

Taxonomic studies in the Acanthaceae: A reappraisal of the genera *Duvernoia* and *Adhatoda* in southern Africa

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A reappraisal of floral and vegetative characters of southern African species of *Adhatoda* Miller and *Duvernoia* E. Mey. ex Nees is made with reference to selected tropical species of *Adhatoda* and to species of the closely related genus *Justicia* L. The generic status of *Duvernoia* is confirmed and the generic characters expanded. The southern African species of *Adhatoda* are clearly distinct from *Duvernoia*. Their relationship to the tropical members cannot be assessed until a full revision of the genus is undertaken. *S. Afr. J. Bot.* 1985, 51: 475–484

'n Herevaluering van die blom- en vegetatiewe kenmerke van Suider-Afrikaanse spesies van *Duvernoia* E. Mey. ex Nees en *Adhatoda* Miller word gedoen met verwysing na geselekteerde tropiese spesies van *Adhatoda* en na spesies van die naverwante genus *Justicia* L. Die generiese status van *Duvernoia* word gehandhaaf en die generiese kenmerke uitgebrei. Die Suider-Afrikaanse spesies van *Adhatoda* is duidelik van *Duvernoia* afgebaken. Totdat 'n volledige hersiening van die genus voltooi is, kan hulle verwantskap met tropiese lede nog nie ge-evalueer word nie. *S.-Afr. Tydskr. Plantk.* 1985, 51: 475–484

Keywords: Acanthaceae, *Adhatoda*, *Duvernoia*, *Justicia*, taxonomy

Introduction

Duvernoia E. Mey. ex Nees, a genus of two species confined to south-east Africa, is closely related to, and often regarded as inseparable from, the widespread genus *Adhatoda* Miller. A brief review of the history of these two generic names and examination of the generic descriptions revealed that distinctions between them have often been confused. Their relationship with *Justicia* L. is also subject to debate. Therefore, an attempt was made to reappraise the characters that have been used to distinguish these genera in the past, using southern African species of *Adhatoda* and *Duvernoia* together with a limited number of specimens of tropical species of *Adhatoda* and a sample of southern African species of *Justicia*.

History of the genera

Although the name was first used in pre-Linnaean literature (Tournefort 1700), the genus *Adhatoda* was first described by Miller (1754) and recognized as distinct from *Justicia* L. Two species of the so-called malabar nut, both tropical Asian woody species, were described, but the formal publication of specific binomials was delayed until Nees' account of the genus included the combination *A. vasica*, which we now propose as the lectotype of the genus. The original generic description included reference to the hooded flower and bilocular fruit with heart-shaped seeds. *Duvernoia* was described by Nees almost 100 years later (1847). Here Nees described *D. adhatodoides*, the type species, very fully and included anther details. In the same publication, Nees considered the genus *Adhatoda* but his concept of this was evidently much broader than that of Miller (1754) for he included within it the Linnaean genus *Justicia* and species now regarded as members of *Monechma* Hochst. and *Siphonoglossa* Oersted. *Adhatoda sensu* Nees was distinguished from *Duvernoia* by its tailed anthers and five-partite calyx, whereas *Duvernoia* anthers lack tails and the calyx was described as four-partite. Bentham & Hooker fil. (1876) ignored differences in anther appendages and amalgamated the two genera under *Adhatoda*. Lindau (1895), basing his generic concepts largely on pollen characters, reassorted the species into an expanded concept of *Duvernoia*, which included some species of *Adhatoda sensu* Nees, the balance being assigned to *Justicia* L. Clarke (1901) recognized two taxa, regarding them as subgenera of *Adhatoda* but remarked that its unusual calyx might be sufficient to support the recognition of the genus *Duvernoia*.

Brief references to these generic problems were made by Meeuse (1956) and Obermeyer (1962) but no detailed studies have been conducted recently. A re-examination of the generic



Commemorating the 75th Anniversary
of the University of Natal



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Accepted 27 June 1985

limits in this complex was therefore carried out to see if correlated features from diverse sources could replace the dependence on single-character classifications of the past. Nature of the pollen and of the anther thecae was not excluded, but was augmented by other data.

The study was based on southern African species of *Duvernoia* and *Adhatoda* and comparisons were drawn between these and some tropical species of *Adhatoda*, including representatives of the type species, *A. vasica*. In the absence of clear evidence of the type of *Justicia*, we used material of South African species currently regarded as true members of the genus (Clarke 1901) as a basis for this aspect of our comparisons. A list of the species selected is given in the Appendix.

Materials and Methods

Material for this study included herbarium specimens (see Appendix) and living material in cultivation locally or collected on field trips and preserved in 70% ethanol. This latter was particularly useful for studies of the inflorescences. Pollen was prepared for examination using a scanning electron microscope by shaking the pollen from dried anthers directly onto brass stubs covered with double-sided tape. Specimens were coated with gold-palladium and viewed in a Jeol 200X scanning electron microscope.

Characters appraised

Inflorescence

The organization of the inflorescence in the Acanthaceae has often been neglected or described superficially. This is

particularly true of those members in which the inflorescences are congested and branching is partly concealed by bracts and bracteoles. Detailed description is particularly difficult when only herbarium material is available. Nevertheless, where inflorescence structure has been analysed, it has proved to be a useful taxonomic tool.

Baden (1981) relied on this character to recognize sections within *Anisotes* Nees, Balkwill & Getliffe Norris (1985) found it valuable as a specific character in *Hypoestes* Soland. ex R. Br. and Immelman (1983) utilized it as one feature characterizing subdivisions within *Justicia*.

A synopsis of the inflorescence types was prepared after the dissection of each species and is presented in Figure 1.

A dichasium is assumed to be the ancestral form of these inflorescences and increase in the number of flowering nodes (Figure 1 A–C), is followed by the suppression of some of the higher order flowers. This is seen in the inflorescence of *A. robusta* C.B. Clarke (Figure 1D) where the former position of the missing flowers is indicated by residual bracts and bracteoles. From this point, we suggest that further suppression of the internodes of lateral branches and loss of the terminal buds could lead to the inflorescence of *D. adhatodoides* Nees (Figure 1E) and, with reduction of the paired lateral buds, to that of *D. aconitiflora* Meeuse (Figure 1F). Derived monochasia of *D. bolomboensis* De Wildeman (Figure 1Ei) and *A. engleriana* C.B. Clarke (Figure 1Fi) would be formed by the suppression of one of each pair of lateral buds in the original dichasium and further reduction in the number of lateral flowers produced. In *A. vasica* (not shown), the reduction proceeded even further and neither lateral bud

