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Source: *Evolution*, Vol. 8, No. 4 (Dec., 1954), pp. 378-388

Published by: Society for the Study of Evolution

Stable URL: <http://www.jstor.org/stable/2405784>

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HYBRIDIZATION AS AN EVOLUTIONARY STIMULUS

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Received July 1, 1954

One of the most spectacular facets of the newer studies of evolution has been the demonstration that evolution has not proceeded by slow, even steps but that seen in the large there have been bursts of creative activity. Some of the evidence for these bursts is from paleontology; Simpson (1953) has recently assembled a wealth of data concerning them and has discussed in detail their possible causes. Paleobotanists are equally aware of such events as the great upsurge of angiosperms in the Cretaceous, and of primitive vascular plants in the Devonian period. Other evidence for evolutionary bursts comes from the existence of large clusters of related endemic species and genera in the modern fauna and flora of certain regions, particularly oceanic islands and fresh water lakes. The snails (*Achatinellidae*) and honey sucker birds (*Drepanidae*) of Hawaii are classical examples, as are also the Gammarid crustaceans of Lake Baikal, and the fishes of Lakes Tanganyika and Nyasa in Africa, and particularly of Lake Lanao in the Philippines (see Brooks, 1950 for a summary and discussion of the data). It is true that some of these examples may represent normal rates of evolution occurring in a restricted area which has been isolated for a very long time, but there can be little doubt that in the case of others evolution has been phenomenally rapid.

As Simpson (1944, 1953) has clearly stated, the cause of this rapid evolution is to be sought in the organism-environment relationship. Along with most authors, however, he has tended to emphasize the peculiar environment present during these evolutionary bursts, and has suggested that one need not postulate

any unusual type of population structure as a contributing factor. Zimmermann (1948) has given a plausible account of the environmental factors operating in the case of oceanic islands; reduction of competition, frequent migration to new habitats, and populations repeatedly reduced to a very few individuals, giving a maximum opportunity for the operation of chance as well as for the rapid action of selection.

To the student of hybridization, however, another factor which may have contributed largely to these evolutionary bursts presents itself. Hybridization between populations having very different genetic systems of adaptation may lead to several different results. If the reproductive isolation between the populations is slight enough so that functional, viable and fertile individuals can result from segregation in the F_2 and later generations, then new adaptive systems, adapted to new ecological niches, may arise relatively quickly in this fashion. If, on the other hand, the populations are well isolated from each other so that the hybrids between them are largely sterile, then one of two things may happen. The hybrids may become fertile and genetically stabilized through allopolyploidy, and so become adapted to more or less exactly intermediate habitats, or they may back cross to one or both parents, and so modify the adjoining populations of the parental species through introgression. This latter phenomenon has now been abundantly documented in the higher plants, and several good examples are known in animals (see bibliographies in Anderson, 1949; Heiser, 1949; Anderson, 1953). By introgressive hybridization elements of an entirely foreign ge-

netic adaptive system can be carried over into a previously stabilized one, permitting the rapid reshuffling of varying adaptations and complex modifier systems. Natural selection is presented not with one or two new alleles but with segregating blocks of genic material belonging to entirely different adaptive systems. A simple analogy will show the comparative effectiveness of introgression.

Let us imagine an automobile industry in which new cars are produced only by copying old cars one part at a time and then putting them together on an assembly line. New models can be produced only by changing one part at a time. They cannot be produced *de novo* but must be built up from existing assembly lines. Imagine one factory producing only model 'T' Fords and another producing model 'T' Fords and also modern station wagons. It will be clear that if changes could only be brought about by using existing assembly lines these would have to proceed slowly in the factory which had only one assembly line to choose from. In the other factory, however, an ingenious mechanic, given two whole assembly lines to work with, could use different systems out of either and quickly produce a whole set of new models to suit various new needs when they arose.

