S.-Afr. Tydskr. Plantk., 1987, 53(3): 194 – 201

Floral development in *Greyia flanaganii* with notes on inflorescence initiation and sympodial branching

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Accepted 19 December 1986

The aerial parts of *Greyia flanaganii* H. Bolus consist of a system of superposed monochasial shoots. The mature lateral inflorescences of this evergreen and probably most primitive species of *Greyia* Hook. & Harv. are primarily terminal. The flowers are adapted to ornithophily, basically diplostemonous and inclined to haplostemony. The 5 floral whorls essentially develop acropetally and alternately, but in flower buds with less than 10 stamens the carpels are epipetalous. The multilayered endothecium-like tissue and additional inner parenchyma form the criteria for considering the anther of *Greyia* as phylogenetically primitive. Similarities in floral morphogenesis of the Greyiaceae and Saxifragaceae *sensu lato* are discussed.

Die bogrondse dele van *Greyia flanaganii* H. Bolus is opgebou uit 'n stelsel van gesuperponeerde monogasiums. Die volwasse bloeiwyses van hierdie bladhoudende en waarskynlik primitiefste spesies van *Greyia* Hook & Harv. word lateraal gedra, maar ontstaan terminaal. Die blomme het aanpassings vir voëlbestuiwing, is diplostemoon en neig na haplostemonie. Die 5 blomgordels ontwikkel akropetaal en afwisselend, maar in blomknoppe met minder as 10 meeldrade is die vrugblare teenoor die kroonblare geplaas. As gevolg van die meerlagige endotekiumagtige weefsel en bykomende parenkiem word die meeldraad van *Greyia* as filogeneties primitief beskou. Ooreenkomste in blommorfogenese tussen die Greyiaceae en Saxifragaceae *sensu lato* word bespreek.

Keywords: Anther development, diplostemony, floral morphogenesis, floral response, *Greyia*

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Introduction

Greyia flanaganii H. Bolus is one of three species comprising the family Greyiaceae — a family endemic to southern Africa. *G. flanaganii* is limited to the steep mountain slopes of the Kei River valley in the eastern Cape Province, whereas *G. radlkoferi* Szyszyl. and *G. sutherlandii* Hook. & Harv. are confined to the eastern Transvaal escarpment and the Natal Drakensberg mountains respectively. The restricted geographical distribution of *Greyia* Hook. & Harv. is paralleled by its isolated taxonomic position, as there is still doubt as to the families with which Greyiaceae should be associated. Evidence from many sources suggests affinities with families included in the Cunoniales, Rosales and Saxifragales (Dahlgren & Van Wyk 1987). A possible link with particularly Francoaceae or Saxifragaceae has been proposed by these authors. An association with the Francoaceae is mainly supported by pollen morphological evidence (Hideux & Ferguson 1976). Additional possible similarities in the androecium of Francoaceae, Greyiaceae and Saxifragaceae have been pointed out (Dahlgren & Van Wyk 1987). Although the androecium should obviously be considered for the purpose of establishing taxonomic affinities, very little factual data is available on the development and structure of the stamens in *Greyia*.

During a leaf morphological/embryological study on *Greyia* (Steyn 1974, 1977), some intriguing aspects concerning the floral response in *G. flanaganii* were encountered. A developmental study of the inflorescence and flowers of this species was subsequently undertaken with special attention given to the development of the stamens before anthesis.

Materials and Methods

Material for this investigation was obtained from plants cultivated in private gardens and gardens of the University of Pretoria. The original stock material was obtained from cuttings taken in 1972 from *G. flanaganii* plants found in their natural habitat in the Komgha district. For comparative purposes, material of *G. sutherlandii* was obtained from plants growing in the Harrismith district. During the blooming season of 1985, inflorescences and buds in various stages of development were dissected and fixed in 2,5% glutaraldehyde in a Na_2PO_4 buffer, dehydrated in a graded alcohol series and imbedded in glycol methacrylate, following the procedures of Feder & O'Brien (1968). Sections *c.* 2 – 3 µm were cut on a Porter Blum microtome, stained with the periodic/Schiff's reaction (Feder & O'Brien 1968) and counterstained with 0,05% toluidine blue (Sidman *et al.* 1961). Flower primordia used for SEM studies were fixed as above, postfixed in 1% Os_5PO_4 and dehydrated in a graded acetone series. After critical point drying the primordia were transferred onto SEM stubs, coated with silver and viewed with a Phillips PSEM 500 at 12kV.

All drawings were made with the aid of a Leitz Wetzlar drawing tube.

Descriptors used to indicate abundance and frequency are based on the proposals of Schmid (1982).

Observations

Initiation of inflorescences and sympodial branching

Under Pretoria conditions most inflorescences of *G. flanaganii* start appearing (Figure 1C) from early January till the end of February when day length is still long and the maximum temperature exceeds 30°C. At this stage the leafbearing shoots are seemingly still in an actively growing stage. Newly formed inflorescences can however still appear up to the end of May.

The inflorescences occupy neither a terminal nor a strictly axillary position. The apical meristem of a shoot is transformed into an inflorescence which is quickly deflected owing to the development of a nearby axillary bud taking over the terminal position and immediately continuing the lengthening of the shoot. The initially terminal inflorescence (Figure 1C) is now positioned laterally and the usurping shoot, (*sensu* Guédès 1982) i.e. the shoot which continues the lengthening of the supporting branch, is a sympodium (Figure 1A).

