

New approaches to the systematics of Saintpaulia and Streptocarpus. Pp. 253-264.

In: Andrews, S., A. Leslie, & C. Alexander (eds.), Taxonomy of Cultivated Plants. Third International Symposium. Kew, U.K.: Royal Botanic Gardens, Kew.

REFNO: 3139

KEYWORDS:

Africa, Cytology, Kenya, Linnaeopsis, Molecular Systematics, Morphology, Saintpaulia, Schizoboea, Streptocarpella, Streptocarpus, Tanzania

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TAXONOMY OF CULTIVATED PLANTS

Third International Symposium

Proceedings of the Meeting held in
Edinburgh, Scotland
20-26 July 1998

Edited by

Susyn Andrews

Royal Botanic Gardens, Kew

Alan Leslie

Royal Horticultural Society, Wisley

Crinan Alexander

Royal Botanic Garden Edinburgh

Published by the Royal Botanic Gardens, Kew, 1999

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First published 1999

Production Editor: S. Dickerson

Cover design by Johnny Willis Fleming, page make up by Media Resources, Information Services
Department.
Royal Botanic Gardens, Kew

ISBN 1 900347 89 X

Printed in Great Britain
by
Whitstable Litho Printers Ltd., Whitstable, Kent

Möller, M. & Cronk, Q.C.B. (1999). New approaches to the systematics of *Saintpaulia* and *Streptocarpus*. In: S. Andrews, A.C. Leslie and C. Alexander (Editors). *Taxonomy of Cultivated Plants: Third International Symposium*, pp. 253–264. Royal Botanic Gardens, Kew.

NEW APPROACHES TO THE SYSTEMATICS OF *SAINTPAULIA* AND *STREPTOCARPUS*

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Abstract

Molecular phylogenies of the genus *Streptocarpus* based on the ribosomal DNA internal transcribed spacer (ITS) sequences show that the genus is paraphyletic; other African genera *Saintpaulia*, *Schizoboea* and *Linnaeopsis* are nested within *Streptocarpus*. The genus *Saintpaulia* has evolved from a caulescent African *Streptocarpus* species in subgenus *Streptocarpella*. This has been confirmed by sequence phylogenies of three additional genes; the chloroplast *trnL* (UAA) intron and the spacer between the *trnL* (UAA) 3' exon and *trnF* (GAA), the chloroplast *ndhF* gene and the putative single copy developmental gene *GCYC*. The ITS phylogenies of *Saintpaulia* reflects its biogeographic distribution. A group of Usambara species, the 'ionantha-complex' show minimal ITS genetic differentiation. The *Streptocarpus* ITS phylogeny is also congruent with the two base chromosome numbers and reflects the existing subgeneric division, with a few phylogenetically interesting exceptions.

Introduction

The flowering plant genera *Saintpaulia* H. Wendl. and *Streptocarpus* Lindl. (*Gesneriaceae* Dumort., subfamily *Cyrtandroideae* Endl., tribe *Didymocarpeae* Endl.) are important horticultural plants with a multi-million pound trade-value world-wide. Although numerous in households, many species are endangered in the wild (Walter & Gillett 1998), and hybrid cultivars of *Saintpaulia* are more common on windowsills than some species are in their natural habitat. *Saintpaulia teitensis* B.L. Burtt, for instance, only occurs as a few hundred specimens in one population in the Teita Hills in Kenya. Despite being well known in horticulture, surprisingly little was understood until recently about the evolutionary relationships between *Saintpaulia* and *Streptocarpus*, and among species within these two genera.

In 1958 B.L. Burtt recognised 19 species of *Saintpaulia* based on morphology, particularly the leaf hairs (Fig. 1) of living and herbarium material. However, *S. amaniensis* E.P. Roberts was later included in *S. magungensis* E.P. Roberts as a subspecies (Burtt 1964), and re-examination of existing and new material resulted in an increase of the number of species to 20 with the recognition of *S. brevopilosa* B.L. Burtt and *S. rupicola* B.L. Burtt (Burtt 1964). The whole genus has a very small area of distribution and occurs only in southern Kenya and northeastern parts of Tanzania (Fig. 2). Since the early work little taxonomic revision has been carried out and the pioneering treatment by Burtt is still the standard work on *Saintpaulia* systematics.