Just as in the example of the two assembly lines, hybrids between the same two species could produce various different recombinations, each of which could accommodate itself to a different niche. When a big fresh water lake was formed *de novo*, hybrids between the same two species could rapidly differentiate into various new types suitable for the various new niches created in the big new lake. A technical point of much significance is that each of the various heterozygous introgressive segments brought in by hybridization would (by crossing over) be capable of producing increased variation generation after generation for periods running into whole geological eras (Anderson, 1939). The enhanced

plasticity due to crossing over in introgressed segments has been shown on theoretical grounds to be present for many generations. Such studies as those of Woodson on *Asclepias* (1947, 1952), of Hall on *Juniperus* (1952) and of Dansereau on *Cistus* (1941) indicate that this does actually happen and that introgressive segments may persist for geological periods and produce effects of continental magnitude.

To students of introgressive hybridization it would seem like an excellent working hypothesis to suppose that when Lake Baikal was formed, and when each new island of the Hawaiian archipelago arose from the ocean, species belonging to different faunas and floras were brought together and that physical and biological barrier systems were broken down. There were increased chances for hybridization in an environment full of new ecological niches in which some new recombinations would be at selective advantages. There is a growing body of experimental data to support such an hypothesis. These data fall largely in two groups (1) Evolution under domestication, (2) Evolution in disturbed habitats.

(1) For evolution under domestication the evidence is overwhelming that by conscious and unconscious selection, man has created forms of plants and animals which are specifically distinct from their wild progenitors. This large body of evidence demonstrates that given a habitat in which novelties (or at least some of them) are at a great selective advantage, evolution may proceed very rapidly. There is presumptive evidence that many of these domesticates originated through introgression but the process began so early that getting exact experimental evidence for the history of any one of them will entail long-continued cooperative research (see, however, Mangelsdorf and Smith (1949), Alava (1952), and Nickerson (1953) for evidence that modern *Zea* is greatly different from the maize of five thousand

years ago and that much of this differentiation may well be the result of introgression from *Tripsacum*). For some ornamentals, domestication is such a recent event that critical evidence is easier to assemble. Anderson (1952) has presented in elementary detail the case of *Tradescantia virginiana*. He shows that in four hundred years by introgression from *T. ohioensis* and *T. subaspera* (unconsciously encouraged by man) it has evolved under cultivation into a variable complex quite distinct from *T. virginiana* as a genuinely wild species.

(2) Evolution in disturbed habitats. It has been repeatedly shown (Anderson, 1949; Heiser, 1949; Epling, 1947) that species which do not ordinarily produce hybrids and backcrosses may readily do so when man or any other agent disturbs the habitat. This phenomenon was referred to as "Hybridization of the Habitat" by Anderson (1948). After citing the work of several authors who have emphasized the role of man in promoting and creating habitats favorable for the perpetuation of hybrids and hybrid derivatives, he reached the following conclusion (1948, p. 6). "Does this mean that introgression as a phenomenon is limited to the areas disturbed by man and that its results are mere artifacts and not genuine natural phenomena? I think not. Though freely admitting that nearly all the introgression which has been studied experimentally (for one exception see Dansereau, 1941) is of the nature of an artifact, I believe that at particular times, and in particular places, introgression may have been a general evolutionary factor of real importance."

The great frequency of hybrid derivatives in disturbed habitats is only in part due to the breaking down of barrier systems, allowing previously isolated species to cross. It can and does occur when the barrier systems are not broken down (see for instance Heiser, 1951). Much more important is the production of new and varying ecological niches; more or less open habitats in which some of the almost

infinitely various backcrosses and occasional types resulting directly from segregation in F_2 and later generations will be at a selective advantage. A particularly significant example was investigated by Anderson (unpublished) who studied *Salvia apiana* and *Salvia mellifera* in the San Gabriel mountains, confirming and extending Epling's (1947) previous studies. He found hybrid swarms not in the chaparral itself where both of these species are native but adjacent to it in cut-over live oaks amidst an abandoned olive orchard. In this greatly disturbed area, new niches were created for the hybrid progeny, which are apparently always being produced in the chaparral but at a very low frequency. In this strange new set of various habitats some of the mongrels were at a greater selective advantage and the population of the deserted olive orchard was composed of hybrids and back-crosses to the virtual exclusion of *S. apiana* and *S. mellifera*.