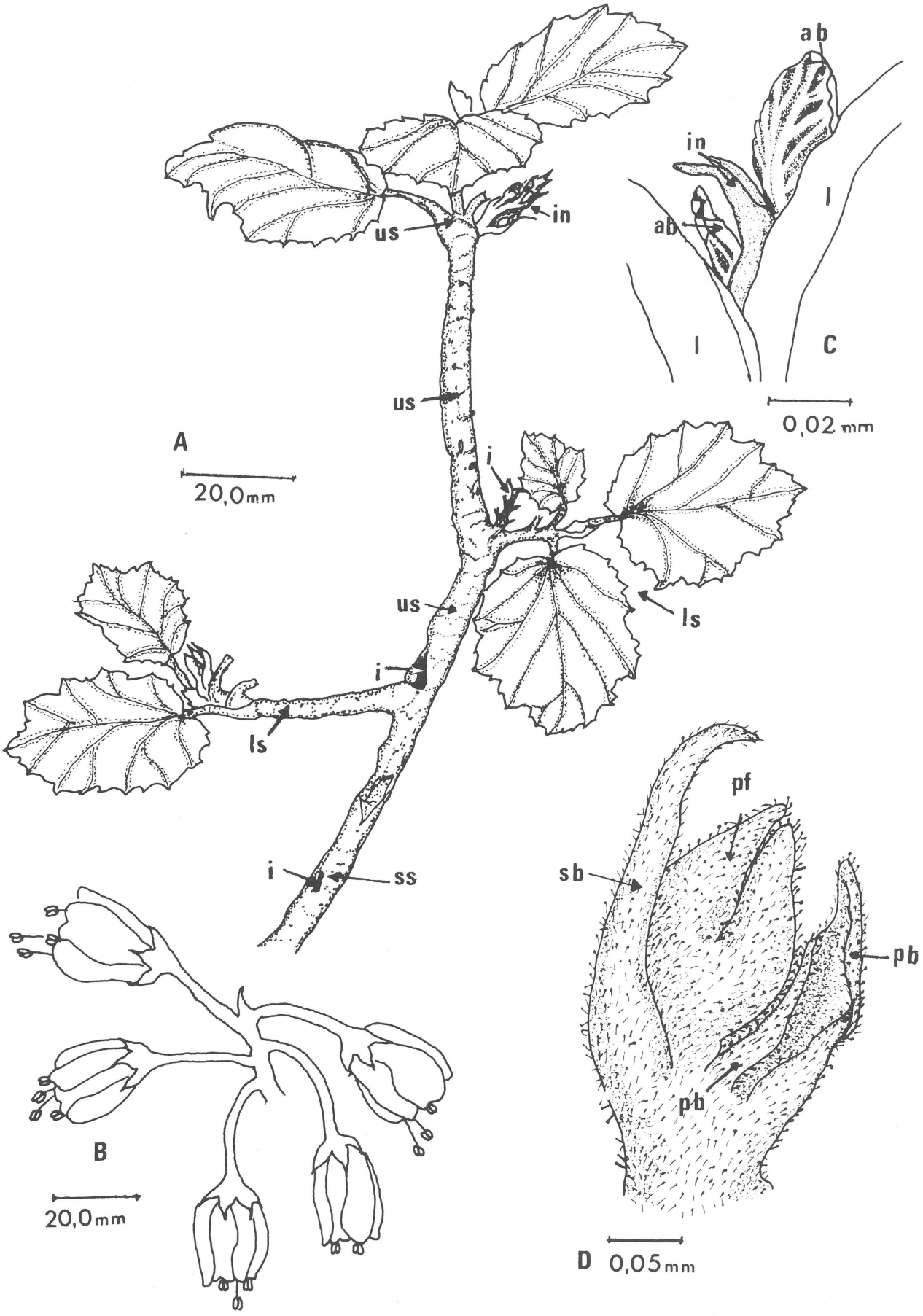

Figure 1 Floral response and sympodial branching in *G. flanaganii*: A. supporting branch (ss) with inflorescences (in), remains of infructescences (i), lateral shoots (ls) and successive usurping shoots (us); B. mature inflorescence; C. shoot apex with distal axillary buds (ab), leaf bases of distal leaves (l) and terminal inflorescence (in); D. apex of inflorescence with sterile distal bracts (pb), distal flower primordium (pf) and subtending bract (sb).

The usurping shoot develops from the axillary bud of the most distal leaf. Usually the axillary bud of the second leaf from the top also develops into a shoot (Figure 1C), but the last mentioned grows plagiotropically and does not overtop the usurping shoot (Figure 1A). New leaves separated by very short internodes are formed in rapid succession on these two shoots, so that the developing inflorescences are protected and obscured by the new growth.

After successive flowering periods (Figure 1A) the supporting branch consists of a succession of sympodial usurping shoots. Consecutive growth flushes are delimited by the dry remains of the infructescences and (usually) by the plagiotropic lateral shoots.

In *G. flanaganii* inflorescence initiation seems to mark the beginning of the new vegetative phase of the plant. As the number of inflorescences increases, the leaves of the previous season's growth show manifestations of senescence by exhibiting autumn colouring, become dry and fall. The supporting shoots become bare, with the new leaves crowded near the apex around the developing inflorescences. Axillary buds, occurring in a 2/5 phyllotaxis around the bare shoot, usually remain dormant but may shoot later in the season, enhancing the leafiness of the shrub. In this respect it is interesting that the tree-like *G. radlkoferi* does not retain its axillary buds during leaf abscission: ". . . except in the case of one or two of the uppermost leaves of a branch the falling leaf usually carries away its axillary bud." (Schonland 1914).

