A Study of Intra- and Interspecific Relations of *Crepis foetida* L.

by

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With 13 Text-figures

Introduction

The genus *Crepis* contains many species which, on the basis of common morphological characteristics, can be assembled into groups, the members of each group having nearly identical karyotypes (Babcock and Cameron, 1934). Yet the individual species within a group may be highly differentiated in certain features, such as length of life-cycle or degree of specialization of the achenes, and they may occupy widely separated geographical areas. As previously stated (Babcock, 1936, p. 31): "These groups of related but well-differentiated species, with very similar chromosomes among the species of each group, are significant in several ways. For one thing, they prove that close similarity in the chromosomes is directly correlated with close taxonomic relationship in *Crepis*. They also indicate that the genetic evolutionary processes involved in speciation within these groups are processes which are not accompanied by many visible changes in the chromosomes."

In a later discussion (Babcock and Emsweller, 1936, p. 357) is the following conclusion: "Thus the inference seems warranted that speciation (in these groups) has been made possible by a limited number of gene mutations or minute structural changes, leaving the main part of the residual genotype unchanged." Here reference was made to certain unpublished data of Jenkins, Cave, and Smith, who worked independently on different groups of species, as evidence in support of the inference quoted above. More recently Jenkins (1938) has reported data and conclusions pertaining to a group of four species, occurring in the Madeira and Canary Islands, three of which are isolated endemics. The evidence from this study definitely supports the generalizations quoted above.

It is the purpose of this paper to report certain data and the conclusions based thereon, concerning a group of three species which are widely distributed in the Mediterranean region. Two of them, *Crepis Thomsonii* Babcock (1938) and *C. eritreënsis* Babcock (op. cit.), are not only widely separated from each other but are completely isolated from the third. Both are fairly uniform except for occasional ecological modifications. *C. Thomsonii* occurs in Punjab and adjacent parts of northwestern India, Baluchistan, and Afghanistan. *C. eritreënsis* has been found only in Eritrea. The third species is *C. foetida* L., which has an extensive range and is extremely polymorphic, especially when considered in the broad sense adopted by the present authors (Babcock, 1938). Taken in this sense, its distribution is in western, central, and southern Europe to the Caspian Sea; Asia Minor and Syria to Transcaucasia and southwestern Persia. Three subspecies have been recognized (Babcock, op. cit.) namely *C. foetida vulgaris*, *rhoeadifolia*, and *commutata*. Each is highly variable, including numerous forms, some of which have been named as species, varieties, or forms.

Materials and Methods

The species, subspecies, and forms used in this investigation are listed below, together with the accession number and source of each of the nine strains, and an abbreviated designation which will be used in this paper. The 9 strains were chosen out of 70 grown the first year, because they were known to have come from natural populations and were therefore considered more representative and dependable than strains obtained from botanic gardens.

Fvt	— *Crepis foetida* subsp. *vulgaris* fa. *typica*	1812	— Spain
Fvg	— ,, ,, subsp. ,, fa. *glandulosa*	2850	— Sicily
Fvi	— ,, ,, subsp. ,, fa. *interrupta*	2047	— Cyprus
Fvf	— ,, ,, subsp. ,, fa. *fallax*	3169	— Syria
Fr	— ,, ,, subsp. *rhoeadifolia*	2318	— Tiflis
Fct	— ,, ,, subsp. *commutata* fa. *typica*	2864	— Crete
Fcl	— ,, ,, subsp. *commutata* fa. *lesboa*	2969	— Lesbos
T	— *Crepis Thomsonii*	3208	— Punjab
E	— *Crepis eritreënsis*	3005	— Eritrea

All the plants were grown on a table in a greenhouse, thus providing fairly uniform conditions. Careful records were kept of all important operations and on numerous character differences between the strains. The seeds were germinated in sterile sand and the seedlings transplanted to 4-inch, then to 6-inch pots. About 3 weeks after placing the seedlings in 6-inch pots, root-tips were taken in the usual way for examination of the somatic chromosomes, using the chrom-acetic-formalin method of killing and fixing (Hollingshead and Babcock, 1930, p. 3) and staining the sections with Heidenhain's iron-haematoxylin. Meiotic chromosomes were examined in smear preparations of pollen mother cells killed and stained in aceto-carmine solution.

Common characteristics of the species

The three species represented are annual herbs, although there are a few rare forms of *C. foetida* which behave as biennials or perhaps short-lived perennials, but no such forms have been used in this study. Under favorable conditions the plant produces a rosette of leaves from the root-crown or caudex before the stem and flower-heads appear. The caudical leaves are oblanceolate, petiolate, denticulate, dentate or pinnately lobed, and with a broad or narrow terminal lobe. Under favorable conditions the stem is more or less branched and the branches bear several or many flower-heads. The involucres are cylindric in anthesis and become turbinate or campanulate at maturity. As is usual in *Crepis*, the involucre consists of outer and inner series of bracts. The outer bracts are unequal, the longest being from about one-half to two-thirds as long as the inner bracts. The inner bracts, in fruiting heads, become strongly carinate, enclosing the marginal achenes. The whole plant is more or less hispid, and the involucre is pubescent with either glandular hairs or glandless bristles or both. The florets are yellow with more or less reddish purple either on the outer face of the marginal florets or restricted to the ligule teeth of all the florets. The achenes are usually dimorphic, the marginal being shorter, thicker, and more shortly or not at all beaked, the inner being long-beaked. But in *C. eritreënsis* the achenes are monomorphic and long-beaked. Also in certain rare forms of *C. foetida* the characteristic marginal achenes are absent, but no such forms were used in this study. The pappus is closely similar in these species, except as to its length. A qualitative feature which appears in all 3 species is the characteristic odor of the crushed leaves from which *foetida* derived its name. This odor occurs in all forms of *foetida vulgaris* and *foetida rhoeadifolia*; whereas it is present in some strains of *foetida commutata* but not in others, at least not very definitely. No attempt has been made to study the inheritance of these differences with respect to herbage odor.

Characteristic differences between the nine strains

Figures 1—8 show individual plants representing all of the strains. Each plant shown is either from the same strain used in this study or from a sister strain which came from the same source, with the following exceptions. In Fig. 4 (Fvf) and Fig. 6, lower (Fct), specimens from the strains used in this study were not available; the specimens shown are from other strains, but they illustrate the habit, leaf-shape, and relative size of the plants satisfactorily.

Table 1 gives a comparison of the 9 strains with reference to 18 characters, several of which were used in the genetic experiments. From these data it is evident that *eritreënsis* and *Thomsonii* show more resemblance to each other than to any of the other strains. In their leaves, size of flower-heads and length of style-branches they are similar, and they are equally precocious. They have lighter colored ligules than any of the other strains and they both have red ligule-teeth on all the florets, a character not found in the other strains. They are the most glandular strains with the exception of Fvg, but in floral characters they show most resemblance to Fvt. In these 3 strains (Fvt, E, T) the flower-heads close before midday and the plants are highly self-compatible. In Fvg the plants are also self-compatible but the flower-heads do not close notably in bright sunlight. Otherwise this strain differs from Fvt only quantitatively.

Although closing of the flower-heads in sunlight, thus facilitating self-pollination, is characteristic of self-compatible strains, except Fvg, yet it can not be the cause of self-compatibility since it was found that mechanical closing of heads of self-incompatible strains does not cause seed setting (see below, Fertility of Hybrids).

The *foetida* strains may be considered in four subgroups on the basis of degree of resemblance:

(1) Fct and Fcl. The *commutata* strains differ from all the others in having paleae on the receptacle and bipinnate leaves; also the pubescence of the involucre consists of both gland-hairs and glandless setae, the latter being very long and spreading. Presence of paleae on the receptacle has long been recognized as an

Table 1

Comparison of the nine strains as to 12 structural, 3 qualitative, and 3 physiological characters

	Fvt	Fvg	Fvi	Fvf	Fr	Fct	Fcl	T	E
Caudical leaves[1]	P	P	P	P	P	P	P	D	d
Lobes or teeth[2]	A	A	R	A	A	A	A	A	A
Lobes or teeth[3]	E	D	E	D	D	P	P	E	E
Central axis[4]	L	L	S	S	L	S	S	S	I
Glands on stem[5]	+	+	—	—	—	—	—	+	+
Glands, inner bracts[5]	+	+	—	+	±	+	±	+	+
Diam. open head (mm)	25	32	32	37	33	37	28	21	15
Bract ratio[6]	2	2	1.7—2	1.7—2	1.7	1.7	2	2	2.5
Style branches (mm)	2.5	3	3.8	4	4.5	2.8	2.9	1.6	2
Pappus length (mm)	6.5	7	4	5.5	5.5	3.5	4.5	5	5
Outer achenes, beak[7]	S	S	S	S	—	S	S	—	L
Paleae[8]	—	—	—	—	—	+	+	—	—
Ligule color[9]	Y	Y	Y	Y	Y	Y	Y	C	L
Red ligule teeth	—	—	—	—	—	—	—	+	+
Leaf spots[10]	—	—	—	—	—	—	—	+	—
Life cycle[11]	6	5.7	5	4.5	5	3.5	4.5	3	3.1
Fl.-Lt. relation[12]	C	O	O	O	O	O	O	C	C
Self-compatibility	high	high	none	low	low	none	none	high	high

[1] P = pinnately lobed; D = deeply toothed; d = shallowly toothed.

[2] A = acute; R = rounded, obtuse.

[3] E = entire; D = dentata; P = pinnata.

[4] L = stem long; S = short; I = intermediate.

[5] + = glands present; — = absent.

[6] Ratio of length inner/longest outer involucral bracts.

[7] Length of beak in marginal achenes: S = short; — = no true beak present; L = long.

[8] Presence or absence of paleae on the receptacle.

[9] Y = yellow; C = cream; L = lemon.

[10] Anthocyanin spots in epidermis.

[11] Number of months from date of planting to first flower.

[12] C = flower-heads in anthesis closing about midday; O = heads remain open in sunlight.

important diagnostic character in the Cichorieae. But in natural hybrids between *commutata* and *rhoeadifolia* paleae are found on plants which in all other respects are *rhoeadifolia* (see below, Inheritance of Paleae). Bipinnate leaves are found in certain strains of *rhoeadifolia* although they are not characteristic of the strain used in this investigation. Glandless setae on the involucre also occur in *rhoeadifolia*, though they are usually shorter and thicker; and still shorter gland-hairs

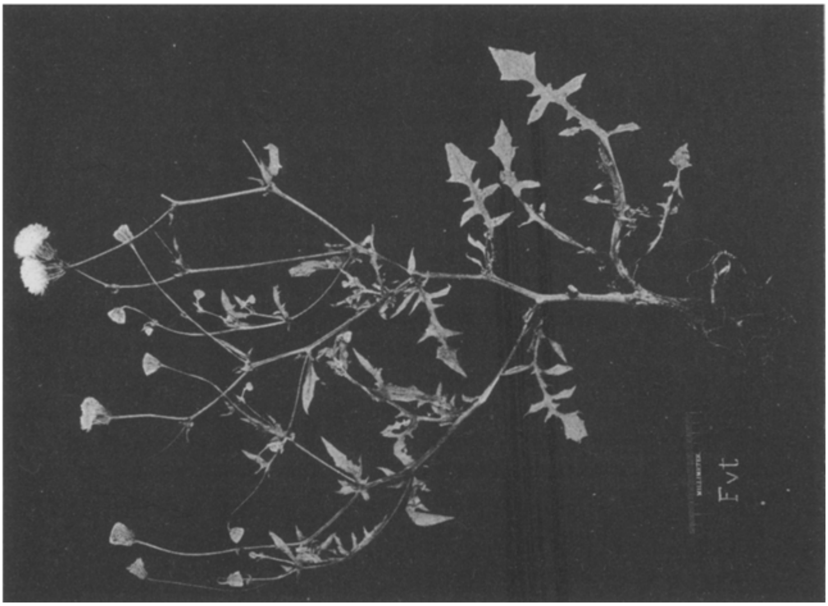

Fig. 1. *Crepis foetida vulgaris* fa. *typica* (28.1812-5).

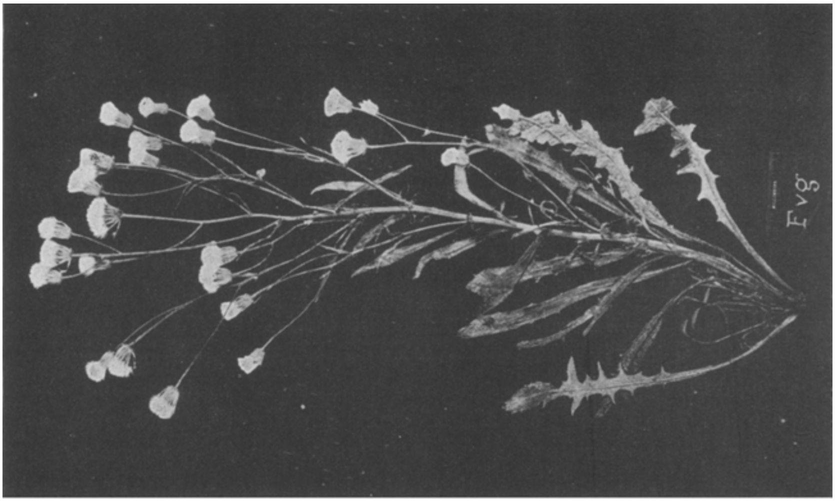

Fig. 2. *Crepis foetida vulgaris* fa. *glandulosa* (30.2307-2).

