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The Rates of Evolutionary Processes

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Introduction. It has often been claimed that evolution progresses by two essentially different types of changes, namely macro- and micro-evolutionary changes; or expressed differently, that major systematic categories like orders and phyla "pass through an orderly series of changes" or "programme evolution," while groups of species "evolve progressively along a certain line of change or 'trend' " (Dobzhansky 1941, Waddington 1939). Paleontology is supposedly responsible for the examples of programme evolution, while genetics offers the available data concerning trend evolution. Needless to say, the geneticist confines his attention to the micro-evolutionary changes which he can attack experimentally. But is the practice of contrasting these types of evolutionary changes necessary or justifiable on the basis of available information?

Paleontologists and geophysicists have taught us to think in immense spans of time, long enough to embrace the vast panorama of organic evolution, and excusably may find it difficult to accept the findings of modern genetics—so far our only experimental approach—based on such incomparably shorter periods of time and limited numbers of generations. Despite their great youth, genetics and the accompanying study of speciation furnish an overwhelming body of pertinent information, which is now fortunately replacing most of the unproductive controversy concerning evolution so widespread only yesterday. It is no longer impossible to visualize evolution in terms of processes known today and within the time limits available for it. This does not imply that all problems have suddenly been answered but certainly that fewer remain to be solved.

The species concept, past and present. Taxonomists are often accused of defining species in a subjective manner and without recourse to a generally applicable species concept. Disregarding the difficulties resulting from abuses of the older species concept, biologists have now come to recognize the fact that species of identical hierarchical value do not exist in the numerous groups of the animal and plant kingdoms. Naturally this realization leads to the practice of distinguishing different kinds of species, not to confuse the taxonomist but rather to interpret correctly the great diversity of forms encountered in nature. If this is so, more than one mode of the "origin of species" must be sought, tested experimentally and recognized as effective evolutionary mechanisms in speciation. These modes are likely to differ in many respects and are bound to progress at different rates. As these processes are analyzed and established on general grounds, the picture of evolution is likely to change. Evolution will not be simplified or reduced to a simple formula.

Rather the evolutionary processes will be removed from speculation and placed in proper perspective.

It can easily be shown that the term species is applied to groups of very different genetical status. Several ways of distinguishing kinds of species can be followed. Thus Darlington (fide Waddington, 1939) lists six types of species variously affected by evolutionary mechanisms and differing in degree of hybridity. Elsewhere (Darlington, 1940) he speaks of genetic systems which make up the various kinds of species. "There are many kinds of species and many kinds of discontinuities between species; there are also many kinds of hybridity and isolation. These differences depend on the different kinds of genetic systems at work in plants and animals; but they cannot be arranged in a simple table because they occur at different levels of integration."

Significantly Sewall Wright (1940) points out that "it has become necessary to shift the emphasis in the definition of species from the essentially physiological concept, kind, to the ecological one, the interbreeding population."

Dobzhansky's (1941) definition, admittedly applicable only to sexual and cross-fertilizing forms, was proposed to "define species as that stage of evolutionary process, 'at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding.'" The emphasis is here clearly placed on the dynamic nature of the species concept, or in his words "the species is a stage in a process, not a static unit." This definition cannot serve as a yardstick for the practical taxonomist. Mayr (1942) considers it "an excellent description of the process of speciation, but not a species definition. A species is not a stage of a process, but the result of a process."

Mayr's (1942) short definition reads as follows: "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Although it may cover most cases, Mayr believes that it is "doubtful whether this species definition applies equally well to plants" in view of the many differences between plants and animals listed by him. Turrill (1942) is of the same opinion, because many good species of plants are not as definitely separated genetically and cytogenetically as required by these definitions.

In his analysis of the species concept Mayr (l.c.) distinguishes *sympatric* species with overlapping or coinciding areas from *allopatric* species with geographically separate areas. The gaps between sympatric species are absolute, whereas those of allopatric species are frequently gradual and relative. These two kinds of species are contemporary or *synchronic*. Their recognition may be difficult at times but never as complicated as that of *allochronic* species belonging to different time levels.

