

# Studies in the *Justicia* and *Siphonoglossa* (Acanthaceae) species of southern Africa: final conclusions

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## ABSTRACT

On the basis of seed surface micromorphology, pollen and inflorescence type, as well as characters of the capsule, seven sections can be distinguished in the southern African species of *Justicia*. The relationship of these to the sections recognised by Graham is discussed. A key to the sections and a synopsis of their main distinguishing characters are presented. One new section, sect. *Minima* Immelman, is described. A short note on the generic position of the *Siphonoglossa* species of the region, following on from a previous paper, is also given.

## UITTREKSEL

Op grond van saadoppervlak-mikromorfologie, stuifmeel en bloeiwysetipe, sowel as kenmerke van die kapsule, word sewe seksies onder die Suider-Afrikaanse *Justicia*-spesies onderskei. Die verwantskap van die seksies met dié van Graham word bespreek. 'n Sleutel tot seksies en 'n oorsig van hul belangrikste onderskeidende kenmerke word gegee. Een nuwe seksie, seksie *Minima* Immelman, word beskryf. 'n Kort nota oor die generiese posisie van die *Siphonoglossa*-spesies van die streek, wat volg op 'n vorige artikel, word ook gegee.

## INTRODUCTION

In the preceding four papers on the southern African species of *Justicia* and *Siphonoglossa*, the various states of indumentum, pollen and seed surface were described. Their possible value both in identifying species and delimiting sections within *Justicia*, was discussed. One of the points made throughout was that none of these organs could be used in isolation in the delimiting of sections.

The species studied were chosen on the basis of their geographical distribution rather than as being (putatively) representative of the whole genus. As was stated by Graham (1988), small sample size created difficulties in the delimitation both of sections and of the genus *Justicia*. She studied 58 species in detail, but concluded that 'It is over-optimistic to hope that all the remaining known species of *Justicia* will fit neatly into the sectional classification proposed here .... However, it is hoped that this study will provide the basis for future work.' The present study of the southern African representatives of *Justicia* and the closely related genus *Siphonoglossa* used Graham's work as a starting point for discussion, since it gives a worldwide perspective on the genus. Graham's sectional treatment will be discussed in the light of results obtained from the detailed study of the  $\pm 30$  southern African taxa traditionally included in *Justicia* and *Siphonoglossa*.

Some confusion surrounds the designation of a type species in *Justicia*. A summary of the problems involved was given by Stearn (1971), and the problem is also dealt with by Graham (1988). She considered the type species to be *J. hyssopifolia* L., as did Hedrén (1989), and this decision is followed here.

## METHODS

All southern African taxa traditionally included in *Justicia* and *Siphonoglossa* were studied, and sections elucidated. The area termed 'southern Africa' is that defined by the *Flora of southern Africa*, i.e. the area south of the Cunene and Limpopo Rivers, including Botswana.

Dried material was examined from the following herbaria: BOL, GRA, KMG, KNP, NBG, NH, NU, SAM, STE and WIND. Living material was collected on trips to the northern Transvaal, northern Natal and Zululand, the eastern Cape and the north-central part of Namibia. Some of this material was grown in the nursery of the National Botanical Institute, Pretoria.

Seed testa surface, indumentum and pollen were examined under the Scanning Electron Microscope. Inflorescence structure was also examined. Various characters of leaves, bracts, calyx, corolla, capsules and habit were taken into consideration in the conclusions reached. Nomenclature of the sections was taken from Graham (1988), and her sectional synonymy and type species are not repeated here.

## RESULTS AND DISCUSSION

In this series of studies, striking correlations between inflorescence form, seed testa morphology and pollen were found in the genus. Largely on this basis, the species studied could be grouped into seven sections, one of them new.

The primitive inflorescence is considered to probably be a thyrses which has been reduced in various ways. Where it has been reduced to sessile cymes/single flowers, these are in some cases re-aggregated to form a more or less dense, terminal synflorescence.

