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# EVOLUTION OF MORPHOLOGICAL NOVELTY: A PHYLOGENETIC ANALYSIS OF GROWTH PATTERNS IN *STREPTOCARPUS* (GESNERIACEAE)

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*Abstract.*—*Streptocarpus* shows great variation in vegetative architecture. In some species a normal shoot apical meristem never forms and the entire vegetative plant body may consist of a single giant cotyledon, which may measure up to 0.75 m (the unifoliate type) or with further leaves arising from this structure (the rosulate type). A molecular phylogeny of 87 taxa (77 *Streptocarpus* species, seven related species, and three outgroup species) using the internal transcribed spacers and 5.8S region of nuclear ribosomal DNA suggests that *Streptocarpus* can be divided into two major clades. One of these broadly corresponds to the caulescent group (with conventional shoot architecture) classified as subgenus *Streptocarpella,* whereas the other is mainly composed of acaulescent species with unusual architecture (subgenus *Streptocarpus*). Some caulescent species (such as *S. papangae*) are anomalously placed with the acaulescent clade. Available cytological data are, however, completely congruent with the two major clades: the caulescent clade is x = 15 and the acaulescent clade (including the caulescent *S. papangae*) is x = 16 (or polyploid multiples of 16). The genera *Linnaeopsis, Saintpaulia,* and *Schizoboea* are nested within *Streptocarpus.* The sequenced region has evolved, on average, 2.44 times faster in the caulescent clade than in the acaulescent clade and this is associated with the more rapid life cycle of the caulescents. Morphological variation in plant architecture within the acaulescent clade is homoplastic and does not appear to have arisen by unique abrupt changes. Instead, rosulate and unifoliate growth forms have evolved several times, reversals have occurred, and intermediate architectures are found. An underlying developmental plasticity seems to be a characteristic of the acaulescent clade and is reflected in a great lability of form.

*Key words.*—Gesneriaceae, phyllomorph, phylogeny, plant architecture, shoot apical meristem, *Streptocarpus.*

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*Streptocarpus* Lindley (Gesneriaceae) is a genus of about 130 species from Africa, Madagascar, and the Comoro Islands from which the familiar Cape primroses of horticulture are derived. *Streptocarpus* species are striking for their nonclassical morphology (Jong 1970, 1973, 1978; Jong and Burtt 1975). The acaulescent species do not form a conventional shoot apical meristem (SAM). Instead, the vegetative portion of the plant is composed of leaves that typically have continued growth of the lamina from a basal meristem and a stemlike petiole (termed a ''petiolode'') formed from a petiolode meristem (an intercalary meristem extending across the base of the midrib, topographically at the level of the groove meristem). Inflorescence shoots and additional leaves arise from a groove meristem (an organogenic meristematic region on the adaxial side of the lamina base). Because these leaves are complex organs that possess up to three separate meristems and combine leaflike and stemlike features, the term ''phyllomorph'' has been coined for them (Jong 1973; Jong and Burtt 1975). Some species (''unifoliates'') do not produce additional leaves at the groove meristem. In these species, the only aboveground vegetative growth consists of a greatly enlarged single cotyledon and associated hypocotyl/mesocotyl (mesocotyl being hypocotyl-like tissue that forms in some species after germination between the two cotyledons causing their vertical separation). This cotyledonary phyllomorph (primary phyllomorph) can be up to 0.75 m long in species such as *S. grandis.* If additional phyllomorphs are iterated from the primary and succeeding phyllomorphs, then a rosettelike plant can be produced (the ''rosulate'' growth form). In some rosulate species, the production of phyllomorphs can be highly regular (Jong 1978).

However, many *Streptocarpus* species produce a normal shoot system with a normal SAM initiating decussate leaf pairs (the ''caulescent'' species). These caulescent species may sometimes have a reduced stem axis and spiral phyllotaxis as in *Saintpaulia* or the Madagascan *Saintpaulia*-like species. Like most Old World Gesneriaceae, all *Streptocarpus* (including these caulescent species) show anisocotyly; some enlargement of one cotyledon after germination. In caulescent *Streptocarpus,* there is a delay in the development of a SAM, which corresponds to the period of cotyledonary enlargement. The extreme developmental variation shown by *Streptocarpus* therefore may be prefigured by the developmental oddity of anisocotyly in the Old World Gesneriaceae as a whole. Indeed, some species of *Chirita,* such as *C. micromusa* can be induced by adverse environmental conditions or short days to flower on the enlarged cotyledon without producing a stem system (Jong 1970). Such plastic caulescence is also found in *S. nobilis* (Lawrence 1943). The genus *Monophyllaea* commonly has a unifoliate habit (Cronk and Möller 1997; Tsukaya 1997), but because it belongs to a different tribe of Gesneriaceae, this is likely to be independently derived (Smith et al. 1997). Unlike *Streptocarpus,* in which there are numerous rosulate species, *Monophyllaea* does not usually iterate further phyllomorphs and the inflorescence appears to be a reduced leafy shoot (Weber 1975). In *Streptocarpus* it has been shown that anisocotyly can be prevented and a shootlike structure induced even in the acaulescent species if high exogenous $GA_3$ is applied or if auxin transport is inhibited (Rosenblum and Basile 1984).

The genus *Streptocarpus* has long been divided into two

subgenera: the caulescent *Streptocarpella* and the acaulescent *Streptocarpus.* This division was strengthened by the discovery of a cytological difference, with subgenus *Streptocarpella* having x = 15 and subgenus *Streptocarpus* x = 16 chromosomes (Lawrence 1940). However the dividing line between the two subgenera is not always clear. Adult specimens of *S. schliebenii* have a normal stem morphology conforming to the *Streptocarpella* pattern and it was accordingly classified in that subgenus by Hilliard and Burtt (1971). However, the juvenile stages of *S. schliebenii* show a phyllomorphic pattern and the chromosome number of x = 16 (Milne 1975), suggesting reclassification in subgenus *Streptocarpus* (Burtt 1999). Another problematic species is *S. decipiens,* in which an initial phyllomorphic morphology is succeeded by the production of a leafy stem, but, as with *S. schliebenii* the balance of morphological and cytological evidence suggests a position in subgenus *Streptocarpus* (Hilliard and Burtt 1971).

The abandonment of the classical leaf/shoot dichotomy by some species of *Streptocarpus* and the existence of such a wide range of growth patterns raises questions about the evolution of morphology in the genus. A previous study using internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA (nrDNA) (Möller and Cronk 1997) based on limited sampling suggested that the truly unifoliate species that were included (*S. dunnii, S. eylesi, S. wittei*) formed a single clade characterized by an approximately 40-bp deletion in ITS2, while the rosulate species formed another clade. If this clear-cut division were maintained, it would imply that the unifoliate/rosulate transition (in whatever direction) represents a unique, irreversible event. Such abrupt morphological innovation would conform to a model of evolution that proceeds by rare but major changes (e.g., Bateman and DiMichele 1994). If, however, morphological transitions within *Streptocarpus* are homoplastic (i.e., reversals have occurred and transitions are associated in the tree with species of intermediate morphology), then a different view of the evolution of this morphological innovation would be promoted. Under this model, genetically controlled developmental variability (e.g., variability in the regulation of the homeotic genes responsible for leaf and shoot determination) would allow repeated variation of form, even in fundamental morphological characters, on which selection can act. The evolution of anisocotyly, varying in degree, in almost all the Old World Gesneriaceae, may be an essential precondition for further developmental plasticity. To test these ideas, we therefore wished to expand the phylogenetic analysis of the genus in order to assess in greater detail the relationships between species with different architectures.

