Is evolution gradual or rectangular? Evidence from living fishes

(speciation/paleobiology/isozymes/evolutionary rates)

JOHN C. AVISE

Department of Zoology, University of Georgia, Athens, Georgia 30602

ABSTRACT The traditional view that most evolutionary change is gradual and cumulative within lineages (phyletic gradualism) has recently been challenged by the proposition that the majority of evolutionary change is concentrated within speciation events (rectangular evolution). The logical implications of these competing hypotheses for the means and variances of genetic distance among living members of rapidly and slowly speciating phylads are examined. An example of a critical test of gradual versus rectangular evolution is provided by electrophoretic analyses of genic composition in 69 species of North American Cyprinidae (minnows), and 19 species of Centrarchidae (sunfish). Rate of protein evolution appears somewhat decelerated, if anything, in the rapidly speciating minnows. Results are inconsistent with predictions of rectangular evolution, but are not demonstrably incongruent with predictions of phyletic gradualism.

A central tenet of traditional or Darwinian evolutionary theory holds that most evolutionary change is gradual and occurs by the slow and even transformation of populations within established species. According to this conventional view, termed *phyletic gradualism* (1), a complete fossil record would consist of a continuous and finely graded series of intermediate forms connecting ancestral and descendant organisms. The many gaps appearing in the fossil record are illusory, due only to inadequate preservation. As Darwin himself stated (2), "Those who believe that the geological record is in any degree perfect, will undoubtedly at once reject (my) theory."

Recently, a serious challenge has been raised to this traditional view by both paleontologists and geneticists, who have independently proposed that much significant evolutionary change (in morphology and in genotype, respectively) is confined to speciation episodes, with phyletic evolution playing a comparatively minor role in the origin of evolutionary novelty (1, 3–10). According to this hypothesis, gaps in the fossil record are real and are a logical consequence of the rapid genetic changes often occurring in geographically localized populations undergoing speciation. Because rapid evolutionary change is concentrated in speciation events, with relatively slow rates of change in the intervening periods of phyletic evolution, this mode of evolution has been termed *rectangular* (3), or evolution through *punctuated equilibria* (1). Antecedents to this view of evolution are traced to Mayr (11), who argued that gene flow coupled with strong homeostatic mechanisms tends to prevent genetic change from occurring within established species, but that speciation events frequently entail "genetic revolutions."

An important consequence of rectangular evolution, which does not hold for phyletic gradualism, is an increase in rate of evolution with splitting (3). Theoretical models have recently been developed which contrast predicted means and frequency

distributions of genetic distance among *living* members of rapidly speciating versus slowly speciating phylads, according to whether evolutionary change is primarily gradual or rectangular (12, 13). Expected results are as follows: (*a*) when genetic distance between species is a function of time since they last shared a common ancestor (phyletic gradualism*), the ratio of *mean* distances separating species in species-rich versus species-poor phylads of comparable evolutionary age is very nearly one, and the ratio of *variances* of distance is less than one; (*b*) when genetic distance between species is a function of rate of speciation in a phylad (rectangular evolution), the ratios of means and of variances of genetic distance in speciose versus depauperate phylads are considerably greater than one, and increase rapidly as the difference in rate of speciation in the two phylads increases. Gradual versus rectangular models of evolution yield predictions that are qualitatively distinct, are independent of the mode of speciation (i.e., sympatric or allopatric), and, importantly, are subject to critical experimental tests with organisms alive today. This report presents one such test, with one currently quantifiable measure of evolutionary change—composition of structural genes. The approach should be generally useful for any measurable characteristics, although the results may differ depending upon what aspect of phenotype or genotype is being assayed.

