

(1) Read the Preface

(2) Just skim the first section on "The Nature and Sources of Variation" primarily to see how Simpson tries to fit his paleo/macroevolutionary view into the genetics of the early Synthesis

(3) Then read pp.160 to 212 on Adaptation and Adaptive Radiation where Simpson makes one of his seminal contributions

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The Major Features of Evolution

Columbia University Press, New York, 1953

Preface

WHEN A REVISION OF *Tempo and Mode in Evolution* was called for, my feeling was that the book had served its purpose and should be allowed to fossilize quietly. That work was written at intervals between the spring of 1938 and the summer of 1942. At that time it was to me a new and exciting idea to try to apply population genetics to interpretation of the fossil record and conversely to check the broader validity of genetical theory and to extend its field by means of the fossil record. That idea is now a commonplace. I like to think that *Tempo and Mode in Evolution* helped to produce its own rapid obsolescence, although of course many others had equal and greater parts in the movement that has brought paleontology, genetics, systematics, and other biological disciplines into a synthesis of evolutionary theory.

Much more work in the field of that book has been done since it was written than in all the years before. The last ten years have produced a veritable revolution in knowledge of evolution and, what is even more important, in the breadth and nature of approach to evolutionary theory. The Society for the Study of Evolution has been founded and has published five volumes of its international journal *Evolution*, every issue of which has contained articles pertinent to the themes of *Tempo and Mode in Evolution*. Innumerable other short studies and monographs in what may be called the new spirit of evolutionary theory have appeared in other journals. The National Research Council's Committee on Common Problems of Genetics, Paleontology, and Systematics completed its deliberations, held a conference in cooperation with Princeton University, and prepared a symposial volume (Jepsen, Mayr, and Simpson, 1949). Other conferences in this general field were held, not only in the United States but also in Great Britain, France, Italy, Australia, and elsewhere.

A number of important summarizing and reviewing volumes in the new spirit of evolutionary theory have also appeared in the last ten

years, outstanding among them those by Huxley (1942),¹ Mayr (1942),¹ Heberer (1943),¹ Rensch (1947), Schmalhausen (1949), Stebbins (1950), Carter (1951), and Dobzhansky (1951).² Even more numerous are works less immediately of this school or in this field, but with a strong bearing on it. Included are important general works on evolutionary theory by such dissenters as Schindewolf (1950) and Cuénot (1951). In annexant fields, merely by way of example, there are the volumes by Mather (1949) and by Darlington and Mather (1950) on some aspects of genetics, by Florkin (1949) and by Blum (1951) on biochemical and biophysical factors in evolution, by de Beer (1951) on embryology and evolution, by White (1945) on cytology and evolution, by Zeuner (1946) on geological time, by Romer (1945) on vertebrate paleontology, by Gregory (1951) on vertebrate phylogeny, and by Emerson (in Allee, Emerson, Park, Park, and Schmidt, 1949) on ecology and evolution. Added to all this is the relevant serial literature, running to some thousands of titles in this period.

When I suggested that *Tempo and Mode in Evolution* could now fade away without great loss, the publishers assured me that it must still have some usefulness because it continued in steady demand. Obviously it was too out of date to permit mere reprinting indefinitely, so I reluctantly undertook revision. The plan was to go through tear sheets and simply delete or reword statements that now seem incorrect or in need of modification. This immediately proved to be completely impractical. So much has been learned and said since 1942 that revision in any such limited sense would leave the book almost as badly out of date as before. Moreover, it is not even the sort of book to publish in 1953. To revise it now would be like installing central heating and air conditioning in a pioneer's log cabin. What is needed is replacement by a modern structure, to fit the city that has grown up around the cabin. So, as revision proceeded, not only were practically all the original sentences discarded or rewritten but also the selection of topics was changed and expanded and the whole sequence and structure radically modified.

This, then, is another book, in the field of *Tempo and Mode in Evo-*

¹ Although *Tempo and Mode in Evolution* was not published until 1944, circumstances prevented my making any changes or additions after the summer of 1942. No note could be taken of these three volumes or of any other publications of latter 1942 and thereafter.

² This revision, essentially a new work, was received after completion of the present manuscript. Some references to it have been inserted.

lution and therefore drawing heavily on that earlier work, but still quite a different book. Its predecessor was a series of technical theses, speculative in large part, developed in a rather personal way, and necessarily thin in background and support. This book, although not an attempt at exhaustive review of a whole field from all points of view, is more rounded and complete within its scope. Then there was embarrassingly little in the way of directly pertinent previous evidence and discussion; now the embarrassment is one of choice among riches. The change is partly due to the fact that the author personally has grown a little less ignorant in the ten years, but it mainly results from the movement and publications referred to above. As just one example among many, the theses now draw some support from plant evolution, which was not even mentioned in the earlier book. This is possible not because I have overcome my botanical incompetence but because Stebbins has summarized the botanical evidence from just this point of view. As regards the original theses, it is gratifying that some quite speculative suggestions can now be firmly supported. Others of course require modification in the light of later knowledge. Whatever measure of originality the preceding book had is now past, but its loss may be compensated by increased solidity.

The purpose of the present book is to consider and to try to explain some of the major features of the evolution of life, as far as this can be done between two covers. These major features are most directly seen in the fossil record, but their explanation must bring in every branch of biological research. In addition to paleontology, population genetics and systematics are the sciences most directly contributing to evolutionary theory today. The fact that the latter two are by practical necessity concerned mainly with minor features of evolution only makes their synthesis in application to major features the more necessary and useful. Perhaps no one is fully competent to treat all the pertinent sciences at once. I, at least, am not; but as I wrote ten years ago: "The effort to achieve such a synthesis is so manifestly desirable that no apology is in order; the intention will hardly be criticized, whatever is said about its execution."

The quotation brings to mind a final prefatory remark. The critics were almost uniformly kind to *Tempo and Mode in Evolution*. Such critical suggestions as were made were almost all constructive and have been followed in the present book. Two reviewers did criticize the intention, however. The most adverse criticism was also the longest. It

ran serially for three weeks in a British Sunday school paper and can be fully paraphrased as saying that I should never have written the book because evolution is all a lie anyway. More important were remarks by a colleague who seemed to imply that it is not quite fair for someone labeled "paleontologist" to base interpretations and conclusions on anything but fossils. I should think that this would make me a better paleontologist when I am being one, but the point here is that for the purposes of this book, at least, I am not a paleontologist. I am trying to pursue a science that is beginning to have a good many practitioners but that has no name: the science of four-dimensional biology or of time and life. Fossils are pertinent to this field when they are treated as historical records (paleontologists do not always treat them so), but *Drosophila* is equally pertinent when it exemplifies changes of populations in time.

Acknowledgments should be made first of all to the many colleagues who wrote critical reviews of *Tempo and Mode in Evolution*, who have considered its theses in the course of their own work, and who have discussed those and related topics with me. It is unfortunately impossible to make explicit mention of all who have helped in those ways. I am again indebted to Dr. Anne Roe for essential encouragement and for reading the whole manuscript for style and comprehensibility. The manuscript was edited by Miss Gladys Fornell for Columbia University Press, and I am further grateful to the Press for care in design and manufacture of the book. The index is by Publications Indexers.

Some of the illustrations are taken without special acknowledgment from *Tempo and Mode in Evolution*. Most of them are new, drawn by the Staff Illustrators Corps of The American Museum of Natural History from my sketches and data. Mr. David Kitts assisted in compilation and some other details. Mrs. Rachel H. Nichols checked some of the bibliographic data.

The final draft of the manuscript was completed in December, 1951, and only minor verbal changes have since been made. A few later publications already known to me in manuscript in 1951 were taken into consideration, but no later revision has been practicable.

G.G.S.

*The American Museum of Natural History
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New York*

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tionary factors most likely to cast light on major aspects of evolution, to discuss them from this particular point of view, and to relate them to the primary evidence of long-range evolution. The factors chosen are as follows:

1. Variation
2. Mutation
3. Population
4. Time and the length of generations
5. Selection
6. Environmental factors, and interaction of all factors in adaptation
7. Isolation and splitting

Factor 1 of this list is discussed in the present chapter; 2 in Chapter IV; 3, 4, and 5 in Chapter V; and 6 in Chapters VI-VII. Factor 7 is incidentally included at several points in the ensuing discussion and explicitly in Chapter XII from the special point of view of major evolutionary patterns. In detail, isolating mechanisms are obviously of crucial importance in evolution, and they have been considered at length by students of recent organisms (e.g., Mayr, 1942; Stebbins, 1950; Dobzhansky, 1951). Their result, when it eventuates in phyletic splitting and the rise of essentially distinct, long-continued lineages, is an essential part of the present subject. The detailed mechanisms in themselves are not, and for the most part the existence and nature of those mechanisms can be taken for granted here.