## METHODS

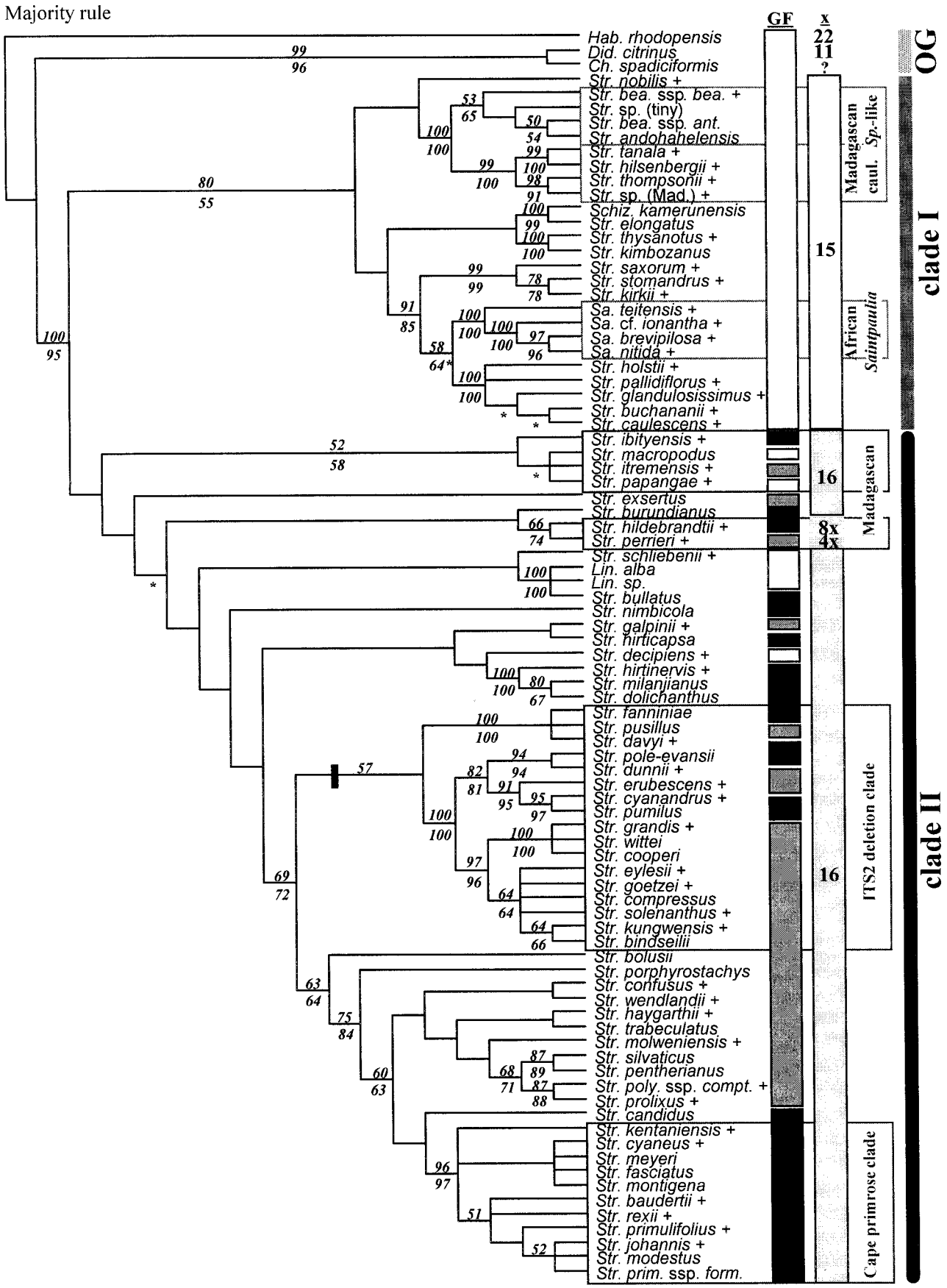
### *Ingroup and Outgroup Selection*

We sequenced 77 species of *Streptocarpus* (Appendix). These include all those assembled over many years in the cultivated collections of the Royal Botanic Garden Edinburgh and several species that were sequenced from herbarium specimens. This represents about 60% of the genus. Although the majority of the African species have been sequenced, a considerably lower representation has been achieved of the less-well-known Madagascan species. Two expeditions to Madagascar by M. Möller attempted to fill this gap.

*Streptocarpus* has been considered a natural group characterized by the twisted fruit. However, it has recently been shown that *Saintpaulia,* a genus without a twisted fruit, is a member of the *Streptocarpus* clade (Möller and Cronk 1997). *Saintpaulia* with its untwisted fruit has been traditionally placed in a genus separate from *Streptocarpus.* This finding prompted us to include other African members of the tribe Didymocarpeae in our analysis, namely *Schizoboea* (one species) and *Linnaeopsis* (two species). Twisted-fruit Gesneriaceae are also found in Asia, but these are divergent in other characters from *Streptocarpus.* However, four Asian species (*S. burmanicus, S. clarkeanus, S. orientalis,* and *S. sumatranus*) are sufficiently similar to *Streptocarpus* to have been retained in that genus pending further examination. We have obtained material of *S. orientalis* from Thailand and find that the ITS and *trn*L-F sequences are highly divergent from African *Streptocarpus* (M. Möller, Q. C. B. Cronk, K. Hellens, and J. Preston, unpubl. data). These Asian *Streptocarpus* were therefore excluded from this analysis. To root the tree unambiguously and to test the monophyly of *Streptocarpus* with respect to the African Didymocarpeae, we have chosen as outgroups three species that are morphologically dissimilar to each other and to *Streptocarpus*: *Chirita spadiciformis* and *Didymocarpus citrinus* from Asia and *Haberlea rhodopensis* from Europe.

### *Molecular Methods*

DNA extraction, polymerase chain reaction (PCR), and DNA sequencing were performed as described previously (Möller and Cronk 1997). For extraction from herbarium specimens, a modified procedure was used: DNA was extracted using the DNeasy genomic plant DNA extraction kit (Qiagen Ltd. Dorking, Surrey, U.K.). This DNA was then additionally purified using the QIAquick PCR purification kit (Qiagen) to remove residual impurities. The complete ITS region was amplified using the modified (Gesneriaceae) primers ITS5P and ITS8P of Möller and Cronk (1997). PCR cycle parameters were set as follows after an initial denaturation step for 3 min at 94°C: denaturation for 1 min at 94°C, primer annealing for 1 min at 55°C, primer extension for 1.5 min at 72°C. After 30 cycles, a final extension step of 5 min at 72°C was added to allow completion of unfinished strands. A negative control (sterile distilled water instead of DNA) was added to each set of reactions. For some herbarium extractions booster-PCR was necessary using primers ITS1 and ITS4 (White et al. 1990), nesting inside primer sites ITS5P and ITS8P, applying the PCR conditions given above. For these samples the complete procedure, starting from DNA extraction to sequencing, was repeated twice to ensure authenticity of the fragments amplified. The spacers were sequenced in four reactions using the dye terminator cycle-sequencing ready-reaction kit (Perkin Elmer, Applied Biosystems Division, Foster City, CA), with AmpliTaq DNA Polymerase, FS, according to the manufacturer's recommendations and analyzed on an ABI377 sequencer. Forward and reverse sequences were compared for sequence confirmation (Möller and Cronk 1997). Individual sequences (GenBank


