

1 ~ Evolutionary Biology

The theory of evolution is quite rightly called the greatest unifying theory in biology. The diversity of organisms, similarities and differences between kinds of organisms, patterns of distribution and behavior, adaptation and interaction, all this was merely a bewildering chaos of facts until given meaning by the evolutionary theory. There is no area in biology in which that theory has not served as an ordering principle. Yet this very universality of application has created difficulties. Evolution shows so many facets that it looks alike to no two persons. The more different the backgrounds of two biologists, the more different have been their attempts at causal explanation. At least, so it was through the history of evolutionary biology (Heuts 1952; Simpson 1949, 1960b; Eiseley 1958), until the many dissenting theories were almost suddenly fused, in the 1930's, into a broad unified theory, the "synthetic theory."

Many of the earlier evolutionary theories were characterized by heavy emphasis, if not exclusive reliance, on a single factor (Table 1-1). The synthetic theory has selected the best aspects from the earlier hypotheses and has combined them in a new and original manner. It attempts to evaluate the respective roles of the numerous interacting factors responsible for evolutionary change. In essence it is a two-factor theory, considering the diversity and harmonious adaptation of the organic world as the result of a steady production of variation and of the selective effects of the environment. It is thus basically a synthesis of mutationism and environmentalism.

Attempting to explain evolution by a single-factor theory was the fatal weakness of the pre-Darwinian and most 19th-century evolutionary theories. Lamarckism with its internal self-improvement principle, Geoffroyism with its induction of genetic change by the environment, Cuvier's catastrophism, Wagner's evolution by isolation, De Vries' mutationism,

all were deficient through focusing on only one aspect of a complex set of interacting factors. These hypotheses tried to explain evolution by a single principle to the exclusion of all others. Even Darwin occasionally fell into this error, as when he wrote, late in his life, that natural selection

Table 1-1. Theories of evolutionary change (in part after Heuts 1952).

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- A. Monistic (single-factor explanations)
1. Ectogenetic: changes directly induced by the environment
 - (a) Random response (for example, radiation effects)
 - (b) Adaptive response (Geoffroyism)
 2. Endogenetic: changes resulting from intrinsic forces
 - (a) Finalistic (orthogenesis)
 - (b) Volitional (genuine Lamarckism)
 - (c) Mutational limitations
 - (d) Epigenetic limitations
 3. Random events ("accidents")
 - (a) Spontaneous mutations
 4. Natural selection
- B. Synthetic (multiple-factor explanations)
- 1(b) + 2(a) + 2(b) = most "Lamarckian-type" theories
 - 1(b) + 2(b) + 2(c) + 4 = some recent "Lamarckian" theories
 - 1(b) + 3 + 4 = late Darwin, Plate, most nonmutationists during first three decades of 20th century
 - 3 + 4 = early "Modern Synthesis"
 - 1(a) + 2(c) + 2(d) + 3 + 4 = recent "Modern Synthesis"
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rather than isolation was responsible for the origin of species, as if the two forces were mutually exclusive (Mayr 1959c). Yet on the whole Darwin was the first to make a serious effort to present evolutionary events as due to a balance of conflicting forces. Indeed, he often went too far in compromising. It has been claimed, not without justification, that one can find support in Darwin's writings for almost any theory of evolution: speciation with geographic isolation or without it, direct effect of the environment or merely selection by the environment, evolutionary importance of large genetic changes or of small ones, and so on. This explains the paradox that the term "Darwinism" means such different things to an American, a Russian, or a French biologist. To be sure, the current theory of evolution—the "modern synthesis," as Huxley (1942) has called it—owes more to Darwin than to any other evolutionist and is built around Darwin's essential concepts. Yet it incorporates much that is distinctly post-Darwinian. The concepts of mutation, variation, population, inheritance, isolation, and species were still rather nebulous in Darwin's day. To avoid confusion, it has been suggested, particularly by Simpson

(1949, 1960b), that the term "neo-Darwinism," originally introduced into biology for Weismann's concepts of evolution, should be dropped.

The development of the modern theory was a slow process. Evolutionary biology was at first in the same situation as sociology, psychology and other vast fields still are today: the available data were too voluminous and diversified to be organized at once into a single comprehensive theory. Individual, specialized theories had to spotlight selected aspects and assist in a preliminary sorting of the data before a complete synthetic interpretation of the field as a whole was feasible. Looking back over the history of the many false starts gives a valuable insight into the process of theory formation. One important lesson is that progress is stepwise and that some sets of data may not have significance until certain concepts are clarified or principles established. For instance, the true role of the environment in evolution could not be understood until the nature of small mutations and of selection were fully comprehended. Polygenes could not be analyzed and understood until the laws of inheritance had been clarified with the help of conspicuous mutations. The process of speciation could not be understood until after the nature of species and of geographic variation had been clarified. Discussions of variation among early evolutionists were utterly confused because they failed to make a clear distinction between geographical "variety" (geographical race) and individual variety. The replacement of the morphological by the biological species concept led to a reevaluation of the "biological race" and to a rather drastic shift in the study of speciation. The analysis of quantitative characters was futile until the principles of particulate inheritance had been fully understood. Genetics, morphology, biogeography, systematic paleontology, embryology, physiology, ecology, and other branches of biology, all have illuminated some special aspect of evolution and have contributed to the total explanation where other special fields failed. In many branches of biology one can become a leader even though one's knowledge is essentially confined to an exceedingly limited area. This is unthinkable in evolutionary biology. A specialist can make valuable contributions to special aspects of the evolutionary theory, but only he who is well versed in most of the above-listed branches of biology can present a balanced picture of evolution as a whole. Whenever a narrow specialist has tried to develop a new theory of evolution, he has failed.

The importance of eliminating erroneous concepts is rarely given sufficient weight in discussions of theory formation. Only in some cases is it true that the new, better theory vanquishes the old, "bad" one. In many

other instances it is the refutation of an erroneous theory that vacates the field for new ideas. An excellent illustration of this is Louis Agassiz's neglect of what seem to us most convincing evolutionary facts because they were inconsistent with his well-organized, harmonious world view (Mayr 1959d). Darwin, who had started the voyage of the *Beagle* with views similar to those of Agassiz, began to think seriously about evolution only after he had found overwhelming evidence that was completely irreconcilable with the idea of an origin of the world fauna and flora by creation. Or, to cite another example, as long as spontaneous generation and the instantaneous conversion of one species into another were universally believed in, even for higher animals and plants (Zirkle 1959), there was no room for a theory of evolution. By insisting on the fixity of species, Linnaeus did more to bring about the eclipse of the concept of spontaneous generation than did Redi and Spallanzani, who disproved it experimentally. Indirectly, Linnaeus did as much to prepare the ground for a theory of evolution as if he had proposed such a theory himself. Weismann, through his theoretical analysis of the relation between germ cells and soma cells, eliminated many of the misconceptions and errors that until then had prevented the recognition of the work of Mendel. These are merely a few illustrations of the importance of eliminating erroneous theories. The refutation of an erroneous idea thus is not a purely negative activity, and in this volume I often give considerable space to the analysis of that alternative of two opposing theories that I consider to be the less well-founded one.

