

## A Theory of Evolution Above the Species Level

(paleontology/paleobiology/speciation)

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**ABSTRACT** Gradual evolutionary change by natural selection operates so slowly within established species that it cannot account for the major features of evolution. Evolutionary change tends to be concentrated within speciation events. The direction of transpecific evolution is determined by the process of species selection, which is analogous to natural selection but acts upon species within higher taxa rather than upon individuals within populations. Species selection operates on variation provided by the largely random process of speciation and favors species that speciate at high rates or survive for long periods and therefore tend to leave many daughter species. Rates of speciation can be estimated for living taxa by means of the equation for exponential increase, and are clearly higher for mammals than for bivalve mollusks.

In reaction to the arguments of macromutationists who opposed Neo-Darwinism, modern evolutionists have forcefully asserted that the process of natural selection is responsible for both microevolution, or evolution within species, and evolution above the species level, which is also known as macroevolution or transpecific evolution (1). It will be shown in the following discussion that the presence of a largely random process (speciation) between the two levels of evolution decouples them, and that large-scale evolution is guided not by natural selection, but by a separate, though analogous, process.

### PHYLETIC GRADUALISM AND THE RECTANGULAR MODEL

Phylogenies have traditionally been characterized as having tree-like patterns. In plots depicting morphologic change on a horizontal scale and time on a vertical scale, continuous phyletic change is typically represented by diagonal branches and twigs. Being based on fragmentary fossil evidence, such plots are interpretive. They represent the concept of evolution that has been called *phyletic gradualism* (2). In reality, gradual phyletic change is recognized for only a few fossil lineages, and in these it is of minor morphologic consequence. Soviet workers (3-5) proposed that we should not expect to find widespread documentation of gradual change in the fossil record. Rather, they alleged, change tends to be concentrated in speciation events, while species evolve rather little after becoming established. These ideas have since been enunciated by American workers (6, 2). They imply that the standard tree of life should be modified to have a more rectangular pattern, with evolution proceeding in a step-wise pattern. This so-called *allopatric model* of evolution (6) represents the geographic concept of speciation propounded by Mayr (7) and others, in which small peripheral populations of estab-

lished species are seen as occasionally becoming separated by geographic barriers to form new species. Most isolates become extinct, but occasionally one succeeds in blossoming into a new species by evolving adaptations to its marginal environment and diverging to a degree that interbreeding with the original population is no longer possible. Mayr has emphasized the stability of the genotype of a typical established species. Most species occupy heterogeneous environments within which selection pressures differ from place to place and oppose each other through gene flow. Furthermore, biochemical systems interact in complex ways. Most genes affect several adaptations and most adaptations are under the influence of several genes. Thus, it is alleged, homeostatic mechanisms oppose wholesale restructuring of the genotype in large, well-established populations. In small, peripheral populations under what might be described as crisis conditions in marginal habitats, such restructuring occasionally takes place. Sympatric speciation, whatever its incidence, can also produce rectangular patterns of phylogeny. Hence, the adjectives *rectangular* and *gradualistic* will be used here to label the alternative models of phylogeny without reference to mode of speciation.

### CRITICAL TESTS

The gradualistic view of phylogeny does not deny geographic or other types of speciation, it simply recognizes no increase in rate of evolution with splitting. The question that must be settled is not whether phyletic change occurs in established species (it must, to some degree), but whether its effect is minor, with most change occurring in speciation events. I do not agree that "the data of paleontology cannot decide which picture is more adequate" (2). Four tests devised to examine this question will be applied in the following discussion. All deal with rates of evolution, for it is the distribution of rates in phylogeny that is really in question. As it turns out, the rectangular model passes each test, and the gradualistic model fails as a dominant pattern of change.

*The Test of Adaptive Radiation.* The first test is whether both models can account for documented episodes of rapid diversification, or adaptive radiation. To evaluate the gradualistic model here we must estimate durations for lineages that change little enough morphologically to be placed within a single species by taxonomic specialists. Looking backward in geologic time, we find that fossil faunas of a given taxon contain fewer and fewer still-living species. Eventually we reach a point on a smooth curve (8) at which living species comprise 50% of fossil faunas. Average species duration will be approximately twice this value. Some species may have become ex-

Abbreviation: My, million years.

