

Trichome complement of *Turnera* and *Piriqueta* (Turneraceae)

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The indumentum of *Piriqueta* and *Turnera* is made up of nine different types of trichomes, which broadly can be divided into glandular and non-glandular. Taking into account foot shape, head size and pedicle size, five variants of glandular trichomes are recognized: microcapitate, stipitate-capitate, sessile-capitate and setiform. The non-glandular trichomes can be simple (unicellular or pluricellular-uniseriate), stellate or porrect-stellate. The setiform glandular hairs are present in most species of *Piriqueta*. Simple unicellular hairs are the most widespread type, frequently being found in combination with other trichomes. Stellate trichomes show a restricted distribution in both genera. Within *Piriqueta*, section *Africana* has only simple trichomes, whereas section *Piriqueta* has also porrect-stellate trichomes; groups of species can be set up according to the presence and type of glandular trichomes. Within *Turnera* the stipitate-capitate trichomes are exclusive to series *Papilliferae*; sessile-capitate trichomes are found in series *Microphyllae*, *Annulares* and in some species of *Salicifoliae*; clavate trichomes are found only in series *Turnera*; setiform glandular hairs are exclusive to *T. collothricha*, whereas the microcapitate trichomes are widely distributed. © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, 143, 000–000.

ADDITIONAL KEYWORDS: epidermis – glandular hairs – leaf – non-glandular – ontogeny – systematic anatomy – vegetative anatomy.

INTRODUCTION

Turneraceae is a tropical and subtropical family, with ten genera. The genus *Turnera* includes about 100 species in America and two in Africa, gathered in nine series, whereas *Piriqueta* has 44 species in America and one in Africa (Arbo, 1995, 1997, 2000).

The indumentum was considered by all those authors who have studied the family. Urban (1883) described six different types of trichomes in his monograph; he was aware of the systematic value of the trichomes, using them to differentiate the genera of Turneraceae, and to separate sections or series within genera.

Berger (1919) described *Piriqueta* with stellate and glandular trichomes, and he placed *Turnera* within the genera that rarely have stellate trichomes and never glandular trichomes; however, both types of trichomes were described and illustrated in both genera.

Trichomes are one of the key characters used to differentiate *Piriqueta* and *Turnera*, the former having simple, porrect-stellate and setiform glandular trichomes (Arbo, 1995), whereas *Turnera* has simple, sometimes stellate, hairs and different types of glandular trichomes. The presence and distribution of the main trichome types was described in taxonomic papers (Arbo, 1981, 1985, 1987, 1993, 1997, 2000). An anatomical study of floral indumentum was made in *Piriqueta racemosa*, *Turnera joelii* and *T. hassleriana* (Gonzalez, 1993). Nevertheless, none of these studies had the structure of the trichomes as a primary focus of the work.

It is against this background that the present study was begun. It aims to provide a detailed description of the anatomy and ontogeny of the trichome complement of *Piriqueta* and *Turnera*, supplying information to elucidate phylogenetic relationships.

MATERIAL AND METHODS

The present research was carried out mainly on material collected during field trips, fixed in FAA (*) or col-

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lected and maintained under cultivation (#). The scarce material that was taken from herbarium specimens (@) was boiled gently before fixation. Voucher specimens are deposited at the Herbarium of the Instituto de Botánica del Nordeste, Corrientes, Argentina (CTES), and they are listed in the Appendix.

Leaves at different stages of development were embedded in paraffin, and sections 10–15 µm thick were cut, stained with a combination of safranin and alcian blue (Luque, Sousa & Kraus, 1996) and mounted in synthetic Canadian balsam. A camera lucida was used for the drawings. For SEM studies specimens were dehydrated in an acetone series, critical-point dried, coated with gold in a sputter coater and observed under a JEOL 5800 LV scanning electron microscope.

RESULTS

The authors who have studied the general structure of trichomes have given different definitions to their components. In this paper the following terms are used: the *foot* is the portion of the trichome placed between the other epidermal cells; *accessory cells* are the cells adjacent to the foot that are different from the ground epidermal cells; *body* is the segment of the trichome that stands out of the epidermis surface (Uphof, 1962). In the glandular trichomes the body can be differentiated in a *pedicle* and an apical gland (Font Quer, 1977), and a portion usually called *head* (Metcalfe & Chalk, 1957; Payne, 1978; Strasburger, 1986). When the subepidermal cells proliferate, the structure is not a trichome but an emergence; in this case the bottom is called *pedestal* (Uphof, 1962).

The indumentum of *Piriqueta* and *Turnera* is made up of nine different types of trichomes, which can be divided into glandular and non-glandular according to whether they are excretory or not.

- Glandular: microcapitate, clavate, stipitate-capitate, sessile-capitate and setiform.
- Non-glandular: simple, unicellular or pluricellular-uniseriate, stellate and porrect-stellate.

GLANDULAR TRICHOMES

They are pluricellular, with a foot and a body, which is composed of a pedicle and a secretory head.

A similar ontogenetic sequence was observed in all the glandular trichomes; they begin with the differentiation of an initial cell with round apex, which projects above the surface. This cell undergoes periclinal or anticlinal divisions, depending on the type of trichome. Once the trichome growth is completed, only the head cells show dense, granular cytoplasm, distinctive of secretory cells; the cytoplasm of the pedicle cells is transparent, and the thickness of the walls is

lightly increased, as is the cuticle covering the foot and pedicle. Old trichomes show the head cells collapsed covered by the intact cuticle, so the secretion is probably transcuticular in most cases.

In some species glandular trichomes are seldom present in adult leaves or stems, but they are generally found in the buds. In this case the trichomes are deciduous and their cells have thin walls.

Five variants of glandular trichomes were found taking into account foot shape, head size and pedicle length.

Microcapitate

These trichomes have a uni-bicellular foot and a bi-triseriate pedicle 5–10 cells high; the head is composed of 1–3 cells that frequently collapse at maturity, under the intact cuticle. The foot has an equal or smaller diameter than the trichome body, and the head can be of equal, smaller or slightly larger diameter than the pedicle. According to these characteristics the shape of the trichome varies among the different species: cylindrical, club-shaped or bottle-shaped (Figs 1, 15–17).

A smooth cuticle covers the whole trichome. Sometimes, while observing the trichome with SEM, a prominent line produced by the cuticle around the base of the head stands out (Figs 1, 3 mic).

Ontogeny. This starts with the enlargement of the initial cell, the cytoplasm becomes dense and stains strongly, it shows many small vacuoles, and its nucleus is larger than those of the neighbouring epidermal cells. This cell divides obliquely (Fig. 12). The basal cell undergoes an anticlinal division to develop into the trichome foot. The apical cell goes through several oblique and periclinal divisions (Figs 13, 14); the intermediate cells develop the pedicle and the apical cell or cells will form the trichome head (Figs 15–17).