More important for the development of the synthetic theory than the rejection of ill-founded special theories of evolution was the rejection of two basic philosophical concepts that were formerly widespread if not universally held: preformism and typological thinking. Preformism is the theory of development that postulates a preformed adult individual in miniature "boxed" into the egg or spermatozoon, ready to "unfold itself" during development. The term evolution is derived from this concept of unfolding, and this connotation continued well into the post-Darwinian period. It was perhaps the reason Darwin did not use the term "evolution" in his *Origin of Species*. Transferred from ontogeny to phylogeny, evolution meant the unfolding of a built-in plan. Evolution, according to this view, does not produce genuine change, but consists merely in the maturation of immanent potentialities. This, for instance, was Louis Agassiz's theory of evolution (Mayr 1959d). Some of the orthogenetic and finalistic theories of evolution are the last remnants of this type of think-

ing. The underlying erroneous assumption that the development of the "type" is essentially the same phenomenon as the development of the individual has also been the reason for much of the search for "phylogenetic laws." Mutationism was the extreme in the reaction to these orthogenetic concepts. The current theory compromises by admitting that genotype and phenotype of a given evolutionary line set severe limits to its evolutionary potential (Table 1-1, A2c,d), without, however, prescribing the pathway of future evolutionary change.

Typological thinking is the other major misconception that had to be eliminated before a sound theory of evolution could be proposed. Plato's concept of the *eidos* is the formal philosophical codification of this form of thinking. According to this concept the vast observed variability of the world has no more reality than the shadows of an object on a cave wall, as Plato puts it in his allegory. Fixed, unchangeable "ideas" underlying the observed variability are the only things that are permanent and real. Most of the great philosophers of the 17th, 18th, and 19th centuries were influenced by the idealistic philosophy of Plato and the modifications of it by Aristotle. The thinking of these schools dominated the natural sciences until well into the 19th century. The concepts of unchanging essences and of complete discontinuities between every *eidos* (type) and all others make genuine evolutionary thinking well-nigh impossible. I agree with those (such as Reiser 1958) who claim that the typological philosophies of Plato and Aristotle are incompatible with evolutionary thinking.

The assumptions of population thinking are diametrically opposed to those of the typologist. The populationist stresses the uniqueness of everything in the organic world. What is true for the human species, that no two individuals are alike, is equally true for all other species of animals and plants . . . All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and the statistics of variation. Averages are merely statistical abstractions; only the individuals of which the populations are composed have reality. The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real. No two ways of looking at nature could be more different (Mayr 1959c).

The replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biol-

ogy. Many of the basic concepts of the synthetic theory, such as that of natural selection and that of the population, are meaningless for the typologist. Virtually every major controversy in the field of evolution has been between a typologist and a populationist. Even Darwin, who was more responsible than anyone else for the introduction of population thinking into biology, often slipped back into typological thinking, for instance in his discussions on varieties and species.

A new conceptual danger to the evolutionary theory at the present time comes not from metaphysics but from physics. Some physicists who believe in reductionism have attempted in recent years to express the laws of evolution in terms of the laws of physics. Statements to the effect that "evolution is one more expression of the general principle of irreversibility embodied in the second law of thermodynamics" are based on a facile analogy that has no operational value. Since every individual is unique, strict evolutionary reversibility is a logical impossibility. Yet acquired specializations may be lost again at later stages of evolution and a type may evolve that has in its essential structure reverted to a prior condition although it is obviously not the same as the ancestral type. The processes in physics and evolution labeled by the same term, "irreversibility," are fundamentally different. To drag the second law of thermodynamics into the discussion of evolutionary irreversibility confuses two distant levels of integration, the atomic level and the level of the phenotype. Those who try to explain the pathway of evolution in terms of the laws of physics do not seem to realize how dangerously close they sail to preformism.

CLARIFICATION OF EVOLUTIONARY CONCEPTS

A comparison of current evolutionary publications with those of only 20 or 25 years ago shows what great conceptual progress has been made in this short period. Since much of this volume is devoted to reporting on this progress, I will barely mention some of these advances in this introductory discussion. Our ideas on the relation between gene and character have been thoroughly revised and the phenotype is more and more considered not as a mosaic of individual gene-controlled characters but as the joint product of a complex interacting system, the total epigenotype (Waddington 1957). Interactions and balances among opposing forces are stressed to an increasing extent. Virtually every component of the phenotype is recognized as a compromise between opposing selection pressures.

The realization that the DNA of the chromosomes carries a code of information has led to great clarification. The phenomena of ontogeny and physiology are now interpreted as manifestations of the decoding of the information embodied in the genotype. Phylogeny, on the other hand, and all the phenomena involving evolutionary change are considered as the production of ever-new codes of information. Nothing could make the difference between ontogeny and phylogeny clearer than stating it in terms of codes of information. We shall come back to this later.

Let me cite some other advances in our understanding. Natural selection is no longer regarded as an all-or-none process but rather as a purely statistical concept. Isolation has been revealed as a dual phenomenon, either the separation of populations by environmental barriers or the maintenance of the genetic integrity of species by isolating mechanisms. The environment is restored to the place of one of the most important evolutionary factors but in a drastically different role than it held in the various "Lamarckian" theories. The new role of the environment is to serve as principal agent of natural selection.

OPEN PROBLEMS

The development of the evolutionary theory is a graphic illustration of the importance of the *Zeitgeist*. A particular constellation of available facts and prevailing concepts dominates the thinking of a given period to such an extent that it is very difficult for a heterodox viewpoint to get a fair hearing. Recalling this history should make us cautious about the validity of our current beliefs. The fact that the synthetic theory is now so universally accepted is not in itself proof of its correctness. It will serve as a warning to read with what scorn the mutationists in the first decade of this century attacked the contemporary naturalists for their belief in gradual changes and in the immense importance of the environment. It never occurred to the saltationists that their own typological and antiselectionist interpretation of evolution could be much further from the truth than the late Darwinian viewpoint of their adversaries. Unfortunately, the synthetic theory is still by some considered a form of mutationism. In my experience, every recent attack on the synthetic theory has really been an attack on crude mutationism rather than a reasoned argument against the actual tenets of the synthetic theory. Everything that is stated in the synthetic theory about mutations is in conflict with the claims of mutationism. We now believe that mutations do not guide evolution; the effect of a mutation is very often far too small to be visible.

Recombination produces far more selectively important phenotypes than does mutation, and the kinds of mutations and recombinations that can occur in a given organism are severely restricted. These statements are entirely consistent with the synthetic theory but they may be quite startling to those who are unaware of the modern developments and who are still fighting the fight of the last generation.

When we reread the volumes published in 1909, on the occasion of the 50th anniversary of the *Origin of Species*, we realize how little agreement there was at that time among the evolutionists. The change since then has been startling. Symposia and conferences were held all over the world in 1959 in honor of the Darwin centennial, and were attended by all the leading students of evolution. If we read the volumes resulting from these meetings at Cold Spring Harbor, Chicago, Philadelphia, London, Göttingen, Singapore, and Melbourne, we are almost startled at the complete unanimity in the interpretation of evolution presented by the participants. Nothing could show more clearly how internally consistent and firmly established the synthetic theory is. The few dissenters, the few who still operate with Lamarckian and finalistic concepts, display such colossal ignorance of the principles of genetics and of the entire modern literature that it would be a waste of time to refute them. The essentials of the modern theory are to such an extent consistent with the facts of genetics, systematics, and paleontology that one can hardly question their correctness. The basic framework of the theory is that evolution is a two-stage phenomenon, the production of variation and the sorting of the variants by natural selection. Yet agreement on this basic thesis does not mean that the work of the evolutionist is completed. The basic theory is in many instances hardly more than a postulate and its application raises numerous questions in almost every concrete case. The discussions throughout this volume are telling testimony to the truth of this statement.