It has been customary to dismiss the evidence of introgression under the influence of man as relatively unimportant to general theories of evolution because nothing quite like it had previously occurred. A little reflection will show that this is not so. Man at the moment is having a catastrophic effect upon the world's faunas and floras. He is, in Carl Sauer's phrase, an ecological dominant but he is not the first organism in the world's history to achieve that position. When the first land vertebrates invaded terrestrial vegetation they must have been quite as catastrophic to the flora which had been evolved in the absence of such creatures. When the large herbivorous reptiles first appeared, and also when the first large land mammals arrived in each new portion of the world there must have been violent readjustments and the creation of new ecological niches.

The last of these (the arrival of the large land mammals) is close enough to us in geological time so that we have witnessed the very end of the process. The

vegetation of New Zealand had had no experience with mammals until the arrival of the Maori in the fourteenth century followed by Europeans in the 18th and 19th centuries. Man, pigs, horses, cattle, rats, sheep, goats, and rabbits were loosed upon a vegetation which had had no previous experience with simians or herbivores. The effect was catastrophic. Hybrid swarms were developed upon the most colossal scale known in modern times. A succession of New Zealand naturalists have occupied themselves with the problem and it has been treated monographically by Cockayne (1923) and by Allen (1937).

The extent to which disturbance of the habitat combined with reorganization of adaptive systems through hybridization could have been responsible for evolutionary bursts, "proliferation," "tachytely" or "quantum evolution" (Simpson 1953) can best be estimated by summarizing the geological and paleontological evidence concerning the time of occurrence of habitat disturbances, and comparing this with probable evolutionary changes in certain groups of organisms which were most likely initiated by hybridization. In such a survey, all three of the possible results of hybridizations—introgression, segregation of new types without backcrossing and allopolyploidy—must be considered. Reference to allopolyploids is particularly important, since hybrid derivatives of this type can easily be distinguished from their parental species by their chromosome numbers, and the time and place of hybridization can often be indicated with a high degree of probability (Stebbins, 1950, Chap. 9).

Preceding the advent of man, the most revolutionary event in the history of the northern continents was the Pleistocene glaciation and the contemporary pluvial periods of regions south of the ice sheet. This involved not only radical oscillations in climate, but also great disturbances of the soil, both in the glaciated regions and in areas to the south of them. In the latter, the extensive deposits of loess im-

mediately south of the ice margin and the masses of alluvium carried for miles down the river valleys must have disturbed these areas almost as much as the ice sheets churned up the areas which they covered.

The activity of hybridization in developing plant populations adapted to these new habitats is amply evident from the frequency of allopolyploids in them. Specific examples are *Iris versicolor* and *Oxycoccus quadripetalus* (Stebbins, 1950); the polyploid complexes of *Salix*, *Betula*, *Vaccinium*, *Antennaria*, *Poa*, *Calamagrostis*, and many others can also be cited. The best example of introgression among species which have invaded the ice-free areas in post-Pleistocene time is in the complex *Acer saccharophorum* (Dansereau and Desmarais, 1947). The numerous examples cited by Anderson (1953) of hybrid and introgressant types which occupy the central Mississippi Valley between the Appalachian, Ozark, and central Texas highlands probably represent late Pleistocene or post-Pleistocene invasion of these areas which were strongly affected by outwash from the ice sheet and from the post-glacial lakes. The origin of *Potentilla glandulosa* subsp. *Hanseni* in the post-Pleistocene meadows of the Sierra Nevada is discussed by Stebbins (1950, p. 279).

During the Tertiary and earlier geological periods three types of changes in the inanimate environment can be singled out which probably gave rise to disturbed habitats favorable to the establishment of hybrid derivatives. These were mountain building movements, advance and retreat of epicontinental seas, and radical changes in the earth's climate.

