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## CATASTROPHIC SELECTION AS A FACTOR IN SPECIATION<sup>1</sup>

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Speciation is generally considered to be a slow process involving gradual change in gene frequencies. At the same time, some patterns of variation and relationship among many groups of organisms seem explicable only on the basis of rapid genetic reorganization. Mayr (1954), for example, has suggested that the conspicuous differences between island populations of many birds and their mainland relatives may represent rapid evolution as a consequence of "genetic revolution" following drastic alteration of genetic background in newly founded peripherally isolated populations. Among flowering plants, patterns of differentiation are found that suggest a rapid process of speciation at the diploid level in ecologically peripheral populations within continental areas. For example, a study of species relationships in the genus *Clarkia* (Onagraceae) has led me to the conclusion that rapid speciation, involving an abrupt shift in adaptive mode and accompanied by barriers to gene exchange, represents the normal mode of speciation. Furthermore, the available evidence strongly suggests that speciation normally involves catastrophic selection in ecologically marginal populations.

Catastrophic selection as a factor in speciation has received little attention. The purpose of this paper, therefore, is to present evidence that it does play a prominent role in *Clarkia*. At the same time, this genus is not unique in its pattern of differentiation. Consequently, one may reasonably assume that a similar mode of speciation characterizes many other groups. Many genera of plants and animals, like *Clarkia*, have closely related species that show gross differences in chromosome arrangement, often accompanied by differences in basic number. Notable examples among plants are *Crepis* (Babcock, 1947) and *Haplopappus* (Jackson, 1962) in which the direction of chromosome change has been demonstrated. Other genera such as *Amsinckia*, *Arabis*, *Brodiaea*, *Calochortus*, *Daucus*, *Hypericum*, *Lesquerella*, *Madia*, *Phacelia*, and *Trifolium*, to mention only a few that are characterized by several basic numbers, have probably had similar histories of differentiation. Other groups of organisms are like *Clarkia* in showing well-defined sequences of adaptation to more xeric habitats associated with chromosomal differentiation. Verne Grant, for example, has shown such trends within the major phylads of the family Polemoniaceae (1959) as well as within particular species groups such as the *Gilia tricolor* complex (1952).

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And of particular significance, Babcock (1947, p. 155) has indicated that in *Crepis*, one of the genetically best-known genera, adaptation to increasing xeric conditions has been of special importance to its evolution.

*Clarkia* comprises some 35 species, all of which are endemic to western North America, except for a polyploid complex in southwestern South America. The diploid species number 24, all of which are indigenous to California and 21 are found nowhere else. The pattern of relationships within the genus is one of diverse lineages, which have sometimes been referred to separate genera, that are tied together by naturally occurring polyploids (Lewis and Lewis, 1955). Polyploidy as a mechanism of species formation in plants is well understood and, aside from indicating that it does serve to knit the entire group together, no further reference to this aspect of the evolution of the group will be made in this paper. In other words, attention will be directed to mechanisms relevant to the more basic problem of speciation among the diploid outcrossing populations.

The species are all annual and occur in more or less discrete colonies of varying size that form a pattern resembling a distribution on an archipelago with the islands consisting of ecologically suitable sites. The limits of the colonies are usually well defined and generally show little variation in extent from year to year. The seeds have no special means of transport and are ordinarily deposited close to the base of the plant on which they are produced. They are, however, used as food by birds and rodents and are undoubtedly transported to some extent, especially over longer distances, by these animals. Rodents, for example, are known to harvest whole capsules or the entire fruiting portion of the plants and may carry them some distance before removing the seeds. Most of the seeds are retained in the capsules during transport because they are held tightly in the capsules which normally open slowly and discharge their seeds during a period of weeks. The seeds have no required

dormancy and germinate readily under cool, moist conditions. All of the species are self-compatible, although most of them are normally outcrossed because the stigma is held above the anthers and does not mature until about the third day after the flower opens, when pollen from the same flower has already been shed. Self-pollination may occur, however, from a pollinator visiting more than one flower on the same plant, and some races and species are normally self-pollinated.

The diploid species, without exception, are separated by strong internal barriers to gene exchange. Some species cannot be crossed with one another; interspecific hybrids that can be produced are sterile, or essentially so, and this sterility is invariably associated with extensive structural rearrangement of the chromosomes, with or without a change in basic number (Lewis, 1953a).

In the course of their evolution, the diploid species, taken as a whole, have become adapted to a diversity of habitats within the plant communities that represent modern derivatives of the Madro-Tertiary Geoflora. Furthermore, there is a strong correlation between habitat preference and phylogenetic sequence; the derivative species occupy more xeric and presumably more recent habitats than their progenitors (Lewis, 1953b).

#### ADAPTATION AND LOCAL EXTINCTION

The factors limiting the occurrence of species and the physiological basis of differential adaptation between them are particularly relevant to their evolution. Consequently, we have conducted two sorts of simple experiments in order to obtain some idea of the determining factors in *Clarkia*. First, several species were grown under controlled environmental conditions in the Earhart Laboratories at the California Institute of Technology where the variables tested were temperature and length of daylight. But no differential response among the species was detected, and we learned little, except in a negative way, about adaptation that might account



the Santa Ana locality and twice at the Piute locality. Furthermore, 1958–59 and 1960–61 were seasons of extreme drought at both sites.

