

STUDIES ON *STREPTOCARPUS* Lindl.

V. SPECIATION AND GENE SYSTEMS

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1. INTRODUCTION

IN previous papers the genetics and chemistry of flower colour in *Streptocarpus* (Lawrence *et al.*, 1939; Lawrence and Sturgess, 1958) and the genetics of flower pattern (Lawrence, 1958) have been described. This paper completes the survey of *Streptocarpus*, gathers up the whole of the results and discusses their meaning.

2. TAXONOMY OF SPECIES

(i) *Habit*

On the basis of habit, *Streptocarpus* Lindl. falls naturally into two perfectly distinct sub-genera (Fritsch, 1904), *Streptocarpella* which comprises the caulescent species with stems (plate I, fig. 1) and *Eustreptocarpus* * the acaulescent species without stems (plates, figs. 2-5). Fritsch further divided *Eustreptocarpus*, again on habit, into two sections, *unifoliati* with one leaf and *rosulati* with many leaves. Burt (1939), however, has pointed out that "there does not seem to be a hard and fast line" between these two sections. From observations I have made in the course of the studies on *Streptocarpus*, it has become clear that selection can produce unifoliates having a large second leaf born opposite the first one, or even a small third leaf. Further, plants raised from seed gathered in the wild from unifoliates may develop a second leaf.

In the large-leaved unifoliates, e.g. *grandis*, *dunnii*, *wendlandii*, the additional leaves could be regarded as aberrant. In certain small-leaved "unifoliates" however, the production of a second or third leaf is characteristic, e.g. *gracilis*; in others, a second leaf is very rarely formed, e.g. *polyanthus*. It will be convenient to distinguish these small-leaved true unifoliates and near-unifoliates as "sub-unifoliates", reserving the term unifoliates for the large-leaved species. The majority of rosulates produce many leaves, e.g. *rexii*, *parviflorus*, but there are some with only 6 or 7, e.g. *meyeri*.

Oehlkers (1938, 1942) has shown that in crosses between *rexii* (rosulate), and *wendlandii* and *grandis* (unifoliates), the F_2 progeny segregate into approximately 15 rosulates to one unifoliate as if two, dominant, supplementary genes controlled the rosulate character, the double recessive being unifoliate. Clearly, if modifiers affect

* Although the current rules of nomenclature require that the typical sub-genus merely repeats the generic name, the previous practice in this series of papers is continued here.

either or both of the recessive genes, or if they differ in their degree of recessiveness, the possibility exists of unifoliate (and sub-unifoliate) producing a second leaf of sorts.

In my material the difference in leaf number between unifoliate and rosulate was obvious. There are, however, two other criteria of importance for the arguments concerning taxonomy and speciation. First, unifoliate and rosulate can be distinguished by their floral systems. The unifoliate are strong-growing plants bearing stout, many-branched inflorescences each carrying roughly 30-60 moderately large flowers (plate I, fig. 3). The sub-unifoliate are weaker-growing plants and the inflorescences are smaller and more slender but each may bear some 30-60 flowers which, in contrast to those of the large-leaved unifoliate, are small (plate I, fig. 2). The rosulate are strong-growing and, typically, bear 1-2 flowers on each inflorescence (plate II, fig. 4) though some may have up to about 12 (plate II, fig. 5). Thus, with respect to the distinction between unifoliate and sub-unifoliate on the one hand and rosulate on the other, flower number appears to be a better taxonomic criterion than leaf number, the distinction being decisive in my material.

The second criterion refers to the time of flowering of the unifoliate and sub-unifoliate. In cultivation, sub-unifoliate and rosulate flower in from 4-6 months from germination, unifoliate in from 12-18 months. A difference in flowering time of this order must be an adaptive response to a major difference in climatic conditions, as must also the difference between monocarpy and polycarpy. Field studies of the distribution of polycarpic and monocarpic species of *Streptocarpus* in relation to environment, especially climate, should prove enlightening.

In the wild the division into (1) unifoliate and sub-unifoliate, and (2) rosulate may not be absolute but it holds for the 27 species (perhaps half of all those recorded) I have grown under standard conditions of good cultivation.

(ii) *Habitat*

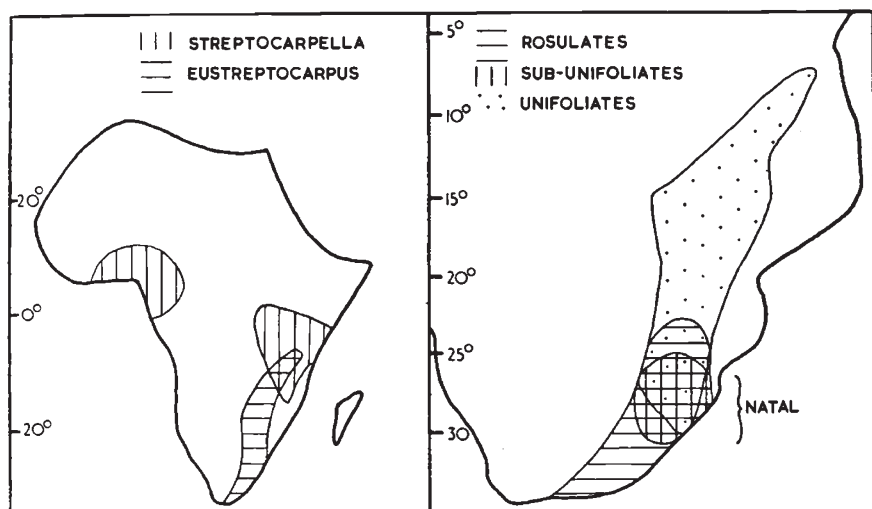
The relevance of these facts concerning habit becomes apparent when the geographical distribution of *Eustreptocarpus* is noted (text-fig.). The centre of diversity is Natal, in which unifoliate and sub-unifoliate are found together with rosulate. The sub-unifoliate known to the author occur mainly in or near Natal. Two unifoliate (*wendlandii*, *grandis*) are found in Natal, the remainder occurring northward in widely spaced areas, usually 200-300 miles apart. The rosulate overlap both unifoliate and sub-unifoliate. Of the individual species, *rexii* has the widest distribution of all, *viz.* from latitudes 25.5° to 34°. Broadly we may say the rosulate inhabit the wooded ravines and valleys of the Drakensburg mountain range and its north and south extensions and the unifoliate the more open country of the high veldt, *i.e.* habit is matched to habitat.

3. EXPERIMENTAL

The experiments described in this section all refer to *Eustreptocarpus*.

(i) Pistil and capsule length

Mean pistil length in the newly opened flower and mean capsule length after adequate fertilisation are given for 23 species and 4 wild varieties in table 1. The species are divided into four groups arranged in order of morphological resemblance, (1) *rexii*-like rosulates, (2) other rosulates, (3) sub-unifoliate and (4) unifoliate. On the whole, there is good correlation between the two lengths, $r = +0.829$. The inheritance of pistil length in F_1 was recorded in 108 species crosses and the calculated mean of parental pistil length compared with the



TEXT-FIG.—Left: distribution of the sub-genera *Streptocarpella* and *Eustreptocarpus* in Africa. Right: the distribution of the three sections of *Eustreptocarpus* in south-east Africa.

observed length (to the nearest mm.) in F_1 . Correlation was so good, $r = +0.978$, that it is possible to predict F_1 pistil length accurately throughout the genus. There were no reciprocal differences. Evidently, pistil length is governed by a polygenic system, common to the genus, with no potency. Analogous phenomena have been discussed in relation to diploid species of *Berberis* (Anderson, 1953).

It will be seen, from table 1, that the four main groups of species listed there are characterised by their mean pistil lengths: *rexii*-type rosulates 37 mm., other rosulates 17 mm., sub-unifoliate 7 mm., unifoliate 26 mm. There is only one case (*montigena*) of overlapping of pistil lengths in the first three groups but group IV overlaps with groups I and II, *i.e.* it is the most heterogeneous group (this is true in a number of respects). When pistil and capsule lengths are taken together, the characterisation of the groups is even more pronounced.

Doubtless there is more variation in pistil and capsule lengths among wild plants than I have observed in my material (in several species Mr B. L. Burtt has noted capsules longer than those given above) but the mean values for the groups are sufficiently different to make it unlikely that they do not represent real distinctions.