THE NATURE AND SOURCES OF VARIATION

It is a truism that all populations of organisms vary. No two individuals are ever exactly alike, not even monozygotic twins. It is equally commonplace nowadays to recognize that some of this variation involves the genotype and some does not, although the still usual custom of speaking of "hereditary" and "acquired" differences does not clarify the distinction. This is another set of false alternatives setting up an unreal problem. What is inherited, mostly but not exclusively through the genotype, is known to be an organized physico-chemical system with a definite growth tendency or pattern. The organism eventuates from the interaction of this system with all environmental influences (in the broadest sense) throughout development and the whole of life. The naive conception that genes correspond with somatic characters

or that the latter are inherited as such is now well known to be untrue in most cases. It is approximately true only when the "character" in question is directly a chemical concomitant of the gene, as, for example, the ability of *Neurospora* to synthesize indole from anthranilic acid (Beadle, 1945), and even in such a case independence from the environment is not absolute.¹ For such morphological characters as here concern us, it is fair to say that they are never *strictly* inherited nor *strictly* acquired, but are both or neither, depending on the point of view.

An "acquired character," or one should say, any character is thus simply a particular variant within the reaction range determined by the given genotype. The important point is that different variants in the range of the same genotype are not materials for evolution. Similarly, differences in genotype are not materials for evolution when the same phenotypic characters develop in their overlapping reaction ranges. With, again, certain exceptions of no particular importance here,² materials immediately available for evolution occur only when *both* phenotype and genotype vary, and vary in a correlated way.

Although both phenotype and genotype are thus concerned, the source of variation available for evolution must be in the genotype. This is simply because differences arising in phenotypes with the same genotype produce no change in the latter whereas differences arising in genotypes with (before the change) the same phenotypes usually do produce differences in the phenotypes. (I do not here propose to discuss neo-Lamarckism or Michurinism, the schools that continue to deny these extremely probable, if not absolutely proven statements.)

Correlated variations of genotype and phenotype within a population, or lineage, are the indispensable materials without which no evolution can occur. Their sources are therefore the basic and most fundamental sources of evolutionary change. As now known to geneticists,³ these sources are as follows:

¹ For instance, the operation depends on presence and amount in the environment of materials for prior synthesis of anthranilic acid, and on a different gene for that synthesis, and presumably the action would be modified if indole were already present.

² Notably cases concerning compatibility of genotypes in conjugation, with selection acting directly on the genotype and not indirectly through the phenotype.

³ In summarizing such genetic data as are here pertinent, it is assumed that authority need not be specified for facts that may be found in any competent, modern, general text on genetics, for example, Sinnott, Dunn, and Dobzhansky (1950).

A. Mutation

1. Of genes
2. Of chromosomes
 - a. Structural (deficiencies, duplications, translocations, inversions)
 - b. Numerical (polyploidy, polysomy, etc.)

B. Recombination

1. Of genes (by crossing over in meiosis)
2. Of chromosomes (by conjugation of gametes with unlike chromosomes)

Although recombination produces new and variant characters and is, in fact, responsible for most of the variation observed in interbreeding populations of sexual organisms, it produces no genetically new materials. Strictly new materials arise by mutation, which is much less common than recombination but which must ultimately supply materials for long-continued evolution. The genetic changes here listed do not (ordinarily) provide immediate materials for evolution unless they are accompanied by changes in phenotype, but as discussed below they may provide cryptic variation which may later become available.

Another point about variation greatly affecting its availability for evolution and its relationship to different evolutionary processes concerns the units in or between which variation is occurring. Obviously variation occurs within individuals, which are never precisely the same throughout life, or for any successive instants. Such variation affects the fate of the individual and may therefore affect evolution in his lineage, but the variation, itself, is not material for evolutionary change. Variation also occurs, so obviously that this is usually meant when "variation" is mentioned without qualification, between contemporaneous individuals within a population of interbreeding individuals or of asexually produced descendants from one (not too distant) ancestor. Variation also occurs between or among two or more such groups, with no (or little) interbreeding. Both intra- and intergroup variation provides material for evolution, but the bearing is quite different in the two cases. With passage of time, intragroup variation is a unit, transferable through the group, material for phyletic change and for initiation of speciation. Intergroup variation cannot be (or can only to limited extent be) transferred from one group to another. It may

VARIATION

condition extinction or survival of any one group or, in combination with intragroup variation, it may be involved in divergence or other relationships among various groups. Finally there is successive variation within groups, lineages or phyla, with the passage of time. This is not material for evolution; it is evolution.

CORRELATED PHENOTYPIC VARIATION

Another aspect of variation is extremely important because it helps to explain some otherwise baffling evolutionary phenomena for which a great variety of speculative and frequently metaphysical hypotheses have been advanced. This is correlated variation in two or more different (or, at least, separately designated) phenotypic characters. By this is not meant that two characters tend to change by equal amounts or in the same direction, but that a variation in one is more likely than not to be accompanied by some particular sort of variation in the other within the same individual. Analogously with variation in general, the correlation is not material for evolution unless it has a genetical basis—that is, the correlation, itself, must be related to something in the mechanism of heredity, and not merely the variations that happen to be correlated. Two characters, such as teeth adapted to a plant diet, and hoofs, may tend to develop together and each may be closely correlated with the genetic mechanism, and yet their rise *together* may not be fixed by that mechanism. If selection is the effective factor, it then acts separately on the two,⁴ each of which must have selective value. In fact, although the hoof-herbivore correlation is usual, as noted by the ancients and made into a law by Cuvier, there have been clawed herbivores. "Environmental correlation," or correlation by selection without genetic correlation, may be difficult to distinguish from genetic correlation, although methods have been developed for doing so in animal breeding (Lerner and Dempster, 1948).

Some truly genetic character correlations may be rather obvious and indicate plainly only that the characters, as analyzed, are parts or aspects of a larger character. Thus if an organ becomes larger as a whole, so will its height, width, and breadth in close correlation with each other. Other cases may be analogous and yet less obvious. For instance, a shift in a growth gradient over a field may produce rather

⁴ Although a trend in one may affect separate selection for the other, see Chapter VIII.

complicated, genetically correlated changes in all the structures in that field, as in a series of teeth, for instance (Butler, 1939, 1946). Allometry, likewise an aspect of growth pattern, may also produce changes actually but not obviously correlated as parts of a single, genetically controlled growth pattern. Other correlations are still more complicated or inexplicable by phenotypic study but have genetical explanations.

Among the mechanisms possibly producing genetic correlation of phenotypic characters are:

1. Genetic control of growth gradients and fields, including allometry, as above
2. Pleiotropy
3. Linkage
4. Incidental inclusion of genes in a genetic system (or among polygenes) integrated on some other basis

There is no doubt that all these mechanisms occur, although there can be dispute as to their relative effectiveness or their applicability in a given example.

Pleiotropy, multiple effect of single genetic factors, is certainly common. Indeed, it may prove to be the rule rather than the exception. Among many examples are the *se* gene in mice, which produces short ears and also lowers the number of ribs (Green and Green, 1946), "vestigial" in *Drosophila*, producing small wings, lowered fecundity and life span, and changes in the halteres, spermathecae, ovaries, and elsewhere (Mohr, 1932), or a mutation in mice producing a remarkable, and remarkably variable, series of malformations in various individuals and various parts of the body (Grüneberg, 1947).⁵ There is no point in multiplying examples here; they can be found in abundance in any work on genetics.

There seems to be no really clear distinction between correlation by linkage and by inclusion in a genetic system or among polygenes,

⁵ The variability of expression is unusual in this case and is due to the fact that the primary effect is production of blisters under the ectoderm which migrate variably and may interfere with development elsewhere. This may not be considered "real" pleiotropy, but it is deliberately mentioned in order to point out that any or all cases of pleiotropy might well prove, if pushed back to chemical effects of the gene, to be diverse consequences of a single primary action. The point is to emphasize that genes do not control characters but are elements in a developmental system, a single change in which may produce changes on any number of different characters. See also Grüneberg, 1948.

and the latter may be a special case of the former in the sense that the correlation or retention in the system would still require some persistent linkage. The long-range effectiveness of linkage to maintain the correlation may be questioned in some cases or as a general rule, although it evidently could be effective, especially as there are mechanisms which impede or prevent crossing over. These are also more difficult cases to establish experimentally, but there are now examples for which no other explanation seems likely. Among these are correlation of physiological (salinity preference) and morphological (plate number) characters in *Gasterosteus*, interpreted as due to linkage groups with impeded recombination (Heuts, 1947), and selection for high and low numbers of abdominal chaetae in *Drosophila* which also produced changes in the spermathecae and other parts, interpreted as incidental to selection on a polygenic system (Mather and Harrison, 1949). Whatever the precise mechanism involved, long experimental selection for a given character is commonly found to have produced correlated changes in other characters. As one more example, MacArthur (1949) selected for large and small size in mice and found that changes in coat color, proportions, litter size, and temperament had also occurred. He interpreted these changes, as far as they were consistent trends, as involving allometry, pleiotropy, and linkage, all three, with drift or sampling effects also producing some nontrend differences between the stocks.