Today all of the alien species have apparently disappeared from these test sites except for *C. deflexa* and *C. dudleyana* at the Piute locality and *C. unguiculata* at Santa Ana. These exceptional survivors occur naturally at low elevations south of the respective experimental sites, whereas the nonsurvivors are found only in more northern areas or at higher elevations where drought is less severe. Considering the general pattern of rainfall in California, the record of survival and elimination leaves little doubt that availability of water is a principal factor determining successful reproduction of species of *Clarkia* within the area of the test plots: the species tested apparently are not adapted to growing in areas where periodic drought is more severe than in their natural habitats.

Not only have most of the species we planted failed to survive at the test sites, but, of particular importance for our present thesis, one of the indigenous species, *C. similis*, has also disappeared from the Santa Ana locality (table 1). It is too early to conclude that viable seeds of this species are no longer present in the ground at this site, but this is not the only instance of local extinction we have observed. For example, a population of *C. williamsonii* near Dunlap in the Sierra Nevada foothills that was studied in 1946 disappeared in 1948, which was a notably dry season, and has not reappeared since. Another example is a population of *C. biloba* that we studied in 1952, which had not only disappeared by 1959 but had been replaced by the closely related species *C. lingulata* (Lewis, 1961). Our observations of *C. xantiana* in the upper Kern River Canyon also show in a very graphic way the extinction of a local population and its replacement by an adjacent race. We first noticed this site in 1949 because of a small colony of white flowered plants adjacent to a very large colony consisting almost entirely of plants with the normal pink color. The two colo-

nies were separated by a distance of less than ten meters (Lewis, 1953a). Annual observations showed no notable change in the composition of the colonies through 1955. But in that year the winter rains stopped a full month earlier than in any other year for which we have record. The following year, in the spring of 1956, the white colony was as large and vigorous as usual but the pink colony had completely disappeared except for a very few individuals at one margin, presumably because it matured very few seeds the previous year. This pink colony has not recovered, and the large area in which it previously occurred is now occupied by the white-flowered race.

Local extinction appears, therefore, to be a frequent event, but the possibility must be considered that we are merely observing instances of prolonged dormancy. Many annual plants adapted to dry climates are known to survive for many years without germinating, only to appear again abundantly in a favorable season. A notable example is that of *Linanthus parryae*, a desert annual for which we have annual observations covering two decades. We know that seeds of this species remain viable in the ground for at least ten years and probably much longer (Epling, Lewis, and Ball, 1960). But apparently no species of *Clarkia* is adapted to sporadic rainfall such as one finds in the desert and consequently must replenish the local seed supply at frequent, almost annual, intervals. Under conditions of dry storage in the laboratory at room temperature, seeds of all of the species are capable of germinating for about 5 years, but no longer. They may also retain this capacity in the soil in their natural habitats, if they are prevented from germinating. However, the requirements for germination are not very rigorous; seeds of all of the species germinate readily and rapidly if the soil remains damp for a week at a temperature of 10°–15° C. Ordinarily these conditions are met throughout the entire distribution area of *Clarkia* every year. But subsequent rainfall is sometimes not adequate to permit

the seedling to mature and reproduce. Because of the ease and uniformity of germination, inability to mature can be disastrous to a local population.

This is not just speculation; we have demonstrated by simple extermination experiments that seeds are not ordinarily stored in the ground from one year to the next in several species and probably all. For example, we selected a small colony of *C. deflexa* in full flower in the Santa Monica Mountains and divided it into two equal areas containing approximately the same number of plants. From one of the areas all *C. deflexa* plants, totaling 578, were removed before a mature seed was shed; the other was left undisturbed. The following year four plants, less than one percent of the number the previous year, were found in the extermination area and were removed. Furthermore, three of these four plants were in a tight cluster suggesting that we had overlooked a small plant the year before and that they had not come from seeds two years old. The adjacent, undisturbed, area had approximately the same number of plants as in the previous year. The following year there was one *Clarkia* in the extermination plot but it was on the side closest to the undisturbed area and may have come from there rather than from a residual seed in the soil of the extermination area. The next year there were no plants in the extermination area, although again plants were abundant in the adjacent control. Similar results have been obtained with other species (e.g., *C. dudleyana*, Snow, 1960).

These simple experiments demonstrate very clearly that at least some *Clarkia* populations are dependent on a frequent, even annual, replacement of seeds, and the local extinctions we have observed suggest that this is generally true. On the other hand, conditions may be so adverse at some sites in some seasons that many or even most seeds do not germinate. Furthermore, with most species, the capsules may retain a few seeds and may remain on dead stalks for a year and sometimes even longer. Such a holdover will account, for example,

for the populations at the Piute test site in 1960 despite the fact that no plant, indigenous or introduced, reached maturity at that site in 1959. But even though we have observed such recoveries, there can be no question that occasionally local, marginal, populations become extinct because all or nearly all of the seeds germinate and none of the seedlings reach maturity.