TABLE 1
Mean pistil and capsule length in 23 species and 4 wild varieties of
Streptocarpus

| | Length (mm.) | | | Length (mm.) | |
|------------------------------|--------------|---------|-------------------------------|--------------|---------|
| | Pistil | Capsule | | Pistil | Capsule |
| Group I | | | Group III | | |
| <i>rexii</i> | 40 | 115 | <i>pusillus</i> | 8 | 14 |
| <i>rexii S</i> | 34 | 96 | <i>daviesii</i> | 9 | 35 |
| <i>rexii B</i> | 39 | 97 | <i>polyanthus</i> | 7 | 27 |
| <i>rexii FB</i> | 36 | 79 | <i>gracilis</i> | 7 | 38 |
| <i>rexii L</i> | 43 | 87 | <i>haygarthii</i> | 8 | 47 |
| <i>insignis</i> | 47 | 115 | <i>comptonii</i> | 5 | 33 |
| <i>polackii</i> | 33 | 97 | <i>pole-evansii</i> | 5 | 9 |
| <i>cyaneus</i> | 26 | 90 | | | |
| <i>gardeni</i> | 38 | 124 | Means | 7 | 29 |
| Means | 37 | 100 | | | |
| Group II | | | Group IV | | |
| <i>montigena</i> | 27 | 64 | <i>grandis</i> | 23 | 43 |
| <i>meyeri</i> | 12 | 40 | <i>wendlandii</i> | 15 | 72 |
| <i>johannis</i> | 13 | 47 | <i>wilmsii</i> | 16 | 52 |
| <i>parviflorus</i> | 17 | 106 | <i>dunnii</i> | 35 | 64 |
| Means | 17 | 64 | <i>micheelmorei</i> | 24 | 53 |
| | | | <i>eylesii</i> | 24 | 45 |
| | | | <i>vandeleuri</i> | 48 | 90 |
| | | | Means | 26 | 60 |

(ii) *Natural pollinations*

Although in the past twenty years I have made repeated enquiries of field botanists and others in South Africa as to the insects that visit *Streptocarpus* in the wild, no information has been forthcoming. One correspondent wrote "bees and other insects visit wide-lobed flowers in my garden". No British insects ever visited my plants, consequently pollinations could be made without protecting the flowers and without fear of contamination.

Some evidence on natural pollination has been obtained by noting the degree to which species set seed naturally in the glasshouse (table 2). No general trends are evident with respect to the four taxonomic groups, therefore specific mechanisms concerned with pollination must come into play. For example, comparison of the relative positions of anthers and stigmas in the different species shows that proximity of these organs is often correlated with good natural

seed-setting and that species with stamens at a lower level than the stigma do not easily set seed naturally. It is clear, however, that anther and stigma positions do not account entirely for ability or inability to set seed. Pollen-tube incompatibility (p. 340) is probably a factor in some species and the highly specialised shape of the corolla tube in e.g. *polyanthus* and *johannis* strongly suggests that such species may be pollinated by long-tongued insects such as moths. Further, the flowers of *vandeleuri* from Pretoria, Transvaal and *eylesii* from Umtali, Rhodesia (600 miles distant) are identically and uniquely scented, which again suggests a specific type of insect visitor. It is unfortunate that so little is known of the pollination of *Streptocarpus*

TABLE 2

Natural seed-setting in the glasshouse

| Seed-setting | | | |
|--|---------------------------------------|---|--|
| Good | Moderate | Poor | Little or none |
| * I <i>rexii</i> I <i>rexii</i> vars. I <i>rexii</i> L I <i>insignis</i> I <i>gardeni</i> III <i>pusillus</i> III <i>polyanthus</i> III <i>haygarthii</i> III <i>comptonii</i> III <i>umtaliensis</i> IV <i>wendlandii</i> | IV <i>grandis</i> IV <i>dunnii</i> | I <i>polackii</i> IV <i>micelmorei</i> | I <i>cyaneus</i> II <i>montigenus</i> II <i>meyeri</i> II <i>johannis</i> II <i>parviflorus</i> III <i>daviesii</i> III <i>gracilis</i> III <i>pole-evansii</i> IV <i>wilmsii</i> IV <i>eylesii</i> IV <i>vandeleuri</i> |

* The numbers refer to the taxonomic groups listed in table 1.

and, therefore, so little can be said of its breeding system from direct observation. No detailed study has been made on inbreeding depression but I have observed it in a number of species (e.g. see p. 341). This, together with the evidence from crossability and certation (pp. 337-342) suggests that most of the *Streptocarpus* species are outbreeders.

(iii) Interspecific crossability and fertility

A summary of the selfing and crossing of species is presented in table 3. One hundred and ninety-one crosses were made involving 24 species, and 71 of the hybrids were selfed. In addition, 23 of the species were selfed. In most cases several flowers were pollinated in each cross or self.

Scoring was made, first on the percentage of inter- or intra-group crosses giving viable seeds in F_1 (= crossability index) and secondly on the number of seedlings per capsule from selfing, and in F_1 and F_2 (= germination or fertility index). Eight fertility classes were

used, arranged on a logarithmic basis to facilitate the distinguishing of the lower fertility classes, as follows :—

| Fertilisation, or germination, failed | No. of seeds germinating per capsule | | | | | | |
|---|--------------------------------------|------|-------|--------|---------|----------|-----------|
| | 1-5 | 6-17 | 18-55 | 56-173 | 174-548 | 549-1730 | 1731-5480 |
| Fertility index—0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |

Ovary length (usually 80-90 per cent. of capsule length) varies greatly from species to species but as the maximum number of seeds per millimetre of ovary length is from 20-30 in successful pollinations, restriction of seed number in species with the shorter ovaries does not affect the general assessment of fertility on the basis of the above fertility index. For example, in general, the maximum number of seeds set in species with long and short ovaries is some 2000 and 500 respectively, hence the potential seed set for nearly all species is indicated by the fertility index 6.0. Only a quarter of the possible crosses between the 24 species were made, nevertheless evidence from several different experiments show that the results may be relied upon as a broad measure of crossability and fertility.

Mean crossability and fertility indices for all combinations are 53 and 2.2 respectively. Corresponding values for rosulates crossed *inter se* are 97 and 5.2, for sub-unifoliates 46 and 1.8 and for unifoliolate crosses 37 and 0.9, *i.e.* the crossability and fertility indices are much higher for rosulate than for non-rosulate crosses and highest of all for crosses between group I rosulates, *viz.* 100 and 5.8.

In both crossability and fertility, the rosulates are distinctly more effective as male parents than the unifoliates. This distinction is real, *e.g.* it can also be seen in a different series of crosses (p. 342 and table 5). Crossability and cross-fertility indices are conspicuously low in group I \times group III, *i.e.* when the species with the longest styles are pollinated by those species with the shortest styles. In the reciprocal cross, group III \times group I, the crossability and cross-fertility indices are three times as high. The same phenomenon can be seen, in decreasing degree, in group III \times group IV and group III \times group II.

The percentage of F_1 plants that produced progeny from selfing was 76 and the fertility index 3.4. The corresponding figures for the rosulates were 100 and 5.6. The fertility index for F_1 plants in group I was 5.9 and for group I crossed group II, 4.9.

Thirteen reciprocal crosses failed in one direction and were successful in the other, the fertility indices ranging fairly evenly, from 0.5 to 6.0. No correlations or trends were evident, except one: 12 of the failures were from the use of species in groups III (7 failures) and IV (5 failures) as male parents, the thirteenth being a Group II

species. Thus the tendency to failure in one direction of reciprocal crossing is associated with the use of pollen from the groups with

TABLE 3

Intra- and inter-group crossability and fertility in Streptocarpus

| ♀ \ ♂ | Group | | | | Means | |
|------------------------|----------------------------|------------------------|-----------------------|-----------------------|-----------------------|-------------------------|
| | I | II | III | IV | | |
| <i>Rosulates</i> | | | | | | |
| Group I | | | | | | |
| <i>rexii</i> L | } C . . F . . FF . . | 100/20 5·8 5·3/6 | 89/9 4·4 ... | 13/15 0·5 ... | 66/15 2·8 ... | 68/59 3·5 ... |
| <i>insignis</i> | | | | | | |
| <i>polackii</i> | | | | | | |
| <i>cyaneus</i> | | | | | | |
| <i>gardeni</i> | | | | | | |
| Group II | | | | | | |
| <i>montigena</i> | } C . . F . . FF . . | 100/7 4·6 ... | 100/1 5·0 4·4/4 | 43/7 0·6 ... | 33/1 1·1 ... | 62·21 2·3 ... |
| <i>meyeri</i> | | | | | | |
| <i>johannis</i> | | | | | | |
| <i>parviflorus</i> | | | | | | |
| <i>Sub-unifoliates</i> | | | | | | |
| Group III | | | | | | |
| <i>pusillus</i> | } C . . F . . FF . . | 38/8 1·5 ... | 50/4 2·0 ... | 46/13 1·8 4·7/6 | 44/11 1·8 ... | 44/36 1·8 ... |
| <i>daviesii</i> | | | | | | |
| <i>polyanthus</i> | | | | | | |
| <i>gracilis</i> | | | | | | |
| <i>haygarthii</i> | | | | | | |
| <i>comptonii</i> | | | | | | |
| <i>pole-evansii</i> | | | | | | |
| <i>Unifoliates</i> | | | | | | |
| Group IV | | | | | | |
| <i>grandis</i> | } C . . F . . FF . . | 72/18 2·4 ... | 50/6 1·5 ... | 29/24 0·8 ... | 37/27 0·9 3·5/7 | 44/75 1·3 ... |
| <i>wendlandii</i> | | | | | | |
| <i>wilmsii</i> | | | | | | |
| <i>dunnii</i> | | | | | | |
| <i>galpinii</i> | | | | | | |
| <i>micelmorei</i> | | | | | | |
| <i>eylesii</i> | | | | | | |
| Means | } C . . F . . FF . . | 81/53 3·8 ... | 70/20 3·0 ... | 31/59 0·9 ... | 46/59 1·6 ... | 53/191 2·2 4·5/23 |
| | | | | | | |
| | | | | | | |

C = crossability index, F = cross-fertility index, FF = self-fertility index.