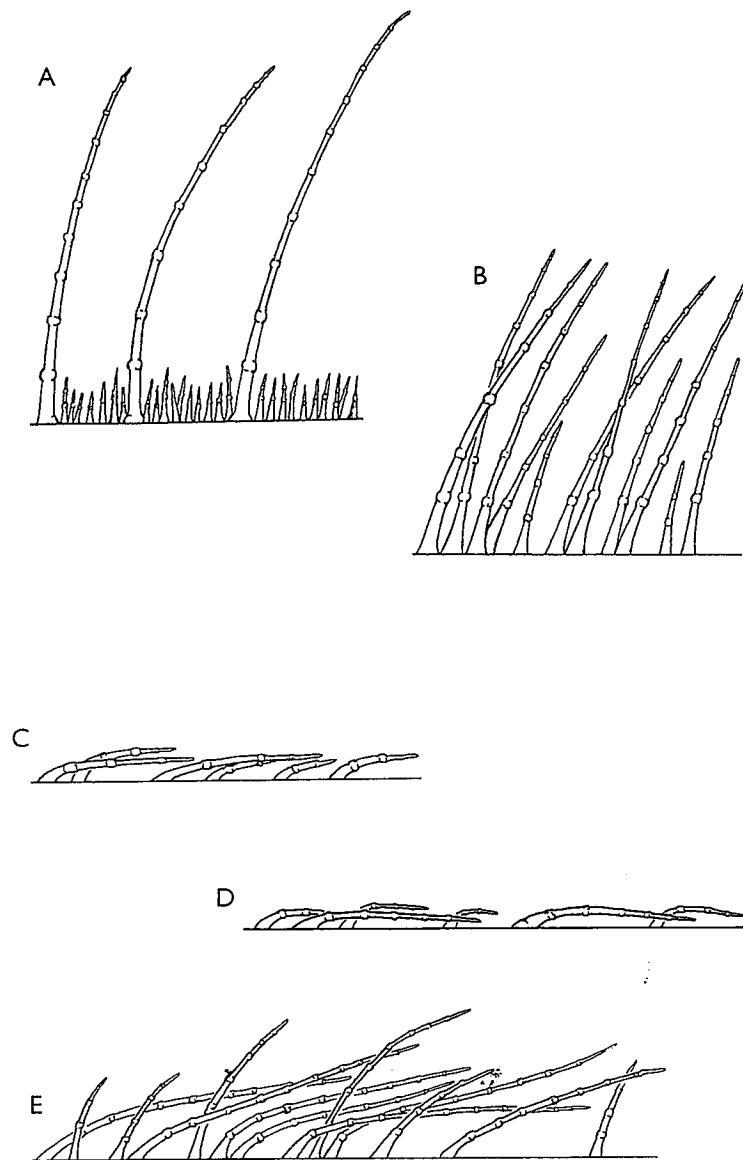


FIG. 1. Indumentum on the upper leaf surface of *Saintpaulia* species. A) *S. diplotricha* B.L. Burt long erect + short erect. B) *S. ionantha* H. Wendl. long erect. C) *S. nitida* B.L. Burt short appressed. D) *S. orbicularis* B.L. Burt long appressed + short appressed. E) *S. intermedia* B.L. Burt long appressed (modified after Burt 1958).

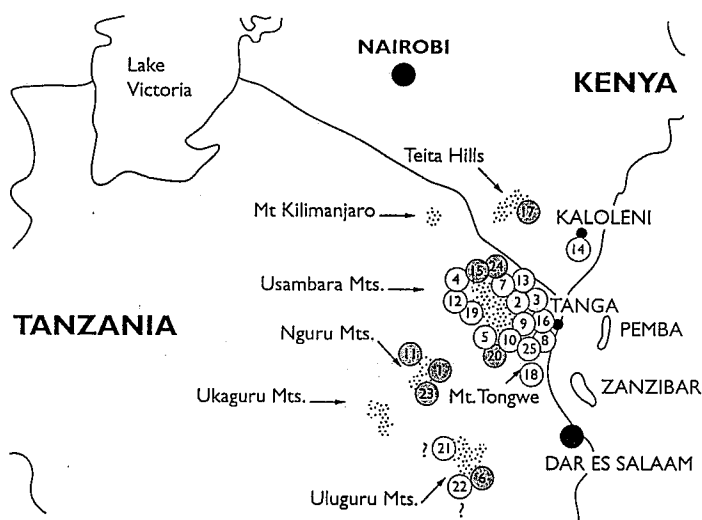


FIG. 2. Guide to the geographical distribution of *Saintpaulia* species. The position of each circle is an indication of the (very approximate) general distribution of the species represented by the number. ○—species belonging to the 'ionantha-complex'. Species are numbered as in Fig. 5; in addition no. 21 = *Saintpaulia inconspicua* B.L. Burt, no. 22 = *S. pusilla* Engl.; *S. goetzeana* Engl. and *S. inconspicua* also occur in the Nguru Mts. and, the latter further south in the Ukaguru Mts.

The genus *Streptocarpus* is distributed in tropical and southern Africa (87 species) and Madagascar and the Comoro Islands (41 species). Another four are described from Asia; these are thought not to be closely related to the African or Madagascan taxa (Hilliard & Burt 1971). The species are currently divided into two subgenera, mainly on vegetative morphological characters (Hilliard & Burt 1971). Subgenus *Streptocarpella* Fritsch (44 species) contains mainly caulescent herbs with 'normal' shoot development, but a few unusual types occur in Madagascar, such as taxa with long-petioled leaves in a basal rosette (reminiscent of African *Saintpaulia*), and shrubby, woody caulescent species. Subgenus *Streptocarpus* Fritsch (88 species) comprises taxa without a shoot apical meristem, and form (in the extreme case) plants with a single, sometimes hugely expanded, cotyledon as the only aerial vegetative organ (Fig. 3B). Inflorescences are formed at the base of the lamina or on a shoot-like petiole, the 'petiolode'. Lamina and petiolode together form the 'phyllomorph'. Re-iteration of the phyllomorphic growth from a meristem on the petiolode results in rosulate forms (Fig. 3C, D) (Jong 1973, 1978). Rosette-type cultivars grown for commercial purposes belong to this type. Since Hilliard and Burt's monograph (1971), based on morphology, the genus has not attracted much systematic study. Phylogenetic work based on morphological characters alone may be hampered, or at least be incomplete when comparing unifoliate with caulescent forms, as the former lack true leaves. However, the African members of tribe *Didymocarpeae* are relatively uniform when compared with the very diverse morphology seen in Asian members. For this reason it has been suggested that the African genera of *Didymocarpeae* are more closely related to each other than to Asian taxa (Hilliard & Burt 1971).

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 E) *S. intermedia* B.L.

