THE TEMPO OF EVOLUTIONARY CHANGE IN PRIMATE KARYOTYPES: speciation mode and phylogenetic inference

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Introduction

Evolutionary inferences made on the basis of cytogenetic data are of considerable value to biologists and anthropologists. Although a considerable amount of data has accumulated on the rates of cytogenetic change among lineages, there has been a general failure to appreciate the implications of these observations for the overall study of the evolutionary processes, and for the interpretation of other bodies of cytogenetic data.

My goals in this paper are to discuss evolutionary rates; to focus on the factors influencing the rate of karyotypic change; and to show how phylogenetic influences may be made from karyotype data -- with special reference to the order Primates.

The Hierarchical Nature of Evolutionary Change

Evolution classically has as its referent the phenotype. The fact of evolution is recognized in the paleontological record as a change in organismal morphology through time. Simpson (1944, 1953) documented and analyzed the differences in evolutionary rates among groups of animals, showing them to be highly variable, but largely dependent upon ecological opportunity.

With the expansion of biochemical genetics in the 1960's, it became possible to study evolutionary rates at another level: the genotypic. Here, both nucleotide substitutions (Kimura and Ohta, 1974; Jukes and King, 1979; Jukes, 1980) and allozyme differences (Sarich and Wilson, 1967; King and Jukes, 1969; King and Wilson, 1975; Wilson et al., 1977) are seen to be occurring across lineages at a rate independent of the rate of morphological change -- indeed, at a rate claimed to be roughly constant.

Karyotypic evolution, however, proceeds at rates independent of either phenotypic or genotypic evolution (Sinnott et al., 1958:294; Darlington, 1978). In a seminal article, Arnason (1972) attempted to associate karyotypic rates of evolution with speciation modes, dichotomizing the large, vagile, continuously distributed marine mammals against the small, less vagile, and discontinuously distributed rodents. The former group is karyotypically conservative, and chromosome changes are presumed not to participate in the speciation process; the latter group is karyotypically diverse, with chromosomal shifts presumable being the agents of reproductive isolation between two species.

Studies of Rates of Chromosomal Evolution

Arnason's study contrasted two types of speciation: allopatric (Mayr, 1942; 1963), associated with slow chromosomal evolution, and stasipatric (White et al., 1967; White, 1968), associated with rapid chromosomal evolution. Allopatric or geographical speciation does not stipulate a structured population -- only that some portion of a parent population is geographically isolated from its conspecifics. As a consequence of this geographical isolation, the subpopulation becomes reproductively isolated from the parent population either by adapting genetically to a new sub-niche (natural selection) or by the founder effect. The role of chromosomal changes is minor in this speciation mode, as the reproductive isolation is presumed to occur through the differential fixation of regulatory point mutations (Bush, 1975).

An alternative mode is the stasipatric speciation model of M.J.D. White, in which a socially structured population of low vagility evolves reproductive isolation through random inbreeding differentially fixing chromosomal variants in small demes. Infertility should theoretically result from the meiotic mechanisms in a chromosomal hybrid.

Wilson et al. (1975) and Bush et al.(1977) invoked the stasipatric speciation model upon finding a high correlation between speciation rate and rate of chromosomal evolution in many groups of mammals. Unfortunately, they combined stasipatric speciation (which invokes chromosomal mutations as adaptively passive agents of reproductive isolation) with Goldschmidt's (1940) discredited idea of chromosomal macromutations (which involves chromosomal mutations as the agents of organismal change, making the unlucky bearer of such a mutation a "hopeful monster").

Another theory to account for the rates of chromosomal change among lineages is the canalization model of karyotype evolution by Bickham and Baker (1979). Here, the assumption is that the karyotype contributes significantly to fitness, and when two related species differ in karyotype, one will out-compete the other as a consequence of that karyotype difference. Karyotypic evolution is considered to be most rapid early in the evolution of a given taxon, and ultimately the karyotype "stabilizes" (i.e., a species with a certain karyotypic configuration is more likely to survive, while other species with other kayrotypic configurations are more likely to become extinct).