Figures after the oblique stroke refer to the number of crosses or selfs made.

the shortest mean style length. The significance of this is discussed in the next section.

The indices for crosses between *polyanthus*, *gracilis* and *haygarthii* reveal an affinity between these species (F_1 's 4·0 to 5·0) closer than that between them and some other members of the group.

The following conclusions can be drawn from the results of species crossing :

- (i) half of the species tested were crossable but mean fertility was very low.
- (ii) the *rexii*-like species (group I) are highly crossable and inter-fertile and their hybrids are fertile.
- (iii) the rosulates (groups I and II) are highly crossable and moderately inter-fertile, and their hybrids moderately fertile.
- (iv) when crossed to sub-unifoliate and unifoliate, the rosulates are more effective as male than female parents.
- (v) all other inter-group crosses show low crossability and low fertility.
- (vi) in general, group crossability and fertility indices are positively correlated with the mean pistil length of the pollen parents.

(iv) Certation

The broad picture of crossability and fertility having been ascertained, a closer examination of the breeding system in *Streptocarpus* was made in two experiments, the first comprising simultaneous self- and cross-pollinations, the second simultaneous dual cross-pollinations.

In the first experiment, self-pollen and pollen from a different variety or species (foreign pollen) were taken in roughly equal amounts, thoroughly mixed and applied in quantity to the stigma of a flower from the plant contributing the self-pollen. The plants selected for the experiment were raised from seed collected in the wild. They ranged from closely to distantly related forms as follows. *rexii*; *rexii* S₁, a white-flowered variety; *rexii* L, a form sufficiently different from *rexii* as, perhaps, to warrant sub-specific rank; *gardeni* and *cyaneus*, species quite distinct from one another and from *rexii*; and *dunnii*, a large-leaved unifoliate, the other five forms being rosulates. The self-fertility indices of these six plants were 6.5, 5.2, 5.8, 4.6, 4.5 and 3.0 respectively. The total number of plants was 3885, comprising 2546 F₁ hybrids and 1339 selfs. The percentage of crossed to selfed progeny in the individual combinations is given in table 4.

Assuming that the proportion of hybrid to selfed progeny is an expression of the relative rates of pollen-tube growth, foreign pollen is seen to compete successfully against self-pollen in 20 of the 30 combinations. But the most striking result is that seen when each species is used, in turn, as pollen parent for all of the other species (columns). The success of foreign pollen is greatest with the *rexii* forms, moderate with *cyaneus*, poor with *gardeni* and least with *dunnii* (the mean value for *dunnii* is inflated by one result, viz. *rexii* L × *dunnii*). No such gradation is to be seen when the species are considered as maternal parents (rows).

At first sight these results might be ascribed to the action of a number of genes comprising an incipient incompatibility system dependent on differential rates of pollen-tube growth, a possibility

which cannot be ruled out. For example, when single plant selection is practised, there is a fairly rapid fall-off in self-fertility, mainly in the unifoliate. Indeed, the self-fertility indices given above for the six species seem to reflect this very behaviour: *rexii* is highly fertile and the other species less so in graded order.

The self-fertility index for *dunnii* is certainly too low, and is a consequence of the inbreeding that ensues when only a small number of plants of each species can be accommodated in a glasshouse. By contrast, plants of *dunnii* from the wild have a much higher self-fertility index.

The prime cause of the graded paternal effect is undoubtedly the difference in size of the pollen grains of the different species. The greater the volume of the pollen grains, the more rapid the growth

TABLE 4
Percentage hybrids from simultaneous self- and cross-pollination

| ♀ \ ♂ | <i>rexii</i> | <i>rexii S</i> | <i>rexii L</i> | <i>cyaneus</i> | <i>gardeni</i> | <i>dunnii</i> | Means |
|--------------------------------|--------------|----------------|----------------|----------------|----------------|---------------|-------|
| <i>rexii</i> 9700 * . . . | ... | 87 | 82 | 63 | 55 | 19 | 58 |
| <i>rexii S</i> , c. 8500 . . . | 54 | ... | 37 | 62 | 24 | 9 | 38 |
| <i>rexii L</i> 9000 . . . | 89 | 96 | ... | 43 | 22 | 63 | 73 |
| <i>cyaneus</i> 7500 . . . | 98 | 89 | 59 | ... | 31 | 14 | 61 |
| <i>gardeni</i> 6300 . . . | 100 | 85 | 100 | 58 | ... | 5 | 59 |
| <i>dunnii</i> 13,000 . . . | 100 | 80 | 78 | 70 | 4 | ... | 81 |
| Means . . . | 91 | 87 | 72 | 59 | 21 | 22 | 65 |

* Mean pollen-grain volume, μ^3 .

of the pollen tube. Although not evident with the few species given in table 4, all of which have long pistils relative to the generic range, a survey of *Streptocarpus* species by my colleague, Dr D. Lewis, has shown that good correlation exists between pollen size and pistil length which, therefore, must be mutually adapted. Correlation between pollen size and rate of pollen-tube growth has been described in heterostyled species of *Primula*, in which "thrum" pollen is twice the volume of "pin" and grows twice as fast (Lewis, 1948).

If the results in table 4 could be attributed to pollen-grain size alone, then all the combinations below the diagonal should have a crossability index greater than 50, and in fact, all of them have but one (*dunnii* \times *gardeni*). The reverse applies to combinations above the line, in which the indices should all be below 50. Six of them are not. These may be due to errors in the mixed pollination technique but it is more probable that they result from incompatibility which slows down the growth of self-pollen tubes to the advantage of the foreign pollen. In this connection, the high proportion of hybrids when *rexii* is crossed by *rexii S* and *rexii L* pollen is of special significance. The same cause would account for the success of foreign pollen in

the *dunnii* combinations (bottom row) where, on pollen size alone, self-pollen should be at a considerable advantage. It has already been pointed out that the self-fertility index for the plant of *dunnii* used in the experiment is exceptionally low, *viz.* 3.0.

Bateman (1956) has described cryptic incompatibility in *Cheiranthus cheiri* which closely resembles the findings in *Streptocarpus*. Artificial pollination gave a full seed set, but in the field, individual plants showed outcrossing of more than 70 per cent. Mixed pollinations showed that self-pollen, though fully capable of fertilisation, could not compete with foreign pollen which, when present in equal amounts, was responsible for over 90 per cent. of the seed set.

In the second certation experiment, pollens from two different species were applied simultaneously to the stigma of a third species and the numbers of the two different hybrids counted in F_1 . All of the parental combinations in these crosses were known to yield progeny in moderate to good numbers, therefore a substantial difference in the proportions of the two hybrids in F_1 could be attributed to differential rates of pollen-tube growth (or, possibly, to competition between the fertilised ovules).

The results of the mixed cross-pollinations are given in table 5. In general, they show that :—

- (1) rosulate pollen competes successfully against unifoliate pollen.
- (2) pollen from a species closely related to the female parent tends to be more successful than pollen from a less closely related species.
- (3) pollen from *rexii* and its varieties is universally successful.

These results from mixed cross-pollinations are in agreement with those from mixed self- and cross-pollinations and together they support the conclusions from crossability. We may conclude that two certation systems operate in the genus, the first and most important dependent on pollen-grain size, the second dependent on incompatibility between pollen and style.

An interesting parallel to the observations given in sections 6 and 7 is described in *Datura* (Buchholz *et al.*, 1935). Ten species, each with $2n = 12$ chromosomes, were crossed in all possible combinations and the percentage of normal pollen tubes which had grown at least half the length of the longest tubes was noted. Half the species had short styles, 30, 38, 40, 40 and 70 mm. in length respectively and half long styles, 120, 135, 140, 150 and 190 mm. in length. It was found that the short-styled species were each "the best cultural media for the pollens of all of the other species" and, conversely, the pollen from each of the long-styled species was the most successful in growing down the styles of the others. Essential reciprocal differences in the behaviour of the pollen tubes were not found among the short-styled species but they did occur in certain crosses between short- and long-styled species. No mention is made of pollen-grain volume.

