Studies in the southern African species of Justicia and Siphonoglossa (Acanthaceae): indumentum

K.L. IMMELMAN*

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ABSTRACT

The trichome types present on all species of Justicia and Siphonoglossa in the southern African region (as defined by the Flora of southern Africa) were examined with the dissecting and with the Scanning Electron Microscope. Both glandular and eglandular trichomes were observed, the former comprising both sessile, peltate glands and stalked glands of various lengths. Eglandular trichomes are either straight or sharply bent (anvil-shaped), and comprise two to many cells. They are either smooth or have raised ornamentation on the cell walls. The presence and morphology of the trichomes on various organs is recorded and measured, and the range of trichomes seen was illustrated. The possible significance of trichome type and ornamentation in the taxonomy and ecology of the genera is discussed.

INTRODUCTION

The indumentum of all species of Justicia and Siphonoglossa found in southern Africa (as defined by the Flora of southern Africa) was examined. Numerous authors, including Ahmad (1974a, b; 1978), Munday (1980), Baden (1981), Balkwill & Getliffe Norris (1985), Hansen (1985) and Manning & Getliffe Norris (1985), have found pubescence and trichome types important as indicators of relationships in various genera of the Justicieae.

METHODS

Several specimens of each taxon were examined with the dissecting microscope and the eglandular and stalked glandular trichomes were measured using a micrometer eyepiece.

Indumentum type present was recorded from the stem, the leaf lamina and petiole/leaf base area, from the bracts, the inner and outer surface of the calyx and from the capsule. Material of one specimen of each species or subspecies recognized by Immelman (1987), except J. parvibracteata, was examined under the SEM. The leaf, outer and inner surface of calyx as well as the bract and the leaf base/petiole area were scanned. This was mounted directly onto 15 mm diameter aluminium stubs and glow-discharge-coated with +400 Å of metallic gold in an Eiko sputter coater. They were then viewed directly in an SEM Hitachi-Akashi (desk top model) SEM at kv 15, and photographed using a Mamiya 6 × 7 camera and Ilford FP 4 125 ASA film. The film was developed in Microdol X.

Where fresh material was available this was critical-point dried before being examined under the SEM. This was found to be preferable to using dried material as the trichomes, especially glandular trichomes, are then not collapsed and their structure can be more accurately observed. The material was dehydrated in 2,2-dimethoxy-propane (DMP), fixed in FAA, and critical-point dried in a Balzer's Union critical-point drier using liquid carbon dioxide. It was then mounted, viewed and photographed as described above. Trichome types were defined and named according to the terminology used by Munday (1980). Presence or absence of the different types was recorded for the different organs mentioned above (Table 1). Figures were prepared illustrating the range of trichome types seen (Figures 1 & 2).

MORPHOLOGY

Two basic types of trichomes were found: 1, eglandular and 2, glandular.

1. Eglandular trichomes (Figure 1 and type 'A' on Table 1) are either straight (varying from long to short) or gradually to sharply bent. They consist of (1)2 to many uniseriate cells with or without ornamentation.

In some species, e.g. J. parvibracteata, the trichomes are two-celled (Figure 1G). J. montis-salinarum A. Meeuse appeared to have one-celled trichomes, but the trichomes were so heavily ornamented that it was not possible to see whether they were 1- or 2-celled (Figure 1H). In most other species one to many additional cells
FIGURE 1.—Eglandular trichomes, all × 420, except where otherwise stated. A, C, *J. protracta* subsp. *rhodesiana*, Germishuizen 974: A, from leaf showing swollen basal cells; C, from calyx. B, *J. cuneata* subsp. *hoerleiniana*, from leaf, with ornamented and non-ornamented heads, Dinter 6403; D, *J. capensis*, from leaf showing small branch on trichome, Immelman 375; E, *J. odoru*, from leaf showing ornamented trichome surface, × 3000, Meeuse 9530; F, *J. kirkiana*, from petiole, × 300, Brummitt & Banda 8539; G, *J. parvibracteata*, from leaf, Esterhuizen 1101; H, *J. montis-salarum*, from leaf, Van Wyk 5536. I, K, *J. protracta* subsp. *protracta*, Balkwill s.n.: I, from bract showing striate joint at cell wall; K, from leaf near petiole, showing eglandular and glandular trichomes in two separate layers, × 120. J, *J. orchioides* subsp. *glabrata*, from bract, Muir 1101.
TABLE 1.—Trichome types present in taxa of *Justicia* and *Siphonoglossa*: A, eglandular trichomes; B, peltate glandular trichomes; C, stalked glandular trichomes