Several students, among them Lerner and Dempster (1948) and Mather and Harrison (1949), have noted that such correlations provide a mechanism by which selection for one character (or character complex) might move another character *against* the pressure of selection. We will return to this point later (Chapter IX).

THE VARIABILITY POOL AND BALANCE

With the unimportant exception of clones still quite near their point of origin, every natural population has a store of correlated genotypical and phenotypical variation. That phenotypical variation is always present is a matter of observation, to which there is no established exception. That a certain proportion of this reflects genotypical variation is also beyond any doubt. Experimental association of genetic variants with phenotypic variants is the basis of the whole science of genetics. It is also often evident that high morphological variation is

Adaptation

ADAPTATION is intimately involved in almost all evolutionary processes, and particularly in those stressed in this book. It is therefore discussed under one aspect or another in every chapter, and it may not be entirely logical to set aside one chapter under this heading. There are, however, some special points regarding adaptation which can be considered separately and for which sufficient groundwork has now been laid. Some of these points are discussed here and others in the following chapter.

COMPLEXITY AND EXTENT OF ADAPTATION

On earlier pages the definition of adaptation has been taken for granted and its universal existence has been considered so obvious as hardly to require exemplification. Now it is necessary to ask more specifically what adaptation is and how widespread is its occurrence, although the subject is so intricate that even here no more than a very general and summary statement can be attempted. For our purposes, an adaptation is a characteristic of an organism advantageous to it or to the conspecific group in which it lives, while adaptation or the process of adaptation is the acquisition within a population of such individual adaptation. What makes a characteristic advantageous, hence adaptive, is a relationship between the organism and (in an extremely broad sense, see below) its environment. Adaptation may be on a basis of individual modification or it may have a hereditary basis. The study of evolution is of course mainly concerned with hereditary adaptation, but it has already been noted that the distinction is hard to maintain and sometimes quite artificial. The *capacity* for individual modification is generally adaptive and has a hereditary basis even though the particular form of modification in a given case does not.

It is obviously advantageous for an individual to remain alive and

for a group to continue reproducing itself—or, if this does not seem obvious, we will define this as a pertinent meaning of “advantageous.” While individuals live and lineages continue they are *ipso facto* adapted, and to this extent, at least, adaptation is clearly universal. There are, however, different degrees and sorts of adaptation. If one group is more successful than another under given (the same or similar) conditions of life, it is fair to conclude that it is better adapted. The surest criterion of such success is increase in relative abundance of the better adapted group.¹ Such increase in relative abundance is evidence of selection (indeed it is genetical selection if the advantageous characters are genetic) and again the relationship of selection to adaptation is confirmed.

Further evidence of the existence and effectiveness of adaptation is provided by adaptive correlations and facies. An animal living in a given environment has many different adaptations all correlated with particular conditions of the environment. A striking example is the lizard genus *Uma*, which lives in the Mojave and Colorado Deserts (Stebbins, 1944; Smith, 1946). These lizards have thick, serrated, overlapping eyelids with a translucent area in the lower lid, peculiar nasal passages, wedge-shaped snout with countersunk jaw, broad depressed body, scale fringes on the toes, granular coloration, and other characters all advantageous for life on and in the sand of its habitat, where it “is the only reptile which shows a decided preference for the mighty barren dunes” (Mosauer, quoted in Smith, 1946). Moreover, in a special sort of habitat different sorts of organisms tend often to have similar adaptations, producing an effect of adaptive facies. Thus in deserts small mammals are often bipedal and ricochet and tend to have large auditory bullae; reptiles, beetles, and some other animals are usually fossorial; most animals tend to be pale in color although some are black; many plants are spiny; and so on. Adaptations to deserts, a

¹ Emerson (1949) criticized an earlier statement of this criterion on the grounds that a rare organism may be better adapted than an abundant one. That is of course true and was not at all contradicted by my statement. Emerson failed to note that the criterion was applied to changes in *relative* abundance in groups in one *certain* or *given* environment, i.e., ecologically horizontal in their relationship. Abundance of one group relative to another may increase even though absolute numbers are small or decreasing, and the criterion cannot apply to two groups adapted to quite different conditions or ecologically vertical as, for instance, parasite and host or predator and prey. Pitelka (1951) has already noted that Emerson's comment was irrelevant. I mention it here, not to reply to a criticism, but to try to clarify a point that must have been obscure.

particularly difficult sort of environment, are often striking and clear in significance so that there has grown up a large and fascinating literature on this subject (e.g., Heim de Balsac, 1936; Kachkarov and Korovine, 1942). Every geographic environment, however, has its own peculiarities which are met by special adaptations of the organisms living in it, as has been rather fully summarized by Hesse, Allee, and Schmidt (1951) for animals, and with some difference in point of view by Cain (1944) for plants, and Newbigin (1948) for both.

Concentration on such strikingly specific adaptations as those of *Uma* for life in the dunes should not make one overlook the fact that most (some students would say "all") of the other characters of such organisms are also adaptations, although they may be of a more general sort. Thus the lungs and circulatory system of *Uma* are adaptations to life in an oxygen-containing atmosphere, and so on through as long a list of characters, anatomical and physiological, as you care to compile. The adaptive significance of such characters may seldom be noted just because they are so necessary or so widely useful and occur in a multitude of different forms, but they are no less, indeed are all the more, adaptive for just those reasons.

Striking examples related to geographical environments may also tend to make us overlook the extreme complexity of the total environment and, correspondingly, of adaptations to it. The physical environment at one geographic locality not only has many different concurrent aspects, such as those of temperature, humidity, substratum, and others less obvious, but also may be radically different for different organisms, for instance for a flying bird, a burrowing mammal, and a soil microorganism. Nor is the physical environment the only one requiring adaptation. It is frequently noted that the biotic environment, the whole local community of plants and animals, has a greater or less degree of mutual adaptation and of individual and specific adaptation to it. Further, from the point of view of adaptation the conspecific breeding or social group of which an organism forms part also has its adaptations and is also part of the environment to which the individual is adapted. Even beyond this, each individual has its own internal environment to which it is also adapted and within which its various parts and functions are correlatively adapted. It seems a little paradoxical to speak of an individual's own body as part of its environment, but the distinction between inside and outside is by no means as clear as at first

appears (Sinnott, 1946). The whole complexity of adaptation cannot be fully grasped without realization that what is adapted to—the "environment" in this sense—includes at least four main, strongly interacting and not sharply separable levels:

1. The physical environment
2. The extrademe biotic environment
3. The deme (conspecific local breeding or social group) environment
4. The individual (or internal) environment

Some students (Emerson, 1949) call adaptation to the first three levels "exoadaptation" and to the last "endoadaptation," but the distinction is not very clear (as Emerson notes). In fact most examples of "endoadaptation" seem merely to be anatomical or physiological correlations and integrations which are the means of achieving "exoadaptation." "Endoadaptations" under the name of "coadaptations" have been stressed by Cuénot (1951 and earlier, see also Corset, 1931; Hovasse, 1950). In a broad sense the term "coadaptation" is defined as an organic character the presence of which makes possible a particular function or sort of behavior. Since all functional characters do this to some extent, the term in this sense is almost meaningless or certainly unnecessary, but it has also been used more specifically for some extraordinary phenomena, notably "coadaptations d'accrochage," in which two anatomical parts arise separately in the embryo and subsequently fit together and cooperate in a common function. They are especially numerous in insects and include, for instance, the femoral groove of the mantis into which the tibia can be folded or the many cases in which different leg segments fit together as seizing devices.²

It is mainly individual morphological adaptation with which this book is concerned. This is the sort most clearly visible in most of the data on long-range evolution, although with improved collecting and broadening viewpoints data for both deme or specific and interspecific

² I mention these here to help exemplify the variety and complexity of adaptation. Cuénot considers them evidence of finalism, and Hovasse explains them by organic selection (of Baldwin) or what he calls "parallel selection." It is unnecessary to discuss their origin here, beyond expressing the opinion that they are explicable in the same ways as any other adaptations and do not really constitute an exceptional and distinct class. That two parts should arise separately and later fit together seems to me no more—and no less—mysterious or finalistic than the fact that in epigenetic development *all* functional structures arise with apparent anticipation of their subsequent functioning.

adaptations are increasingly available. In any case, proper interpretation must be made against the broader background of adaptation in general. Much adaptation is physiological or behavioral rather than morphological although, again, the distinction is not really sharp or clear. Physiological and behavioral factors are limited by and correlated with morphology, and in a sense the adaptive characteristic of morphology is seldom strictly morphological but arises from the dynamic, i.e., physiological and behavioral, functioning of the anatomy.

