Inflorescence and floral development in *Streptocarpus* and *Saintpaulia* (Gesneriaceae) with particular reference to the impact of bracteole suppression

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Abstract. Floral development and inflorescence structure within *Streptocarpus* and *Saintpaulia* were investigated using Scanning Electron Microscopy (SEM). We discuss the structure and development of the pair-flowered cyme and the floral ontogeny found in the Gesneriaceae in a phylogenetic context with particular reference to an East African clade of *Streptocarpus* and *Saintpaulia*. Current phylogenetic hypotheses divide the caulescent East African *Streptocarpus* species into two distinct clades, in relation to which the position of *Saintpaulia* is not yet clear. Variation in the branching of the inflorescence showed phylogenetic significance and included dichasial, monochasial and unbranched patterns. In four of the East African *Streptocarpus* species sampled a single lateral bracteole was present on the first to third axes, after which the inflorescence was ebracteolate. Our results indicate that there may be some link between bracteole suppression and an alteration in the order of sepal initiation. The loss or suppression of lateral bracteoles also appears to result in the precocious development of the lateral cyme meristem.

Key words: *Streptocarpus*, *Saintpaulia*, Gesneriaceae, Floral development, Ontogeny, Initiation sequence, SEM.

The genus *Streptocarpus* Lindl. comprises approximately 130 species distributed in Africa, Madagascar and the Comoros Islands (Hilliard and Burtt 1971). Several closely related genera, including *Saintpaulia* Wendl., are now believed to be nested within *Streptocarpus* based on molecular phylogenetic analyses (Möller and Cronk 1997, 2001a, b; Smith et al. 1998; Smith et al. 1997). *Streptocarpus* itself comprises two long-established subgenera, *Str.* subgenus *Streptocarpella* Fritsch and *Str.* subgenus *Streptocarpus*, and support has been found for two main clades (I & II) which largely correspond to the subgenera (Möller and Cronk 1997, 2001a, b). Clade I comprises mainly caulescent species from Madagascar, East and West Africa and includes the genus *Saintpaulia*. Clade II comprises mainly acaulescent species from the African mainland but also includes several Malagasy species, some of which are caulescent and woody. Within Clade I, phylogenetic hypotheses have subdivided the caulescent East African *Streptocarpus* species into two distinct clades which together may be sister to a monophyletic *Saintpaulia* (Möller and Cronk 1997), or alternatively *Saintpaulia* may be nested within the East African clade, sister to the clade comprising *Str. caulescens*, *Str. pallidiflorus*, *Str. glandulosissimus*, *Str.*

holstii and *Str. buchananii* (Möller and Cronk 2001a, b; Smith et al. 1997). In this paper we investigate the inflorescence and floral variation found in Clade I, particularly in the Malagasy and caulescent East African *Streptocarpus* species and the East African *Saintpaulia*.

Within *Streptocarpus* there is a diversity of growth forms from more or less annual monophyllous or rosette-forming herbs to woody shrubs 1.5 m high. Although *Saintpaulia* species are generally rosulate herbs, there are also caulescent species with creeping or trailing stems. There is also a diversity of floral morphology within *Streptocarpus* from the small, 5–7.5 mm long, pouch-shaped flowers of the Malagasy *Str. andohahelensis* to the long funnel-shaped flowers up to 55 mm long found in the type species, *Str. rexii* Lindl. (Harrison et al. 1999, Hilliard and Burtt 1971). In comparison there is very little variation shown between the almost rotate flowers within *Saintpaulia*.

The branching structure of the inflorescence in the Gesneriaceae is highly diverse, although it is now considered to be based on a single underlying structure of an indeterminate thyrse composed of a series of axillary pair-flowered cymes (Hilliard and Burtt 1971; Weber 1973, 1982, 1995; Wiehler 1983). Each cyme unit generally comprises a hypopodium (cyme unit peduncle) which terminates with a pair of lateral bracteoles, above which both a terminal and an associated front flower are carried (Fig. 1). The terminology adopted here for the bracteoles follows that of Weber (2004) although the terms prophylls and bracts have both been used previously for these structures (Hilliard and Burtt 1971; Weber 1978, 1982, 1995). Additional cyme units frequently develop in the axils of the lateral bracteoles and the inflorescence may show monochasial to dichasial branching ranging from a single dichasium to a highly branched structure carrying numerous flowers on a single inflorescence. The front flower was originally believed to be adventitious, but Weber (1982, 1995) has suggested that it is,

in fact, a regular axillary flower in which the subtending bracteole (γ-bracteole) is nearly always suppressed or aborted. The sequence of initiation of the inflorescence structure in the Gesneriaceae has been described as acropetal (but see Wang and Li 2002; Weber 1982, 1995) starting with: 1) lateral bracteoles; 2) front flower bracteole (γ-bracteole); 3) lateral cyme meristem; 4) front flower meristem. This can be equated with a transformation mode of Hufford (1995) or a developmental sequence of Smith (2001, 2003) facilitating comparison between species by representing morphological change as part of a series of events in the context of an active ontogenetic process. The front flower bracteole is, in fact, rarely present in the family and its absence allows the front flower meristem to proceed directly to organogenesis whilst the establishment of the lateral bracteole causes a delay in the development of the lateral meristems resulting in the apparent precocious development of the front flower (Weber 1982, 1995). In flowers in which the lateral bracteoles are also suppressed then one may expect a corresponding change in the developmental sequence, allowing the lateral meristems to proceed directly to the development of floral organs, which may therefore develop earlier than the front flower. In some species of Gesneriaceae lateral bracteoles may be displaced or absent (Weber 1982, 1995).