The latest botanical counterpart to the practice of distinguishing these types of species based essentially on ecological criteria is *biosystematy*, which is characterized by Camp and Gilly (1943) as an expanded phase of classical taxonomy employing new techniques and a new outlook, primarily genetical criteria. According to these authors: "biosystematy seeks (1) to delimit the natural biotic units and (2) to apply to these units a system of nomenclature adequate to the task of conveying precise information regarding their defined limits, relationships, variability, and dynamic structure." Biosystematy requires genetical analyses in addition to morphological and biogeographical studies. This practice will lead to different results from those based on conventional taxonomic procedure, or, as Turrill (1942) puts it: "the genetical species or other group does not necessarily coincide with the taxonomic." Hogben (1940) states it in another way: "the word 'species' has no single meaning. Hence there is no one problem of the origin of species. There are many problems of the origins of species."

Using a genetical approach, Camp and Gilly employ two primary criteria in their work: "(1) the appearance of species-populations in the field and (2) the genetic systems operative within these populations."

On this basis they recognize two major kinds of species: a) species in which apomixis is not present, and b) species in which apomixis is present. The species without apomixis are of ten kinds: homogeneon, phenon, parageneon, dysploidion, euploidion, alloploidion, micton, rheogameon, cleistogameon, and heterogameon. The species exhibiting apomixis, on the other hand, belong to one of two kinds, apogameon and agameon.

The subspecific categories recognized in biosystematy are: phenogen, subspecies, forma, and stropha.

Throughout their study a sincere effort is made to recognize the attainments of genetics and the accomplishments of taxonomy in order to find a common basis for future work and mutual understanding.

Despite certain differences of definition and delimitation, all of these concepts agree in their dynamic approach, in their attack on the problem via speciation or the various modes of speciation. As ecology profited once by the introduction of the dynamic viewpoint, taxonomy may benefit equally from this almost revolutionary change in its outlook, orientation, and methodology.

Modes of speciation. It is impossible to attempt here a complete enumeration of all known and probable processes of speciation. This has never been done and seems, for the time being, somewhat premature, because experimental work is still too young and in a state of flux. Dobzhansky (1941) lists the following patterns of evolution: "gene mutation, chromosome changes, restriction of the population size, natural selection, and development of the isolating mechanisms are the known common denominators of many, if not all, evolutionary histories. Different phylogenetic lines vary, however, in that one or the other of these evolutionary agents may become limiting at different stages of the process. Polyploidy, self-fertilization, apogamy, and asexual reproduction create very special conditions, . . ." sometimes very sudden or "cataclysmic" changes.

"From the viewpoint of a zoologist" Mayr (1942) lists the following modes of speciation:

A) geographic, with its five stages;
B) semigeographic (origin of species gaps in zones of intergradation); taneous or gradual.
C) nongeographic (sympatric speciation), which may be either instantaneous or gradual.

Geographic speciation is by far the most common, whereas little evidence supports the nongeographic modes.

Geographic speciation includes two processes: "the development of diversity and the establishment of discontinuities between the diverging forms." It is not an abrupt but gradual and continuous process, because all imaginable levels of speciation are found in nature. A vast amount of pertinent information is supplied by the author to illustrate this most effective mode of speciation.

Mayr also emphasizes certain differences between plants and animals, which are reflected in their respective modes of speciation. Actually so far no similar and equally exhaustive treatise of speciation in plants has come to the speaker's attention, irrespective of many excellent monographic studies.