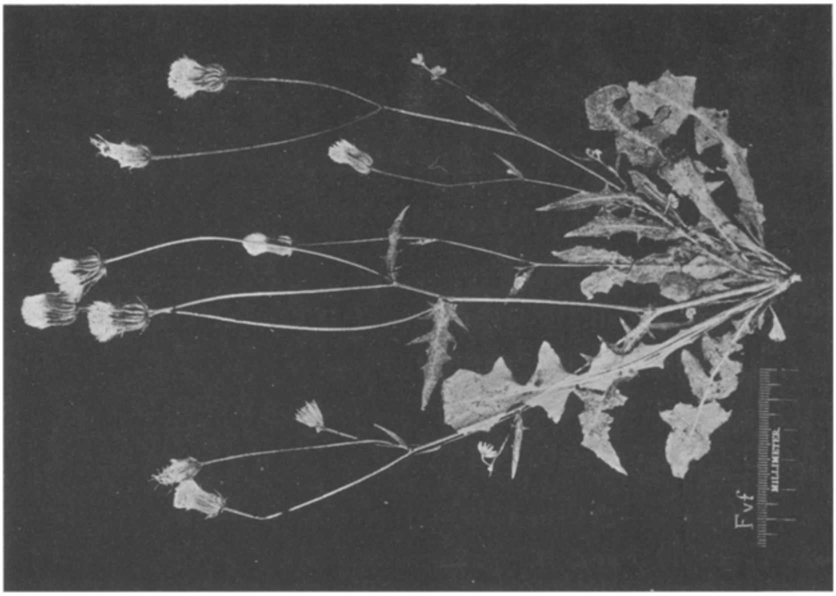

Fig. 4

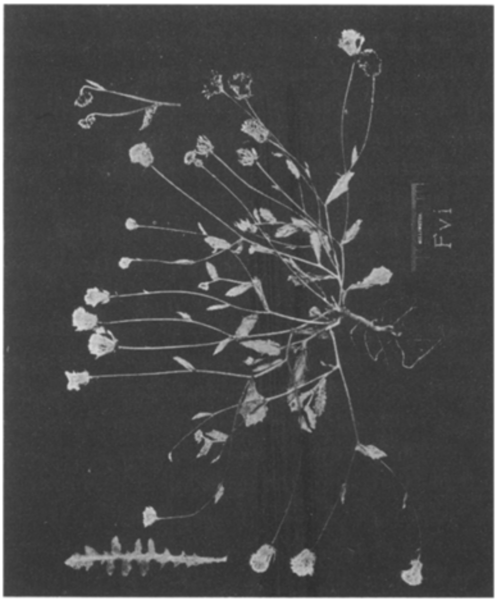

Fig. 3

Fig. 3.
Crepis foetida vulgaris fa. *interrupta* (28.2048-7).

Fig. 4.
Crepis foetida vulgaris fa. *fallax* (31.2863-5).

sometimes occur on the inner bracts in *rhoeadifolia*. Fct has the shortest life cycle of all *foetida* strains and Fcl is equalled in precocity only by Fvi. Both *commutata* strains differ from all the others, except Fvi, in being completely self-incompatible.

(2) Fvt and Fvg. The *foetida vulgaris typica* and *glandulosa* strains are closely similar and they differ from all the other *foetida* strains in high self-compatibility. In *glandulosa* the plant tends to be more robust, the heads are larger, and they do not close in sunlight. It is worth noting also that in some other strains of *glandulosa* the leaves are bipinnate just as in certain *rhoeadifolia* strains.

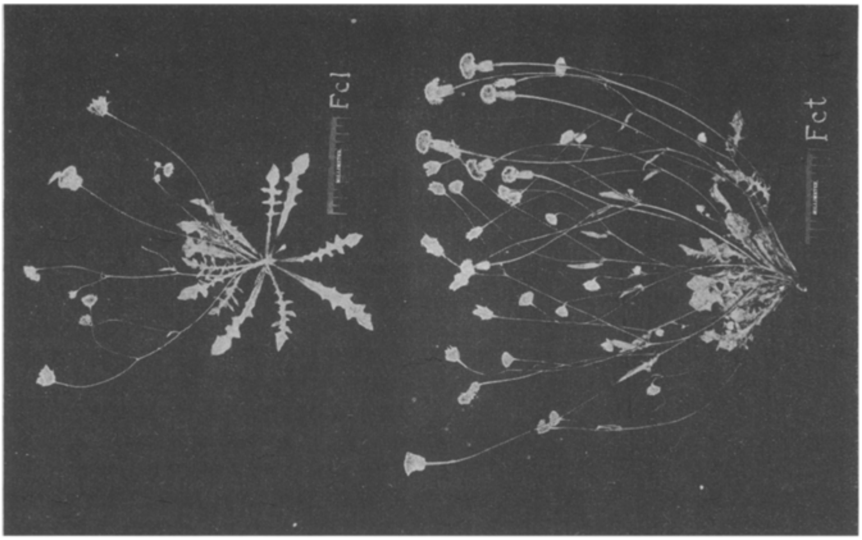

Fig. 6. *Crepis foetida commutata*; below, fa. *typica* (30.2219-6); above, fa. *lesboa* (31.2970-6).

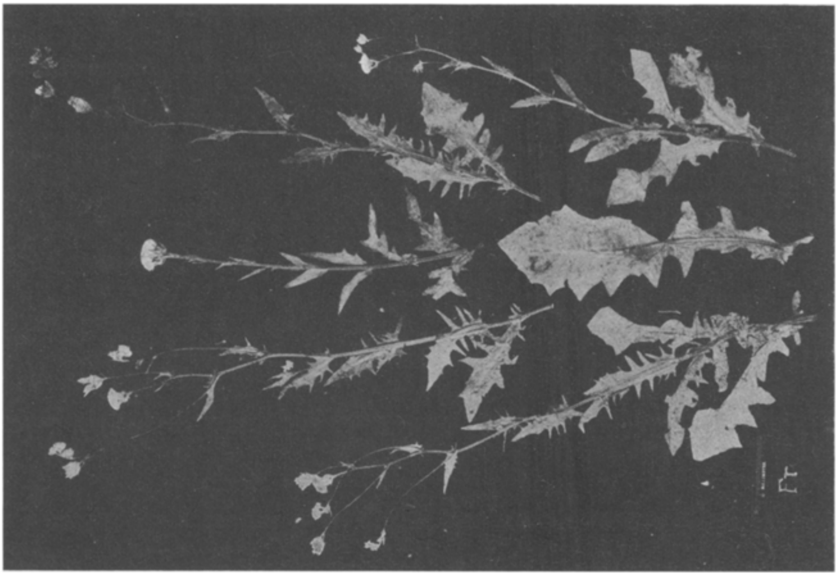

Fig. 5. *Crepis foetida rhoeadifolia* (28.2318-2).

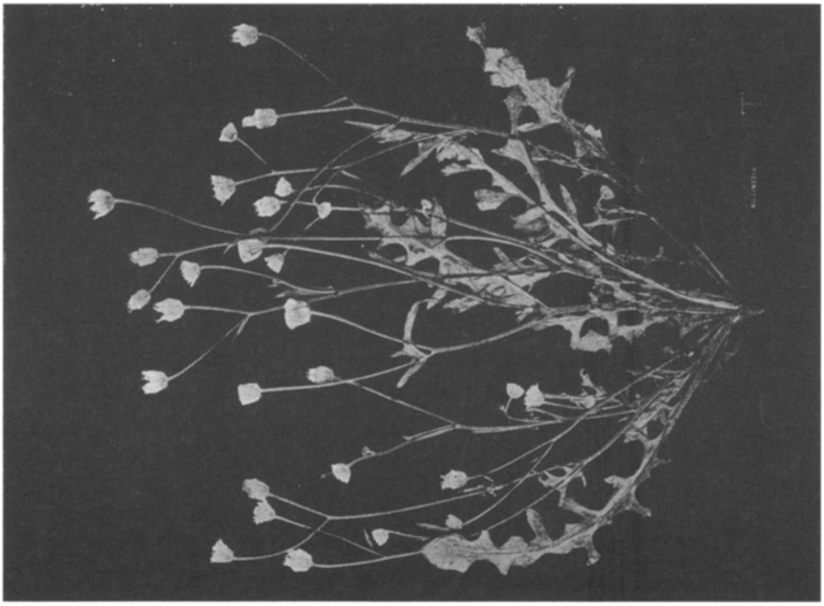

Fig. 7. *Crepis Thomsonii* (38.3208-5).

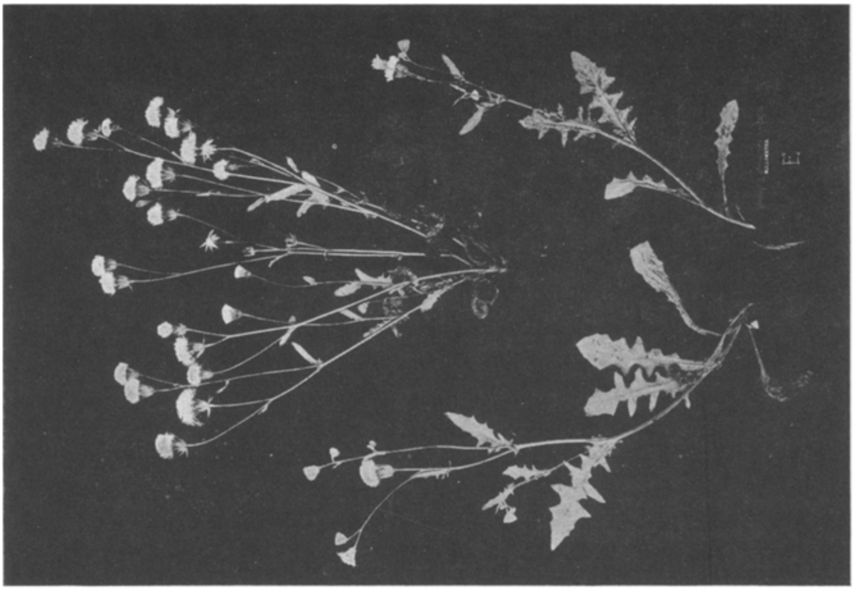

Fig. 8. *Crepis eritreënsis*; below, B32.3005a-4, grown in greenhouse; above, PA32.3005c-5, grown in open.

(3) Fr. The *foetida rhoeadifolia* strain used in this study has been shown to have certain characters in common with *commutata*. It approaches *commutata* also in its low self-compatibility. In certain other characters, however, it resembles *typica* and *glandulosa*, especially the latter. It is usually very robust,

with a tall central axis; the heads are large and the style-branches long. It differs from all the other *foetida* strains in having beakless outer achenes. In some other strains of *rhoeadifolia,* however, the outer achenes have a short, coarse beak. Certain strains of *rhoeadifolia* are apparently somewhat self-compatible, but the strain used in this study was self-incompatible.

(4) Fvi and Fvf. The remaining two *foetida* strains, *interrupta* and *fallax,* are also intermediate. Fvi is intermediate between *typica* and *rhoeadifolia* in the degree of coarseness of the glandless setae on the involucre, in length of style-branches, and length of the outer achenes; also the ratio of length of inner to outer involucral bracts varies between the modes of the putative parents. Whereas Fvi has no gland-hairs on the stem and, in head size, flower-light relation, and self-incompatibility it resembles *rhoeadifolia,* yet it also has the entire leaf-lobes, yellow style-branches the dark brown, shortly beaked achenes of *typica.*

Fvf is intermediate between *typica* and *commutata* in length of pappus, while the bract ratio varies as in *interrupta.* Fvf is like *typica* in the complete absence of paleae; the leaf shape is more nearly as in *typica*; and in shape and pubescence of the involucre it more nearly resembles *typica.* The habit of the plant, though variable, is more as in *commutata*; there are no glands on the stem; and in size of involucre, color and shape of the outer achenes, head size, and flower-light relation it resembles *commutata.* Also Fvf is highly self-incompatible.

