

SPECIATION AND THE FOUNDER PRINCIPLE

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INTRODUCTION

Can an entire new species arise as a population descended from a single individual of an ancestral species? That this is indeed possible in the special circumstance of allopolyploidy is readily admitted by most evolutionary biologists. In the schemes of WALLACE (1959) and WHITE (1968), furthermore, single individuals could also be pivotal, but these cases require a complex role to be played by a special chromosomal 'tour de force.' Thus, the precise question that is being raised here can be more precisely stated as follows. Can an aberration-free, sexually reproducing and cross-fertilizing diploid species produce a single fertilized propagule which is competent to produce a new species?

In view of our modern knowledge of population genetics and speciation, this 'Adam and Eve' idea seems simplistic and improbable at first sight. It recalls some of the crude notions produced by adherents of the mutation theory in the early part of the present century. Accordingly, the idea being set forth here is not the same as speciation by saltation, macromutation or through 'hopeful monsters.' Further, although random drift would certainly be an important associate of single-founder populations, it would not necessarily be associated with speciation. Therefore, the scheme cannot be placed with those theories advanced by some authors (but not Sewall WRIGHT) that species 'can arise by genetic drift.' The species concept being employed in this paper is that which is commonly called 'the biological species' (MAYR 1950), fully subject to the well-known laws of population genetics.

The idea that a single founder could form a species probably first suggested itself to DARWIN as he contemplated the biota of the Galapagos Islands. During his visit there early in the last century, he already recognized these oceanic islands as having 'derived a few stray colonists' from the adjacent American continent, five to six hundred miles away. As every evolutionist knows, the fact that the Galapagos species are largely endemic and are not just slight variations of mainland species, was a major influence on DARWIN's thinking.

For the most part, evolutionary events surrounding the origin of present-day species are not directly observable at this time level. This is in contrast to certain adaptational events which have been observed historically (e.g. industrial melanism in moths) or followed as microevolutionary events in population cages (e.g. DDT resistance in *Drosophila*). The origin of a species, it seems, can only be traced by piecing together its past history with whatever meager evidence remains in existing or fossil organisms. Thus, on the face of it, it would seem to be impossible to prove that an existing species arose from a single founder. On the other hand, if single founders are involved in some way in the formation of species it should be possible, through laboratory manipulations, to bring the process under close observational and experimental scrutiny.

In this paper, I will adduce evidence that indicates, in some cases at least, that passage through a single founder individual has occurred as a pre-condition for speciation. Even if a strong case is made for this, however, the question remains as to how widespread this scheme may be in diverse biological situations. Could it be that geographical speciation frequently operates in this way? Because of the obvious difficulties of observing the role of founder individuals in speciation, it may not be possible to apply the idea universally but there is no intrinsic reason why, if it can occur at all, it could not occur very widely indeed. In any event, if it can occur at all, it would appear to be worth consideration as a limiting, if exceptional, case.

The founder principle was proposed by MAYR (1942) and considerably elaborated in his 1954 paper. Still later (1963), this author defined the principle as referring to the:

"establishment of a new population by a few original founders (in an extreme case, by a single fertilized female) which carry only a small fraction of the total genetic variation of the parental population."

No mention is made in this definition as to whether the founding event leads to new species or not. Thus, it could equally well refer to simple colonization of a field by a weed. Nevertheless, the emphasis in my paper will be on MAYR's extreme case, i.e., that of single individuals and will attempt to relate the founding event specifically to species formation.

Most discussions of the founder principle, like those of MAYR, do not deny a role for single founder individuals. Nevertheless, the subject is treated with the attitude that at least a small number of individuals must usually be involved in a successful founding event (see, for example, CARLQUIST 1966, MACARTHUR and WILSON 1967). Generally, the discussions relegate the single species-founder case to a relatively unimportant position within the framework of the theory.

As DOBZHANSKY (1970) has pointed out, the founder principle embodies features which would lead to random drift of gene frequencies (WRIGHT 1955). As developed in the present paper, furthermore, it represents an example of what WRIGHT has called an 'unique event' in its effect on gene frequencies.

After reviewing the evidence for the role of single founders, I will consider the possible genetic effects of such extreme conditions, addressing myself to the question of the extent to which genetic systems are capable of withstanding such drastic reductions in population size.

Consideration will be given to the question whether certain organisms have a genetic system which would prevent them from forming other species through single founders. This will lead into the subject of genetic competence of a population for speciation.

Finally, consideration of the single-founder cases raises the possibility that the process of adaptation is somehow drastically altered at the time the founding event occurs. A model will be suggested which attempts to separate, in part, the events leading to the origin of a new species from the processes whereby new adaptations are attained.

GENETICS OF INSULAR POPULATIONS

Very little attention has been given to the genetics of natural populations of insular terrestrial organisms, particularly those found on oceanic islands. This neglect is all the more remarkable because of the important role such organisms have played in the development of modern evolutionary theory. The conditions on oceanic islands have always been considered by evolutionists to have a useful relative simplicity. The historical aspects of volcanic islands are simpler than their volcanic counterparts on the continents. Not only this, but the organisms are fewer in number and occupy much smaller areas. Oceanic archipelagos sometimes permit the tracing of several evolutionary phases in a geographically sequential fashion. Although the terrestrial ecology of volcanic islands may seem to be as refractory to analysis as a comparable area on a continent, geographical, altitudinal and climatic restrictions aid simplification.