(v) *Heterosis*

Apart from the various morphological characters employed in the identification of selfed and hybrid progenies in the experiments on certation, it was evident very early in the life of the seedlings that hybrid vigour was not only common but a conspicuous character differentiating hybrids from selfs (plate II, figs. 6-7). The comparative vigour of the different selfed and hybrid progenies was

TABLE 5
Simultaneous cross-pollinations using mixed pollens

| Ref. no. | Parent species | | No. of plants in F ₁ | Ref. no. | Parent species | | No. of plants in F ₁ |
|----------|----------------|--------------------------------------|---------------------------------|----------|-------------------|---------------------------|---------------------------------|
| | ♀ | ♂ | | | ♀ | ♂ | |
| 1 | <i>rexii</i> | <i>rexii S</i> <i>rexii L</i> | 133 169 | 11 | <i>rexii B</i> | <i>rexii dunnii</i> | 226 13 |
| 2 | „ | <i>rexii S</i> <i>cyaneus</i> | 64 37 | 12 | „ | <i>gardeni dunnii</i> | 142 61 |
| 3 | „ | <i>rexii L</i> <i>parviflorus</i> | 46 46 | 13 | <i>rexii L</i> | <i>rexii B dunnii</i> | 233 6 |
| 4 | „ | <i>rexii B dunnii</i> | 209 6 | 14 | „ | <i>cyaneus dunnii</i> | 52 58 |
| 5 | „ | <i>cyaneus johannis</i> | 170 0 | 15 | „ | <i>gardeni wendlandii</i> | 218 2 |
| 6 | „ | <i>cyaneus wendlandii</i> | 440 0 | 16 | <i>wendlandii</i> | <i>rexii johannis</i> | 20 9 |
| 7 | <i>rexii S</i> | <i>rexii B</i> | 57 42 | 17 | <i>dunnii</i> | <i>rexii michelmorei</i> | 100 0 |
| 8 | „ | <i>rexii cyaneus</i> | 135 51 | | | | |
| 9 | „ | <i>gardeni dunnii</i> | 54 186 | | | | |
| 10 | „ | <i>parviflorus johannis</i> | 162 39 | | | | |

assessed by calculating the area (cm.²) from the length and breadth of the first leaf of the 28-week-old seedlings, a method reasonably satisfactory for the strap-shaped leaves of young *Streptocarpus* plants. The families were raised simultaneously, under the same conditions, and scored on the same day.

First, the leaf areas of the parent species were estimated by calculating the mean for all the selfed seedlings in those families in which a given species was used as female. These means are given along the diagonal in table 6 and they show that leaf size, at the time of scoring, differed considerably among the six species, *i.e.* their rate of growth differed.

Secondly, the mode of inheritance of leaf area was examined by plotting the mean of the parent species against the mean of their hybrids, first by considering a species as maternal parent, and secondly as paternal parent, a comparison which will show up any general reciprocal difference. The summed results for the species are $r = +0.816$, $P = 0.001$ and $r = +0.725$, $P = 0.001$. The corresponding regression coefficients are $y = 2.046x - 25.879$ and $y = 2.406x - 35.583$, and the difference between them is not significant. These data show that (1) inheritance of leaf area is quantitative, (2) the behaviour of the species in the aggregate when considered alternatively as maternal and paternal parents is closely similar.

TABLE 6
Heterosis as expressed in leaf area of species hybrids

| $\begin{array}{c} 40 \\ \swarrow \\ \delta \end{array}$ | <i>cyaneus</i> | <i>rexii S</i> | <i>rexii L</i> | <i>rexii</i> | <i>dunnii</i> | <i>gardeni</i> | Heterosis index |
|---|----------------|----------------|----------------|--------------|---------------|----------------|-----------------|
| <i>cyaneus</i> | 21 | 1.56 | 1.51 | 1.19 | 1.39 | 2.00 | 1.55 |
| <i>rexii S</i> | 1.28 | 42 | 1.60 | 1.69 | 1.40 | 1.59 | 1.53 |
| <i>rexii L</i> | 1.49 | 1.37 | 53 | 1.09 | 2.68 | 1.85 | 1.74 |
| <i>rexii</i> | 1.85 | 1.17 | 1.37 | 61 | 1.69 | 2.84 | 1.83 |
| <i>dunnii</i> | 1.45 | 1.42 | 2.10 | 1.05 | 67 | 1.75 | 1.57 |
| <i>gardeni</i> | 1.65 | 1.39 | 1.95 | 1.96 | 1.42 | 76 | 1.67 |
| Heterosis index | 1.56 | 1.37 | 1.77 | 1.42 | 1.72 | 2.02 | 1.66 |

italic = parental leaf area (sq. cm.)

roman = heterosis index $\left(\frac{\text{hybrid leaf area}}{\text{mean of parents}} \right)$

Thirdly, the degree of vigour, or heterosis index, was assessed by computing the ratio of mean hybrid leaf area to the mean of the parents. The heterosis indices are given in table 6 and range from 1.05 to 2.84. They show that in every cross, hybrid leaf area is greater than the parental mean although in a few cases it is obvious that it cannot be significantly greater. Individual reciprocal differences are seen to occur, the greatest being 1.69 : 1.05.

Lastly, the grand mean leaf area of all parents may be compared in the form of a ratio with that of the hybrids. The three values are, parents 1.0, species as females 1.57, species as males 1.75. Positive heterosis, therefore, predominates in these species crosses.

What is the nature of this heterosis or luxuriance? Although measurements were not made on very young seedlings, the reciprocal differences in leaf size were evident to the eye at the earliest stage that comparisons would be valid. This suggests that the heterosis observed in *Streptocarpus* results from the attainment of a high growth rate very soon after germination (Whaley, 1952), *i.e.* after a very short "lag" phase (Lewis, 1955).

Detailed information has been obtained by Beuttel (1939) who measured embryo, seed and cotyledon dimensions in *rexii*, *wendlandii*, *grandis* and their hybrids, also the rate of growth of the leaves. No heterosis was found in hybrid embryos and seeds and none worth mentioning in chlorophyll content, transpiration, percentage dry weight and ash content. Heterosis was apparent in the rate of growth of leaves and in the regenerative capacity of the hybrids when propagated from leaves. Beuttel states that the heterosis arises from the increased rate of cell division.

So far we have been speaking of inter-specific heterosis, or luxuriance. That intra-specific heterosis also occurs is shown by the inbreeding depression found in some species, e.g. *dunnii*, but the intra-specific heterosis is much less in magnitude than the inter-specific.

Finally, although the evidence from so few as six species can serve only as a pointer, it may be significant that comparison of pistil

TABLE 7

| Class 1 | Class 3 |
|--|---|
| <i>wendlandii</i> <i>comptonii</i> | <i>rexii</i> <i>cyaneus</i> <i>gardeni</i> <i>parviflorus</i> <i>pole-evansii</i> <i>grandis</i> <i>dunnii</i> <i>micelmorrei</i> <i>? galpinii</i> |
| Class 2 | |
| <i>polyanthus</i> <i>gracilis</i> <i>haygarthii</i> <i>johannis</i> | |

length with leaf area of the species, and with leaf area of the hybrids, suggests that these characters are positively correlated. In particular, when the *rexii*-like species are considered as female parents it will be seen that the heterosis index of their hybrids increases with increase of the leaf area of the species.

(vi) Cytoplasmic inheritance

Reciprocal species hybrids in *Streptocarpus* often differ quantitatively, e.g. in size of plant, size, shape, colour and colour pattern of flowers. One conspicuous difference involves the sexual organs: A × B is normal, B × A is male sterile. Characteristically the male sterility results from aborted anthers or their entire absence, filaments which are adnate for part of their length, often thin and coiled back and sometimes missing. In less extreme cases the anthers are reduced in size and without pollen, and separate instead of cohering. In one extreme case, *wendlandii* × *cyaneus*, the anthers were stigmatic. No attempt was made to record the minor degrees of abnormality often associated with male sterility (Oehlkers, 1938), the stamens being scored simply as normal or abnormal.

In my experiments, the species fell into three cytoplasmic classes (table 7). *wendlandii* crossed, as female parent, with the species in

class 3 gave abnormal (male sterile) F_1 's, the reciprocal crosses being normal hermaphrodite. *comptonii* crossed with *rexii* and *pole-evansii* (both class 3) also gave abnormal, *i.e.* behaved the same as *wendlandii*.

The results with class 2 species are given in table 8. *johannis*, *polyanthus* and *gracilis* gave normal progeny crossed to *wendlandii*, as if they belonged to class 1; and the results when these species are crossed *inter se*, also with *haygarthii*, are in agreement with this view. Yet *polyanthus* and *haygarthii* when used as female parents in crosses with class 3 species, give normals. These species therefore cannot be allotted either to classes 1 or 3 and along with *johannis* and *gracilis* are considered to form the intermediate class 2. It is of interest that

TABLE 8
Occurrence of normal and abnormal anthers in species hybrids

| Cyto- plasmic group | | | | | | | | Group 3 | |
|---------------------------|--|---|--------------|---------------|-------------|--------------|--------------|------------|-------------|
| | ♀ | ♂ | <i>wend.</i> | <i>compt.</i> | <i>joh.</i> | <i>poly.</i> | <i>grac.</i> | | <i>hay.</i> |
| 1 | <i>wendlandii</i> . . . | | | N | N | N | N | ... | A |
| | <i>comptonii</i> . . . | | F | | F | F | F | N | A |
| 2 | <i>johannis</i> . . . | | N | ... | ... | | ... | ... | F |
| | <i>polyanthus</i> . . . | | N | F | N | | N | ... | N |
| | <i>gracilis</i> . . . | | ... | F | ... | N | ... | ... | F |
| | <i>haygarthii</i> . . . | | F | F | ... | N | ... | ... | N |
| 3 | <i>rexii</i> , and other class 3 species. | | N | N | N | N | F | F | N |

N = normal stamens
A = abnormal stamens
F = cross failed

johannis, a rosulate, occurs in class 2, along with the three sub-unifoliate. *johannis* is almost certainly a natural hybrid between *polyanthus* and *rexii* (p. 351). As we have seen, the latter is much more likely to have been the pollen parent than *johannis* and in this case *johannis* would be expected to carry class 2 cytoplasm.

