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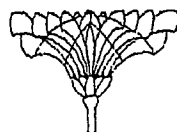
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Phylogenetic studies in *Streptocarpus* (Gesneriaceae): reconstruction of biogeographic history and distribution patterns

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Abstract. – Molecular phylogenies have been generated to investigate relationships among species of *Streptocarpus* Lindl., the largest genus of Gesneriaceae in Africa. Of the around 146 species described, 77 have been included in a parsimony analysis using the internal transcribed spacer (ITS) of ribosomal DNA. The studies show that *Streptocarpus* is paraphyletic and at least three other genera are nested within the genus. Incongruence occurs in relation to the subgeneric division. *Streptocarpus* is currently divided into two subgenera, *Streptocarpella* and *Streptocarpus*, mainly on morphological grounds; the former including basically caulescent species with a functional shoot apical meristem, while the latter includes mainly unifoliate and rosulate species with an abnormal shoot apical meristem. On the African continent the geographic distribution of caulescent species of subgenus *Streptocarpella* ranges across tropical Africa from Sierra Leone to the Indian Ocean, while species of subgenus *Streptocarpus* occur in central and eastern parts of Africa. The molecular data suggest a southwards migration and “progressive latitudinal speciation” of subgenus *Streptocarpus* in Africa. Some evidence suggests an origin of the genus on Madagascar but this is equivocal. The subgeneric split probably occurred before interchange between mainland Africa and Madagascar ceased, after the geological separation of Madagascar, and is consistent with the hypothesis of a land bridge connection between 45-26Mya.

Key words: biogeography, dispersal, Gesneriaceae, migration, phylogeny, *Streptocarpus*.

Abbreviations: bp, base pairs; BS, bootstrap support; CI, consistency index; JK, jackknife support; RC, rescaled consistency index; RI, retention index; ITS, internal transcribed spacers; rDNA, ribosomal DNA; cpDNA, chloroplast DNA.

Résumé. – Etudes phylogénétiques chez *Streptocarpus* (Gesneriaceae): reconstruction de l'histoire biogéographique et modèles de distribution. Des phylogénies moléculaires ont été générées afin d'étudier les relations entre espèces chez *Streptocarpus* Lindl., le plus grand genre de Gesneriaceae en Afrique. Parmi les 146 espèces décrites, 77 ont été utilisées dans une analyse de parcimonie en

différences morphologiques; le premier regroupe des espèces caulescentes à méristème apical fonctionnel, alors que le deuxième inclut principalement des espèces dont les individus, unifoliés ou en rosette, présentent un méristème apical anormal. Sur le continent africain, la distribution utilisant l'ITS du DNA ribosomique. Les études montrent que *Streptocarpus* est paraphylétique et qu'il regroupe au moins trois autres genres. La division subgénérique est problématique. *Streptocarpus* est actuellement divisé en deux sous-genres, *Streptocarpella* et *Streptocarpus*, principalement sur base de géographique des espèces caulescentes du sous-genre *Streptocarpella* s'étend des régions tropicales de la Sierra Leone à l'Océan Indien, alors qu'on trouve les espèces du sous-genre *Streptocarpus* en Afrique centrale et orientale. Les données moléculaires suggèrent une migration vers le sud et une "spéciation latitudinale progressive" du sous-genre *Streptocarpus* en Afrique. L'origine malgache du genre est envisagée mais reste équivoque. La différenciation des sous-genres a probablement eu lieu avant que l'échange entre le continent africain et Madagascar ait pris fin suite à la séparation géologique de Madagascar. Elle est en accord avec l'hypothèse d'une connexion terrestre entre 45-26 Mya. Traduit par le journal.

1 Introduction

The genus *Streptocarpus* Lindl. (Gesneriaceae) has recently been the focus of intensive phylogenetic studies (Möller & Cronk 1997a, 1997b, 2001; Smith et al. 1997). The majority utilised molecular data of the internal transcribed spacer (ITS) sequences of ribosomal DNA (rDNA). These studies found the genus to be paraphyletic with another important African genus, *Saintpaulia* Wendl., nesting within *Streptocarpus* (Möller & Cronk 1997a). *Streptocarpus* is a genus of considerable morphological flexibility that includes acaulescent (unifoliolate, rosulate) and caulescent species. It includes 146 described species and has long been divided into two subgenera: the caulescent *Streptocarpella* and the acaulescent *Streptocarpus*. This division is strengthened by the discovery of a consistent cytological difference, with subgenus *Streptocarpella* having $x = 15$ and subgenus *Streptocarpus* $x = 16$ chromosomes (Lawrence 1939). On molecular data the dividing line between the two subgenera is not so clear. Some caulescent species such as the African *S. schliebenii* Mansfeld and a group of woody caulescent Malagasy species, are found to reside basally within the subg. *Streptocarpus* clade (Möller & Cronk 2001). Their chromosome number, however, supports such a placement (Milne 1975). The evolutionary interplay of the three basic growth forms (unifoliolate, rosulate, caulescent) has been explicitly analysed using an extended ITS data set (Möller & Cronk 2001). It was shown that the diverse growth forms evolved several times, in contrast to the first impression from an analysis which included only three unifoliolate taxa (Möller & Cronk 1997a).