Modern research is directed primarily toward three areas: evolutionary phenomena that do not yet appear to be adequately explained by the synthetic theory, such as stagnant or explosive evolution; the search for various subsidiary factors that, although inconspicuous at casual inspection, exercise unexpected selection pressures; and, perhaps most important, the interplay among genes and between genotype and environment resulting in the phenotype, the real "object" of natural selection.

Most contemporary arguments concern the relative importance of the various interacting factors. One will get highly diverse answers if one asks a number of contemporary evolutionists the following questions:

How important are random events in evolution?

How important is hybridization in evolution?

How important is interpopulation gene flow?

What proportion of new mutations is beneficial?

What proportion of genetic variability is due to balanced polymorphism?

Other areas in which there is still wide divergence of opinion are the importance of phenotypic plasticity, the pathway to adaptation, evolutionary mechanisms in higher and lower organisms, the origin of sexuality, and the origin of life. It must be stressed, for the benefit of nonevolutionists, that none of these arguments touches upon the basic principles of the synthetic theory. It is the application of the theory that is involved, not the theory itself. And with respect to application we still have a long way to go. There are vast areas of modern biology, for instance biochemistry and the study of behavior, in which the application of evolutionary principles is still in the most elementary stage.

THE MAJOR AREAS OF EVOLUTIONARY RESEARCH

Important contributions to our understanding of the evolutionary process have been made by virtually every branch of biology. During the past 100 years most of the research has been concerned with a number of discrete areas, progress within which has been unequal:

The fact of evolution,

The establishment of phylogenies,

The origin of discontinuities (speciation),

The material of evolution,

Rates of evolution,

Causes of evolution, and

The evolution of adaptation.

The amount of attention given to each of these areas has changed with time. To establish unequivocally the fact of evolution was after 1859 the first concern of the young science of evolutionary biology. The study of phylogeny soon became predominant, at least in zoology. Indeed, even today there still are some zoologists to whom the term "evolution" signifies little more than the determination of homologies, common ancestors, and phylogenetic trees. By far the majority of evolutionary biologists, however, have shifted their interest to a study of the causes and mechanisms of evolutionary change and to an attempt to determine the role and relative importance of various factors. A study of the difference in response to these factors displayed by different types of organisms is also

receiving increasing attention. Evolutionary biology is beginning to become truly comparative.

The attack on evolutionary problems can be compared to an attack on a many-walled city by a number of separate armies. A breach in one of these walls made by the army of the geneticists improves the strategic situation of the paleontologists and systematists, and vice versa. Each factual or conceptual advance in one field will have an impact on the thinking in the others. Each branch of evolutionary biology occupies, so to speak, a special niche and is uniquely qualified to illuminate some special problem.

The geneticist is mainly concerned with the individual, the stability or mutability of loci, the modification of the phenotype, the interaction of parental genes in the production of the phenotype and the effect of this interaction on fitness, in short, all the problems concerning the gene and its interaction with other genes and with the environment. The development of population genetics led to an expansion from the gene to the gene pool of the population.

The contribution of genetics to the understanding of the process of evolution has not yet been evaluated objectively (Mayr 1959c). The assumption made by some geneticists, that it was quite impossible to have sensible ideas on evolution until the laws of inheritance had been worked out, is contradicted by the facts. Everyone admits that Darwin's evolutionary theories were essentially correct and yet his genetic theories were about as wrong as they could be. Conversely, the early Mendelians, the first biologists (except for Mendel himself) who truly understood genetics, misinterpreted just about every evolutionary phenomenon. Some of their contemporaries among the naturalists, on the other hand, though they did not understand genetics and even believed in some environmental induction (Geoffroyism), presented a remarkably correct picture of speciation, adaptation, and the role of natural selection. It would be going too far to claim that it is immaterial whether one believes the source of genetic variation to be De Vriesian or Lamarckian, yet it is true that it is less important for the understanding of evolution to know how genetic variation is manufactured than to know how natural selection deals with it (Waddington 1957). Replacing the erroneous belief in blending inheritance by the theory of particulate inheritance is the greatest single contribution of genetics. It has been the basis of all subsequent developments. The genetic material presented in Chapters 7-10 and 17 shows to what extent the modern genetic theory can explain many phenomena

that the naturalist has long known and correctly described, but has been unable to interpret.

The study of long-term evolutionary phenomena is the domain of the paleontologist. He investigates rates and trends of evolution in time and is interested in the origin of new classes, phyla, and other higher categories. Evolution means change and yet it is only the paleontologist among all biologists who can properly study the time dimension. If the fossil record were not available, many evolutionary problems could not be solved; indeed, many of them would not even be apparent.

The taxonomist, who deals primarily with local populations, subspecies, species, and genera, is concerned with the region that lies between the areas of interest and competence of the geneticist and of the paleontologist, overlapping with both but approaching problems in the area of overlap from a somewhat different viewpoint. The species, the center of his interest, is one of the important levels of integration in the organic world. Neglect of this level in much of our biological curriculum is rather puzzling. We do not even have a special term for the study of the species, corresponding to cytology, the study of cells; histology, the study of tissues; and anatomy, the study of organs. Yet the species is not only the basic unit of classification, but also one of the most important units of interaction in ecology and ethology. The origin of new species, signifying the origin of essentially irreversible discontinuities with entirely new potentialities, is the most important single event in evolution. Darwin, who had devoted so much of his life to the systematics of species, fully appreciated the significance of this level, as he made clear in the choice of title for his classic *On the Origin of Species*.

The emphasis in the present volume is deliberately on those aspects of evolution that involve the species. Other aspects, of greater interest to the geneticist or paleontologist, and adequately treated by Dobzhansky (1951), Simpson (1953a), Rensch (1960a), and other modern writers, will be neglected or treated only incidentally. Evolutionary biology has become far too vast a field to be covered adequately in a single volume.

The basic structure of this volume is as follows. The *characteristics of species* will be dealt with in Chapters 1-6; the *structure and genetics of populations* in Chapters 7-10; the (population) *structure and variation of species* in Chapters 11-14; and the *multiplication of species* in Chapters 15-18. Chapter 19 will be devoted to a discussion of the role of *species in transpecific evolution* and Chapter 20 to a review of the possible consequences of our findings for *man*.

2 ~ Species Concepts and Their Application

Darwin's choice of title for his great evolutionary classic, *On the Origin of Species*, was no accident. The origin of new "varieties" within species had been known since the time of the Greeks. Likewise the occurrence of gradations, of "scales of perfection" among "higher" and "lower" organisms, was a familiar concept, though usually interpreted in a strictly static manner. The species remained the great fortress of stability and this stability was the crux of the antievolutionist argument. "Descent by modification," true biological evolution, could be proved only by demonstrating that one species could originate from another. It is a familiar and often-told story how Darwin succeeded in convincing the world of the occurrence of evolution and how—in natural selection—he found the mechanism that is responsible for evolutionary change and adaptation. It is not nearly so widely recognized that Darwin failed to solve the problem indicated by the title of his work. Although he demonstrated the modification of species in the time dimension, he never seriously attempted a rigorous analysis of the problem of the multiplication of species, of the splitting of one species into two. I have examined the reasons for this failure (Mayr 1959a) and found that among them Darwin's lack of understanding of the nature of species was foremost. The same can be said of those modern authors, for instance Goldschmidt (1940), who attempted to solve the problem of speciation by saltation or other heterodox hypotheses. They all failed to find solutions that are workable in the light of the modern appreciation of the population structure of species.