The garden forms of *Streptocarpus*, derived from artificial hybridisation of *rexii*, *parviflorus* and *dunnii* (Lawrence, 1958), should fall into class 3 since these parents are themselves in class 3, and the results from several crosses with garden forms fulfilled this expectation. $73/37 \times (rexii \times wendlandii)$ gave normals, but $(wendlandii \times rexii) \times 73/37$ gave abnormal as did also *wendlandii* when crossed by 1/33 and 59/36. Other crosses that gave normals are: $73/37 \times (rexii \times comptonii)$, $polyanthus \times 1/33$, $rexii \times (rexii \times comptonii)$, $(rexii \times comptonii) \times comptonii$ and $(rexii \times comptonii)$ selfed. All these results are consistent with the threefold classification described above.

The behaviour of class 1 and class 3 species when crossed reciprocally

is attributable to interaction of nuclear and cytoplasmic factors such that class 1 genomes are able to function in class 3 cytoplasm to produce normal hermaphrodite plants but group 3 genomes in class 1 cytoplasm cannot. This view assumes that in fertilisation, little or no cytoplasm is contributed by the male gametes.

That the constitution of the cytoplasm is fundamental to the phenomena observed is especially evident from an F_2 raised from selfing the hybrid *wendlandii* \times *cyaneus*, a few flowers of which bore a little pollen. Three F_2 families were raised from three different pollinations and yielded 4, 5 and 5 plants respectively, all of which bore abnormal flowers, though the degree of abnormality varied. Thus, although gene segregation must have occurred, and probably accounted for the variation observed, the cytoplasm was essentially of the same constitution as in the F_1 plant.

The *wendlandii* \times *cyaneus* hybrid was also crossed as male parent to a normal garden form and gave 41 individuals. The first flower to open on each of these individuals was scored for the condition of the anthers; 25 were found to be normal and 16 had separated, *i.e.* aberrant, anthers. Three weeks later, when the family was in full flower, only an occasional flower was found in which the anthers were separated. Thus in class 3 cytoplasm the F_1 nuclei reacted normally, though there seems to have been either a lag in the mutual adjustment of nuclei and cytoplasm or a small contribution of cytoplasm was made by the male gametes.

This same phenomenon was also observed in two plants derived from (*wendlandii* \times *gardeni*) \times *wendlandii*, which again shows that the nuclear factors play a large part in the nuclear-cytoplasmic interaction.

Oehlkers (1938), studied cytoplasmic inheritance in *Streptocarpus* in detail and found that (1) species could be grouped for their cytoplasm, (2) the expression of sex depended on both cytoplasmic and nuclear factors, and (3) there were grades of femaleness and maleness, *i.e.* deviation from the normal hermaphrodite condition in the abnormal segregates. We may note in particular that Oehlkers found *wendlandii* and *comptonii* to comprise one class and *rexii*, *grandis*, *solenanthus* and garden forms another. *polyanthus* \times *wendlandii*, the reciprocal cross, and (*polyanthus* \times *wendlandii*) \times *polyanthus* gave nothing but normals, but in the backcross (*wendlandii* \times *polyanthus*) \times *polyanthus* half the progeny were normal and half abnormal. Further, the F_2 from *wendlandii* \times *polyanthus* gave three-quarters normal and one-quarter abnormal progeny. Oehlkers concludes that *polyanthus* is an intermediate form between *rexii* and *wendlandii*.

The evidence on cytoplasmic inheritance in *Streptocarpus* may be summarised as follows :—

- (i) 15 species tested fell into 3 distinct classes.
- (ii) the two species comprising the smallest class have the most specific cytoplasm and come from Natal (*wendlandii*,

- unifoliate) and the extreme south-east Transvaal (*comptonii*, sub-unifoliate), *i.e.* in or fairly near Natal.
- (iii) the species comprising class 2 are mainly sub-unifoliate and are distributed in or around Natal. The class is intermediate to classes 1 and 3.
 - (iv) the species comprising class 3 are either unifoliate or rosulate which are distributed from Natal to the extreme north (unifoliate) and to the extreme south (rosulate) of the *Streptocarpus* area.

4. DISCUSSION

The special aspects of *Streptocarpus* discussed in this paper fall into three categories: habit and habitat, the breeding system, speciation. To these three categories can be added a fourth, descriptive of the genus in general terms and concerned with gene systems.

(i) *Habit and habitat*

As we have seen, the unifoliate and the rosulate are two very distinct types with respect to their habit of growth. Their geographical distributions also are distinctly different, that of the unifoliate being discontinuous and northward of Natal in the high plains, while the rosulate distribution is more or less continuous and mainly southward of Natal, in shady valleys and woods. Although this correlation of habit and habitat is not absolute, without doubt it is an important criterion in considering speciation and evolution in the genus.

Oehlkers' finding that certain rosulate and unifoliate species are apparently differentiated with respect to leaf number by only two major genes is of much interest. It suggests that, first, leaf number is of major ecological importance and secondly, during speciation in *Eustreptocarpus* genes affecting leaf number were brought together (linked) in each of two groups to constitute the two postulated major genes. It also raises the question to what extent this simple Mendelian control of habit bears on the stabilisation, migration and evolution of species. An analogous example of control of different habits by a single gene has been reported by Correns (1904) for annual and biennial varieties of *Hyoscyamus niger*.

Turning to the sub-unifoliate, their distribution is striking in that they overlap the point of juncture of the unifoliate and the rosulate. Again, this criterion is not absolute but the facts are too obvious to be overlooked or lack significance. Thus the sub-unifoliate bridge the "gap" between unifoliate and rosulate on the criteria of both habit and habitat. It is not impossible that some, or all, of the sub-unifoliate also bridge this gap with respect to the genes controlling leaf number, *e.g.* rosulate *AABB*, unifoliate *aabb* and sub-unifoliate *A(A)bb* or *aaB(B)* plus, of course, "modifying" genes specific to a given species.

Another feature that broadly characterises the sub-unifoliate is

their cytoplasmic heredity. This time, however, the geographical pattern is not so much a linear one as with habit and habitat but roughly concentric, class 1 species being moderately near, or in, the centre, class 2 (mainly sub-unifoliate) occupying an inner ring and class 3 the outer northern and southern extensions of the *Streptocarpus* area.

Heterosis may be considered here as a component of habit. Inter-specific heterosis, *i.e.* luxuriance, predominates in *Eustreptocarpus* to an extent that justifies its being described as a generic characteristic and it occurs regardless of whether the parent species are distantly or closely related. Heterosis is not found in pistil and capsule length or in pollen-grain size, *i.e.* in floral characters. Heterosis, therefore, is expressed mainly in the vegetative system, *i.e.* in the highly specialised leaf structure and growth, in which one of the sessile cotyledons dies and the other develops by proliferation of the meristematic tissue at its base into a leaf (Hill, 1938). A few leaves are later developed in the rosulates. The specialised single leaf of the unifoliate, also the relatively few leaves of the rosulates, must be adapted to equally specialised ecological factors.

The common occurrence of heterosis in *Eustreptocarpus* can be explained by postulating that each species carries a different combination of dominant genes controlling the rate of growth of the leaves, the combination in a given species serving to regulate growth so that an excessively fast or slow rate is avoided. Species crossing then results in a larger number of dominant growth genes being brought together than is found in the individual species, with a consequent enhancement of rate of growth.

It would be of interest to ascertain the comparative character of inter- and intra-specific heterosis in unifoliate, sub-unifoliate and rosulate species respectively, whether heterosis is found in the caulescent species and, if so, what the relationship of the caulescent heterosis is to the acaulescent.

(ii) *The breeding system*

It has been established that a positive correlation exists between pistil length and pollen-grain size in *Streptocarpus*. The inheritance of pistil length is quantitative or polygenic, with no potency, hence, by inference, so also is the inheritance of pollen-grain size. Also, species with large pollen grains are more effective as male parents in species crossing than those with smaller pollen grains. This behaviour has also been demonstrated in mixed pollinations, *i.e.* other things being equal, large pollen grains produce the faster-growing pollen tubes.

To what extent could, or do, these factors constitute the mechanism of a generic breeding system? Broadly, selection leading to increase in pollen-grain size would seem to be an advantage for a species in which a measure of cross-pollination also was an advantage, *i.e.* pollen size may be regarded merely as one of a number of devices for promoting outbreeding. More precisely, the answer, so far as

pollen size alone is concerned, depends on the variation that occurs within species and between closely related sub-species and species. There is no evidence on the former but in *rexii*, *rexii S* and *rexii L* the differences in mean pollen sizes are not inconsiderable, *viz.* 9700, 8500 and 9000 μ^3 respectively.