Flower initiation

The initiation of the flower primordia is preceded by the development of 12 – 20 bracts which are formed acropetally in a 2/5 phyllotaxis around the rachis. The bracts are already well-developed when flower primordia start developing acropetally in their axils. While the two distal bracts are being formed, the apical meristem of the inflorescence becomes inactive and ceases to function. These two bracts are poorly developed and no flower primordia are formed in their axils (Figure 1D). Two sterile distal bracts have also been encountered in *G. sutherlandii* and they seem to be characteristic of the *Greyia* inflorescence. The reason for their sterility is unknown. Perhaps these bracts are, on account of their reduced size, inadequate to synthesize the floral hormone complex necessary for the initiation of flower primordia.

The subtending bracts are densely covered with numerous, uniseriate, glandular hairs consisting of a stalk, which is sometimes branched, with a glandular head. The heads secrete a very sticky, clear substance, covering the developing flower primordia. The bracts are glued together, and to the rachis, isolating and protecting the developing flower primordia. Nevertheless, most of the primordia abort at an early stage along with their subtending bracts and the initial 2/5 phyllotaxis of the inflorescence becomes obscured. The mature inflorescences (Figure 1B) contain 2 – 10 flowers. In nature even fewer flowers reach maturity.

Formation and arrangement of the foral parts

In the bisexual, pentamerous and hypogynous flower of *G. flanaganii* the floral parts are arranged in five whorls which develop acropetally. The sepals are therefore formed first, followed by the petals, the outer and inner stamen whorls and the congenitally fused carpels.

The five broadly based sepals are formed well ahead of the inner whorls. Although the sequence in which the sepals had been formed was not followed, they are imbricate, but in such a way that one sepal overlaps two adjacent ones, three sepals have one margin overlapped and the fifth sepal is overlapped on both sides (Figure 3B). Like the bracts, the sepal primordia are covered with stalked glandular hairs. Although the sepal primordia are free they become glued together by the secretion and interlocking of the hairs. The inner floral whorls are completely surrounded and covered by the sepal primordia and enveloped by the sticky secretion. These primordia must therefore be removed to facilitate penetration of fixatives. Attempts to dissolve this as yet unknown secretion was only partly successful so that an extensive SEM study was not attempted.

The petal and stamen whorls are formed in quick succession (Figure 2) and their primordia resemble each other at this early developmental stage before marginal growth of the petal primordia becomes pronounced. At this stage the flower primordium looks like a pentagon when viewed from above, with the broad bases of the excised primordia representing the sides of the pentagon. The five narrow-based petal primordia are pressed into the inner corners of the pentagon. They alternate with the sepal primordia and are arranged in the same imbricate manner as the sepals (Figure 3B).

The 10 stamen primordia are formed in two acropetal whorls alternating with each other. The petal primordia alternate with the outer and older (from now on called the episepalous) stamen primordia and lie opposite the inner (from now on called the epipetalous) stamen primordia (Figure 2).

Evidence of this initial diplostemonous arrangement of the stamen primordia is also found in young flower buds. In a transverse section of the receptacle the procambial traces supplying the stamens are arranged in two whorls. The episepalous traces are larger and lie outside the epipetalous traces (Figure 3A). Higher up in the same bud the episepalous stamens are also larger and more to the outside than the epipetalous stamens (Figure 3B).

A time-lapse occurs between the formation of the epipetalous stamen primordia and the carpel primordia (Figure 2). Although the initial stages in the development of the carpels were not seen with the SEM, it is evident from transverse sections of young flower buds that the congenitally fused carpel primordia form opposite the episepalous stamen primordia. The dorsal procambial traces of the carpels and the episepalous stamen traces lie opposite the sepal traces in the receptacle (Figure 3A) and higher up in the same bud the carpels (Figure 3B) lie opposite the sepals.

Basically 10 stamen primordia are formed, but a reduction may occur in the basic number. One of the epipetalous stamen

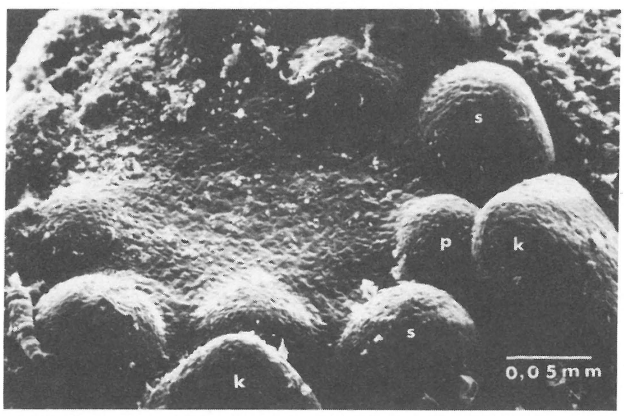

Figure 2 Scanning electron micrograph of a flower primordium of *G. flanaganii* during formation of the petals (k), the epipetalous stamens (p) and the episepalous stamens (s).

primordia often does not develop (Figure 3D & H) and only 9 stamens with 9 stamen traces in the receptacle (Figure 3E & G) then occur. In these buds the locules of the ovary lie opposite the petals (Figure 3D) and in the receptacle the dorsal carpel traces lie opposite the epipetalous stamen traces. Occasionally two stamens and their traces are lacking.