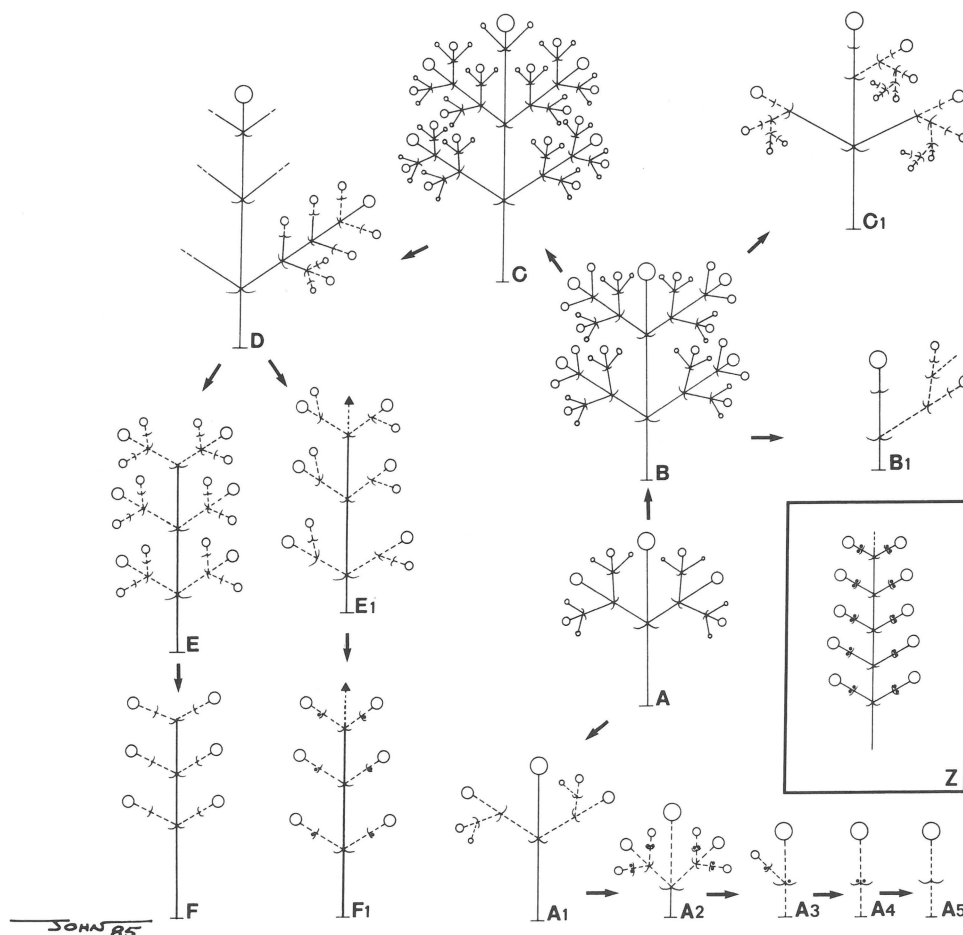
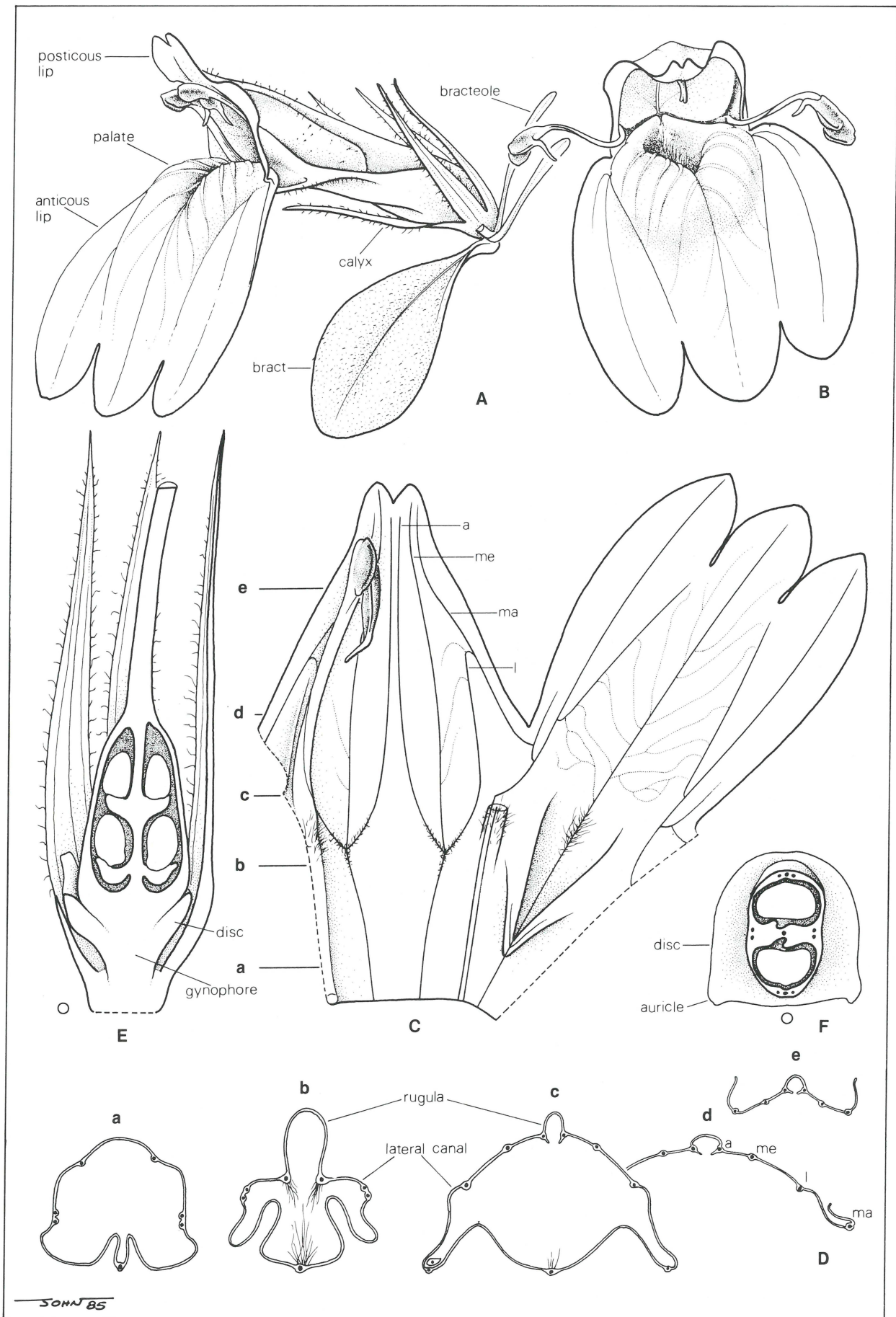


Figure 1 Synopsis of inflorescence types and their possible derivation from a compound dichasium (A). Two major lines of evolution are represented by the sequences A–A5 and A–F & Fi. A–C. Hypothetical ancestors, A1. *Adhatoda maculata*; A2–4. *Adhatoda andromeda* and *A. densiflora*; A5. *Justicia pallidior*; B1. *J. bolusii*; C1. *J. campylostemon*; D. *Adhatoda robusta*; E. *Duvernoia adhatodoides*; E1. *Adhatoda bolomboensis*; F. *Duvernoia aconitiflora*; F1. *Adhatoda engleriana*; Z. synflorescence of *Adhatoda andromeda* and *A. densiflora*.



○ position of bract

Figure 2 Floral organization in the tribe Justicieae: the flower of *J. petiolaris*. **A.** Flower, lateral view at anthesis; **B.** flower, anterior view after anthesis, showing the elongated style and the reflexed stamens; **C.** perianth opened out: a — axial vein, ma — marginal vein, me — median vein, l — lateral vein; **D.** transverse sections of the perianth sectioned at positions marked with matching letters in C; **E.** gynoecium in longitudinal section; **F.** ovary and disc in transverse section. Magnification: A–D × 4; E & F × 8.

is formed in the axils of the bracteoles. In these highly derived spike-like thyrsiform inflorescences, the opposition of flowers and their multibracteate condition distinguish them from true spikes.

The species of *Duvernoia* are well characterized, and separated from others examined, by the abortion of the first order apical bud, and represent an offshoot from one of the main lines of inflorescence evolution. Their particular form of spike-like inflorescences is unique and apparently not matched in *Adhatoda*. In addition, many species of *Adhatoda* with strobilate spike-like inflorescences have very large, broadly ovate bracts (*A. engleriana*, *A. schimperiana* Nees, *A. vasica*) quite unlike those of *Duvernoia*.

Two highly modified derivatives of early stages in this proposed sequence are the inflorescences of *J. bolusii* C.B. Clarke (Figure 1Bi) and *J. campylostemon* T. And.

The second trend is believed to involve the reduction of the dichasia to congested monochasia by the suppression of axillary buds, and the condensation of lateral axes. These reduced axillary inflorescences are aggregated into terminal synflorescences (A1–5). This line is associated with herbaceous perennials and thus is found in *Adhatoda andromeda* (Lindau) C.B. Clarke, *A. densiflora* (Hochst.) Manning as well as many species of *Justicia*.