Tests of gradual versus rectangular evolution with living species

By all available evidence, two families of fishes in North America have undergone grossly different rates of speciation since their origin on the continent in early to mid-Cenozoic. The North American minnows (Cyprinidae, primarily subfamily Leuciscinae) are extremely diverse, with more than 200 living species currently placed in about 40 genera. The largest genus of minnows, *Notropis*, dates from the Pliocene and contains about 100 species. By contrast, the relatively depauperate sunfish (Centrarchidae) are represented by only 30 species in 9 genera, the largest genus, *Lepomis*, contributing 11 living species. Evidence for the exceptionally rapid rate of speciation in Cyprinidae is discussed in more detail elsewhere (12, 14) and

---

---

* Phyletic gradualism does not propose an exact correspondence between genetic divergence and time in all lineages. Environmental changes alter selection pressures to which organisms respond by adaptation through genetic change. Although selection pressures may fluctuate through time and across character states, the fluctuations are likely to cancel out when averages are made over many character states and long periods of time, if consistent trends (such as speciation rates) with important effects do not persist in different lineages. Thus genetic distance should be positively correlated with time on the average, under phyletic gradualism. The models are sufficient to elucidate only main effects. Also, because neutrality theory predicts a positive correlation of genetic distance and time, tests of the models are not likely to provide critical evidence to resolve another current controversy—the role of natural selection versus neutral mutation in molecular evolution.

Table 1.   Taxonomic and evolutionary information on minnows (Cyprinidae, and its largest genus, *Notropis*) and sunfish (Centrarchidae, and its largest genus, *Lepomis*)*

Attribute	Cyprinidae	Centrarchidae	*Notropis*	*Lepomis*
Number of living species worldwide	~2000	~30	~100	~11
Number of living genera worldwide	~250	~9	—	—
Number of living N. American species	~200	~30	~100	~11
Number of living N. American genera	~40	~9	—	—
Number of known fossil species in N. America	≥28	≥8	—	—
Number of fossil genera in N. America	≥16	≥6	—	—
Earliest known N. American fossils	Miocene	Eocene(?)–Miocene	Pliocene	Miocene–Pliocene boundary
Probable ancestors of N. American forms	One or a few members of the subfamily Leuciscinae from Eurasia	Forms similar to Serranidae (sea basses)	—	—

* Information from refs. 15–20.

is summarized in Table 1. If most evolutionary change has been confined to speciation episodes in these fishes, mean genetic distances among randomly chosen living representatives of Cyprinidae should be considerably greater than mean distances among Centrarchidae; but if genetic change is primarily a function of time, mean distances in the two families should be roughly the same.

We have determined, using standard techniques of starch-gel electrophoresis, allele frequencies at 11–24 genetic loci in 69 species of North American Cyprinidae, and in 19 species of Centrarchidae (Table 2).[†] Species were chosen for study solely on the basis of availability, and should provide an adequate representation of Centrarchidae and Cyprinidae, unbiased with respect to level or pattern of genetic differentiation in the two families. Proteins reliably scored in at least some species of Cyprinidae are as follows: (*a*) lactate dehydrogenase (EC 1.1.1.27; 2 loci); (*b*) malate dehydrogenase (EC 1.1.1.37; 1–3 loci, depending on the species); (*c*) esterase (EC 3.1.1.2; 1–3 loci); (*d*) isocitrate dehydrogenase (EC 1.1.1.41; 1 locus); (*e*) phosphohexose isomerase (EC 5.3.1.9; 2 loci); (*f*) phosphoglu-comutase (EC 2.7.5.1; 1 locus); (*g*) 6-phosphogluconate dehydrogenase (EC 1.1.1.43; 1 locus); (*h*) glutamate oxaloacetate transaminase (EC 2.6.1.1; 2 loci); (*i*) tetrazolium oxidase (1 locus); (*j*) alcohol dehydrogenase (EC 1.1.1.1; 1 locus); (*k*) α-glycerophosphate dehydrogenase (EC 1.1.99.5; 1 locus); (*l*) triosephosphate dehydrogenase (EC 1.2.1.9; 1 locus); (*m*) general proteins (5 loci). Analogous loci encoding proteins *a*–*i* plus a single peptidase (1 locus) were scored in most centrarchid species.

As new species were added to the study, protein mobilities at each locus were compared side-by-side on gels with products of alleles in previously assayed species. This procedure is necessary to permit computation of statistics appropriate to test predictions of the models: genetic distances among all possible pairwise comparisons of species. Using Nei's (22) formulas, totals of 1806 and 171 mean genetic distances across loci were calculated among different pairs of cyprinid and of centrarchid species, respectively. Frequency distributions of observed genetic distances are presented in Figs. 1 and 2, and the relevant statistics are summarized in Table 3.