tinct by termination of their lineages, while others have suffered what is often called phyletic extinction or pseudoextinction by gradual evolution into new species. Although termination is clearly important, let us assume for the moment that all extinction is phyletic. Then we can obtain *minimum* estimates for average phyletic duration of species of higher taxa. Using a curve for Cenozoic mollusks of Venezuela (8), we find that the 50% extant level is reached about 3.5 million years (My) ago, in the Late Pliocene. This gives an estimate of species duration (D) of about 7 My. Using other considerations and taking into account estimates of earlier workers, Durham (9) arrived at an estimate of 6 My for species durations of marine invertebrates in general. There is no reason to believe that such values should have varied significantly with geologic time. To Durham they posed a problem with respect to the high diversity exhibited by the Echinodermata and other phyla present in the Cambrian. He reasoned, in effect, that many species would have had to be stacked end-to-end for one class of echinoderms to emerge from another and that a long Precambrian interval of echinoderm evolution must have preceded the Cambrian. We now have a wealth of evidence suggesting that the origin and initial diversification of most invertebrate phyla occurred during only a few tens of millions of years (10). The gradualistic model cannot account for such rapid change. Rapid speciation, on the other hand, can easily account for the required rate of diversification.

The same argument holds for the adaptive radiation of the placental Mammalia in the early Cenozoic. The major orders of mammals arose from primitive ancestors during an interval of the Paleocene and earliest Eocene (11) that could not have greatly exceeded 12 My (12). It is true that species durations for mammals are shorter than those for marine invertebrates. The figure is less different, however, than many workers have assumed from the order-of-magnitude disparity found for average durations of genera in the two groups (1, 13). These durations cannot be converted into relative durations of species. An average living genus of mammals contains about three species, whereas an average genus of bivalves contains almost 20, and all species of a genus must die out for the genus to become extinct. The species is the basic unit of extinction, and we must focus upon it directly. The well-documented late Cenozoic record of mammals offers good data for turnover rates, and hence average durations for mammal species. Kurtén compiled data for Pleistocene mammals of Europe that yield average durations for species of about 1 My. Extinction rates were, of course, unusually high in the Pleistocene. Data from Webb (14) yield average durations for North American genera of about 5 My for the Pliocene and 3 My for the Pleistocene, suggesting that average durations for pre-Pleistocene species may have been closer to 2 My. Again, the estimate is a minimum for phyletic duration within on-going lineages because it assumes that no species disappeared by termination. The estimate shows that observed phyletic rates cannot account for the initial Cenozoic divergence of the Mammalia. The time interval of the radiation allows for a succession of only about 5 or 10 species of normal longevity to produce the enormous amount of evolutionary change required for the origin of each of nearly 20 mammalian orders, including the Chiroptera (bats) and Cetacea (whales). It is inconceivable that rates of phyletic change could have been accelerated sufficiently to account for the rate of evolution shown here by the fossil record. Extraordinarily high selection pressures

would have had to be sustained in diverse habitats and upon diverse taxa over a period of about 12 My. What is quite obviously documented, instead, is the rapid occupation by speciation of sets of niches (adaptive zones) that are known to have been vacated shortly before by dinosaurs and other reptilian groups.

*The Test of the Pontian Cockles.* We can directly test rates of gradual change within established lineages against rates produced by speciation by examining the history of a small group of animals known to have undergone large-scale speciation locally, while speciating little in other areas, where it therefore had to change chiefly by phyletic evolution. A natural test of this type is found in the history of the cockles (Cardiacea) during the existence of the low-salinity Pontian "Sea," the predecessor of the modern Caspian. As has also been known to happen in other large, isolated lakes, there occurred widespread speciation of a few taxonomic groups that gained access to the Pontian. During an interval not greatly exceeding 5 My, a new cockle family, the Limnocardidiidae, arose here and developed over 30 new genera representing five subfamilies and including a truly remarkable array of morphologies (15-17). Nearly all limnocardidiids have since become extinct as a result of salinity change. The important point is that all seem to have evolved from the single genus *Cerastoderma*. What happened to this genus elsewhere? It simply persisted with little change and survives today in the form of the common European cockle and a few other living species (two others, for example, in Britain and one in the United States). Modern representatives of the genus look much like those of the Late Oligocene, when it first appeared. The slow rate of phyletic change of the genus is by no means unusual compared to rates seen in other Cenozoic bivalve genera, but stands in marked contrast to the rapid change produced by speciation in the Pontian "Sea."

