

THE BREAKDOWN OF TRIMORPHIC INCOMPATIBILITY IN *OXALIS* SECTION CORNICULATAE

ROBERT ORNDUFF

Department of Botany, University of California, Berkeley, Calif.

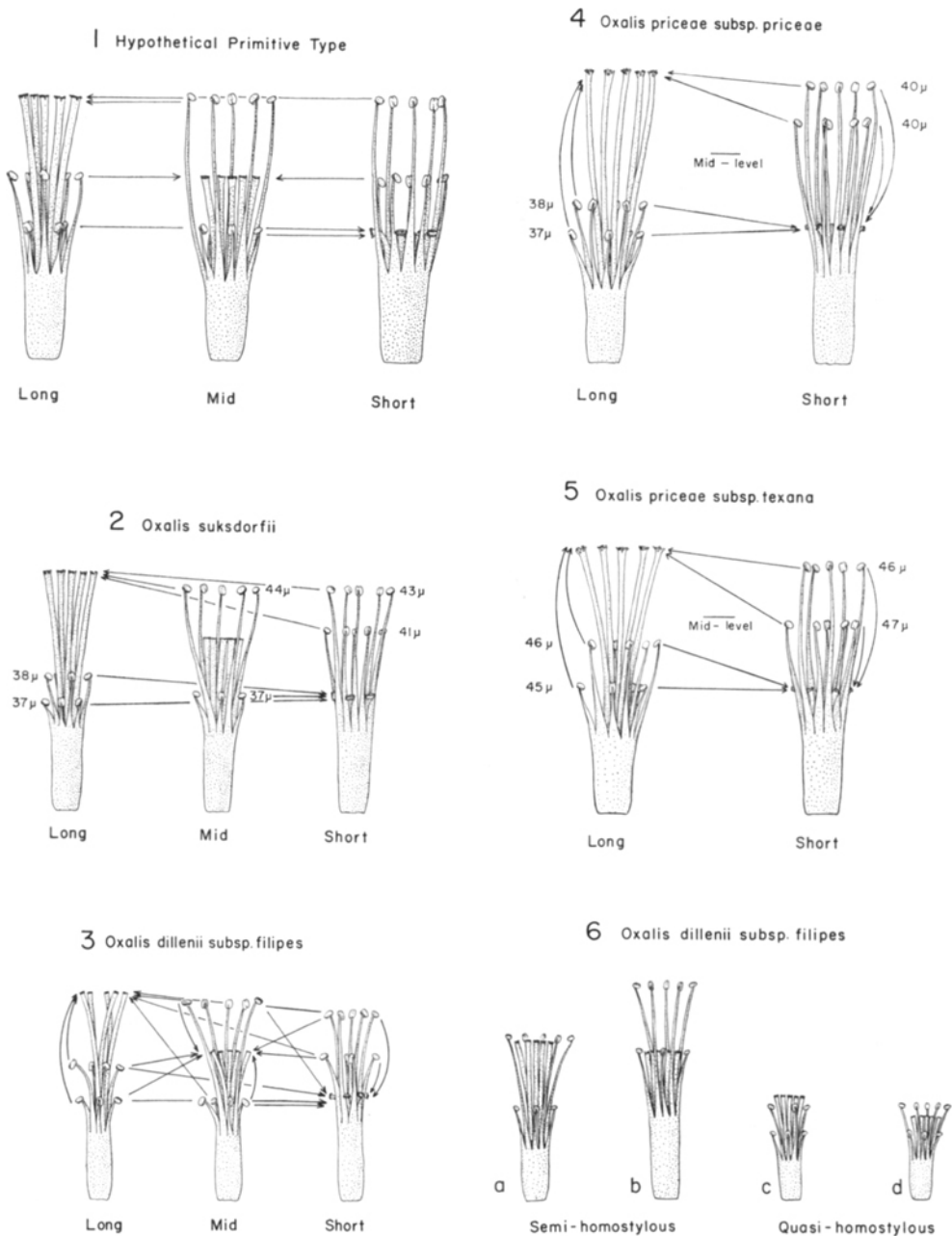
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Among the most complex outcrossing systems in flowering plants are those in which floral heteromorphism is associated with a physiological incompatibility system. Such heteromorphic incompatibility systems can arise only as a result of strong selective pressures exerted over a long period of time. There is excellent evidence that when the selective pressures regulating the maintenance of these systems are relaxed or altered in their direction, the integrated syndrome of morphological and physiological traits characteristic of heteromorphic incompatibility may rapidly break down, usually in the direction of increased inbreeding. There are several evolutionary routes which the breakdown of heteromorphic incompatibility may follow. The diverse breeding systems of the American representatives of *Oxalis* section Corniculatae (Oxalidaceae) are most probably derived from an ancestral trimorphic incompatibility system. This paper presents a study of the breeding systems of several members of this group and briefly discusses the genetic and ecological circumstances leading to the development of these derivative systems.

Oxalis section Corniculatae recently has been the subject of a taxonomic monograph by Eiten (1963), whose nomenclature will be followed here. As circumscribed by Eiten, the section contains 14 species of caulescent, non-bulbous, yellow- or orange-flowered herbs with trifoliate leaves. Members of this section occur mostly in North and South America and the Greater Antilles, but two species are believed to have a natural amph-Pacific range in North America and eastern Asia.