That all of this applies at different levels also involves marked differences in the significance and nature of adaptation. A character adaptive in one respect may not be so in another. Adaptive alternatives may exist such that adaptation to one precludes adaptation to another. Development of armor is, for instance, a frequent adaptation for defense, but it lessens the possibility of rapid motion, which is also a frequent adaptation for defense in other animals and has generally wider usefulness than has armor. More subtle and possibly more important is the contrast between individual and group advantage in adaptation.

That contrast is, indeed, usually absent. An adaptation advantageous to the individual is also likely to be advantageous to the species. It used to be assumed rather generally that this is always true—or the question was not raised at all. This was when selection was understood and discussed in purely Darwinian terms, and Darwinian selection usually (but even it not always) acts for the advantage of the species by favoring individuals of some sorts and eliminating those of other sorts. Even selection on social aggregates generally favors the individual, his integration into the group being favorable to survival and adaptive for him, as well as the group, its social structure being favorable for continuing reproduction of the whole unit. Genetical selection as well as Darwinian selection produces no contradiction between individual and specific adaptation in such cases.

Haldane (1932) has, however, pointed out that there are "altruistic" adaptations that favor the group at the expense of the individual, that is, they shorten the lives of their individual possessors but prolong the survival of the group, as in insect societies organized as if to ensure the survival of only the small minority of reproductive members. Among others, Allee (1943) has also emphasized this situation, and Wright (1945) has suggested a genetical mechanism for it involving small, incompletely isolated populations, with intergroup selection favoring

local populations in which the individually disadvantageous gene has become fixed by chance and with gene migration permitting spread of the character from the selectively increasing population. In a stimulating discussion of this whole subject, Huxley (1942, Chapter 8) has also emphasized the opposite effect, i.e., individual adaptation deleterious to the group, exemplified by development of bizarre ornamentation and overelaborate weapons by intragroup selection.

I must confess to a little skepticism regarding some of the examples on both sides, that is, as to whether "altruism" in, say, insects does develop when it is actually disadvantageous for most individuals and whether sexual characters are favored by selection if while the selection is actually operating they are disadvantageous to the group. Of course there may be in both cases a balance of advantages so that selection as a whole carries a character as far as advantages outweigh disadvantages, which may not be quite the same thing as to say that there is selection for the group and against the individual or the other way around. There is clearly also the sort of balance previously noted between narrow variation, favoring survival of more individuals but potentially fatal to the group if conditions change, and wide variation, producing more misfit individuals at the time but favoring ultimate survival of the group. But in such cases, too, one may question looking at the matter as individual *versus* group. It is rather a question of short and long range adaptation. Both group and individuals are favored by narrow variation while conditions are not changing, and both are favored by wide variation while conditions are changing.

Judgment as to whether characters are actually adaptive and if so in what way is quite easy in a majority of cases, which are likely to be overlooked just because they arouse no argument. This is usually because the adaptation is widespread and not specific: adaptations for respiration, reproduction, broad types of metabolism or of locomotion, and the like. It is generally only as regards characters of less basic importance, highly specific and peculiar characters, or differences between similar groups that doubt often arises and argument begins. Part of the difficulty lies in the necessarily arbitrary nature of what is called a "character" in taxonomy, which may be a purely incidental result of what is really the adaptive character. For instance, color is one of the commonest of "taxonomic characters" and we are inclined to think that if it is adaptive it is so because of its visual characteristics. Certainly

this is true much of the time, but it is not necessarily true all of the time. Desert animals tend to be light in color, as mentioned, and this is generally protective coloration or, and possibly at the same time, it is protective by increasing reflection. But there is also a less common desert color facies of black animals. Are they inadaptive in color? It has been suggested that the color may protect from high-frequency radiation or that it may increase resistance to low humidity. It may actually be disadvantageous as a color, but merely the manifestation of some obscure or physiological character of outweighing advantage. That such can be the case, although with reversed value for black, has been known for many years: melano mice usually have a higher death rate than their siblings of normal color, and surely not because of their blackness, as a color. (See Haldane, 1942.) Similarly obscure correlations occur in nature. Some minor variations in scale characters of snakes, of no evident adaptive significance, are significantly associated with juvenile mortality (Dunn, 1942); the example is especially striking because this is just the sort of taxonomic character often cited as of "no conceivable survival value."

Human judgment is notoriously fallible and perhaps seldom more so than in facile decisions that a character has no adaptive significance because we do not know the use of it. The case of the European banded snails, *Cepaea nemoralis*, will probably become notorious and may cause a swing too far the other way. These snails are highly polymorphic in banding, with considerable stability in local variation and in differences between populations. The polymorphism has long been cited as selectively neutral and as firm evidence of occurrence of nonadaptive characters (e.g., still so cited in Carter, 1951). Recently, however, conclusive evidence has been produced that selection and adaptation are involved (Cain and Sheppard, 1950).

In dealing with extinct organisms, the difficulties may be even greater. Appearance of a character known in recent animals or plants and known to be adaptive in them warrants the inference that it was adaptive in the same way in the fossil group. But fossils sometimes have characters quite unknown in living animals, and evaluation of them is hazardous and often purely speculative. The complex suture lines of ammonites have no recent parallel and there is a widespread idea that they were nonadaptive, although to others the very consistency of their histories implies adaptation, and adaptive advantage is possible.

at least, for example as body anchorage and leverage in varying conditions and positions or as resistance to pressures in shells of different shape and size. There are no clawed ungulates today, but such developed several times in the past. In this case few have doubted that the claws were adaptive, but there is no clear consensus as to what the adaptation was. Use for digging tubers or for clinging to trees are among the numerous, inconclusive suggestions. An even more baffling case may really be solved, although there is no possible way to establish this with certainty: extraordinary dorsal fins developed independently in several lines of Permian reptiles (pelycosaurs). Romer (1948, 1949) has shown that these have just the size and other relationships that would be expected if they were body-heat regulating mechanisms.

In view of all the difficulties and obscurities in discovering the adaptive significance of some characters, it is impossible to adduce rigid proof for any case that a character has no adaptive significance, either in itself or as an incidental effect of another feature that is adaptive. Since no one doubts that many characters are adaptive and since none can be proved *not* to be adaptive, some students maintain that all characters should be assumed to be adaptive (e.g., Ford, 1945b). Others maintain that the universal affirmative is equally unproven and that with so many characters that are not known to be adaptive and do not seem to be so it is illogical to suppose without proof that all are so. They therefore assign a significant role to nonadaptive change (e.g., Carter, 1951) or sometimes even the major role in evolution (e.g., Goldschmidt, 1940). Theoretical considerations from population genetics, previously reviewed, are cited on both sides of the argument. Those students favoring universal adaptation cite Fisher (with whom, in fact, Wright apparently does not disagree on this point) to the effect that no character is likely to be or, at least, long to remain neutral to the effects of selection, which therefore eventually tends to eliminate any nonadaptive character. Those assigning a role to nonadaptive change cite Wright to the effect that this is likely to occur in spite of selection in sufficiently small populations, and it was noted above that for characters of low selection value (positive or negative) the populations in question may be judged of moderate or even rather large size.

Aspects of this problem of particular importance for the present

inquiry center around differences between taxonomic groups and will be somewhat further discussed in that connection.

ADAPTATION AND DIFFERENCES BETWEEN TAXONOMIC GROUPS

It is not surprising to find that opinion as to the adaptive significance of differences between taxonomic groups varies from belief that such differences have no adaptive value to the claim that they are always adaptive. Opinion often depends on whether the groups in question are of low rank, demes, subspecies, and species, or high, families and upward. It is here recognized (or perhaps I should say concluded) that there is no absolute difference of kind as regards characters and their adaptive status in the sequence of different levels in the hierarchy, but it remains possible if not probable that there is a graded quantitative difference between low and high levels. The two will therefore be discussed separately before trying to reach a general conclusion.