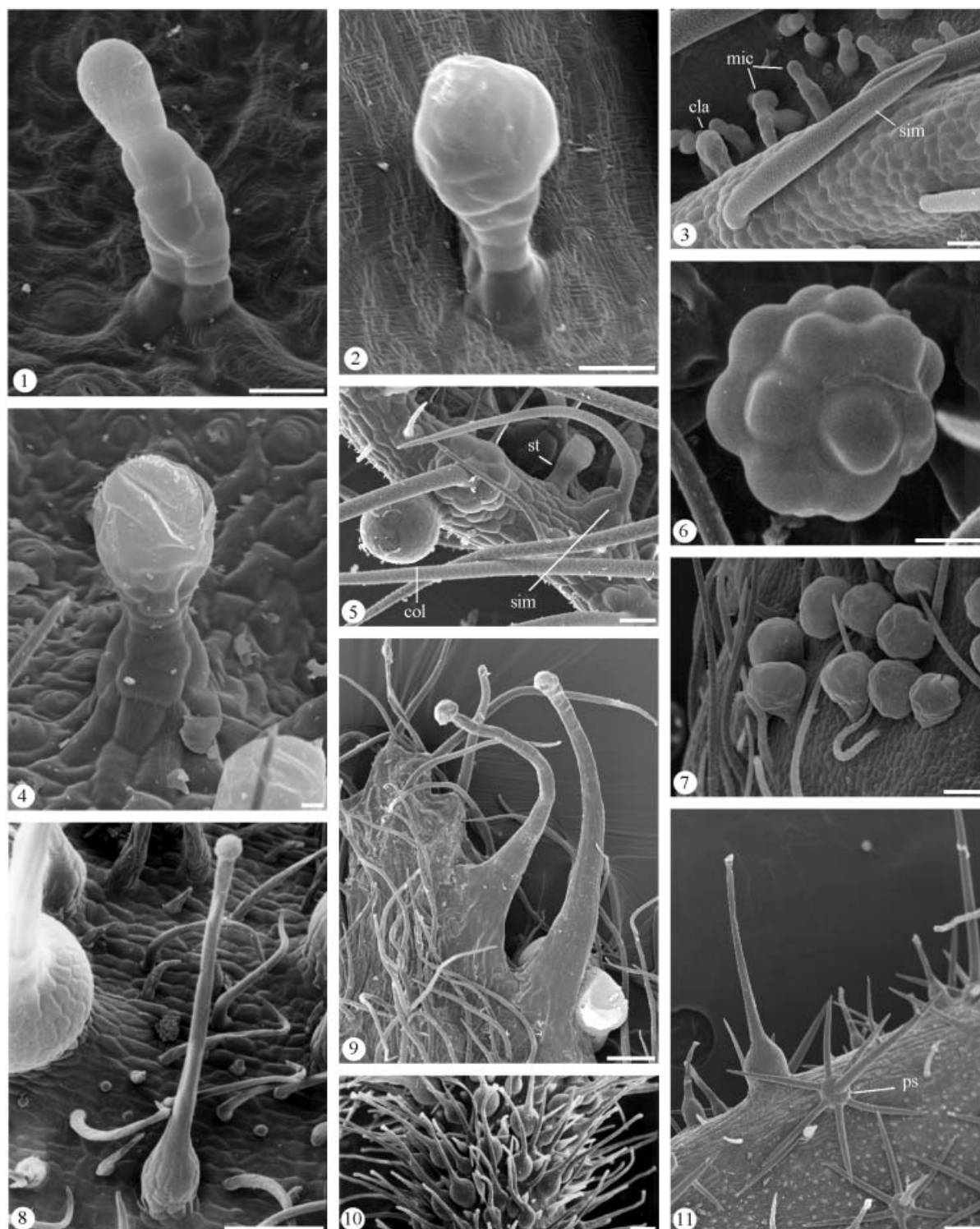
Clavate

These trichomes have a bicellular foot, a uni-triseriate pedicle 2–4 cells high and a multicellular club-shaped head, formed by 6–9 radial cells located at the pedicle apex, covered by a thin cuticle, lightly thickened at the trichome base. The foot and pedicle are thinner than the head (Figs 2, 3, cla; Fig. 23).

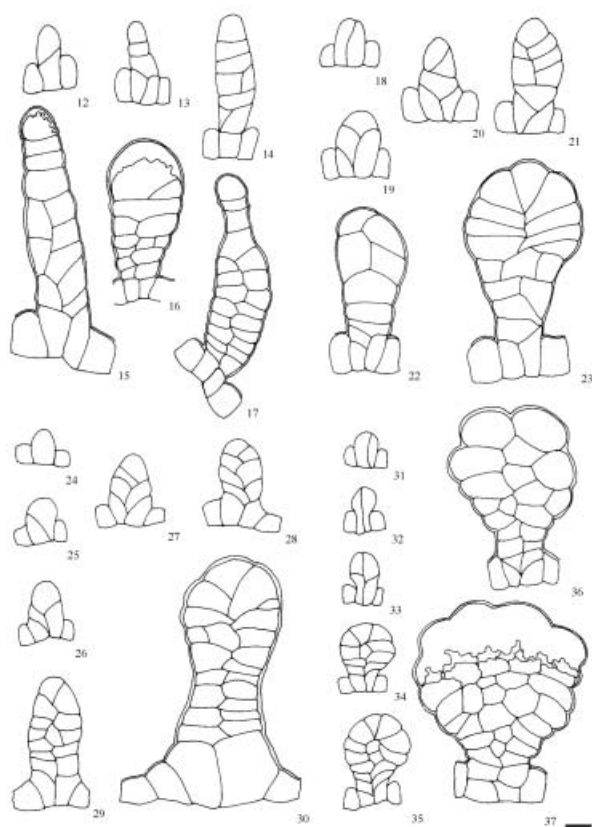
Ontogeny. The initial cell undergoes first an anticlinal division (Fig. 18) and then forms the foot and pedicle by oblique divisions (Figs 19–21). The last divisions are radial to develop the head (Figs 22, 23).

Stipitate-capitate

These have a trapezoidal foot, formed by 3–5 cells frequently containing tannin, taller than the ground epidermal cells; the pedicle is 2–4 seriate, of a smaller



Figures 1– 11. SEM photographs of glandular trichomes. Figs 1–3. *T. joelii*. Fig. 1. Microcapitate trichome. Scale bar = 10 µm. Fig. 2. Clavate trichome. Scale bar = 10 µm. Fig. 3. Adaxial side of the leaf. Scale bar = 50 µm. Figs 4, 5. *T. chamaedrifolia*. Fig. 4. Stipitate-capitate trichome. Scale bar = 10 µm. Fig. 5. Leaf margin. Scale bar = 50 µm. Fig. 6. Sessile-capitate trichome of *T. diffusa*. Scale bar = 20 µm. Fig. 7. Sessile-capitate trichome of *T. annularis*. Scale bar = 50 µm. Figs 8–11. Setiform trichome. Figs 8, 10, 11. *P. morongii*. Scale bars = 0.1 mm. Fig. 9. *T. colotricha*. Scale bar = 0.1 mm. Abbreviations: cla: clavate, col: colleter, mic: microcapitate, ps: porrect-stellate, sim: simple trichome.



Figures 12–37. Ontogeny of glandular trichomes. Scale bar = 10 μ m. Figs 12–17. Microcapitate trichome. Figs 12–15. *T. velutina*. Fig. 16. *T. melochioides*. Fig. 17. *T. joelii*. Figs 18–23. Clavate trichome of *T. velutina*. Figs 24–30. Stipitate-capitate trichome of *T. chamaedrifolia*. Figs 31–37. Sessile-capitate trichome of *T. diffusa*.

diameter than the foot, and it becomes gradually thicker towards the apex to form the head, where the cells are radial (Fig. 30), so that 8–10 cells can be seen in the head CS. When observed with SEM, the contour of the head cells with a smooth cuticle is visible (Figs 4, 5 st).

Ontogeny. The initial cell grows longer and becomes divided obliquely (Figs 24, 25); both daughter cells divide again in the same way giving four cells; the following divisions always occur in the apical cells, so that the resulting cells stand imbricate (Figs 26–28). The head is formed by radial divisions of apical cells (Figs 29, 30). The foot cells accumulate tannins (especially in the trichomes located on the abaxial epidermis of the leaves) and they increase in size, developing a projection on top of which the pedicle is placed. At maturity, the head cells collapse and their remains can be seen on top of the pedicle cells. The foot cells and the pedicle do not degenerate, looking intact even in old trichomes.

