

CYTOGENETICS AND SYSTEMATICS OF THE ANTHROPOIDEA,
WITH SOME THOUGHTS ON MACROEVOLUTION

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The chromosomes of the primates are potentially extremely powerful tools for eliciting a deeper understanding of primate systematics. Their utility lies largely in the fact that chromosomes are of extremely high heritability (to take an analogy from quantitative genetics: nearly all chromosomal variation in a population is inherited; the only exceptions being *de novo* chromosomal mutations). The chromosomes do not exhibit the plasticity in response to direct environmental pressure characteristic of gross organismal morphology, which makes them rather "purer" indicators of genetic affinity. Further, a chromosomal inversion or translocation is an effectively unique event, which means that parallel evolution in the karyotype will be exceedingly rare.

The chromosomes hold a position of rough intermediacy between genotype and phenotype. As genes exist in the genotype and are expressed in the phenotype, they are nevertheless housed in the karyotype. The rates of genotypic and phenotypic evolution are now generally acknowledged to be independent, although they proceed in parallel directions (e.g., Sarich and Wilson 1967; Dickerson 1972; Byles 1976). However, frequently accompanying that observation is the inference that karyotype change causes phenotype evolution, based on the recently resurrected "chromosomal repatterning" theory of Richard Goldschmidt (Goldschmidt 1940; Wilson *et al.* 1974a, 1974b, 1975; Stanley 1979:146ff.). In this view, a "systemic mutation" will alter the gross morphology of the organism by changing the expression of genes involved in a karyotype mutation, or "repatterning." Actually, however, there are few data to support this view; and very many to contradict it. First, data from clinical genetics overwhelmingly affirm that balanced chromosomal alterations (i.e., those which do not involve either the gain or loss of chromosomal material, but only the rearrangement thereof) do not generally have a detectable effect upon the individual phenotype (e.g., Moorhead 1976). Second, there are several known instances of organisms which are morphologically very similar, yet karyotypically very different; e.g., the muntjacs (Wurster and Benirschke 1970) and the gibbons (Myers and Shafer 1979, cf. below). Finally, there are cases of morphologically different organisms with identical karyotypes, for example, the "homosequential" *Drosophila* species (Carson *et al.* 1970; White 1978: 45).

A much more reasonable view than the Goldschmidt-Wilson "systemic mutation" concept is the recognition, long held among evolutionary cytogeneticists, that morphological change and karyotypic change do not proceed apace. "Thus," we read, "the degree of morphological divergence... and of the differentiation of the chromosome structure do not necessarily go hand in hand in evolution" (Sinnott *et al.* 1958:294). And again, "(By 1932), the chromosomes were seen to have evolved according to rules of their own not clearly related to any properties of the organisms whose heredity they were supposedly carrying" (Darlington 1978).

The chromosomes, therefore, are best viewed as a third, semi-autonomous "level" of evolution, evolving in parallel with the DNA and the gross organismal morphology, but at a rate independent of either (Marks, in prep.). A convincing example from the higher primates is within the family Hylobatidae, who exhibit "chromosomal tachytely." By that phrase I mean that the rate of evolution is accelerated in this lineage relative to related lineages (as in the sense of Simpson's [1944] "tachytely") -- but this observation applies to the chromosomal level. The gibbon (Hylobates sp.) and the siamang (Symphalangus syndactylus) are similar ecologically and morphologically, differing mainly in size, calls, and coloring (Chivers 1972). Across the entire genome, the two animals are genetically so close that they have produced viable hybrid offspring (Myers and Shafer 1979). They thus provide an ideal test for the Goldschmidt-Wilson hypothesis. If indeed, karyotypic changes cause morphological changes, then here in the Hylobatidae we should expect that these organisms so similar in morphology, ecology, and lifestyle should be similar karyotypically as well. Such, however, is not the case: the two hylobatids, similar enough genetically to hybridize, differ in chromosome number (H. moloch $2n=44$; S. syndactylus $2n=50$); and differ in chromosomal banding patterns to such an extent that there is only one detectable interspecific homologue among the 22-25 pairs of chromosomes (Myers and Shafer 1979).

If the Goldschmidt-Wilson theory of morphological evolution were to hold, then Hylobates should be vastly different from Symphalangus, as their chromosomes have been rather extensively repatterned. The morphological differences between the two genera are more likely related to their genetic, rather than genomic, differences.