TRISTYLOUS INCOMPATIBILITY AS AN ANCESTRAL CONDITION

The ancestral condition from which the breeding systems of the modern members of the Corniculatae were derived was probably one combining tristylous flowers and a strong incompatibility system (Ornduff, 1964). This type of system occurs in species of diverse affinities, such as *Oxalis valdiviensis* Barn. (section Laxae), *O. regnellii* Miq. (Articulatae), *O. purpurea* L. (Stictophyllae), and others (Hildebrand, 1867, 1871, 1887; Darwin, 1877). However, no extant member of the Corniculatae is known to possess this primitive morphological-physiological character combination in its complete expression, although some of the species approach it (see below). For purposes of understanding the various derivative breeding systems in the Corniculatae, the functional aspects of a fully developed tristylous incompatibility system will be considered briefly. In species having such a system plants of three kinds exist (Fig. 1): those having flowers with long styles and anthers at two levels below the stigmas ("Longs"); those having flowers with mid-length styles and one set of anthers above the stigmas and the other set below them ("Mids"); and those having flowers with a short style and anthers at two levels above the stigmas ("Shorts"). The stigmas of Longs are at approximately the same height above the ovary as the anthers of the longer set of stamens of Mids and Shorts; likewise, the stigmas of Mids and Shorts are at the same levels as one set of anthers of the other floral forms. Thus in any flower there are three positions available for the two sets of anthers and one set of stigmas: the long, mid, and



FIGS. 1-6. Illustrations of portions of flowers of *Oxalis* species in section *Corniculatae*, showing relative positions of anthers and stigmas in the various floral forms. Arrows running from anthers to stigmas indicate compatible pollinations that are possible, based on data in Table 1. Numbers adjacent to anthers refer to size of pollen grains from that set of anthers. The flower shown in Fig. 1 is for comparative purposes only and is not known to occur in any extant member of the *Corniculatae* ($\times 3$).

short position. Often associated with these differences in length of reproductive parts are differences in size of pollen grains from the three sets of anthers, in pubescence of filaments and styles, and in size and orientation of the stigmas.

The usual interpretation of the positions of reproductive structures of heterostylous flowers is that these enhance outcrossing by promoting pollinations between anthers at a given level and stigmas at an equivalent level in flowers of other plants (Fig. 1). Such pollinations are termed "legitimate" pollinations in Darwinian terminology (1877). Legitimate pollinations presumably are accomplished by the deposition of pollen on various portions of the bodies or appendages of visiting pollinators from the anthers at three positions and the subsequent removal of this pollen by stigmas of an equivalent height. According to this interpretation, pollen from the longest set of anthers of Mids or Shorts is transferred to stigmas of Longs, etc. Correlated with these differences in the position of stigmas and anthers in the three floral forms is an incompatibility system that functions to prevent illegitimate pollen (i.e., from the "wrong" level of anthers) from participating in fertilizations. Some of the members of *Oxalis* sect. *Corniculatae* have retained the morphological features of tristylly, but in none of the species examined does the incompatibility system function in the manner just described. The following paragraphs discuss the various modifications of a heteromorphic incompatibility system that have evolved in the *Corniculatae*.

ANDRODIOECISM AND TRISTYLY

Oxalis suksdorfii Trel. is a woodland species that ranges along the Pacific coast from southern British Columbia to central California. In its floral morphology and in most aspects of its breeding system it approaches the self-incompatible tristylous ancestor of the *Corniculatae* more closely than does any other species of the section. The species is morphologically tristylous and there are some corresponding differ-

ences among the three floral forms in pollen size, stigma size and orientation, and stilar pubescence. Its floral morphology and breeding system have been discussed elsewhere (Eliot, 1892; Trelease, 1892; Ornduff, 1964) and will be summarized here. Longs are weakly self-compatible and show little if any differentiation in pollen size or incompatibility relationships of pollen from both sets of anthers. Shorts show slight pollen-size differentiation and are self-incompatible. Mids have strongly differentiated pollen but produce few seeds after either illegitimate or legitimate pollinations (see Fig. 2, Table 1). This is due partly to failure of legitimate pollen-tube growth in its styles and partly to failure of embryo-sac formation. In view of the functionally staminate condition of Mids, *O. suksdorfii* is androdioecious; this phenomenon is unknown in other heterostylous genera. Nevertheless, Mids are present in all populations sampled and, although the proportion in which they occur fluctuates from population to population, Mids represents about $\frac{1}{3}$ of the total individuals sampled.

