

## Morphological variation and phylogenetic relationships in the genus *Anginon* (Apiaceae)

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The variation in habit and morphology of the twelve species of *Anginon*, a poorly known southern African genus of woody Apiaceae, is discussed and illustrated. The genus *Glia* is shown to be the obvious outgroup, sharing with *Anginon* two convincing synapomorphies: 1, the reduction or partial reduction of the laminar part of the leaves, and 2, the heavily cutinized outer walls of the fruit epidermis. Several characters of the internal structure of the fruit, together with other morphological characters, have been analysed by the cladistic method. Our interpretation of character evolution within the genus and a first hypothesis of phylogenetic relationships, showing three distinct infrageneric groups, is presented.

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### Introduction

*Anginon* Raf. is an interesting and taxonomically isolated genus of Apiaceae endemic to southern Africa. In a recent revision, 12 species were distinguished, of which no less than 5 were described as new (Allison & Van Wyk 1997). In view of the woody habit and relative abundance of the species, it is surprising that most of them are poorly known and rarely collected. As a result, very few diagnostic characters were known, so that the delimitation of species was most unsatisfactory. Burt (1988, 1991) made important contributions to the generic concept, but pointed out the need for further study. Despite the paucity of characters and the variability of character states, it is possible to give here a summary of our interpretation of character evolution within the genus *Anginon* and also an explicit hypothesis (cladogram) of phylogenetic relationships amongst the species.

### Materials and methods

Specimens from all the major southern African herbaria and some European herbaria were included in our study (BOL, GRA, JRAU, K, M, NBG, NH, PRE, S, SAAS (now part of PRE), SAM, STE (now part of NBG), UPS, WIND) and all the species except *A. streyi* were studied in habitat over the period 1988 to 1994. A major difficulty was to obtain flowers and fruit of some of the rare species, so that some of the localities were revisited several times. Our own collections are listed in the taxonomic revision (Allison & Van Wyk 1997). A list of voucher specimens for the anatomical study of flowers and fruit is given here (other voucher specimens are listed in the captions of the figures). All the samples comprised mature fruit except for those marked with an asterisk, where flowers, young fruit and mature fruit were sampled. Authorities for names are the same as in Allison & Van Wyk (1997) and are not repeated elsewhere. *A. difforme* (L.) B. L. Burt: Allison 50 (NBG), Van

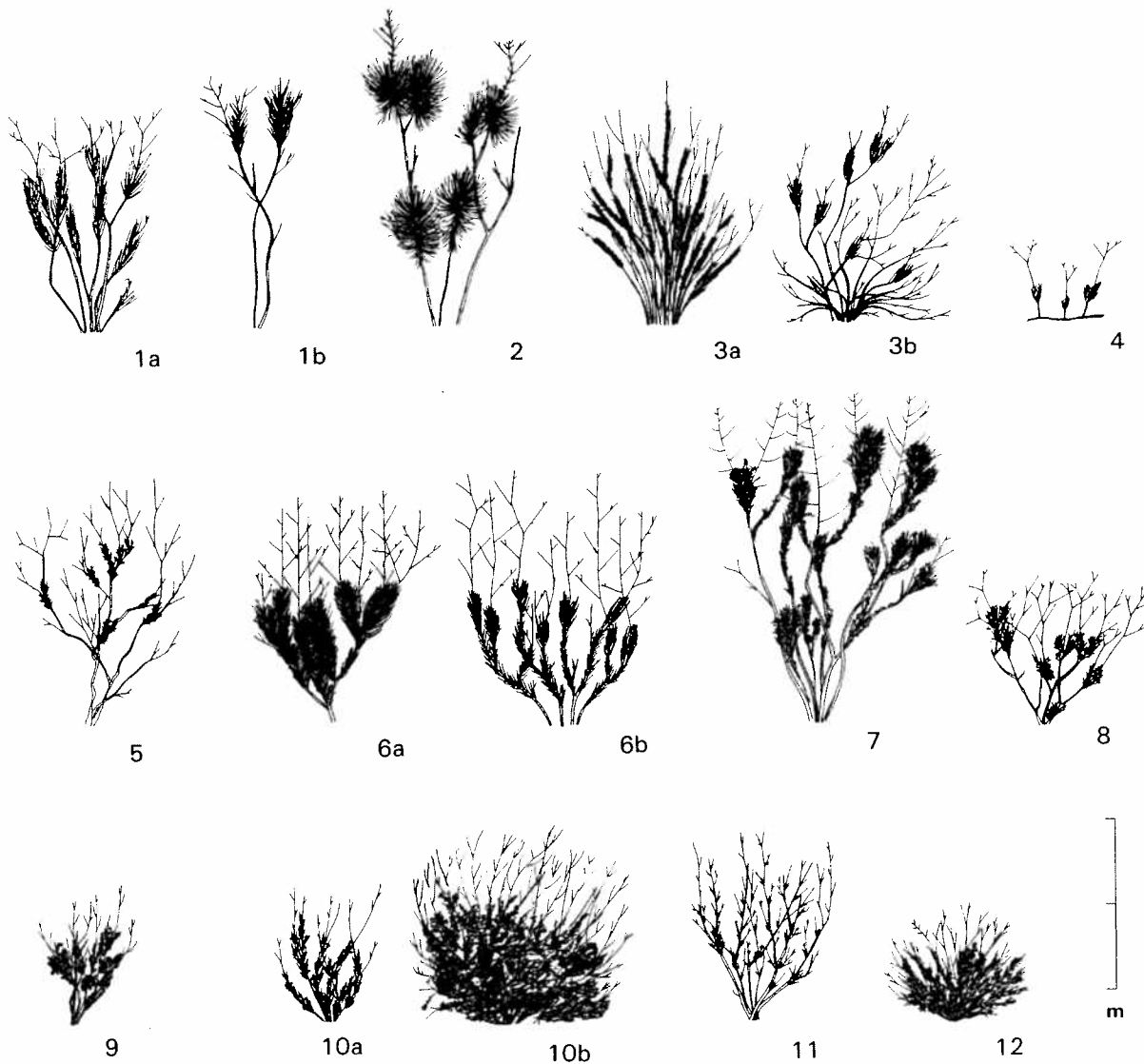


Fig. 1. The habit of all the species of *Anginon*, to show the variation in size, branching pattern, leafiness and inflorescence structure. 1a. *A. difforme* (Robinson Pass); 1b. *A. difforme* (Paardepoort); 2. *A. ternatum* (Gifberg Pass); 3a. *A. fruticosum* (Hex River Pass); 3b. *A. fruticosum* (Calvinia); 4. *A. pumilum* (De Hoop); 5. *A. tenuior* (Oudeberg Pass); 6a. *A. swellendamense* (Oudtshoorn); 6b. *A. swellendamense* (Hex River Pass); 7. *A. paniculatum* (Matsikamma Mountain); 8. *A. rugosum* (Paterson); 9. *A. streyi* (drawn from herbarium material); 10a. *A. verticillatum* (Numeesberg); 10b. *A. verticillatum* (Ploegberg); 11. *A. intermedium* (Kamiesberg); 12. *A. jaarsveldii* (Pella Mountain). – All except 9 drawn to scale from colour slides.

Wyk 2944\* (JRAU); *A. fruticosum* Allison & Van Wyk: Van Wyk 3050a, 3050b (PRE), Vlok 2288 (JRAU); *A. intermedium* Allison & Van Wyk: no fruit available; *A. jaarsveldii* B. L. Burt: Allison 166\* (JRAU), 167 (K), 168 (NBG); *A. paniculatum* (Thunb.) B. L. Burt: Van Wyk 3025, 3337\* (JRAU); *A. pumilum* Allison & Van Wyk: Acocks 23003 (PRE), Allison 154 (JRAU); *A. rugosum* (Thunb.) Raf.: Archibald 3955 (PRE), Allison 210 (JRAU); *A. streyi* (Merxmüller) Al-

lison & Van Wyk: Strey 2154 (M); *A. swellendamense* (Eckl. & Zeyh.) B. L. Burt: Allison 61 (BOL), 82 (PRE), Van Wyk 2963 (PRE), 3013 (JRAU); *A. tenuior* Allison & Van Wyk: Lewis 1793 (NBG), Van Wyk 3334 (PRE); *A. ternatum* Allison & Van Wyk: Van Wyk 3028 (PRE); *A. verticillatum* (Sond.) B. L. Burt: Allison 178 (JRAU). Flowers, young fruits and mature fruits were collected in FAA or in some cases, mature fruits were removed from rich herbarium collections.

