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Plant Syst. Evol. 224: 173-182.

REFNO: 3024

KEYWORDS:

**Africa, Chromosome numbers, Comoro Islands, Cytology, Madagascar,
Morphology, Streptocarpella, Streptocarpus**

New chromosome counts in *Streptocarpus* (Gesneriaceae) from Madagascar and the Comoro Islands and their taxonomic significance

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Received September 9, 1999

Accepted June 28, 2000

Abstract. This study records the chromosome numbers of 10 species of *Streptocarpus*; nine of the counts are new. With the exception of *S. buchananii* of mainland Africa, all the results are for plants endemic to Madagascar and the Comoro Islands. While there is a strong correlation between basic number and growth form in the two subgenera of the genus on the African mainland ($x = 15$ among caulescent species in subgenus *Streptocarpella*; $x = 16$ among acaulescent species in subgenus *Streptocarpus*), the situation appears more complex among Madagascan and Comoro Island species. One notable example of deviation from this correlation is shown by *S. papangae*, a shrubby caulescent species, with $2n = 32$ ($x = 16$). Polyploidy in the genus appears to be absent on mainland Africa, but is present in Madagascar and the Comoro Islands, ranging from tetraploidy to octoploidy. Evolutionary implications of the cytological observations are considered.

Key words: Gesneriaceae, *Streptocarpus*. Chromosome numbers, growth patterns, taxonomy, Africa, Comoro Islands, Madagascar.

The tremendous diversity in growth forms present in the genus *Streptocarpus* Lindl. (Gesneriaceae, subfamily Cyrtandroideae, tribe Didymocarpeae) poses a challenge to

taxonomists. These forms range from highly unusual acaulescent types to more or less caulescent ones. As typical of Old World Gesneriaceae, the seedlings display anisocotily, where one of the cotyledons continues to grow after germination, while the other remains very small. Among acaulescent species are those with a distinctive unifoliate habit consisting of only a single unusually enlarged cotyledon, flowering from the base of the lamina, and rosulates i.e. rosette-like plants as well as forms that are apparently orthodox rosettes (as exemplified in *Saintpaulia* Wendl.). Caulescent species typically have aerial shoots with decussate leaves and axillary buds. The enlarged cotyledon (macrocotyledon) possesses mixed characteristics of shoot and leaf and is known as a 'phyllomorph' (Jong 1970, 1973, 1978; Jong and Burt 1975). Thus, unifoliate consists of a single phyllomorph, whereas the rosulates, an assemblage of phyllomorphs.

The unifoliate together with the rosulates, are placed in the subg. *Streptocarpus*, and the caulescent species in the subg. *Streptocarpella*. With few exceptions (Hilliard and Burt 1971, p. 117), this subgeneric division is basically clear cut amongst mainland African species.

The situation, however, becomes more complex when species from Madagascar and the Comoro Islands (one species) are taken into consideration; almost one third of all species of *Streptocarpus* are found on these islands (Hilliard and Burt 1971, Humbert 1971). The morphology of many of these is unusual and has yet to be studied in detail; some of these cannot be easily placed in either of the two subgenera; Hilliard and Burt (1971) recognise at least three groups not found on mainland Africa:

- Group 1: plants with long-petiolate leaves in a basal rosette, reminiscent of *Saintpaulia*, e.g. *S. beampingaratrensis*,
- Group 2: plants with leaves in a basal rosette, often narrowing gradually at the base, with ascending veins that branch further up, e.g. *S. variabilis*,
- Group 3: caulescent plants with opposite decussate leaves that can be described as woody shrubs, e.g. *S. papangae*.

Currently, members of Group 1, of acaulescent habit with long-petiolate leaves, axillary inflorescences and verruculose seeds, and those of Group 3, of woody shrubs, are placed in subg. *Streptocarpella*, and those in Group 2, acaulescent forms with very different leaf morphology, in subg. *Streptocarpus*. Hilliard and Burt (1971), however, had long anticipated that a further understanding of the developmental bases of the morphological diversity of Madagascan plants "may eventually add a new dimension to our understanding of *Streptocarpus* and lead to a revision of the subgeneric groupings." In this paper we present strong cytological evidence that the dichotomy into two subgenera will have to be reassessed, although the number of species examined is not yet sufficient for a full revision to be made.