Our observations add up, therefore, to the simple and by no means novel conclusion that the ecological margins of distribution of a species are commonly in a state of flux. The conclusions from our observations of *Clarkia* can be summarized as follows: (1) The geographical limits of distribution of a given species within the area occupied by the genus are determined primarily by its ecological range of tolerance and to only a minor extent, if at all, by limitations of seed dispersal. (2) Climatic factors that limit distribution act intermittently: The limiting conditions may occur infrequently. (3) Marginal populations become periodically extinct. (4) Availability of soil moisture is the determining factor causing extinction in the particular instances observed. (5) Following local extinction, the site may again be occupied by the same or by a closely related race or species.

#### PATTERN OF DIFFERENTIATION

Periodic extinction and recolonization such as we have observed has, I believe, played a dominant role in the establishment of genetic deviants and evolutionary novelties, some of which may represent new departures in adaptive potential and an abrupt shift in adaptive mode. This does not mean, however, that geographical speciation as we ordinarily conceive of the process does not occur, but merely that one sees little evidence of it in this genus. Ecogeographical differentiation has, in fact, been detected in all species studied, except those with an extremely limited area of distribution, but this does not seem to have led to the formation of sibling species. At the same time, closely related pairs of species are common in *Clarkia* and several of

these have been studied in detail: *C. biloba*-*C. lingulata* (Lewis and Roberts, 1956; Lewis, 1961); *C. amoena*-*C. rubicunda* and *C. rubicunda*-*C. franciscana* (Lewis and Raven, 1958); *C. unguiculata*-*C. exilis* (Vasek, 1958); *C. mildrediae*-*C. virgata* and *C. mildrediae*-*C. stellata* (Mosquin, 1961). In every instance the evidence, particularly that based on chromosome relationships and breeding habit, demonstrates or strongly suggests that one member of the pair is derived from the other. In other words, species pairs in *Clarkia* are related as parent to offspring rather than as siblings.

Evidence of any process that cannot be observed directly is best indicated by intermediate stages. But such stages are not likely to be found in the case of rapid or abrupt speciation because of its very nature. One does find, however, many deviant, marginal populations that differ from the parental species in varying degrees and in various ways, and these serve to indicate that abrupt discontinuities frequently arise.

Deviant marginal populations are so frequent in *Clarkia* that one often stumbles onto them without making a deliberate or systematic search. They may differ from the parental species in any one or more ways, including morphology, genetic compatibility, breeding structure, and chromosome arrangement. They all have, however, two features in common; they are ecologically marginal, and the discontinuity with the parental populations is abrupt.

One may assume that most deviant marginal populations are ephemeral and destined to become extinct *in situ*. Few warrant taxonomic recognition, but some have persisted and flourished as distinct species, and occasionally, we may suppose, a deviant may set the stage for a successful new phylad of species (Lewis, 1953a). New phylads may result particularly from those deviants that differ from the parental population in basic chromosome number. In the Onagraceae, for example, most genera are characterized by a single basic number, although the number differs from genus to genus (Lewis and Raven, 1961). This sug-

gests that a change in basic number such as characterizes some of the derivative species of *Clarkia* may in some instances set the stage for the evolution of genera.

#### CHARACTERISTICS OF DERIVATIVE SPECIES

The future of any deviant population or species is, of course, entirely speculative, but its origin can sometimes be determined with confidence, particularly when quantitative chromosomal changes are involved or the sequence of structural changes in the genome can be determined.

The most intensively studied example of a derivative species in *Clarkia* is *C. lingulata* (Lewis and Roberts, 1956), and its origin as an independently evolving population at the margin of the parental species, *C. biloba*, is particularly relevant to the thesis of this paper. Consequently, the salient facts concerning the relationship and ecological adaptation of these species will be reviewed briefly as a basis for reconstructing the events that led to speciation.

*Clarkia lingulata* is known from only two colonies at the southern margin of distribution of *C. biloba*, a polytypic species with a moderately extensive distribution in the foothills of the central Sierra Nevada of California. *Clarkia lingulata* differs from *C. biloba* in only one character of external morphology, the shape of the petal (for illustration see Lewis and Roberts, 1956, fig. 2). Nevertheless, they differ markedly in chromosome composition; *C. lingulata* ( $n=9$ ) has an additional chromosome, not present in *C. biloba* ( $n=8$ ), which is homologous to parts of two chromosomes of *C. biloba*. In other words, part of the basic genome of *C. biloba* is duplicated in *C. lingulata*. This of itself indicates the direction of the change. In addition, the genomes differ by a large translocation and at least two paracentric inversions (only one was reported in the original account). Because of these chromosomal differences, the hybrids between them are sterile. In essence, *C. lingulata* is a marginal population of *C. biloba* which differs by a simple morphological trait, several chromosomal differences, and,

as we shall see, in ecological adaptation. Together these differences are sufficient to warrant recognition of *C. lingulata* as a species. At the same time, the closeness of the relationship permits us to reconstruct with a high degree of confidence the steps in the speciation process. Furthermore, this example serves as an appropriate model for the entire genus because the chromosomal repatterning that distinguishes *C. lingulata* from *C. biloba* is comparable to that which characterizes all species of *Clarkia*. Inasmuch as all species are characterized by gross chromosomal differences, we can reasonably assume that chromosome repatterning is an integral part of the speciation process in this genus, and that the same factors are involved. In addition, *C. lingulata* is also representative of derivative diploid species of *Clarkia* because, like the others, it occurs at the ecological margin of distribution of its progenitor.