Sessile-capitate

These trichomes have a biserial narrow foot; the brief pedicle is 1–2 cells high, bi-triseriate, and supports a prominent pluricellular head, where the more or less globe-shaped cells are arranged in no perceptible order (Figs 6, 7); its distal portion can have 15–18 cells in CS. At maturity, the head cells collapse progressively from the apex towards the base, until they are wrinkled against the pedicle. The head remains as a cuticular bag, which inherits the preceding cellular contours, and the cuticle is stretched but intact and completely smooth (Figs 6, 37); this can be seen in dried and also in fixed material. When observed with SEM the shape of the head cells can be discerned (Fig. 6).

Ontogeny. The initial cell becomes longer and suffers an anticlinal division (Figs 31, 32), and each daughter cell becomes oblique or transversely divided. The brief pedicle is formed at the base by periclinal divisions, and the head at the apex by horizontal, vertical and oblique divisions (Figs 33–37).

Setiform

These trichomes have a multicellular swollen pedestal, a biserial pedicle and a generally unicellular small head (Figs 8–10). Secretion can be noteworthy, such that some species are sticky. These trichomes are the only ones in which frequent rupture of the cuticle and disruption of the head cells were observed (Fig. 11).

Ontogeny. They start from one or two initial cells that grow longer; then by repetitive oblique divisions they develop a swelling (Fig. 58) where the cells overlap (Figs 59, 60). The apical cells become longer and by means of oblique and longitudinal divisions develop the long narrow pedicle (Figs 61, 62), and the distal cell becomes the secreting unicellular head (Fig. 63). Continued divisions in different planes in the cells of the basal portion form the trichome's swollen pedestal. The size of these structures is extremely variable, the smaller ones being trichomes whereas the larger ones are emergences because the subepidermal cells also participate in the origin of the pedestal.

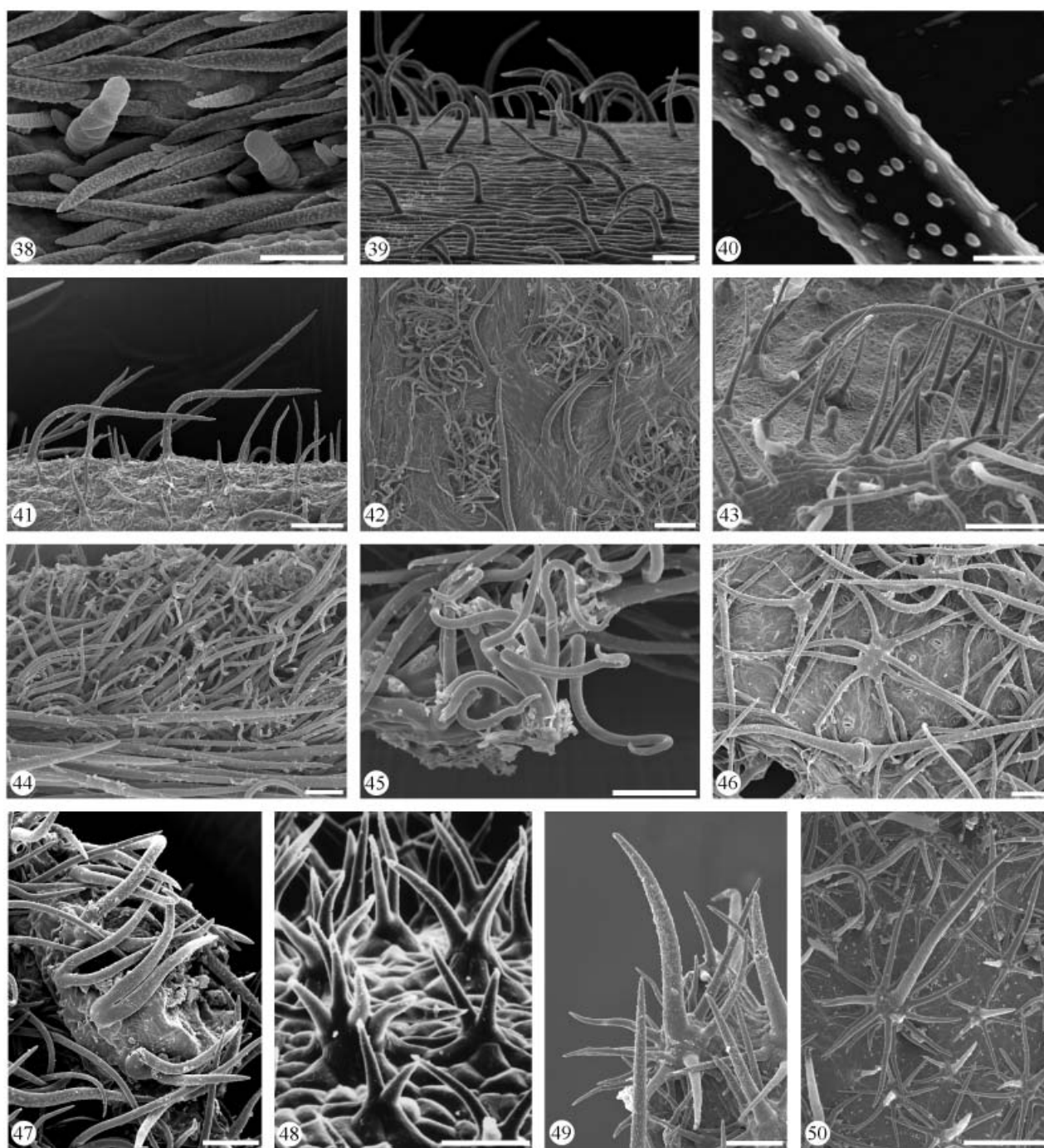
NON-GLANDULAR TRICHOMES

They can be simple or stellate, with smooth or ornamented walls, generally lignified; at maturity they generally lack protoplasm. The following types are recognized: simple, stellate and porrect-stellate.

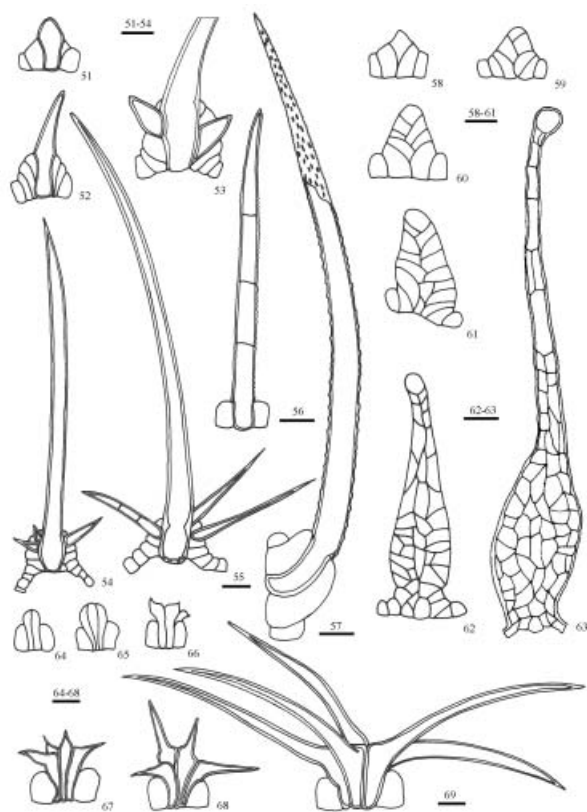
Simple

They can be unicellular or pluricellular-uniseriate.

