

Streptocarpus redefined to include all Afro-Malagasy Gesneriaceae: Molecular phylogenies prove congruent with geographical distribution and basic chromosome numbers and uncover remarkable morphological homoplasies

Kanae Nishii,^{1,4} Mark Hughes,¹ Marie Briggs,² Elspeth Haston,¹ Frieda Christie,¹ Margaret J. DeVilliers,³ Thea Hanekom,³ Wiets G. Roos,³ Dirk U. Bellstedt³ & Michael Möller¹

1 Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, Scotland, U.K.

2 Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, England, U.K.

3 Department of Biochemistry, University of Stellenbosch, Private Bag XI, Matieland 7602, South Africa

4 Tokyo Gakugei University, 4-1-1 Nukuikitamachi, Koganei, Tokyo 184-8501, Japan

Author for correspondence: Michael Möller, m.moeller@rbge.ac.uk

ORCID: KN, <http://orcid.org/0000-0001-8141-8908>; MH, <http://orcid.org/0000-0002-2168-0514>; MB, <http://orcid.org/0000-0003-2988-0032>; EH, <http://orcid.org/0000-0001-9144-2848>; MM, <http://orcid.org/0000-0002-2819-0323>

DOI <http://dx.doi.org/10.12705/646.8>

Abstract The taxonomy of the African, Madagascar and Comoro Island (Afro-Malagasy) Gesneriaceae attracts a large amount of interest given the horticultural importance of Cape Primroses (*Streptocarpus*) and African Violets (*Saintpaulia*). Earlier studies indicated that the Afro-Malagasy genera form a strongly supported clade, and recent classifications have included some of the genera within an expanded *Streptocarpus*. Given the global importance of this group, we carried out a comprehensive molecular phylogenetic analysis of all Afro-Malagasy genera in subfamily Didymocarpoideae, tribe Trichosporeae, subtribe Streptocarpinae, to investigate species relationships in these genera as the basis for a new classification. Phylogenetic analyses of the nuclear ribosomal spacer (ITS, 5S NTS) and chloroplast intron and spacer regions (*rpl20-rps12* spacer, *trnL* intron, *trnLF* spacer) of 226 samples were performed, including all Streptocarpinae genera, except the monotypic *Nodonema*. The molecular phylogenies demonstrate that the genera with non-twisted fruits are nested within *Streptocarpus* which has twisted fruits. Two main clades were found, one comprising herbaceous caulescent *Streptocarpus* that also included *Saintpaulia*, the caulescents *Hovanella* and *Schizoboea*, and the unifoliates *Acanthonema* and *Trachystigma*. The second clade comprises the woody caulescents and acaulescent *Streptocarpus*, *Colpogyne* and *Linnaeopsis*. Altogether, twelve well-supported subclades can be recognized, each with a combination of distinct morphological characteristics. A new classification of tribe Streptocarpinae, de facto *Streptocarpus*, is presented, retaining the two subgenera, *Streptocarpus* and *Streptocarpella*, and dividing them into five and seven sections respectively. *Nodonema* is attributed to subg. *Streptocarpus* for morphological reasons. The former genus *Saintpaulia* is classified as *Streptocarpus* subg. *Streptocarpella* sect. *Saintpaulia* with ten species recognized.

Keywords *Acanthonema*; *Colpogyne*; *Hovanella*; infrageneric classification; *Linnaeopsis*; *Nodonema*; *Saintpaulia*; *Schizoboea*; *Trachystigma*.

Supplementary Material The Electronic Supplement (Tables S1–S2; Figs. S1–S18) is available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>; matrices and trees have been submitted to TreeBase (<http://purl.org/phylo/treebase/phylovs/study/TB2:S17292>).

■ INTRODUCTION

Cape Primroses (*Streptocarpus* Lindl.) and African Violets (*Saintpaulia* H.Wendl.) have a significant economic importance with an estimated annual world trade value of over \$30 million (Buta & al., 2010). The taxonomy of such important horticultural plants is of interest for horticulturists and botanists alike, for the global trade and the communication of research findings. A recent classification has synonymised *Saintpaulia* with *Streptocarpus* but did not consider the many

other African and Madagascar and Comoro Island (Afro-Malagasy) Gesneriaceae genera (Christenhusz, 2012). A new family classification for the Gesneriaceae was published recently, following molecular phylogenetic relationships (Weber & al., 2013). Here, we follow this approach for the Afro-Malagasy Gesneriaceae. *Saintpaulia* and *Streptocarpus* are among the 10 Gesneriaceae genera in the subfamily Didymocarpoideae occurring in Africa, Madagascar and the Comores (Möller & Clark, 2013; Weber & al., 2013). The other genera are *Epi-thema* Blume, *Acanthonema* Hook.f., *Colpogyne* B.L.Burtt,

Hovanella A.Weber & B.L.Burt, *Linnaeopsis* Engl., *Nodonema* B.L.Burt, *Schizoboea* (Fritsch) B.L.Burt and *Trachystigma* C.B.Clarke (Burt & Wiehler, 1995; Weber, 2004). Within the subfamily Didymocarpoideae, *Epithema* belongs to tribe Epithemateae, subtribe Epithematinae, a South and Southeast Asian group, with only *E. tenue* C.B.Clarke occurring in Africa (Mayer & al., 2003). The other nine genera belong to subtribe Streptocarpinae in tribe Trichosporeae (Weber & al., 2013), and are the subject of the study presented here. One of them, *Streptocarpus*, is characterized by twisted capsules, while the remainder have straight (non-twisted) capsules (Weber, 2004; Weber & al., 2013).

Most genera in the Streptocarpinae are monotypic (*Colpogyne*, *Nodonema*, *Schizoboea*, *Trachystigma*), or small (*Acanthonema* 2 spp., *Hovanella* 2–3 spp., *Linnaeopsis* 3 spp.), with only *Streptocarpus* being large (154 spp.; Hilliard & Burt, 1971; Skog & Boggan, 2007; Möller & Clark, 2013). *Acanthonema*, *Linnaeopsis*, *Nodonema*, *Saintpaulia*, *Schizoboea*, and *Trachystigma* are endemic to Africa and *Colpogyne* and *Hovanella* endemic to Madagascar. *Streptocarpus* is the most widespread genus, occurring in Africa (111 spp.), Madagascar and the Comores (43 spp.) and Asia (4 spp.; Hilliard & Burt, 1971), although the Asian species are not allied to the Afro-Malagasy species (Hellens & al., 1999; Möller & al., 2009) and fall outside the new classification proposed in this paper.

Earlier molecular phylogenetic analyses have shown that subtribe Streptocarpinae forms a strongly supported clade (Möller & Cronk, 1997a, b; Möller & al., 2009, 2011a; Weber & al., 2011a). Phylogenetic studies using the internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA (nrDNA) indicated that *Saintpaulia*, *Linnaeopsis* and *Schizoboea* are nested within *Streptocarpus* (Möller & Cronk, 1997a, 2001a, b; Möller & al., 1999). The nested position of *Saintpaulia* was supported by chloroplast DNA (cpDNA) *ndhF* sequence data (Smith & al., 1998). Later analyses using additional cpDNA sequences (*trnLF*, *atpB-rbcL*: Möller, 2003; Möller & al., 2009) showed that *Acanthonema*, *Colpogyne* and *Hovanella* are also nested within *Streptocarpus*. Thus far, all Streptocarpinae analyzed are phylogenetically nested within *Streptocarpus*. Only *Nodonema* and *Trachystigma* have not been placed using DNA sequence data to date.

On the basis of molecular phylogenies, several genera have already been synonymized with *Streptocarpus*, namely *Linnaeopsis* (Darbyshire, 2006), *Saintpaulia*, *Schizoboea*, *Colpogyne* and *Hovanella* (Christenhusz, 2012). With respect to *Saintpaulia*, these studies also considered a number of the 21 species accepted by Burt (1958a, 1964) to be synonyms, reducing the number of accepted species to 6 (Darbyshire, 2006) and a further 2 species being considered as synonyms by Christenhusz (2012). However, molecular phylogenetic relationships among species (e.g., Möller & Cronk, 1997b) appear not to have been taken into consideration fully.

Once the first molecular phylogenies became available, it became apparent that the generic and infrageneric circumscription within subtribe Streptocarpinae was in need of revision (e.g., Möller & Cronk, 1997a, b; Smith & al., 1998; Möller & Cronk, 1999). The division of *Streptocarpus* into two

subgenera was based on morphological and cytological grounds (Hilliard & Burt, 1971). *Streptocarpus* species, like most Old World Gesneriaceae (Burt, 1970), have unequally developing seedling cotyledons (anisocotily) due to the extended activity of a basal meristem in one cotyledon (macrocotyledon) (e.g., Jong, 1970; Jong & Burt, 1975). The macrocotyledon of caulescent species grows for a few days or weeks only and then becomes petiolated (Jong, 1970). In acaulescent species, to which unifoliate and rosulate belong, the macrocotyledon continues to grow for months, and in extreme cases, for years in some unifoliate, until inflorescences are produced (Hilliard & Burt, 1971). Because of the extended period of growth and the bearing of inflorescences, Jong (1970) termed the macrocotyledonary leaf a phyllomorph. In unifoliate only the seedling cotyledonary phyllomorph is produced, while in rosulate further phyllomorphs are produced from a meristem at the base of the lamina of a preceding phyllomorph. Based on chromosome data then known, Hilliard & Burt (1971) placed the acaulescent species into subg. *Streptocarpus*, and the caulescent ones into subg. *Streptocarpella*, with the former having $x = 16$, and the latter $x = 15$. The subgeneric division based on chromosome number showed inconsistencies when it was found that the basic chromosome number for the caulescent *Streptocarpus schliebenii* Mansf. was $x = 16$ (Milne, 1975). The molecular phylogenetic position of this species in the genus was, however, consistent with chromosome counts, since this species fell among acaulescent species of subg. *Streptocarpus* (Möller & Cronk, 2001a, b). In their monograph, Hilliard & Burt (1971) pointed out that many Madagascar species were insufficiently known, and that groups of species exist which cannot be easily assigned to either of the two subgenera: (i) herbaceous species with leaves in a basal rosette with long petioles, sharply marked off from the orbicular blades, unbranched veins arising from the midrib, filaments fused to about a third of the corolla tube; (ii) herbaceous species with leaves in a basal rosette (rarely solitary), often attenuate at the base (petiole ill-defined), veins ascending from the base and branched, filaments fused to about a third of the corolla tube; and (iii) species of shrubby-woody habit, unbranched veins arising from the midrib, characterized also by short filaments arising at the base of the corolla. The presence of sclereids and non-coherent anthers can be added as further synapomorphies for the last group of shrubby *Streptocarpus* species (Hilliard & Burt, 1971; Jong & al., 2012). The shrubby species share the basic chromosome number of $x = 16$ (Jong & Möller, 2000; Möller & Kiehn, 2004) and form a clade with acaulescent species (Möller & Cronk, 2001a, b; Möller & al., 2009, 2011a). Members of group (iii) were placed in subg. *Streptocarpella* by Hilliard & Burt (1971), although there are other compelling reasons not to place them there. Members of group (i) were also placed in subg. *Streptocarpella* and those of group (ii) in subg. *Streptocarpus* (Hilliard & Burt, 1971). However, since increased morphological, cytological and molecular phylogenetic information for the Malagasy Streptocarpinae species has become available, it is time to propose a new classification.

Molecular phylogenetic studies that include samples of subtribe Streptocarpinae are somewhat scattered and did not include large combined datasets of both nuclear and chloroplast

genes. Here we present data of two nuclear and three chloroplast intron-spacer regions (ITS at genus level; 5S non-transcribed spacer of nrDNA [5S NTS] at sectional level for *Saintpaulia*; *rpl20-rps12* spacer, *trnL* intron, *trnLF* spacer) for 260 samples covering ~80% of species of subtribe Streptocarpaceae, including all genera except the monotypic genus *Nodonema* for which no suitable material for DNA extraction was available. Furthermore, several species morphologically linked to *Str. schliebenii*, that had not been included in previous molecular studies, i.e., *Str. montanus* Oliv. and *Str. parensis* B.L.Burt from Tanzania have also been included with multiple samples here, as well as early diverging lineages of *Saintpaulia*. These samples cover important gaps in the morphological diversity of the Afro-Malagasy Gesneriaceae.

The aim of our study is to provide a state of the art classification for Afro-Malagasy Gesneriaceae, based on our current knowledge of phylogeny, morphology and cytology. We present phylogenies augmented with a considerable amount of new data, both in terms of taxon and gene sampling. The phylogenies shed light on the geographic relationships among the species and the distribution of key morphological and basic chromosome numbers of the species. Based on this evidence, a new infrageneric division of *Streptocarpus* with two subgenera and 12 sections is proposed. We also aim to re-evaluate and adjust the species delimitations in the erstwhile genus *Saintpaulia*.

■ MATERIALS AND METHODS

Plant materials. — For simplicity, we have adopted the generic concept of Möller & Clark (2013) and Weber & al. (2013), who recognized nine genera among the Afro-Malagasy Streptocarpaceae. We gathered 260 samples including 189 samples of *Streptocarpus* (116 out of 154 described species, 75%), 58 samples of *Saintpaulia* (including all species and infraspecific taxa described, except for the doubtful *Sa. amaniensis* F.Roberts; see Burt, 1958a), 4 samples of *Linnaeopsis* (1 out of 3 species), two of *Hovanella* (2 out of 2 species), 2 of *Acanthonema* (1 out of 2 species), 2 each of the monotypic *Schizoboea* (*Sch. kamerunensis* (Engl.) B.L.Burt) and *Colpogyne* (*C. betsiliensis* (Humbert) B.L.Burt), and 1 of the monotypic *Trachystigma* (*T. mannii* C.B.Clarke) (Appendices 1, 2).

Outgroup taxa for the *Streptocarpus* analyses were chosen on the basis of previous work (Möller & Cronk, 1997a, b, 2001a, b; Möller & al., 2009, 2011a; Weber & al., 2011a). All came from tribe Trichosporeae and include the European *Haberlea rhodopensis* Friv. of subtribe Ramondinae, *Paraboea rufescens* (Franch.) B.L.Burt of subtribe Loxocarpaceae, and two samples of subtribe Didymocarpaceae, *Didymocarpus citrinus* Ridl. and *Primulina spadiciiformis* (W.T.Wang) Mich. Möller & A.Weber.

DNA extraction, PCR, and direct sequencing. — Genomic DNA was extracted following Möller & al. (2009) and De Villiers & al. (2013). DNA extractions from herbarium material were carried out using the CTAB method (Doyle & Doyle, 1987, 1990), but with a longer precipitation time that increased the amount of recovered DNA.

PCR and sequencing approaches followed that of Möller & Cronk (1997a), Mayer & al. (2003) and De Villiers & al. (2013). For the ITS region, containing the internal transcribed spacers 1 and 2 and the intervening 5.8S gene, the primers used were ITS5P and ITS8P (Möller & Cronk, 1997a), for *trnL* intron and *trnLF* spacer (*trnLF*), primers c and f (Taberlet & al., 1991), and for *rpl20-rps12*, primers rpl20 and 5'-rps12 (Hamilton, 1999).

For partially degraded DNA from herbarium specimens, internal primers ITS2G and ITS3P (Möller & Cronk, 1997a) were used for ITS, primers d and e (Taberlet & al., 1991) for *trnLF*, and rpl20-3r and rpl20-2f for *rpl20-rps12*, which were designed in this study (rpl20-3r: 5'-CGT TGT GAA AGA CCT ATT ACT GGA T-3'; rpl20-2f: 5'-TCT TCT CTA TAC ACC GGA GCC-3') to PCR amplify the regions in smaller fragments. For low yield DNA extracts, booster PCR was carried out for the ITS region, by re-amplifying PCR products that were initially amplified with ITS5P and ITS8P with primers ITS1 and ITS4 (White & al., 1990).

PCR conditions for amplifying ITS, *trnLF*, and *rpl20-rps12* were according to De Villiers & al. (2013). The short fragments obtained using internal primers were amplified under the following conditions: 94°C for 5 min, then 35 cycles of 94°C for 30 s, 55°C for 30 s, 72°C for 30 s, with a final extension at 72°C for 10 min. The amplified PCR fragments were purified with ExoZAP-IT (Affymetrix U.K., Voyager, U.K.) and cycle-sequenced in both forward and reverse directions (Terminator Ready Reaction Mix, Applied Biosystems, Foster City, California, U.S.A.), using the PCR primers following the manufacturer's protocol and analyzed on a capillary sequencer ABI3730 at the GenePool facilities of the University of Edinburgh, U.K. The electropherograms were assembled and sequences edited in Sequencher v.4.7 (Gene Codes, Ann Arbor, Michigan, U.S.A.). Base polymorphisms detected in both forward and reverse direction electropherograms were IUB coded. The GenBank accession numbers of these newly acquired sequences are indicated in Appendices 1, 2.

Phylogenetic analyses. — The newly acquired sequences and sequences downloaded from GenBank were added to existing sequence matrices (ITS: Möller & Cronk, 2001a; *trnLF*, *rpl20-rps12*: De Villiers & al., 2013) and manually aligned by eye. We assembled matrices with data for ITS, the *trnL* intron, *trnLF* spacer and *rpl20-rps12* spacer sequences that included all available Afro-Malagasy samples assembled, 21 out of the 66 *Saintpaulia* samples representing 19 taxa, plus the 4 outgroup samples, and rooted on *Haberlea* (Möller & al., 2009, 2011a). This matrix contained a total of 226 samples ("Str226"), of which 117 (*rpl20-rps12* spacer), 130 (*trnL* intron), 130 (*trnLF* spacer) and 75 (ITS) were newly acquired (Appendix 1). Additionally, to test for incongruences in phylogenetic signal between the nuclear and chloroplast markers, the ITS and plastid matrices (combined *trnL* intron, *trnLF* spacer, *rpl20-rps12* spacer sequences) for both sampling levels were analysed individually. Due to missing samples for cpDNA data in the large analysis, this matrix contained only 209 samples ("Str209-cpDNA").

To investigate the phylogenetic relationships and taxon coherence among the *Saintpaulia* samples in detail, a matrix containing ITS and 5S NTS nrDNA sequences was assembled

that included 57 *Saintpaulia* samples with multiple samples per taxon and *Streptocarpus caulescens* Vatke as outgroup and root (“Sa58”), based on the large analysis and previously published work (Möller & Cronk, 2001a, b). Forty ITS sequences were newly acquired, while all 5S NTS sequences were downloaded from GenBank. These were essentially those generated by Lindqvist & Albert (1999, 2001) and had been generated for the same accessions as the ITS data (Appendix 2). The ITS region resides in the tandemly arranged 18S, 5.8S and 26S ribosomal genes that are clustered in the nucleolar organizer region (NOR; Hillis & Dixon, 1991). The 5S gene, between which the 5S NTS resides, is also tandemly repeated but not linked to the other three genes in plants except bryophytes and can exist on separate chromosomes (Murata & al., 1997; Sone & al., 1999). Thus, to test for phylogenetic congruences, separate analyses were carried out for the ITS region and 5S NTS sequences on matrices of both sampling levels. Due to missing sequences of the larger set, the ITS matrix contained 47 (“Sa47-ITS”), and the 5S NTS matrix 49 sequences (“Sa49-5S”).

All matrices and trees have been submitted to TreeBase, study no. TB2: S17292 (<http://purl.org/phylo/treebase/phylogs/study/TB2:S17292>).

It is well known that homoploid hybridization is widespread in *Streptocarpus*, particularly among members of the South African Cape Primrose clade (Hilliard & Burt, 1971; De Villiers & al., 2013). To assess the impact of this on the phylogenetic analysis we compared topology differences among the individual marker analyses with reference to major clades (that we use as the basis for the classification here) for the *Streptocarpus* analyses and “species” monophyly for the *Saintpaulia* analyses. Incongruences supported by higher than 75% bootstrap values and/or 0.95 posterior probabilities would be regarded as significant.

A limited proportion of within-electropherogram single nucleotide polymorphisms were found in ITS and 5S NTS (Electr. Suppl.: Table S1), amounting to 0.06% for the *Streptocarpus* matrices and 0.02%–0.39% for the *Saintpaulia* matrices. These polymorphisms may have their origin in past hybridisation and incomplete lineage sorting events (De Villiers & al., 2013). Alternatively, they may result from incomplete concerted evolution across the two NOR sites known to be present in *Streptocarpus* (Möller & al., 2008). Mutations arising here may sometimes be transiently present in evolutionary terms (others may become homogenised in parallel with speciation events; Hughes & al., 2005), reducing their significance in phylogenetic analyses. Polymorphisms may also arise as artefacts of PCR and/or sequencing protocols (cf. Möller, 2000). Because of the complex nature of polymorphisms in the multicopy ribosomal DNA sequences, their low levels of occurrences in the matrices and the fact that the matrices consisted of a mix of sequences downloaded from GenBank and newly acquired sequences, the scoring of polymorphisms was not necessarily uniformly performed, and so these polymorphisms were treated as uncertainties in the phylogenetic analyses.

Maximum parsimony (MP) and Bayesian inference (BI) analysis were run in PAUP* v.4.0b10 (Swofford, 2002), and MrBayes v.3.2.2 (Ronquist & al., 2012), respectively. The MP

analysis followed Möller & al. (2009). Best-fitting models for the BI analyses were obtained independently for each gene region using MrModeltest v.2.3 (Nylander, 2004). Under the Akaike information criterion (Akaike, 1974), GTR+I+G was given for *rpl20-rps12*, GTR+G for *trnL* intron and *trnLF* spacer, SYM+I+G for both the 5.8S gene region and ITS spacers for matrix Str226. For matrix Sa58, K80+I was given for the 5.8S gene, SYM+G for the ITS spacers, and K80+G for the 5S NTS sequences. For matrix Str226 10 million generations and for Sa58 5 million generations were run in two independent parallel runs and sampled every 1000th generation. The first 500 (Str226) or 250 (Sa58) trees (5%) were discarded as burn-in prior to calculating the BI consensus trees and posterior probabilities (PP). The statistics for each analysis are shown in Figs. S1, S4, S7, S10, S13, S16 (Electr. Suppl.), as run online under AWTY (Nylander & al., 2008). RAxML analysis was carried out using the raxmlGUI (Silvestro & Michalak, 2012), with GTRGAMMA setting and 1000 bootstrap replicates. Partitions were set for *rpl20-rps12*, *trnL* intron and *trnLF* spacers, ITS1, 5.8S, ITS2 and 5S NTS sequences (Marx & al., 2010).

Geography, morphology and cytology. — Geographical and morphological data were taken from living plants cultivated in the research collection at the Royal Botanic Garden Edinburgh (RBGE), herbarium specimens at E, and consultation of the relevant literature, primarily Hilliard & Burt (1971) for *Streptocarpus*, and for other genera as cited hereafter in the relevant sections. Living material was either fixed in Farmer’s Fluid to aid clearing (Jong & al., 2012), or directly observed under a dissecting microscope. Some material used came from the RBGE spirit collection and was preserved in Copenhagen mix.

Streptocarpus species display an array of morphological diversity (Jong, 1970; Hilliard & Burt, 1971; Jong & Burt, 1975). We categorized the species into the main forms irrespective of herbaceous or woody habit, including caulescents with stems and decussate leaf arrangement (Fig. 1A), plants with creeping rhizomatous stem and alternate leaf arrangement (Fig. 1B), *Saintpaulia*-like rosettes (Fig. 1C), acaulescents lacking a stem and shoot apical meristem and either producing leaves in an irregular rosette (rosulates; Fig. 1D), or only retaining a single enlarged cotyledon as the sole photosynthetic organ (unifoliate; Fig. 1E).

We used the categorization into floral types of Harrison & al. (1999) for *Streptocarpus* flowers, these included the small pouch (Fig. 1F), open tube (Fig. 1G), personate (having the lower lip pushed upward so as to close the gap between the lips, as in the snapdragon; Fig. 1H), keyhole (where the opening of the corolla is laterally compressed to a narrow vertical slit; Fig. 1I), *Saintpaulia*-type (Fig. 1J), and bird-pollination (possessing a red tubular flower; Fig. 1K). We distinguished a further two types, the Acanth-type (Fig. 1L) for the recently described *Str. lilliputana* Bellstedt & T.J. Edwards that exhibits an extremely long proximate alignment channel (viz. Westerkamp & Claßen-Bockhoff, 2007), and the labellanthus-type with a forward directing lip and reduced upper lip (Fig. 1M).

Seeds were either categorised as reticulate, where the lateral testa cell walls form a raised reticulum on the seed surface, and verruculose where the outer testa cell walls produce a papilla.

Data for basic chromosome numbers were taken predominantly from the RBGE WebCyt2 (Möller & Pullan, 2015–), from Briggs (2004), or obtained from mitotic chromosome counts according to Jong & Möller (2000).

■ RESULTS

Phylogenetic congruence between the individual marker matrices. — A comparison of the topologies of the ITS with the cpDNA trees for the *Streptocarpus* analyses revealed no strong conflict in relationships between the main clades (Electr. Suppl.: Figs. S1–S6; summarised in Table S2). Some “clades”,

such as “h” and “i” were not resolved as monophyletic in some analyses, especially those involving ITS matrices, but no strongly supported topological conflict existed. A similar situation was revealed for clades “k” and “l”. All clades received predominantly high support in the combined ITS & cpDNA analyses. For *Saintpaulia*, the MP, ML and BI analyses of neither ITS nor 5S NTS separately indicated strongly supported incongruences in topologies (Electr. Suppl.: Figs. S7–S12). A few instances occurred of changing relationships between ITS and 5S NTS trees. None received consistently strong support. As the *Streptocarpus* and *Saintpaulia* analyses revealed no strong topological incongruences, our report is based on the results of the combined analyses only.

