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Colleters in *Turnera* and *Piriqueta* (Turneraceae)

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The anatomy of colleters was examined by light and scanning electron microscopy in 25 species of *Turnera* and nine species of *Piriqueta*. Based on morphology, four categories of colleters were recognized: standard, sessile, lachrymiform and trochleariform, all of which differ in shape and length/width ratio. They all have a similar anatomy: they consist of an axis of parenchymatous cells, sheathed by a palisade epidermis. The standard type is the most widespread in the studied taxa; the lachrymiform example was found in those species of *Piriqueta* with setiform glandular hairs; only one trochleariform example appeared in *T. diffusa*. The sessile type is considered to be a morphological transitional form between extrafloral nectaries and colleters. This is the first record of sessile, lachrymiform and trochleariform colleters. The anatomy of colleters is compared with other secretory structures such as glandular trichomes and extrafloral nectaries.

ADDITIONAL KEY WORDS:—bud-glue – emergences – epidermis – extrafloral nectaries – glandular hairs – leaf – ontogeny – systematic anatomy – vegetative anatomy.

CONTENTS

INTRODUCTION

Colleters are glandular structures that consist of a short, multicellular axis bearing an expanded disc or knob of secretory cells (Foster, 1949). They are thought to protect young differentiating leaves or their stipules from desiccation (Kronestedt-Robards & Robards, 1991).

According to Foster (1949), the term "colleter" was introduced by Hanstein in 1868. Such structures have received different names: "shaggy hair" (Solereder,

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1908), "secretory trichomes" (Horner & Lersten, 1968), and "squamellae" (Ramayya & Bahadur, 1968). Strasburger (1986) called them emergences because they arise from both epidermal and subepidermal layers. Their secretions have been called "blastocolla" (Hanstein, 1868) or "bud-glue" and they contain carbohydrates, mucilages, and proteins or lipophilic substances (Kronestedt-Robards & Robards, 1991).

Colleters are mainly found on young foliar organs and examples have been described in different parts: cataphylls of *Aesculus, Rosa, Carya* (Foster, 1949); stipules of Rubiaceae (Horner & Lersten, 1968; Lersten, 1974a, b, 1975) and *Rhizophora mangle* (Rhizophoraceae; Lersten & Curtis, 1974); ochreas of *Rheum* and *Rumex* (Metcalfe & Chalk, 1979); young foliar teeth of *Aphanopetalum* (Saxifragaceae; Dickison *et al.*, 1994); leaves of *Malus pumila* Mill. var. Jonathan (Blaser & Einset, 1948; Lewis, 1968).

In the Turneraceae, colleters have been cited as "glandular emergences" (González, 1993), located at the margins of the prophylls of *Turnera hassleriana* Urban. In her revision of *Piriqueta*, Arbo (1995) described them as stipules or prophylls reduced to glandular prominences.

In this paper, I report for the first time the presence of colleters in nine species of *Piriqueta* and 25 of *Turnera* belonging to seven series, including their description and illustration, and discuss their systematic importance.

MATERIAL AND METHODS

The list of the species used and their sources is given in the Appendix. Voucher specimens are deposited at CTES (Herbarium of Instituto de Botánica del Nordeste). Plant material used was fresh and fixed in FAA; in exceptional cases it was dried.

Light Microscopy

Buds, flowers, fruits and leaves were fixed in FAA (formalin-acetic acid —70% alcohol), and processed as outlined in González & Cristóbal (1997). Dried material was previously boiled for several minutes in water. Transverse (TS) and longitudinal sections (LS) were cut 8–12 μm thick and stained with safranin-Astra blue combination (Luque, Sousa & Kraus, 1996). Observations were made on Olympus BMAX and WILD M 20 microscopes equipped with camera lucida.

Scanning electron microscopy (SEM)

Both fresh and FAA fixed material was used. Living material was fixed in 3% glutaraldehyde in phosphate buffer, at pH 7.2 for 4 h at 4°C and washed in the same buffer. The material was dehydrated in a graded acetone series, critical point dried with CO_2, mounted on a stub and coated with a thin layer of gold (Sorrivas de Lozano & Morales, 1992). Observations were carried out using a JEOL 35CF scanning electron microscope operating at 5 kV.

RESULTS

The colleters are abundant in young parts of the plant, but they are mostly found on the borders of leaf primordia and prophylls. In some species they replace the