The initiation sequence of the sepals is not always described in the literature, but is often visible from published figures and plates. Within the Gesneriaceae, a unidirectional adaxial to abaxial sequence of sepal initiation is present in *Epithema* (Weber 1995), *Sinningia* (Weber 1982, 1995) and *Whytockia* (Wang 2001, Wang and Li 2002). This unidirectional adaxial to abaxial initiation sequence was also observed in *Streptocarpus* and *Saintpaulia* (Harrison 1998). However, Harrison (1998) found variation in the sepal initiation sequence between the terminal and the front flowers of *Saintpaulia* in which she observed a reversed unidirectional abaxial to adaxial sequence.
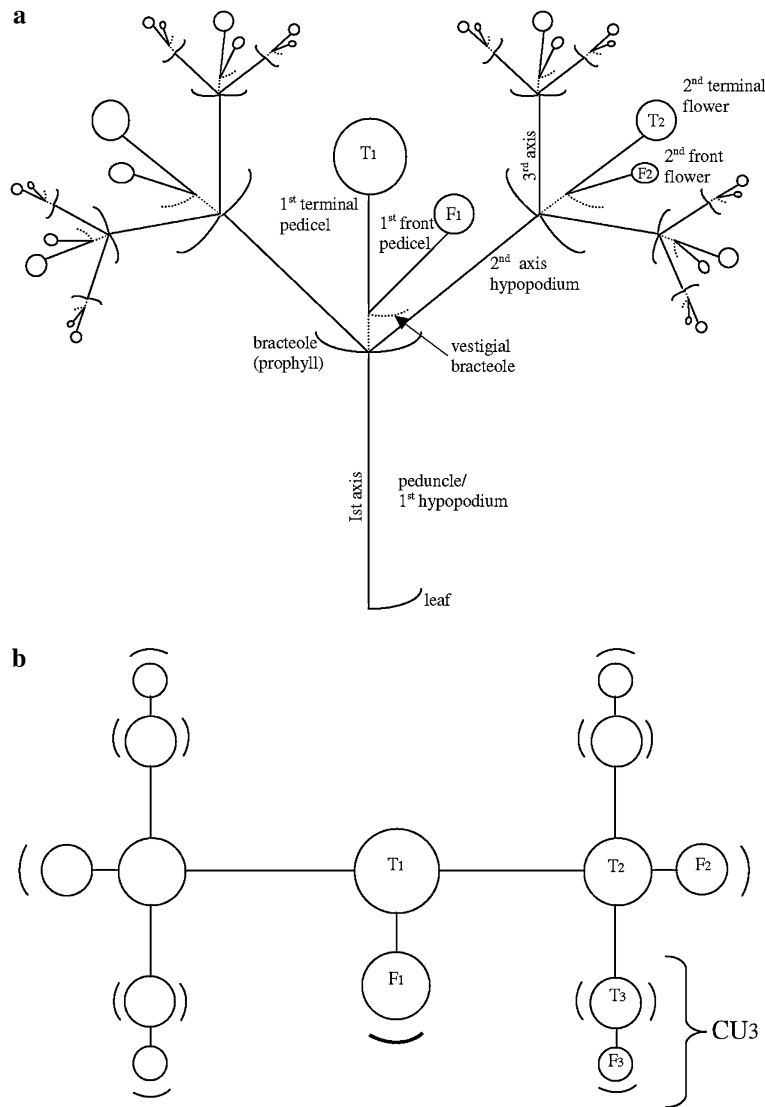
a

b

Fig. 1. Diagrams illustrating the pair-flowered inflorescence structure found in the Gesneriaceae. **a** Lateral view of a dichasially branching inflorescence. The internode below the initiation of the front flower marked here with a dotted line is compressed and not generally visible. The front flower bracteole is generally supressed and is also marked by a dotted line here. **b** Plan view of the same inflorescence with vestigial front flower bracteoles (γ-bracteoles) not shown. T = terminal flower, F = front flower, with the number indicating the branching level of inflorescence axis. CU = a single cyme unit comprising a hypopodium (cyme unit peduncle) which terminates with a pair of lateral bracteoles, above which both a terminal and an associated front flower are carried

Preliminary observations within the genus *Streptocarpus* found structural and sequential variation in inflorescence and floral development. This level of variation, combined with the availability of a phylogenetic hypothesis of relationships, prompted further investigation of selected developmental characters. We aim to investigate possible phylogenetic patterns in the branching of the inflorescence, bracteole presence or absence, and sepal initiation. We

also aim to explore the relationship between bracteole presence or absence and the sequence of sepal initiation. In addition, we are interested in testing the hypothesis, extrapolated from the work of Weber (1982, 1995), that the suppression of the lateral bracteoles may influence the sequence of development in the inflorescence structure.

Materials and methods

Inflorescences of nine species of *Streptocarpus* and six species of *Saintpaulia* were collected at different developmental stages from plants in the living collections at The Royal Botanic Garden Edinburgh (Appendix 1). Material was immediately fixed in FAA before being transferred to 70% ethanol. Preliminary dissection was carried out in 70% ethanol before the material was subjected to a dehydration series of 70% ethanol for 15 mins, 95% ethanol for 10 mins, 100% ethanol for 5 mins, 100% acetone dried with a molecular sieve for two × 5 mins. The samples were then placed in a precooled K850 Critical Point Dryer and cp-dried for ten × 1 min before being dissected further, mounted on stubs and coated with platinum-palladium using an Emitech K575 sputter coater. Material was examined using a Leo Supra 55VP scanning electron microscope at a working distance of 9–15 mm at 3–5 kV.

Three morphological characters were scored and optimised on to a consensus of the alternative phylogenetic hypotheses based on molecular data (Möller and Cronk 1997, 2001a, b; Smith et al. 1997). The character optimisation was carried out using MacClade version 4.0 (Maddison and Maddison 2000) showing all most parsimonious states at each node.

Results

Variation was observed in the structural and sequential development of the inflorescence and floral organs, including the inflorescence branching patterns, the presence or absence of one or both lateral bracteoles, the order of sepal initiation and the order of initiation and development within the inflorescence. The following sections describe this variation more fully.