*The Test of Living Fossils.* If the rectangular model is correct, we can predict that groups of taxa that have survived at consistently low diversities over long periods of time should exhibit very little evolutionary change. They should not have undergone sufficient speciation for their basic body plans to have been greatly altered. Such groups are, in fact, well known and contain most of the classic "living fossils." Among them are the linguloid brachiopods, the monoplacophoran mollusks, the rhynchocephalian reptiles, the mytilid and pinnid bivalve mollusks, the sclerosponges, and the lungfishes. All these groups have persisted in low diversity for hundreds of millions of years. The body plans of most changed rapidly only during earlier periods of rapid diversification. The Dipnoi (lungfishes) will serve as an example (18, 1). Assigned scores for net degree of morphological advancement, genera of lungfishes show that the Dipnoi underwent rapid evolutionary change early in their evolution and little change thereafter (Fig. 1A and B). This well-known example of evolutionary stagnation has remained a curiosity in treatises on macroevolution because the gradualistic model, which has been assumed, offers no explanation. Viewed in light of the rectangular model, however, it is easily explained. Fig. 1C shows that rate of morphologic diversification correlates with taxonomic diversification at the generic level, which clearly reflects rate of speciation. (Diversity for the Paleozoic Era would be even higher relative to that of the Mesozoic and Cenozoic if we could remove the inadequacies of the early fossil record.)

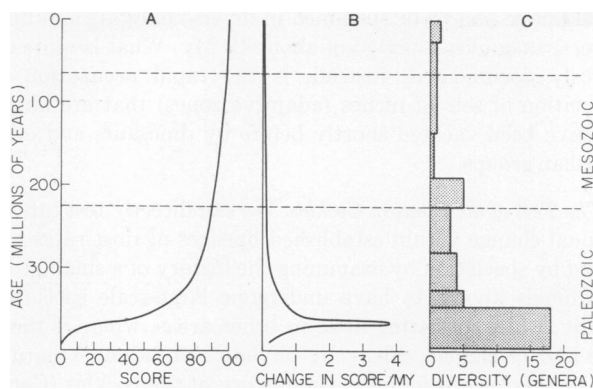


FIG. 1. Rate of evolution of Dipnoi (lungfishes) from their time of origin. (A) Change in score, which represents composite degree of morphologic advancement of a fossil genus. (B) Rate of change of score. (C) Generic diversity through time. (A) and (B) modified from Westoll (17) and Simpson (1). Data for (C) from Romer (11).

The lungfishes form but one example. It can hardly be accidental that no taxonomic group seems to have persisted for relatively long periods of geologic time at low species diversity while exhibiting substantial evolutionary change.

*The Test of Generation Time.* The assumption that gradual change within established species is the dominant process of evolution has led many workers to predict that differing rates of evolution among taxa should correlate with generation time because the fate of each generation represents, in effect, a single event of natural selection. The demonstrated absence of such a correlation (19, 20) can be taken as a failure of the gradualistic model. If speciation is the dominant source of evolutionary change, however, rate of evolution should be related not to generation time, but to an equivalent parameter for speciation. The latter relationship is, in fact, observed in the fossil record, as will be documented in the final portion of this paper. Again the rectangular model is upheld.

*A Disclaimer.* It must be emphasized that the above tests do not demonstrate that no gradual change occurs within established species, but only that such change is generally slow and of minor consequence relative to changes that frequently occur in speciation events. The pattern of phylogeny is not perfectly rectangular, only crudely so.

### SPECIES SELECTION

If, as just concluded, evolutionary change tends to be concentrated in speciation events, most evolutionary trends are not simple directional features that pass continuously along lineages that we divide arbitrarily into species. Rather, a typical trend must represent net change within a complex pattern of species proliferation (2).

In fact, the process of speciation is to a large extent random. Isolation frequently arises accidentally, through the operation of external agents. It is impossible to predict at what time or in what type of subenvironment it will occur. In addition, most populations are spatially heterogeneous, and the local gene pool "sampled" by isolation is therefore often randomly determined. Furthermore, the sample of individuals being isolated may itself be taken at random, as when a few happen to reach a new, isolated habitat (the Founder Effect in speciation). Noting the largely random nature of speciation, Mayr

(7) has compared speciation to mutation, which is an entirely random process.