[†] Detailed data descriptions for Centrarchidae are given in ref. 21, and comparable information for Cyprinidae, including systematic implications of the electrophoretic data, will be presented elsewhere. Preliminary data for a few cyprinids are in ref. 14. Results for 62% of the 79 species assayed, and for nearly 90% of the 1977 pairwise species comparisons, are presented here for the first time.

Mean genetic distances in minnows and sunfish are incompatible with predictions of the rectangular model of evolution (Table 4). Average genetic distance ($\bar{D}$) between species of *Notropis* equals 0.619 ± 0.007, not significantly different from $\bar{D}$ in *Lepomis*, which equals 0.626 ± 0.028. North American Cyprinidae as a whole show significantly smaller genetic distances on the average ($\bar{D}$ = 0.663 ± 0.006) than do all assayed Centrarchidae ($\bar{D}$ = 1.123 ± 0.036), exactly the opposite of predictions from the theory that genetic change is a function of speciation rates. Even if the most extreme comparison is made, all of North American Cyprinidae versus *Lepomis*, the ratio of $\bar{D}$s in the two groups remains 1.06. If anything, minnows have evolved more slowly genically, on the average, despite a far more rapid rate of speciation in their evolutionary history.

The results (except for the comparison of *Notropis* versus *Lepomis*) also appear somewhat inconsistent with the time-divergence model. However, two important assumptions of the theoretical models are crucial in determining the exact expected ratios of distance in species-rich versus species-poor phylads
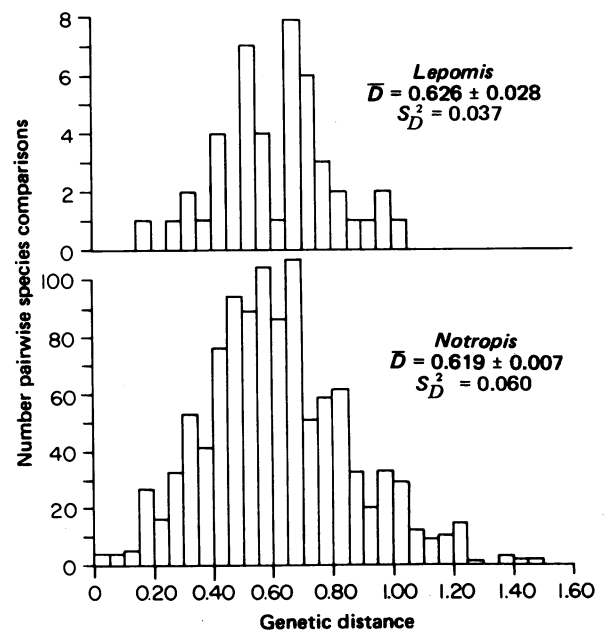

FIG. 1.   Frequency distributions of genetic distances between species within the genera *Lepomis* (Centrarchidae) and *Notropis* (Cyprinidae). S_D^2 is the variance of distance.

Evolution: Avise

Proc. Natl. Acad. Sci. USA 74 (1977) 5085

Table 2. Species of Cyprinidae and Centrarchidae assayed in the present study and the number of loci scored for genetic distances