#### THE PROBLEM OF CHROMOSOME REPATTERNING

The key to understanding the origin of *C. lingulata*, and hence speciation at the diploid level in the genus, is to explain the accumulation of several consistent gross chromosomal differences within a single population that differentiate it from all other populations. One alternative is that the structural and quantitative changes in the chromosomes accumulate as homozygotes one by one over a long period of time through random fixation or because the homozygotes have a selective advantage in the population concerned. The other alternative is that the reorganization of the genomes is a rapid process in which all of the differences became consolidated within a few generations. These alternatives have been considered elsewhere (Lewis and Raven, 1958) and the first alternative has been rejected on the basis of evidence of several sorts, although none alone is conclusive: (1) The derivative species is of very recent origin; (2) the parental species is chromosomally homomorphic or essentially so; (3) the chromosomal differences are not of the same sort as those found as

variable elements within populations; (4) chromosome arrangement is generally stable within all species of the genus. These arguments with respect to *C. lingulata* and *C. biloba* will be restated very briefly.

The morphological similarity between *C. lingulata* and *C. biloba*, their degree of chromosome homology despite rearrangement, and their relative geographical occurrence, indicate beyond reasonable doubt that *C. lingulata* is of recent origin and not a relictual remnant of a species that has had a long history of differentiation. All populations of *C. biloba australis*, the race from which *C. lingulata* is derived, are apparently chromosomally homomorphic. If gradual accumulation of chromosomal differences were involved in the differentiation of *C. lingulata* one might expect some evidence of chromosomal differentiation among populations of the parental race. The chromosome differences that distinguish *C. lingulata* from *C. biloba* are not like those found as variable elements within species. For example, some species of *Clarkia*, but not *C. biloba*, are characterized by high frequencies of translocation heterozygotes and supernumerary chromosomes in wild populations, which might suggest differentiation by the gradual accumulation of chromosomal changes. But the translocation heterozygotes that occur in natural populations invariably show a regular alternate segregation, whereas the translocation that distinguishes *C. lingulata* from *C. biloba* is not regular in its dissociation in the hybrid. Naturally occurring supernumerary chromosomes are found in many species, although again not in *C. biloba*. But in species in which they do occur, they differ in three major respects from the extra chromosome that characterizes *C. lingulata*: they are variable in number; they have a strong tendency to increase in maternal transmission; and they do not pair with the basic genome even when only one extra chromosome is present. Inversions are apparently extremely rare within species of *Clarkia*; in fact, among the several thousand wild plants that have been examined by various work-

ers, only two have been detectably heterozygous for a paracentric inversion and neither of these was among the many individuals of *C. biloba* that have been examined. Nevertheless, *C. lingulata* differs from its close relative by at least two paracentric inversions. In other words, there is no suggestion that variation of the sort required to form *C. lingulata* exists today in populations of *C. biloba*.

A comparable situation apparently exists throughout the genus. Despite the extensive genome reorganizations that characterize different species, chromosome arrangements within a species appear to be remarkably stable and several species are apparently chromosomally homorphic. Even the two chromosomally most variable and most widely occurring diploid species, *C. amoena* and *C. unguiculata*, are each characterized by one arrangement that is most abundant throughout all or nearly all of the area of distribution (Håkansson, 1942; Mooring, 1958). In other words there is little tendency in this genus to form chromosome races within species, notable exceptions being the two chromosome races of *C. speciosa* (Lewis, 1959) and the chromosomal differentiation in *C. dudleyana* (Snow, 1960).

If the chromosomal differences that distinguish *C. lingulata* did not accumulate gradually, then some mechanism must be responsible for rapid reorganization. One possibility is interspecific hybridization and another is a mutator genotype. The latter seems more probable on the basis of present evidence, although the possibility of interspecific hybridization as a mechanism can not be excluded.

Spontaneous chromosome breakage due to particular genotypes has been reported for several organisms, and of particular significance may be genes such as Ives (1950) has recovered from wild populations of *Drosophila* which give rise to a number of chromosome rearrangements in the stocks in which they occur. Although we have not yet discovered such a genotype in *Clarkia*, it offers an attractive pos-

sibility for producing the raw material for a rapid reorganization of the genomes.

