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The Major Features
of Evolution

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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.

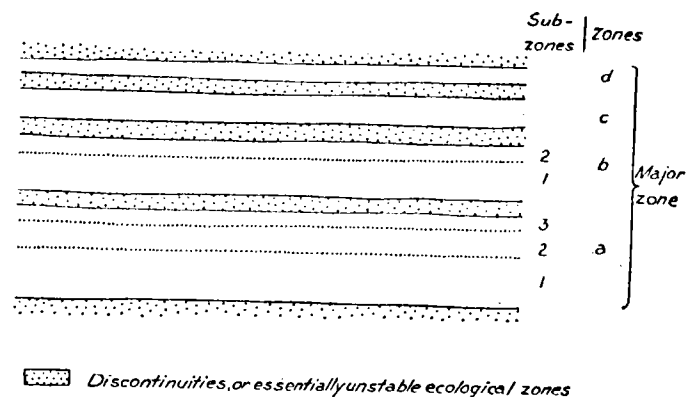


FIGURE 22. DIAGRAM SUGGESTING THE NATURE OF AN ADAPTIVE GRID. The real grid is incomparably more complex than the diagram because it may have a very large number of dimensions or number and grades of subdivision.

(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.²

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

² I now find part of my earlier discussion of this subject (Simpson, 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

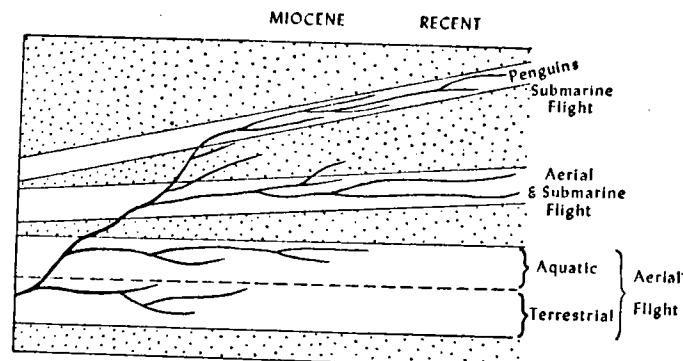


FIGURE 23. GRID DIAGRAM OF PENGUIN EVOLUTION. (From Simpson, 1946.)

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 grazing 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 parcelling 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.³ 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

³ 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 machairodontine (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 impelling 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 cricetid 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, nonrecurrent 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.⁶

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-

⁶ 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.⁶

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 progressive⁷ 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

⁶ 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.

⁷ 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.

the well-known comparative anatomical sequences from "primitive"⁸ to "advanced" or "specialized" among contemporaneous recent animals: Lemuroidea, Cercopithecoidea, Hominoidea; *Squalus*, *Rhinobatus*, *Raja*; Dasyuridae, Phalangeridae, Macropidae; *Drepanis pacifica*, *Drepanis funerea*; and so on. Almost all of the innumerable "phylogenies" that have been based on living animals and plants are of this sort. Incidentally, with possible very rare exceptions at the level of subspecies or, at most and still more rarely, species, none of these really are phylogenies.

Although persistence, with more or less change, of populations in both lower and higher zones is thus quite common in such a situation, extinction in either lower or higher zones or, indeed, in both, is also common. One of these outcomes, survival of the less specialized, has been dignified by recognition as an evolutionary principle. Such a "principle," however, is merely a description of what sometimes happens and this one should be accompanied by all possible alternatives, all of which also frequently occur: survival of both more and less specialized (as above), survival of the more specialized, and extinction of both more and less specialized. The real point is not that one of these happens more than another or is the characteristic outcome in evolution, but that each tends to happen under certain conditions that we should seek to identify.

Survival of the more specialized, in the higher adaptive zone, is the usual outcome when the zones are not so distinct as to preclude competition, i.e., when they do overlap in some essential respect even though separated by discontinuity in all others (Fig. 24A). Many of the examples of ecological replacement of one group by another are probably of this sort, although it may be difficult to judge relative degree of specialization and to avoid the fallacy that a replacing group is *ipso facto* more specialized than the one replaced. Yet this effect is almost certainly one, at least, of the factors in such cases as the replacement of the least specialized creodonts, the Arctocyonidae, by more specialized condylarths, on one hand, and other creodonts, on the other, and then the later replacement of condylarths by still more specialized

⁸ I use quotes because this is a frequent comparative anatomical designation but one that is often incorrect in its implications. No recent animal is primitive in the sense of being early or ancestral and none was ever primitive in the sense of being generalized. Most living "primitives" also have some "advanced" or strongly specialized characteristics.

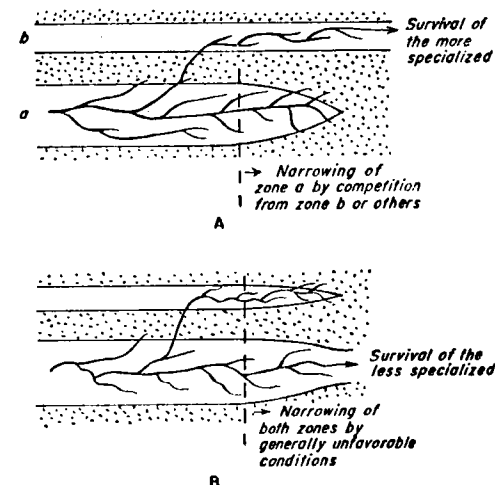


FIGURE 24. SURVIVAL OF THE MORE AND OF THE LESS SPECIALIZED.

ungulates and of creodonts by generally more specialized fissipeds. In other instances a factor in the extinction of a less specialized group is competition with still other groups with which more specialized relatives do not compete or over which they have an advantage. Ultimate extinction of all the earliest, in some sense less specialized horses and survival of only one type, which was the latest to arise and among the more specialized, was probably largely due to this factor. It is highly unlikely that competition between grazing and browsing horses was lethal, but the browsing horses had heavier competition from other groups, especially various artiodactyls. A third sort of survival of the more specialized is largely nominal: transformation of an ancestral group into its more advanced descendants, as of *Hyracotherium* into *Ephippus* and so on. This is not a sequence involving lower and higher zones but evolution of and in a single, changing zone.

Survival of the less specialized may result when conditions become generally unfavorable for all populations in related zones (Fig. 24B). Greater adaptability of the less specialized group, both in that it has, so to speak, more room for maneuvering in its wider zone and in that it often has more opportunity to change zones, then gives it greater chances for survival. Among many examples probably involving this general advantage is that of the Caenolestoida, a group of South

American marsupials that occupied four distinct adaptive zones with a clear sequence of increasing specialization (Fig. 25).⁹ The most specialized group became extinct first, then the two of intermediate specialization, and the least specialized still survives. A related factor

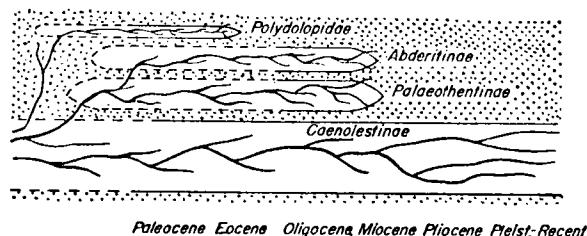


FIGURE 25. EVOLUTION OF THE CAENOLESTOIDEA. Progressive extinction of more specialized and survival of the least specialized groups. (This is a grid diagram, in which widths of bands represent relative scope of adaptive type, not abundance or variety of the animals.)

in survival of the less specialized perhaps operative in such examples and quite clearly so in others is that more restricted, narrow specialization means greater susceptibility to any pertinent environmental change, even to a single or a random change rather than any general deterioration of conditions. If a less specialized group feeds on *a*, *b*, *c*, and *d* and a more specialized group only on *a*, general scarcity of food is likely to lead to extinction of the more and survival of the less specialized; disappearance of *a*, with *b*, *c*, and *d* still abundant, is sure to cause extinction of the more specialized group while the less specialized survives. Such an effect seems to be involved in extinction of the Machairodontinae and survival of the Felinae in the example discussed later in this section (Fig. 28).