Majority rule
GF
x
22
11
?
Hab. rhodopensis
Did. citrinus
Ch. spadiciformis
Str. nobilis +
Str. bea. ssp. bea. +
Str. sp. (tiny)
Str. bea. ssp. ant.
Str. andohahelensis
Str. tanala +
Str. hilsenbergii +
Str. thompsonii +
Str. sp. (Mad.) +
Schiz. kamerunensis
Str. elongatus
Str. thysanotus +
Str. kimbozanus
Str. saxorum +
Str. stomandrus +
Str. kirkii +
Sa. teitensis +
Sa. cf. ionantha +
Sa. brevipilosa +
Sa. nitida +
Str. holstii +
Str. pallidiflorus +
Str. glandulosissimus +
Str. buchananii +
Str. caulescens +
Str. ibityensis +
Str. macropodus
Str. itremensis +
Str. papangae +
Str. exsertus
Str. burundianus
Str. hildebrandtii +
Str. perrieri +
Str. schliebenii +
Lin. alba
Lin. sp.
Str. bullatus
Str. nimbicola
Str. galpinii +
Str. hirticapsa
Str. decipiens +
Str. hirtinervis +
Str. milanjianus
Str. dolichanthus
Str. fanniniae
Str. pusillus
Str. davyi +
Str. pole-evansii
Str. dunnii +
Str. erubescens +
Str. cyanandrus +
Str. pumilus
Str. grandis +
Str. wittei
Str. cooperi
Str. eylesii +
Str. goetzei +
Str. compressus
Str. solenanthus +
Str. kungwensis +
Str. bindseilii
Str. bolusii
Str. porphyrostachys
Str. confusus +
Str. wendlandii +
Str. haygarthii +
Str. trabeculatus
Str. molweniensis +
Str. silvaticus
Str. penthierianus
Str. poly. ssp. compt. +
Str. prolixus +
Str. candidus
Str. kentaniensis +
Str. cyaneus +
Str. meyeri
Str. fasciatus
Str. montigena
Str. baudertii +
Str. rexii +
Str. primulifolius +
Str. johannis +
Str. modestus
Str. prim. ssp. form.
Madagascan caul. Sp.-like
15
African Saintpaulia
16
Madagascan
8x
4x
16
ITS2 deletion clade
Cape primrose clade
OG
clade I
clade II

numbers AF316898–AF316984) and the aligned matrix (as Popset) have been submitted to GenBank.

### *Analytical Methods*

The ITS1, ITS2, and 5.8S sequences for all 87 ingroup and outgroup taxa were aligned as described previously (Möller and Cronk 1997). Only unambiguously alignable regions were used in the analyses, with gaps treated as missing data and character states unordered. All phylogenetic analyses were conducted using PAUP versions 4.0b2a and 4 (Swofford 1998). Due to the large size of the data matrix, a three-step maximum-parsimony (MP) search strategy was implemented to optimize the search for most parsimonious trees (see Soltis and Soltis 1997). First, a heuristic search was performed with SIMPLE ADDITION sequence, TREE BISECTION-RECONNECTION (TBR), COLLAPSE (max), and MULTREES on. Second, 10,000 replicates of RANDOM ADDITION were performed, with NEAREST NEIGHBOUR INTERCHANGES (NNI) swapping, MULTREES, and STEEPEST DESCENT deactivated, terminating each replicate after saving not more than two trees of length (n). This length (n) was established empirically in the first heuristic search. Third, the saved trees were subjected to TBR swapping with MULTREES and STEEPEST DESCENT and COLLAPSE (max) on. This strategy is designed to detect multiple islands of most parsimonious trees if they exist.

Descriptive tree statistics (consistency index [CI], retention index [RI], rescaled consistency index [RC]) were derived as described previously (Möller and Cronk 1997), except using PAUP version 4.0b2a. Branch support values were obtained by fast jackknifing (JK) with 33% character deletion (10,000 replicates) and by heuristic bootstrapping (BS) with TBR and MULTREES off (10,000 replicates) (Spangler and Olmstead 1999). To examine the effect of weighting, the characters were reweighted by the mean value of the RC for each character in the most parsimonious trees that were recovered using the procedure above. An additional heuristic search was then performed, using the reweighted characters, collapsing branches with minimum length of zero. The ratio of transitions to transversions was obtained using MacClade 3.01 (Maddison and Maddison 1992).

The constraint option in PAUP was used to analyze tree length increases (over unconstrained trees) when we enforced the respective monophyly of unifoliate, rosulate, and caulescent growth forms. Heuristic search procedures were identical to the previous searches. A similar constraint strategy was applied to test the parallel origin of rosette-caulescent Madagascan *Streptocarpus* species and *Saintpaulia* species. The significance of differences between constrained and unconstrained trees was tested using the Templeton (Wilcoxon signed-ranks) (Templeton 1983) option (TW) in PAUP (Swofford 1998). The three main growth forms were mapped onto the tree. Character mapping was performed on the single MP tree based on reweighted characters (identical in topology to the majority rule consensus tree). Both accelerated (ACCTRAN) and delayed (DELTRAN) character state optimization were employed using equal weighting of gains and losses and terminal polytomies (resulting from the collapse of zero length branches) were resolved randomly using MacClade 3.01 (Maddison and Maddison 1992). Because the MP majority rule tree, the reweighted single tree, and the ML tree (below) all have identical or nearly identical topology, this is the most appropriate phylogenetic hypothesis presently available on which to base the character mapping. However, sensitivity analyses were performed to assess the effect on character mapping of alternative resolution of the most weakly supported internal nodes and of alternative random resolution of the terminal polytomies.

All available ML models were tested using a nested hierarchical approach with Modeltest version 3.0 (Posada and Crandall 1998) under PAUP (Swofford 1998). The model with the highest score under the Akaike information criterion (AIC) was chosen: SYM + I + G. This uses a general time-reversible model with equal base frequency (SYM), variable proportions of invariable sites (I), and gamma-distributed among-site rate variation (G). As a comparison, we also tested the commonly used HKY model, which gave identical results except for some minor changes in the terminal part of the tree.

The hypothesis of a molecular clock was examined in two ways using the appropriate options in PAUP. The significance of branch length variation between clade I (subgenus *Streptocarpella*) and clade II (subgenus *Streptocarpus*) was tested using a likelihood-ratio test (Page and Holmes 1998), either on the MP tree with the highest likelihood score (without ML search routine) including all taxa or on a subset of 21 taxa (with a complete ML search) using the PAUP batch routine (*www.bioss.sari.ac.uk/~frank/newton/lrtclock.nex*). The branch length difference between clades I and II was estimated from the depth of subtrees (as substitutions per site) based on pruned subsets of the taxa (clade I and clade II) separately imposing a molecular clock (ML) (D. Baum, pers. comm.).

## RESULTS

### *Sequence Characteristics and Analysis*

The 87 ingroup and outgroup ITS and 5.8S sequences formed an aligned data matrix of 743 bp in length. The sequences confirm patterns already revealed in a previous anal-