The close correspondence between basic chromosome number ($x = 16$ in subg. *Streptocarpus*, $x = 15$ in subg. *Streptocarpella*), and growth form is of great evolutionary interest. This correlation was first recognised by Lawrence et al. (1939), and has been confirmed by

the subsequent more extensive chromosome surveys of Ratter and his co-workers (Ratter and Prentice 1967, Ratter and Milne 1970, Milne 1975, Ratter 1975). To date, the chromosome numbers of 51 species (Ratter 1975) out of 132 recognised in *Streptocarpus* (Hilliard and Burt 1971) are known. The majority of the published counts are for species of the African mainland. Very few counts have previously been reported for species from Madagascar and the Comoro Islands. Since some of these represent growth forms that are not readily interpretable in terms of the phyllo-morph concept, the present chromosome survey has been undertaken both to add to cytological knowledge of the genus and to test the consistency of the correlation between basic number, growth form and subgeneric division. This study complements a wider molecular and phylogenetic study of the genus being conducted at the Royal Botanic Garden Edinburgh (Möller and Cronk 1997, Möller and Cronk in press).

Materials and methods

Plant material. During a recent expedition to Madagascar, living specimens were collected by the second author (M.M.) for molecular, cytological and other investigations (see Table 1 for collecting localities and accession numbers). This study was based mainly on root tips harvested from pot-grown specimens or from cuttings grown in tap water. Some counts were also obtained from the basal meristems of cotyledons of young seedlings from seeds germinated on filter paper in petri-dishes. These seedlings were grown in a 20 °C growth chamber, on a 12 hr light/dark cycle. They were harvested when about 10 days old.

Voucher herbarium specimens and flowers preserved in Copenhagen mixture (methylated spirit, glycerol and distilled water: 5.5:0.5:3.5 v/v) were lodged in the RBGE Herbarium (E). Colour photographs of flowering specimens were deposited in the RBGE Library slide collection.

Cytological protocols. Root tips or whole seedlings were pre-treated either in saturated aqueous 1-bromonaphthalene for 2 to 2.5 hr, at room temperature (a) or for 20 hr at 5 °C (b) or

Table 1. Species of *Streptocarpus* cytologically investigated

Taxon	Accession number	Origin	2n	Subgenus /Group
<i>S. beampingaratrensis</i> Humbert subsp. <i>beampingaratrensis</i>	1997 2884	Madagascar; Tuléar, Col de Beampingaratra	30*	SA/1
<i>S. variabilis</i> Humbert	1994 1333	Comoro Islands, Anjouan	96	SS/2
<i>S. perrieri</i> Humbert	1997 2892	Madagascar; Antananarivo, Mt. Ibity	64*	SS/2
<i>S. papangae</i> Humbert	1997 2886	Madagascar; Tuléar, Col de Beampingaratra	32*	SA/3
<i>S. ibityensis</i> Humbert	1997 2888	Madagascar; Antananarivo, Mt. Ibity	32*	SS
<i>S. itremensis</i> B.L. Burt	1997 2889	Madagascar; Antananarivo, Mt. Ibity	32*	SS
<i>S. tanala</i> Humbert	1997 2882	Madagascar; Tuléar, Analaro, Andranohela	30*	SA
<i>S. thompsonii</i> R. Br.	1997 2890	Madagascar; Antananarivo, Mt. Ibity	30	SA
<i>S. thompsonii</i> R. Br.	1994 1334	Madagascar; locality unknown; seed from American Gloxinia & Gesneriad Society	30	SA
<i>S. thompsonii</i> R. Br.	1992 3189	Madagascar; locality unknown; seed from Royal Botanic Gardens, Kew	60*	SA
<i>S. sp.</i>	1993 1445	Madagascar; Fianarantsoa, Itremo Massif	30*	SA
<i>S. buchananii</i> C.B. Clarke	1996 1895	South Africa; Malawi; Zomba Distr., Mt. Zomba	30*	SA