The geographical range of the genus includes Africa, Madagascar and the Comoro Islands. Although four species are found in Asia, they are not thought to be closely related to the African/Malagasy taxa. This was clearly demonstrated by molecular data (ITS and *trnL-F*) for *S. orientalis* Craib from Thailand which is more closely related to other Asiatic taxa with twisted fruits than to African/Malagasy taxa (Möller, Cronk, Hellens & Preston unpublished). On the African continent a marked partition exists between the geographic distribution of caulescent species of subg. *Streptocarpella*, which ranges across tropical Africa from Sierra Leone to the Indian Ocean, and subg. *Streptocarpus* which occur in the centre and in the eastern half of Africa (Hilliard & Burt 1971).

In order to correlate the biogeographic pattern with the complex pattern of morphological evolution, a closer investigation of the distribution of the genus in relation to the molecular phylogenetic hypothesis was envisaged. To this end we here use the phylogenetic tree obtained in the previous investigation (Möller & Cronk 2001) to map and interpret the geographic distribution pattern.

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2 Materials and methods

2.1 Species selection and molecular methods

Seventy seven species of *Streptocarpus* (Möller & Cronk 2001) were included from both cultivated collections of the Royal Botanic Garden Edinburgh and from herbarium specimens. This represents about 60% of the genus. These included 14 Malagasy species collected during two expeditions to Madagascar by M.M. Molecular methods are as described (Möller & Cronk 1997a, 2001).

2.2 Analytical methods

The ITS1, ITS2 and 5.8S sequences for all 87 ingroup and outgroup taxa were obtained and aligned as described previously (Möller & Cronk 1997a, 2001). Only unambiguously alignable regions were used, with gaps treated as missing data and unordered character states. Due to alignment ambiguities 100 characters had to be excluded, including a 77 base pairs (bp) section in ITS2 containing a ca. 40 bp deletion site shared by a group of species.

We used a three step maximum parsimony (MP) search strategy to optimise the search for most parsimonious trees (see Soltis & Soltis 1997). The steps are as follows: (1) a heuristic search was performed with SIMPLE ADDITION sequence, TREE BISECTION-RECONNECTION (TBR), COLLAPSE (max.) and MULTREES on. (2) 10000 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 treelength (n). This treelength (n) was established empirically in the first heuristic search. (3) TBR swapping on the saved trees with MULTREES and STEEPEST DESCENT and COLLAPSE (max.) was used to detect any multiple islands of most parsimonious trees (MPTs).

Descriptive tree statistics (CI, RI, RC; Farris, 1989) were derived as described previously (Möller and Cronk 1997), except using PAUP4.0b2a. "Fast" jackknifing with 33% character deletion (10000 replicates) and full heuristic bootstrapping with TBR and MULTREES off (10000 replicates) (Spangler and Olmstead 1998) were used to obtain branch support values.

The constraint option in PAUP 4.0b2a was used to analyse tree length increases (over unconstrained trees) of trees which enforced the respective monophyly of African and Malagasy species, with otherwise identical heuristic search procedures. A Templeton (Wilcoxon signed-ranks) test was performed to test the significance between unconstrained and constrained trees (Swofford 1998).

Character mapping was performed on the MP majority rule consensus tree. Both accelerated (ACCTRAN) and delayed (DELTRAN) character state optimisation were employed and terminal polytomies (resulting from the collapse of zero length branches) were resolved randomly using MacClade 3.01 (Maddison & Maddison 1992).

3 Results

3.1 Matrix characteristics

A full description of the sequence analysis is given in Möller & Cronk (2001). Therefore a summary of the important facts relevant to the present study is given here. The aligned data matrix of 87 ingroup and outgroup ITS and 5.8S sequences was 743 bp long. Numerous indel events have occurred in the dataset, the most notable of which is a ca. 40 bp deletion characteristic of 17 species in one clade (fig. 1). Of the 643 unambiguously alignable characters, 364 (56.6%) were variable of which 262 (40.5%) were potentially informative in parsimony analysis.