Finally, Rensch (1939) discusses first speciation and then the origin of higher categories. He explains even transformations of the body as a whole by undirected mutation and selection, and claims that the evolutionary phenomena recognized in paleontology can be understood without the assumption of any inner unfolding impulse. Although irreversibility is known, it has theoretically been disproved by reverse mutations. The actual irreversibility is said to be due to the complex conditions of life, which render a return to identical situations for mutation and selection practically impossible. Orthogenetic series are explained largely through continued selection of larger variants and resulting changes in proportion due to heterogonic growth of single organs, or orthoselection. "Explosive development of new forms and later diminution of species formation should not be ascribed to varying rates of mutation, since mutation is steady, but to increasing occupation of the available biotopes with competing forms. Ageing and extinction of evolutionary series is to be explained by an increased restriction to narrow habitats and specialization due to selection, by selectively caused increase in size, and by the consequent development of monstrous organs." "Even the perfection and the higher development of organisms is due to no unknown law of development, but merely to the fulfillment of the available possibilities, including increase in complication and physiological amelioration and simplification."

Estimated and known rates of evolutionary processes. Now that the principal modes of the origin of higher and lower systematic categories are established, there remains the question of determining what is known regarding the rates of the processes involved introducing them. As will be clear from the following discussion, our knowledge in this respect is quite scanty and unequal.

Ritchie (1941) emphasizes strongly the slowness of evolution. To illustrate the point, he gives a new estimate of the evolution of the modern horse (*Equus*) from its precursors during Eocene times. He states that "the whole gamut of changes which modified the four toed forelimb of *Eohippus* into the single toe of *Equus*, from lower Eocene to Upper Pliocene, occupied about 57 million years. It took some 17 million years to reduce the four effective digits of *Eohippus* (Lower Eocene) to three in *Mesohippus* (Lower Oligocene), and 22 million more to raise the two lateral digits clear of the ground (in *Merychippus*, Middle Miocene). The penultimate stage of reducing the ineffective side digits to vestigial splints (in *Plesippus*, Upper Pliocene) occupied some 16 million years, and the gradual reduction of these vestiges to the condition seen in the modern horse (*Equus*, Upper Pliocene) probably took about another two million more."

These estimates concerning the evolution of various genera leading up to the modern horse should certainly cover speciation within these groups. Other examples of slow evolution could probably be provided but perhaps with less definite estimates of the periods of time involved.

Evolution obviously progresses more rapidly in other cases, especially in organisms less widely distributed. After reviewing the geological and entomological evidence Zimmerman (1942) for instance concluded: "There appear to be no indigenous elements in the eastern oceanic insect faunas that demand as great or greater age for their developments as for such creatures as the horse and elephant, or, for that matter, man, who, it is believed, developed from Miocene primates derived from the Eocene lemuroides of North America." Ernst Mayr (in litt.) concurs with this thesis.

The post-glacial development of many animals and plants has been realized for a long time despite the varying time limits set for these processes by different authors. Ritchie sets a maximum of 20,000 years for the evolution of seven different and distinctive species of mammals endemic in the outer islands of Scotland.

An excellent botanical example is given by Marie-Victorin (1938). The freshwater tidal shore of the St. Lawrence River is characterized by the presence of many estuarine endemics of post-glacial origin. This author believes that this area represents the "richest Oenothera territory in Quebec and possibly in the whole of northeastern America." The factors claimed to be responsible for this accelerated development of endemic species[1] in post-pleistocene times are the double daily cycle of emersion and immersion, diminished competition, the operation of efficient devices for seed dispersal, etc.

Man has permanently influenced and determined the course of evolution followed by many cultivated plants and domesticated animals. Three examples should illustrate this sufficiently. On the basis of archaeological and botanical evidence Mangelsdorf and Reeves (1939) concluded that teosinte (*Euchlaena mexicana*) originated in Guatemala between 600 A.D. and 900 A.D. by the hybridization of Zea and Tripsacum.

The other two cases involved even shorter spans of time. Marie-Victorin (1938) has shown that "under favorable circumstances, a period of two or three hundred years is sufficient to produce, in some genera

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[1] Regarded as geographical races by Cleland (1944).

at least, by mutation or otherwise, a marvelous outburst of species, or at any rate, of recognizable forms." This conclusion is based on extensive studies of Crataegus and Oenothera populations[2] in the immediate neighborhood of the older Canadian cities like Quebec, Montreal, Toronto, and old Hudson Bay forts. Apparently deforestation and settlement during the short colonial period resulted in considerable migration and multiplication of recognizable forms.