The canalization model is actually a broad invocation of the controversial concept of "species selection" popularized by the paleontologists Stanley (1975; 1979) and Gould and Eldredge (1977). Bickham (1981) has shown that chromosomal evolution in the turtles has apparently been decelerating and interprets this as evidence in favor of the canalization model. But the objections to accepting this model as a general paradigm for the dominant role of karyotype shifts in evolution are as follows: 1) evidence from many areas (especially human genetics) suggests quite strongly that karyotype changes are adaptively neutral, not advantageous (e.g., Moorhead, 1976); 2) the model predicts a close parallel between karyotype and phenotype evolution, yet there are numerous cases of disparity between karyotype and phenotype for which the model cannot account

(Baker and Bickham, 1980); 3) the model predicts a strong correlation between antiquity of a lineage and stability of karyotypes -- yet this is frequently not the case. For example, the ancient primate suborder Prosimii is certainly no less karyotypically diverse than the more recent suborder Anthropoidea (Chiarelli et al., 1979).

Bengtsson (1980) has elucidated the speciation model, which is more consistent with available data than any model of karyotypic adaptation, and argues that the tendency towards stasipatric (rather than allopatric) speciation involves primarily the size of the organism and its concomitant reproductive strategy. While this correlation may well be significant, basic population biology would suggest that social structure is of at least equal importance in determining the evolutionary rate; and most likely, of paramount importance.

Chromosomal Tachytely

There are numerous examples of groups of species very similar at the morphological and genetic levels, but grossly dissimilar at the chromosomal level: the most famous of these is in the genus *Muntiacus* (Cervidae), wherein *M. reevesi* has 2n=46 in both sexes, and *M. muntjak* has 2n=6 in the female and 2n=7 in the male (Wurster and Benirschke, 1970; Shi Liming et al., 1980). The situation is also common among the rodents; for example, among the species *Sigmodon hispidus*, *S. arizonae*, and *S. mascotensis*, which are karyotypically diverse (Elder, 1980).

Bickham and Baker (1980) have acknowledged this phenomenon and called it "karyotypic megaevolution" -- a highly inappropriate and ambiguous term. Simpson (1944) coined "megaevolution" to refer to the evolution of taxonomic categories above the genus level, juxtaposing it against both "microevolution" (below the species level) and "macroevolution" (above the species level). By 1953, however, Simpson abandoned the term as it served merely to obscure the continuity of process along the evolutionary hierarchy. To resurrect a term originally used to apply to the development of supra-generic categories and re-apply it to what is obviously a rate-phenomenon in karyotype evolution is very unfortunate.

The cases of the muntjacs and cotton rats cited above are ones in which evolution of the chromosomes has proceeded much more rapidly than evolution of either the organism or its genes. Simpson (1944) did coin a useful term that can be transferred to the chromosomal level and applied here: tachytely, which he defined as a rate of evolution faster than the modal rate for the group under study (cf. also Raup and Marshall, 1980).

The application of Simpson's "tachytely" to the chromosomal level of evolution must differ from his original formulation in two respects: 1) Simpson plotted a measure of macroevolution (the survivorship of supraspecific taxa) versus absolute time; and 2) he defined tachytely relative to a modal rate of evolution for a group, horotely.

Unfortunately for the study of rates of chromosomal evolution, we have no measure of absolute time against which to plot chromosome rearrangement, insofar as the fossil record reveals nothing about the karyotype of the fossil animal. Bickham's (1981) attempt to reconstruct the karyotypes of fossil turtles centers around the equation of morphological change with karyotypic change -- which certainly does not hold for the mammals. Further, there is no useful way to measure the "amount" of karyotypic rearrangement in a lineage: with inversions, fissions, fusions, duplications, deletions, translocations, NOR-variants, and heterochromatin shifts all being qualitatively different, and their relative contributions to evolution being largely unknown -- one cannot at present give a simple numerical value for the amount of karyotypic change in a given lineage. Finally, a corollary of the quantitation problem is that in a group like the primates, there is such great variety in kind and amount of chromosomal change that the prospect of establishing a "modal rate" for the group is all but nil.