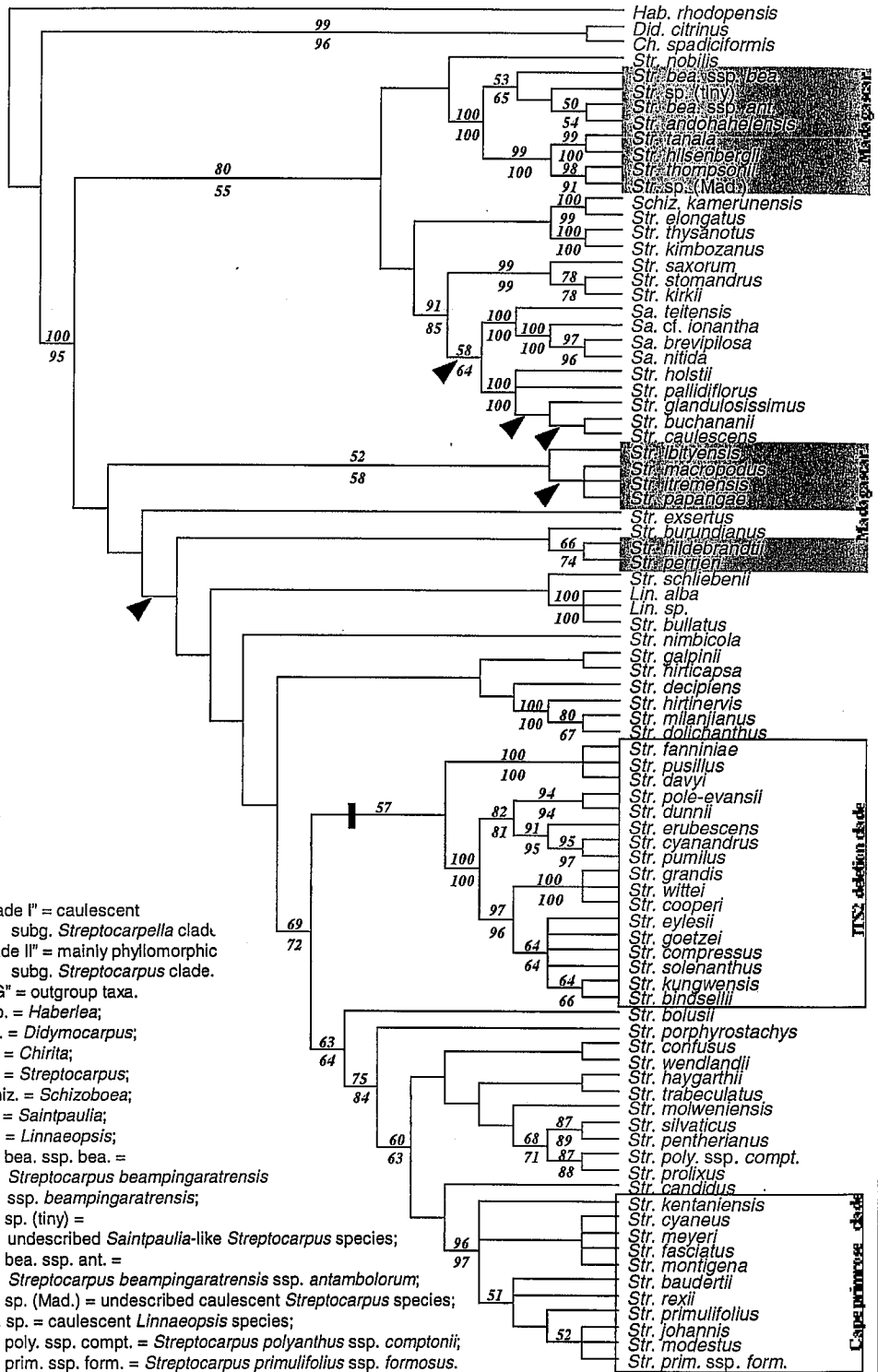
3.2 Sequence divergences

The sequence divergence ranged from 0-24.3% (*Streptocarpus hilsenbergii* R.Br. – *S. elongatus* Engler) between ingroup taxa and 12.1% (*Haberlea rhodopensis* Friv. – *S. schliebenii*) and 25.8% (*Chirita spadiciformis* W.T.Wang – *S. elongatus*) between ingroup and outgroup taxa. Within subgenera *Streptocarpella* and *Streptocarpus* sequence divergence was 0.4-24.3% and 0-10.8%

Majority rule consensus tree of 1455 most parsimonious trees of 1107 steps, based on ITS1, 5.8S and ITS2 sequence data. The MP trees had a CI of 0.503, RI of 0.753 and a RC of 0.379 with uninformative characters included. The numbers above the branches are BS values, and the numbers below the branches are JK values; missing values indicates branch support values of less than 50%. Nodes that collapse in the strict consensus are indicated by black arrowheads. The black vertical bar indicates a shared ca. 40 bp deletion event (see text).

Single phylogram of 1107 steps based on ITS1, 5.8S and ITS2 sequence data. Branches in bold indicate BS or JK support of > 80%. Inset A depicts a plot of BS versus JK support values with linear regression line. Inset B illustrates a plot of branch lengths of clade I and II versus BS support values.