The last case of this sort is the domestication of the European rabbit, *Oryctolagus cuniculus*, which among mammals is second only to the dog in variability. The facts (Nachtsheim 1936) are as follows: the development of at least fifty well marked breeds began with the sixteenth century; mutants can be traced historically and concern characters other than coat color, etc.; five mutants of coat color were known by the end of the sixteenth century, seven around 1700, three more appeared by 1850, three additional ones by 1900, and six between 1900 and 1935.

A normal minimum for distinct subspeciation of 5,000 years was determined by Moreau (fide Huxley 1942) on the ground that the Nile Delta has in part become land within the last 5,000 years and lacks endemic passerine subspecies, and has only a limited number of others. Additional cases of this sort are given by Huxley (1942) and Mayr (1942).

Only a few years seem to have been required for the separation of two distinct local populations of a moth, *Oporabia autumnata*, known to inhabit two ecologically distinct woodlands. These populations are said to differ in size, color, and certain physiological characters (fide Huxley 1942).

After determining by extensive collections the number of species of the genus Cynips known to occur in Mexico and Southwest, Kinsey (1936) estimated the rather low number of mutations needed to account for their existence. The group originated in the Miocene, some ten or twenty million years ago. "One mutation in 20,000 years would, if properly timed and placed, account for the 100 species of *Cynips* known in this area. The laboratory rate of plus mutations even in *Drosophila* would, if extended over the thousands of square miles and tens of millions of years involved, be ample to account for the condition we find in nature."

On paleobotanical grounds Zimmermann (1930) attempted similar estimates. A low estimate places the boundary between the Miocene and Pliocene some two million years ago. The fossil flora of Oeningen is well known and mostly made up of woody species fairly close to living species. If one assumes that it requires on an average twenty years for these woody species to produce flowers and set fruit, one could translate this time into 100,000 generations. If only one viable mutation occurred per every 1,000 generations, one hundred mutations would appear during the available time. Two plants differing in 100 genes should at least belong to two different species. Surely within the span of 1,000 generations one mutation of selective value could be expected to appear. Speciation ("phylogenetischer Artschritt") has, in other words, two million years

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[2] See footnote 1.

at its disposal, an assumption which is easily compatible with present genetical knowledge. By the same token, herbaceous plants require correspondingly less time, e.g., two to three years after the seeds are sown, fruits are likely to be produced. Since the present angiosperm families appeared largely during the Cretaceous, at least thirty million years ago, it is possible to apply 15 times the time limit set for speciation. On that basis these plants should be far enough differentiated barely to be included in the same family. This means, roughly speaking, that thirty million years would permit the development of different families. Later Zimmermann (1938) reduced his estimate for speciation to 500,000 years or the appearance of 1,000 visible mutations, assuming that one large mutation would appear every 500 years or per 100 generations. Intraspecific evolution would, of course, require correspondingly shorter spans of time.

The foregoing discussion is based on estimates derived from various sources and by different ways of calculation. A review of the highly significant mathematical studies concerning this problem by R. A. Fisher (1930), Sewall Wright and others cannot be attempted in this paper.

In recent years the problem has been approached experimentally and summarized by Timoféeff-Ressovsky (1940), who concluded "that the total mutation rates per generation are rather low and in the order of magnitude of 1-10 per cent. Variation in the factors of the normal environment of the organisms have little or no influence upon the mutability. Different single mutation-steps have different rates of change, lying in the order of magnitude of 0.001-0.00001 per cent."[3]