Nevertheless, in many cases of comparative cytogenetic studies, what are observed are clearly rate-related phenomena -- in which a lineage is observed to be karyotypically very diverse relative to either antiquity of the lineage or amount of biochemical diversity within the lineage (e.g., Ryder et al., 1978, for the Equidae). And since at another evolutionary level, "tachytely" refers to "fast" evolution, albeit in a more quantifiable and precise sense, it would seem both justified and reasonable to utilize that term as a referent for rapid evolution at the chromosomal level as well.

A classic example of such chromosomal tachytely is to be found within the primate family Hylobatidae, the gibbons. The family is comprised of two genera, *Hylobates* and *Symphalangus*, which differ mainly in size, calls, and coloring -- although they are broadly very similar morphologically and ecologically (Chivers, 1972), as well as genetically (Dene et al., 1976). The two genera, similar enough to produce a viable offspring, nevertheless differ chromosomally to such an extent that there is only one distinguishable intergeneric homologue in their karyotypes (Myers and Shafer, 1978).

Although *Hylobates moloch* and *H. lar* (2n=44) are karyotypically similar (Tantravahi et al., 1975), *H. concolor* (2n=52) has few homologies with its congenerics (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).

The likely explanation for the karyotypic diversity among the gibbons lies not in different adaptations, but in their socio-ecology, which dictates a monogamous, arboreal, territorial existence (Carpenter, 1940; Ellefson, 1968; Chivers, 1977; Roonwal and Mohnot, 1977; Gittins and Raemaekers, 1980). The discontinuous distribution of animals, small deme size, and relative lack of gene flow are the very kinds of demographic factors which should facilitate stasipatric speciation -- where these randomly inbreeding subpopulations will become fixed for different chromosomal variants, and so induce reproductive isolation.

It is of interest that what I have called chromosomal tachytely is apparently common among arboreal primates: it has been shown in the highly speciose genus Cercopithecus (Eckhardt, 1979); Aotus (Ma, 1981); and Lemur (Rumpler and Dutrillaux, 1976; Hamilton and Buettner-Janusch, 1977). It would seem to be the case that the socio-ecological exigencies imposed by arboreal life dispose a primate population to speciate stasipatrically, which should lead to a high degree of karyotypic diversity relative to either organismal adaptations or genetic distance.

Chromosomal Bradytely

The converse situation, retarded chromosomal evolution, can be found among the terrestrial monkeys of the family Cercopithecidae. Although diverse at the morphological level, and comparable in genetic distance to the gibbons (Dene et al., 1976), these monkeys display an astonishing degree of karyotypic conservatism.

Papio papio and P. anubis (2n=42) are karyotypically identical (Dutrillaux et al., 1979), identical also to P. ursinus and P. hamadryas (Bernstein et al., 1980), and to P. cynocephalus (Soulie and de Grouchy, 1981). 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 M. fascicularis and M. mulatta to be identical. A broader comparison of unbanded karyotypes (Chiarelli et al., 1979) finds the genera Macaca, Papio, Mandrillus, Theropithecus, and Cercocebus identical.

The phenomenon of exceedingly slow evolutionary rates was termed "bradytely" by Simpson (1944). Appropriating this term for the chromosomal level of evolution, we can visualize chromosomal bradytely as karyotypic conservatism within a taxonomic group, relative to other related groups.

Again, the rate of karyotypic change can be related to the evolutionary forces which emerge from the sociobiology of these terrestrial monkeys. Although cercopithecine social organizations vary, they are quite different from that of the gibbons, and several generalizations can be made.

Cercopithecine social structure is generally characterized by a mobile troop (with one or several males); polygyny without pair-bonding (except Papio hamadryas, which is apparently polygynous and pair-bonded); lack of territoriality; and extensive gene flow in the form of peripheral males (Hall and DeVore, 1965; Crook and Gartlan, 1966; Kummer, 1968; Lindburg, 1969; Rowell, 1969; Packer, 1975; Itani, 1977).

This general form of terrestrial social organization inhibits the operation of genetic drift, for the effective population size is large and the population itself is not genetically sub-divided. Indeed, because of the extensive gene flow within these terrestrial cercopithecines, we should expect that cladogenetic events (evolutionary splittings) due to non-adaptive chromosomal modifications will be impaired, since the effect of gene flow is to reduce between-group variation.