For reasons of accessibility to the laboratory and ease of handling, most of *Drosophila* species which have been used for studies of the genetics of natural populations are widespread continental forms. Thus, the *obscura*, *virilis*, *robusta*, *willistoni*, *melanica*, *repleta*, *cardini* and *affinis* groups, on which so much analytical work has been done are all basically continental forms. Although some of these groups have insular species or subspecies in the Caribbean or Mediterranean areas, the islands involved are mostly continental ones or, if oceanic, they are so imperfectly isolated that they lack the distinctive features of the true oceanic islands or archipelagos such as Galapagos, Hawaii, Tristan da Cunha or Lord Howe-Norfolk Islands.

GENETICS OF HAWAIIAN DROSOPHILA

A preliminary approach to the filling of this need has been made by a team which recently undertook a study of the *Drosophila* species found on the Hawaiian islands (see CARSON et al. 1970 for a review). Although it was one of the original objectives of this work, only very minor progress has been made in developing a basis for a genuine comparative population genetics of insular and continental forms. Such a comparison may yet be possible and yield fruitful insights. On the other hand, attainment of this goal has been delayed by the uncovering of many remarkable and unexpected aspects of the basic genetics and evolution of the insular forms. In short, this has led to more of the initial effort being put into the gathering of data on the broader aspects of the evolutionary biology of these flies, especially phylogenetic patterns. This has led to data which bear to a considerable extent on the founder effect, the general subject of this paper. As will be shown below, however, some of the phylogenetic data provide a new insight into the peculiarities of the genetics of insular evolution. In short, they have aided in the pinpointing of those species and those populations which are currently the most active in a microevolutionary sense.

Accordingly, it may be useful to recount, in summary fashion, some of the basic facts which pertain to the Hawaiian *Drosophila* (details will be found in CARSON et al. 1970).

1. THE NUMBER OF SPECIES

In 1948, ZIMMERMAN estimated the number of endemic species in the family Drosophilidae from Hawaii as 57. When he became aware of the discoveries of D.E. HARDY, made during the ensuing ten years, ZIMMERMAN (1958) raised his estimate to 300 and made a dramatic call for the study of the situation. With the publication of HARDY's

monograph in 1965, more than 400 endemic species had been described. In CARSON et al. (1970), HARDY states that about 500 have been presently described and now estimates that the total fauna may reach 650 to 700.

For those who think in terms of mainland *Drosophila* flies, a word or two about the taxonomy of these species may be helpful. Thus, the list contains few, if any, cryptic species distinguished only by tests of reproductive isolation. They are what most taxonomists would refer to as 'alpha' species, one easily characterized by simply-observed morphological traits.

2. SIZE OF THE ISLANDS

The Hawaiian land mass is relatively small, being less than 6500 square miles. Between one-third and one-half of this terrain furthermore, is unsuitable for *Drosophila*, so that the flies are in effect concentrated in mountainous areas between 1000' and 5000' elevation. Accordingly the species are even more restricted than the simple geographical facts would indicate.

3. GEOLOGICAL FEATURES OF THE ARCHIPELAGO

The drosophilid fauna is essentially confined to the six islands of major size at the southeastern end of the archipelago (Figure 1, upper). These extend for about 400 miles and are separated by channels of various widths. Potassium-argon dating studies reveal that the oldest lava flows are on the most northwestern island (Kauai), with dates indicating an age of between five and six million years. As one proceeds southeastward, the islands give evidence of being progressively younger. The lava flows from the oldest of the five volcanos of the island of Hawaii appear to be no more than 700,000 years and two of the volcanos are still active.

The entire archipelago is one of the most isolated in the world. At the present time, it is more than 2000 miles to the nearest land mass in any direction. The leeward islands, to the north and west of the main islands, are low atolls and seamounts, having no relevant fauna today. Evidence exists, however, that at one time these were high islands capable of colonization from some mainland source. In view of this, it seems prudent to consider the age of the archipelago as approaching 10 million years, with these islands representing the oldest.

THE ULTIMATE ORIGIN OF THE HAWAIIAN DROSOPHILIDAE

In a landmark study of the comparative anatomy of the endemic Hawaiian *Drosophila*, THROCKMORTON (1966) made the remarkable discovery that all of them could be assigned to one or the other of two major groups, which may be called the scaptomyzoids and the drosophiloids. This finding was unexpected because of the development in many species and species groups of bizarre features of external morphology. These characters so impressed the earlier taxonomists that a number of genera and subgenera were erected for them. THROCKMORTON's work revealed that most of this variation was phylogenetically superficial and that underlying similarity in basic anatomical features was striking.

About 110 of the species are large, conspicuous forms mostly characterized by maculations on the wings ('the picture-winged species'). CARSON and STALKER, in a series of papers (e.g. 1969,