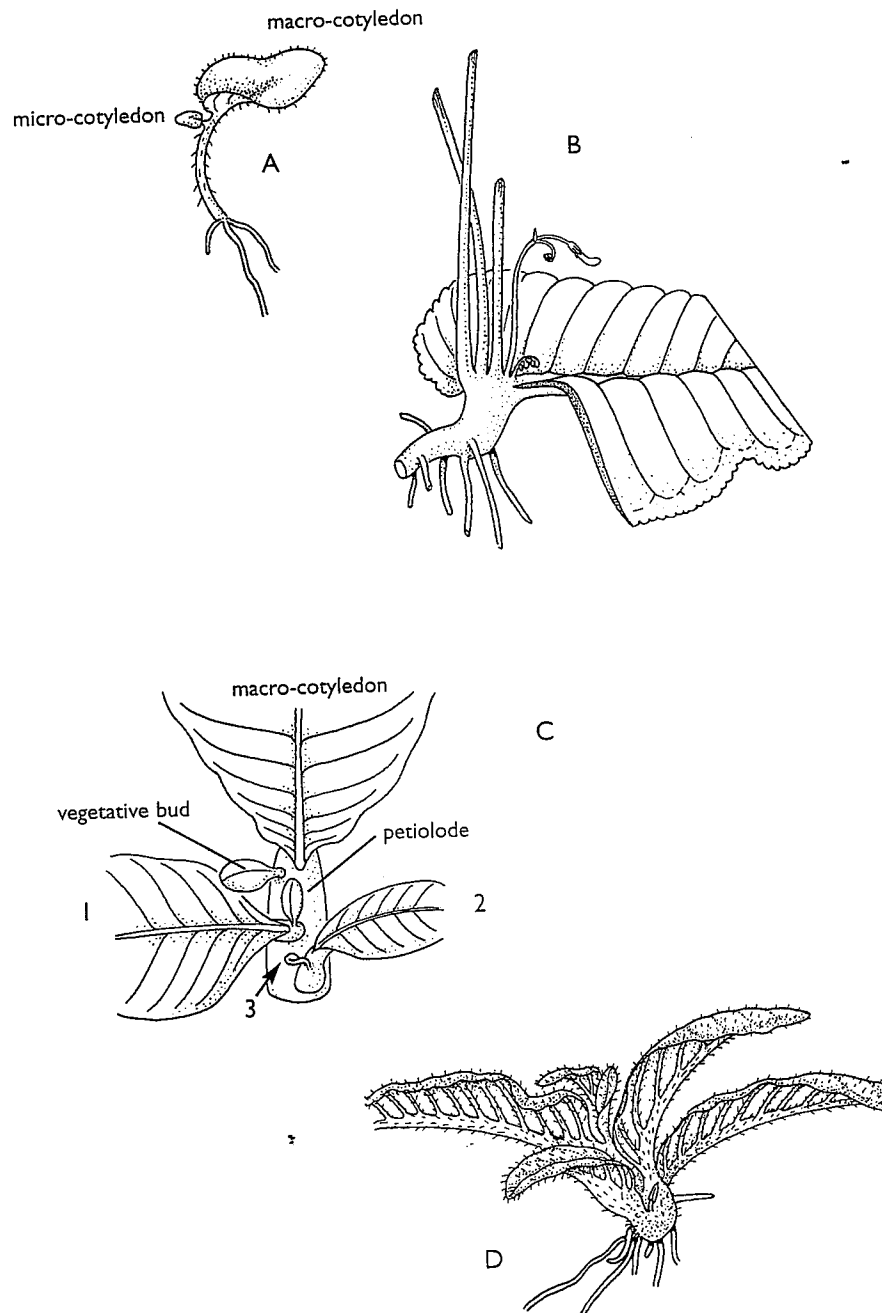


FIG. 3. Seedling stage and various growth forms of *Streptocarpus*. A) Seedling showing micro- and macro-cotyledon. B) *S. wendlandii* Spreng., a unifoliate form. C) Schematic sketch of a 'typical' rosulate, showing the formation of successive phyllomorphs (1, 2 & 3) on the petiolode of the macro-cotyledon. D) *S. primulifolius* Gand., a rosulate form (modified after Hilliard & Burt, 1971 and Jong 1978).

The present work summarises the results of recent molecular work at the Royal Botanic Garden Edinburgh on African taxa of *Gesneriaceae*, with particular reference to *Streptocarpus* and *Saintpaulia*, complemented by newer findings. The genes chosen for various aspects of this research involve the chloroplast *trnL* (UAA) intron and the spacer between the *trnL* (UAA)3' and *trnF* (GAA) exons (Fig. 4C), the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (Fig. 4B), and a putative *Gesneriaceae* homologue of the *Antirrhinum* L. single copy developmental gene *CYCLOIDEA* (Fig. 4A), which we have called *GESNERIACEAE CYCLOIDEA* (*GCYC*) (Möller *et al.* 1999) involved in the expression of flower symmetry (Cronk & Möller 1997). Previous work has also used the chloroplast gene *ndhF* (Smith *et al.* 1998). The chloroplast DNA (cpDNA) sequences are relatively conserved and thus suitable for phylogenetic reconstruction at genus level. In contrast, ITS sequences are about 5 times faster evolving than cpDNA in *Gesneriaceae*, and are suitable for resolution at the species level. The nuclear developmental gene *GCYC* has an intermediate substitution rate about three times faster than the chloroplast intron/spacer region (Möller *et al.* 1999).