One sort of specialization has been mentioned, sequential occupation of zones decreasing in width (Fig. 26A). The same sort of effect, movement of populations into narrower zones, may arise in at least two other ways readily represented on an adaptive grid. One of these is for a population occupying a considerable part or even the whole

⁹ My previous discussions of this example (e.g., 1944a, Fig. 21) erred in showing the most specialized group, Polydolopidae, as derived from the next lower in specialization, Abderitinae. Evidence since found suggests that the Polydolopidae arose independently from the least specialized group, Caenolestinae. This complicates the phylogeny, but it does not change the order of increasing specialization or the fact that extinction followed this order in reverse.

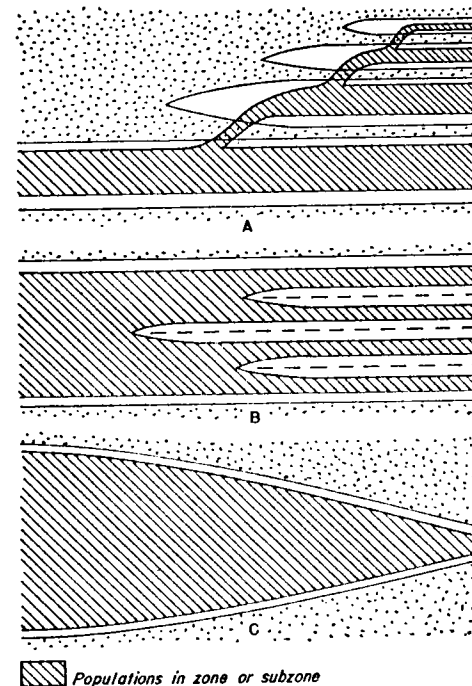


FIGURE 26. THREE PATTERNS OF INCREASING SPECIALIZATION BY DECREASING BREADTH OF ADAPTATION. A, successive occupation of narrower zones. B, segregation into subzones. C, narrowing zone.

of a broad zone to split up (by speciation) into separate populations each of which is narrower and covers only a part, of the original zone (Fig. 26B). Although this effect is not shown in the diagram, a usual concomitant and indeed, in a sense, result of this process is that the narrow zones tend to diverge from each other and eventually to cover a considerably greater total span than the broad, unified ancestral zone. This seems to be a very common relationship between speciation and the evolution of adaptation. It is perhaps seen in its purest or most clearly separable form in such examples as the differentiation among descendants of relatively unspecialized immigrants on isolated archipelagos, e.g., the Geospizidae on the Galápagos (Lack, 1947).

Another process of movement into a narrower zone involves phylo-

genetic progression in a zone that becomes narrower as time goes on (Fig. 26C). This, too, may be common, although one must guard against the conclusion that progressive and irreversible structural change implies in itself that adaptation is narrowing. Man, for instance, has undergone considerably more progressive change than, say, an Eocene lemuroid but obviously occupies a tremendously broader adaptive zone. Actual narrowing of adaptation in the course of phylogeny within one general zone is probably less common than change of adaptation, which has no special correlation with narrowing adaptation but is often mistaken for it. Change means loss of ancestral functions and we sometimes overlook the fact that new functions usually compensate the loss. I have the impression that progressive specialization in the sense of narrowing of adaptive zone in phyletic evolution is much less common than has generally been supposed. Yet it surely does occur, for instance in host-specific parasites and monophagous animals some of which must have arisen from less specific or polyphagous ancestors (e.g., Thorpe, 1930, 1940). But most of these and analogous cases may involve not so much the narrowing of a zone as its subdivision by speciation, as discussed above. Indeed it may be a rule that when a zone seems to narrow, and really does so for populations continuing in it, this is usually the result of occupation of subzones in that zone by other populations. At any rate, when there is no parceling out of subzones by related species or encroachment on a zone by related or unrelated populations, I see no evidence that progressive adaptation within a zone tends as a general rule toward narrower adaptation.

In passing, it should be noted that the sort of specialization just discussed is specified as narrowing of adaptive range or zone. The word "specialization" has been used loosely in many ways and only confusion results if conclusions relevant to one usage are applied to another. A wholly different but also common usage applies "specialization" to changes that limit further possibilities for change, or seem to. For instance, the specialization, in this sense, of the foot of *Equus* seems to preclude any further essential change in that structure, but I see no reason to think it gives *Equus* a narrower adaptive range than its three-toed ancestors. Some discussions seem almost to imply that any change is necessarily a specialization. The subject will again be mentioned in a later chapter (IX) in connection with the concept of overspecialization.

To turn to a different topic, it is a common evolutionary pattern for a group to expand successively into a sequence of adaptive zones which involve different sorts but not necessarily different breadths of adaptation, although narrowing in the higher or later zones is commonly present also as in the examples first discussed in this section. In this pattern, each zone normally has a considerable degree of stability when

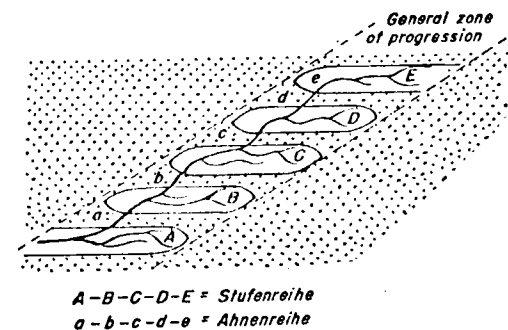


FIGURE 27. EVOLUTION INVOLVING SUCCESSIVE OCCUPATION OF ADAPTIVE ZONES AND SUCCESSIVE CLOSING OF OLDER ZONES. The Stufenreihe, A-E, indicates the general direction and nature of the progression of the Ahnenreihe, a-e, but in fact none of the populations of A-E are evolving in that direction.

occupied, and populations in each tend to survive, expand, and adapt further even while other populations are making the change to the next zone in the sequence. All or several zones may remain in existence and be occupied simultaneously, but it also frequently happens that each zone overlaps the next lower in some respect or is so related to it that occupation of a zone tends to change the next lower and to make conditions less favorable to populations in the latter. In such a case there is not only successive occupation of zones but also successive extinction of their occupants following more or less regularly at intervals after zonal occupation and in the same sequence, a situation shown diagrammatically in Figure 27.

This rather complicated pattern might be judged a priori to be so special as to be unusual in nature. Although of course the perfect regularity of the diagram is not usual, the fact is that examples clearly of this sort are very common in the fossil record. The populations evolving within a zone are frequently abundant and widespread. They are

likely to be found as fossils and they provide a sequence both temporal and structural which closely simulates a phylogeny. Then the steps in the sequence are really discontinuous. The populations through which phylogenetic continuity occurred are those that moved from one zone to the next, not those that expanded within the zones. The populations in the true phylogenetic lineages that moved between zones are almost always smaller, in total numbers, and also more restricted geographically than those in each zone. Moreover, although all the interzonal transitions sometimes occur in one area, different steps may occur in quite different regions. Thus the chances of finding any interzonal line are smaller than for finding a zonal population and the chances of finding all interzonal lines in a long sequence are very slight.

