

Natural hybridization in the genus *Eriosema* (Leguminosae) in South Africa

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ABSTRACT

Both spontaneous and introgressive hybridization occur naturally in *Eriosema* in South Africa. One case of hybrid swarming is reported and a catalogue of six hybrids is presented and discussed in detail.

RÉSUMÉ

HYBRIDATION NATURELLE DANS LE GENRE ERIOSEMA (LEGUMINOSAE) EN AFRIQUE DU SUD

L'hybridation naturelle et introgressive survient naturellement chez l'*Eriosema* d'Afrique du Sud. Un cas d'essaimage d'hybride est rapporté dans un catalogue de six hybrides et est présenté et discuté en détail.

INTRODUCTION

Although hybridization is today widely recognized as having played a major role in the evolution of the plant kingdom, there is still disagreement (Heiser, 1973) as to how it should be defined. For example, Sibley (1957) defined it as interbreeding between populations in secondary contact, regardless of taxonomic rank, whereas Solbrig (1970) differentiated clearly between the crossing of different taxa, calling that between species, or taxa of higher rank, 'hybridization', and that within species 'recombination'. In this paper the term hybridization is used in Mayr's (1942) sense of 'the crossing of individuals belonging to two unlike natural populations that have secondarily come into contact'.

Most authors who have written on this subject recognize two main types of hybridization: spontaneous hybridization and introgressive hybridization. Naturally occurring interspecific hybrids, presumably individuals of the first filial generation (henceforth referred to as the F_1), are known in all major groups of plants and in all well studied floras (Grant, 1971). According to this author the F_1 generation may be fertile, semi-sterile, highly sterile, or completely sterile, and in all but the last case it can produce some later-generation progeny. The partially fertile F_1 hybrid may reproduce sexually, be selfing, or there may be crossing with sister hybrid plants, or backcrossing to one or both parental species. The resulting second-generation progeny can then go on to cross with one another and with the original plants. This results in a hybrid swarm, an extremely variable mixture of species, hybrids, backcrosses, and later-generation recombination types.

In this study the term 'spontaneous hybridization' is used in reference to the production of occasional or sporadic natural hybrids, whereas the term 'introgressive hybridization' refers to the repeated backcrossing of a natural hybrid to plants of one, or both, parental populations.

Three hybrid situations have been encountered in the present study. These are:

- (a) *spontaneous hybridization* between two species, with the hybrid progeny sterile;
- (b) *introgressive hybridization* between two species, with the hybrid progeny semi-sterile or fertile;
- (c) *hybrid swarming* between four species with the hybrid progeny of variable fertility.

Representative examples of spontaneous and introgressive hybridization have been selected from the hybrid catalogue and are presented in detail. The only hybrid swarm encountered is briefly referred to, as its detailed analysis was considered beyond the scope of this work. The three hybrid situations listed above form the framework on which the hybrid catalogue has been compiled. It is presented in the last section.

The structure of populations of plants derived through hybridization have been evaluated almost exclusively on the basis of morphological criteria (Levin, 1967). Their analysis has been possible by the development of a number of techniques such as Anderson's (1949, 1953, 1956, 1957) pictorialized scatter diagrams and hybrid indices and to a lesser extent Hatheway's (1962) weighted hybrid index. However, as Levin (1967) clearly pointed out, these techniques, although they provide considerable information about the gross population structure, the direction and extent of gene flow, and the correlation and segregation of species characters, they nevertheless may fail to provide a basis of ascertaining the specific nature of each hybrid. As a consequence of dominance, character cohesion, epistasis, complex mode of inheritance, varying degrees of expressivity and phenotypic plasticity Levin (1967) considers any judgements concerning parentage of individual organisms to be unreliable. Clearly comparative morphology alone is inadequate in portraying the dimensions and significance of hybridization: it can however, indicate its physical presence and, from a practical taxonomic viewpoint, can provide an adequate preliminary tool of analysis.

For over 30 years Anderson's paradigm of character coherence, the basis of his concept of introgressive hybridization, has been very useful to taxonomists dealing with hybrid populations. There is now, however, sufficient data to suggest that this paradigm should be considerably modified (Flake, Rudloff & Turner, 1969; Adams & Turner, 1970; Heiser, 1973; Anderson & Harrison, 1979; Grant, 1979; Wells, 1980). The Andersonian theory has been succinctly summarized by Grant (1979) as follows: 'Character coherence is a diagnostic feature of natural hybrid populations. The character coherence is due primarily to multifactorial linkage and secondarily to pleiotropy and environmental selection. Selection in nature normally favours parental types and thus works in the same direction as linkage'. What has troubled Grant (1979) and other authors is the limiting scope of Anderson's theory as well as the misleading interpretations that can arise from its faulty techniques. The latter has been clearly shown

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by Wells (1980). The biggest stumbling block in Andersonian theory is the finding (Grant 1979) that different hybrid populations may have marked differences in character coherence. Grant has suggested, therefore, that character coherence is not a constant, but rather a variable feature of natural hybrid populations. Two new techniques are now available to detect this (Grant 1979; Wells, 1980). The nub of Grant's conclusion is that multifactorial linkage and recombination are opposing tendencies and that in hybrid populations they work in balance such that their respective expressions of character coherence and character recombination will reflect a balance or compromise between opposite extremes. He suggests that 'the balance is affected by various internal and external factors. The components of the recombination system of the plant group comprise the internal factor (see Grant 1975, Chap. 3); the chief external factor is natural selection. The interplay between these factors determines the point of equilibrium between character coherence and character recombination and so will vary from hybrid population to hybrid population depending on the controlling factors involved.