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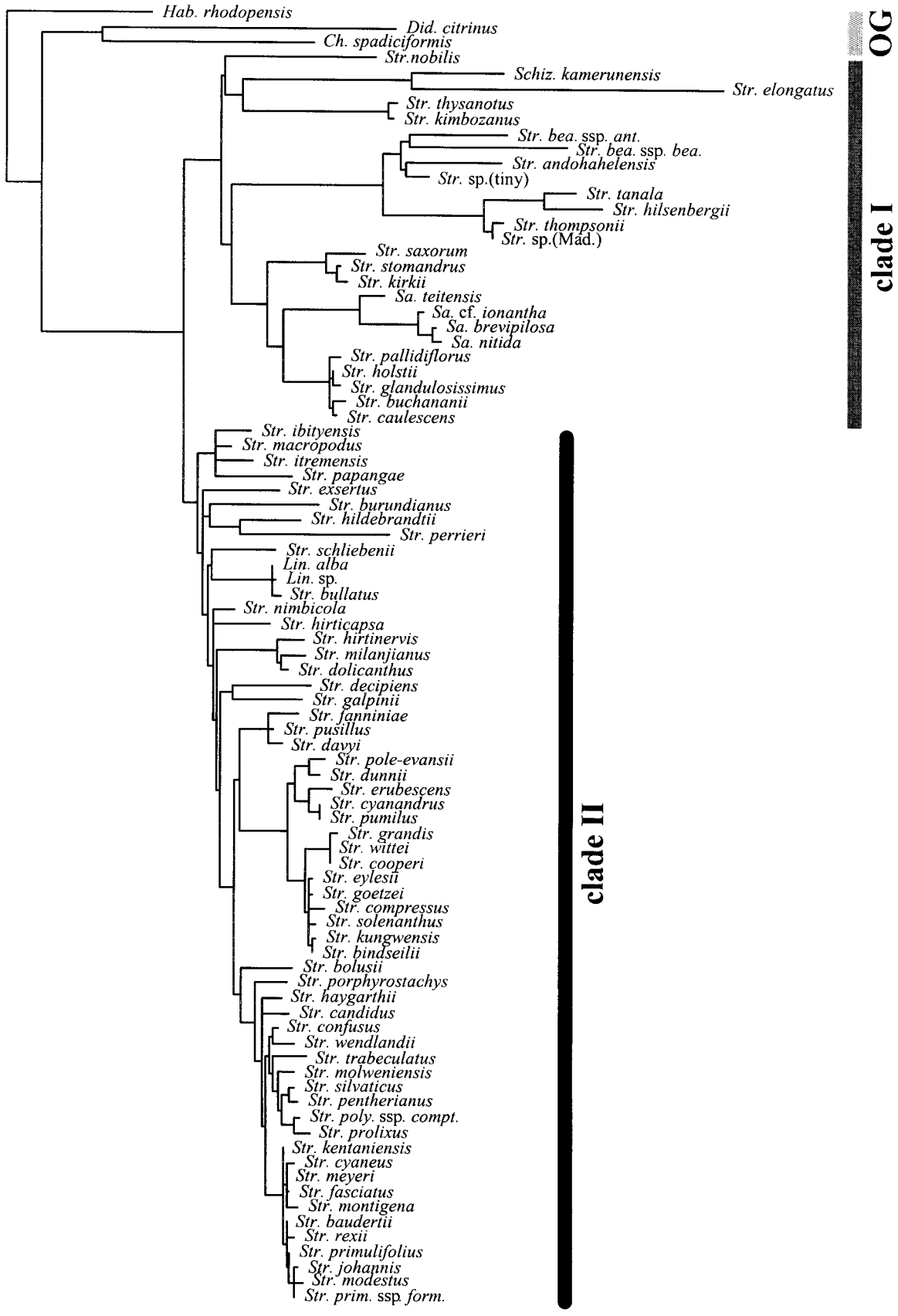
FIG. 1. Majority-rule consensus tree of 1455 most parsimonious trees of 1107 steps, based on ITS1, 5.8S, and ITS2 sequence data. The numbers above the branches are bootstrap values, and the numbers below the branches are jackknife values. This tree is identical in topology to the single maximum-parsimony reweighted tree recovered from the weighted analysis (the polytomies result from the collapse of zero length branches). GF, growth forms defined according to the three major divisions: caulescent, white; unifoliate/plurifoliate, gray; rosulate, black; x, basic chromosome numbers and for *Streptocarpus hildebrandtii* and *S. perrieri* (x = 16), the ploidy level. The majority of species in both clades have been counted (plus sign). The black vertical bar (within the tree) indicates a shared approximately 40-bp deletion event (see text). Clade I refers to the caulescent, subgenus *Streptocarpella* clade; clade II refers to the phyllomorphic, subgenus *Streptocarpus* clade. OG are the outgroup taxa. Nodes that collapse in the strict consensus are indicated by asterisks.


Hab. rhodopensis
Did. citrinus
Ch. spadiciformis
Str.nobilis
Schiz. kamerunensis
Str. elongatus
Str. thysanotus
Str. kimbozanus
Str. bea. ssp. ant.
Str. bea. ssp. bea.
Str. andohahelensis
Str. sp.(tiny)
Str. tanala
Str. hilsenbergii
Str. thompsonii
Str. sp.(Mad.)
Str. saxorum
Str. stomandrus
Str. kirkii
Sa. teitensis
Sa. cf. ionantha
Sa. brevipilosa
Sa. nitida
Str. pallidiflorus
Str. holstii
Str. glandulosissimus
Str. buchananii
Str. caulescens
Str. ibityensis
Str. macropodus
Str. itremensis
Str. papangae
Str. exsertus
Str. burundianus
Str. hildebrandtii
Str. perrieri
Str. schliebenii
Lin. alba
Lin. sp.
Str. bullatus
Str. nimbicola
Str. hirticapsa
Str. hirtinervis
Str. milanjianus
Str. dolicanthus
Str. decipiens
Str. galpinii
Str. fanniniae
Str. pusillus
Str. davyi
Str. pole-evansii
Str. dunnii
Str. erubescens
Str. cyanandrus
Str. pumilus
Str. grandis
Str. wittei
Str. cooperi
Str. eylesii
Str. goetzei
Str. compressus
Str. solenanthus
Str. kungwensis
Str. bindseilii
Str. bolusii
Str. porphyrostachys
Str. haygarthii
Str. candidus
Str. confusus
Str. wendlandii
Str. trabeculatus
Str. molweniensis
Str. silvaticus
Str. pentherianus
Str. poly. ssp. compt.
Str. prolixus
Str. kentaniensis
Str. cyaneus
Str. meyeri
Str. fasciatus
Str. montigena
Str. baudertii
Str. rexii
Str. primulifolius
Str. johannis
Str. modestus
Str. prim. ssp. form.
OG
clade I
clade II
— 0.01 substitutions / site

ysis (Möller and Cronk 1997) in that ITS2 is more length variable than ITS1. Numerous indel events have occurred, the most notable of which is an approximate 40-bp deletion characteristic of 17 species in one clade (Fig. 1). Secondary structure analyses (data not shown) reveal that this deletion corresponds to the end of arm one of the ITS2 RNA folding conformation. Due to alignment ambiguities, 100 characters had to be excluded, including a 77-bp section in ITS2 containing the 40-bp deletion site. Of the 643 unambiguously alignable characters, 364 (56.6%) were variable, of which 262 (40.5%) were potentially informative in parsimony analysis. The sequence divergence ranged from 0.0% (e.g., *S. cyanandrus–S. pumilus*) to 24.3% (*Streptocarpus hilsenbergii–S. elongatus*) between ingroup taxa and from 12.1% (*Haberlea rhodopensis–S. schliebenii*) to 25.8% (*Chirita spadiciformis–S. elongatus*) between ingroup and outgroup taxa. The transition/transversion ratio (Ti/Tv) from the MP analysis was 1.8 across the whole matrix. The ML tree (ln = 6638.09) is almost completely congruent with the MP strict consensus tree (1455 most parsimonius trees of length 1107 steps) except for the position of *S. nobilis,* which in the ML tree is sister to a clade comprising the African species *S. kimbozanus, S. thysanotus, S. elongatus,* and *Schizoboea kamerunensis.* In the MP tree *S. nobilis* is sister to the Madagascan caulescent clade. The MP trees have a CI of 0.503, RI of 0.753, and, therefore a RC of 0.379. Reweighting recovered a single MP tree identical in topology to Figure 1 (CI = 0.725, RI = 0.866, RC = 0.628).

### *Clade Structure of Streptocarpus*

The majority of the caulescent *Streptocarpus* species form a single well-supported (BS = 80, JK = 55) clade (clade I, the ''*Streptocarpella* clade''; see Figs. 1, 2). Two other genera, *Saintpaulia* and *Schizoboea,* are nested within this clade. The Madagascan caulescent species (including the *Saintpaulia*-like species) form a single subclade nested within the African caulescent species (the ''Madagascan caulescent clade'') (BS = 100, JK = 100). Within caulescent clade I, the *Saintpaulia*-like (rosette-caulescent) growth form has arisen twice, once in the genus *Saintpaulia* (BS = 100, JK = 100) and once in the Madagascan *Saintpaulia*-like species (BS = 53, JK = 65). Constraining these two clades to be monophyletic results in a significantly less parsimonious tree (extra 28 steps), significant at the $P < 0.0001$ level in a Templeton (Wilcoxon signed-rank) test (Templeton 1983).