Although considerable information is on hand regarding induced mutations and the frequency of their appearance, less is apparently known concerning spontaneous mutation rates and the causes affecting them (Plough 1941). Nevertheless Plough believes that increases in mutation frequency can speed up "the automatic processes of natural evolution," although they can not change their direction. While studying unstable genes, Demerec (1941) found genes which affect the mutability of other genes and which, in *Drosophila melanogaster*, seem to increase the mutability of the whole gene complex. Neel (1942), who recently found a case of high mutation rate, states that at present at least two factors are known which have a definite effect on mutation rate in Drosophila. Other cases have, however, been reported since. In Neel's opinion, future studies may disclose that much of the mutation found in nature may occur in "such spurts, resulting in the formation of localized populations of relatively high genetic heterogeneity." If this should be so, "a mechanism which may rank in importance with geographical isolation in the process of species differentiation, and one which, in any

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[3] According to Timoféeff-Ressovsky (1940) rate of mutation means "the percentage of gametes or haploid genomes containing a mutation. In this case, by 'total mutation rate' is meant the percentage of gametes (of one generation) containing any kind of mutation." Other mutation rates can of course be determined for special types of mutations etc. Elaborate and variously effective methods have been worked out. Recently Stevens (1942) has compared various methods regarding their statistical accuracy.

event, offers a valuable supplement to isolation" would then become known.

Two other cases of genes increasing mutation rates are now reported. Tiniakov (fide Huxley 1942) detected in wild drosophilas "a gene increasing mutation-rate at least 40 times, and possibly to a level higher than that induced by X-rays." According to Mampell (1943) a case of abnormally high mutation rate in *Drosophila pseudoöbscura*, race B, is due to the presence and action of a "mutator gene." The latter increases the normal spontaneous rate about 34 times in heterozygous condition and about 70 times when homozygous. The increase in mutation rate is in this case linear with the dosage of the mutator gene.

Rhoades (1941) has found "a situation in maize where an extremely stable gene is made highly unstable when subjected to a specific genetic environment". Other genes in maize are known to vary greatly in their spontaneous mutation rates. Obviously more information on mutation rates in other plants would be very desirable.

Hybridization apparently increases the mutation rate in some cases. Sturtevant (1939) studied backcrosses from hybrids between the two races (A and B) of *Drosophila pseudoöbscura* and recorded about 9 per cent of lethals and one-half of 1 per cent sex-linked visibles. He also believes that "natural selection must operate to keep the general mutation rate of a species at a minimum." Shapiro (1939) reached essentially the same conclusion.

By comparison Berg (1941-1942) claims that "hybridization disturbs the mechanisms assuring high mutability that have been created during the course of evolution." Furthermore Berg contends that mutation rates are not reduced during evolution and believes that they may even increase under certain conditions. The main factor of increase is "selection for adaptability, which proceeds against a background of struggle among separate groups." Finally Berg showed that mutation rate decreases as isolation increases near the boundary areas of the species distribution. He also reached this important conclusion: "the stability of the variation of the mutation rate under identical conditions, as well as the similarity of the rate under varying conditions, should be taken to mean that mutability is an adaptive character of the species."

The shortest possible time for changes in gene arrangements found to date has recently been reported by Dobzhansky (1943) for certain populations of *Drosophila pseudoöbscura.* In some localities the relative frequencies of the gene arrangements change in these populations from month to month and show thus a cyclic and seasonal cycle reflecting apparently the annual climatic cycle. While populations of a certain locality are apparently alike at any one time, they may readily be permanently different if occurring 10 or 15 miles apart. These changes are ascribed to "natural selection favoring the carriers of different gene arrangements at different seasons of the year". Although different sampling might alter the data obtained, this case illustrates an instance of rapid transformation of populations.

Little, if anything, has so far been said regarding lower organisms and their behavior in this respect. After comparing the rates at which variants appear in viruses, bacteria, and Drosophila, Gowan (1941) concluded that they are of the same order of magnitude and nature (mutations). (See also Luria and Delbrück (1943) for additional data on mutation rates in bacteria). An exceedingly high mutation rate, 38 to 87 per cent with a rise of temperature from 10° to 35°, was recorded by Sonneborn (1942) for *Paramecium aurelia*, variety 1. This rate seems to compare favorably with Mampell's values.