Some of the direct effects of mountain buildings are the rapid creation of raw, unoccupied habitats (such as lava flows, for instance), in which plants belonging to very different ecological associations may temporarily mingle and gain a chance to hybridize. In central California the canyon of the Big Sur River is a typical example of the mixing together of spe-

cies belonging to very different floras in a region of recent uplift which has a rugged, youthful topography. Here yuccas and redwoods grow within a stone's throw of each other. An example of hybridization in this area is between two species of *Hieracium*; *H. albiflorum*, which is typical of northern California, the Pacific Northwest, and the Rocky Mountains, and *H. argutum*, a Southern California endemic which here reaches its northern limit except for one known station in the Sierra foothills. Examples such as this could undoubtedly be multiplied by a careful study of any youthful mountain region.

The retreat of epicontinental seas in the latter part of the Pliocene period, plus faulting in the Pleistocene and recent times, has been largely responsible for the present topography of coastal California with its flat valleys and abrupt mountain ridges. One hybrid polyploid which appears to have spread as a result of these changes is the octoploid *Eriogonum fasciculatum* var. *foliolosum* (Stebbins, 1942); another is probably the tetraploid *Zauschneria californica* (Clausen, Keck, and Hiesey, 1940). A series of hybrid swarms which may have arisen in response to the same topographical changes is that of *Quercus Alvordi* (Tucker, 1952). *Delphinium gypsophilum* is a relatively well stabilized species, probably of hybrid origin, endemic to this same recently emerged area of California (Epling, 1947), and the species of *Gilia* considered by Grant (1953) to be of hybrid origin have the same general distribution. In the Old World, Dansereau (1941) has suggested that *Cistus ladaniferus* var. *petiolatus*, which occupies the recently emerged coast of North Africa, is a product of hybridization between typical *C. ladaniferus* and *C. laurifolius* both of which occur in the more ancient land mass of the Iberian Peninsula.

Among the radical changes in the earth's climate which occurred recently enough so that their effect on the vegeta-

tion can be recorded, is the advent of the Mediterranean type of climate with its wet winters and dry summers in most of California. The time of this climatic change is now fully documented by the fossil record; it took place during the middle part of the Pliocene period. It was preceded by a general decrease in precipitation, with biseasonal maxima (Axelrod, 1944, 1948).

The effects of this climatic change on the woody vegetation of the area are also well documented by the fossil record. One very probable example of a hybrid swarm exists in a fossil flora. In the Remington Hill Flora, which was laid down in the Sierra foothills at the beginning of the Pliocene, there is a great abundance of oak leaves corresponding to the modern *Q. morehus*, a hybrid between the mesophytic, deciduous *Q. Kelloggii*, and the xerophytic, evergreen *Q. Wislizenii* (Condit, 1944). That these fossil leaves were borne by hybrid trees is evidenced not only by their very unusual and characteristic shape, but also by their great variability and the fact that no similar leaves are found in any of the numerous Miocene and Pliocene floras of California. Furthermore, the Remington Hill is the only one of these fossil floras which contains the counterparts of both parental species. At present, the *Q. Kelloggii* × *Wislizenii* hybrid is frequent in the Sierra foothills, but it usually grows as single trees in company with dense stands of *Q. Wislizenii* and *Q. Kelloggii*. The populations of the parental species growing in the vicinity of the hybrids appear little or not at all different from those occurring by themselves, far from any other species of this complex. On the other hand, *Q. Wislizenii* shows considerable geographic variation, with the more northerly and more coastal variants, i.e., those adapted to increasingly mesic climates, possessing an increasingly greater resemblance to *Q. Kelloggii* in habit, leaves, buds, and fruits. This suggests that the present variation pattern in *Q. Wislizenii* is the

result chiefly of extensive introgression from *Q. Kelloggii*, which began with the hybrid swarms of Mio-Pliocene time, and has since been ordered into a regular, clinical series of variants by the selective action of the changing Pliocene and Pleistocene climates. Tucker (oral comm.) has suggested that *Q. Douglasii*, a completely unrelated oak with a similar geographical distribution, may have also originated from one or more hybrid swarms of a similar geological age. The modern variation pattern of the common chaparral species *Adenostoma fasciculatum* (Anderson, 1952) could be interpreted on the same basis, while less thorough observations by the junior author suggest that several other examples can be found in the California flora.