The classification of these 2 intermediate forms is necessarily arbitrary. The authors find it convenient to place them in subsp. *vulgaris.*

The Chromosomes

All the strains have 5 pairs of chromosomes, and the haploid sets of the three species have been illustrated (Babcock and Cameron, 1934, p. 316). The 5 chromosome types are so closely similar in all three species that it is hardly worth while to go into detail concerning them in the present paper. The junior author made a few measurements of armlength of all the chromosomes in E, Fcl, and Fvg. Differences were found in the range of values obtained for the 3 strains, but these differences were not sufficient to insure discrimination between the chromosomes in the hybrids. The chromosomes of *eritreënsis* appear to be the longest, those of *foetida commutata* the shortest, while those of *foetida vulgaris* are intermediate. These observations agree with the published illustrations (Babcock and Cameron, loc. cit.). In one of the strains (Fvi) the "D" chromosomes bear larger satellites than those found in any other strains. Since this is the only accession of this strain that has been studied cytologically, it is not known whether this cytological peculiarity is constant in nature. There is no evidence that polyploidy or heteroploidy exists in naturally occurring forms of the three species under investigation.

Crossability

All possible hybridizations of the 9 strains were attempted. Some crosses which were made only once and were unsuccessful were repeated the following year and F_1 hybrids were obtained. It was not possible to repeat all the unsuccessful crosses, but of the 72 possible combinations (each strain being used both as female and male parent) 44 were obtained; and of the 36 possible combinations (regardless of which strain was used as female and which as male) 31 were successful. Only the following 5 combinations were unsuccessful in both directions: Fvt—E; Fvt—Fvf; Fvg—Fvi; Fvg—T; and Fvi—Fct. Of these crosses only Fvt × Fvf and the reciprocal were repeated the second year and these were again unsuccessful. Since E, T, Fvt, and Fvg are all self-compatible, castration of the individual florets was necessary and this definitely limited the number of florets that could be crossed. In view of the large proportion of successful crosses actually obtained, it seems likely that all 5 of these hybrid combinations could be made with a sufficient number of attempts; and even if some of these particular strains could not be crossed, it is not unlikely that different strains of the species and subspecies represented in these failures would cross successfully.

The nine strains were either very self-compatible or entirely self-incompatible when a plant was placed under a cage. The procedure in using the self-incompatible strains (Fr, Fvi, Fct, Fcl) as female parent was to omit castration and merely wash off the pollen with a jet of water. It was found that Fvf was also self-incompatible under cages, but this was not known until the crosses on it had been made by castration.

Without further attempts to obtain the 5 combinations which failed, it can not be said that there are certainly any differences in crossability among the 9 strains; consequently no inferences can be made from the data on crossability concerning degree of relationship. The list of hybrids and number of F_1 plants grown are given in columns 1 and 2 of Table 2.

Hybrid Fertility

In Table 2, column 3, the comparative fertility of the F_1 hybrids is recorded. This was estimated from the number of achenes produced by selfing those hybrids which were self-compatible and interpollinating sister plants when they were self-incompatible. The evidence for lack of fertility or low fertility in some of the hybrids can not be considered as significant, firstly because covering the flowers with bags or even enclosing the plants with cages in the greenhouse often prevents normal seed setting, and secondly because a too strong fumigation of the greenhouse with sulfur fumes had injurious effects on some of the hybrids before they had produced seed and this may have been responsible for their low fertility. But the fact that 16 of the 36 possible strain combinations produced highly fertile hybrids must be significant. The distribution of these highly fertile combinations among the 9 strains is shown in Fig. 9. From this representation it is evident that the hybrid congruity, as indicated by fertility in F_1 is as high in crosses between either *Thomsonii* or *eritreënsis* and several of the *foetida* strains as between the *foetida* strains themselves.

Germination of the F_2 seeds ranged from less than 50 per cent. to 100 per cent. and the seed from most of the highly fertile hybrids gave better than 50 per cent. germination. When germination of the F_2 seeds was high only a portion

Table 2

List of successful crosses with number of hybrids grown in F_1 and F_2. (Column 3 gives the degree of fertility of the F_1 hybrids, as estimated from the number of achenes produced by selfing plants that were self-compatible or interpollinating sibs when self-incompatible. But low fertility in this case is not necessarily significant — see text.)

Hybrid	No. of F_1 plants	F_1 fertility under bag	F_2 achenes placed on agar	F_2 achenes transferred to pots	No. of mature F_2 plants
Fvt × Fvg	1	very high	100 +	50	47
Fvt × Fvi	3	high	100 +	98[1]	91
Fvt × Fr	1	self-sterile			
Fvt × Fcl	5	low	100 +	58[1]	48
Fvg × Fcl	2	nil			
Fvi × Fvt	2	very low	1	1	1
Fvi × Fvf	10	high	100 +	67[1]	66
Fvi × Fr	14	low	100 +	34[1]	33
Fvi × Fcl	10	high	100 +	77[1]	64
Fvf × Fvi	10	high	100 +	50	43
Fvf × Fvg	2	nil			
Fvf × Fr	3	nil			
Fvf × Fct	5	nil			
Fvf × Fcl	5	nil			
Fr × Fvt	5	low	19	19[1]	12
Fr × Fvg	5	low	not sown		
Fr × Fvi	21	high	100 +	62[1]	62
Fr × Fvf	5	nil			
Fr × Fct	19	nil			
Fr × Fcl	8	high	100 +	100	94
Fct × Fvt	5	nil			
Fct × Fvg	5	low	not sown		
Fct × Fvf	5	nil			
Fct × Fr	1	self-sterile			
Fcl × Fvt	19	low	15	12[1]	10
Fcl × Fvg	16	high	100 +	50	46
Fcl × Fvi	27	high	100 +	78[1]	60
Fcl × Fvf	24	high	100 +	125	123
Fcl × Fr	19	high	100 +	50	42
Fcl × Fct	16	very high	100 +	50	50
Fcl × T	2	nil			
T × Fvt	2	low	22	15[1]	13
T × Fvi	2	high	100 +	55[1]	52
T × Fvf	2	high	100 +	46[1]	32
T × Fr	4	nil			
T × Fct	4	high	100 +	58[1]	57
T × E	2	very high	100 +	51	50
E × Fvg	5	very low	9	8[1]	6
E × Fvi	3	high	100 +	64[1]	57
E × Fvf	4	high	100 +	40[1]	38
E × Fr	1	very low	8	7[1]	3
E × Fct	10	high	100 +	52[1]	49
E × Fcl	3	high	100 +	64[1]	48
E × T	4	very high	100 +	50	50

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[1] In these progenies all the achenes which germinated on agar were transferred to pots or flats.

of the germinating seeds were planted in pots or flats. The proportion of germinating F_2 seeds planted which grew into mature plants ranged from 70 to 100 per cent. No record was kept concerning the relative vigor of these F_2 plants, but the junior author observed that the great majority of them were apparently normal and at least fairly vigorous.

Both T and E are very self-compatible. The reciprocal hybrids were self-compatible and fully as fertile as the parents; and all the F_2 plants were also self-compatible. This fact seems especially noteworthy in view of the wide geographic separation of the two species. For it not only confirms the close relationship of the two species but also indicates that self-compatibility is a more primitive condition than self-incompatibility in this group of species, a concept which agrees with other evidence on phylogeny (p. 154). This is further supported by the fact that, of the *foetida* strains, the farthest removed geographically from E and T, namely Fvt and Fvg are also self-compatible. In the case of these 2 *foetida* strains, the F_1 and F_2 hybrids between them are as self-compatible as the parents themselves.

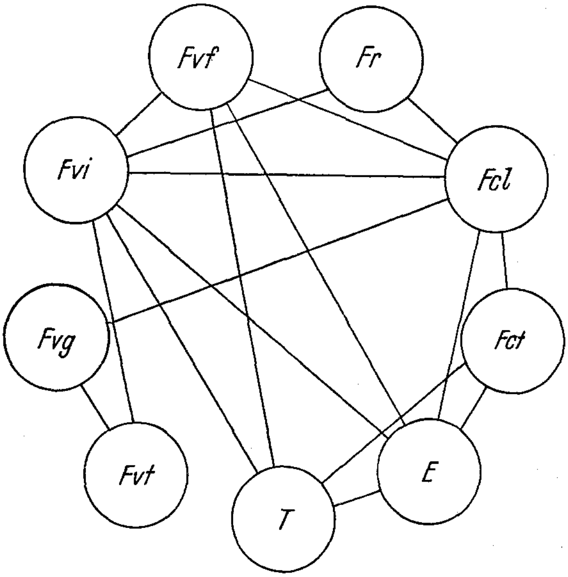

Fig. 9. Crosses which produced highly fertile F_1 hybrids.

Fct and Fcl are both self-incompatible but the plants produce seed when the flowers of different plants are rubbed together. This holds true also for the F_1 and F_2 hybrids, thus indicating that these two strains are also more closely related to each other than to any other strains.

From the crosses involving the three groups: (1) E and T; (2) the Fv strains; and (3) the Fc strains; it appears that, although hybrids between (1) and (2) give many less F_2 plants than do hybrids between (1) and (3), yet the hybrids between (3) and (2) are as fertile as the hybrids between (3) and (1). These facts point to a common origin of Fc with E, T, and Fv.

Meiosis in Parents and F_1

Pollen mother cells in diakinesis and early metaphase stages were examined in two of the 9 strains, E and Fct, in both of which 5 bivalents were seen regularly. The former strain is highly self-compatible. whereas the latter is self-incompatible, and seeds are obtained only by rubbing together the heads of two different plants. Similar material was examined in certain plants in all the hybrid populations grown the first year. In every case associations of 5 bivalents were the general rule. The only exception was that 4 bivalents and 2 univalents were seen in occasional isolated cells. Apparently this was due to precocious separation of a bivalent, since the other cells showed 5 bivalents consistently. No observations were made on chiasma frequency in these hybrids. However, it has been reported by JENKINS (1938, and oral communication) that many *Crepis* species are characterized by a low number of chiasmata in spite of the large size of the chromosomes. "At late diakinesis there are usually one, sometimes 2 chiasmata, and rarely 3." In so far as this criterion may be of value, it indicates that these species are very closely related.

There is no evidence of chromatin rearrangements in these species. The same was found to be true in the group of closely related species (*Crepis divaricata, C. Noronhaea, C. canariensis,* and *C. vesicaria*) studied by JENKINS (op.cit.). As was pointed out by JENKINS, it may therefore be assumed that the genes have a similar arrangement in the several species in each of these two groups; and this evidence supports the assumption that similar chromosome morphology in closely related *Crepis* species indicates structural similarity of the chromosomes in those species. Hence the comparison of karyotypes is of value in determining genetic relationship in this genus.

The genetic nature of self-incompatibility

That genetic factors, conditioning self-compatibility and self-incompatibility, exist in these species is strongly indicated by the data on F_1 and F_2 progenies from crosses between the strains used.' It is realized that the available data are very inadequate as a basis for generalization, especially on such a complicated problem; but they appear to be of unusual interest. It must be kept in mind, however, that the strains used were not pure lines (nor inbred lines in case of the self-incompatible strains); and that in each of 3 reciprocal crosses different sibs of one strain were used. Also in deriving 3 of the F_2 families, it was necessary, on account of the small numbers of plants and self-incompatibility, to interpollinate plants of two different F_1 families from the same cross. However, in two of these cases the strain represented by the two different F_1 plants was self-compatible and very uniform. In spite of all these uncertainties, it seems worth while to present the data, since they seem to indicate another type of inheritance of self-incompatibility in plants. In Table 3 are reported the results of 32 crosses involving all 9 strains. In this table C indicates self-compatible, N, self-incompatible. These abbreviations will be used in the following discussion.