In association with the functionally staminate condition of Mids, pollen from mid-level anthers of Longs and Shorts is able to participate in illegitimate fertilizations between Longs and Shorts. The pollen of Longs is not only undifferentiated in size, but the mid-level anthers (i.e., the longer set of anthers) are no longer positioned at the level of the nonfunctional Mid stigmas. Instead, they are nearer the level of Short stigmas and presumably participate in illegitimate but fertile pollinations of Shorts (Table 1; Fig. 2). In contrast, the position of the mid-level anthers of Shorts is approximately that of Mid stigmas. However, pollen from such anthers can effect fertilizations only after transfer to Long stigmas. It is not clear why the mid-level anthers of Shorts have not undergone a change in position similar to that which has occurred in the mid-level anthers of Longs. Nor is it clear why Mids continue to be retained in popula-

TABLE 1. *Results of legitimate and illegitimate pollinations in Oxalis sect. Corniculatae.*

Cross made	Number of flowers pollinated	Total number of seeds obtained	Average number of seeds per pollination
<i>Oxalis suksdorfii</i>			
Legitimate pollinations:			
Long × long/short ¹	129	1,317	10.4
Long × long/mid	106	1,052	9.9
Total legitimate pollinations of long	235	2,369	10.1
Mid × mid/long	100	13	0.1
Mid × mid/short	95	22	0.2
Total legitimate pollinations of mid	195	35	0.2
Short × short/mid	128	1,027	8.0
Short × short/long	146	1,334	9.1
Total legitimate pollinations of short	274	2,361	8.6
Illegitimate pollinations:			
Long × long	482	702	1.5
Long × mid/short	89	782	8.8
Long × short/mid	102	137	1.3
Total illegitimate pollinations of long	673	1,621	2.4
Mid × mid	64	13	0.2
Mid × long/short	57	0	0
Mid × short/long	0	0	0
Total illegitimate pollinations of mid	121	13	0.1
Short × short	396	77	0.2
Short × mid/long	162	1,470	9.1
Short × long/mid	126	54	0.4
Total illegitimate pollinations of short	684	1,601	2.3
Summary of all legitimate pollinations	704	4,765	6.8
Summary of all illegitimate pollinations	1,478	3,235	2.2
<i>Oxalis dillenii</i> subsp. <i>filipes</i>			
Legitimate pollinations:			
Long × long/short	33	649	19.7
Long × long/mid	28	645	23.0
Total legitimate pollinations of long	61	1,294	21.2
Mid × mid/long	15	447	29.8
Mid × mid/short	14	425	30.4
Total legitimate pollinations of mid	29	872	30.1
Short × short/mid	17	470	27.6
Short × short/long	39	1,003	25.7
Total legitimate pollinations of short	56	1,473	26.3
Illegitimate pollinations:			
Long × long	125	2,703	21.6
Long × short/mid	24	515	21.5
Long × mid/short	26	487	18.7
Total illegitimate pollinations of long	175	3,705	21.2
Mid × mid	102	2,522	24.7
Mid × long/short	23	572	24.9
Mid × short/long	15	346	23.1
Total illegitimate pollinations of mid	140	3,440	24.6
Short × short	142	3,854	27.1
Short × long/mid	34	740	21.8
Short × mid/long	38	904	23.8
Total illegitimate pollinations of short	214	5,498	25.7
Summary of all legitimate pollinations	146	3,639	24.9
Summary of all illegitimate pollinations	529	12,643	23.9

TABLE 1. (Continued).

Cross made	Number of flowers pollinated	Total number of seeds obtained	Average number of seeds per pollination
<i>Oxalis grandis</i>			
Legitimate pollinations:			
Long × long/mid	11	156	14.2
Mid × mid/long	29	300	10.3
Illegitimate pollinations:			
Long × mid/long	12	62	5.2
Long × short/long	4	33	8.2
Long × short/mid	17	196	11.5
Total illegitimate pollinations of long	33	291	8.8
Mid × long/mid	12	135	11.3
Mid × short/mid	18	215	11.9
Mid × short/long	29	283	9.8
Total illegitimate pollinations of mid	59	633	10.7
Summary of all legitimate pollinations	40	456	11.4
Summary of all illegitimate pollinations	92	924	10.0
<i>Oxalis priceae</i> subsp. <i>texana</i>			
Legitimate pollinations:			
Long × long/short	36	919	25.5
Short × short/long	26	399	15.3
Illegitimate pollinations:			
Long × short/long	24	486	20.3
Long × long/long	40	962	24.1
Long × mid/short	28	666	23.8
Total illegitimate pollinations of long	92	2,114	23.0
Short × mid/short	32	471	14.7
Short × long/short	23	379	16.5
Short × mid/long	40	626	15.7
Total illegitimate pollinations of short	95	1,476	15.5
Summary of all legitimate pollinations	62	1,318	21.3
Summary of all illegitimate pollinations	187	3,590	19.2
<i>Oxalis priceae</i> subsp. <i>priceae</i>			
Legitimate pollinations:			
Long × long/short	22	277	12.6
Short × short/long	29	448	15.4
Illegitimate pollinations:			
Long × mid/long	23	236	10.3
Long × short/long	18	227	12.6
Long × mid/short	31	443	14.3
Total illegitimate pollinations of long	72	906	12.6
Short × mid/short	41	645	15.7
Short × long/short	52	889	17.1
Short × mid/long	42	588	14.0
Total illegitimate pollinations of short	135	2,122	15.7
Summary of all legitimate pollinations	51	725	14.2
Summary of all illegitimate pollinations	207	3,028	14.6

¹ Notation to be read: long-styled ♀ × pollen from long stamens of short-styled flower. Data for *O. suksdorfii* taken from Ornduff, 1964.

TABLE 2. Measurements of pollen grains from the 2 sets of anthers of each floral form of trimorphic populations of *O. dillenii* subsp. *filipes*, subjected to Student's *t* test for testing the means of two samples. A 1:1 hypothesis is rejected at the 5% level.

