

Chromosomal change and rectangular evolution in North American cyprinid fishes*

By J. R. GOLD

Genetics Section, Texas A & M University, College Station,
Texas 77843, U.S.A.

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SUMMARY

An important question in evolutionary biology concerns the manner and tempo in which organismal and/or genetic changes that promote evolutionary divergence occur. One recent hypothesis, termed *rectangular evolution*, holds that most significant evolutionary change occurs during occasional or periodic speciation episodes, with long periods of evolutionary stability in the interim. An alternative view, termed *phyletic gradualism*, holds that evolutionary divergences proceed by the slow and even accumulation of genetic differences within populations of established species. Two brief tests of rectangular evolution are presented using chromosomal data from North American cyprinid fishes (minnows), a group known to have experienced heterogeneous rates of splitting. Within the rapidly speciated genus *Notropis*, rates of chromosomal evolution appear slower relative to other, less rapidly speciated confamilial genera. Species of *Notropis* also are less divergent chromosomally, on the average, than are species from other cyprinid genera. These results are incompatible with a rectangular mode of chromosomal divergence in these fishes. The results also reveal inconsistencies with a gradual mode of chromosomal divergence, but at present this hypothesis cannot be falsified. Consideration of these and other data suggests that different levels of the cyprinid genome may follow independent evolutionary paths.

1. INTRODUCTION

A recent controversy involving both geneticists and paleontologists concerns whether major evolutionary divergences are primarily gradual or rectangular (Carson, 1975; Eldredge, 1971; Eldredge & Gould, 1972; Stanley, 1975; Ruzhentzev, 1964). By definition, these terms refer to alternative modes of phylogeny (Stanley, 1975); although, as recent arguments point out (e.g. Eldredge & Gould, 1972), the central distinction between the two lies in the different manner and

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tempo (Simpson, 1944) in which organismal and/or genetic changes that promote evolutionary divergence occur.

The gradualistic mode, termed *phyletic gradualism* (Eldredge & Gould, 1972), is essentially Darwinian in that most genetic change is thought to occur gradually, primarily in response to natural selection. Divergence proceeds by the slow accumulation of genetic differences within populations of established species, and new species, when they occur, arise from the slow and even transformation of populations into reproductively isolated units. Evolution above the species level is considered to proceed in essentially the same manner, and result in the slow and gradual divergence of forms (the 'stately unfolding' of Eldredge & Gould, 1972, p. 109).

The opposing view, termed *rectangular evolution* (Stanley, 1975) or evolution through *punctuated equilibria* (Eldredge & Gould, 1972), holds that much significant genetic change occurs during speciation episodes. Here, a lineage's history is viewed to normally include long periods of evolutionary stability, interrupted or punctuated occasionally by rapid genetic change accompanying bursts of speciation. Because major evolutionary changes in morphology and in genotype occur only periodically during speciation episodes, with relatively slow rates of change in the interim, the resulting phyletic patterns should be stepwise or rectangular. Evolution above the species level under a rectangular mode is thus effectively distinct from evolution within species, and may be guided by a process termed *species selection* (Stanley, 1975) which is analogous to, but different from, natural selection.

Rectangular versus gradualistic evolution represent extreme hypotheses, and as such yield testable predictions which are qualitatively distinct. One important prediction of rectangular evolution, which does not hold for phyletic gradualism, is an increase in evolutionary rate with splitting (Stanley, 1975). Avise (1977) tested this prediction at the structural gene (allozyme) level by comparing means and variances of genetic distance between species pairs from two fish groups known to have experienced widely divergent rates of splitting (see also Avise & Ayala, 1975, 1976; Avise, 1978). His findings were generally inconsistent with rectangular evolution, but not with expectations of phyletic gradualism. More importantly, Avise's (1977) study demonstrated a conceptual framework from which tests of gradual versus rectangular evolution may be carried out using quantifiable measures of evolutionary change in living members of appropriately chosen groups. In the following, two such tests of rectangular evolution are briefly presented, using rearrangements of gross chromosome structure as the quantifiable unit of evolutionary change.

(i) *Test of evolutionary rates*

Because rectangular evolution predicts an increase in evolutionary rate with splitting, a simple but effective test need only compare evolutionary rates between taxa known to exhibit divergent rates of splitting. Under a rectangular mode, more rapidly speciated groups would be expected to display significantly increased

rates of evolution. Examination of evolutionary rates (Table 1) within North American genera of the fish family Cyprinidae (minnows) affords such a comparison. The genus *Notropis*, which contains well over 100 living members (Miller, 1965), appears to have undergone considerably faster splitting than all other genera ($\bar{x} = 6.9$ species/genus) for which appropriate data are available. The net speciation rate (R) within *Notropis* is almost twice that of other con-familial genera, and although extinction rate (E) within *Notropis* could not be estimated, the highly significant, positive correlation between net speciation rates (R) and corrected speciation rates (S , where $S = R + E$) among vertebrates ($r^2 = 0.73$, from Bush *et al.* 1977) strongly suggests that S values within *Notropis* also are appreciably higher than within other genera.