Besides the vast differences between the karyotypes of Hylobates moloch and Symphalangus syndactylus, H. Lar ($2n=44$) and H. moloch have been shown to be very similar (Tantravahi et al. 1975), but H. concolor ($2n=52$) has very few homologies to its congeners (Dutrillaux et al. 1975). Hylobates hoolock, H. klossi, and H. agilis each have $2n=44$, but none has been systematically examined (de Grouchy et al. 1978).

Quite the opposite situation is found among the anthropoid subfamily Cercopithecinae, wherein Papio papio and P. anubis ($2n=42$) are karyotypically identical to each other (Dutrillaux et al. 1979) and to P. ursinus and P. hamadryas (Bernstein et al. 1980). A "minor change in the T-staining of a short fragment" yields the karyotype of Macaca mulatta; and an additional inversion yields M. fascicularis (Dutrillaux et al. 1979), although de Vries et al. (1975) found the karyotypes of M. fascicularis and M. mulatta to be identical. These, in turn, differ mainly by heterochromatin gains/losses from Cercopithecus aethiops (Stock and Hsu 1973); Miopithecus talapoin (Ponsa et al. 1980) and Erythrocebus patas (Dutrillaux et al. 1978).

Both the Cercopithecinae and Hylobatidae (or their only extant subfamily, Hylobatinae, to make the taxa strictly comparable) are of comparable age (Simons 1972). However, although the Cercopithecinae have eight extant genera to the two Hylobatinae genera, the former subfamily

is characterized by chromosomal conservatism (bradytely)*, while the latter subfamily is characterized by extensive chromosomal alterations (tachytely). The recognition of different rates of evolution is hardly novel or arcane (cf. Simpson 1944, 1953). Yet it seems to elude Bernstein et al. (1980);

"[The] similarity of the G-band pattern between so many of the baboon chromosomes and those of man confirms the findings of Dutrillaux et al. (1978). In contrast, comparative studies on the gibbon (Hylobates lar) showed a relatively great evolutionary distance between the gibbon and man (Miller 1977); this suggests that evolutionary divergence of the baboon and man from a common progenitor occurred more recently than did that of the gibbon and man."

Bernstein et al. (1980) are able to draw this absurd conclusion because they are comparing overall similarity of chromosomes, instead of relying on synapomorphies (shared derived characters) as the only similarities of phylogenetic relevance. This latter methodological axiom has been popularized in the school of phylogenetic systematics (Hennig 1966; Wiley 1975; Tattersall and Eldredge 1976; Cracraft and Eldredge 1979) or cladistics. Although there is much more to cladistics which is of dubious utility in evolutionary studies (i.e., evolution occurs exclusively by the splitting of lineages; phylogeny logically precedes classification; all taxa must be monophyletic), the preeminence of shared derived characters in constructing phylogenetically significant groups is an important contribution. Thus Simpson writes:

"I believe that [cladistics] includes a major contribution to the methodology of phylogenetic research, apart from questions as to how phylogeny is to relate to classification. Greatly oversimplified, the main point is this: characters of the ancestry of a group of organisms tend to change in the course of time; as the group diversifies, the ancestral conditions will tend to be retained in some but not all the descendants; derived conditions shared by some but not all members of the larger group indicate origin from a later common ancestry. The essential is discrimination between primitive and derived characters at different levels..."

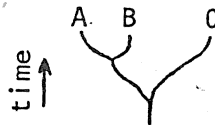
* Actually, the highly speciose genus Cercopithecus is also tachytelic at the chromosomal level. This is related to its arboreality and most likely, social structure, and thus supports the ideas developed herein. I retain the term Cercopithecinae as a matter of convenience, although any broad statements usually refer to the Terrestrial cercopithecines.

"In fact students of phylogeny have been following procedures similar to Hennig's for years, but they have rarely if ever done it quite so carefully and consistently or so clearly demonstrated the theoretical basis in a hierarchic sequence of derived characters as the sole (or at worst most reliable) criterion for cladistic succession."

(Simpson 1975:14)

Although Simpson seems ambiguous in his usage of "derived characters" (i.e., apomorphies) and "shared derived characters" (i.e., synapomorphies; as opposed to unique derived characters or autapomorphies), it must be pointed out that any grouping must be based on the sharing of traits, and thus an autapomorphy cannot give any information about relationships among lineages; it is a derived character definitionally held by only one lineage. Synapomorphies are the storehouses of phylogenetic relationships; the indications which are yielded by examination of autapomorphies and symplesiomorphies merely concern the tempo of evolution.