Branching patterns. Dichasial, monochasial, and unbranched inflorescences were observed, as well as an intermediate form which showed dichasial branching in the first axis followed by monochasial branching in the subsequent axes. The branching patterns are presented here in diagrammatic form (Fig. 2). Of the Malagasy species, *Streptocarpus beampingaratrensis* subsp. *antambolorum* and *Str. andohahelensis* produced dichasially branching pair-flowered cymes (Fig. 2a) although *Str. andohahelensis* mainly produced unbranched inflorescences, some of which had only a solitary flower (Fig. 2d). The branching of the East African caulescent species was monochasial (rarely with vestigial lateral cyme development), resulting in a scorpioid cyme, or cincinnus (Fig. 2b). However, the East African species, *Str. saxorum*, was unbranched and commonly produced a single flower (Fig. 2d). In *Saintpaulia*, most of the species observed here formed a double cincinnus, showing dichasial branching of the first axis only, followed by monochasial branching of each subsequent axis (Fig. 2c), although in *Sa. rupicola* only a single cincinnus was present (Fig. 2b). The amount of branching in the cincinnus was variable. Where dichasial branching was present, the development of each pair of lateral cyme units was often unequal, one side developing markedly before the other.

Order of initiation and development of inflorescence structure. The developmental stage of the terminal flowers was used as the principle point of reference for the inflorescence. It proved difficult in many cases to mark the absolute point of initiation of the front flower and the lateral bracteole and cyme meristems but in all material examined lateral bracteoles, where present, initiate very early in the development of the inflorescence, apparently before the initiation of the front flower meristem (Fig. 3a). Where paired bracteoles are present, the front flower meristem appears to initiate next, before the lateral cyme meristem (Fig. 3c,d,f). In the Malagasy *Streptocarpus andohahelensis* and *Str. beampingaratrensis* subsp. *beampingaratrensis* and in *Saintpaulia*
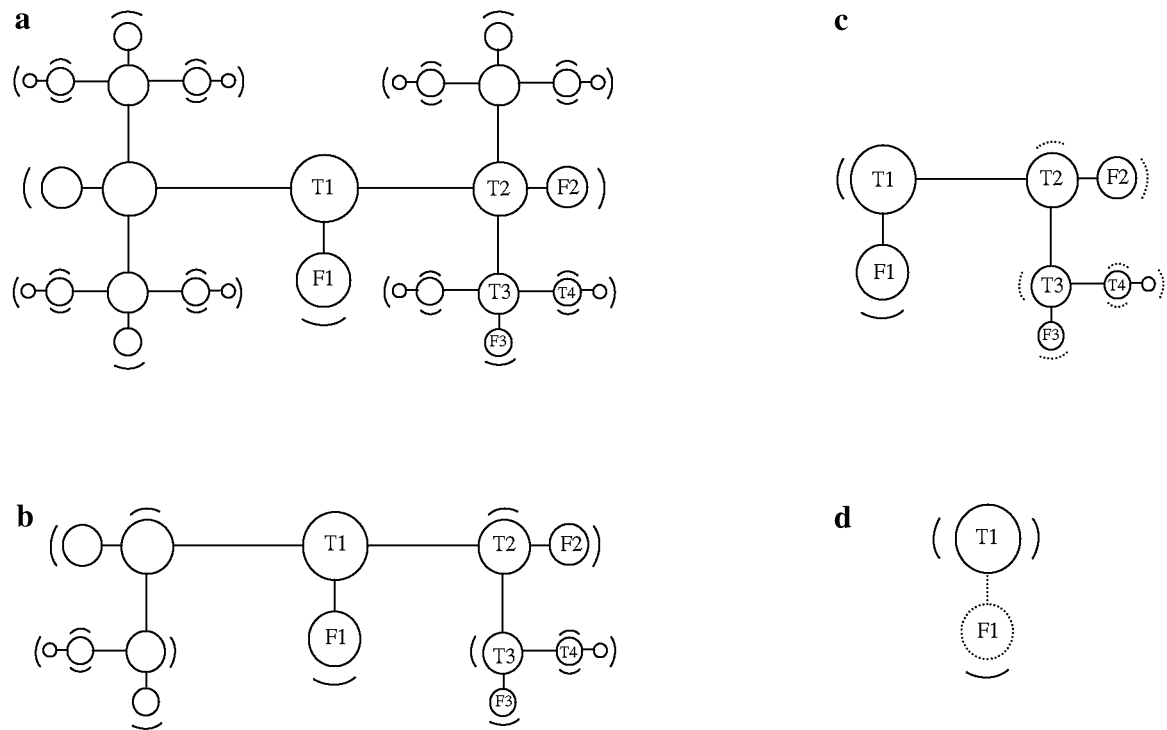
Fig. 2. Branching patterns observed in the taxa included in our study: **a** dichasial branching, **b** monochasial branching, **c** dichasial to monochasial branching, **d** unbranched. Bracteoles shown with a dotted line in the monochasial inflorescence (**c**) are consistently either present or absent within species. The front flower shown with a dotted line in the unbranched inflorescence (**d**) may be variably present or absent within species

the initiation and development of the lateral cyme meristem usually occurs after the terminal flower has produced sepals, and often not until the petal primordia are also visible (Fig. 3i) although lateral development was rarely observed in *Str. andohahelensis*. In *Streptocarpus glandulosissimus*, *Str. holstii* and *Str. pallidiflorus*, the lateral axis which lacks a bracteole proceeds directly to cyme meristem initiation and development (Fig. 4b,c).