Abbreviations: SA = subg. *Streptocarpella*; SS = subg. *Streptocarpus* [Assignments to subgenera and groups 1 to 3 after Hilliard and Burt (1971)]. * indicates new chromosome counts

in 0.002 M 8-hydroxyquinoline for 4 to 5 hr at 13 °C (c), and then fixed in freshly prepared Farmer's Fluid (3 ethanol:1 glacial acetic acid). After hydrolysis for 20 min in 5 M HCl at room temperature, followed by washing through several changes of distilled water, the roots or whole seedlings were transferred to Feulgen Reagent prepared according to Fox (1969) for 2 to 3 hr. To facilitate squashing, the stained material was usually treated with an enzyme mixture of 5% pectinase (Sigma 2401) and 5% cellulase (BDH or Calbiochem 21947) at 35 °C for 20 min. and squashed in 45% acetic acid or in an aceto-carmin counterstain. Due to their small size, chromosomes mounted in 45% acetic acid are more clearly seen when observed under phase contrast. Counterstaining with dilute aceto-carmin (0.4%), however, greatly enhances viewing under bright field. This also reduces the likelihood of fading in permanent slides produced according to a modification of Conger & Fairchild's quick-freeze method (1953, in Jong 1997). Kodak

Technical Pan Film at ISO 100, developed in Suprol Developer (1:4 water) for 3 min at 20 °C, was used for photomicrography.

Results

Chromosome numbers observed in the present investigation are listed in Table 1. Nine of the counts are new (marked by an asterisk) and two are of new accessions of species for which published results already exist.

Whereas the Madagascan *S. ibityensis*, *S. itremensis* (subg. *Streptocarpus*) and *S. tanala*, *S. thompsonii*, and *S. sp.* (subg. *Streptocarpella*) possess a gross morphology that can be easily assigned to the respective subgenera, the other taxa represent morphologically unusual plants and are thus given in the groupings suggested by Hilliard and Burt (1971).

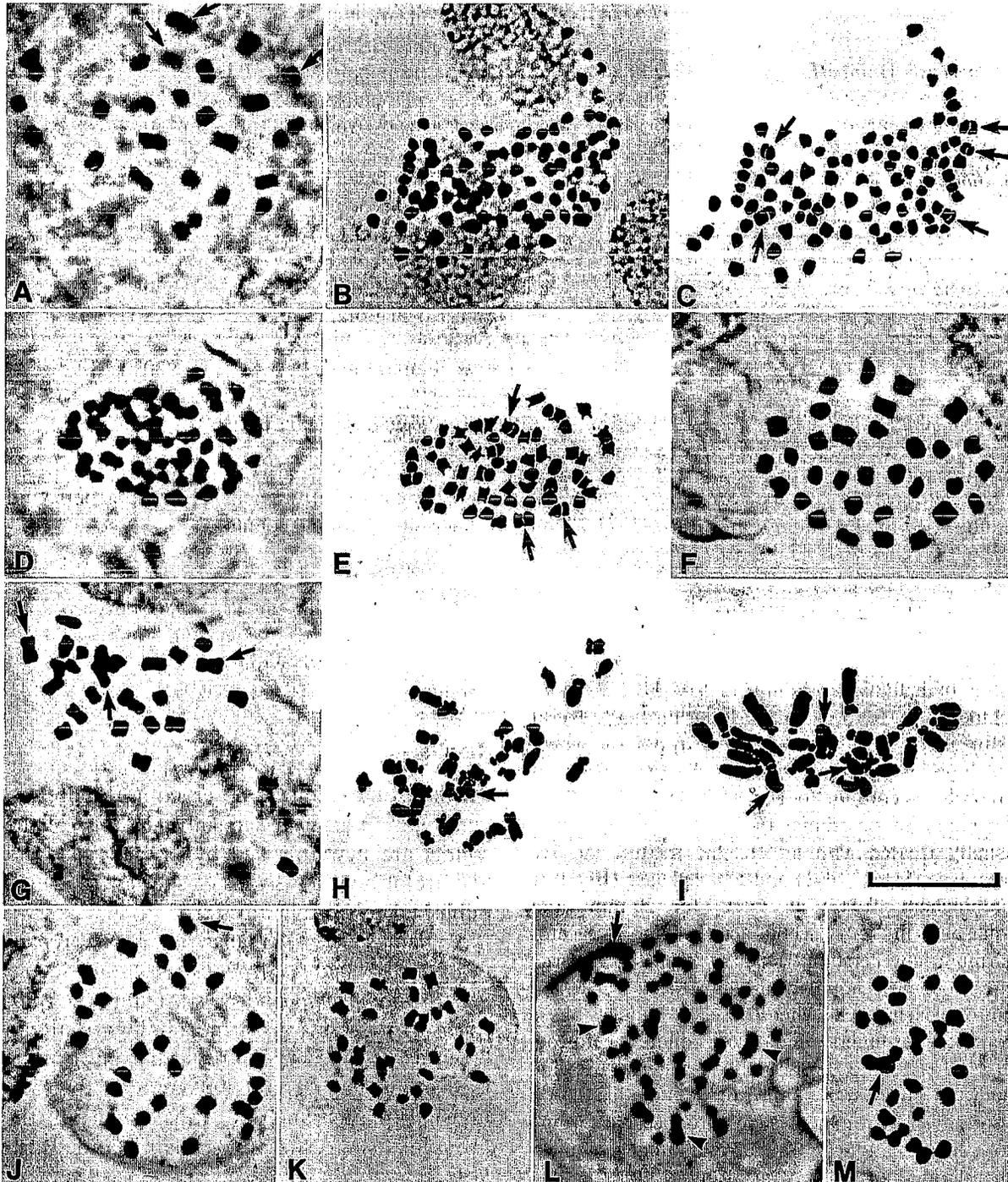
Group 1 Taxon:

Streptocarpus beampingaratrensis Humbert
 subsp. *beampingaratrensis* - $2n = 30$. This
 has leaves with long petioles and ovate-subor-
 bicular lamina arranged in a rosette closely
 resembling that of a *Saintpaulia*. Its somatic

number is $2n = 30$. The root tip chromosomes
 show marked association in twos (Fig. 1A).

Group 2 Taxa:

Streptocarpus variabilis Humbert - $2n = 96$.
 This rosette plant with broad sessile subgla-



brous leaves and prominent ascending veins belongs to a group with a combination of characters that is unique within subg. *Streptocarpus*. The two different accessions examined were from the Comoro Islands, possibly originating from a single collection; both had an unusually high chromosome number of $2n = 96$ (Fig. 1B, C), which is in accord with the gametophytic number of $n = 48$ previously reported by Milne (1975).

Streptocarpus perrieri Humbert - $2n = 64$. Counts obtained from petri-dish grown seedlings indicate that *S. perrieri* has a somatic number of $2n = 64$ (Fig. 1D, E). This perennial unifoliolate, together with the rosulate *S. variabilis* and *S. hildebrandtii* Vatke, a perennial rosulate with $n = 64$ (Milne 1975), are all polyploids sharing the basic number $x = 16$. The two last-mentioned species form regular bivalents thus behaving meiotically as diploids (Ratter 1975).

Group 3 Taxa:

Streptocarpus papangae Humbert - $2n = 32$. The most unusual group of species found on Madagascar comprises tall shrubby plants with woody stem bases, of which *S. papangae* was the only representative available in this investigation. While its caulescent habit places it in subg. *Streptocarpella* (Hilliard and

Burt 1971), its chromosome number of $2n = 32$ (Fig. 1F, G) is clearly inconsistent with such a placement. The chromosomes are mostly metacentric to submetacentric (Fig. 1G).

Additional Taxa:

Subgenus *Streptocarpus*

Streptocarpus ibityensis Humbert - $2n = 32$. This is a rosette plant with silvery hirsute leaves without petioles, and has $2n = 32$ in accord with the basic number $x = 16$ observed in other acaulescents in subg. *Streptocarpus*. It has, however, a distinctive karyotype consisting largely of acrocentric chromosomes (Fig. 1H), a karyotypic composition not previously reported in *Streptocarpus*. A similar karyotype also occurs in *S. itremensis* (see below).