Unicellular. Each hair is formed by one cell with thick, lignified, smooth or ornamented walls (Figs 38–43,



Figures 38–50. SEM photographs of non-glandular trichomes. Fig. 38. *T. stenophylla*, adaxial side of the leaf. Scale bar = 50 μ m. Figs 39, 40. *T. panamensis*, simple unicellular trichomes. Fig. 40. Detail of the ornamented wall. Scale bar = 1000 μ m. Fig. 41. *T. sidoides* ssp. *carnea*, short and long simple trichomes. Scale bar = 100 μ m. Fig. 42. *T. discolor*, simple and crisped trichomes. Scale bar = 100 μ m. Fig. 43. *T. sidoides* ssp. *integrifolia*, adaxial side of leaf. Scale bar = 0.25 mm. Figs 44, 45. *T. revoluta*. Fig. 44. Adaxial side of the leaf with simple and stellate crisped trichomes. Scale bar = 20 μ m. Fig. 45. Stellate trichomes. Scale bar = 50 μ m. Fig. 46. *T. sidoides* ssp. *sidoides*, stellate trichomes on adaxial side of leaf. Scale bar = 50 μ m. Figs 47, 48. *T. blanchetiana*. Fig. 47. Two-armed trichomes on extrafloral nectary. Scale bar = 100 μ m. Fig. 48. Stellate trichomes 2–5-armed on adaxial side of leaf. Scale bar = 50 μ m. Figs 49, 50. Porrect-stellate trichomes. Fig. 49. *P. taubatensis*. Scale bar = 100 μ m. Fig. 50. *P. sidifolia*. Scale bar = 0.25 mm.



Figures 51–69. Ontogeny of non-glandular trichomes. Figs 51–55. Porrect-stellate trichomes of *P. racemosa*. Scale bars in Figs 51–54 = 10 µm, in Fig. 55 = 50 µm. Fig. 56. Simple pluricellular trichome of *P. racemosa*. Scale bar = 50 µm. Fig. 57. Simple unicellular trichome of *T. weddelliana*. Scale bar = 50 µm. Figs 58–61. Setiform trichomes of *P. nanuzae*. Scale bars in Figs 58–61 = 10 µm, in Figs 62, 63 = 50 µm. Figs 64–69. Stellate trichomes of *T. blanchetiana*. Scale bars in Figs 64–68 = 10 µm, in Fig. 69 = 50 µm.

57). These trichomes can be straight, erect or appressed (Fig. 3 sim), antrorse, i.e. curved towards the apex of the organ (Figs 39, 41) or crisped (Fig. 42). Two layers of simple trichomes are found on different organs of many species, the hairs being different in length and degree of curvature (Fig. 41). Arbo (1985, 1997) described them as short and long trichomes, the former may being straight or crisped and the latter erect or antrorse. The base of the long trichomes is frequently surrounded by a rosette of accessory cells with tannins (Fig. 5 sim; Figs 43, 57).

Ontogeny. The initial cell grows longer; the apex becomes thinner, and it curves away in antrorse trichomes; the nucleus increases its volume notably. Accessory cells enlarge slightly and accumulate tannins.

Pluricellular-uniseriate. Each hair is a string of 2–5 cells with narrow, frequently ornamented walls (Fig. 56). Most are found in young organs; they are very delicate and easily detached.

Stellate

They are sessile, with 2–8 arms made up by a single cell with thick smooth walls (Figs 45–48, 69). The foot comprises the basal portion of the arm cells.

Ontogeny. The initial cell becomes longer, its distal end is slightly discoidal, flattened, and it becomes longitudinally divided in as many cells as arms in the developed trichome (Figs 64, 65). Each arm begins growing, the wall gets thicker while the apex forms a sharp tip (Figs 66–68).

Porrect-stellate

They differ from the stellate hairs in having a central arm greatly enlarged, surrounded by the other arms, sometimes arranged like a crown; each arm is unicellular or pluricellular-uniseriate, with lignified walls (Fig. 11 ps; Figs 49, 50). Some species show hairs with a very low number of short arms, sometimes only one.

Frequently they have accessory cells taller than the ground epidermal cells, which develop into a protrusion on which the trichome is placed (Fig. 55).

Ontogeny. An epidermal cell increases its height; its distal portion grows quickly and sharpens, forming the trichome's central arm (Figs 51, 52). The cells that surround it also grow and undergo anticlinal divisions; some of these will lengthen forming the lateral arms (Figs 53–55), which in some species can be divided in several cells (Fig. 55).

DISTRIBUTION AND TAXONOMIC CORRELATION

The distribution of the different trichomes in the studied organs of each species is shown in Table 1. Observations were made mainly on leaves, stem, calyx (floral tube) and ovary.

Piriqueta

This genus shows three types of glandular trichomes: clavate, microcapitate and setiform. The clavate and microcapitate trichomes are found in vegetative organs like stem, leaves, floral peduncle and pedicel. Setiform glandular trichomes, by contrast, are found even on the calyx abaxial epidermis and on the external surface of the ovary, close to simple unicellular trichomes. *P. dentata* is the only species that does not show setiform glandular hairs in the ovary. *P. capensis* is the only species of this genus without glandular trichomes in the analysed leaves (herbarium material).

Table 1. Trichome types and distribution among *Piriqueta* and *Turnera*.

	Glandular					Non-glandular			
	Clavate	Micro-capitate	Setiform	Stipitate-capitate	Sessile-capitate	Simple			Porrect-Stellate
						Unicellular	Pluricellular	Stellate	
PIRIQUETA									
<i>P. capensis</i>						H			
<i>P. cistoides</i>		H,T				O,T			T,H,K
<i>P. racemosa</i>		H,T				O,T	T		T,H,K
<i>P. carnea</i>			H,T,K,O			T,H,O			T,H,K
<i>P. dentata</i>			H,T,K			T,K,O			T,H,K
<i>P. densiflora</i>			T,K,H,O			T,O			T,H,K
<i>P. duaricana</i>			H,T,K,O			T,O	T		T,H,K
<i>P. guianensis</i>			T,H,K,O			T,O	T		T,H,K
<i>P. morongii</i>			T,H,K,O			T,O			T,H,K
<i>P. nanuzae</i>			T,H,K,O			T,O			T,H,K
<i>P. ochroleuca</i>			T,H,K,O			T,O			T,H,K
<i>P. sidifolia</i>			O,H,T,K			H,T,O	T	H	T,H,K
<i>P. suborbicularis</i>	T,H					T,O			T,H,K
<i>P. taubatensis</i>	T,H					T,O			T,H,K
TURNERA									
Annulares									
<i>T. odorata</i>					H	H			
<i>T. annularis</i>					H	H			
Anomalae									
<i>T. bahiensis</i>		H,T,O				T,K,O,H			
<i>T. blanchetiana</i>		H,T,O						H,K,T	
<i>T. cearensis</i>		H,O				K,O		H,K,T	
Capitatae									
<i>T. capitata</i>		H				H,O,T,K			
<i>T. maracasana</i>		H				H			
Leiocarpae									
<i>T. coccinea</i>		H,O,K,T				H,K,O,T			
<i>T. discolor</i>		H				H			
<i>T. genistoides</i>		H				H			
<i>T. hassleriana</i>		O,H,K,T				H,T,K,O			
<i>T. melochioides</i>		H,K,T,O				H,T,K,O			
<i>T. nervosa</i>		H,K,T,O				H,T,K,O			
<i>T. oblongifolia</i>		H				H,T,K,O			
<i>T. opifera</i>		H,K,T,O				H,K,T,O			
<i>T. pumilea</i>		H,K,T,O				H,T,K,O			
<i>T. revoluta</i>		H				H		H	
<i>T. sidoides</i>									H,T,O,K
<i> carnea</i>		H,T							H,T,O,K
<i> integrifolia</i>		H,T							H,T,O,K
<i> holosericea</i>		H,T							H,T,O,K
<i> pinnatifida</i>									H,T,O,K
<i> sidoides</i>									
<i>T. coccinea</i>						H			
Microphyllae									
<i>T. diffusa</i>					H,T,O,K	H,T,K,O			
<i>T. collotricha</i>			H,K			H,T,K,O			
<i>T. hebetata</i>					H,T,O,K	H,T,O,K			
Papilliferae									
<i>T. caatingana</i>				H,T,O,K		H,T,O,K			
<i>T. chamaedrifolia</i>				H,T,O,K		H,T,O,K			
Salicifoliae									
<i>T. brasiliensis</i>					T,K	H,T,O,K			