Locality	Floral form	Sample size	Pollen diameter, long-level anthers (μ)	Pollen diameter, mid-level anthers (μ)	Pollen diameter, short-level anthers (μ)	<i>t</i>	Difference significant ?
Lancaster County, South Carolina	Long	30	—	32.6	31.2	2.93	Yes
	Mid	30	32.4	—	30.9	3.28	Yes
	Short	30	31.6	31.6	—	—	No
Berkeley County, South Carolina	Long	80	—	34.0	32.6	0.47	No
	Mid	40	36.6	—	35.3	2.33	Yes
	Short	40	34.2	33.6	—	2.32	Yes
Stanly County, North Carolina	Long	30	—	33.1	33.2	0.24	No
	Mid	30	35.1	—	33.1	3.05	Yes
	Short	30	36.3	33.6	—	4.68	Yes

tions of *O. suksdorfii*, since there are no apparent genetic obstacles preventing the elimination of this form which seems to contribute rather little to the peculiar reproductive system of the species.

The representation of the three forms in populations of *Oxalis suksdorfii* deviates from equality (Ornduff, 1964), as it does in the tristylous *O. grandis* (discussed below; Finney, 1952; Fabergé, 1959). Certain features of the reproductive behavior of these two species may account for these deviations, however. Under stable ecological conditions, increase in population size of both species is largely by vegetative propagation. In natural populations one floral form may occupy an area of several square meters and in many instances these monomorphic stands are surely the result of extensive clonal growth. Sexual reproduction in well established populations seems to be rare and may occur only after ecological disturbances such as fire, road building, or clearing of land. Such sexual reproduction seems to be associated largely with populating newly available habitats rather than with producing progeny on the site of the parent populations. With clonal development and only occasional sexual reproduction, the composition of the founding population would strongly influence the pattern of representation of forms in the population derived from it. This com-

position might vary from equality of representation as a result of the composition of the parent population from which it was derived.

SELF-COMPATIBLE TRISTYLY

The variable *Oxalis dillenii* Jacq. subsp. *filipes* (Small) Eiten occurs in stable or disturbed habitats from eastern Canada southward to Florida and westward along the Coastal Plain to southeastern Missouri, southwestern Arkansas, and eastern Texas. This subspecies possesses tristylous races, discussed here, and semi- and quasi-homostylous races to be discussed in a later section. Plants used in this study originated in North and South Carolina.

The fully tristylous races of *Oxalis dillenii* subsp. *filipes* show a good correspondence of anther position and stigma position of the three forms (Fig. 3). Measurements of pollen diameters from flower samples collected in three tristylous populations give variable results (Table 2). In the three populations examined, pollen from the two sets of anthers shows a significant size difference in two of the three floral forms. Longs of two populations exhibit no pollen-size dimorphism, but in a third population it is Shorts which have uniform pollen.

Seed production following illegitimate pollinations of Longs and Shorts is equal to their seed production after legitimate

pollinations indicating that these forms lack a self-incompatibility system (Table 1). The seed production of legitimately pollinated Mids is above that of illegitimately pollinated flowers of this form, indicating that a residual incompatibility is present in this form.

One population sample of *Oxalis dillenii* subsp. *filipes* from Lancaster County, South Carolina, gave 41 Longs, 26 Mids, and 16 Shorts. A sample from another population of this subspecies in Stanly County, North Carolina, gave 33 Longs, 12 Mids, and 11 Shorts. The proportional representation of the three forms in these two populations is similar and strongly deviates from equality with a predominance of Longs. The explanation for this may lie partly in certain seasonal phenological changes in the subspecies. The first flowers produced by the tristylous races of *O. dillenii* subsp. *filipes* in the spring are relatively large. Despite the self-compatibility of this subspecies, it is likely that a large proportion of these flowers are outcrossed. As the season progresses, however, the size of flowers gradually decreases by as much as one-third. Although these reduced flowers are fully heterostylous and maintain the same positional relationships among the stigmas and the two sets of anthers, the smaller absolute distance between stigmas and anthers in these flowers likely results in an increased amount of selfing during the visits of pollinators. This selfing during a portion of the flowering season possibly accounts for the unequal representation of the three forms in the populations of *O. dillenii* subsp. *filipes* that were sampled. The excess of Longs may result from the fact that Longs produce only Long offspring upon selfing, but certain genotypes of Mids and Shorts produce long offspring as well (Table 3). Fluctuations or long-term changes in proportional representation of the three forms would be dependent upon the genotypes present in the founding populations, but the results of population samples may suggest that seedling establishment in these

TABLE 3. Probable genetics of tristylty in the *Corniculatae* and changes in relative proportions of floral forms in two successive generations as a result of continued self-pollination.

Genotype (P ₁)	F ₁ phenotype (%)			F ₂ phenotype (%)		
	Long	Mid	Short	Long	Mid	Short
Long						
<i>ssmm</i>	100	—	—	100	—	—
Mid						
<i>SsMm</i>	25	75	—	37.5	62.5	—
<i>ssMM</i>	—	100	—	—	100	—
Short						
<i>Ssmm</i>	25	—	75	37.5	—	62.5
<i>SsMm</i>	6.25	18.75	75	14.1	23.4	62.5
<i>SsMM</i>	—	25	75	—	37.5	62.5
<i>SSmm</i>	—	—	100	—	—	100
<i>SSMm</i>	—	—	100	—	—	100
<i>SSMM</i>	—	—	100	—	—	100

populations as a result of self-pollination is more common than that resulting from outcrossing.