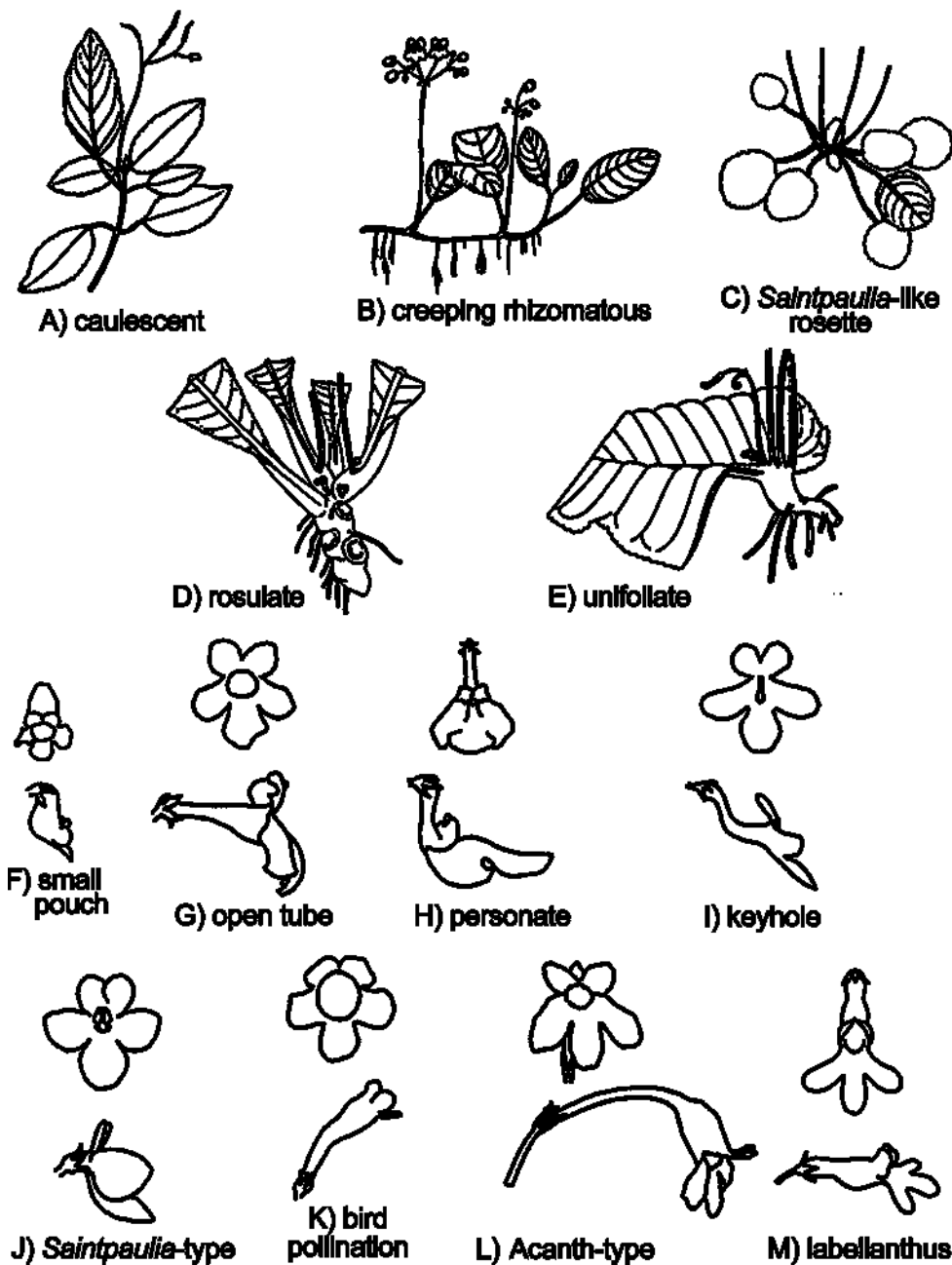


Fig. 1. Major growth forms (A–E) and floral types (F–M) found among the Afro-Malagasy Gesneriaceae. A & C, modified from Humbert (1971: figs. XIII4, X8, © Publications Scientifiques du Muséum national d’Histoire naturelle, Paris); B, from Weigend (2000: fig. 2:5, © Elsevier Ltd. Oxford); D–E, from Hilliard & Burt (1971: figs. 2, 5, © University of Natal Press, Pietermaritzburg); F–K, from Harrison & al. (1999: fig. 1A, © Oxford University Press); L, from Bellstedt & Edwards (2004: fig. 1D–E, © Cambridge University Press); M, modified from Hilliard & Burt (1975: figs. 1Aa–1Ab, © Royal Botanic Garden Edinburgh).

Characteristics and phylogenetic relationships revealed by the Str226 analysis. — The combined *rpl20-rps12* spacer, *trnL* intron, *trnLF* spacer and ITS matrix included 2589 characters, of which 1526 (58.9%) were constant, 298 (11.5%) were parsimony uninformative and 765 (29.6%) parsimony informative.

The MP analysis resulted in 48,847 most parsimonious trees of a length of 3021 steps (consistency index [CI] = 0.5144, retention index [RI] = 0.8610). The BI tree of the same matrix had a topology very similar to the RAxML tree and MP consensus tree (Electr. Suppl.: Figs. S13, S14, S15 respectively). The subclades relevant for the subgenus and sectional division were identical in all analyses, with minor differences in unsupported topologies within subclades. The Bayesian inference phylogenies are presented in the main text, with branch support values from the BI, ML and MP analyses shown for main branches (Fig. 2A–B). The individual analyses with all support values are given in Figs. S13–S15 (Electr. Suppl.).

Two strongly supported large clades were identified, one (Clade I, PP = 1.00; ML = 99%; BS = 84%; Fig. 2A) being composed mainly of subg. *Streptocarpella* and *Saintpaulia*, and the other (Clade II, PP = 1.00; ML = 100%; BS = 92%; Fig. 2B) including mostly subg. *Streptocarpus*, but also some caulescent species (see below). Within Clade I, several subclades were strongly supported; subclade “a” contains *Str. nobilis* C.B. Clarke, *Trachystigma* and the *Acanthonema* samples (PP = 1.00; ML = 97; BS = 75%), subclade “b” (PP = 1.00; ML = 100%; BS = 99%) contains the Madagascan species of group (i) of Hilliard & Burt (1971). Subclade “c” (PP = 1.00 ML = 100%; BS = 100%) contains the Madagascan herbaceous species and the two *Hovanella* species. Subclade “d” (PP = 1.00; ML = 99%; BS = 92%) was composed of *Str. thysanotus* Hilliard & B.L. Burt, *Str. kimbozanus* B.L. Burt, *Str. elongatus* Engl. and the *Schizoboea* samples. Subclade “e” (PP = 1.00; ML = 100%; BS = 100%) included three species, *Str. saxorum* Engl.,

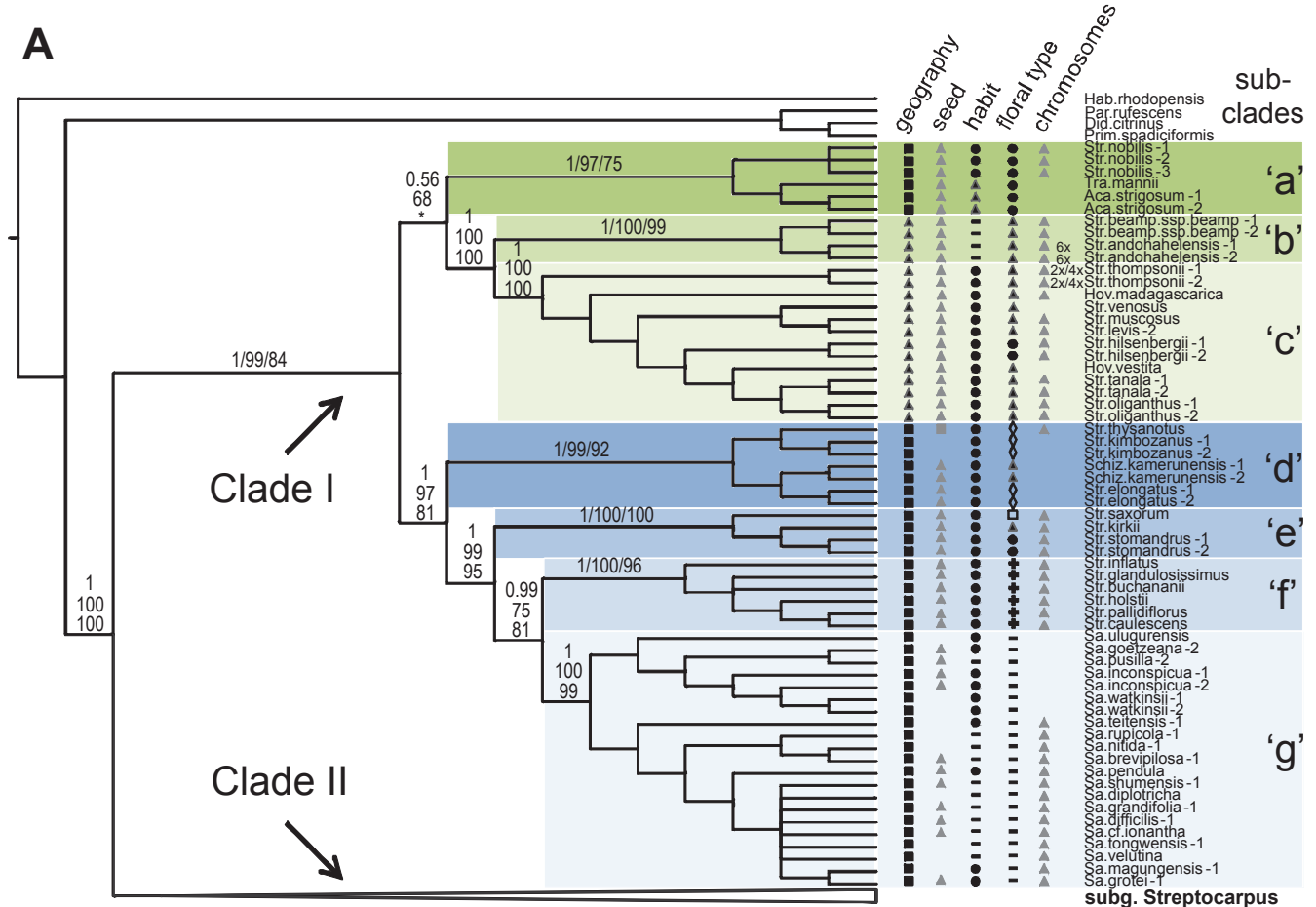


Fig. 2A–B. Bayesian inference tree for matrix Str226 of combined ITS, *trnL* intron, *trnLF* spacer and *rpl20-rps12* spacer sequences, with branch support (BI/ML/MP) along the branches, indicated for branches supporting sections and higher-level taxa. For intrasectional branch support values see Electr. Suppl.: Figs. S1A, S2, S3. * indicates branches receiving values less than 0.5 (BI) or 50% (ML, MP). Characters for subg. *Streptocarpella* (A) and subg. *Streptocarpus* (B) are indicated. First column, country of origin (geography): ■ Africa, ▲ Madagascar and Comores. Second column, seed ornamentation (seed): ▲ verruculose, ■ reticulate. Third column, growth form (habit): ● caulescent, ★ creeping rhizomatous stem, ■ rosulate, - *Saintpaulia*-like rosette, ▲ unifoliate, + shrubby. Fourth column, floral types: ▲ small pouch, ◇ labellanthus, □ keyhole, ● open tube, - *Saintpaulia*, + personate, + bird-pollination, ★ Acanth. Fifth column, basic chromosome number (chromosomes): ▲ x = 15, ■ x = 16; ploidy level: given as numbers to the right. Gaps indicate missing data.

Str. kirkii Hook.f., and *Str. stomandrus* B.L.Burt. The species with personate flowers were in subclade “f” (PP = 1.00; ML = 100%; BS = 96%). The final subclade in Clade I, subclade “g” (PP = 1.00; ML = 100%; BS = 99%), contained all *Saintpaulia* species included in this analysis. Relationships between the subclades were found to be identical in the three phylogenetic analyses of the Str226 dataset and well supported in the BI (PP = 0.98–1.00), ML (75%–100%) and MP (BS = 81%–100%) analyses, except for the position of subclade “a”, which was sister to subclade “b” and “c” in the BI and ML analyses (Electr. Suppl.: Figs. S13–S14), but collapsed into a basal polytomy in Clade I in the MP analysis (Electr. Suppl.: Fig. S15).

Clade II showed similar resolution but overall less branch support in the MP, but high branch support in the BI and ML analyses (Figs. 2–3; Electr. Suppl.: Figs. S13–S15). Two subclades, “h” (PP = 1.00; ML = 98; BS = 86%) containing the shrubby Madagascan species of group (iii) of Hilliard & Burt (1971), and subclade “i” (PP = 1.00; ML = 98%; BS = 88%) including Madagascan *Streptocarpus* species with a dense woolly indumentum, plus *Colpogyne*, formed sister clades (PP = 1.00; ML = 97%; BS = 86%) on the earliest diverging lineage in Clade II. The two samples of *Str. exertus* Hilliard & B.L.Burt and *Str. capuronii* Humbert were resolved in different positions in the different analyses, either in a polytomy with the remaining subclades in the BI analysis (Electr. Suppl.: Fig. S13), in a basal polytomy of Clade II in the MP analysis (Electr. Suppl.: Fig. S15), or resolved in grades between the two subclades “h” and “i” in the ML analysis (Electr. Suppl.: Fig. S14), although never with significant branch support. Subclade “j” (PP = 1.00; ML = 81%; BS = 85%) included species of group (ii) of Hilliard & Burt (1971) with ascending veins, and subclade “k” (PP = 0.98, ML = 75%; BS = 59%) contained the African species *Str. bullatus* Mansf., *Str. montanus*, *Str. parensis*, *Str. schliebenii*, and the *Linnaeopsis* samples. The remaining 107 samples were unifoliate and rosulate African species and formed subclade “l” (PP = 1.00; ML = 80%; BS < 50%). Within this subclade there were several larger supported clades, such as the ITS2 deletion clade (PP = 1.00; ML = 98%; BS = 90%) and an extended Cape Primrose clade (sensu Möller & Cronk 2001a, b) (PP = 1.00; ML 91%; BS < 78%) (see Figs. S1A, S2, S3 in Electr. Suppl.), that includes exclusively rosulate species geographically restricted to the northern and eastern provinces of South Africa and Swaziland.

Characteristics and phylogenetic relationships revealed by the Sa58 analysis. — The combined ITS, 5S NTS nrDNA matrix had 991 characters of which 690 (69.6%) were constant, 97 (9.8%) uninformative and 204 (20.6%) parsimony-informative in matrix Sa58.

In the MP analysis 13,925 most parsimonious trees were found of 469 steps (CI = 0.8081, RI = 0.9112). In the MP majority consensus tree, BI and ML trees, sequences of samples from the Uluguru Mts. (PP = 1.00; ML = 97%; BS = 94%), Teita Hills (PP = 1.00; ML = 100%; BS = 100%), and Nguru Mts. (PP = 1.00; ML = 98%; MP = 98%) were retrieved in respective clades, with identical topologies between these clades in all three analyses and high branch support (Electr. Suppl.: Figs. S16–S18; summarized in Fig. 4). Within each of

these clades, the samples fell into species-specific clades in the case of *Sa. watkinsii* Haston (PP = 1.00; ML = 100%; BS = 98%), *Sa. inconspicua* B.L.Burt (PP < 0.50; ML < 50%; BS < 50%), *Sa. pusilla* Engl. (PP = 1.00; ML = 97%; BS = 85%), *Sa. goetzeana* Engl. (PP = 1.00; ML = 100%; BS = 100%), *Sa. teitensis* B.L.Burt (PP = 1.00; ML = 100%; BS = 100%), *Sa. brevopilosa* B.L.Burt (PP = 1.00; ML = 100%; BS = 91%), and *Sa. nitida* B.L.Burt (PP = 1.00; ML = 98%; BS = 86). Only for *Sa. inconspicua* were different topologies of the individual samples found between the analyses, as sister pair in the MP, in grades in the ML and in separate positions in the BI analysis (Electr. Suppl.: Figs. S16–S18). This might be linked to the fact that of *Sa. cf. inconspicua*-1, only ITS1 sequences were available and no 5S NTS data.

The clade of the West Usambara Mts. species *Sa. shumensis* B.L.Burt (PP = 1.00; ML = 100%; MP = 91%) fell between the Nguru Mts. clade and the remainder of the *Saintpaulia* samples. These were the Usambara Mts. samples and the Kenyan samples of *Sa. rupicola* B.L.Burt that formed a clade without support, and the latter in a separate clade (PP = 1.00; ML = 96%; BS = 92%) within the former. Where multiple taxon samples existed within the *Sa. ionantha* complex (sensu Möller & Cronk, 1997b) none, except *Sa. rupicola*, formed a taxon-specific clade.

Character distribution. — As the relationships at the base of Clade II were unresolved, and the *Saintpaulia* analyses showed a polytomy for the *Sa. ionantha* complex (= *Str. ionanthus* complex), the characters for geographic origin, morphology and cytology were presented next to the taxa in the phylogenetic trees (Fig. 2, summarized for the *Streptocarpus* analysis in Fig. 3, Fig. 4), rather than carrying out a character optimization, and their utilization for the classification discussed.

DISCUSSION

In this study we have assembled the most comprehensive molecular dataset to date for the Afro-Malagasy didymocaroid Gesneriaceae, that include the well-known African Violets and Cape Primroses, covering about 83% out of the 211 taxa in 176 species (equivalent to 76% sampling at the species level). On the basis of the phylogenetic trees reconstructed, we assess morphological character states and their use in a new classification. Such an approach has been widely applied before (e.g., Marx & al., 2010; Möller & al., 2011b; Weber & al., 2011b; Iles & al., 2012). Our results are in stark contrast to previous classifications of the Afro-Malagasy Gesneriaceae that viewed the traditional genera as independent evolutionary lineages (Hilliard & Burt, 1971; Weber, 2004; Weber & al., 2013). The results are particularly significant for the horticulturally important genus *Saintpaulia*, which can be distinguished morphologically from an archetypical *Streptocarpus* such as the rosulate *Str. rexii* (Bowie ex Hook.) Lindl. or the caulescent *Str. caulescens* (Hilliard & Burt, 1971). However, with the increased knowledge of the Madagascan species these morphological boundaries became weakened (Briggs, 2004), and its inclusion in *Streptocarpus* seems a viable option. The ramifications of

our findings with view to a new classification of the Afro-Malagasy Gesneriaceae are discussed in detail here.

Molecular phylogenetic structure. — Overall, we found that the reconstructed phylogenies showed few incongruences between the plastid and nuclear datasets at the clade level, and none were strongly supported. The largest matrix with combined ITS, *trnL* intron, *trnLF* spacer and *rpl20-rps12* spacer sequences resulted in a well-resolved and generally well-supported tree topology. The high resolution is perhaps the effect of the combination of fast evolving ITS with slower evolving plastid intron and spacer sequences, a well-known observation (e.g., Sullivan, 1996; Gontcharov & al., 2004). This is despite the fact that this matrix was incomplete and had data gaps in the plastid sequence

partitions. The effect of missing data on phylogenies has been investigated previously and their effect on retrieving accurate topologies found to be minimal (e.g., Wiens, 2003, 2006; also in Gesneriaceae, Möller & al., 2009).

Based on our phylogenetic analyses using three different approaches, BI, ML, and MP, we retrieved very strong support for the finding that all Afro-Malagasy Gesneriaceae genera with non-twisted fruits included in this analysis, i.e., *Acanthonema*, *Colpogyne*, *Hovanella*, *Linnaeopsis*, *Saintpaulia*, *Schizoboea* and *Trachystigma*, have evolved from within the genus *Streptocarpus* (Figs. 2–3). We found only small differences in branch support between the BI, ML, and MP analyses, increasing the confidence for inferences regarding sectional coherence and

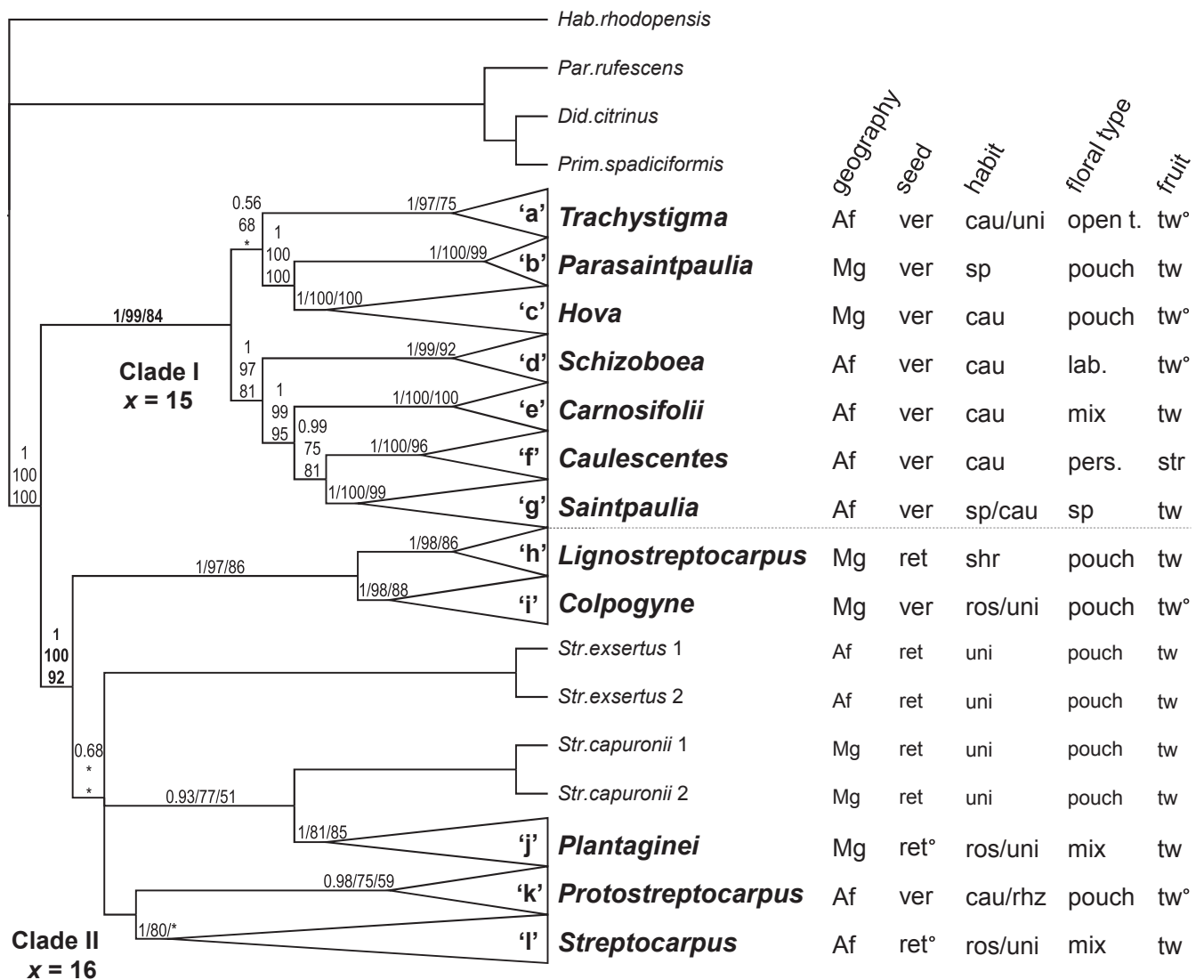


Fig. 3. Summary of phylogenetic relationships among sections of *Streptocarpus* based on BI, ML, and MP analyses with branch support (BI/ML/MP) indicated for branches supporting sections and higher-level taxa, for the Str226 analysis. * indicates branches receiving values less than 0.5 (BI) or 50% (ML, MP); °, with minor exceptions. Lowercase letters a–l identify sections (names in bold italics). First column, geographic origin (geography): Af., Africa; Mg; Madagascar and Comores. Second column, seed ornamentation (seed): ret, reticulate; ver, verruculose. Third column, growth form (habit): cau, caulescent; rhz, creeping rhizomatous; ros, rosulate; shr, shrubby; sp, *Saintpaulia*-like rosette; uni, unifoliate. Fourth column, floral type: pouch, small pouch; lab., labellanthus-type; mix, mixed subclades; open t., open tube; pers., perianate; sp, *Saintpaulia*-type. Fifth column, fruit development: str, not twisted; tw, twisted.

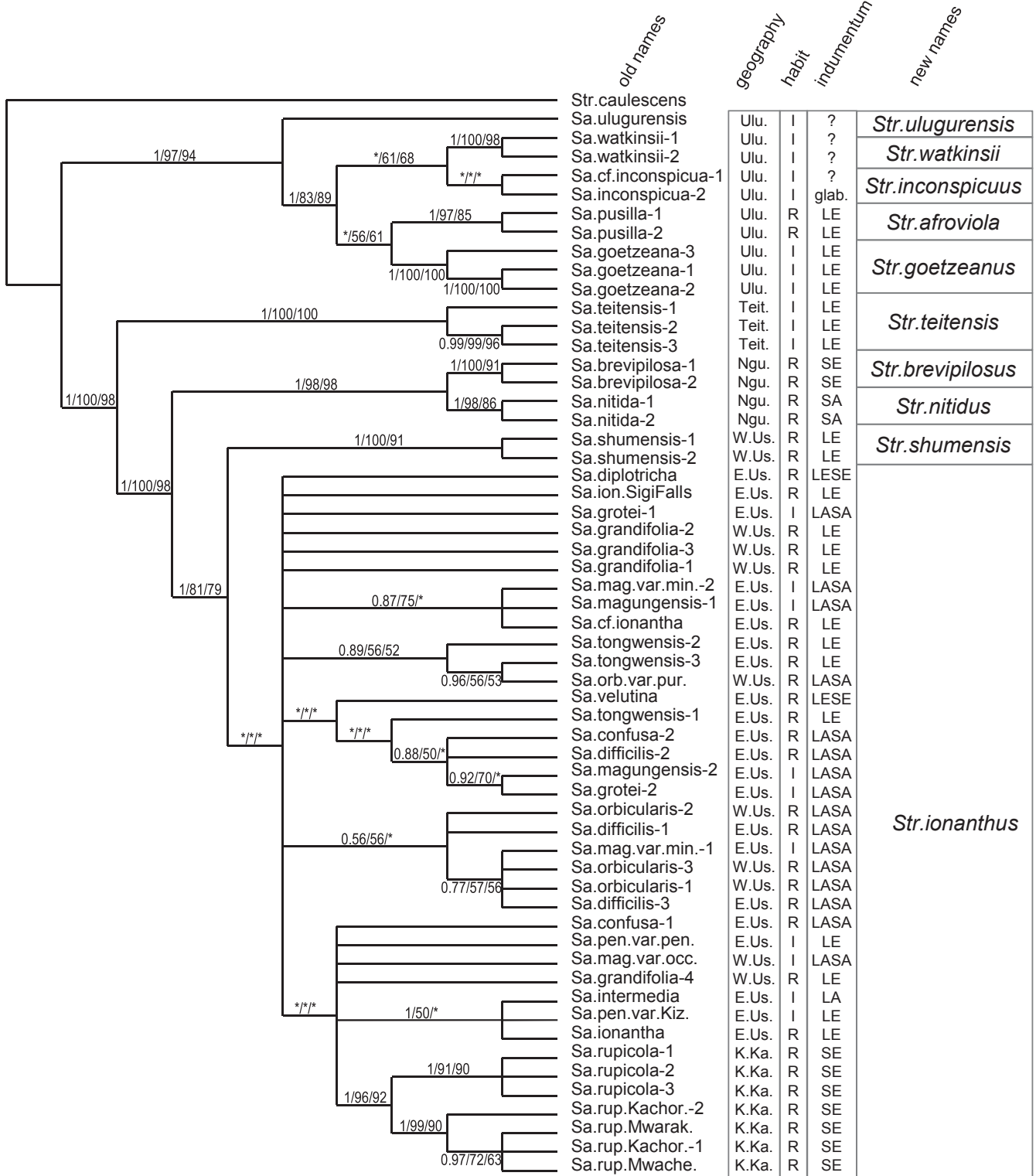


Fig. 4. Majority-rule consensus tree of the maximum parsimony analysis of the *Saintpaulia* Sa58 matrix comprised of combined ITS and 5S NTS nrDNA data, with branch support values indicated along branches (BI/ML/MP). * indicates branches receiving values less than 0.5 (BI) or 50% (ML, MP). First column, old names: Sa, *Saintpaulia*; Str, *Streptocarpus*. Second column, geographic origin (geography): E.Us., East Usambara Mts.; K.Ka., Kenya, Kaloleni; Ngu., Nguru Mts.; Teit., Teita Hills; Ulu., Uluguru Mts.; W.Us., West Usambara Mts. Third column, growth form (habit): I, opposite leaves and conspicuous internodes; R, alternate leaves in rosette. Fourth column, leaf indumentum (indumentum): A, appressed hairs; E, erect hairs; glab., glabrous; L, long hairs; S, short hairs. Fifth column, new names at species rank.

relationships where they were strongly supported. In our phylogenetic analyses, we found two strongly supported clades. Clade I is comprised of the herbaceous caulescent *Streptocarpus* species of subg. *Streptocarpella* including samples of five non-twisted genera, i.e., *Acanthonema*, *Hovanella*, *Saintpaulia*, *Schizoboea*, and *Trachystigma*. Clade II primarily included species of subg. *Streptocarpus* and samples of *Colpogyne* and *Linnaeopsis* possessing non-twisted fruits. Since no molecular data could be generated for *Nodonema*, its taxonomic placement was decided on the basis of morphological features shared with members of subg. *Streptocarpus* (see below).

Character evolution. — Despite the low resolution at the base of Clade II that precludes a full character optimization analysis, several conclusions can be drawn from the molecular phylogenies and consequently for the new infrageneric classification presented here. We follow a character order of decreasing congruence with infrageneric clade topology.