The reduction in the number of epipetalous stamen primordia is often accompanied by a reduction in the number of carpel primordia. A young flower bud may therefore contain 10 or 9 stamens and 5 or 4 fused carpels (Figure 3B & H) with the corresponding number of traces in the receptacle (Figure 3A & G).

Although 10 or 9 stamens are initially formed, older buds often contain less stamens, as abortion of both the epipetalous and episepalous stamens may take place during the development of the anthers and the ovary. The crushed remains (Figure 3D) and the vascular traces of the aborted stamens (Figure 3E) can however still be seen. As the filaments are initially short, the developing anthers and ovary lie in the same horizontal plane. The enlarging anthers of the epipetalous and episepalous stamens are not only of the same size, but are now arranged in a single series. Furthermore, the surrounding imbricate petals are also encroaching into this space by marginal growth. The anthers are no longer symmetrical in shape, but are usually distorted and some are so crushed that they abort. Abortion is therefore obviously a result of the confinement of space.

In the flower primordia of *G. sutherlandii* the five fused

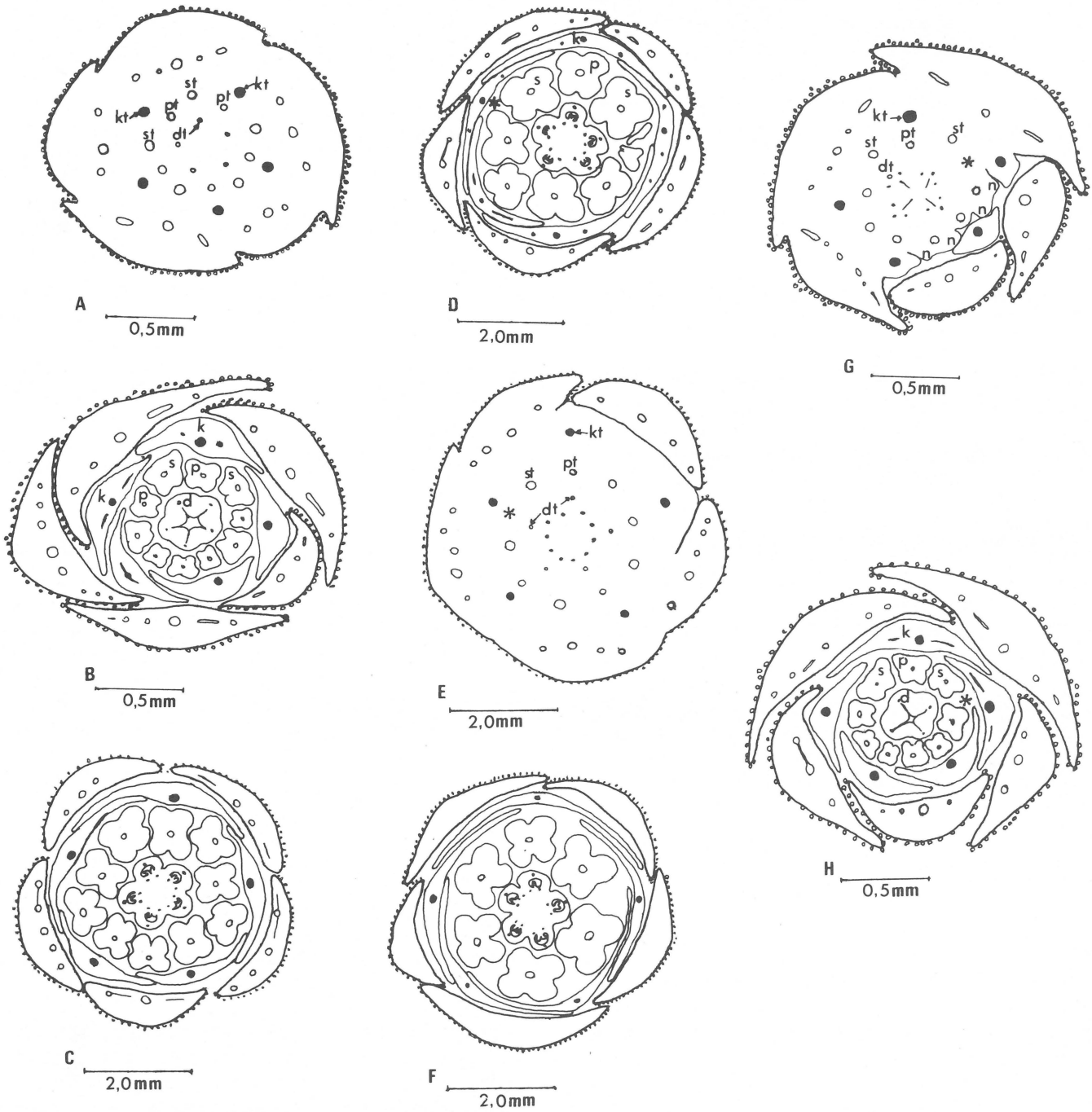

Figure 3 Transverse sections of *G. flanaganii* flower buds: A. receptacle of bud B; B. very young bud with 5 carpels and 10 stamens; C. older bud with 5 carpels and 10 stamens; D. bud with 5 carpels and 9 stamens, 2 of which have aborted; E. receptacle of D; F. older bud with 6 stamens; G. receptacle of H with staminode primordia; H. very young bud with 4 carpels and 9 stamens. (d) centre of carpel, (dt) dorsal carpel trace, (k) petal, (kt) petal trace, (n) staminode primordia, (p) epipetalous stamen, (pt) epipetalous stamen trace, (s) episepalous stamen, (st) episepalous stamen trace.