Majority rule



"Clade I" = caulescent subg. *Streptocarpella* clade.
 "clade II" = mainly phylomorphic subg. *Streptocarpus* clade.
 "OG" = outgroup taxa.
 Hab. = *Haberlea*;
 Did. = *Didymocarpus*;
 Ch. = *Chirita*;
 Str. = *Streptocarpus*;
 Schiz. = *Schizoboea*;
 Sa. = *Saintpaulia*;
 Lin. = *Linnaeopsis*;
 Str. bea. ssp. bea. = *Streptocarpus beampingaratrensis* ssp. *beampingaratrensis*;
 Str. sp. (tiny) = undescribed *Saintpaulia*-like *Streptocarpus* species;
 Str. bea. ssp. ant. = *Streptocarpus beampingaratrensis* ssp. *antamborum*;
 Str. sp. (Mad.) = undescribed caulescent *Streptocarpus* species;
 Lin. sp. = caulescent *Linnaeopsis* species;
 Str. poly. ssp. compt. = *Streptocarpus polyanthus* ssp. *comptonii*;
 Str. prim. ssp. form. = *Streptocarpus primulifolius* ssp. *formosus*.

OG

clade I

clade II

Madagascar

Madagascar

ITS deletion clade

Esape primrose clade

rhodopensis
 rinus
 adiciformis
 hills
 ssp. bea
 (tiny)
 ssp. ant.
 onahelensis
 ala
 enbergii
 mpsonii
 (Mad.)
 kamerunensis
 ngatus
 sanotus
 bozanus
 orum
 mandrus
 ii
 ensis
 onantha
 vipilosa
 ia
 stii
 lidiflorus
 ndulosissimus
 hananii
 iescens
 tensis
 ropodus
 mensis
 argaei
 ortus
 undianus
 ebrandtii
 ietia
 liebenii
 a
 latus
 bicola
 pinii
 icapsa
 piens
 hervis
 anjanus
 chanthus
 niniae
 illus
 yi
 e-evansii
 inii
 bescens
 andrus
 illus
 ndis
 el
 peri
 ssii
 tzei
 ipressus
 ananthus
 gwensis
 tsellii
 tsii
 yprostachys
 fusus
 idlandii
 garthii
 eculatus
 weniensis
 aticus
 therianus
 r. ssp. compt.
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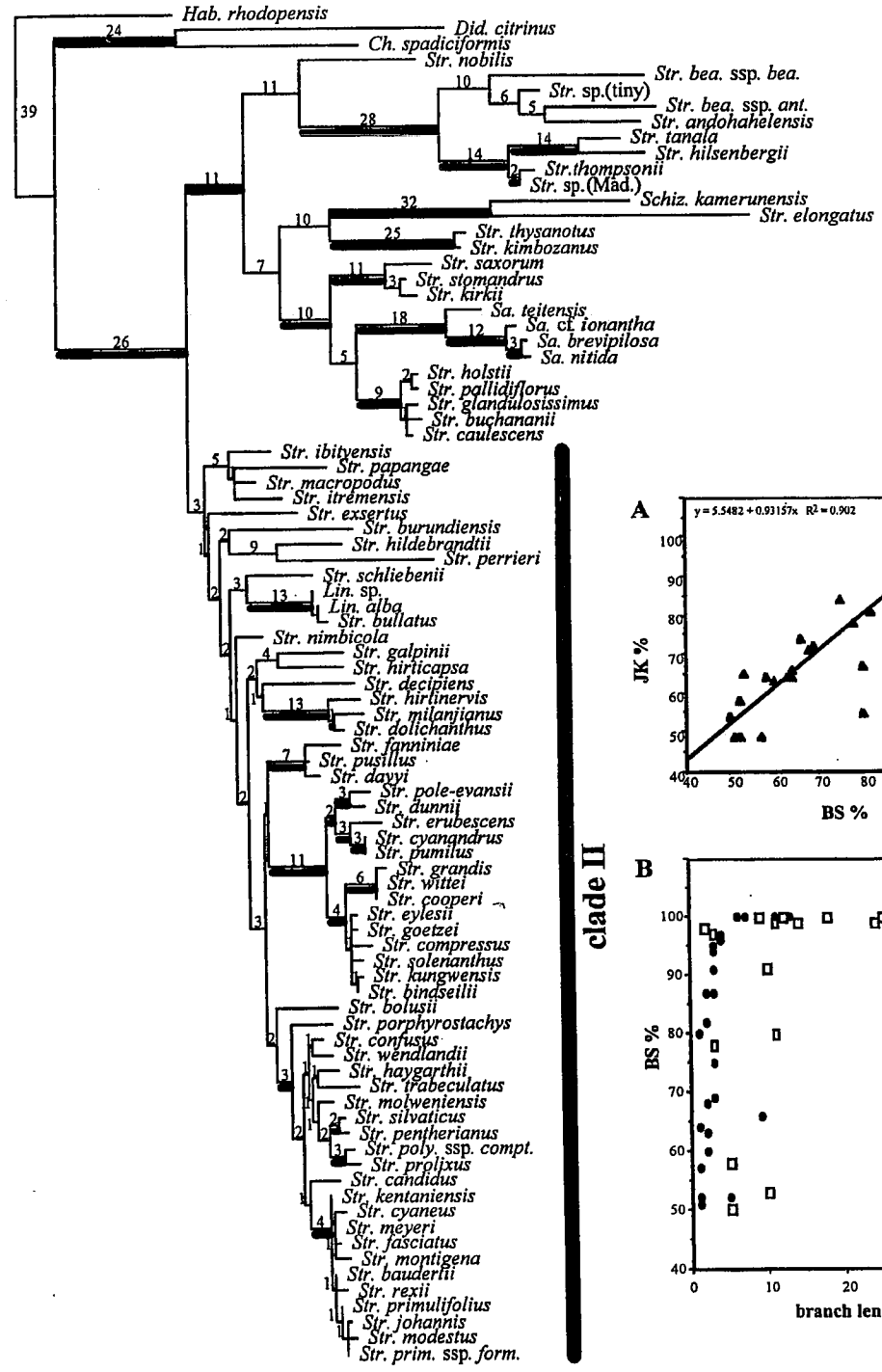
OG