Because of the unique character of the results, a brief discussion of the methods of obtaining the data is in order. The F_1 data, at least, may be considered dependable, since persistent efforts were made to obtain selfed seeds. Each F_1 plant that failed to produce seeds under bag was enclosed in a cage in order to give it good ventilation while excluding insects. If it continued to produce no seed under cage, it was recorded as N, and sibs were interpollinated by rubbing heads in order to obtain F_2 seeds. It will be seen (Table 3) that in 15 of the 16 crosses, C × N and N × C, the F_1 was N. This was a wholly unexpected result since, in the recent work on self-incompatibility, such crosses always produced at least some self-compatible plants in F_1. The possibility that this

Table 3

Inheritance of self-compatibility and self-incompatibility in F_1 and F_2 (C indicates self-compatible; N indicates self-incompatible)

Hybrid	Parents	F_1	F_2
Fvt × Fvg	C × C	1 C	47 C
Fvt × Fvi	C × N	3 N	84 N : 7 C
Fvt × Fr	C × N	1 N	no F_2
Fvt × Fcl	C × N	5 N	47 N : 1 C
Fvi × Fvf	N × N	9 N	64 N : 2 C
Fvi × Fr	N × N	12 N	33 N
Fvi × Fcl	N × N	8 N	64 N
Fvf × Fvi	N × N	9 N	36 N : 1 C
Fr × Fvt	N × C	3 N	9 N : 3 C
Fr × Fvi	N × N	7 N	63 N
Fr × Fct	N × N	7 N	no F_2
Fr × Fcl	N × N	7 N	92 N : 2 C
Fcl × Fvt	N × C	5 N	9 N : 1 C
Fcl × Fvg	N × C	7 N	41 N : 5 C
Fcl × Fvi	N × N	8 N	60 N
Fcl × Fvf	N × N	12 N	122 N
Fcl × Fr	N × N	12 N	41 N
Fcl × Fct	N × N	8 N	50 N
Fcl × T	N × C	2 N	no F_2
T × Fvt	C × C	2 C	13 C
T × Fvi	C × N	2 N	42 N : 1 C
T × Fvf	C × N	2 N	18 N : 11 C
T × Fr	C × N	4 N	no F_2
T × Fct	C × N	4 N	54 N : 3 C
T × E	C × C	2 C	50 C
E × Fvg	C × C	5 N!	1 N : 5 C
E × Fvi	C × N	3 N	53 N : 3 C
E × Fvf	C × N	4 N	21 N : 17 C
E × Fr	C × N	1 N[1]	3 N
E × Fct	C × N	10 N	46 N : 34 C
E × Fcl	C × N	3 C!	29 N : 20 C
E × T	C × C	4 C	50 C

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[1] This plant produced three achenes which were viable.

unexpected result was due to the accidental overdose of sulfur fumes, mentioned above, is obviated by the fact that over half of these 15 F_1 hybrids had been tested before the sulfuring occurred. In the F_2 generation the plants were much more numerous and, since they were grown in flats, they could not be covered with cages. Each F_2 plant was tested by covering 1 of the earliest heads with folded tissue paper held in place with a pin. If no seeds were produced in the first test, often but not always a second head was tested; and, in every case, when the first head gave no seed the second head was also sterile. Although these tests were too limited to insure an accurate measure of each plant's behavior, yet the records of self-compatibility are certainly dependable. Furthermore, the results in F_2 are mostly consistent with the F_1 results; also they are mostly consistent with a single hypothesis as to the nature of the genetic factors conditioning self-incompatibility. It seems worth while, therefore, to consider them in some detail. For convenience in comparison of the results of strain crosses, the original data are rearranged below according to type of cross, with numbers in italics representing observed numbers of plants. In each segregating population the observed numbers are followed by the assumed type of Mendelian segregation in parentheses, the calculated numbers, the strains represented in the cross, and the population and plant numbers of the parents used in the cross.

C × C

1 F_1 family *5* all N
1 F_2 family segregated
1 N : *5* C (see text) (E × Fvg) 3005(20)-4, (11)-3 × 2850-1

4 F_1 families *9* all C
4 F_2 families *160* all C
47 (Fct × Fvg) 1812-1 × 2850-2 *50* (T × E) 3208-3 × 3005(11)-3
13 (T × Fvt) 3208-6 × 1812-4 *50* (E × T) 3005(11)-4 × 3208-6

N × N

11 F_1 families *99* all N (1 gave no F_2)
7 F_2 families *433* all N
33 (Fvi × Fr) 2047-3 × 2318-6 *122* (Fcl × Fvf) 2969-1 × 3169-4
63 (Fr × Fvi) 2318-6 × 2047-3 *41* (Fcl × Fr) 2969-1 × 2318-6
64 (Fvi × Fcl) 2047-3 × 2969-1 *50* (Fcl × Fct) 2969-1 × 2864-7
60 (Fcl × Fvi) 2969-1 × 2047-3

3 F_2 families segregated
64 N : *2* C (63 : 1) 65 : 1 (Fvi × Fvf) 2047-3 × 3169(3)-2
36 N : *1* C (63 : 1) 36.4 : 0.6 (Fvf × Fvi) 3169-7 × 2047-3
92 N : *2* C (63 : 1) 92.5 : 1.5 (Fr × Fcl) 1916-3 × 2969-1

C × N

1 F_1 family *3* all C
1 F_2 family segregated
29 N : *20* C (38 : 26) 29.1 : 19.9 (E × Fcl) 3005(20)-6 × 2969-1

11 F_1 families *39* all N (1 gave no F_2)
(1 F_1 family *1* "N" produced in F_2 *3* N) (E × Fr) 3005(11)-6 × 2318(1)-1
9 F_2 families segregated
84 N: *7* C (15 : 1) 85.3 : 5.7 (Fvt × Fvi) 1812-3 × 2047-3
47 N: *1* C (63 : 1) 47.3 : 0.7 (Fvt × Fcl) 1812-3 × 2969-1
42 N: *1* C (63 : 1) 42.3 : 0.7 (T × Fvi) 3208-3 × 2047-2
54 N: *3* C (15 : 1) 53.4 : 3.6 (T × Fct) 3208-8 × 2864-7
18 N : *11* C (38 : 26) 17.2 : 11.8 (T × Fvf) 3208-8 × 3169-4, (3)-2
53 N: *3* C (15 : 1) 52.5 : 3.5 (E × Fvi) 3005(11)-4, (20)-4 × 2047-3
21 N : *17* C (38 : 26) 22.6 : 15.4 (E × Fvf) 3005(11)-6 × 3169(3)-2
46 N : *34* C (38 : 26) 47.5 : 32.5 (E × Fct) 3005(20)-4 × 2864-7

N × C

4 F_1 families *17* all N (1 gave no F_2)
3 F_2 families segregated
41 N : *5* C (15 : 1) 43.1 : 2.9 (Fcl × Fvg) 2969-1 × 2850-2
9 N : *3* C (3 : 1) 9 : 3 (Fr × Fvt) 2318-6 × 1812-1
9 N : *1* C (15 : 1) 9.4 : 0.6 (Fcl × Fvt) 2969-1 × 1812-1

From the above representation it is clear that C × C crosses produce only C plants in F_1 and F_2, with one exception (E × Fvg) which will be considered later. Also N × N crosses produce only N plants in F_1 while F_2 may segregate or consist of only N plants. But in C × N and N × C crosses F_1 is always N, with 1 or 2 exceptions, and F_2 segregates in proportions of N and C plants which approximate 63 : 1, 15 : 1 or 3 : 1, except in four families which fit most closely to the modified trihybrid ratio, 38 : 26. (In most cases the observed numbers fit closely to the numbers calculated on the basis of the assumed ratio. Hence it was not considered worth while to calculate probability values for purposes of this wholly tentative discussion.)

Ignoring for the moment the above mentioned exceptions, including the 38 : 26 ratios, the most logical assumption is that self-incompatibility in *C. foetida* is conditioned by 1, 2, or 3 dominant genes. Then the C strains carry the recessive allelomorphs of these genes; whereas the N strains may have various combinations of the 3 dominant genes. The 38 : 26 ratios can be interpreted as due to the presence of a dominant gene in E and T which, in certain combinations with one or two of the dominant incompatibility genes, will cause self-compatibility[1]. There is actually some precedent for such an interpretation in the discovery by

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[1] A purely hypothetical scheme of gene relationship is suggested. If two dominant genes for self-incompatibility be represented by **U** and **V**, and a dominant gene for self-compatibility, by **A**; and if **A** is epistatic to **U** and/or **V** in all genotypes where the proportion of **A**'s to **U**'s and/or **V**'s is as 2 is to 3 or larger; then the following genotypes would develop into C plants: (2) **AAUuVV**; (2) **AAUUVv**; (4) **AAUuVv**; (1) **AAUUvv**; (2) **AAUuvv**; (4) **AaUuvv**; (1) **AAuuVV**; (2) **AAuuVv**; (4) **AauuVv**; (1) **AAuuvv**; (2) **Aauuvv**; (1) **aauuvv**. On this basis 26/64 of the F_2 plants from the cross **AAuuvv** × **aaUUVV** would be self-compatible.

Kakizaki (1930) of stimulating alleles in *Brassica.* However, this assumption is not supported by one cross (T × Fct) which gave a 15 : 1 ratio in F_2.

Regarding the other exceptions already noted: E × Fvg (C × C) gave 5 F_1 plants, all N, and in F_2 1 N : 5 C, a wholly anomalous ratio but of no significance due to the small numbers; E × Fcl (C × N) gave 3 F_1 plants, all C, and in F_2 29 N : 20 C which is almost exactly 38 : 26; E × Fr (C × N) gave 1 F_1 plant, which was recorded as "N", although it produced 3 achenes, and the 3 F_2 plants were N (probably a case of pseudo-fertility in the F_1 plant). It is noteworthy that the same E strain was one of the parents in all three of these exceptional crosses. Also, that of the 4 crosses giving 38 : 26 ratios in F_2 three had the same E strain as one parent. Obviously there is something peculiar about the genetic factors conditioning self-compatibility in *eritreënsis*; and there is a suggestion (T × Fvf) that a similar condition exists in *Thomsonii.* Furthermore, the reciprocal crosses (T × E and E × T) gave only C plants in F_1 and F_2. Thus it appears that these two species differ more from the *foetida* strains, in the genetic nature of their self-compatibility, than the *foetida* strains differ among themselves. This inference appeals to the authors as a valid additional reason for the recognition of *eritreënsis* and *Thomsonii* as species.

If the assumption which best explains the majority of the F_2 segregating families, i. e., that self-incompatibility is conditioned by 1, 2, or 3 dominant factors, can be verified by further research on *Crepis,* it will reveal just the opposite genetic relationship between self-compatibility and self-incompatibility, from that which exists in most of the plant species thus far investigated. Correns (1912) reported on experiments with *Cardamine pratensis* which led him to the hypothesis that self-incompatibility in this species depends on two dominant allelomorphic factors which are inherited according to Mendelian principles. East (1929) points out several difficulties with this hypothesis and suggests that Correns was probably dealing with material in which pollen-tube growth was easily shifted from sterility to fertility by conditions. But Correns (1913, pp. 397—398) reported evidence that the normally germinating pollen failed to penetrate the stigma in self-fertilized plants of *Cardamine pratensis.*

Brieger (1930) adopts the two types of self-sterility first proposed by Correns (1928): the Cruciferentypus, exemplified by *Cardamine pratensis* with two dominant allelomorphs for self-incompatibility (Correns, 1912); and the Personatentypus, in which there is a dominant factor for self-compatibility and recessive alleles for self-incompatibility, as demonstrated in *Nicotiana* (East and Park, 1917; East and Mangelsdorf, 1925); *Verbascum* (Sirks, 1917, 1926); *Antirrhinum* (Baur, 1919; East, 1926; Filzer, 1926); and *Veronica* (Filzer, 1926). In *Crepis foetida* self-incompatibility appears to be of the Cruciferentypus, since the data indicate that it is conditioned by dominant factors. But apparently there is an important difference between *Cardamine pratensis* and *Crepis foetida,* since in the latter these factors are not allelomorphic but duplicate or triplicate, if the data presented above are dependable.

The first published research on self-incompatibility in a genus of the Compositae led to no definite conclusion regarding inheritance. Stout (1916), working with *Cichorium intybus,* observed so much variability in the results of his crosses that he concluded that self-incompatibility is a highly variable phenomenon. But East (1926) maintains that Stout failed to remove as many variables as possible and was therefore unable to obtain consistent evidence. East (1929) also suggests that Stout was working with factors which were generally close to the borderline between compatibility and incompatibility. Babcock and Hall (1924, pp. 60—62) in a genetico-taxonomic study of *Hemizonia congesta,* a self-incompatible species, reported evidence which indicates that genetic factors for intersterility between certain individual plants exist in this species and which demonstrates the existence of intrasterile classes, comparable to classes known to occur in *Nicotiana*, etc. *Hemizonia congesta*, therefore, appears to belong to the Personatentypus with respect to intrasterile classes. The evidence from *Crepis foetida* certainly supports the generalization that self-incompatibility has a genetic basis. The available evidence, however, indicates that in this species the phenomenon is of the Cruciferentypus.

As for the physiological concepts involved in attempting to interpret self-incompatibility in *Crepis foetida,* very little can be said at present except to mention several alternative types of failure in the normal fertilization process. (1) Differential growth rates of self and foreign pollen tubes may be the explanation, although the total time required for penetration of the pollen tube to the embryo-sac is probably extremely short. Gerassimova (1933) reports that in *Crepis capillaris* the pollen tubes reach the embryo sac in from 35 to 75 minutes as extremes, and the majority in from 50 to 60 minutes. Poddubnaja-Arnoldi and Dianowa (1934) report that in *Taraxacum kok-saghys* fertilization is completed in from 15 to 20 minutes after pollination. If the time required in *C. foetida* is also very short, it is conceivable that any pollen tubes which penetrate into the style would succeed in reaching embryo-sacs regardless of their genotypes. (2) Failure of the normally germinating pollen to penetrate through the stigmatic surface was observed by Correns (1912) and was considered the "cause" of self-incompatibility in *Cardamine.* Although East (1929) considers differential pollen-tube growth to be the more reasonable explanation, yet this has not actually been demonstrated in *Cardamine.* It would not seem likely that failure of selfed pollen to penetrate the stigma is only an extreme manifestation of the same inhibiting effect as that which causes differential growth rate of the pollen tubes in the style. (3) Failure of the plant's own pollen to germinate on the stigma has been observed in various species (Brieger, 1930, pp. 31—35). But there is no evidence that this is a "cause" of self-incompatibility in any cases that have been analyzed genetically. (4) Failure of some of the gametes to unite in selfed F_1 hybrids from the interspecific cross, *Crepis capillaris* × *C. tectorum,* is reported by Gerassimova (1933). Selective fertilization occurs generally in hybrids between species with different chromosome numbers. But in hybrids, either interspecific or intraspecific, which are characterized by normal meiotic behavior, selective fertilization would not be expected to cause self-incompatibility. In fact it has been shown by East and Park (1917) that "self-sterility behaves as a sporophytic character and is not the result of incompatibility between gametes". The first 3 possibilities, however, should all be investigated in *C. foetida.*

It was with reluctance that the authors decided to publish the above report on self-incompatibility. But unavoidable circumstances made it impossible to continue the investigation and it is uncertain when it can be resumed. It is planned to purify the strains by inbreeding with the expectation that it will be possible to attack the problem later. Therefore, this preliminary statement is made as a matter of record.