A thorough understanding of the biological properties of species is necessary not only for the evolutionist, but for every biologist. Every biologist, even the biochemist, constantly works with species or with com-

pounds and systems that are species specific. Unawareness of this fact by some physiologists and ecologists has been the cause of much confusion in the literature. The failure properly to define and distinguish species has had far-reaching practical effects in the fields of economic entomology, parasitology, and medical entomology.

In view of this apparent importance of the species it is a curious paradox that since time immemorial it has been contended that species have no existence in nature. Such claims have been made by philosophers who think in terms of philosophical categories and consider species as something man-made (see Mayr 1957a for historical notes). They have come from taxonomists (including Darwin) who had unsuitable species criteria and became bewildered by the variability of their material. And finally, such claims have come from paleontologists, who work in the time dimension and who are therefore indeed unable in certain cases to delimit species against each other. From the discussions of the negators of species it is very apparent that they deal with only a few aspects of a very complex problem.

Among naturalists the attitude toward the species has greatly fluctuated in the course of history. For the ancients and for some naturalists as recently as the nineteenth century (Agassiz) or even the present, species are merely man-made "categories of thought." Folklore took it for granted that one species can change readily into another (Zirkle 1959), and a belief in the spontaneous generation even of higher animals and plants was almost universal far into the eighteenth century. In spite of Redi's and Spallanzani's experiments, spontaneous generation was used by the philosopher Schopenhauer as late as 1851 to explain the origin of species and higher categories. It is the great merit of Linnaeus (Mayr 1957a) to have challenged and decisively defeated the folklore belief of the easy mutability of species. The whole concept of evolution would be meaningless if species were the arbitrary and ephemeral units of the pre-Linnaean period. It was Linnaeus' insistence on the constancy and objectivity of species that posed the problem of the origin of species, a problem previously nonexistent in that form (see also Poulton 1903).

The supremacy of the Linnaean species extended from the 1750's to 1859. Two characteristics of species were stressed during this period: their constancy and their sharp delimitation against each other (their "objectivity"). The general assumption of the period was that these two characteristics "are strictly correlated and that one must make a choice of either believing in evolution (the 'inconstancy' of species) and then

having to deny the existence of species except as purely subjective, arbitrary figments of the imagination, or, as most early naturalists have done, believing in the sharp delimitation of species but thinking that this necessitated denying evolution" (Mayr 1957a). Darwin, the evolutionist, simply denied the existence of nonarbitrary species: "I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other . . . it does not essentially differ from the term variety which is given to less distinct and more fluctuating forms" (Darwin 1859). By eliminating the species as a concrete natural unit, Darwin also neatly eliminated the need for a solution to the problem of how species multiply (Mayr 1959a). In retrospect it is apparent that Darwin's failure, as well as that of the antievolutionists, resulted to a large extent from a misunderstanding of the true nature of species. There is a great need, then, for an impartial investigation of species criteria, species characteristics, species concepts, and species definitions. For recent literature on the species problem see Mayr (1957a), Sylvester-Bradley (1956), Beaudry (1960), and Simpson (1961).

SPECIES CRITERIA

How to allocate the variable individuals in nature to species has been a problem for the naturalist since earliest times. The first author to express this in relatively modern terms was Ray (1686):

In order that an inventory of plants may be begun and a classification of them correctly established, we must try to discover criteria of some sort for distinguishing what are called "species." After a long and considerable investigation, no surer criterion for determining species has occurred to me than the distinguishing features that perpetuate themselves in propagation from seed. Thus, no matter what variations occur in the individual or the species, if they spring from the seed of one and the same plant, they are accidental variations and not such as to distinguish a species . . . Animals likewise that differ specifically preserve their distinct species permanently; one species never springs from the seed of another nor vice versa. (From Beddall 1957.)

The three themes of Ray's discussion dominated the thinking of the next 50 years: first, the implied rejection of spontaneous generation; second, the morphological definition of the species; and third, the endeavor to reconcile the observed variation with the typological species concept. Production by the same parents is the "common descent" of which such antievolutionists as Cuvier and von Baer spoke in their species definitions (Mayr 1957a).

Degree of morphological difference remained the dominant species

criterion in taxonomy through the entire Linnaean period, and even in Darwin's writings. This concept was carried to the logical extreme by the proposal of mathematical formulas that would permit an unambiguous answer to the question whether or not a certain population is a species: "A given population is to be considered a species with respect to another closely related population when the degree of intergradation (overlap of the observed samples) is not more than 10 percent" (Ginsburg 1938:260). A revival of this sort of thinking can be found in the writings of some of the contemporary "numerical taxonomists." The weaknesses of this purely morphological approach will be discussed in more detail later (Chapter 3). It may be remarked here that nearly all of the older species definitions, including those of Buffon, Lamarck, and Cuvier, refer to the morphological similarity of the individuals of which species are composed.

Yet Ray's species characterization contained also the germ of the modern species concept, which considers reproductive relationship to be the principal species criterion. Instead of concentrating on the degree of difference in the offspring of a pair of parents, one can equally well concentrate on the degree of difference between potential mates and their ability to interbreed. As early as 1760 Koelreuter had stated that all those individuals belong to a species that are able to produce fertile offspring. With increasing frequency since then, interbreeding has been considered a decisive criterion in species definitions. Unfortunately, this criterion has often been narrowed down to a single aspect of successful interbreeding, that of fertility. Cross-fertility was accepted as the decisive species criterion in much of the genetic and botanical literature until naturalists pointed out that fully cross-fertile species of animals may live side by side without interbreeding because their reproductive isolation is maintained by isolating mechanisms other than the sterility barrier. Authors like myself, who have consistently advocated that the noninterbreeding of natural populations rather than the sterility of individuals be taken as the decisive species criterion, have nevertheless been accused by hasty readers of having a species concept "based on cross-sterility."

The history of the many attempts to find universally satisfactory species criteria has been given elsewhere (Mayr 1957a). The difficulties encountered are a strong indication not only of the great diversity of population phenomena and of types of species found in nature but, alas, also of much muddled thinking. It is evident that the word "species" has meant and still means different things to different people. There is no hope for ultimate unanimity unless one understands the various basic concepts to which the term has been applied.

SPECIES CONCEPTS

Several different species concepts coexist in the biological literature. There are at least two categories of such concepts. Terms like "practical," "sterility," or "genetic," when used to describe species concepts, refer to criteria one may apply to concrete situations. They deal with the evidence that, as Simpson (1961) would say, one uses in order to determine whether a given taxon belongs to the category species or not. Yet these secondary, "applied" concepts are based on underlying primary or theoretical concepts. A study of all the species definitions published in recent years indicates that they are based on three theoretical concepts, neither more nor less. An understanding of these three concepts is a prerequisite for the investigation of the problem of speciation.

(1) *The Typological Species Concept.* This is the simplest and most widely held species concept. Species here means "a different thing," something that "looks different" (from the Latin *specere*, to look at, to regard), "a different kind." This is the concept the mineralogist has in mind when he speaks of "species of minerals" or the physicist who speaks of "nuclear species."