There seems to be a consensus that differences between subspecies and species are usually adaptive but sometimes nonadaptive. This is the opinion of both Mayr (e.g., 1942) and Rensch (e.g., 1929, 1947), who have devoted as much attention to the question as anyone.³ Mayr tends to stress adaptive differences and Rensch nonadaptive, but it is hardly possible to take a complete census and both do agree that adaptive differences are usual but not universal. There is the strongest sort of evidence for the usually adaptive nature of low-category taxonomic differences. This evidence is especially of the following sorts:

1. Distinct but similar and related species fully established in any region have some ecological distinctions of habit, habitat, or both. In especially close cases they may overlap in some niches, but their modal populations are in different niches. For instance it has often been noted that among multiple species of rodents in any given area, unless one is clearly driving another out by competition, each has some distinction of habitat or food preference, or both.

2. There is often an observable correlation of habit and diagnostic structure among related species, e.g., in the Drepaniidae, birds with long beaks and tubular tongues regularly feed on nectar, those with short beaks and nontubular tongues do not (Amadon, 1950).

³ Both are ornithologists, but both have extraordinarily broad grasp of neontological systematics.

3. Geographic variation generally shows graded and regular distribution of characters and this can often be correlated with environmental factors, e.g., Bergmann's rule that in warm-blooded vertebrates related forms tend to be smaller in warmer and larger in colder regions (e.g., Hesse, Allee, and Schmidt, 1951).

4. Vicarious parallel, and convergent species tend to develop similar characters in correlation with degrees of similarity of habits and habitat, e.g., the same adaptations are found independently developed in reptiles in American and African deserts (Mosauer, 1932), and in each case these characters distinguish them from their closer relatives of different habitat.

So impelling is this and related evidence that one must agree with Mayr (1949a), that "the adaptation of local populations and its causation by selection can be considered a fact" and further (1949b), that "speciation is . . . an adaptive process," but without conceding at this point that it must always and exclusively be so. The question, then, is whether nonadaptive differences also occur and, if so, whether they are common enough to have distinct significance in evolution. Evidence for nonadaptive differentiation is, in the main, the reverse of that for adaptive differentiation, hence, using the same numbers as above:

1. The rule of the ecological incompatibility of distinct groups with very similar or the same adaptive characteristics was based largely on terrestrial vertebrates. Such forms are not highly multispecific in any one habitat, and the rule seems to apply to them without known exceptions. The few apparent exceptions are explicable as involving zones of marginal contact, areas of recent invasion of a competing form, or cases of obscure but real or of periodic rather than discontinuous ecological distinction. Among other organisms, adaptive differences between related, sympatric species are certainly very common, also. I must say that it requires a measure of faith to conclude that they are universal in exuberantly multispecific communities such as, for instance, the gammarids of Lake Baikal, the molluscs or crustacea (among other groups) of a tropical reef, or the trees of a rain forest. Even in such cases faith finds support from such observations as that the gammarids of Lake Baikal do have zonal depth distribution and other adaptive differences, although the evident ecological distinctions are much less numerous than the species. The question seems still to be open,

either the ancestral population in its earlier adaptation or the descendant population in its later adaptation. This is not to say that the evolutionary movement goes contrary to a direction of some adaptation at any time or that the population must at any point be considered absolutely inadaptive, although it may become so and may become extinct if it fails to cross the threshold successfully. (In fact, the threshold may move away from it and leave it inadaptive.)

The fact that a population in this situation is relatively inadaptive—or let us say to avoid any possible misunderstanding that it is distinctly less well adapted than either of two existing alternatives—involves very high selection pressure on any population that crosses a threshold. Exceptionally high rates of evolution are therefore to be expected in any group that does successfully pass a threshold, with later deceleration as the new adaptation is more completely realized. This effect is, indeed, clearly evident in sequences with thresholds. Horse hypsodonty illustrates the occurrence of this in the midst of a sequence. It is more broadly illustrated by the general observation that phylogenetic rates of evolution are often much more rapid in early than in late phases of a group arising with a decided change in adaptive type, as previously exemplified by the lungfishes.

The rapid evolutionary movement into new adaptation after a threshold is crossed concerns not only "key" characters and other pre-threshold prospective adaptations but also and often more particularly other characters of genotype and phenotype involved in integration and expansion in the new adaptive relationship. This process has been called "postadaptation," in analogy with "preadaptation," and the term perhaps may still be retained without confusion. It refers specifically to one particular phase of adaptation, readjustment to a new adaptive position after crossing a threshold. It grades into usual progressive adaptation and is not sharply distinguishable from the latter, being a phase of the whole adaptive process and not a qualitatively different sort of adaptation.

CHAPTER VII

The Evolution of Adaptation

THE PRECEDING DISCUSSIONS have led to the conclusion that most evolution involves adaptation. Absolutely or relatively inadaptive phases occur and organisms develop nonadaptive and inadaptive characteristics, but over-all patterns of evolution are predominantly adaptive and adaptation has been seen to be the usual orienting relationship even in minor details of the pattern. Adaptation, itself, evolves. We do not simply have on one side a discrete something called "environment" with a neatly fixed set of prospective functions packaged into niches and on the other side discrete things called "organisms" or "populations" the evolution of which consists of progressive occupation of the niches. That is a process that happens in the course of evolution or, at least, it is one way of stating one of the aspects of what happens. For purposes of analysis of some phases of evolution it is a valid and useful manner of speaking. For fuller understanding, however, it is equally or more useful to focus neither on environment nor on organisms but on the complex interrelationship in which they are not really separable. The present subject, then, is the evolution of this relationship, of adaptation, and the way it is reflected in the actual phylogenetic histories of organisms.

ADAPTIVE ZONES AND THE ADAPTIVE GRID

At any instant in time, the realized functions of environments and organisms define a broader or narrower field or type of adaptation. This is not precisely the same for any two organisms, but it is almost the same for individuals in the same deme, somewhat less so for demes of the same species, and decreasingly similar but still with some common ground for species of the same genus, genera of the same family, and so on. In other words, at each of these levels there is a characteristic adaptive aspect which becomes narrower and more particular in

the direction from higher levels down to individuals, broader and more general in the opposite direction. Although this adaptive relationship correlates with taxonomy as suggested, it is not confined or defined by taxonomy. It is quite common for taxonomically distinct units, of different phylogenetic origin, to share an adaptive aspect with each other but not with other members of their respective taxonomic groups. Thus the thylacine, a marsupial of Australia and Tasmania long extinct in the former and possibly now extinct in the latter also, shares with the placental Canidae an easily definable adaptive type entirely distinct from that of, say, a kangaroo on one hand or a seal on the other. Nevertheless thylacines are more closely related phylogenetically to kangaroos and dogs, in about the same degree, to seals.

The definition of adaptive types has an arbitrary element. It is in part merely a matter of what analysis we care to make of an exceedingly complex and extensive continuum. Choice in such cases depends on the particular aim of the study, the nature of the relationships involved, and the taste or experience of the analyst. Thus a not literally infinite¹ but extremely large number of different definitions and arrangements of adaptive types is possible, all valid or real in the sense of corresponding to facts in nature but all arbitrary in the way those facts are analyzed. The breadth or scope assigned to such types and the number and delimitation of steps in a scale of increasing scope may also be set arbitrarily in a very large number of different ways.

Consideration of the situation with any accepted classification of adaptive types shows, however, that the distinctions of type are not merely arbitrary. They correspond with discontinuities in nature, which may tend to be more rather than less obvious the broader the scope involved. Sibling birds in the same nest do not really have absolutely identical adaptive types, but the adaptive difference between them

¹ Some readers may be interested in the somewhat abstruse but, I think, important distinction between "infinite" and "extremely" or even "inconceivably large," which has a bearing on the theory and philosophy of classification. Any realized adaptive type is a class to which one or more real organisms are referred. The greatest possible number of such classes (only a minute proportion of which would have biological significance, i.e., would correspond with real adaptive types) is defined by the number of combinations of individuals in groups of from one upward by integers to the total number of really existing individuals. Since this total number is finite, the number of combinations, although extremely large, is also finite and so is the number of possible adaptive types, smaller than and limited by the number of combinations.