Inheritance of "leaf-shape"

The general form of the caudical leaves in all the strains is oblanceolate, but they differ in degree of dissection and, when lobed, in the shape of the lobes. It is to these differences in degree of dissection and shape of the lobes that "leaf-shape" refers. The range of variation in dissection among the various strains is from shallowly dentate to almost bipinnately lobed; and the lobes vary in shape and degree of dentation. These facts alone suggest that a considerable number of genetic factors may be involved in these variations.

One cross, however, gave results which show a monogenic relation between the type of early caudical leaves in two subspecies of *foetida.* In Fvi the early caudical leaves (about 6 cm. long) are narrowly oblanceolate and have definitely rounded lateral lobes; whereas in Fcl the caudical leaves at the same stage are relatively broader, more nearly spatulate, and merely dentate or beginning to develop triangular lateral lobes. From the cross Fvi ♀ × Fcl ♂ the Fvi type of early caudical leaves was fully dominant in F_1 and in F_2 there was sharp segregation into 3 Fvi : 1 Fcl as is shown by the following data:

Cross	F_1	F_2	F_2 expected
Fvi × Fcl	9 Fvi	58 Fvi : 19 Fcl	57.75 : 19.25
Fcl × Fvi	16 Fvi	38 Fvi : 15 Fcl	39.75 : 13.25

The sharpness of the segregation is clearly illustrated by Fig. 10 which shows part of one of these F_2 families. This result is in striking contrast with the observations on form of the later caudical leaves in F_1 and F_2 hybrids between the strains.

In respect to form of the later caudical leaves, most of the F_1 plants were

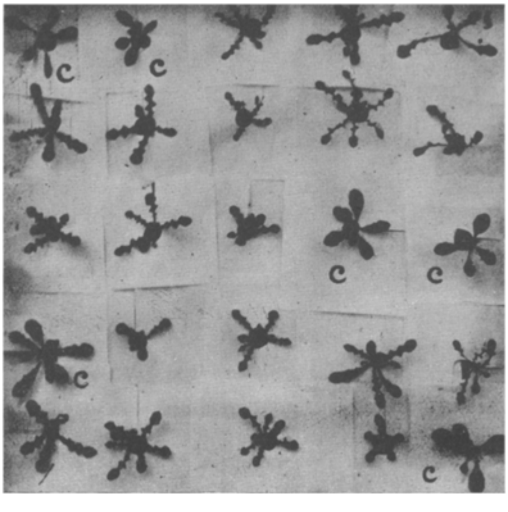

Fig. 10. Part of an F_2 family from the cross Fvi × Fcl showing 3 Fvi : 1 Fcl segregation for type of early caudical leaves (c indicates Fcl).

either intermediate between the parental types or closely similar to the male parent. Data on shape of the later caudical leaves were taken from 43 F_1 families, among which all 9 strains were involved. In 20 of the F_1 families the later caudical leaves were intermediate between the leaf-types of the parent plants; in 4 of the F_1 families some of the plants were intermediate and some resembled the male parent; in the other 19 F_1 families the later caudical leaves were almost identical with those of the male parent, with the exception of one plant. In the first cross reported in Table 4 (Fvt × Fcl) there were 5 F_1 plants; 4 were like the male parent (Fcl) whereas 1 closely resembled the female parent and there was no doubt about its being a hybrid because it had paleae on the receptacle which must have come from the male parent. In just one other cross (Fct × Fvf, omitted in Table 4 because no F_2 data were obtained) 3 out of 5 F_1 plants were recorded as like the female parent, but it is not certain that they were hybrids.

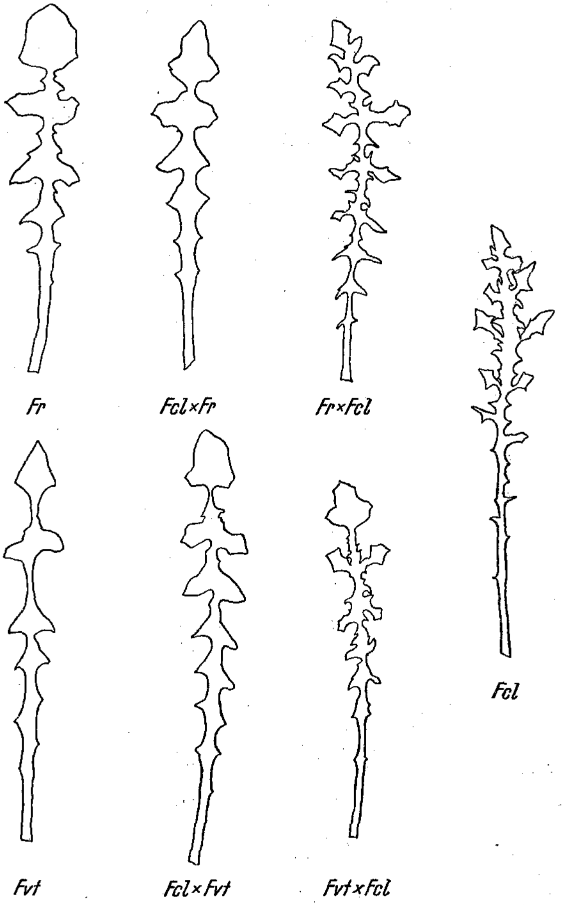

Fig. 11. Late caudical leaves from parent strains and their reciprocal hybrids showing close resemblance to the male parent in F_1. In each cross the female parent is given first.

Fig. 11 shows the parental and F_1 leaf types in two reciprocal crosses between *foetida* strains. This tendency of F_1 hybrids to resemble the male parent in leaf-shape has been noted before in *Crepis* hybrids (Jenkins, unpublished). How much significance may be attached to it is at present uncertain, owing to lack of knowledge concerning the genotypic nature of the plants crossed. In no case were pure lines available and there is little doubt that the individual plants in most of the parent strains were more or less heterozygous. Furthermore, in most of the reciprocal crosses obtained, either one or both strains were represented by different individuals in the two crosses. For these same reasons little is to be gained from a study of the F_2 families derived from these crosses. The

Table 4

Inheritance of form in late caudical leaves. (Strain symbols, Fcl, Fvi, etc., in F_1 and F_2 indicate close resemblance to the parental types; I indicates an intermediate condition. Only those crosses from which F_2 families were grown are reported.)

Crosses	F_1	F_2
Fvt × Fcl	Fcl[1]	11 Fcl : 4 I : 4 Fvt[2]
Fvi × Fvt	I	1 Fvi
Fr × Fvt	I	12 Fr
Fr × Fvi	Fvi	3 Fvi : 2 I : 7 Fr[2]
Fr × Fcl	Fcl	49 Fr : 17 I : 34 Fcl
Fcl × Fvt	Fvt	7 Fvt : 5 I
Fcl × Fvg	I	18 Fcl : 19 I : 13 Fvg
Fcl × Fr	Fr	15 Fcl : 8 I : 27 Fr
T × Fvt	Fvt	13 Fvt
T × Fvi	Fvi	14 Fvi : 2 I
T × Fct	Fct	17 Fct : 31 I : 9 T
T × E	I	38 T : 13 E
E × Fvg	Fvg	1 E : 3 I : 2 Fvg
E × Fvi	Fvi	12 E : 20 I : 5 Fvi
E × Fvf	Fvf	4 E : 5 I : 30 Fvf
E × Fr	Fr	2 E : 1 Fr
E × Fct	Fct	1 E : 11 I : 40 Fct
E × Fcl	I	40 E : 3 I : 6 Fcl
E × T	I	24 E : 26 T

data are reported in Table 4. It is worthy of note that, in nearly all the crosses between different *foetida* strains or between a *foetida* strain and either E or T, there are some intermediate plants in F_2 with respect to character of the lobes on later caudical leaves. In only 2 or 3 families, however, do the observed numbers approach a 1 : 2 : 1 segregation. Apparently the numbers in the F_2 classes have no relation to the dominant or intermediate condition in F_1. It certainly appears that these differences in leaf-shape are conditioned by more than one gene.

Inheritance of stem length and associated branching habit

The strains in which the plant normally has a long central axis and erect habit are Fvt, Fvg, and Fr. Those characterized by a short central axis and a spreading habit are Fvi, Fvf, Fct, Fcl, and T. The stem length in E is intermediate. These typical habits of growth are very definite in healthy potted plants.

In the F_1 of crosses between strains with long and short stems, the short stem (and consequent spreading habit) was dominant, except in Fcl × Fvt, Fcl × Fvg, and T × Fvt, in which the habit was intermediate. In crosses be-

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[1] One of the 5 F_1 hybrids resembled Fvt.

[2] Leaf-shape was not recorded for all the plants in these 2 families.

tween E, with intermediate stem length, and the strains with short stems the spreading habit is again dominant except in T × E and E × T, in which the intermediate type of E is dominant and in F_2 all the plants were intermediate. The F_1 between E (intermediate) and Fvg (tall) was tall.

The F_2 families showed all degrees of stem length and habit between the two parents. An attempt was made to classify the F_2 plants as being more like one parent, more like the other, or intermediate. Even though the low, spreading habit was dominant in F_1, there were more tall than low plants in the F_2 populations, except in the case of Fr × Fvi. An indication of multiple, possibly cumulative, factors is seen in the fact that F_2 families derived from F_1 spreading plants contain a larger proportion of spreading plants than F_2 families grown from intermediate F_1 families (Table 5). Further evidence of multiple factors comes from crosses in which the parents have the same type of branching habit but which produce F_2 families containing plants of the opposite habit type. Especially striking is the F_2 from Fcl × Fvf, both parents being short and spreading. In this F_2 family only one very spreading plant was found, whereas 113 tall and 8 intermediate plants occurred. These plants were grown in flats

Table 5

Inheritance of stem length. (L indicates long central axis and erect plant; S indicates short central axis and spreading plant; I, intermediate.)

Crosses	Parental types	F_1	F_2
Fvt × Fvi	L × S	S	37 S: 18 I: 37 L
Fvt × Fcl	L × S	S	19 S: 7 I: 22 L
Fvi × Fvf	S × S	S	64 S: 1 I: 1 L
Fr × Fvt	L × L	S	3 S: 2 I: 7 L
Fr × Fvi	L × S	S	44 S: 12 I: 6 L
Fr × Fcl	L × S	S	15 S: 12 I: 67 L
Fcl × Fvt	S × L	I	9 S: 10 L
Fcl × Fvi	S × S	S	5 S: 9 L
Fcl × Fvg	S × L	I	2 S: 5 I: 39 L
Fcl × Fvf	S × S	S	1 S: 8 I: 113 L
Fcl × Fr	S × L	S	12 S: 11 I: 19 L
T × Fvt	S × L	I	1 S: 1 I: 11 L
T × Fvi	S × S	S	14 S: 2 I: 15 L
T × Fvf	S × S	S	17 S: 13 L
T × E	S × I	I	50 I
E × Fvg	I × L	L	3 I: 3 L
E × Fvi	I × S	S	3 S: 26 I: 3 L
E × Fvf	I × S	S	31 S: 7 I
E × Fct	I × S	S	37 S: 12 I
E × Fcl	I × S	S	6 S: 42 I: 1 L
E × Fr	I × L	S	2 S: 1 L
E × T	I × S	I	50 I

close together. But this could not have caused this result since other F_2 families, grown under similar conditions, contained erect and spreading plants growing side by side.

Inheritance of ligule color

The ligules are chrome yellow in all the strains except T and E. In E they are lemon yellow and in T, cream. In all crosses the F_1 resembled the darker colored parent. In hybrids between lemon and chrome the F_1 was chrome and in F_2 there were approximately 15 yellow : 1 cream (Table 6). Here yellow is used to designate any deeper yellow tint, including lemon. It was impossible to distinguish with certainty in F_2 between the various shades of yellow other than cream. However, since about 1/16 of the F_2 plants had cream ligules, the chrome strains must differ from E (lemon) with respect to 2 pairs of genes. Therefore, the chrome strains may be assigned the genotype **XXyy**, the gene **X** conditioning chrome ligules; E has the genotype **xxYY**, the gene **Y** conditioning lemon ligules; and T, with cream ligules, would then be **xxyy**.