The remainder of the ingroup form a single clade in all the most parsimonious trees (Fig. 1) and a single remaining clade is also recovered by ML analyses (Fig. 2). There is, however, no meaningful bootstrap support for this grouping, and further data is needed to confirm the existence of this provisional clade (clade II, the ''subgenus *Streptocarpus* clade''). The subgenus *Streptocarpus* clade is overwhelmingly acaulescent, but a few caulescent growth forms do occur, notably *Streptocarpus papangae, S. macropodus,* and *S. schliebenii*; these species will be discussed below. Sister to the remainder of the subgenus *Streptocarpus* clade is a clade of Madagascan rosulate polyploids (see below) and the caulescent species *S. papangae* and *S. macropodus* (the ''subgenus *Streptocarpus* basal clade''). Also supported in the analysis is a southern African clade of 40 rosulates and unifoliates (BS = 69, JK = 72), which includes two subclades, an ''ITS2 deletion clade'' (BS = 57, JK = <50), comprising the 17 species with an approximate 40-bp deletion in their ITS2 sequences (positions 491–535 in the aligned matrix) and a ''Cape primrose clade'' (BS = 96, JK = 97), which includes the most southerly distributed species and those species (notably *S. rexii*) from which the Cape primroses of commerce have been principally derived. Other notable groupings include the grouping of the genus *Linnaeopsis* with *S. bullatus* (BS = 100, JK = 100) and a ''polyploid clade,'' the grouping of *S. perrieri* (4x) and *S. hildebrandtii* (8x) (BS = 66, JK = 74). There is morphological, cytological, and partial sequence evidence that *S. variabilis* (6x) also belongs in this clade. *Streptocarpus variabilis* has been excluded from this analysis because difficulties with amplification and sequencing have led to only partial sequence data being available.

As noted above, morphology is not perfectly congruent with the major clade structure because caulescent species such as *S. papangae, S. macropodus,* and *S. schliebenii* occur with the acaulescent, subgenus *Streptocarpus* clade. However, cytological data (Skog 1984) is perfectly congruent with the postulated clade structure: All the members so far cytologically examined in the *Streptocarpella* clade have x = 15, whereas all the members of the subgenus *Streptocarpus* clade so far examined have x = 16 (or polyploid multiples of 16). This applies even to *S. papangae* (Jong and Möller 2000) and *S. schliebenii* (Milne 1975). The major clades show some geographical patterning. The *Streptocarpella* clade is mainly tropical African or Madagascan. The crown group of the subgenus *Streptocarpus* clade is South African, whereas the basal members of this clade tend to be Madagascan or tropical African. This is suggestive of a north-to-south migration of the genus within Africa.

### *Constrained Trees and Character Mapping*

Unconstrained MP trees had a length of 1107 steps, and when the monophyly of unifolate and rosulate taxa is enforced, the tree length increased by 74 steps (6.7%; TW: $P < 0.0001$). Constraining the tree topology to force monophyly of all three major growth forms increased tree length by 77 steps (7.0%; TW: $P < 0.0001$). When the growth forms were constrained individually to be monophyletic, all resultant trees were significantly longer (TW: $P < 0.0001 - 0.0003$). The greatest increase was observed for rosulates (65 steps, 5.8%; TW: $P < 0.0001$). An approximate indication of the frequency of transitions between morphological types was obtained by character mapping (Fig. 3). The topology

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FIG. 2. Maximum-likelihood tree (ln = −6638.09) showing branch lengths, based on ITS1, 5.8S, and ITS2 sequence data. Clade I indicates the caulescent, subgenus *Streptocarpella* clade; clade II indicates the phyllomorphic, subgenus *Streptocarpus* clade (see text); OG are the outgroup taxa.

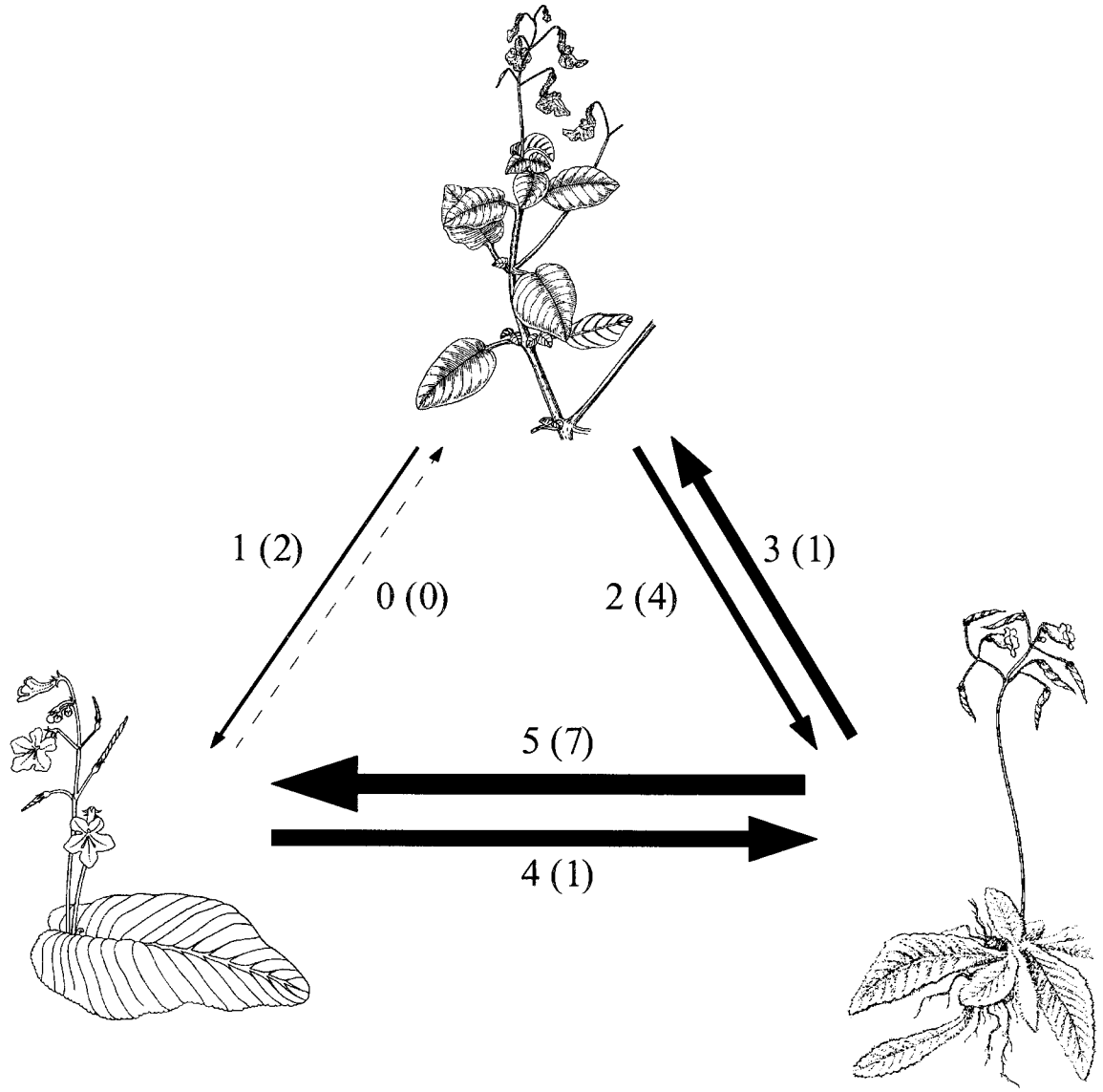


FIG. 3. Representatives of the three major growth forms (unifoliate/plurifoliates [left], caulescent [top], and rosulate [right]) connected by arrows showing hypothetical evolutionary transitions of the taxa included. The width of the arrow indicates the frequency of transitions using ACCTRAN optimization (the figures using DELTRAN optimization are given in parentheses) based on the maximum-parsimony majority rule consensus tree. Plant drawings are modified from Hilliard and Burtt (1971) and Humbert (1971).

of the single most parsimonious reweighted tree (identical to that of the majority rule consensus, Fig. 1) is used as the best supported phylogenetic hypothesis presently available. Under this phylogenetic hypothesis, all growth forms appear to have multiple origins (Fig. 3). Investigation of the effect of the collapse and alternative resolution of weak nodes (asterisks in Fig. 1) did not reveal major changes to the numbers of transitions and all growth forms appear to have multiple origins even under these alternative resolutions.