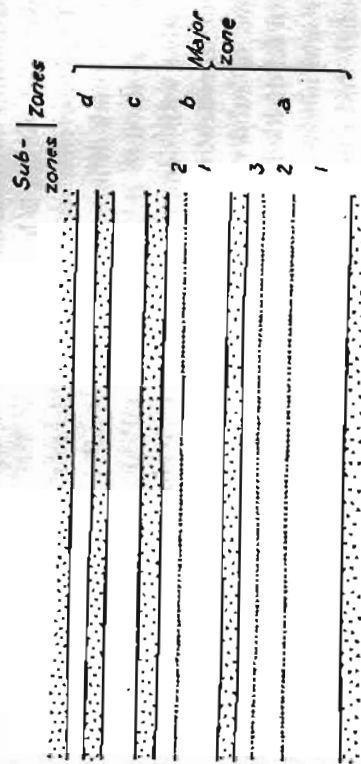


FIGURE 22. *Discontinuities, or essentially unstable ecological zones*

FIGURE 22. DIAGRAM SUGGESTING THE NATURE OF AN ADAPTIVE GRID. The real grid is incomparably more complex than the diagram because it may have a very large number of dimensions or number and grades of subdivision.

(which is a real discontinuity) has no practical or theoretical significance for most purposes or, at least, for our present purposes. (Even so, it does matter in some sorts of studies.) On the other hand a paramecium in a pond and a man reading this book, a fish in the sea and a bird in the air, an opossum up a tree and a bat in a cave, or a cat stalking a mouse and a dog chasing a rabbit clearly and significantly represent sharply discontinuous adaptive types with, in the sequence of examples, characteristic differences in the breadth of the discontinuity.

A visualization of some of these relationships, useful as long as one bears in mind that it involves abstraction, analogy, and oversimplification, is to represent adaptive types as zones which can be diagrammed on paper as bands or pathways, together simulating in some examples a sort of grid (Fig. 22). A broader zone represents a more general adaptive type and a wider space between contiguous zones indicates greater discontinuity of type. Adaptive types may be defined in part and in some cases in geographic or physical environmental terms, but it is essential to remember that what we are talking about here is not a geographic, physical, or even in the broadest sense environmental zone but an adaptive zone, representing a characteristic reaction and mutual

relationship between environment and organism, a way of life and not a place where life is led.¹

To give even a semblance of reality to this visualization, it is necessary to think of most broad zones as subdivided into narrower zones, these again into subzones, and so on down to narrowest bands correlative with demes or even with individuals. For example, a major zone of rodentlike adaptation might, as one of numerous possible systems of subdivision, include zones one of which is squirrellike, in turn subdivided perhaps into arboreal and terrestrial subzones, the latter into nonfossorial and fossorial or maybe noncommunal and communal, and so on down to a sub-subzone representing the particular and special adaptive type of one colony of *Cynomys gunnisoni zuniensis* (such as the one visible to me as I write these lines) or of one family or individual in that colony. To be sure, somewhere along the descending scale is a point below which existing differences in adaptation are not consistently correlated with genetical or with heritable phenotypic variation and therefore do not concern us here. In the example, adaptive differences down to the deme (the colony or "prairie-dog town") probably have some correlation with heredity and those within the deme do not; this is a usual situation.

Changes in adaptation involve, figuratively, movement of phylogenetic lines within or between zones. Such movement may be an expansion or restriction, more often the latter as when a group covering a broader zone becomes specialized and more narrowly confined to one of its subzones. Movement may also be interzonal, for any level between major zones and subzones. Thus differentiation of prairie-dogs from ground squirrels was subzonal, rather far down the scale but not at its lowest levels. Change of penguin ancestors from aerial to aquatic adaptation was interzonal at a rather high level.

Discontinuities between zones as seen now or at any other point in time are generally quite clear and fixed. Canidae and Felidae are now in different, sharply discontinuous zones within a major zone of terrestrial, predaceous carnivores. Even the cheetah, a doglike animal as cats go, does not contradict the fact that animals fully intermediate in adaptive type between cats and dogs would be anomalous in the existing ecological system. Coming down the scale, there are also distinct

¹ I now find part of my earlier discussion of this subject (Stimpson, 1944a) somewhat confusing in this respect.

but lesser discontinuities between, say, pantherlike and lionlike subzones, and going upward there are distinct and larger discontinuities between, for instance, terrestrial and aquatic carnivores. (Designation of zones in taxonomic terms, as "felid" or "canid," is also a convenience and a convention, as is their occasional designation in environmental terms, but is still not to be allowed to obscure the fact that it is adaptation, not organism or environment, that defines the zones.)

Since the divergence of dogs and cats in the Eocene, dogs have changed less in adaptive type. In a sense, the cats have moved from a broadly canid zone (more precisely a viverrid zone) into the felid zone. As the grid appears today, this suggests that they crossed an adaptive discontinuity. There is no doubt that such events do occur. When they do, the discontinuity corresponds with the adaptively unstable conditions around a threshold, as discussed in the last chapter. It is, however, an important additional fact that the zones themselves, and their relationship to each other, evolve. Environments change and organisms change. As they do, so do both the existing and the possible relationships between them, which are symbolized as adaptive zones. The adaptive relationship may and usually does show steady secular change. The existing canid zone is not the same as the Eocene canid zone from which the cats moved, nor was the felid zone then like the recent felid zone. The discontinuity between them was thus not the same as that now existing, and it does not follow that it was equally large or even that it was then present at all.

Many of the problems of the evolution of adaptation involve the existence and origins of discontinuities in and between adaptive zones. Some discontinuities are inherent in the ecological situation over the periods involved in an adaptive change or may even be regarded as permanently required by the environment. Thus a discontinuity between aerial and aquatic life seems inherent in the permanent physical distinction between air and water. We may be quite sure that regardless of continuous evolution of both aerial and aquatic adaptive zones, a discontinuity did have to be crossed when the penguins evolved. This example shows, nevertheless, that the inherent discontinuity may not be as great or of quite the same sort as appears at first sight. In fact there is an adaptive zone with only slight discontinuity from the strictly aerial zone and yet nearer the aquatic zone. (Fig. 23.) This intermediate zone is now occupied by oceanic birds that fly both in the

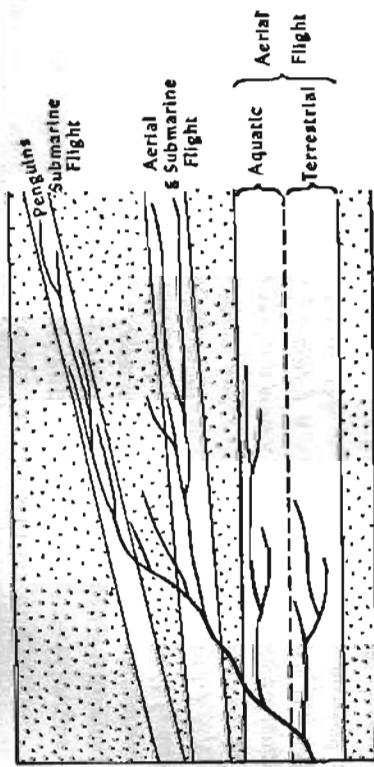


FIGURE 23. GRID DIAGRAM OF PENGUIN EVOLUTION. (From Simpson, 1946.)

air and under water, among them some of the Procellariiformes, e.g., *Pelecanoides*, diving petrels. There is still a distinct discontinuity between the adaptation of forms like this and that of the earliest true penguins. Its threshold was the point where selection for underwater flight became stronger than for aerial flight, with the ultimate effect that the former was perfected and the latter lost. Once over this threshold, the penguins had progressive and complex postadaptation to the new environmental relationship, and this, in itself, has further removed the penguin zone from that of *Pelecanoides* and still more, of exclusively aerial flight (Simpson, 1946). Incidentally, although there is now an increased discontinuity between *Pelecanoides* and the present penguin zone, that genus, perhaps with some others of similar habits, may be a rare instance of a recent animal near a major primary threshold. Study of selection on it would doubtless be extremely difficult but would also be extremely interesting.

Other inherent discontinuities include that between aquatic and land life, which was crossed, as in the somewhat reversed case of the penguins, by forms whose adaptation was alternatively to both habitats, either facultatively or at different periods in ontogeny. Discontinuities that seem to be inherent only for a particular group in the ecological situation at a given time are illustrated by such cases as change from browsing to grazing in horses. Intermediate types do occur and evidently can persist stably in other groups, but for the horses when the change

occurred either alternative was advantageous over intermediate positions.