Crosses between T and E produced the 3 : 1 ratio in F_2 as would be expected (Table 6). But it will be noted that the plants with darker colored ligules were classified as yellow for the same reason as before. Furthermore, in this cross (and other crosses involving T) there appeared among the F_2 plants with yellow

Table 6

Inheritance of ligule color (chr indicates chrome; lem, lemon; cre, cream; yel, yellow when chrome, lemon, or other shades of yellow were not distinguished; for genic relations see text.)

Crosses	Parental colors	Parental genotypes	F_2 observed	F_2 calculated
E × T	lem × cre	xxYY × xxyy	40 yel : 10 cre	37.5 : 12.5
T × E	cre × lem	xxyy × xxYY	38 yel : 13 cre	38.3 : 12.7
E × Fvi	lem × chr	xxYY × XXyy	48 yel : 8 cre	52.5 : 3.5
E × Fvf	,, × ,,	,, × ,,	36 yel : 2 cre	35.6 : 2.4
E × Fct	,, × ,,	,, × ,,	44 yel : 5 cre	45.9 : 3.1
E × Fcl	,, × ,,	,, × ,,	45 yel : 4 cre	45.9 : 3.1
T × Fct	cre × chr	xxzzMM × XXZZMM	53 yel : 4 cre	50.7 : 6.3
T × Fvf	,, × ,,	,, × ,,	24 yel : 5 cre	25.7 : 3.3
T × Fvi	,, × ,,	,, × ,,	37 yel : 1 cre	33.6 : 5.4
T × Fvt	,, × ,,	,, × ,,	13 yel : 0 cre	11.6 : 1.4

Backcrosses	Colors	Genotypes	Observed	Calculated
(Fcl × T) × Fcl	chr × chr	XxZzMm × XXZZmm	16 chr	all chr or yel
(Fcl × T) × T	chr × cre	XxZzMm × xxzzMM	3 chr : 1 cre	3 cre (or yel) : 1 cre
Fcl × (Fcl × T)	chr × chr	XXZZmm × XxZzMm	30 chr	all chr or yel
(T × Fr) × T	chr × cre	XxZzMm × xxzzMM	1 chr : 2 cre	2.2 chr (or yel) : 0.8 cre

ligules some which had a definite tinge of orange in the ligules. The numbers were too small to determine significant ratios, but apparently T contains a gene which modifies yellow to orange when in certain combinations with other genes. This aids somewhat in our analysis of the remaining data.

Crosses between T (xxyy) and 4 of the chrome strains (**XXyy**) did not produce the 3 : 1 ratio in F_2. The recessive class was always too small. Even though the total number in some F_2 families was very small, still the recessive class was too low for a 3 : 1 distribution. Apparently there are modifying genes which cause some of the **xxyy** plants to be yellow. If it be assumed that two other genes, **Z** and **M**, have a complementary relation, independent of **X**, for the production of yellow pigmentation of a deeper shade than cream, and if the chrome strains are **XXyyZZmm** and T is **xxyyzzMM**, then an F_2 population derived from crossing plants of these genotypes would consist of 57 yellow (including all shades darker than cream) : 7 cream, because 9/16 of the **xxyy** plants would be yellow. The observed numbers in F_2 from the four crosses of T with chrome strains closely approximate these proportions. It may be that the gene **M**, postulated above as contributed by *Thomsonii*, is the gene which conditions orange ligules in certain genotypic combinations. Among the 78 "yellow" plants in the combined F_2 from E × T and T × E, there were 29 with the orange tinge in the ligules. This proportion of orange-liguled plants would be approximated if the genotypes **YYMM**, **YyMM**, and **YYMm** conditioned orange color. Although the data are too meager to warrant any definite hypothesis, the available evidence shows that there are at least 3 or 4 gene differences affecting ligule color in these species. Furthermore, it is clear that T and E both differ genetically from F as to ligule color.

Inheritance of paleae on the receptacle

The only strains which are characterized by having paleae on the receptacle are Fct and Fcl. However, small palea-like structures were noted occasionally on plants of Fr but no study of their inheritance was made. This tendency of Fr to develop paleae on the receptacle may have some bearing on its origin and will be mentioned again.

In all crosses involving Fct or Fcl as one parent the F_1 plants had paleae which were nearly as numerous and long as in the parents. In F_2 the number and size of the paleae are very variable so that the only classification of F_2 plants attempted was as to presence or absence of paleae. Even so, in some cases the paleae may have been overlooked since they are occasionally greatly reduced in size and number. This fact may explain the deviations of observed from calculated numbers in the crosses T × Fct and E × Fct (see Table 7).

The F_2 families involving Fvt, Fvg, T, E, and one particular plant of Fr can all be interpreted in terms of the 15 : 1 ratio. This would indicate that in *foetida commutata* there are duplicate genes for paleae. These genes may be represented by **R** and **S**. Although there were no plants with paleae in the F_2 from T × Fct and E × Fct, yet these deviations from the 15 : 1 ratio would be expected to occur in from 5—7 per cent. of trials in a population consisting of only 49 plants (Table 7).

Table 7

Inheritance of paleae on the receptacle. (R and S represent duplicate genes for paleae; I, a dominant inhibitor of one duplicate gene but hypostatic to the other. In the observed F_2 ratios P indicates presence, and p absence of paleae. In all F_1 hybrids paleae were present.)

Crosses	Parental genotypes	F_2 observed	F_2 calculated
Fcl × Fvg	RRSS × rrss	45 P: 1 p	43.1: 2.9 (15: 1)
Fvt × Fcl	rrss × RRSS	46 P: 2 p	45 : 3 (15: 1)
T × Fct	„ × „	57 P: 0 p[1]	53.4: 3.6 (15: 1)
E × Fct	„ × „	49 P: 0 p[2]	45.9: 3.1 (15:1)
E × Fcl	„ × „	48 P: 1 p	45.9: 3.1 (15: 1)
Fr × Fcl	„ × „	90 P: 4 p	88.1: 5.9 (15: 1)
Fcl × Fr	RRSS × rrs's'	27 P: 14 p	30.7 : 10.3 (3 : 1)[3]
Fvi × Fcl	rrssII × RRSSii	51 P: 13 p	51 : 13 (51 : 13)
Fcl × Fvi	RRSSii × rrssII	51 P: 9 p	47.8 : 12.2 (51 : 13)
Fcl × Fvf	„ × „	100 P: 22 p	97.1 : 24.9 (51 : 13)

Backcrosses	Genotypes	Observed	Expected
(Fcl×T)×T	RrSs × rrss	3 P: 1 p	3: 1
(Fcl×Fvi)×Fvi	RrSsIi × rrssII	21 P: 21 p	21 : 21
Fvi×(Fcl×Fvi)	rrssII × RrSsIi	16 P: 28 p[2]	22 : 22

It will be noted that, whereas the F_2 from Fr × Fcl gives a normal ratio for independent duplicate genes, yet the F_2 of the reciprocal cross closely approximates a monohybrid ratio (Table 7). Two different Fr plants of the same strain were used in these crosses. The plant (32.2318-6), which was used in making the cross Fr × Fcl, was also used in the cross T × Fr. This latter cross produced a highly sterile F_1 but, by backcrossing to T, 3 plants were obtained which had small palea-like structures on the receptacle. It might be assumed that the gene s mutated to s' in the plant 32.2318-6, and that s' inhibits R but is recessive to S. Under these conditions a monohybrid F_2 ratio should be produced. This same s' might also have conditioned the small paleae found on the receptacle of the backcross plants in (T × Fr) × T, though the original Fr plant and the F_1 were not examined for this character. This evidence for the existence of genic variability in Fr with respect to the occurrence of paleae is of some theoretical interest in connection with the problem of the origin of Fr.

In the crosses of Fcl with Fvi and Fvf the observed numbers in F_2 approximate the ratio 51 with paleae : 13 without paleae (Table 7). In order to

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[1] This deviation has a probability of 5 per cent.

[2] This deviation has a probalility of 7 per cent.

[3] See text.

account for these results it is necessary to assume that the Fvi and Fvf plants carried a dominant gene (I) which inhibits one of the two genes, **R** and **S**, but not the other. The 3 F_2 families are in close agreement with this hypothesis. The one backcross family available shows a rather wide deviation but one that should occur in 7 per cent. of trials under conditions of chance alone. This indication of a gene inhibiting paleae in Fvi and Fvf is also of interest in connection with the origin of these strains and will be mentioned later.

Inheritance of certain other characters

Glandular hairs on the involucre. — The presence or absence of gland-hairs on the inner involucral bracts was observed in all the strains and a number of crosses. In Fvt, Fvg, Fvf, Fct, E, and T all the plants had gland-hairs on the inner bracts. In Fvi these gland-hairs were always absent whereas in Fr and Fcl they were sometimes present and sometimes absent in plants of the same population, and these differences were found to be inherited. The number of gland-hairs varies between and within the strains and these variations also are probably genetic in nature. But in the F_2 families only the presence or absence of gland-hairs was recorded. The data indicate that at least two pairs of genes are concerned with presence or absence of the gland-hairs, but the data are too meager to substantiate dihybrid ratios in many instances.

Position of young flower-heads, nodding vs. erect. — The young flower-heads before anthesis may be either nodding or erect in *C. foetida*; but it happens that Fcf was the only strain in which both of these characters occurred in the material used in this study. In both E and T as far as known, the plants always have nodding buds. The nodding position is dominant in F_1 and the F_2 families appear to segregate in monohybrid fashion. POOLE (1932) reported monohybrid inheritance for these characters in hybrids between *C. rubra* and *C. foetida*.

Color of style-branches. — The style-branches are yellow in all the strains except Fr in which some plants have the style-branches green and the green color varies from very dark to almost yellow. Evidently green is dominant over yellow and the colors are conditioned by one pair of genes; but apparently other genes modify the depth of the green color.

Red vs. yellow ligule-teeth. — Only *Thomsonii* and *eritreënsis* have red ligule-teeth on all the florets. In *foetida* the marginal florets are usually more or less reddish purple on the outer face and when this is intense the color may extend into the teeth. But, in *foetida*, when a young head is viewed from above after the marginal florets have opened out it will be seen that all the remaining florets have yellow ligule-teeth. In crosses between T or E and the 7 *foetida* strains all the F_1 plants had red ligule-teeth, and in 6 F_2 families there was a close approximation to the 3 : 1 ratio; but there were 4 F_2 families which showed extreme deviations from calculated expectations. These have not been satisfactorily explained and unfortunately could not be investigated further.

Monomorphic vs. dimorphic achenes. — In all the strains except E the achenes are of two shapes. The marginal achenes are shorter, thicker, and either unbeaked or shortly and coarsely beaked. The inner achenes are longer, more slender, and have a much longer and finer beak. E, with the inner and marginal achenes all alike, and T, with no beak on the thick marginal achenes, are the extreme types. In reciprocal crosses between E and T the F_1 plants were intermediate in their marginal achenes, and the F_2 families segregated very definitely in the 1 : 2 : 1 ratio. Thus it is clear that a single pair of genes conditions this very striking morphological difference between the two species.

Anthocyanin leaf spots. — Anthocyanin spots have been seen in some strains of Fr, Fct, and Fcl, and they are always present on the leaves of T. But such spots were absent from the leaves of E and from all the *foetida* strains used in these crosses. In crosses between T and 7 other strains all the F_1 plants had anthocyanin spots on the leaves. The F_2 families showed for the most part very good agreement with expectations for the monohybrid ratio. One exceptional F_2 family (from T × Fct) showed an extreme deviation which it was not possible to study further. In this case apparently more complicated genic relations were involved.

Review of the evidence on relationship

Comparative morphology. — *Crepis eritreënsis* and *C. Thomsonii* show more resemblance to each other in their leaves and flowers than to any of the *foetida* strains, but in their fruits they differ as much from each other as from *foetida*. In floral characters they show most resemblance to *C. foetida vulgaris typica* and, like it, their flower-heads close before midday and the plants are highly self-compatible. On this basis, *Thomsonii* and *eritreënsis* are closer to *foetida vulgaris typica* than to any other forms of *foetida*; and the resemblance is so marked that the hypothesis of a common origin for the 3 species appears fully warranted.

Cytology. — The karyotype is almost identical in every respect in the 3 homoploid species except for slight differences in sizes of the chromosomes and the presence of a larger satellite in one *foetida* strain. The pairing of the chromosomes at metaphase of the first meiotic divisions in pollen mother cells is almost perfectly regular in all the F_1 hybrids between these species. No chains, rings, or chromatin bridges were observed. This is taken to indicate a common basic genom and essentially the same arrangement of the genes in these species. Thus the cytological evidence is in harmony with the morphological evidence for a monophyletic origin of these species.