| Species            | Stem | Lf base | Lf lam. | Bract | Calyx (outer surface) | Calyx (inner surface) | Capsule |
|--------------------|------|---------|---------|-------|------------------------|------------------------|---------|
| *Justicia*         |      |         |         |       |                        |                        |         |
| anagalloides       | A    | A       | B       | A     | B                      | B                      | A       |
| anselliana         | A    | A       | A       | A     | A                      | B                      | A       |
| betonica           | A    | A       | B       | A     | B                      | A                      | B       |
| bolusii            | A    | A       | A       | A     | C                      | —                      | A       |
| campylodestemon    | A    | A       | B       | A     | B                      | —                      | C       |
| capensis           | A    | A       | B       | A     | B                      | A                      | A       |
| *Siphonoglossa*    |      |         |         |       |                        |                        |         |
| leptantha           |      |         |         |       |                        |                        |         |
| subsp. late-ovata   | A    | C       | A       | A     | A                      | ?                      | A       |
| subsp. lepantha     | A    | C       | A       | A     | A                      | ?                      | A       |
| linifolia           | A    | A       | A       | A     | ?                      | ?                      | —       |
| nkandidensis        | A    | A       | A       | A     | ?                      | ?                      | —       |

are present, these being progressively narrower than the basal cell. The upper cells are frequently set at an angle to the one below, so that the trichome is gradually or sharply bent or even appressed to the surface of the organ on which they occur. The sharply bent condition (Figure 1A) has been described as anvil-shaped by Munday (1980). The basal cell of the eglandular trichomes is thicker and set into the epidermis. It is sometimes surrounded by a ring of swollen epidermal cells (e.g. *J. protracta* (Nees) T. Anders.—Figure 1A). In anvil-shaped trichomes, it is usually the second cell which is set at an angle to the basal cell. The terminal cell is usually pointed but in *J. cuneata* subsp. *hoerleiniana* (P. G. Mey.) Immelman it is swollen, with one end rounded and the other more pointed (Figure 1B). The terminal cell of *J. cuneata* subsp. *hoerleiniana* is either smooth or ornamented. Rarely, a branched trichome was encountered, as in *J. capensis* Thunb. (Figure 1D). The cells of the upper tiers are usually ornamented, except in those trichomes found on the inner surface of the calyx lobes. The ornamentation is striate to papillose (Figure 1E, cf. Figure 1F) but, as these types intergrade, no attempt was made to draw a distinction between them. The area of the joint between two cells is smooth and not ornamented except for a ring of vertical striations (Figure 1G).

In a number of taxa the eglandular and glandular trichomes form discrete layers with the eglandular being the longer, e.g. in *J. protracta* subsp. *protracta* (Figure 1K).

2. Glandular trichomes: two main types were recorded, peltate and stalked glands.

2.1 Peltate glands (Figure 2A–C; type ‘B’ in Table 1)

These glands consist of a solitary basal cell set as a wedge into the epidermis (Figure 2B). The head, set on the basal cell, is broad and flattened, and is probably four-celled. No sections were cut to confirm this, but the head is marked with two lines at right angles (probably cell walls, Figure 2A). The top of the head is sometimes marked with a faint ring where the lines cross. In *J. anagalloides* (Nees) T. Anders. (Figure 2C), each cell of the head has a single papilla on the outer edge. This feature is unique among the species of *Justicia* seen in this study.

2.2 Stalked glands (Figure 2D–G; type ‘C’ in Table 1)

The basal cell of stalked glands is similar to that of the peltate glands.
The stalk varies in length (0.02 mm in *J. protracta* subsp. *rhodesiana* (S. Moore) Immelman to 1.56 mm in *J. petiolaris* (Nees) T. Anders. subsp. *petiolaris*) and in the number of cells, and is not ornamented. Long-stalked glands on certain organs are characteristic of some species, e.g. the bracts of *J. kirkiana*, *J. petiolaris* subsp. *petiolaris* (Figure 2E), and sometimes of *J. flava* (Vahl) Vahl, have very long glandular trichomes.