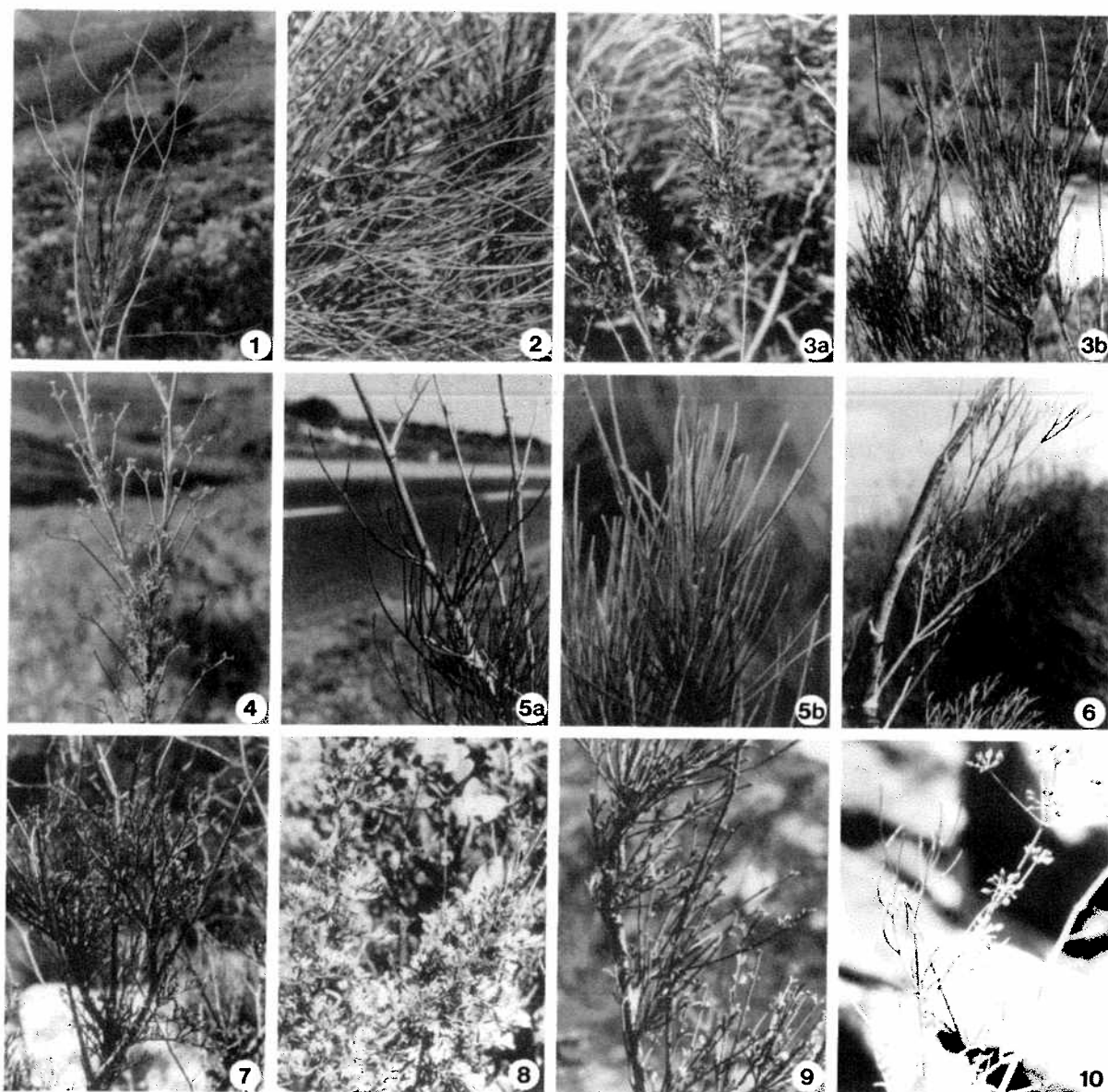


Fig. 2. Mature foliage of the species of *Anginon* to show the differences in structure and appearance of the leaves. 1. *A. difforme* (Zuurberg); 2. *A. ternatum* (Gifberg); 3a. *A. fruticosum* (Doringrivier); 3b. *A. fruticosum* (Ladismith); 4. *A. tenuior* (Oudeberg Pass); 5a. *A. swellendamense* (Oudtshoorn); 5b. *A. swellendamense* (Hex River Pass); 6. *A. paniculatum* (Matsikamma mountain); 7. *A. rugosum* (Paterson); 8. *A. verticillatum* (Kamiesberg); 9. *A. intermedium* (Kamiesberg); 10. *A. jaarsveldii* (Pellaberg).

The latter were rehydrated in tubes with distilled water by heating slowly to boiling point for approximately one hour and then fixing in FAA for at least 24 hours. The material was embedded in glycol methacrylate (GMA) according to a modification of the method of Feder & O'Brien (1968) for sectioning on a Porter Blum MT-1 ultramicrotome. This modification involves infiltrating the material in the GMA for a minimum of

24 hours between the first two changes and for a longer period (usually at least five days) before placing in the gelatin capsules, which are then heated in an oven at 60 °C for 24 hours to polymerise. Mounted sections were stained according to the so-called Periodic Acid - Schiff / Toluidine Blue (PAS/TB) staining method and photographed using a Leitz Wetzlar microscope and Ilford FP4 (ASA 125) film. Fruits from several other collec-

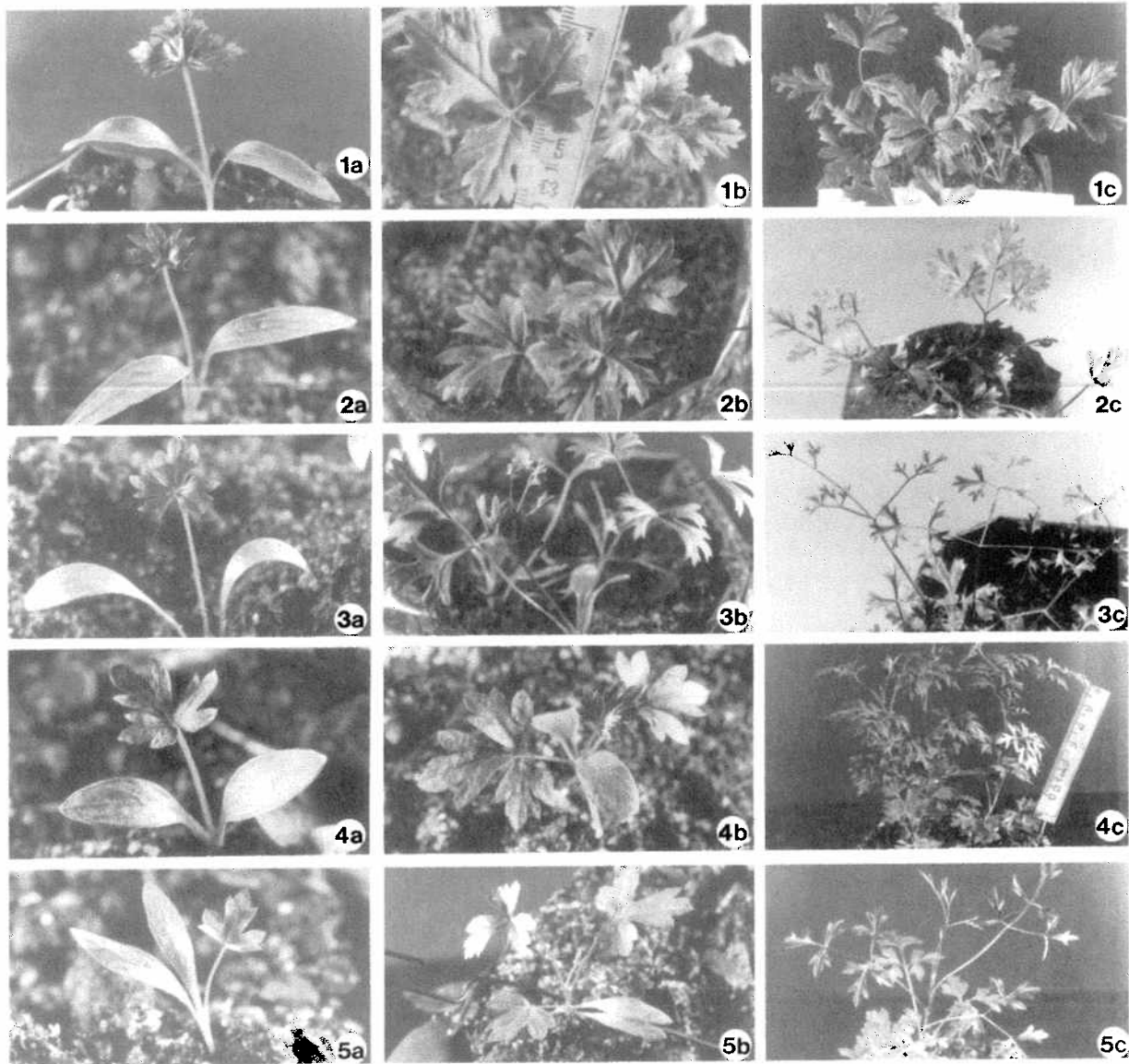


Fig. 3. Seedling leaves (a) and young juvenile leaves (b & c) of some species of *Anginon* to show the early stages of reduction from a "normal" laminate leaf to a more or less phyllodinous mature leaf. Species differences in the mature leaves are not visible at the seedling stage. 1. *A. paniculatum* (Van Wyk 3025, Citrusdal); 2. *A. swellendamense* (Van Wyk 3013, Worcester); 3. *A. tenuior* (Van Wyk 3334, Oudeberg Pass); 4. *A. fruticosum* (Van Wyk 3050, Hex River Pass); 5. *A. difforme* (Allison 50, Robinson Pass).

tions (not listed above) were sectioned by hand to study the distribution and variability of character states within the species. For histochemical study (to differentially stain the cutin of the epidermal cells), GMA sections were also treated with Sudan black B and mounted in glycerine-jelly (Jensen 1962). For the study of seedling characters, fresh fruits from several species were germinated and the seedlings grown under glass. For compar-

ative studies of the internal structure of leaves, seedling leaves from cultivated plants, as well as sequences of juvenile to mature leaves, collected in situ, were used. Sections of leaves were mostly hand-cut with a razor blade, stained in aqueous Toluidine blue and studied under a light microscope. Diagrammatic drawings (e.g. Figs 5, 8 and 11) were done with the aid of a drawing tube (camera lucida) mounted on a Wild M3Z binocular