Woody tropical species of *Adhatoda* have inflorescences of the sequence A–Fi, the exception being *Adhatoda maculata* C.B. Clarke (Figure 1Ai). *A. maculata* also differed florally from other species examined and its position in the genus may prove to be incorrect on further study.

Floral features

These attractive flowers have a common basic floral organization which is illustrated in Figure 2.

The bracteate flower is markedly zygomorphic and bilabiate with a distinct corolla tube convoluted below (Figure 2Da–e) and expanding abruptly into a bifid upper rugulate lip and a tripartite lower lip with a distinct palate which may be prominently swollen. The palate is often faintly coloured and the veins deeply coloured, probably functioning as nectar guides.

The flowers are markedly protandrous, the style remaining enclosed within the rugula until after anthesis when it extends (*Duvernoia*) or arches downwards (*Justicia*) to expose the stigma. The flowers of *Adhatoda* and *Justicia* are also hercogamous in that the filaments reflex after anthesis carrying the anthers away from the palate or, rarely, tucking them into the corolla throat (*J. protracta*). In *Duvernoia* the anther filaments are restricted by their position in lateral rugulae but elongate conspicuously so that the anthers descend onto the lower lip. This alteration of the position of the anthers correlated with protandry must favour xenogamy.

(i) Calyx

Despite Nees's statement (1847) that the calyx of *Duvernoia* was four-partite, we found five-partite calyces in this and all the genera studied. There is, however, a distinction between the deeply divided calyces of *Adhatoda* and the campanulate calyces of *Duvernoia* which have lobes approximately as long as the tube.

(ii) Corolla

Aspects of corolla symmetry and aestivation feature prominently in the subdivision of the family (Lindau 1895) and often serve to distinguish genera. Within the *Justicieae* the corolla is very uniform. In the course of this study,

however, attention was drawn to the form and venation of the upper lip (Figure 2C), the degree of subdivision and shape of the lobes of the lower lip and the nature of the palate. These subtle differences provided interesting taxonomic data.

The southern African and all but one tropical species of *Adhatoda* examined have markedly hooded, arched upper corolla lips without lateral channels, and with the lateral traces joining the marginal traces in the proximal half of the lip (Figure 2C). The lower lip is deeply or shallowly divided with a prominent rugose, channelled palate restricted to the hypochile (Figures 2B and 3B & C). *Adhatoda maculata* differed in that its palate was narrow and extended into the epichile and the lateral and marginal traces do not fuse (Figure 3A).

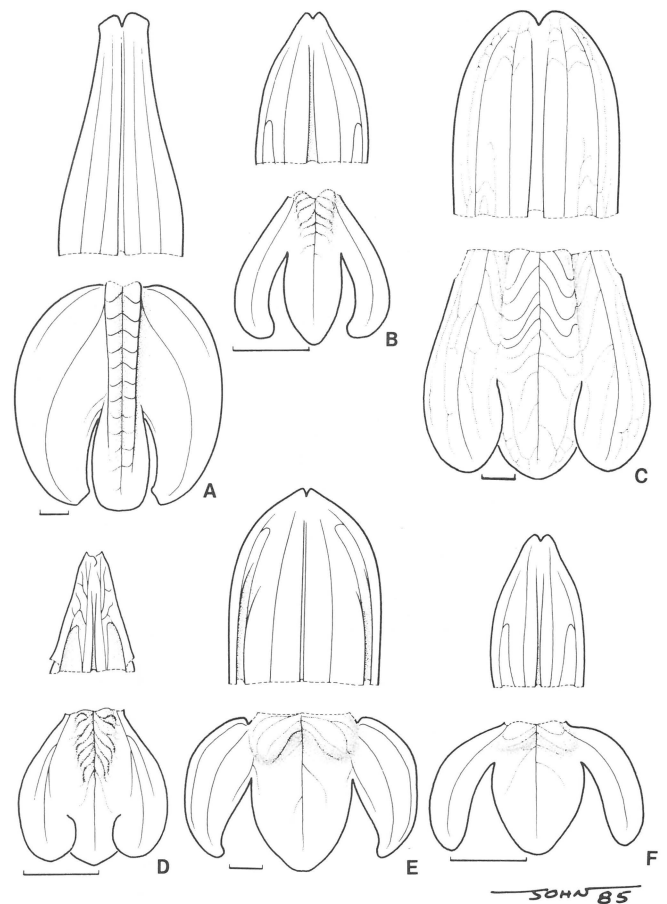


Figure 3 Upper and lower lips of the corolla of: A. *Adhatoda maculata*; B. *A. andromeda*; C. *A. vasica*; D. *Justicia protracta*; E. *Duvernoia aconitiflora*; F. *J. campylostemon*. Scale = 2 mm.

The upper lip of *Duvernoia* is shallowly hooded and possesses lateral channels in which the filaments are held (shaded in Figure 3E). The lateral traces of this lip fuse with the marginal traces very near to the apex (Figure 3E). The lower lip is divided at least half way and the lateral lobes are falcate. A smooth palate is raised into two tumuli (Figure 3E). This form of palate was also seen in *J. campylostemon* (Figure 3F) but other features of the corolla did not match those of *Duvernoia*. No *Justicia* species examined had lateral channels, nor were the lateral and marginal traces free for more than half their length. Although frequently as deeply divided as in *Duvernoia*, the lower lip differed in that the lobes were obtuse or truncate and not falcate (Figure 3D). Most southern African *Justicia* species have a rugose palate with conspicuous coloured veins (Figure 3D).

(iii) Anther

Characteristics of the androecium feature prominently in the taxonomy of the Acanthaceae. Stamen number is used at the subfamily level (Bremekamp 1965); the number of anther thecae distinguishes genera such as *Hypoestes* (monothecate) from the allied genera *Peristrophe* and *Dicliptera* (bithecate); the relative heights of the anther thecae distinguish between *Adhatoda* and *Duvernoia* (Dyer 1975) and the presence of anther appendages characterizes *Thunbergia* and *Hygrophila* and is a feature of the Justicieae.

Nees (1847) remarked on the spurred thecae of *Adhatoda* (including *Justicia*, *Monechma* and *Siphonoglossa* of other authors) and Burkill & Clarke (1900) also relied on this character.

Once again a careful comparison of this feature revealed that it is not a constant characteristic of *Justicia* although when used with caution it may help to distinguish this genus from *Duvernoia* and *Adhatoda*. Variants on the anther form in *Justicia* are illustrated in Figure 4 (A–D).