Table 1. Continued

	Glandular					Non-glandular			
	Clavate	Micro-capitate	Setiform	Stipitate-capitate	Sessile-capitate	Simple			Porrect-Stellate
						Unicellular	Pluricellular	Stellate	
<i>T. panamensis</i>						H,T,O,K	T		
<i>T. steyermarkii</i>						H,T,O,K			
<i>T. weddelliana</i>		H,T,O,K				H,T,O,K			
Stenodietyae									
<i>T. acuta</i>		H				H,T,K,O			
Turnera									
<i>T. aurelii</i>		H,T,O				H			
<i>T. cuneiformis</i>		H,T				H			
<i>T. grandidentata</i>	H,T	H,T,K				H,T,K			
<i>T. grandiflora</i>	H,T	H,T,K				H,T,K			
<i>T. hermannioides</i>	H	H,K,T,O				T,O		H,T,K,O	
<i>T. joelii</i>	H	H,K,T,O				H,T,K,O			
<i>T. simulans</i>	H,T	O,K,H				H,T,K,O			
<i>T. stenophylla</i>	H,T	O,K				H,T,K,O			
<i>T. ulmifolia</i>		H, T				H,T,O,K			
<i>T. velutina</i>	H,T	H,T,K,O				H,T,K,O			

Non-glandular trichomes: many species share porrect-stellate and simple unicellular trichomes in vegetative and reproductive organs. The occurrence and distribution of these trichomes is described in the general part of the monograph of the genus and in the morphological descriptions (Arbo, 1995).

Interestingly, the simple trichomes found in vegetative organs are unicellular, erect, inconspicuous and slightly crisped, with smooth or ornamented walls; the ones located on the ovary external surface are antrorse, with a thick smooth wall. Simple pluricellular-uniseriate trichomes, with walls relatively thin and ornamented, were observed only in the stem of some species (Table 1).

In *P. racemosa* unicellular lateral arms with smooth walls and pluricellular-uniseriate ones with ornamented walls were observed in the same porrect-stellate trichome (Fig. 55).

Turnera

Series Anomalaе. Microcapitate trichomes were found in all the analysed species; they are located mainly in the adaxial epidermis of the leaves on the veins or near them. They were not found in the calyx, and they were very abundant on the ovary of *T. bahiensis*.

T. cearensis and *T. blanchetiana* have stellate trichomes, small and very abundant in the latter species, with 2–5 arms (Figs 47, 48). The ovary indumentum in *T. cearensis* and *T. bahiensis* is composed of microcapitate and simple unicellular trichomes, whereas in

T. blanchetiana there are microcapitate and stellate trichomes.

In *T. bahiensis* and *T. cearensis*, simple trichomes were observed on the adaxial epidermis at the petals midvein base, and on the basal portion of the styles.

Series Annulares. *T. odourata* and *T. annularis* show sessile-capitate glandular trichomes, plentiful on the abaxial epidermis of the leaf, and on the two lower thirds of the ovary in the latter species (Fig. 7). Simple unicellular trichomes are found on both sides of the leaves.

Series Capitataе. In *T. capitata*, simple unicellular trichomes were observed on the entire plant whereas microcapitate trichomes were located only on the abaxial epidermis of leaves. In *T. maracasana*, leaves are glabrescent; in young leaves microcapitate and simple unicellular trichomes were observed. Adult leaves of *T. marmorata* are glabrous.

Series Leiocarpae. *T. sidoides* is a taxon with five subspecies, which have simple unicellular trichomes, frequently arranged in two layers: short crisped layers and long structurally similar layers, erect, antrorse or appressed (Fig. 41). In the ssp. *sidoides* the short trichomes are stellate (Fig. 46), whereas the ssp. *integri-folia* generally has only long erect or curved simple hairs (Arbo, 1985). Microcapitate glandular hairs were observed occasionally on the abaxial face of foliar pri-

mordia (Fig. 43). They were not observed in the ssp. *sidoides* and *pinnatifida*.

The other species of this series have microcapitate and simple unicellular trichomes distributed over the whole plant.

Turnera discolor also presents two types of simple trichomes, long straight trichomes on the veins and crisped trichomes on the areoles (Fig. 42). *T. revoluta* has ericoid leaves with glabrous adaxial epidermis; trichomes are restricted to the abaxial epidermis, there are simple straight hairs on the midvein, and crisped simple and stellate trichomes in the grooves between the midvein and the blade's revolute margins (Figs 44, 45).

Series Microphyllae. *T. diffusa* (Fig. 6) and *T. hebeptala* show sessile-capitate glandular trichomes and simple unicellular ones on the entire plant. In *T. hebeptala* there are simple hairs even on the adaxial face of petals. *T. colotracha* is the only species of the genus that shows setiform glandular hairs (Fig. 9).

Series Papilliferae. This series has only two species, which are characterized by the presence of stipitate-capitate trichomes (Figs 4, 5). They have also simple unicellular trichomes on the whole plant.

Series Salicifoliae. *T. brasiliensis* has sessile-capitate trichomes; in *T. weddelliana* microcapitate trichomes were observed; *T. steyermarkii* and *T. panamensis* do not have glandular trichomes in adult organs, only microcapitate trichomes in very young foliar primordia. All these species show also simple unicellular trichomes (Figs 39, 40).

Simple pluricellular-uniseriate trichomes with thin walls were observed in the stem of *T. panamensis*. This species also shows trichomes at the base of the inner face of the ovary; they are simple unicellular and pluricellular-uniseriate hairs with very thin walls.

Series Stenodictyae. The adult leaves of *T. aurantiaca* and *T. castilloi* are glabrous. The observed material of *T. acuta* shows microcapitate and simple unicellular trichomes on the leaves and only simple ones on the floral tube.

Series Turnera. Almost all the species have microcapitate and/or clavate trichomes (Figs 1–3, 15–17, 23); the latter are not very frequent and they are found particularly on young stems and abaxial epidermis of leaves. Microcapitate trichomes are more frequent and are scattered over the entire plant.

The ovary's indumentum is composed of simple unicellular and microcapitate trichomes; clavate hairs were not observed in any of the analysed species.

Turnera hermannioides is the only species of the series with stellate trichomes; it also has two-armed trichomes at the extrafloral nectaries border. All the other species have simple unicellular trichomes. Two layers of simple unicellular trichomes can be observed on the leaves of *T. aurelii* and *T. orientalis*; long trichomes are 0.6–1 mm long and possess a rosette of accessory cells with tannins, short trichomes are not longer than 0.3 mm, they lack accessory cells and can be slightly crisped.

T. hermannioides and *T. stenophylla* show a particular feature: they have small simple unicellular trichomes with thick lignified walls at the locule's base, on the inner face of the ovary.