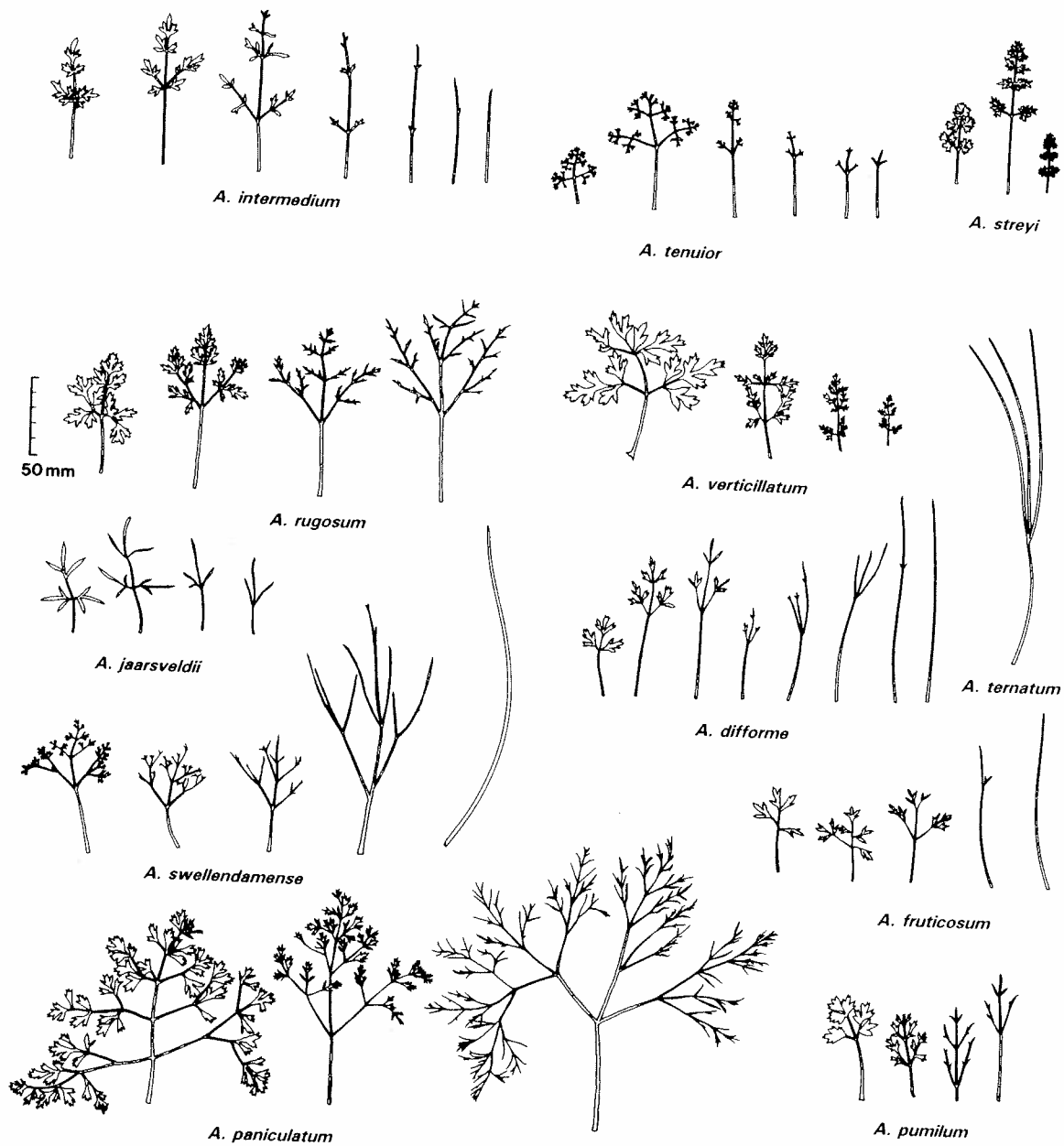


Fig. 4. Juvenile to mature leaves (from left to right) of the genus *Anginon* to illustrate the salient differences between all the species. The various stages (juvenile to mature) that are shown for each of the species were taken from a single plant (a few exceptions are given below). Junciform mature leaves (unbranched, needle-like) are characteristic of *A. difforme*, but also occur occasionally in *A. intermedium*, *A. rugosum* and in *A. swellendamense*. In all the other species, the mature leaves are pinnately dissected to various degrees. In *A. ternatum*, the mature leaves are invariably divided into three needle-like segments. Such leaves are also commonly found in *A. difforme*, but only on coppice shoots and not on mature branches. *A. jaarsveldii* (all from Allison 163); *A. intermedium* (all from Allison 190); *A. verticillatum* (all from Allison 171); *A. streyi* (all from Strey 2154); *A. rugosum* (all from Allison 210); *A. paniculatum* (all from Allison 122); *A. swellendamense* (first four from Allison 82, last one from Allison 118); *A. tenuior* (all from Van Wyk 3334); *A. pumilum* (all from Allison 158); *A. fruticosum* (all from Allison 113); *A. ternatum* (from Allison 128, juvenile and intermediate stages not known); *A. difforme* (all from Allison 46).

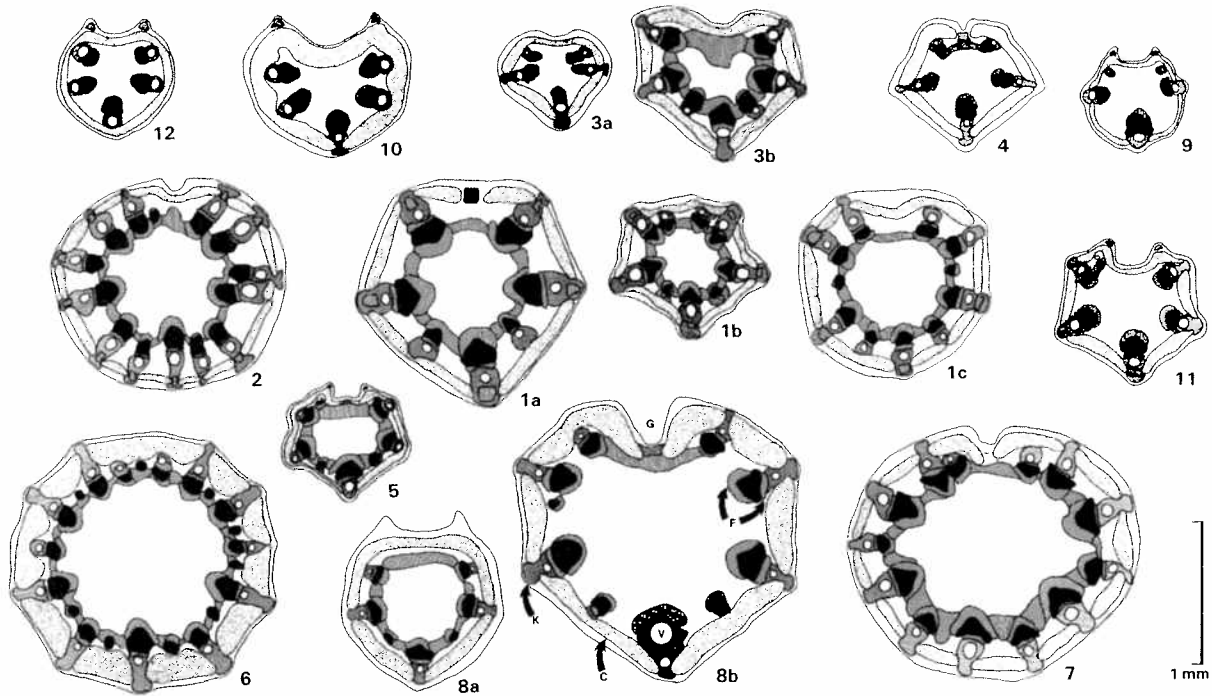


Fig. 5. Transverse sections of mature leaves of all the species of *Anginon* to show the range of variation found in a much larger sample. Sections were made through the middle of the petiole or, in the case of phyllodinous leaves, at a corresponding height. Note the absence or presence of an adaxial groove (G), the degree of sclerification (F = fibres; K = collenchyma) and the number of vascular bundles (V), the number of discontinuities within the chlorenchyma (C) and the number of vittae, shown as open circles within the collenchyma. 1. *A. difforme* (1a = Allison 50, 1b = Pearson 5783, 1c = Allison 41); 2. *A. ternatum* (Allison 91); 3. *A. fruticosum* (3a = Allison 53, 3b = Allison 96); 4. *A. pumilum* (Allison 158); 5. *A. tenuior* (Viviers & Vlok 449); 6. *A. swellendamense* (Allison 88); 7. *A. paniculatum* (Taylor 11271); 8. *A. rugosum* (8a = Liebenberg 7725, 8b = Allison 208); 9. *A. streyi* (Strey 2154); 10. *A. verticillatum* (Allison 170); 11. *A. intermedium* (Viviers 2112); 12. *A. jaarsveldii* (Allison 164).

microscope or a Zeiss light microscope. Morphological characters were quantified using an image processing system (FIPS) comprising a central processing unit with an image acquisition board connected to a video camera mounted on a Wild M3C binocular microscope (Merbold 1994). The data were analysed statistically using a standard software (SYSTAT), mainly to generate the measurements used for the formal species descriptions in Allison and Van Wyk (1997). Only some of the phylogenetically informative patterns are reported here. For the sake of brevity, sample sizes are not given except for the four characters included in Fig. 7. These are given in the same order as in the figures. (For Figs 7a, 7b & 7c, 20 individual rays, styles and fruits were measured on each plant or specimen, the values below thus refer to the number of plants/specimens included; for Fig. 7d, the values below refer to the number of individuals/provenances of which three fruits (where possible) were measured in transverse section. Fig. 7a: 13=3, 1=22, 2=2, 3=7, 4=2, 5=2, 6=8, 7=2, 8=1, 9=1, 10=2,

11=1, 12=2; Fig. 7b: 13=2, 1=3, 2=2, 3=3, 4=1, 5=1, 6=3, 7=2, 8=2, 9=2, 10=2, 11=1, 12=2; Fig. 7c: 13=2, 1=9, 2=1, 3=5, 4=1, 5=1, 6=4, 7=5, 8=1, 9=1, 10=1, 11=0, 12=2; Fig. 7d: 13=3, 8=2, 4=2, 5=2, 6=3, 7=3, 9=1, 12=3, 10=1, 2=1, 3=3, 1=3.