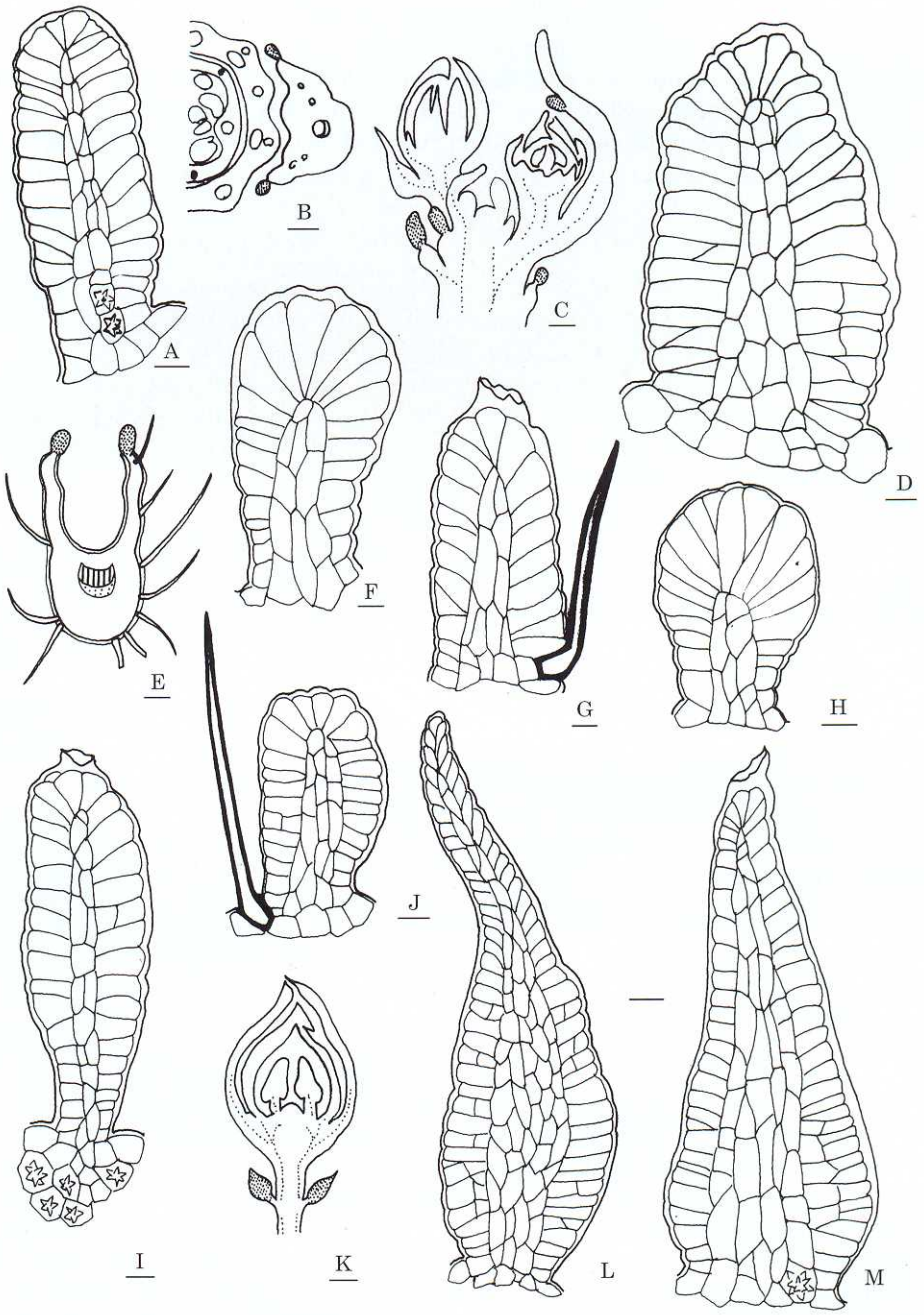

Figure 1. Standard and lachrimiform colleters in Turneraceae. A–J: standard colleters. A & B, *T. velutina*. A, scale bar = 10 μm. B, TS flower and prophyll with colleters on the margins. Scale bar = 0.25 μm. C & D, *T. nervosa*. C, LS floral buds with colleters on stipules and prophylls. Scale bar = 0.1 mm. D, scale bar = 20 μm. E & F, *T. cearensis*. E, TS foliar primordia with colleters on the margins. Scale bar = 50 μm. F, scale bar = 10 μm. G, *T steyermarkii*. Scale bar = 10 μm. H, *T. chamaedryfolia*. Scale bar = 10 μm. I, *P. racemosa*. Scale bar = 10 μm. J, *P. suborbicularis*. Scale bar = 20 μm. K–M, lachrimiform colleters. K & L, *P. carnea*. K, LS young flower showing the colleters in the place of the prophylls. Scale bar = 0.1 μm. L, Scale bar = 20 μm. M, *P. morongii*. Scale bar = 20 μm.

prophylls and stipules. They can be solitary or in groups of two to four (Fig. 3 B). In leaves they are found on the teeth or crenatures.

When the organ on which they are found is fully developed, the colleters commonly dry up and fall off, although some of them remain on the leaves and prophylls. The secreted liquid can be observed with SEM (Fig. 3 B, C). In living young material it appears like a viscous fluid but in older organs it stays as a yellowish crust on the colleter.

Based on their shape, four types of colleters may be distinguished:

Standard. Cylindrical, claviform with a narrow base, or conoidal with a wide base and round apex. Their size varies between 70–380 μm long and 50–110 μm wide, the length/width (l/w) ratio being 1.25–3/1 (Figs 1A–J, 3A–D).

The axis consists of elongated parenchymatous cells, which may contain druses or prismatic crystals. This axis may be cylindrical and formed by 2–5 cells or conical and up to 20 cells. The axis is surrounded by a palisade-like epidermis of 1–2 layers, composed of secretory cells with conspicuous nucleus and dense, intensely stained cytoplasm. In some species, these cells contain deposits of tannin. The colleter is completely covered with a smooth, thin cuticle, slightly thicker in the basal portion.