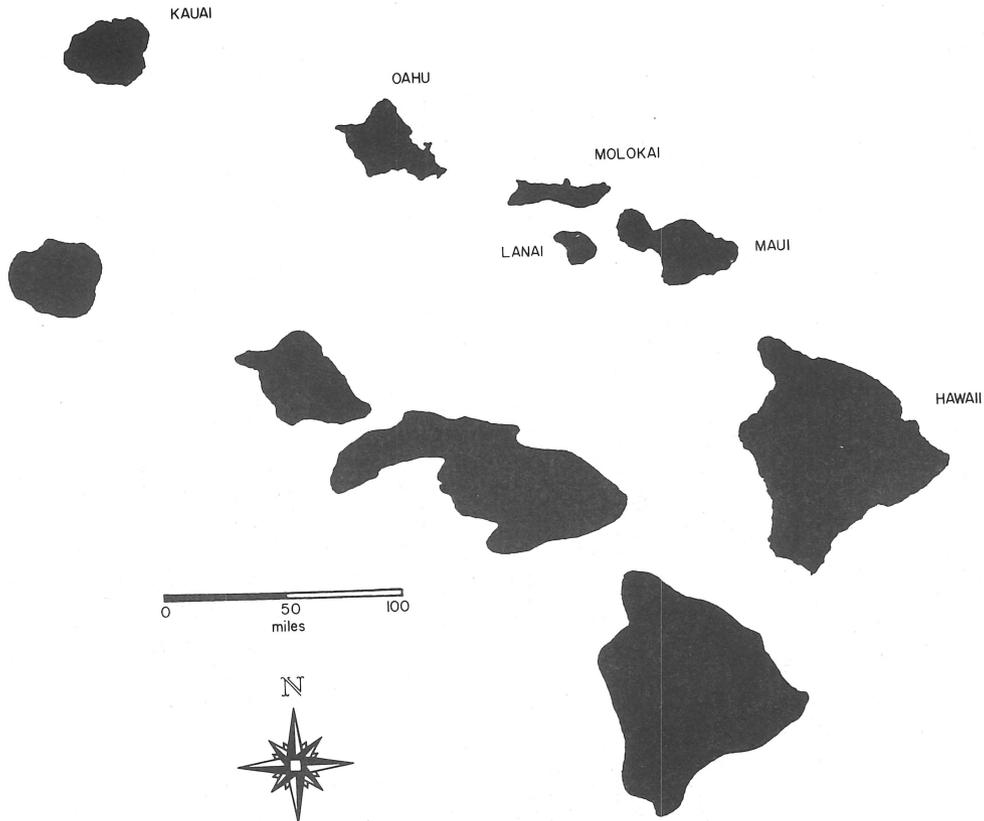


Figure 1. The major Hawaiian islands. Upper: The islands at the present stage of the level of the sea. Below: The appearance of the islands at 1000 feet below present sea level (after ZIMMERMAN 1943).

and CARSON 1971) showed that these flies can be described in terms of a single set of polytene chromosome standard sequences, that is, the sequences of the chromosomes were not so altered by inversions as to prevent the 'reading' of the number of steps whereby the changes occurred. This permitted the grouping together in a close phylogenetic scheme of such morphological oddities as *D. setosifrons*, which has reduced ocellar bristles and in their place there is a dense patch of black setae and the 'idiomyias,' a complex of species, mostly of giant size, with an extra wing-vein.

A third major method whereby elements which appeared biologically disparate was shown to be unified was through the studies of behavior by SPIETH (e.g. 1968). These observations provided an independent assessment of the two phyletic lines recognized by THROCKMORTON, the scaptomyzoids and the drosophiloids.

In discussing the fact that the Hawaiian flies seem to fall into these two major groups, THROCKMORTON (1966) says that at most two introductions (Trans-Pacific colonizations) . . . "presumably of a single individual each" . . . would be required as ancestors of the scaptomyzoids and the drosophiloids. On the other hand, THROCKMORTON reports on a number of unusual species from Hawaii which appear to lie in a position intermediate between these two rough groups (see also KANESHIRO 1969). Nowhere else in the world does the generic distinction between *Scaptomyza* and *Drosophila* tend to be blurred by the existence of quasi-intermediate forms. This has led THROCKMORTON to suggest that the scaptomyzoids, indeed the genus *Scaptomyza*, originated on Hawaii from drosophiloid-like ancestors.

This theory, which is strongly supported by many relevant facts, carries the implication that, first, the world-wide genus *Scaptomyza* had its origin in Hawaii and, what is more important in the present connection, that there may have been only a single original trans-Pacific colonization of Hawaii as a founder of the endemic *Drosophilidae*. This is postulated to have been a single specimen with drosophiloid affinities.

If this is true, and the weight of anatomical and behavioral evidence indicates it is, this means that this one chance migrant, of about five million years ago, was ancestral to around six to seven hundred existing species. Of course, one does not need to use only the case of *Drosophila* of Hawaii to find evidence for such founder events. Thus the 'finches' of Galapagos, the honey-creepers and many other groups of Hawaii (see ZIMMERMAN 1948) provide independent evidence for the operation of the single-founder principle. Nevertheless, the very striking nature and broadly based evidence of the Hawaiian *Drosophila* case is compelling. As will be seen shortly, further operation of the founder principle is evident.

The geographical origin of the founder of the Hawaiian *Drosophilidae* is of course not known. There is, nevertheless, evidence these flies are derived from certain Palearctic or Nearctic elements THROCKMORTON 1966). STALKER (1968) has reported on a study in which he has compared photographic salivary gland chromosome maps of members of different species groups of *Drosophila*. In a number of cases, visibly homologous chromosome segments are found and in some cases deductions as to the phylogenetic relationships between groups are possible. Of the various mainland species groups, STALKER has found that the robusta group is the most closely related to the Hawaiian flies which he has studied. Of the Hawaiian flies, one of the closest is *D. primaeva* of Kauai which stands in an intermediate position between the mainland forms and all of the other picture-winged species on the newer islands.