Genotypes producing a relatively high level of chromosome breakage would be so disruptive to the populations in which they occur that the gene or gene combination concerned might not persist for long in a given population, and the chances of finding such a genotype may be relatively remote. One might also suppose that most of the chromosome changes resulting from a mutator genotype, particularly those associated with greatly reduced fertility as heterozygotes, would also be eliminated rapidly unless they were highly adaptive as heterozygotes. The general absence of such heterozygotes as variable elements in populations suggests that this is true. We know from one of our experiments, however, that chromosome differences producing low fertility as heterozygotes are not necessarily eliminated immediately, but may persist in a population without significant change in frequency for several generations.

In the experiment designed to test the persistence of chromosomal variation, populations were initiated in natural habitats, as described above, by sowing seeds derived from hybrids between *C. biloba* and *C. lingulata*. Although this hybrid has very low fertility, a few seeds were obtained from extensive backcrossing (Lewis and Roberts, 1956). The backcross progenies, which included individuals of various fertilities and chromosome compositions, were self-pollinated or backcrossed a second time to the parental species. Progenies from these crosses were grown in a block in the experimental field and open pollinated seeds were used for the sowing experiment. From the data on fertility and cytology of the block of garden plants, estimates were made of the initial frequencies of the various chromosome arrangements in the samples sown. The chromosomal differences that were scored are indicated in table 2. The two translocations are easily scored and identified as heterozygotes. One of them ( $T_1$ ) distinguishes the two species and greatly reduces fertility when

TABLE 2. Change in chromosome composition in a synthetic population of hybrid derivatives of *Clarkia biloba* × *C. lingulata*. See text for details

	Translocations heterozygotes		L-chromosome	Inversion heterozygotes	
	T <sub>1</sub>	T <sub>2</sub>		1 inversion	2 inversions
Initial frequency (estimated per cent)	32	13	15	34	17
Frequency after five generations (per cent).					
<i>N</i> = 75	43	14	4	29	14

T<sub>1</sub>. Translocation that distinguishes *C. lingulata* from *C. biloba*; heterozygotes nondisjunctional.

T<sub>2</sub>. Translocation from *C. biloba brandegeae*; heterozygotes disjunctional.

L-chromosome. Additional chromosome of *C. lingulata* that distinguishes it from *C. biloba*.

heterozygous; the other (T<sub>2</sub>), obtained from a population of *C. biloba brandegeae*, segregates regularly as a heterozygote, and causes no reduction in fertility. The additional chromosome from *C. lingulata* is easily identified. Plants monosomic for this chromosome have low fertility, whereas disomics and nullisomics are fully fertile. The inversions could not be distinguished.

Two of the three initial populations have not survived; one was apparently in an area of inadequate rain, and the site of the other was removed by flood. The third population still survives and was examined after five generations. At that time a sample of 75 plants showed that every detectable chromosomal difference in the initial population was still present. The translocations had not notably decreased in frequency and one may even have increased, although this is questionable in view of the possible magnitude of error in estimating the initial frequency. The duplicated chromosome from *C. lingulata* had decreased in frequency but was still in the population, in every instance as a monosomic. Both inversions were still present and probably had not changed significantly in frequency.

The persistence of these chromosomal differences in the experimental population

for five generations suggests that new chromosome arrangements that arise from a mutator genotype, or from hybridization, may remain for a few generations in a population without being eliminated, even when the heterozygote greatly reduces fertility.

#### OBLIGATE ALLOPATRY

*Clarkia biloba* and *C. lingulata* are unable to form stable mixed populations because pollinators apparently do not discriminate between them and sterile interspecific hybrids are produced as readily as intraspecific progeny. As a consequence, the species producing the smaller number of flowers in a mixed population loses a higher proportion of its progeny in the production of sterile hybrids and is soon eliminated. This has been shown by the results from a series of experimental mixed populations (Lewis, 1961). For example, one of the most vigorous of the experimental populations (Kaweah River) was initiated with a seed mixture made up of about two thirds *C. biloba* and one third *C. lingulata*. The two species apparently germinated equally well and grew and flowered with equal vigor, but within four generations *C. lingulata* had been eliminated.

The inability to persist in mixed populations explains the natural spacing of these two species in the Merced River Canyon. In this area each species forms distinct colonies that are not mixed and that do not overlap except at one point of contact. In contrast, each grows mixed to some extent with a closely related species, *C. dudleyana*, in this same area, but no hybrids with this species have been found. At one point where *C. biloba* and *C. lingulata* come into contact, their distributions overlap by about 3 meters and hybrids are frequent within and immediately adjacent to this narrow zone. The overlap is very recent (Lewis, 1961), and is maintained by the integrity of the populations adjacent to it. This boundary is undoubtedly not stable and will change until one or the other species occupies the entire site.

