

The Nature and Origins of Primate Species

LAURIE GODFREY AND JONATHAN MARKS
*Department of Anthropology, University of Massachusetts, Amherst,
Massachusetts 01003 (L.G.); and Departments of Anthropology and
Biology, Yale University, New Haven, Connecticut 06511 (J.M.)*

KEY WORDS Speciation, Species, Primates, Evolution, Hybridization

ABSTRACT The living world has genetic discontinuity in it, and morphological discontinuity as well. Patterns of these discontinuities overlap to a large extent. When they do, species discrimination is unambiguous. But directly at the point of cladogenesis, there are parallel sets of processes occurring, which result in patterns that can be difficult to reconcile in a single term such as speciation. Primate "species," living and extinct, exhibit various degrees of morphological discontinuity and genetic incompatibility, which implies that a single concept of speciation may be difficult to apply universally.

The species is a fundamental unit of biology. It marks the boundary between macroevolutionary and microevolutionary processes, the virtual cessation of genetic contact among populations, and the difference between the practices of microtaxonomy and macrotaxonomy. In general, while there is broad conceptual agreement on just what a species is, it is as difficult to define "species" precisely and satisfactorily as it is for anthropologists to define "culture" (Kroeber and Kluckhohn, 1952). In this review, we examine why this is the case: processes of speciation are pluralistic; genetic discontinuities do not map precisely onto morphological discontinuities; and, within the primates, different patterns of diversification exist.

SPECIES AND SPECIATION

A species is widely recognized to be a unit in a biological hierarchy, composed of organisms, as organisms are composed of cells (Novikoff, 1945; Hull, 1980; Eldredge and Salthe, 1984; Vrba and Eldredge, 1984). The component cells of an organism bear a special relationship to one another (they are clonally derived), and the component organisms of a species bear a special relationship (they are potential mates). In addition, the component organisms of a species are genetically similar to one another, and are visually similar to one another. A species also occupies a particular niche, or has a unique way of life, in the natural world. Finally, a species is an enduring entity through time, whose longevity transcends that of any of its component organisms. These properties of a species have all been emphasized to greater or lesser extents by different schools of biological philosophy.

Species differ in the composition of their respective gene pools and in external characteristics such as skins, horns, or decorations, body size, form, and behavior. In general, there is strong concordance between species as clusters of phenotypically similar individuals with common niche specializations and as clusters of reproducing individuals with common mate-recognition and fertilization systems. Yet it is precisely because phenotypes and fertilization systems are not strictly concordant that species are hard to define and to recognize. Since, by and large,

good mammalian species are both genetically and morphologically distinct, this distinction might appear to be moot. But it is not at all moot if we consider the question of species *origins*. Genetic processes that generate reproductive isolation among closely related lineages may be phenomenologically distinct from those processes that produce a diversity of morphologically discrete forms. This is not to say that morphological divergence and genetic discontinuity cannot arise in association with one another, or as by-products of the same underlying mechanisms. However, genetic isolation can occur in the absence of any significant morphological change, and highly significant, easily discernible morphological change can occur among populations that are potentially (or even actually) interfertile. If we are interested in processes of change, and if those processes that generate morphological discontinuity are not the same as those that generate genetic isolation, then these processes could more profitably be addressed independently.

The process of speciation also impacts upon other aspects of evolutionary biology and anthropology, for example in the determination of phylogenetic relationships. In this case, as Nelson (1989) has pointed out, speciation by founder effect,¹ thought to be a dominant mode of species-formation, produces parapatry in the parent species. Figure 1 shows that as a daughter population buds off from a parent population, the daughter population is more closely related to part of the parent population than other parts of the parent population may be to one another. To attempt to infer phylogenetic relations long after the daughter population has achieved species status would therefore require a great deal of information on genetic polymorphism, both past and present.

Discussing the nature of the standpoint of physical anthropology requires recognizing that a unicellular species may be different from a multicellular species, and that a zoological species may be different from a botanical species. To the extent that primates are multicellular animals, our discussion of species is necessarily "zoocentric" (Stebbins, 1987).

Two other distinctions must be made. (1) There is a difference between the nature of a species *taxon* and the nature of the species *category*. In other words, one can explore "what is a species" (in relation to another species) apart from "what is the species" (in relation to the subspecies and the genus). The species (category) is a class, the specific instances of which are unique species (taxa) (Chiselin, 1988). (2) The nature of a species and the assignment of individual organisms to it are in principle different things. The assignment of an organism to a species is based upon judgments of its anatomical or genetical attributes, a process called "identification" by Simpson (1961). However, when we discuss the nature of species, we are concerned with the nature of populations of organisms, and not with the attributes of particular organisms.