The difference between *rexii* and the acyanic wild variety *rexii S* is of interest. Like many other white-flowered varieties of plants, *rexii S* is a little smaller, in many respects, than the type. The only known genetical difference between the two genotypes is that *rexii* is homozygous dominant for the gene *F* producing anthocyanin in the flowers, whereas *rexii S* is homozygous recessive. If mutation of such a gene as *F* results in a smaller plant, including smaller pollen, then, apart from other considerations, hybridisation with the type is likely to lead, through certation, to the rapid elimination of the mutant form from the population.

This concept, however, is too simple for it does not take into consideration the probable existence of a second outbreeding mechanism in *Streptocarpus*, namely, pollen-incompatibility. When *rexii* was used as female parent in mixed self- and cross-pollinations, pollen from *rexii S* and *rexii L* was distinctly more successful than self-pollen, despite the larger size of the latter, *i.e.* a degree of self-incompatibility operates to the advantage of the foreign pollen. Such is not the case when wider crosses are made, *e.g.* *rexii* crossed by *cyaneus* or *gardeni*. The fact that the smaller pollen of *rexii S* and *rexii L* competes successfully against pollen of *rexii* indicates that pollen size and pollen-incompatibility are independent factors in certation, at least in some cases.

Now, by inference, inheritance of pollen-grain size in *Streptocarpus* is polygenic, hence it would probably be least efficient as an outbreeding mechanism in the closest crosses, *e.g.* sib-crosses. Conversely the success of an incompatibility system is dependent on simple gene differences, *e.g.* S_1 , S_2 , etc., and this system would be most efficient in sib-crosses. In other words, pollen size is quantitative and incompatibility qualitative in inheritance and function and together these systems could comprise a sensitively balanced mechanism promoting outbreeding within a species and, possibly, between sub-species. Variability would be stored within the population, as well as within the individual, facilitating adaptation to new or changing environments. That *rexii* populations, even from very small areas, are heterogeneous is beyond doubt. For example, quantitative variation in flower colour and pattern is characteristic of this species and the frequency with which recessive genes have turned up in material from the wild, supports the inference from visual assessment.

This brings us to a closer examination of *rexii* in relation to speciation. The seeds of *Streptocarpus* are exceedingly small, some 50,000 per gram, and in *rexii* very numerous, probably 2000 to 20,000 per plant per season. Such small seeds would often be carried on the

feet of birds and small animals some scores of feet from the parent plant and occasionally to much greater distances. Provided the territory was suitable, colonisation would proceed rapidly. Actually, *rexii* ranges from the wooded country of the south of Cape Province, in a narrow belt across the furrowed eastern slopes of the Drakensburg mountains, into Natal, and from thence northward as far as Barberton in the south-east of the Transvaal. This extensive area can be described, broadly, as hilly and wooded, with a characteristic rainfall. Locally, this stretch of country may vary greatly, in altitude, soil type, shelter, rainfall, etc. It is obvious that this topographical variation is matched by the actual and potential genetical variation that characterises *rexii*. All other species have, by comparison, restricted geographical ranges and not infrequently they are highly restricted.

What is it that differentiates *rexii* as the most successful species? Of the various *Streptocarpus* characters studied by the author none is unique to *rexii*. On the other hand, several rare or extreme characters are combined in *rexii*. Thus, the trumpet-shaped flower with an expanded limb is only exceeded in size by *rexii* L and *insignis* among the rosulates and by *vandeleuri* among the unifoliates. All three of these species have a highly localised distribution. Pistil length in *rexii* is among the longest in *Streptocarpus*, and crossability, freedom of seed setting and germination are exceptionally high. Only *rexii* L, *insignis* and *vandeleuri* have longer pistils and these forms are less fecund than *rexii*. Of the species examined, pollen size in *rexii* is exceeded only by that of *dunnii*, but this species is confined to one area in the Transvaal. In the glasshouse, natural seed setting, in terms of the number of capsules set, is equalled by *gardeni*, *pusillus*, *polyanthus*, *haygarthii*, *comptonii* and *wendlandii* but all these species have delimited distributions. Thus, the combination of features that differentiate *rexii* from all other species refer to its floral or reproductive mechanism; large flowers and pollen grains, long pistils and capsules, and high fecundity.

Finally, although from field studies there is no direct evidence that hybridisation of species occurs in the wild, the results of hybridisation in the glasshouse lend support to the probability of its occasional occurrence. Thus, the hybrid *rexii* × *polyanthus* strikingly resembles the rosulate *johannis*, a species whose distribution (lat. 31-32°) apparently does not now overlap with that of *polyanthus* (lat. 29-30°). In the hybrid the rosulate was dominant to the sub-unifoliate habit and in this connection it will be noted that *johannis* occupies rosulate, not sub-unifoliate territory.

Another plant from Natal, presumably a natural hybrid, closely resembled the hybrid obtained in the glasshouse by crossing *gardeni* with an unnamed and very distinct species sympatric with *gardeni* and the other two forms. It may be significant that the anthers of the presumed natural hybrid carried a large percentage of bad pollen.

In speaking of crossability it must not be assumed that species

crossing in *Streptocarpus* is either common or successful in the wild. On the contrary, many species are spatially isolated and the sympatric species seem to be physiologically isolated. Similarly, it must not be assumed that hybrids and their progeny would usually survive successfully. Disharmony of genetic factors would, as a rule, lead to degeneration of hybrid progeny, especially in unifoliate crosses.

(iii) Speciation

Eustreptocarpus comprises species showing much morphological diversity, even within a single group, e.g. sub-unifoliate. In the first place, this phenotypic diversity is clearly related to diversity of habitat. The mountains, valleys, woods and high veldt of south-east Africa provide locally, many different combinations, in different degrees, of insolation, precipitation, wind velocity, temperature, soil factors, and so forth, including seasonal changes in climate.

Secondly, the different species must have colonised the various habitats by reason of the high genic variability that characterises this outbreeding genus, and which is the outcome of a degree of hybridisation. Direct evidence on the frequency of hybridisation of *Streptocarpus* in the wild and of hybrid swarms is lacking. But there is evidence that new species have arisen from *rexii* at the periphery of its area of distribution, viz. *insignis* around Port St John, C.P., and *polackii* in the Barberton region of the Transvaal. *rexii* L, a subspecies of *rexii*, also is found in a peripheral area, East London, C.P., and may well be an incipient species in the process of colonising the maritime strip.

Thirdly, *rexii* is outstanding, partly on account of its wide distribution, therefore in its ability to adapt to a large range of environmental conditions; and partly because of its potentiality to act as universal "donor" in pollination and fertilisation. In speaking of the wide distribution of *rexii* it should not be overlooked that if it occupies territory intermediate between the climatic extremes, then this territory is the most extensive type and therefore offers the greatest potential for colonisation.

The corollary of the propositions mentioned above is that the relative rate of gene-flow within and from *rexii* is high, therefore while *rexii* will show a moderate degree of phenotypic stability it will carry a large store of genetic variability. In other words, *rexii* will exhibit a degree of stabilisation or constancy at the phenotypic level which results from, and conceals, heterogeneity at the genotypic level.

Fourthly, it is evident that evolution in *Streptocarpus* has proceeded to the point where, on the one hand, a major genetic disjunction, also almost complete spatial isolation, have been established between *Streptocarpella* ($2n = 30$) and *Eustreptocarpus* ($2n = 32$) but, on the other hand, evolution is, by inference, still actively proceeding in *Eustreptocarpus*, where at one extreme inter-specific or sub-specific

hybridisation may still occur, and at the other, specific discontinuities are clearly established.

Colonisation of new territory by *Eustreptocarpus* cannot occur in a southern or eastern direction where the sea is a barrier; nor to the west where the barrier is the arid central plateau. Only to the north is expansion possible. As we have seen, the unifoliate occupy the northern region of the *Eustreptocarpus* area, but the species usually are separated by wide distances. The future of the unifoliate therefore is problematical: they could be regarded as the vanguard of a new colonisation to the north or as species surviving at the extremity of the *Eustreptocarpus* range by close adaptation to special conditions. The sub-unifoliate could expand southwards, but only in competition with the more successful rosulate. There is no obvious barrier to their expansion northward, except that they are, in general, weak-growing species rather sharply delimited in distribution and apparently adapted to special environments.

The sub-unifoliate could, of course, be supposed to be the immediate ancestral forms from which the rosulate and unifoliate have diverged and migrated southwards and northwards respectively. This view would seem to be supported by the fact that the cytoplasmic constitution of the sub-unifoliate is different from, but compatible in degree, with that of the other two cytoplasmic groups. Even so, the potentiality for the further evolution of new forms in the sub-unifoliate would seem to be remote.