The result is that paleontological sequences related to this pattern usually include the successive but discontinuous zonal populations, forming what Abel (1929 and earlier) called a "Stufenreihe," "step series." Representation of the interzonal, actually phylogenetic sequence, the "Ahnenreihe" or "ancestral series," is usually less good, and the whole of that series is seldom known for any long time span. Many paleontological "phylogenies" are really Stufenreihen or include parts that are Stufenreihen along with parts of Ahnenreihen, rather than being Ahnenreihen and hence real phylogenies throughout. The Stufenreihen are analogous to the comparative anatomical "phylogenies" mentioned above and are due to the same general sort of phenomenon, but they do usually more nearly approximate true phylogeny. They have correct and given time sequence of the stages and each is nearer to an actual phylogenetic ancestor than are the comparative anatomical stages, especially as regards the so-called "primitive" ones among the latter.

The phylogeny of the Equidae, as followed in Europe and in North America, is an example of this pattern that is unusually close to the diagram and that is open to no other reasonable interpretation because here we have not only a Stufenreihe in both regions but also very nearly, at least, the whole Ahnenreihe in one of them (see Chapter XI, Fig. 46). The lungfish phylogeny of Dollo (1896), rightly considered a triumph of the first half century of phylogenetic paleontology, was really a Stufenreihe (Abel, 1911). An example at a lower taxonomic level, of interest in showing how an Ahnenreihe can sometimes be reconstructed in almost all its detail from a Stufenreihe, is Kaufmann's *Olenus* series

elsewhere discussed (Chapter VIII, Fig. 31). Other examples are legion. In fact most long paleontological series show the Stufenreihe-Ahnenreihe pattern, symbolized in Figure 27, as one element among others.

As an example of application of the adaptive grid symbolic analogy to analysis of more complex real sequences, the history of the Felidae may be summarized in this way (Fig. 28). In this diagram, innumerable complications have been omitted; all could also be analyzed in this way by using separate diagrams at successively lower taxonomic levels. The purpose here is to give an over-all picture of the evolution of a

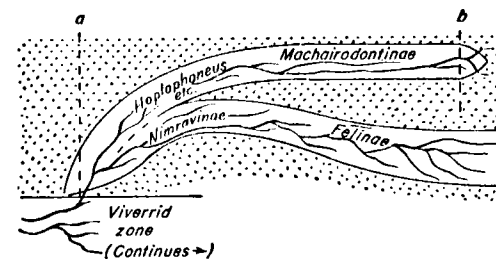


FIGURE 28. BROADEST FEATURES OF THE EVOLUTION OF THE FELIDAE. At *a* the felid zone opens by extinction of the creodonts and evolution of the herbivores. At *b* many large, slow herbivores became extinct and the machairodontine zone disappeared thereafter. For other features, see text.

large group of animals as an example only. The indicated phylogeny, which is highly schematic, is essentially that of Matthew (1910), whose views still seem to me most probable in such major points as are represented in the diagram, although Scott (e.g., 1937) has supported an interpretation radically different in some respects and Hough (1951) has suggested greater complexity and somewhat different relationships for the machairodont group. Their views could equally well be shown on such a diagram, but the purpose of exemplification of the method would be no better served.

An adaptive zone for the Felidae as a whole became available with the rise of various herbivores and the decline of creodont carnivores. It was occupied by a considerable variety of animals derived from prospectively adapted viverrids. The wide, more basal viverrid zone has persisted and is still richly occupied. The early felid major zone, which as a whole was somewhat more like the Pleistocene sabertooth than

the Pleistocene or Recent cat zone, tended toward subdivision into two zones, not then very distant from each other and both rather finely sub-zoned among a variety of types. These two zones were occupied respectively by hoplophoneines and nimravines. Lineages of general hoplophoneine type evolved in a continuing zone which changed considerably but maintained about the same level of specialization and of differentiation from a basal, more or less viverridlike fissiped zone. Late occupants of this zone were the Machairodontinae, including the widely known genus *Smilodon*, popular exemplar of the sabertooths (or "sabertoothed tigers," a most misleading popularization). Lineages of more or less nimravine type also evolved in a continuing zone which changed more appreciably, as regards the dentition, at least, so as to become less sabertoothlike than the early Nimravinae. The Felinae arose in this zone and occupied it in later stages. Change mainly in the nimravine-feline zone tended to move the two (speaking broadly) felid zones farther apart, producing greater discontinuity between them and reducing marginal competition, which was doubtless a factor in their divergence.

In the late Cenozoic there were two quite distinct zones, the machairodontine, with adaptation particularly to preying on rather large, slow, thick-skinned herbivores,¹⁰ and the feline, with less specific adaptation on the whole but particularly related to preying on smaller and more agile animals. By the end of the Pleistocene, the sort of prey for which machairodontines could most successfully compete had become markedly less varied and abundant all over the world and the specifically machairodontine zone effectually came to an end. Its occupants at the time, the Machairodontinae, probably had sufficient prospective adaptation to change to a contiguous zone had one been open but could not do so in the face of existing, already well adapted occupants in such zones, notably the hyaenids in a carrion-eating zone and the felines in a broad ambush and pursuit zone. The Machairodontinae became extinct.

ADAPTIVE RADIATION AND ITS SEQUELS

It is strikingly noticeable from the fossil record and from its results in the world around us that some time after a rather distinctive new

¹⁰ Bohlin (1940) thinks that they were carrion-eaters, but this seems most unlikely to me (Simpson, 1941) and in either case it is probable that this is the kind of animal they ate, whether they killed them personally or not.

adaptive type has developed it often becomes highly diversified. This may follow soon after the origin of such a type or may be long delayed (a point discussed in the next section), but it is more likely than not to occur sooner or later if the type does survive and become well established. Diversification may be brief or prolonged and may be of limited scope or may ramify into the most extraordinarily varied zones covering a breadth of total adaptation that would have been wholly unpredictable and incredible if we were aware only of the beginning of the process. (This, by the way, is one reason why I continue to be somewhat skeptical of the idea, stated in Huxley, 1942, and in work by that student not yet published at this writing, that evolution has essentially ended except in man.)

The same sort of diversification follows, and in this case begins almost immediately, when a group spreads to new and, for it, ecologically open territory. The extent of adaptive diversity eventually reached tends, although rather roughly, in the first case to be proportional to the distinctiveness of the new adaptive type and in the second to the extent and diversity of the new territory. In both cases the more direct factor may be said to be the extent of adaptive opportunity provided by the change or, in other words, the number of prospective adaptive zones opened more or less simultaneously to the groups involved. In many instances it is, however, by no means obvious when a new adaptive type is arising how distinctive it will eventually become or what zones will later open to it or develop with it. Indeed the early stages of what later becomes a strikingly novel adaptive type may have only the slightest distinction from its ancestors or collateral contemporaries, a fact which is, of course, related to delay in diversification of such groups and which does not contradict an over-all correlation of distinctiveness of type with eventual diversity.

So far as adaptive radiation can be distinguished from progressive occupation of numerous zones, a phenomenon with which it intergrades, the distinction is that adaptive radiation strictly speaking refers to more or less simultaneous divergence of numerous lines all from much the same ancestral adaptive type into different, also diverging adaptive zones. Progressive occupation of such zones is not simultaneous and usually involves in any one period of time the change of only one or a few lines from one zone to another, with each transition involving a distinctly different ancestral type. Theoretically, at least, the whole of the diversity of life is explicable by these two not sharply distinct

processes plus the factor of geographic isolation which may permit essential duplication of adaptive types by different organisms in different regions.

There has been a highly irregular and yet fairly general tendency for existing diversity to increase throughout the history of life. This involves a concomitant tendency for the adaptive zones still remaining open to occupation to become narrower in scope as well as fewer in number. Because adaptive radiation, like any change of adaptive type, depends on availability of adaptive zones and because it further requires that several or many of these be available simultaneously (or nearly so on the geological scale, at least) there has also been a tendency for the scope of adaptive radiation to decrease. This has been further accentuated by the fact that major radiation requires considerable geological time. The tendency has, again, been extremely irregular but its effect is evident.