This study has utilized Andersonian techniques as these were all that were available at the time. Unfortunately the present author has no further opportunities to continue this study and presents the results in the hope that someone will reassess the problem in greater depth using chemical and cytological data and a revised Andersonian paradigm.

Eriosema is one of the few papilionoid genera in southern Africa which is known to have undergone hybridization. The reason for this propensity is unknown. It is interesting that *Rhynchosia*, a genus close to and often confused with *Eriosema*, has not a single recorded case of hybridization. Judging from reported cases hybridization among papilionoid legumes is an apparently rare phenomenon. This may, however, be due to a lack of appreciation by taxonomists of its role in plant variation. The chemotaxonomic studies of *Baptisia* by Alston and Turner and co-workers remain the classic case of hybridization analysis in the Papilionoideae (Alston, 1959; Alston, Turner, Lesters & Horne, 1962; Alston & Turner, 1963; Alston & Hempel, 1964; Alston, 1965) and a useful model to follow if suitable facilities are available.

1. SPONTANEOUS HYBRIDIZATION

While collecting specimens on vacant commonage at Hayfields, Pietermaritzburg (Fig. 1), I found a large population of yellow flowered *E. salignum* E. Mey., growing below a ridge on a gentle slope. South of this was an extensive population of prostrate, bright red, orange and yellow flowered *E. cordatum* E. Mey. In the adjacent area between the two species and also within the *E. cordatum* population were about twenty semi-erect, pale pink and yellow-flowered plants (Fig. 2), most of which bore withered flowers and fruits. Some of the fruits were fully formed but the enclosed seeds had shrivelled. The vesture of hairs of these twenty proved to be intermediate between those borne by plants of *E. salignum* and *E. cordatum* that grew in the same general area. I decided to analyse the entire population.

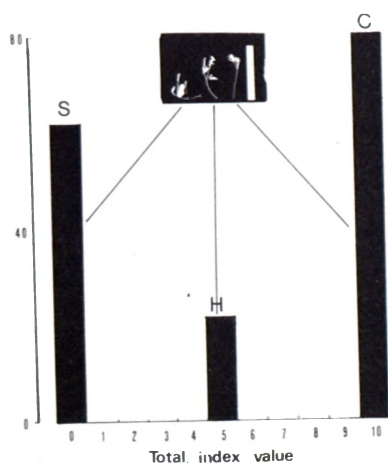
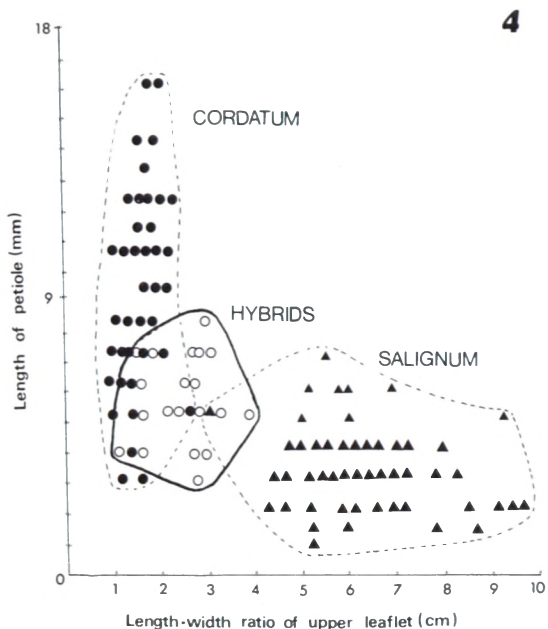
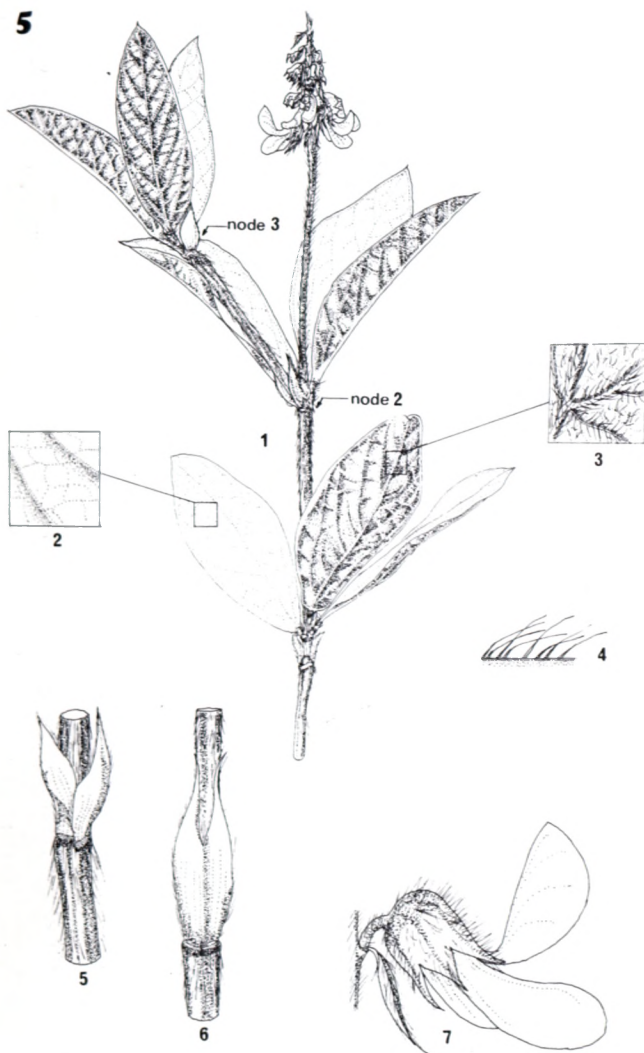
After considering the possible influence of slope, shade and soil type, I laid out four transects that provided an adequate sample of the area. I collected all plants of *Eriosema* that grew within 1 m of these lines. At 50 m intervals, I then made right-angled transects along which I also collected all plants within 1 m distance from the transect.