Cytology. — The basic chromosome number is the only character that is, to our present knowledge, fully congruent with the tree topology, albeit only to support the split between Clade I and Clade II. An interesting aspect is the occurrence of polyploidy. This has only been detected in the four species on Madagascar and the Comoro Islands (*Str. variabilis* Humbert on Anjouan), and in both main evolutionary lineages (Fig. 2). This recalls the idea of island colonization for which polyploidy has been argued to be particularly advantageous (Stebbins, 1950; Barrier & al., 1999).

Geography. — Our phylogeny of the Streptocarpaceae shows a strong geographic pattern (Fig. 2). It is interesting to note that the species resolved into clades of either African, or Madagascan and Comores distributions in both Clade I and, to a lesser extent, in Clade II. This confirms that interchanges between the two geographic regions were rare events (as previously suggested by Möller & Cronk, 2001b). Because of the polytomy at the base of Clade II, it is not possible to state with certainty whether the Streptocarpaceae originated in Africa or Madagascar, or whether there were one or two geographic exchanges in Clade II.

Seed ornamentation. — The seed testa cell surface ornamentation of the Streptocarpaceae is either reticulate (Fig. 5K) or verruculose (Fig. 5L). The correlation between caulescence and verruculose seeds, and acaulescence and reticulate seeds in *Streptocarpus* on the African continent and the lack of this correlation in Madagascan and Comores species has been observed before (Hilliard & Burt, 1971). We can define this pattern more precisely here. Most members of Clade I have verruculose seeds irrespective of their geographic origin (Fig. 2A), while those in Clade II exhibit a more complex pattern (Fig. 2B). The few exceptions in Clade I are likely to be incorrect reports and are dealt with in detail below. The absence of reticulate seeds in Clade I, the mixed reticulate/verruculose subclades in the basal lineages and the predominantly reticulate seeds of the derived subclade “1”, may suggest that verruculose seed testa ornamentation is the ancestral state from which reticulate seeds have evolved. However, a conclusive answer to the evolutionary scenario here is hampered by the low basal resolution in Clade II. However, the presence of verruculose seeds in some members in subclade “1” (*Str. dunnii* Hook.f., *Str. decipiens*

Hilliard & B.L.Burt, *Str. hirtinervis* C.B.Clarke, *Str. nimbicola* Hilliard & B.L.Burt, and some populations of *Str. galpinii* Hook.f.) are clearly homoplastic.

Fruit twist. — This study shows that this character, traditionally used to define the genus *Streptocarpus*, is perhaps the most labile of all the morphological characters used to define it. The repeated loss of this character is not unprecedented in Gesneriaceae, and has also been observed in *Paraboea* (C.B.Clarke) Ridl. (Puglisi & al., 2011). In *Streptocarpus*, the twisted fruit was lost on at least seven occasions (Fig. 2). Given that the fruit twist has perhaps evolved only once or twice in Gesneriaceae (Möller & al., 2009), the results here and perhaps for *Paraboea* (Puglisi & al., 2011) are an interesting demonstration of uni-directionality in character evolution.

Floral types. — Similar to other genera of Didymocarpoideae, such as *Oreocharis* Benth. (Möller & al., 2011b), or *Petrocodon* Hance (Weber & al., 2011b), *Streptocarpus* exhibits a high diversity of floral sizes and forms which can be ascribed to several main types (Harrison & al., 1999; Hughes & al., 2006). However, this rough grouping does not fully reflect floral diversity in *Streptocarpus*. Among the small-flowered type, there is a group of species in subclade “d” with a forward directing lip and reduced upper lip that cannot be adequately described as a small pouch type and is described here as labellanthus-type (Fig. 6D). The open flower type exhibits perhaps the most diversity, and may contain several subtypes, without or with distinct pollination chambers (viz. Westerkamp & Claßen-Bockhoff, 2007), such as the Acanth-type present in *Str. lilliputana* (Bellstedt & Edwards, 2004; De Villiers & al., 2013). However, differences are often only slight and some flowers are difficult to classify. Cases of parallelisms in the evolution of main floral types occur, such as for the key-hole flower for example (Fig. 6E), occurring in *Str. saxorum* in Clade I, and several species in Clade II (Fig. 2). However, several subclades have more conserved flower characteristics (Fig. 2A), such as subclade “d” with the labellanthus-type, subclade “f” with personate flowers (Fig. 6F) or the flat-faced corollas of *Saintpaulia* (Figs. 6G–H). Such cases have been utilized for our classification here.

Growth form. — After the Madagascan species of Humbert (1967, 1971) became known, the subdivision of *Streptocarpus* into the unranked groups *Caulescentes*, *Rosulati* and *Unifoliati* of Fritsch (1894) was considered not to capture the breadth of morphological diversity in this genus. With the phylogenetic inclusion of other genera of subtribe Streptocarpaceae into *Streptocarpus*, there are at least two more fundamental growth patterns that can be recognized, (1) *Saintpaulia*-like rosette plants (group (i) of Hilliard & Burt, 1971; Fig. 7B) and (2) shrubby caulescent plants (group (iii) of Hilliard & Burt, 1971; Fig. 7I). Species with a creeping rhizomatous stem (Fig. 8C–E) could be regarded as a subform of caulescents, while those with leaves with branched veins ascending from the base (Fig. 7J; group (ii) of Hilliard & Burt, 1971) are best described as a subform of acaulescents, since they include rosulates and unifoliates (Fig. 2).

The evolution of growth form has been studied previously in *Streptocarpus* and the habit found to be rather plastic (Möller & Cronk, 2001a). In the expanded phylogenies presented here,

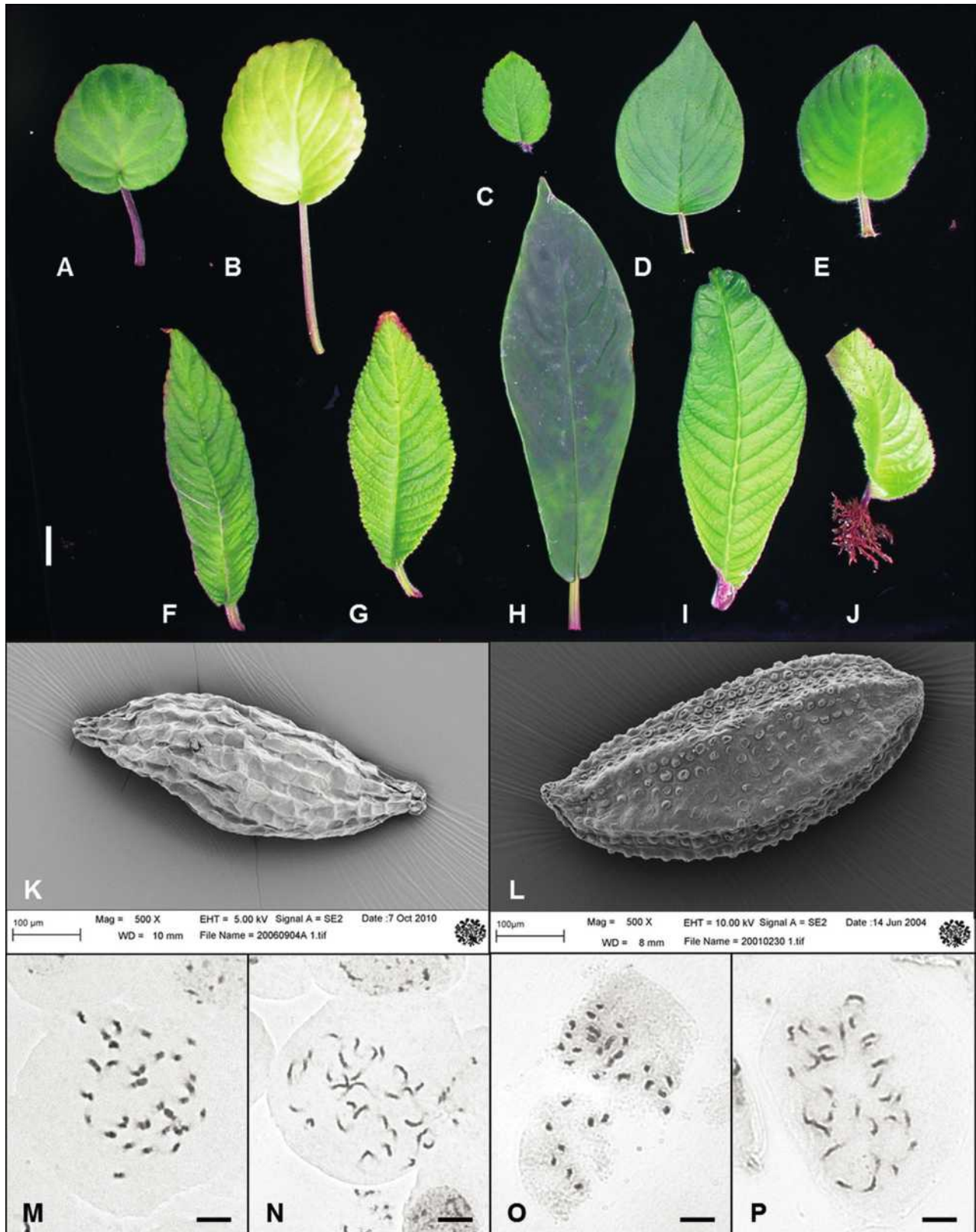


Fig. 5. Leaves, seeds, and chromosome numbers of selected *Streptocarpus* species. **A**, *Str. beampingaratrensis* subsp. *antambolorum*; **B**, *Str. ionanthus* subsp. *grotei*; **C**, *Str. levis*; **D**, *Str. glandulosissimus*; **E**, *Str. stomandrus*; **F**, *Str. schliebenii*; **G**, *Str. parensis*; **H**, *Str. papangae*; **I**, *Str. rexii*; **J**, *Str. wendlandii*; **K**, *Str. rexii*; **L**, *Str. vestitus*; **M**, *Str. vestitus*, late prometaphase; **N**, *Str. vestitus*, prometaphase; **O**, *Streptocarpus* sp. nov., early metaphase; **P**, *Streptocarpus* sp. nov., prometaphase. — Scale bars: A–J = 1 cm; K–L = 100 μ m; M–P = 10 μ m. Photos: A–J, M–P by M. Möller, RBGE; K, L by F. Christie, RBGE.



Fig. 6. Floral form (front and side view) of representative species of sections of *Streptocarpus*. **A**, sect. *Trachystigma*: *Str. nobilis* (open tube); **B**, sect. *Parasaintpaulia*: *Str. beampingararensis* (small pouch); **C**, sect. *Hova*: *Str. muscosus* (small pouch); **D**, sect. *Schizoboea*: *Str. thysanotus* (labellanthus); **E**, sect. *Carnosifolii*: *Str. saxorum* (keyhole); **F**, sect. *Caulescentes*: *Str. caulescens* (personate); **G**, sect. *Saintpaulia*: *Str. ionanthus* (*Saintpaulia*-type); **H**, sect. *Saintpaulia*: *Str. goetzeanus* comb. nov. (*Saintpaulia*-type); **I**, sect. *Lignostreptocarpus*: *Str. papangae* (small pouch); **J**, sect. *Plantaginei*: *Str. hildebrandtii* (small pouch); **K**, sect. *Colpogyne*: *Str. ibityensis* (small pouch); **L–M**, sect. *Protostreptocarpus* (small pouch); **L**, *Str. montanus*; **M**, left to right: *Str. bullatus*, *Str. montanus*, *Str. parensis*, *Str. schliebenii*; **N–O**, sect. *Streptocarpus*: **N**, *Str. rexii* (open tube); **O**, *Str. dunnii* (bird pollination). — Scale bars: 5 mm. All photos by M. Möller, RBGE.

most morphs form separate subclades and have been found useful in the classification of the Streptocarpaceae, with the exception of the unifoliate and rosulate, but sometimes with parallelisms such as the *Saintpaulia*-rosette, that has evolved once in Africa and once in Madagascar. The unifoliate form shows a high level of homoplasy, and has most likely evolved

several times, at least twice in Clade II within the African and the Madagascan acaulescents and once among the caulescents of Clade I.

There is an enormous wealth of publications devoted to the study of growth and development of *Streptocarpus* plants. However, a detailed discussion of the historic (e.g., Crocker,



Fig. 7. Habit and growth form of representative species of sections of *Streptocarpus* subg. *Streptocarpella* and subg. *Streptocarpus*. **A**, sect. *Trachystigma*: *Str. nobilis* (facultative caulescent); **B**, sect. *Parasaintpaulia*: *Str. beampingararensis* (rosette); **C**, sect. *Hova*: *Str. muscosus* (caulescent); **D**, sect. *Schizoboea*: *Str. elongatus* (caulescent); **E**, sect. *Carnosifolii*: *Str. saxorum* (caulescent); **F**, sect. *Caulescentes*: *Str. caulescens* (caulescent); **G**, sect. *Saintpaulia*: *Str. ionanthus* (rosette); **H**, sect. *Saintpaulia*: *Str. goetzeanus* comb. nov. (caulescent); **I**, sect. *Lignostreptocarpus*: *Str. papangae* (caulescent); **J**, sect. *Plantaginei*: *Str. hildebrandtii* (acaulescent); **K**, sect. *Colpogyne*: *Str. lanatus* (rosulate); **L**, sect. *Colpogyne*: *Str. betsiliensis* (rosulate). — Photos: A–C, E–H, J–L by M. Möller, RBGE; D by Matt Walters; I by L. Wilson, RBGE.

1860; Jong, 1970) and evolutionary developmental work (e.g., Jong & Burtt, 1975; Harrison & al., 2005; Nishii & al., 2010) would be beyond the scope of this work.

Inter- or infrageneric division. — In our phylogenetic analyses, we retrieved strong support for a subdivision within the main clades and we found additional support from vegetative,

floral, seed morphological characters and basic chromosome number or combinations thereof. These are used here to propose a new classification for the Streptocarpaceae. The question arises as to the rank at which to divide them. There are different options to classify the Afro-Malagasy Streptocarpaceae. These options include:

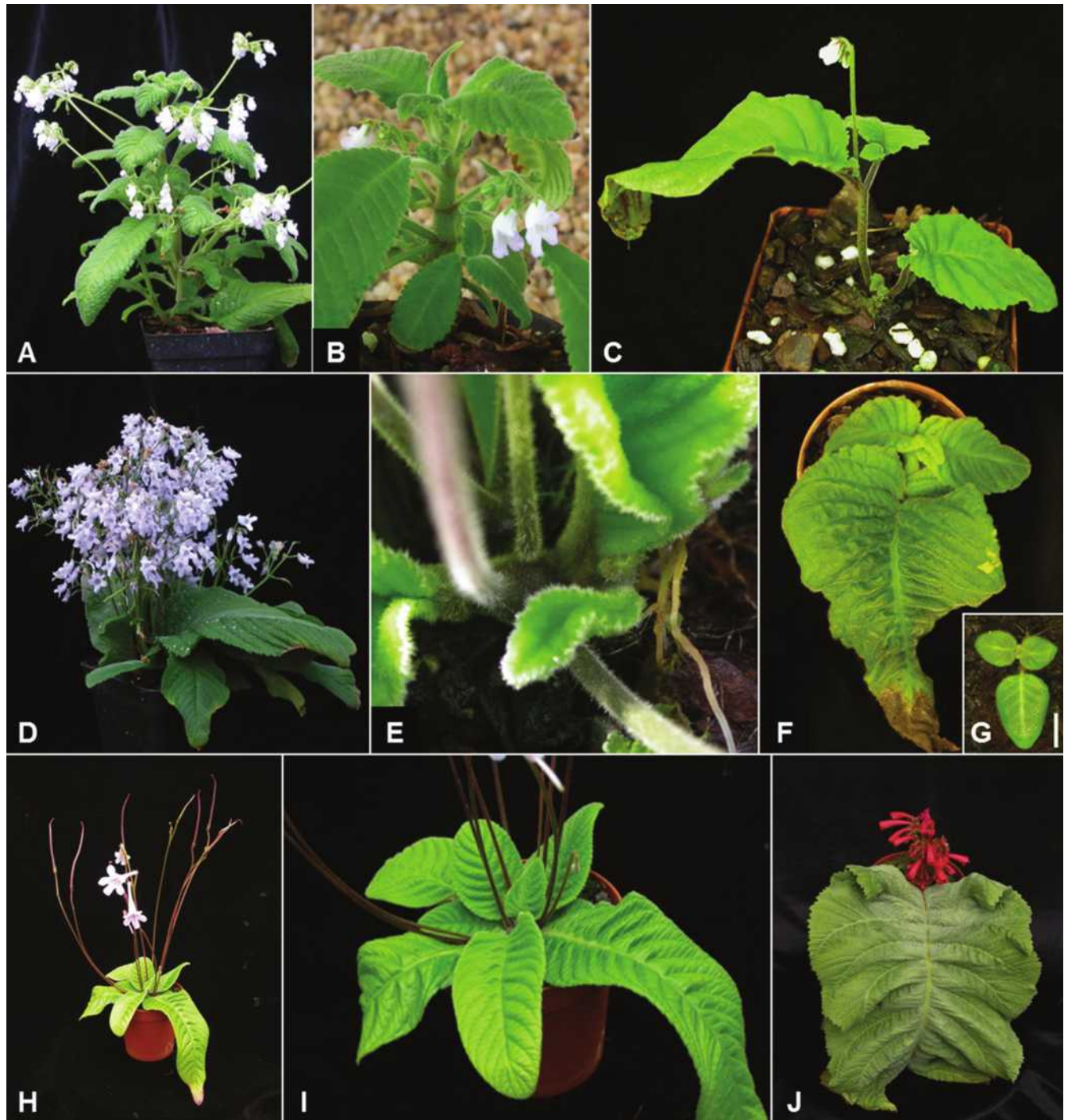


Fig. 8. Habit and growth form of representative species of sections of *Streptocarpus* subg. *Streptocarpus*. **A–F**, sect. *Protostreptocarpus*: **A–B**, *Str. parensis* (caulescent); **C**, *Str. bullatus* (creeping rhizomatous); **D–E**, *Str. montanus* (creeping rhizomatous); **F**, seedling of *Str. schliebenii* (caulescent); **G**, sect. *Carnosifolii*: seedling of *Str. kirkii* (caulescent); **H–J**, sect. *Streptocarpus*: **H–I**, *Str. rexii* (rosulate); **J**, *Str. dunnii* (unifoliate). — All photos by M. Möller, RBGE.

1. Retaining all nine genera in subtribe Streptocarpinae with no nomenclatural changes, but leaving a paraphyletic *Streptocarpus*.
2. Assigning *Streptocarpus* species to other genera with which they form subclades in order to obtain monophyletic genera. This would involve extreme splitting, with new genera needing to be established from within paraphyletic *Streptocarpus* subclades, resulting in over 20 (often small) genera, sometimes even requiring the splitting of genera such as *Hovanella* whose two species were not sister to each other in any of our analyses. The morphological definition and differentiation between these “genera” would also be weak. Raising subclades “a–l” to monophyletic genera would still result in around a dozen genera, with the recurring issue of difficulty in their delineation sometimes on the basis of a single character, e.g., flower form (e.g., subclades “f” and “g”), geography (e.g., subclades “c”, and “k”), or basic chromosome number (subclades “d” and “k”) and much nomenclatural change. For all other characters used in the traditional classification of the Streptocarpinae exceptions exist (e.g., *Str. thysanotus* does not have verruculose seeds, despite its placement in Clade I, and similar exceptions exist in subclade “j” and “l”). For growth form and floral form, exceptions exist in 9 out of the 12 subclades. Furthermore, the existence of morphologically intermediate species, such as *Str. semijunctus* B.L.Burt, *Str. stenosepalus* B.L.Burt or *Str. tsimihetorum* Humbert, would, without additional data, only allow an uncertain or no generic placement, further destabilizing the classification. The 12-genus approach would thus raise the level of uncertainty in the generic placement of new species, that has caused the misplacement of species in genera among the Chinese Gesneriaceae, a situation that was resolved by enlarging genera such as *Oreocharis* or *Petrocodon* along phylogenetic boundaries and their redefinition using synapomorphies (Möller & al., 2011b; Weber & al., 2011b). Finally, the uncertainty of a phylogenetic placement of species such as *Str. exsertus* and *Str. capuronii*, and the insufficient knowledge of the morphology and affinities of another seven species would result in unplaced species at the genus level. Their existence in a taxonomic limbo is not desirable.
3. Establishing two genera divided along Clade I and Clade II species. The only clear synapomorphy for such a division would be the basic chromosome number.
4. Sinking the genera with non-twisted fruits into *Streptocarpus*. This would result in a single genus, *Streptocarpus*, encompassing all Afro-Malagasy species with two subgenera.

Nomenclatural considerations. — The alternatives of subdividing the Streptocarpinae have different nomenclatural consequences. In option 3, the two genera would comprise Clade I, hitherto subg. *Streptocarpella* and *Saintpaulia*, and Clade II, species of the former subg. *Streptocarpus* including the generic type *Str. rexii*. The oldest genus name in Clade I is *Acanthonema* (Hooker, 1862), and this name would have to be used as a genus name for this clade under the *International*

Code of Nomenclature (ICN, McNeill & al., 2012). However, this is a small genus with two species, and would require 63 new combinations to accommodate the remaining species in this genus. For the horticulturally important name *Saintpaulia* to be used, a proposal to conserve this name over *Acanthonema* (and any other older genus names) would be required. An argument for conserving *Saintpaulia* could be the fact that some species placed in subg. *Streptocarpella* by Hilliard & Burt (1971), group (i), do resemble *Saintpaulia* very closely in vegetative habit, and that some *Saintpaulia* species of basal lineages have prominent internodes and erect habit, and decussate leaf arrangement (e.g., Fig. 7H, see also below). The globose-ovoid non-twisted capsules of derived *Saintpaulia* species occur also in *Acanthonema*, further blurring the morphological boundaries between *Saintpaulia* s.str. and other taxa in Clade I.

The single-genus solution, *Streptocarpus*, in option 4, could contain two subgenera, *Streptocarpus* and *Streptocarpella*, with expanded circumscriptions, and several sections, one to accommodate *Saintpaulia*. *Saintpaulia* has a single synapomorphy in the tubeless flat corolla to support this section. Of all the above options, this would keep the morphological concept of *Saintpaulia* most intact, though at the rank of section. The plants are of significant horticultural importance, and the name well established in the trade and the public. The retention of the name at section rank would enable it to be used in colloquial terms. The option of a single genus *Streptocarpus* requires the fewest name changes, and provides a phylogenetic-taxonomic framework across the genus with sufficient support at the infrageneric level and we propose this option in our classification.

Subdivision in *Streptocarpus*. — Fritsch (1894: 151) recognized three unranked groups in *Streptocarpus*, which Engler (1921) later established as sections, i.e., sect. *Unifoliati*, sect. *Rosulati* and sect. *Caulescentes*, the last of which Fritsch (1904: 158) raised to subg. *Streptocarpella* and combined the former two into subg. *Eustreptocarpus* (now correctly *Streptocarpus*, Art. 22 of the ICN, McNeill & al., 2012). Fritsch established subg. *Streptocarpella* to comprise herbaceous caulescent species, while in subg. *Streptocarpus* he included the unifoliolate and rosulate species known at the time. Hilliard & Burt (1971) expanded the concept to accommodate some Madagascan groups of species that did not fit well into either subgenus. Not having seen nor studied these species in the field, they included the shrubby species (group iii) and species with leaves in a basal rosette with long petioles (group i) in subg. *Streptocarpella*, and those with leaves in basal rosettes with veins ascending from the leaf base (group ii) in subg. *Streptocarpus* although they admitted to place these taxa for convenience rather than conviction until more data became available. With the additional information now available, we retain a subdivision into two subgenera and establish a separate section for each of the three Madagascan groups, but with the shrubby species falling into subg. *Streptocarpus*. This is supported by cytology and perhaps leaf base morphology, which is attenuate in subg. *Streptocarpus* and cordate in subg. *Streptocarpella* (Fig. 5A–J, M–P). The only further subdivision within subgenera was attempted by Engler (1921) for subg. *Streptocarpella*, who recognized seven

“Gruppen” which Hilliard & Burt (1971) interpreted as series. None of Engler’s Gruppen form a natural group and we refrain from using these as section names. New sections have been established here to accommodate the diversity now known in the genus. A key to the subgenera and sections is provided.

In the new circumscription, the genus *Streptocarpus* includes all species of *Acanthonema*, *Colpogyne*, *Hovanella*, *Linnaeopsis*, *Nodonema*, *Saintpaulia*, *Schizoboea* and *Trachystigma*. These names are cited as synonyms under the section into which their types fall. Some of the former genus names were adopted as sectional names for nomenclatural stability (e.g., *Colpogyne*, *Saintpaulia*), some had to be used for priority reasons (e.g., *Hova*, *Schizoboea*, *Trachystigma*). Out of the 176 species in the newly defined *Streptocarpus* only 9 could not be placed to section because of uncertainties in their phylogenetic placement or insufficient knowledge of their morphology. A table is provided listing the species in their respective sections (Appendix 3).

■ TAXONOMY AND NOMENCLATURE

Key to subgenera and sections in *Streptocarpus*

- 1. $x = 15$ chromosomes; herbaceous caulescents with short phyllomorphic phase of petiolated macrocotyledon (Fig. 6G), or unifoliate with non-twisted fruits subg. *Streptocarpella* — 2
- 1. $x = 16$ chromosomes; woody caulescents, or herbaceous caulescents with extended phyllomorphic phase of apetalated macrocotyledon (Fig. 6F), or unifoliate and rosulates with twisted fruits subg. *Streptocarpus* — 8

Streptocarpus subg. *Streptocarpella* (includes *Acanthonema*, *Hovanella*, *Saintpaulia*, *Schizoboea*, *Trachystigma*)

- 2. Unifoliate with fruits not twisted, or facultative unifoliate with twisted fruits sect. *Trachystigma* (“a”)
- 2. Rosette or caulescent herbs, fruits twisted or not twisted 3
- 3. Rosette herbs, or herbs with distinct internodes, corollas flat 4
- 3. Caulescent herbs with tubular corollas 5
- 4. Rosette or herbs with distinct internodes, corollas flat, fruits not twisted sect. *Saintpaulia* (“g”)
- 4. Rosette herbs, corollas tubular, fruits twisted sect. *Parasaintpaulia* (“b”)
- 5. Endemic to Madagascar and the Comoro Islands sect. *Hova* (“c”)
- 5. Endemic to Africa 6
- 6. Small-flowered (≤ 10 mm corolla tube length), often with forward directed lip and reduced upper lip sect. *Schizoboea* (“d”)
- 6. Larger-flowered (≥ 15 mm corolla tube length) 7
- 7. Succulent leaves with thick subepidermis, flowers not \pm personate sect. *Carnosifolii* (“e”)
- 7. Leaves thinner, flowers \pm personate sect. *Caulescentes* (“f”)

Streptocarpus subg. *Streptocarpus* (includes the former *Colpogyne*, *Linnaeopsis*, *Nodonema*)

- 8. Unifoliate and rosulates, lateral leaf veins ascending from the base of the lamina sect. *Plantaginei* (“j”)
- 8. Shrubs, unifoliate, rosulate and caulescent herbs, lateral leaf veins spreading at right angle to midrib 9
- 9. Shrubs, anthers not coherent, some species with sclereids sect. *Lignostreptocarpus* (“h”)
- 9. Unifoliate, rosulate and caulescent herbs, anthers coherent, sclereids absent 10
- 10. Unifoliate and rosulate, leaves with very dense and long indumentum sect. *Colpogyne* (“i”)
- 10. Unifoliate, rosulate and caulescent herbs, leaves glabrous or slightly hairy 11
- 11. Caulescent herbs, with erect or rhizomatous stems, leaves alternate or opposite, leaves without abscission zones, seeds verruculose sect. *Protostreptocarpus* (“k”)
- 11. Unifoliate or rosulate, leaves with abscission zones, seeds mostly reticulate sect. *Streptocarpus* (“l”)

Streptocarpus Lindl. in Bot. Reg. 14: t. 1173. 1828 – Type: *Streptocarpus rexii* (Bowie ex Hook.) Lindl. in Bot. Reg. 14: t. 1173. 1828 \equiv *Didymocarpus rexii* Bowie ex Hook., Exot. Fl. 3: 227. 1827.