This simple concept of everyday life was made the basis of the *eidos* in Plato's philosophy (Chapter 1). Different authors have stressed different aspects of Plato's *eidos*, some its independence of perception, others its transcendent reality, and still others its eternity and immutability. All these concepts take for granted that there is an unchanging essence, an *eidos*, which alone has objective reality. Objects, on the other hand, are for Plato and his adherents merely varying manifestations ("shadows") of the *eidos*. The individuals of a natural species, being merely shadows of the same "type," do not stand in any special relation to each other. Variation, under this concept, is due to the imperfections in the visible manifestations of the "idea" implicit in each species.

There are, however, limits to the amount of variation that can be ascribed to the varying manifestations of a single *eidos*. Where it transgresses these limits, more than one *eidos* must be involved. Degree of morphological difference, thus, determines species status. The two aspects of the typological species concept, subjectivity and definition by degree of difference, depend on each other and are logical correlates. The typological species concept, translated into practical taxonomy, is the morphologically defined species.

In recent years most systematists have found this typological-morpho-

logical concept inadequate and have rejected it. They have pointed out that this concept treats the individuals of a species like an aggregation of inanimate objects, a singularly inappropriate treatment for a reproductive community. They have also called attention to the fact, discussed in Chapters 3 and 7, that the morphological species criterion is highly misleading in cases of polymorphic diversity within species or of morphologically extremely similar species. Where the taxonomist applies morphological criteria, he uses them as secondary indications of reproductive isolation.

(2) *The Nondimensional Species Concept.* This concept is based on the relation of two coexisting natural populations in a nondimensional system, that is, at a single locality and at the same time (sympatric and synchronous). This is the species concept of the local naturalist (Mayr 1946b). If one studies the birds, the mammals, the butterflies, or the snails near his home town, he finds each species clearly defined and sharply separated from all other species. This is sometimes better appreciated by primitive natives than by modern civilized man. Some 30 years ago I spent several months with a tribe of superb woodsmen and hunters in the Arfak Mountains of New Guinea. They had 136 different vernacular names for the 137 species of birds that occurred in the area, confusing only two species. It is not, of course, pure coincidence that these primitive woodsmen arrive at the same conclusion as the museum taxonomists, but an indication that both groups of observers deal with the same, non-arbitrary discontinuities of nature.

This striking discontinuity between sympatric populations is the basis of the species concept in biology. The two taxonomists who, more than anyone else, were responsible for the acceptance of species in biology were local naturalists, John Ray in England and Carolus Linnaeus in southern Sweden. But anyone can test the reality of these discontinuities for himself, even where the morphological differences are slight. In eastern North America, for instance, there are four rather similar species of the genus *Catharus* (Table 2-1), the Veery (*C. fuscescens*), the Hermit Thrush (*C. guttatus*), the Olive-backed or Swainson's Thrush (*C. ustulatus*), and the Gray-cheeked Thrush (*C. minimus*). These four species are sufficiently similar visually that they confuse not only the human observer, but also silent males of the other species. The species-specific songs and call notes, however, permit easy species discrimination, as experimentally substantiated by Dilger (1956a). Rarely more than two species breed in the same area and the overlapping species $f + g$, $g + u$,

a limited number of adaptive peaks, and that ecological factors have given the former continuum a taxonomic structure." Each adaptive peak is occupied by a different "kind" of organisms and if each "kind" is sufficiently different from other kinds it will be legitimate to call such a cluster of genotypes a species (see also Chapter 15).

Various proposals have been made to resolve the difficulty that asexuality raises for the biological species concept. Some authors have gone so far as to abandon the biological species concept altogether and return to the morphological species for sexual and asexual organisms. I can see nothing that would recommend this solution. It exaggerates the importance of asexuality, which is both secondary and limited in its extent, and reintroduces the subjectivity and arbitrariness of the morphological species (see Hairston 1958 and Simpson 1961 for illuminating discussions of this problem).

A second solution, that of using a neutral term ("binom") for kinds of asexual organisms and restricting the term species to biological species of sexual organisms (Grant 1957), is logical and consistent. It minimizes, however, the fact that the word "species" signifies not only the biological unit of a reproductively isolated population, but also the classifying unit of a kind of organism. It is perhaps this consideration that has induced most practicing taxonomists to be frankly dualistic: they define the term species biologically in sexual organisms and morphologically in asexual ones. The fact that degree of genetic difference is on the whole responsible both for reproductive isolation and for morphological difference gives this procedure biological justification. To draw conclusions from the degree of morphological difference on the probable degree of reproductive isolation is a method of inference that has long been applied successfully to isolated populations in sexual organisms. There is no reason not to extend its application to asexual types. It results in the combining in a single species of those asexual individuals that display no greater morphological difference from each other than do conspecific individuals or populations in related sexual species. Subjectivity and arbitrariness cannot be avoided in such situations, particularly when there are no related sexual species.

Cain (1954a), Meglitsch (1954), and Simpson (1961) speak of asexual or uniparental "populations." However, every individual and its descendants are reproductively isolated in asexual organisms, and I am at a loss to define the term "population" in such organisms. Simpson

(1961) states that uniparentally reproducing individuals can be treated as species because their unity "is maintained by community of inheritance, by the capacity for genes to spread throughout the population (which therefore has a gene pool), and by the inhibition of their spread to other populations." It seems to me that these statements are contradicted by the known facts. Cases like that of the bdelloid rotifers show that community of inheritance does not help to define uniparental species and I know of no evidence that genes in uniparental species have a capacity to spread to individuals other than descendants (excepting phenomena of paraxuality). I feel, for these reasons, that introducing the term "population" into the definition of asexual or uniparental species is not legitimate.

Is the biological species concept invalidated by the difficulties in its application that have been listed?

One can confidently answer this question: "No!" Almost any concept is occasionally difficult to apply, without thereby being invalidated. The advantages of the biological species are far greater than its shortcomings. Difficulties are rather infrequent in most groups of animals and are well circumscribed where they do occur. Such difficulties are least frequent in nondimensional situations where (except in paleontology) most species studies are done. Indeed the biological species concept, even where it has to be based on inference, nearly always permits the delimitation of a sounder taxonomic species than does the morphological concept.

THE IMPORTANCE OF A NONARBITRARY DEFINITION OF SPECIES

Whoever, like Darwin, denies that species are nonarbitrarily defined units of nature not only evades the issue, but fails to find and solve some of the most interesting problems of biology. These problems will be apparent only to the student who attempts to determine species status of natural populations. The correct classification of the many different kinds of varieties, of polymorphism (Chapter 7), of polytypic species (Chapter 12), of biological races (Chapter 15), would all be meaningless, indeed would be ignored, but for an interest in arranging natural populations and phenotypes into biological species. Application of the concept has led to advances in the sorting of fossil specimens (Sylvester-Bradley 1936). Even though the evidence is largely morphological, an interpretation of fossil specimens based on biological concepts forces the paleontologist to make clear-cut decisions: morphologically different specimens found in the same exposure (the same sample) must be either different

Table 2-1. Characteristics of four eastern North American species of *Catharus* (from Dilger 1956a).