The length of the tail on the lower theca in *Justicia* is extremely variable. Those of *J. campylostemon* are so short that the anther is scarcely tailed, but this species is anomalous in other respects too. In all of the *Justicia* species examined, however, the anther thecae are disposed slightly one above the other. *Adhatoda* anther thecae are also obliquely inserted on the connective and at least the lower theca is briefly tailed (Figure 4E–G). The southern African species (Figure 4E) are very similar, in this respect, to the tropical species including the type *A. vasica*. In *Duvernoia* both anther thecae are slightly elongated but scarcely tailed (Figure 4H&I). The

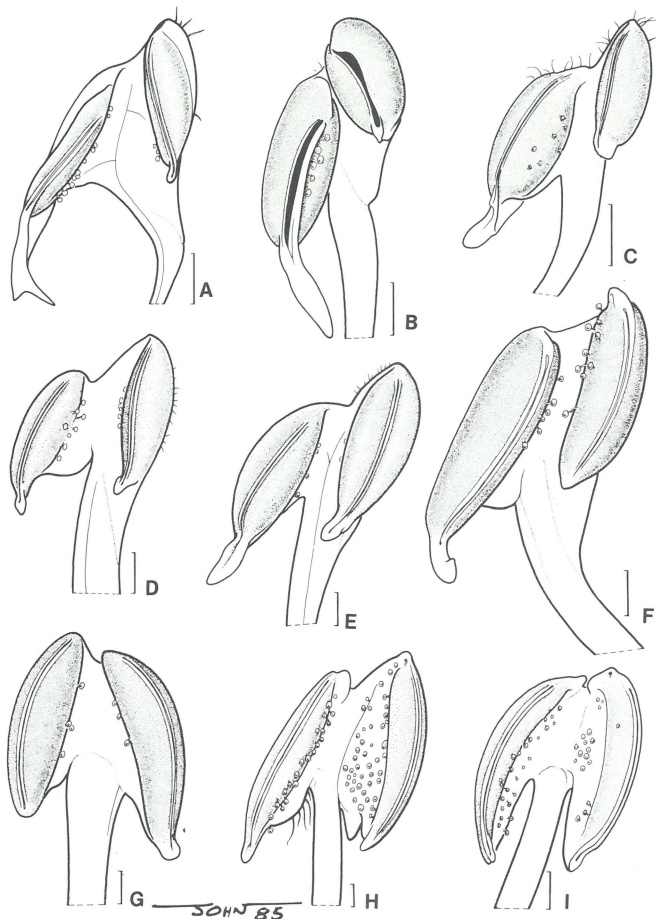


Figure 4 Anther form in: A. *Justicia campylostemon*; B. *J. bolusii*; C. *J. pallidior*; D. *J. protracta*; E. *Adhatoda andromeda*; F. *A. engleriana*; G. *A. vasica*; H. *Duvernoia adhatodoides* and I. *D. aconitiflora*. Scale = 0,5 mm.

character 'anther tailed' must therefore be used with caution.

(iv) Pollen

Radlkofer (1883) was the first to distinguish different pollen types in this eurypalynous family and Lindau (1895), with almost fanatical zeal, applied differences in pollen in his classification of infra-familial groups. Pollen studies are therefore a prerequisite of any taxonomic study in the family and are undoubtedly of immense value, although perhaps not as useful as generic markers at the tribal level. Lindau (*l.c.*), probably as a result of the limited number of species examined, described *Justicia* pollen as tuberculate, but recent studies (Immelman 1983) demonstrated that this is not invariably so. Indeed, most of the recent studied on pollen of acanthaceous genera have resulted in revisions of the original concepts of taxa within the family (De 1968; Baden 1981; Immelman 1983).

Within Justicineae, pollen is typically, and primitively, isopolar, prolate, 3-colporate with pseudocolpi (Baum *et al.* 1983) separated from the colpi by entire margocolpi ('colpoid streaks' *sensu* Immelman 1983, *et al.*). Apparently independently in the different genera, derived 2-aperturate grains and derived areolate margocolpi occur (Figure 5A).

Immelman (1983) reported that in *Justicia* pollen may be 2- or 3-aperturate, with entire or areolate margocolpi. *Adhatoda* pollen is 2-colporate with areolate margocolpi (Figure 5A) or 3-colporate with entire margocolpi (Figure 5B&C). The grains of southern African species are 3-colporate with entire margocolpi (Figure 5B&C) as are those of some of the tropical species studied (*A. maculata* and *A. robusta*). *A. vasica* pollen, and that of *A. schimperiana* and *A. engleriana*, is however 2-aperturate with areolate margocolpi. This is correlated with pedunculate, strobilate inflorescences and large imbricate bracts subtending showy flowers. On palynological and morphological grounds these three tropical species form a well defined group distinct from the remaining species ascribed to this genus. These three species constituted the section *Vasica* in Lindau's (1895) treatment of *Justicia*. *Duvernoia* pollen is 2-colporate with entire margocolpi (Figure 5D&E).

(v) Ovary, fruit and seed

Hitherto unrecorded characteristics of the ovary, fruit and nectariferous disc lend weight to the opinion that *Duvernoia* is a separate natural unit. The nectariferous disc in the two species of this genus is conspicuously cupulate and encloses almost half the ovary. The rounded, finely downy ovaries (Figure 6A&B) contrast markedly with the elongate, sparsely pubescent ovaries of the other species examined (Figure 6).

The nectariferous disc in species of *Adhatoda* is not as conspicuous (Figure 6C–F). *Justicia* species have distinctive auriculate discs (Figure 6G–J).

Within the Justicineae, stipitate fruits are the norm although in *Justicia* there is a series from long-stipitate through intermediates to sessile capsules (Figure 7A–D). The latter are not known in *Duvernoia* or *Adhatoda* and appear to be an apomorphic feature.

Crystals in the cells of the testa noted in *Justicia* by Immelman (1983) apparently do not occur in either *Duvernoia* or *Adhatoda*.

In *Duvernoia* the capsules have a stipe which is very long when compared with that in *Adhatoda* and a characteristic facies in dorsal view (Figure 7F) which is not found in other long-stipitate ovaries. These differences are of degree only but support the close relationship between *D. aconitiflora* and *D. adhatodoides* and their separation from other genera examined.