Streptocarpus subg. *Streptocarpella* Fritsch, Keimpfl. Gesneriaceen: 158. 1904 \equiv *Streptocarpus* [unranked] *Caulescentes* Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 151. 1894 (“§ 1.”) – Type (designated by Burt in Notes Roy. Bot. Gard. Edinburgh 21: 208. 1954): *Streptocarpus caulescens* Vatke in Linnaea 43: 323. 1882.
See Figs. 5A–E, 6A–H, 7A–H.

Description. – In its broader circumscription, this subgenus comprises plants with $x = 15$ chromosomes and verruculose seed ornamentation, and includes forms with the following vegetative character combinations, (a) herbaceous caulescent with decussate leaves at least in the seedling stage (for *Saintpaulia* see below) with a distinctly short phyllomorphic phase of the macrocotyledon, and strongly petiolated macrocotyledon that is seldom larger than the subsequent cauline leaves (Hilliard & Burt, 1971: 118) (Fig. 8G), and (b) unifoliate with non-twisted fruits.

Notes. – This subgenus contains ca. 65 taxa in 49 species and includes the former genera *Acanthonema*, *Hovanella*, *Saintpaulia*, *Schizoboea* and *Trachystigma* (Clade I in Fig. 2A). The fruit type in this subgenus is diverse, due to the inclusion of the five genera with non-twisted fruits. *Acanthonema* and *Saintpaulia* have globose or ovoid fruits, while *Hovanella*, *Schizoboea* and *Trachystigma* have slender cylindrical fruits. The spiral leaf arrangement of leaves in mature *Saintpaulia* species in the *Sa. ionantha* complex is the result of a shift in leaf position and disjunct leaf development in a pair, superficially resembling anisophylly. Fritsch (1904: fig. 1) observed that seedlings of *Sa. ionantha* H.Wendl. develop their first few pairs of leaves in decussate arrangement and only later, due to initial bending of the long petioles and shifts of the insertion

points of leaves of a pair, the phyllotaxis becomes spiral. Hilliard & Burt (1971) found a clear separation between their aculescent *Streptocarpus* ($2n = 32$) and caulescent *Streptocarpella* ($2n = 30$) species, but at that time chromosome counts for the herbaceous caulescent *Str. schliebenii* ($2n = 32$; Milne, 1975) and woody caulescent species (i.e., *Str. papangae* Humbert and *Str. suffruticosus* Humbert both $2n = 32$; Jong & Möller, 2000) were unavailable. So far, basic chromosome numbers for species of this clade representing subg. *Streptocarpella* are consistent with $x = 15$ (24 species out of 49 now included). The seed ornamentation is known for 38 taxa out of 65 in this subgenus. All but three have verruculose seeds. Reticulate seed testa cell surfaces were reported for *Acanthonema strigosum* Hook.f. and *Sa. inconspicua*. The report for *A. strigosum* (Beaufort-Murphy, 1983: 287, based on Mann 1948, P) is, on closer inspection of the published SEM image, perhaps based on the analysis of an immature seed, since the specimen appears shrivelled and not fully formed. Specimens observed in the MNHN herbarium in Paris (*R. Letouzey 12925*) clearly showed verruculose seed ornamentation for *A. strigosum*. The report for *Sa. inconspicua* (Beaufort-Murphy, 1983: pl. 20F) came from a herbarium specimen which we have now seen (*Pócs T. & al. 6296*, E); the testa sculpturing in Beaufort-Murphy (1983) is more like that found in seeds of other genera, such as certain *Cyrtandra* J.R.Forst. & G.Forst. (Beaufort-Murphy, 1983: pls. 6–9; Mühlbauer & Kiehn, 1997) or *Didissandra* C.B.Clark (e.g., *D. elongata* (Jack) C.B.Clark or *D. sprengelii* C.B.Clark; Beaufort-Murphy, 1983: pl. 18I; Sontag & Weber, 1998). However, on reexamining seeds of *Pócs T. & al. 6296*, we find that the seeds, while more strongly ribbed than other *Saintpaulia* seeds clearly possess verruculose seed testa cells. The only species possessing seeds with a confirmed absence of a bladder-like protrusion or papilla is *Str. thysanotus*. The phylomorphic phase of seedlings of herbaceous caulescent *Streptocarpus* subg. *Streptocarpella* species is decidedly short and their macrocotyledon cordate and strongly petiolated (Fig. 8G; Jong, 1970; Hilliard & Burt, 1971).

Streptocarpus* sect. *Trachystigma (C.B.Clark) Mich.Möller & Nishii, **comb. nov.** \equiv *Trachystigma* C.B.Clark in Candolle & Candolle, Monogr. Phan. 5: 131. 1883 \equiv *Roettlera* sect. *Trachystigma* (C.B.Clark) Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 148. 1894 – Type: *Trachystigma mannii* C.B.Clark in Candolle & Candolle, Monogr. Phan. 5: 131. 1883 \equiv *Roettlera mannii* (C.B.Clark) Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 148. 1894 \equiv *Streptocarpus mannii* (C.B.Clark) Mich.Möller & Nishii (see below). — Figs. 6A, 7A.
 \equiv *Acanthonema* Hook.f. in Bot. Mag. 88: t. 5339. 1862 – Type: *Acanthonema strigosum* Hook.f. in Bot. Mag. 88: t. 5339. 1862 \equiv *Streptocarpus strigosus* (Hook.f.) Nishii & Mich.Möller (see below).
 \equiv *Streptocarpus* [unranked] *Brevilobati* Engl. in Bot. Jahrb. Syst. 57: 210. 1921 (“§”) – Type (designated by Hilliard & Burt, Streptocarpus: 120. 1971): *Streptocarpus princeps* Mildbr. & Engl. in Bot. Jahrb. Syst. 57: 211. 1921 (\equiv *S. nobilis* C.B.Clark).

Description. – Facultative unifoliate caulescents with decussate leaf arrangement and twisted fruits, and unifoliate with non-twisted fruits. Seeds verruculose. Distributed in western tropical Africa.

Notes. – Subclade “a” (Fig. 2A). Contains five species, including *Str. nobilis*, which become unifoliate under unfavorable conditions such as short day length (Lawrence, 1943). Other members of the section are *Acanthonema strigosum*, *A. diandrum* (Engl.) B.L.Burt, and *Trachystigma mannii*, three obligate unifoliate species. It appears that in these plants the transition to the unifoliate state is irreversible, as opposed to *Str. nobilis*, and the plants only produce one macrocotyledon as the sole photosynthetic organ. *Streptocarpus nobilis* shares a relatively large infundibuliform dark purple corolla with *Acanthonema strigosum*. There are characters that differentiate *Acanthonema* and *Trachystigma* from the former delimitation of *Streptocarpus*, not least the non-twisted fruits of both genera, but also the ovoid-globose shape of the capsule, flattened toothed filaments, unilateral disc and bilocular ovary for *Acanthonema*, and the cylindrical capsule opening along the median line of the upper carpel for *Trachystigma* (Hilliard & Burt, 1971: 115; Weber & Skog, 2007–). However, they share characters with *Streptocarpus* such as being unifoliate, having an acropetal succession of inflorescences on the leaves, two coherent fertile stamens in anterior position, and unilocular ovaries (*Trachystigma* only) that place them firmly in the genus. Interestingly, *Acanthonema* and *Trachystigma* share toothed filaments, and the phylogenetic work retrieves them as strongly supported sister taxa. This suggests that the toothed filament has evolved prior to a split between the two taxa, and that characters pertaining to the ovary and fruit morphology have evolved more rapidly. This section is essentially of western tropical African origin (Cameroon, Fernando Po Island off the west coast of Cameroon), with *Str. nobilis* the most widespread (from Gambia, through Cameroon to Central African Republic).

Streptocarpus diandra (Engl.) Nishii & Mich.Möller, **comb. nov.** \equiv *Carolofritschia diandra* Engl. in Bot. Jahrb. Syst. 26: 362. 1899 \equiv *Acanthonema diandrum* (Engl.) B.L.Burt in Bull. Mus. Natl. Hist. Nat., B, Adansonia, ser. 4, 3(4): 416. 1982 (“1981”) – Syntypes: CAMEROUN. Um Lolodorf, März 1895, *Staudt 118* (B, destr.; BM barcode BM001122850!); zwischen Lolodorf und Carantschiamasdorf, Mai 1907, *Zenker 1381* (B, destr.; BM barcode BM000984380!, E barcode E00632283!, P barcode P00057466!).

Streptocarpus mannii (C.B.Clark) Nishii & Mich.Möller, **comb. nov.** \equiv *Trachystigma mannii* C.B.Clark in Candolle & Candolle, Monogr. Phan. 5: 131, pl. 14. 1883 \equiv *Roettlera mannii* (C.B.Clark) Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 148. 1894 \equiv *Didymocarpus mannii* (C.B.Clark) Wonisch in Sitzungsber. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Cl., Abt. 1, 118: 483. 1909 – Holotype: Africa occidentalis tropica. Sinus Corisco, in montibus Sierra del Crystal, *Mann 1682* (K barcodes K000378484! & K000378485!).

Streptocarpus strigosus (Hook.f.) Nishii & Mich.Möller, **comb. nov.** \equiv *Acanthonema strigosum* Hook.f. in Bot. Mag. 88: pl. 5339. 1862 – **Neotype (designated here):** CAMEROUN, Fernando Po, epiphyte on rocks and trees, corolla dark purple, calyx brown[red], 1–2000 feet, Nov 1860, Mann 569 (K barcode K000378483!).

Note. – In the protologue, Hooker (1862) refers only to “living plants were sent home by M. Gustav Mann from an elevation of 4000–5000 feet in the plains of Fernando Po, where it grows on rocks and epiphytically on trees.”

Streptocarpus sect. *Parasaintpaulia* Mich.Möller & Nishii, **sect. nov.** – Type: *Streptocarpus beampingaratrensis* Humbert in Adansonia, sér. 2, 7: 287. 1967. — Figs. 6B, 7B.

Description. – Leaves in basal rosette, long petioles sharply marked off from the (sub-)orbicular blades, axillary inflorescence, small short wide corollas and relatively short spirally twisted fruits. Seeds verruculose. Distributed in Madagascar.

Notes. – Subclade “b” (Fig. 2A). Six taxa in three species. The section is named for their similarity in vegetative morphology with African *Saintpaulia*. This section corresponds to group (i) of Hilliard & Burtt (1971), for which they recognized a close affinity to the African *Saintpaulia*, but which can be distinguished easily by their tubular corolla and twisted fruits. A section that includes polyploids, all with a basic number of $x = 15$ (Fig. 2).

Streptocarpus sect. *Hova* (C.B.Clarke) Mich.Möller & Nishii, **comb. nov.** \equiv *Didymocarpus* sect. *Hova* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 5: 108. 1883 \equiv *Hovanella* A.Weber & B.L.Burtt in Beitr. Biol. Pflanzen 70: 333. 1998 – Type: *Didymocarpus madagascariensis* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 5: 108. 1883 \equiv *Streptocarpus madagascariensis* (C.B.Clarke) Christenh. in Phytotaxa 46: 8. 2012. — Figs. 6C, 7C.

\equiv *Streptocarpus* [unranked] *Longiflori* Engl. in Bot. Jahrb. Syst. 57: 216. 1921 (“§”) – Type (designated by Hilliard & Burtt, *Streptocarpus*: 120. 1971): *Streptocarpus hilsenbergii* R.Br. in Bennett, Pl. Jav. Rar.: 119. 1840.

Description. – Herbaceous caulescent plants with decussate leaves, axillary inflorescences, mostly with small, short-tubed pouch flowers. Seeds verruculose. Distributed in Madagascar.

Notes. – Subclade “c” (Fig. 2A). Seventeen taxa in 13 species plus 4 varieties. Species in this section have the strong tendency to possess small corollas (mostly 5–10 mm) with short tubes (4–8 mm), which are the ancestral type in the genus (Hughes & al., 2006). The exception is *Str. hilsenbergii* R.Br. with the largest flower of all Madagascan and Comores Gesneriaceae, although within this species flower size varies greatly (25–45 mm corollas with 20–30 mm tubes), indicating an inherent flexibility in these characteristics. Its phylogenetic position in the middle of this section indicates an isolated co-speciation event with a long-tongued pollinator (Potgieter & Edwards, 2005). Section *Hova* includes the erstwhile genus *Hovanella*. The main character distinguishing it from *Streptocarpus* s.str. is the non-twisted fruit. The

two species included here have distinctive fruit orientations and dehiscence. In *H. madagascariensis* (C.B.Clarke) A.Weber & B.L.Burtt they are plagiocarpic, held horizontally at a \pm right angle to the pedicel and dehiscence follicle-like, only along the dorsal suture, whereas in *H. vestita* (Baker) A.Weber & B.L.Burtt they are in line with the pedicel and dehiscence along the dorsal and ventral suture. It is no surprise to find that they were not sister species in the phylogenetic trees, and that the losses of fruit twist in *Hovanella* represent parallel, independent events. Seven chromosome counts are available for species in this section, most with $2n = 30$ (Möller & Pullan, 2015–). The one of $2n = 28$ by Kiehn for *Hovanella madagascariensis* should be treated with caution since the count is based on field-fixed flower bud material. Preliminary counts exist for two further taxa, *H. vestita* and a putative new species, with $2n = 30$ (Fig. 5M–P).

Streptocarpus sect. *Schizoboea* (Fritsch) Mich.Möller & Nishii, **comb. nov.** \equiv *Roettlera* sect. *Schizoboea* Fritsch in Engler & Prantl, Nat. Pflanzenfam. Nachtr. 1: 300. 1897 \equiv *Schizoboea* (Fritsch) B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 33: 266. 1974 – Type: *Didymocarpus kamerunensis* Engl. in Bot. Jahrb. Syst. 18: 79. 1894 \equiv *Schizoboea kamerunensis* (Engl.) B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 33: 266. 1974 \equiv *Streptocarpus kamerunensis* (Engl.) Christenh. in Phytotaxa 46: 7. 2012. — Figs. 6D, 7D. \equiv *Streptocarpus* [unranked] *Ventricosi* Engl. in Bot. Jahrb. Syst. 57: 210. 1921 (“§”) – Type: *Streptocarpus gonjaensis* Engl. in Bot. Jahrb. Syst. 57: 210. 1921. \equiv *Streptocarpus* [unranked] *Elongati* Engl. in Bot. Jahrb. Syst. 57: 213. 1921 (“§”) – Type (Art. 22.6): *Streptocarpus elongatus* Engl. in Bot. Jahrb. Syst. 18: 76. 1894.

Description. – Short-lived herbaceous caulescent plants with decussate leaf arrangement, with mostly long-pedunculate axillary inflorescences and small, strongly bilabiate flowers. Distributed in tropical Africa.

Notes. – Subclade “d” (Fig. 2A). A section with six species, which forms a link between species in East and West Africa (Hilliard & Burtt, 1975). They are characterized by a forward directed lower lip and a reduced upper lip of the corolla, the labellanthus-type (Fig. 7D). They are annuals with a sappy stem and long-pedunculate axillary inflorescences. The section includes the erstwhile genus *Schizoboea*. Characters shared between this genus and *Streptocarpus* subg. *Streptocarpella* include axillary few-flowered cymes, small corolla, two fertile stamens in anterior position (Burtt, 1974), and verruculose seeds (Beaufort-Murphy, 1983). Initially described in *Didymocarpus* (Fritsch, 1894), on the basis of the straggling creeping habit and subglabrous entire leaves, Burtt (1974) suggested that the true affinity of the erstwhile *Schizoboea* does not lie with *Didymocarpus* Wall., but with the little-known African *Saintpaulia inconspicua*, and in that he was not far off the mark. Our molecular data suggest that both *Saintpaulia* and *Schizoboea* have evolved from within *Streptocarpus* and belong in subg. *Streptocarpella* (Fig. 2). *Schizoboea* is sister to *Str. elongatus* with which it shares a bilabiate white corolla. The straight, sometimes slightly falcate capsule, dehiscing into 4 valves and

the lateral, sclerified vascular bundles, are seemingly another isolated evolutionary event that *Streptocarpus* is prone to, but is by no means unique in the Gesneriaceae.

Streptocarpus* sect. *Carnosifolii Mich.Möller & Nishii, **sect. nov.** – Type: *Streptocarpus saxorum* Engl. in Bot. Jahrb. Syst. 19: 154. 1894 (“1895”). — Figs. 6E, 7E.

– *Streptocarpus* [unranked] *Pauciflori* Engl. in Bot. Jahrb. Syst. 57: 216. 1921 (“§”) – Type: *Streptocarpus saxorum* Engl. in Bot. Jahrb. Syst. 57: 216. 1921.

Description. – Long-lived caulescent herbs or shrubs with a sometimes woody stem base and succulent decussate leaves, axillary inflorescences and twisted fruits. Seeds verruculose. Distributed in tropical East Africa.

Notes. – Subclade “e” (Fig. 2A). A group of six species with a distribution in Tanzania and Kenya, usually with large corollas, but very divergent floral types, ranging from keyhole flowers in *Str. saxorum* (Fig. 6E), strongly bilabiate flowers in *Str. stomandrus*, to almost campanulate corollas in *Str. kirkii*. The species are often long-lived plants that possess relatively fleshy leaves with an extremely thick hypodermis of up to seven layers in *Str. saxorum* (Sahasrabudhe, 1970).

Notes. – Subclade “e” (Fig. 2A). A group of six species with a distribution in Tanzania and Kenya, usually with large corollas, but very divergent floral types, ranging from keyhole flowers in *Str. saxorum* (Fig. 6E), strongly bilabiate flowers in *Str. stomandrus*, to almost campanulate corollas in *Str. kirkii*. The species are often long-lived plants that possess relatively fleshy leaves with an extremely thick hypodermis of up to seven layers in *Str. saxorum* (Sahasrabudhe, 1970).

Streptocarpus* sect. *Caulescentes (Fritsch) Engl. in Bot. Jahrb. Syst. 57: 203. 1921 ≡ *Streptocarpus* [unranked] *Caulescentes* Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 151. 1894 (“§ 1.”) ≡ *Streptocarpus* [unranked] *Porrectilobati* Engl. in Bot. Jahrb. Syst. 57: 214. 1921 (“§”) – Type (designated by Hilliard & Burtt, *Streptocarpus*: 120. 1971): *Streptocarpus caulescens* Vatke in Linnaea 43: 323. 1882. — Figs. 6F, 7F.

Description. – Herbaceous caulescent plants with decussate leaves, axillary inflorescences, enantiostyly (the deflection of the style either to the left or right side of the floral axis) with personate corollas and twisted fruits. Seeds verruculose. Distributed in tropical East Africa.

Notes. – Subclade “f” (Fig. 2A). The species in this section were placed in “Gruppe” *Porrectilobati* by Engler (1921), but for reasons of priority the name *Caulescentes* has to be used (McNeill & al., 2012). The six species in this section have a very similar corolla form, in which the bend of the lower lip more (*Str. holstii* Engl.) or less (*Str. pallidiflorus* C.B.Clarke, *Str. inflatus* B.L.Burtt) closes the corolla tube (Fig. 6F).

Notes. – Subclade “f” (Fig. 2A). The species in this section were placed in “Gruppe” *Porrectilobati* by Engler (1921), but for reasons of priority the name *Caulescentes* has to be used (McNeill & al., 2012). The six species in this section have a very similar corolla form, in which the bend of the lower lip more (*Str. holstii* Engl.) or less (*Str. pallidiflorus* C.B.Clarke, *Str. inflatus* B.L.Burtt) closes the corolla tube (Fig. 6F).

Streptocarpus* sect. *Saintpaulia (H.Wendl.) Mich.Möller & Haston, **comb. & stat. nov.** ≡ *Saintpaulia* H.Wendl. in Gartenflora 42: 321, pl. 1391, fig. 66. 1893 – Type: *Saintpaulia ionantha* H.Wendl. in Gartenflora 42: 321. 1893 ≡ *Petocosmea ionantha* (H.Wendl.) Rodigas in Ill. Hort. 42: 108. 1895 ≡ *Streptocarpus ionanthus* (H.Wendl.) Christenh. in Phytotaxa 46: 6. 2012. — Figs. 6G–H, 7G–H.

Description. – Herbaceous caulescent plants with leaves in a basal rosette (opposite as seedlings), or decussate with distinct internodes, long petioles, axillary inflorescences, flower with flat corollas and enantiostyly. Fruits ovoid to linear-cylindric, not twisted. Seeds verruculose. Distributed in Tropical East Africa.

Description. – Herbaceous caulescent plants with leaves in a basal rosette (opposite as seedlings), or decussate with distinct internodes, long petioles, axillary inflorescences, flower with flat corollas and enantiostyly. Fruits ovoid to linear-cylindric, not twisted. Seeds verruculose. Distributed in Tropical East Africa.

Notes. – Subclade “g” (Fig. 2A). This section represents the former genus *Saintpaulia* which has received various treatments resulting in 21 (Burtt, 1958a, 1964), 8 (Darbyshire, 2006) or 6 species (Christenhusz, 2012). Our phylogenetic analysis revealed 10 distinct genetic entities which we treat as species in sect. *Saintpaulia*. *Saintpaulia ulugurensis* Haston was previously sunk into *Sa. ionantha* subsp. *grandifolia* (B.L.Burtt) I.Darbysh. (Darbyshire, 2006) (= *Str. ionanthus* subsp. *grandifolius* (B.L.Burtt) Christenh.; Christenhusz, 2012), although they are distant both phylogenetically (Figs. 2A, 4) and geographically. Morphologically, they can be differentiated by the decussate leaf arrangement, distinct internodes and bicolored flowers of the former (Haston, 2009a), and spiral leaf arrangement, rosette habit and deep violet flowers of the latter (Burtt, 1958a). Consequently, we give it species status in *Streptocarpus*. *Saintpaulia watkinsii* was reduced to *Str. afroviola* subsp. *watkinsii* (Haston) Christenh. (Christenhusz, 2012). However, it is distinct from *Str. afroviola* in having violet-blue colouration on the lower lobes of the otherwise white flower whereas the flowers of *Str. afroviola* are white with the two upper lobes mauve to blue. In addition, the upper leaf surface of *Str. afroviola* has sparse, long, erect to arching hairs, rather than the more dense, short, appressed hairs of *Str. watkinsii*. Moreover, the molecular data suggest that its phylogenetic affinity is with *Str. inconspicuus* (Fig. 4), from which it differs by the short appressed hairs on the upper leaf surface as opposed to the nearly glabrous upper leaf surfaces of *Str. inconspicuus* (B.L.Burtt) Christenh. (Burtt, 1958a; Haston, 2009b). We raised the subspecies to species rank in *Streptocarpus*. *Saintpaulia brevopilosa* was previously included in *Sa. ionantha* subsp. *velutina* (B.L.Burtt) I.Darbysh. (Darbyshire, 2006) (= *Str. ionanthus* subsp. *velutinus* (B.L.Burtt) Christenh.; Christenhusz, 2012), although the two species are geographically and phylogenetically distant (Fig. 4). They also differ in indumentum and leaf texture from each other (Burtt, 1958a, 1964), thus we raise them to species level in *Streptocarpus*. *Saintpaulia nitida* was included within *Sa. ionantha* as *Sa. ionantha* subsp. *nitida* (B.L.Burtt) I.Darbysh. (Darbyshire, 2006) (= *Str. ionanthus* subsp. *nitidus* (B.L.Burtt) Christenh.; Christenhusz, 2012). The two species occur in separate mountain ranges, at different altitudes and are phylogenetically distant (Fig. 4), and the former has short appressed hairs which are not present in the latter (Burtt, 1958a). We therefore raise *Sa. nitida* to species rank as *Str. nitidus* in *Streptocarpus* (see below). The oversimplified taxon boundaries in Darbyshire (2006) and Christenhusz (2012) have led to unforeseen consequences in a recent biogeographic study of *Saintpaulia* (Dimitrov & al., 2012), extending the distribution of *Sa. ionantha* across the entire range of *Saintpaulia* skipping only the Uluguru Mts., and resulting in individual taxa such as *Sa. ionantha* subsp. *nitida* or *Sa. ionantha* subsp. *velutina* each having disjunct distributions in the Nguru Mts. and East Usambara Mts. Given published molecular data, it is more likely that the plants designated cf. subsp. *nitida* and cf. subsp. *velutina* in Lindqvist & Albert (1999) belong to new taxa. Previous studies (Möller & Cronk, 1997b; Lindqvist & Albert, 2001; Dimitrov & al., 2012) and the results presented here show that there is no strongly supported phylogenetic structure and

discernible taxon monophyly, except perhaps for *Sa. rupicola*, in the *Sa. ionantha* complex (= *Str. ionanthus* complex in Fig. 4). Putative ancestral characters of growth form and leaf indumentum are very homogeneous within the mountain ranges (Fig. 4), but are mixed and combined (e.g., leaf indumentum states) in the *Sa. ionantha* complex, suggestive of past hybridization events. This would explain the mixed phylogenetic signals from 5S NTS nrDNA spacer data and the base polymorphisms detected in the ITS data (Möller & Cronk, 1997a, present study). In such a hybridization scenario, morphological heterogeneity would have resulted and taxon boundaries would have been blurred, perhaps pointing to a reconsideration of the need for the diverse subspecies and varieties in the *Sa. ionantha* complex.

Streptocarpus brevipilosus (B.L.Burt) Mich.Möller & Haston, **comb. nov.** ≡ *Saintpaulia brevipilosa* B.L.Burt in Notes Roy. Bot. Gard. Edinburgh 25: 193. 1964 – Holotype: TANZANIA: Morogoro Dist., Nguru Mts., Lulaga, *Punter ref.* 59/4350, cultivated at RBG Edinburgh, C.3827 (E barcode E00009668!).

Streptocarpus nitidus (B.L.Burt) Mich.Möller & Haston, **comb. nov.** ≡ *Saintpaulia nitida* B.L.Burt in Notes Roy. Bot. Gard. Edinburgh 22: 564. 1958 ≡ *Saintpaulia ionantha* subsp. *nitida* (B.L.Burt) I.Darbysh. in Beentje & Ghazanfar, Fl. Trop. E. Africa: 69. 2006 ≡ *Streptocarpus ionanthus* subsp. *nitidus* (B.L.Burt) Christenh. in Phytotaxa 46: 7. 2012 – Holotype: TANZANIA. Morogoro District: Nguru Mts., near Morogoro, Aug 1959, Harvey Cox ref. A, cultivated at RBG Edinburgh, C1557 (E sheet 1 barcode E00009655!, sheet 2 barcode E00009656!; isotypes: K barcode K000378659!, P barcode P00568966!).

Streptocarpus ulugurensis (Haston) Haston, **comb. nov.** ≡ *Saintpaulia ulugurensis* Haston in Bot. Mag. 26(3): 273 (–276, pl. 656, fig.). 2009 – Holotype: Cultivated at RBGE from wild material collected from Tanzania, Morogoro, Uluguru Mountains, *Haston 246* (NHT, n.v.; isotypes: E barcode E00708368!, K, n.v.).

Streptocarpus watkinsii (Haston) Haston, **comb. nov.** ≡ *Saintpaulia watkinsii* Haston in Bot. Mag. 26(3): 278 (277–280, pl. 657, fig. 1). 2009 ≡ *Streptocarpus afroviola* var. *watkinsii* (Haston) Christenh. in Phytotaxa 46: 6. 2012 – Holotype: TANZANIA. Morogoro, Uluguru Mts., *Haston 99* collected with *John Mejissa* (NHT, n.v.; isotype: E barcode E00201489!).