Oxalis priccae subsp. *colorea* (Small) Eiten is also tristylous (Eiten, 1963; Mulcahy, 1964) and "exhibits a high degree of self-fertility" (Mulcahy, 1964). I have not examined this subspecies.

Another member of the *Corniculatae*, *Oxalis grandis* Small, is a tall woodland species occurring in upland areas from Pennsylvania and Illinois south to Georgia and Alabama. This species is morphologically tristylous throughout its range (Eiten, 1963), although I have not obtained measurements of the length of floral organs. Examination of pollen of herbarium specimens indicates that there are no consistent differences in pollen size among the anthers at three levels. Seed production figures for Longs and Mids from North Carolina (the only forms available to me as living plants) suggest that Long has a moderate self-incompatibility but that Mid does not, since in Mid average seed production after illegitimate pollinations is equal to that after legitimate pollinations (Table 1).

Fabergé (1959) has reported that a population of *Oxalis grandis* in southern Indiana was composed of 1305 Longs, 661

Mids, and 623 Shorts, proportions which represent a strong departure from equality. My observations on two smaller populations in North Carolina revealed compositions of 9 Longs, 20 Mids, and 2 Shorts (McDowell County), and 16 Longs, 10 Mids, and 1 Short (Madison County). These figures agree with those of Fabergé in their deviation from equality of representation of the three forms, although in one of the North Carolina samples Mid rather than Long predominates. The factors which may lead to these unequal population structures are discussed under *O. suksdorfii*, which in many respects is the western ecological counterpart of *O. grandis*.

DERIVED DISTYLY

Oxalis priceae Small subsp. *priceae* (Fig. 4) and *O. priceae* subsp. *texana* (Small Eiten (Fig. 5) are distylous, possessing only Longs and Shorts. Pollinations of *O. priceae* subsp. *texana* from Louisiana indicate that Shorts are fully self-compatible and that perhaps a slight incompatibility system is present in Longs (Table 1). Pollinations of subsp. *priceae* from Tennessee indicate that both forms are fully self-compatible (Table 2; see Mulcahy, 1964).

Pollen of *Oxalis priceae* subsp. *texana* and subsp. *priceae* is monomorphic. Mid-level stigmas are no longer present in either subspecies, but in the samples of *Oxalis priceae* subsp. *texana* examined the mid-level anthers of Shorts and, to a lesser extent, those of Longs occupy a mid-level position (Fig. 5). In contrast, the "mid-level" anthers of Longs and Shorts of *O. priceae* subsp. *priceae* occupy a level that is nearer the other set of anthers of these flowers than to the true mid-level (Fig. 4; Mulcahy, 1964). The floral morphology of *O. priceae* subsp. *priceae* more closely approaches that of a truly dimorphic species than does the floral morphology of subsp. *texana* because of the position of the mid-level stamens of the first subspecies. Thus, it is possible that loss of the Mid form has occurred more recently in the evolution of subsp. *texana* than it has in

subsp. *priceae*. Whatever the explanation, subsp. *priceae* shows a better morphological adjustment to the absence of Mids than does subsp. *texana*.

Data concerning the population structure of *Oxalis priceae* subsp. *texana* are not available. In four of five populations of subsp. *priceae* sampled by Mulcahy (1964) the ratio of Longs to Shorts approached 2 : 1, suggesting either inbreeding or differential mortality of Shorts.

SEMI- AND QUASI-HOMOSTYLY

Relatives of heterostylous taxa sometimes have anthers and stigmas at the same level. As a consequence, such homostylous plants are self-compatible if not largely autogamous. The homostylous derivatives of tristylous ancestors rarely, if ever, have both sets of anthers at the same level as the stigmas. In some instances, one set of anthers occupies this position and the second set occurs above or below the stigmas. This condition has been termed "semi-homostyly" (Lewis, 1954, after Stout, 1925) and occurs in some members of the Corniculatae (Fig. 6a and b). A second type of derived floral structure which occurs in the section is one in which the position of stamens and stigmas is still fundamentally a heterostylous one, but because of the highly reduced flowers the distance between anthers and stigmas is very small and results in autogamy (Fig. 6c and d). Because this floral structure has a closer functional affinity to homostyly than to heterostyly, I am designating such flowers as "quasi-homostylous."

The flowers that I have examined of *Oxalis dillenii* subsp. *dillenii* are either quasi-homostylous Mids with the stigmas occupying a position between the upper and lower sets of anthers (as in Fig. 6d), or quasi-homostylous Longs (as in Fig. 6c). The lower set of anthers in both forms is sometimes sterile, a condition also present in some races of *O. corniculata* L. The quasi-homostylous races of *O. dillenii* subsp. *dillenii* are outcrossing. Eiten (1959) also describes semi-homostylous

and "quite heterostylous" races of this subspecies.