Unfortunately, studies of the genetic differences between groups of terrestrial monkeys have proven difficult to evaluate, since most of these have revealed complex patterns of diversity and homogeneity in the genetic composition of the populations; and many demographic mechanisms have been postulated to account for these patterns (Buettner-Janusch et al., 1974; Olivier et al., 1974; Duggleby, 1977, 1978; Cheverud and Buikstra, 1978; Cheverud et al., 1978; Ober et al., 1978). Nevertheless, the rare studies of chromosomal diversity within a primate species have found a surprisingly low prevalence of chromosomal variations in Papio cynocephalus (Soulie and de Grouchy, 1981), and high amounts of structural and numerical variation in the arboreal monkey Alouatta seniculus (Yunis et al., 1976). It may be expected that a cytogenetic survey of other primate species (for example, the chimpanzee) would reveal greater levels of karyotypic diversity due to differing socio-ecological factors (Marks, in prep.).

What exist, then, are near-optimum conditions for the establishment of chromosomal variants in the gibbon (much genetic drift, which increases between-groups variation; but little gene flow to act as a homogenizing agent between demes) -- and the reverse situation among the baboons, leading to greater karyotypic uniformity. The latter situation of little genetic drift and extensive gene flow likely exists, although for obviously different reasons, among the Cetacea and Pinnipedia, accounting for Arnason's (1972) observation of chromosomal bradytely in those groups.

The rate of chromosomal evolution for a given group appears to be attributable to the interaction of the following five socio-ecologic parameters:

1. Selective value of the homozygous chromosomal configurations; these are presumed to be generally nearly neutral (Lande, 1979), but one cannot exclude the possibility of adaptive shifts to account for the occasional directional trends in karyotype evolution.

2. Continuous versus discontinuous substrate (Arnason, 1972), where savannah and ocean are continuous substrates, but gene flow for an arboreal population would be more restricted.

3. Social organization (Bush et al., 1977), where populations structured into small interbreeding units (demes) should be more karyotypically heterogeneous than populations not so structured.

4. Size and reproductive strategy (Bengtsson, 1980), where small, rapidly reproducing animals may fix new mutations more rapidly in populations than large animals.

5. Vagility (Arnason, 1972), where more territorial animals are expected to express more between-group variation than highly vagile groups.

The interaction of these five factors (which need not, of course, be acting in harmony) will apparently account for most of the rate differences in primate karyotype evolution, and perhaps in mammalian karyotype evolution as well.

Phylogenetic Inference

With the knowledge that different groups of primates evolve at different rates at the karyotypic level, the next question involves predicting and interpreting the distribution of shared chromosomal characters within these groups.

Evolution proceeds by the modification of any given character in a group of organisms such that the modified character is carried by some subset of the descendants of the original group (Simpson, 1975). The original state is termed ancestral, or plesiomorphous; the modified state is derived, or apomorphous (Hennig, 1966). Since any given chromosomal mutation can be considered an effectively unique event, the sharing of a derived karyotypic feature is a strong indication of evolutionary closeness. However, since an ancestral character is likely to be retained independently in several different lineages, the sharing of ancestral characters is _not_ a good criterion for establishing phylogenetic relationships. Similarly, a character which is derived, but not shared by any other group, cannot give any information about the phylogenetic relationships of that group (Eldredge, 1979).

The failure to recognize the importance of these shared derived characters (synapomorphies) as "the sole (or at worst, most reliable) criterion for cladistic succession" (Simpson, 1975) has been an unnecessary handicap to several recent, and otherwise excellent, studies of primate cytogenetics.

If traits other than those which are shared evolutionary novelties, or synapomorphies, are used to infer phylogenetic proximity, the problem of differential evolutionary rates among lineages will obscure the true relationships of the organisms. An excellent example of this occurs in a recent paper by Bernstein et al. (1980). After commenting on several homoeologies between the karyotypes of the chacma baboon (_Papio ursinus_) and human, the authors go on to say:

> In contrast, comparative studies on the gibbon (_Hylobates lar_) shows 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., 1980:61).