Crossability. — Only 5 of the 36 possible combinations, made in either direction, among the 9 strains used, failed to produce hybrids. Since 7 of the 9 strains are represented among these unsuccessful combinations, these failures are not considered as significant. In other words complete crossability among all 9 strains in all possible combinations is considered highly probable. This evidence, being positive, gives further support to the concept that the 9 strains have a close genetic relationship.

Hybrid fertility. — The fertility of the F_1 hybrids between the strains ranged from complete absence to "very high". The negative evidence found in a few hybrids with low or no fertility is not considered as significant since injury resulting from fumigation may have caused the sterility. Positive evidence of close relationship between all the strains is found in the fact that 16 of the 36 possible strain combinations produced highly fertile hybrids, that all 9 strains are represented among these highly fertile combinations, and that the seed produced by most of the highly fertile hybrids gave more than 50 per cent. germination. Furthermore, of the F_2 seeds which germinated and were planted, from 70 to 100 per cent. developed into mature plants.

On the basis of hybrid fertility alone, therefore, the 9 strains could be considered as constituting a single species. But when the various degrees of hybrid fertility are considered, together with the inheritance of self-compatibility and self-incompatibility, the 9 strains fall into 4 groups, namely E and T, Fvt and Fvg, Fct and Fcl, and the 3 remaining strains, Fvi, Fvf, and Fr. In the first 3 groups the intra-group hybrids are more highly fertile than any inter-group hybrids. However, when this evidence is coordinated with the evidence from morphology, cytology, geographic distribution, and the occurrence of hybrids in nature, the 9 strains fall naturally into 3 groups: *C. eritreënsis* (E); *C. Thomsonii* (T); and *C. foetida* (Fvt and Fvg; Fr; Fct and Fcl; while Fvi and Fvf are actually intermediate between Fv and either Fr or Fc).

Hybrid segregation. — Although the available data are very limited, some cogent generalizations are possible. Self-incompatibility appears to be conditioned by duplicate or triplicate dominant factors which are present in Fc, Fr, and in Fvi and Fvf. Such quantitative characters as length of stem and shape of leaves are evidently conditioned by multiple genes; and the differences with respect to these genes may be just as great between closely related strains as between more distantly related strains within the three species. Less complicated structural differences, such as the presence or absence of paleae, erect or nodding flower-buds, and presence or absence of glands on the involucre, are conditioned by 1, 2, or at most 3 pairs of genes in any of the strains. The same is true of such qualitative characters as color of the style-branches and color of the ligule-teeth, but in the case of ligule color it appears that *Thomsonii* differs from *foetida* in 2, 3, or possibly 4 genes. The regularity of the F_2 monohybrid, dihybrid, and trihybrid ratios is consistent with the meiotic regularity of the F_1 hybrids and indicates the absence of any elimination of gametes in F_1. There is sufficient evidence to show conclusively that the three species are very similar genetically, although there are important differences between them with respect to such characters as receptacular paleae and self-incompatibility.

Geographic distribution

Crepis eritreënsis and *C. Thomsonii* occupy relatively restricted areas, the former in Eritrea and the latter in northwest India and adjacent districts to the west. They are, therefore, completely isolated from each other and from *C. foetida* which occurs in southern Europe, Asia Minor, and eastward into the Caucasus, Transcaucasia, and western Persia. Furthermore, *C. Thomsonii* is not only isolated from *C. foetida* by a considerable gap between their respective distributional areas, but also by the occurrence of *C. Bureniana* in the intervening region. *C. Bureniana* is certainly related to *Thomsonii* and *foetida*, but since it has only 8 chromosomes, any natural hybrids between it and the other two species would probably be highly sterile. Between *foetida* and *eritreënsis* the gap between the areas of distribution is even greater than that between *foetida* and *Thomsonii*. *C. foetida* does not occur in southern Palestine and the Sinai Peninsula, and neither *foetida* nor *eritreënsis* has been reported from Arabia.

Within *C. foetida*, the present distribution of the subspecies and forms is important in explaining the development of this group of forms as it exists today (Fig. 12). Subsp. *vulgaris* fa. *typica* is the only form indigenous in southwest Europe, but it extends eastward through the Balkan region into Asia Minor and southward into northern Palestine. Fa. *glandulosa* occurs in Sicily and southern Italy, in southern Greece, and at several localities in a small area near the coast of northern Syria. This distribution of Fvg is important in connection with one hypothesis as to the origin of subsp. *rhoeadifolia*. The other two forms of subsp. *vulgaris*, namely *interrupta* and *fallax*, both occur in the eastern Balkan Peninsula, the Aegean Archipelago, and here and there in Asia Minor and Syria. Subsp. *rhoeadifolia* occurs throughout Asia Minor and eastward to the Caspian Sea, in southern Russia, the northern Balkan Peninsula, and into central Europe. Subsp. *commutata* is distributed from Crete northward through the Aegean Archipelago from eastern Greece to southern Bulgaria, in Asia Minor and northern Syria, and eastward to western Persia. All the subspecies and forms of *C. foetida* are usually found at low altitudes, so that where the distributional areas overlap the different forms or subspecies are apt to occur in close proximity to one another.

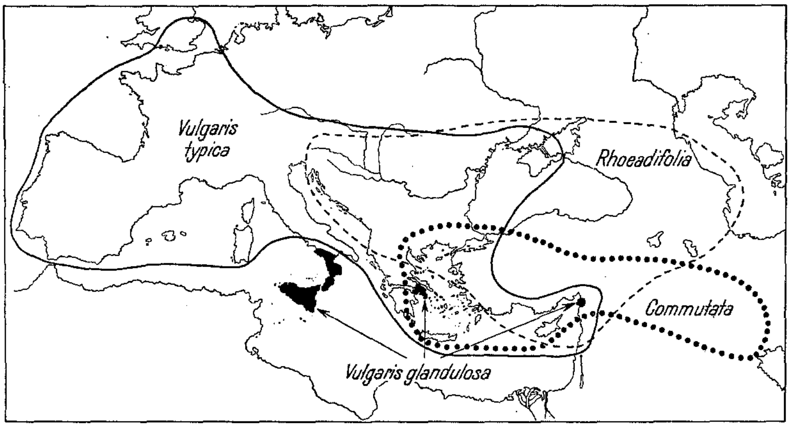

Fig. 12. Map showing the approximate distributional areas of the 3 subspecies of *Crepis foetida*: *vulgaris*, *rhoeadifolia*, and *commutata*. — Note that only the 2 geographically important forms of *C. foetida vulgaris* i. e., *typica* and *glandulosa*, are shown. The other 2 forms of this subspecies, *fallax* and *interrupta*, as well as numerous other forms, which for convenience are classified under one or other of the subspecies, are not shown. They occur mostly in the area of overlapping of the subspecies, are actually intermediate, and probably arose through hybridization.

It will be noted (Fig. 12) that the size of the overlapping areas of the subspecies is large as compared with the areas occupied by the 3 subspecies separately. The question may therefore arise as to whether *C. foetida* sen. lat. is a "Rassenkreis" in the strict meaning of the classical definition of the term. RENSCH (1929) defines a Rassenkreis as composed of geographic races which have developed separately, but which overlap in distribution and then produce fertile hybrids; whereas in his definition of geographic race he stipulates that each race occupies an area in which no other race lives. This leaves the impression that the overlapping areas are relatively small as compared with the separate areas of the races; and this relation seems to hold generally in animals, from which RENSCH drew most of his illustrations. His definition contains nothing definite concerning the relative sizes of the separate and overlapping areas in a Rassenkreis, for obvious reasons. Hence the critical question is whether each geographic race (or subspecies) occupies a separate geographic area. As for *C. foetida*, the number of collections from the eastern part of its range are too small to provide very reliable data on the distributional limits of the subspecies in that region. But supplementing the data on specimens seen by the authors with such information as is available in floras makes it possible to depict the approximate areas as shown in Fig. 12. Although *vulgaris* and *rhoeadifolia* overlap widely, they have large separate areas; but both of them include much of the *commutata* area within their limits. However, it is fairly certain that neither *vulgaris* nor *rhoeadifolia* occurs in the eastern part of the *commutata* area; and it is possible that the eastern limit of *commutata* extends farther into Persia. Thus the critical question is answered in the affirmative and *C. foetida* may be considered essentially a Rassenkreis.

The occurrence of hybrids in nature

There are, of course, no natural hybrids between *eritreënsis* and *Thomsonii* nor between either of them and *foetida*, because their geographic isolation makes it impossible. It is this fact, together with their distinctive morphological, qualitative, and physiological traits, and the evidence that they are distinct genetically with respect to some of these traits, that calls for the recognition of *eritreënsis* and *Thomsonii* as species. Within *foetida*, on the other hand, natural hybrids occur, and it is believed that natural hybridization has been largely responsible for the development of the Rassenkreis which we designate as *Crepis foetida* sen. lat.

Most important of the natural hybrids known to occur within the Rassenkreis are the hybrids between *rhoeadifolia* and *commutata*. Indisputable evidence that natural crossing occurs and produces fertile hybrids between these 2 subspecies has been obtained from recent collections made in Asia Minor by Dr. K. KRAUSE. Among plants of the same wild population various intermediate combinations occur, including *rhoeadifolia*-like plants with receptacular paleae; and the seeds from such plants, sown at Berkeley, produced quite variable progenies. These facts, combined with the experimental evidence that one strain of *commutata* (cf. Fcl, Tables 2, 3) produced highly fertile hybrids with *rhoeadifolia* which behave like both parents as to self-incompatibility, are sufficient grounds for treating *commutata* and *rhoeadifolia* as subspecies of the same species. The significance of this genetic evidence needs emphasis, perhaps, on account of the importance which has been attached by earlier taxonomists to a single morphological character, like presence or absence of paleae on the receptacle as a diagnostic criterion. Our study of the inheritance of this character shows that it has a simple genetic basis and, therefore, that two forms of the same ancestral species, one having paleae and the other lacking them, could arise through the occurrence of one or two gene mutations.

Next in importance is the well known fact that variable intermediate forms between *rhoeadifolia* and *vulgaris typica* occur in Asia Minor, the Balkan Peninsula, and east-central Europe where the two subspecies come into contact. Although the 5 F_1 plants which were obtained from the cross Fr × Fvt (Table 2) had low fertility, yet 60 per cent. of the F_2 seeds which were planted produced mature plants. Furthermore, many earlier experiments on crossing *rhoeadifolia* with *vulgaris typica* were made by C. W. HANEY (unpublished). Records on 14 of these crosses are available. The F_1 hybrids were vigorous and more or less intermediate in quantitative characters; and their fertility ranged from approximately 25 to 50 per cent. of potential seed production. In F_2 the segregation for certain characters was observed such as erect vs. nodding young flower-heads. From one of these crosses, herbarium specimens from over 20 F_2 fruiting plants are available; and, although these exhibit great variability in production of fertile achenes, there are always some good seeds produced and in some plants the fertility is high. These experimental results support the inference, drawn from the frequent occurrence of intermediate forms, that these two subspecies cross freely in nature, producing highly variable intergrades, some of which may persist or give rise to local races when isolated.

Finally, subsp. *vulgaris* fa. *fallax* has apparently produced natural hybrids with both subsp. *vulgaris typica* and subsp. *rhoeadifolia*. In 1930 the senior author collected seed of *C. foetida* in Athens which produced progeny the following year at Berkeley. These combined the smaller heads and shorter pappus of *fallax* with achenes characteristic of *typica*. Progeny grown the following year were more variable than their parents. Both *vulgaris typica* and *vulgaris fallax* occur in southern Greece and presumably these intergrading forms were hybrids between them. Other intergrades between *fallax* and *typica* have been collected in Syria. The situation is similar with respect to the occurrence of intergrading forms between *fallax* and *rhoeadifolia* in both Syria and Bulgaria; also between *fallax* and *commutata* in southwest Persia.

Phylogenetic relations

The data from comparative morphology, cytogenetics, and geographic distribution all point to the conclusion that *Crepis eritreënsis*, *C. Thomsonii*, and *C. foetida* sen. lat. had a monophyletic origin in the narrowest sense. It may be assumed that the ancestral stock had paleae on the receptacle and that the plants were self-compatible, since these are presumably more primitive characters than absence of paleae and self-incompatibility[1]. This ancestral stock was probably located in Asia Minor which is central with reference to the 3 outlying regions, Eritrea, India, and southwest Europe.

Differentiation within the ancestral stock undoubtedly progressed as a result of gene mutation, natural selection, and geographic isolation. Among the numerous gene mutations involved in the gradual process of differentiation, those conditioning absence of paleae and self-incompatibility appear to have been of primary importance. Through these and other genic variations two divergent lines arose. One of these led to the present-day group of forms which we call *C. foetida commutata* but which may have been isolated over a long period from the other present-day subspecies of *foetida* as well as from *eritreënsis* and *Thomsonii* through the migration of all the latter away from the common center. The other line broke up into divergent lines leading to *eritreënsis*, *Thomsonii*, and the forms we now know as *foetida vulgaris glandulosa* and *foetida vulgaris typica* (Fig. 13).