Cyprinidae	Cyprinidae (continued)	Centrarchidae
Notropis atherinoides; 16	*Notropis telescopus;* 16	*Lepomis auritus;* 14
Notropis atrapiculus; 16	*Notropis texanus;* 16	*Lepomis cyanellus;* 14
Notropis baileyi; 16	*Notropis topeka;* 16	*Lepomis gibbosus;* 14
Notropis bellus; 16	*Notropis trichroistius;* 16	*Lepomis gulosus;* 14
Notropis boops; 16	*Notropis umbratilis;* 16	*Lepomis humilis;* 14
Notropis buchanani; 15	*Notropis uranoscopus;* 15	*Lepomis macrochirus;* 14
Notropis callisema; 15	*Notropis venustus;* 15	*Lepomis marginatus;* 14
Notropis chalybaeus; 16	*Notropis volucellus;* 16	*Lepomis megalotis;* 14
Notropis chrosomus; 16	*Notropis whipplei;* 16	*Lepomis microlophus;* 14
Notropis chrysocephalus; 16	*Notropis xaenurus;* 14	*Lepomis punctatus;* 14
Notropis coccogenis; 16	*Notropis zonatus;* 15	*Acantharchus pomotis;* 11
Notropis cornutus; 16	*Notropis zonistius;* 16	*Ambloplites rupestris;* 11
Notropis cummingsae; 15	*Campostoma anomalum;* 15	*Archoplites interruptus;* 11
Notropis dorsalis; 15	*Dionda nubila;* 15	*Centrarchus macropterus;* 11
Notropis euryzonus; 15	*Ericymba buccata;* 15	*Elassoma evergladei;* 11
Notropis fumeus; 16	*Gila bicolor;* 24	*Elassoma okefenokee;* 11
Notropis galacturus; 16	*Hesperoleucus symmetricus;* 24	*Enneacanthus obesus;* 11
Notropis gibbsi; 16	*Hybopsis lineapunctata;* 15	*Micropterus salmoides;* 11
Notropis greenei; 16	*Hybopsis sp. (undescribed);* 14	*Pomoxis nigromaculatus;* 11
Notropis hudsonius; 15	*Hybopsis storeriana;* 14	
Notropis hypselopterus; 16	*Lavinia exilicauda;* 24	
Notropis leedsi; 15	*Mylopharodon conocephalus;* 24	
Notropis longirostris; 16	*Nocomis leptocephalus;* 15	
Notropis lutipinnis; 14	*Nocomis micropogon;* 15	
Notropis lutrensis; 15	*Notemigonus crysoleucas;* 24	
Notropis maculatus; 15	*Orthodon microlepidotus;* 24	
Notropis niveus; 15	*Phoxinus erythrogaster;* 13	
Notropis ozarcanus; 15	*Pimephales notatus;* 13	
Notropis petersoni; 16	*Pimephales vigilax;* 15	
Notropis pilsbryi; 16	*Pogonichthys macrolepidotus;* 24	
Notropis rubellus; 15	*Ptychocheilus grandis;* 24	
Notropis signipinnis; 15	*Rhinichthys cataractae;* 15	
Notropis spilopterus; 13	*Richardsonius egregius;* 24	
Notropis sp. (undescribed); 16	*Semotilus atromaculatus;* 15	
Notropis stramineus; 16		

when genetic distance is a function of time: (*a*) the phylads must be of comparable evolutionary age; and (*b*) speciation events must have occurred at regular time intervals in all lineages. Neither of these assumptions is likely to be met exactly in Cyprinidae and Centrarchidae (the assumptions are not critical to predictions of the rectangular model—if genetic change is a function of number of speciations, it does not matter when speciation events occur). For example, if the Centrarchidae are in fact considerably older than the North American Cyprinidae, or if a disproportionately large number of cyprinid speciations have taken place relatively recently, the observed genetic distances might be very closely related to time. For present purposes, to argue on the basis of genetic distances that many centrarchid genera are older than cyprinid genera, or that many more cyprinid species are of relatively recent origin, would clearly represent circular reasoning, Thus, with respect to electrophoretically detectable alleles in these two families of fishes, the rectangular mode of evolution can be falsified; the time-divergence model cannot presently be falsified.

Similar conclusions are reached by an examination of variances of genetic distance in Cyprinidae and Centrarchidae. The observed ratio of variances in Cyprinidae versus Centrarchidae is 0.29, fairly close to the expected ratio under the time-divergence model (0.58) but extremely different from the expected ratio under rectangular evolution (1.50). However, the comparison of variances of distance in *Notropis* versus *Lepomis* would appear to favor the rectangular model (Table 4). Again,

these results may not be inconsistent with time-divergence predictions if, as is currently thought by some ichthyologists, *Notropis* is in part an artificial assemblage of North American minnows, containing some species whose affinities lie elsewhere in the family and which may have diverged from a common ancestor to the remainder of *Notropis* at an earlier date. The slightly increased variance in *Notropis* would then be attributable to the inclusion of increased distances among some species, coupled with exceptionally small distances among other pairs of species that may have separated very recently (Fig. 1).