Although the observation is accurate, the interpretation is not. Their conclusion only follows if the rates of karyotypic evolution are held to be constant and equal among the human, gibbon, and baboon lineages: i.e., if there is a chromosomal "evolutionary clock." Despite the fact that this assumption is not made explicit, it is clearly the only way their conclusion can follow from the data they adduce -- namely, that humans and baboons are karyotypically more similar than humans and gibbons.

Yet, as we have seen, some gibbons are highly distinct chromosomally from other gibbons -- they simply evolve rapidly at the chromosomal level. Consequently, if we are to use "overall karyotypic similarity" as the criterion for elucidating the phylogenetic branching sequence of these primates, we would be forced to conclude that the lar gibbon and the siamang are very distantly related, despite their overwhelming similarity at other levels of analysis.

The data upon which the conclusion of Bernstein et al. should have been based is a comparison of the synapomorphies of the groups. Thus, if the baboon and human share derived features and the gibbon retains primitive features, their conclusion would stand. Based on considerations of evolutionary tempo, however, it is probably rather the case that humans and baboons, evolving more slowly, share many ancestral karyotypic traits; and that the gibbons, evolving more rapidly, possess uniquely derived chromosomes. But in the absence of shared derived characters linking the groups, no phylogenetic reconstruction is theoretically justifiable. Nevertheless, at other levels of analysis, the gibbon shares several derived characters with the pongids and hominids, notably the lack of a tail, the Y-5 molar cusp pattern, and tendency toward orthograde posture. Genetic distance studies also argue that the human-gibbon link is tighter than the human-baboon link.

Similarly, when Miller (1977) proposed the heterodox hypothesis that gorillas and humans are more closely related than gorillas and chimpanzees, it was based in part on unique derived characters in the chimpanzee karyotype. The chimpanzee is the only representative of the pongid-hominid lineage to lack a DNA fraction homologous to human DNA Satellite II (Jones, 1976; Gosden et al., 1977). Although Miller used that observation to unite Gorilla and Homo, the fact that the orangutan also has the DNA fraction strongly suggests that the chimpanzee lineage has simply lost it; i.e., that the state possessed by Pan is a unique derived character, and the condition shared by Gorilla and Homo is ancestral.

On the other hand, a constellation of telomeric C-bands is shared by Pan and Gorilla, and they are the only primates in the hominoid lineage to have them (Paris Conference 1971, Supplement 1975). This implies that either the telomeric C-bands have been gained or lost independently in several lines, or that they represent a true synapomorphy linking Pan and Gorilla -- as indeed the anatomical evidence would suggest.

Conclusions

Of the putative roles assigned to chromosomal shifts in evolution, the most likely appear to be in speciational, rather than adaptational, events. Among the primates, arboreal species tend to have more rapidly evolving karyotypes than terrestrial groups -- leading to the inference that the population dynamics associated with arboreal life (along with other factors) may dispose these populations to diverge genetically according to the stasipatric mode of speciation.

Since the stasipatric mode predicts rapid evolution of the karyotype for a given lineage and the allopatric mode predicts slow karyotypic change, rates of chromosomal evolution are expected and found to vary widely. However, the variation in evolutionary rates can obscure true phylogenetic affinities. It is thus of paramount importance to consider differential rates of chromosomal evolution and their implications before establishing an evolutionary branching sequence based on cytogenetic data.

References

Arnason, U.
1972 The role of chromosomal rearrangement in mammalian speciation with special reference to Cetacea and Pinnipedia. *Hereditas* 70: 113-118.

Baker, R.J., and Bickham, J.W.
1980 Karyotypic evolution in bats: Evidence of extensive and conservative chromosomal evolution in closely related taxa. *Syst. Zool*. 29:239-253.

Bengtsson, B.O.
1980 Rates of karyotype evolution in placental mammals. *Hereditas* 92:37-47.

Bernstein, R.; Pinto, M.; Morcom, G., and Bielert, C.
1980 A reassessment of the karyotype of *Papio ursinus*: Homoeology between human chromosome 15 and 22 and a characteristic submetacentric baboon chromosome. *Cytogenet. Cell Genet*. 28:55-63.