Bracteoles. Variation was observed in the presence (Fig. 3) or absence (Fig. 4) of one or both lateral bracteoles. They may be present as paired structures throughout the inflorescence, as single structures on one side only of each cyme unit or as a single structure on the side of the first to third cyme units only. Paired bracteoles subtending lateral cyme units throughout the inflorescence were present in *Streptocarpus andohahelensis*, *Str. beampingaratrensis* subsp. *antambolorum* and *Str. beampingaratrensis* subsp. *beampingaratrensis* (Fig. 3c,e) In the double cincinnus of *Saintpaulia* the lateral bracteoles were also paired, and therefore in all but the first cyme unit only one of the bracteoles subtended a lateral cyme meristem (Fig. 3g). This pattern was also seen in the single cincinnus of *Streptocarpus stomandrus*, in which the bracteole not subtending a lateral cyme meristem was generally smaller (Fig. 3j). In *Str. caulescens*, *Str. pallidiflorus*, *Str. glandulosissimus* and *Str. holstii*, the bracteoles are present as single structures on one side only of each cyme unit (Fig. 4a–c, g), although in *Str. caulescens* and *Str. pallidiflorus* only the bracteoles of the first two axes develop, ;the subsequent ones remain vestigial or are absent respectively (Fig. 4e,h). Finally, in the unbranched *Str. saxorum*, the lateral
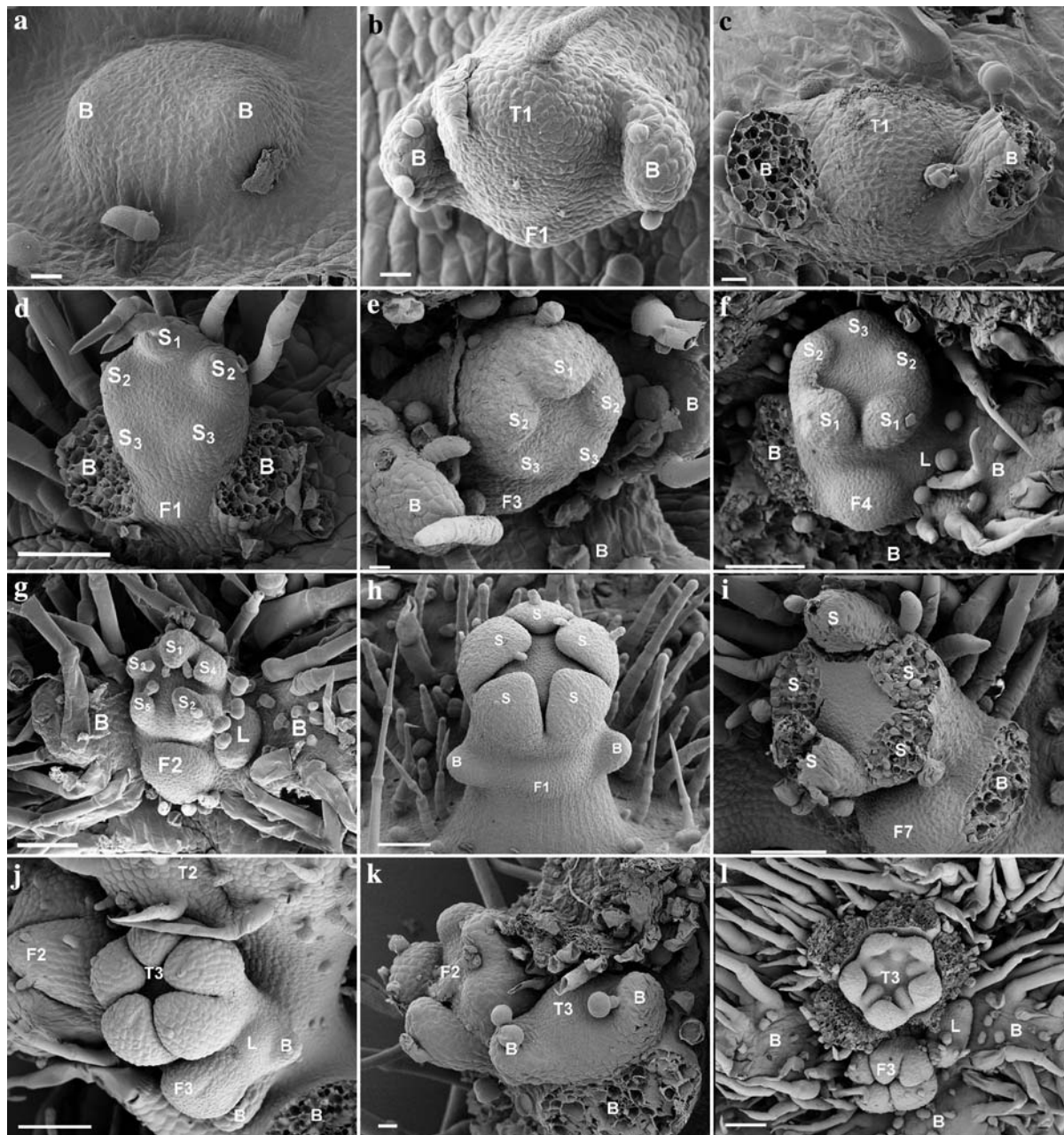
Fig. 3. Inflorescence development in species with paired bracteoles. **a–c.** Initiation of lateral bracteoles and terminal and front flowers. **a** *Streptocarpus saxorum*, **b** *Saintpaulia teitensis* **c** *Str. beampingaratrensis* subsp. *beampingaratrensis.* **d, e.** Development of lateral bracteoles and unidirectional adaxial to abaxial initiation of sepals on the terminal flower. **d** *Str. teitensis* **e** *Str. beampingaratrensis* subsp. *antambolorum.