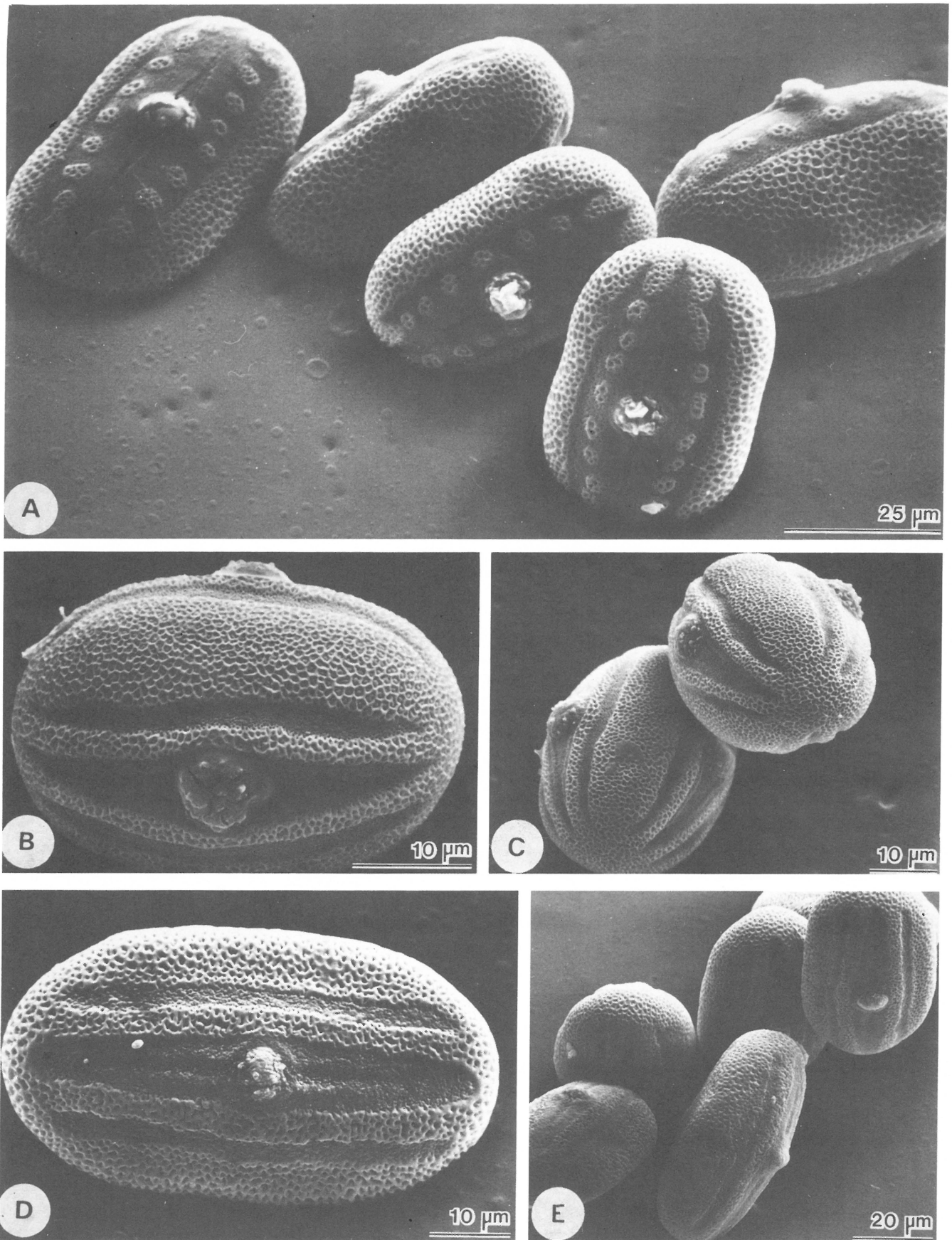


Figure 5 A. Two-aperturate pollen with areolate margocolpi of *Adhatoda* spp. (*A. schimperiana* Polhill and Paulo 984); B & C. three-colporate pollen with entire margocolpi of *A. andromeda* (Phelan 112); D & E. two-colporate pollen with entire margocolpi of *Duvernoia adhatodoides* (Balkwill & Manning 384).

Leaf epidermal features

The taxonomic and phylogenetic value of epidermal trichomes in the Acanthaceae have been demonstrated by many (Metcalf & Chalk 1950; Singh & Jain 1975; Ahmad 1978 and

references therein). In this study, we recognized three types of glandular and three types of eglandular trichomes on the leaves (Figure 8A – F). Most hair types were found in more than one of the genera under discussion, but type B trichomes

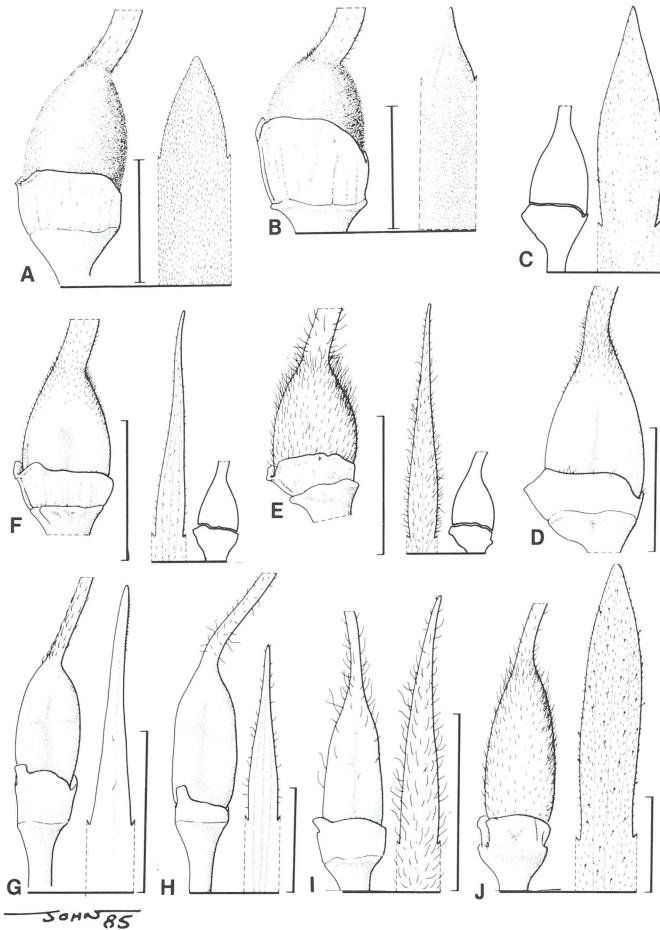


Figure 6 Ovary and adjacent calyx lobe in: **A.** *Duvernoia aconitiflora*; **B.** *D. adhatodoides*; **C & D.** *A. vasica* (Anderson s.n.) with ovary enlarged in D; **E.** *A. densiflora* (Moll 2626); **F.** *A. andromeda* (Trauseld 2284); **G.** *J. campylostemon*; **H.** *J. protracta*; **I.** *J. flava* and **J.** *J. bolusii*. (All *Justicia* species in cultivation at the University of Natal, Pietermaritzburg). Scale = 2 mm.

characterized the genus *Duvernoia*. In addition, the leaf epidermal cells in *Duvernoia* were unusually small and had straight walls (Figure 9A) while those of *Adhatoda* and *Justicia* were larger and had ripple walls (Figure 9B).

Conclusions

The genus *Duvernoia* is reliably distinguished from related genera by its campanulate calyx which is unique in the *Justiceae*. We have found that this character correlates with several other features and suggest that *Duvernoia* can be defined as follows:

- (i) Small trees or strongly branching shrubs,
- (ii) inflorescences subverticillate, on nude peduncles, determinate by the abortion of the first order apical bud,
- (iii) bracts never subrotund nor imbricate and never partly concealing the flowers,
- (iv) calyx 5-fid, tube campanulate,
- (v) upper corolla lip with two lateral channels containing the filaments; the lateral veins anastomosing with the marginal traces in the distal third of the lip,
- (vi) lower corolla lip deeply lobed, lateral lobes falcate,
- (vii) palate of two smooth tumuli,
- (viii) anthers with thecae at slightly different heights and slightly divergent; thecae acute or equally acuminate at the base,
- (ix) pollen prolate bilateral, 2-colporate; margocolpi entire,
- (x) disc cup-shaped, not auriculate,

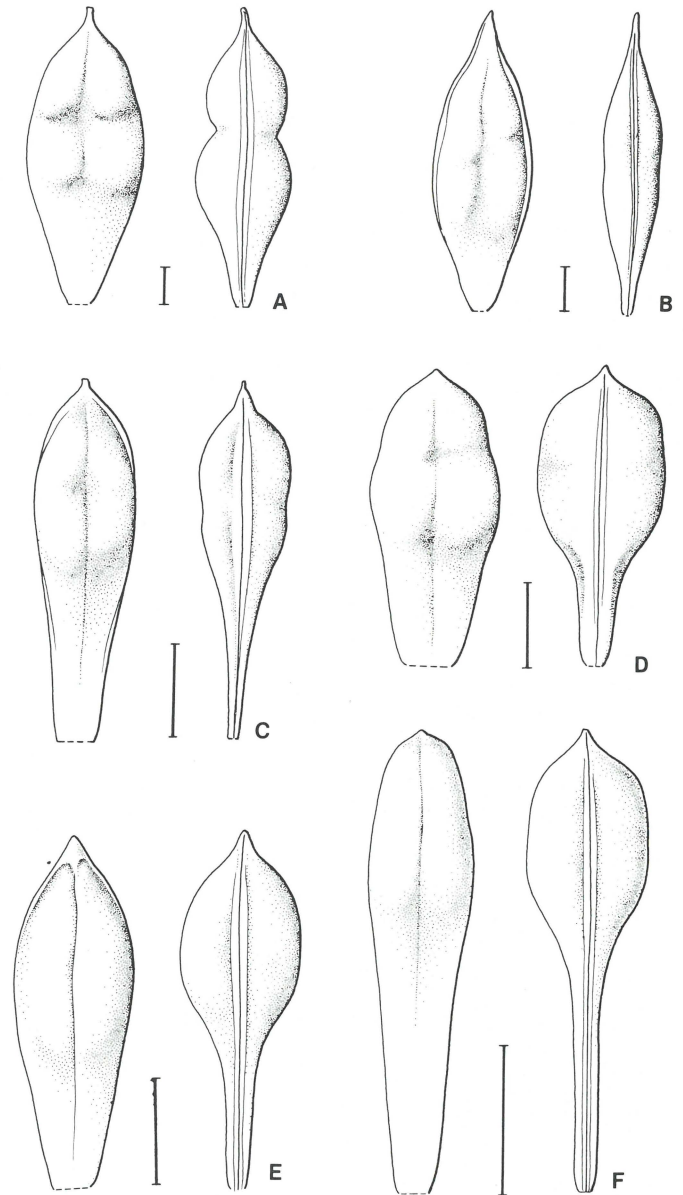


Figure 7 Dorsal and lateral faces of fruit of: **A.** *Justicia flava*; **B.** *J. protracta*; **C.** *J. campylostemon*; **D.** *J. betonica*; **E.** *Adhatoda andromeda* and **F.** *Duvernoia adhatodoides*. Scale = natural size of fruit.