Phylogenetic Relationships between *Saintpaulia* and *Streptocarpus*

A. The Phylogenetic Origin of *Saintpaulia*

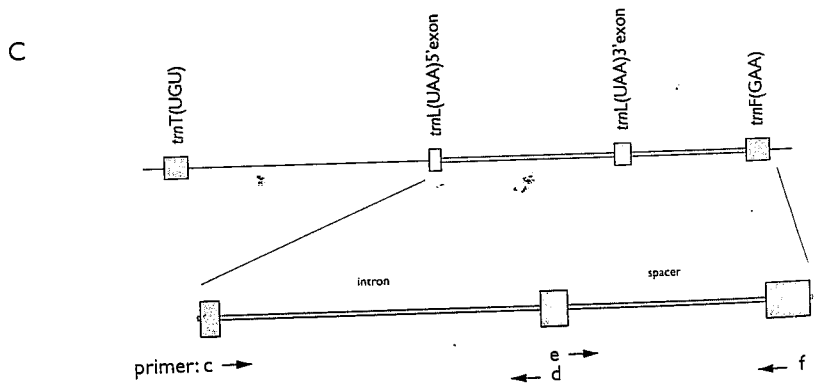
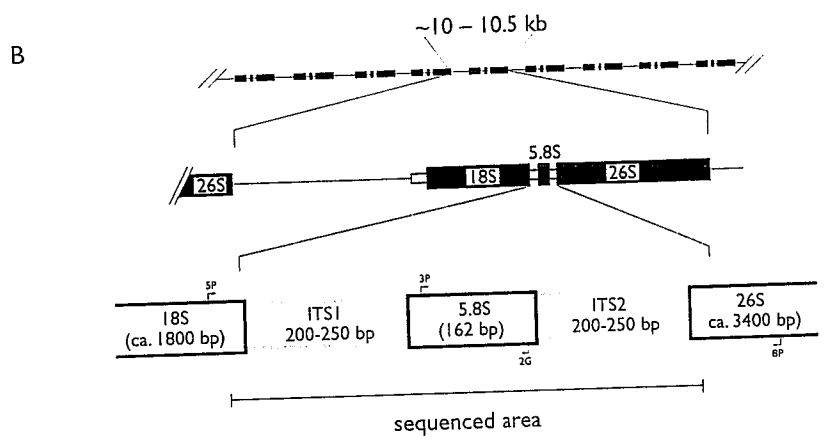
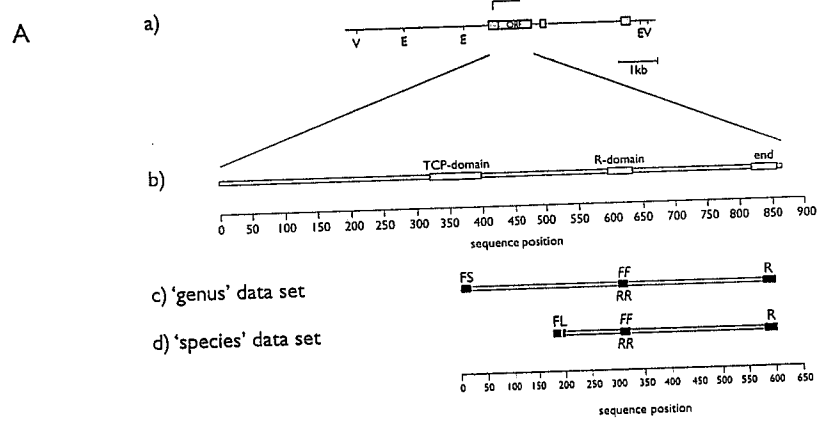
Initially, *Saintpaulia* species were included in the molecular work to serve as potential outgroup taxa for studies in *Streptocarpus*. However, the ITS phylogenies indicated that *Streptocarpus* is not monophyletic, but rather that a monophyletic *Saintpaulia* is nested within a paraphyletic *Streptocarpus* (Fig. 6) (Möller & Cronk 1997a). The results clearly showed that *Saintpaulia* has evolved from within the genus *Streptocarpus* subgenus *Streptocarpella*. This supports Hilliard and Burt's (1971) suggestion of a close relationship among African genera of *Gesneriaceae*, tribe *Didymocarpeae*.

The apparent evolution of *Saintpaulia* from within *Streptocarpus* was surprising, and provoked the study of additional genes to test the validity of the phylogeny based on the multicopy nuclear ribosomal DNA sequences. However, all additional phylogenies, inferred from *trnL+F* cpDNA sequences (Fig. 4C) and *GCYC* nucleotides and amino acid data (Fig. 4Ac) showed the same *Streptocarpus-Saintpaulia* relationships as those inferred from ITS data (Möller *et al.* 1999); in all cases the sister group of *Saintpaulia* comprises caulescent *Streptocarpus* species. This has also been confirmed independently in a cladistic analysis using sequences from another cpDNA gene, *ndhF* (Smith *et al.* 1998). The close relationship between *Saintpaulia* and *Streptocarpus* subgenus *Streptocarpella* is strengthened by shared morphological and cytological features; both have verruculose seeds and the same base chromosome number ($x=15$), while the majority of species in subgenus *Streptocarpus* have reticulate seeds and a base chromosome number of $x=16$ (Ratter 1975).

The major differences between typical *Streptocarpus* subgenus *Streptocarpella* and *Saintpaulia* are a reduction of the aerial stem (*Saintpaulia* mainly being rosette herbs) and the absence of a marked corolla tube in the latter. These features may be related to habitat, as many chasmophytes (e.g. *Saxifraga* L.) growing on wet cliffs (the main habitat of many *Saintpaulia* species) are typically rosette plants. The absence of a marked corolla tube may be associated with the loss of specialist long-tongued pollinators and a switch to generalist short-tongued insects (Cronk & Möller 1997). The two large exerted yellow anthers of *Saintpaulia* species also imply that they evolved pollen flowers rather than retaining the nectar flowers of *Streptocarpus*, further supporting a pollinator switch theory. A third significant difference between

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Taxonomy of Cultivated Plants



Saintpaulia and *Streptocarpus* is the absence of a twisted fruit in *Saintpaulia*. It is the main generic character of *Streptocarpus*, but is also found in other *Gesneriaceae* taxa, such as *Boea* Juss., *Dichiloboa* Stapf, *Ornithoboa* C.B. Clarke, *Paraboa* Ridl., *Rhabdothamnopsis* Hemsl. and *Triseptalum* C.B. Clarke. It is interesting that fruits of *Streptocarpus capuronii* Humbert and *S. lanala* Humbert have only a very slight or no twist, indicating that this trait is relatively easily lost; this has apparently happened several times independently in *Streptocarpus*, as indicated by an extended ITS phylogenetic analysis (Möller & Cronk in prep.) of the position of *Schizoboa* B.L. Burt and *Limnecopsis* Engl., two other genera with straight fruits having apparently evolved from within *Streptocarpus*. The evolutionary function of the twisted fruit may be related to an extension of the period of seed dispersal (Hilliard & Burt 1971).