### *Molecular Clock*

The hypothesis that the ITS region of *Streptocarpus* has evolved in a clocklike fashion was rejected after tests on the single complete tree ($\chi^2 = 280.08$, $P = 0.001$) and the ML search on a subset ($\chi^2 = 120.15$, $P = 0.001$) were performed. Inspection of the ML subtrees reveals that the branch lengths in the subgenus *Streptocarpella* clade are 2.44 times longer than the branches in the subgenus *Streptocarpus* clade. Apparently ITS molecular evolution has been progressing, on average, more than twice as fast in subgenus *Streptocarpella* than in subgenus *Streptocarpus*. This could be due to acceleration in clade I, deceleration in clade II, or both.

## DISCUSSION

### *Three Other Genera Are Nested within Streptocarpus*

The genus *Streptocarpus* is conveniently defined as African and Madagascan gesneriads with a twisted fruit. For this reason, members of the *Streptocarpus* lineage that have lost their twist have been placed in other genera. The molecular

data suggest that this loss of twist has occurred three times in Africa independently, with the genera *Saintpaulia, Schizoboea,* and *Linnaeopsis* being nested within *Streptocarpus. Linnaeopsis,* as well as having lost its twist, appears to have reverted to caulescence within the acaulescent clade along with *Streptocarpus schliebenii.* The possible reversion to caulescence in *S. papangae* (suggested by ACCTRAN optimization only) is a separate event. We have discussed the evolution of *Saintpaulia* elsewhere (Möller and Cronk 1997). *Schizoboea kamerunensis,* like *Saintpaulia,* belongs in the caulescent clade. It has a disjunct distribution in east and west Africa, thus providing a potential biogeographical link between the east African caulescents such as *Streptocarpus saxorum* and the west African caulescents such as *S. elongatus.* It would be interesting to sample *Schizoboea kamerunensis* from both ends of its range in order to test the monophyly of this species.

### *Nuclear Ribosomal DNA Has Evolved 2.44 Times Faster in Subgenus Streptocarpella than in Subgenus Streptocarpus*

Molecular clock tests indicate considerable rate variation in the evolution of nrDNA, with the caulescent clade being on average 2.44 times faster. *Streptocarpus elongatus* is on the longest branch, and thus appears to be the fastest evolving lineage. We observe from herbarium specimens that *S. elongatus* frequently produces flowers when very small, with only one or two pairs of leaves. As a diminutive epiphyte from the relatively aseasonal rain forests of Cameroon, *S. elongatus* may have several generations per year. Even the larger caulescents commonly flower abundantly six months after sowing (at least in cultivation). In contrast, species in the acaulescent clade commonly take longer to build phyllomorphs robust enough to sustain flowering. Some unifoliates, such as *S. dunnii,* also require vernalization for inflorescence formation. In the wild these factors may translate into a three- or four-year period before flowering (Hilliard and Burtt 1971). Thus, it is the plants with the faster life cycle that have the higher rate of molecular evolution (cf. Gaut et al. 1996).

### *All Three Major Growth Forms Have Multiple Origins in Streptocarpus*

As noted in the Results, cytology is completely congruent with the two major putative clades, but morphology is not. The formal subdivision of the genus by Fritsch (1894, p. 151) into three sections (*Unifoliati, Rosulati,* and *Caulescentes*) based solely on morphology is not tenable. Forcing the monophyly of morphological types significantly increased parsimony tree lengths (by 77 steps). In the acaulescent clade there are two apparent independent origins of a caulescent habit: *S. papangae* and *S. schliebenii.* In addition, there are some pseudocaulescent species, such as *S. fanniniae,* which although phyllomorphic, iterate numerous long petiolodes and so come to resemble caulescent plants. Furthermore, inspection of Figure 1 shows that unifoliate and rosulate plants are mixed in an apparently haphazard way on the tree, implying that there have been several evolutionary transitions from unifoliate to rosulate and vice versa. Optimization (using both ACCTRAN and DELTRAN models on unweighted transitions) of the distribution of the three major growth forms on the majority-rule consensus tree (using MacClade) is shown in Figure 3. ACCTRAN optimization suggests that the caulescent form is primitive and that there have been two transitions from caulescent to rosulate, five transitions from rosulate to unifoliate, and four transitions from unifoliate to rosulate. The suggestion by Hill (1938) that the original growth form in *Streptocarpus* was acaulescent (and that the caulescent species represent secondary developments from this) is not borne out. However, some reversion to caulescence from acaulescent species has definitely occurred. It is also interesting to note that one caulescent species is conditionally unifoliate—a state of affairs also found in species of *Chirita* (e.g., *Chirita micromusa*). It is therefore not impossible that the conditional unifoliate/caulescent habit (as in *S. nobilis*) may be primitive.

The existence of evolutionary transitions from rosulate to unifoliate is interesting in the light of Oehlkers's (1964) finding that the unifoliate habit seems to result from two recessive alleles. Oehlkers took this to imply that the unifoliate may have arisen by loss of function mutations from a rosulate progenitor with the dominant alleles. Such a transition appears to have occurred several times and accords with the notion that evolution in *Streptocarpus* proceeds by recessive mutations of major effect in developmental genes. However, the existence of unfoliate to rosulate transitions is evidence against this idea (as reversing a loss of function mutation is likely to be difficult). The suggestion by Hilliard and Burtt (1971) that the unifoliate form precedes the rosulate (on the grounds that a caulescent to unifoliate transition, by paedomorphosis, represents a developmentally more plausible change) is not directly supported by our phylogeny (Figs. 1, 3). The apparent frequency of unifoliate to rosulate transitions, however, means that this cannot be ruled out. It is certainly true that the formation of an abscission zone on the leaf blade of all African acaulescents, implies a unifoliate ancestor because this characteristic makes greater ecological sense in unifoliates (unifoliates cannot regulate leaf area by abscising whole leaves). Alternatively, as the rosulate habit is dominant, the restoration of this habit in unifoliate lineages may be due to introgression of the relevant genes by hybridization with rosulate plants. Hybrids between growth forms are readily produced under cultivation. What is clear, however, is that the numerous transitions between growth forms of the taxa analyzed is indicative of the intrinsic lability of form present in *Streptocarpus.* The adaptive and developmental significance of this is discussed below.

### *Adaptive Morphological Evolution in Streptocarpus*

It is characteristic of the Old World Gesneriaceae that their seedlings exhibit continued growth of one cotyledon (by basal meristematic activity) and the delayed formation of a plumule. Burtt (1970) suggested that this ''anisocotyly'' is an adaptation to the growth of *Streptocarpus* in deep shade while possessing small dust-like seeds with almost no endosperm. Such growth is advantageous where light is a limiting factor, as the production of photosynthetic area instead of stem structures is more efficient. However, the delay of SAM development and the continued growth of the cotyledon requires

an uncoupling of the strict developmental linkage between meristematic activity and the shoot apex. This uncoupling may be a preadaptation underlying the evolutionary lability of form in *Streptocarpus.* It may result from gain-of-function dominant mutations in plant-meristem-determining genes such as shootmeristemless (*stm*) (Long et al. 1996). Where conditions are extreme, it may be advantageous to delay plumular growth indefinitely while further developing a meristematic cotyledon. This would either result in a unifoliate form or, if the cotyledon can produce further leaves, a rosulate form. The production of further leaves is reminiscent of weak loss of function mutations at the *stm* locus in *Arabidopsis.* These have phenotypes in which further leaves are produced on the hypocotyl (Barton and Poethig 1993). The suppression of further leaves by subsequent (recessive) mutations could also give rise to the unifoliate growth form.

The unifoliate forms are photosynthetically efficient by having no self-shading or stem production. However, they die after a single burst of flowering. Rosulate forms are perennial and can flower over many years. The interplay of reproductive strategy and photosynthetic economy in different ecological niches will favor different growth forms. Lawrence (1958) suggested that the unifoliate and rosulate species have different ecological preferences, and very broadly this is probably true. However, rosulates and unifoliates are often to be found growing together (Hilliard 1966; Hilliard and Burtt 1971). In Madagascar, *S. itremensis* (unifoliate) and *S. ibityensis* (rosulate) can be found adjacent to each other. It should be noted, however, that even though they are growing together and thus have the same habitat preference, they may be occupying different niche space, particularly in reproductive features (i.e., the ''regeneration niche,'' Grubb 1977) to which the different growth forms may contribute. It seems that *Streptocarpus* species have an intrinsic developmental lability that has allowed the differentiation of morphologies adapted to different environmental conditions.