Below the head is a collar cell, which is shortly cylindrical and usually narrower than the rest of the stalk (Figure 2D).

The glandular heads are of various types, and are occasionally species-specific. In *J. betonica* L., for instance, the glands on the petiole (when present) have elongated clavate heads, while those on the calyx have the heads broad at the base and narrowing towards the apex (Figure 2G). In some species the head is longitudinally faintly striate (?cell walls). It is either the same width as the stalk and longer than wide (Figure 2E) or much wider than the stalk and wider than long (pin-shaped glands) (Figure 2D, F, G).

The number of cells in the head is uncertain, as no sections were cut, but accounts in the literature (Ahmad 1978) record from 1 to 17 cells in trichomes of the family.

**TAXONOMIC VALUE**

On the basis of indumentum morphology, *Siphonoglossa* could not be distinguished from *Justicia*. It was also not possible to delimit sections within these genera, or in the related genus *Monechma*, solely on indumentum features. Some of the trichome types Munday (1980) found in *Monechma* are very rare or absent altogether from the species of *Justicia* seen in this study. These types are glandular papillae with the tip not wider than the stalk, T-shaped eglandular trichomes, flattened uniseriate eglandular trichomes, and dendroid trichomes. Anvilshaped trichomes having broad flattened shoe-like heads were rare in *Justicia* but relatively common in *Monechma*. However, as none of these trichomes were exclusive to either of the genera, they cannot be used to distinguish them at generic level.

At species and subspecies level, however, the trichomes in *Justicia* provide many useful characters, and are sometimes characteristic of one or a few species. The following species, for example, have very long-stalked glands on the bracts: *J. kirkiana*, *J. flava* (Figure 2D), *J. dinteri* and *J. petiolaris* subsp. *petiolaris* (Figure 2E). In the case of *J. kirkiana* and *J. dinteri*, these glands give the bracts a cottony appearance. Some species, such as *J. parvibracteata* and *J. montis-salinarum*, are puberulous, with a dense indumentum of short, heavily ornamented trichomes. One species pair among the southern African species of *Justicia* is most easily distinguished on pubescence characters. Because differences also exist in other characters it seems reasonable to maintain these taxa at specific rank. They are *J. platysepala*, which has leaves with sparse to dense pubescence, whereas in the closely related *J. guerkeana* the leaves are usually completely glabrous. In *J. guerkeana* the leaves are also three-veined from the base and there is a difference in distribution.

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**FIGURE 2.** — Glandular trichomes, all × 600, except where otherwise stated. A, B, D, *J. flava*, Immelman 249: A, leaf, peltate gland; B, leaf base, peltate gland showing wedge-shaped basal cell; D, bract, stalked gland with long stalk, × 240. C, *J. anagalloides*, leaf base, peltate gland showing small protuberances at outer margin of each cell; E, *J. petiolaris*, calyx, stalked gland with long stalk; F, *J. protracta* subsp. *protracta*, inner surface of calyx, stalked gland with short stalk, Baldovil s.n.; G, *J. betonica*, calyx, stalked gland with short stalk, Immelman 178.
The pubescence is the most reliable morphological feature for distinguishing certain subspecies. Because there was also a degree of geographical separation, they were recognized at subspecific rank. *J. cuneata*, for example, has the following three subspecies: subsp. *latifolia* is glabrous except on the stems and on the inside of the calyx lobes, subsp. *cuneata* is densely puberulous on all vegetative parts as well as the exterior of the calyx, and subsp. *hoerleiniana* has a dense covering of broad-headed anvil-shaped trichomes. Another example, *J. protracta* subsp. *protracta*, has multicellular eglandular trichomes averaging 0.47 mm in length (on the leaf lamina), whereas in subsp. *rhodesiana* the whole plant is densely puberulous with short, two-celled eglandular trichomes, of which the average length (on the leaf lamina) is 0.04 mm. *J. orchioides* subsp. *orchioides* has stiff opaque white trichomes on stem and leaves while subsp. *glabrata* is glabrous.