The secretion is exuded through a cuticular apical pore, which does not exceed 4–6 μm in diameter. At the tip of a young colleter the cuticle is slightly detached, probably because the bud-glue accumulates between the wall and the cuticle. SEM observations of uncoated colleters verify that bud-glue arises from a pore at the gland apex (Fig. 3 A, C). In old colleters the cuticle is very distended (Fig. 3 D).

Lachrymiform. Tear-shaped, with acute apex. These are the biggest colleters: 200–420 μm long × 80–140 μm wide, l/w ratio: 2.2–3.8/1 (Figs 1 K–M, 3 F). They have a pluricellular axis, tear-shaped or conical, composed of parenchymatous cells, covered by a palisade-like epidermis, 1–2 layered (Fig. 1 L, M). The cuticle is thicker at the base, and thinner at the apex.

Sessile. Hemispherical, these are the smallest colleters, about 70–100 μm long and 60–75 μm wide, l/w ratio: 0.6–1/1(Figs 2 A–F, 3 E). The axis is hemispherical or slightly conoidal, formed by 6–20 parenchymatous cells. The glandular epidermis is 1–2 layered. The cuticle is thinner at the apex, where it can be distended and detached from the epidermal cell wall. It may have a pore to let the secretion out.

Trochleariform. Stalked, with a broad flat or concave apex. L/w ratio is less than 1.1/1, and their size varies between 90–125 μm long × 150–190 μm wide (Figs 2 G, H, 3 G). The parenchymatous axis is cylindrical, with rounded apex, and the subepidermal layer is tanniferous. The apex is shaped by the different heights of the epidermal cells: they are 2–4 layered on the margin and 1 layered in the centre. The external wall of the latter is convex or slightly nipple-shaped. The cuticle has little wedges which encrust the epidermal cells, and it may be separated from the epidermis. No cuticular ruptures or interruptions were observed.

Ontogeny

The ontogeny of the standard colleters located at the prophyll apex of *T. grandiflora* (Fig. 2 I–L) and those which, replace the stipules in *T. melochioides* (Fig. 2 M–P) has been investigated.