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## APPENDIX

Accessions of 77 *Streptocarpus* taxa, together with species of *Saintpaulia, Schizoboea, Linnaeopsis,* and three outgroup taxa (*Haberlea rhodopensis, Didymocarpus citrinus,* and *Chirita spadiciformis*) examined for ITS1, 5.8S, and ITS2 sequence variation. The wider distribution, of those species present in more than one country, is indicated in parentheses. GenBank accession numbers refer to the ITS sequences stored in GenBank.

| Taxon | Origin (distribution) | RBGE acc. no.[1] | GenBank acc. no. |
|---|---|---|---|
| *Haberlea rhodopensis* Friv. | Ex cult. (Europe, Greece) | 1975 4106 | AF316900 |
| *Didymocarpus citrinus* Ridl. | Malaya, Parlis Stae, N. side of Kedat Peak (Malaysia) | 1983 0510 | AF316899 |
| *Chirita spadiciformis* W. T. Wang | Smithsonian Institution 94-087 (China) | 1995 1205 | AF316898 |
| *Schizoboea kamerunensis* (Fritsch) B. L. Burtt | Ex herb. (E): Burundi; Muramuya, Mt. Teza (Cameroon, Fernando Po, Burundi, Zaire, Tanzania) | No 6693 | AF316901 |
| *Linnaeopsis* sp. nov. | Ex herb. (E): Tanzania; Uluguru Mts. above Morogoro town, Palata ridge | 8656/c | AF316932 |
| *Linnaeopsis alba* (E. A. Bruce) B. L. Burtt | Ex herb. (E): Tanzania; Uluguru Mts. above Morogoro town, NW side of Lupanga ridge | 86106/D | AF316933 |
| *Saintpaulia brevipilosa* B. L. Burtt | Tanzania; Kanga forest, Mt. Kanga (Nguru Mts.) | 1970 0909 | AF316924 |
| *Saintpaulia* cf. *ionantha* H. Wendl. | Tanzania; Tanga, Sigi River | 1971 0860 | AF316923 |
| *Saintpaulia nitida* B. L. Burtt | Tanzania; Nguru Mts. | 1992 3186 | AF316925 |
| *Saintpaulia teitensis* B. L. Burtt | Ex herb. (E): Kenya; Coast Region, Teita Hills, Mbololo forest | C 3771 | AF316922 |
| *Streptocarpus andohahelensis* Humbert | Madagascar; Tulear, Ranomafana-Col de Beampingaratra | 1997 2885 | AF316903 |
| *Streptocarpus baudertii* L. L. Britten | E. Cape, Transkei (South Africa) | 1996 1858A | AF316978 |
| *Streptocarpus beampingaratrensis* Humbert ssp. *antambolorum* Humbert | Madagascar; Tulear, Ranomafana-Col de Beampingaratra | 1997 2887 | AF316902 |
| *Streptocarpus beampingaratrensis* Humbert ssp. *beampingaratrensis* | Madagascar; Tulear, Ranomafana-Col de Beampingaratra | 1997 2884 | AF316905 |
| *Streptocarpus bindseilii* Eb. Fisch. | Rwanda; S. Nyakabuye | ex Bonn | AF316960 |
| *Streptocarpus bolusii* C. B. Clarke | Ex herb. (E): South Africa; Natal, Mt. Ngeli (Natal, E. Cape) | C 5115 | AF316961 |
| *Streptocarpus buchananii* C. B. Clarke | Ex Cult. (AGGS), (Malawi, S. Tanzania, N. Moçambique) | 1997 2911 | AF316919 |
| *Streptocarpus bullatus* Mansf. | Ex herb. (E): Tanzania; Uluguru Mts., E. of Nagari Peak | C 6297 | AF316942 |
| *Streptocarpus burundianus* Hilliard and B. L. Burtt | Ex herb. (E): Burundi; NE corner of Lake Tanganika | C 8336 | AF316940 |
| *Streptocarpus candidus* Hilliard | South Africa; Natal, Zululand, Ngome forest | 1977 1204 | AF316965 |
| *Streptocarpus caulescens* Vatke | Tanzania; Uluguru Mts., Morogoro region (Tanzania, Kenya) | 1971 1199 | AF316920 |
| *Streptocarpus compressus* B. L. Burtt | Ex herb. (E): Tanzania, Songea Distr., Matengo Hills, Luiri Kitesi | C 2965 | AF316957 |
| *Streptocarpus confusus* Hilliard ssp. *lebomboensis* Hilliard and B. L. Burtt | South Africa; Natal, Nr Hluhluwe game reserve, Makowe Mt. (Natal, Transvaal, Swaziland, Moçambique) | 1991 2546 | AF316966 |
| *Streptocarpus cooperi* C. B. Clarke | South Africa, Natal, Nkandla Distr., Andeni forest (Natal, Orange Free State) | 1993 3029 | AF316954 |

APPENDIX. Continued.