## Results and discussion

In the following discussion of characters and character states, we use the species concepts and nomenclature as presented in the taxonomic revision (Allison & Van Wyk 1997).

### Habit

*Anginon* is an interesting example of a taxonomically isolated woody member of the family (see Introduction in Burtt 1991). All the species are woody shrubs or

shrublets and vary in height from less than 0.7 m (*A. pumilum*, the only species with rhizomatous subterranean stems) to 4 m in *A. paniculatum* and *A. ternatum*. There are subtle differences between the species in terms of the number of stems, the branching pattern and the leafiness of the stems. These differences in habit and appearance are illustrated schematically in Fig. 1.

## Leaves

A characteristic feature of *Anginon* species is the interesting modification of the mature leaves to branched or unbranched needle-like phyllodes (Fig. 2). The phyllodinous nature of the leaf has been discussed in some detail by Briquet (1897a) and Wolff (1910). In all the species, there is a partial or complete loss of the laminar part of the leaf, and in most species also a reduction in the number of leaf segments. In its extreme form (as in *A. difforme*), the mature leaves are all unbranched and junciform. The first seedling leaves have a broad lamina (Fig. 3), but as the plant matures the leaves become progressively more phyllodinous. These modifications from juvenile to mature leaves within each of the species are illustrated in Fig. 4. The mature leaves are sometimes diagnostically different (see key to the species and formal descriptions in Allison & Van Wyk 1997) but the juvenile stages are often very similar (Fig. 4) and the seedling stages (Fig. 3) appear to be identical in all the species studied.

In transverse section, the mature leaves differ markedly in shape and symmetry, and also in the number of vascular bundles and the number of resin ducts. The range of variation in these character states in the genus is illustrated schematically in Fig. 5. In those species where the mature leaves are only partially modified to phyllodes (e.g. *A. streyi*, *A. verticillatum* and *A. jaarsveldii*, respectively 9, 10 & 12 in Fig. 5), the petioles are bilaterally symmetrical with a distinct adaxial groove, and with only a small number of vascular bundles. This morphology is typical of seedling leaves of all the species. However, where the mature leaves are completely phyllodinous and junciform (as in *A. difforme* and *A. swellendamense*, 1 & 6 in Fig. 5), the petioles – and indeed the whole leaf – are radially symmetrical, without an adaxial groove and with a large number of vascular bundles.

## Inflorescence and flowers

The terminal umbel of the inflorescence is compound in all the species of *Anginon* but the lateral (lower) umbels are invariably simple only in *A. verticillatum*, *A. jaarsveldii* and *A. intermedium* (Fig. 6) but rarely also in *A.*

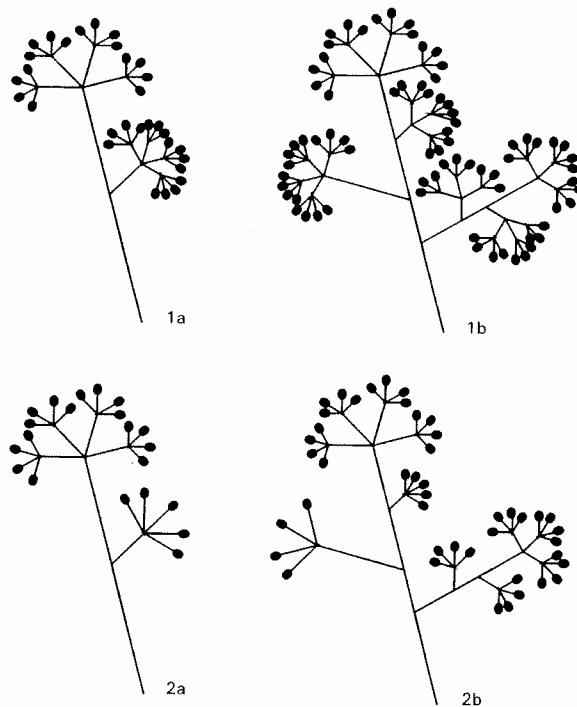


Fig. 6. The inflorescence structure of *Anginon* species, showing terminal and lateral racemes with compound umbels (1a & 1b), as in most species of *Anginon* (and in *Glia*) or terminal racemes with compound umbels, lateral racemes with simple umbels (2a & 2b), as in *A. jaarsveldii*, *A. verticillatum*, *A. intermedium* and rarely also in *A. streyi*. Note that some lateral umbels may be compound in these species (as shown in 2b) but then the tertiary umbels are simple.

*streyi*. This interesting character was discussed by Burt (1991), p. 146. The terminal umbels are often strictly compound, because the rays sometimes do not arise from exactly the same point on the main axis, or sometimes are verticillately arranged on the main axis. This modification of the basic inflorescence type of the Apiaceae was also illustrated by Wolff (1921). The simple umbels of the lateral racemes are of diagnostic value to distinguish between the closely related *A. verticillatum* and *A. streyi*, or between *A. intermedium* and *A. fruticosum*, but seems to have limited value at higher taxonomic levels. In *A. verticillatum* and related species, the rays are often exceptionally long (Fig. 7a) but the long rays are not logically correlated with the inflorescence structure. Burt (1991) mentioned the sterile scale-leaves, commonly found in small "clusters" within the inflorescences of *A. difforme*, which are also present in *A. ternatum* and *A. fruticosum*. In the other species, these small bracts are dispersed along the peduncles and pedicels and are never congested. It is in-

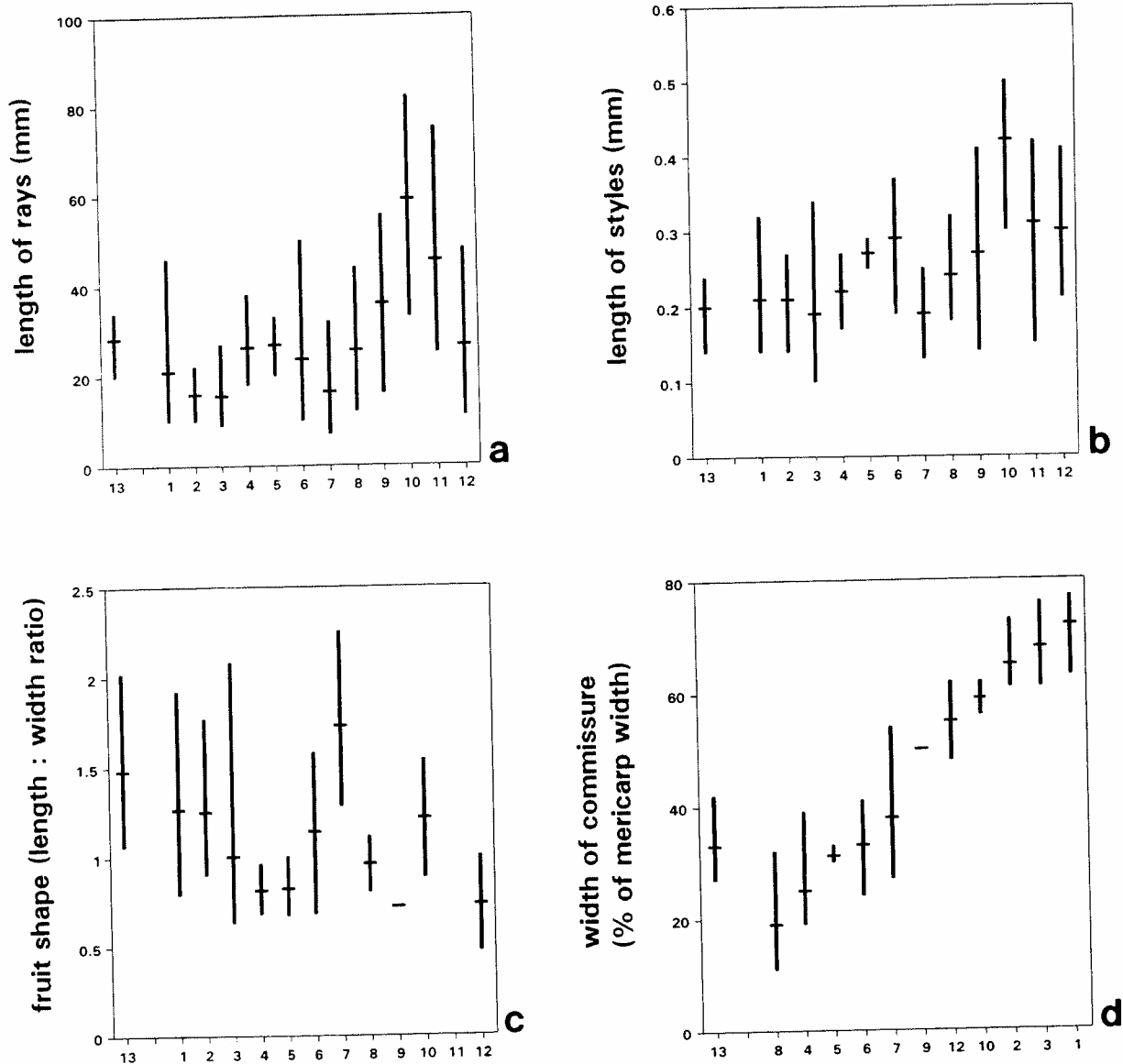


Fig. 7. Variation in ray length, style length, fruit shape and width of the commissure in *Anginon* species. a, ray lengths (often longer than 30 mm in *A. intermedium*, *A. verticillatum* and *A. streyi*). b, style lengths (often longer than 0.3 mm in *A. jaarsveldii*, *A. intermedium*, *A. verticillatum* and *A. streyi*; see also Fig. 8). c, fruit shape (length to width ratio of less than 1.0 in *A. pumilum*, *A. rugosum*, *A. tenuior*, *A. streyi* and *A. jaarsveldii*). d, width of the commissure, expressed as a percentage of the total width of the fruit (see also Fig. 10). The commissure is narrow (generally less than 40 % of total fruit width) in *Glia* and in all the species of *Anginon* with glaucous leaves (i.e., *A. rugosum*, *A. paniculatum*, *A. swellendamense*, *A. tenuior* and *A. pumilum*). The commissure is moderately wide (50 to 60 % of total fruit width) in *A. jaarsveldii*, *A. verticillatum* and *A. streyi*. A wide commissure (invariably more than 60 % of total fruit width) is found only in *A. fruticosum*, *A. ternatum* and *A. difforme*. (Species are numbered as in Fig. 1; *Glia* = 13)

interesting to note that this character, which was not included in the analysis due to its sporadic occurrence, provides additional support for the *A. difforme* clade (see Fig. 13).