Bickham, J.W.
1981 Two-hundred-million-year-old chromosomes: deceleration of the rate of karyotypic evolution in turtles. *Science* 212:1291-1293.

Bickham, J.W., and Baker, R. J.
1979 Canalization model of chromosomal evolution. *Bull. Carnegie Mus. Nat. Hist.* 13:70-84.

Buettner-Janusch, J.; Mason, G.A.; Dame, L.; Buettner-Janusch, V.; and Sade, D.S.
1974 Genetic studies of serum transferrins of free-ranging rhesus macaques of Cayo Santiago, *Macaca mulatta* (Zimmerman 1780). *Amer. J. Phys. Anth*. 41:217-232.

Bush, G.L.
1975 Modes of animal speciation. *Ann. Rev. Ecol. Syst*. 6:339-361.

Bush, G.L.; Case, S.M.; Wilson, A.C.; and Patton, J.L.
1977 Rapid speciation and chromosomal evolution in mammals. *Proc. Nat. Acad. Sci*. 74:3942-3946.

Carpenter, C.R.
1940 A field study in Siam of the behaviour and social relations of the gibbon, *Hylobates lar*. *Comp. Psych. Monog*. 16:1-212.

Cheverud, J.M.; Buettner-Janusch, J.: and Sade, D.
1978 Social group differentiation and the origin of intergroup genetic differentiation among the rhesus monkeys of Cayo Santiago. Amer. J. Phys. Anth. 49:449-456.

Cheverud, J.M.; and Buikstra, J.E.
1978 A study of intragroup biological change induced by social group fission in Macaca mulatta using discrete cranial traits. Amer. J. Phys. Anth. 48:41-46.

Chiarelli, B.; Koen, A.L.; and Ardito, G.
1979 Comparative karyology of primates. Mouton, The Hague.

Chivers, D.J.
1972 The siamang and the gibbon in the Malay peninsula. In D.M. Rumbaugh, ed., Gibbon and siamang, vol. 1: Evolution, ecology, behavior, and captive maintenance. S. Karger, Basel.

1977 The feeding behavior of siamang (Symphalangus syndactylus). In T. Clutton-Brock, ed., Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes, pp. 355-382. Academic Press, New York.

Crook, J.H.; and Gartlan, J.S.
1966 Evolution of primate societies. Nature 210:1200-1203.

Darlington, C.D.
1978 A diagram of evolution. Nature 276:447-452.

Dene, H.T.; Goodman, M.; and Prychodko, W.
1976 Immunodiffusion evidence on the phylogeny of the primates. In M. Goodman, R.E. Tashian, and J.H. Tashian, eds., Molecular anthropology, pp. 171-196. Plenum, New York.

Duggleby, C.
1977 Blood group antigens and the population genetics of Macaca mulatta on Cayo Santiago. II. Effects of social group division. Yearbook of Phys. Anth. 20:263-289.

1978 Blood group antigens and the population genetics of Macaca mulatta on Cayo Santiago. I. Genetic differentiation of social groups. Amer. J. Phys. Anth. 48:35-40.

Dutrillaux, B; Biemont, M.C.; Viegas-Pequignot, E.; and Laurent, C.
1979 Comparison of the karyotypes of four cercopithecoidae (sic): Papio papio, P. anubis, Macaca mulatta, and M. fascicularis. Cytogenet. Cell Genet. 23:77-83.

Dutrillaux, B; Rethore, M.O.; Aurias, A.; and Goustard, M.
1975 Analysis of the karyotype of two species of gibbons (Hylobates lar and H. concolor) by various banding techniques. Cytogenet. Cell Genet. 15:81-91.

Eckhardt, R.B.
1979 Chromosome evolution in the genus *Cercopithecus*. *In* B. Bhiarelli, A.L. Koen, and G. Ardito, eds., *Comparative* karyology of primates, pp. 39-46. Mouton, The Hague.

Elder, F.F.B.
1980 Tandem fusion, centric fusion, and chromosomal evolution in the cotton rats, genus *Sigmodon*. *Cytogenet. Cell Genet.* 26: 199-210.

Eldredge, N.
1979 Cladism and common sense. *In* J. Cracraft and N. Eldredge, eds., Phylogenetic analysis and paleontology, pp. 165-198. Columbia University Press, New York.