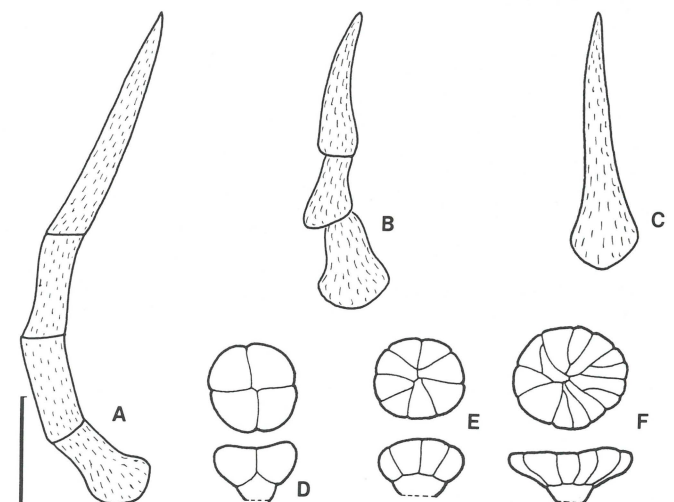


Figure 8 **A-C.** Three types of eglanular trichomes and **D-F.** three types of glandular trichomes on leaves of species of *Duvernoia*, *Adhatoda* and *Justicia* spp. Scale = 50 µm.

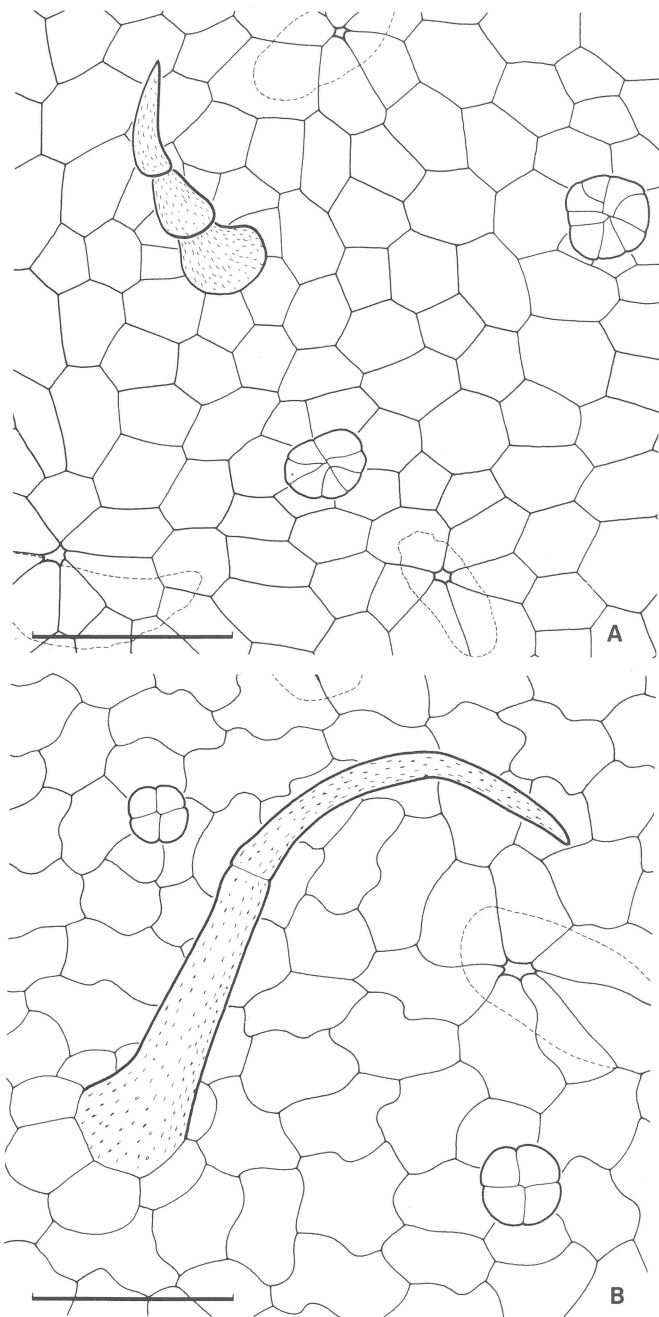


Figure 9 A. Upper leaf epidermis of *Duvernoia* species, with straight-walled epidermal cells and B. upper leaf epidermis of *Adhatoda* with ripple-walled epidermal cells. Dotted lines represent the position of subepidermal cystoliths. Scale = 100 μ m.

- (xi) capsules long-stipitate, slender and truncate in dorsal view, pubescent,
- (xii) leaf epidermal cells with straight walls, and
- (xiii) leaf epidermal trichomes of type B and glandular trichomes with 8 or more head cells.

The limits of *Adhatoda* are rather wide and a comprehensive survey over its entire range may well support segregates of at least sectional rank, if not separate genera. At present the genus seems to be characterized as follows:

- (i) Shrubs or perennial herbs with a woody rootstock,
- (ii) inflorescences axillary, open or congested, usually cymose, sometimes sessile and congested so as to become pseudo-terminal synflorescences,
- (iii) bracts in southern African species, linear-lanceolate and not concealing the flowers but in tropical species, large subtrotund and partly concealing the flowers,

- (iv) calyx 5-partite almost to the base,
- (v) upper corolla lip deeply naviculate, rarely shallow, lateral veins anastomosing with the marginal traces within the proximal half of the lip,
- (vi) lower corolla lip fused almost to the tip or deeply 3-partite, lateral lobes arched, usually oblong and obtuse, rarely tapering,
- (vii) palate median, channelled, rugose, usually restricted to the hypochile,
- (viii) anthers with thecae at slightly different heights, slightly diverging, rounded or with the lower thecae tailed at the base,
- (ix) pollen prolate, 2- or 3-colporate, margocolpi entire or areolate,
- (x) ovary ovoid, variously pubescent; disc cupulate, not auriculate,
- (xi) capsule stalked, pubescent,
- (xii) leaf epidermal cells with ripple walls, and
- (xiii) leaf epidermal trichomes of type A and glandular trichomes with up to 8 head cells.

Adhatoda vasica and its two close associates *A. schimperiana* and *A. engleriana* form a discrete group characterized by their woody habit, pedunculate, strobilate inflorescences (Figure 1E&F), subtrotund imbricate bracts and 2-aperturate areolate pollen. Further investigation may reveal that the genus *Adhatoda* should be restricted to species that share these distinctive features. The southern African species are perennial herbs, have synflorescences of variously reduced axillary cymes (Figure 1A1–5), linear lanceolate bracts, and 3-aperturate pollen with entire margocolpi. Until a revision of the genus throughout its range is complete, it would be premature to recommend that these species be removed from *Adhatoda*.