Table 1. *Evolutionary rates within genera of North American Cyprinidae.*

Group	Net speciation rate (R)	Extinction rate (E)	Corrected speciation rate (S)	Chromo- some number changes/ lineage/ Myr*	Arm number changes/ lineage/ Myr*
N. A. Cyprinidae	0.40	0.25	0.65	0.012	0.056
<i>Notropis</i>	0.66	—	—	0.000	0.018
Other N.A. genera	0.37	0.25	0.62	0.015	0.069

* Myr = Million years. Speciation and extinction rates represent species per lineage (genus) per million years, and were computed using equations in Stanley (1975) and Bush *et al.* (1977). Rates of karyotypic change were computed after Bush *et al.* (1977), using the methodology outlined in Gold *et al.* (1978), and the data summarized in Gold, Karel & Strand (1979). Ages for cyprinid genera were based on the first appearance of a genus in the fossil record (Miller, 1965; Kimmel, 1975; Smith, 1975), and absolute ages for geological times were taken from Savage (1975). Chromosomal data for *Notropis* includes 22 species; data for other North American genera includes 17 species from 7 genera.

In contrast, rates of karyotypic change (in chromosome number and arm number) appear far slower within *Notropis* than within other genera (Table 1). No changes in chromosome number have yet been detected among 22 *Notropis* species assayed, and the rate of arm number change within *Notropis* is only one-fourth that within other genera. Clearly, the rate of gross chromosomal evolution within *Notropis* does not reflect the rapid rate of speciation in this genus. Rather, by comparison with the other North American cyprinids for which chromosomal data are available, the rate of chromosomal alteration is considerably less in the more speciose *Notropis*.

(ii) *Test of mean chromosomal distances and variances*

The second test employs the logic of theoretical models developed by Avise & Ayala (1975, 1976) and Avise (1977, 1978), which contrast expected means and variances of genetic distance among living members of rapidly versus slowly speciating taxa. Briefly, if genetic distance between species is a function of time

(gradual evolution), the ratio of mean genetic distances separating species in species-rich versus species-poor taxa should be very nearly one, and the ratio of variances should be less than one. If genetic distance between species is a function of speciation episodes (rectangular evolution), the ratios of both means and variances of genetic distance in species-rich versus species-poor taxa should be considerably greater than one.

By using a difference of one in haploid karyotype to represent one unit of chromosomal distance, mean chromosomal distances and variances between species pairs of North American Cyprinidae were calculated (Table 2). Again, the appropriate comparison is between *Notropis* (rapidly speciated group) and all other

Table 2. Mean chromosomal distances between species of North American Cyprinidae

Comparisons among	Chromosome number		Arm number	
	$\bar{D} \pm \text{s.e.m.}$	Variance	$\bar{D} \pm \text{s.e.m.}$	Variance
North American Cyprinidae (62:50)	0.157 \pm 0.009	0.139	1.866 \pm 0.051	3.227
<i>Notropis</i> (22:22)	0.000 \pm 0.000	0.000	1.104 \pm 0.064	0.954
Other N. A. genera (40:28)	0.240 \pm 0.016	0.198	1.791 \pm 0.098	3.625

Parentheses refer to the number of species used in pairwise comparisons (chromosome number:arm number). Chromosome data are from Gold, Karel & Strand (1979).

North American cyprinid genera (slowly speciated group). If chromosomal changes are rectangular, then both mean and variance of chromosomal distance between species pairs of *Notropis* should be greater than mean and variance of chromosomal distance between species pairs from other, less rapidly split genera. However, means and variances of distances in both chromosome number and arm number between *Notropis* species are appreciably less than means and variances of distances between species from other genera (Table 2), exactly the opposite of expectations based on rectangular evolution. Species of *Notropis* appear, in fact, to have evolved much more slowly chromosomally than might be expected based on a history of accelerated evolution.

(iii) *Are chromosomal changes in cyprinids gradual?*

The data in Tables 1 and 2 may also be used to examine whether chromosomal divergence in cyprinids has been primarily time dependent or gradualistic. Here, the general expectations are (1) that rates of chromosomal change over long periods of time should be more or less equivalent among cyprinid subgroups; and (2) that genetic (chromosomal) distances between species should exhibit a positive correlation with elapsed time. However, rates of change in both chromosome and arm number appear distinctly heterogeneous between *Notropis* and the other genera examined (Table 1), despite differences in generic age or number of species. *Notropis* dates to the Pliocene (10 Myr) and contains over 100 living species; whereas the average age and number of species for the other genera examined were 6.23 Myr and 6.9 species/genus, respectively (references in Table 1).

Further, *Notropis* species on the average are less distinct chromosomally than species from other genera (Table 2); yet based on appearances in the fossil record, *Notropis* is older than most of these genera.

The results are inconsistent with a gradualistic mode of chromosomal evolution. However, both expectations are based on the assumptions that chromosomal changes occur linearly at regular intervals through time and that homoplasmy plays a relatively unimportant role. Neither of these assumptions is likely to be met in cyprinids. It may be that a disproportionate number of chromosomal rearrangements have occurred relatively recently in some genera, but not in others; or it may be that the similarities of many cyprinid karyotypes are derived from convergent or parallel evolution. Either way, until these questions are resolved, the gradualistic mode cannot be falsified.