The flowers are relatively uniform within the genus, but the variation of some characters and character states is illustrated in Fig. 8. In the petals of five of the species, the median vitta (resin duct) is branched into three

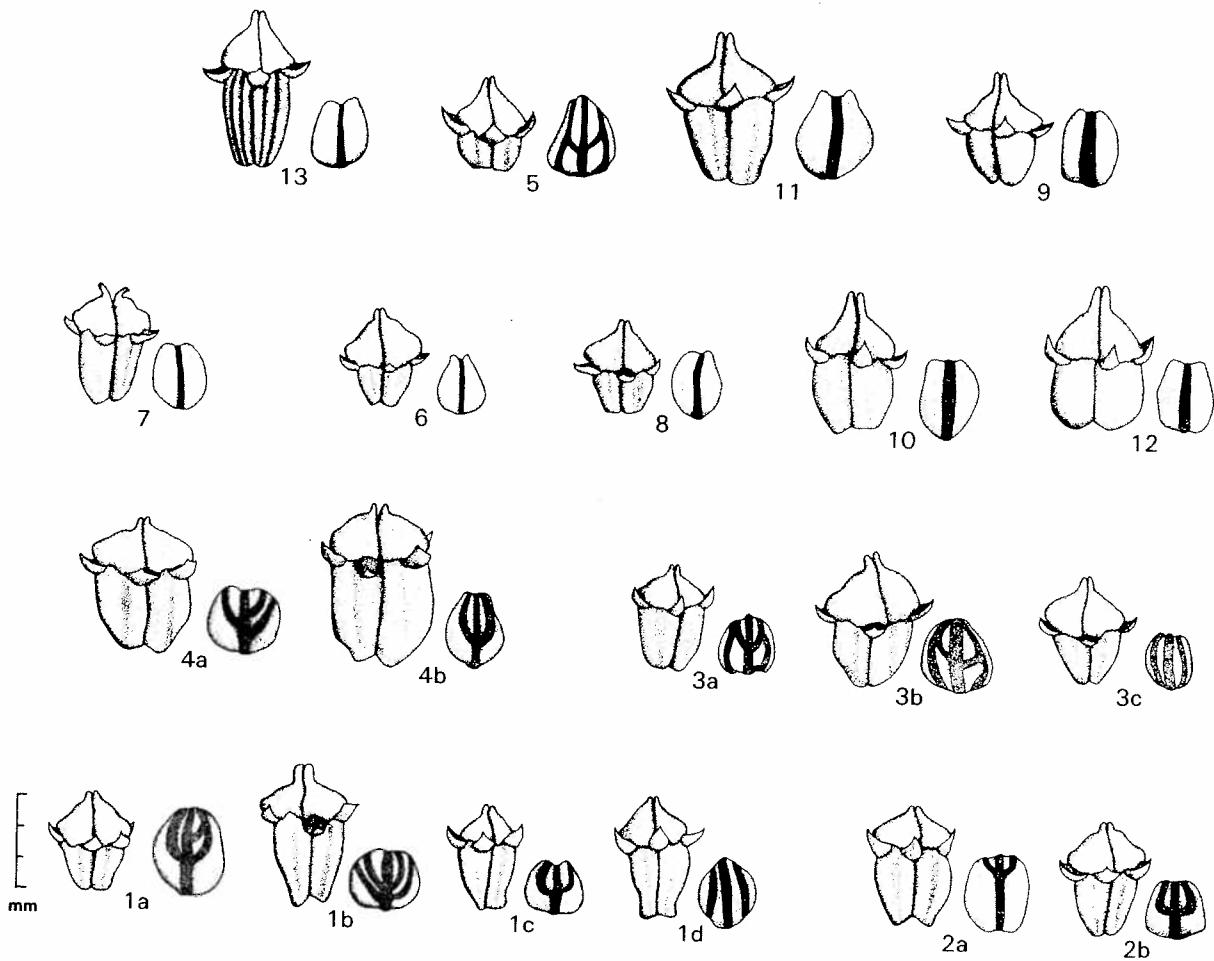


Fig. 8. Flowers of all the species of *Anginon* to show the range of variation found in a much larger sample (flower with petals removed shown on the left, single petal in dorsal view on the right). There are general trends in the size and shape of the ovary, stylopodium and style, but none of these appear to be of diagnostic value. Note, however, the remarkable difference in the vittae (resin ducts) of the petals (unbranched or branched) which divides the species into two distinct groups: those with a single median vitta (as in *Glia*) and those with branched vittae. 1. *A. difforme* (1a = Adamson 1020, 1b = Bayliss 6078, 1c = C.M. van Wyk 703, 1d = Lewis 5192); 2. *A. ternatum* (2a = Van Wyk 3028, 2b = Hugo 1048); 3. *A. fruticosum* (3a = Compton 6760, 3b = Hanekom 2493, 3c = Rehmann 2779); 4. *A. pumilum* (4a = Lewis 5145, 4b = C.M. van Wyk 2254); 5. *A. tenuior* (Van Wyk 3333); 6. *A. swellendamense* (Compton 10270); 7. *A. paniculatum* (Van Wyk 3027); 8. *A. rugosum* (Ecklon & Zeyher 2193); 9. *A. streyi* (Strey 2154); 10. *A. verticillatum* (Allison 173); 11. *A. intermedium* (Viviers 2112); 12. *A. jaarsveldii* (Allison 167); 13. *Glia prolifera*, note the distinctly ribbed ovary (Haynes 1111).

or more (so that two or more lateral vittae are visible). This seemingly unique and taxonomically useful character has gone unnoticed in previous studies. Variations in the length of the rays (Fig. 7a), the length of the styles (Fig. 7b), and in the shape and size of the flowers and the stylopodia (Fig. 8) show general trends in some species or species groups but have limited diagnostic value. As shown in Fig. 7b for example, the range of style lengths exceeds 0.4 mm in only four of the species (compare also Fig. 8).

### Fruit

Externally, the fruits of *Anginon* species are relatively uniform but there are slight differences in shape, size and surface sculpturing. The mature fruits are more or less ovate or obovate and without any distinct ribs or wings. Fig. 9 gives a broad comparison of the range of variation within the genus. The shape and tuberculate surface sculpturing of the fruits of *A. difforme* are usually quite distinct, but even in this species the diagnostic value is limited by considerable variation within and be-