Streptocarpus itremensis B.L. Burt - $2n = 32$. This unifoliolate also has $2n = 32$ (Fig. 1I). The chromosomes are mostly acrocentric. Unfortunately insufficient metaphases were available for a more detailed examination of the karyotype. These preliminary observations suggest that there is a close karyotypic similarity between this species and *S. ibityensis*.

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Fig. 1. Root tip and macrocotyledonary mitotic chromosomes of *Streptocarpus*. Scale bar: 10 μ m. All figures approx. 2000 \times . **A** *S. beampingaratrensis* subsp. *beampingaratrensis*. Root-tip-chromosomes, $2n = 30$. Note close association in twos of certain chromosomes. Arrows point to chromosomes out of focus. **B, C** *S. variabilis*. Root tip prometaphase, $2n = 96$. **C** drawing of **B**, overlapping chromosomes arrowed. **D, E** *S. perrieri*. Macrocotyledonary basal meristem prometaphase, $2n = 64$. **E** drawing of **D**, closely associated/overlapping chromosomes arrowed. **F, G** *S. papangae*. Root tip chromosomes. **F** late prometaphase, $2n = 32$. **G** partial metaphase showing mostly meta- to submetacentric chromosomes. Noticeably larger chromosomes arrowed. **H** *S. ibityensis*. Drawing of macrocotyledonary basal meristem metaphase, $2n = 32$. Chromosomes mostly acrocentric. Arrow points to a group of four overlapping chromosomes. **I** *S. itremensis*. Drawing of macrocotyledonary basal meristem metaphase, $2n = 32$. Chromosomes mostly acrocentric. Arrows indicate groups of overlapping chromosomes. **J** *S. tanala*. Root tip metaphase, $2n = 30$. Arrowed chromosome belongs to neighbouring metaphase. **K** *S. thompsonii*, accession No. 1997 2890. Root tip metaphase, $2n = 30$. **L** *S. thompsonii*, accession No. 1992 3189. Root tip metaphase, $2n = 60$. Note close association of some chromosomes. Arrow points to out-of-focus chromosome, arrowheads to overlapping chromosomes. **M** *S. buchananii*. Root-tip metaphase, $2n = 30$. Arrow indicates two closely associated overlapping chromosomes in a group of four

Subgenus *Streptocarpella*

Within the herbaceous caulescent group of subg. *Streptocarpella*, three Madagascan representatives were counted, namely *S. tanala*, *S. thompsonii* and an unnamed species.

***Streptocarpus tanala* Humbert** – $2n = 30$. This species is ecologically unusual since, unlike any other *Streptocarpus* (except for *S. fanninae* [Harvey ex] C.B. Clarke in Africa), it grows very close to river edges, almost in waterlogged conditions. Morphologically, it differs from other species of the subgenus in its creeping habit and barely twisted fruits. Its chromosomes are predominantly metacentric to submetacentric (Fig. 1J), and its chromosome number of $2n = 30$ is consistent with its subgeneric placement.

***Streptocarpus thompsonii* R.Br.** – $2n = 30, 60$. In *S. thompsonii*, a typical herbaceous caulescent species, two accessions (accession number 1994 1334 and 1997 2890) had the expected number $2n = 30$ (Fig. 1K), in agreement with a previous count of $n = 15$ in *S. thompsonii* var. *bojeri* reported by Milne (1975). Accession 1992 3189 had a tetraploid number of $2n = 60$ (Fig. 1L). Morphologically this accession can be easily distinguished by its larger flowers. It is unclear, however, whether the tetraploid condition is typical of a wild population or has arisen over many generations of cultivation from seed, as information on the origin of the accession is scant. In both the diploid and tetraploid plants, there is a strong association of chromosomes in twos (Fig. 1K, L).

***Streptocarpus* sp.** – $2n = 30$. This caulescent species is morphologically closely associated with *S. thompsonii*, and the observed chromosome number of $2n = 30$ (data not shown) is in accordance with its subgeneric placement in *Streptocarpella*.