Other pairs of closely related species are also obligatorily allopatric. For example, *C. rubicunda*, which we have argued elsewhere is a derivative of *C. amoena* (Lewis and Raven, 1958), replaces its putative progenitor geographically without overlap in the Coast Ranges of California near San Francisco Bay. The morphological similarity and cytogenetic relationship of these two species closely parallels that of *C. lingulata* and *C. biloba*. They also differ by a single character in external morphology, in this instance by the position of the red spot of color on the petals, a difference which has a simple genetic basis (Hiorth, 1940). The two species have the same chromosome number ( $n = 7$ ), but differ by at least six gross differences in chromosome arrangement (Håkansson, 1947; Lewis and Raven, 1958) which cause the hybrids to be sterile. As in the case of *C. biloba* and *C. lingulata*, mixed colonies do not occur even in the areas where they grow close to each other, with one known exception which was found by Dr. Peter H. Raven after a thorough search for just such a situation. In this instance a few individuals of *C. amoena* and several hybrids were found in a colony of *C. rubicunda* (1.5 miles south of Fairfax, Marin County). The *C. amoena* plants, together with the hybrids, were localized near one margin of the population. Information from garden crosses and field observations leaves no doubt that hybrids are produced as readily as intraspecific progeny, and that pollinators make little if any distinction between the two species. Consequently, a mixed population such as the one that was found undoubtedly represents a transient situation.

The inability of species pairs such as *C. biloba-C. lingulata*, and *C. amoena-C. rubicunda* to persist sympatrically indicates with certainty that the derivative species in each instance must have been spatially separated from the parental race at the time the various differences, particularly the chromosomal differences, became consolidated to produce a self-perpetuating population. Otherwise an innovation com-

parable to the derivative species would undoubtedly be eliminated by hybridization if it arose as a unique or minority element in a population. At least this would be true in the absence of very strong, essentially catastrophic, selection that would in effect prevent all but the unique individual from reproducing at a particular site.

#### CATASTROPHIC SELECTION

Catastrophic selection has been repeatedly noted as a phenomenon, particularly in the spontaneous development of resistant races of insects following application of insecticides, and is regularly used as a technique for obtaining organisms resistant to various pathogens and other stringent environments. But selection in these instances has not resulted in the formation of new species. Furthermore, environments that cause catastrophic selection are generally assumed to be rare and of little if any consequence in species formation. But the factors that cause sudden extinction of peripheral populations, such as we have observed, could produce catastrophic selection; the difference is merely whether or not an affected population includes one or more "resistant" individuals capable of maturing seed when all others are prevented by the environment from doing so. The probability that such individuals are present in a given population is undoubtedly very small. At the same time, extinction of ecologically marginal populations may be a relatively frequent event, as we have seen in *Clarkia*. It follows that if environments which eliminate whole populations are common, vast numbers of individuals are in time screened for exceptional adaptation. The occasional survival of unique genotypes among such numbers becomes inevitable.

Catastrophic selection is of particular significance in the process of speciation because it produces, by elimination of the parental population, immediate spatial isolation of the survivors and their progenies. As we have indicated, isolation is essential for the establishment of derivative species

such as *C. lingulata* and *C. rubicunda*. Furthermore, individuals isolated as a result of catastrophic selection are in a habitat highly suitable for a derivative population to develop. The availability of a habitat in which parental genotypes are absent is particularly important if the survivors have reduced or low fertility relative to the parental population, because selection for full fertility may then occur in the absence of competition with the parental race. In other words, there is an opportunity for the population derived from the survivors to pass through a "bottleneck" of low fertility which would not be possible in the presence of the parental race.

Full occupancy of a given site by the derivatives of a unique survivor, even if many or all of the initial progeny were structural heterozygotes characterized by low fertility, would probably take a very short time not only because of the normal exponential increase in numbers permitted by an unoccupied site but also because of an increase in potential seed production that follows from low population density. The increase in plant size and seed set of many annual plants under conditions of reduced environmental stress is tremendous. For example, the average seed set per individual in one natural population of *C. williamsonii* in 1961 was about 50, whereas plants from seeds of the same population grown under cultivation at Los Angeles produced about 75,000 seeds each. The latter figure is seldom approached in nature except in disturbed sites along roads where the population is sparse and runoff from the road provides ample water. However, the correlation between density and seed set per individual is evident in wild populations of *C. williamsonii* (Wedberg, 1962), and is suggested by some of our extermination experiments. In these experiments, which closely approximate the conditions following catastrophic selection, the few survivors in the decimated plots often produce more flowers than the individuals in the adjacent undisturbed control area.

Once a derivative population has become

established following catastrophic selection, the parental race will be excluded from the site it previously occupied if hybrids of low fertility are readily formed with the derivatives. Even if a parental individual became established within the population of the derivative, all or nearly all of its progeny would be hybrid. At the same time, the derivative species would be unable to effectively migrate into a population of the parental species and displace it unless and until barriers to hybridization develop. The derivative species would, however, be likely to colonize an adjacent or near-by site where the parental species has been eliminated by the environment. Such replacement probably accounts for the recently observed expansion of the range of *C. lingulata* in the Merced River Canyon (Lewis, 1961). In the same manner, expansion of the range of *C. rubicunda* has probably occurred as marginal populations of *C. amoena* have been eliminated by the environment.