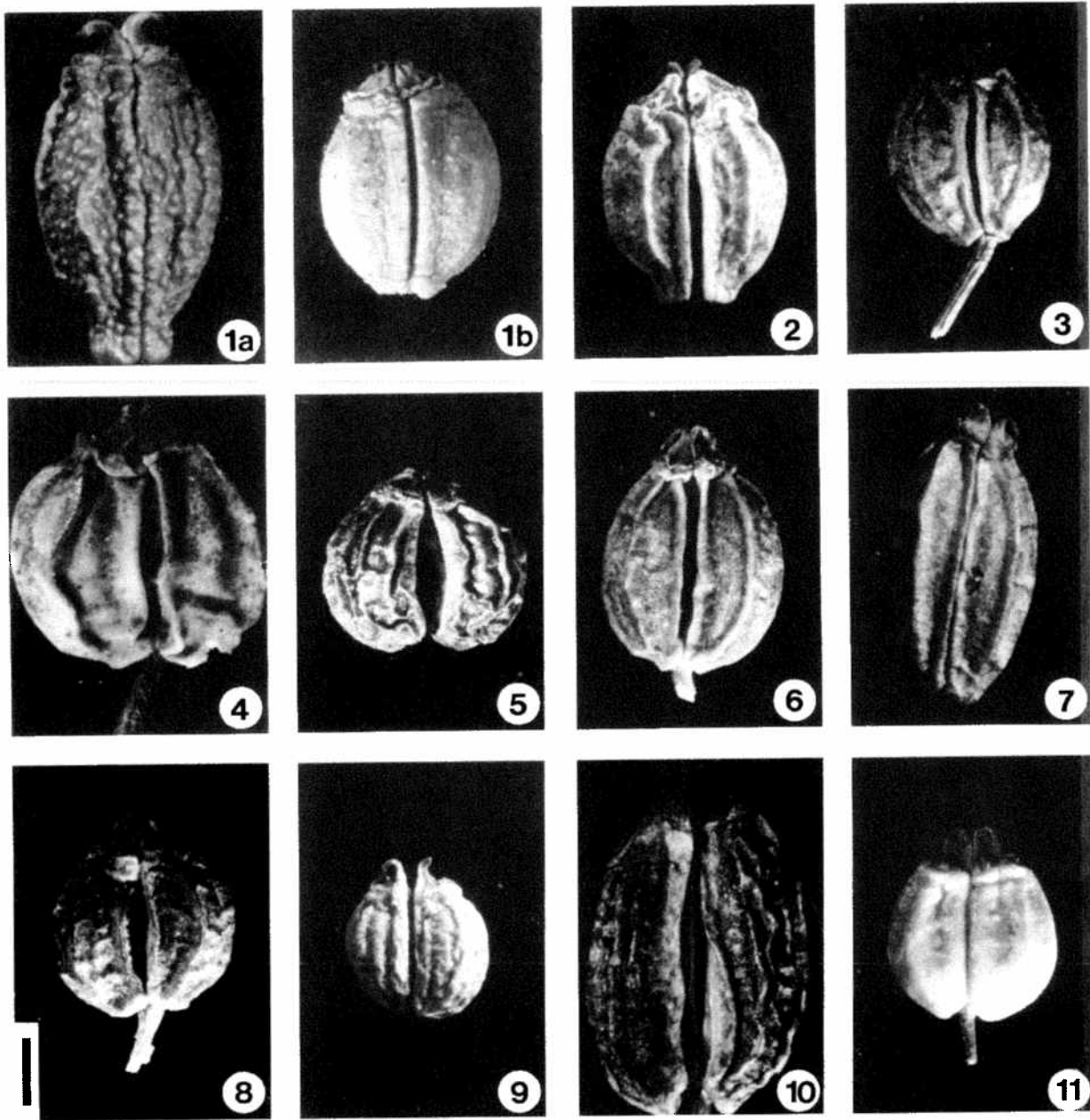


Fig. 9. Mature fruits of *Anginon* species to show the range of variation in size, shape and surface sculpturing. The surface varies from smooth to rugose in most of the species, but rarely tuberculate (most samples of *A. difforme*). 1. *A. difforme* (1a = Allison 207, 1b = Allison 129); 2. *A. ternatum* (Van Wyk 3028); 3. *A. fruticosum* (Van Wyk 3050); 4. *A. pumilum* (Allison 159); 5. *A. tenuior* (Van Wyk 3334); 6. *A. swellendamense* (Van Wyk 3013); 7. *A. paniculatum* (Van Wyk 3344); 8. *A. rugosum* (Paterson 456); 9. *A. streyi* (Strey 2154); 10. *A. verticillatum* (Allison 178); 11. *A. jaarsveldii* (Allison 164).

tween populations – compare 1a in Fig. 9 (“typical”, strongly tuberculate *A. difforme* fruit from Uniondale) with 1b in Fig. 9 (more or less smooth, obovate fruit of *A. difforme* from the Kamiesberg). *Anginon pumilum*,

the smallest of the species in terms of habit, has amongst the largest fruits in the genus (4 in Fig. 9). The fruits of *A. pumilum*, *A. tenuior*, *A. rugosum*, *A. streyi* and *A. jaarsveldii* are relatively broad, with a length to

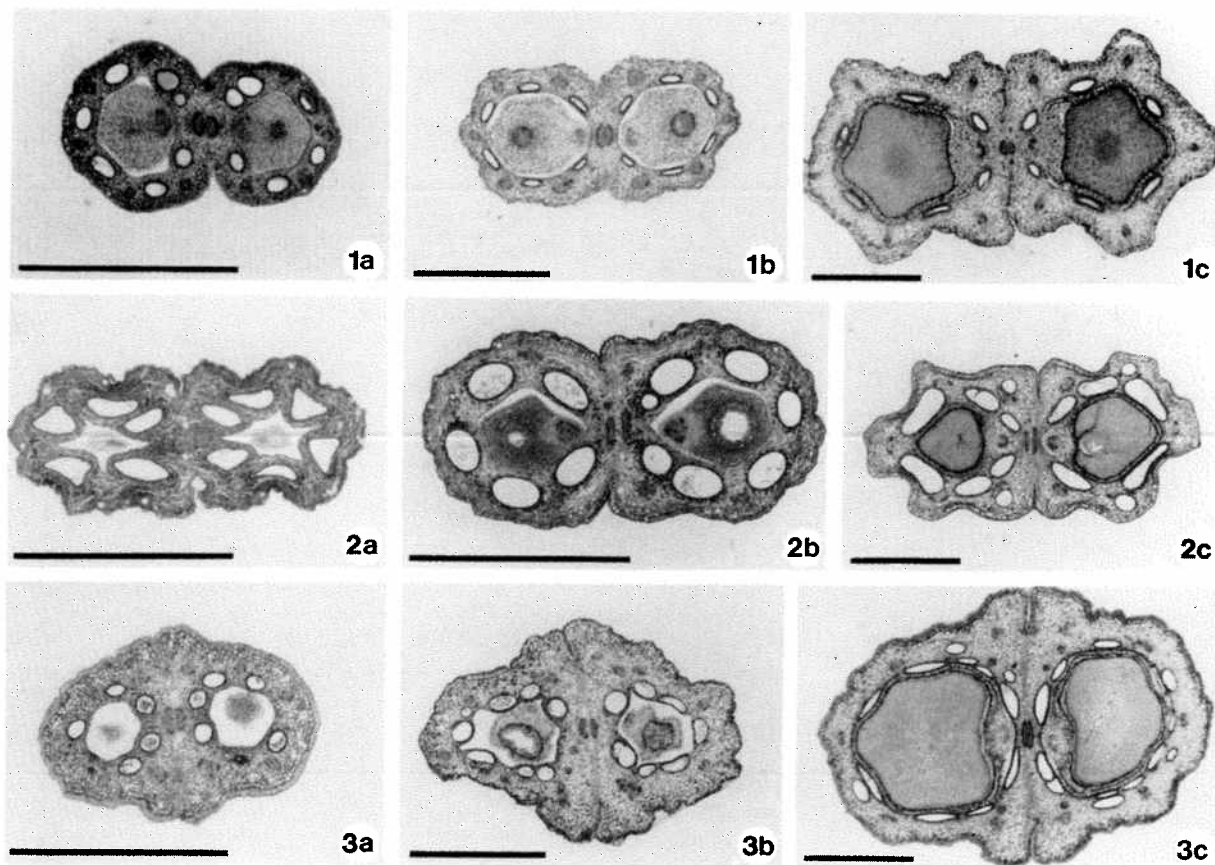


Fig. 10. Transverse sections of a flower (a), young fruit (b) and mature fruit (c) of three species of *Anginon* to show the range of variation in the genus. 1. *A. paniculatum*, note the narrow commissure, weakly developed ribs and small vascular bundles (all from Van Wyk 3337); 2. *A. jaarsveldii*, note the somewhat wider commissure (all from Allison 166); 3. *A. difforme*, note the wide commissure, the absence of ribs except at the commissure, the small vascular bundles and the large number of vittae (all from Van Wyk 2944).

width ratio of less than 1 (Fig. 7c). Thus this character proved to be convergent within the genus, but *A. pumilum* and *A. tenuior* are the only species with the fruit widely depressed ovate (see Fig. 13).

Briquet (1897b) and Wolff (1910) reported anatomical differences between three species of *Anginon*, but there is uncertainty about the identity of the species which they investigated. Nevertheless, the potential value of fruit anatomy details was clearly demonstrated. We studied the internal fruit structure of practically all the species and several characters could be used for phylogenetic interpretations (Tab. 1), including differences in the size and shape of the fruits, the width of the commissure, the size, position and number of vittae in the mature fruits, the size of substomatal chambers, the presence of lignified cells in the commissural area and the shape and wall thickness of the epidermal cells. To gain a better understanding of how the variation should be interpreted, we studied the flowers, young fruits and

mature fruits of three different species (Fig. 10). It is interesting to note that most of the characters are congenital, while some are visible only at a late stage of development. When compared with the outgroup (*Glia*), *A. difforme* appears to have the most highly specialized fruits of all the species; it usually has a tuberculate surface, an exceptionally thick cuticle, a very wide commissure (with prominent commissural ribs), a large number of vittae (usually 12 per mericarp) and distinct groups of lignified cells in the commissural region. The width of the commissure varies considerably, with *A. rugosum* and *A. difforme* at the two extremes (Fig. 7d). The commissure is narrow in the former (often less than 20 % of the total width of the fruit), while it is broad and "Peucedanum-like" in *A. difforme*. A schematic summary of the range of variation in fruit structure is given in Fig. 11, which shows transverse sections through the middle of the fruits of all the species except *A. intermedium*. In contrast to *Glia* (where the fruit is