The last example, however, probably also involved and perhaps could be wholly explained by a very widespread effect that causes or increases discontinuity as and after a new zone is occupied. The effect of such occupation, in itself, tends to eliminate adaptive stability in any closely adjacent or overlapping zone. Development of specialized grazinging horses placed at a selective disadvantage any less specialized grazing forms and also those in which grazing or browsing was facultative, as long as grazing was in fact continuously possible. This effect, which results in a sort of parceling out of a total ecological situation into a number of specialized and more or less sharply discontinuous adaptive zones, is very general in evolution. Examples on a grand scale will be noted toward the end of this chapter. On a small scale, the effect is a normal concomitant of speciation. After adaptive differentiation of two populations, wherever they come in contact there is a tendency to eliminate variants adaptively intermediate between them. As long as considerable gene flow continues, the contact zone is rather a line of tension than a discontinuity, but when for any reason gene flow decreases or stops (speciation, *sensu stricto*, occurs) discontinuity develops. (See, e.g., Huxley, 1939; Mayr, 1942.)

Probably almost all small and most large discontinuities between adaptive zones arise in that general way, i.e., develop along with the adaptive differentiation of the groups evolving in the two zones between which the gap arises.² Incidents of the opposite sort, with adaptive change initiated across a preexisting unstable zone or inherent adaptive discontinuity, seem to be relatively fewer in number. There is, however, reason to believe that they have been absolutely numerous in the course of geologic time and have been particularly important with respect to more marked changes of adaptive types and the origin of higher taxonomic categories.

In the course of the evolution of adaptation, zones not only change

² Although this does not represent a strong change in opinion, I formerly (1944a) failed to make this point quite clear and also stressed the less common, but frequently even more important, cases where threshold effects occur across a preexisting gap. Günther (1949) has used that treatment in support of his view that almost any change of adaptive type means crossing a discontinuity or unstable zone and has further generalized (contrary to my opinion, as he recognized) that random preadaptation is usually involved.

constantly in specificity (width) and character (direction or position) but also appear and disappear. Within the general felid zone, a *chairodontine* (*sabertooth*) subzone early developed as a consequence of the spread of numerous rather slow-moving and thick-skinned herbivores and the subzone disappeared, with extinction of its occupants, when such prey became markedly less abundant during the Pleistocene. (The example is discussed in more detail in the next section.) On a broader scale, evolution of numerous small flying insects opened a zone for aerial insectivores, still richly occupied (many birds, most bats), and more broadly still a whole sequence of wide zones successively subdivided arose progressively as vascular plants spread to the land and evolved there.

It is abundantly clear that despite periodic elimination of many adaptive zones, mostly rather minor in extent, there has been tremendous increase in the number of broad adaptive zones and in the fineness and multiplicity of subdivision of these in the course of geologic time. The broadest zones of all tended to open and be occupied early and, while such a statement depends considerably on personal definition of such zones, most of them were apparently in existence and occupied by the end of the Paleozoic. A balance toward increase in number of zones of lesser scope, at least, continued much later, probably well into the Cenozoic. Whether the balance still is tending toward increase is a moot point. There has perhaps been a decrease in the late Cenozoic, but it is impossible to say whether this indicates that the earth is, so to speak, full at last or whether much further adaptive extension and subdivision will eventually occur. If it were not for the quite unpredictable activities of man, who is eliminating many adaptive zones (or subzones) and creating many others, I would favor the latter alternative, simply as a guess subject to no verification and backed by no compelling evidence.

THE OCCUPATION OF ADAPTIVE ZONES

A basic evolutionary sequence, an element entering into most of the more complex evolutionary patterns, is the occupation by a group of organisms of an adaptive zone new to them, their subsequent diversification and phylogenetic change in that zone, and their eventual extinction in it, if this has yet occurred. For a zone to be occupied, it must first of all exist as a prospective or realized set of environmental

functions, and there must be a population able to move into it. Existence of a prospective zone may involve appearance of a new environment unoccupied as far as the adaptive type in question is concerned, or new access to such an environment. Any change in the whole environmental complex (which includes the organisms in it) does produce new environments, but slow and accustomed changes usually lead not to new occupation of zones but to secular evolution of the zones (and of course of their occupants) already present. The opening of quite new zones is rather by evolutionary changes such as those indicated in the last section (e.g., spread of vascular plants on the land), by rather abrupt and widespread geographic events (rise or fall of relative sea level, advance and retreat of glaciers, etc.), or by new access (rise of a land bridge, piercing of an isthmus, waif or sweepstakes dispersal, etc.)

To enter a new zone, a group must have physical, evolutionary, and ecological access to it, all three. The need and significance of physical access are obvious. The zone must occur where the group is or where it can and does reach by dispersal. By "evolutionary access" in the present connection, I mean that the group must have at least minimal prospective adaptation for the new zone, as discussed in the last chapter. Acquisition, by any process, of such prospective adaptation may and frequently does lead to occupation of a new zone without involving physical movement of the group or ecological change around it, except such as follows its own movement into the zone. This is a relatively clear-cut event when a threshold occurs. The horses that became grazers did not go anywhere to do so, and there was no particularly relevant ecological change around them.⁴

By "ecological access" is meant that the zone must be occupied by organisms for some reason competitively inferior to the entering group or must be empty. It is highly doubtful whether a group entering an occupied zone is ever competitively superior when it is actually in the process of significant change of adaptation or when its adaptation for the new zone is prospective rather than effectively realized. Prob-

⁴ It might be objected that spread of prairie grasses was a concomitant ecological change. It was a necessary preliminary in bringing the grazing adaptive zone into possible existence, but not otherwise relevant to the actual event of change in zone by the horses. Also the apparent evidence (Elias, 1942) that prairie grasses did spread in the Miocene, just when the horses took to grazing, may be a coincidence. What seem clearly to have been grazing mammals of other groups had evolved much earlier elsewhere, in the Eocene and Oligocene.

ably no group ever shifted to a distinctly new zone by progressive adaptation to it while it was already occupied by well-adapted organisms sympatric with the former group and therefore with the possibility of direct competition from the start. For success against a group already established, it seems to be a rule with few possible exceptions that the entering group must already be well-adapted to just the same zone, or to a subzone of that zone, or to an overlapping zone or one near enough to be competitive (which really means that there is at least some overlap). The first of these three situations cannot arise and the other two are unlikely to arise, if they can at all, unless the entering group evolved its adaptive type elsewhere and the "entrance" was an actual movement, geographical migration or expansion.

It follows that occupation by a different group of a zone already occupied usually, perhaps always, involves change in distribution; a geographically invading group, if the invasion is successful, ousts one already established in a region. This is a very important conclusion for, among other things, interpretation of the fossil record, which is in all cases incomplete as regards geographic sampling. It means that when one group replaces another of similar adaptive type, a common phenomenon in the record, much the most probable interpretation is that one or the other evolved elsewhere and is a rather recent migrant where found—"rather recent" because its current adaptive type has not essentially changed since it was developed elsewhere. Among many examples, that of the mammalian faunal interchange between North and South America is particularly good, because here we know with one possible exception (the opossums) where all the many groups involved came from, when the exchange began within reasonable limits, and what happened to all the groups. A fairly detailed analysis has been given elsewhere (Simpson, 1950b). In brief, there was on both continents but especially in South America rather extensive entrance into occupied faunal zones by animals *already* adapted to them on the other continent. With no exceptions, this duplication within faunal zones was temporary, one group or the other becoming extinct in a geologically short time. In most cases it was the invading type that survived, as would be expected because the ability to invade in the face of occupation implies probable competitive superiority although this might not, in exceptional cases, extend to longer competition or endure in rapidly changing conditions.

There are a number of apparent exceptions to the rule that replacement of one group by another in an adaptive zone indicates geographic invasion. I question whether any of these exceptions really are such. Some of them are clearly artifacts of classification. For instance, fissiped carnivores replaced creodonts (both suborders of Carnivora) in the late Eocene and Oligocene (Fig. 19, Chapter VI), including replacement in western United States where these groups had lived together without decided tendency toward replacement for a very long time, from the middle Paleocene. Over-all, it is entirely correct to say that fissipeds arose from creodonts and replaced the latter, but not without invasion. The fissipeds that long lived with creodonts were not competing types but a family with its own well-defined adaptive zone, Miacidae. The actually competing and replacing types probably arose from this family, in a broad sense, but not in the area of observation, where no transitional forms are found. The actual replacers are clearly invaders when they appear. Analysis at the family rather than subordinal level shows this clearly, for the invaders already belonged to other and more progressive families than the Miacidae. In fact, they replaced the native Miacidae (more similar to them in adaptive type) more quickly than they did many of the creodonts.