Accordingly, this evidence indicates that *D. primaeva* is indeed primitive and that the rest of the picture-winged flies are phylogenetically more recent. This is, of course, in agreement with data which indicate that the southeastern islands of the archipelago are geologically more recent than Kauai. The colonization patterns of these islands are thus directional and permit more accurate inferences concerning the operation of the founder principle.

Such inferences are made somewhat easier by several other considerations. Study of the geology of the archipelago (STEARNS 1966) indicates that, if the level of the sea were 1000 feet lower than at present, the three islands of Maui, Molokai and Lanai would be joined to form a single island ("the Maui complex"). There is indeed strong evidence that such fluctuations in sea level have occurred during the Pleistocene and that these three islands were joined together into one at least twice in the not too distant past. Accordingly, for long-range historic and biogeographical purposes, the number of major islands may be reduced from six to four (Figure 1, lower).

SINGLE ISLAND ENDEMISM

Of the approximately 110 picture-winged species now known in collections, 95 have been analyzed cytologically at the time of writing. This figure includes material from thirteen species for which the data are still unpublished. All but two of the total, that is 93/95, are single-island endemics, in other words, are geographically confined to one island alone. These are distributed as follows: Kauai 9, Oahu 26, Maui Complex 35 and Hawaii 23.

Cytological analysis of the banding pattern of the giant chromosomes has been carried out for these species. All species can be related by visual analysis of chromosome inversions to a single set of standard sequences for each chromosome; namely, those found in *Drosophila grimshawi*. As detailed by CARSON and STALKER (1968, 1969), CARSON et al. (1970) and CARSON (1971) it is possible in the first place to group, as genetically related, those species having specific fixed inversions in common. Secondly, particular sequences or inversion combinations can be utilized as tracers to estimate the chromosomal makeup of putative ancestral founders as the colonization of the southeastern islands has proceeded. This has been done and a list of 23 putative founders has been prepared (see CARSON et al. 1970).

THE FOUNDER PRINCIPLE AND THE ISLAND OF HAWAII

There are several reasons for choosing the Island of Hawaii for special consideration. The island is large and geologically new; there are no lava flows, in fact no geological formations known, for which K-Ar dates are older than 700,000 years. The closest island, Maui, is 30 miles away across an abysmally deep channel, so that it is clear that the two islands were never joined. Despite its larger size, Hawaii has fewer picture-winged species than Maui. Furthermore, all 23 of the species which have been studied represent unique species endemic to the island.

The very fact that the island of Hawaii has only endemic species appears remarkable, especially in view of its great ecological similarity to nearby east Maui. Ecologies are of course never identical, but one is greatly struck, especially in the wet forests, by the fact that the major plant associations seem transplanted bodily from Maui. The plant species which support the common picture-winged species, *Cheiodendron*, *Clermontia*, *Charpentiera*, *Dracaena* and *Pisonia*, for example, are basically unchanged and colonization in most of these

appears to have occurred without speciation. Yet, so far, not a single authenticated case of a colonization without speciation is known in the case of the picture-winged *Drosophila*.

The twenty-three species of *Drosophila* from the island of Hawaii fall into eleven groupings (Table 1). Each grouping shows an unique combination of gene sequences. The five major chromosome arms are designated: X, 2, 3, 4, 5. When this designation alone is given, the standard gene order, as found in *D. grimshawi*, is designated. Arrangements differing by fixed inversions are indicated by lower-case letters, occasionally with superscripts. Each combination given in the table serves to 'trace' or identify the members of each grouping. Within the groupings the flies are either very close or identical in giant chromosome banding order. Between the groupings, however, there is strong disparity such that the members of a grouping are more closely related to species known on other islands than they are to the members of another group on Hawaii. Examination of Table 1 will show that in nine of these groupings one or more candidates for an ancestor are present on the neighboring island of Maui. Each is considered to be a case of descent from an interisland founder which is given a number in the table. In the other two cases, the required ancestral chromosomal conditions are known on Kauai and Oahu. Accordingly, founders No. 3 and 10 are postulated to have been derived from these two islands respectively.

Details of most of these cases have been published in the references referred to above but several interesting cases are new. The first such case refers to one of the descendants of proposed founder No. 21, called *n. sp.* No. 1. This is of interest because the specimens concerned resemble *D. grimshawi* which is one of the two species of the 95 studied which is found on more than one island. Thus, specimens of *D. grimshawi* from Oahu, Kauai and the Maui complex give no evidence of reproductive isolation. F₁ hybrids so far studied are fertile.

Although *D. grimshawi* is an abundant fly on Maui, only three specimens resembling this species are known from Hawaii. The reason for its rarity is not known. On two of these three specimens no breeding information was obtained. The third, a male, was collected in the Kohala Mountains in August 1970 by Mr. K. Y. KANESHIRO. When this male was crossed to virgin females from Maui, carrying the standard gene arrangements, the result was sterile F₁ males but fertile F₁ females. Such hybrid male sterility frequently accompanies true specific differentiation.

A second case involves a species (*n. sp.* No. 2, Table 1) resembling *D. villitibia* of Maui of which stocks were obtained from the Puuwaawaa area on Hawaii for the first time in December 1969. The results of a cross of virgin females from one of these stocks by a male *D. villitibia* from Maui made by Mr. KANESHIRO again produced sterile males as in the first case. It is concluded that the Puuwaawaa flies also constitute a new species and represents a separate introduction (No. 24, Table 1) into the island of Hawaii.