The floral morphology of the semi-homostylous races of *Oxalis dillenii* subsp. *filipes* (Small) Eiten is variable. In some individuals it is the upper set of anthers which is opposite the stigmas (Fig. 6a). In others, the lower set of anthers is adjacent to the stigmas (Fig. 6b). Such spatial arrangements of reproductive organs seem to be confined to large-flowered semi-homostylous races. In quasi-homostylous races of this subspecies and particularly in those which have small flowers, the stigmas may be positioned between the two sets of anthers, slightly above them, or slightly below them (Fig. 6c and d). Some populations of *O. dillenii* subsp. *filipes* are exclusively heterostylous; others consist only of one type of semi-homostylous or quasi-homostylous plants. Other populations may contain as many as three types of semi-homostylous plants or both semi- and quasi-homostylous plants. Still other populations are made up of fully heterostylous individuals as well as semi- and quasi-homostylous ones. The population dynamics of these mixed populations deserves further study.

Because of the variation in flower size and length of the reproductive structures of the semi-homostylous races of *Oxalis dillenii* subsp. *filipes* it is difficult to determine the evolutionary origin of these races, but the variability strongly suggests that semi-homostyly has had multiple origins in this subspecies. The style-length and the location of stigmas of some semi-homostyles suggest that they are modified Mids. The position of reproductive structures of the flower illustrated in Fig. 6b suggests that the styles are mid-length and the stamens are positioned as in Shorts. Fig. 6a perhaps illustrates a "Long" with Mid anthers. In other plants with the same positional relationships of anthers and stigmas, the style length is equivalent to that of Shorts, suggesting that these races represent modified Shorts. However, it is probable that some of these latter

races consist of Longs in which the entire flower size and length of reproductive structures have been substantially reduced. The semi- and quasi-homostylous races of this subspecies are largely self-pollinated, although it is probable that the large-flowered semi-homostylous plants may participate in the pollination of heterostylous ones when the two occur together.

Although I have not examined other members of the Corniculatae in detail, Eiten (1959) indicates that the self-compatible and (at least in the weedy races) autogamous *Oxalis corniculata* L. is mostly semi-homostylous with the styles equal in length to the longer set of stamens. However, he also indicates that this species is sometimes "slightly mid- or long-styled." A similar description is given for *O. albicans* H. B. K., although *O. albicans* subsp. *pilosa* (Nutt.) Eiten is described as sometimes "strongly heterostyled (mid-styled or long-styled)." Whether mixed populations occur is not clear. Similarly, *O. stricta* L. is described as "homostylous or slightly or strongly long-styled, or rarely slightly short- or mid-styled."

In the South American species, Eiten (1959) states that heterostyly and homostyly occur in *O. bisfracta* Turcz. and *O. sexenata* Sav.; only mid-styled forms have been described in *O. rufescens* Turcz.; *O. calachaccensis* Knuth is said to be homostylous or rarely mid-styled; and *O. filiformis* H. B. K. is homostylous or heterostylous with long- and mid-styled forms. Of the Antillean species, *O. theloxys* Focke is described as "slightly or strongly long-styled" and *O. rugeliana* Urb. as "neither strictly homo- or heterostylous." Eiten's description of the latter species indicates that it is a semi-homostyle in which the rather short styles are equal in length to the shorter set of stamens. Although nothing is known of the breeding systems of the Antillean and South American species, the analogy of their floral structure with that of the North American species which have been studied suggests that all these species are probably self-compatible and

some of them undoubtedly are largely autogamous.

EVOLUTIONARY CONSIDERATIONS

The genetic data available for *Oxalis priceae* subsp. *colorca* of the Corniculatae suggest that the tristily of this subspecies is governed by a two-locus system similar to that of *O. valdiviensis* Barn. of section Laxae (von Uebisch, 1921; Barlow, 1923; Fyfe, 1950; Mulchay, 1964; see Table 1). In this system, Long is homozygous recessive at both loci (*ssmm*), Mid is dominant to Long (Mid: *sM-*), and Short is epistatic to Mid (Short: *S---*). Preliminary studies of *O. dillenii* subsp. *filipes* (Ornduff, unpub.) also are consistent with this model. Although different genetic systems govern tristily in other sections of the genus, I assume that the "*O. valdiviensis* system" is present in other tristylous members of the Corniculatae since it already is known to occur in two species of the section.

Loss of incompatibility.—An early stage in the breakdown of a trimorphic incompatibility system in the Corniculatae was the reduction and, in some species, loss of self-incompatibility. In general where self-incompatibility and self-compatibility occur in closely related taxa, the latter is considered to be a derivative condition (Lewis, 1954; Stebbins, 1957). In distylous species the development of self-compatibility may occur via the origin of homostyles without corresponding mutation at the incompatibility locus. In such plants, the incompatibility alleles may continue to function, but because pollen having the incompatibility characteristics of one floral form is combined with carpels of the other form in a single flower, self-compatibility is achieved and the outbreeding function of the self-incompatibility alleles is circumvented. In some species of the Corniculatae, however, self-compatibility occurs in the absence of homostyly, although self-compatible homostyly also is present in the section. Moderate to strong self-compatibility exists in some or all of

the floral forms of the heterostylous *Oxalis grandis*, *O. priceae*, and *O. dillenii* subsp. *filipes*. Therefore, it is clear that in the Corniculatae the development of self-compatibility preceded the development of homostyly, whereas in many other genera self-compatibility has been possible only as a consequence of homostyly.