In summary, the logical consequences of a rectangular model of evolution for the Centrarchidae and Cyprinidae lack congruence with the observed patterns of genetic differentiation among living representatives of these phylads. Although the hypothesis that genetic divergence is strictly a function of time cannot be falsified with the present data, rate of protein evolution appears decelerated, if anything, in the rapidly speciating minnows.

Possible caveats

Some objections may be raised to the above conclusions:

Rate of speciation appears greater in minnows because the group has been "oversplit." Species of Cyprinidae (and Centrarchidae) have been described primarily on morphological grounds, and biological species criteria may not be met in all cases. Although species limits cannot be delineated by an ar-

Table 3.   Summary of genetic distances between 19 species of Centrarchidae and between 69 species of North American Cyprinidae

Comparisons among	No. pairwise species comparisons	$\overline{D} \pm$ SEM	Variance
Centrarchidae			
Species of *Lepomis*	45	0.626 ± 0.028	0.037
Other genera	35	1.356 ± 0.078	0.215
Other genera versus *Lepomis*	90	1.287 ± 0.040	0.143
All assayed species	171*	1.123 ± 0.036	0.224
Cyprinidae			
Species of *Notropis*	1081	0.619 ± 0.007	0.060
Other genera (eastern U.S.)	73	0.676 ± 0.029	0.062
Other genera (western U.S.)	36	0.568 ± 0.051	0.092
Other genera versus *Notropis*	611	0.752 ± 0.010	0.059
All assayed species	1806*	0.663 ± 0.006	0.065

* Slightly greater than sum of above rows because of additional comparisons among species within other genera.

bitrary level of genetic distance, nonetheless reasonable estimates can now be made of the *maximum* degree to which excessive splitting has increased the apparent number of North American minnows.

Recent surveys of genetic differentiation in a wide variety of animal groups have overwhelmingly led to the conclusion that distances among conspecific populations are usually ≤0.10, and only rarely does $\overline{D}$ reach 0.20, while among "good" biological species, distances are usually >0.15 (23, 24). Although minnows are not more distinct genically than sunfish, they are by no means closely similar in allelic composition (about 0.66 electrophoretically detectable allelic substitutions per locus differentiate species, on the average). Of 1806 assayed pairs of cyprinid species, only 17 exhibit $\overline{D} \leq 0.15$ (Fig. 2). If for the sake of argument each such pair or cluster is considered a single species, the 69 assayed minnows are reduced to 56 species, and proportionately, only 163 "good" minnow species are living in North America. Because, for example, *Hesperoleucus symmetricus* and *Lavinia exilicauda* exhibit $\overline{D} = 0.055$ but remain largely distinct even where sympatric (25), the above estimate of probable number of "good" minnow species is minimal, and in any event represents more than five times the number of living sunfish.

FIG. 2.   Frequency distributions of genetic distances between all assayed species in the families Centrarchidae (sunfish) and Cyprinidae (minnows).

Speciation rates are similar in sunfish and minnows, but rates of extinction have been greater in Centrarchidae. This hypothesis finds no support in the fossil record, but is perhaps impossible to eliminate as a theoretical possibility, in fishes or in other groups of organisms. If different rates of extinction rather than different rates of speciation characterize Cyprinidae and Centrarchidae, and if extinctions in both groups are random across lineages, the observed genetic distances would be compatible with either time-dependent or speciation-dependent models of evolutionary change.