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The pollen in the genus is three- or two-colporate or two-porate, with entire or areolate margocolpi. The sexine is reticulate to lophate in all species, with a pseudocolpus (colpoid streak) on either side of the colpus (Immelman 1989a). The area between the colpus and the pseudocolpus (the margocolpus, see Immelman 1989a) is either entire or divided into circular areolae. In the southern African taxa, as well as in seven tropical African species examined later, the inflorescence and pollen types are closely correlated and valuable in dividing the genus into sections.

Seed surface, described simply as 'rough' in earlier accounts of the genus, is one of the characters that is used to distinguish *Justicia* from the related genus *Monechma* Hochst. (Munday 1980). It is, however, very varied in *Justicia*, and under the SEM reveals a number of useful characters, a fact also noted by Graham (1988). In a number of cases seed surface also correlates with the sections, which lends weight to their naturalness. It is considered unlikely that a number of characters, taken from three different organs, viz. pollen, inflorescence and seeds, would have evolved in parallel.

A number of other characters were considered, and some were found to reinforce these divisions, especially capsule texture. Capsule shape is mainly useful at generic level. Munday (1980) considered a clavate capsule characteristic of *Monechma*, as it was constant in the genus, being correlated with the two-seeded condition. Some *Justicia* species (also two-seeded) also have this type of capsule, but in most cases it can be used to distinguish the two genera. (It is possible that *Monechma* should be considered congeneric with *Justicia*, as no one character or combination of characters could be found to completely separate the two genera, but this will not be discussed here.)

The capsule of *Justicia* is usually cylindrical-clavate with an apiculate apex and a short or long stipe. The stipe is laterally flattened. The fertile portion contains four seeds, sometimes reduced to two or one, each subtended by a hook-shaped retinaculum. The texture of the capsule varies from woody and thick-walled (sects. *Raphidospora*, *Justicia*) or papery and thin-walled (sects. *Tyloglossa*, *Minima*), most species of sect. *Harnieria* and sect. *Ansellia*. Intermediate between these two extremes are the capsules of, for example, sect. *Betonica* and some species of sect. *Harnieria*.

As stated in the introduction, the sections were proposed on the basis of a study of southern African material only. However, *Justicia* is probably a tropical genus, with southern Africa being at the southern end of its distribution range in Africa and it was therefore considered important to assess whether the apparent pattern seen in the southern African species also existed north of the Cunene and Limpopo Rivers. As a test, therefore, seven tropical species (listed in Immelman 1989a) were selected from a number of the sections, their probable section being first assessed by examining the type of inflorescence present. The pollen of each was then viewed under the SEM and it was found that in every case it was of the pollen type expected for the section in which they had provisionally been placed (Immelman 1989a). It was not, unfortunately, possible to examine seeds of the species.

#### KEY TO SECTIONS IN SOUTHERN AFRICAN SPECIES OF *JUSTICIA*

- 1a Pollen three-colporate; inflorescence of pedunculate lax axillary cymes, or sessile condensed cymes aggregated into a terminal inflorescence:
- 2a Pollen with entire margocolpi:
  - 3a Seeds one per capsule, smooth; inflorescence a simple axillary cyme; flowers with a pouched throat ..... II sect. *Justicia*
  - 3b Seeds 2–4 per capsule, rough; inflorescence a terminal or axillary simple cyme or a compound axillary cyme; flowers without a pouched throat:
    - 4a Inflorescence terminal, an aggregate of sessile cymes, each usually reduced to a single flower; seed testa with shortly sinuate-dentate pattern ..... III sect. *Betonica*
    - 4b Inflorescence axillary, a lax branching raceme-like compound cyme; seed testa either with long barbed scales or reticulate with each cell outlined by minute papillae ..... I sect. *Raphidospora*
- 2b Pollen areolate:
  - 5a Calyx four-lobed; inflorescence a terminal elongated 'spike'; seeds without crystals in testa; flowers small and white ..... V sect. *Minima*
  - 5b Calyx five-lobed; inflorescence a terminal aggregate of sessile cymes; seeds with crystals in testa; flowers medium to large, yellow or blue ..... IV sect. *Tyloglossa*
- 1b Pollen two-colporate or two-porate; inflorescence of axillary lax or condensed cymes:
  - 6a Pollen with entire margocolpi; shrubs, sometimes woody; cymes often reduced to a single axillary flower; bracts and leaves often reduced ..... II sect. *Justicia*
  - 6b Pollen areolate; plants herbaceous or shrubby; inflorescence rarely reduced to a single flower:
    - 7a Pollen porate, small (22–36  $\mu\text{m}$  long); inflorescence an axillary elongate 'spike'; flowers white, small; herbaceous; seeds irregularly rugose at high magnifications ..... VII sect. *Ansellia*
    - 7b Pollen colporate, medium-sized (34–60  $\mu\text{m}$  long); inflorescence of axillary sessile cymes; flowers and habit various; seeds usually papillate at high magnifications, sometimes reticulate ..... VI sect. *Harnieria*