THE CASE FOR SINGLE FOUNDERS

In accordance with the theme proposed at the outset of this paper, I wish to advance the hypothesis that these eleven founding events were accomplished by eleven single gravid females, each derived from a population ancestral to certain present-day species on the donor island.

In support of this hypothesis, the argument may be advanced that if colonization of an ecologically similar area is accomplished by a

Table 1. Origin of the species endemic to the island of Hawaii.

Species on the island of Hawaii	Founder number	Probable island origin	Chromosome tracers*
<u>grimshawi subgroup species</u>			
hawaiiensis silvarentis heedi	19	Maui	Xa ² 2 3g 4u
murphyi ciliaticrus engyochracea	20	Maui	Xg
n. sp. No. 1 sproati	21	Maui	X 2 3 4 5
ochracea claytonae	22	Maui	5a
n. sp. No. 2	24	Maui	2b
conspicua alsophila assita	18	Maui	X 2 3 4b 5
macrothrix	23	Maui	3i 5d
<u>planitibia subgroup species</u>			
setosifrons	3	Kauai	3de 4hij 5e
silvestris heteroneura	17	Maui	Xpqrst 3d
<u>adiastola subgroup species</u>			
setosimentum ochrobasis	15	Maui	Xm ² 3l 4b ²
<u>punalua subgroup species</u>			
basisetae paucipuncta prolaticilia	10	Oahu	Xef 3z 4efg

*for explanation, see text.

series of propagules from the same donor species population, the net result should be the simple colonization of the new area by the donor species rather than the founding of a population leading to a new species. The degree of biological disparity between old and new populations, under the circumstances of multiple propagules would be expected to be biologically minor and at most to represent subspecific differentiation. This expectation is based on observations of colonization patterns of less isolated areas or cases where it can be proved that colonization is regular and continual.

Conversely, the hypothesis holds that if colonization is accomplished by a rare single propagule, the break in the gene pool may be significant enough to result in drastic reconditioning of the gene pool of the new colony, much in the manner envisaged by MAYR (1954) and called by him a "genetic revolution."

The further argument may be advanced that single founders may be more likely to become successfully established and serve as a species-founders if the competition is low at the colonizing site. A

geologically new island, such as Hawaii, would be expected to provide ecological conditions under which competition would be minimized.

Conditions of low competition might lead, following the founding event, to another phenomenon, the population flush. In 1968, I considered the genetic consequences of such sudden population spurts and suggested that relaxed selection, increase in population size and genetic recombination could lead to great genetic differences in the population remnants or demes which are left after the inevitable population crash occurs. Such changes would be expected to be initially unrelated to the forging of new adaptations and might indeed represent a basically non-adaptive phase of evolutionary change. Such an abrupt series of events might be an initial genetic move in the direction of speciation essentially divorced from the monitoring effects of natural selection. I will return to a discussion of this later.

GENETIC PROPERTIES OF FOUNDERS

The question arises whether a large, normally cross-fertilized population can be forced through a single pair of individuals and retain a promising evolutionary future. I have already reviewed the evidence that some large groups of species can arise through single founders. This indicates that, when a population derived from a single founder expands, the loss of genetic variability expected through random drift can be expected to be temporary and can be compensated for by new mutations. Even in experimental work, when single sexual individuals are used as founders of lines or laboratory stocks, the reduction of total variability is only temporary if expansion of the population again ensues. It should be remarked, however, that very little specific experimental information on this topic is available.

In any event, a species founder will be expected to carry only a small fraction of the genetic variability present in the ancestral population. SELANDER et al. (1969) cite evidence that a single individual wild house mouse may carry about 1/5th of the genetic variability present in the population from which it was drawn. Compared to the estimates on *Drosophila* this is relatively low. The amount of heterozygosity among kangaroo rats is about the same (JOHNSON and SELANDER 1971) but some species have extremely low mean heterozygosity values. For a successful founding event such very low individual heterozygosity values would be required.

HOMOSEQUENTIAL SPECIES AS SOURCES OF FOUNDERS

Earlier discussions (e.g. CARSON 1959, 1965) stressed marginal populations of continental polytypic species as sources of new species. The arguments supporting this view need not be repeated here except to reiterate the essential point. If chromosomal polymorphism is extensive in the species, the greatest amount of sectional heterozygosity appears to be concentrated in the center of the species range whereas the margins tend to be sectionally monomorphic.

This should impose restrictions on recombination in the center of the range but leave the margins as sites for free recombination. Given equal amounts of basic genetic variability, the marginal populations should be the more capable of responding to selection and thus have a greater capacity to produce an evolutionary novelty.

Although the recombinational difference is considered the pertinent one from this point of view, the question has sometimes been raised whether the total genetic variability, not just inversion variability, is also less in marginal populations. CARSON (1959)

found that marginal populations respond well to selection, in fact, they respond better than central populations. This indicates that much genetic variability is present. Furthermore, PRAKASH et al. (1969), using 24 randomly chosen allozyme loci, showed that the marginal and central populations of *Drosophila pseudoobscura* do not differ in their basic amounts of genic polymorphism. These facts enable us to reemphasize the well-known fact that inversion polymorphism is basically a phenomenon which affects genetic recombination. The gross amount of sectional chromosome variability present in a population does not necessarily serve as an indicator of the amount of genetic variability present.