Electrophoretic methods are inadequate to measure true levels of genetic distance. The distinctness of the predictions of the gradual and rectangular models of evolution are dependent upon the assumption that parallel and convergent evolution are relatively unimportant, in other words that the proportion of the genome that is free to diverge is large and is roughly equal in the two phylads. Although this assumption may be closely met at the level of nucleotide composition, it is certainly only incompletely met with respect to protein bands (electromorphs), which may often represent clusters of distinct proteins sharing an electrophoretic mobility. Electrophoretic techniques underestimate genetic divergence, although the problem can be partly alleviated with statistical corrections (Nei's $\overline{D}$ statistic does this). However, if the number of differentiable character states (electromorphs) at a locus is very small, varying evolutionary rates of conversion between electromorphs

Table 4.   Observed and expected ratios of means and variances of genetic distance in the species-rich North American Cyprinidae versus the species-poor Centrarchidae

Comparison	Ratio of mean distances			Ratio of variances of distance		
	Expected when differentiation is proportional to			Expected when differentiation is proportional to		
	Time	No. of speciations	Observed	Time	No. of speciations	Observed
Notropis vs. *Lepomis*	1.06	2.01	0.99	0.61	1.87	1.62
Cyprinidae vs. Centrarchidae	1.06	1.78	0.59	0.58	1.50	0.29

Expected ratios were calculated according to procedures developed in refs. 12 and 13, using the following values for t (time units since origin of phylad) and k (equal to t/m, in which m is the number of time units between speciation events): Centrarchidae ($t = 40, k = 5$); Cyprinidae ($t = 40, k = 8$); *Lepomis* ($t = 28, k = 4$); *Notropis* ($t = 28, k = 7$). The number of species arising per speciation episode (1) was assumed to equal 2 in all cases. As described in the text, expected ratios are not precise, particularly for the time-divergence model, but are intended to exemplify the contrast in predictions of phyletic gradualism versus rectangular evolution.
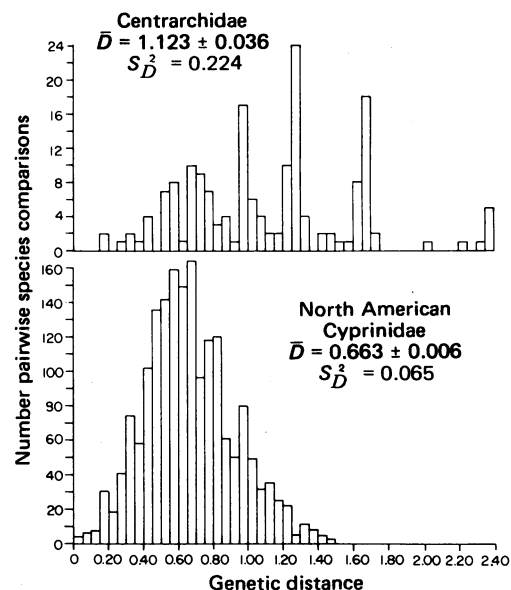
Evolution: Avise

Proc. Natl. Acad. Sci. USA 74 (1977)   5087

will have little effect on final distributions of measurable genetic distances in various phylads.

Phyletic gradualism or rectangular evolution?

The process of speciation remains one of the final realms of evolutionary biology not yet successfully integrated into the rubric of neo-Darwinism. Population genetics, true to its name, has dealt primarily with the mechanistic processes of transformation of gene frequencies within populations, and the broader diversification of life forms was assumed to follow as a logical extension of these processes through time, coupled with reproductive isolation. But if recent suggestions are correct, that most organismal and/or genetic change accompanies speciation episodes, and that phyletic evolution accounts only for "fine-tuning" of ground plans laid down during speciation, then the speciation process is effectively decoupled from phyletic evolution, and much of the theory of phyletic gradualism is simply irrelevant to important evolutionary patterns.

Phyletic gradualism and rectangular evolution represent extreme hypotheses with a large range of intermediate likelihoods. Nonetheless, given our considerable ignorance about the relative roles of speciation versus phyletic change in evolution, amplified arguments should help clarify the logical consequences of these distinct evolutionary modes. The present study demonstrates that one logical prediction of rectangular evolution is not even closely approximated with respect to levels and patterns of genic differentiation among living members of two families of fishes characterized by greatly different rates of speciation. Despite an unusually rapid rate of speciation, protein evolution has, if anything, been decelerated in North American Cyprinidae (although the hypothesis that genic divergence is a linear function of time cannot presently be falsified). On the other hand, if a positive relationship between rate of genic divergence and rate of speciation had been observed, this would not necessarily imply correctness of the rectangular evolution model—it could be that whenever phyletic evolution is occurring at a faster rate (for whatever reasons), speciation events occur with greater probability. Also, results of the present study do not necessarily contradict other predictions of the rectangular model—that speciation often occurs relatively rapidly or in geographically localized populations. We simply have not observed an increase in evolutionary rate with splitting.