The origins of the members of this tribe are probably in tropical arborescent forms and *Duvernoia* and *Adhatoda* from tropical Africa probably represent early derivatives of this woody core. The southern African species of *Adhatoda* may represent the most highly derived members of their genus in that the arborescent habit has been replaced by a suffrutescent habit in which robust woody perennial rootstocks give rise to annual flushes of short flowering stems. Our observations over the past two growing seasons support the theory that this derived habit has evolved in response to fire, for unless the surrounding grass cover is removed, the annual flush of flowering shoots is not produced. *Justicia* species have perhaps diverged furthest from the ancestral woody stock as they invaded drier habitats and acquired an herbaceous habit, derived pollen, derived anthers and highly condensed inflorescences. An anomaly in this genus is the shrubby woodland species, *J. campylostemon*.

To sink *Adhatoda* and *Duvernoia* into *Justicia* would conceal what appears to be considerable evolutionary divergence.

Synopsis of the genera in southern Africa

1. Inflorescences axillary, verticillate, on nude peduncles, never of scorpioid cymes; calyx 5-fid up to half way, densely puberulous; upper corolla lip with two lateral staminal canals extending into the distal half; palate with two smooth tumuli; ovary downy-pubescent, half enclosed in a cupulate disc; pollen 2-colporate, margocolpi entire
..... *Duvernoia*

Inflorescences sessile or segregated into terminal synflorescences, sessile or pedunculate, panicle-like or of scorpioid cymes; calyx 5-partite nearly to the base, variously pubescent, rarely densely and finely puberulous; upper corolla lip without lateral staminal canals, or these weakly developed in the proximal half; palate rarely with two smooth tumuli (*J. campylostemon*), commonly rugose; ovary sparsely pubescent, disc less than half the length of ovary; pollen

2- or 3-colporate, margocolpi entire or areolate 2
 2. Inflorescences diffuse, pedunculate, helicoid cymes; lower corolla lip deeply divided, palate of two smooth tumuli; pollen 3-colporate, margocolpi entire **J. campylostemon**

Inflorescences sessile or pedunculate but then strobilate; lower corolla lip deeply or shallowly divided, palate median, rugose; pollen various 3

3. Corolla lips subequal, upper arched, usually deeply hooded; lower anther theca rounded at the base or shortly tailed; testa cells never with crystals; capsules stipitate **Adhatoda**

Upper corolla lip usually much shorter than lower; anther theca short- or long-tailed; testa occasionally with epidermal crystals; capsules shortly stipitate or subsessile **Justicia**

Duvernoia E. Mey. ex Nees in DC, Prodr. 111: 322 (1847); Phillips, The Genera of South African Flowering Plants 713 (1951); Dyer, The Genera of southern African Flowering Plants 1: 597 (1975). Type: *Duvernoia adhatodoides* E. Mey. ex Nees.

Adhatoda subgenus *Duvernoia* E. Mey ex Nees C.B. Clarke in Thiselton-Dyer (ed.), Fl. Cap. 5(1): 76 (1901).

Adhatoda pp. *sensu* Bentham & Hooker fil., Genera Plantarum 2(2): 112 (1876).

Adhatoda Miller, Gard. Dict. Abr. ed. 4: 39 (1754); Nees in Wallich, Pl. As. Rar. 3: 102 (1832); Bentham & Hooker fil., Genera Plantarum 2(2): 112 (1876); C.B. Clarke, in Thiselton-Dyer (ed.), Fl. trop. Afr. 5: 221 (1900); and in Thiselton-Dyer, Fl. Cap. 5(1): 75 (1901); Phillips, The Genera of South African Flowering Plants 715 (1951); Dyer, The Genera of southern African Flowering Plants 1: 599 (1975). Lectotype, here designated, *Adhatoda vasica* Nees (Flora Zeylanensium, *Hermann 16* (B.M.)).

Justicia p. *minore parte sensu* Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4.3B: 346 (1895).

In his synonymy of the species *A. vasica*, Nees (1832) included, amongst others, *J. adhatoda* L. and *A. zeylanensium* Herm. Both of these were based on a specimen in the Hermann Herbarium and the same material was the source of Miller's description of the genus (1754). It thus seems certain that the Hermann gathering numbered 16, is the type of the genus and that the earliest correct combination is *Adhatoda vasica* Nees. The Hermann Herbarium is now housed in the British Museum of Natural History.

Justicia L., Sp. Pl. 15 (1753), p.p.: Lindau in Engler & Prantl, Nat. Pflanzenfam. 4.3.B: 346 (1895); C.B. Clarke, in Thiselton-Dyer, Fl. Cap. 5(1): 55 (1901); Thonner, The Flowering Plants of Africa 512 (1915); Phillips, The Genera of South African Flowering Plants 714 (1951); Dyer, The Genera of southern African Flowering Plants 1: 598 (1975). Type not determined.

Justicia adhatoda L. cited as the type of the genus by Farr *et al.* (1979) was transferred to *Adhatoda* Miller (Medikus 1790, *vide* Farr *et al.* l.c.).

Acknowledgements

We gratefully acknowledge the financial support of the CSIR and the University Research Fund. Special thanks are due to Professor O.M. Hilliard and Mr B.L. Burt for their pertinent observations and discussions and to Mr B.L. Burt for his assistance in typifying *Adhatoda*.

We gratefully acknowledge the assistance of the Electron Microscope Unit and of our colleagues involved in similar studies in this challenging family.

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Appendix

Specimens examined

Adhatoda andromeda (Lindau) C.B. Clarke

ORANGE FREE STATE. — 2829 (Harrismith): Sterkfontein (–AC), *Blom 60* (PRE).

NATAL. — 2828 (Bethlehem): Royal Natal National Park, Mahai River (–DB), *Galpin 9573* (PRE); Royal Natal National Park, Mont aux Sources, *Trauseld 284* (PRE, NU); Bergville, Mont aux Sources (–DD), *Schweickerdt 726* (PRE).

2829 (Harrismith): Between Bergville and National Park (–CB), *Galpin 9573* (PRE); Cathedral Peak (–CC) *Buch 1468* (PRE); *ibidem*, *Killick 1615* (NU, PRE); Cathedral Peak, near Hotel, *Schelte 833* (NU); Ennersdale (–DD), *Whyllie com Wood 10584* (NH).

2929 (Underberg): Loskop dist., Cathkin Peak (– AB), *Howlett* 87 (NU, PRE); Estcourt dist., Dalton Bridge (? – BB), *Acocks* 10623 (NH, PRE); Estcourt, *Miller* 436 & 454, (PRE); Polela, on Mr Gold's farm near Underberg (– CA), *Dyer* 3278 (NH, PRE); Upper tributaries S of Mkomazi River (– CB), *Hilliard & Burt* 15670 (NU); Coleford, S of Nature Reserve above Endawana River (– CD), *Hilliard & Burt* 9568 (NU); Loteni Nature Reserve (– DA), *Jacobsz* 3934 (PRE); ibidem, *Killick* 3885 (PRE); ibidem *Phelan* 112 (NU); Polela dist., Sunset Farm (– DC), *Rennie* 66 (NU); Eastwolds (– DD), *Strey* 9232 (PRE).

2930 (Pietermaritzburg): Hela Hela Mountain Game Valley Estates (– CC), *Schrire* 951 (NH).

TRANSKEI. — **3029** (Kokstad): mountains around Clydesdale (– BD), *Tyson* 2063 (PRE).

3030 (Port Shepstone): 1/2 km S of Highflats (– AD), *Acocks* 13305 (PRE).