As fruiting and flowering were almost completed at time of first locating the population, emphasis had to be placed upon the morphological form of vegetative characters. A record was made of each plant's habit of growth, the degree of senescence of the stipules and the type and density of stem and leaf vesture. The length and width of the terminal (upper) leaflet of the mature trifoliolate leaf subtending the first produced inflorescence, and the length of the petiole of the same leaf were also noted. The qualitative morphological characters are listed in the left hand column of Table 1. Each character was divided into three states. Those states representative of plants of *E. salignum* were given the value 0; those representative of plants of *E. cordatum* carried the value 2, while intermediates were represented by value 1. One hundred and fifty two plants were scored for these character states. The sum of the index values for all character states of an individual comprises its total index value. Theoretically the total index value for plants of *E. salignum* was thus 0, that for plants of *E. cordatum* was 10, while for hybrid plants scores from 1-9 were possible. Plants with similar total index

TABLE 1. — Characters and index values used in scoring the hybrid population at Hayfields, Pietermaritzburg

Characters	0	1	2
Habit	erect	semi-erect	prostrate
Form of stipules	free	connate at base	connate, 2/3 of length
Persistence of stipules	senescent	senescing	persistent, green
Stem vesture	dense, fine appressed	dense, shaggy appressed	sparse, shaggy patent
Pubescence of undersurface of leaflet	appressed hairs along veins, woolly in intercostal areas	surface dull, hairs semi-erect on veins and in intercostal areas	surface shiny, with sparsely scattered erect hairs

1. SPONTANEOUS



FIGS 1 — 5.—Spontaneous hybridization. 1, fallow commonage near Scottsville. 2, *Stirton* 736: plant collected at Hayfields, Pietermaritzburg (1974–02–21). 3, frequency distribution of total index values of the *Eriosema* population at Hayfields, Pietermaritzburg (S, *E. salignum*; H, 'hybrid'; C, *E. cordatum*). 4, pictorialized scatter diagram of population of *E. salignum* and *E. cordatum*, and putative hybrids growing at Hayfields, Pietermaritzburg (sampled 1974–12–01). 5, *Stirton* 1601: plant collected at Hayfields, Pietermaritzburg (1975–01–22), probably a hybrid between *E. cordatum* and *E. salignum* — 1, stem with flowers, $\times 0.5$; 2, glabrous abaxial surface of lateral leaflet, $\times 3$; 3, hairy adaxial surface of terminal leaflet, $\times 3$; 4 semi-erect hairs of stem and adaxial surfaces of leaflets; 5 free stipules at node 2, $\times 2.8$; 6, fused stipules at node 3, $\times 2.8$; 7, flower, $\times 4.3$.

values were grouped into a frequency distribution (Fig. 3). The 21 intermediate plants all fell into class 5 of the frequency distribution. The 61 plants which had individual total index values of 0 were considered to belong to *E. salignum*, whereas those plants which had a total index value of 10 were considered to belong to *E. cordatum*. Only one group of plants was found to be intermediate, namely those falling within class 5.

Quantitative parameters were combined with the qualitative character states by constructing a pictorialized scatter diagram (Fig. 4). In this diagram the value of the ratio of leaflet length/leaflet width was plotted against the length of the petiole.

In Fig. 4 the hybrids (open circles) are seen to occupy an area of the graph intermediate between the main area of variation occupied by each putative parent. The hybrid is not entirely discrete spatially as a number of specimens of both putative parents fall within its range.

Fig. 4 and Table 1 both indicate the presence of a group of plants with characters that are not those of *E. salignum* nor those of *E. cordatum* but more or less intermediate between these.

A resampling of this population on the 22-10-1975 produced a plant (Fig. 5) which, although clearly within the range of the intermediate plants referred to above, showed some features that are worth special mention. The stipules, instead of senescing, persisted and remained green. They also varied from free and overlapping at the base (Fig. 5.5) to fused for two-thirds their length (Fig. 5.6). It would be advantageous to monitor an area such as the one described, for hybrids and hybrid variation throughout several years to attempt to obtain information relating to maternal and pollen parents of the hybrids that grew and flowered at different times and especially to ascertain whether the nature of the spontaneous hybrids varied over time.

In the Hayfields area the location of the hybrid plants in relation to the populations of both putative parental species suggested that the hybrids arose from seed shed by *E. cordatum*. Plants of *E. cordatum* always set abundant seed, whereas those of *E. salignum* produced a poor, erratic seed set. This level of seed set has been found to be consistent for these

taxa throughout their range. Bruchid damage was also heavier in seeds of *E. salignum*.