B. Limitations of ITS for the Phylogenetic Reconstruction in *Saintpaulia*

The ITS of ribosomal DNA in *Saintpaulia* has evolved both by base substitutions and by insertion/deletion events, with a maximum sequence divergence of 15.8% between *S. goetzeana* Engl. and *S. nitida* B.L. Burt (Möller & Cronk 1997b). However, *Saintpaulia* is unusual in that a large group (12 accessions in the 'ionantha-complex', Figs. 5 & 2) was found to have sequence divergences too low for clear phylogenetic resolution, and in an extended ITS analysis several accessions had identical sequences (Fig. 5) (Möller & Cronk 1997b, Möller *et al.* in prep.). To resolve further the relationships between species within the 'ionantha-complex', *GCYC* sequences (Fig. 4Ad) were obtained for 22 species and subspecies of *Saintpaulia*, representing all areas of geographical distribution. We have shown that the evolutionary mutation rate of *GCYC* is higher than in ITS of closely related species (Möller *et al.* 1999). However, despite the higher divergence rate for *GCYC* at low divergence level, the phylogenetic resolution found was not higher when compared to ITS. Other gene sequences and molecular techniques are currently being evaluated at the Royal Botanic Garden Edinburgh with the aim of further characterising and differentiating taxa within the 'ionantha-complex'. These include DNA fingerprinting using interspersed short sequence repeats (inter SSRs; Tsumura *et al.* 1996); the results of these studies are so far inconclusive.

The Evolution of *Streptocarpus*

A. The Phylogenetic Relationships within *Streptocarpus*

The genus *Streptocarpus* is, at least in vegetative morphology, one of the most diverse in the plant kingdom. Phylogenetic analyses based on ITS sequences clearly separate the species analysed into the two subgenera; the unifoliolate/rosulate group (subgenus *Streptocarpus*) and the caulescent forms from Africa and Madagascar (subgenus *Streptocarpella*) (Fig. 6). Moreover, the two growth forms within subgenus *Streptocarpus*, the unifoliolate (*S. dunnii* Hook.f., *S. eylesii* S. Moore and *S. willetii* De Wild.), and the



FIG. 4. Structures and maps of the genes sequenced. A) a) *CYCLOIDEA* (*CYC*) locus. Exons and predicted open reading frame (ORF) are indicated in rectangles; the arrow indicates the direction of transcription; restriction enzyme sites: E - *EcoRI*, V - *EcoRV*, (modified after Luo *et al.* 1996); b) The *CYC* ORF and the location of conserved regions (open boxes). Fragment of *CYC* sequenced for c) the 'genus' and d) for the 'species' data set and the PCR primer positions (closed boxes). B) ITS of ribosomal DNA, illustrating primer position and regions sequenced. C) cpDNA, illustrating the *trnL* (UAA) intron and the spacer between the *trnL* (UAA)3' exon and *trnF* (GAA) sequenced.