| Taxon | Origin (distribution) | RBGE acc. no.[1] | GenBank acc. no. |
|---|---|---|---|
| *Streptocarpus cyanandrus* B. L. Burtt | Ex herb. (E): Zimbabwe; Inyanga Downs | C 3674 | AF316947 |
| *Streptocarpus cyaneus* S. Moore | Swaziland; Mbabane, Sebebe Mts. (Swaziland, South Africa: Natal) | 1991 1950 | AF316975 |
| *Streptocarpus davyi* S. Moore | Ex herb. (E): Swaziland; Mbabane | C 5174 | AF316946 |
| *Streptocarpus decipiens* Hilliard and B. L. Burtt | Ex herb. (E): South Africa; E. Transvaal | 6000 | AF316938 |
| *Streptocarpus dolichanthus* Hilliard and B. L. Burtt | Ex herb. (E): Malawi; Mt. Mulanje, Litelenya Plateau | J. D. and E. G. Chapman 8496 | AF316937 |
| *Streptocarpus dunnii* Hook.f. | Swaziland; N. Mbabane (Swaziland, South Africa: Transvaal) | 1994 1745 | AF316951 |
| *Streptocarpus elongatus* Engl. | Ex herb. (E): Nigeria; Taraba State, Mambila plateau, NgeNyaki forest (Cameroon, São Thomé, Nigeria) | Spurrier 705 | AF316913 |
| *Streptocarpus erubescens* Hilliard and B. L. Burtt | Ex herb. (E): Malawi; Ndirandi Mts. (Malawi, Moçambique) | C 5108 | AF316949 |
| *Streptocarpus exsertus* Hilliard and B. L. Burtt | Ex herb.: Kenya, Lolokwe Mt., NE slopes of Onulbeys | Gilbert 5358 | AF316939 |
| *Streptocarpus eylesii* S. Moore ssp. *eylesii* | Zimbabwe; Mt. Nyangoi (Tanzania, Zambia, Malawi, Zimbabwe) | 1993 2790 | AF316955 |
| *Streptocarpus fanniniae* Harv. | South Africa; Natal, Lion's River distr., Bridgewood, Dargle | 1977 1324 | AF316944 |
| *Streptocarpus fasciatus* T. J. Edwards and C. Kunhardt | Ex cult.: South Africa (Transvaal) | 1996 2086 | AF316977 |
| *Streptocarpus galpinii* Hook.f. | Ex herb. (E): Swaziland; Mbabane (South Africa: Transvaal, Swaziland) | C 5154 | AF316943 |
| *Streptocarpus glandulosissimus* Engl. | Ex cult. (Congo, Rwanda, Rurundi, Uganda, Tanzania, Kenya) | 1965 2118 | AF316918 |
| *Streptocarpus goetzei* Engl. | Ex cult. (Tanzania, Moçambique, Malawi) | 1997 2033 | AF316956 |
| *Streptocarpus grandis* N. E. Br. | South Africa: Natal, Zululand, Ngome forest (South Africa: Natal, Zimbabwe, Moçambique) | 1977 1210 | AF316952 |
| *Streptocarpus haygarthii* N. E. Br. ex C. B. Clarke | South Africa, Natal, mid-Illovo (South Africa: Natal, E. Cape) | 1993 3030 | AF316964 |
| *Streptocarpus hildebrandtii* Vatke | Ex cult. (PBZT) (Madagascar) | 1997 2891 | AF316930 |
| *Streptocarpus hilsenbergii* R. Br. | Madagascar; Mandrake Valley, 70 km from Tana | 1963 1505 | AF316907 |
| *Streptocarpus hirticapsa* B. L. Burtt | Zimbabwe; Chimanimani National Park | 1993 2793 | AF316962 |
| *Streptocarpus hirtinervis* C. B. Clarke | Ex herb. (E): Malawi, Mt. Mulanje | C 8233 | AF316935 |
| *Streptocarpus holstii* Engl. | Ex cult. (Tanzania, E. Usambara Mts.) | 1959 2272 | AF316917 |
| *Streptocarpus ibityensis* Humbert | Madagascar; Antananarivo, Mt. Ibity | 1993 2867 | AF316926 |
| *Streptocarpus itremensis* B. L. Burtt | Madagascar; Antananarivo, Mt. Ibity | 1997 2889 | AF316928 |
| *Streptocarpus johannis* L. L. Britten | South Africa; Natal (South Africa: Natal, E. Cape) | 1969 0450 | AF316981 |
| *Streptocarpus kentaniensis* L. L. Britten and Story | South Africa; Cape Province, E. Transkei, Kei Mouth | 1992 3050 | AF316974 |
| *Streptocarpus kimbozanus* B. L. Burtt | Ex herb. (E): Tanzania; Kimboza forest reserve | C 8334 | AF316911 |
| *Streptocarpus kirkii* Hook.f. | Tanzania; Tanga Region, E. Usambara Mts. (Kenya: Teita Hills; Tanzania: Uluguru Mts.) | 1994 1332 | AF316916 |
| *Streptocarpus kungwensis* Hilliard and B. L. Burtt | Ex herb.: Tanzania, W. slopes of Musenabantu | C 4673 | AF316959 |
| *Streptocarpus macropodus* B. L. Burtt | Ex herb. (E): Madagascar | Lewis et al. 1043 | AF316927 |
| *Streptocarpus meyeri* B. L. Burtt | South Africa; E. Cape Province | 1996 1800A | AF316976 |
| *Streptocarpus milanjianus* Hilliard and B. L. Burtt | Malawi; Mt. Mulanje | C 8227 | AF316936 |
| *Streptocarpus modestus* L. L. Britten | South Africa; Transkei, Magwa Falls | 1994 3058 | AF316982 |
| *Streptocarpus molweniensis* Hilliard | Ex herb. (E): South Africa; Natal, Molveni River, Everton | C 4013 | AF316968 |
| *Streptocarpus montigena* L. L. Britten | Ex herb. (E): South Africa; E. Cape, top of Katberg Pass | C 4788 | AF316980 |
| *Streptocarpus nimbicola* Hilliard and B. L. Burtt | Ex herb. (E): Malawi, Mt. Mulanje | C 5364 | AF316934 |
| *Streptocarpus nobilis* C. B. Clarke | Ex cult. (W. tropical Africa) | 1966 1728 | AF316912 |
| *Streptocarpus pallidiflorus* C. B. Clarke | Tanzania; Arusha Reg., Masai Distr., Longido Mts., Longido Stream | 1969 1121 | AF316921 |
| *Streptocarpus papangae* Humbert | Madagascar; Tulear, Col de Beampingaratra, Maloto River | 1997 2886 | AF316929 |
| *Streptocarpus pentherianus* Fritsch | Ex cult. (South Africa: Transvaal, Swaziland, Natal) | 1997 2034 | AF316971 |
| *Streptocarpus perrieri* Humbert | Madgascar; Antananarivo, Angavo near Ankazobe | 1997 2892 | AF316931 |

APPENDIX. Continued.

| Taxon | Origin (distribution) | RBGE acc. no.[1] | GenBank acc. no. |
|---|---|---|---|
| *Streptocarpus pole-evansii* Verd. | Ex cult. (Transvaal) | 1996 1908 | AF316950 |
| *Streptocarpus polyanthus* Hook. ssp. *comptonii* (Mansf.) Hilliard | South Africa; E. Cape, Transkei, Nsikasa (South Africa: Transvaal, Swaziland, Natal) | 1992 3045 | AF316972 |
| *Streptocarpus porphyrostachys* Hilliard | South Africa; E. Cape, Transkei, Mkabati nature reserve (South Africa: E. Cape, Natal) | 1990 2311 | AF316963 |
| *Streptocarpus primulifolius* Gand. (blue) | South Africa, SW Cape, Table Mt. | 1966 0432 | AF316983 |
| *Streptocarpus primulifolius* Gand. ssp. *formosus* Hilliard and B. L. Burtt | South Africa; Natal (South Africa: E. Cape, Natal) | 1992 3046 | AF316984 |
| *Streptocarpus prolixus* C. B. Clarke | South Africa, Natal, Pinetown Distr., Everton | 1977 2035 | AF316973 |
| *Streptocarpus pumilus* B. L. Burtt | Zimbabwe, Domboshawa | 1993 2787 | AF316948 |
| *Streptocarpus pusillus* Harv. ex C. B. Clarke | Ex herb.: South Africa, Natal, Anne Rennies's Mountain sunset farm, Bulwer (Lesotho, South Africa: Natal, Orange Free State, E. Cape) | Kew (1983 1816) | AF316945 |
| *Streptocarpus rexii* Lindl. | South Africa, Cape Province, Grahamstown, Foraway Estate (South Africa: E. Cape, Natal) | 1987 0333 | AF316979 |
| *Streptocarpus saxorum* Engl. | Tanzania, Usambara, Tanga region (Kenya: Teita Hills; Tanzania: Nguru, Uluguru Mts.) | 1972 1499 | AF316914 |
| *Streptocarpus schliebenii* Mansf. | Ex herb. (E): Tanzania, Ukaguru Mts. | C 8433 | AF316941 |
| *Streptocarpus silvaticus* Hilliard | South Africa; Natal Province, Lion's River Distr., Karkloof range, Benvie (South Africa: E. Cape, Natal) | 1991 2181 | AF316970 |
| *Streptocarpus solenanthus* Mansf. | Malawi (Tanzania, Zambia, Malawi, Zimbabwe) | 1997 2037 | AF316958 |
| *Streptocarpus* sp. (Madagascar) | Madagascar, Fianarantsoa, Itremo Massif | 1993 1445 | AF316909 |
| *Streptocarpus* sp. (tiny) | Madagascar, Maloto river, 430 m | 1997 2895 | AF316904 |
| *Streptocarpus stomandrus* B. L. Burtt | Tanzania, Nguru Mts. | 1971 1392 | AF316915 |
| *Streptocarpus tanala* Humbert | Madagascar; Tulear, Analaro, Andranohela River | 1997 2882 | AF316906 |
| *Streptocarpus thompsonii* R. Br. | Ex cult. (AGGS) (Madagascar) | 1994 1334 | AF316908 |
| *Streptocarpus thysanothus* Hilliard and B. L. Burtt | Ex herb.: Tanzania; Morogoro Distr., Kimboza | 1997 3246 | AF316910 |
| *Streptocarpus trabeculatus* Hilliard | Ex cult. (South Africa: E. Cape, Natal) | 1997 2032 | AF316969 |
| *Streptocarpus wendlandii* Sprenger | Natal; Mtunzini Distr., Ngoye forest | 1997 0108 | AF316967 |
| *Streptocarpus wittei* De Wild. | Malawi, Rumpi Distr., Nyika (Congo, Zambia, Malawi) | 1987 1695 | AF316953 |

[1] These numbers were also used as voucher numbers.