Mainland Africa Taxon:

***Streptocarpus buchananii* C.B. Clarke** – $2n = 30$. This caulescent species from Malawi with personate flowers not found in any

Madagascan species has $2n = 30$ (Fig. 1M), a new count which conforms with $n = 15$ reported for other members of subg. *Streptocarpella* of mainland Africa.

Discussion

Possible links between subgenera in Madagascar. From the cytotaxonomic point of view, Madagascar provides interesting examples of deviation from the neat pattern of correlation between growth form, subgeneric position, and chromosome number found in mainland Africa. This deviation is reported here for the first time for *S. papangae*. This unusual shrubby, woody species has $2n = 32$ instead of $2n = 30$ generally observed in other caulescent species in subg. *Streptocarpella*. As this is the sole representative of Group 3 for which we have cytological data, further information from other members of this group is highly desirable, but, as yet, no other species is in cultivation. The presence of apparently anomalous chromosome numbers is perhaps not surprising, for molecular data indicate that *S. papangae* and other related species hold the key to understanding the phylogenetic development within the genus (Möller and Cronk in press). With this combination of $x = 16$, generally found in subg. *Streptocarpus*, and the caulescent habit found in subg. *Streptocarpella*, the species-group around *S. papangae* may represent a link between the two subgenera.

Streptocarpus beampingaratrensis subsp. *beampingaratrensis*, a rosette plant has $2n = 30$ instead of $2n = 32$ typical of other acaulescent species of subg. *Streptocarpus*. Interestingly, based on its gross morphology (long petiolate leaves, axillary inflorescences, verruculose seeds) this species (together with a number of other species) is placed in subg. *Streptocarpella* (Hilliard and Burt 1971), where the basic number $x = 15$ is prevalent. Evidence from recent molecular studies indicates that this species may have evolved from Madagascan caulescent ancestor (Möller and Cronk in press), most probably by shortening

of the shoot axis, without any accompanying changes in basic chromosome number. It may be deduced that the split, on the one hand, between acaulescent forms of subg. *Streptocarpus*, i.e. the unifoliate, rosulate and Group 2 taxa, and on the other, caulescent forms of subg. *Streptocarpella*, (associated with a change in basic chromosome number) most likely preceded the independent evolution of *S. beampingaratrensis* and its related species in Group 1 from within subg. *Streptocarpella* (Möller and Cronk in press). This deduction about the origin of *S. beampingaratrensis* in turn further suggests that its acaulescent habit is not necessarily homologous with acaulescence present in subg. *Streptocarpus*. This may explain the lack of conformity to the correlation generally found between growth form and chromosome number in the two subgenera.

Quite apart from unconfirmed counts of $n = 14$, $2n = 28$ (cited in Ratter 1975), it should further be noted that the predominant chromosome number of *Saintpaulia* is also $2n = 30$ (Ratter 1975, Skog 1984). The similarity in gross morphology and chromosome number between *S. beampingaratrensis* and *Saintpaulia* could be open to at least two possible interpretations: that it is an indication of a close relationship between the two taxa, or that the resemblance is largely superficial. The second seems the more probable, for although molecular evidence strongly supports the hypothesis that *Saintpaulia* evolved within *Streptocarpus* subg. *Streptocarpella* (Möller and Cronk 1997, Smith et al. 1998, Möller et al. 1999), the data further suggest that the evolution of *S. beampingaratrensis* and *Saintpaulia* followed separate, parallel evolutionary routes (Möller and Cronk in press).

Polyploidy. Polyploid taxa have not yet been found amongst mainland African *Streptocarpus*. On Madagascar and the Comoro Islands, however, three polyploid species (in Group 2) are now known, their polyploidy ranging from the tetraploid (*S. perrieri*, $2n = 64$), hexaploid (*S. variabilis*, $2n = 96$) to the octoploid (*S. hildebrandtii*, $2n = 128$, Milne 1975) level. This polyploid series is based

on $x = 16$, the number characteristic of subg. *Streptocarpus* in which these species are currently placed. This may suggest a close affinity of this polyploid group to the phyllomorphic taxa in this subgenus and hence its current placement there. The tendency to polyploidy, however, together with a combination of morphological features not known amongst other members of subg. *Streptocarpus* (rosette growth habit, leaves with ascending veins, and axillary inflorescences) suggest that these taxa may form an independent line of evolution.