Taxonomy of Cultivated Plants

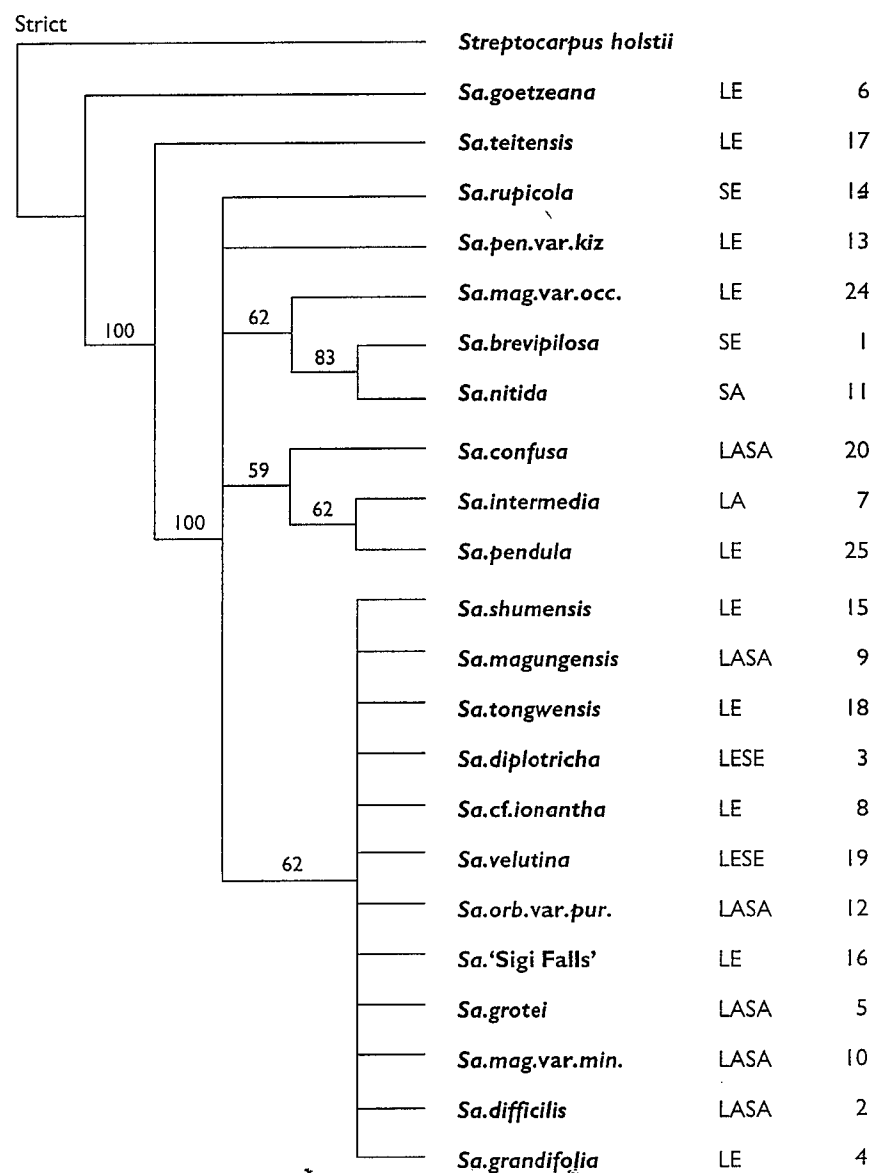


FIG. 5. Strict consensus tree of eight most parsimonious trees of 126 steps based on combined ITS 1 and ITS 2 sequence data (CI: 0.913; RC: 0.779), and the respective leaf hair type of 22 *Saintpaulia* accessions. Numbers above branches are heuristic bootstrap values of 1000 replicates. *Sa.* - *Saintpaulia*, *Sa.mag.var.occ.* - *Saintpaulia magungensis* E.P. Roberts var. *occidentalis* B.L. Burt, *Sa.orb.var.pur.* - *Saintpaulia orbicularis* B.L. Burt var. *purpurea* B.L. Burt, *Sa.mag.var.min.* - *Saintpaulia magungensis* E.P. Roberts var. *minima* B.L. Burt, *Sa.pen.var.kiz.* - *Saintpaulia pendula* B.L. Burt var. *kizarae* B.L. Burt; L - long hairs on upper surface of leaves, S - short, E - erect, A - appressed. Numbers beside hair types refer to the general distribution of the species in Fig. 2.

LE	6
LE	17
SE	14
LE	13
LE	24
SE	1
SA	11
LASA	20
LA	7
LE	25
LE	15
LASA	9
LE	18
LESE	3
LE	8
LESE	19
LASA	12
LE	16
LASA	5
LASA	10
LASA	2
LE	4

rosulate forms, were clearly separated into two distinct clades (Fig. 6). However, in an extended ITS analysis the subgeneric division is no longer clear cut (Möller & Cronk in prep.). Caulescent species such as *S. macropodus* B.L. Burtt, *S. papangae* Humbert and *S. schliebenii* Mansf. are placed in the subgenus *Streptocarpus* (acaulescent) clade in this analysis, which may indicate that the ancestor of unifoliate/rosulate taxa was caulescent. In our first ITS analysis (Fig. 6), the unifoliate taxa analysed were characterised by a large deletion in ITS2, but in the extended analysis a group of 17 taxa share this character (Möller & Cronk in prep.). This group is made up of unifoliate, plurifoliate and rosulate taxa. The rosulate habit appears in more than one clade, one of which consists of typical rosulate species of the *S. rexii* aggregate, including the most horticulturally important species. This indicates that the rosulate habit evolved independently several times.

Streptocarpus subgenus *Streptocarpella* includes 19 species in tropical mainland Africa, and 21 species from Madagascar. The molecular phylogenies indicate independent evolution of 'true rosette' growth forms (with long-petiolate leaves and axillary inflorescences) from caulescent ancestors in both Africa and Madagascar (*Saintpaulia* on the African mainland is one example). The 'true rosette' type from Madagascar, such as *Streptocarpus andohahelensis* Humbert and *S. beampingaratsensis* Humbert, (with vegetative morphology reminiscent of *Saintpaulia*), is the result of independent evolution from Madagascan caulescent species (Möller & Cronk in prep.). Fruit twisting is a diagnostic character of the genus *Streptocarpus*. This has resulted in the exclusion from *Streptocarpus* of African taxa which lack this character, including *Saintpaulia*. Molecular ITS phylogenies, however, indicate that at least two other genera have evolved from within *Streptocarpus* (Möller & Cronk in prep.). *Schizoboea*, originally part of *Didymocarpus* Engl., has straight fruits, but is otherwise very similar to caulescent *Streptocarpus* taxa (Burtt 1974). *Linnaeopsis* (another genus with straight fruits, but with flowers closely resembling those of rosulate *Streptocarpus* taxa) is also in this category.

B. The Cytology of *Streptocarpus*

The cytology of the genus is relatively uniform, subgenus *Streptocarpus* having $2n=32$ chromosomes while subgenus *Streptocarpella* has $2n=30$ (Ratter 1975, Jong & Möller in prep.). This is clearly reflected in the ITS topology (Fig. 6). The only exception appears to be confined to a clade of characteristically polyploid Madagascan species, with *S. perrieri* Humbert being tetraploid and *S. hildebrandtii* Vatke being octoploid. A third taxon belonging to this group (also characterised by branched veins ascending from the leaf base), *S. variabilis* Humbert, is hexaploid (Jong & Möller in prep.). The morphology different from other rosulate species and the tendency to form high polyploids, set this group apart from other *Streptocarpus* species. The close affinity of species within this group is also substantiated by molecular data (Möller & Cronk in prep.).