2. INTROGRESSIVE HYBRIDIZATION

Of common occurrence in *Eriosema* in South Africa are populations in which two species are readily recognized but in which a range of 'intermediates' are also present.

The example discussed in this section was located near Sobantu village, Pietermaritzburg (Fig. 6). Two species occurred: *E. cordatum* and *E. preptum* C. H. Stirton.

The habitat consisted of heterogeneous soil conditions that ranged from clay in burnt grassveld to deep sand on the lip of a bare roadbank. The latter site formed the limit of distribution. The roadbank was fully exposed to the sun, whereas the grassland had a fair number of plants of *Acacia* that provided shade.

Plants were analysed as in the example described previously. A field assessment of their range of variation revealed two characters with marked quantitative variation, namely the length of the inflorescence and the length of the terminal leaflet of a mature trifoliolate leaf. Measurements were recorded for 136 plants.

The qualitative characters are listed in the left hand column of Table 2. Each character was divided into 3 or 4 states. The numerical value of the character states provides an index value. Total index values were compiled for each plant and then used in the compilation of a frequency distribution (Fig. 7) by the method used previously. The scoring of individual plants was such that a typical plant of *E. preptum* would score 0, one of *E. cordatum* would score 9, whereas plants with characters of either putative parent would score from 1 to 8.

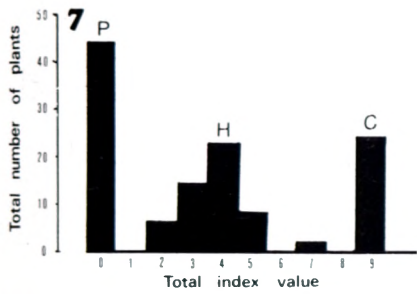
Fig. 7 shows that nearly 50 % of the plants scored fell between the two putative parents. Fig. 8 is typical of the plants falling in group 4 in Fig. 7. From Fig. 7 it appears that there was backcrossing of the interspecific hybrids with plants of *E. preptum*.

The quantitative characters were combined with the various qualitative character states and are presented in a pictorialized scatter diagram (Fig. 9). It

TABLE 2. — Characters and index values used in scoring the hybrid population at Sobantu Village, Pietermaritzburg

Characters	0	1	2	3
Stem vesture	short white with longer appressed hairs interspersed	semi-erect short white hairs with spreading yellow hairs interspersed	ferruginous, stiff spreading hairs only	
Gland colour on calyx	yellow	orange	white	
Habit of growth	erect	semi-erect or ascending	prostrate	
Under-surface of leaflets	dense white woolly with longer appressed hairs on veins yellow glands interspersed	sparsely woolly, longer hairs more erect, yellow glands	scattered hairs, erect, orange glands, surface dull	scattered hairs erect, white glands, surface shiny

2. INTROGRESSIVE



STEM PUBESCENCE

- short white hairs with longer appressed hairs interspersed
- ◐ short white hairs with spreading yellow hairs interspersed
- stiff, spreading, ferruginous hairs

GLAND COLOUR ON CALYX

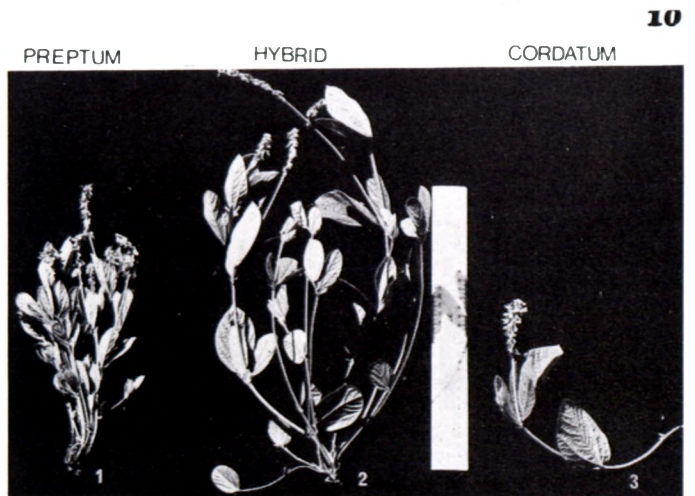
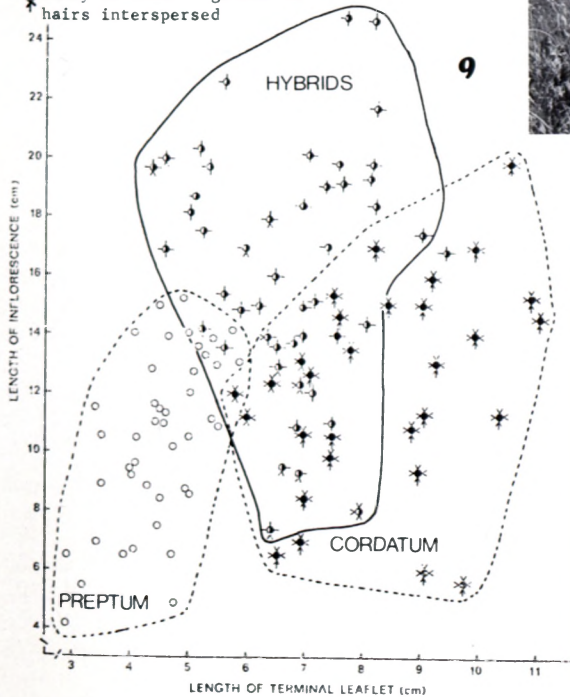
- yellow
- ◐ orange
- white