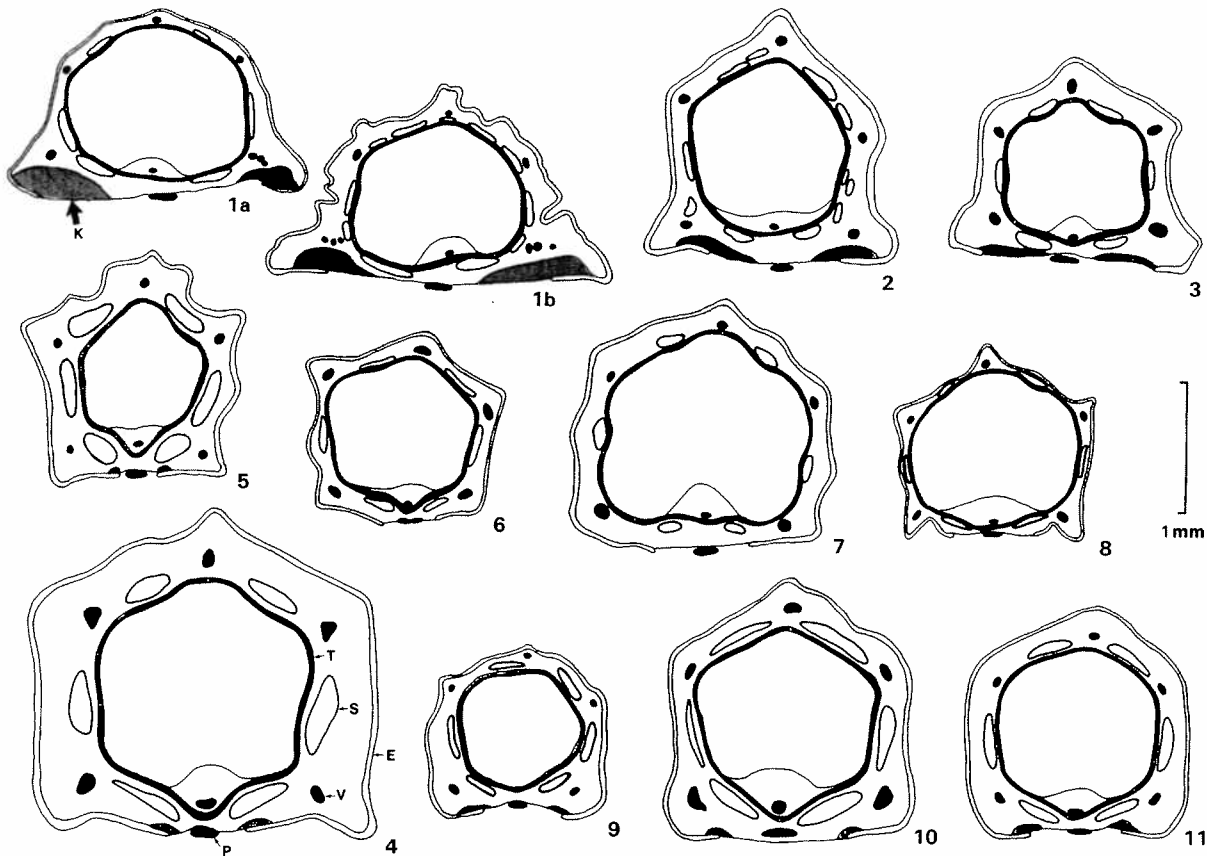


Fig. 11. Transverse sections of mature mericarps of *Anginon* species (all except *A. intermedium*), showing the shape and size, as well as the thick, cutinised epidermis (E), the carpophore (P), the vittae (S), the testa (T) and the vascular bundles (V). Large groups of lignified cells (K) are present in the commissural area in *A. difforme*, *A. ternatum* and *A. fruticosum*; a few lignified cells are usually visible in *A. pumilum*, *A. tenuior*, *A. streyi*, *A. verticillatum* and *A. jaarsveldii*. All the species have six (very rarely eight) resin ducts (vittae) except *A. difforme* and *A. ternatum*, where there are usually eight to twelve. Size differences are not very useful but the fruit of *A. pumilum* are generally larger than those of the other species. 1. *A. difforme* (1a = B-E & M van Wyk 1235, 1b = Van Breda 1634); 2. *A. ternatum* (Van Wyk 3028); 3. *A. fruticosum* (Moffett & Steensma 4123); 4. *A. pumilum* (Allison 154); 5. *A. tenuior* (Van Wyk 3334); 6. *A. swellendamense* (Van Wyk 3013); 7. *A. paniculatum* (Taylor 11271); 8. *A. rugosum* (Paterson 456); 9. *A. streyi* (Strey 2154); 10. *A. verticillatum* (Allison 178); 11. *A. jaarsveldii* (Allison 168).

distinctly ribbed), the fruit ribs are generally indistinct or absent in *Anginon*. Six vittae are usually present in each mericarp, but seven or eight occur sporadically in some species (see 2b & 2c in Fig. 10 for example). *A. difforme* (3 in Fig. 10, 1 in Fig. 11) and *A. ternatum* (2 in Fig. 11) are exceptional in the much larger number of vittae (up to 13 in each mericarp). The additional vittae often do not run along the entire length of the fruit but form so-called "island-vittae" (Burt 1991). The vittae are often larger in *A. pumilum* (4 in Fig. 11) and *A. tenuior* (5 in Fig. 11) than in the other species. Mature fruits of *A. jaarsveldii* have a "gland-dotted" appearance at maturity, due to large substomatal chambers, a character apparently unique to this species. As shown in Fig. 11, there is also variation in the degree of lignifica-

tion of cells in the commissural area. A few thick-walled cells are usually present in most of the species (see 4, 5, 9, 10 and 11 in Fig. 11) but large groups of lignified cells appear to be limited to *A. difforme*, *A. ternatum* and *A. fruticosum* (respectively 1, 2 and 3 in Fig. 11). Most of the interesting anatomical characters do not show distinct discontinuities and are therefore of limited diagnostic value at the species level but they nevertheless show interesting trends within the genus as a whole. Some trends seem to be directional and mutually correlated and as such provide new ideas about character evolution within *Anginon*. The way in which some characters could be polarised is shown in Tab. 1.

The outer walls of the epidermal cells of the fruit are heavily thickened and cutinised in all the species of *Anginon*.

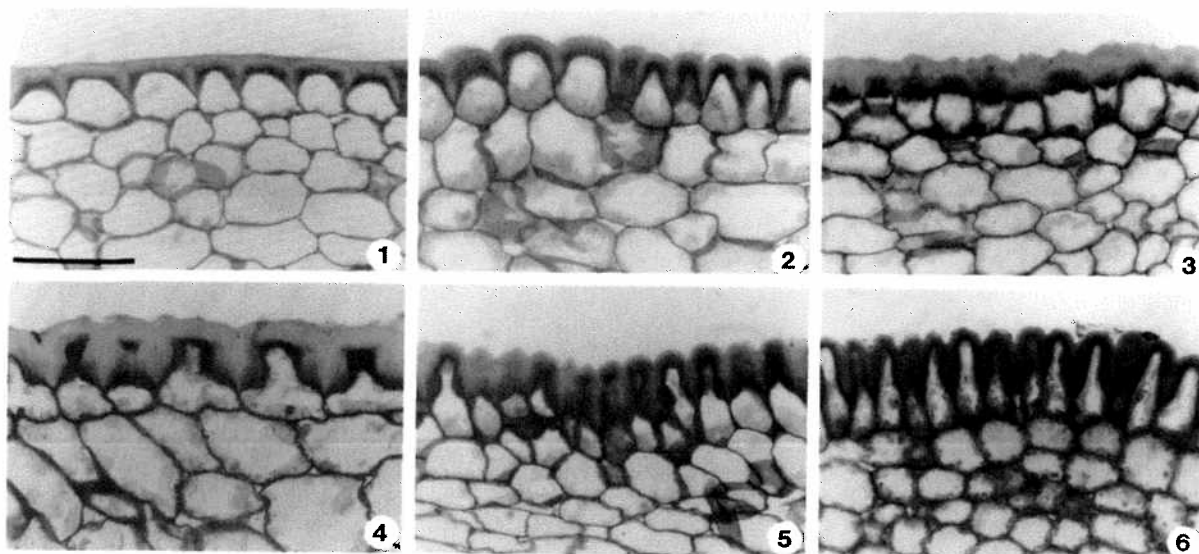


Fig. 12. The heavily cutinised fruit epidermis of *Anginon* species, showing the range of variation found in all the species studied. 1. *A. rugosum*, cells not bottle-shaped (Allison 210); 2. *A. swellendamense*, cells somewhat pointed (Van Wyk 2963); 3. *A. verticillatum*, outer cell wall constricted (Allison 178); 4. *A. pumilum*, cells slightly bottle-shaped (Acocks 23003); 5. *A. fruticosum*, cells distinctly bottle-shaped (Van Wyk 3050); 6. *A. difforme*, cells distinctly bottle-shaped (Van Wyk 2944).

*ginon*, and also in the monotypic genus *Glia*. This unusual feature is not only a useful diagnostic character to distinguish *Anginon* and *Glia* from all other genera, but provides convincing evidence that the two genera constitute a monophyletic group. Generic circumscriptions in the Apiaceae are often based on superficial similarities and relationships are little understood, so that it is useful to find such a remarkably unambiguous character. Fig. 12 shows the range of variation in the shape of the epidermal cells and the thickness of the cuticle. The peculiar bottle-shaped epidermal cells of two species were reported by Briquet (1897b) and Wolff (1910) and this character is visible in most of the species, at least near the commissural area. The polarity of the character is shown in Tab. 1. The shape varies from short and broad (gemmate) as in *A. rugosum* (1 in Fig. 12), to oblong and distinctly bottle-shaped as in *A. difforme* (6 in Fig. 12). Some species (and *Glia*) have the epidermal cells slightly bottle-shaped, i.e. somewhat elongated and constricted (see 3 and 4 in Fig. 12).

### Phylogenetic relationships

Based on general trends in the vegetative and reproductive morphology, the species can be grouped together or arranged in sequences reflecting their degree of specialization. We used the cladistic method to explore patterns of character state distributions and to

present an explicit hypothesis of relationships and groupings within *Anginon*. Similar approaches were taken by Winter & Van Wyk (1996) for the genus *Heteromorpha* Cham. & Schlecht. and Roux et al. (1978) for the genus *Bupleurum* L., but there are few examples of generic level cladistic studies in Apiaceae. By selecting *Glia* as outgroup (with the heavily cutinised epidermal cells of the fruit as convincing synapomorphy) it was possible to logically polarise 19 different characters (Tab. 1). This data set was analysed by means of the computer program HENNIG86 (Farris 1988). Using the "ie" option (which guarantees the shortest possible tree or trees), a single, fully resolved topology was found, shown as the cladogram in Fig. 13. The cladogram gives a summary of the most likely sequence of character evolution within *Anginon* and provides a first hypothesis of phylogenetic relationships at the species level in this genus.