Catastrophic selection must act with respect to some physiological difference, which in the case of *C. biloba* and *C. lingulata* is probably the rate of maturation. This is indicated by results from the experimental mixed populations described above, in which *C. lingulata* consistently flowered somewhat earlier than *C. biloba*; the flowering periods overlapped greatly but the peak of flowering differed by about two weeks (Lewis, 1961). The capacity of *C. lingulata* to mature seeds two weeks earlier than *C. biloba* becomes particularly significant when one considers the rainfall gradient along the Sierra Nevada where these species occur. Not only is there generally less rainfall from north to south at a given elevation, but within areas of comparable amounts of precipitation, the number of storms decreases southward. Consequently, in the south the rains may start later in the season and end earlier, and the length of time between effective rains is often greater.

In view of this pattern of rainfall, the occurrence of *C. lingulata* in the Merced River Canyon at the southernmost limit of

*C. biloba* can scarcely be considered a coincidence, because this is the area where populations of *C. biloba* are most susceptible to local elimination as a consequence of drought. It follows from our argument that the two sites now occupied by *C. lingulata* were earlier occupied by *C. biloba*, and I would suggest that *C. lingulata* probably had its origin at one of them. According to the thesis developed in this paper, *C. biloba* was eliminated, perhaps repeatedly, by drought from these sites. But coincident with one of these eliminations, one or more early maturing plants, differing from the norm by several chromosomal alterations, remained as the founders of the population that became *C. lingulata*. Drought of the order that we assume produced the initial selection is an exceptional event. With the return of the environment to its former norm, an essentially stable situation would obtain and might persist for a number of generations. During this stable period the derivative, *C. lingulata*, would not expand its range, but following subsequent periods of exceptional drought, it might do so as a consequence of the extinction or contraction of local populations of *C. biloba*.

Catastrophic selection may occur frequently in marginal populations without the formation of new species. For speciation to occur, the result of selection must be essentially irreversible. In the absence of barriers, notably chromosomal differences, which effectively prevent gene exchange, migration from the parental population might rapidly restore the original genetic norm, particularly if the parental race were better adapted than the derivative to all but the exceptional season. In other words, with free gene exchange, not only is speciation impossible following catastrophic selection, but the resulting ecological differentiation may be ephemeral.

Ecologically differentiated geographical races are evident in many species of *Clarkia*, but these interfertile and often intergrading races have apparently evolved, for the most part, in response to more or less constant environmental factors such as

edaphic differences or contrasting (e.g., coastal vs. inland) climatic regimes rather than infrequent environmental extremes. Furthermore, these races do not seem to represent a stage in the normal speciation process; at least no pairs of closely related diploid species seem to have had such an origin. In this genus, then, speciation and the formation of ecogeographical races appear to be quite distinct phenomena.

#### UNIDIRECTIONAL ADAPTATION AND SPECIATION

The most notable evolutionary trend in *Clarkia* is that all of the derivative diploid species occupy more xeric habitats than their respective progenitors. This uniformity in the direction of adaptation within the genus undoubtedly reflects the conditions under which speciation has occurred.

*Clarkia* has no fossil record, but inasmuch as all of the diploid species are characteristically associated with plant communities derived from the Madro-Tertiary Geoflora (Axelrod, 1958), one may reasonably assume that the history of the genus has been intimately associated with the development of this geoflora and its subsequent migration and differentiation in response to increasing aridity and change in the seasonal distribution of rainfall.

*Clarkia* comprises seven distinct diploid phylads, taxonomically recognized as sections (Lewis and Lewis, 1955). Three of these, *Primigenia*, *Myxocarpa*, and *Eucharidium*, include species that have genomes consisting of seven relatively large chromosomes similar to those that undoubtedly characterized the ancestral *Oenothera*-like stock from which the genus evolved; the other four lineages, on the basis of chromosome evidence, are more recent derivatives. Each of the three older phylads has one species, *C. amoena*, *C. mildrediae*, and *C. concinna*, respectively, that grows in the ecotone between the most mesic woodland derived from the Madro-Tertiary Geoflora and the adjacent forests of Arcto-Tertiary derivation. These three species, which occur in the most mesic habitats occupied by the genus, are apparently the oldest in

their respective phylads (Lewis, 1953b; Lewis and Raven, 1958; Mosquin, 1961). Furthermore, such habitats have been in existence at least since the Oligocene, as is indicated by the plants associated in the Florissant beds of central Colorado, where one finds *Sequoia* and other elements of the Arcto-Tertiary Geoflora together with evergreen oaks and other plants of the Madro-Tertiary Geoflora (MacGinitie, 1952). One may reasonably suppose, therefore, that species of *Clarkia* comparable to the three listed above have long occurred in the ecotone between these two major geofloras. It seems not unlikely that the prototype of *Clarkia* may have been adapted to such a habitat. We have no knowledge of when the differentiation occurred that led to the three oldest phylads, or the factors involved, but all subsequent diploid speciation, which in some instances has led to new groups of species, has apparently involved adaptation to more xeric habitats. This adaptation consists, generally, of more rapid maturation which permits the derivatives to reproduce within a shorter growing season. But these seasons must occur regularly; *Clarkia* has not developed germination inhibitors which, by reserving a large portion of the population as seeds, permit many annual plants to occupy desert habitats where rainfall is sporadic. Seemingly such adaptation lies outside of the genetic potential of the genus, with the consequence that no desert species have evolved.