Streptocarpus* subg. *Streptocarpus [*Streptocarpus* subg. *Eustreptocarpus* Fritsch, Keimpfl. Gesneriaceen: 158. 1904, nom. illeg. (Art. 21.3 & 22.2)] – Type: *Streptocarpus rexii* (Bowie ex Hook.) Lindl. in Bot. Reg. 14: pl. 1173. 1828 ≡ *Didymocarpus rexii* Bowie ex Hook., Exot. Fl. 3: t. 227. 1827. . — Figs. 5F–J, 6I–O, 7I–L, 8A–J.

Description. – Species in this enlarged subgenus share a basic chromosome number of $x = 16$ (41 counts), and include

woody and herbaceous caulescents with decussate or alternate leaf arrangement, unifoliate and rosulate, with a long seedling phylomorphic phase and apetiolar macrocotyledons with attenuate bases (Fig. 8F) and mostly twisted fruits. It represents an extension of the subg. *Streptocarpus* concept of Hilliard & Burt (1971). While the subgenus clearly forms a separate clade with distinct subclades, delimitation of all sections by growth form alone (as in the woody Madagascan species for example), such as herbaceous caulescents, rosulate or unifoliate, is not possible, and supporting characters from seeds, leaves and flowers are required.

Notes. – This subgenus contains ca. 138 taxa in 119 species. Includes the former *Colpogyne*, *Linnaeopsis* and *Nodonema*. (Clade II in Fig. 2B).

Streptocarpus* sect. *Lignostreptocarpus Mich.Möller & Bellstedt, **sect. nov.** – Type: *Streptocarpus papangae* Humbert in Adansonia, sér. 2, 7: 293. 1967. — Figs. 6I, 7I.

Description. – Woody shrubs with decussate leaves, axillary inflorescences, small pouch flowers, short filaments arising at the base of the corolla with non-coherent anthers, seeds long and pointed at both ends and distinctly larger (0.9–1.2 mm) than in other species (0.3–0.7 mm; Jong & al., 2012). Distributed in Madagascar.

Notes. – Subclade “h” (Fig. 2B). Seven species with 10 taxa. This section is most readily defined by the extensive woodiness of the stems and is equivalent to group (iii) of Hilliard & Burt (1971). There is not necessarily a link between the peculiarly short filaments and the non-coherent anthers as species with coherent anthers can have short filaments, such as *Str. levis* in sect. *Hova* (Hilliard & Burt, 1971; Jong & al., 2012). Section *Lignostreptocarpus* is sister (with strong support) to the next section, a group of unifoliate and rosulate also from Madagascar. This again highlights the flexible morphology (in evolutionary terms) of *Streptocarpus*. The woody caulescents in sect. *Lignostreptocarpus* represent a break from the correlation between caulescence and basic chromosome number ($x = 15$) as previously described for subg. *Streptocarpella*. The two species for which chromosomes have been counted to date (*Str. papangae* and *Str. suffruticosus*) both have $2n = 32$ (Jong & Möller, 2000; Möller & Kiehn, 2004).

Streptocarpus* sect. *Colpogyne Mich.Möller & Bellstedt, **comb. & stat. nov.** ≡ *Colpogyne* B.L.Burt in Fl. Madagasc., Fam. 180: 150. 1971 – Type: *Colpogyne betsiliensis* (Humbert) B.L.Burt in Fl. Madagasc., Fam. 180: 150. 1971 ≡ *Streptocarpus betsiliensis* Humbert in Adansonia, sér. 2, 7: 289. 1967. — Figs. 6K, 7K–L.

Description. – Unifoliate and rosulate, leaves with dense, long, woolly indumentum, small flowers and deep invagination (*colpus*) in the ovary walls. Seeds verruculose. Distributed in Madagascar.

Notes. – Subclade “i” (Fig. 2B). A section with five species including the former genus *Colpogyne*. *Colpogyne* was initially included in *Streptocarpus* by Humbert (1971), but then established as a separate genus on the basis of its short and non-twisted fruits (Hilliard & Burt, 1971: 115). There are other

features that led to its exclusion from *Streptocarpus* such as the deep invagination in the ovary walls; however, this is also found in *Str. itremensis*, *Str. lanatus* and *Str. ibityensis* (Humbert, 1971: fig. IX), the latter a species which Hilliard & Burttt (1971) see as most similar in vegetative characters to *Colpogyne*, and it is indeed this species that is phylogenetically most closely related to *Colpogyne betsiliensis* (\equiv *Str. betsiliensis*), hence its inclusion in sect. *Colpogyne*. The straight fruit in *Str. betsiliensis* is another case of loss of fruit twist.

***Streptocarpus* sect. *Plantaginei* Mich.Möller & Bellstedt, sect.**

nov. – Type: *Streptocarpus hildebrandtii* Vatke in *Linnaea* 43: 324. 1882. — Figs. 6J, 7J.

Description. – Unifoliates and rosulates with leaves in a basal rosette, often attenuate at the base (petiole ill-defined), veins ascending from the base and branched. Distributed in Madagascar.

Notes. – Subclade “j” (Fig. 2B). This section includes 14 species and essentially represents group (ii) of Hilliard & Burttt (1971: 104). It includes a few species with less conspicuous ascending venation and petiolated leaves. It is morphologically the most complex group. This is also seen in the seed ornamentation of its members, being reticulate in most, but verruculose in *Str. brevistamineus* Humbert and *Str. lokohensis* Humbert. The occurrence of unifoliates and rosulates in this Madagascar subclade is similarly mixed. This highlights again, as previously observed by Fritsch (1904), Hilliard & Burttt (1971) and Möller & Cronk (2001a) for African members, that transitions between the two growth forms have occurred frequently. Intermediate forms also exist, such as *Str. hildebrandtii* with two similarly sized leaves (Fig. 7J), one representing the macrocotyledon, the other a true leaf (Humbert, 1971: fig. III–3). Interestingly, the three chromosome counts for members of this section all reveal polyploidy of the basic number $x = 16$, with *Str. perrierii* Humbert being tetraploid, *Str. variabilis* being hexaploid and *Str. hildebrandtii* octoploid (Möller & Pullan, 2015–).

***Streptocarpus* sect. *Protostreptocarpus* Mich.Möller & Bell-**

stedt, sect. nov. – Type: *Streptocarpus montanus* Oliv. in *Trans. Linn. Soc. London, Bot.* 2: 344. 1887. — Figs. 6L–M, 8A–G.

= *Linnaeopsis* Engl. in *Bot. Jahrb. Syst.* 28: 483. 1900 – Type: *Linnaeopsis heckmanniana* Engl. in *Bot. Jahrb. Syst.* 28: 483. 1900 \equiv *Streptocarpus heckmannianus* (Engl.) I.Darbysh., *Fl. Trop. E. Africa, Gesner.*: 33. 2006.

= *Nodonema* B.L.Burttt in *Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér.* 4, 3(4): 415. 1982 (“1981”) – Type: *Nodonema lineatum* B.L.Burttt in *Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér.* 4, 3(4): 416. 1982 (“1981”) \equiv *Streptocarpus lineatus* (B.L.Burttt) Mich.Möller & M.Hughes (see below).

Description. – A group of species of variable habit (rhizomatous perennial herbs, or caulescents with alternate or opposite leaves) with extended seedling phylomorphic phase. Small, more or less campanulate flowers. Seeds verruculose. Distributed in tropical Africa.

Notes. – Subclade “k” (Fig. 2B). A group of 10 taxa in 8 species with a narrow distribution in Kenya and Tanzania, and one outlier in Nigeria and Cameroon (*Nodonema lineatum*). The section includes a variety of vegetative forms and can be regarded as a transition from caulescents to acaulescents. It includes the previously recognized genera *Linnaeopsis* and *Nodonema*. The closeness of *Linnaeopsis* to *Streptocarpus* is emphasized by the tightly twisted fruits of one species, *Str. subscandens* (B.L.Burttt) I.Darbysh. (*L. subscandens* B.L.Burttt; Weigend, 2000). It had not been described in *Streptocarpus* since the specimens available for the description had no intact fruits (Burttt, 1958b). The alternate leaf arrangement, verruculose seeds, and inflorescences borne in series on the petiole of the former *Linnaeopsis* and *Nodonema* (Weigend, 2000) are all reminiscent of *Streptocarpus*, and with view to leaf arrangement, particularly of *Str. bullatus*. In fact this species was found to be the closest relative of the *Linnaeopsis* samples included here. Another strongly supported sister species pair found in sect. *Protostreptocarpus* comprises the morphologically very similar caulescents *Str. parensis* and *Str. schliebenii*. *Streptocarpus schliebenii* represents another break from the correlation of herbaceous caulescence and $x = 15$ found in subg. *Streptocarpella*. Morphologically, the two species can readily be distinguished from other species in subg. *Streptocarpella* by differences in seedling development. This includes a long lag phase of the plumule development during which the macrocotyledon continues to expand (Fig. 8F), by the activity of the basal meristem, similar to the well-studied rosulate *Str. rexii* (Jong, 1970; Nishii & al., 2010). *Streptocarpus montanus* represents a further step towards the typical rosulate morphotype, as represented by the type *Str. rexii*. It has $2n = 32$ chromosomes (Ratter & Milne, 1970), and, apart from the verruculose seeds, its leaf insertion is much looser. The “rhizome” only superficially resembles that of “typical” rosulates of sect. *Streptocarpus* (below) such as *Str. primulifolius* Gand., and differs by the fusion of the petiolodes (structures with functions of stem and petiole sensu Jong & Burttt, 1975) in their entirety to form the rhizome stock, whereas in *Str. primulifolius* it is only the bases of successive petiolodes that do so. The effect is that in *Str. montanus* old inflorescences remain attached to the rhizome and appear axillary in origin, similar to caulescent species (Hilliard & Burttt, 1971). *Nodonema* could not be included in our molecular analysis. The verruculose seeds (Weigend, 2000), pair-flowered axillary cymes, few-flowered cymes with small infundibuliform bilabiate white corollas, with purple lines in the throat and two fertile stamens in anterior position (Weber & Skog, 2007–), link the genus to *Streptocarpus*. The short, subglobose fruit may suggest a closer relationship with *Acanthonema* or *Saintpaulia*, but the rhizomatous habit with apparently alternate leaves does not occur in subg. *Streptocarpella*, and resembles *Str. montanus* in this section.

***Streptocarpus lineatus* (B.L.Burttt) Mich.Möller & M.Hughes, comb. nov.** \equiv *Nodonema lineatum* B.L.Burttt in *Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér.* 4, 3(4): 416. 1982 (“1981”) – Holotype: CAMEROUN. Crête du Nta Ali (1266 m),

entre cotes 1009 et 1202, 30 km SE Mamfe, *Letouzey 13873* (P barcode P00057467!; isotypes: E barcode E00632294!, P barcodes P00057468! & P00057469!, YA barcode 0032423, n.v.).

Streptocarpus* sect. *Streptocarpus – Type: *Didymocarpus rexii* Bowie ex Hook. in Exot. Fl. 3: pl. 227. 1827 ≡ *Streptocarpus rexii* (Bowie ex Hook.) Lindl. in Bot. Reg. 14: pl. 1173. 1828.

See Figs. 6N–O, 8H–J.

= *Streptocarpus* sect. *Rosulati* (Fritsch) Engl. in Bot. Jahrb. Syst. 57: 217. 1921 ≡ *Streptocarpus* [unranked] *Rosulati* Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 151. 1894 (“§ 2.”) – Type (designated by Burttt in Notes Roy. Bot. Gard. Edinburgh 21: 208. 1954): *Streptocarpus rexii* (Bowie ex Hook.) Lindl. in Bot. Reg. 14: pl. 1173. 1828.

= *Streptocarpus* sect. *Unifoliati* (Fritsch) Engl. in Bot. Jahrb. Syst. 57: 217. 1921 ≡ *Streptocarpus* [unranked] *Unifoliati* Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 151. 1894 (“§ 3.”) – Type (designated by Burttt in Notes Roy. Bot. Gard. Edinburgh 21: 208. 1954): *Streptocarpus polyanthus* Hook. in Bot. Mag. 81: pl. 4850. 1855.

Description. – Rosulate, plurifoliate and unifoliate herbs, with greatly extended seedling phyllocladous phase, the formation of abscission zones, and inflorescences usually at the base of the lamina. Seeds reticulate, with few exceptions. Distributed in Africa.

Notes. – Subclade “1” (Fig. 2B). The largest section with 85 species (99 taxa) and a distribution from Ethiopia in the north to the Western Cape Province in South Africa in the south. This section includes a wide range of floral forms and sizes with a trend of a north to south speciation pattern (Möller & Cronk, 2001b) and an accompanying increase in corolla size southwards (Hughes & al., 2006). Section *Streptocarpus* includes only acaulescent species, with the exceptions of *Str. decipiens* and *Str. fanniniae* Harv. ex C.B. Clarke which have unusual growth forms. *Streptocarpus fanniniae* is branching and has extremely long petiolodes, but does not possess a shoot apical meristem or axis and is acaulescent (Jong & Burttt, 1975). *Streptocarpus decipiens* was initially considered to belong to subg. *Streptocarpella* by Hilliard & Burttt (1971: 227), because of the axillary inflorescences and verruculose seeds. However, basal leaves, presence of abscission zone, origin of the “stem” from the base of the petiolode and attenuate leaf base place it in sect. *Streptocarpus*. Abscission zones are thus far only reported for members of sect. *Streptocarpus* and have not been observed in any of the Madagascan acaulescent species (Hilliard & Burttt, 1971: 118; M. Möller, pers. obs.), here placed in sect. *Plantaginei* and sect. *Colpogyne*. Within sect. *Streptocarpus*, a clear evolutionary trend from verruculose to reticulate seeds is observed. Only a few species on early-branching lineages in sect. *Streptocarpus* possess verruculose seed ornamentation, such as *Str. nimbicola*, *Str. hirtinervis*, *Str. decipiens*, and *Str. galpinii* (a few populations only). *Streptocarpus dunnii*, in a more nested position, also has verruculose seeds. Growth form and other characters (e.g., presence of abscission zone) firmly place all these species in this section.

■ CONCLUSIONS

The present work is based significantly on the enormous body of work and careful observations by O.M. Hilliard, B.L. Burttt and K. Jong and draws on their many publications. Since then, more species have been described in *Streptocarpus*, but the generic concept has changed little until recently, principally including Afro-Malagasy taxa with twisted fruits. The reliance on this character led Burttt (in Humbert, 1971) to remove *Colpogyne* from *Streptocarpus*. With the advent of molecular methods it has become clear that the evolution of morphology is more complex, and that some characters, such as twisted fruits, may not evolve often but can be lost relatively easily (Möller & al., 2009, 2011a; Puglisi & al., 2011). Burttt (1984) himself gave preference to indumentum characters over fruit characters and redefined the genus *Paraboea* to include species with and without twisted fruits and was shown to be correct in his approach (Puglisi & al., 2011). This is the broad approach to characters we have taken here in uniting all Streptocarpaceae genera into *Streptocarpus* to bring taxonomy in line with phylogeny. While the twisted fruit is no longer a defining characteristic of the genus, it was not without exceptions before; i.e., *Str. capuronii* has capsules “not or scarcely (through one turn of the spiral only) twisted” (Hilliard & Burttt, 1971: 310), and *Linnaeopsis subscandens* on the other hand has strongly twisted fruits (Weigend, 2000: 49). With the inclusion of the seven Streptocarpaceae genera with non-twisted fruits, the circumscription of the genus *Streptocarpus* has been widened, and can now be defined as including woody caulescents with twisted fruits, herbaceous caulescents with twisted or non-twisted fruits, and rosulates and unifoliates with twisted, non-twisted cylindrical or globose fruits.

Within *Streptocarpus* there are strong correlations between geographic distribution and phylogenetic relatedness, reflected in sections that are strictly either Madagascan or African. Both subgenera include subclades from the two regions. Hilliard & Burttt (1971) often drew morphological links across this geographic divide (pp. 44–46), but none have been substantiated here. Neither has Engler’s section *Elongati* been found to represent a natural group, in which he included the Madagascan *Str. thompsonii* R.Br. and African *Str. elongatus* (Engler, 1921), here placed in separate sections. It appears that geography rather than morphology is the key to understanding the evolution of *Streptocarpus*.

Although nine species remain unplaced to section, our work represents a huge step forwards in the classification of *Streptocarpus* and a stable baseline for future refinement.

■ ACKNOWLEDGMENTS

The authors thank the horticulturists at the Royal Botanic Garden Edinburgh (RBGE) for their excellent work in maintaining and accurately curating the living Gesneriaceae collections, in particular S. Barber and L. Galloway who also collected critical material of Tanzanian species for study without which this work would not have been possible. We are extremely grateful to J. McNeill, R. Mill

(both RBGE) for a critical revision of the nomenclatural aspects of the manuscript, and to D. Middleton (Singapore Botanic Gardens) for helpful comments, M. Walters, University of Canterbury, New Zealand, for images of *Str. elongatus*, O. Poncy and M. Gaudeul at the Paris herbarium and curators at BM and K for access to specimens, and publishers for permission to use illustrations in Fig. 1. We are also grateful to two anonymous reviewers for their constructive comments on the manuscript. Initial research funds to M. Möller came from the Leverhulme Trust (grant no. F/00 771 A-0735) and the Carnegie Trust for the Universities of Scotland. Funding was granted by the South African National Research Foundation to D. Bellstedt as part of the South African Biodiversity Initiative (SABI). We would also like to acknowledge the Sibbald Trust (project 2012#9) of the RBGE and the Japan Society for the Promotion of Science (JSPS KAKENHI Grant Number 15K18593) for support for the phylogenetic work of K. Nishii. We thank M. Hart, L. Forrest, R. Hollands for useful comments and help at the molecular laboratories at RBGE. RBGE is supported by the Rural and Environment Science and Analytical Services division (RESAS) in the Scottish Government.

■ LITERATURE CITED

- Akaike, H.** 1974. A new look at the statistical model identification. *IEEE Trans. Automatication Control* 19: 716–723. <http://dx.doi.org/10.1109/TAC.1974.1100705>
- Barrier, M., Baldwin, B.G., Robichaux, R.H. & Purugganan, M.D.** 1999. Interspecific hybrid ancestry of a plant adaptive radiation: Allopolyploidy of the Hawaiian silversword alliance (Asteraceae) inferred from floral homeotic gene duplications. *Molec. Biol. Evol.* 16: 1105–1113. <http://dx.doi.org/10.1093/oxfordjournals.molbev.a026200>
- Beaufort-Murphy, H.T.** 1983. The seed-surface morphology of the Gesneriaceae, utilizing the scanning electric microscope and a new system for diagnosing seed morphology. *Selbyana* 6: 220–422.
- Bellstedt, D.U. & Edwards, T.J.** 2004. A new species of *Streptocarpus* (Gesneriaceae) from the Pondoland Coast, South Africa. *Edinburgh J. Bot.* 60: 409–414.
- Briggs, M.** 2004. *The taxonomy of Madagascan Saintpaulia-like Streptocarpus*. M.Sc. Dissertation, University of Edinburgh, Scotland, U.K.
- Burt, B.L.** 1958a. Studies in the Gesneriaceae of the Old World XV: The genus *Saintpaulia*. *Notes Roy. Bot. Gard. Edinburgh* 22: 547–568.
- Burt, B.L.** 1958b. Studies in the Gesneriaceae of the Old World XVII: A new species of *Linnaeopsis*. *Notes Roy. Bot. Gard. Edinburgh* 22: 581–582.
- Burt, B.L.** 1964. Studies in the Gesneriaceae of the Old World XXV: Additional notes on *Saintpaulia*. *Notes Roy. Bot. Gard. Edinburgh* 25: 191–195.
- Burt, B.L.** 1970. Studies in the Gesneriaceae of the Old World XXXI. Some aspects of functional evolution. *Notes Roy. Bot. Gard. Edinburgh* 30: 1–10.
- Burt, B.L.** 1974. Studies in the Gesneriaceae of the Old World XXXVII: *Schizoboea*, the erstwhile African *Didymocarpus*. *Notes Roy. Bot. Gard. Edinburgh* 33: 265–267.
- Burt, B.L.** 1984. Studies in the Gesneriaceae of the Old World: XLVII. Revised generic concepts for *Boea* and its allies. *Notes Roy. Bot. Gard. Edinburgh* 41: 401–452.
- Burt, B.L. & Wiehler, H.** 1995. Classification of the family Gesneriaceae. *Gesneriana* 1: 1–4.
- Buta, E., Cantor, M., Buta, M. & Zaharia, A.** 2010. The effect of rooting substrates on the development of leaf cuttings in *Saintpaulia*. *Analele Univ. Craiova* 15: 110–119.
- Christenhusz, M.J.M.** 2012. On African Violets and Cape Primroses – towards a monophyletic *Streptocarpus* (Gesneriaceae). *Phytotaxa* 46: 3–9.
- Crocker, C.W.** 1860. Notes on the germination of certain species of Cyrtandreae. *J. Proc. Linn. Soc. Bot.* 5: 65–66. <http://dx.doi.org/10.1111/j.1095-8312.1860.tb01039.x>
- Darbyshire, I.** 2006. Gesneriaceae. Pp. 1–75 in: Beentje, H.J. & Ghazanfar S.A. (eds.), *Flora of tropical East Africa*. Richmond: Royal Botanic Gardens, Kew.
- De Villiers, M.J., Pirie, M.D., Hughes, M., Möller, M., Edwards, T.J. & Bellstedt, D.U.** 2013. An approach to identify putative hybrids in the “coalescent stochasticity zone”, as exemplified in the African plant genus *Streptocarpus* (Gesneriaceae). *New Phytol.* 198: 284–300. <http://dx.doi.org/10.1111/nph.12133>
- Dimitrov, D., Nogués-Bravo, D. & Scharff, N.** 2012. Why do tropical mountains support exceptionally high biodiversity? The Eastern Arc mountains and the drivers of *Saintpaulia* diversity. *PLoS ONE* 7: e48908. <http://dx.doi.org/10.1371/journal.pone.0048908>
- Doyle, J.J. & Doyle, J.L.** 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.
- Doyle, J.J. & Doyle, J.L.** 1990. Isolation of plant DNA from fresh tissue. *Focus* 12: 13–15.
- Engler, A.** 1921. Gesneraceae africanae. IV. Neue Arten und das Auftreten von Kleistogamie sowie Reduktion der Assimilationstätigkeit auf einen laubblattartigen Kotyledon bei kauszenten Arten von *Streptocarpus*. *Bot. Jahrb. Syst.* 57: 202–219.
- Fritsch, K.** 1893–1894. Gesneriaceae. Pp. 133–144 (1893) & 145–185 (1894) in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, IV/3(b). Leipzig: Engelmann, 1895. <http://dx.doi.org/10.5962/bhl.title.4635>
- Fritsch, K.** 1904. *Die Keimpflanzen der Gesneriaceen mit besonderer Berücksichtigung von Streptocarpus, nebst vergleichender Studien über die Morphologie dieser Familie*. Jena: Fischer.
- Gontcharov, A.A., Marin, B. & Melkonian, M.** 2004. Are combined analyses better than single gene phylogenies? A case study using SSU rDNA and *rbcL* sequence comparisons in the Zygnematomyceae (Streptophyta). *Molec. Biol. Evol.* 21: 612–624. <http://dx.doi.org/10.1093/molbev/msh052>
- Hamilton, M.B.** 1999. Four primer pairs for the amplification of chloroplast intergenic regions with intraspecific variation. *Molec. Ecol.* 8: 521–523.
- Harrison, C.J., Möller, M. & Cronk, Q.C.B.** 1999. Evolution and development of floral diversity in *Streptocarpus* and *Saintpaulia*. *Ann. Bot. (Oxford)* 84: 49–60. <http://dx.doi.org/10.1006/anbo.1999.0887>
- Harrison, C.J., Möller, M., Langdale, J., Cronk, Q.C.B. & Hudson, A.** 2005. The role of *KNOX* genes in the evolution of morphological novelty in *Streptocarpus*. *Pl. Cell* 17: 430–443. <http://dx.doi.org/10.1105/tpc.104.028936>
- Haston, E.M.** 2009a. 656. *Saintpaulia ulugurensis*. *Bot. Mag.* 26: 270–276. http://dx.doi.org/10.1111/j.1467-8748.2009.01660_2.x
- Haston, E.M.** 2009b. 657. *Saintpaulia watkinsii*. *Bot. Mag.* 26: 277–281. <http://dx.doi.org/10.1111/j.1467-8748.2009.01661.x>
- Hellens, K., Preston, J., Cronk, Q.C.B. & Möller, M.** 1999b. Phylogenetic position of *Streptocarpus orientalis* inferred from nuclear and chloroplast DNA sequences. P. 10 in: Curry, G. (ed.), *Systematics Association Second Biennial Conference, University of Glasgow, 23–27 August 1999: Poster Abstracts*. Glasgow: University of Glasgow. <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.195.2404&rep=rep1&type=pdf>
- Hilliard, O.M. & Burt, B.L.** 1971. *Streptocarpus*: An African plant study. Pietermaritzburg: Natal University Press.
- Hilliard, O.M. & Burt, B.L.** 1975. Studies in the Gesneriaceae of the Old World XXXVIII: A new species of *Streptocarpus* from East Africa. *Notes Roy. Bot. Gard. Edinburgh* 33: 467–469.