A very different case is that of an experimentally produced race (chromosome doubling in haploid gametophyte, $n = 10$) of *Bryum caespiticium* (normally dioicous) studied by Wettstein (1937). This race, *B. caespiticium bivalens*, is an autopolyploid (diploid, $n = 20$) and a gigas type of high sterility. It undergoes a gradual transformation of its entire genetical constitution which is equally shown in the original plant, its vegetative offspring and the offspring raised from spores. In the course of the experiment one individual of F_1 generation was raised from a spore and showed increased production of sporogones, while it reduced its cell size to that of normal haploid plants within eleven years without change in the chromosome number. This new plant, called *Bryum Corrensii*, is completely fertile and produces normal spores. But more significant than this fact is that Wettstein succeeded in finding a wild type (related species with $n = 20$ and monoicous gametophyte) which is also polyploid and fertile and which, in all probability, arose in the same manner as *B. Corrensii*. This is at least one case demonstrating the importance of polyploidy in the origin of some new species and the time required for it (see also Dobzhansky 1941, p. 231, and Fagerlind 1941).

Judging by these estimated and known values of mutation rates, we may agree with Huxley who states that "in general it seems that from the standpoint of mathematical theory, existing mutation-rates will in moderately abundant species suffice, with the aid of selection, for the distinctly slow processes of evolutionary change to be observed in fossils".

It must be pointed out in this connection that mutation rates are not the only effective factors determining the speed of evolutionary processes. Highly significant in this respect are also various ecological factors such as population size, dispersal, natural selection and others. The intricate operation and interaction of these have been elaborately described and substantiated by Dobzhansky (1941) and Mayr (1942), whereas some mathematical possibilities have been explored by S. Wright (1940).

Higher Systematic Categories and Mutations. It is by now a time-worn accusation that mutations are too small and injurious to be of sufficient magnitude to account for superspecific evolutionary processes, irrespective of their cumulative values. I mention only two recent examples, namely Willis' evolution by differentiation and Goldschmidt's systemic mutations (1940). What is the evidence which can be brought to bear on this objection?

Hurst (1933) showed clearly that mutations affecting specific, generic, and family characters immediately become varietal and Mendelian in behavior, or as he puts it, the mutation "loses its high status." He cites the case of the mutant "tricarpel" found by Blakeslee in Datura. This is obviously an exception to the two-celled ovary of the Solanaceae, an important taxonomic character of the family. Zimmermann (1938) described several noteworthy mutations in *Anemone Pulsatilla*, an archichlamydeous (dialypetalous) species. Of these one mutant was definitely gymnospermous and died without setting fruit. Another mutant was characterized by the fusion of the petals and the last showed a modified cotyledon leaving the other one functional. The characters involved are typical of the angiosperms, of the Archichlamydeae or better the Dialypetaleae, and of the Dicotyledoneae. As far as the appearance of beneficial mutations is concerned, the known cases are definitely on the increase in such carefully studied organisms as Drosophila and Ephestia as well as others. Muller (1939) points out that the occurrence of reverse mutations is a further argument for the refutation of this objection.

According to Hurst (1933) varietal, specific, generic, and family characters do not differ in kind but merely in the degree of stability and mutability in nature. On this basis—and there is ample evidence for it—the characters distinguishing the present higher groups appeared during geological history at various time levels and, in Hurst's opinion, as mutants. Since he regards the species as composed of many homozygous dominant specific characters, many mutants are required to form a new species. These mutants undergo selection while the climate may pass through extreme changes in different geological periods. Ultimately the new species will have to attain some degree of sterility.