Before any taxonomic regrouping can be made based on these observations, however, detailed examination of the growth patterns of Madagascan species is essential. For example, while stemless rosulate plants and unifoliate of mainland Africa are generally phyllomorphic in structure (Jong 1970, 1973, 1978; Jong and Burt 1975), this is apparently not the case in rosette forms of species such as *S. variabilis* or *S. beampingaratrensis*.

Mainland African *Streptocarpus*. Among African mainland *Streptocarpus*, only few examples of apparent deviation from the morphology/chromosome number correlation are known (e.g. *S. schliebenii* Mansf. and *S. decipiens* Hilliard and Burt). *S. schliebenii* seems to combine seedling aspects of an acaulescent plant with the subsequent growth patterns of a caulescent species (B. L. Burt, pers. comm.). In an addendum to her paper, Milne (1975) reports a gametophytic number of $n = 16$ for this species. Herbarium sheets of cultivated specimens (C 8433, accession number 1972 2140) look unmistakably caulescent, with opposite petiolate leaves and axillary inflorescences, while the scant information on the early ontogeny of this species pointed to a definite elongation of the macrocotyledon with wide-spreading venation, suggestive of a phyllomorphic structure. *S. decipiens* might represent an even more likely link between the two subgenera as it combines the characters of opposite leaves, axillary inflorescences and verruculose seeds of subg. *Streptocarpella*, with phyllomorphic features commonly found in subg. *Streptocarpus*, namely basal leaves, a

well marked abscission zone on these, and the origin of shoots from buds at the base of a petiole-like structure ('petiolode'). Cytologically, the chromosome number $2n = 32$ (Ratter and Milne 1970) supports its current position in subg. *Streptocarpus*. Molecular data also indicate that the characters linking this species to subg. *Streptocarpella* are most probably the result of convergent evolution (Möller and Cronk in press).

Basic Number, polyploid and dysploid derivation. The presence of the basic number $x = 16$ in *S. schliebenii* and *S. decipiens* and in *S. papangae*, apparently linking the two subgenera, is highly interesting and informative in a discussion of the possible cytological condition in putative ancestors of *Streptocarpus*.

In a survey of chromosome numbers in Old World members of the Gesneriaceae, Ratter (1975) points out that patterns of chromosomal variation can be strikingly different in the larger genera of the subfamily Cyrtandroideae to which *Streptocarpus* belongs, and suggests that the ancestral basic number of the subfamily was probably $x = 8$ or 9 found today in species of *Boea*, *Chirita* and *Henckelia* (Kiehn et al. 1997) and that the numbers $n = 15$, 16 , 17 and 18 are of tetraploid derivation.

In some allopolyploid plants, bivalents at first metaphase of meiosis are not randomly distributed but occur in pairs or groups. This was interpreted to reflect genetic similarity or affinity between bivalents. Lawrence (1931), who provided a general review on the subject, and Darlington (1937) were both emphatic that secondary association is not an artefact caused by fixatives. Using the common allohexaploid wheat with suitable chromosome markers, Riley (1960) provided the first experimental evidence that such associations do indeed occur between genetically similar chromosomes.

In view of the high numbers $n = 15$ and $n = 16$, and prevalence of secondary association among bivalents in pollen mother cells, Lawrence et al. (1939) suggested that the chromosome numbers in *Streptocarpus* may

have been derived from a lower ancestral number through allopolyploidy. In the present study, somatic chromosomes of certain species also show a marked tendency to associate in twos (Fig. 1A, L). Such chromosome associations, therefore, occur not only in pollen mother cells but also in somatic cells. Quadrivalent formation in *Streptocarpus*, however, has not been reported in the literature. There is at present no other line of evidence to indicate whether *Streptocarpus* arose through autopolyploidy or allopolyploidy. Meiotically at least, the investigated species, including the high polyploids from Madagascar and the Comoro Islands, behave like diploids (Ratter 1975, Milne 1975). That the promotion of bivalent formation in polyploids (i.e. diploidisation) can have a genetic basis has been well demonstrated in cultivated breadwheats, and appears to be implicated in some ornamentals, for example, in the evolution of the polyploid garden *Dahlia* (Gatt et al. 1998). Such genetic evidence is lacking for *Streptocarpus*.