I. Sect. **Raphidospora** (Nees) T. Anders. (sect. III in Graham: 587). Species included: *J. glabra* Koenig ex Roxb., *J. campylostemon* (Nees) T. Anders.

*Inflorescence* of axillary laxly-branching thyrses. Pterophylls and prophylls reduced, subulate. *Pollen* 3-colporate, with entire margocolpi. *Capsule* relatively large, hard and woody, with a long stipe. *Seeds* four, reticulate or with long barbed scales.

The inflorescence and pollen are considered in most respects to be the most primitive in southern Africa. The seeds of the two southern African species, however, differ greatly and, in *J. glabra* at least, may be considered highly advanced, as they are covered with long barbed scales (Immelman 1990a).

All except one species of *Justicia* seen have anthers with the lower locule spurred, *J. campylostemon* being an occasional exception. A few specimens were seen where the anther locules were not spurred, but only mucronate. This is the regular condition in *Siphonoglossa*. However, as this is variable within *J. campylostemon*, and its other characters are typical of *Justicia*, it was not considered a species of *Siphonoglossa*.

From the three-colporate pollen with entire margocolpi and the laxly branching inflorescence of sect. *Raphidospora*, a number of lines of specialization can be traced.

II. Sect. **Justicia** (sect. VI in Graham: 595). Species included: *J. bolusii* C.B. Cl., *J. orchioides* L.f., *J. cuneata* Vahl, *J. thymifolia* (Nees) C.B. Cl., *J. guerkeana* Schinz and *J. platysepala* (S. Moore) P.G. Mey.

*Inflorescence* of stout-peduncled axillary elongated thyrses or nearly sessile or flowers solitary, pedicelled or sessile. Pherophylls and prophylls reduced and subulate or large and lanceolate to broadly obovate. *Flowers* hooded or upper line straight, with or without pouched throat. *Pollen* two- or three-colporate, with entire margocolpi. *Capsule* relatively large, hard and woody, with a long stipe. *Seeds* one (two), smooth or rough. Shrubby, in *J. bolusii* with suckers from stems below ground.

*J. bolusii* is a rare eastern Cape endemic, and in flowers, seeds and pollen, differs from other species of the section in the southern African region. The pollen type is the same as sect. *Raphidospora*. *J. bolusii* and *J. campylostemon* were formerly placed together in sect. *Gendarussa* by Clarke (1901) (= sect. *Raphidospora*), but *J. bolusii* differs from both *J. campylostemon* and *J. glabra* in the single smooth seed, the pouched corolla throat and the unbranched inflorescence.

*J. bolusii* is probably most similar to some East African species of *Justicia*, e.g. *J. cordata* (Nees) T. Anders., a common species in East Africa. *J. bolusii* and *J. cordata* are very similar in appearance, both have a pouched throat in the corolla, a clavate capsule and a similar inflorescence, in addition to the unusual smooth seeds. Graham (1988) states that the pollen of *J. cordata* is 2-colporate, but under the SEM, it was seen to be 3-colporate as in *J. bolusii* (Immelman 1989a). It is reasonable to surmise that the section to which *J. bolusii* and *J. cordata* belong was once more widely distributed in Africa, *J. bolusii* being a relict of this distribution.