Genetics and Paleontology. Several instances of the apparent compatibility of paleontological and genetical knowledge have been presented thus far. Two additional cases may serve to illustrate the successful transfer of genetical concepts into paleontological theory and interpretation. Axelrod (1941) in the course of paleobotanical studies of Tertiary floras found it useful to apply the concept of ecospecies to the fossil equivalents of modern endemic trees and shrubs, which occupied habitats widely differing from those occupied by their nearest descendants. The modern endemics survived in habitats different from those occupied by their related fossil forms as a result of the elimination of biotypes during the late Cenozoic. Mason (1942) suggests a similar interpretation for the extremely localized populations (or species) of Ceanothus found in certain parts of northern California.

The other case is based on the demonstration by Wehrli (fide Weigelt 1942) of geographical races among the fossil horses of Europe. So far the European representatives of Anchitherium have been classified as *A. aurelianense* which lived in central and western Europe for about two to three million years. These forms range through the whole Miocene and Lower Pliocene. Wehrli was able to work out a good phylogenetic series based on tooth characters. The significant thing is that evolution along this line progressed more rapidly in France than in southern Germany, e.g., the French race gets larger more rapidly than the dwarf type of southern Germany and Switzerland. Contrary to the views held by Stirton (1940) et al., Wehrli claims that American fossil horses of Kalobatippus and Hypohippus are indistinguishable from the European forms of *A. aurelianense*. All told three stocks were found and recognized, namely small, normal, and large, but were retained in *A. aurelianense*. The American species *A. matthewi*, more appropriately designated as *Megahippus matthewi*, apparently branched off from the large stock and attained giant size which was never reached in Europe. Here is a fine example of the presence of parallel lines of evolution pointing in the same direction but followed through at different rates. Most likely similar cases can be found in the literature or may become known as certain localities are worked intensively.

Finally we may turn our attention briefly to another frequently voiced opinion which is held by those who are apparently unwilling to interpret the fossil record correctly. According to these authors (Bertalanffy and particularly Frieling 1940) the evolution of the major groups has come to an end and only genera are developed anew or often only species (Bertalanffy 1937). Frieling limits evolution to intraspecific processes which are the only ones possible at the present, because speciation stopped with the advent of man. Such claims are obviously ill founded and outside the domain of biological science.

As should be evident from what was said regarding the time factor, evolution progresses in different groups at different rates. But it is difficult to see, why it should have come to an end at the present time. In fact, Ritchie paints a rather gloomy picture of the future of mankind as we try to look ahead as far as we can look back into man's past. Here, at least, he seems to have the evidence on his side.

The foregoing discussion of the kinds of species recognized today, of the various modes of origin known and of the speeds with which they progress, clearly shows the great variation of the existing mechanisms of evolution "even from genus to genus, so that it is becoming increasingly difficult to formulate general 'laws' of evolution, and the universal applicability of such 'laws' as have been derived from paleontology and morphology is becoming more and more doubtful" (White 1937).

But in all this flux limits are set preventing further changes. In this sense evolution is a process of "sequential stabilization of genetic patterns," as Ferris (1943) puts it, involving "loss and limiting of capacities as well as the attainment of them."

Summary. The term species is applied to groups of very different ecological and genetical status. As a result speciation must progress by various modes and definitely at different rates. Examples of estimated and known rates of evolutionary processes affecting both higher and lower systematic categories are presented, including cases of slow (modern horse) as well as rapid evolution (by mutator genes, ploidy, etc.). The compatibility of genetical and paleontological knowledge is also demonstrated. Although the occurrence of unstable genes, mutation rates, hybridization, ploidy, etc., are admittedly not the only effective evolutionary factors, they represent some of the most important agencies

and indicators of evolutionary changes. The rates of evolutionary processes differ so greatly that they can not be expressed in simple mathematical terms.

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[4] For additional examples the reader is referred to Chapter 25, Rate of Evolution and Speciation (pp. 383-396) of *Foundations of Plant Geography,* by Stanley A. Cain, Harper & Brothers, New York, 1944, and the *Report of Meetings of the Committee on Common Problems of Genetics and Paleontology,* National Research Council, Division of Geology and Geography, Washington, 1943 (15 pp., mimeographed), which came to the writer's attention while the present paper was in press.

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