As far as environmental possibilities are concerned the very broadest possible scope for adaptive radiation existed when life first arose, even though the further evolution of life has itself from time to time opened very broad possibilities. Actual occurrence of a radiation requires, again like any adaptive change, not only this possibility in the form of prospective adaptive zones but also the existence of organisms with prospective adaptations. Protists seem inherently limited in prospective adaptation for any but subzones of their own broad zone. After metazoan organization had become well established, there came a time when maximum prospective adaptation among them coincided with maximum scope of prospective adaptive zones in a world empty of life other than protists and a restricted range of truly primitive multicellular plants and animals. Radiation of most of the animal phyla ensued. Much of the long discussion of the rather sudden appearance of the phyla (although Cloud, 1949, has pointed out that "sudden" here involves time on the order of some tens of millions of years) seems quite beside the point because it overlooks the great probability that this was an adaptive radiation which is, to the degree required by the actual record, a "sudden" process. Each of the major phyla (i.e., those clearly warranting that grade rather than having it conferred on them because we do not know the relationships of some aberrant relict) does stem from a distinctive and basic adaptive type. When this is not obvious, the obscurity is due to later radiations within the phylum, the diversity

of which overlays the relative unity of original adaptive type. No later radiation has developed the scope of this particular one, not only because there has been less time but also because the great radiation had, in a sense, preempted the broadest possibilities.

Not all origins of phyla can be assigned to the postulated great radiation. The Chordata perhaps cannot, because the first sure chordates appear rather late for a phylum (late Ordovician) and because there is on anatomical grounds some possibility that chordates arose from echinoderms (De Beer, 1951).¹¹

The now existing major adaptive types of chordates do not owe their origin to early adaptive radiation in the phylum, which occurred but which involved lesser adaptive differences. The major types, corresponding to the classes in taxonomy, arose partly by radiation and partly by successive occupation of major zones: the Placodermi by succession from Agnatha, the Chondrichthyes and Osteichthyes probably as the most successful branches of a (poorly known) radiation in the Placodermi, the Amphibia by succession from Osteichthyes and the Reptilia by succession from Amphibia, the Aves and Mammalia, finally, as the most successful branches of a radiation in the Reptilia. The complexity of the process and the lack of definite distinction between radiation and succession is, however, shown by the fact that even when the relationship as between classes is successional the particular lineage that made the adaptive shift was one of many involved in lower-level radiation.

Within the Mammalia, early radiations evidently occurred but what little we know about them suggests that they were of small scope, involving few major adaptive zones and with less scope than, say, some contemporaneous single orders of reptiles. Much later occurred the combination of, on one side, primitive placental mammals occupying an adaptive zone already rather broad, the organisms with extensive prospective adaptation, and on the other side a wide range of virtually empty adaptive zones. The emptiness of these zones was due in part to extinction of many groups of Mesozoic reptiles, a series of events that no one has satisfactorily explained in separate detail for each, although the general principle back of them is clear. In part, and it may be in greater part, lack of occupation of zones for which mammals became

¹¹ On the other hand, there is also some possibility that the graptolites were chordates (Kozłowski, 1947) and graptolites appear early enough (late Cambrian) to have been possible results of the great radiation although there remains some slight additional possibility that they arose from the still older echinoderms.

prospectively adapted around the Mesozoic-Cenozoic transition was due to the fact that reptiles had not developed prospective adaptation for numerous zones that nevertheless became potential as evolution proceeded through the Mesozoic. Physical and ecological access to these zones existed; evolutionary access did not until mammalian evolution (a ramification of reptilian radiation) reached a certain point, a great threshold beyond which lay not only one but many diverging adaptive zones.

In the great, basic radiation of primitive placentals (nominally insectivores), which probably began in latest Cretaceous time and clearly continued through the Paleocene, various lines reached adaptive zones basic for almost the whole range later so richly developed by mammals. These most basic zones may be roughly equated with the taxonomic orders, among which at least the following rather surely arose from the great primary placental radiation: Insectivora, strictly speaking (a bundle of radiating lines that did not happen to move significantly far from the major ancestral zone), Dermoptera, Chiroptera, Primates, Tillodontia, Tactiodonta, Edentata, Lagomorpha, Rodentia, Cetacea, and Carnivora in a very broad sense (the early members were not carnivorous). For most of these, the nature and range of basic adaptation is fairly obvious, although it must be emphasized (and will be again) that when really early members are known, these are remarkably similar in all the groups named. The zones diverged and developed really clear-cut distinctions only with further evolution. For instance, the many known lineages of more or less insectivorelike and more or less primateline mammals in the Paleocene and Eocene are all similar except in endlessly varied detail. There is no character or complex of characters, no clear-cut difference of adaptive type, that warrants dividing the lines decisively between Insectivora and Primates. Yet among these lineages were small adaptive differences that were to evolve into the tremendous adaptive discontinuity between, say, a man and a mole.

A secondary but still major, complex radiation, begun while the primary radiation was still under way, produced from primitive carnivore-condylarth or ferungulate stock a great array of carnivores, in a stricter sense, and an even greater array of ungulates and their allies. Still another radiation followed from physical access to the ecologically varied and (for mammals) empty continent of South America. There several major adaptive types, already differentiated as such, radiated simul-

taneously: primitive marsupials, edentates, and omnivorous to herbivorous ferungulates (condylarths and condylarthlike). In descending scale, with reference to the distinctions eventually developed between the adaptive zones occupied and the range of adaptation eventually covered by the various zones, radiation from the condylarth zone in South America gave rise to Litopterna, Notoungulata, Astrapotheria, Xenungulata, and Pyrotheria. The notoungulates, most successful of these groups, radiated early and exuberantly through late Paleocene and Eocene into what were, in the Oligocene, nine adaptive zones distinct enough to correspond with taxonomic families. Each of these zones in turn was subdivided by lesser radiation. For instance in the Notoungulata (a group with some adaptive similarity to horses, as the name implies, but no phylogenetic relationship) at least five early Oligocene genera were present simultaneously in a rather restricted area.

In such cases radiation of a minor sort, taxonomically at about the specific level, doubtless also occurred in many or most of the generic and familial zones, although geographic distribution of paleontological samples is inadequate to show the full scope of these minimal radiations. Radiation at these low levels is clearly shown in the finches and tortoises of the Galápagos or the honeycreepers, land snails, and many groups of insects of the Hawaiian Islands. It is also evident but not generally so isolable as a single event in many polytypic genera of animals and plants all over the world.

In exemplifying adaptive radiation and its scope, I have run down the scale from phyla to species. It is, however, seriously misleading as to the complexity and the true nature of the process to look at it (as some students have) only as a sequence of radiations of regularly decreasing scope. The actual phylogenetic process is not first a radiation of phyla, then of classes in each phylum, then of orders in each class, and so on down until finally a radiation of species occurs. What actually occurs when any radiation is going on is simply a divergence of populations, which are or are becoming separate species, into different adaptive zones. These zones themselves then evolve, as has been emphasized. Their characteristics, what are seen *in retrospect* to have been their potentialities, interactions between them, and the amount of time elapsed all react together to determine how distinctive they eventually become. Whether we represent the outcome as radiation of genera, orders, or phyla, depends, so to speak, on how far back we

stand, how much of the whole picture we take in and how much we generalize on a pattern which is in detail no more and no less than constantly recurring radiation of populations and constantly occurring succession of adaptive changes in populations. This touches on other problems, particularly concerning the nature and origin of higher categories, that will require further discussion in this and later chapters (especially Chapter XI).