When considered in conjunction with morphology and other data, $x = 16$ might be considered ancestral, from which $x = 15$ has been derived. The African *Streptocarpus decipiens*, *S. schliebenii* and the shrubby Madagascan *S. papangae* perhaps hold the key, with their $2n = 32$ which, probably through chromosomal rearrangement followed by dysploid reduction, led to $2n = 30$ that characterises all other mainland African and Madagascan species of subg. *Streptocarpella*. The main $x = 16$ line of subg. *Streptocarpus* may have been established early, most likely prior to the final geographical isolation of Madagascar from the African mainland, because of the presence of the subgeneric links in both geographical regions. The genome differentiation has now become so strongly established that attempted crosses between the two subgenera meet with failure (Lawrence 1940, Oehlkers 1940). This failure to hybridise is in marked contrast to intergeneric cross-compatibility between other taxa in tribe Didymocarpeae (Halda 1989). Cross-incompatibility in

Streptocarpus may of course reside in many other possible causes which remain to be explored. It would be highly instructive, for example, to test the crossability of *S. papangae* with other caulescent as well as acaulescent species.

Variation in karyotype. The somatic chromosomes of *Streptocarpus* are small, and analysable somatic metaphase figures are scarce. Many of the present counts were based on prometaphases. Details of chromosome morphology can be gleaned, however, from favourable mitotic spreads, as for example in *S. ibityensis* and *S. itremensis*. Here, the chromosomes are predominantly acrocentric (Fig. 1H, I) as compared with for example *S. papangae* where they are predominantly meta-centric to submetacentric (Fig. 1G). It may be deduced that much chromosome repatterning had occurred, at least among Madagascan taxa. This highlights the potential value of, and need for, a careful comparative karyotype study, not only of Madagascan species, but also of mainland African ones. Such studies, including the measurement of DNA quantitative variation, the use of molecular-cytological techniques, e.g. in situ DNA hybridisation, to further investigate genomic affinities, may well yield valuable insights into cytological evolution of the genus as a whole.

Conclusions

The cytological evidence presented here, when considered in conjunction with the diverse morphology of *Streptocarpus* species displayed in Madagascar and the Comoro Islands, suggests that a split into two subgenera based only on morphology is far too simple a treatment. Furthermore, within the unifoliate/rosulate and caulescent groups, at least two distinctive subgroups can be recognised; a group of high polyploid species with leaf veins ascending from the base, and another group of taxa with rosettes of strongly petiolate leaves, reminiscent of *Saintpaulia*. This investigation demonstrates that the long established correlation between growth habit, subgeneric posi-

tion, and basic chromosome number breaks down in Madagascar.

It is with great pleasure to extend grateful thanks to the Carnegie Trust for the Universities of Scotland, the Davis Expedition Fund of the University of Edinburgh, and the Percy Sladen Memorial Fund for financial assistance that enabled M. Möller to undertake field studies and to collect living material from Madagascar (Republic of Malagasy) for this investigation. We thank A. Andrianjafy, G. Rafamontanantsoa and S. Irapanarivo from PBZT for logistic field support there. We extend our thanks to the Regius Keeper and staff at the Royal Botanic Garden Edinburgh for the use of research facilities, especially to J. Main and D. Mitchell for the maintenance of the Gesneriaceae collection, to S. Scott, A. Reid and U. Gregory (horticultural staff) for their willing help in growing the plants. We also greatly appreciate the critical comments on our draft manuscript from Mr. B.L. Burtt, Drs. J.A. Ratter and Q.C.B. Cronk of the Royal Botanic Garden Edinburgh, and Professor A. Weber and Dr. M. Kiehn of the Botanical Institute of the University of Vienna. The help of L. Forrest in providing the first tentative somatic chromosome count for *Streptocarpus variabilis* is gratefully acknowledged. Thanks also to M. Mendum for help in composing the illustrations.

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