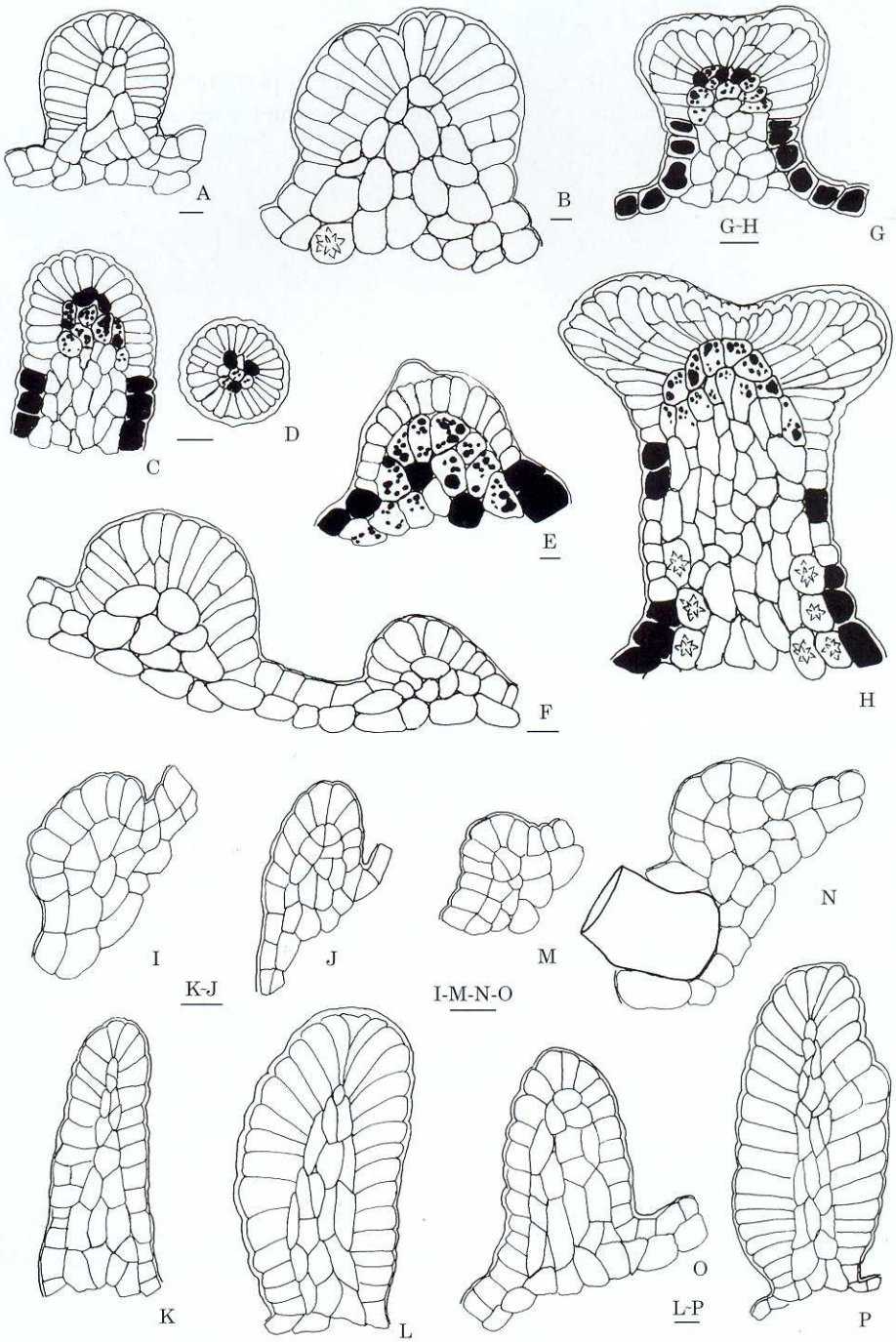

Figure 2. Sessile and trochleariform colleters in Turneraceae. A–F, sessile colleters. A, *T. hebepetala*. Scale bar = 10 μm. B, *P. taubatensis*. Scale bar = 10 μm C & D, *T. diffusa*. C, LS of stipule with a sessile colleter in the apex. Scale bar = 20 μm. D, TS colleter. Scale bar = 20 μm. E, *T. bahiensis*. Scale bar = 10 μm. F, *T. sidoides*. Scale bar = 20 μm. G & H, Trochleariform colleters in *T. diffusa*. Scale bar = 20 μm. I–P, colleters ontogeny. I–K, *T. grandiflora*. Scale bar = 10 μm. L, *T. grandiflora*. Scale bar = 20 μm. M–O, *T. melochioides*. Scale bar = 10 μm. P, *T. melochioides*. Scale bar = 20 μm.

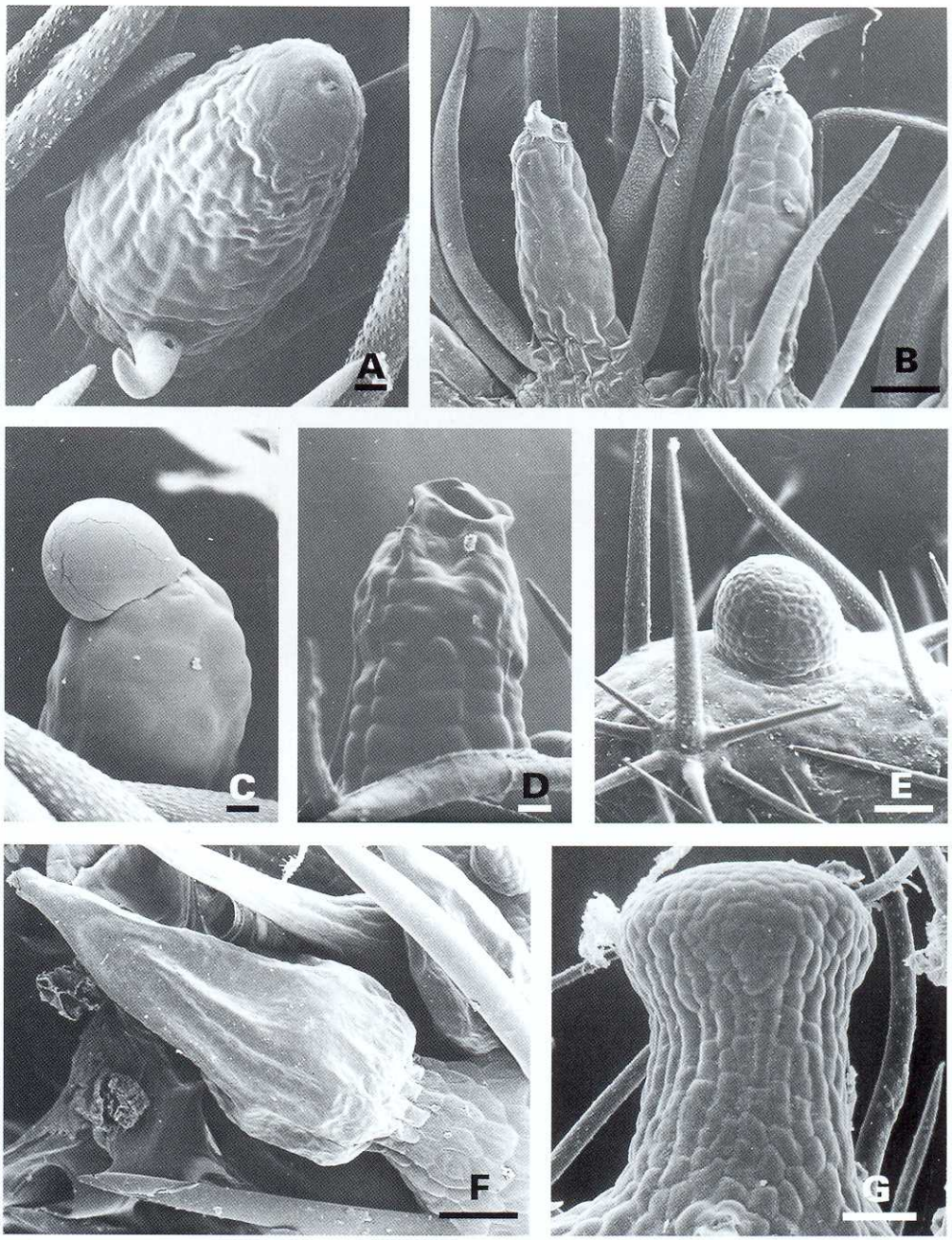

Figure 3. SEM photographs of colleters in Turneraceae. A, standard colleter of *P. suborbicularis*. Scale bar = 10 μm. B, standard colleters of *T. hermannioides*. Scale bar = 50 μm. C, *T. velutina*, standard colleter with a drop of the bud-glue. Scale bar = 10 μm. D, *T. hassleriana*, old standard colleter. Scale bar = 10 μm. E, sessile colleter of *P. suborbicularis*. Scale bar = 50 μm. F, *P. morongii*, lachrimiform colleter. Scale bar = 50 μm. G, trochleariform colleter of *T. diffusa*. Scale bar = 50 μm.