Consider the following evolutionary tree:



Lineages A and B are, in fact, more closely related than lineage C. Let us now postulate differential rates of evolution in the three lineages: in particular, let us suppose that lineage A evolves more rapidly than lineages B and C. This would mean that lineage A contains many derived characters not shared by B (autapomorphies); and B and C contain more overall similarity to each other than either does to A -- except that this similarity is based on primitive traits (symplesiomorphies). The only way to elicit the true phylogenetic relationships of these three lineages is on the basis of the distribution of synapomorphies. And, indeed, this is the very situation we find ourselves in when we examine the chromosomes of the Hylobatidae, Pongidae, and Cercopithecinae.

The phylogenetic speculation by Bernstein *et al.* (1980) quoted above is not valid because it relies on the distribution of symplesiomorphies. In fact, by that criterion, *Hylobates lar* and *H. concolor* would have to be quite distantly related, since they have few chromosomal homologies. In point of fact, however, the unique derived characters of the gibbon karyotypes tell us no more than that they are evolving rapidly at the chromosomal level. The phylogenetic relationships of these three groups of higher primates can only be ascertained through the distribution of synapomorphies, which the analysis by Bernstein *et al.* (1980) has not revealed.¹ The only way in which the statement by Bernstein *et al.* (1980) could be true is if there were a chromosomal evolutionary clock; i.e., if the accumulation of chromosomal mutations were a direct

function of time since lineage divergence -- and there is certainly no evidence to support such a contention.

The difference in the rates of chromosomal evolution between these Old World anthropoid primates is most likely related to their population structure. The social structure of the cercopithecines* is generally characterized by a mobile troop (with one or several males); lack of pair-bonding between males and females (except for Papio hamadryas, which is apparently bonded and polygynous) and gene flow in the form of peripheral males (Hall and DeVore 1965; Kummer 1968; Crook and Gartland 1966; Itani 1977). On the other hand, what is known of hylobatine social organization suggests that they are permanently pair-bonded, nuclear-family structured, and territorial (Ellefson 1968; Chivers 1972).

The differences in social organization will play a profound role in the rate of chromosomal evolution in these lineages for several reasons: 1) the gibbons, being highly territorial, thus have their gene flow curtailed -- the baboon troop is a highly mobile unit, frequently encountering other large troops; 2) deme size is substantially larger in baboons, whose basic social unit is the troop, which makes genetic drift more unlikely than among gibbons; and 3) the vagility of the baboon troop, along with the dominance hierarchy and the existence of peripheral males, makes it likely that the baboon demes would be more genetically homogeneous than the gibbon demes. Where a baboon peripheral male can fight his way into a dominant role in a new social group, and so impregnate many females, the gibbon male contacts fewer individuals, impregnates one -- and consequently does not perform qualitatively the same function in terms of gene flow between groups that the baboon male does.

What we have, then, are near-optimum conditions for the establishment of chromosomal variants in the gibbons (much genetic drift and little gene flow) -- and the reverse situation among the baboons, leading to greater uniformity of populations.** We should expect, then, that the cercopithecines would be characterized by much more stable and uniform karyotypes than the gibbons, since their social structure does not promote the homozygosity and fixation of chromosomal variants that the gibbon social organization does.

We have, then, forceful evidence to uphold the view that there are not two levels of evolution as King and Wilson (1975) suggest, but three: molecular, chromosomal, and morphological -- each proceeding at its own rate. This recognition has important consequences for the overall synthetic view of evolution.

*Obviously there is much variety in social structure among cercopithecine species. However, this is minimized when compared with the hylobatines, which are wholly different. Thus, although the hamadryas baboon may be pair-bonded (unlike the other baboons), the major social unit is still the troop, which is quite unlike anything in the gibbons.

**Although the "dominance effect" (i.e., one male establishing dominance and impregnating many of the females) is certainly a form of non-random mating in baboons, this would actually tend to be a force of genetic cohesion between troops, since the male who establishes dominance is likely to be from another troop.

Macroevolution, besides being the illegitimate linguistic offspring of Greek and Latin parents, has the general usage in evolutionary science as evolution above the level of the species (e.g., Simpson 1944; Rensch 1959:1; Dobzhansky 1970:429). This is distinguished from microevolution, or change within a species. The former category is appropriated by the paleontologist, who tends to define "evolution" in terms of morphological change: thus, "Species are rather stable in an evolutionary sense: once formed, they tend to evolve slowly" (Stanley 1979:3, my emphasis).