In early phases of an adaptive radiation, particularly one that does reach considerable or great scope of total adaptive range, there is usually an evident and sometimes almost a dramatic release of variability. A radiation does not occur unless prospectively adapted populations exist, and it is an aspect of their prospective adaptation that they have (as in fact do most populations, but in these cases probably to unusual degree) large pools of potential genetic variability (see Chapter III). Increase in total population, even though this is distributed among descendant species, relaxation of centripetal selection, and a centrifugal pattern of selection away from the ancestral condition and into a variety of diverging adaptive zones are concomitants of the situations in which adaptive radiation does occur. All these factors tend to release variation from existing pools of variability and also to increase the probability and rate of fixation of new variability arising by mutation.¹² One would then expect a phase in adaptive radiation in which intragroup variation was large and intergroup variation still larger and increasing rapidly. In addition to this, there would be a considerable number of adjacent and overlapping adaptive zones the boundaries of which were not yet clear and discontinuities between which were still small and fluctuating. A further expectation would therefore be development, for a time, of a great variety of adaptive types, rather poorly differentiated from each other, and partly conflicting and adaptively unstable.

These expectations are wholly fulfilled when we happen to get the appropriate early phases of an adaptive radiation. An unusually good example is provided by the Notoungulata (and some other groups) in the late Paleocene and early Eocene of South America (Riochican of Argentine Patagonia and Brazil, Casamayoran of Argentina, see Simp-

¹² There is also the possibility of selection for increased mutation rates in such a situation but it is questionable whether this is an appreciable factor or whether in any one lineage it would have time to operate before the lineage was sufficiently adjusted in its adaptive zone to make high mutation rates again disadvantageous.

son, 1948, also continuation of that work still in manuscript and studies by de Paula Couto now in progress). Intragroup variation is great, intergroup variation is unusual and is plainly increasing, the notoungulates as a whole are protean almost beyond parallel, and there are so many transitional types that the taxonomic problem seems almost hopeless.

In theory such a condition cannot persist indefinitely and in fact it does not in the known examples. It may be prolonged in a major radiation like that of the Notoungulata by the fact that the actually primary process, the splitting of populations, does not really go on all at once but now in one and now in another segment of the whole taxonomic group and in renewed bursts as new adaptive levels are reached in succession. Such a radiation, or rather, series of radiations, may thus continue in the expanding, highly variable phase for spans on the order of millions of years (see the next section of this chapter). Even in this phase, weeding out of populations and adaptive types is constantly going on; extinction rates are high although origination rates are still higher. The most prolonged radiation, however, finally reaches a time when rates of origination, averaged over the whole, fall off rapidly. In this phase rates of extinction are also usually decreasing but less rapidly, and they come to be higher than contemporaneous origination rates so that the net result is decrease in total numbers of groups present. In terms of the evolution of adaptation what is then happening is that existing adaptive zones have been occupied and appearance of new zones (a result inherent in the expansion of adaptive types) has slowed down or stopped. At the same time, overlap of zones is being eliminated, their boundaries are sharpening, discontinuities are developing between them, and intermediate or intergrading populations lose what adaptive stability they may have had and become extinct. Long range adaptive possibilities have developed and are being parceled out among a smaller number of more distinctive zones. Populations outside those zones are weeded out.

In the example of the notoungulates these effects are evident by late Eocene time and the phase, which of course is not sharply distinguishable from those preceding and following it, continued more or less throughout the Oligocene. In the Eocene there were nine families, primary products of the basic radiation. In the Oligocene there were also nine, five continuing from the Eocene and four the more highly

divergent products of Eocene radiation. In the early Miocene, when the phase of parceling out and weeding out had been essentially completed, there were only six families and all of these had already been sharply distinct in the early Oligocene.

After divergence is complete and the long range main adaptive zones have become sharply defined and decidedly discontinuous from each other there follows a phase during which each main zone evolves independently with no evident further divergence or interaction between them. The radiation as such has definitely ended, both as regards its expanding phase, radiation strictly speaking, and its contracting or weeding out phase. For the notoungulates, as far as a time can be designated in a continuous, slowly shifting sequence, this change came around the end of the Oligocene. Thereafter progressive changes in the separate major zones continue and within each there are progressions between and changes within subzones, but the radiation by which the zones arose has no evident influence in these late events. There may even be renewed radiation in or from one of the zones, as a new and separate occurrence. (This did not happen among later notoungulates except on quite a minor scale within zones.)

This sequence of phases is a striking and often repeated element in the whole evolutionary pattern, but it is not the only element. It arises from time to time and on a smaller scale or a larger when a concatenation of circumstances results in the previously specified conditions for adaptive radiation. It is not constant, nor is it the only way in which stable, long range adaptive zones arise or are occupied. Their origin may be due at least as often to secular processes in the total evolution of adaptation and their occupation to successional evolution from zone to zone, and not to episodic radiation. Or both the secular and episodic elements may be involved, or again something between the two.

CYCLIC AND EPISODIC EVOLUTION

Adaptive radiation is a clear example of episodic evolution. With all its complications, prolongations, and repetitions at different levels of effects, an instance of adaptive radiation is an episode set off from preceding and following events at comparable levels and defined by a beginning and an end. It also has a characteristic course which may be closely similar in different episodes of adaptive radiation. Such ob-

servations have often suggested to students that the evolutionary process as a whole or some aspects of it might be cyclic, that is, that it might consist of episodes of the same sort recurring at more or less regular intervals. Two principal sorts of theories of cyclic evolution have been proposed: that a group or characteristic sort of organisms tends to go through a kind of racial life cycle repeated in each successive group, and that geologic history and biologic history consist over-all of a series of repeating, simultaneous physical and evolutionary cycles.

Theories of a racial life cycle usually recognize three phases described more or less as follows: an initial, relatively short phase of vigorous expansion and diversification, a longer stable phase of slow change and little increase in diversity unless among minor adaptive or geographically local types, and a final phase, again relatively short, showing more or less marked diversification into monstrous, overspecialized, degenerate, or generally inadaptive forms, followed by extinction. Numerous different terms have been proposed for these phases. Schindewolf (e.g., 1950a), who is among the few well-informed recent students who believe that such phases really do follow each other with noteworthy regularity, calls them the phases of typogenesis, typostasis, and typolysis, respectively. An analogy is often drawn with individual life and its juvenile, adult, and senile phases—an analogy obviously perilous because these individual ontogenetic phases are known to be defined and conditioned by factors that could not possibly apply to ancestral and descendant sequences of populations and that do not even have any known or likely analogy in the factors affecting such sequences.¹³

The first of these postulated phases is in general like the first phase of adaptive radiation as described above and the second suggests the phase of mainly intrazonal evolution that often follows after the radiation has quieted down and an intermediate phase of weeding out (which is not invariably present as a distinct time phase) has intervened. Adaptive radiation is common in evolution, so is stable intrazonal evolution, and to this extent the postulated phases certainly occur. That they fol-

¹³ Schindewolf extends the same analogy to human cultural history also and concludes (in German) that "these manifold analogies make it probable that all temporal-historical development follows the same sort of patterns and that phylogenetic evolution to this extent falls into a higher category of generalization (by which, to be sure, nothing is yet expressed as to the inner determinants of these phenomena, which in themselves are only analogous)." (Italics his.)

low each other inevitably, that major radiation is the constant pattern of a "young" group, or that all of evolution can be realistically analyzed in such terms is not true.

The sequence radiation-intrazonal evolution is usual, simply because radiation does not occur unless there are diverse zones within which evolution will follow. Occasionally, nevertheless, something happens to close the zones so soon that the radiation is curtailed or the intrazonal phase is even shorter than the radiation. The camarate crinoids, for instance, seem to have been in the full swing of a radiation when they all became extinct in the Carboniferous. Occupation of a new zone and subsequent intrazonal evolution may also occur without radiation or a "youthful" phase, unless the whole scheme is reduced to mere wordage by saying that change from one zone to another is radiation or a "youthful" phase. No radiation seems to have been involved in the rise of the Stylinodontinae (Patterson, 1949) and none occurred among them during their whole history. Common as adaptive radiation is, such examples are also rather common, although probably less so from the mere fact that radiation may reach any extent and opportunities for radiation of small extent are likely to occur for any group that long survives.