The ultimate problem is to account for the differentiation of *Streptocarpella* and *Eustreptocarpus* in form, space and time. Hill (1938) states that a number of caulescent gesneriads, e.g. *Chirita viola* Ridl., have unifoliate varieties, or develop the unifoliate character under certain environmental conditions. This suggests that the actual and potential difference between the two forms is governed by a single gene or, at most, by a simple Mendelian situation. As we have seen, such a difference distinguishes the unifoliate from the rosulate. Evidently the major morphological characters that differentiate groups of species, sub-genera and even families, may be determined by one or two genes, though, of course, such genes cannot be the causal agents for the evolution of taxa.

Hill discussed the caulescent and acaulescent phenomena in detail and concluded that the unifoliate genera and species may be considered to represent the primitive condition from which caulescent forms are derived. On the other hand, Mr B. L. Burt kindly informs me that *Streptocarpus montanus*, an apparent rosulate which is found 20° north of the northernmost rosulate, in company with caulescent species, though not at the same general altitude, has a definite abbreviated axis with well marked leaf-scars, which suggests it is a condensed caulescent rather than an acaulescent species. In this case, it is not impossible that the caulescent form is the primitive type from which have evolved the rosulate and unifoliate habits.

If specialisation continues in the sub-unifoliate, it might well lead to an evolutionary cul-de-sac and the disappearance of the section. The unifoliate would then occupy the northern part of south-east Africa and the rosulate the southern half, with little, or perhaps no, overlapping. A similar event in the past could account for the present position of the acaulescent and caulescent sub-genera, *Streptocarpella* and *Eustreptocarpus*, i.e. expansion northwards and southwards from an ancient centre of origin and diversity with the ultimate elimination of the intermediate group. On the above postulation, an evolution sequence becomes evident. The centre of origin later becomes the centre of diversity and, still later, the centre of extinction.

(iv) Gene systems

In this and four previous papers, Lawrence *et al.* (1939), Lawrence (1947), Lawrence and Sturges (1958), and Lawrence (1958), accounts have been given of the genetics and chemistry of flower colour, the genetics of flower pattern and of sub-lethality, also of such features as morphology (habit), geographical distribution, crossability, certation, heterosis and cytoplasmic inheritance displayed by the various species.

In all these investigations one and the same feature has been outstanding. The characters studied do not occur in all possible combinations, i.e. are not distributed at random, but fall into groups or systems. These systems characterise the genus and its divisions and are the expression of gene systems concerned with form and function.

There are six major systems, two concerned with growth and four with reproduction. The nature of these systems is summarised in table 9. The first four are described and discussed in this paper. The flower-pattern system is controlled by a supergene having four components, the dominant and recessive members of which vary from species to species. Groups of species are characterised by certain combinations of the supergene components. In the flower-colour system some ten independently inherited major genes govern anthocyanin and anthoxanthin production and modification, and these genes control a syndrome in which, by gene interaction in pigment synthesis, the production of wild-type colour (malvidin 3 : 5-dimono-side) is given a high factor of safety.

Looking at the gene systems as a whole, two aspects are of note. First, the systems not only characterise, differentially, the species, sub-genera and other taxa but are themselves characterised it seems, by a duality of function, namely the simultaneous conservation of phenotypic stability and genetic variability. Secondly, the mechanism of conservation varies from system to system. In the habit system major genes would conserve stability and modifying genes would permit variability. In the certation system pollen size would conserve stability and pollen-incompatibility variability. In the flower-pattern

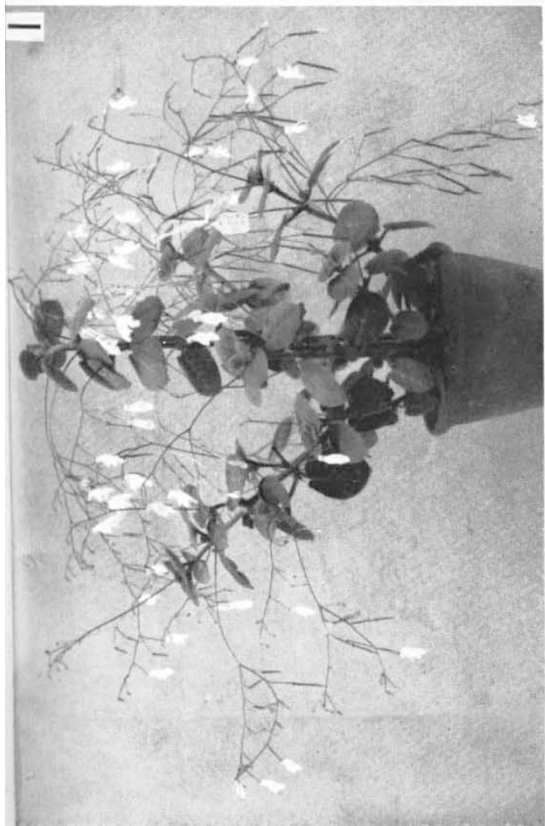
Plate I

FIG. 1.—A typical acaulescent species, *Streptocarpus kirkii*.

FIG. 2.—A sub-unifoliate species, *Streptocarpus polyanthus*.

FIG. 3.—A typical large-leaved unifoliate species, *Streptocarpus dunii*.