* **f** Unidirectional abaxial to adaxial initiation of sepals in the terminal flower in *Sa. rupicola.* **g** Initiation of lateral cyme and helical initiation of the sepals on the terminal flower in *Sa. brevipilosa.* **h** Paired lateral bracteoles in *Str. saxorum.* **i** Relatively late initiation of the front flower but still earlier than lateral cyme initiation in *Str. beampingaratrensis* subsp. *antambolorum.* **j–l.** Development of subsequent axes of the inflorescence showing unidirectional abaxial to adaxial sepal initiation in the front flower. **j** *Str. stomandrus*, **k** *Sa. tongwensis*, **l** *Sa. brevipilosa.* (B = bracteole, T = terminal flower with number inidicating level of axis, F = front flower with number indicating level of axis, L = lateral cyme, S = sepal with numbers indicating order of initiation. In a–c, e and k scale bar = 20 μm; in d, f–j and l scale bar = 100 μm)
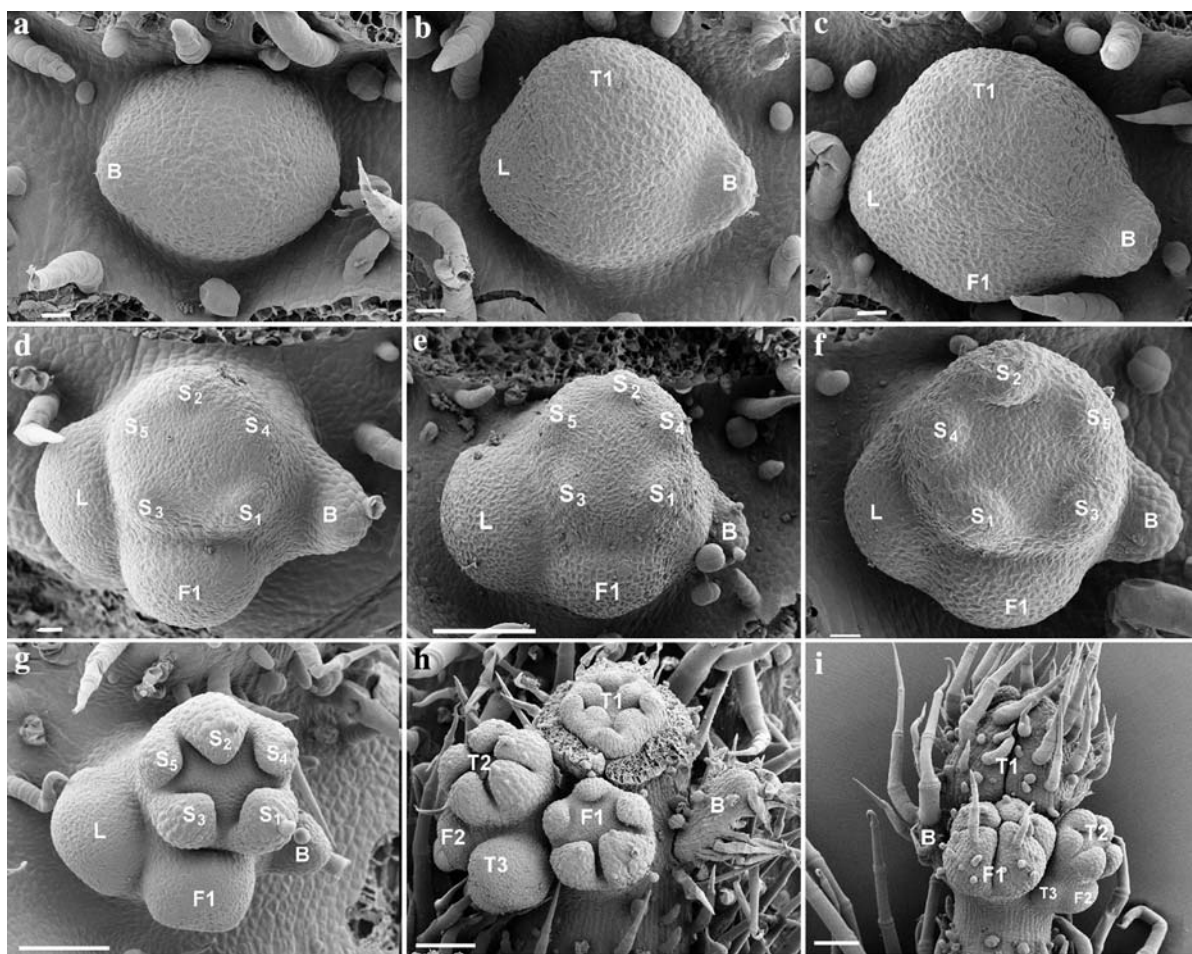
Fig. 4. Inflorescence development in partially ebracteolate species. **a–c.** Initiation of lateral bracteole and cyme, and terminal and front flowers in *Streptocarpus glandulosissimus*. **d–g.** Development of lateral bracteole and cyme and helical initiation of sepals on the terminal flower. **d** *Streptocarpus holstii*, **e** *Str. pallidiflorus*, **f** *Str. glandulosissimus*, **g** *Str. holstii*. **h, i.** Development of subsequent axes of the inflorescence showing monochasial branching and unidirectional abaxial to adaxial sepal initiation in the front flower. **h** *Streptocarpus pallidiflorus*, **i** *Str. glandulosissimus*. (B = bracteole, T = terminal flower with number indicating level of axis, F = front flower with number indicating level of axis, L = lateral cyme, S = sepal with numbers indicating order of initiation. In a–d and f scale bar = 20 μm; in e and g–i scale bar = 100 μm)