Conditions favorable for the origin and spread of hybrid derivatives are made not only by changes in the inanimate environment, but also by the advent and disappearance of various types of animals. Previous to man and his associated domesticates, some of these disturbances were as follows. In the Eocene and Oligocene periods, large grazing mammals made their first appearance on the earth. Their effect on the woody vegetation cannot be detected in the fossil record, and probably was not great. The herbaceous plants, however, must have been greatly affected by their inroads, and if these smaller plants had been abundantly preserved as fossils, we might be able to record a burst of evolution in them during these early Tertiary epochs. Babcock (1947, p. 132), after careful consideration of all lines of evidence, has suggested the latter part of the Oligocene as the time of origin of the genus *Crepis*, one of the larger, more specialized, and probably more recent genera of Compositae. On this basis, one might suggest that the greatest period of evolution of genera in this largest of plant families was during late Eocene and Oligocene time. The junior author, from his studies of various grass genera of temperate

North America, believes that many facts about their present distribution patterns could best be explained on the assumption that they began their diversification during the Oligocene epoch. They appear to have attained much of their present diversity by the middle of the Miocene, by which time many of the now extensive polyploid complexes, such as those in *Bromus*, *Agropyron*, and *Elymus*, had begun to be formed. The extensive Miocene record of species belonging to the relatively advanced tribe Stipeae (Elias, 1942) would support such an assumption.

At an earlier period, namely the beginning of the Cretaceous, the world saw for a relatively short time the dominance of the largest land animals which have ever existed, the great herbivorous dinosaurs. These monsters must have consumed huge quantities of the fern and gymnosperm vegetation which prevailed at the time, and it is difficult to see how these plants, with their relatively slow growth and reproduction, could have kept up with such inroads. It is very tempting, in fact, to speculate that over grazing on the part of giant dinosaurs contributed toward the extinction of the Mesozoic gymnospermous vegetation, as well as of the larger dinosaurs themselves, during the middle of the Cretaceous period. At the same time, shallow epicontinental seas were advancing and retreating, leaving coastal plain areas open for plant colonization; other significant events during this period were the rise of modern birds and of Hymenoptera, particularly bees.

The writers venture to suggest that these four nearly or quite concurrent events—retreat of seas, overgrazing by dinosaurs, advent of a diversified avifauna which transported seeds long distances, and rise of flower pollinating bees and other insects—all contributed to the greatest revolution in vegetation which the world has even seen; the replacement of gymnosperms by the predominant angiosperm flora of the upper part of the Cretaceous period. One should note that all of these conditions would favor hy-

bridization and the spread of hybrid derivatives, by giving unusual opportunities for previously separated types to be brought together by wide seed dispersal, by permitting cross pollination between types previously isolated from each other, and by opening up new areas for colonization by the hybrid derivatives. The suggestion has been made elsewhere (Stebbins, 1950, p. 363) that differentiation of genera and sub-families among primitive angiosperms took place partly via allopolyploidy; the time of origin of this polyploidy may well have been during the Cretaceous period. Evidence of introgression at so remote a time is probably impossible to obtain; by an analogy we should assume that in the past as now, conditions favorable for allopolyploidy also promoted introgression.

Going still further into the past, let us speculate on the events which must have taken place at the time when vascular plants and vertebrates first spread over the land. The principal geological period involved is the Devonian. At the beginning of this period comes the first extensive fossil record of vascular plants, all belonging to the primitive order Psilophytales. By the end of the Devonian, forms recognizable as club mosses (Lycopsidea), ferns (primitive Filicales), and seed plants (Pteridospermae) were already widespread. We shall, of course, never know what chromosome numbers existed in these extinct groups of primitive vascular plants. But their nearest living descendants are nearly all very high polyploids, as has now been most elegantly demonstrated by Manton (1950, 1953). She has suggested that the living Psilotales, which have gametic numbers of about 52, 104, and over 200, "are the end-products of very ancient polyploid series which date back to simple beginnings. . . ." The relationship between the modern Psilotales and the Devonian Psilophytales is not clear, but to the present authors they appear to resemble each other nearly enough so that they could belong to the same complex