The pouched corolla throat of *J. bolusii* and *J. cordata* is like that described for *Monechma* (Munday 1980) and so are the 1- or 2-seeded capsules and smooth-surfaced seeds. It was therefore considered whether *J. bolusii* should not be better placed in that genus than in *Justicia*, but the inflorescence and pollen are not like those of *Monechma*. *Monechma* usually has sessile cymes or single sessile or pedicellate flowers and has two-colporate areolate pollen, whereas *J. bolusii* has inflorescences as described above and 3-colporate pollen with entire margocolpi. The one or two smooth seeds and pouched corolla throat are considered to be a parallel adaptation in *Monechma*, rather than indicating relationship between it and *J. bolusii*.

Sect. *Justicia* sensu Graham (1988) also includes *J. orchioides* L.f. and *J. platysepala* (S. Moore) P.G. Mey. This has been accepted here with some hesitation, as it is felt that differences exist. However, the whole of sect. *Justicia* is in need of revision, which would have to include more tropical African species. Graham states that *J. orchioides* and *J. platysepala* have 'type 4' pollen, i.e. 2-porate with two raised bands (entire margocolpi), which applies to these species but not to *J. bolusii* or *J. cordata*, which are both 3-colporate. These two groups do not resemble each other in inflorescence or seed testa either. It is possible to place them in separate sections.

Within the second group (*J. orchioides*, *J. thymifolia*, *J. platysepala* and *J. guerkeana*) there is a tendency to increased woodiness and to a reduction in the size of the bracts and the number of flowers in the cyme, the three trends progressing together. *J. guerkeana* and *J. platysepala* have numerous flowers in the cyme, broad bracts with green centres and white membranous margins, and rather soft shrubby stems, whereas *J. thymifolia* is woody, has small bracts and still has multiflowered cymes. *J. orchioides* and *J. cuneata* invariably have small bracts, solitary axillary flowers and are hard-stemmed (in *J. orchioides* sometimes spiny) shrublets. It is not suggested that any of these is the direct ancestor of any other species.

III. Sect. **Betonica** (Nees) T. Anders. (sect. II in Graham: 585). Species included: *J. betonica* L., *J. montis-salinarum* A. Meeuse.

*Inflorescence* a terminal spike-like aggregate of axillary cymes reduced to 1(3) flowers each. Pherophylls and prophylls reduced and subulate or large and green-veined. *Pollen* 3-colporate, with entire margocolpi. *Capsule* relatively large, semi-woody, with a long stipe. *Seeds* 4, rough.

The common and widespread *J. betonica* (South Africa to India) and the narrowly endemic *J. montis-salinarum* (Soutpansberg of the Transvaal) have pollen similar to that of sect. *Raphidospora*, being 3-colporate with entire margocolpi, but the cymes have been reduced to 1 (rarely 3) axillary flower(s) each. These flowers have been secondarily aggregated to form a dense, terminal 'spike'. In *J. betonica* there are large, colourful, imbricate pherophylls and prophylls, whereas in *J. montis-salinarum* there appears to have been even further reduction, with both pherophylls and prophylls being small and subulate. In both species, the seed testa is drawn into sinuate, dentate structures, which in *J. betonica* have a micro-structure of colliculate individual cells and in *J. montis-salinarum* are finely striate. A sinuate or dentate testa was not seen in any other species in the genus. Although the two species placed in this section are very different superficially, their similar pollen and inflorescence structure, and their distinctive seed testa, indicate they should be placed together.

IV. Sect. **Tyloglossa** (Hochst.) Lindau (sect. IV in Graham: 390). Species included: *J. petiolaris* (Nees) T. Anders. (with three subspecies), *J. flava* (Vahl) Vahl and *J. kirikiana* T. Anders.

*Inflorescence* terminal, a dense or lax aggregate of sessile axillary cymes. Pherophylls and prophylls reduced, oblanceolate to obovate. *Pollen* 3-colporate, areolate. *Capsule* of medium size, texture papery, stipe short. *Seeds* 4, reticulate, with crystals in testa.

This is a well-defined section, one of the major unifying characters of the section being the seeds, which under the SEM are seen to have one to many cubic or rectangular crystals in each cell of the testa. This character is unique to the section. The pollen is 3-colporate and areolate.