PLANT HABIT

- erect
- ◐ semi-erect or ascending
- prostrate

UNDERSURFACE OF LEAVES

- dense white woolly with longer appressed hairs on the veins. Yellow glands interspersed
- ◐ sparsely woolly with longer erect hairs, and yellow glands interspersed
- ◑ dull with orange glands and scattered erect hairs interspersed
- shiny with white glands and scattered erect hairs interspersed



FIGS 6-10.—Introgressive hybridization. 6, open grassland with scattered *Acacia* trees near Sobantu Village, Pietermaritzburg. 7, frequency distribution of total index values of the *Eriosema* population near Sobantu Village, Pietermaritzburg (P, *E. preptum*; H, 'intermediate plants'; C, *E. cordatum*) 8, Stirton 1602: putative hybrid plant between *E. cordatum* and *E. preptum*. 9, pictorialized scatter diagram of hybridizing population of *E. preptum* and *E. cordatum*, near Sobantu Village, Pietermaritzburg (sampled 1974-11-20); the terminal leaflet of the leaf subtending the second produced inflorescence was measured. 10, representative specimens of the *Eriosema* population near Sobantu Village, Pietermaritzburg: 1, *E. preptum*; 2, part of hybrid intermediate showing hybrid vigour; 3, *E. cordatum*.

can be seen that plants of *E. cordatum* mostly had longer terminal leaflets than did plants of *E. preptum*. The tendency of the hybrids to produce longer inflorescences than those of either putative parent is also apparent. What is not clearly shown is the hybrid vigour of the putative hybrids, but this may be seen in Fig 10.

The hybrid plant (half the specimen was photographed) shown in Figs 8 & 10 is a robust intermediate, and of all the different 'introgressants' is, with others like it, the least likely to be found in the proximity of either parent.

The hybrids were found scattered throughout the total population but tended to be aggregated in micro-localities not particularly favoured by either parent.

Although the overall population at Sobantu Village has been interpreted as exhibiting signs of introgressive hybridization, it is quite likely that this may be an incorrect explanation as a number of alternatives are theoretically plausible. Firstly, individuals having characters of two species may represent the remnants of the ancestral population out of which the two species differentiated (Dobzhansky, 1941). This does not appear to be the case here as the introgressants were mostly sterile and were found in the more recently disturbed areas of the total population.

A second alternative might be that the variation arose through mutation. Heiser (1973) pointed out that this is probably not uncommon and quoted Mayr (1942) as saying that it is known that the basic potentialities of related species tend to be similar and so the mutational channels are therefore more or less prescribed. This, however, also seems unlikely in view of the numbers of 'intermediates' observed.

The third possible explanation is more complex. It involves population intergradation. There are two types of intergradation. Primary intergradation (Mayr, 1942) occurs in populations that are in continuous contact, whereas secondary intergradation occurs between populations that have come together after a previous separation. Heiser (1973) pointed out that the former involved recombination and the later hybridization. Secondary intergradation could result in introgression. But as Mayr (1963) also pointed out, these two types of intergradation are not easy to distinguish, and because of this, the effects of primary intergradation would be difficult to distinguish from those of introgressive hybridization. Heiser (1973) quoted Barber & Jackson (1957) as stating that 'in a region of great ecological change one can expect simultaneous clinal variation in the frequencies of genes at a number of loci. Variability under the control of selection may reach a peak and decay on both sides of this peak'. This would lead to the loose association of variables that Anderson (1953) considered diagnostic of introgression. This would then mean that highly variable populations resulting from primary intergradation would be quite similar to those resulting from introgression. Both putative parents are widely distributed in the drier areas of Pietermaritzburg. For the most part they are allopatric but at least three localities are known where they overlap. In all the overlapping localities there is hybridization of the type reported in this section. It seems that these examples conform to Mayr's (1963) statement, that 'belts of highly variable populations in a meeting zone between rather uniform populations are almost invariably zones of secondary intergradation'.

Heiser (1973) mentioned two further possible interpretations of what is known as introgression. The first involved segmental allopolyploidy where segregates approaching one or both parents may occur. From the available cytological evidence (Baudet, 1977; Turner & Fearing, 1959), it seems that polyploidy is absent in the subtribe Cajaneae to which *Eriosema* belongs. It seems unlikely, therefore, that the intermediates of the Sobantu population were segregates produced by a polyploid species.

Heiser's second interpretation concerned the production of introgression-like effects which might result from inbreeding and selection in autogamous plants following an initial hybridization. Heiser (*l.c.*) stressed that although occasional hybridization between autogamous species did allow for the possibility of introgression, the lack of backcrossing after the initial hybridization would imply that the variation observed, while like introgression, was not the outcome of this phenomenon.

Field and laboratory experiments which involved bagging and emasculation of flowers revealed that both putative parents of the Sobantu Village population failed to set seed if the inflorescences were isolated from pollinators.