In the Corniculatae the evolution of self-compatibility has been the result of a stepwise series of genetic changes. Different degrees of self-compatibility are present in various of the species, and within some species certain of the floral forms exhibit stronger self-compatibility than do others. The genetic basis for these changes is unknown, but the occurrence of this graded series suggests that a multiallele and/or polygenic system governs the operation of the incompatibility-compatibility system in this section.

Derived dimorphism.—The initial step in the evolution of the Long-Short distyly characteristic of two subspecies of *Oxalis priceae* was the loss of the *M* allele, after which only Longs (*ssmm*) and Shorts (mostly *Ssmm*, some *SSmm*) are present in populations. In the absence of the *M* allele, this system is similar to the diallelic systems which occur in distylous species of other families. This genetic system has been shown to exist in *O. priceae* subsp. *priceae* (Mulchay, 1964) and subsp. *texana* (Ornduff, unpub.). Subsequently, additional genetic changes have occurred which reinforce this morphological dimorphism; the most obvious of these are reflected in the change of position of the mid-level anthers away from the true mid-level position in the direction of the long and short levels.

The derived dimorphism which seems to have evolved in addition to homostyly in *Oxalis albicans* and perhaps *O. filiformis* is one in which Longs and Mids only are present. Such a system can be explained by loss of the *S* allele, with the result that Shorts no longer appear in any progenies of the two remaining forms. Eiten's descriptions of these species suggest that

some or perhaps all of the populations of their heterostylous races are monomorphic, with either Longs or Mids present in a population but not both. Genetically, such populations can be explained by the absence of the *M* and *S* alleles in populations of Longs (*ssmm* only) and of the *m* and *S* alleles in populations of Mids (*ssMM* only). At the ultimate end of this allelic-loss series are species such as *O. rufescens*, known as Mids only, and *O. theloxys*, which seems to be made up of Longs only.

The origin of homostyly.—By analogy with the postulated structure of genes governing distyly (Lewis, 1954), it seems likely that in the Corniculatae the *S* and *M* loci are each occupied by a “supergene,” which is fundamentally a series of extremely tightly linked adjacent genes each of which governs some feature of the morphological-physiological syndrome that is associated with the expression of tristily. On this basis, one genetic explanation for the origin of semi-homostyly is that it is a result of crossing-over or mutation within a supergene, specifically involving those loci which are concerned with the morphological features of heterostyly. Such genetic alterations could easily result in the production of plants having flowers which show, for example, the style length of one form combined with a length of one set of stamens that is characteristic of another form. Since this type of recombinant homostyly has occurred in a number of dimorphic genera, it is reasonable to assume that a similar mechanism may be responsible for the semi-homostyly in the Corniculatae.

The quasi-homostyly of various races of *Oxalis dillenii*, *O. corniculata*, and some of the South American species is one in which the positional relationships of anthers and stigmas is basically a heterostylous one. The length of these reproductive structures and the overall size of flowers are strongly reduced and autogamy prevails. Such quasi-homostyles probably largely retain the genetic apparatus which governs the morphological as-

pects of tristily; this is supported by the appearance of fully heterostylous, large-flowered Longs and Shorts in progenies of crosses between a quasi-homostylous race (a reduced Long, as in Fig. 6c) of *O. dillenii* subsp. *dillenii* and both forms of the distylous *O. priceae* subsp. *texana* (Ornduff, unpub.). In quasi-homostylous races a system of genetic modifiers which serves primarily to reduce the overall size or length of the perianth, styles, and stamens is probably associated with the genes governing tristily. Further support for these speculations concerning the genetic basis of semi- and quasi-homostyly could be verified by detailed study of *O. dillenii* subsp. *jilipes*, since this subspecies exhibits nearly the full range of variation in floral structure that occurs in the Corniculatae.

Most of the morphological and physiological changes in the breeding systems of the Corniculatae have been in the direction of increased inbreeding. The initial alteration in the evolutionary sequence leading to autogamy was a reduction and eventual loss of self-incompatibility. The development of self-compatibility per se does not necessarily increase inbreeding, but there is evidence that under natural conditions a high proportion of illegitimate pollination of heterostylous flowers may occur (as in the saxifragaceous genus *Jepsonia*; Ornduff, 1970; 1971). Under these circumstances inbreeding would be enhanced as a result of illegitimate fertilizations. It is probable that in the self-compatible heterostylous Corniculatae an increased degree of inbreeding is a consequence of selfing and near-neighbor matings. In addition, in some heterostylous taxa such as *Oxalis dillenii* subsp. *jilipes*, inbreeding is further augmented by the production of the smaller mostly autogamous flowers that are produced as the flowering season progresses. In connection with the gradual loss of an incompatibility system is the loss of associated “secondary” morphological characters such as differences in pollen size and stylar orientation. In some phyletic lines of the Corniculatae the degree of inbreed-

ing has been further enhanced by the origin of autogamous semi- or quasi-homostyles as well as by cleistogamy. Coupled with these trends has been the gradual development of autogamous monomorphism, which may be viewed as the final development of one phyletic sequence.

