

Figure 3. Types of glandular trichomes on the adaxial surface of the leaf-blade of *Mendoncia*. **A.** *M. riedeliana*. **B.** *M. blanchetiana*. **C.** *M. cowanii*. **D.** *M. puberula*. **E.** *M. rizziniana*. **F.** *Mendoncia* sp.. Scale bars: 10 µm (Specimens analysed in Table 1).

trichomes (Type 1) and dendritic trichomes without enlarged basal cells (Type 4) in two African species [*M. camerounensis* (Fig. 1L) and *M. phytocrenoides*]. One African species has only dendritic trichomes (*M. combretoides*). Trichome types 2 and 3 are so far restricted to Neotropical species. Interestingly, one of the Paleotropical clades recovered by Borg (2012) has species with dendritic trichomes (*M. combretoides* + *M. phytocrenoides*) suggesting the importance of this trichome type as a potential synapomorphy for this group.

Trichome basal cells in other plant groups

Despite the importance of the indumentum in the evolution of plant species, few plant groups have been surveyed regarding these structures and their taxonomic significance. A few examples include Melastomataceae (Wurdack 1986), megagenus *Croton* L. in the Euphorbiaceae (Webster *et al*. 1996; Feio *et al*. 2018; Pinto-Silva *et al*. in press) and Neotropical Bignoniaceae (Nogueira *et al*. 2013). Apart from the branched, basally stellate trichomes recorded for *Arabidopsis thaliana* Schur (Perazza *et al*. 1999), we were unable to find trichomes with well developed basal cells in other plant families. We highlight that types 2 and 3 appear to be restricted to Neotropical *Mendoncia*.

Conclusion

Mendoncia species lack true stellate trichomes. Whereas Paleotropical *Mendoncia* have dendritic trichomes, the Neotropical species have only asymmetric epidermal cells arranged radially around the base of uniseriate trichomes. These epidermal cells may be prolonged to a lesser (*M. bivalvis* – Fig. 1A), or a more dramatic (*M. meyeniana* – Fig. 1I) extent. Characters such as number and length of radiated epidermal cells have shown some overlap within the same species and the different types were not easily distinguished between morphologically similar species. Therefore, the use of trichome characters in isolation is not recommended for subgeneric classification of Neotropical *Mendoncia*. Neotropical *Mendoncia* trichomes with well developed, bilaterally oriented epidermal cells appear to be unique to this group, without equal in any other plant family.

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Authors contributions

Fabio Araújo da Silva: collected, prepared material and carried out the SEM imaging, wrote and edited the manuscript.
Daniela C. Zappi: conceived the study and sampled African species at RBG, Kew, co-wrote and edited the manuscript.
Ana Carla Feio: advised on techniques, edited the manuscript.
Cíntia Kameyama: edited the manuscript.
Ranielle de Araújo Mendonça: prepared the light microscopy slides and photographed the samples.

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