network of allopolyploids, which developed its greatest diversity in the Devonian period. In the genus *Ophioglossum*, generally regarded as one of the three most primitive genera of true ferns, we have the highest chromosome numbers known to the plant kingdom, namely $n = \text{ca. } 256$ in the northern *O. vulgatum* and $n = \text{ca. } 370$ in the tropical *O. pendulum*. These ferns are not preserved in the fossil record because of their soft texture, but their origin during the Devonian period is a fair inference. There is very good reason to believe, therefore, that the great proliferation of genera and families of vascular plants during this earliest period of their dominance was accompanied by allopolyploidy just as it has been in the more recent periods of very active evolution. Where allopolyploidy was widespread, we can also suspect abundant introgression.

The reader may well ask at this point whether any of this evidence contributes to the central theme of the present discussion, namely the hypothesis that these extensive hybridizations, both ancient and relatively modern, gave rise to really new types, which formed the beginnings of families, orders, and classes having different adaptive complexes from any plants previously existing. It is undoubtedly true that the results of introgression and allopolyploidy are chiefly the blurring of previously sharp distinctions between separate evolutionary lines, and the multiplication of variants on adaptive types which were already established during previous cycles of evolution. Nevertheless, the fact must not be overlooked that conditions favorable for introgression and allopolyploidy, namely the existence of widely different and freely recombining genotypes in a variety of new habitats, also favor the establishment and spread of new variants. Establishment of new adaptive systems is under any circumstances a relatively rare event; in any group of organisms we have hundreds of species and subspecies which are variants of old adaptive types to one which repre-

sents a really new departure. Hence we cannot expect to recognize introgressive or polyploid complexes which have given rise to such new types until we have carefully analyzed hundreds of those which have not. Furthermore, our methods of recognizing these complexes almost preclude the chance of identifying the new types which have arisen from them. We make the assumption that hybrid derivatives, whether introgressants or allopolyploids, have characteristics which can all be explained on the basis of intermediacy between or recombination of the characteristics of the putative parents, and then devise methods of verifying this assumption. The new types, falling outside of this assumption, would be rejected by our methods.

The junior author can suggest two examples known to him of new and distinctive morphological characteristics which may have arisen in recent hybrid derivatives. One of these is the presence in *Ceanothus Jepsonii*, a species narrowly endemic to the serpentine areas of northern California, of flowers with six and seven sepals, petals, and anthers (Nobs, 1951). This characteristic is not known anywhere else in the family Rhamnaceae or even in the entire order Rhamnales, an order which almost unquestionably dates back to the Cretaceous period. Mason (1942) has given strong evidence for the recent origin of *Ceanothus Jepsonii*. It inhabits an environment which is certainly recent, since the mountains on which it occurs were covered by a thick layer of volcanic rocks even as late as the end of the Pliocene epoch, and the serpentine formations to which it is endemic were not exposed until after the faulting which occurred at the beginning of the Pleistocene (Mason, 1942). It belongs to a complex of closely related species and subspecies, among which hybridization is still very actively taking place (Nobs, 1951). In characteristics other than sepal and petal number, it is intermediate between various ones of its relatives rather than an extreme type.

Hence there is a good reason to suspect that *Ceanothus Jepsonii* represents a species of relatively recent (i.e. Pleistocene) hybrid origin which has evolved a morphological characteristic previously unknown in its family, and in fact one which is relatively uncommon in the entire subclass of dicotyledons.

The other example is in the grass species *Sitanion jubatum*. This species is distinguished by possessing glumes which are divided into a varying number of linear segments, a characteristic not found elsewhere in the tribe Hordeae, and one which is the basis of a distinctive mechanism for seed dispersal (Stebbins, 1950, p. 141). *Sitanion jubatum* is endemic to Pacific North America, being most abundant in the coast ranges and foothills of central California. Its nearest relative is *S. hystrix*, a species found in the montane areas of the same region, and extending far eastward and southeastward. The two species are distinguished only by the degree of division of the glumes, and in fact appear to grade into each other. Field observations suggest that they actually consist of a large swarm of genetically isolated microspecies, such as has been demonstrated experimentally to exist in the related *Elymus glaucus* (Snyder, 1950).