Characteristic compared	<i>C. fuscescens</i>	<i>C. guttatus</i>	<i>C. ustulatus</i>	<i>C. minimus</i>
Breeding range	Southernmost	More northerly	Boreal	Arctic
Wintering area	No. South America	So. United States	C. America to Argentina	No. South America
Breeding habitat	Bottomland woods with lush undergrowth	Coniferous woods mixed with deciduous	Mixed or pure tall coniferous forests	Stunted northern fir and spruce forests
Foraging	Ground and arboreal (forest interior)	Ground (inner forest edges)	Largely arboreal (forest interior)	Ground (forest interior)
Nest	Ground	Ground	Trees	Trees
Spotting on eggs	Rare	Rare	Always	Always
Relative wing length	Medium	Short	Very long	Medium
Hostile call	veer pneu	chuck seeeep	peep chuck-burr	beer
Song	Very distinct	Very distinct	Very distinct	Very distinct
Flight song	Absent	Absent	Absent	Present

and $u + m$ usually differ considerably in their foraging habits and niche preference, so that competition is minimized with each other and with two other thrushes, the Robin (*Turdus migratorius*) and the Wood Thrush (*Hylocichla mustelina*), with which they share their geographic range. In connection with their different foraging and migratory habits the four species differ from each other (and from other thrushes) in the relative length of wing and leg elements and in the shape of the bill. The rather extraordinary number of small differences between these at first sight very similar species has been worked out in detail by Dilger (1956a,b). Most importantly, no hybrids or intermediates among these four species have ever been found. Each is a separate genetic, behavioral, and ecological system, separated from the others by a complete biological discontinuity, a gap.

Indeed the most characteristic attribute of a species in such a non-dimensional system is that it is separated by a gap from other units in this system. The gap that surrounds a species is the core of the species concept. The term "species" signifies a very definite mutual relation between sympatric populations, between units in a nondimensional system, namely that of reproductive isolation. The great advantage of the cri-

terion of interbreeding between two populations in a nondimensional system is that its presence or absence can be determined unequivocally. Reproductive isolation thus supplies an objective yardstick; a completely nonarbitrary criterion, for the determination of species status of a population. The word "species" indicates a relationship, like the word "brother." Being a brother is not an inherent property of an individual, as hardness is the property of a stone. An individual is a brother only with respect to someone else. A population is a species only with respect to other populations. To be a different species is not a matter of difference but of distinctness.

(3) *The Interbreeding-population Concept.* The concept of the multidimensional species is a collective concept. It considers species as groups of populations that actually or potentially interbreed with each other. Such populations, in order to retain their identity, cannot coexist at the same place and at the same time. The multidimensional-species concept thus deals with allopatric and allochronic populations, populations distributed in the dimensions of space and time, and classifies them on the basis of mutual interbreeding.

This concept has the weakness of all collective concepts, that of practical difficulties of delimitation: which discontinuous populations shall be judged "potentially" interbreeding? Even though the multidimensional concept comes much closer to reality than the nondimensional concept, it is evident that it lacks the latter's objectivity.

SPECIES DEFINITIONS

When the term species is applied to inanimate objects, as in "species of minerals," it is based on the typological species concept. When the term is used in biology, it is based to a greater or lesser degree on the two other concepts, the nondimensional ("reproductive gap") and the multidimensional ("unlimited gene exchange"). Parts of these two concepts have been incorporated into nearly all species definitions in biology in the last 100 years. Most of the definitions proposed in the last 25 years have avoided all reference to morphological distinctness. For instance, I defined species (Mayr 1940) as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups," and Dobzhansky (1950) defined the species as "the largest and most inclusive . . . reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool."

Definitions that stress this dual biological significance of species, re-

productive isolation and community of gene pools, are usually referred to as "biological" species definitions. This designation has been questioned, for instance by Simpson (1961), on the grounds that this is not an exclusive terminology, since many of the other species definitions also refer to living species and their biological attributes. This cannot be denied and yet the designation "biological species" would seem best for the modern concept for three reasons. First, it has never been used for any other species concept or definition; no confusion can arise as to the intent of an author who uses this terminology. Second, this terminology emphasizes that the underlying concept is based on the biological meaning of the species, that is, to serve as a protective device for a well-integrated, co-adapted set of gene complexes. Third, alternative terminologies are even more ambiguous. This is true, for instance, of the term "genetical concept," preferred by Simpson (1961). This term is full of ambiguity, since it has been applied to the most diverse species definitions. The "genetic species concept" of De Vries, Lotsy, Shull, Bateson, and other Mendelians was a strictly typological species concept that had nothing to do with the biological concept. A later generation of geneticists adopted a genetic species concept based on the sterility criterion, and the result was the recognition of cenospecies and other entities having little to do with the biological species. Nothing in a genetic species concept requires it to stress those particular genetic differences that are essential for species status, those that provide reproductive isolation. The term "biological species concept" for a concept emphasizing interbreeding within the population system and reproductive isolation against others is now so widely adopted and so uniformly used that it could hardly lead to misunderstanding. A history of the development of the biological species concept is given by Mayr (1957a).

If we wanted to single out the aspects most frequently stressed in recent discussions of the biological species concept, we would list these three:

- (1) Species are defined by distinctness rather than by difference;
- (2) Species consist of populations rather than of unconnected individuals; and
- (3) Species are more unequivocally defined by their relation to non-conspecific populations ("isolation") than by the relation of conspecific individuals to each other. The decisive criterion is not the fertility of individuals but the reproductive isolation of populations.

The typological species concept treats species as random aggregates of

individuals that have in common "the essential properties of the type of the species" and that "agree with the diagnosis." This static concept ignores the fact that species are reproductive communities. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction. A multitude of devices insure intraspecific reproduction in all organisms (Spurway 1955). The species is also an ecological unit that, regardless of the individuals composing it, interacts as a unit with other species with which it shares the environment. The species, finally, is a genetic unit consisting of a large, intercommunicating gene pool, whereas the individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time.

These three properties raise the species above the typological interpretation of a "class of objects." The nonarbitrariness of the biological species is the result of this internal cohesion of the gene pool (Chapter 10) and of the biological causation of the discontinuities between species (Chapters 16 and 17).

DIFFICULTIES IN THE APPLICATION OF THE BIOLOGICAL SPECIES CONCEPT

The general adoption of the biological species concept has done away with a bewildering variety of "standards" followed by the taxonomists of the past. One taxonomist would call every polymorph variant a species, a second would call every morphologically different population a species, and a third would call every geographically isolated population a species. This lack of a universally accepted standard confused not only the general biologists who wanted to use the work of the taxonomist, but the taxonomists themselves. Agreement on a single yardstick, the biologically defined category species, to be applied by everybody, has been a great advance toward mutual understanding.

Yet not all difficulties were eliminated by the discovery of this yardstick. Some taxonomists confused themselves and the issue by failing to understand that there is a difference between the species as a category and the species as a taxon. The species as category is characterized by the biological species concept. The practicing taxonomist, however, deals with taxa, with populations and groups of populations, which he has to assign to one category or another, for instance either to the category species or to the category subspecies. The nonarbitrary criterion of the category species, biologically defined, is that of the interbreeding or noninterbreeding. When confronted with the task of having to assign a taxon to

the correct category, the occurrence or potentiality of interbreeding is usually only inferred. This, as Simpson (1961) has stressed, poses in most cases only a pseudo problem. Whether a given taxon deserves to be placed in the category species is a matter of the total available evidence.

The evidence that the definition is met in a given case with a sufficient degree of probability is a different matter [from the validity of the concept]. The evidence is usually morphological, but to conclude that one therefore is using or should use a morphological concept of the category (not taxon) species is either a confusion in thought or an unjustified relapse into typology. The evidence is to be judged in the light of known consequences of the genetical situation stated in the definition [of the category] (Simpson 1961:150).