Unless, again, the whole problem is made meaningless by calling any short-range diversification, such as the nearly universal and continual pattern of geographic speciation, "youthful," "typogenesis," or the like, it is also untrue that radiation regularly follows the appearance of a new group. It will shortly be shown that periods of most rapid diversification may occur at any time in the history of a group but seem to be less common just at its beginning than later. Note, for one example, the Mammalia, in which there was little marked or apparently basic diversification for at least 75 million years after the class arose. Nor is it literally true that basic differentiation into major adaptive zones regularly occurs within a group by one radiation (early or late), with subsidiary cycles later filling in the chinks, in a manner of speaking. Something descriptively like this can occur, as in the Paleocene origin of many of the orders of mammals, although even in such cases the divergence of the major groups, the thing that makes us call them "major groups" a posteriori, was a long and later process. In other cases not even this exiguous agreement with the racial life history theory appears. The vertebrates, for instance, certainly did not radiate into their major adap-

tive types in any "typogenetic" phase, but developed the major types, in large part by successive occupation of zones, over some 200 million years.

The supposed last phase of a racial life cycle, that of senility followed by death, brings up the general problem of extinction, to which this concept is only ancillary. Extinction will be discussed in Chapter IX. At this point it need only be said that the concept of senility, as applied to evolving populations, seems to be a false analogy and that a phase even analogical with old age does not appear really to occur in evolution. The whole theory of racial cycles is an overgeneralization and invalid interpretation of some phenomena that are real (buttressed by some that probably are not) but that do not really have the claimed relationships to evolution over-all.

Distinctive adaptive types and corresponding taxonomic groups are likely to be numerically small when they arise and thereafter to increase more or less in numbers and variety if they survive long. That is a necessary concomitant of any usual mode of development that can be ascribed to them. Once the group is established, it inevitably varies in size and diversity and so must have a maximum point at some time or other. In some cases the phenomena of expansion and contraction seem to have no more interest than this casual fact. In most groups there are, however, one or more well-defined maxima which clearly are not casual but represent definite and important episodes in the history of the group. Fossil sampling permits no fully reliable determination of absolute numbers of taxonomic units in a group, but at levels from genera upward, less commonly for species, it is probable that determinations of rise and fall and of times of maxima and minima are reasonably reliable for groups fairly common as fossils. Not even an approximation of figures for census population is possible except in the vaguest terms, but it may often be a reasonable (although it is not a necessary) assumption that total numbers of individuals in any one group tend to vary with numbers of taxonomic groups. (Of course this assumption is not even roughly permissible in comparison of groups of quite different adaptive types.)

Something was said about peaks of taxonomic diversity in Chapter II from the point of view of their tabulation and of the rates of evolution leading to (and from) them. The purpose here is to consider them as episodes in the evolution of adaptation, related to the subject of adap-

tive radiation (also of racial cycles, already discussed) and also to the theory of simultaneous geologic and biologic cycles.

Sudden rises in taxonomic diversity have frequently been discussed as examples of "explosive evolution." The term is ill chosen, as has been pointed out a number of times, for instance by Cloud (1949), although it has a certain unintended humor. These are explosions that commonly take millions of years from fuse to bang (which is silent). Cloud has suggested "eruptive evolution," which is better, surely, but still suggests an inept mental picture to me, at least. Rensch (1947) follows Wedekind in speaking of "Virenzperioden," which is better yet but might carry some undertone of the life-cycle analogy. Various other picturesque terms have been used, but I shall call these events more primly "episodes of proliferation," not a very snappy metaphor but at least a reasonable designation.

Many different factors in the complex web of evolution may underlie any given episode of proliferation. Rapid phyletic evolution, for instance, runs up the number of taxonomic units existing (although not simultaneously) in a given period of time and occurs during episodes of proliferation. The one feature probably present and determinative in all these episodes, however, is adaptive radiation. That conclusion has been questioned and it can hardly be shown to lack exceptions, but examination of many examples always reveals what seems to me clearly adaptive radiation related to each episode. This is especially convincing when more than one episode has occurred in a large group. Episodes of proliferation after the first generally (always, as far as I have found) turn out to be due to adaptive radiation in included groups. Thus in the Osteichthyes the first episode of proliferation follows an adaptive radiation in the Chondrostei, the second another such radiation in the Holostei, and the third still another in the Teleostei. In the Spiriferaceae the first peak is really a resultant of more or less independent radiations in several families and the second is mainly due to an adaptive radiation of the Athyridae.¹⁴ (See Chapter II.)

¹⁴ Query should hardly arise at this point as to how it is known that the radiation, which is factual, really is adaptive, which is an interpretation. Sufficient has already been said to indicate that speciation, the basic process of radiation, is normally adaptive. The general evidence for mainly adaptive control in such events is so impelling that it cannot be doubted even when, as with species or genera of brachiopods, the precise adaptive significance of each form may be dubious. In other cases, as for the teleosts, the adaptive significance is reasonably known for some if not for all of the groups involved.

It was also stated and exemplified in Chapter II that episodes of proliferation may come early, middle, or late in the history of a group. This confirms the conclusion that adaptive radiation is episodic but not cyclic. Radiations occur when certain conditions are produced by the whole concatenation of previous historical events influencing the organism and environment relationship, and not from anything regularly inherent in the organisms. The peak of an episode of proliferation follows some time (usually quite a long time) after radiation begins. This does not mean that incidence is completely random, nor would this be expected in view of the fact that there are some broad but pertinent similarities between the episodes and between the whole adaptive histories of the groups involved in them. There is, in fact, some evidence that although the peaks *may* occur at any time whatever in the span of a group they are *most likely* to occur during the first half but not the earliest part of that span.

Innumerable complications arise in attempting to compile data on such a point. Apparently objective data may merely reflect a subjective approach. For instance, as noted, the Osteichthyes had a peak of generic proliferation in the Cenozoic, near the end of their span. But this was almost entirely in the Teleostei, which originated much later than the Osteichthyes as a whole. Moreover, this peak may be considered a resultant of radiation within lines which had themselves, for the most part, arisen in an adaptive radiation in the Cretaceous. The peaks of the same episode of proliferation are different for different levels of radiation. In spite of these difficulties, an experienced paleontologist can usually designate with some assurance an epoch or period in which a group reached its generally highest point of abundance and differentiation. For instance Stromer (1944) has indicated such high points for 35 groups of about the average scope of orders, 16 invertebrate and 19 vertebrate.¹⁵ It is an advantage for our purpose that Stromer did not select these groups to show the distribution of the high points, but for quite a different purpose (incidence of gigantism). If the spans are divided into deciles, the distribution of high points is as shown in Table 21. This is not a random distribution. The peak in the third

¹⁵ Stromer omitted high points for two mammalian groups that he nevertheless put in his table and I have supplied these: late Paleocene—early Eocene for the "Prosimiae" and latest Cretaceous—Paleocene for the Multituberculata. I have also made some small corrections in his data, e.g., the Multituberculata as now defined are unknown before late Jurassic.

TABLE 21

RELATIVE POSITIONS OF "HIGH POINTS" IN EVOLUTION OF VARIOUS ANIMALS
(Calculated from a table by Stromer, see text)

Decile	Invertebrates	Vertebrates	Both
1	1	2	3
2	2	0	2
3	3	6	9
4	0	4	4
5	2	0	2
6	1	1	2
7	1	1	2
8	1	2	3
9	2	0	2
10	3	3	6
	16	19	35

decile is statistically significant and seems also to be biologically so. The peak in the last decile is also significant statistically but probably is not biologically. It is due mainly to Cenozoic high points of groups still living, hence of indeterminate span. It is practically certain that these peaks will not be in the last part of total span since the groups concerned (e.g., Rodentia) are flourishing and give no signs of approaching extinction. With allowance made for this factor, it seems probable that very late high points, in the ninth or tenth deciles, are relatively few.