The inflorescence in the section is basically composed of sessile cymes, as in the preceding section, but these are aggregated into a terminal compound 'spike' with

numerous flowers at each node. The pherophylls and prophylls are somewhat reduced, usually spatulate and often with very long-stalked glandular hairs (Immelman 1990b). Though the inflorescence type of *J. petiolaris* subsp. *incerta* and subsp. *bowiei* tends towards that of the sect. *Harnieria*, being more open than in subsp. *petiolaris*, the pollen and seeds are quite different from those of sect. *Harnieria*.

V. Sect. **Minima** *Immelman*, sect. nov. Type species: *J. minima* A. Meeuse.

*Inflorescentia* terminalis elongata simplex spiciformis e cymis flore solitario redactis composita. Pherophylla prophyllaque redacta subulata. *Calyx* quadrilobatus. *Pollinis* grana tricolporata areolata. *Semina* quatuor, testa reticulata.

*Inflorescence* a terminal, elongate, unbranched spike-like aggregate of cymes reduced to a single flower each. Pherophylls and prophylls reduced and subulate. *Calyx* four-lobed. *Pollen* 3-colporate, areolate. *Seeds* 4, testa reticulate.

*J. minima* is a rare endemic from the Waterberg of the Transvaal. It is not here considered closely related to any of the southern African species, and its affinities probably lie north of the South African border. Its pollen is similar to, though much smaller than that of sect. *Tyloglossa* (above), but its inflorescence is a terminal, unbranched, lax 'spike' (actually a reduced series of cymes forming a terminal inflorescence) similar to that of sect. *Ansellia*. Both pherophylls and prophylls are greatly reduced, and the calyx is four-lobed. The reticulate micro-pattern of the seed surface did not aid in placing the seed surface, as the reticulate pattern is scattered in the genus, e.g. *J. campylostemon* and *J. capensis* Thunb., and therefore was not considered significant. This species does not key out in Graham's key to sections, the nearest being sect. *Rostellaria* subsect. *Anisostachya* (if the bracts are ignored) or subsect. *Ansellia* (if the number of calyx lobes, the pollen and the details of the seed are ignored).

VI. Sect. **Harnieria** (*Solms-Laub.*) *Benth.* (sect. V in Graham: 591). Taxa included: *J. capensis* Thunb., *J. protracta* (Nees) T. Anders. (with two subspecies), *J. heterocarpa* subsp. *dinteri* (S. Moore) Hedrén, *J. parvibracteata* Immelman and *J. odora* (Forssk.) Vahl. A very complete synonymy for the section is given in Hedrén: 62 (1989).

*Inflorescence* of scattered sessile axillary cymes, or these reduced to a single flower. Pherophylls and prophylls foliose, bracteoles reduced and subulate or absent. *Pollen* 2-colporate, areolate. *Capsule* of medium size, texture papery, stipe short or, in one species, hard and woody with long stipe (*J. cuneata*) with *J. odora* and *J. capensis* intermediate. *Seeds* 4, or only one in the dimorphic capsules of *J. heterocarpa* subsp. *dinteri* and (rarely) *J. protracta* subsp. *protracta*. Seed surface varied, usually papillate or reticulate.

Both pollen and inflorescence in this section are specialized with respect to the condition seen in sect. *Raphidospora*, the pollen being 2-colporate and areolate and the inflorescence reduced to pedunculate or sessile

axillary cymes with up to five flowers, scattered in the leaf axils. The seeds of four of the five species in the section have a micro-pattern of a single papilla in the centre of each cell of the testa, but in *J. capensis* the seed testa is reticulate. I would agree with Hedrén (1989) in considering *J. capensis* and *J. odora* as belonging in sect. *Harnieria*, while being in some respects very different from the majority of species in the section.