Of these two *foetida* forms, *vulgaris glandulosa* appears to be the more primitive because of its tall stature, robust habit, larger heads, and the combination of self-compatibility with the tendency for the flower-heads to remain open in sunlight, in which respect it resembles *commutata*. *Vulgaris glandulosa* is now known only from Sicily and a few other isolated points in the Mediterranean and Syria. Apparently it is a relic form, whereas *vulgaris typica* is an aggressive form which has become wide-spread in southern Europe and has even migrated into Asia Minor.

The origin of *foetida rhoeadifolia* is an interesting problem since two possibilities suggest themselves. This group of forms, which we treat today as a subspecies, may have developed as a distinct species in the Caucasus region (just as *eritreënsis* and *Thomsonii* developed in their isolated regions) and later spread into Asia Minor and southern Europe. This method of origin has already been suggested (BABCOCK, 1938). On the other hand, *rhoeadifolia* may have originated through hybridization between *commutata* and *vulgaris glandulosa*, perhaps in northern Asia Minor, and then spread eastward and westward around the Black Sea and into southern Russia. Although the former alternative may appear at

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[1] From his review of the literature on self-incompatibility BRIEGER (1930, p. 252) concludes: "daß gar keine Beziehungen zwischen der systematischen Stellung einer Art und den bei ihnen beobachteten Sterilitätserscheinungen besteht." Hence there is no logical objection to the a priori assumption that self-compatibility is a more primitive characteristic than self-incompatibility. This assumption has in its favor the fact that self-incompatibility induces maximum heterozygosity in the population, and heterozygosity is generally considered as advantageous to the species. The objection might be raised that *commutata*, although self-incompatible, has paleae on the receptacle and presence of paleae is considered primitive. The authors believe that none of the existing species and subspecies in this group represents the ancestral type — all have become differentiated, some retaining self-compatibility, and *commutata* keeping paleae on the receptacle. Regarding self-compatibility then, *commutata* has apparently become differentiated from its closest relatives through a succession of dominant gene mutations preventing self-compatibility.

first to be more reasonable, yet there are a number of reasons why the hypothesis of origin through hybridization is also tenable. In the first place, *rhoeadifolia* has been shown (Table 1; pp. 127—132) to combine certain morphological and physiological features found in *glandulosa* and *commutata*. The tendency for occasional *rhoeadifolia* plants to have small palea-like structures on the receptacle is particularly suggestive, although this and all the other morphological peculiarities can also be attributed to a common origin with *commutata*. Second, the relations as to hybrid fertility between *rhoeadifolia* and *commutata* (Table 2) can be interpreted in terms of the hybrid origin of *rhoeadifolia*, together with obvious genetic differences affecting hybrid fertility in the two strains of *commutata*. Unfortunately the F_2 seeds from the cross between *rhoeadifolia* and *glandulosa* were not sown. But, on the basis of available data, *rhoeadifolia* is intermediate in its hybrid fertility relations between *vulgaris* and *commutata*. Third, the data on inheritance of paleae in hybrids between *rhoeadifolia* and *commutata* indicate unique genic relations with respect to this character in *rhoeadifolia* (p. 148). Fourth, *rhoeadifolia* is evidently variable as to its genetic factors conditioning self-incompatibility. Fifth, some cultivated strains of typical *rhoeadifolia* have been observed to have low fertility. POOLE (1931) reported that in such a strain (no. 1539) he found meiotic irregularities caused by nonconjunction of one pair of chromosomes, which would account for the observed sterility. Partial sterility in *rhoeadifolia* is indicated by the occurrence of sterile achenes in herbarium specimens collected in the wild. In 17 specimens of *rhoeadi-*

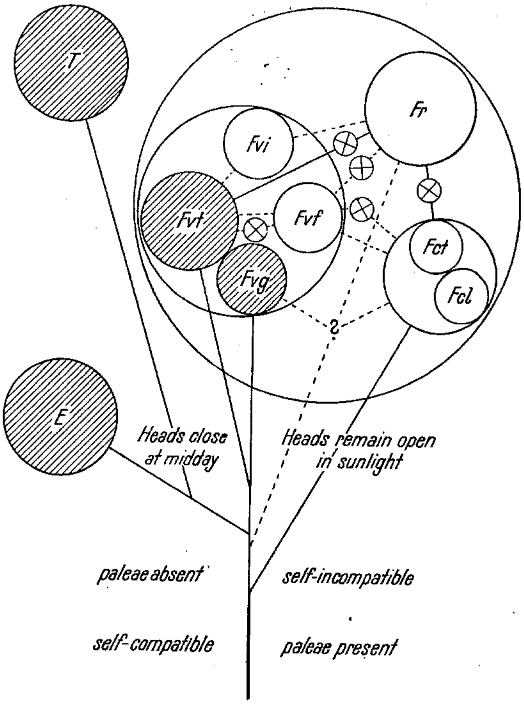

Fig. 13. Diagram representing the phylogenetic relations of *C. eritreënsis* (E), *C. Thomsonii* (T), and *C. foetida* (F). Within *foetida* the 3 subspecies, *vulgaris* (Fv), *commutata* (Fc) and *rhoeadifolia* (Fr) are represented by the 3 larger circles. Within *vulgaris*, the 4 forms, *typica* (Fvt), *glandulosa* (Fvg) *fallax* (Fvf), and *interrupta* (Fvi) are shown as smaller circles. Similarly within *commutata* the 2 forms, Fct and Fcl, are shown. The very small circles enclosing a cross represent natural hybrids. Purely hypothetical connections are represented by dotted lines. Shaded circles indicate self-compatibility; unshaded circles, self-incompatibility.

folia with fruiting heads, collected at different localities in Asia Minor and Bulgaria, it was found that 9 specimens or over 50 per cent. contained numerous sterile achenes in the heads. Although none of these bits of evidence alone proves anything, yet altogether they lend considerable support to the hypothesis of hybrid origin of *rhoeadifolia.*

The other two strains of *foetida vulgaris* used in this investigation, *interrupta* and *fallax,* may also have arisen through hybridization. They are actually intermediate in morphology, *interrupta* combining certain characters of *vulgaris typica* and *rhoeadifolia,* and *fallax* combining certain characters of *vulgaris typica* and *commutata.* But, since they never have paleae and show definite resemblance to *vulgaris typica* in certain characters, they have been included in that subspecies. The absence of paleae can be explained on the basis of the genetic evidence (p. 149) which indicates that these strains carry a dominant inhibiting gene. Both *interrupta* and *fallax,* as represented by the strains used in this study, are self-incompatible. This is to be expected in view of the great preponderance of self-incompatible progeny in F_2 from the crosses between self-compatible and self-incompatible strains. At the same time it is also to be expected that among the host of intergrading forms between *vulgaris, rhoeadifolia,* and *commutata* which exist in nature one might occasionally be found to be self-compatible.

Finally, it should be pointed out that our phylogenetic diagram (Fig. 13) is much too simple a picture of the variability within *C. foetida.* Besides the many intergrading forms, some arising through gene mutation and some through hybridization between the subspecies, there are many environmental modifications which also tend to make classification difficult. In other words, *C. foetida* sen. lat. is essentially a Rassenkreis in which the 3 subspecies, in their more typical forms, are very distinct and easily recognized, but in which there are also many intermediate forms which must be classified more or less arbitrarily.

We consider *foetida* to be a Rassenkreis, whereas *Thomsonii* and *eritreënsis* are distinct species. Some biologists may question the advisibility of recognizing *Thomsonii* and *eritreënsis* as species on the basis of their geographical isolation plus certain morphological differences, rather than treating them as subspecies because of their close genetic relationship with *foetida,* as revealed by experimental crosses. Rensch proposes that, "when the distribution area of the whole Rassenkreis is not continuous", the sum of morphological and physiological differences between the geographically separated forms and the rest of the Rassenkreis will show approximately whether fertile hybrids would be formed in case of invasion. In the opinion of the present authors, such an indefinite criterion is likely to lead to taxonomic confusion. After all, practicability in systematics is a primary consideration. Even though the testing of hybrid fertility by experimental crosses is more often possible in plants than in animals, yet it is sometimes impracticable in plants. Furthermore, even if fertile hybrids can be obtained experimentally between isolated forms, this does not prove that fertile hybrids would certainly occur in nature — some environmental factor might interfere.

These objections to hybrid fertility as the primary criterion for the recognition of species also apply to the genecological system of TURESSON (1929) as somewhat modified by CLAUSEN, KECK, and HISEY (1936). According to this scheme, the ecospecies (Linnaean species) are kept distinct by an inner genetical mechanism, so that when hybrids are produced they are partly sterile; whereas the ecotypes (subspecies) produce fertile hybrids and are kept distinct by their geographical or ecological isolation. The difficulty in applying this scheme to the group of forms under consideration in this paper becomes obvious when individual forms are considered. For example, *rhoeadifolia* is quite variable as to the fertility of the hybrids which it produces with the other forms. How can a norm or mode for the whole of *rhoeadifolia* in this respect be obtained? Furthermore, as JENKINS (op. cit.) has pointed out, in order to apply hybrid fertility as the primary criterion, it becomes necessary to fix some arbitrary degree of hybrid fertility in order to distinguish species from subspecies on this basis alone. But since both *Thomsonii* and *eritreënsis* produce highly fertile hybrids with 4 forms of *foetida*, they would become subspecies on this basis, even though it is not known that they will ever hybridize with *foetida* in nature.

On the other hand, complete isolation, either geographical or ecological, is a definite criterion which can serve for the present as a sound basis for the recognition of genetically close species, even when experimental hybrids between them are highly fertile. If they should later occupy the same area and produce fertile hybrids in nature, it will of course be necessary then to recognize them as one species. The present authors prefer to follow this rule, at least until the majority of taxonomists agree that a definite amount of hybrid fertility is to supersede isolation as a criterion when dealing with forms which are very close genetically.

Summary

1. Nine strains of *Crepis*, representing 3 closely related species, *C. eritreënsis* BABC., *C. Thomsonii* BABC., and *C. foetida* L. sen. lat., were studied as to comparative morphology, geographic distribution, chromosome number and morphology, crossability, meiotic regularity, and the inheritance of certain quantitative and qualitative differences.

2. The species are readily distinguished by means of certain characters of the flowers, fruits, and involucres (for a key to the species cf. BABCOCK, 1938).

3. The chromosome number is the same in these species and the chromosomes are closely similar in size and shape. Meiosis is regular in the parent strains and in the F_1 hybrids.

4. Segregation in F_2 families from strain crosses gave monohybrid, dihybrid, and trihybrid ratios for several structural or qualitative differences, whereas certain quantitative differences (leaf shape, stem height) and self-compatibility vs. self-incompatibility displayed extremely variable proportions in F_2. These characters are presumably conditioned by several or numerous genes.

5. The three species are so close genetically that, if their distributional areas overlapped they would probably form one Rassenkreis, since there is

nothing to indicate that either physiological or ecological isolation would exist. It happens, however, that *eritreënsis* and *Thomsonii* are widely separated from each other and from *foetida*. Since they are also distinguished by definite morphological characters and several known genetic factors, they should be recognized as species and have been so recognized (Babcock, 1938).

6. *C. foetida* sen. lat. is a Rassenkreis in which the major subdivisions, subspp. *vulgaris*, *commutata*, and *rhoeadifolia*, are connected by many intergrading forms. Since some of these forms are known to have arisen through crossing in nature, it is inferred that many others arose in this way, including two of the strains used in this investigation, i. e., *C. foetida vulgaris* fa. *interrupta* and fa. *fallax*.

7. Based on the foregoing evidence, a picture of the assumed phylogenetic relations of the 3 species has been presented.

Supplementary note. — Since the foregoing was written, an article on "Self-Sterility in *Antirrhinum* and *Petunia*" has come to hand (Hsien-Po Tseng, Jour. Genetics 36 (1), 127—138, 1938). Regarding the inheritance of self-fertility and self-sterility in *Petunia hybrida*, the author concludes that: (1) dominant self-fertility is probably based upon one factor pair F/f; (2) recessive fertility is due to at least one other factor pair (called provisionally A/a), the effect of A/a being dependent upon the assortment of modifiers present; (3) self-sterile plants must be ff, but may be AA, Aa, or even aa, according to the particular combination of modifiers present. Here we have additional evidence for at least one dominant factor for self-sterility (self-incompatibility). In the comprehensive review of the literature by Stout (1938) which has just appeared, several cases like that of *Petunia hybrida* are classified under the "Associate Type" of incompatibility. In these cases two different series of alleles are involved, one opposing and the other favoring fertilization. The genetic basis of incompatibility in *Crepis foetida*, *C. eritreënsis* and *C. Thomsonii* does not appear to be of this Associate Type; nor is it of the Personate Type. Furthermore, it does not correspond with the genetics of incompatibility in *Cardamine pratensis* in which polyploidy is involved. — The Authors.

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