In both species a group of protodermal cells enlarge radially and divide anticlinally. Some subepidermal cells also divide to form a bulge. The former develops in the colleter epidermis and the latter in the axis. Some epidermal cells can undergo periclinal divisions, forming partially bilayered portions.

Although I was unable to study the ontogeny in the other colleter types, the presence of a palisade epidermis and a core of parenchymatous cells suggests that they probably have a similar ontogenetic development.

Taxonomic distribution

Turnera

1. Series Canaligerae: 22 species, 12 of them in the *T. ulmifolia* complex (Arbo, 1986). Eight species were surveyed, five of them belonging to the *T. ulmifolia* complex. Standard colleters were found in all of them, mainly on the stipules, prophyll margins and on the leaf teeth. The colleter axis has 3–5 cells in cross section, l/w ratio: 2.6–3/1. (Figs 1 A, B, 3 B, C).

2. Series Leiocarpae: 39 species (Arbo, 1986). In the majority of the analysed species (*T. nervosa, T. hassleriana, T. melochioides, T. opifera* and *T. oblongifolia*) the colleters are standard (Figs 1 C, D, 3 D). They are very abundant on the stipules or they replace them. They are also found on the teeth of leaf primordia and on prophylls of young flowers. L/w ratio: 1.25–2.8/1.

T. pumilea has rosette-arranged leaves in the apex of the branches, the flower-bearing leaves become abruptly smaller (Arbo, 1987). The colleters are standard, they occur on the teeth of the external leaves and also replace the stipules. They were not found on the prophylls.

T. sidoides has standard colleters in the three subspecies analysed: *integrifolia, camea* and *pinnatifida*. They are found on the prophyll borders, l/w ratio: 1.25–1.37/1. These taxa also have sessile colleters on the border of the basal portion of the prophyll, in place of the stipules and on the leaves teeth. L/w ratio is less than 1/1 (Fig. 2 F). The cuticle shows a bulge at the apex of the sessile colleter, when observed with SEM.

3. Series Papilliferae: two species, *T. chamaedryfolia* and *T. caatingana* (a new species placed in this series by Arbo, pers. comm.). Both have standard colleters (Fig. 1 H). Some of them have conoidal axis, their size varying between 80–180 μm long and 60–100 μm wide; l/w ratio: 1.35–1.8/1.

The colleters of *T. chamaedryfolia* have a little pore in the apex, scarcely 2 μm in diameter, and observed with SEM. The bud-glue flows up through this pore.

4. Series Salicifoliae: 12 species (Arbo, 1997). The two analysed species have standard colleters, with a conoidal axis; l/w ratio 2.5–3/1. In *T. weddelliana* the colleters are very abundant at the base and margins of the prophylls and stipules; they also accur on the margins of the young leaf. In *T. steyermarkii* the colleters are mainly found in place of the stipules (Fig. 1 G); some of them can be 380 μm long.

5. Series Anomalae: Urban (1883) only mentioned *T. cearensis* as belonging to this series, but Arbo (pers. comm.) also includes *T. bahiensis, T. blanchetiana* and *T. stipularis.*

T. cearensis has standard colleters located on the prophyll borders and on apical leaf teeth (Fig. 1 E, F).

T. blanchetiana has standard colleters, which are scarce and mainly found on the prophylls.

The standard colleters were not found on the prophylls or stipules of *T. bahiensis*. The most distal foliar teeth have sessile colleters (Fig. 2 E). All tissues of this species are tanniferous except for the cauline apical meristems and the anther walls.

6. Series Capitatae: 5 species (Arbo, pers. comm.). In *T. capitata* the colleters are grouped on the stipules, on the prophylls borders and on the teeth of the leaves. They are standard, with conoidal axis.

7. Series Microphyllae: 4 species (Arbo, pers. comm.). *T. diffusa*, the same as *T. bahiensis*, has tannin in most of the tissues. It has trochleariform colleters on the leaf teeth; l/w ratio: 0.8–1.1/1 (Figs 2 G, H, 3 G) and has sessile colleters on the stipule apex; l/w ratio 1/1 (Fig. 2 C, D). Colleters are not found on prophylls.

T. hebepetala has standard colleters on prophylls and on the apex of the young stipules, l/w ratio 1.9/1; by the mature stipule stage the colleter has accumulated considerable tannin and finally falls off. It has sessile colleters on the basal leaf teeth (Fig. 2 A) and standard colleters on the apical ones.

Piriqueta

1. *P. racemosa*, *P. cistoides*, *P. suborbicularis* and *P. taubatensis* have standard colleters. In *P. racemosa* and *P. cistoides* they are thin and long, their diameter does not exceed 55 µm in the widest portion; l/w ratio: 1.4–3/1; they are found on the small prophylls, in place of the stipules and on the leaf crenatures. The apical portion with distended and broken cuticle was observed in sections. The subepidermal tissues have many druses but they are not present on the colleters (Fig. 1 I).