Taxonomy is not alone in encountering difficulties when trying to assign concrete phenomena to categories. Most of the universally accepted concepts of our daily life encounter similar difficulties. The transition in category from subspecies to species is paralleled by the transitions from child to adult, from spring to summer, from day to night. Do we abandon these categories because there are borderline cases and transitions? Do we abandon the concept tree because there are dwarf willows, giant cactuses, and strangler figs? Such conflicts are encountered whenever one is confronted with the task of assigning phenomena to categories.

There are several classes of difficulties one may encounter when trying to apply this yardstick to concrete situations. These have recently been discussed by Mayr (1957b) and Simpson (1961), and for plants by Grant (1957). Such difficulties are caused by lack of information, by evolutionary intermediacy (speciation incomplete), or by genuine inapplicability of the concept (owing to asexuality, that is, uniparental reproduction).

Lack of Information

The Ranking of Variant Individuals. Whether certain morphologically rather distinct individuals belong to the same species or not is a routine problem of taxonomy. The types of variation that are particularly bothersome have been discussed by Mayr, Linsley, and Usinger (1953), who also give hints on how to resolve some of the difficulties. It is important to emphasize the difficulties, caused by sexual dimorphism, age differences, genetic polymorphism, and nongenetic habit differences, which face the student of insects, of parasites, and indeed of any group of living animals, because some paleontologists seem to believe that it is only

in work with fossils that one has to cope with the difficulty of having to draw inferences from morphological types.

No one will deny that the application of the biological species concept to fossil specimens is a difficult task. Yet, in principle, it does not differ from the task of the neontologist who only rarely can study natural populations but is usually forced to classify preserved specimens. The task of the paleontologist is clarified if he remembers that fossils are the remains of formerly living organisms that, when they were alive, were members of genetically defined populations exactly as the species living today are. Morphological criteria are used by the paleontologist as inferences on the natural populations that left the fossil remains. There is no justification for abandoning the biological approach merely because it is sometimes difficult to decide whether or not several morphological types in a sample are conspecific. No one makes the absurd demand that the paleontologist test the reproductive isolation of the species he recognizes. Yet by proper consideration of all the available morphological, ecological, stratigraphic, and distributional evidence it can usually be inferred with high probability whether certain specimens when living were or were not members of the same population. The problems in the application of the species concept to fossils have been discussed by Simpson (1951b, 1961) and Imbrie (1957), and by several contributors to a symposium on the species concept in paleontology (Sylvester-Bradley 1956).

The Ranking of Populations. The criterion of species status, "sympatric coexistence without interbreeding," raises practical problems also where two populations occur in contiguous geographic areas but in very different habitats. Where the evergreen rain forest of central Africa comes in contact with open-country vegetation, one may find the forest drongo *Diorurus ludwigii* within 50 meters of the very similar savanna drongo *D. adsimilis*, but not on the same tree. Indeed they never interbreed. The same is true of other closely related species pairs wherever habitats meet along a sharp border. Even though such species replace each other spatially they must nevertheless be considered sympatric. The potential mates are within cruising range of each other during the breeding season, and could freely interbreed if they were not kept apart by specific isolating mechanisms. The terms "sympatric" or "coexistence" in species definitions must be conceived broadly, to include populations the individuals of which are within cruising range of each other during the breeding season, even though the habitats in which they occur do not overlap in space (Cain 1953).

Incompleteness of Speciation

Evolution is a gradual process and, in general, so is the multiplication of species (except by polyploidy). As a consequence one finds many populations in nature that have progressed only part of the way toward species status. They may have acquired some of the attributes of distinct species and lack others. One or another of the three most characteristic properties of species—reproductive isolation, ecological difference, and morphological distinguishability—is in such cases only incompletely developed. The application of the species concept to such incompletely speciated populations raises considerable difficulties. The various situations usually encountered can be classified under six headings.

(1) *Evolutionary continuity in space and time.* Species that are widespread in space or time may have terminal populations that behave toward each other like distinct species even though they are connected by an unbroken chain of interbreeding populations. Cases of reproductive isolation among geographically distant populations of a single species are discussed in Chapter 16. For instance, when Leopard Frogs (*Rana pipiens*) from the northern United States are crossed with frogs from southern Florida or from Texas most of the embryos die during development (Moore 1949).

Intermediacy of populations between successive species would be the normal situation in paleontology if all populations had left a fossil record. Actually the breaks in the fossil record are so frequent that it has been possible in only a few cases to piece together unbroken lineages connecting good species. The evolution from *Micraster leskei* through *M. cortestudinarium* to *M. coranguinum* (Fig. 2-1) is one such case (Kermack 1954; see also Nichols 1959). In other cases, cited in the literature, the differences in the lineages are so slight that neontologists would be inclined to consider the consecutive forms merely subspecies of a single polytypic species. Even though the number of cases causing real difficulties to the taxonomist is very small, it cannot be denied that an objective delimitation of species in a multidimensional system is an impossibility.

(2) *Acquisition of reproductive isolation without equivalent morphological change.* This group of cases raises a difficulty more practical than fundamental. When the reconstruction of the genotype in an isolated population has resulted in the acquisition of reproductive isolation, such a population must be considered a biological species, regardless of how

little it may have changed morphologically. Such sibling species are discussed in Chapter 3.

(3) *Morphological differentiation without acquisition of reproductive isolation.* The acquisition of isolating mechanisms in isolated populations