- Hillis, D.M. & Dixon, M.T. 1991. Ribosomal DNA: Molecular evolution and phylogenetic inference. *Quart. Rev. Biol.* 66: 411–453. <http://dx.doi.org/10.1086/417338>
- Hooker, J.D. 1862. *Acanthonema strigosum*. Strigose Acanthonema. *Bot. Mag.* 88 [= ser. 3, 18]: pl. 5339.
- Hughes, M., Möller, M., Bellstedt, D.U., Edwards, T.J. & De Villiers, M. 2005. Refugia, dispersal and divergence in a forest archipelago: A study of *Streptocarpus* in eastern South Africa. *Molec. Ecol.* 14: 4415–4426. <http://dx.doi.org/10.1111/j.1365-294X.2005.02756.x>
- Hughes, M., MacMaster, G., Möller, M., Bellstedt, D.U. & Edwards, T.J. 2006. Breeding system of a plesiomorphic floral type: An investigation of small flowered *Streptocarpus* (Gesneriaceae) species. *Pl. Syst. Evol.* 262: 13–24. <http://dx.doi.org/10.1007/s00606-006-0453-6>
- Humbert, H. 1967. Espèces nouvelles de *Streptocarpus* (Gesneriaceae) a Madagascar. *Adansonia*, sér. 2, 7: 275–294.
- Humbert, H. 1971. Gesnériacées, Pp. 47–163 in: Leroy, J.F. (ed.), *Flore de Madagascar et des Comores*. Paris: Muséum national d'Histoire naturelle. <http://dx.doi.org/10.5962/bhl.title.6600>
- Iles, W.J.D., Rudall, P.J., Sokoloff, D.D., Remizowa, M.V., MacFarlane, T.D., Logacheva, M.D. & Graham, S.W. 2012. Molecular phylogenetics of Hydatellaceae (Nymphaeales): Sexual-system homoplasy and a new sectional classification. *Amer. J. Bot.* 99: 663–676. <http://dx.doi.org/10.3732/ajb.1100524>
- Jong, K. 1970. *Developmental aspects of vegetative morphology in Streptocarpus*. Ph.D. Dissertation, University of Edinburgh, Scotland, U.K.
- Jong, K. & Burtt, B.L. 1975. The evolution of morphological novelty exemplified in the growth patterns of some Gesneriaceae. *New Phytol.* 75: 297–311. <http://dx.doi.org/10.1111/j.1469-8137.1975.tb01400.x>
- Jong, K. & Möller, M. 2000. New chromosome counts in *Streptocarpus* (Gesneriaceae) from Madagascar and the Comoro Islands and their taxonomic significance. *Pl. Syst. Evol.* 224:173–182. <http://dx.doi.org/10.1007/BF00986341>
- Jong, K., Christie, F., Paik, J.H., Scott, S.M. & Möller, M. 2012. Unusual morphological and anatomical features of two woody Madagascan endemics, *Streptocarpus papangae* and *S. suffruticosus* (Gesneriaceae), and their potential taxonomic value. *S. African J. Bot.* 80: 44–56. <http://dx.doi.org/10.1016/j.sajb.2012.02.004>
- Lawrence, W.J.C. 1943. Cleistogamy in *Streptocarpus*. *Gard. Chron.*, ser. 3, 113: pl. 56.
- Lindley, J. 1828. *Streptocarpus rexii*. Cape Streptocarpus. *Bot. Reg.* 14: pl. 1173.
- Lindqvist, C. & Albert, V.A. 1999. Phylogeny and conservation of African violets (*Saintpaulia*: Gesneriaceae): New findings based on nuclear ribosomal 5S non-transcribed spacer sequences. *Kew Bull.* 54: 363–377. <http://dx.doi.org/10.2307/4115813>
- Lindqvist, C., & Albert, V.A. 2001. A high elevation ancestry for the Usambara Mountains and lowland populations of African violets (*Saintpaulia*, Gesneriaceae). *Syst. & Geogr. Pl.* 71: 37–44. <http://dx.doi.org/10.2307/3668751>
- MacMaster, G., Möller, M., Hughes, M., Edwards, T.J. & Bellstedt, D.U. 2005. A new species of *Streptocarpus* (Gesneriaceae) endemic to Madagascar. *Adansonia*, ser. 3, 27: 131–136.
- Marx, H.E., O'Leary, N., Yuan, Y.-W., Lu-Irving, P., Tank, D.C., Múlgura, M.E. & Olmstead, R.G. 2010. A molecular phylogeny and classification of Verbenaceae. *Amer. J. Bot.* 97: 1647–1663. <http://dx.doi.org/10.3732/ajb.1000144>
- Mayer, V., Möller, M., Perret, M. & Weber, A. 2003. Phylogenetic position and generic differentiation of Epithemateae (Gesneriaceae) inferred from plastid DNA sequence data. *Amer. J. Bot.* 90: 321–329. <http://dx.doi.org/10.3732/ajb.90.2.321>
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'Homme Van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (eds.) 2012. *International Code of Nomenclature for algae, fungi, and plants* (“Melbourne Code”): Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011, online ed. Bratislava: International Association for Plant Taxonomy. <http://www.iapt-taxon.org/nomen/main.php> (retrieved 20 Dec 2012).
- Milne, C. 1975. Chromosome numbers in the Gesneriaceae: V. *Notes Roy. Bot. Gard. Edinburgh* 33: 523–525.
- Möller, M. 2000. How universal are universal rDNA primers? A cautionary note for plant systematists and phylogeneticists. *Edinburgh J. Bot.* 57: 151–156.
- Möller, M. 2003. Gesneriaceae. Pp. 421–425 in: Goodman, S.M. & Benstead, J.P. (eds.), *The natural history of Madagascar*. Chicago: The University of Chicago Press.
- Möller, M. & Clark, J.L. 2013. The state of molecular phylogenetic work in the family Gesneriaceae: A review. *Selbyana* 31: 95–125.
- Möller, M. & Cronk, Q.C.B. 1997a. Origin and relationships of *Saintpaulia* (Gesneriaceae) based on ribosomal DNA internal transcribed spacer (ITS) sequences. *Amer. J. Bot.* 84: 956–965. <http://dx.doi.org/10.2307/2446286>
- Möller, M. & Cronk, Q.C.B. 1997b. Phylogeny and disjunct distribution: Evolution of *Saintpaulia* (Gesneriaceae). *Proc. Roy. Soc. London, ser. B, Biol. Sci.* 264: 1827–1836. <http://dx.doi.org/10.1098/rspb.1997.0252>
- Möller, M. & Cronk, Q.C.B. 1999. New approaches to the systematics of *Saintpaulia* and *Streptocarpus*. Pp. 253–264 in: Andrews, S., Leslie, A. & Alexander, C. (eds.), *Taxonomy of cultivated plants, Third International Symposium*. Richmond: Royal Botanic Gardens, Kew.
- Möller, M. & Cronk, Q.C.B. 2001a. Evolution of morphological novelty: A phylogenetic analysis of growth patterns in *Streptocarpus* (Gesneriaceae). *Evolution* 55: 918–929. [http://dx.doi.org/10.1554/0014-3820\(2001\)055\[0918:EOMNAP\]2.0.CO;2](http://dx.doi.org/10.1554/0014-3820(2001)055[0918:EOMNAP]2.0.CO;2)
- Möller, M. & Cronk, Q.C.B. 2001b. Phylogenetic studies in *Streptocarpus* (Gesneriaceae): Reconstruction of biogeographic history and distribution patterns. *Syst. & Geogr. Pl.* 71: 545–555. <http://dx.doi.org/10.2307/3668699>
- Möller, M. & Kiehn, M. 2004. A synopsis of cytological studies in Gesneriaceae. *Edinburgh J. Bot.* 60: 425–447.
- Möller, M., Clokie, M., Cubas, P. & Cronk, Q.C.B. 1999. Integrating molecular phylogenies and developmental genetics: A Gesneriaceae case study. Pp. 375–402 in: Hollingsworth, P.M., Bateman, R.M. & Gornall, R.J. (eds.), *Molecular systematics and plant evolution*. London & New York: Taylor and Francis.
- Möller, M. & Pullan, M. 2015–. RBGE WebCyte2 – An updated Gesneriaceae cytology database. <http://elmer.rbge.org.uk/webcyte/>
- Möller, M., Kokubugata, G. & Jong, K. 2008. Aspects of genome evolution in Gesneriaceae: Patterns of 45S-nrDNA site evolution based on evidence from fluorescent in situ hybridization (FISH). *Int. J. Pl. Sci.* 169: 667–676. <http://dx.doi.org/10.1086/533609>
- Möller, M., Pfosser, M., Jang, C.G., Mayer, V., Clark, A., Hollingsworth, M.L., Barfuss, M., Wang, Y.Z., Kiehn, M. & Weber, A. 2009. A preliminary phylogeny of the “Didymocarpoideae Gesneriaceae” based on three molecular data sets: Incongruence with available tribal classifications. *Amer. J. Bot.* 96: 989–1010. <http://dx.doi.org/10.3732/ajb.0800291>
- Möller, M., Forrest, A., Wei, Y.G. & Weber, A. 2011a. A molecular phylogenetic assessment of the advanced Asiatic and Malesian didymocarpoideae Gesneriaceae with focus on non-monophyletic and monotypic genera. *Pl. Syst. Evol.* 292: 223–248. <http://dx.doi.org/10.1007/s00606-010-0413-z>
- Möller, M., Middleton, D.J., Nishii, K., Wei, Y.G., Sontag, S. & Weber, A. 2011b. A new delineation for *Oreocharis* incorporating an additional ten genera of Chinese Gesneriaceae. *Phytotaxa* 23: 1–36.

- Mühlbauer, I. & Kiehn, M. 1997. Seed morphology of *Cyrtandra* (Gesneriaceae). *Scripta Bot. Belg.* 15: 117.
- Murata, M., Heslop-Harrison, J.S. & Motoyoshi, F. 1997. Physical mapping of the 5S ribosomal RNA genes in *Arabidopsis thaliana* by multi-color fluorescence in situ hybridization with cosmid clones. *Plant J.* 12: 31–37. <http://dx.doi.org/10.1046/j.1365-3113X.1997.12010031.x>
- Nishii, K., Möller, M., Kidner, C., Spada, A., Mantegazza, R., Wang, C.N. & Nagata, T. 2010. A complex case of simple leaves: Indeterminate leaves co-express *ARP* and *KNOX1* genes. *Developm. Genes Evol.* 220: 25–40. <http://dx.doi.org/10.1007/s00427-010-0326-4>
- Nylander J.A. 2004. MrModeltest, version 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Sweden.
- Nylander, J.A., Wilgenbusch, J.C., Warren, D.L. & Swofford, D.L. 2008. AWTY (are we there yet?): A system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24: 581–583. <http://dx.doi.org/10.1093/bioinformatics/btm388>
- Potgieter, C.J. & Edwards, T.J. 2005. The *Stenobasipteron wiedemanni* (Diptera, Nemestrinidae) pollination guild in Eastern Southern Africa. *Ann. Missouri Bot. Gard.* 92: 254–267.
- Puglisi, C., Middleton, D.J., Triboun, P. & Möller, M. 2011. New insights into the relationships between *Paraboea*, *Trisepalum*, and *Phylloboea* (Gesneriaceae) and their taxonomic consequences. *Taxon* 60: 1693–1702.
- Ratter, J.A. & Milne, C. 1970. Chromosome numbers in the Gesneriaceae: IV. *Notes Roy. Bot. Gard. Edinburgh* 30: 183–187.
- Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. <http://dx.doi.org/10.1093/sysbio/sys029>
- Sahasrabudhe, S. 1970. *Phylogenetic studies in the Gesneriaceae*. Ph.D. Dissertation, University of Manchester, U.K.
- Silvestro, D. & Michalak, I. 2012. raxmlGUI: A graphical front-end for RAxML. *Organisms Diversity Evol.* 12: 335–337. <http://dx.doi.org/10.1007/s13127-011-0056-0>
- Skog, L.E. & Boggan, J.K. 2007. World Checklist of Gesneriaceae. Washington, D.C.: Dept. of Botany, Smithsonian Institution. <http://botany.si.edu/Gesneriaceae/Checklist>
- 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* subgenera *Streptocarpus* and *Streptocarpella* (Gesneriaceae). *Edinburgh J. Bot.* 55: 1–11. <http://dx.doi.org/10.1017/S0960428600004315>
- Sone, T., Fujisawa, M., Takenaka, M., Nakagawa, S., Yamaoka, S., Sakaida, M., Nishiyama, R., Yamato, K.T., Ohmido, N., Fukui, K., Fukuzawa, H. & Ohyama, K. 1999. Bryophyte 5S rDNA was inserted into 45S rDNA repeat units after the divergence from higher land plants. *Pl. Molec. Biol.* 41: 679–685. <http://dx.doi.org/10.1023/A:1006398419556>
- Sontag, S. & Weber, A. 1998. Seed coat structure in *Didissandra*, *Ridleyandra* and *Raphiocarpus* (Gesneriaceae). *Beitr. Biol. Pflanzen* 70: 179–190.
- Stebbins, G.L. 1950. *Variation and evolution in plants*. New York: Columbia University Press.
- Sullivan, J. 1996. Combining data with different distributions of among-site rate variation. *Syst. Biol.* 45: 375–380. <http://dx.doi.org/10.1093/sysbio/45.3.375>
- Swofford, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4. Sunderland, Massachusetts: Sinauer.
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Molec. Biol.* 17: 1105–1109. <http://dx.doi.org/10.1007/BF00037152>
- Weber, A. 2004. Gesneriaceae. Pp. 63–158 in: Kubitzki, K. & Kadereit, J.W. (eds.), *The families and genera of vascular plants*, vol. 7, *Flowering plants: Dicotyledons; Lamiales (except Acanthaceae including Avicenniaceae)*. Berlin & Heidelberg: Springer.
- Weber, A. & Skog, L.E. 2007–. The genera of Gesneriaceae: Basic information with illustration of selected species, ed. 2. <http://www.genera-gesneriaceae.at>
- Weber, A., Middleton, D.J., Forrest, A., Kiew, R., Lim, C.L., Rafidah, A.R., Yao, T.L. & Möller, M. 2011a. Molecular systematics and remodelling of *Chirita* and associated genera (Gesneriaceae). *Taxon* 60: 767–790.
- Weber, A., Wei, Y.G., Puglisi, C., Wen, F., Mayer, V. & Möller, M. 2011b. A new definition of the genus *Petrocodon* (Gesneriaceae). *Phytotaxa* 23: 49–67.
- Weber, A., Clark, J.L. & Möller, M. 2013. A new formal classification of Gesneriaceae. *Selbyana* 31: 68–94.
- Weigend, M. 2000. A synopsis of the genus *Linnaeopsis* (Gesneriaceae), an “Uluguru *Streptocarpus*”. *Flora* 195: 45–50.
- Westerkamp, C. & Claßen-Bockhoff, R. 2007. Bilabiate flowers: The ultimate response to bees? *Ann. Bot. (Oxford)* 100: 361–374. <http://dx.doi.org/10.1093/aob/mcm123>
- White, T.J., Bruns, T., Lee, S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.), *PCR protocols*. London: Academic Press. <http://dx.doi.org/10.1016/b978-0-12-372180-8.50042-1>
- Wiens, J.J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Syst. Biol.* 52: 528–538. <http://dx.doi.org/10.1080/10635150390218330>
- Wiens, J.J. 2006. Missing data and the design of phylogenetic analyses. *J. Biomed. Inf.* 39: 34–42. <http://dx.doi.org/10.1016/j.jbi.2005.04.001>

Appendix 1. Origin of the material used in the phylogenetic analyses of matrix Str226.

Taxon, locality, collector(s), collector number, herbarium code, and ITS, *rpl20-rps12*, and *trnLF* GenBank accession numbers. Asterisk indicates newly generated sequences.

Acanthonema strigosum Hook.f. 1, Cameroon, *Macinder B. BM491* (K), FJ501306, *KR703824, FJ501454. *Acanthonema strigosum* Hook.f. 2, Cameroon, *Plana V. VP88* (E), *KR704038, *KR703825, *KR703921. *Colpogyne betsiliensis* (Humbert) B.L.Burtt 1, Madagascar: Fianarantsoa, Mt Itremo, *Moeller M. & al. MMO0122* (E), *KR704039, *KR703826, *KR703922. *Colpogyne betsiliensis* (Humbert) B.L.Burtt 2, Madagascar: West Betsileo, *Humbert H. 28225* (E), *KR704040, –, –, *Didymocarpus citrinus* Ridl., Malaysia: Perlis, Kedah Peak, *Davis P.H. 69437* (E), DQ912669, *KR703821, AJ492293. *Haberlea rhodopensis* Friv., ex cult (Bulgaria, Greece), *s.n.* (E), AF316898, *KR703820, AJ492296. *Hovanella madagascariensis* (C.B.Clarke) A.Weber & B.L.Burtt, Madagascar: Antananarivo, Maromiza, *Moeller M. & Andriantiana J. MMO0115* (E), *KR704042, *KR703828, *KR703923. *Linnaeopsis alba* (E.A.Bruce) B.L.Burtt, Tanzania: Uluguru Mts, above Morogoro town, NW side of Lupanga ridge, *Pócs T. & Pócs S. 86106/D* (E), AF316933, *KR703829, –, *Linnaeopsis sp.* 1, Tanzania: Uluguru Mts, above Morogoro town, Palata ridge, *Pócs T. & Pócs S. 8656C* (E), AF316932, *KR703830, *KR703924. *Linnaeopsis sp.* 2, Tanzania: Morogoro, N.W. Uluguru Mts, Palata track, *Mabberley D.J. 1254* (E), *KR704043, –, –, *Linnaeopsis sp.* 3, Tanzania: Uluguru Mts, above Morogoro

Appendix 1. Continued.

town, Pócs T. & Pócs S., 8656C (E), *KR704044, *KR703831 (short), *KR703925. *Paraboea rufescens* (Franch.) B.L.Burtt, China: Yunnan, Möller M., Qi Y.D. MMO1-99 (E), FJ501316, *KR703823, FJ501469. *Primulina spadiciformis* (W.T.Wang) Mich.Möller & A.Weber, China: unknown locality, ex Smithsonian Institution 94-087 (E), AF316900, *KR703822, AJ492291. *Saintpaulia brevopilosa* B.L.Burtt_1, Tanzania: Kanga forest, Mt. Kanga (Nguru Mts), Pócs T. s.n. (E), AF316924, *KR703832, *KR703926. *Saintpaulia* cf. *inconspicua* B.L.Burtt_1, Tanzania: Uluguru Mts, unknown locality, Watkins C. CW430/01/03 (C.Watkins), *KR704050, *KR703839, *KR703933. *Saintpaulia* cf. *ionantha* H.Wendl., Tanzania: Tanga, Sigi River, Moors D.R. s.n. (–), AF316923, –, *KR703934. *Saintpaulia difficilis* B.L.Burtt_1, Tanzania: Tanga Region, Bogner J. BNR (E), *KR704045, *KR703833, *KR703927. *Saintpaulia diplotricha* B.L.Burtt, Tanzania: Tanga Region, Munich Univ., s.n. (E), *KR704046, *KR703834, *KR703928. *Saintpaulia goetzeana* Engl._1, Tanzania: Uluguru Mts, Evans M.J. (AGGS) s.n. (Ephoto), *KR704047, *KR703835, *KR703929. *Saintpaulia grandifolia* B.L.Burtt_1, ex cult. (Tanzania: E. Usambara Mts), ex Hannover B.G./Marburg B.G. MMOG-240 (E), *KR704048, *KR703836, *KR703930. *Saintpaulia grotei* Engl._1, Tanzania: E. Usambara Mts, Munich Univ. s.n. (E), *KR704049, *KR703837, *KR703931. *Saintpaulia inconspicua* B.L.Burtt_2, Tanzania: Uluguru Mts, unknown locality, Watkins C. s.n. (E), *KR704051, *KR703838, *KR703932 (short). *Saintpaulia magungensis* E.P.Roberts_1, ex cult. (Tanzania), ex RBG Kew 1983-8183 (E), *KR704052, –, *KR703935. *Saintpaulia nitida* B.L.Burtt_1, ex cult. (Tanzania: Nguru Mts), ex RBG Kew 1987-1566 (E), AF316925, –, *KR703936. *Saintpaulia pendula* B.L.Burtt, Tanzania: NE Usambara Mts, ex Phillipps Univ. Marburg B.G. s.n. (E), *KR704053, *KR703840, *KR703937. *Saintpaulia pusilla* Engl._2, Tanzania: Uluguru Mts, Mabberley D.J. 1362 (E), *KR704054, –, *KR703938 (short). *Saintpaulia rupicola* B.L.Burtt_1, ex cult. (Kenya), ex Hannover B.G. VS2.2 (E), *KR704055, *KR703841, –, *Saintpaulia rupicola* B.L.Burtt_1, Kenya: Kaloleni, ex RBG-Kew 1987-1283 (E), –, –, *KR703939. *Saintpaulia shumensis* B.L.Burtt_1, ex cult. (Tanzania: W. Usambara Mts, Mt Shume), ex Clements T. s.n. (E), *KR704056, –, *KR703940. *Saintpaulia teitensis* B.L.Burtt_1, Kenya: Mbololo, Taita Hills, Punter W.R. s.n. (E), AF316922, –, –, *Saintpaulia tongwensis* H.Wendl._1, Tanzania: Tanga Region, ex Clements T. Mather 2 (–), FJ501303, *KR703842, FJ501446. *Saintpaulia ulugurensis* Haston, Tanzania: Morogoro, Uluguru Mts, Haston E. 102 (E), *KR704057, *KR703843, *KR703941. *Saintpaulia velutina* B.L.Burtt, Tanzania: Usambara Mts, ex Munich University s.n. (E), FJ501304, *KR703844, AJ492303. *Saintpaulia watkinsii* Haston_1, Tanzania: Morogoro, Morogoro-Rural, Lusangalala area, Tegetero, Uluguru Nature Reserve, Barber S. & Galloway L. TZBG65 (E), *KR704058, *KR703845, *KR703942. *Saintpaulia watkinsii* Haston_2, Tanzania: Morogoro, Uluguru Mts, Haston E. 99 (E), *KR704059, *KR703846, –, *Schizoboea kamerunensis* (Engl.) B.L.Burtt_1, Burundi: unknown locality, Lewalla 6603 (E), FJ501305, *KR703847, FJ501453. *Schizoboea kamerunensis* (Engl.) B.L.Burtt_2, unknown origin, Drummond & Hemsley D.&H1590 (E), *KR704085, *KR703848, *KR703943. *Streptocarpus andohahelensis* Humbert_1, Madagascar: Tulear, Ranomafana, Moeller M. & Rafanantsoa G. MM9717B (E), *KR704086, *KR703849, *KR703944. *Streptocarpus aylae* T.J.Edwards, South Africa: Eastern Cape, Msikaba, Edwards T.J. & Styles D. s.n. (Bews Herbarium, PMB), HQ719017, HQ719134, HQ718937. *Streptocarpus baudertii* L.L.Britten_1, South Africa: KwaZulu-Natal, Otterspoort, Hughes M. & al. MH1067 (E), HQ719049, HQ719166, *KR703945. *Streptocarpus baudertii* L.L.Britten_2, South Africa: Eastern Cape, Collywobbles, Hughes M. & al. MH1189 (E), *KR704087, *KR703850, *KR703946. *Streptocarpus beampingararensis* subsp. *beampingararensis* Humbert_1, Madagascar: Tulear, Ranomafana, Bellstedt D.U. DUB1234 (STE), *KR704088, –, *KR703947. *Streptocarpus beampingararensis* subsp. *beampingararensis* Humbert_2, Madagascar: Tulear, Ranomafana, Moeller M. & Rafanantsoa G. MM9715 (E), *KR704089, *KR703851, FJ501448. *Streptocarpus bindseili* E.Fischer, Rwanda: S. Nyakabuye, ex Munich B.G. [ex Bonn] s.n. (E), AF316960, *KR703852, *KR703948. *Streptocarpus bolusii* C.B.Clarke_1, South Africa: Satans Pass, Ngcobo, Eastern Cape, Badenhorst L. 60 (NBG) (STE), HQ718999, HQ719116, HQ718923. *Streptocarpus bolusii* C.B.Clarke_2, South Africa: Satans Pass, Ngcobo, Eastern Cape, Badenhorst L. 60 (NBG) (STE), HQ719000, HQ719117, HQ718924. *Streptocarpus brevistamineus* Humbert, Madagascar: Antsiranana, Mai-kampango forest, Moeller M. & Andriantiana J. MM9888A (E), *KR704090, *KR703853, *KR703949. *Streptocarpus buechananii* C.B.Clarke, ex cult. (Malawi, S. Tanzania, N. Mocambique), ex AGGS s.n. (E), AF316919, *KR703854, *KR703950. *Streptocarpus bullatus* Mansf._1, Tanzania: Morogoro, Uluguru Mts, E. of Magari peak, Pócs, Kondela & Nchimbi 6297 (E), AF316942, –, –, *Streptocarpus bullatus* Mansf._2, Tanzania: Morogoro, Mvomero, Beho-beho area, Barber S. & Galloway L. TZBG41 (E), *KR704091, *KR703855, *KR703951. *Streptocarpus bullatus* Mansf._3, Tanzania: Morogoro, Morogoro-Rural, Kigadu area, Barber S. & Galloway L. TZBG58 (E), *KR704092, *KR703856, *KR703952. *Streptocarpus caeruleus* Hilliard & B.L.Burtt_1, South Africa: Limpopo, Lajuma, Bellstedt D.U. DUB1011a (STE), HQ719018, HQ719135, HQ718938. *Streptocarpus caeruleus* Hilliard & B.L.Burtt_2, South Africa: Limpopo, Blouberg, Bellstedt D.U. DUB1065 (STE), HQ719019, HQ719136, HQ718939. *Streptocarpus candidus* Hilliard, South Africa: KwaZulu-Natal, Ngome Forest, Edwards T.J. s.n. (Bews Herbarium, PMB), HQ719007, HQ719124, HQ718927. *Streptocarpus capuronii* Humbert_1, Madagascar: Antsiranana, Mt Ambodilaitra, Moeller M. & Andriantiana J. MM9885A (E), *KR704093, –, *KR703953. *Streptocarpus capuronii* Humbert_2, Madagascar: unknown locality, Gautier L. LG3936 (G), *KR704094, *KR703857, *KR703954. *Streptocarpus caulescens* Vatke, ex cult. (Tanzania, Kenya), Mr & Mrs I La Crox 1481 (E), AF316920, *KR703858, *KR703955. *Streptocarpus cf. mangindranensis* Humbert, Madagascar: unknown locality, Gautier L. LG3477 (G), MacMaster & al. (2005), –, MacMaster & al. (2005). *Streptocarpus* cf. *michelmorei* B.L.Burtt_1, Zimbabwe: Manicaland Province, Chimanimani National Park, Clark 458 (STE), *KR704095, *KR703859, *KR703956. *Streptocarpus* cf. *michelmorei* B.L.Burtt_2, Zimbabwe: Manicaland Province, Chimanimani National Park, Clark 459 (STE), *KR704096, *KR703860, *KR703957. *Streptocarpus compressus* B.L.Burtt, Tanzania: Songea Distr., Matengo Hills, Luiiri Kites, Redhead M. & Taylor 8982A (E), AF316957, –, –, *Streptocarpus confusus* Hilliard, South Africa: Natal, Near Hluhluwe Game Reserve, Makowe Mt., Harrison E.R. s.n. (E), AF316966, –, –, *Streptocarpus cooksonii* B.L.Burtt, South Africa: Jamisons Drift, Edwards T.J. s.n. (Bews Herbarium, PMB), *KR704097, HE861712, HE956758. *Streptocarpus cooperi* C.B.Clarke, South Africa: Natal, Nkandla distr. Qudeni forest, Edwards T.J. s.n. (E), AF316954, –, –, *Streptocarpus cyanandrus* B.L.Burtt, Zimbabwe: Inyanga Downs, Wild H. 4943 (E), AF316947, *KR703861, *KR703958. *Streptocarpus cyaneus* S.Moore_1, South Africa: Limpopo, Mariepskop, Hughes M. & al. MH1329 (E), HQ719024, HQ719141, HQ718943. *Streptocarpus cyaneus* S.Moore_2, South Africa: Mpumalanga, Josephsdal, Hughes M. & al. MH1355_02 (E), HQ719025, HQ719142, HQ718944. *Streptocarpus cyaneus* subsp. *longi-tommii* Weigend & T.J.Edwards, South Africa: Mpumalanga, DieGeut, Hughes M. & al. MH1232 (E), *KR704098, –, *KR703959. *Streptocarpus cyaneus* subsp. *nigridens* Weigend & T.J.Edwards, South Africa: Limpopo, Soutpansberg, Bellstedt D.U. DUB1077_01 (STE), HQ719023, HQ719140, HQ718942. *Streptocarpus daviesii* N.E.Brown ex C.B.Clarke, South Africa: Kwa-Zulu Natal, Laager Farm, Wartburg, Bellstedt D.U. DUB955 (STE), *KR704099, HE861713, HE956759. *Streptocarpus davysi* S.Moore, Swaziland: Mbabane, Burtt B.L. 3551 (E), AF316946, *KR703862, *KR703960 (short). *Streptocarpus decipiens* Hilliard & B.L.Burtt, South Africa: E. Transvaal, Hilliard O.M. & Burtt B.L. H&B6000 (E), AF316938, *KR703863, *KR703961. *Streptocarpus denticulatus* Turrill_1, South Africa: Mpumalanga, Belfast, Bellstedt D.U. DUB1096a (STE), HQ718991, HQ719108, HQ718915. *Streptocarpus denticulatus* Turrill_2, South Africa: Mpumalanga, Belfast, Bellstedt D.U. DUB1096b (STE), HQ718992, HQ719109, HQ719108. *Streptocarpus dolichanthus* Hilliard & B.L.Burtt, Malawi: Mt. Mulanje, Litelenya Plateau, Chapman J.D. & Chapman E.G. 8496 (E), AF316937, *KR703864, *KR703962. *Streptocarpus dunnii* Hook.f._1, South Africa: Mpumalanga, Uitvlugt Farm, Hughes M. & al. MH1268 (E), HQ718988, HQ719105, HQ718912. *Streptocarpus dunnii* Hook.f._2, South Africa: Mpumalanga, Slaaihoek, Hughes M. & al. MH1273 (E), HQ718989, HQ719106, HQ718913. *Streptocarpus dunnii* Hook.f._3, South Africa: Mpumalanga, Angle Station, Hughes M. & al. MH1371 (E), HQ718990, HQ719107, HQ718914. *Streptocarpus elongatus* Engl._1, Nigeria: Taraba state, Mambilla Plateau, Nge Nyaki Forest, Spurrier M. N705 (E), AF316913, *KR703865, *KR703963. *Streptocarpus elongatus* Engl._2, Nigeria: Taraba state, Mambilla Plateau, Nge Nyaki Forest, Spurrier M. N705 (–), *KR704100, *KR703866, *KR703964. *Streptocarpus erubescens* Hilliard & B.L.Burtt, Malawi: Ndirandi Mts, Cram. 66-1294 (E), AF316949, *KR703867, *KR703965. *Streptocarpus exsertus* Hilliard & B.L.Burtt_1, Kenya: Lolokwe Mt., Samburu District., Bellstedt D.U. & Bytebil B. 564 (NMK Nairobi), *KR704101, –, *KR703966. *Streptocarpus exsertus* Hilliard & B.L.Burtt_2, Kenya, Lolokwe Mt., NE slope of Onulbeys, Gilbert 5358 (E), AF316939, *KR703868, *KR703967. *Streptocarpus eylesii* S.Moore, Zimbabwe: Nyanga Mountains, Rukotso area, Clark 518 (STE), *KR704102, *KR703869, *KR703968. *Streptocarpus fanniniae* Harvey ex C.B.Clarke_1, South Africa: Natal, Lion's distr., Bridgewood, Dargle, Dale J.E. s.n. (E), AF316944, –, *KR703969. *Streptocarpus fanniniae* Harvey ex C.B.Clarke_2, South Africa: KwaZulu-Natal, Mt. Gilboa, Bellstedt D.U. DUB1025 (STE), HQ718982, HQ719099, HQ718906. *Streptocarpus fuscicatus* T.J.Edwards & C.Kunhardt, South Africa: Mpumalanga, Crocodile River Gorge, Hughes M. & al. MH1291(MMOG237C) (E),

Appendix 1. Continued.