bracteoles appear to develop as paired structures before the development of the front flower (Fig. 3a,h). In one of the samples examined however, the development of the front flower appeared to be replaced by the development of a front flower bracteole (γ-bracteole), with no lateral bracteole development (Fig. 5a). A vestigial front flower bracteole was observed in *Streptocarpus ando-hahelensis* (Fig. 5b).

Sepal initiation. Variation was observed in the sequence of sepal initiation not only between species but also between the terminal and front flowers within species. In the terminal flowers the initiation sequence was unidirectional or helical. The order of sepal initiation in the Malagasy species, *Streptocarpus andohahelensis* and *Str. beampingaratrensis* subsp. *antambolorum*, was unidirectional start-ing with the single adaxial sepal, followed by
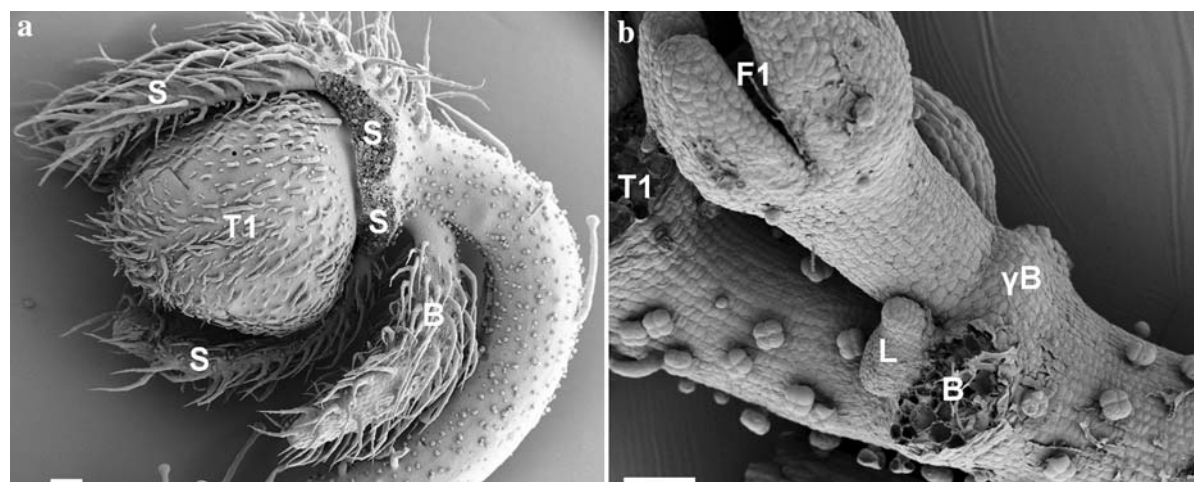
Fig. 5. a *Streptocarpus saxorum* showing an unusual development of a bracteole appearing to replace the front flower. **b** *Streptocarpus andohahelensis* showing vestigial development of a front flower bracteole (γ-bracteole). *B* = bracteole, γ*B* = front flower bracteole (γ-bracteole), *T* = terminal flower with number indicating level of axis, *F* = front flower with number inicating level of axis, *L* = lateral cyme, *S* = sepal

the two lateral and finally the two abaxial sepals (Fig. 3e). In nearly all the East African caulescent species the terminal flower showed 2/5 helical initiation patterns, generally starting with one of the two abaxial sepals (Fig. 4c–g). *Streptocarpus saxorum* appears to show unidirectional adaxial to abaxial sepal initiation although more observations are needed to confirm the consistency of this state (Fig. 3h). Within *Saintpaulia*, the order of initiation in *Sa. grotei*, *Sa. ionantha* and *Sa. teitensis* was unidirectional from the adaxial to abaxial side (Fig. 3d), but in *Sa. brevipilosa* there appeared to be a helical sequence of initiation similar to that found in the East African caulescent *Streptocarpus* species (Fig. 3g). In *Sa. rupicola* the order of initiation appears to be variably modified and either starts with the two abaxial sepals followed by the adaxial sepal and finally the lateral sepals or presents an abaxial to adaxial unidirectional sequence (Fig. 3f). The initiation sequence of *Sa. tongwensis* is not yet clear.

In all the East African caulescent species and in *Saintpaulia* the front flower showed a unidirectional order of initiation but in an abaxial to adaxial sequence (Figs. 3k, 4h).

Although sepal initiation in the front flower was not observed in *Streptocarpus andohahelensis* and *Str. beampingaratrensis* subsp. *antambolorum*, slightly older flowers suggest that initiation may also be unidirectional from the abaxial to adaxial side. This initiation sequence in the front flowers does not appear to be universal in the genus *Streptocarpus* and may be restricted to Clade I (unpubl. data).

Discussion

A large extent of the diversity in the inflorescence branching structure of the Gesneriaceae is found within the single genus *Streptocarpus*. We mapped the observed branching patterns onto a consensus of the alternative phylogenetic hypotheses based on molecular data (Möller and Cronk 1997, 2001a, b; Smith et al. 1997). The variation in inflorescence structure corresponds largely with the phylogenetic structure within the species sampled, suggesting that branching structure is relatively conserved at this hierarchical level (Fig. 6a). However, the amount of branching within the inflorescence appears to be less

fixed, which may affect the type of branching observed in some species. The sampling here is not sufficient to determine any trend towards a reduction series in the branching pattern.