In contrast to the situation in many widespread continental species, the amount of chromosomal polymorphism is low among the Hawaiian species of picture-winged *Drosophila*. Of the 95 species studied, 65 or close to 70%, are monomorphic for gene arrangement. Of the species which show chromosomal polymorphism at all, it is usually minimal, with only one or two inversions present. Several species, however, are highly polymorphic for inversions, as will be pointed out below.

The observation that most of the Hawaiian species are monomorphic seems to render it likely that most founders derived from these species would also be monomorphic. This conclusion is particularly strengthened by the data available on the homosequential nature of many of the Hawaiian species (see CARSON et al. 1967 and CARSON et al. 1970).

Two or more species may be designated as homosequential if they share a common set of standard gene sequences. Two species may carry polymorphism for inversions but still have a standard set of gene arrangements in common. For example, *D. grimshawi* and *D. disjuncta* are considered homosequential even though in some populations *D. grimshawi* is polymorphic for a particular inversion in Chromosome 4 (gene arrangement 4a). *D. disjuncta* carries the same Standard Chromosome 4 (i.e. is homosequential with *D. grimshawi*) but some of its populations are heterozygous for another inversion, 4v.

Tables 2 through 5 give the basic data on homosequential species. In the summary (Table 5), it will be noted that 59 of the 95 species of picture wings are involved in homosequential groupings. The largest group is composed of eight; all these are homosequential for the Standard gene arrangements. Of the 59 species, 41 are both homosequential and without inversion polymorphism (right-hand column of Table 5).

There seems to be a strong tendency toward monomorphism in certain subgroups. Of a total of eight species in the punalua subgroup, all but one (*D. prolaticilia* of the Island of Hawaii) are wholly monomorphic and five of the species are homosequential. As the species are widely distributed throughout the islands (Kauai-1, Oahu-3, Maui Complex-1, Hawaii-3) it is clear that the founders forming them must have been monomorphic. This same situation can be documented in a number of other cases by recourse to the data in Tables 2 through 4.

The adiastola subgroup, comprising 14 species, also provides data which suggest that the founders of many of these species must have been homokaryotypic in all chromosomes as well as homosequential with the parent species. Thus, Table 6 documents the remarkable fact that at the present time, inversion polymorphism is unknown in 12 of the 14 species of this subgroup. The samples on which this conclusion is based are in some cases quite large. Despite this widespread monomorphism in existing species, however, the members of this subgroup form only a moderate number of homosequential species. This indicates that indeed some heterozygosity has existed in the past within populations of species ancestral to the existing species.

Table 2. Homosequential species among Hawaiian Drosophila grimshawi subgroup: standard 4 phylad; * = have intraspecific polymorphism.

Species	Island	Chromosomal formula				
grimshawi	Kauai, Oahu, Maui Molokai, Lanai					
new sp. No. 1	Hawaii					
villosipedis	Kauai					
atrimentum	Oahu					
*bostrycha	Molokai	X	2	3	4	5
*disjuncta	Maui					
*orphanopeza	Maui					
new sp. No. 2	Oahu					
sejuncta	Kauai					
limitata (6R)	Maui	X	2	3	4	5a
ochracea	Hawaii					
*flexipes	Oahu					
villitibia (6R)	Maui	X	2b	3	4	5
*new sp. No. 4	Hawaii					
musaphilia	Kauai					
gymnobasis	Maui					
*recticilia	Maui	Xa ²	2b	3g	4u	5
*hawaiiensis	Hawaii					
*silvarentis	Hawaii					
heedi (6R)	Hawaii					
balioptera	Maui, Molokai, Lanai	Xg	2	3	4	5
*murphyi	Hawaii					
sobrina	Oahu					
new sp. No. 3	Oahu	Xg	2	3o	4	5
*ciliaticrus	Hawaii					

Table 3. Homosequential species among Hawaiian *Drosophila grimshawi* subgroup: 4b phylad.

Species	Island	Chromosomal formula				
glabriapex	Kauai					
pilimana	Oahu					
vesciseta	Maui	X	2	3	4	5
*aglaia	Oahu					
assita	Hawaii					
montgomeryi (6R)	Oahu	Xk ³ l ³	2	3	4b	5
tarphytrichia	Oahu					
spaniothrix	Oahu					
psilophallus (6R)	Oahu	X	2	3i	4b	5d
odontophallus	Maui					
*macrothrix	Hawaii					
distinguenda	Oahu					
divaricata	Oahu	Xc ³ d ³	2r	3	4	5
inedita	Oahu					
punalua subgroup						
ocellata	Kauai					
punalua	Oahu					
uniseriata (6R)	Oahu	Xef	2	3z	4befg	5
paucicilia	Oahu					
paucipuncta	Hawaii					

Table 4. Homosequential species among Hawaiian Drosophila planitibia subgroup: Xijkopqs

Species	Island		Chromosomal formula			
*neopicta *obscuripes substenoptera	Molokai, Maui Maui Oahu	X	2	3d	4b	5
*oahuensis *neoperkinsi hanaulae	Oahu Molokai	Xt	2	3d	4b	5
planitibia *heteroneura *silvestris	Maui Hawaii Hawaii	Xtr	2	3d	4b	5
adiastola subgroup: Xikouvvyz						
cilifera peniculipedis adiastola	Molokai Maui Maui, Lanai	X	2cd	3fjk	4bopq	5f
varipennis paenehamifera hamifera	Molokai Maui Maui	Xy ²	2cd	3fk	4bopq	5f

Table 5. Homosequential species among Hawaiian Drosophila.