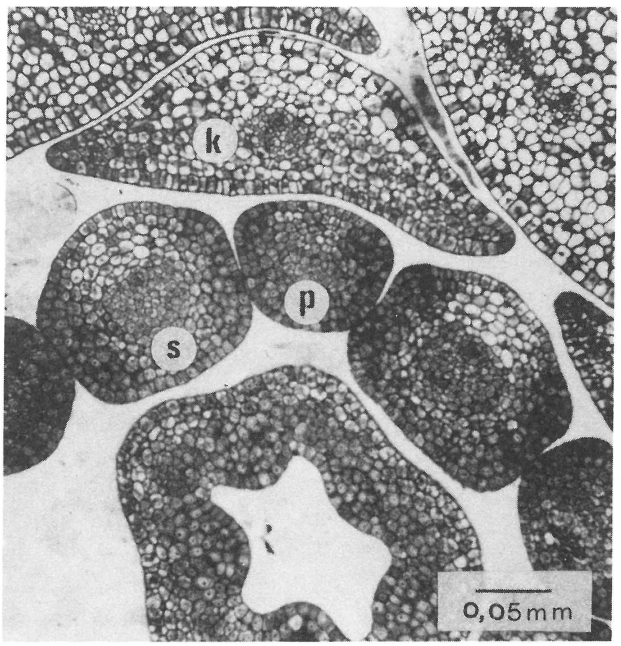

Figure 4 Transverse section of a very young bud of *G. sutherlandii* with 5 fused carpel primordia opposite the petals (k) and alternating epipetalous (p) and episepalous (s) stamen primordia.

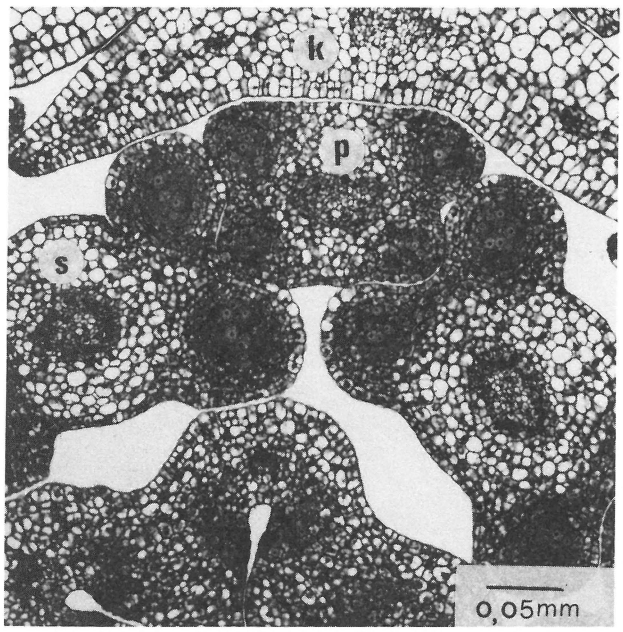

Figure 5 Transverse section of an obdiplostemonous bud of *G. sutherlandii* with carpels opposite the petals (k), small epipetalous stamens (p) and episepalous stamens (s).

carpel primordia develop opposite the petals (Figure 4). The 10 stamen primordia lie in a single series, the smaller epipetalous primordia alternating with the larger episepalous primordia. When the lobes of the anthers and the locules of the carpels develop (Figure 5), the problem of constricted space is solved in another way than in *G. flanaganii*: the epipetalous stamens not only remain much smaller than the episepalous stamens, but are now outside the episepalous whorl. Young buds of *G. sutherlandii* are therefore distinctly obdiplostemonous.

Development of the anther and filament

The first indication of anther development is the appearance of four slight symmetrically spaced bulges on the primordium. Each bulge represents a developing pollen sac (Figure 6A – F) of the tetrasporangiate anther. The flow diagram in Figure 7 depicts this development.

Underneath the protoderm of the pollen sac the cells of the archesporium divide periclinally and anticlinally (Figure 6A). The inner initials constitute the primary sporogenous cells while the outer initials constitute the primary parietal cells. Division and differentiation of the sporogenous initials leads to the formation of a center core of pollen mother cells (Figure 6B – D) in each pollen sac. The parietal initials repeatedly divide periclinally so that the pollen mother cells are separated from the protoderm by four layers of radially orientated, tangentially flattened cells (Figure 6B). These cells represent the secondary parietal layers (Davis 1966). Laterally to these layers, periclinal divisions (Figure 6B & D) occur in the adjacent subprotodermal cells, spreading around the circumference of the pollen mother cells. While the latter proliferate by divisions in many planes, (Figure 6C & D) the radial arrangement of the four layers is disturbed.