If most evolutionary change occurs during speciation events and if speciation events are largely random, natural selection, long viewed as the process guiding evolutionary change, cannot play a significant role in determining the overall course of evolution. Macroevolution is decoupled from microevolution, and we must envision the process governing its course as being analogous to natural selection but operating at a higher level of biological organization. In this higher-level process species become analogous to individuals, and speciation replaces reproduction (Table 1). The random aspects of speciation take the place of mutation. Whereas, natural selection operates upon individuals within populations, a process that can be termed *species selection* operates upon species within higher taxa, determining statistical trends. In natural selection types of individuals are favored that tend to (A) survive to reproduction age and (B) exhibit high fecundity. The two comparable traits of species selection are (A) survival for long periods, which increases chances of speciation and (B) tendency to speciate at high rates. Extinction, of course, replaces death in the analogy. The two traits are not totally distinct in that speciation succeeds through the initial survival of a peripheral isolate. The idea that selection of some type operates at the species level is not new (21, 22, 2). Darwin himself viewed large-scale evolution as a race among evolving species. Others (21, 2) have more closely approached the ideas set forth in the present paper.

Species selection, which must largely determine the overall course of evolution, is most analogous to natural selection in asexual organisms. A new species, like a mutant arising in an asexual group, contributes to the future population solely through the selection of its direct descendants. The descendants form what has traditionally been termed a clade. A clade is, therefore, comparable to a clone of asexual organisms. Within sexual species beneficial mutations can be spread among individuals by recombination. In the higher-level process, by the very definition of species, comparable mixing of useful traits of species seldom occurs. There is a higher incidence of mixing among plant species, which hybridize extensively, than among animal species, but nothing as extreme as reproductive panmixia occurs. A given plant species can generally breed with only a few others.

The randomness of speciation generally disallows long-term phyletic trends in evolution. A trend becomes a net direction in a complex pattern of change guided by species selection. The net direction will reflect a lateral shift in the average phylogenetic position at which new species arise. Two factors can contribute to the shift: first, certain types of species will tend to survive for long periods and, therefore, produce a disproportionate number of descendent species and, second, certain types of species will tend to speciate at especially high rates. Differential survival is in response to the basic agents of nonaccidental extinction: predation, competition, and habitat alteration (23). Even many aspects of the latter are biological in nature. We must conclude that biological interactions play a major role in governing large-scale evolutionary trends. Critical factors will vary from taxon to taxon. Predator-limited groups, for example, will tend to shift toward efficient predator avoidance and food-limited groups, toward efficient food capture. Adaptive breakthroughs in the form of morphologic innovations will improve chances for survival in certain

TABLE 1. Analogous features of natural selection and species selection

Process	Unit of selection	Source of variability	Type of selection
Microevolution	Individual	Mutation/recombination	Natural selection A. Survival against death B. Rate of reproduction
Macroevolution	Species	Speciation	Species selection A. Survival against extinction B. Rate of speciation

clades and may also accelerate rates of speciation by increasing the incidence of survival of peripheral isolates.

**RATES OF SPECIATION AND ADAPTIVE RADIATION**

Fisher's Fundamental Theorem of Natural Selection states that rate of phyletic change within a population is proportional to genotypic variance. It also, of course, increases with selection pressure, which is the source of directional change. Similarly, rate of large-scale evolution will reflect both rate of speciation, as the source of variability, and intensity of species selection. An increase in one or both of these factors must account for rapid evolution, like that occurring in adaptive radiation. As we have seen in the previous sections, the critical factor must usually be rate of speciation. The selection coefficient of population biology may be important in simple examples to which the Fundamental Theorem is applied because only brief intervals of time are considered and uniform environmental pressures can be assumed. For an adaptive radiation like that of the early Cenozoic mammals to be caused by intensification of species selection, however, would require the simultaneous onset and continuation for millions of years of numerous environmental pressures that would propel diverse lineages of varied species occupying varied habitats in various directions at extraordinary rates. This scenario is clearly preposterous. Let us then focus upon the critical role of speciation in determining rates of adaptive radiation.

Speciation is a splitting process analogous to that of population growth. Taxonomic diversification can saturate habitats, just as population growth does on a smaller scale. By analogy, we can predict that uninterrupted taxonomic diversification should follow a sigmoid curve (24-26). The sigmoid logistic curve of population biology is formed by modifying the basic exponential growth curve with a term that reflects crowding. In considering adaptive radiation we are concerned only with the earliest portion of the curve, where crowding has little effect. This segment will reflect unrestrained rates of specia-

tion as a new adaptive zone is occupied. Thus, we can adapt to our purpose the simple exponential equation for population growth:

$$\frac{dN}{dt} = RN$$

where  $N$  is number of species,  $t$  is time, and  $R$  is an intrinsic rate of increase in number of species analogous to  $r$  of population growth. Integrating:

$$N = N_0 e^{Rt}$$

where  $N_0$  is the initial number of species (one for strict monophyly). Exponential diversification undoubtedly accounts for the pinched tail at the base of empirically constructed balloon diagrams depicting species diversity through time.