One real difficulty in interpreting the Sobantu population is that there is, as Heiser (1973) pointed out, some confusion between the definition of introgression and of hybrid swarming. Whether the Sobantu population consisted of hybrid populations out of genetic contact with the putative parents, or whether it consisted of hybrid plants repeatedly backcrossing to the parental forms clearly cannot be solved without detailed genetic experiments. The unlikely possibility also exists that the introgressants are nothing more than F_1 hybrids showing a marked degree of environmental plasticity.

3. HYBRID CATALOGUE

In the hybrid catalogue I have endeavoured to include all the putative hybrids that have been found in *Eriosema* in southern Africa (Fig. 11). This hybrid list will, I hope, encourage further studies within *Eriosema*. I hope it will also indicate to future workers that hybridization probably contributes materially to the extensive variation represented within *Eriosema* in southern Africa.

Each pair of putative parents has been named and numbered as representing a case of interspecific hybridization.

Under the numbered putative parents (for example H_1), each individual hybrid specimen known has been cited, together with its putative parents where these have been suspected. Each set of citations is followed by a general discussion.

H_1 *Eriosema cordatum* E. Mey. × *E. salignum* E. Mey. (yellow-flowered form)

LESOTHO.—2828 (Bethlehem): Malaoaneng (—CC), Dieterlen 866 (PRE); Leribe (—CC), Dieterlen 104 (PRE).

SOUTH AFRICA.—2628 (Johannesburg): Germiston (—AA), Rogers 12199e (BOL). 2732 (Ubombo): top of Pongola Poort (—CA), Stirton 506 (PRE), putative parents Stirton 503 & 507 (PRE). 2830 (Dundee): Buyahlanga Mountain, between Wasbank and Elandslaagte (—AC), Stirton 1364 (PRE), putative parents Stirton 1362 & 1363 (PRE). 2831 (Nkandla): Eshowe (—DC), Lawn 2271 (NH); Mtunzini (—DD), Stirton 417, 1271 (PRE), putative parents Stirton 414 & 419 (PRE). 2930 (Pietermaritzburg): Hilton Road (—CB), Ford s.n. (NH); Hayfields, Pietermaritzburg (—CB),

Stirton 736 (PRE), putative parents *Stirton 737* & *738* (PRE); also *Stirton 1169* (PRE), and *Stirton 1368* (PRE) with putative parents *1367* & *1369* (PRE); Voortrekker Road, Clarendon (-CB), *Stirton 1240* (PRE), putative parents *Stirton 1238* & *1239* (PRE); Baynesfield (-CB), *Stirton 704* (PRE), putative parents *Stirton 702* & *701* (PRE). 3029 (Kokstad): 2 km from Harding to Umzimkulu (-DB), *Storv 646* pro parte (PRE). 3030 (Port Shepstone): Hazlewood, Umzinto (-BC), *Bajinath 418* (NU), putative parent *Bajinath 419* (NU).

Dieterlen 866, a hybrid, was the basis for the incorrect inclusion of *Eriosema parviflorum* E. Mey. in the flora of Lesotho. *Dieterlen 104* (PRE) has five specimens on the sheet but only the robust specimen is a hybrid. *Rogers 12199e* is included with uncertainty.

Putative hybrids between *E. cordatum* and *E. salignum* (yellow-flowered form) have been found over a wide range yet the plants that are of suspected hybrid progeny are everywhere remarkably uniform. No specimens have been found which might be considered backcrosses between the intermediate hybrid and either of the two putative parents.

Hybrids, in general, are not common and thus are likely to be rare in any locality. The *Stirton 736* Hayfields population, however, numbered over 20 plants spread over four hectares. Some of these plants had very large rootstocks and were considered to be at least five years old.

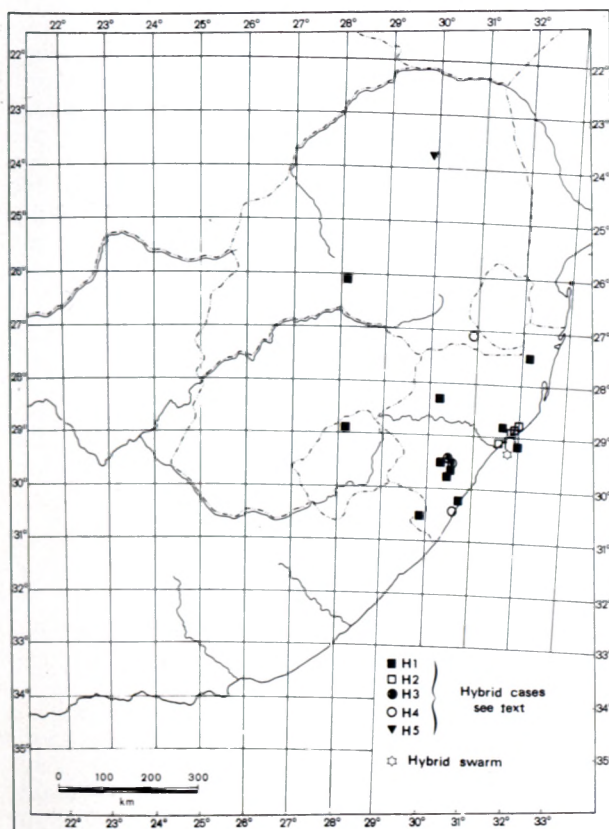


FIG. 11. — Known distribution of hybrid populations of *Eriosema* in southern Africa.