Microevolution, on the other hand, is largely the domain of the geneticist -- and aside from being merely intra-specific, it also tends to be viewed in terms of genetic alteration.² Thus, "Evolution proceeds by the occurrence and fixation of quantitative or qualitative changes in DNA" (Gosden *et al.* 1977). This sort of "evolution," however, is complicated by the fact that much of the change of this sort is probably unexpressed as morphological change, and therefore insignificant as regards macroevolutionary patterns (Wilson *et al.* 1977; Kimura 1979; Jukes 1980).

This problem of disharmony in evolution can most fruitfully be viewed as a genotype-phenotype translation problem. The geneticists, viewing evolution from the standpoint of molecular substitutions, find it a practical impossibility to translate these into morphological changes. On the other hand, when a paleontologist states that species are "stable" or "not evolving," he has no basis on which to suggest that those species are not fixing DNA variants -- he merely observes no phenotypic change in the animal. This is not surprising: it is axiomatic that, 1) genetic change is the sine qua non of evolution; but that 2) genetic change does not map directly on to the phenotype.

Gould (1980b), in delineating a processual hierarchy of evolution (variation within populations, speciation, and patterns of macroevolution), attempts to effect a theoretical divorce between paleontology and genetics. After all,

"(i)f every evolutionary principle can be seen in a Drosophila bottle or in the small and immediate adjustment of local populations on the Biston betularia model, then paleontology may have nothing to offer biology beyond exciting documentation. But if evolution works on a hierarchy of levels (as it does), and if emerging theories of macroevolution have an independent status within evolutionary theory (as they do), then paleontology may become an equal partner among the evolutionary disciplines."

(Gould 1980a)

Gould's claim is absolutely justified: the macroevolutionary process should be considered an emergent phenomenon, but not so that paleontology students should not have to suffer through a semester of genetics. On the contrary,

it is precisely because of the genetic axiom that the phenotype is an emergent relative to the genotype that macroevolution is an emergent relative to microevolution.

Further, there is persuasive evidence to suggest that, at least among the mammals, the speciation process may occur largely according to the "stasipatric model of M.J.D. White, wherein the agents of reproductive isolation (i.e., speciation sensu stricto) are suggested to be chromosomal mutations in peripheral populations (White 1968; Arnason 1972; Wilson et al. 1975; Bush et al. 1977; Marks, in prep.). Thus, Gould's hierarchy of evolutionary process (microevolution, speciation, macroevolution) is likely to be an epiphenomenon of a more fundamental hierarchy of genetic process (genotypic change, karyotypic change, phenotypic change).

I do not mean to suggest that genotypic change is microevolutionary, karyotypic change is speciation and phenotypic change is macroevolutionary; i.e., that the levels of our three-tiered hierarchies map directly on to each other. Certainly, for example, there is chromosomal and phenotypic variation within a given species. I am suggesting, however, that Gould's hierarchy of evolutionary process exists only because there is a fundamental genetic hierarchy: the relationships of genotype-karyotype-phenotype underlie the relationships of microevolution-speciation-macroevolution; and since all three elements of the genetic hierarchy evolve at independent rates, there need be no direct or immediate links between the emergent tiers of the evolutionary hierarchy.

This suggestion certainly does not invalidate the profound observation that evolution is indeed a hierarchical set of processes, any one of which is not simplistically reducible to another. It simply reinforces the fundamental tenet of the evolutionary "synthesis" of this century: that first and foremost, evolutionary change is genetic change. This should also enable the "macroevolutionists" to attend themselves to patterns of supra-specific diversity, without feeling obligated to bolster them with specious genetic arguments. The problem of connecting phenotypic alteration with a genetic change is the central problem of genetics, and it should remain so. Evolution is quintessentially genetics, but the evolutionary effects of the separate levels of the genetic hierarchy form a hierarchy of evolutionary process, any level of which will have to contain its own corpus of theory.

Footnotes

¹ Indeed, at the chromosomal level, it is possible that there may be no detectable synapomorphies between the gibbons and the other anthropoids, due to the extreme rapidity of chromosomal evolution in that lineage. Certainly, however, the distribution of shared evolutionary novelties at other levels (biochemical, morphological) suggests a closer affinity of the Pongidae with the gibbons than with the Cercopithecidae.

- 2 "Microevolution," unfortunately, is hampered by a semantic ambiguity: on the one hand, the term denotes intra-specific variation of any sort (i.e., genotypic, karyotypic, phenotypic); on the other hand, it connotes specifically the fixation of point mutations in DNA. Gould (1980a and b) does not distinguish between these two "microevolutions," and it lends an element of vaguity to his discussion, which is necessarily carried over in my discussion. I shall treat this matter further under separate cover.

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