A feature of interest in this section is the dimorphic capsules that are present in two members, regularly in *J. heterocarpa* subsp. *dinteri* and encountered once in *J. protracta* subsp. *protracta*. These are also occasionally seen in *Siphonoglossa leptantha* (Nees) Immelman subsp. *leptantha*. Specimens of *J. protracta* and *S. leptantha* showing this condition are preserved at PRE and NU (*Balkwill* 217 (NU), *Balkwill* 649 (NU, PRE), *Immelman* s.n. (630291 in PRE)). As well as the normal four-seeded capsule, a smaller, one-seeded, non-opening (indehiscent) capsule is produced, with four irregularly serrate wings. The seed does not differ from those in the normal capsules except in being larger (Immelman 1990a). This was also seen by Hedrén (1989) in a number of tropical African taxa in sect. *Harnieria*. The possession in common of a specialised type of capsule is evidence of a close relationship between *Justicia* sect. *Harnieria* and *Siphonoglossa*.

The seed of *Siphonoglossa*, like that of most of the species of sect. *Harnieria*, is papillate, the pollen is similar, and its inflorescence is also of many-flowered scattered sessile axillary cymes. In Hedrén (1989), the *J. striolata* species group of sect. *Harnieria* corresponds to *Siphonoglossa* as recognised by me (non Oerst, Immelman 1989b), and he has placed *Siphonoglossa* sensu Moore non Oerst. in the synonymy of sect. *Harnieria*. He found it to separate rather widely from the rest of the section on MDS ordination, but nevertheless retained it in *Justicia* sect. *Harnieria*. Though I gave it as my opinion (Immelman 1989b) that there are reasons for not combining the two genera, if *Siphonoglossa* sensu Moore is placed in *Justicia*, I feel it might best be as a separate section close to sect. *Harnieria*.

Note on the genus *Siphonoglossa*: when I published my paper on *Siphonoglossa* and *Aulojusticia* (Immelman 1989b), I was not aware of the existence of a series of papers by Henrickson & Hilsenbeck (1979) and Hilsenbeck (1990a, 1990b) on the South American representatives of *Siphonoglossa*. Hilsenbeck's opinion is that there are three, or possibly four diverse taxa included under the name *Siphonoglossa*, which are held together mainly by having in common a long narrow corolla tube (Hilsenbeck 1990b).

After comparing the South African species with his descriptions of the South American taxa, I would agree that they do not belong together in a common genus, separate from *Justicia*. Rather the South African (and other African) taxa should be placed either in a section/sub-section of *Justicia* (the latter being the course followed by Hedrén), or in a genus with a name other than *Siphonoglossa*, the type species of *Siphonoglossa* being a South American species. *Aulojusticia*, which already exists, would be a suitable name. Before either of these is done, however, it would be necessary to compare the South African species with the South American species and the tropical African species placed in *Justicia*

sect. *Harnieria* species group *J. striolata* by Hedrén, looking especially at pollen, inflorescence structure and seed testa.

VII. Sect. *Ansellia* (C.B. Cl.) *Ensermu*. Species included: *J. anselliana* (Nees) T. Anders., *J. crassiradix* Burkill & C.B. Cl. and *J. anagalloides* (Nees) T. Anders.

Sect. *Rostellaria* T. Anders. subsect. *Ansellia* (C.B. Cl.) V.A.W. Graham (sect. VIIb in Graham: 598).

*Inflorescence* axillary, an elongated, slender-peduncled spike-like aggregate of cymes reduced to a single flower each. Pterophylls and prophylls greatly reduced, subulate. *Pollen* 2-porate or shortly 2-colporate, areolate. *Capsule* of medium size, texture papery, stipe short. *Seeds* 4, rough. Herbaceous, may be annual or creeping and rooting at the nodes.

This well-defined section has inflorescence and flowers resembling those of the sect. *Minima*, but the inflorescences are axillary not terminal, the calyx is five- not four-lobed and the pollen is quite different. The two upper (adaxial) lobes of the calyx are noticeably longer than the three lower (abaxial) lobes. The pollen, which is the smallest in the genus in southern Africa, is areolate and either 2-porate or shortly 2-colporate. In *J. crassiradix* there were short colpi present and it is considered probable that the porate condition seen in *J. anagalloides* and *J. anselliana* is derived from the colporate by gradual reduction of the colpus length.

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