Field studies in the Hayfields population showed that *E. salignum* and *E. cordatum* usually had very little overlap in the time and duration of anthesis but on cloudy days both species showed fully reflexed flowers (i.e. flowers ready for pollination with the standard folded back) throughout the day. Sporadic hybrids were found to occur in the locality of this

population and may well have been the result of such an environmental influence. It is possible that isolating mechanisms other than time of flower reflexion may be in general operation to maintain the integrity of the two parental species. This needs further study.

Field studies during the present work have suggested that plants of *E. cordatum* and *E. salignum* hybridize more frequently than any other known cases of hybridizing species in the genus in southern Africa.

E. cordatum E. Mey. × *E. salignum* E. Mey. (yellow-flowered form) can be separated from its putative parents by the characters listed below.

<i>E. salignum</i> (yellow-flowered form)	Hybrid	<i>E. cordatum</i>
Plants erect	Plants semi-erect or ascending	Plants decumbent
Stipules becoming senescent, before young leaflets expand	Stipules senescent to halfway up stem	Stipules persistent, green
Stipules free	Stipules slightly connate at base, to ± ¼ total length	Stipules connate, at base to ¾ total length
Under surface of leaflets woolly with longer appressed hairs on veins	Under surface of leaflets dull with semi-erect hairs on veins and in intercostal areas	Under surface of leaflets shiny with sparsely scattered erect hairs
Stem pubescence dense, appressed, finely hairy	Stem pubescence dense, shaggy and appressed.	Stem pubescence shaggy ferruginous or white, patent.
Flowers yellow	Flowers orange (or pale pink) and yellow	Flowers red and yellow

H2 *Eriosema cordatum* E. Mey. × *E. salignum* E. Mey. (red and yellow flowered form)

SOUTH AFRICA.—2831 (Nkandla): Ngoye Forest (-DD), *Stirton 1278* (PRE), putative parent *Stirton 1279* (PRE); Twinstreams Farm, Mtunzini (-DD), *Stirton 1285* (PRE), putative parents *Stirton 1283* & *1284* (PRE); University College of Zululand (-DD), *Venter 690* (ZULU), putative parent *Venter 691* (ZULU). 2930 (Pietermaritzburg; Kloof (-DD), *Galpin s.n.* (24-6-1932. BOL), mixed sheet with *E. salignum*. 2931 (Stanger): Tugela Beach (-AB), *Johnson 407* (NBG).

The suspected hybrids of putative parents *E. cordatum* and *E. salignum* (red and yellow-flowered form) are different from those cited under Case H1.



FIG. 12.—Rootsystems of 1, *Eriosema salignum*; 2, hybrid *E. cordatum* × *E. salignum*; 3, *E. cordatum*.

This evidence suggests that there may be two distinct taxa presently included in *E. salignum* and this probability is still being investigated. Case H2 hybrids are more erect with very dark green shiny upper leaf surfaces and have ovate leaflets with the bases cordate. The leaflets of Case H2 hybrids are more commonly unifoliolate than in the Case H1 hybrids.

The hybrid situation on Mr I. Garland's farm at Mtunzini was particularly interesting. The hybrids were numerous and occurred wherever the putative parents were sympatric. There was a very large hybrid population at the bottom of the front lawn of his house. The hybrids were intermediate in nearly all characters, the most striking being the intermediate root system (Fig. 12). In this figure, the hybrid plant lies between the two putative parents: it can be seen to have features both of the straight daucate rootstock of *E. cordatum* and of the constricted rootstock of *E. salignum*. (Intermediate rooting systems are very characteristic of hybrids in the genus as a whole.) There was a marked hybrid vigour in this Mtunzini population. The hybrids were tall, suberect or ascending and stood out against other plants of the population.

H3 *Eriosema cordatum* E. Mey. × *E. preptum* C. H. Stirton

SOUTH AFRICA.—2930 (Pietermaritzburg): Hilton College farmlands (—CB), *Khan s.n.* (NU 45857); behind S.P.C.A. kennels, Scottsville, Pietermaritzburg (—CB), *Stirton 713* (PRE, this is a mixed collection containing both putative parents) and *Stirton 1243* (PRE), putative parents *Stirton 1241* & *1242* (PRE); near Sobantu Village (—CB), *Stirton 1411* (PRE), putative parents *Stirton 1409* & *1410* (PRE).

The *Stirton 1409–1411* population was analysed under Introgressive Hybridization. In the Sobantu Village and Scottsville populations there was marked hybrid vigour and an intermediate type of rooting system. The main differences between the hybrids and the putative parents are summarized below. It must be stressed, however, that in dealing with an introgressed population the choice of characters are to some extent arbitrary. Overlap must therefore be expected.