Tabulation of absolute times of high points after appearances of the groups would be less significant for present purposes because of the very great differences in duration and rates of evolution in the various groups (vertebrates as a whole having decidedly shorter durations and faster rates than invertebrates). It is, however, of some interest that high points for Stromer's selection of vertebrates range from 10 or 15 (Prosimii, Mystacoceti) to more than 250 (Selachii) and average about 55 million years after appearance of the group, while for invertebrates the range is about 20 (Protodonata) to perhaps 450 (Foraminifera, Pelecypoda, Gastropoda¹⁶) with a mean of about 180 million years. At any rate, it is clear that considerable time elapses before a group of much scope reaches a high point and that a high or the highest point (not necessarily the first) may appear after a very long time.

¹⁶ There is, however, little doubt that these groups now at or near maximum had earlier high points as well.

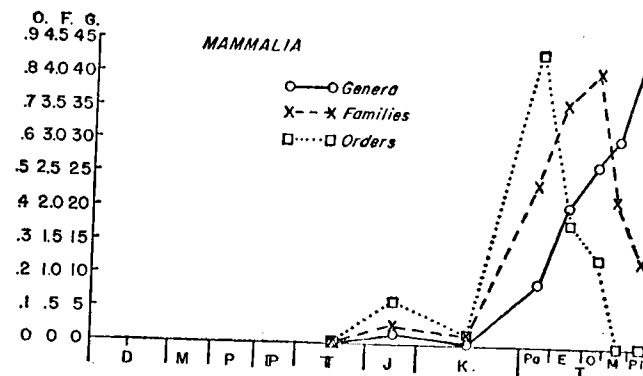


FIGURE 29. FIRST APPEARANCES PER MILLION YEARS FOR MAMMALIAN ORDERS (O), FAMILIES (F), AND GENERA (G).

Another point before now only touched on in passing, or obliquely, demands special comment. If time frequency curves are plotted for the same group in terms of different taxonomic levels, the peaks for higher categories usually appear earlier than those for lower categories. This is evident, for example, in the data for origination rates in aquatic vertebrates in Figure 9 (Chapter II), for mammals in Figure 29, and for vertebrates as a whole in Table 22. Even when, using the coarse scale of periods, peaks for different categories are in the same period, those of higher categories are earlier in the period as the data for mammals show.

Offhand, this fact suggests that orders arise first, then families, then genera, and so on, as Schindewolf has so often insisted.¹⁷ Closer study

¹⁷ Schindewolf's theories are so frequently criticized here that it should be pointed out that critical reference to them is worth while just because Schindewolf is among the few paleontologists (such men are few in any science) who have really broad grasp and subtle, theoretical minds. He has paid more attention than most to the really important theoretical problems of his science. His views are based, as in this case, on real evidence and must be taken seriously. The points on which I disagree naturally require more specific notice of his work than do those on which I agree.

On the present point, Schindewolf seems to mean quite literally that the higher categories of a group arise as such before the lower. Our disagreement is not entirely fundamental if this is taken as a manner of speaking, a broad and figurative view of the net result rather than a description of the process. This is the position of Wright (1949a), with which I agree in essentials. Schindewolf (1950b) has quoted two sentences from this paper of Wright's as indicating agreement with his views. The rest of that paper and, indeed, Wright's whole great body of work show that his agreement extends only as far as does mine with Schindewolf. The point actually

TABLE 22

PEAKS OF FREQUENCY OF APPEARANCE OF DIFFERENT TAXONOMIC CATEGORIES IN THE VERTEBRATE CLASSES

Period	Peak for orders	Peak for families	Peak for genera
Tertiary	Mammalia	{Mammalia Osteichthyes 3	{Mammalia Osteichthyes 3 Chondrichthyes 2
Cretaceous	Osteichthyes 3
Jurassic	Chondrichthyes 2	Chondrichthyes 2
Triassic	Osteichthyes 2	Osteichthyes 2	Osteichthyes 2
Permian	Reptilia 1	Reptilia 1	Reptilia 1
Pennsylvanian	Amphibia	Amphibia
Mississippian	Amphibia	{Osteichthyes 1 Chondrichthyes 1	{Osteichthyes 1 Chondrichthyes 1
Devonian	{Osteichthyes 1 Chondrichthyes 1	Placodermi	Placodermi
Silurian	{Placodermi Agnatha	Agnatha	Agnatha

shows quite clearly, I think, that this is a misleading statement as to the processes actually involved. One reason why it is misleading is evident if one considers the result of a single, isolable incident of adaptive radiation such as that of, say, the Geospizidae on the Galápagos. It would be true in a formal sense to say in this case that the family rose before most of its genera or species and before the generic peak which in turn probably came before the specific peak. But in an example so clear in most details down to the level of species (thanks largely to Lack), this is obviously only a manner of speaking or even an artifact of classification. Now that the adaptive radiation is complete, we recognize the result as a family (or subfamily). Looking backward from here, we consider that the family arose when its first species was differentiated. That species probably differed very little from its immediately ancestral species (which is, however, unknown in this example without paleontological support). The family did not arise as such but as a *species*. The family resulted from the whole radiation, and its first species is placed in it in retrospect. The peak for genera (4) obviously had to be

at issue is whether an order, say, arises and develops by processes of selection acting on ordinary mutations and in the basic form of speciation under special and necessarily infrequent circumstances (since orders are infrequent relative to species), or whether it is the immediate result of one large mutation without benefit of selection or of speciation in any ordinary sense. In the paper cited and elsewhere, Wright has been fully explicit in his opposition to the latter view.

later than the appearance of the first species now placed in the family and that for species (14) had to be later than the generic peak unless, as is improbable, the two monotypic genera arose after speciation was complete in the two polytypic ones.

In major episodes of proliferation, such as those of the vertebrate classes, analysis shows that adaptive radiation is clearly involved but that we are not dealing with a single and isolable episode of radiation corresponding with or leading to a single, short peak. There is, instead, an extremely complex series of radiations all of which began basically at the specific level but which in retrospect had different final net results. In fact it may be said that an episode of proliferation, no matter how high the level, is simply exuberant speciation irregularly continual over a long period plus a considerable amount of phyletic divergence among the lineages thus arising. Earlier radiations eventually have more far-reaching aspects not only from the simple fact that they are earlier and that their lines therefore have time to diverge farther but also because it is these lines that start the occupation of a broad new adaptive zone and that therefore have inherently more space for eventual divergence. Reviewing the whole phenomenon in retrospect and putting it into taxonomic form, we generalize by running the origins of larger subzones, corresponding with higher categories, farther back to earlier radiations than those of smaller subzones. It does not follow and when we have the crucial evidence it is found not to be a fact (as will be exemplified and further discussed in Chapter XI) that what are taxonomically the earliest representatives of, say, an order were ordinarily distinct from their contemporaries in the sense of having anything like the degree of morphological or adaptive distinction and discontinuity that we associate with the concept of an order in considering the final results of the process. If, indeed, we can trace the lines back to the point where the actual biological splitting of one order from another occurred (unfortunately an impossibility in most cases), the distinction existing when the fundamental discontinuity actually arose is only specific. There is, indeed, a genus in the early Paleocene (*Protogonodon*) some species of which are *by morphological definition* members of the Order Carnivora and others members of the Order Condylarthra.