Although we described the foliar appendages in the inflorescence of Gesneriaceae as bracteoles, they represent subtending leaves (prophylls) or bracts. Within the axils of these bracteoles the lateral cyme units show
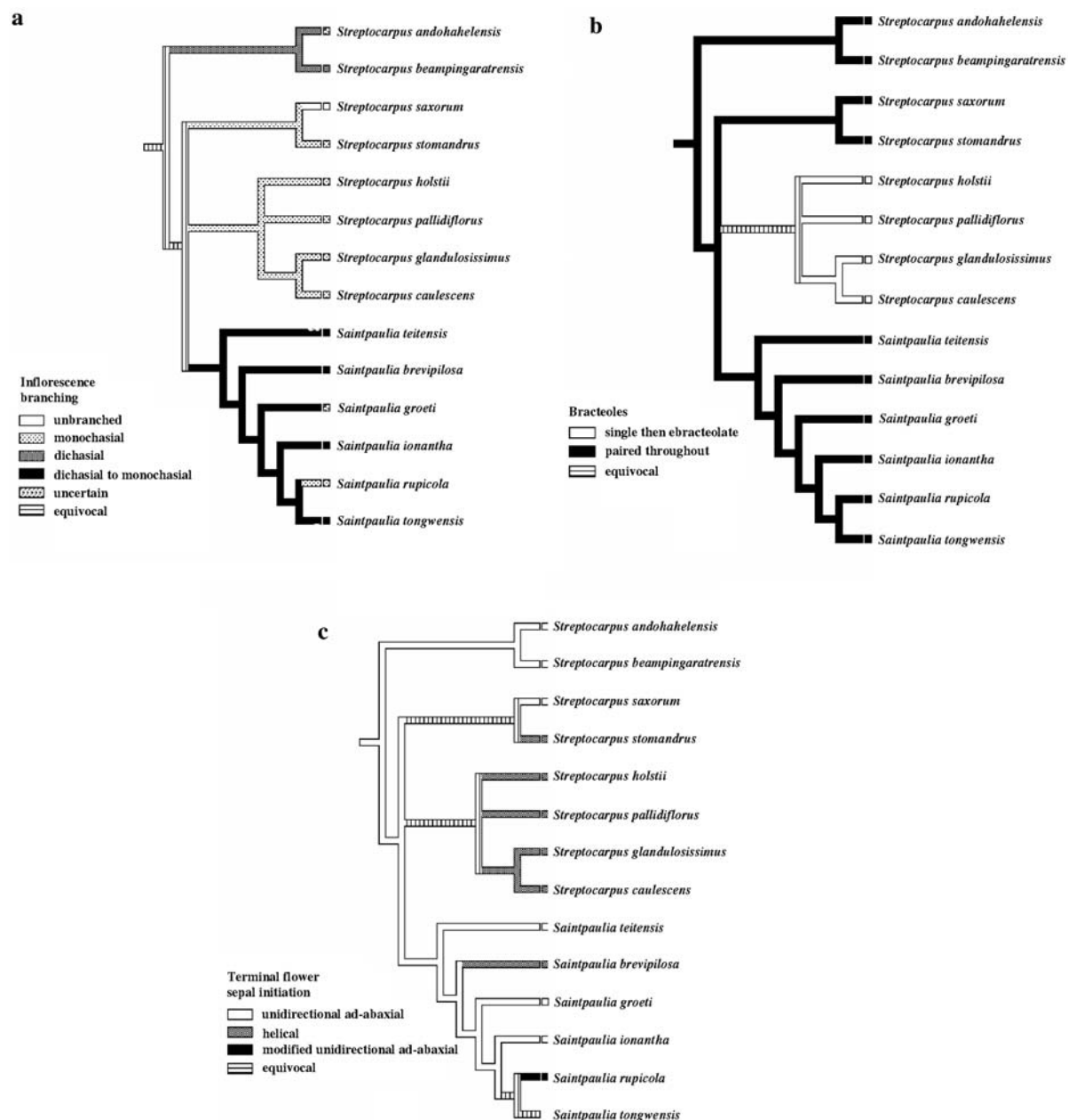

Fig. 6. Inflorescence and floral characters optimised onto a consensus of the alternative phylogenetic hypotheses based on molecular data (Möller and Cronk 1997, 2001a, b; Smith et al. 1997). **a** Inflorescence branching, **b** bracteole presence/absence, and **c** sepal initiation sequence of the terminal flowers

symmetric or asymmetric development. Extreme asymmetry resulting in monochasial branching has been elsewhere observed in the family. Mapping lateral bracteole presence or absence onto the consensus tree suggests that the partial loss of lateral bracteoles within the caulescent East African *Streptocarpus* species is the result of a single evolutionary event (Fig. 6b). In the *Streptocarpus saxorum* clade, *Streptocarpus saxorum* and *Streptocarpus stomandrus* both retain paired bracteoles although the unbranched *Str. saxorum* has only a single pair, and the bracteoles are both reduced in *Str. stomandrus* with the bracteole not subtending the lateral cyme being markedly smaller. The partially ebracteolate species of *Streptocarpus* also have monochasial branching. It is not yet clear how consistently loss of lateral bracteoles is associated with monochasial branching in the family.

There are indications in our results that there is some link between the suppression of one or both lateral bracteoles and an alteration in the order of sepal initiation in *Streptocarpus* (Fig. 6c). A helical initiation sequence was observed in the caulescent East African *Streptocarpus* which also showed the suppression of one or both lateral bracteoles, but a unidirectional adaxial to abaxial initiation pattern was present in *Streptocarpus saxorum* which notably exhibited paired lateral bracteoles. However, a helical initiation pattern was also present in the bracteolate *Streptocarpus stomandrus* and *Saintpaulia brevipilosa* indicating that further study is necessary before any definite conclusions can be drawn. The position of *Saintpaulia*, either as sister to the East African caulescent *Streptocarpus* species or nested within them, becomes more critical for reconstructing the evolution of sepal initiation. The modified pattern of unidirectional sequence initiation observed in *Saintpaulia rupicola* in addition to the two previously discussed patterns suggests that sepal initiation may be more labile in this part of the phylogeny. Additional observations are

needed to determine the extent of variation within *Saintpaulia*.