*KR704103, *KR703870, *KR703970. *Streptocarpus fenestra-dei* Weigend & T.J.Edwards, South Africa: Mpumalanga, GodsWindow, *Hughes M. & al. MH1305* (E), *KR704104, –, *KR703971. *Streptocarpus floribundus* M.Weigend & T.J.Edwards, South Africa: KwaZulu-Natal, *KRanskop, *Edwards T.J. s.n.* (Bews Herbarium, PMB), HQ19026, HQ19143, HQ18945. *Streptocarpus formosus* (Hilliard & B.L.Burt) T.J.Edwards_1, South Africa: Eastern Cape, Mzamba, *Burring J. 27* (Bews Herbarium, PMB), HQ19063, HQ19180, HQ18969. *Streptocarpus formosus* (Hilliard & B.L.Burt) T.J.Edwards_2, South Africa: Eastern Cape, Oribi Gorge, *Bellsiedt D.U. DUB1136_01* (STE), HQ19065, HQ19182, HQ18971. *Streptocarpus galpinii* Hook.f., Swaziland: Mbabane, *Burt B.L. 3552* (E), AF316943, *KR703871, –, *Streptocarpus gardenii* Hook_1, South Africa: KwaZulu-Natal, Hoha Forest, *Bellsiedt D.U. DUB0560_01* (STE), HQ19008, HQ19125, HQ18928. *Streptocarpus gardenii* Hook_2, South Africa: KwaZulu-Natal, Mt. Gilboa, *Bellsiedt D.U. DUB1027_02* (STE), HQ19011, HQ19128, HQ18931. *Streptocarpus glandulosissimus* Engl., ex cult. (Congo, Rwanda, Rurundi, Uganda, Tanzania, Kenya), *Hilliard O.M. s.n.* (E), AF316918, *KR703872, *KR703972. *Streptocarpus goetzei* Engler, ex cult. (Tanzania, Moçambique, Malawi), *La Croix I.F. s.n.* (E), AF316956, *KR703872, *KR703973. *Streptocarpus grandis* N.E.Brown_1, South Africa: KwaZulu-Natal, NW of Inanda Mt., *Styles D.G.A. 3007_01* (STE), HQ18993, HQ19110, HQ178917. *Streptocarpus grandis* N.E.Brown_2, South Africa: KwaZulu-Natal, Kingscliff Farm, *Styles D.G.A. 3019_02* (STE), HQ18994, HQ19111, HQ178918. *Streptocarpus haygarthii* N.E.Brown ex C.B.Clark, South Africa, Natal, mid-Illovo, *Edwards T.J. s.n.* (E), AF316964, –, –, *Streptocarpus hildebrandtii* Vatke, ex cult. Madagascar: Parc Botanique et Zoologique de Tsimbazaza, *Moeller M. & Rafanantsoa G. MM9725* (E), AF316930, *KR703874, MacMaster & al. (2005). *Streptocarpus hilsenbergii* R.Brown_1, Madagascar: Asaranitra, Andringitra, *Bellsiedt D.U. DUB1274* (STE, TAN), *KR704105, *KR703875, *KR703974. *Streptocarpus hilsenbergii* R.Brown_2, Madagascar: Ambohimahaso, Fianarantsoa District, *Bellsiedt D.U. DUB1280* (STE, TAN), *KR704106, HE861719, HE956765. *Streptocarpus hirticapsa* B.L.Burt_1, Zimbabwe; Manicaland Province, Chimanimani National Park, *Weigend M. s.n.* (E), AF316962, *KR703876, *KR703975. *Streptocarpus hirticapsa* B.L.Burt_2, Zimbabwe; Manicaland Province, Chimanimani National Park, *Clark 456* (STE), *KR704107, *KR703877, *KR703976. *Streptocarpus hirticapsa* B.L.Burt_3, Zimbabwe; Manicaland Province, Chimanimani National Park, *Clark 456* (STE), *KR704108, *KR703878, *KR703977. *Streptocarpus hirtinervis* C.B.Clark, Malawi: Mt. Mulanje, *Burt B.L. 71-0126* (E), AF316935, *KR703879, *KR703978. *Streptocarpus holstii* Engl., ex cult. (Tanzania, E. Usambara Mts), ex *Cornell Univ. (Bail. Hort) 88* (E), AF316917, *KR703880, AJ492304. *Streptocarpus huamboensis* B.L.Burt, Angola: Mount Moco, Huambo Province, *Harrower A. AGH4492* (Kirstenbosch NGB), *KR704109, HE861720, HE956766. *Streptocarpus ibityensis* Humbert_1, Madagascar: Antananarivo, Mt. Ibity, *Fischer E. 250/93* (E), AF316926, –, FJ501455. *Streptocarpus ibityensis* Humbert_2, Madagascar: Antananarivo, Mt. Ibity, *Moeller M. & al. MMO0132b* (E), *KR704110, –, *KR703979. *Streptocarpus ibityensis* Humbert_3, Madagascar: Antananarivo, Mt. Ibity, *Moeller M. & al. MMO0132ca* (E), MacMaster & al. (2005), *KR703881, MacMaster & al. (2005). *Streptocarpus inflatus* B.L.Burt, Tanzania: Udzungwa Mts, *Luke Q. (MMOG-112)* (E), *KR704111, *KR703882, *KR703980. *Streptocarpus itremensis* B.L.Burt_1, Madagascar: Antananarivo, Mt. Ibity, *Moeller M. & al. MMO0138Ba* (E), MacMaster & al. (2005), *KR703883, MacMaster & al. (2005). *Streptocarpus itremensis* B.L.Burt_2, Madagascar: Antananarivo, Mt. Ibity, *Moeller M. & Rafanantsoa G. MM9723* (E), AF316928, –, MacMaster & al. (2005). *Streptocarpus itremensis* B.L.Burt_3, Madagascar: Fianarantsoa, Mt Itremo, *Bellsiedt D.U. DUB1302* (STE, TAN), *KR704112, –, *KR703981. *Streptocarpus itremensis* B.L.Burt_4, Madagascar: Fianarantsoa, Mt Itremo, *Moeller M. & Andriantiana J. MM9898B* (E), *KR704113, *KR703884, *KR703982. *Streptocarpus johannis* L.L.Britten_1, South Africa: Eastern Cape, Emboty, *Bellsiedt D.U. DUB0840* (STE), HQ19054, HQ19170, HQ18965. *Streptocarpus johannis* L.L.Britten_2, South Africa: KwaZulu-Natal, Hebron Road, *Bellsiedt D.U. DUB0714* (STE), HQ19056, HQ19171, HQ18966. *Streptocarpus kantaniensis* L.L.Britten & Story_1, South Africa: Cape province, E. Transkei, Kei Mouth, *Kunhardt, M. s.n.* (E), AF316974, –, *KR703983. *Streptocarpus kantaniensis* L.L.Britten & Story_2, South Africa: Eastern Cape, Kentani, *Joannou J. 6* (STE), HQ19014, HQ19131, HQ18934. *Streptocarpus kimbozanus* B.L.Burt_1, Tanzania: Kimboza Forest reserve, *Pócs T. 72-1700* (E), AF316911, *KR703885, *KR703984. *Streptocarpus kimbozanus* B.L.Burt_2, Tanzania: unknown locality, *Polhill & Lovett 4911* (E), *KR704114, *KR703886, *KR703985. *Streptocarpus kirkii* Hook.f., Tanzania: Tanga region, E Usambara Mts, *Johnston-Stewart N.G.B. s.n.* (E), AF316916, *KR703887, *KR703986. *Streptocarpus kungwensis* Hilliard & B.L.Burt, Tanzania: W. slope of Musenabantu, *Harley & Raymond M. 9370* (E), AF316959, –, –, *Streptocarpus kunhardtii* T.J.Edwards, South Africa: Mpumalanga, Itala, *Edwards T.J. s.n.* (Bews Herbarium, PMB), *KR704115, –, *KR703987. *Streptocarpus lanatus* MacMaster_1, Madagascar: Fianarantsoa, Mt Itremo, *Bellsiedt D.U. DUB1285* (STE, TAN), *KR704116, –, *KR703988. *Streptocarpus lanatus* MacMaster_2, Madagascar: Fianarantsoa, Mt Itremo, *Moeller M. & al. MMO0119a2* (E), MacMaster & al. (2005), *KR703888, MacMaster & al. (2005). *Streptocarpus lanatus* MacMaster_3, Madagascar: Fianarantsoa, Mt Itremo, *Moeller M. & al. MMO0119a1* (E), MacMaster & al. (2005), –, MacMaster & al. (2005). *Streptocarpus levis* B.L.Burt_2, Madagascar: Tulear, Andranohela River, *Moeller M. & Rafanantsoa G. MM9709* (E), *KR704117, *KR703889, *KR703989. *Streptocarpus lilliputana* D.U.Bellsiedt & T.J.Edwards_1, South Africa: Eastern Cape, Lupatana Gorge, *Bellsiedt D.U. DUB0611* (Bews Herbarium, PMB), HQ19015, HQ19132, HQ18935. *Streptocarpus lilliputana* D.U.Bellsiedt & T.J.Edwards_2, South Africa: Eastern Cape, Upper Fraser Falls, Fraser Gorge, *Bellsiedt D.U. DUB0627* (Bews Herbarium, PMB), HQ19016, HQ19133, HQ19016. *Streptocarpus lokohensis* Humbert, Madagascar: Antsiranana, Mt Ambodilaitra, *Moeller M. & Andriantiana J. MM9886A* (E), MacMaster & al. (2005), *KR703890, MacMaster & al. (2005). *Streptocarpus longiflorus* (Hilliard & B.L.Burt) T.J.Edwards, South Africa: Limpopo, Blouberg, *Bellsiedt D.U. DUB1064_01* (STE), HQ19020, HQ19137, HQ18940. *Streptocarpus macropodus* B.L.Burt, Madagascar: Andringitra, Camp IV, *Lewis & al. 1038* (E), AF316927, *KR703891, –, *Streptocarpus makabengensis* Hilliard, South Africa: Limpopo, Machabengberg, *Truter J. s.n.* (–), *KR704118, HE861721, HE956767. *Streptocarpus meyeri* B.L.Burt_1, South Africa: Eastern Cape, Bastervoetpad, *Bellsiedt D.U. DUB0913_01* (STE), HQ19027, HQ19144, HQ18946. *Streptocarpus meyeri* B.L.Burt_2, South Africa: Eastern Cape, Bastervoetpad, *Bellsiedt D.U. DUB0913_07* (STE), HQ19028, HQ19145, HQ18947. *Streptocarpus meyeri* B.L.Burt_3, South Africa: Eastern Cape, Somerset East, Glen Craig Farm, *Bellsiedt D.U. DUB0896_02* (STE), HQ19036, HQ19153, HQ18953. *Streptocarpus meyeri* B.L.Burt_4, South Africa: Eastern Cape, Bavianskloof, *Jamieson R. s.n.* (–), HQ19038, HQ19155, HQ18954. *Streptocarpus meyeri* B.L.Burt_5, South Africa: Eastern Cape, Zuurburg, *Bellsiedt D.U. DUB0844* (STE), HQ19040, HQ19157, HQ18956. *Streptocarpus meyeri* B.L.Burt_6, South Africa: Eastern Cape, Graaff-Reinet, *Bellsiedt D.U. DUB0776_01* (STE), HQ19041, HQ19158, HQ18957. *Streptocarpus micranthus* C.B.Clark_1, South Africa: Mpumalanga, Shia Longubu dam, *Hughes M. & al. MH1375* (E), *KR704121, –, *KR703990. *Streptocarpus micranthus* C.B.Clark_2, South Africa: Mpumalanga, Graskop Resort, *Bellsiedt, D.U. DUB581* (STE), *KR704122, –, –, *Streptocarpus milanjanus* Hilliard & B.L.Burt, Malawi: Mt. Mulanje, *Burt B.L. 6385* (E), AF316936, *KR703892, *KR703991. *Streptocarpus modestus* L.L.Britten_1, South Africa: Eastern Cape, Upper Fraser Falls, *Bellsiedt D.U. DUB0624_01* (STE), HQ19060, HQ19177, HQ18967. *Streptocarpus modestus* L.L.Britten_2, South Africa: Eastern Cape, Upper Fraser Falls, *Bellsiedt D.U. DUB0624_02* (STE), HQ19061, HQ19178, HQ18968. *Streptocarpus molweniense* Hilliard, South Africa: Kwa-Zulu Natal, Dlinza Forest, Eshowe, *Bellsiedt D.U. DUB1357* (STE), *KR704123, HE861724, HE956768. *Streptocarpus monophyllus* Welwitsch_1, Angola: Huila Province, Humpata District, Zootechnica, *Bellsiedt D.U. DUB1172* (STE), *KR704124, HE861725, HE956769. *Streptocarpus monophyllus* Welwitsch_2, Angola: Huila Province, Humpata District, Zootechnica, *Bellsiedt D.U. DUB1179* (STE), *KR704125, HE861726, HE956770. *Streptocarpus montanus* Oliv_1, Kenya: Taita Taveta, Mbololo Forest, *Bytebier B. BB1937* (–), HQ18981, HQ19098, –, *Streptocarpus montanus* Oliv_2, Tanzania: Kilimanjaro, Mvomero, S. Pare Mts, *Barber S. & Galloway L. TZBG71* (E), *KR704126, *KR703893, *KR703992. *Streptocarpus montanus* Oliv_3, Tanzania: Morogoro, Mvomero, Kolweza Mts, *Barber S. & Galloway L. TZBG4* (E), *KR704127, *KR703894, *KR703993. *Streptocarpus montigena* L.L.Britten_1, South Africa: Eastern Cape, Elandsberg, *MacMaster C. s.n.* (STE), HQ19045, HQ19162, HQ18961. *Streptocarpus montigena* L.L.Britten_2, South Africa: Eastern Cape, Katberg Pass, *Bellsiedt D.U. DUB0897_02* (STE), HQ19048, HQ19165, HQ18964. *Streptocarpus muscosus* C.B.Clark, Madagascar: Tulear, Col de Tanatana, *Moeller M. & Rafanantsoa G., MM9703* (E), *KR704128, *KR703895, *KR703994. *Streptocarpus nimbicola* Hilliard & B.L.Burt, Hilliard O.M., Malawi: Mt. Mulanje, *Burt B.L. 67-0252* (E), AF316934, *KR703896, *KR703995. *Streptocarpus nobilis* C.B.Clark_1, ex cult. (W. Tropical Africa), ex *Vienna Univ. B. G. s.n.* (E.photo), AF316912, *KR703897, *KR703996. *Streptocarpus nobilis* C.B.Clark_2 (W. Tropical Africa), *Jongkiad & Abbw 1919* (Leiden), *KR704129, *KR703898, *KR703997. *Streptocarpus nobilis* C.B.Clark_3, cult. origin, ex *Berlin Botanic Garden 63-1823* (E), *KR704130, –, –, *Streptocarpus occultus* Hilliard, South Africa: Mpumalanga, Warburton, *Truter J. s.n.* (–), *KR704131, HE861727, HE956771. *Streptocarpus oliganthus* B.L.Burt_1, Madagascar: Antsiranana, Marojezy

Appendix 1. Continued.

RN12, *Moeller M. & Andriantiana J. MM9866* (E), *KR704132, *KR703899, *KR703998. *Streptocarpus oliganthus* B.L.Burt 2, Madagascar: Antsiranana, Mt Ambodilaitra, *Moeller M. & Andriantiana J., MM9882* (E), *KR704133, –, *KR703999. *Streptocarpus pallidiflorus* C.B. Clarke, Tanzania: Arusha region, Masai distr., Longido Mts, Longido Stream, *Carmichael Rev. W. s.n.* (E), AF316921, *KR703900, *KR704000. *Streptocarpus papangae* Humbert 1, Madagascar: Tulear, Col de Beampingaratra, *Moeller M. & Rafanantsoa G. MM9718* (E), AF316929, –, FJ501444. *Streptocarpus papangae* Humbert 2, Madagascar: Tulear, Col de Beampingaratra, *Moeller M. & Rafanantsoa G. MM9718* (E), HQ718980, HQ719097, HQ718905. *Streptocarpus parensis* B.L.Burt 1, Tanzania: Kilimanjaro, Mvomero, S. Pare Mts, *Barber S. & Galloway L. TZBG70* (E), *KR704134, *KR703901, *KR704001. *Streptocarpus parensis* B.L.Burt 2, Tanzania: Kilimanjaro, Mvomero, S. Pare Mts, *Barber S. & Galloway L. TZBG66* (E), *KR704135, *KR703902, *KR704002. *Streptocarpus parviflorus* Hook.f. 1, South Africa: unknown locality, *La Croix I.F. s.n.* (E), *KR704136, –, *KR704003. *Streptocarpus parviflorus* Hook.f. 2, South Africa: Limpopo, Magoebaskloof Hotel, *Hughes M. & al. MH1292* (E), HQ719021, HQ719138, *KR704004. *Streptocarpus parviflorus* subsp. *soutpansbergensis* Weigend & T.J. Edwards, South Africa: Limpopo, Soutpansberg, *Bellstedt D.U. DUB1075* (STE), HQ719022, HQ719139, HQ718941. *Streptocarpus petherianus* Fritsch, ex cult. (South Africa: Transvaal, Swaziland, Natal), ex *Chiltern Seeds s.n.* (E), AF316971, –, –, **Streptocarpus perrieri* Humbert, Madagascar: Antananarivo, Angavo near Ankazobe, *Moeller M., Rafanantsoa G. & Irapanarivo S. MM9726* (E), AF316931, *KR703903, MacMaster & al. (2005). *Streptocarpus polevansii* Verdoorn, ex cult. (South Africa: Transvaal), *La Croix I.F. s.n.* (E, photo), AF316950, –, *KR704005. *Streptocarpus polyanthus* Hook. 1, South Africa: KwaZulu-Natal, Shelter Falls, *Hughes M. & al. MH1022* (E), HQ719002, –, *KR704006. *Streptocarpus polyanthus* Hook. 2, South Africa: KwaZulu-Natal, Ferncliff, *Hughes M. & al. MH1031* (E), HQ719004, HQ719121, *KR704007. *Streptocarpus porphyrostachys* Hilliard 1, South Africa: E. Cape, Transkei, Mkabati nature reserve, *Kunhardt C. KNT60* (E), AF316963, –, *KR704008. *Streptocarpus porphyrostachys* Hilliard 2, South Africa: Eastern Cape, Mtentu Gorge, *Bellstedt D. DUB0984* (STE), HQ719001, HQ719118, HQ718925. *Streptocarpus primulifolius* Gand. 1, South Africa: Eastern Cape, Port Shepstone, Rooivaal, *Hughes M. & al. MH1088* (–), HQ719082, HQ719199, *KR704009. *Streptocarpus primulifolius* Gand. 2, South Africa: KwaZulu-Natal, Table Mt., Inanda, *Edwards T.J. s.n.* (Bews Herbarium, PMB), HQ719071, HQ719188, HQ718977. *Streptocarpus primulifolius* Gand. 3, South Africa: Eastern Cape, Msikaba, *Bellstedt D.U. DUB0965_01* (STE), HQ719072, HQ719189, HQ718978. *Streptocarpus primulifolius* Gand. 4, South Africa: KwaZulu-Natal, Stone's Farm, *Hughes M. & al. MH1052* (E), HQ719074, HQ719191, *KR704010. *Streptocarpus primulifolius* Gand. 5, South Africa: Eastern Cape, Endliniyokozi, *Hughes M. & al. MH1126* (E), HQ719075, HQ719192, *KR704011. *Streptocarpus primulifolius* Gand. 6, South Africa: Eastern Cape, Dwalana Forest, *Bellstedt D.U. DUB0587* (STE), HQ719079, HQ719196, *KR704012. *Streptocarpus prolixus* C.B. Clarke, South Africa: Natal, Pinetown Distr., Everton, *Leep & Pasche E. LEP72/2* (E), AF316973, –, –, **Streptocarpus pumilus* B.L.Burt, Zimbabwe, Domboshawa, *Weigend M. s.n.* (E), AF316948, *KR703904, *KR704013. *Streptocarpus pusillus* Harvey ex C.B. Clarke 1, South Africa: KwaZulu-Natal, Mt. Gilboa, *Bellstedt D.U. DUB1029a* (STE), HQ718983, HQ719100, HQ718907. *Streptocarpus pusillus* Harvey ex C.B. Clarke 2, South Africa: Natal, Anne Rennie's Mountain sunset farm, Bulwer, ex *RBG Kew 1983-1816* (K), AF316945, –, *KR704014. *Streptocarpus rexii* (Bowie ex Hook.) Lindl. 1, South Africa: Eastern Cape, Kologha center, *Hughes M. & al. MH1149* (E), HQ719088, HQ719205, *KR704015. *Streptocarpus rexii* (Bowie ex Hook.) Lindl. 2, South Africa: Eastern Cape, Tsitsikamma, *Hughes M. & al. MH1180* (E), HQ719096, HQ719212, *KR704016. *Streptocarpus rimicola* Story 1, South Africa: Limpopo, Thabazimbi, *Bellstedt D.U. DUB1047* (STE), HQ718997, HQ719114, HQ718921. *Streptocarpus rimicola* Story 2, South Africa: Limpopo, Thabazimbi, *Bellstedt D.U. DUB1048* (STE), HQ718998, HQ719115, HQ718922. *Streptocarpus roseo-albus* Weigend & T.J. Edwards, South Africa: Mpumalanga, Agnes Mine, *Hughes M. & al. MH1353* (E), *KR704137, –, *KR704017. *Streptocarpus sambiranensis* Humbert, Madagascar: Antsiranana, Sambirano basin, *Humbert H. HH18583* (E), *KR704138, *KR703905, *KR704018. *Streptocarpus saundersii* Hook. 1, South Africa: KwaZulu-Natal, Inanda, *Styles D.G.A. DGA3013_02* (Bews Herbarium, PMB), HQ719006, HQ719123, HQ718926. *Streptocarpus saundersii* Hook. 2, South Africa: Ozwatini Plateau, *Styles D.G.A. DGA3021* (Bews Herbarium, PMB), –, HE861728, HE956772. *Streptocarpus saxorum* Engl., Tanzania: Usambara, Tanga region, *Mather S. 1330* (E), AF316914, *KR703906, *KR704019. *Streptocarpus schliebenii* Mansf. 1, Tanzania: Ukaguru Mts, *Burt B.L. s.n.* (E), AF316941, *KR703907, *KR704020. *Streptocarpus schliebenii* Mansf. 2, Tanzania: Ukaguru Mts, *Mabberley D.J. 1398* (E), *KR704139, –, –, **Streptocarpus schliebenii* Mansf. 3, Tanzania: Morogoro, Gairo, Mnyera Peak, Ukaguru Mts, *Barber S. & Galloway L. TZBG37* (E), *KR704140, *KR703908, *KR704021. *Streptocarpus silvaticus* Hilliard, South Africa: Natal Province, Lion's River Distr., Karkloof range, Benvie, *Hilliard O.M. & Burt B.L. HBT19107* (E, photo), AF316970, *KR703909, *KR704022. *Streptocarpus solenanthus* Mansf., Malawi: unknown locality, *La Croix I.F. s.n.* (E), AF316958, –, –, **Streptocarpus sp. nov.* 1, South Africa: Laager farm, *Styles D.G.A. DGA3014* (Bews Herbarium, PMB), *KR704119, HE861723, –, **Streptocarpus sp. nov.* 2, South Africa: Inanda Mountain, towards Wartberg, *Styles D.G.A. DGA3006* (Bews Herbarium, PMB), *KR704120, HE861722, –, **Streptocarpus stomandrus* B.L.Burt 1, Tanzania: Nguru Mts, *Mabberley D.J. 687C* (E), AF316915, *KR703910, *KR704023. *Streptocarpus stomandrus* B.L.Burt 2, Tanzania: Morogoro, Mvomero, Manyangu Forest, *Barber S. & Galloway L. TZBG23* (E), *KR704141, *KR703911, *KR704024. *Streptocarpus suffruticosus* Humbert, Madagascar: Antsiranana, Marojezy RN12, *Moeller M. & Andriantiana J. MM9877A* (E), MacMaster & al. (2005), *KR703912, MacMaster & al. (2005). *Streptocarpus tanala* Humbert 1, Madagascar: Tulear, Analara, Andranohela River, *Moeller M. & Rafanantsoa G. MM9710* (E), AF316906, *KR703913, *KR704025. *Streptocarpus tanala* Humbert 2 (C & E Madagascar), *Lowry II P.P. 4364* (TAN), *KR704142, –, *KR704026. *Streptocarpus thompsonii* R. Brown 1, Madagascar: Analalava Forest, Andringitra, *Bellstedt D. DUB1258* (STE, TAN), *KR704143, –, *KR704027. *Streptocarpus thompsonii* R. Brown 2, Madagascar: Antananarivo, Angavo, *Moeller M. & Rafanantsoa G. MM9851* (E), *KR704144, *KR703914, *KR704028. *Streptocarpus thysanotus* Hilliard & B.L.Burt, Tanzania: Morogoro Distr., Kimboza, ex *AGGS (Moeller M. MMOG-90)* (E), AF316910, *KR703915, *KR704029. *Streptocarpus trabeculatus* Hilliard, ex cult. (South Africa: E. Cape, Natal), ex *Chiltern Seeds s.n.* (E), AF316969, –, –, **Streptocarpus tsaratananensis* Humbert ex B.L.Burt, Madagascar: unknown locality, *Gautier L. LG3600* (G), MacMaster & al. (2005), –, MacMaster & al. (2005). *Streptocarpus umtaliensis* B.L.Burt, Zimbabwe, Manicaland Province, Leopard Rock Hotel, Bvumba, *Clark 498* (STE), *KR704145, *KR703916, *KR704030. *Streptocarpus vandeleurii* E.G. Baker & S. Moore 1, South Africa: Limpopo, Thabazimbi, *Bellstedt D.U. DUB1055* (STE), HQ718995, HQ719112, HQ718919. *Streptocarpus vandeleurii* E.G. Baker & S. Moore 2, South Africa: Limpopo, Thabazimbi, *Bellstedt D.U. DUB1055* (STE), HQ718996, HQ719113, HQ718920. *Streptocarpus variabilis* Humbert 1, Madagascar: Anjouan Island, *Pócs T. 9282A* (E), *KR704146 (short), –, *KR704031. *Streptocarpus variabilis* Humbert 2, Madagascar: Anjouan Island, *Pócs T. 9282A* (E), *KR704147, *KR703917, *KR704032. *Streptocarpus variabilis* Humbert 3, Madagascar: Road to Beolamana, *Moeller M. MMOG32* (E), *KR704148, *KR703918, *KR704033. *Streptocarpus venosus* B.L.Burt, Madagascar: Tulear, Andranohela River, *Moeller M. & Rafanantsoa G. MM9711* (E), *KR704149, *KR703919, *KR704034. *Streptocarpus wendlandii* Spreng. 1, ex cult. (South Africa: Natal; Mtunzini Distr., Ngoye forest), ex *Hannover B.G. s.n.* (E), AF316967, –, *KR704035. *Streptocarpus wendlandii* Spreng. 2, South Africa: KwaZulu-Natal: Ngoye Forest, Mtunzini., *Bellstedt D.U. DUB1336/1345* (STE), *KR704150, HE861729, HE956773. *Streptocarpus wilmsii* Engl., South Africa: Mpumalanga, God's Window, *Potgieter C. CP907* (Bews Herbarium, PMB), *KR704151, HE861730, HE956774. *Streptocarpus wittei* DeWild., Malawi: Rumpi Distr., Nyika, *La Croix I.F. s.n.* (E), AF316953, –, *KR704036. *Trachystigma manii* C.B. Clarke (Gabon), *deWilde, Sosef & Van Nek 10139* (Leiden), *KR704152, *KR703920, *KR704037.