clade I

clade II

ITS2 deletion clade

Cape primrose clade

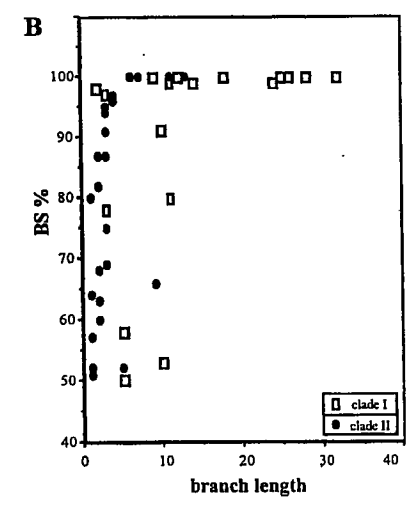
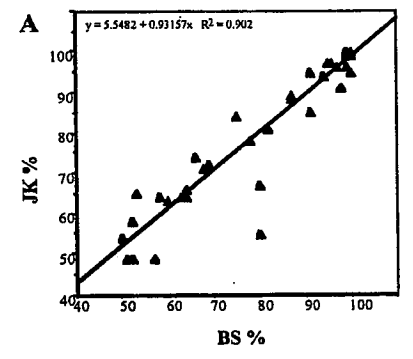


OG

clade I

clade II

— 5 changes



respectively, and 2.1–20.5% between the subgenera. Maximum sequence divergence within groups of African and Malagasy species of subg. *Streptocarpella* was 19.5% (African species) and 11.1% (Malagasy species) and subg. *Streptocarpus* 8.6% (African species) and 8.9% (Malagasy species). When contrasting African and Malagasy species, sequence divergence within subg. *Streptocarpella* was between 9.9% and 24.3% and within subg. *Streptocarpus* 4.8% and 10.8%, respectively.

3.3 Summary of clade structure of *Streptocarpus*

Branch support ranged from 51–100% (BS) and 54–100% (JK) respectively (fig. 1). A high linear correlation was found between BS and JK values ($r^2 = 0.902$) (fig. 2 inset A), indicating that the parameter settings in both branch support analyses (see 2.2 Analytical methods) result in similar support values. Branches with high support values (>80%) were found across the tree (figs. 1 and 2). Comparing branch length of a randomly chosen most parsimonious tree, depicted as phylogram (fig. 2), with BS support values shows a correlation over a very narrow range of branch length 0–4 for clade II ($P < 0.01$) but there is no correlation for clade I (fig. 2 inset B). There was a slight tendency for branches in clade II to have higher support values compare to clade I.

The majority of the caulescent *Streptocarpus* species form a single well-compared supported (BS=80, JK=55) clade (clade I, the “*Streptocarpella* clade”), with *Saintpaulia* and *Schizoboea* B.L.Burtt nested within this clade (fig. 1). The Malagasy caulescent species (including the *Saintpaulia*-like species) form a single subclade nested within the African caulescent species (the “Malagasy caulescent clade”) (BS=100, JK=100).

The remainder of the genus forms a single clade in all most parsimonious trees (clade II, the “subg. *Streptocarpus* clade” - fig. 1). There is no bootstrap support for this clade but preliminary results based on cpDNA *trnL-F* intron/spacer data supports this grouping (O’Sullivan unpublished). Although the subg. *Streptocarpus* clade includes mainly African species, two groups of Malagasy species occur basal or near the base of clade II; a clade of Malagasy rosulate polyploids (*S. hildebrandtii* Vatke, *S. perrieri* Humbert) and a clade of mixed morphology including the unifoliate *S. itremensis* B.L.Burtt, the rosulate *S. ibityensis* Humbert and the caulescent species *S. papangae* Humbert and *S. macropodus* B.L.Burtt. Inserted in-between these two Malagasy clades reside two of the most northerly distributed African species of subgenus *Streptocarpus*, *S. exsertus* Hilliard & Burtt (NW Kenya) and *S. burundianus* Hilliard & Burtt (Burundi). Below the Malagasy clades follow several clades with no branch support along the backbone.