DISCUSSION

Urban (1883) described two sets of trichomes: the tector hairs (covering hairs) and the glandular ones. Among the former he mentioned simple unicellular, simple articulated and stellate trichomes, and amid the glandular trichomes, he mentioned secretory setae, multicellular round papillae and stipitate hairs.

Berger (1919) described the same categories within the tector hairs, and he added clavate hairs among the secretory ones.

GLANDULAR TRICHOMES

The name used by Urban (1883) for the trichomes of *T. chamaedrifolia* is kept taking into account that the term 'stipitate' clearly describes their shape. This was the main character used by Urban (1883) to distinguish series *Papilliferae* from the other series of *Turnera*. Berger (1919) described the hairs of *T. chamaedrifolia* with a short pluricellular pedicle subtending a large unicellular spherical head, but in disagreement with this description, in his drawings the head shows several cells. He described the glandular hairs of *T. diffusa* as similar to those of *T. chamaedrifolia*, with a large unicellular head; however, in the figures the head is formed by one to three cells.

Theobald, Krahulik & Rollins (1979) described and illustrated a trichome of *T. diffusa* with pluricellular pedicle and unicellular head. Urban (1883) named them multicellular round papillae with a shape similar to that of the *Rubus*' fruit and Berger (1919) called them pluricellular papillae. According to our analysis the trichomes of this species have a pluricellular head; at maturity the cells collapse and shrink while the cuticle remains intact. These trichomes are called sessile-capitate following Arbo (1997). They may be found in the series *Microphyllae* and *Annulares* and also in some species of the series *Salicifoliae*.

Berger (1919) cited clavate trichomes for *P. racemosa*, *P. caroliniana*, *T. ulmifolia*, *T. velutina*,

T. genistoides and *T. weddelliana*. Arbo (1995) found them in *P. suborbicularis* and *P. taubatensis*. In some species of the series *Turnera* these trichomes are found together with microcapitate ones.

Most species of *Piriqueta* have setiform glandular trichomes; their presence or absence is generally a useful taxonomic character (Arbo, 1995). They may be strictly epidermal or may include subepidermal tissues in which case they must be considered as emergences. Urban (1883) called them secretory setae sometimes with bulbous base, and quotes them also for *Wormskioldia* and *Streptopetalum*. The anatomy of this type of trichome was studied by Berger (1919) in species of the three genera. Arbo (1981, 2000) found setiform glandular hairs, similar to those of *Piriqueta*, in *Turnera colotracha* Arbo.

The term microcapitate was selected for the remaining glandular trichomes, which are characterized by the presence of a small head, even though they show different shapes. They are the most frequent glandular trichomes in *Turnera*, and may be found in the stem, leaves, calyx and ovary; in *Piriqueta* they were found only in leaves and young stems of *P. racemosa* and *P. cistoides*. Berger (1919) recognized these trichomes as secretory hairs and illustrated them in several species; he named them as pluricellular papillae in *T. melochioides* and as clavate hairs in *P. racemosa*.

According to Urban (1883), *T. melochioides* and *T. opifera* of the series *Leiocarpae* have sessile-capitate trichomes, but we found that the glandular hairs of these species belong to the microcapitate type, with a short pedicle.

All the glandular trichomes analysed have acropetal development. According to Uphof (1962) this sequence is the most widespread in capitate glandular trichomes.

The secretion is transcuticular in stipitate-capitate, clavate, sessile-capitate and microcapitate trichomes, whereas in setiform trichomes it occurs by means of the rupture of the cuticle of the head cells. In the first group the head's shape is preserved after the secretion takes place, a feature that was observed previously in glandular peltate trichomes of *Compositae* and *Labiatae* (Uphof, 1962).

The taxonomic value of these appendages in the systematic treatment of *Turneraceae* is undeniable, at generic, intrageneric and specific levels. Within *Piriqueta*, section *Africana* has only simple trichomes, whereas section *Piriqueta* has also porrect-stellate trichomes (Arbo, 1995). Groups of species can be set according to the presence and type of glandular trichomes:

- *P. capensis* lack of glandular hairs
- *P. racemosa* and *P. cistoides* microcapitate hairs

- *P. suborbicularis* and *P. taubatensis* clavate hairs
- remaining species setiform hairs

Within *Turnera* the stipitate-capitate trichomes are exclusive to series *Papilliferae*; sessile-capitate ones are found in series *Microphyllae*, *Annulares* and in some species of *Salicifoliae*; clavate trichomes are found only in series *Turnera*; setiform glandular hairs are exclusive to *T. colotracha*, whereas the microcapitate trichomes are widely distributed.

Glandular trichomes are a useful taxonomic character in these genera because most species show just one type of trichome. Only some species of series *Turnera* have microcapitate hairs together with clavate trichomes.

NON-GLANDULAR TRICHOMES

Simple unicellular trichomes are the most widespread type in the family; they are found nearly in the whole plant, in combination with other trichomes. In some species in which apparently they were the only type of trichome (*T. steyermarkii*, *T. panamensis* and some subspecies of *T. sidoides*), microcapitate glandular trichomes were found in leaf primordia. Size and array of simple trichomes is quite variable. Arbo (1985) used the presence of one or two layers of simple hairs to differentiate between subspecies of *T. sidoides* and species of the *T. ulmifolia* complex.

Urban (1883) reported simple articulate trichomes (simple pluricellular-uniseriate hairs) in *Wormskioldia* and *Streptopetalum*. In other genera these trichomes have a limited distribution. Berger (1919) described them in *P. racemosa* and *T. chamaedrifolia*. Arbo (1997) found them at the leaves, axils and buds of *Erblichia*. In this study they were found only on young stems of some species of *Piriqueta* and in *T. panamensis*.

The presence of unicellular trichomes at the base of the ovary locule is an attribute limited to a few species: *T. hermannioides*, *T. stenophylla* and *T. panamensis*.

Within the stellate hairs, Urban (1883) and Berger (1919) described the trichomes of *Turnera* with arms of the same length and the trichomes of *Piriqueta* with the central arm stretched out as a bristle. The latter hairs were later named as porrect-stellate trichomes. The term was introduced by Roe (1971) for *Solanum* and used for *Piriqueta* in Theobald *et al.* (1979) and Arbo (1995). These trichomes are a generic attribute of *Piriqueta*, absent in the known species of *Turnera*. Their nature and distribution was described in the monograph for the genus (Arbo, 1995).

Stellate trichomes show a restricted distribution in both genera; they may be found in some species of *Piriqueta* (*P. constellata* and *P. plicata*) and *Turnera* (*T. blanchetiana*, *T. cearensis*, *T. hermannioides*, *T. sidoides* ssp. *sidoides* and *T. revoluta*).

The connotation of trichomes in the systematic arrangement of the family is clearly illustrated in the taxonomic studies carried out on the different genera. In *Piriqueta* and *Turnera* the indumentum is one of the characters most frequently used in the identification keys. Table 1 confirms that the trichome complement provides valuable information for intrageneric and even intraspecific segregation.

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APPENDIX

Voucher specimens and collection localities of plants used as sources of material. Cultivated in the greenhouse (#), fixed in FAA during collecting trips (*), dried specimens (@).

*PIRIQUETA**Section Africana*

1. *Piriqueta capensis* (Harv.) Urb., @Schlechter 4597, South Africa, Transvaal pr. Sandrivier, 880 m.