In *P. taubatensis* and *P. suborbicularis* the standard colleters are thicker, l/w ratio: 1; 4–1.5/1; they are on the reduced prophylls or they replace the stipules. There are also sessile colleters on the teeth of the apical leaves, each with an apical pore (Fig. 3 A, E).

2. *P. morongii*, *P. camea*, *P. densiflora and P. sidifolia* have lachrymiform colleters placed on apical leaf teeth and on reduced prophylls, or replacing them (Figs1 K–M, 3 F).

3. Colleters were not found in *P. nanuzae*, which instead has an abundant indument of setiform glandular hairs.

DISCUSSION

Strasburger (1986) describes colleters as emergences in *Viola tricolor*. This term is too broad because it refers not only to the tissues of which they are composed, but also includes other structures like prickles and stinging hairs. The term 'colleter' is more appropriate because it also refers to the sticky nature of the secretion. This term is nowadays used by different authors (Lersten, 1974a; Metcalfe & Chalk, 1979; Dickison *et al.*, 1994) to describe these glandular structures found in young foliar organs (Esau, 1974). This study confirms that Turneraceae colleters are emergences, as described previously in *T. hassleriana* (González, 1993).

In the majority of the Turneraceae, I found colleters on prophylls and on stipules,

or replacing them. Colleters also occur on crenatures and on teeth of young leaves. Their position in the plant coincides with that reported by other authors in other families (Blaser & Einset, 1948; Foster, 1949; Lersten, 1974 a).

The colleters of *Piriqueta* species included in the present work were previously described as glandular prominences by Arbo (1995). Berger (1919) studied the anatomy of numerous Turneraceae but did not mention the occurrence of colleters.

According to Esau (1974) the colleters wither when the leaves unfold. In Turneraceae, when the development of the foliar organ is finished, the colleters may fall off or persist as dried, wrinkled structures. In *T. hebepetala*, the colleters store tannic compounds before falling off.

The structure of Turneraceae colleters, with an axis and a palisade epidermis, is the same as the one described by classical authors in other plants (Solereder, 1908; Foster, 1949; Esau, 1974).

In the Rubiaceae, Lersten (1974a, b, 1975) and Robbrecht (1988) recognized several types of colleters. The standard type is considered to be the most pervasive in the family, the remainder (dendroid, reduced standard, brushlike, etc.) are deviations from it, and can be regarded as derived forms, and of more recent origin (Lersten, 1974a). These authors proposed their use as a taxonomic character at the generic level.

In *Malus pumila* Mill. var. Jonathan (Lewis, 1968), the colleters have the same structure described as standard. This author also observed cytoplasm with a reddish-brown pigment as in Turneraceae.

The resin glands of *Salix lucida* Muhl. (Curtis & Lersten, 1980) have the same 'standard' anatomy, in spite of the fact that they are vascularized and that they exceed the colleter in size. The resin of these glands is expelled in the form of thin filaments through a pore in the cuticle at the gland tip.

In the standard colleter of the Turneraceae, the thin cuticle is distended before the secretion, as it is observed by optical microscopy. Only with SEM was a cuticular pore observed. The bud-glue flows through this pore. In old colleters the cuticle appears wrinkled.

The exudate is released by the rupture of the apex in the case of lachrymiform colleters. The sessile type may either possess or lack a cuticular pore when observed with SEM. Trochleariform colleters do not possess a pore, the cuticle is distended but not ruptured.

The widespread standard colleters are the most common type in both genera; they are present in the majority of the groups analysed.

All species of Canaligerae and Leiocarpae series (except *T. sidoides*) included in the present work possess extrafloral nectaries, which are born on the petiole apex or at the base of the leaf blade. The paired nectaries are distinctly cupular or discoid, their size varies from 0.3 to 2 mm and they are supplied with vascular strands (González, 1996).

The standard colleter is the only colleter type in Canaligerae. The nectaries of the series Canaligerae are considered to be the most advanced because they possess a conspicuous and elaborate 'pore' (González, 1996). According to its floral morphology, this series is also considered the most specialized in *Turnera* (Arbo, 1986; González, 1993).

In the series Leiocarpae, all species have standard colleters. *T. sidoides* is a complex composed of five subspecies, being the only species in this series that possesses rugose fruits and crested seeds (Arbo, 1985). Most analysed subspecies in this group have

standard colleters and they are the only ones that possess sessile colleters in the Leiocarpae series.

The species of the series Papilliferae, Capitata and Salicifoliae analysed also have standard colleters. Both species of series Papilliferae have abundant stalked glandular hairs. They are smaller than the colleters and different from them because they have a conspicuous stalk or pedestal of tanniferous cells and a head of 8–10 secretory cells.

T. capitata (series Capitata), *T. steyermarkii* (series Salicifoliae) and the species surveyed in the series Anomalae also possess discoidal vascularized extrafloral nectaries on the basal leaf teeth or on the border near the base of the leaf blade (González, in prep.). In these species the colleters occur in apical leaf teeth. In *T. bahiensis* the nectaries decrease in size towards the foliar apex, where morphologically they gradually become sessile colleters.