The cells of the outer secondary parietal layer divide anticlinally only, except underneath the stomata, where periclinal divisions occur (Figure 6E & F). This layer represents the endothecium. At later stages, when the pollen mother cells have become mature and during the development of tetrahedral tetrads (Figure 6E), a single-layered endothecium can no longer be distinguished from the underlying parenchyma. This multilayered parenchymatous tissue has developed from the second and third secondary parietal layers. During the development of the pollen wall (Figure 6F) fibrous wall thickenings develop simultaneously in the cell walls of the endothecium and the cell walls of the underlying parenchyma. The inner parenchymatous layers, however, do not develop fibrous wall thickenings (Figure 6F).

The inner secondary parietal layer covers the pollen mother cells on the outside and represents the primordial tapetum. Laterally to and along the inside of the pollen mother cells the cells of the adjacent conjunctive tissue divide (Figure 6C) to contribute towards the primordial tapetum (Figure 6C). When the pollen mother cells reach maturity the tapetal layer consists of well-developed, large cells with large nuclei. The latter divide when tetrads are formed so that the tapetal cells become at least binucleate.

Prior to anthesis the septum between two microsporangia on each side of the tetrasporangiate anther breaks down and the anther becomes bilocular. It is evident at this stage that dehiscence of the anther will be latrorse.

In floral buds initiated in January, meiosis of the pollen mother cells takes place in early June, i.e. in mid-winter. All the buds of an inflorescence are in the same developmental stage although they have been formed acropetally.

During meiosis the anthers are enclosed by the petals which are as long as the sepals. The overlapping sepal margins are glued together by the secretion of the glands. The sepals cover the inner floral parts completely until meiosis has taken place and the massive anther wall has been formed. The dividing pollen mother cells are therefore well-protected. Towards the end of pollen formation the petals elongate and their scarlet tips become visible. The filaments of the stamens now start to elongate, pushing the anthers upwards.

At the bases of the filaments the 10 disc lobes (Schonland 1914) or staminodes (Guerke 1896) which occur in one (two?)