The fact that *S. papangae* has a base chromosome number of $x=16$ (typical of subgenus *Streptocarpus*) (Jong & Möller in prep.), but has caulescent morphology typical of subgenus *Streptocarpella* indicates that the caulescent growth form may be ancestral with regard to the subgenus *Streptocarpus*. This is reflected in the basal position of *S. papangae* in the clade containing most *Streptocarpus* in the extended ITS phylogeny (Möller & Cronk in prep.).

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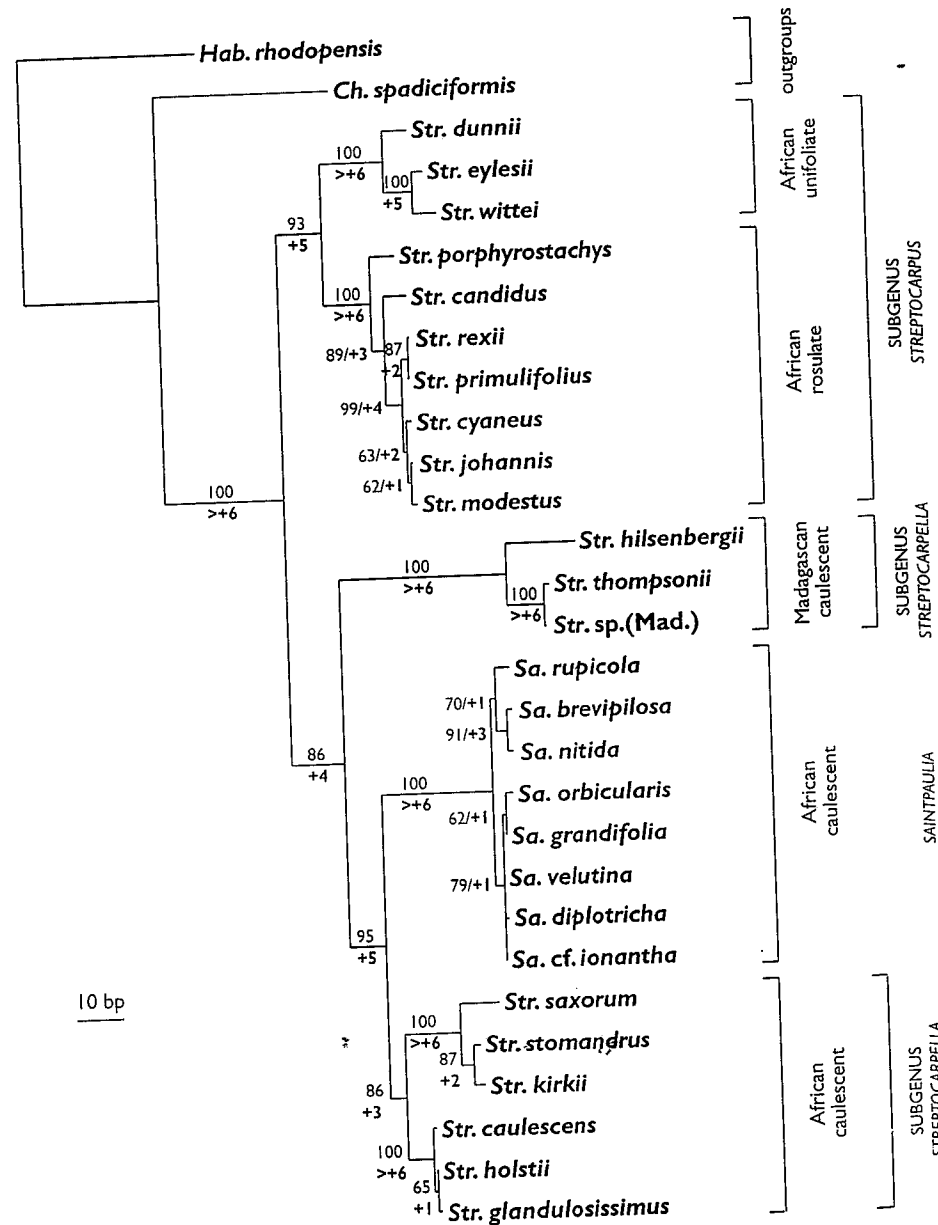


FIG. 6. Single most parsimonious tree for *Streptocarpus* and *Saintpaulia* of 419 steps length based on parsimony analysis of the combined ITS 1 and ITS 2 sequence data plus the alignment gap matrix (CI: 0.778; RC: 0.711). Upper numbers are bootstrap values of 1000 replicates. Lower (boldface) numbers are decay indices (the numbers of steps necessary to cause collapse of monophyletic groups) modified after Möller & Cronk (1997a). Hab. = *Haberlea*, Ch. = *Chirita*.