Several species of *Clarkia*, such as *C. lingulata* and *C. rubicunda*, discussed earlier, are undoubtedly of very recent origin, probably since the last glacial maximum. During this time increasing drought has shifted the geographic distribution of species generally northward and to higher elevations. Peripheral populations at the retreating margin have been eliminated at particular sites, perhaps repeatedly. These are the conditions that would be opportune for new species to arise as a consequence of survival of an exceptional individual in a suitable habitat from which the parental species has been eliminated.

Although several of the diploid species

of *Clarkia* have probably had their origin during the present major cycle of increasing drought, surely the entire genus has not evolved during this time. On the reasonable assumption that species of *Clarkia* were extant during a previous period, when rainfall was increasing, these species presumably migrated in the opposite direction, and populations at the more mesic margins of distribution must have been progressively eliminated. But seemingly this shift did not lead to speciation.

The apparent absence of speciation during wet cycles in contrast to dry may be a consequence of the manner in which peripheral populations of *Clarkia* are affected by the two situations. With extreme drought, a population may be drastically reduced in size or may be completely eliminated. When elimination is not complete, the opportunity exists for restoration of the population by the few survivors, including those with unique genomes. In contrast, with a season of exceptionally high rainfall these annuals respond by growing larger and producing more seeds. A sustained increase in rainfall, however, would result in a gradual change in the composition of the vegetation, which would render a given site unsuitable for *Clarkia*. But elimination under these circumstances would be relatively slow rather than sudden as in the case of exceptional drought. Furthermore, if a population of *Clarkia* is reduced to one or a few individuals as a consequence of a change in the whole community, the habitat would be generally unsuitable and the progeny of the last survivors, even though possessing a unique genome, would not find themselves in an open habitat that would provide an opportunity for a decimated population to pass through a bottleneck of low fertility in the course of reoccupying the parental site; there would be no suitable site to reoccupy.

The consistent direction of adaptation associated with speciation in *Clarkia* can be explained, therefore, by the abrupt but temporary reduction in population size produced by exceptional drought which thereby sets the stage for the development

of unique genotypes in the absence of competition with the parental population.

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#### SUMMARY

Evidence is presented to indicate that catastrophic selection in ecologically marginal populations has had a prominent role in speciation in the genus *Clarkia*.

The following observations compellingly suggest that speciation at the diploid level in this genus ordinarily involves a rapid reorganization of the genome associated with ecological differentiation, a reorganization that involves an intermediate stage of low fertility: Closely related pairs of species bear a relationship of parent to offspring and not one of siblings. They invariably differ by several gross structural rearrangements of the chromosomes, and sometimes by a change in basic number; as a consequence, hybrids between them are essentially sterile. Recent derivatives occur at the margin of distribution of the parental species, but the two species are unable to form stable mixed populations because sterile hybrids are formed as readily as intraspecific progenies; the derivative populations must, therefore, have arisen in isolation. In all instances, derivative species occupy ecologically different, invariably more xeric, habitats than their progenitors.

Catastrophic selection, whereby an entire population is suddenly eliminated by an environmental extreme except for one or more exceptionally adapted individuals, provides the conditions necessary for the establishment of a population characterized by deviant genomes. By elimination

of the parental population, catastrophic selection isolates the survivors and their progenies in an open habitat to which they are adapted. If initial fertility is low because of structural or quantitative chromosomal heterozygosity, selection for full fertility and hence chromosomal homozygosity can occur in the absence of competition with the parental race. Once a fertile derivative population characterized by chromosome rearrangement becomes established, the parental race will be excluded because any migrant would produce only sterile hybrids. At the same time, the derivative would be unable to invade populations of the parental race until and unless barriers restricting hybridization become established.

Direct evidence for catastrophic selection in *Clarkia* consists of the observation that ecologically marginal populations in several species have suddenly become extinct. In one instance, a rare genotype marked by flower color survived when genotypes of the normal color suddenly disappeared. Extinction in all instances resulted from exceptional drought, which throughout the history of the genus has been the most likely cause of catastrophic selection associated with speciation. The physiological basis for the survival of unique genotypes in the material studied has been early seed set.

The absence of derivative species adapted to more mesic habitats than their parents is explained on the basis of response to increased rainfall. Unlike extreme drought, exceptionally high rainfall does not result in the sudden extinction of populations and hence the opportunity for catastrophic selection.

Differentiation of ecogeographic races within species is prevalent in *Clarkia*, but seems to bear little relation to speciation. Ecogeographical races apparently result from more or less continuous and steady selection pressures due to such factors as edaphic differences or climatic regimes rather than to highly intermittent environmental extremes that may result in catastrophic selection.

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