The monophyly of *Anginon* is supported by three apomorphies (the reduced leaves, the absence of medullary vascular bundles in mature leaves and the absence of ribs or wings in the fruit). The species form three monophyletic groups, each distinguished by at least two apomorphies: a basal group (*A. jaarsveldii*, *A. intermedium*, *A. verticillatum* and *A. streyi*) with at least slightly laminar mature leaves, and with the lateral racemes terminating in simple umbels (albeit rarely so in *A. streyi*); an intermediate group (*A. rugosum*, *A. paniculatum*, *A. swellendamense*, *A. tenuior* and *A. pumilum*)

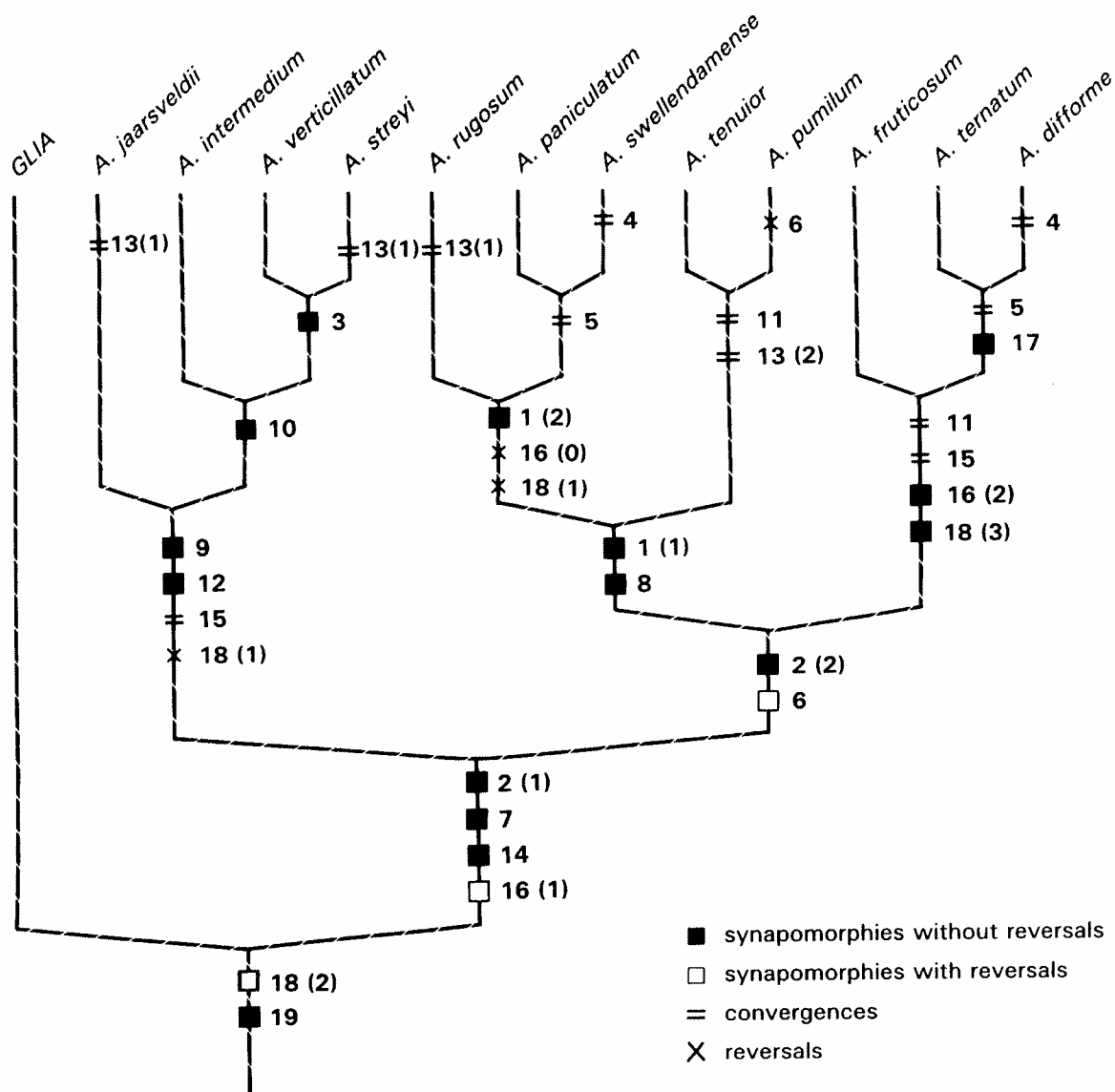


Fig. 13. Single, fully resolved cladogram of the genus *Anginon*, with *Glia* as outgroup, showing phylogenetic relationships between all the species. Characters and character states are numbered as in Tab. I. The result was obtained with HENNIG86, using the "ie" option (consistency index 70; retention index 83).

with glaucous stems and leaves, and with long, sparse, widely branched inflorescences; and lastly a highly specialised group (*A. fruticosum*, *A. ternatum* and *A. difforme*), with needle-like phyllodes and distinctive fruit structural characters, such as the distinctly bottle-shaped epidermal cells and the wide, "Peucedanum-like" commissure. The cladistic approach taken in this study has, contrary to initial expectations, contributed significantly to a better understanding of relationships within the genus *Anginon*, despite sample limitations

and considerable variability in characters and character states.

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Tab. 1. Characters and polarization of character states in the genus *Anginon*, used to construct the cladogram in Fig. 13.

Species	Characters and character states			
	1 to 5	6 to 10	11 to 15	16 to 19
<i>Glia prolifera</i>	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 2 1
<i>A. difforme</i>	0 2 0 1 1	1 1 0 0 0	1 0 0 1 2	2 1 3 1
<i>A. fruticosum</i>	0 2 0 0 0	1 1 0 0 0	1 0 0 1 2	2 0 3 1
<i>A. intermedium</i>	0 1 0 0 0	0 1 0 1 1	0 1 0 1 ?	?? ? 1
<i>A. jaarsveldii</i>	0 1 0 0 0	0 1 0 1 0	0 1 1 1 1	1 0 1 1
<i>A. paniculatum</i>	2 2 0 0 1	1 1 1 0 0	0 0 0 1 0	0 0 1 1
<i>A. pumilum</i>	1 2 0 0 0	0 1 1 0 0	1 0 2 1 0	1 0 2 1
<i>A. rugosum</i>	2 2 0 0 0	1 1 1 0 0	0 0 1 1 0	0 0 1 1
<i>A. streyi</i>	0 1 1 0 0	0 1 0 1 1	0 1 1 1 1	1 0 1 1
<i>A. swellendamense</i>	2 2 0 1 1	1 1 1 0 0	0 0 0 1 0	0 0 1 1
<i>A. tenuior</i>	1 2 0 0 0	1 1 1 0 0	1 0 2 1 0	1 0 2 1
<i>A. ternatum</i>	0 2 0 0 1	1 1 0 0 0	1 0 0 1 2	2 1 3 1
<i>A. verticillatum</i>	0 1 1 0 0	0 1 0 1 1	0 1 0 1 1	1 0 1 1

1. Leaves, stems and/or inflorescence: green = 0; slightly glaucous (at least in some specimens) = 1; invariably glaucous = 2.
2. Ultimate segments of mature (upper) leaves: distinctly laminar = 0; at least slightly laminar = 1; completely and invariably phyllodinous = 2.
3. Mature (upper) leaves: laminar segments absent, or if present, then reduced in number (but not much reduced in size) = 0; laminar segments not reduced in number but much reduced in size = 1.
4. Petiole of mature (upper) leaves: adaxially grooved = 0; terete, without a groove = 1.
5. Petiole of mature (upper) leaves in transverse section: bilaterally symmetrical = 0; radially symmetrical = 1.
6. Petiole of mature leaves (number of vascular bundles): 3 to 5 = 0; several (>5) = 1.
7. Petiole (number of medullary bundles): several (4 to 6) in most leaves except those directly below the inflorescence = 0; usually absent, rarely 1 or 2, but then mostly in seedling leaves = 1.
8. Inflorescence length: shorter than the branches = 0; longer than the branches = 1.
9. Lateral racemes: terminate in compound umbels = 0; terminate in simple umbels (rarely so in *A. streyi*) = 1.
10. Length of rays: normal = 0; very long (usually >30 mm) = 1.
11. Vittae in petals: single (unbranched) = 0; branched = 1.
12. Style length: short (up to 0.3 mm) = 0; range exceeds 0.4 mm = 1.
13. Fruit shape: ovate/obovate = 0; widely ovate/obovate = 1; widely depressed ovate = 2 (see 4 and 5 in Fig. 9).
14. Fruit ribs: with distinct ribs = 0; without ribs = 1.
15. Width of commissure: narrow = 0; medium = 1; wide = 2.
16. Lignified cells in commissural area: none = 0; few = 1; many = 2.
17. Number of vittae per mericarp: usually 6 = 0; 6 to 12 = 1.
18. Shape of epidermal cells: not bottle-shaped = 0; slightly bottle-shaped, at least in the commissural area = 1; slightly bottle-shaped, in the commissural area and elsewhere = 2; distinctly bottle-shaped = 3.
19. Outer wall of fruit epidermal cells: thin = 0; thick and heavily cutinised = 1 (not used in the analysis).

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