In the series Microphyllae, *T. hebepetala* possesses sessile colleters on the basal leaf teeth and standard colleters on the apical ones. *T. diffusa* has sessile and trochleariform colleters. Berger (1919) described the latter structures in *T. pringlei* (= *T. diffusa*, Arbo, pers. comm.) as extrafloral nectaries with vascular traces. According to my own observations, no vascularization was observed in these structures.

The species of *Piriqueta* that lack glandular setiform hairs, like *P. racemosa*, *P. cistoides*, *P. suborbicularis* and *P. taubatensis*, possess standard colleters. *P. suborbicularis* and *P. taubatensis* are similar to *T. bahiensis*. They have sessile colleters in apical leaf teeth and extrafloral nectaries on the basal ones. The paired nectaries are opposite and located on the base of the leaf blade of *P. suborbicularis*; *P. taubatensis* has small nectaries on all basal crenatures of the leaf instead. The morphological transition between nectaries and colleters is more gradual in *P. taubatensis*, in which the nectaries are smaller. The absence of vascular traces in the colleter is the main anatomical difference between both structures, besides the conspicuous sugary secretion, confirmed with glucose indicator strips. The secretion of the colleters could not be analysed as it was too exiguous (González, in prep.).

Lachrymiform colleters are present only in species of *Piriqueta* that possess setiform glandular hairs; these species lack any other type of colleter. The lachrymiform colleter shape is similar to the wide base of these hairs, but the latter are different because they have a bristle crowned by a head, are not differentiated into axis and palisade-like epidermis, and all the cells are more or less isodiametric. In early stages of development, before the growth of the bristle, the apex of the setiform glandular hairs consists of several rows of cells; in the young colleter the apex possesses palisade-arranged cells.

P. nanuzae, which was placed in a different group (Arbo, 1995), has smooth fruits, and is the only species that lacks colleters.

Figure 4 is a summary diagram showing the various types of colleters found among the taxa studied, and their possible evolutionary relations.

The lachrymiform type may be placed among the primitive features: it is present only in those species of *Piriqueta* with less specialized characters like setiform glandular hairs. Arbo (1995) concluded that the absence of setiform glandular hairs and the presence of such characters as smooth fruit, glabrous seeds and glabrescent calyx inner lobes are derived or specialized in *Piriqueta*. The standard colleters encountered in *Piriqueta* species without setiform glandular hairs and also found in the majority of *Turnera* series should be included among these characters.

The sessile colleter is not a very common derived type, being found in only a few

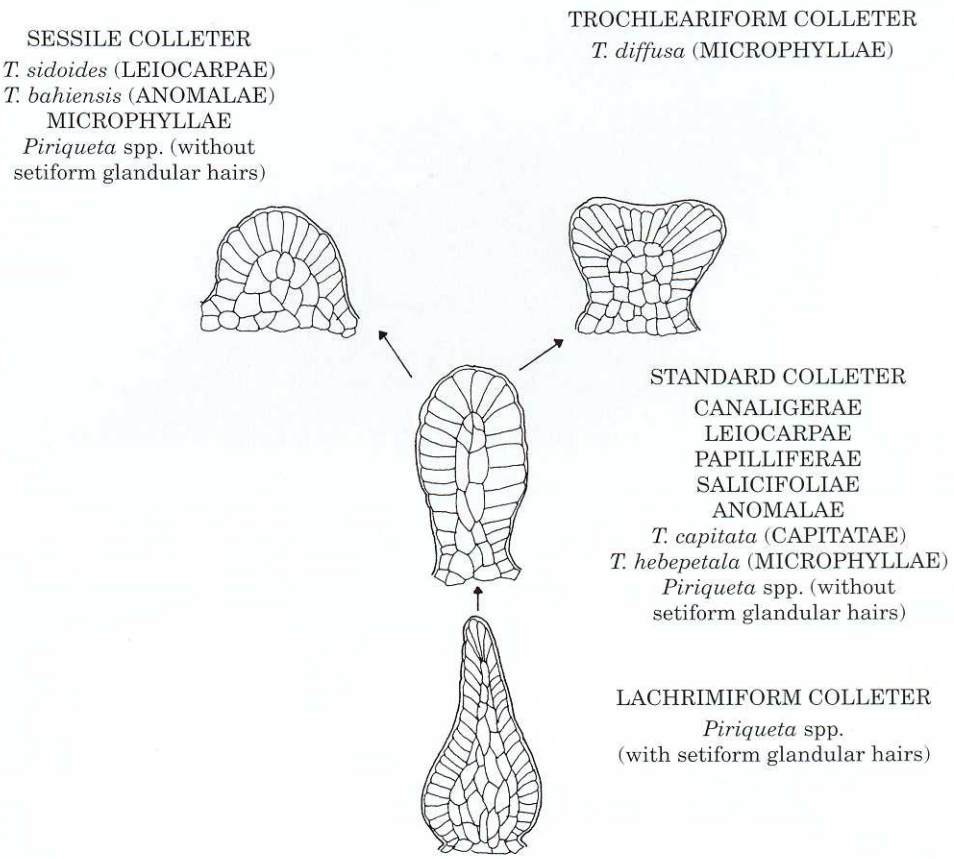

Figure 4. A diagrammatic scheme of possible evolutionary relationships among colleter types in Turneraceae.

species from both genera. The sessile colleters of *P. taubatensis* and *T. bahiensis* seem to be a morphological transition from the extrafloral nectaries, from which they differ in their lack of vascular traces.