In *Justicia*, four taxa from arid areas have dense to moderately dense long pubescence: *J. dinteri*, *J. anseliana*, *J. guerkeana* and *J. cuneata* subsp. *hoerleiniana*. The last taxon, a woody shrub, has an indumentum type unique in the genus, though present in the related *Monechma*. The very dense eglandular trichomes have large swollen shoe-shaped heads which sit at 45–90° to the stalks.

In some taxa, the indumentum is reduced or even lacking (except for the sessile glands, see Table 1). Examples are *J. orchioides* subsp. *glabrata*, *J. crassinervis* and *J. odora*.

**ECOLOGICAL SIGNIFICANCE**

A number of probably closely related pairs of *Justicia* species or subspecies are known of which one member occurs in a more arid environment, and possesses an indumentum markedly different from that of the other. These are *J. montis-salinarum* and *J. betonica*, *J. protracta* and *J. dinteri*, *J. protracta* and *J. parvibracteata*, *J. protracta* subsp. *protracta* and *rhodesiana* and *J. cuneata* subsp. *cuneata* and *hoerleiniana*. The last taxon occurs in the most arid environment of any of the southern African taxa of *Justicia*, in the Sperrgebiet of southern Namibia.

Johnson (1975), after reviewing the evidence for the presence and density of pubescence in geographical areas of different moisture stress, concludes that 'It thus seems clear that ecogeographic relationships of pubescence must involve factors in addition of moisture. It is even possible, he suggests, that the presence of trichomes increases the rate of transpiration, and that their function may rather be to act as a light shield in areas with intense radiation. Uphof & Hummel (1962) make a similar suggestion, though they stress that experimental proof is lacking. The bent shape and heavier ornamentation of trichomes of some species would seem to add to the effectiveness of such trichomes as light shields. They state: '... the faculty to function as a screen against the light would depend on the presence of a large number of light-dispersing centres. The latter may be present in the form of knobs on the cell-wall or on the cuticle only or in that of more or less sharp bends in the trichomes.'

This provides a possible explanation for the predominance of short dense pubescence, consisting of bent trichomes having heavy ornamentation, in many of those species of *Justicia* occurring in arid or semi-arid areas.

Species with such a dense puberulous indumentum in which the trichomes are shorter and more heavily ornamented than is generally found in species from moister areas include *J. cuneata* subsp. *cuneata* (W Karoo), *J. protracta* subsp. *rhodesiana* (Namibia, Botswana, N Transvaal, Zimbabwe), *J. parvibracteata* (N Cape) and *J. montis-salinarum* (Outpansberg of the Transvaal). When examined under a dissecting microscope these species all appear minutely puberulous. When the trichomes are examined under the SEM, they are seen to be reduced to (1)2 cells. If the trichome is 2-celled, then the upper cell is at an angle to the basal cell. The whole surface is heavily ornamented with papillae, which are noticeably denser and more projecting than in other species of the genus.

*Monechma*, a genus predominantly of dry areas, was found by Munday (1980) to have many species with puberulous leaves, especially those occurring in the southern part of Namibia. There are, however, exceptions to this tendency, as in *Justicia*, where *J. orchioides* subsp. *glabrata* from the Karoo is glabrous.

Taxa with reduced or even lacking indumentum (except for the sessile glands) (see Table 1) are found in both arid regions (e.g. *J. orchioides* subsp. *glabrata* from the Karoo), and in moist, even marshy, habitats, e.g. *J. crassinervis*, *J. odora* and sometimes *J. capensis*.

It is considered probable that the function of the trichomes in reflecting light is more significant than in water conservation, and their shape and ornamentation may be important in this regard. However, no clear-cut picture has emerged, where a single type of indumentum (or even its absence) could be consistently correlated with aridity or geographical distribution.

**CONCLUSIONS**

Two basic types of trichomes were found: eglandular and glandular. In most species both types are present. It was not possible to distinguish genera or sections on the basis of indumentum morphology. At species and subspecies level, however, trichomes provide many taxonomically useful characters. No clear-cut correlation was found between indumentum and habitat, but a predominance of short, dense pubescence was noted in many *Justicia* species from arid and semi-arid areas.

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