Ellefson, J.D.
1968 Territorial behavior in the common white-handed gibbon, *Hylobates lar* Linn. *In* P.C. Jay, ed., Primates: studies in adaptation and variability, pp. 180-199. Holt, Rinehart, and Winston, New York.

Gittens, S.P.; and Raemaekers, J.J.
1980 Siamang, lar, and agile gibbons. *In* D.J. Chivers, ed., Malayan forest primates, pp. 63-105. Plenum, New York.

Goldschmidt, R.B.
1940 The material basis of evolution. Yale University Press, New Haven.

Gosden, J.R.; Mitchell, A.R.; Seuanez, H.N.' and Gosden, C.M.
1977 The distribution of sequences complementary to human satellite DNAs I, II, and IV in the chromosomes of chimpanzee (*Pan troglodytes*), gorilla (*Gorilla gorilla*), and orangutan (*Pongo pygmaeus*). Chromosoma 63:253-271.

Gould, S.J.; and Eldredge, N.
1977 Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiol.* 3:115-150.

Grouchy, J. de; Turleau, C.; and Finaz, C.
1978 Chromosomal phylogeny of the primates. *Ann. Rev. Genet.* 12: 289-328.

Hall, K.R. L.; and DeVore, I.
1965 Baboon social behavior. *In* I. DeVore, ed., Primate behavior. Holt, Rinehart, and Winston, New York.

Hamilton, A.E.; and Buettner-Janusch, J.
1977 Chromosomes of lemuriformes. III. The genus *Lemur*: Karyotypes of species, subspecies, and hybrids. *Ann. N.Y. Acad. Sci.* 239: 125-159.

Hennig, W.
1966 Phylogenetic systematics. University of Illinois Press, Urbana.

Itani, J.
1977 Evolution of primate social structure. J. Hum. Evol. 6:235-243.

Jones, K.W.
1976 Comparative aspects of DNA in higher primates. In M. Goodman, R. Tashian, and J. Tashian, eds., Molecular anthropology, pp. 357-368. Plenum, New York.

Jukes, T.H.
1980 Silent nucleotide substitutions and the molecular evolutionary clock. Science 210:973-978.

Jukes, T.H.; and King, J.L.
1979 Evolutionary nucleotide replacements in DNA. Nature 281:605-606.

Kimura, M.; and Ohta, T.
1974 On some principles governing molecular evolution. Proc. Nat. Acad. Sci. 71:2848-2852.

King, J.L.; and Jukes, T.H.
1969 Non-Darwinian evolution. Science 164:788-798.

King, M.C.; and Wilson, A.C.
1975 Evolution at two levels in humans and chimpanzees. Science 188: 107-116.

Kummer, H.
1968 Social organization of hamadryas baboons: a field study. University of Chicago Press, Chicago.

Lande, R.
1979 Effective deme sizes during long-term evolution estimated from rates of chromosomal rearrangement. Evolution 33:234-251.

Lindburg, D.G.
1969 Rhesus monkeys: Mating season mobility of adult males. Science 166:1776-1778.

Ma, N.S.F.
1981 Chromosome evolution in the owl monkey, Aotus. Amer. J. Phys. Anth. 54:293-304.

Marks, J.
in prep. Population cytogenetics of the common chimpanzee, Pan troglodytes. Ph.D. dissertation, Dept. of Anthropology, University of Arizona.

Mayr, E.
1942 Systematics and the origin of species. Clumbia University Press, New York.

1963 Animal species and evolution. Belknap, Cambridge.

Miller, D.A.
1977 Evolution of primate chromosomes. Science 198:1116-1124.

Moorhead, P.S.
1976 A closer look at chromosomal inversions. Amer. J. Hum Genet. 28:294-296.

Myers, R.H.; and Chafer, D.A.
1978 Hybrid ape offspring of a mating of gibbon and siamang. Science 205:308-310.

Ober, C.; Olivier, T.J.; and Buettner-Janusch, J.
1978 Carbonic anhydrase heterozygosity and F_{st} distributions of Kenyan baboon troops. Amer. J. Phys. Anth. 48:95-100.