Let us now consider taxa to which the exponential equation can be applied for estimation of  $R$ : living taxa having fossil records and presently undergoing initial adaptive radiations. For such taxa we have  $N$ , the number of living species, and, to a good approximation,  $t$ , the age of the taxon. Assuming  $N_0 = 1$  for such a group, we can calculate  $R$ . The advantage of this approach is that it circumvents the basic inadequacies of the fossil record. In some instances we have substantial evidence of approximate monophyly. For others its assumption can be relaxed to establish boundary conditions for the comparison of different taxa. (Its effect is relatively weak anyway, since it does not appear in the exponent.) There is no space here to make detailed estimates of  $R$ , or the other parameters that will be related to it below, for numerous taxa. The present goal will be to show how the basic technique permits estimation and comparison of rates of speciation.

Just as  $r$ , the intrinsic rate of natural increase in population growth, equals birth rate minus death rate,  $R$  equals speciation rate ( $S$ ) minus extinction rate ( $E$ ). To obtain  $S$ , we have  $R$ , and  $E$  is easily estimated from species duration ( $D$ ), which was discussed earlier; it equals  $1/D$ . For example if  $D = 10$  My, one

TABLE 2. Estimates of  $R$ ,  $S$ , and  $E$

	$t$ (My)	$N$ (species)	$R$ (My <sup>-1</sup> )	$\bar{R}$ (My <sup>-1</sup> )	$E$ (My <sup>-1</sup> )	$S$ (My <sup>-1</sup> )
<b>Bivalvia</b>						
Veneridae	120	2400	0.06			
Tellinidae	120	2700	0.07	0.07	0.17	0.24
<b>Mammalia</b>						
Bovidae	23	115	0.21			
Cervidae	23	53	0.17			
Muridae	23	844	0.29			
Cercopithecidae	23	60	0.18	0.20	0.50	0.70
Cebidae	28	37	0.13			
Cricetidae	35	714	0.19			

in 10 species will become extinct every million years. Table 2 gives preliminary estimates of  $R$ ,  $S$ , and  $E$  for several groups of mammals and bivalve mollusks that are in the midst of rapid diversification. The Veneridae and Tellinidae seem to be radiating at higher rates than nearly all other major bivalve families. The other families occupy a similar position in the Mammalia. Ironically, while the basic technique for estimating both  $E$  and  $R$  avoids the major inadequacies of the fossil record, number of living species is not known for many higher taxa, including bivalves. Estimates for the two bivalve families have been made by combining the estimate of 15,000 total living bivalve species with representation of the two families in regional faunas. Because  $N$  appears in the calculation only as  $\ln N$ , exact values are unnecessary. The striking outcome is that both  $R$  and  $E$  tend to be about three times as large for mammals as for bivalves. Crude calculations using other mammal and bivalve families yield similar values. Thus, although refinement of the estimates should be possible using additional data, the gross disparity in  $S$  for the two classes will certainly remain. It is assumed here that  $E$  reflects only termination of lineages because phyletic change is demonstrably very slow. Granting a small incidence of pseudoextinction by phyletic transition, the rate of extinction by termination, which is the appropriate value for the calculations, should be reduced somewhat. For comparative purposes we can simply assume that the incidence of pseudoextinction is the same for mammals and bivalves. Degree of polyphyly can also be assumed to be comparable for the two groups. Even if we postulate monophyly for bivalves and polyphyly for mammals, an average mammal family would have had to arise from over 20 ancestral species for  $R$  to be equal for the two groups, using the data of Table 2. Such a difference in degree of polyphyly is clearly outrageous, and even if it were to exist,  $E$ , and hence  $S$ , would still be much larger for mammals. Speciation rates are obviously much higher for mammals than for bivalves. Various factors probably contribute to the disparity. For one thing, dispersal mechanisms are more effective for most marine invertebrates than for terrestrial vertebrates, making speciation less likely. In addition, behavioral isolating mechanisms are very common among closely related mammal species, but of little importance to many invertebrate groups, especially ones employing external fertilization.