† these collections from KwaZulu Natal Province, South Africa will be described "*Streptocarpus medley-woodii*" in sect. *Streptocarpus*.

Appendix 2. Origin of the material used in the phylogenetic analyses of matrix Sa58.

Taxon, locality, collector(s), collector number, herbarium code, and ITS and 5S NTS GenBank accession numbers. Asterisk indicates newly generated sequences.

Saintpaulia brevipilosa B.L.Burtt_1, Tanzania: Kanga forest, Mt. Kanga (Nguru Mts), Pócs, T. s.n. (E), AF316924, AF307025. *Saintpaulia brevipilosa* B.L.Burtt_2, Tanzania: unknown locality, RBG Kew 1995-503 (K), –, AF108733. *Saintpaulia* cf. *inconspicua* B.L.Burtt_1, Tanzania: Uluguru Mts, unknown locality, Watkins C. CW430/01/03 (–), *KR704050, –. *Saintpaulia* cf. *ionantha* H.Wendl., Tanzania: Tanga, Sigi River, Moors D.R. s.n. (–), AF316923, AF307034. *Saintpaulia confusa* B.L.Burtt_1, Tanzania: Usambara Mts, Smith J. R6677 (E), *KR704060, AF307027. *Saintpaulia confusa* B.L.Burtt_2, Tanzania: unknown locality, RBG Kew 1974-2873 (K), *KR704061, AF108728. *Saintpaulia difficilis* B.L.Burtt_1, Tanzania: Tanga Region, Bogner J. BNR (E), *KR704045, AF307028. *Saintpaulia difficilis* B.L.Burtt_2, Tanzania: Tanga Region, Mather I.C. MAT1 (E), *KR704062, AF324926. *Saintpaulia difficilis* B.L.Burtt_3, Tanzania: E Usambara Mts, Kwamkoro, Lindqvist C. Kiganga.1 (–), AF307019. *Saintpaulia diplotricha* B.L.Burtt, Tanzania: Tanga Region, ex Munich Univ. s.n. (E), *KR704046, AF307029. *Saintpaulia goetzeana* Engl._1, ex cult. (Tanzania: Uluguru Mts), Evans M.J. (AGGS) s.n. (E, photo), *KR704047, AF307030. *Saintpaulia goetzeana* Engl._2, Tanzania: Mbete–Lupanga peak, N Uluguru Forest Reserve, Morogoro, Lindqvist C. Lupanga.1 (–), *KR704063, AF108734. *Saintpaulia goetzeana* Engl._3, Tanzania: Kilangala, South Uluguru Forest Reserve, Morogoro, Lindqvist C. Kilangala.1 (–), *KR704064, AF108735. *Saintpaulia grandifolia* B.L.Burtt_1, ex cult. (Tanzania), ex Hannover B.G./Marburg B.G., MMOG–240 (E), *KR704048, –. *Saintpaulia grandifolia* B.L.Burtt_2, Tanzania: Tanga Region, W Usambara Mts, Mather I.C. MAT13 (E), *KR704065, AF307031. *Saintpaulia grandifolia* B.L.Burtt_3, ex cult. (Tanzania), ex Hannover B.G./Marburg B.G. s.n. (E), *KR704066, –. *Saintpaulia grandifolia* B.L.Burtt_4, Tanzania: W Usambara Mts, Lindqvist C. Nkoloi Stream.3 (–), –, AF307021. *Saintpaulia grotei* Engl._1, Tanzania: E. Usambara Mts, ex Munich Univ. s.n. (E), *KR704049, AF307032. *Saintpaulia grotei* Engl._2, Tanzania: Usambara Mts, ex RBG Kew 1995-511 (K), –, AF108729. *Saintpaulia inconspicua* B.L.Burtt_2, Tanzania: Uluguru Mts, unknown locality, Watkins C. s.n. (E), *KR704051, –. *Saintpaulia intermedia* B.L.Burtt, Tanzania: E Usambara Mts, Kigongoi, ex Phillips Univ. Marburg B.G. s.n. (E), *KR704067, AF307033. *Saintpaulia ionantha* H.Wendl. ‘Sigi Falls’, Tanzania: Tanga, Sigi Falls ex RBG Kew 1987-1280 (–), *KR704068, AF307035. *Saintpaulia ionantha* H.Wendl., Tanzania: Ulang Distr., Uzyngwa Mts, ex RBG Kew 1987-8132 (K), *KR704069, AF108732. *Saintpaulia magungensis* E.P.Roberts var. *minima* B.L.Burtt_1, Tanzania: E Usambara Mts, Marvera, Punter W.R. 1181 (E), *KR704070, AF307038. *Saintpaulia magungensis* E.P.Roberts var. *minima* B.L.Burtt_2, Tanzania: unknown origin, ex RBG Kew 1963-42311 (K), –, AF108738. *Saintpaulia magungensis* E.P.Roberts_1, ex cult. (Tanzania: E. Usambara Mts), ex RBG Kew 1983-8183 (E), *KR704072, AF307037. *Saintpaulia magungensis* E.P.Roberts_2, Tanzania: Usambara Mts, Lindqvist C. Magunga.4 (–), *KR704052, AF108737. *Saintpaulia magungensis* var. *occidentalis* B.L.Burtt, Tanzania: Usambara Mts, Mather I.C. MAT15 (–), *KR704071, AF307039. *Saintpaulia nitida* B.L.Burtt_1, ex cult. (Tanzania: Nguru Mts), ex RBG Kew 1987-1566 (E), AF316925, –. *Saintpaulia nitida* B.L.Burtt_2, Tanzania: Nguru Mts, ex Basel Univ. B.G. CL8/99 (E), *KR704073, AF324927. *Saintpaulia orbicularis* B.L.Burtt_1, Tanzania: Ambangulu–Kunga Road, West Usambara Mts, Lindqvist C. Kwabulu.5 (–), –, AF108740. *Saintpaulia orbicularis* B.L.Burtt_2, Tanzania: W Usambara Mts, Ambangulu Tea Estate, ex RBG Kew 1987-1370 (K), –, AF108739. *Saintpaulia orbicularis* B.L.Burtt_3, Tanzania: W Usambara Mts, Ambangulu Tea Estate (ex cult.), ex Munich Univ. B.G. s.n. (E), *KR704075, AF324928. *Saintpaulia orbicularis* var. *purpurea* B.L.Burtt, Tanzania: W Usambara Mts, Ambangulu, Punter W.R. s.n. (E), *KR704074, AF307041. *Saintpaulia pendula* B.L.Burtt, Tanzania: E Usambara Mts, E of Mawera Tea Estate, Smith J., JS10 (E), *KR704076, AF307043. *Saintpaulia pendula* var. *kizarae* B.L.Burtt, ex cult. (Tanzania: NE Usambara Mts), ex Phillips Univ. Marburg B.G. s.n. (E), *KR704053, AF307042. *Saintpaulia pusilla* Engl._1, Tanzania: Magari Peak, North Uluguru Forest Reserve, Morogoro, Lindqvist C. Magari.1 (–), *KR704077, AF108741. *Saintpaulia pusilla* Engl._2, Tanzania: unknown locality, Mabberley D.J. 1362 (E), *KR704054, –. *Saintpaulia rupicola* B.L.Burtt ‘Kacharoroni’_1, Kenya: Kacharoroni, Lindqvist C. CL–97003 (–), *KR704078, AF108743. *Saintpaulia rupicola* B.L.Burtt ‘Kacharoroni’_2, Kenya: Kilifi Distr., Kacharoroni Gorge, Smith J. R+L5126 (E), *KR704079, AF307045. *Saintpaulia rupicola* B.L.Burtt ‘Mwache’, Kenya: Mwache Forest Reserve, Pearce 543-94-530.1 (–), *KR704080, AF108744. *Saintpaulia rupicola* B.L.Burtt ‘Mwarakaya’, Kenya: Kaloleni, Mwarakaya, Smith J. JS02 (E), *KR704081, AF307046. *Saintpaulia rupicola* B.L.Burtt_1, ex cult. (Kenya), ex Hannover B.G. VS2.2 (E), *KR704055, AF307044. *Saintpaulia rupicola* B.L.Burtt_2, Kenya: Chasimba, Lindqvist C. CL97002.1 (–), *KR704082, AF108742. *Saintpaulia rupicola* B.L.Burtt_3, Kenya: Mwarakaya, Simiyu S. 169-96-1739 (NMK), –, AF108745. *Saintpaulia shumensis* B.L.Burtt_1, ex cult. (Tanzania: W. Usambara Mts, Mt Shume), Clements T. s.n. (E), *KR704056, AF307047. *Saintpaulia shumensis* B.L.Burtt_2, Tanzania: West Usambara Mts, Shume Hill, Lindqvist C. Shume.1 (–), –, AF108746. *Saintpaulia teitensis* B.L.Burtt_1, Kenya: Mbololo, Teita Hills, Punter W.R. s.n. (E), AF316922, AF307048. *Saintpaulia teitensis* B.L.Burtt_2, Kenya: Teita Hills, Mbololo, Wallace B.J. & Forlonge L.J. WFO336 (–), *KR704083, AF307049. *Saintpaulia teitensis* B.L.Burtt_3, Kenya: Teita Hills, Mbololo, Lindqvist C. CL-97001 (–), *KR704084, AF108747. *Saintpaulia tongwensis* B.L.Burtt_1, Tanzania: Tanga Region, Clements T. Mather 2 (–), FJ501303, AF307050. *Saintpaulia tongwensis* B.L.Burtt_2, Tanzania: Tongwe Mt., Tongwe Forest Reserve, Lindqvist C. Tongwe.9 (–), –, AF108730. *Saintpaulia tongwensis* B.L.Burtt_3, Tanzania: Tanga Region, Pangani Falls, Lindqvist C. Pangani Falls.97010 (–), –, AF108748. *Saintpaulia ulugurensis* Haston, Tanzania: Morogoro, Uluguru Mts, Haston E. 102 (E), *KR704057, –. *Saintpaulia velutina* B.L.Burtt, ex cult. (Tanzania: Usambara Mts), ex Munich University s.n. (E), FJ501304, AF307051. *Saintpaulia watkinsii* Haston_1, Tanzania: Morogoro, Morogoro–Rural, Lusangalala area, Tegetero, Uluguru Nature Reserve, Barber S. & Galloway L. TZBG65 (E), *KR704058, –. *Saintpaulia watkinsii* Haston_2, Tanzania: Morogoro, Uluguru Mts, Haston E. 99 (E), *KR704059, –. *Streptocarpus caulescens* Vatke, Tanzania: Morogoro Region, Uluguru Mts, Harris B. HRR4091 (E), AF316920, AF108727.

Appendix 3. List of species by section of *Streptocarpus*. * indicates placement based on morphological grounds. Remaining species included in the molecular phylogeny. Types of section names in bold italics.

| | |
|---|--|
| <i>Streptocarpus</i> subg. <i>Streptocarpella</i> Fritsch | (“c”) sect. <i>Hova</i> (C.B. Clarke) Mich.Möller & Nishii, comb. nov. |
| (“a”) sect. <i>Trachystigma</i> (C.B. Clarke) Mich.Möller & Nishii, comb. nov. | <i>Streptocarpus hilsenbergii</i> R.Br. var. <i>hilsenbergii</i> |
| <i>Streptocarpus diandra</i> (Engl.) Nishii & Mich.Möller, comb. nov. | <i>Streptocarpus hilsenbergii</i> var. <i>angustifolius</i> Humbert ex B.L.Burtt |
| <i>Streptocarpus insularis</i> Hutch. & Dalziel | <i>Streptocarpus integrifolius</i> B.L.Burtt* |
| <i>Streptocarpus mannii</i> (C.B. Clarke) Nishii & Mich.Möller, comb. nov. | <i>Streptocarpus leandrii</i> Humbert* var. <i>leandrii</i> |
| <i>Streptocarpus nobilis</i> C.B. Clarke in DC | <i>Streptocarpus leandrii</i> var. <i>robustus</i> B.L.Burtt* |
| <i>Streptocarpus strigosus</i> (Hook.f.) Nishii & Mich.Möller, comb. nov. | <i>Streptocarpus levis</i> B.L.Burtt |
| (“b”) sect. <i>Parasaintpaulia</i> Mich.Möller & Nishii, sect. nov. | <i>Streptocarpus linguatus</i> B.L.Burtt |
| <i>Streptocarpus andohahelensis</i> Humbert | <i>Streptocarpus madagascariensis</i> (C.B. Clarke) Christenh. |
| <i>Streptocarpus beampingaratrensis</i> Humbert subsp. <i>beampingaratrensis</i> | <i>Streptocarpus muscosus</i> C.B. Clarke. |
| var. <i>beampingaratrensis</i> | <i>Streptocarpus oliganthus</i> B.L.Burtt |
| <i>Streptocarpus beampingaratrensis</i> subsp. <i>antambolorum</i> Humbert | <i>Streptocarpus prostratus</i> Humbert* var. <i>prostratus</i> |
| <i>Streptocarpus beampingaratrensis</i> subsp. <i>antankarana</i> Humbert* | <i>Streptocarpus prostratus</i> var. <i>major</i> B.L.Burtt* |
| <i>Streptocarpus beampingaratrensis</i> subsp. <i>beampingaratrensis</i> var. | <i>Streptocarpus tanala</i> Humbert |
| <i>brevicarpus</i> Humbert* | <i>Streptocarpus thompsonii</i> R.Br. var. <i>thompsonii</i> |
| <i>Streptocarpus mandrerensis</i> Humbert* | <i>Streptocarpus thompsonii</i> var. <i>bojeri</i> (R. Br.) C.B. Clarke* |

Appendix 3. Continued.

- Streptocarpus venosus* B.L.Burtt in Humbert
Streptocarpus vestitus (Baker) Christenh.
(“d”) sect. *Schizoboea* (Fritsch) Mich.Möller & Nishii, comb. nov.
Streptocarpus elongatus Engl.
Streptocarpus gonjaensis Engl.*
Streptocarpus kamerunensis (Engl.) Christenh.
Streptocarpus kimbozanus B.L.Burtt
Streptocarpus muscicola Engl.*
Streptocarpus thysanotus Hilliard & B.L.Burtt
(“e”) sect. *Carnosifolii* Mich.Möller & Nishii, sect. nov.
Streptocarpus bambuseti B.L.Burtt*
Streptocarpus euanthus Mansf.*
Streptocarpus hirsutissimus E.A.Bruce*
Streptocarpus kirkii Hook.f.
Streptocarpus saxorum Engl.
Streptocarpus stomandrus B.L.Burtt
(“f”) sect. *Caulescens* (Fritsch) Engl.
Streptocarpus buchananii C.B.Clarke
Streptocarpus caulescens Vatke
Streptocarpus glandulosissimus Engl.
Streptocarpus holstii Engl.
Streptocarpus inflatus B.L.Burtt
Streptocarpus pallidiflorus C.B.Clarke
(“g”) sect. *Saintpaulia* (H. Wendl.) Mich.Möller & Haston, comb. & stat. nov.
Streptocarpus afroviola Christenh.
Streptocarpus brevipilosus (B.L.Burtt) Mich.Möller & Haston, comb. nov.
Streptocarpus goetzeanus (Engl.) Christenh.
Streptocarpus inconspicuus (B.L.Burtt) Christenh.
Streptocarpus ionanthus (H.Wendl.) Christenh. subsp. *ionanthus* var. *ionanthus*
Streptocarpus ionanthus subsp. *grandifolius* (B.L.Burtt) Christenh.
Streptocarpus ionanthus subsp. *grotei* (Engl.) Christenh.
Streptocarpus ionanthus subsp. *ionanthus* var. *diplotrichus* (B.L.Burtt) Christenh.
Streptocarpus ionanthus subsp. *mafiensis* (I.Darbysh. & Pócs) Christenh.
Streptocarpus ionanthus subsp. *occidentalis* (B.L.Burtt) Christenh.
Streptocarpus ionanthus subsp. *orbicularis* (B.L.Burtt) Christenh.
Streptocarpus ionanthus subsp. *pendulus* (B.L.Burtt) Christenh.
Streptocarpus ionanthus subsp. *rupicolus* (B.L.Burtt) Christenh.
Streptocarpus ionanthus subsp. *velutinus* (B.L.Burtt) Christenh.
Streptocarpus nitidus (B.L.Burtt) Mich.Möller & Haston, comb. nov.
Streptocarpus shumensis (B.L.Burtt) Christenh.
Streptocarpus teitensis (B.L.Burtt) Christenh.
Streptocarpus ulugurensis (Haston) Haston, comb. nov.
Streptocarpus watkinsii (Haston) Haston, comb. nov.
- Streptocarpus* subg. *Streptocarpus***
(“h”) sect. *Lignostreptocarpus* Mich.Möller & Bellstedt, sect. nov.
Streptocarpus campanulatus B.L.Burtt*
Streptocarpus coursii Humbert*
Streptocarpus glabrifolius Humbert*
Streptocarpus macropodus B.L.Burtt
Streptocarpus papangae Humbert
Streptocarpus suffruticosus Humbert var. *suffruticosus*
Streptocarpus suffruticosus var. *hirtellus* Humbert*
Streptocarpus suffruticosus var. *pachycarpus* B.L.Burtt*
Streptocarpus suffruticosus var. *sericeus* B.L.Burtt*
Streptocarpus tsaratananensis Humbert ex B.L.Burtt
(“i”) sect. *Colpogyne* Mich.Möller & Bellstedt, comb. & stat. nov.
Streptocarpus ibityensis Humbert
Streptocarpus itremensis B.L.Burtt
Streptocarpus lanatus MacMaster
Streptocarpus revivescens Humbert ex B.L.Burtt*
Streptocarpus betsiliensis Humbert
(“j”) sect. *Plantaginei* Mich.Möller & Bellstedt, sect. nov.
Streptocarpus boinensis Humbert*
Streptocarpus brevistamineus Humbert
Streptocarpus cordifolius Humbert*
Streptocarpus hildebrandtii Vatke
Streptocarpus lokohensis Humbert
Streptocarpus mangindranensis Humbert
- Streptocarpus perrieri* Humbert
Streptocarpus plantagineus Vatke*
Streptocarpus polyphyllus Humbert*
Streptocarpus sambiranensis Humbert
Streptocarpus stellulifer B.L.Burtt*
Streptocarpus suborbicularis B.L.Burtt in Humbert
Streptocarpus variabilis Humbert
Streptocarpus velutinus B.L.Burtt in Humbert
(“k”) sect. *Protostreptocarpus* Mich.Möller & Bellstedt, sect. nov.
Streptocarpus albus (E.A.Bruce) I.Darbysh. subsp. *albus*
Streptocarpus albus subsp. *edwardsii* (Weigend) I.Darbysh.*
Streptocarpus heckmannianus (Engl.) I.Darbysh. subsp. *heckmannianus**
Streptocarpus heckmannianus subsp. *gracilis* (E.A.Bruce) I.Darbysh.*
Streptocarpus subscandens (B.L.Burtt) I.Darbysh.*
Streptocarpus bullatus Mansf.
Streptocarpus montanus Oliver
Streptocarpus parensis B.L.Burtt
Streptocarpus schliebenii Mansf.
Streptocarpus lineatus (B.L.Burtt) Mich.Möller & M.Hughes, comb. nov.
- (“l”) sect. *Streptocarpus***
Streptocarpus actinoflorus T.J.Edwards & M.Hughes*
Streptocarpus arcuatus Hilliard & B.L.Burtt*
Streptocarpus aylae T.J.Edwards
Streptocarpus baudertii L.L.Britten
Streptocarpus bindseili Eb. Fisch.
Streptocarpus bolusii C.B.Clarke
Streptocarpus brachynema Hilliard & B.L.Burtt*
Streptocarpus breviflos (C.B.Clarke) C.B.Clarke in Dyer*
Streptocarpus burttianus T.Pócs*
Streptocarpus caeruleus Hilliard & B.L.Burtt
Streptocarpus candidus Hilliard
Streptocarpus compressus B.L.Burtt
Streptocarpus confusus Hilliard subsp. *confusus**
Streptocarpus confusus subsp. *lebomboensis* Hilliard & B.L.Burtt
Streptocarpus cooksonii B.L.Burtt
Streptocarpus cooperi C.B.Clarke
Streptocarpus cyanandrus B.L.Burtt
Streptocarpus cyaneus S.Moore subsp. *cyaneus*
Streptocarpus cyaneus subsp. *longi-tommii* Weigend & T.J.Edwards
Streptocarpus cyaneus subsp. *nigridens* Weigend & T.J.Edwards
Streptocarpus cyaneus subsp. *polackii* (B.L.Burtt) Weigend & T.J.Edwards*
Streptocarpus daviesii N.E.Br. ex C.B.Clarke
Streptocarpus davyi S.Moore
Streptocarpus decipiens Hilliard & B.L.Burtt
Streptocarpus denticulatus Turill
Streptocarpus dolichanthus Hilliard & B.L.Burtt
Streptocarpus dunnii Hook.f.
Streptocarpus erubescens Hilliard & B.L.Burtt
Streptocarpus eylesii S.Moore subsp. *eylesii*
Streptocarpus eylesii subsp. *brevistylus* Hilliard & B.L.Burtt*
Streptocarpus eylesii subsp. *chalenis* I.Darbysh.*
Streptocarpus eylesii subsp. *silvicola* Hilliard & B.L.Burtt*
Streptocarpus fanniniae Harvey ex C.B.Clarke
Streptocarpus fasciatus T.J.Edwards & C.Kunhardt
Streptocarpus fenestra-dei Weigend & T.J.Edwards
Streptocarpus floribundus Weigend & T.J.Edwards
Streptocarpus formosus (Hilliard & B.L.Burtt) T.J.Edwards
Streptocarpus galpinii Hook.f.
Streptocarpus gardenii Hook.
Streptocarpus goetzei Engl.
Streptocarpus grandis N.E.Br. subsp. *grandis*
Streptocarpus grandis subsp. *septentrionalis* Hilliard & B.L.Burtt*
Streptocarpus haygarthii N.E.Br. ex C.B.Clarke
Streptocarpus hilturtianus T.J.Edwards*
Streptocarpus hirticapsa B.L.Burtt
Streptocarpus hirtinervis C.B.Clarke
Streptocarpus huamboensis Hilliard & B.L.Burtt*
Streptocarpus johannis L.L.Britten
Streptocarpus katangensis DeWild. & T.Durand*
Streptocarpus kentaniensis L.L.Britten & Story
Streptocarpus kungwensis Hilliard & B.L.Burtt

Appendix 3. Continued.

Streptocarpus kunhardtii T.J.Edwards
Streptocarpus latens Hilliard & B.L.Burtt*
Streptocarpus leptopus Hilliard & B.L.Burtt*
Streptocarpus lilliputana Bellstedt & T.J.Edwards
Streptocarpus longiflorus (Hilliard & B.L.Burtt) T.J.Edwards
Streptocarpus makabengensis Hilliard
Streptocarpus meyeri B.L.Burtt
Streptocarpus michelmorei B.L.Burtt
Streptocarpus micranthus C.B.Clarke
Streptocarpus milanjanus Hilliard & B.L.Burtt
Streptocarpus modestus L.L.Britten
Streptocarpus molweniensis Hilliard subsp. *molweniensis*
Streptocarpus molweniensis subsp. *eshowicus* Hilliard & B.L.Burtt*
Streptocarpus monophyllus Welw.
Streptocarpus montigena L.L.Britten
Streptocarpus montis-bingae Hilliard & B.L.Burtt*
Streptocarpus myoporoides Hilliard & B.L.Burtt*
Streptocarpus nimbicola Hilliard & B.L.Burtt
Streptocarpus occultus Hilliard
Streptocarpus parviflorus Hook.f. subsp. *parviflorus*
Streptocarpus parviflorus subsp. *soutpansbergensis* Weigend & T.J.Edwards
Streptocarpus pentherianus Fritsch
Streptocarpus pogonites Hilliard & B.L.Burtt*
Streptocarpus pole-evansii I.Verd.
Streptocarpus polyanthus Hook. subsp. *polyanthus*
Streptocarpus polyanthus subsp. *comptonii* (Mansf.) Hilliard*
Streptocarpus polyanthus subsp. *dracomontanus* Hilliard*
Streptocarpus polyanthus subsp. *verecundus* Hilliard*
Streptocarpus porphyrostachys Hilliard
Streptocarpus primulifolius Gand.
Streptocarpus prolixus C.B.Clarke
Streptocarpus pumilus B.L.Burtt
Streptocarpus pusillus Harvey ex C.B.Clarke
Streptocarpus rexii (Bowie ex Hook.) Lindl.
Streptocarpus rhodesianus S.Moore subsp. *rhodesianus**
Streptocarpus rhodesianus subsp. *grandiflorus* I.Darbysh.*

Streptocarpus rimicola Story
Streptocarpus roseo-albus Weigend & T.J.Edwards
Streptocarpus saundersii Hook.
Streptocarpus silvaticus Hilliard
Streptocarpus solenanthus Mansf.
Streptocarpus trabeculatus Hilliard
Streptocarpus umtaliensis B.L.Burtt
Streptocarpus vandeleurii Baker f. & S.Moore
Streptocarpus wendlandi Spreng.
Streptocarpus wilmsii Engl.
Streptocarpus wittei DeWild.

Uncertae sedis

Streptocarpus burundianus Hilliard & B.L.Burtt — Note: No molecular data available and morphologically incompletely known.
Streptocarpus exsertus Hilliard & B.L.Burtt — Note: See the Results section under “Characteristics and phylogenetic relationships revealed by the Str226 analysis.”
Streptocarpus masiensis DeWild. — Note: No molecular data available and morphologically incompletely known.
Streptocarpus mbeyensis I.Darbysh. — Note: No molecular data available and morphologically incompletely known.
Streptocarpus phaeotrichus B.L.Burtt — Note: No molecular data available and morphologically incompletely known.
Streptocarpus capuronii Humbert — Note: See the Results section under “Characteristics and phylogenetic relationships revealed by the Str226 analysis.”
Streptocarpus semijunctus B.L.Burtt — Note: No molecular data available and morphologically incompletely known.
Streptocarpus stenosepalus B.L.Burtt — Note: No molecular data available and morphologically incompletely known.
Streptocarpus tsimhetorum Humbert — Note: No molecular data available and morphologically incompletely known.

Uncertain and doubtful taxa

?*Streptocarpus zimmermanii* Engl.