Two interpretations are possible concerning the origin of derived dimorphism in the Corniculatae. One of these is that dimorphism is a means of achieving a stable balance between inbreeding and outbreeding. Dimorphism perhaps results in a higher degree of outbreeding than does trimorphism, since the chance of a legitimate pollination occurring between nearest neighbors is $\frac{2}{3}$ for a trimorphic taxon and $\frac{1}{2}$ for a dimorphic one. An alternative explanation for the origin of derived dimorphism lies in the possibility that one of the forms of the ancestral trimorphic taxon has a lower fitness than the other two. For example, Mid of *Oxalis suksdorfii* produces little seed. Likewise, it has been suggested that under conditions of inbreeding in *O. prickeae* subsp. *colorea*, Mids will be selected against because they produce fewer surviving offspring than do either Longs or Shorts (Mulcahy, 1964). The reproductive behavior of Mids in *O. dillenii* subsp. *filipes* is also somewhat different from that of Longs and Shorts. Although reproductive data are not available for Shorts of *O. grandis*, the reproductive traits of its Mid are different from those of Long. Thus, there is evidence that in the Corniculatae Mids often play a role in the reproductive system that is different from that of Longs and Shorts; it is possible that these differences account for the elimination of Mids in some phyletic lines.

The changes in the breeding systems of various members of the Corniculatae are associated with changes of ecological characteristics in the group. Species with relatively conservative outcrossing systems such as *Oxalis grandis* and *O. suksdorfii* occupy stable, geologically old plant communities and have relatively restricted geographical ranges. In contrast, the inbreeding *O.*

corniculata, *O. stricta*, and *O. dillenii* subsp. *dillenii* are well known wide-ranging weeds of disturbed habitats whose distribution and colonizing ability are undoubtedly enhanced by their largely autogamous breeding system. Although the distributional and ecological contrasts between these two groups of species with different breeding systems are striking, the outcrossing members of the Corniculatae show two characteristics that seem preadaptive to the weedy condition of the derived inbreeders. One of these traits is the ability to multiply individuals by means of natural vegetative propagation and the other is the general restriction of seedling establishment to periods of ecological disturbance; both characteristics have been discussed above in reference to *O. suksdorfii*. Once increased inbreeding as a result of autogamy became superimposed on those ecological characteristics, the result was (1) an assurance of seed-set without the necessity of external pollinating agents, (2) a reduced generation time, since fertilization occurs before anthesis, and (3) ability to produce large quantities of essentially uniform highly adapted genotypes as a consequence of (1). This combination of characters eventually enabled the autogamous members of the Corniculatae to become characteristic occupants of permanently disturbed habitats rather than of only occasionally disturbed ones. Consequently, in their ecological characteristics, the weedy Corniculatae provide a striking contrast with their progenitors.

It is also clear that reproductive systems in the Corniculatae are still in a state of evolutionary flux. This is particularly evident in *Oxalis dillenii* subsp. *filipes*, in which the diversity of floral structure encompasses virtually the range that occurs in the entire section.

SUMMARY

The degree of outcrossing that is associated with a trimorphic incompatibility system apparently is disadvantageous to the members of *Oxalis* section Corni-

culatae. As a consequence, nearly every evolutionary strategy leading to breakdown of trimorphic incompatibility has been adopted in this group.

The first change that occurred in the breakdown of trimorphic incompatibility was a reduction and eventual loss of self-incompatibility. Concomitant with this loss of incompatibility was a disappearance of various secondary morphological characters (such as pollen-size heteromorphism) that are associated with floral trimorphism, although the trimorphism in style and stamen length was retained in some taxa. In certain phyletic lines (leading to quasi-homostyly) the morphological apparatus of heterostyly has been retained, but because of highly reduced flower size and certain changes in phenology (such as anther dehiscence prior to anthesis) autogamous seed production prevails. In other phyletic lines, alterations at the genetic loci associated with the maintenance of tristily and accumulation of a series of modifier genes have resulted in various semi-homostyly types which combine in a single flower the style- and stamen-lengths characteristic of two forms. The result of these changes is increased selfing which has been further enhanced in some taxa by a decrease in flower size.

Loss of one or two of the floral forms in some taxa has resulted in derived di- or monomorphism which presumably is associated with the loss of one or more of the alleles that govern the expression of tristily. Such a loss may have occurred as a result of chance or as a result of selection against certain genotypes. There is evidence that in some taxa Mids have a reproductive capacity that is different from that of Longs and Shorts. This may account for the disappearance of Mids in some phyletic lines. In some taxa with a derived Long-Short dimorphism, adjustments in position of mid-level anthers has occurred as an adaptation to the absence of Mid stigmas.

Nearly all of the changes in breeding systems that have occurred in the Corni-

culatae are in the direction of increasing inbreeding, although the selective factors that have led to these changes are not clear. In several species increased inbreeding is associated with weediness, whereas those species of relatively stable habitats have retained a more conservative morphological and physiological expression of heterostyly. Nevertheless, certain features of the ecology of the latter species suggest a preadaptation to occupancy of permanently disturbed habitats.

The diversity of floral structure and the associated varying degrees of autogamy within certain taxa of the Corniculatae suggest that reproductive systems within this group are continuing to respond to strong selective pressures in the direction of increased inbreeding.

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