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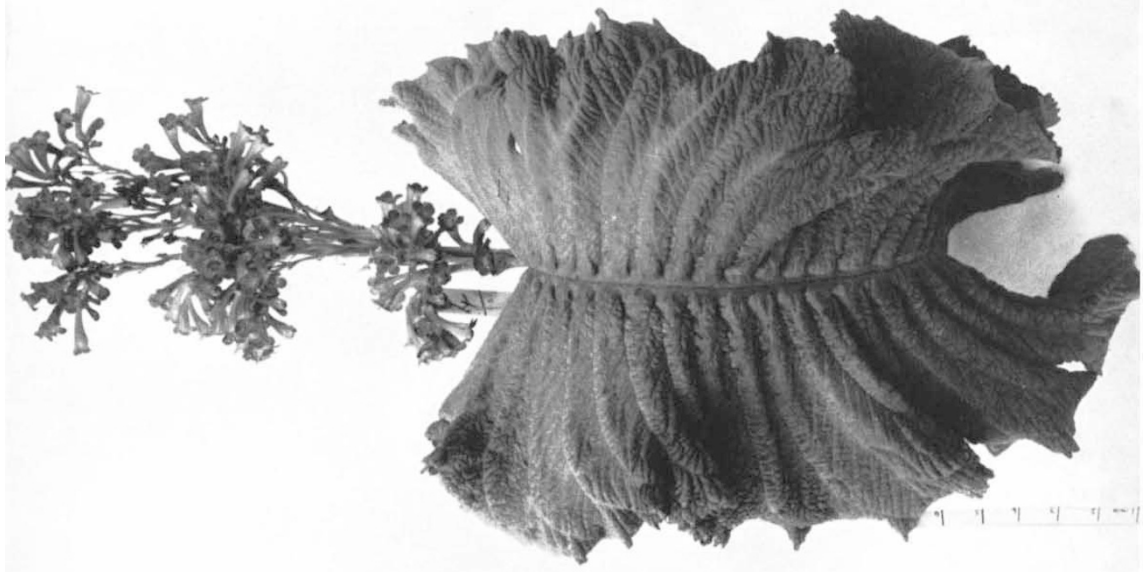
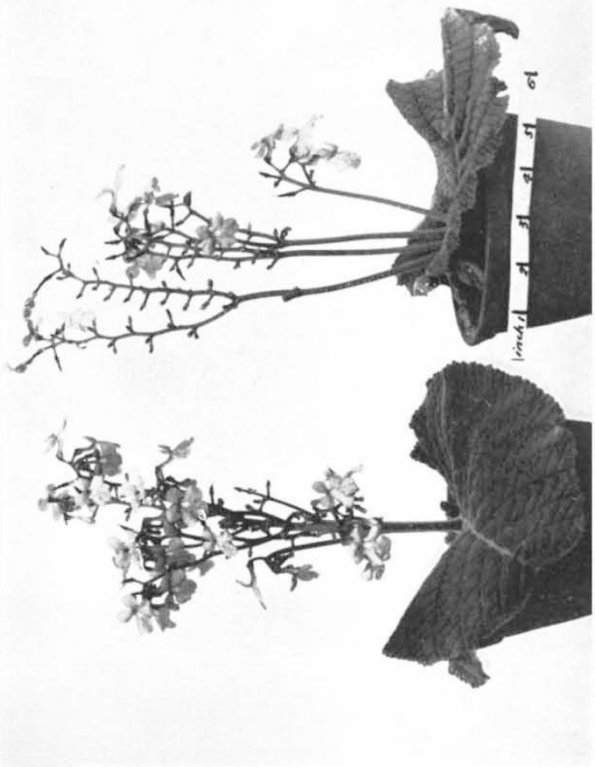
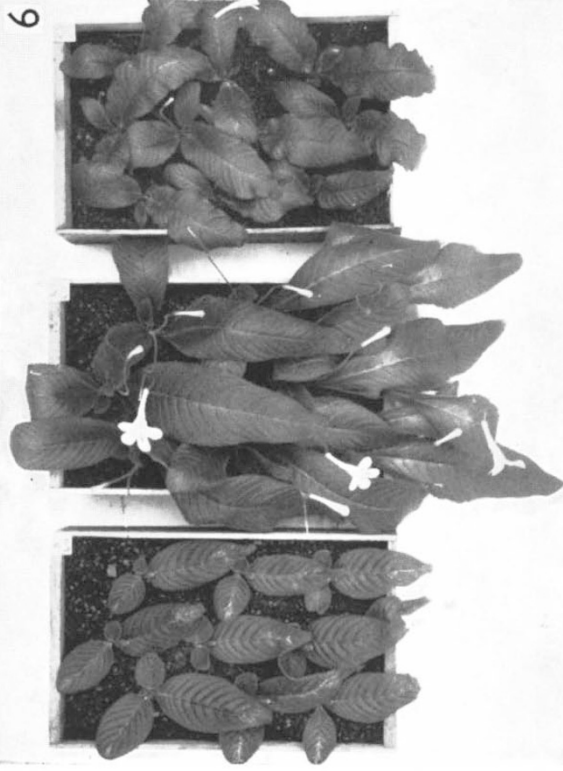
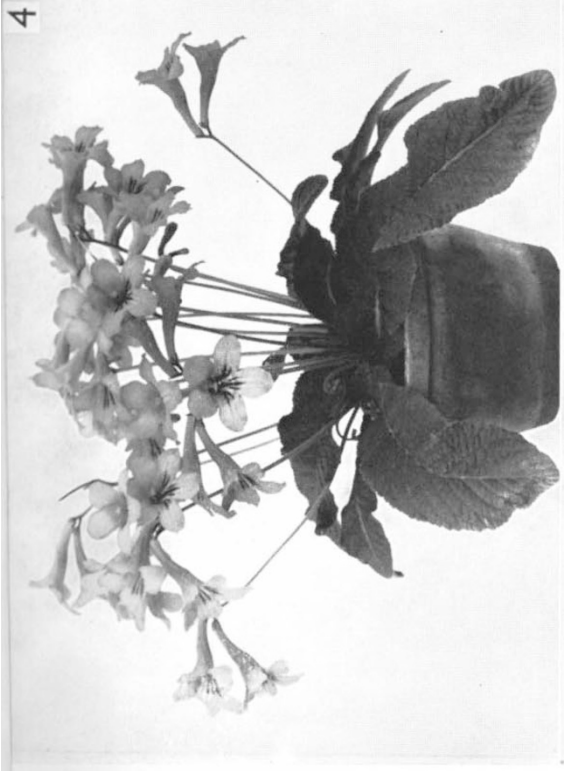
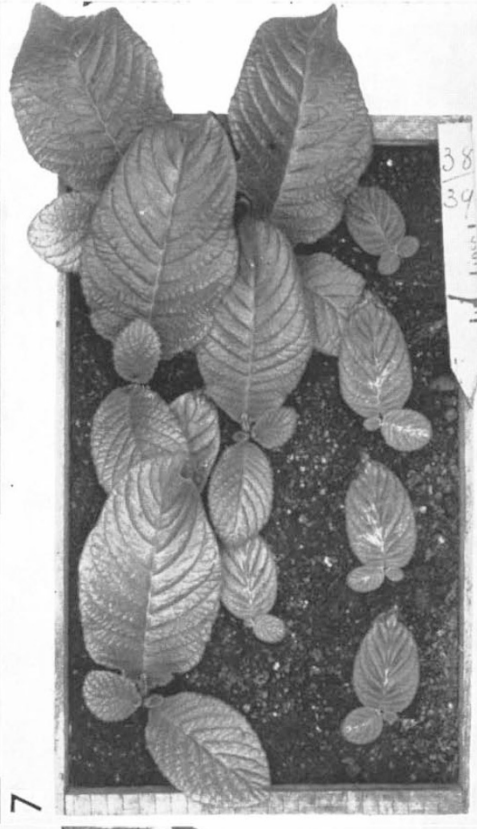
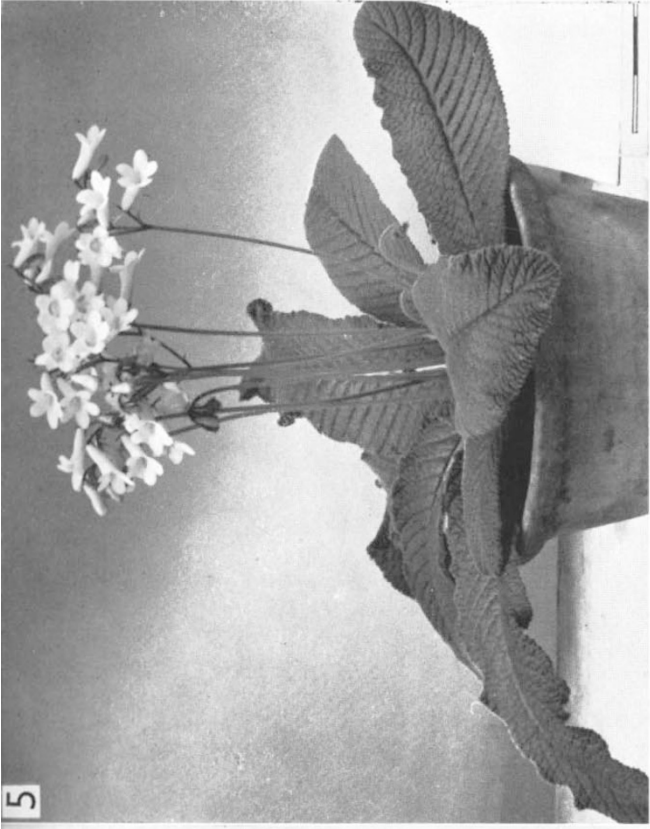


Plate II

- FIG. 4.—A rosulate species, *Streptocarpus textii*, with two flowers on each inflorescence.
- FIG. 5.—A rosulate species, *Streptocarpus parviflorus* with up to 12 flowers on each inflorescence.
- FIG. 6.—Heterosis in the rate of growth of the leaves in *Streptocarpus*. Left, *textii*; Centre, *textii* × *gardenii*; Right, *gardenii*.
- FIG. 7.—Progeny from simultaneous self- and cross-pollination in *textii* × *gardenii*. Note heterosis in the hybrids.



system, stability is conserved, largely at the habit-group level, by a chromosomal mechanism, the supergene, but rare mutation or crossing-over would permit variation. In the flower system phenotypic stability is secured at the generic level by a chemico-genetical mechanism but recessive mutants, by subtly affecting competition for a common substrate, maintain the genetic potential for variation.

5. CONCLUSION

The characters studied in this and in previous surveys on *Streptocarpus* are not distributed at random in the genus but occur in specific combinations or systems and characterise the taxa at various levels. Each system can be seen to have the dual function of conserving

TABLE 9
Gene systems of Streptocarpus

| System | Mode of Inheritance | Characters involved |
|------------------------|---------------------|--|
| <i>Growth</i> | | |
| Habit | Mendelian | Leaf no. and size |
| Heterosis | Quantitative | Leaf growth rate |
| <i>Reproduction</i> | | |
| Certation | Quantitative | Pollen-tube growth rate (i) pollen-size (ii) incompatibility |
| Cytoplasm | Quasi-Mendelian | Gynodioecy and sex modification |
| Flower pattern | Mendelian | Gene linkage (supergene) |
| Flower colour | Mendelian | Gene interaction (syndrome) |

phenotypic stability while permitting genotypic variability. The mechanism of conservation varies from system to system.

6. SUMMARY

1. A broad survey is made of growth habits, habitats, inter- and intra-crossability and fertility, heterosis and cytoplasmic inheritance in some 27 species of the African genus, *Streptocarpus*.

2. Habit is shown to be related to habitat, both at the sub-generic level and especially within the sub-genus, *Eustreptocarpus*, which comprises species with unifoliate, sub-unifoliate and rosulate habits, having well-defined geographical distributions. The centre of diversity is Natal where all three habit groups occur, the unifoliate species ranging northward and the rosulates mainly southward from the centre.

3. Pistil length varies from about 5 to 50 mm. in *Streptocarpus*. The inheritance of pistil length is governed by a polygenic system with no potence. The different habit groups are characterised by their mean pistil (and capsule) lengths.

4. In intergroup crosses, the crossability and fertility indices are positively correlated with the mean pistil length of the species used as pollen parents.

5. This behaviour results from pistil length being positively correlated with pollen-grain volume, the largest pollen producing the fastest-growing pollen tubes. In certain crosses the rate of pollen-tube growth appears also to be controlled by pollen-incompatibility factors.

6. Heterosis, or luxuriance, in the rate of growth of the leaves which, in *Streptocarpus* are specialised organs, is evident in almost all species crosses. Heterosis is not expressed in the floral system.

7. Fifteen species tested fell into three distinct classes for cytoplasm. Class 1 \times class 3 gave male sterile F_1 's, the reciprocals being normal. Class 2 gives normal F_1 's with both classes 1 and 3. Class 2 species are distributed in and around Natal and are mainly sub-unifoliates, *i.e.* habit, habitat and cytoplasm type are, largely, dependent factors.

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