Another derived type is the trochleariform colleter, which appears only in *T diffusa*. Although it was originally described as an extrafloral nectary by Berger (1919), I consider it to be a colleter due to its lack of vascularization and due to its being totally mature in very young organs.

It would be very informative to study the chemical nature of the secretion and check whether or not it is correlated with the different anatomical types of colleters.

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REFERENCES

Arbo MM. 1985. Notas taxonómicas sobre Turneráceas Sudamericanas. *Candollea* **40**: 175–191.

Arbo MM. 1986. Paraguay: centro importante de especiación en las Turneráceas. *Candollea* **41**: 211–218.

Arbo MM. 1987. Turneraceae. *Flora del Paraguay. Conservatoire et Jardin botaniques de Genève.* Missouri Botanical Garden, 1–65.

Arbo MM. 1995. Turneraceae. Parte I. *Piriqueta. Flora Neotrópica.* Monograph 67, 157 pag.

Arbo MM. 1997. Estudios Sistemáticos en *Turnera* (Turneraceae). I. Series Salicifoliae y Stenodictyae. *Bonplandia* **9**: 151–208.

Berger MG. 1919. Etude organographique, anatomique et pharmacologique des Turnéracées. Thèse. Lille.

Blaser H, Einset J. 1948. Leaf development in six periclinal chromosomal chimeras of apple varieties. *American Journal of Botany* **35**: 473–482.

Curtis JD, Lersten NR. 1980. Morphology and anatomy of resin glands in *Salix lucida* (Salicaceae). *American Journal of Botany* **67**: 1289–1296.

Dickison WC, Hills MH, Lucansky TW, Stern WL. 1994. Comparative anatomy and systematics of woody Saxifragaceae: *Aphanopetalum*, Endl. *Botanical Journal of the Linnean Society* **114**: 167–182.

Esau K. 1974. *Anatomia Vegetal.* Madrid: H. Blume Ed.

Foster A. 1949. *Practical Plant Anatomy.* 2nd ed. New Jersey: Van Nostrand.

González AM. 1993. Anatomía y vascularización floral de *Piriqueta racemosa*, *Turnera hassleriana* y *Turnera joelii* (Turneraceae). *Bonplandia* **7**: 143–184.

González AM. 1996. Nectarios extraflorales en *Turnera*, series Canaligerae y Leiocarpae. *Bonplandia* **9**: 129–143.

González AM, Cristóbal CL. 1997. Anatomía y ontogenía de semillas de *Helicteres Lhotzkyana* (Sterculiaceae). *Bonplandia* **9**: 287–294.

Hanstein J. 1868. Die Scheitelzellgruppe im Vegetationspunkt der Phanerogamen. *Festschr. Niederrhein Ges. Natur- und Heilkunde*, 109–134.

Horner HTR, Lersten N. 1968. Development, structure and function of secretory trichomes in *Psychotria bacteriophila* (Rubiaceae). *American Journal of Botany* **55**: 1089–1099.

Kronestedt-Robards E, Robards A. 1991. Exocytosis in gland cells. In: Hawea C, Coleman J, Evans D, eds. *Endocytosis, exocytosis and vesicle traffic in plants.* Society for Experimental Biology Seminar Series 45. Cambridge: Cambridge University Press, 199–232.

Lersten NR. 1974a. Colleter morphology in *Pavetta*, *Neorosea* and *Tricalysia* (Rubiaceae) and its relationship to the bacterial leaf nodule symbiosis. *Botanical Journal of the Linnean Society* **69**: 125–136.

Lersten NR. 1974b. Morphology and distribution of colleters and crystals in relation to the taxonomy and bacterial leaf nodule symbiosis of *Psychotria* (Rubiaceae). *American Journal of Botany* **61**: 973–981.

Lersten NR, Curtis JD. 1974. Colleter anatomy in red mangrove, *Rhizophora mangle* (Rizophoraceae). *Canadian Journal of Botany* **52**: 2277–2278.

Lersten NR. 1975. Colleter types in Rubiaceae, especially in relation to the bacterial leaf nodule symbiosis. *Botanical Journal of the Linnean Society* **71**: 311–319.

Lewis S. 1968. The gross morphology of the glandular trichome of the leaf of Jonathan Apple. *Botanical Gazette* **129**: 89–91.

Luque R, Sousa HC, Kraus JE. 1996. Métodos de coloração de Roeser (1972) – modificado – e Kropp (1972) visando a substituição do azul de astra por azul de alcião 8 GS ou 8 GX. *Acta Botanica Brasilica* **10**: 199–212.

Metcalfe C, Chalk L. 1979. *Anatomy of the dicotyledons.* Vol. I. Oxford: Clarendon Press.

Ramayya N, Bahadur B. 1968. Morphology of "squamellae" in the light of their ontogeny. *Current Science* **37**: 520–522.

Robbrecht E. 1988. Tropical woody Rubiaceae. *Opera Botanica Belgica* **1**: 64–68.

Solereder H. 1908. *Systematic Anatomy of the Dicotyledons* Vol. I–II, New Delhi, Indian Reprints 1986.

Sorrivas de Lozano V, Morales A. 1992. *Introducción a la Microscopía Electrónica.* Argentina, Bahía Blanca, CRIBABB Ed.