Cytogenetically, both species of *Sitanion* are allotetraploids (Stebbins, Valencia, and Valencia, 1946). Extensive chromosome counts from various parts of the ranges of both species plus still more numerous measurements of sizes of pollen and stomata have failed to reveal any form of *Sitanion* which could be diploid. Furthermore, the chromosomes of both species are strongly homologous with those of *Elymus glaucus*, as evidenced by complete pairing in the F_1 hybrid. All of this evidence suggests that *S. jubatum* did not have any diploid ancestors which possessed its distinctive glumes, but has evolved out of a complex of allopolyploids which has existed in western North America for a long

time, probably since the middle of the Tertiary period.

The forms of *S. jubatum* which have the most extreme division of the glumes occupy habitats which are recent, and which in some ways are intermediate between the most extreme habitats occupied by *Sitanion* and those characteristic of *Elymus glaucus*. They are known from the shore of San Francisco Bay, in northeastern Marin County, from the eastern edge of the Sacramento Valley north and east of Sacramento and from the Sierra foothills in Mariposa county. In growth habit, these races of *S. jubatum* could be regarded as intermediate between the most extreme xerophytes found in *Sitanion* on the one hand, and *E. glaucus* on the other.

Experimental evidence (Stebbins, unpublished) has now indicated that the complex of microspecies within the taxonomic species *Elymus glaucus* originated partly if not entirely through introgression. The probability is strong that *Sitanion* consists of a similar swarm of microspecies which originated also by introgression. The extensive subdivision of the glumes in some of these microspecies, therefore, may well have originated through the establishment of new mutations, or of new types of gene interaction, in genotypes produced by hybridization and introgression between morphologically very different and genetically well isolated species.

When all of this evidence has been considered, the writers can hardly escape the conclusion that hybridization in disturbed habitats has produced the conditions under which the more familiar processes of evolution, mutation, selection, and the origin of reproductive isolation barriers, have been able to proceed at maximum rates. Far from being insignificant because much of it is in habitats greatly disturbed by man, the recent rapid evolution of weeds and semi-weeds is an indication of what must have happened again and again in geological history whenever any

species or group of species became so ecologically dominant as greatly to upset the habitats of their own times.

SUMMARY

(1) It has been established by recent work in Palaeontology and Systematics that evolution has not proceeded at a slow even rate. There have instead been bursts of evolutionary activity as for example when large fresh water lakes (Baikal, Tanganyika, and Lanao) were created *de novo*.

(2) Recent studies of introgression (hybridization and subsequent back-crossing) have demonstrated that under the influence of man evolution has been greatly accelerated. There has been a rapid evolution of plants and animals under domestication and an almost equally rapid evolution of weed species and strains in greatly disturbed habitats.

(3) The rapidity of evolution in these bursts of creative evolution may well have been due to hybridization. At such times diverse faunas and floras were brought together in the presence of new or greatly disturbed habitats where some hybrid derivatives would have been at a selective advantage. Far from being without bearing on general theories of evolution, the repeated demonstrations of accelerated introgression in disturbed habitats are of tremendous significance, showing how much more rapidly evolution can proceed under the impact of a new ecological dominant (in this case, Man). Such an agent may bring diverse faunas and floras into contact. Even more important is the creation of various new, more or less open habitats in which novel deviates of partially hybrid ancestry are at a selective advantage. The enhanced evolution which we see in our own gardens, dooryards, dumps and roadsides may well be typical of what happened during the rise of previous ecological dominants. The first vertebrates to enter isolated continents or islands, the first great herbivorous reptiles, the first herbiv-

orous mammals must have created similar havoc upon the biotae of their own times. Introggression must have played the same predominant role in these disturbed habitats as it does today under the impact of man. These arguments are supported by a homely analogy (page 379) and by various kinds of experimental and taxonomic data.

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