Another sort of apparent exception is involved in the last fact stated. A successfully invading group often tends to diversify in the invaded area, to undergo adaptive radiation as it occupies contiguous adaptive zones and specializes into subzones of its original zone. In the course of this process it may, or at least may seem to, spread progressively into zones occupied by natives but not immediately entered by the original invaders. Invading fissipeds forthwith took over the miacid zone and some creodont zones but only much later knocked out the last creodonts. Similarly in South America invading crioetid rodents almost at once replaced the natives most similar in adaptation, but since then have been expanding greatly and progressively entering more diversified zones or subzones while the natives continue to dwindle, a process probably still going on although some of the natives with distinctive adaptive zones retain these completely.

Some of this apparent expanding replacement is not really such but is the effect of repeated invasion by new groups of differing adaptive types overlapping different zones occupied by natives. Part of it seems, nevertheless, to be a real phenomenon, and yet it probably does not

really represent evolution, *in situ*, of a replacing and replaced group. Some of it is due to allopatric evolution and later invasion on a smaller scale. (The areas of the examples are whole, varied continents.) Some of it is probably due to what might be called intercalary replacement. The eventually replacing groups evolve not in but between the zones of those eventually replaced. When this happens with a good many groups each of which has some, even very slight, marginal overlap on an older occupied zone, the total effect may be to make that zone untenable. The effect is not so much actual replacement in that zone as disappearance of the zone by encroachment of contiguous zones. An oversimplified model may make this clearer. Suppose a carnivore *A* is especially adapted for preying on a rodent *a*, but can supplement this diet when *a* is scarce by feeding on *b*, *c*, *d*, and *e* as available and needed. This is no serious impediment to adaptation of another carnivore to feed mainly or wholly on *b*, another on *c*, another on *d*, and another on *e*. None of these competes with *A* for *a*, its principal food, each competes for only one supplemental food of no vital importance to *A*, and they do not compete with each other. Their various adaptive subzones are intercalated around that of *A* and between it and other older carnivore adaptive types not here specified. But among them they compete with *A* for *all* its supplementary food and are severally better adapted to take each sort of this. *A* then cannot supplement its diet and it becomes extinct when *a* is in periodic low supply. The effect may, of course, apply to any environmental conditions and not to food alone. A similar effect may ensue when two groups otherwise quite differently adapted nevertheless have some one need (such as water, nesting space, etc.) for which they compete.

In the preceding model, the zone of *A* was not actually occupied by another group. It simply became empty except as different, adjacent zones might eventually cover it by combined overlap. Or, after the zone is empty, some other group may enter it by narrower specialization requiring no overlap with the surrounding zones. Then, on a small scale, there is delayed rather than competitive replacement in the zone of *A*. This is a fairly common and rather puzzling phenomena on a much grander scale. Bats (and to some extent birds) replaced pterodactyls in their adaptive zone, but not until long after the pterodactyls were extinct and the zone empty for some millions of years. Similarly cetaceans replaced ichthyosaurs long after their extinction. So, in a gen-

eral way and as regards some adaptive types, did mammals replace the dinosaurs, and contrary to a popular impression this was delayed. There is no evidence of competition between mammals and dinosaurs, and mammals that most nearly occupied zones opened by dinosaur extinction did so millions of years after that extinction.

Such events are completely incomprehensible if it is supposed that a particular adaptive zone was continuously open and essentially unchanging throughout the history, for no way is known or even conceivable (to me, at least) in which a group adapted to an essentially unchanging zone can become extinct without competitive replacement (which, as a matter of fact, is a change in the zone if everything is considered). The only possible explanation is that the zone did change, but that later groups could move into the changed zone, or into one defined (more or less arbitrarily in some respects) by some of the same characteristics. After all, such analysis is always oversimple. There are very decided differences in *total* adaptation between cetaceans and ichthyosaurs, and it is an abstraction of ours when we consider the special aspects of adaptive similarity and speak of them as being in the same adaptive zone. To be more concrete, as an example of the sort of process that may occur although this particular one probably did not, a change in the total environment of the ichthyosaurs may have required thermal regulation for their survival. They did not have prospective adaptation for this change and became extinct. It was a long time before another group with prospective adaptations for the ichthyosaur zone (locomotion, aquatic life, food, etc.) plus thermal regulation developed.

In some short range processes it is possible that a transient, non-recurrent catastrophe might cause extinction without longer alteration of an adaptive zone and that this zone would, potentially, then be open as quite the same. In general, however, it is inaccurate to speak simply of extinction as a way in which empty zones arise. The *same* zone as that formerly occupied is irretrievably gone in the complex flux of historical process. *New* zones similar in some respects or defined by the same partial specifications may arise, at once or much later, as a sequel to the extinction.

In a more or less strict sense, empty zones thus seem normally to be new zones, which are constantly arising as the whole complex of adaptations evolves. As previously suggested, such zones may arise from

any sort of environmental change or any sort of evolutionary change in organisms, since any change in either obviously makes possible new relationships between them. The great majority of actually empty zones are those that never have been occupied. The most spectacular examples are provided by islands literally empty when formed and eventually reached somehow (usually by sweepstakes dispersal) by plants and animals, a sequence especially clear and well-studied in the Galápagos (Lack, 1947) and Hawaiian (Zimmerman, 1948; Amadon, 1950) islands.

Generally less obvious but nevertheless more widely important have been cases where access to an empty zone involved more evolutionary than geographic movement. In the case of new minor zones or sub-zones adaptively contiguous to those already occupied, prospective adaptation for them usually occurs even when they are arising and their occupation tends to occur as soon as they appear or soon thereafter. More strikingly distinct zones may require prospective adaptations not in being when they arise and they then may remain empty for long periods of time. For instance, a broad and potentially intricately subdivisible zone for flying insectivores arose when flying insects evolved, but there were then no existing organisms with prospective adaptation for that zone and it was many millions of years before any developed. Flying insects were already common in the Pennsylvanian, and the first possibly flying insectivores (small pterodactyls) do not appear in the fossil record until the Jurassic. It seems probable (to me; some other students think it flatly impossible) that unoccupied major zones now exist. There is, for instance, no true aerial plankton although I see nothing impossible in the eventual evolution of one. If it did appear, this in turn would create other major zones. Whether prospective adaptations for this and other possible developments will appear and such zones will be occupied perhaps comes under the heading of idle speculation.⁸

EVOLUTIONARY SEQUENCES AND PRINCIPLES ON THE ADAPTIVE GRID

The same evolutionary events can be studied from many different points of view and expressed in many different terminologies. The un-

⁸ Or would be a large source of material for science fiction, which has so far been singularly unimaginative and uninstructed in dealing with possible future evolutionary developments here on earth.

derlying principles, also often expressible in quite different ways with equal validity, are likely to appear more clearly and to be better understood if approaches and handling of the data are varied. With certain types of material, analogical diagrams based on the concept of the adaptive grid have proved to be enlightening for those students, at least, who habitually handle abstraction by relational symbols or visual images. For students (among them some outstanding authorities on evolutionary theory) who deal with theoretical or abstract concepts in other forms, such as purely verbal symbols, such diagrams seem to have little explanatory content. In spite of this psychological difficulty, it seems worth while briefly to pursue here the idea of grid representation for a few examples of evolutionary processes that are especially suited to this method.⁹

When a new major zone or a complex of related zones is occupied, the lower zone, so to speak, or the first one entered is commonly the widest, representing least specific adaptation or least specialization for the organisms. Successively contiguous higher zones, of which there may be a large number, are frequently (although not necessarily) narrower. They may be occupied in sequence by populations splitting off from the next lower zone in each case; this is one of several ways in which progressive specialization occurs (Fig. 26A, below). Higher zones may also be occupied by populations from other origins. In either case, the result is the coexistence of groups of different but similar adaptive types some of which are more specialized than others. When the distinction between the zones is well defined, with considerable adaptive discontinuity, and when conditions affecting this relationship are fairly stable, such groups may coexist for a long time or even, so far as we yet know, as long as life persists. On the grandest scale, that is the situation of the major phyla of animals. It is also a very common situation at lower levels in all groups of animals and plants. Hence

⁹ These remarks doubtless apply also to the other relatively abstract diagrams in this book. At least, I have found that some of them, such as Figure 37, give some students extensive, pleasurable insight while they merely baffle and annoy others. Perhaps every author should define his own mental processes. I habitually visualize abstractions, but I have made an attempt in this book also to verbalize them sufficiently for those who handle abstraction in words. A difficulty in this respect is keeping the words from being merely descriptions of the visual images.

¹⁰ I am here and elsewhere in this book using "progressive" as descriptive of any sequence in which each step systematically develops from the last, i.e., in a progression. This study is not concerned with the more philosophical question as to possible progress, change for the better, in evolution.