Section Piriqueta

2. *Piriqueta carnea* Urb., * Arbo *et al.* 5330, Brazil, Bahía, Mun. Gentio do Ouro, elev. 500–550 m, alrededores de Santo Inácio y hasta 9 km al N, camino a Xique-Xique, serra de Açuruá, c. 11°05'S, 42°44'W.
3. *Piriqueta cistoides* (L.) Griseb., ssp. *caroliniana* (Walt.) Arbo, # Hatschbach *et al.* 56981, cult. proc. de Brazil, Bahía, Iaçú, ponte sobre o Rio Paraguauçu.
4. *Piriqueta densiflora* Urb., * Arbo *et al.* 5322, Brazil, Bahía, Mun. Gentio do Ouro, elev. 500–550 m, alrededores de Santo Inácio y hasta 9 km al N, camino a Xique-Xique, serra de Açuruá, c. 11°05'S, 42°44'W.
5. *Piriqueta dentata* Arbo, @ Arbo 7468, Brazil, Bahía, 12 km al NW de Morro do Chapéu, camino a Irecé, 11°31'S, 41°16'W, elev. 1000 m.
6. *Piriqueta duarteana* (Cambess.) Urb. var. *duarteana*, * Arbo *et al.* 5312, Brazil, Bahía, Mun. Palmeiras, BR-242, 18 km W de la entrada a Lençóis, c. 12°27'S, 41°30'W; * Arbo *et al.* 7386, Brazil, Bahía: Serra de Tombador, 19 km NW de Jacobina, BR-324, 11°05'S, 40°40'W.
7. *Piriqueta guianensis* N.E.Br., ssp. *elongata* (Urb. et Rolfe), Arbo, * Crepaldi 2, Brazil, Bahía, Mun. Feira de Santana, Campus da UEFS.
8. *Piriqueta morongii* Rolfe, # Arbo *et al.* 6040, Argentina, Corrientes, Department Ituzaingó, Villa Olivari, Fiplasto, costa del río Paraná, elev. 0–100 m # Gonzalez 32, Argentina, Corrientes, ruta 12 y entrada a Sta. Ana.
9. *Piriqueta nanuzae* Arbo, * Arbo *et al.* 2540, Brazil, Bahía, Mucujé.
10. *Piriqueta ochroleuca* Urb., * Gonzalez *et al.* 17, Paraguay, Department Cordillera, Caacupé, barrio Kennedy.
11. *Piriqueta racemosa* (Jacq.) Sweet., # Krapovickas *et al.* 38807 bi, cultivada en Corrientes procedente de Brazil, Bahía, 1 km N de Baixa Grande.
12. *Piriqueta sidifolia* (Cambess.) Urb. var. *multiflora* Urb., * Mello Silva *et al.* 614, Brazil, Minas Gerais,

Buenópolis, elev. 650, Curimataí, lugar llamado Simão a orillas de la cachoeira del riacho y alrededores, 17°51'S, 43°57'W.

13. *Piriqueta suborbicularis* (A.St.-Hil. & Naud.) Arbo, # Arbo *et al.* 6155, Paraguay, Department Itapúa, elev. 0–100 m, 9 km SE de General Delgado. # Gonzalez *et al.* 28, Paraguay, Itapúa, 9 km SE de Delgado. # Gonzalez *et al.* 29, Paraguay, Itapúa, 9 km. NW de Cnel. Bogado.
14. *Piriqueta taubatensis* (Urb.) Arbo, # Schinini *et al.* 27589, Argentina, Misiones, Puerto Candelaria, Loreto. # Gonzalez 33, Argentina, Misiones, Ayo. Zaimán. # Gonzalez 39, Argentina, Corrientes, Department Ituzaingó, ruta 34, camino a San Carlos.

TURNERA

Series Annulares

1. *Turnera annularis* Urb., * J. Jardim 1032, Brazil, Bahía, Faz. Monte Alegre, entrada a c. 1 km na estrada para Itacaré, c. 10 km na entrada.
2. *Turnera odourata* Richard, @ Rosales & Briceño 254, Venezuela, Bolívar, Mun. Autónomo Piar, El Frío, parcelas de regeneración.

Series Anomalae

3. *Turnera bahiensis* Urb., * Arbo *et al.* 5753, Brazil, Bahía, Barra da Estiva, elev. c. 890 m, 22 km NE Barra da Estiva, 2 km antes de Sincorá Velho, approx. 13°31'S, 41°14'W. @ Arbo *et al.* 5362, Brazil, Bahía, Mun. Morro de Chapéu, 16 km do Morro de Chapéu, camino a Utinga, approx. 11°38'S, 41°16'W.
4. *Turnera blanchetiana* Urb. var. *subspicata* Urb., * Pott, Gonzalez *et al.* 3242, Brazil, Mato Grosso do Sul, Mun. Ladario, estrada indo para fazenda Urúba, 19°04'S, 57°30'W
5. *Turnera blanchetiana* Urb. var. *capituliflora* Urb., * Arbo *et al.* 7323, Brazil, Bahía, 15 km al W de Itiúba, camino a Filadelfia, approx. 10°43'S, 40°W. @ Arbo *et al.* 7434, Brazil, Bahía, BA-426, 7 km S de Varzêa Nova, camino a Morro de Chapéu, approx. 11°48'S, 40°58'W.
6. *Turnera cearensis* Urb., * Arbo *et al.* 5777, Brazil, Bahía, Mun. Andaraí, elev. c. 400 m, 39 km NE de Mucujé, camino a Nova Redenção, approx. 12°47'S, 41°11'W. @ Arbo *et al.* 7326, Brazil, Bahía, 22 km al W de Itiúba, camino a Filadelfia, approx. 10°43'S, 40°03'W.

Series Capitatae

7. *Turnera capitata* Cambess., * Catharino & Gonzalez 2154, Brazil, São Paulo, Parque Estadual das Fontes de Ipiranga, trilhas do nucleo de lazer.

8. *Turnera maracasana* Arbo, * Arbo *et al.* 7708, Brazil, Bahía, Faz. dos Pássaros, 24 km al E de Maracas, camino a Itiruçu, approx. 13°20'S, 40°13'W.

Series Leiocarpace

9. *Turnera coccinea* Arbo *nov. sp. ined.*, * Mello Silva *et al.* 760, Brazil, Minas Gerais, BR-251, extremo N de serra da Bocaina, próximo a las nacientes del rio Ventania, approx. 16°15'S, 42°53'W.
10. *Turnera discolor* Urb., @ Kral & Wanderley 75022, Brazil, Goiás, 10 km NW de Alto Araguaia em direção a Rondonópolis.
11. *Turnera genistoides* Cambess., @ Simão-Bianchini 89, Brazil, Minas Gerais, Diamantina, estrada para Biribiri.
12. *Turnera hassleriana* Urb., # Vanni *et al.* 395, Paraguay, Department Concepción, 12 km NE de Loreto, camino a Paso Barreto, Hugua Poi, 205 m s.n.m. # Arbo *et al.* 6082, Paraguay, Paraguari, 2 km E de ruta Piribebuy-Paraguari, sobre el desvío a Itá-Morotí y Valenzuela, elev. c. 200 m * Gonzalez *et al.* 22, Paraguay, Paraguari,
13. *Turnera melochioides* Cambess., * Gonzalez *et al.* 55, Paraguay, Department Amambay, Parque Nac. Cerro Corá, camino de Administración a monumento histórico. @ Arbo *et al.* 7372, Brazil, Bahía, BR-324, 12 km NW a Jacobina, camino a Umburanas, 11°06'S, 40°36'W.
14. *Turnera nervosa* Urb., # Arbo 2076, Argentina, Corrientes, Department Ituzaingó, Rincón Ombú Chico.
15. *Turnera oblongifolia* Cambess., * Mello Silva *et al.* 603, Brazil, Minas Gerais, Buenópolis, estrada para Curimataí.
16. *Turnera opifera* Mart., * Mello Silva *et al.* 636, Brazil, Minas Gerais, Itacambira, estrada Itacambira-Pau-d'Oleo, 16 km de Itacambira. * Mello Silva *et al.* 641, Brazil, Minas Gerais, Botumirim, Serra da Canastra, extremidade Norte da Serra proximo a estrada para Itacambira, base da Serra Tinoco, 970 m s.n.m.
17. *Turnera pumilea* L., # Krapovickas *et al.* 38624 bi, cult. proc. de Brazil, Piauí, 3 km W de Oeiras.
18. *Turnera revoluta* Urb., @ Pirani *et al.* CFSC 12193, Brazil, Minas Gerais, Mun. Santana do Riacho, Serra de Lapinha, macizo NW de Serra do Cipó, proximo a la salida de Lapinha, 50 km da rodovia. @ Lewis *et al.* CFSC 7805, Brazil, Minas Gerais, Mun. Santana do Riacho, ao longo da rodovia Belo Horizonte-Conceição do Mato Dentro
19. *Turnera sidoides* L. ssp. *carnea* (Cambess.) Arbo, # Solís Neffa *et al.* 271, Uruguay, Department Cerro Largo, Bañado Medina, ruta 44, 409 km.
20. *Turnera sidoides* L. ssp. *holosericea* (Urb.) Arbo, # Solís Neffa *et al.* 418, Uruguay, Department Tac-