Subgroup	Number of homosequential groupings	Summary	
		Number of species in groupings	Number of species without inversion polymorphism
grimshawii	10	8,6,5,4,3,3, 3,3,2,2 = 39	27
planitibia	3	3,3,3 = 9	3
punalua	1	5 = 5	5
adiastola	2	3,3 = 6	6
Total:	16	8,6,5,5,4,3, 3,3,3,3,3,3, 3,3,2,2 = 59	41

The foregoing considerations suggest that the initial founder is likely to be chromosomally monomorphic (but not, of course, necessarily homozygous at gene loci). Although this may be so, evidence in some cases requires that certain founders be heterokaryotypic for at least one inversion at the time the founding event occurred. Thus, CARSON et al. (1970) list five pairs of species in which the two members of the pair have an identical polymorphism. This can be best explained as a case wherein two descendent species have retained a polymorphism which was present in an ancestral population. I have pointed out earlier (1959) that such cases appear to be very rare in continental species, suggesting that at its origin, a new species is forced through a bottleneck which very frequently results in a monomorphism of the species at its inception. This is clearly not a universal pattern but it does underline the fact that most chromosomal polymorphisms are unique to the species in which they have arisen.

CHROMOSOMAL POLYMORPHISM IN *DROSOPHILA SETOSIMENTUM*
AND *D. OCHROBASIS*

The *adiastola* subgroup has fourteen members; twelve are monomorphic (Table 6). Accordingly, it is very striking that the two geologically most recent species of this subgroup found on the island of Hawaii, are highly polymorphic chromosomally. The two species appear to be derived from a common founder stemming from an ancestral population close to that of present-day *D. adiaastola* of Maui (CARSON 1970). Preliminary investigation of these two species has revealed about nine inversion polymorphisms in each species. The two species do not appear to share any polymorphisms. In *D. setosimentum*, the X as well as the major autosomes all show inversion polymorphism. Some of this variability is widely distributed in the species whereas some of it is restricted geographically.

Table 6. Chromosomal monomorphism in twelve species of the *D. adiaastola* subgroup.

Species	Wild chromosomes examined:		Total
	Autosomes 2, 3, 4 and 5	X Chromosomes	
<i>ornata</i>	72	14	86
new sp. No. 5	24	4	28
<i>neogrimshawi</i>	24	5	29
<i>clavisetae</i>	96	22	118
<i>paenehamifera</i>	16	3	19
<i>hamifera</i>	24	5	29
<i>varipennis</i>	24	5	29
<i>truncipenna</i>	24	5	29
<i>spectabilis</i>	112	21	133
<i>cilifera</i>	112	28	140
<i>penicillipedis</i>	84	18	102
<i>adiaastola</i>	984	190	1174
Total	1596	320	1916

SPECIES FORMATION THROUGH SINGLE FOUNDERS
A PROPOSED SCHEME

The following is proposed as the mode of evolution of new species through single founders. A single propagule, capable of producing a large number of sexual zygotes, arrives by chance in a geologically new environment which is not so saturated with similar species that competition is high. Chance also dictates that this propagule finds itself in an area which is at least moderately favorable to it, so that, in the absence of competition, a population flush occurs. The ensuing large population size permits new mutations to arise and the lowered natural selection during the flush results in the survival of these mutants, at least during the flush phase. Some of these mutants might indeed be dysgenic and might be eliminated if natural selection were more stringent. Released and recombinant genic variability will be maximal if the propagule has a high recombination index, due to relatively high chromosome numbers and absence of sectional restraints on crossing-over, such as polymorphic inversions.

A population which produces propagules with the foregoing properties of the genetic system may be referred to as competent for speciation. Lack of competence is implied, for example, by fixed heterozygosity for inversions or translocations, very low chromosome numbers and obligatory schemes of outbreeding which would lead to inbreeding depression following the founding event. It should be emphasized that such species might be competent for colonization of a new area without speciation. We are especially concerned here, however, with the shifts in the genetic system which are characteristic of the species level of evolutionary differentiation.

To return to the new population stemming from a single founder, we may note that a population crash may be expected to follow the flush, reducing the new colony to a small number of isolated demes. Some of these demes may survive to participate in another flush and crash. This may be repeated a number of times. In volcanic terrain, certain of these demes may find themselves in ecologically suitable areas which are strongly isolated by lava flows.

Under these circumstances, one would expect the gene pool of the new population or populations descended from the founder to be extensively changed genetically when compared with the population ancestral to the founder. The essentially dispersive character of the founding event, the flush-crash cycle and the isolation and inbreeding in demes is considered to be largely responsible for this difference rather than natural selection.

It is proposed that some of these differences, by their chance pleiotropic effects, can be responsible for the origin of characters leading to reproductive isolation. In this view, then, the evolutionary events leading to speciation are separable in time, to a considerable degree, from those which lead to adaptation, as will now be argued.

ADAPTATION AND SPECIATION

Evolution proceeds through two major processes, adaptation and speciation. In their most powerful form, both processes must operate in and be subject to, the laws of population genetics in sexually-reproducing, cross-fertilizing populations. Because of this, of course, the two processes have much in common. Indeed, many evolutionists appear to hold the view that there is no essential difference between them and conclude that the conditions which promote adaptation must equally promote speciation.