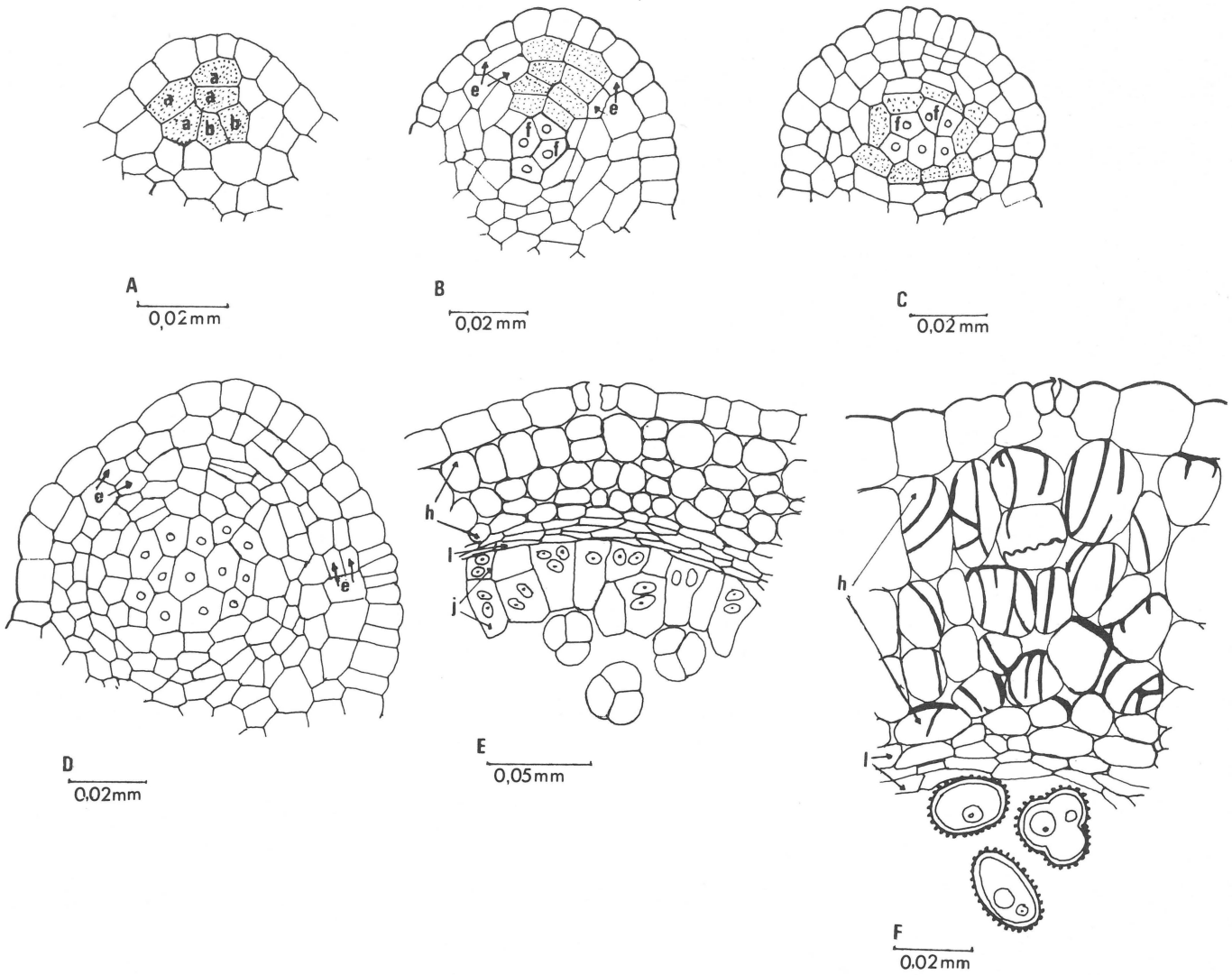

Figure 6 Development and structure of the anther in *G. flanaganii*: A – D, transverse sections of developing pollen sacs, A. with archesporium (stippled) and periclinal (a) and anticlinal (b) divisions; B. with secondary parietal layers (stippled), adjacent periclinal divisions (e) and pollen mother cells (f); C. with tapetal layer (stippled) and pollen mother cells (f); D. with radial orietation of wall layers disturbed and periclinal divisions (e); E. & F. transverse sections of anther wall after meiosis: endothecium and endothecium-like tissue (h), glandular tapetum (j) and persistent inner parenchyma (l).

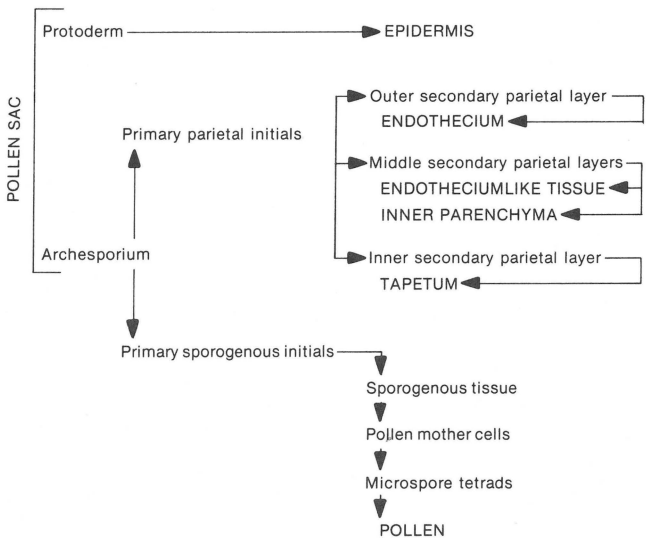

Figure 7 Flow diagram showing anther development.

whorls between the stamens and the petals keep pace with the lengthening of the filaments. These conspicuous, though controversial structures were formed as lateral outgrowths of the bases of the episepalous stamen primordia when the filaments of the latter had been demarcated (Figure 6). In *G. flanaganii* these structures do not resemble stamens at any stage during their development. Although they are vascularized they are not supplied by separate traces from the vascular cylinder. Detailed studies on the development of these structures which are provisionally refered to as staminodes are under way and will be reported elsewhere.

Discussion

A study of the floral response in *G. flanaganii* revealed that sympodization (*sensu* Guédès 1982) is a consequence of flowering. The inflorescences in this evergreen species are therefore primarily terminal and their lateral position is in turn a result of sympodization. In the deciduous *G. sutherlandii* and *G. radlkoferi* where vegative growth is delayed till after the flowering season the inflorescences remain terminal and they are deflected at a much later stage.

The aerial parts of *G. flanaganii* are made up of a series of superposed monochasial shoots. This species therefore fits into the Sixth Type of Guédès' system of tree and shrub architecture (Guédès 1982). The shoot originating from the bud in the axil of the second leaf from the top develops into

a lateral shoot and does not overtop the usurping shoot. This lateral shoot, however, develops concomitantly with the usurping shoot. According to Guédès (1982) the phenomenon of axillary buds developing into lateral branches as soon as they are formed, is rare in temperate woody plants but occurs frequently in the tropics. This characteristic therefore probably denotes a tropical origin for the evergreen *G. flanaganii*. While the latter retains its axillary buds, these buds are shed with the falling leaves in *G. radlkoferi* (Shonland 1914). This characteristic may be an adaptation to a warm-temperate climate with summer rainfall where seasonal alternation between favourable and unfavourable conditions has been the principle selective agent in promoting the evolution of the deciduous habit (Stebbins 1974). Hence it is speculated that *Greyia* has evolved from a tropical ancestral stock before confinement to its current temperate southern Hemispherical range.

Initially the inflorescences of *G. flanaganii* contain many flower primordia, most of which abort at an early stage together with the subtending bracts. Due to this abortion only 2 – 10 flowers reach maturity in contrast to the many-flowered inflorescences of *G. sutherlandii* and *G. radlkoferi*.

A comparison of floral morphogenesis in *G. flanaganii* and the Saxifragaceae *s.l.* (Gelius 1967; Klopfer 1973) indicated some similarities. In both taxa the floral parts are arranged in five whorls which essentially develop acropetally and alternate with each other. A strong development of the sepals is characteristic of *G. flanaganii* as well as of the Saxifragoideae, *Ribes* L., *Francoa* Cav. and *Parnassia* L., while in *Brexia* Nor and *Francoa* a long interval between the development of the sepals and the petals was encountered (Klopfer 1973). In *G. flanaganii* the sepals are well-suited for protecting the inner floral parts during their early development. This outer whorl is formed well ahead of the inner whorls and is covered adaxially with numerous stalked glands. These glands also occur on both the leaves and stamens of *Greyia* (Steyn 1974). The chemical nature of the glandular secretion is unknown but chemotaxonomical work on *Greyia* at the University of British Columbia (B.A. Bohm, pers. comm.) may contribute towards this aspect. The unique imbricate aestivation of the sepals and petals of *Greyia* (Figure 3) does however not characterize the pentamerous members of the Saxifragaceae *s.l.* (Gelius 1967; Klopfer 1973).