With these relationships in mind, it is seen that the spread between, for instance, ordinal and generic peaks for an episode of proliferation in a class tends to reflect the length of time during which a complex

sequence of adaptive radiation continued. The ordinal peak follows, probably by quite a long interval, the beginning of important adaptive radiation in the originally relatively unified primitive representatives of the class. Other radiations then occur among the various lines from the earliest radiation, and yet others among the more and more numerous lines as radiation continues. Separate radiations at the basic level, as far as they can be separated, are quite irregularly distributed in time and also among the lineages present, but the total resultant is increase in number of *species* while the process continues. When it ends, what is taxonomically the last peak, that for species, occurs. The ending of the process in this sense does not necessarily mean that *all* adaptive radiation ceases—this is not usually the case in a very large group, at least—but that the over-all total begins to decline because extinction has overtaken origination.

The total time involved in such a major episode is large. In the vertebrate classes, the generic peaks occur 25 to 50 million years after the corresponding ordinal peaks. Since significant radiation must begin well before an ordinal peak and may not end until well after the generic peak, the whole of one of these episodes is indeed a grand event occurring over a minimum span of about 30 million years and perhaps in exceptional cases extending over 70 or more million years. Certainly we have in such episodes some of the most truly major and long-range elements of evolutionary history. Of course there are also lesser episodes of proliferation, either as parts of major episodes or as separate events, which run over much shorter spans. A lower limit cannot be fixed, but it seems unlikely that a minimal, single radiation, recognizable as such, could normally occur in much less than a million years. (Yet these are all "explosions"!)

The weeding-out effect noted in discussion of adaptive radiation is also evident in most episodes of proliferation and it begins long before the episode has run its course. On a small scale it goes on all the time, but it becomes evident on a large scale when the major subdivision, e.g., that into orders in the Mammalia, has reached a peak. It naturally affects first the results of the first radiation and so first becomes predominant over origination in the most rapidly and basically divergent groups. In a large episode of proliferation, as opposed to a single adaptive radiation, much of the weeding out is likely also to be by replacement of early groups by groups evolved in later radiations within the

episode as a whole and able to reenter older zones competitively. Replacement of condylarths by perissodactyls and artiodactyls or of creodonts by fissipeds is of this sort. The result of these effects is a tendency for higher categories to decline in number while lower categories, by later radiations in the more adaptively successful, surviving higher categories, are still increasing in frequency. This, too, is striking in the Mammalia, with ordinal peak in the Eocene and generic in the Pliocene.

When one group is replaced by another in a major adaptive zone it frequently, perhaps usually, happens that both have episodes of proliferation overlapping in such a way that the earlier group is in the last expanding phases of its episode while the replacing group is beginning expansion. Thus in replacement of Agnatha by Placodermi and of Placodermi by Chondrichthyes and Osteichthyes, jointly, the ordinal peak for replacing groups coincides approximately with the generic peak of the group later replaced.

The last topic to be considered in this chapter is the theory, or rather the various theories, that involve correlated geological and biological cycles. One such theory, formerly widely held and still occasionally advanced, e.g., by Umbgrove (1942), is that there are recurrent cycles of world-wide mountain building each of which is accompanied or immediately followed by a major evolutionary outburst or "explosive" evolution on a large scale. However, even if the tectonic cycles are taken as given, there is no real correlation with major episodes of proliferation, as Umbgrove's own data show (see Simpson, 1949b). Indeed it seems rather pointless to look for a correlation when it becomes clear that such episodes of proliferation do not occur with sharp definition in time but have phases extending over as much as 50 million years or more, a figure of the same order as the average length of intervals between the supposed major tectonic episodes. It has also been assumed that the origins of major groups or the beginnings of episodes of proliferation might correlate with the tectonic episodes, but there seems to be no reliable evidence of this, either. As if to put the last nail in the coffin of this now apparently moribund group of theories, there is a growing belief among geologists (e.g., Gilluly, 1949) that the geological part of the theories was wrong, anyhow, and that the postulated tectonic phases did not occur, that is, that such phases are not really either regularly cyclic or world-wide. The least one can say is that

the regularities and simple relationships demanded by the theories in question are unproven and very improbable on present evidence, but this does not quite close the subject.

There have been rather definite times in earth history when an unusual amount of evolutionary movement of one sort or another was going on in so many groups that pure coincidence seems almost out of the question and in such a variety of organisms that inherent evolutionary similarities in them as opposed to some broad environmental change also seem almost ruled out. For the vertebrates such episodes clearly occurred three times:

1. Devonian. Rapid turnover from earlier to later major groups of aquatic vertebrates with extremely high extinction rates for the former and high-category origination rates for the latter. Origin of Amphibia.

2. Permian to Triassic. Rapid turnover among both aquatic (especially Osteichthyes) and terrestrial (especially Reptilia) vertebrates with high extinction rates in the Permian or both Permian and Triassic for some groups, and high origination rates in the Triassic.

3. Cretaceous to Tertiary. Some change among aquatic vertebrates (perhaps not of crisis proportions near the era boundary). Very high turnover among terrestrial vertebrates.

Schindewolf (1950b) has made a similar list based on "turning points" (which are in general climaxes of what I have called "turnover" above) in a wider variety of organisms, including the vertebrate classes and also fourteen major groups of invertebrates and the plants as a whole. Three of his times of general evolutionary intensity are the same as those listed above for vertebrates alone. (He puts the first between Devonian and Mississippian rather than in the Devonian, but the dating is not sharp enough to give such a difference any importance.) He also lists two more:

- a. Cambrian to Ordovician. Rapid turnover of marine invertebrates.

- b. Triassic to Jurassic. Again considerable turnover of marine invertebrates and some of the vertebrates, but in both cases this seems less profound than the Permian-Triassic turnover.

Unquestionably still another major episode of this sort should be listed: the pre-Cambrian-Cambrian change.

For these crucial evolutionary times Schindewolf shows that, like major episodes of proliferation, they do not correlate with supposedly

world-wide physical events as listed by Umbgrove and other geologists.

The wrong correlations have been sought and the situation is not as simple as was formerly believed, or perhaps hoped. The outstanding periods of fairly general evolutionary crisis are episodic and not cyclic and are not especially connected with mountain-building. Nevertheless it does seem likely that physical events influenced and helped to determine the times of these crises although they may not have been primary causes. What the record strongly suggests is that these crises followed periods of widespread hard times, that is, of deteriorating conditions in many established adaptive zones. They must almost certainly be imputed to changing environments in the broadest sense of that word. The changes involved may not have been, indeed, probably were not, the same in all crises or for all organisms concerned in one crisis. Precisely what the changes were cannot now be clearly specified in any case. Study of past environments, in the full sense of the word and on a broad scale, is one of the most difficult and one of the least advanced subjects in paleontology and geology although progress is being made. In the meantime, hints and possibilities are not lacking. For instance, the Permian-Triassic and the Cretaceous-Tertiary crises do coincide (as nearly as such very long episodes can coincide) with exceptionally great land emergence and, in the case of the earlier, with considerable evidence of abnormal climates. (Abnormal climate is also frequently claimed around the time of the Cretaceous-Tertiary crisis, but the concrete evidence is still very unconvincing.)

Given the way adaptation evolves, it is probable that most or all of the turnovers that occurred in these crises would have occurred sooner or later in any case. Their tendency to group together suggests that their occurring just when they did was influenced by widespread environmental factors, quite possibly physical in part, at least.

To avoid any misunderstanding it may be well to restate the obvious fact that the physical environment and the history of the earth have certainly and strongly influenced the history of life. The influence is always there, as so much of the history of life is the evolution of adaptation and physical environment is always an important factor in adaptation. Sometimes the influence of geologic history is quite obvious, for instance in the shifting relationships of land and sea connections. Often

its influence is inferred but the exact bearing is obscure. As of now, it does not seem to be true that rhythms or cycles of the earth are simply and directly reflected in cycles of evolution. It does still seem probable that episodic earth changes have had an effect on the timing, at least, of episodic crises in evolution.