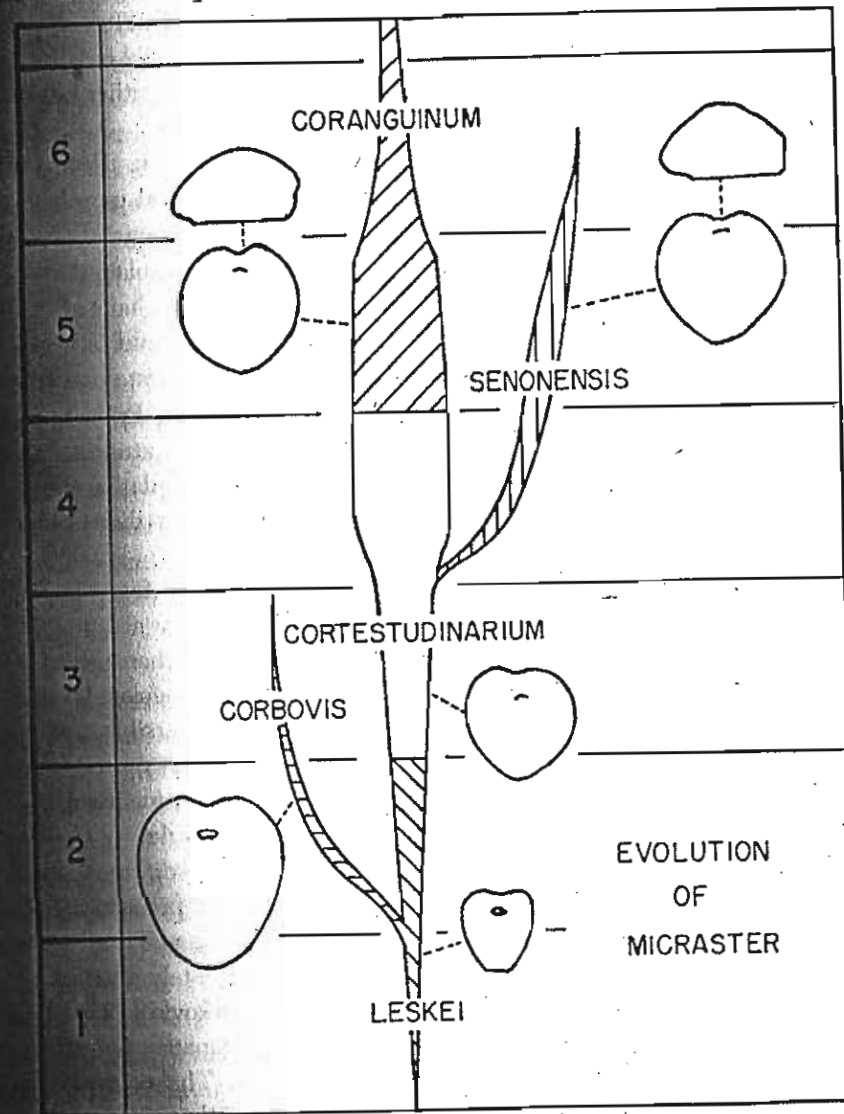


Fig. 2-1. Gradual speciation in time. The echinoid genus *Micraster* changes in the Cretaceous of southern England through six successive geological levels from *M. leskei* through *M. cortestudinarium* to *M. coranguinum*. (From Imbrie 1957.)

sometimes lags far behind morphological divergence (Grant 1957, Mayr 1957a). Such populations will be as different morphologically as good species and yet interbreed indiscriminately where they come in contact. The West Indian snail genus *Cerion* illustrates this situation particularly well. Whenever reproductive isolation and morphological differentiation do not coincide, the decision as to species status must be based on a broad evaluation of the particular case. The solution is generally a rather unsatisfactory compromise.

(4) *Reproductive isolation based on habitat isolation.* Numerous cases have been described in the literature in which natural populations acted toward each other like good species (in areas of contact) as long as their habitats were undisturbed. Yet the reproductive isolation broke down as soon as the characteristics of these habitats were changed, usually by the interference of man. The toads *Bufo americanus* and *B. fowleri* in North America (Blair 1941), and the flycatchers *Terpsiphone rufiventer* and *T. viridis* (Chapin 1948) are well-known examples. Prior to the habitat disturbance no one would have questioned the status of these species, but afterward they behaved like conspecific populations. Such cases of secondary breakdown of isolation will be further discussed in Chapter 6.

(5) *The incompleteness of isolating mechanisms.* Very few isolating mechanisms are all-or-none devices (see Chapter 5). They are built up step by step (except in polyploidy) and most isolating mechanisms of an incipient species will be imperfect and incomplete. Species level is reached when the process of speciation has become irreversible, even if some of the (component) isolating mechanisms have not yet reached perfection (see Chapter 17). To determine whether or not an incipient species has reached the point of irreversibility is often impossible.

(6) *Attainment of different levels of speciation in different local populations.* The perfecting of isolating mechanisms may proceed at different rates in different populations of a polytypic species. Two widely overlapping species may, as a consequence, be completely distinct at certain localities but may freely hybridize at others. Lorković (1953) has described such cases in butterflies. Many cases of sympatric hybridization discussed in Chapter 6 fit this characterization. The compromise solution that the practicing taxonomist often adopts, other things being equal, is to compare the sizes of the areas of undisturbed sympatry and of hybridization. Whichever is the larger determines species status.

The species is a population separated from others by a discontinuity,

but not every discontinuity entitles the isolated population to species rank. If we designate as an *isolate* any more or less isolated population or array of populations, we can distinguish in sexually reproducing organisms between geographical, ecological, and reproductive isolates, of which only the last are species. The unspoken assumption made by certain authors, that the three kinds of isolates coincide, is not supported by the known facts and has led to unwarranted conclusions regarding the pathways of speciation.

The six types of phenomena described in the preceding paragraphs are consequences of the gradual nature of the ordinary process of speciation. Determination of species status of a given population is difficult or impossible in many of these cases.

The Difficulties Posed by Asexuality

The criterion of interbreeding among natural populations, the ultimate test of conspecificity in the higher animals, is unavailable in uniparentally reproducing organisms. It is evident that the absence of this criterion provides the most formidable and most fundamental obstacle to the application of the biological species concept. What should the evolutionist consider the "unit of evolution" in such organisms?

Asexuality in existing organisms is almost certainly a secondary phenomenon (Dougherty 1955; Stebbins 1960). All existing asexual organisms seem to be derived from sexual forms. Asexually reproducing lines have, sooner or later, one of three fates: they are lost by extinction, or they mutate, or they exchange genes with some other line by some process of recombination (Pontecorvo 1958). Indeed clandestine sexuality appears to be rather common among so-called asexual organisms. The expression "uniparental reproduction" is being used increasingly, instead of "asexual reproduction," to overcome this and other difficulties. Many biologists, for instance, are reluctant to refer to parthenogenesis as asexual reproduction.

It is too early for a definitive proposal concerning the application of the species concept to asexually or uniparentally reproducing organisms. If mutation and survival were random among the descendants of an asexual individual, one would expect a complete morphological (and genetic) continuum. Yet discontinuities have been found in most carefully studied groups of asexual organisms and this has made taxonomic subdivision possible. For this phenomenon I have advanced the explanation (Mayr 1957b) "that the existing types are the survivors among a great number of produced forms, that the surviving types are clustered around

species or intrapopulation variants (excepting the relatively rare instances of secondary deposits).

It was not possible to state the problem of the multiplication of species with precision until the biological species concept had been developed. Only after the naturalists had insisted on the sharp definition of local species was there a problem of the bridging of the gap between species. And only then did the problem arise whether or not the species is a unit of evolution, and what sort of unit (Simpson 1951b; Thoday 1951).

It should be evident from these comments that the species problem is of great importance in evolutionary biology and that the growing agreement on the concept of the biological species has resulted in a uniformity of standards and a precision that have been beneficial for practical as well as theoretical reasons.

3 - Morphological Species Characters and Sibling Species

The morphological species concept, which dominated animal taxonomy during the 19th and early 20th centuries, is steadily losing ground. Yet much contemporary thinking about species still rests on it. In view of the historical importance of this concept and the correctness of some of its elements, it deserves more detailed discussion than was possible in the over-all treatment of species concepts in the preceding chapter.

The argument of proponents of the morphological species concept runs about as follows: "Natural populations considered by general consent to be species are morphologically distinct. Morphological distinctness is thus the decisive criterion of species rank. Consequently, any natural population that is morphologically distinct must be recognized as a separate species." The conclusion is fallacious, even though based on the correct observation of a general correlation between reproductive isolation and morphological difference. It is fallacious because it overlooks the strictly secondary role of morphological differences. The primary criterion of species rank of a natural population is reproductive isolation. The degree of morphological difference displayed by a natural population is a by-product of the genetic discontinuity resulting from reproductive isolation. This consideration necessitates a reevaluation of morphological characters as species criteria. Since sympatry of natural populations indicates reproductive isolation, we can use the amount of morphological difference among sympatric species as a yardstick in the evaluation of the taxonomic status of related isolated populations. The application of the biological species concept is thus facilitated by the proper evaluation of morphological differences.