Olivier, T.J.; Buettner-Janush, J.; and Buettner-Janusch, V.
1974 Carbonic anhydrase isozymes in nine troops of Kenya baboons, Papio cynocephalus (Linnaeus 1766). Amer. J. Phys. Anth. 41: 175-190.

Packer, C.
1975 Male transfer in olive baboons. Nature 255:219-220.

Paris Conference(1971), Supplement (1975)
1975 Standardization in human cytogenetics. Birth defects: Original article series. vol. 11, no. 9. The National Foundation, New York.

Raup, D.M.; and Marshall, L.G.
1980 Variation between groups in evolutionary rates: a statistical test of significance. Paleobiol. 6:9-23.

Roonwal, M.L.; and Mohnot, S.M.
1977 Primates of South Asia. Harvard University Press, Cambridge.

Rowell, T.
1969 Long-term changes in a population of Ugandan baboons. Folia primat. 11:241-154.

Rumpler, Y.; and Dutrillaux, B.
1976 Chromosomal evolution in Malagasy lemurs: 1. Chromosomal banding in the genuses (sic) Lemur and Microcebus. Cytogenet. Cell Genet. 17:268-281.

Ryder, O.A.; Epel, N.C.; and Benirschke, K.
1978 Chromosome banding studies of the Equidae. Cytogenet. Cell Genet. 20:323-350.

Sarich, V.M.; and Wilson, A.C.
1967 Immunological time scale for hominid evolution. Science 158: 1200-1202.

Shi Liming; Ye Yingying; and Duan Xingsheng
1980 Comparative cytogenetic studies on the red muntjac, chinese muntjac, and their F_1 hybrids. Cytogenet. Cell Genet. 26: 22-27.

Simpson, G.G.
1944 Tempo and mode in evolution. Columbia University Press. New York.

1953 The major features of evolution. Columbia University Press. New York.

1975 Recent advances in methods of phylogenetic inference. In W.P. Luckett and F.S. Szalay, eds., Phylogeny of the primates, pp. 3-19. Plenum, New York.

Sinnott, E.W.; Dunn, L.C.; and Dobzhansky, T.G.
1958 Principles of genetics. McGraw-Hill, New York.

Soulie, J.; and de Grouchy, J.
1981 A cytogenetic survey of 110 baboons (Papio cynocephalus). Amer. J. Phys. Anth. 56:107-113.

Stanley, S.M.
1975 A theory of evolution above the species level. Proc. Nat. Acad. Sci. 72:646-650.

1979 Macroevolution: pattern and process. W.H. Freeman, San Francisco.

Tantravahi, R.; Dev, V.G.; Firschein, R.L.; Miller, D.A.; and Miller, O.J.
1975 Karyotype of the gibbons Hylobates lar and H. moloch. Cytogenet. Cell. Genet. 15:192-202.

Vries, G.F. de; France, H.F. de, and Schevers, J.A.M.
1975 Identical giemsa banding patterns of two Macaca species: Macaca mulatta and M. fascicularis. Cytogenet. Cell. Genet. 14:26-33.

White, M.J.D.
1968 Modes of speciation. Science 159:1065-1070.

White, M.J.D.; Blackith, R.E.; Blackith, R.M.; and Cheney, J.
1967 Cytogenetics of the viatica group of morabine grasshoppers. I. The 'coastal' species. Austr. J. Zool. 15:263-302.

Wilson, A.C.; Bush, G.L.; Case, S.M.; and King, M.C.
1975 Social structuring of mammalian populations and rate of chromosomal evolution. Proc. Nat. Acad. Sci. 72:5061-5065.

Wilson, A.C.; Carlson, S.S.; and White, T.J.
1977 Biochemical evolution. Ann. Rev. Biochem. 46:573-639.

Wurster, D.H.; and Benirschke, K.
1970 Indian muntjac, Muntiacus muntjak: a deer with a low diploid chromosome number. Science 168:1364-1366.

Yunis, E.J.; Caballero, O.M.T. de; Ramirez, C.; and Ramirez Z., Efrain
1976 Chromosomal variation in the primate Alouatta seniculus seniculus. Folia primat. 25:215-224.