Between the Malagasy clades and the remainder of the species resides a group of species occurring predominantly in Malawi and *S. galpinii* J.D.Hooker from Swaziland and *S. hirticapsa* B.L.Burtt from Zimbabwe. A southern African clade of 40 rosulates and unifoliate (bootstrap support, BS=69, jackknife support, JK=72), includes two subclades, an “ITS2 deletion clade” (BS=57), comprising 17 species with a ca. 40 bp deletion in their ITS2 sequences and a “Cape primrose clade” (BS=96, JK=97). Whereas the latter is geographically restricted to the eastern provinces of South Africa and Swaziland, continuing a north – south migration/speciation, the former clade shows a reversed south – north trend (clade 1–5, fig. 3) with clade 5 (BS=64, JK=64) the most derived clade reaching north to Rwanda (*S. bindseilii* Eb.Fisch.).

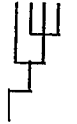
3.4 Biogeography mapping and constrained trees

Frequency mapping indicated three independent migration events from Africa to Madagascar under both ACCTRAN and DELTRAN optimisation. While unconstrained MP trees had a length of 1107 steps, enforced monophyly of Malagasy taxa increased the tree length by 11 steps (1%). However, according to a Templeton (Wilcoxon signed-ranks) test this was not significantly different from the unconstrained tree ($P = 0.078$).

Figure 3. Biogeographic distribution of *Streptocarpus* species of clade II analysed in relation to their phylogeny, based on the majority rule consensus tree in figure 1 illustrating the progressive latitudinal speciation (lines) of subg. *Streptocarpus*. Dotted lines relate to branches of the cladogram without BS or JK support; dashed lines indicate branches on the cladogram with BS and JK support. Solid grey squares = caulescent species, solid black squares = rosulates, open black squares = unifoliate; bold numbers 1–5 define clades in the ITS2 deletion clade; vertical bar as in figure 1. Species abbreviations as in figure 1. An. = Angola; Bot. = Botswana; Bu. = Burundi; Ke. = Kenya; Le. = Lesotho; Ma. = Malawi; Mad. = Madagascar; Mo. = Mozambique; Na. = Namibia; Rv. = Rwanda; SA = South Africa; So. = Somalia; Sw. = Swaziland; Tan. = Tanzania; Ug. = Uganda; Zai. = Zambia; Zim. = Zimbabwe.

SA-Natal ECape
SA-Sw ECape
SA-Natal ECape
SA-T Transkei
SA-Natal ECape

Xir. primifolius
Xir. johannis
Xir. modestus
Xir. prim. ssp. form.