The final question to be considered here is whether rate of speciation alone can account for observed differences in rates of appearance of higher taxa in different groups of organisms. Continuing with the comparison already begun, we can consider the fact that the Mammalia have tended to produce many more families per million years in adaptive radiation than have the Bivalvia. An explanation offered elsewhere (25) is that degree of divergence per speciation event may be greater for the Mammalia, in which interspecific competition is more intense, than for the Bivalvia. In theory, at least, a test can be made to determine whether difference in rate of speciation for the two groups may itself be sufficient to produce the observed difference at the family level. We can simply estimate the total number of species ( $\hat{N}$ ) that would have arisen in a rapid radiation for which we know the duration and number of families produced. This will be given by

$$\hat{N} = \int_0^t e^{St} dt = 1/S \cdot e^{St} - 1/S$$

Assuming that a family of mammals is phenotypically equivalent to a family of bivalves, the ratio of species-to-families can be compared for adaptive radiation of the two groups. This sort of calculation is vulnerable to greater sources of inaccuracy than the mere calculation of  $E$  or  $S$ , particularly because the estimated parameter  $S$  appears in the exponent. Use of the calculation will therefore be deferred to future studies. It will be sufficient here to conclude that speciation rates are higher for mammals than for bivalves and must to some degree contribute to the higher rates of evolution observed for mammals at the family level.

## DISCUSSION

The recognition of a process of macroevolution analogous to, but differing from, the process of natural selection in microevolution is of great consequence for population biology. Contrary to the prevailing belief, natural selection seems to provide little more than the raw material and fine adjustment of large-scale evolution. The reductionist view that evolution can ultimately be understood in terms of genetics and molecular biology is clearly in error. We must turn not to population genetic studies of established species, but to studies of speciation and extinction in order to decipher the higher-level process that governs the general course of evolution.

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1. Simpson, G. G. (1953) *The Major Features of Evolution* (Columbia Univ. Press, New York).
2. Eldredge, N. & Gould, S. J. (1972) in *Models in Paleobiology*, ed. Schopf, T. J. M. (Freeman, Cooper, and Co., San Francisco), pp. 82-115.
3. Ruzhentsev, V. Ye. (1964) *Int. Geol. Rev.* 6, 2204-2213.
4. Nevesskaya, L. A. (1967) *Paleont. J.* 1, 1-17.
5. Ovcharenko, V. N. (1969) *Paleont. J.* 3, 57-63.
6. Eldredge, N. (1971) *Evolution* 25, 156-167.
7. Mayr, E. (1963) *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, Mass.).
8. Raup, D. M. & Stanley, S. M. (1971) *Principles of Paleontology* (W. H. Freeman, San Francisco).
9. Durham, J. W. (1971) *Proc. N. Amer. Paleont. Convention* 2, 1104-1132.
10. Stanley, S. M. (1975) *Geol. Soc. Amer. Bull.*, in press.
11. Romer, A. S. (1966) *Vertebrate Paleontology* (Univ. Chicago Press, Chicago).
12. Harland, W. B., Smith, A. G. & Wilcock, B. (1964) *The Phanerozoic Time-Scale* (Geol. Soc. London, London).
13. Van Valen, L. (1973) *Evol. Theory* 1, 1-30.
14. Webb, D. S. (1969) *Evolution* 23, 688-702.
15. Gillet, S. (1946) *Rev. Sci., Paris* 84, 343-353.
16. Ebersin, A. G. (1965) *Voprosy Teorii i Prikladnoi Malokollogi* (Tezisy Dokl., Sb. 2, Izd. Zool. in-ta AN SSSR).
17. Runnegar, B. & Newell, N. D. (1971) *Amer. Mus. Nat. Hist. Bull.* 146, 1-66.
18. Westoll, T. S. (1949) in *Genetics, Paleontology, and Evolution*, eds. Jepsen, G. L., Simpson, G. G. & Mayr, E. (Princeton Univ. Press, Princeton, N.J.), pp. 121-184.
19. Zeuner, F. E. (1931) *Fortschr. Geol. Paleont.*, ser. 9, 28, 1-160.
20. Kurtén, B. (1968) *Pleistocene Mammals of Europe* (Aldine Publ. Co., Chicago).
21. Wright, S. (1967) *Wistar Inst. Symp. Monogr.* 5, 117-120.
22. Lewontin, R. C. (1970) *Annu. Rev. Ecol. Syst.* 1, 1-18.
23. MacArthur, R. H. (1972) *Geographical Ecology* (Harper and Row, New York).
24. Cisne, J. L. (1971) *Geol. Soc. Amer. Ann. Meet. Abstr.* 3, 525.
25. Stanley, S. M. (1973) *Evolution* 27, 1-26.
26. Stanley, S. M. (1973) *System. Zool.* 22, 486-506.
27. Walker, E. P. (1968) *Mammals of the World* (Johns Hopkins Press, Baltimore).