A variety of yardsticks can be used to measure evolutionary change—morphology, ecology, cytology, genic composition, etc. Results using different assays may not agree, because complex and obscure relationships often exist between genotype and various phenotypic expressions, and because different methodologies may be preferentially monitoring different types of genes (or genes whose dynamics are under different types of control). The utility of the conceptual approach exemplified in this study lies primarily in the use of comparisons among living members of appropriately chosen phylads. No longer need we rely solely on evidence from fossil remains to resolve the rectangular evolution–phyletic gradualism controversy. We can now make reliable inferences directly from the mor-

phologies, gene products, chromosomes, or DNA of organisms, alive today.

The single test presented in this report is of course not sufficient for a more general falsification of the rectangular evolution model. The final issue will only be settled after results of many tests with diverse organisms and diverse aspects of phenotype and genotype are available. Whatever the final outcome, proponents of rectangular evolution have provided an extremely valuable service to science. Rectangular evolution satisfies the highest standards of a scientific hypothesis (26): it is reasonable, its logical implications are rich in empirical content, and it is subject to potential falsification.

1. Eldredge, N. & Gould, S. J. (1972) in *Models in Paleobiology,* ed. Schopf, T. J. M. (Freeman-Cooper, San Francisco, CA).
2. Darwin, C. (1859) *The Origin of Species* (New American Library Edition, New York, 1958) p. 312.
3. Stanley, S. M. (1975) *Proc. Natl. Acad. Sci. USA* 72, 646–650.
4. Stanley, S. M. (1975) *Science* 190, 382–383.
5. Stanley, S. M. (1976) *Science* 192, 267–268.
6. Ruzhentsev, V. Y. (1964) *Int. Geol. Rev.* 6, 2204–2213.
7. Carson, H. L. (1968) in *Population Biology and Evolution,* ed. Lewontin, R. C. (Syracuse Univ. Press, Syracuse, NY).
8. Carson, H. L. (1975) *Am. Nat.* 109, 83–92.
9. Gould, S. J. (1977) *Nat. Hist.* 86, 12–16.
10. Eldredge, N. (1971) *Evolution* 25, 156–167.
11. Mayr, E. (1963) *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA).
12. Avise, J. C. & Ayala, F. J. (1975) *Genetics* 81, 757–773.
13. Avise, J. C. (1977) *Heredity,* in press.
14. Avise, J. C. & Ayala, F. J. (1976) *Evolution* 30, 46–58.
15. Branson, B. A. & Moore, G. A. (1962) *Copeia* 1962, 1–108.
16. Gosline, W. A. (1971) *Functional Morphology and Classification of Teleostean Fishes* (Univ. Press of Hawaii, Honolulu).
17. Gosline, W. A. (1974) *Jpn. J. Ichthyol.* 21, 9–15.
18. Miller, R. R. (1959) *Am. Assoc. Adv. Sci. Pub.* 51, 187–222.
19. Miller, R. R. (1965) in *The Quaternary of the United States,* eds. Wright, H. E., Jr. & Frey, D. G. (Princeton Univ. Press, Princeton, NJ).
20. Romer, A. S. (1966) *Vertebrate Paleontology* (Univ. Chicago Press, Chicago, IL).
21. Avise, J. C. & Smith, M. H. (1977) *Syst. Zool.,* in press.
22. Nei, M. (1972) *Am. Nat.* 106, 283–292.
23. Avise, J. C. (1974) *Syst. Zool.* 23, 465–481.
24. Ayala, F. J. (1975) *Evol. Biol.* 8, 1–78.
25. Avise, J. C., Smith, J. J. & Ayala, F. J. (1975) *Evolution* 29, 411–426.
26. Popper, K. (1972) *The Logic of Scientific Discovery* (Hutchinson Pub. Group, London).