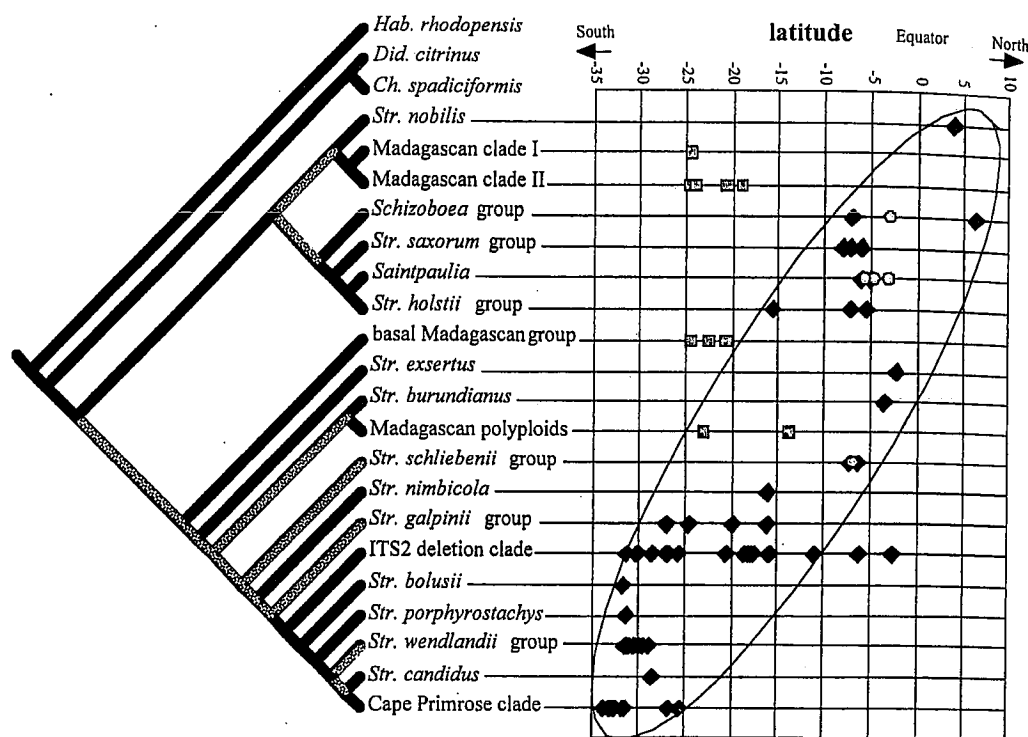


Figure 4. Plot of distribution ranges versus simplified phylogeny of *Streptocarpus* and related genera based on figure 1 illustrating the southern migration and speciation of the genus.

Points indicate most southerly distribution of species for individual clade members or species. Black diamonds = African taxa; grey squares = Malagasy taxa; open circles = other genera. Shaded areas on the cladogram indicate branches with no BS or JK support. An elliptical circle is inserted to emphasise the latitudinal trend.

4 Discussion

4.1 Origin of the genus: Africa or Madagascar?

The genus *Streptocarpus* is defined as African and Malagasy gesneriads with a twisted fruit. For this reason members of this lineage of Gesneriaceae with straight or untwisted fruits were placed in other genera. However, four Asian taxa with twisted fruit are morphologically close enough to be placed in *Streptocarpus* (Hilliard & Burt 1971). Their closest allies, however, are other Asian genera with twisted fruits (Möller, Cronk, Hellens & Preston unpublished).

Character mapping weakly suggests that *Streptocarpus* colonised Madagascar from Africa three times, once as caulescents (clade I) and twice out of clade II. This is in contrast to the distribution of morphological diversity, which is significantly greater in Madagascar. That implies a longer residence of the genus there. The origin of the genus, whether in Africa or Madagascar, must still be regarded as equivocal and more data is therefore urgently needed. Enforced monophyly of Malagasy / Comoro Island species does not result in a significantly longer tree, and the occurrence of a single colonisation event is possible. On the other hand, while branch support for the two single events in clade II is lacking, an extended taxon sampling supports a single colonisation event from Africa to Madagascar in the unifoliate / rosulate clade (Möller unpublished data), and the event in clade I of caulescent species is well

supported (fig. 1). This is in support of the idea of colonisation events after the evolution of the basic morphological types (Möller & Cronk 2001).

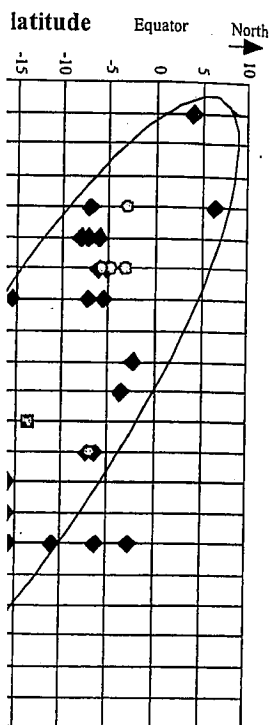
4.2 Dispersal and disjunct distribution: Madagascar and Africa

Of the 128 African/Malagasy species described by Hilliard & Burt (1971) 41 occur on Madagascar and the Comoro Islands, the rest on mainland Africa. No species occurs in both locations, indicating that these colonisation events are extremely rare and have not occurred recently. Representatives of both subgenera occur in both geographical areas. This distribution pattern could be the result of long-distance dispersal. This is highly unlikely as *Streptocarpus* seeds are small, but not dust-like as in orchids, and are unlikely to be dispersed far by wind. The plants also usually occur in moist, shaded, forested locations, sheltered from strong winds. Further, the seeds do not possess any specialised dispersal mechanisms (seed appendices, hooks etc.) facilitating exozoochorous transport. For endozoochorous dispersal the seed testa is too weak for this to be plausible.

Separation by continental drift during Gondwanaland break-up is another scenario that could possibly explain the modern day distribution of *Streptocarpus*. However, the break-up of the Gondwana landmass started 150Mya, at the end of the Jurassic, with Madagascar and India drifting initially south. Geological separation from the mainland Africa was complete at about 130 Mya. Madagascar then separated from India in the late Cretaceous around 88 Mya, probably due to hot spot volcanism and sea-floor spreading (Storey et al. 1995) and India continued drifting north-wards to later collide with Asia. At that time, however, few angiosperm families had evolved and earliest fossil pollen of Scrophulariales *s.l.* appear only in the mid Eocene (47 Mya) (Muller 1985). Divergence times within the genus *Streptocarpus* are incongruent with a continental drift hypothesis; although not without criticism, molecular clocks have been applied to ITS sequence data (Suh et al. 1993; Sang et al. 1994; Wendel et al. 1995). Even a conservative estimate of 0.79-1.57% nucleotide substitutions per My (Sang et al. 1994, 1995), and a maximum sequence divergence between African (*S. elongatus*) and Malagasy (*S. hilsenbergii*) *Streptocarpus* species of 31.8% (uncorrected, excluding 5.8S sequences), would result in a maximum divergence time of 50-25 My. This is too short to be the result of geological separation by continental drift.