According to Weber (1982, 1995), the loss of the front flower bracteole leads to the precocious initiation of the front flower and an apparently basipetal initiation. Although we found that the front flower develops precociously in association with the absence of a bracteole there are exceptions, e.g. where no front flower develops in *Streptocarpus andohahelensis* and *Str. saxorum*. The loss of lateral bracteoles in some of the species included in this study enabled us to examine the effect of this loss on the developmental sequence of the whole inflorescence structure. In particular, it allowed us to test the hypothesis that suppression of lateral bracteoles would result in the precocious development of the lateral cyme meristem. In *Streptocarpus glandulosissimus*, *Str. holstii* and *Str. pallidiflorus* there did indeed appear to be a change in the developmental sequence. However, it is clear that an inflorescence comprises more than one meristematic region or growth centre, each of which forms a developmental sequence which is independent to some extent. There may also be an association between regions so that a change in one regional sequence may invoke a change in another. The overall developmental sequence of the inflorescence is thus a combination of different regional sequences. Thus the generalised developmental sequence of the inflorescence in Gesneriaceae postulated by Weber (1982, 1995) may be viewed as four interrelated steps: 1) development of the lateral meristematic region (bracteoles), 2) development of the front meristematic region (front flower bracteole), 3) development of the lateral meristematic region (cyme), 4) development of the front meristem (flower) (Fig. 7a). From this generalised pattern of development, Weber's hypothesis of precocious development of the front flower was viewed as the following alteration in the developmental sequence: 1) development of the lateral meristematic region (bracteoles), 2) development of the front meristem (flower), 3)
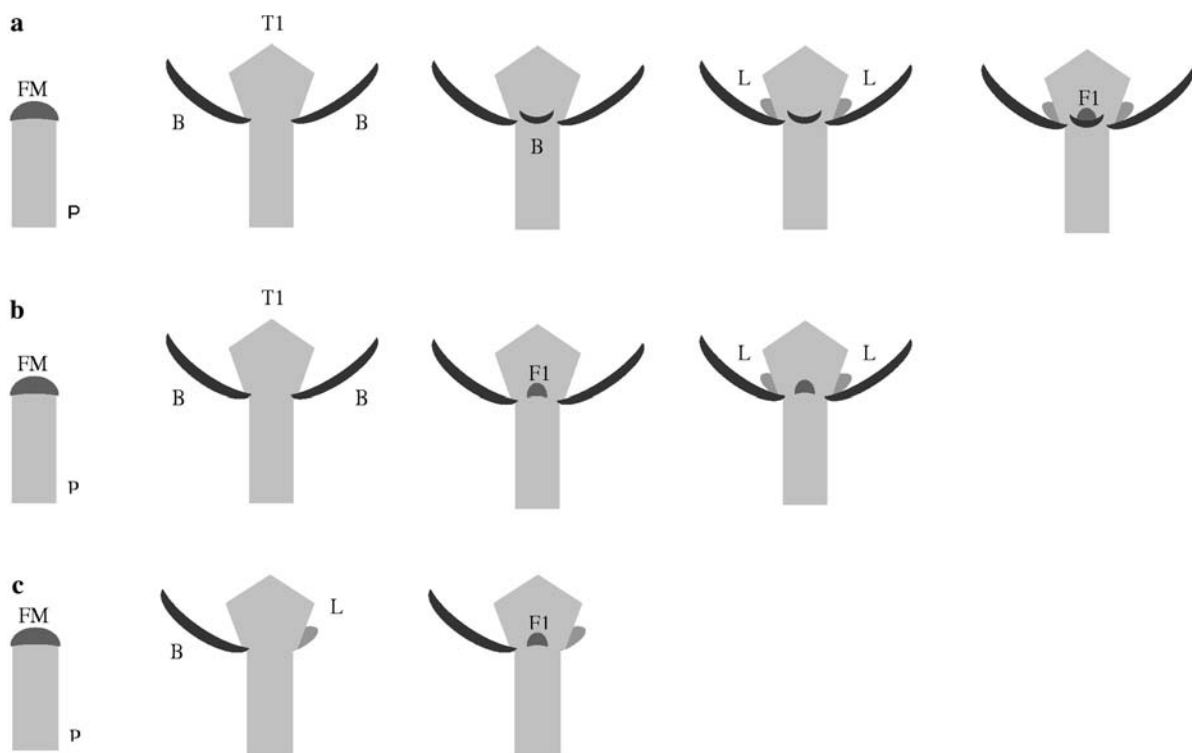
Fig. 7. Diagrammatic representation of the inflorescence development sequences: **a** generalised development sequence with front flower bracteole (γ-bracteole) present based on Weber (1982, 1995), **b** development sequence showing precocious development of the front flower resulting from the absence of the front flower bracteole, **c** precocious development of the lateral cyme meristem resulting from the absence of the lateral bracteole

development of the lateral meristematic region (cyme) (Fig. 7b). In inflorescences where the lateral and front bracteoles are absent this pattern would be simply altered in a shortened developmental sequence: 1) development of the lateral meristematic region (cyme), 2) development of the front meristematic region (flower) (Fig. 7c).

These results suggest that the loss of the lateral bracteole does indeed result in the precocious development of the lateral cyme meristem, thus indirectly supporting the suggestion by Weber (1982, 1995) that the absence of the front flower bracteole results in the precocious development of the front flower meristem and an apparently basipetal sequence of inflorescence development. This indicates that bracteole initiation delays the initiation of the axillary meristem, and that these meristems initiate only when bracteoles have attained a certain size.

Appendix 1. List of species included in the study with Royal Botanic Garden Edinburgh accession numbers and locality information

Name	Accession	Locality/Distribution
Streptocarpus andohahelensis Humbert	19972885	Madagascar
Str. beampingaratrensis Humbert subsp. *antambolorum* Humbert	19972887	Madagascar
Str. beampingaratrensis Humbert subsp. *beampingaratrensis*	19972884	Madagascar
Str. caulescens Vatke	19751215	East Africa
Str. glandulosissimus Engl.	19961868	East Africa
Str. holstii Engl.	19990086	East Africa
Str. pallidiflorus C.B.Clarke	19961879	East Africa
Str. saxorum Engl.	19721499	East Africa
Str. stomandrus B.L.Burtt	20020591	East Africa
Saintpaulia brevipilosa B.L.Burtt	19700909	East Africa
Sa. grotei Engl.	19872171	East Africa
Sa. ionantha Wendl.	19970091	East Africa
Sa. rupicola B.L.Burtt	19850676	East Africa
Sa. teitensis B.L.Burtt	20031340	East Africa
Sa. tongwensis B.L.Burtt	19850668	East Africa

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