uarembó, ruta 5, 343 km, a 500 m del arroyo La Quebrada Grande.

21. *Turnera sidoides* L. ssp. *integrifolia* (Griseb.) Arbo, # Solís Neffa *et al.* 310, Argentina, Entre Ríos, Department Colón, puerto.
22. *Turnera sidoides* L. ssp. *pinnatifida* (Juss. ex Poir.) Arbo, * Schinini 19532, Argentina, Jujuy, Department Ledesma, ruta 34, 4 km S de Fraile Pintado. * Schinini 19536, Argentina, Jujuy, Department El Carmen, Pampa Blanca. # Solís Neffa *et al.* 307, Argentina, Corrientes, Department Mercedes, ruta 123, 5 km E de la entrada a Yofre.
23. *Turnera sidoides* L. ssp. *sidoides*, # Solís Neffa *et al.* 401, Uruguay, Department Maldonado, Piríapolis, cerro San Antonio.
24. *Turnera trigona* Urb., @ Lombardi 584, Brazil, Minas Gerais, Furnas.

Series Microphyllae

25. *Turnera colotracha* Arbo, @ Hatschbach *et al.* 69774, Brazil, Minas Gerais, Mun. Gouveira, Córrego do Tigre.
26. *Turnera diffusa* Willd. ex Schult., * Arbo *et al.* 5354, Brazil, Bahía, Mun. Morro do Chapéu, elev. c. 1000 m, BR-052, 14 km WNW de Morro do Chapéu, camino a América Dourada, approx. 11°30'S, 41°17'W.
27. *Turnera hebetata* Urb., * Hatschbach *et al.* 65059, Brazil, Bahía, Barauninha, Mun. Santana do Riacho.

Series Papilliferae

28. *Turnera caatingana* Arbo, * Arbo *et al.* 5645, Brazil, Bahía, Mun. Caetité, 20 km E de Caetité, camino a Brumado, approx. 14°08'S, 42°15'W. @ Arbo *et al.* 7643, Brazil, Bahía, BR-030, 7 km al E de Caetité, camino a Brumado, 14°05'S, 42°26'W.
29. *Turnera chamaedrifolia* Cambess., # Noblick 3175 bi, cultivada en Corrientes procedente de Brazil, Bahía, Feira de Santana, Faz. Boa Vista, Serra de São José, 12°15'S, 38°58'W.

Series Salicifoliae

30. *Turnera brasiliensis* Willd. ex Schult., @ Fróes 33620, Brazil, Amazonia, Estado do Pará, Região do Rio Capim, Rio Candirú-Açú.
31. *Turnera panamensis* Urb., * Shore s/número. Procedente de Panamá.

32. *Turnera steyermarkii* Arbo, * Berry *et al.* 5856, Venezuela, Amazonas, Laja Suiza, Río Guasacavi, 3.5 km SSW de Santa Cruz, 3°14'N, 67°24'W.
33. *Turnera weddelliana* Urb. & Rolfe, # Gonzalez *et al.* 25, Paraguay, Paraguari, Cerro Capilla.

Serie Stenodictyae

34. *Turnera acuta* Willd. ex Schult., @ Vázquez & Jaramillo 10236, Perú, Department Loreto, Mainas, Iquitos, Pto. Almendras. * Castillo 5476, Venezuela, Amazonas, Mun. Autana, Río Cuao, entre Raudal del Danto y Caño la Raya. 4°54' – 5°3'N, 67°34' – 67°46'W.

Serie Turnera

35. *Turnera aurelii* Arbo, # Schinini 23860, Paraguay, río Salado, camino de Limpio a Emboscada.
36. *Turnera cuneiformis* Poir., # Arbo *et al.* 4985, Brazil, Minas Gerais, Conceição do Mato Dentro.
37. *Turnera grandiflora* (Urb.) Arbo, # Gonzalez & Arbo 1, Argentina, Formosa, Department Laishi, ruta 11, alrededores de Tatané.
38. *Turnera grandidentata* (Urb.) Arbo, # Gonzalez & Arbo 10, Paraguay, Department Central, Cerro Coi, 1 km S de Areguá, sobre el camino a Capiatá.
39. *Turnera hermannioides* Cambess., # Arbo *et al.* 5680, Brazil, Bahía, approx. 14°12'S, 41°26'W, elev. c. 500 m.
40. *Turnera joelii* Arbo, # Barrett & Shore 1373, Brazil, Bahía, río Juremal.
41. *Turnera simulans* Arbo, * Arbo *et al.* 5710, Brazil, Bahía, Mun. Barra da Estiva, 8 km S Barra da Estiva, camino a Ituaçu: Morro do Ouro y Morro da Torre, elev. 1190–1290 m @ Arbo *et al.* 7603, Brazil, Bahía, Rio das Contas, Cachoeira do Fraga, 13°34'S, 41°49'W.
42. *Turnera stenophylla* Urb., * Arbo *et al.* 5319, Brazil, Bahía, Mun. Gentio do Ouro, 500–550 m alrededores de Santo Inácio y hasta 9 km al N de camino a Xique-Xique, Serra de Açuruá. @ Arbo *et al.* 7488, Brazil, Bahía, 20 km S de Xique-Xique, camino a Santo Inácio, 11°01'S, 42°43'W.
43. *Turnera ulmifolia* L., # Arbo 2698, cult. proc. de U.S.A., Florida, Miami.
44. *Turnera velutina* C.Presl, # Koch & Fryxell 78341 bi, cult. proc. de México, Oaxaca, Santo Domingo.

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Insert 'superior' character	/ through character or ⤴ where required	γ under character e.g. γ
Insert 'inferior' character	(As above)	⤵ over character e.g. ⤵
Insert full stop	(As above)	⦿
Insert comma	(As above)	,
Insert single quotation marks	(As above)	γ and/or γ
Insert double quotation marks	(As above)	γ and/or γ
Insert hyphen	(As above)	⊖
Start new paragraph	⤴	⤴
No new paragraph	~	~
Transpose	⤴	⤴
Close up	linking c letters	∩
Insert space between letters	⤴ between letters affected	#
Insert space between words	⤴ between words affected	#
Reduce space between letters	↑ between letters affected	↑
Reduce space between words	↑ between words affected	↑