In *G. flanaganii* the petal primordia are small and are pressed into the inner corners of the pentagon formed by the sepal bases. The development of these primordia is rapidly followed by the development of first the episepalous, then the epipetalous stamen primordia. A pentagonal flower primordium, small petal primordia and the almost immediate development of the outer stamen whorl were also reported in the Saxifragoideae and *Ribes*, while in the Hydrangoideae as well as *Francoa, Parnassia* and *Escalonia* Mutis a time-lapse occurs between the development of the large-petal primordia and the next whorl (Klopfer 1973). Although the bases of the petals remain small these floral parts are strongly developed in *Greyia* and they take over the protection of the bud following meiosis in the anthers.

The strong development of the petals in *Greyia* should also be seen as part of a ornithophilous syndrome. According to Vogel (1954) all species of *Greyia* are pollinated by birds. In the urceolate flowers of *G. flanaganii* the pollen is smeared on to the base of the beak and the head of the bird (Vogel 1954). In Pretoria gardens sun birds have a preference for *G. flanaganii* plants coming into bloom, pecking vigorously at the scarlet buds even before they have opened. In fact, *Greyia* exhibits many of the characteristics of bird-pollinated flowers (Raven 1972; Faegri & Van der Pijl 1979). The petals are scarlet and in addition, retain their colour when dry (Dahlgren & Van Wyk 1987). Anthesis is diurnal. The floral parts are rigid, e.g. the anthers are basifixed, non-versatile. In addition, the presence of interstaminal ridges radiating from the ovary probably contributes towards the rigidness of the flower, thereby protecting it against damage by the probing beaks of the birds. The flowers are odourless without a nectar-guide, producing copious, not too viscous nectar, concealed by the urceolate corolla in *G. flanaganii*.

The most striking adaptation to ornithophily perhaps occurred in the androecium of *Greyia* where the staminodes arising from the same primordia as the episepalous stamens were transformed into conspicuous, nectariferous structures. *Greyia* may therefore be in a transitional evolutionary stage between a nectar (and pollen) flower with many stamens (Faegri & Van der Pijl 1979) and a nectar flower with few stamens. The tendency towards a reduction of the epipetalous stamens in *G. flanaganii* supports this theory.

In the buds of *Greyia*, the 10 stamens are essentially diplostemonous but in *G. sutherlandii* they become decidedly obdiplostemonous at an early stage. Both diplostemony and obdiplostemony occur in the Saxifragaceae *s.l.* (Gelius 1967; Klopfer 1973) and the latter position of the stamens is invariably seen as a secondary adaptation to make the most of the limited space in the bud.

According to Eckert (1966) a flower is more markedly obdiplostemonous if the petals are retarded in growth and the antipetalous stamens are diminished. The small petal bases and retarded development of the epipetalous stamens therefore account for obdiplostemony in *G. sutherlandii*. In *G. flanaganii* the epipetalous stamens develop as strongly as the episepalous stamens but there is a tendency towards a reduction of the epipetalous stamen primordia and an abortion of developing stamens. This species is therefore inclined towards haplostemony which also occurs in some Saxifragaceae as well as in *Ribes, Parnassia, Itea* L. and *Escalonia* (Gelius 1967; Klopfer 1973).

As a consequence of the normal alternation of floral parts, the carpels of *G. flanaganii* essentially lie episepalous. An interruption of the alternation occurs in the gynoecium of *G. sutherlandii* and in flowers of *G. flanaganii* with less than 10 stamens. This alternative position of the carpels can be explained by Hofmeister's principle stating that the new primordia (i.e. the carpel primordia) are formed in the middle of the available space (according to Stebbins 1974). In *G. flanaganii* the missing epipetalous stamen primordium provides the necessary space. In *G. sutherlandii* the retarded development and the slightly more outward position of these primordia account for the epipetalous position of the carpels.

Epipetalous carpels and obdiplostemonous or haplostemonous stamens are therefore derived conditions in *Greyia*. As *G. flanaganii* is still evolving towards these aims, this evergreen species which has also retained some of the characteristics of its proposed tropical ancestral stock (see above) is considered as more primitive than *G. sutherlandii* (and in effect the closely related *G. radlkoferi*).

Whether the above-mentioned similarities between the Saxifragaceae *s.l.* and *Greyia* are taxonomically significant is questionable. At least the latter does not seem out of place among the families included in the Cunoniales, Saxifragales and Rosales complex. The archaic (Davis 1966) structure of the massive anther wall in *Greyia* however, has not been reported for Saxifragaceae *s.l.* but in many of the latter, details

of anther wall development are not available (Davis 1966). According to Bhandari (1984) a massive anther wall is characteristic of primitive angiosperm families like the Magnoliaceae, Degeneriaceae and Ranunculaceae. This primitive wall structure in *Greyia* may therefore denote a more ancestral position for the Greyiaceae.

Acknowledgements

Miss I. von Teichman, Prof Dr Jannie Coetzee and Mr Chris v.d. Merwe are thanked most sincerely for their assistance in various ways during the preparation of the manuscript. Thanks are also due to a unknown referee for proposing a flow diagram to elucidate the development of the multilayered anther wall.

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