The facts presented in this paper dealing with the founder effect and speciation suggest that it may be profitable to reexamine the relationship between the processes of adaptation and speciation. In particular, I would like to explore the possibility that the two processes may be capable of being viewed separately.

THE GENETICS OF ADAPTATION

Since the theoretical work of FISHER, HALDANE and WRIGHT nearly 40 years ago, adaptation has been basically well understood in theoretical outline. It occurs when a large, genetically variable population with free genetic recombination is faced by a new environmental challenge. Natural selection operates to increase, generation by generation, the frequencies of those genes and gene combinations which provide the genetic basis for the newly adapted state.

A great mass of experimental and observational data serve to emphasize that the change is basically one in which individuals in the population having genetically-based adaptations come to characterize a very high proportion of the individuals in the population. Indeed, selection tends to lead toward permanent fixation of the genes conferring adaptation.

Adaptation is a phyletic process. This means that there must be an original condition in which the population concerned is characterized by individuals which are not adapted to a relevant environmental state. After some evolutionary time, of which the sexual generation is the unit, the population comes to be characterized by adapted individuals.

Theoretical and experimental investigations have firmly established that microadaptation does not differ from macroadaptation. By this I mean that adaptations are for the most part forged from the genetic raw materials by the relatively slow inexorable force of natural selection working on gene frequencies in populations. There is no reason to suspect that the adaptations which so impress the ecologist and paleontologist are the outcome of anything other than the basic processes observed in population cages of *Drosophila* or in the historic development of adaptive genetic changes in certain natural populations.

THE GENETICS OF SPECIATION

There is no incontrovertible evidence that speciation, like adaptation, is accomplished gradually in a microevolutionary fashion. Perhaps the most widely held view is that local subspecies and ecotypes are in fact incipient species (MAYR 1963). This view has been perhaps most strongly challenged by GOLDSCHMIDT (1940). He considered that "microevolution, especially geographic variation, does not lead beyond the confines of the species . . ." and ". . . geographic races are not incipient species."

On the other hand, GOLDSCHMIDT's positive view that "Species . . . originate in single macroevolutionary steps as completely new genetic systems" does not seem well founded, especially insofar as the role of what GOLDSCHMIDT called "systemic mutation" is concerned.

I would not go so far as to maintain that no subspecies is an incipient species. On the other hand, where single founders on oceanic islands are concerned, it is quite clear that speciation has not been accomplished by the gradual accumulation of differences as in a subspecies. The appearance of the species gap appears to be abrupt, without intermediate stages. In fact, the differences between

species on the islands of an oceanic archipelago seems to be of a different order of magnitude and of a different nature than the differences within the species. This "gap" between species and subspecies is a phenomenon widely seen in geographical genetics and was the basis of a long and cogent argument by GOLDSCHMIDT.

Cases of circular overlap (e.g. MAYR 1970) are generally considered important as providing very strong evidence that subspecies can reach the specific level in a gradual manner. MAYR, in fact, refers to them as ". . . the perfect demonstration of speciation. . . ." Examination of these cases, however, yields no data which preclude geographical speciation through single founders in the manner proposed above.

In this discussion, it is important to note that the single-founder theory is basically an extreme form of geographical speciation. It need not carry the implication that species formation is possible only by sudden jumps, or macromutations.

If speciation occurs through single founders, the genetic changes which immediately follow the founding event would be expected to be the crucial ones with regard to the origin of reproductive isolation. These changes, not adaptive ones, represent the really critical point in the process of formation of the new species. Chance, not natural selection, plays a principal role in the initial arrival of the founder, in the first population flush and in deme formation. It follows that the genetic changes which would be expected to accompany such events would not be mediated primarily by natural selection and might indeed be unrelated to adaptation.

In this sense, therefore, the key genetic shifts leading to the crucial species differences may be non-adaptive. I suggest that they may precede, in time, an adaptive phase wherein a large genetically variable population is exposed to the usual and well known forces of natural selection.

When one compares two closely related species, differences in adaptation as well as genetic differences producing reproductive isolation are present. Direct observation provides no clue as to whether the two sets of genetic differences are in fact correlated or not. This paper suggests that they may arise and be incorporated into the genome in two separate phases and that their apparent correlation may be spurious.

Finally, this theory is a relatively simple one and is capable of being tested. Competent single propagules can be obtained, an artificial flush and crash cycle induced and the results examined. cursory attempts have already been made to observe speciation under controlled conditions. Failure to observe any significant changes could be due to a number of causes. Little attention, for example, has been given to the subject of competence of a population for speciation or to the careful avoidance of directional natural selection during crucial stages of the flush and crash cycle.

SUMMARY

The proposal is advanced that many species, both in oceanic archipelagos and on continents, arise through single founder individuals. Relevant data are presented on the genetic properties of the putative interisland species founders of Hawaiian *Drosophila*. In order to be competent for speciation, the founder must carry only a small portion of the genetic variance of the ancestral species population and have the capacity to expand, producing a flush. Capacity for genetic recombination throughout the genome must be maximized. It

is argued that the demes formed at the new site following the population crash may undergo a genetic revolution leading to the formation of a gene pool greatly altered relative to the ancestral one. The suggestion is made that in many instances some genetic components of reproductive isolation may arise during an initial developmental stage of the new population. This essentially separates in time the key speciation changes from those relating to adaptation. Speciation, therefore, is thought to have a strong chance element; it may be separated in process from adaptation, which would follow it in time and would be mediated by the well-known force of natural selection.

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