2. DISCUSSION

The above examples demonstrate that observed chromosomal divergence in North American Cyprinidae does not follow a rectangular evolutionary pattern. The rate of chromosomal evolution within *Notropis* does not reflect the rate of speciation in this genus, nor are *Notropis* species more distinct chromosomally on the average than are species of other, less speciose cyprinid genera. The data also appear inconsistent with a gradualistic mode of chromosomal evolution in cyprinids, although at present this hypothesis cannot be falsified.

Objections to the above may be raised at several levels: (1) the taxonomy (classification) of these fishes does not reflect biological reality: *Notropis* may be 'oversplit' with respect to 'good' biological species, or alternatively, many *Notropis* species may have true affinities elsewhere in the group, having diverged from a *Notropis*-like ancestor at a very early date; (2) the cyprinid fossil record in North America is too incomplete, especially for *Notropis*, to accurately reflect times of origin and extinction of taxa; or (3) present methods of fish cytogenetics do not reveal important 'hidden' variation which might be uncovered with higher resolution techniques (e.g. banding).

Both (1) and (2) are impossible to eliminate as theoretical possibilities. However, Avise's (1977) suggestion based on allozyme criteria that only 80% of all North American cyprinids may be 'good' biological species still leaves proportionally about 80 species of *Notropis*, well over ten times the number of living species in almost all other North American cyprinid genera. In regard to (2), the critical assumption made here was that extinction rate within *Notropis* is at least comparable to that within other genera. Given the correlation between net and corrected speciation rates among vertebrates (see above), this assumption is certainly reasonable. Finally, application of banding techniques (C bands, G bands, etc.) may in fact reveal cryptic chromosomal variation. However, to fit a rectangular mode, the variation and rate of change in banded chromosomal phenotypes would have to be greater within *Notropis* than within other genera, exactly the reverse of observed patterns of change in gross chromosome structure. Comparative

studies of variation in standard versus banded karyotypes among other animal groups are not extensive but have thus far shown that in general the rates of both types of chromosomal change (standard versus banded) are more or less equivalent, and that groups which are conservative in standard karyotypes tend also to be conservative in banded karyotypes (Árnason, 1974; Baker, Bass & Johnson, 1979; Bickham, 1979; Bickham & Baker, 1976; Mascarello, Stock & Pathek, 1974; Patton & Baker, 1978; Stock & Hsu, 1973; Stock, Arrighi & Stepnos, 1974; Yosida & Sagai, 1973). Regardless, there is ample evidence that changes in gross chromosome structure are important evolutionary events and represent viable measures of evolutionary divergence (White, 1973, 1977, 1978). Further, to the extent that they initiate or reinforce reproductive isolation and/or significantly alter patterns of gene regulation (Wilson, 1975, 1976), major chromosomal changes may also be important to the speciation process itself.

As pointed out by Avise (1977), rectangular evolution and phyletic gradualism represent extreme hypotheses, with a large range of intermediate possibilities. Nonetheless, the two models are important to consider since if rectangular patterns exist then much of the theory of phyletic gradualism becomes unimportant to the general course of evolution. The two tests presented in this paper do not suffice as a general falsification of rectangular evolution, but rather serve to illustrate that while rapid splitting may occur (e.g. *Notropis*), not all measurable evolutionary characteristics need follow the same pattern. Indeed, Avise (1977, 1978) showed that structural gene divergence in *Notropis* (and in most North American cyprinids) may follow a time-divergence (gradual) mode rather than a rectangular one. On the other hand, morphological evolution in North American cyprinids apparently has been relatively extensive, as evidenced by the large number of species (>200) and genera (35-40) described primarily on morphological grounds. Many cyprinid species show anatomical or behavioral differences indicative of major evolutionary change, yet possess either identical gross karyotypes and/or levels of genic similarity comparable to that between conspecific populations of other species (Avise, Smith & Ayala, 1975; Gold *et al.* 1978, 1980). In short, despite a relatively rapid rate of speciation and concomitant morphological change, protein and chromosomal evolution in North American Cyprinidae appear, if anything, decelerated (Avise, 1977; this paper). This is particularly well emphasized in *Notropis*.

These observations suggest that separate levels of the cyprinid genome may follow independent evolutionary paths, a thesis not inconsistent with the bulk of evolutionary-genetic data from other organisms, including fishes (Gottlieb, 1976; Kornfield *et al.* 1979; Prager & Wilson, 1975; Prager, Fowler & Wilson, 1976; Turner, 1974; Wilson, Maxson & Sarich, 1974a; Wilson, Sarich & Maxson, 1974b). In the future, it will be important to evaluate patterns, modes and rates of change in several evolutionary parameters, as well as compare differences in modes for similar parameters across taxa. Only then will the issue of rectangular versus gradual evolution be possibly resolved.

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