<i>E. cordatum</i>	Hybrid	<i>E. preptum</i>
Plants prostrate	Plants semi-erect or ascending, very robust	Plants erect
Stem vesture consisting of stiff, spreading, ferruginous hairs	Stem vesture consisting of short white hairs with spreading yellow hairs interspersed	Stem vesture consisting of short white hairs with longer appressed white hairs interspersed
Under surface of leaflets shiny with white glands and scattered erect hairs interspersed	Under surface of leaflets either sparsely woolly with longer erect hairs and yellow glands interspersed or dull with orange glands and scattered erect hairs interspersed	Under surface of leaflets dense white woolly with longer appressed hairs on the veins. Yellow glands interspersed
White glands on calyx	Orange glands on calyx.	Yellow glands on calyx.
Rootstock carrot-like with occasional right-angled extensions; short stylopodium	Long central carrot-like rootstock often very thick and constricted with or without numerous small beaded offshoots.	Rootstock with long stylopodium: thin and beaded when young but tending towards slightly wavy or constricted but carrot-like when old
Flowers red and yellow	Flowers pink, orange and yellow	Flowers orange with red veins, or yellow-orange

H4 *Eriosema cordatum* E. Mey. × *E. kraussianum* Meisn.

SOUTH AFRICA.—2730 (Vryheid): 18 km from Vryheid to Paulpietersburg (—DB), *Stirton 1323* (PRE), putative parent *Stirton 1324* (PRE), *E. kraussianum* seen but not collected). 3030 (Port Shepstone): Turnoff to Greenhart on Port Shepstone Road (—DD), *Stirton 1402, 1405* (PRE), putative parents *Stirton 1403, 1404* (PRE).

The *Stirton 1402–1405* population shows characteristics associated with introgression. Two clear-cut intermediates were noted in the field. *Stirton 1402* showed hybrid vigour and was morphologically close to *E. cordatum*, whereas *Stirton 1405* was a stunted, multistemmed plant approximating *E. kraussianum*. The first plants that I found on locating the population were 'introgressants' that I was unable to relate to any species. They grew in deep sand along a road. After studying them for some time two factors drew my attention, namely, their pinkish flowers, and their abortive or irregular seed set. The overall facies of these plants led me to postulate that they were hybrids and that one of the putative parents was *E. cordatum*. After a search down the left-hand side of the road I found a large colony of *E. cordatum* growing on a sandy bank near the end of the road, about 500 m from the first 'introgressants'. I returned down the opposite side and discovered a strange collection of very stunted plants that gave an immediate impression of *E. kraussianum*. These orange and yellow-flowered plants were growing on the damp sandy lip of an irrigation canal. After further searching I found a small colony of *E. kraussianum* within the same general locality. In trying to reconstruct how the various plants became distributed, I noticed that the soils of the two hybrid colonies had been removed from the general vicinity of the parental populations during road-building operations. The two hybrid colonies were established in local habitats that were different in both water availability and aspect. It was possible that the hybrids had resulted from seed or roots being transported in the sand. If putative parents had also been transported, it could be that these were unable to survive the harsher environmental conditions of the hybrid localities.

The second example, *Stirton 1323*, was an isolated plant growing in a very disturbed intermediate habitat. It had numerous ascending to erect stems and showed marked hybrid vigour.

H5 *Eriosema transvaalense* C. H. Stirton × *E. angustifolium* Burt Davy

SOUTH AFRICA.—2329 (Pietersburg): near the Magoebaskloof Hotel, (—DB), *Stirton 1442a, 1442b*, putative parents *Stirton 1445* & *1444* (PRE).

The facies of the *Stirton 1442–1445* population is similar in many ways to that described for the *Stirton 1409–1411* population of *E. cordatum* E. Mey. × *E. preptum* C. H. Stirton. In both instances the habitat had been subjected in the past to burning. The soil cover and type was also rather variable. *Stirton 1442a* (sheet 1) showed the greatest hybrid vigour. This population may be backcrossing to either parent as *Stirton 1442a* (sheet 2) and *Stirton 1442b* were intermediates between *Stirton 1442a* (sheet 1) and *E. transvaalense* (*Stirton 1445*) and *E. angustifolium* (*Stirton 1444*) respectively. The hybrids were spread randomly throughout the population and were readily distinguishable on habit and flower colour. *E. transvaalense* has pink and yellow flowers and is a prostrate, softly pubescent densely matted plant whereas *E. angustifolium* is an erect, stiffly haired yellow-flowered species. The hybrids tended to have

pale pink flowers and to vary from prostrate, ascending to erect in habit.

E. transvaalense and *E. angustifolium* are sympatric species but this small population is the only one in which I have found hybridization between the two species.

H6 Hybrid swarm

SOUTH AFRICA.—2931 (Stanger): 1 km past Gingindlovu to Durban (—BA), Stirton 1259, 1260 (PRE), putative parents *E. salignum* [Stirton 1257 (PRE)], *E. psoraloides* [Stirton 1258 (PRE)], *E. cordatum* [Stirton 1261 (PRE)] and *E. preptum* [Stirton 1262 (PRE)].

This population was spread over a disturbed, recently-felled *Eucalyptus* plantation. Stirton 1259 had yellow flowers and was semi-erect, whereas Stirton 1260 was pale pink-flowered, numerous stemmed and prostrate. These two collections formed the limits of the range of variation. There was a wide range of 'intermediates' between the four 'putative' parents. I attempted to analyse this population using the techniques described earlier but could not make any sense of the results. As there was no time available to pursue the problem it is reported here in case difficulties may be encountered in identifying plants collected in the Gingindlovu area.

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UITTREKSEL

Beide spontane en introgressiewe verbastering kom in die natuur in Eriosema in Suid-Afrika voor. Daar word verslag gegee van een geval van hibriede-geswerm en 'n lys van ses hibriede word aangebied en tot in besonderhede bespreek.

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