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Conclusions

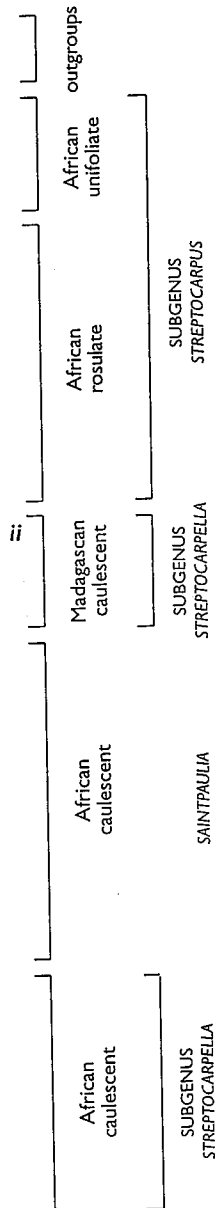
The evolution of the genus *Saintpaulia* from *Streptocarpus* is now undisputed. The shared characters of chromosome number and seed coat structure combined with molecular evidence from four independent genes form a strong base for a close relationship between *Saintpaulia* and taxa belonging to *Streptocarpus* subgenus *Streptocarpebella*. This might suggest that *Saintpaulia* species should be transferred to *Streptocarpus* or that *Streptocarpus* should be dismembered, if strictly monophyletic groups are considered desirable. However, the morphological differences between the two taxa are very clear and consistent. Furthermore, two other genera were found also to be nested within the genus *Streptocarpus*, which would then also need to be sunk into the genus *Streptocarpus*. This would make the diagnostic character of fruit twisting an unsuitable character for generic delimitation. Any revision of generic boundaries is premature, however, as further African and Madagascan genera of the tribe *Didymocarpeae* (*Acanthonema* Hook.f., *Trachystigma* C.B. Clarke, *Colpogyne* B.L. Burtt, *Hovanella* A. Weber & B.L. Burtt), which are possibly closely related to *Streptocarpus* have not yet been available for study, as they are rare in the wild and mostly not in cultivation. Until the relationships of these genera have been assessed by further morphological and molecular study, the *status quo* should be maintained.

Acknowledgements

The authors thank B.L. Burtt for stimulating discussions; H. Shuiman, J. Preston and C. Guihal for their technical support; U. Gregory, S. Scott, D. Mitchell and J. Main for the maintenance and expansion of the Edinburgh *Gesneriaceae* collection, and the Regius Keeper, and staff at the Royal Botanic Garden Edinburgh for research facilities. We thank A. Andrianjafy, G. Rafamontanantsoa and S. Irapanarivo from PBZT for logistic support during plant collections in Madagascar. We further thank the Institute of Cell and Molecular Biology, University of Edinburgh, for access to sequencing facilities and N. Preston for assistance. The receipt of a Leverhulme Trust Award, No. F/771/B, a research grant from the Systematics Association and the African Violet Society of America, and expedition funds from the Davis Expedition Fund of the University of Edinburgh, the Carnegie Trust for the Universities of Scotland and the Percy Sladen Memorial Fund, are gratefully acknowledged.

References

- Bawa, K.S. (1994). Pollinators of tropical dioecious angiosperms: a reassessment? No, not yet. *Amer. J. Bot.* 81(4): 456–460.
- Burtt, B.L. (1958). Studies in the *Gesneriaceae* of the Old World XV: The genus *Saintpaulia*. *Notes Roy. Bot. Gard. Edinburgh* 22(6): 547–568.
- Burtt, B.L. (1964). Studies in the *Gesneriaceae* of the Old World XXV: Additional notes on *Saintpaulia*. *Notes Roy. Bot. Gard. Edinburgh* 25(3): 191–195.
- Burtt, B.L. (1974). Studies in the *Gesneriaceae* of the Old World XXXVII: *Schizoboea*, the erstwhile African *Didymocarpus*. *Notes Roy. Bot. Gard. Edinburgh* 33(2): 265–267.
- Cronk, Q.C.B. & Möller, M. (1997). Genetics of floral symmetry revealed. *Trends Ecol. Evol.* 12: 85–86.
- Hilliard, O.M. & Burtt, B.L. (1971). *Streptocarpus*: an African plant study. 410 pp. University of Natal Press, Pietermaritzburg.



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- Jong, K. (1973). *Streptocarpus* (Gesneriaceae) and the phyllomorph concept (abstr.). *Acta Bot. Neerl.* 22(3): 244.
- Jong, K. (1978). Phyllomorphic organisation in rosulate *Streptocarpus*. *Notes Roy. Bot. Gard. Edinburgh* 36(2): 369-396.
- Luo, D., Carpenter, R., Vincent, C., Copsey, L. & Coen, E. (1996). Origin of floral asymmetry in *Antirrhinum*. *Nature*, 383: 794-799.
- Möller, M. & Cronk, Q.C.B. (1997a). Origin and relationships of *Saintpaulia* H. Wendl. (Gesneriaceae) based on ribosomal DNA internal transcribed spacer (ITS) sequences. *Amer. J. Bot.* 84(7): 956-965.
- Möller, M. & Cronk, Q.C.B. (1997b). Phylogeny and disjunct distribution: evolution of *Saintpaulia* (Gesneriaceae). *Proc. Roy. Soc. London, Series B, Biol. Sci.* 264: 1827-1836.
- Möller, M., Clokie, M., Cubas, P. & Cronk, Q.C.B. (1999). Integrating molecular and developmental genetics: a Gesneriaceae case study. In P.M. Hollingsworth, R.M. Bateman & R.J. Gornall (eds). *Molecular Systematics and Plant Evolution*, pp. 375-402. Taylor & Francis, London.
- Ratter, J.A. (1975). A survey of chromosome numbers in the Gesneriaceae of the Old World. *Notes Roy. Bot. Gard. Edinburgh* 33(3): 527-543.
- Smith, J.F., Kresge, M.E., Möller, M. & Cronk, Q.C.B. (1998). A cladistic analysis of *ndhF* sequences from representative species of *Saintpaulia* and *Streptocarpus* sections *Streptocarpus* and *Streptocarpella* (Gesneriaceae). *Edinburgh J. Bot.* 55(1): 1-11.
- Tsumura, Y., Ohba, K. & Strauss, S.H. (1996). Diversity and inheritance of inter-simple sequence repeat polymorphisms in Douglas-fir (*Pseudotsuga menziesii*) and sugi (*Cryptomeria japonica*). *Theor. Appl. Genet.* 92: 40-45.
- Walter, K.S. & Gillett, H.J. (eds). (1998). 1997 IUCN Red list of threatened plants. 862 pp. IUCN, The World Conservation Union, Gland, Switzerland and Cambridge, UK.