Recent studies of the Mozambique channel, however, revealed the possibility of the existence of a land bridge connecting mainland Africa and Madagascar from the mid-Eocene to the early Miocene (45-26Mya) (McCall 1997). This appears to be more congruent with the estimated age of the genus and the divergence time between African and Malagasy species, and would also fit the distribution and speciation pattern of Malagasy endemic mammals (Yoder et al. 1996).

In contrast, a different kind of colonisation event must explain the occurrence of *S. variabilis* Humbert on Anjouan and *S. thompsonii* R.Br. on Grande Comoro, Comoro Islands. There is morphological, cytological and partial ITS sequence evidence that *S. variabilis* (6x) belongs in a polyploid clade with *S. perrieri* and *S. hildebrandtii* (Möller & Cronk 2001; Jong & Möller 2000). The Comoro Islands are very young volcanic islands, the oldest, Mayotte, has been pushed up from the sea floor only 5.5Mya, Anjouan 1.2Mya, and the youngest, Grande Comore, is merely 130,000 years old (Emerick & Duncan 1982). These islands must have therefore come into existence long after the land bridge disappeared, and the only plausible explanation for the existence of *Streptocarpus* on the Comoro Islands would be long distance dispersal (some 330 km to Anjouan, and 460 km to Grande Comore from Madagascar), by means, however, that remain elusive. The fact that long distance dispersal appears to have occurred twice among Malagasy species over this short period of time may indicate that this represents a more regular event and may refute a land bridge hypothesis in favour of a long distance dispersal event between Africa and Madagascar. However, the distance between Africa and Madagascar is about 700 km, too long to be easily bridged by wind dispersal. It is also interesting to note that the two species concerned are not endemic to the Comoro Islands, but occur on Madagascar as well (*S. thompsonii* is a



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in clade II is lacking, an
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morphologically diverse species widespread across the island). This lack of endemism is probably due to the very recent timing of the dispersal / isolation event.

4.3 Migration patterns on mainland Africa

While African species of subg. *Streptocarpella*, clade I, are mainly restricted to tropical Africa, clade II species in Africa occur mainly along the eastern area from Ethiopia to the Cape (fig. 3). When mapping the molecular phylogeny of the African clade II taxa against their biogeographic origin, a clear trend can be discerned, starting with *S. exertus* in NW Kenya and *S. burundianus* in the north to the crown group including *S. rexii* Lindl., the Cape Primrose, in the south (fig. 4). The sister clade to this rosulate group includes unifoliate species. These groups appear to have evolved sympatrically, as the distribution of the species overlap considerably. However, there is some evidence that the two growth forms, unifoliate and rosulate, occupy different ecological niches (Möller & Cronk 2001). In the ITS2 deletion clade there is some reversal of the north-south trend. This group also shows the widest geographical range, from Swaziland to Rwanda (fig. 3, 4).

African caulescent *Streptocarpus* species and basal members of the phyllomorphic clade are largely restricted to wet and relatively aseasonal tropical forests of equatorial Africa. These species have no abscission layer and no adaptations to withstanding cold and drought. The clade of phyllomorphic *Streptocarpus* species that occur further south generally have the ability to form an abscission layer across the lamina to deal with unfavourable environmental conditions (Hilliard & Burt 1971). This may constitute a "key innovation" (Givnish 1997) which has allowed phyllomorphic species to disperse south while the caulescent species are confined to equatorial Africa.

The "progressive latitudinal speciation" that seems to have accompanied the southwards dispersal of the genus needs to be seen against a background of Pleistocene climatic change. Forest cover relative to grassland has changed in extent markedly both as a result of climate deterioration since the late Miocene and as a response to Pleistocene glacial cycles (Coetzee et al. 1978). During warm, wet periods we would expect a slow southwards migration of *Streptocarpus*. However, allopatric speciation might be expected to occur during cold, dry periods when forest area fragments. It appears that *Streptocarpus* species are still actively radiating at the southern end of their range, as evidenced by species showing great morphological variation (such as *S. johannis* L.L.Britten, *S. haygarthii* C.B.Clarke, *S. grandis* N.E.Br.) and species groups of closely related ill-defined species (such as *S. aggr. rexii*).

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 form an abscission layer
 (Möller & Burt 1971). This may
 allow species to disperse south

eastwards dispersal of the
 forest cover relative to
 the time since the late Miocene
 warm, wet periods we
 think speciation might be
 easier than that of *Streptocarpus*
 recorded by species showing
 C.B. Clarke, *S. grandis*
 (gr. *rexii*).

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