Adhatoda densiflora (Hochst.) J.C. Manning

NATAL. — **2930** (Pietermaritzburg): Lions River (– AC), *Moll* 1043 (NU, PRE); Karkloof, Benvie, *Wylie com Wood* 10073 (NH); Otto's Bluff (– AD), *Young s.n.* (PRE); Pietermaritzburg, Hawthorns Hill (– CB), *Allsopp* 423, 534, 675 & 713 (NU); Pietermaritzburg, Ketelfontein area, Worlds View, *Balfour-Cunningham* 37 (NU); Clarendon, *Comins* 871 (PRE); Pietermaritzburg, *Fisher* 329 (NU); ibidem, *Mogg* 2245 (PRE); ibidem, *Sidey* 3013 (PRE); ibidem, *Shuter* 1 (NU); ibidem, *Wood* 11937 (PRE); Pietermaritzburg, Worlds view, *Moll* 2626 (NU, PRE); Pietermaritzburg, Town Bush Valley, *Ross* 393 (NU); Intshaŋga (– DA), *Wood* 4653 (PRE); Inanda (– DB), *Wood* 174 (NU), 304 (NH) & 1512 (PRE); 21 km from Merrivale on Boston road, *Kunhardt* 31 (NH).

2931 (Stanger): Umhlali (– AB), *Wood* 1137 (NH, NU, PRE); Durban (– CC), *Mogg* 11099 (NH); Port Natal, *Sutherland s.n.* (PRE).

3029 (Kokstad): 2 miles from Harding on Umzimkulu road (– DB), *Story* 654 (PRE).

3030 (Port Shepstone): Ixopo (– AA), *Shirley s.n.* (NU).

Adhatoda engleriana (Lindau) C.B. Clarke

TANZANIA. — (Tanganyika): Lushoto Township, *Semsei* 2903 (PRE).

KENYA. — Kwale dist., Pengo Hill area on the road to Shimba Hills settlement, *Magoga & Glover* 139 (PRE); Machakos dist., *Verdcourt* 3693 (PRE).

Adhatoda eylesii S. Moore

ZAMBIA. — (Northern Rhodesia): Miengwe dist., *Fanshawe F.* 2814 (PRE).

ZIMBABWE. — Salisbury, near Pote River, *Chase* 6322 (PRE).

Adhatoda maculata C.B. Clarke

ZAIRE. — (Belgian Congo): Yangambi, *Louis* 10893 (PRE) (as *Duvernoia classensis* De Wild.).

CAMEROUN. — Lobé River, falls 7 km S of Kribi 2°53'N, 9°54'E, *Bos* 3589 (PRE).

Adhatoda robusta C.B. Clarke

CAMEROUN. — 5 km SW of Madjwe, *Leeuwenberg* 6221 (PRE).

GUINEA. — (Guinie Francophone): Village H20, *Jacques-Georges* 6332 (PRE).

Adhatoda schimperiana Nees

ETHIOPIA. — Ansella, *De Wilde & De Wilde Duyfjes* 9227 (PRE).

KENYA. — Malindi dist., *Rawlins* 698 (PRE); Taita dist. Taveta, *Polhill & Paulo* 984 (PRE).

Adhatoda vasica Nees

INDIA. — Rajpur 3000' Mussoorie, *A. Anderson s.n.* (E).

Duvernoia aconitiflora Meeuse

MOZAMBIQUE. — Little Lebombo, 30 mls from Lourenço Marques, *Bews s.n.* (NH); Banks of Boane River, Lourenço Marques, *Törre* 6501 (PRE).

SWAZILAND. — **2731** (Louwsburg): Hlatikulu, Ingwavuma Poort (– BB), *Compton* 28631 & 29797 (PRE).

TRANSVAAL. — **2530** (Lydenburg): Lydenburg (– AB), *Repton* 595 (PRE).

2531 (Komatipoort): Komatipoort, banks of Komati River (– BD) *Pole Evans* 3492 (70) (PRE); M'Pondurine on top of Lebombo mt., *Strey* 4031 (PRE); 12 km from Kaap Muiden to Nelspruit (– CB), *Van Jaarsveld* 465 (PRE).

Duvernoia adhatodoides Nees

TRANSVAAL. — **2430** (Pilgrim's Rest): Mariepskop (– DB), *Bos* 1090 (PRE); ibidem, *V.d. Schijff* 514 (PRE); Mariepskop Forest Reserve, *De Winter & Killick* 8950 (PRE); Pilgrim's Rest (– DD), *V.d. Schijff* 5030 & 6041 (PRE).

2531 (Komatipoort): Barberton (– CC), *Strey* 4031 (PRE).

NATAL. — **2732** (Ubombo): Ingwavuma, Gwalaweni Forest (– AA), *Scottshaw* 157 (NU); Gwalaweni Forest (– AC), *Vahrmeijer & Hardy s.n.* (PRE).

2831 (Nkandla): Nkandla Forest (– CA), *Codd* 6967 (NU, PRE); ibidem, *Edwards* 1367 (NU, PRE); ibidem, *Guy & Tinley* 6 (PRE); ibidem *Wells & Edwards* 3 (NU, PRE); Nkandla, *De Winter* 8256 (PRE); ibidem, *Forester* 3A (PRE); ibidem, *Lambinon & Reekmans* 82/262 (PRE); Entumeni Nature Reserve (– CD), *Bourquin* 975 (NU); Eshowe, Ngotshe Forest, *Hilliard* 20201 (NU).

2930 (Pietermaritzburg): Table Mountain (– DA), *Killick* 335 (NU); Camperdown, Nagle Dam (sterile specimen), *Wells* 1712 (NU).

2931 (Stanger): Stanger, 4 miles Mapumulo/Kranskop (– AA), *Moll* 2978 (NU); Durban (– CC), *Moll* 3426 (PRE); Durban, Edgewood, *Moll* 3426 (NU).

3030 (Port Shepstone): Infane River, South Coast (– AC), *Bayer* 867 (NU); Ixopo dist., Jolivet, Rosslea Estate (– AD), *Hilliard* 3119 (NU); Ifafa (– BC), *Bayer* 867 (PRE); Paddock, Elliot's Farm (– CC), *Strey* 7159 (NH, NU, PRE).

CAPE. — **3326** (Grahamstown): Albany (– BC), *Jacot-Guillarmod* 4433 (PRE).

TRANSKEI. — **3029** (Kokstad): Eastern Cape, Ngqueleni, Ookama (– DC), *Acocks* 12819 (PRE).

3128 (Umtata): Elliotdale dist., Cwebe Forest (– BB), *Breitenbach* 1352 (PRE).

3129 (Port St. Johns): Lusikisiki (– BC), *Abernethy s.n.* (PRE); Kokstad, Esjossa Forest, *Dist. Forest Officer s.n.* (PRE); ibidem, *Sim* 2721 (NU); ibidem, *Strey* 8923 (NU, PRE); Lusikisiki, *Taylor* 2382 (PRE); 2 miles along road Mbotyi/Lusikisiki, *Van Wyk* 1564 (PRE); Umgazana River near Port St. Johns (– CB), *Codd* 9746 (PRE); Near Canzibe Mission, 45 km from Umtata on Mtata River Road (– CC), (PRE); *Ward* 8699 (PRE); Port St. Johns (– DA), *Blenkiron (C.E. Moss* 16442) (PRE); ibidem, *Flanagan* 2505 (PRE); ibidem, *Galpin s.n.* (PRE); ibidem, *Howlett* 19 (PRE); ibidem, *Venter* 5227 (PRE); Port St. Johns, Noxolweni Forest, *Mogg s.n.* (PRE); Prope flum, Omgazi, *Bolus s.n.* (PRE).

3228 (Butterworth): Willowvale dist., Dumessa Forest (– AD), *Wood* 167 (NU).

Duvernoia (= *Adhatoda*) *bolomboensis* De Wildeman

ZAIRE. — (Belgian Congo): Yangambi dist., *Louis* 3140 (PRE).

Justicia sp. (*Duvernoia pynaerti* De Wildeman)

ZAIRE. — (Belgian Congo): Befall, *Errard* 2908 (PRE).

Other *Justicia* species used in the study are in cultivation at the University of Natal, Pietermaritzburg.