This distinction is critical, for it bears upon views of the evolutionary processes. For "gradualism," a school of evolutionary thought derived from Fisher's population genetics and forming the dominant school of the post-WWII era, the discontinuities observable in nature are taxonomic artifacts: retreating through time, all species become more similar to one another. Thus, "gaps" between species are mainly the result of taxonomists *diagnosing* species, and do not require explanation by recourse to evolutionary processes. More eclectic views, deriving from the popularity of "punctuatedism," do not take that assumption for granted. Rather, they permit the inference—arguably the *observation*—that species are formed very rapidly relative to the extent of their durations. Consequently, when traced back through time, they may appear to remain stable. Thus the "gaps" between species are the results of the process of speciation, and require explanation.

¹This paper contains a glossary of concepts and terms from cognate fields, notably genetics, statistics, and systematics. The Glossary appears before the Literature Cited at the end of the paper.

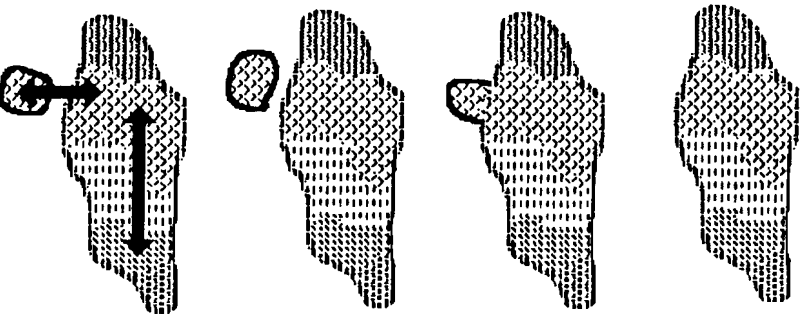


Fig. 1. The origin of a species through founder effect produces parapatry. A member of the daughter species may be more closely related genetically to a member of the cosmopolitan parent species than two members of the parent species are to one another, in spite of the reproductive isolation that divides the parent and daughter species.

THE NATURE OF SPECIES

There have been two fundamentally different conceptions of species widely accepted in this century; each has a number of variants with different emphases, and each has proved useful in certain contexts. The first is morphological, the second genetic. A third explicitly attempts to integrate the two.

Morphospecies: Species concepts based on phenotypes and their distribution

Morphological species (or morphospecies) are ultimately defined by reference to a suite of characteristics possessed by their constituent members, and absent from the members of other species. Here, some sort of phenotypic discontinuity is the key to defining a species.

The classical Platonic, typological, or essentialist species, against which Mayr (1963, 1970) has juxtaposed post-Darwinian thought, conceives of a species as a class of organisms sharing key features considered to be transcendent and meta-

physical. The philosophy underlying this particular cluster of species concepts is that each member partakes in some "essence," from which individuals may diverge slightly.

In this view, however, a species is a class or set composed of members, whose inclusion in the class is based upon the possession of attributes (Ghiselin, 1966). One important consequence of this definition is that it precludes the evolution of species for the attributes used to define the species are fixed. For a species to evolve (or for speciation to occur) in this view, one would simply have to redefine the criteria by which the species is recognized (Ghiselin, 1981).

The shared "essence," however, could be conceived materially as a morphological pattern, in which case the application would be less metaphysical. More recent versions of morphospecies adopt this approach (Sokal and Sheath, 1963). During the process of assigning individuals to species, the characteristics employed are indeed morphological, and to a large extent allocation of individuals to species and the definition of the species are identical.

Contemporary variants emphasize ways in which a trait-based species concept need not be arbitrary. For example, a species may be conceived as a group of organisms whose characteristics define a fundamental niche (or demographic function). Alternatively, there is the phylogenetic species concept of Cracraft, "an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent" (1989: 35; cf. also Nixon and Wheeler, 1990). Here the species is defined only in terms of the diagnosable apomorphies (derived characters) of its members. While the apomorphies may be genetic as well as morphological, a species is nevertheless fundamentally still a class of objects defined by the properties of its members, and the species definition collapses into the process of identification. In practice, however, this is the manner in which paleontologists may be obliged to regard species (Tattersall, 1991). Kluge's (1990) version, "the smallest historical individual within which there is a parental pattern of ancestry and descent," forms a bridge to the next category of species concepts, which we will designate as biospecies.

Biospecies: Species concepts based on gene flow and its interruption.

The most widely cited biospecies concept is the isolation concept, which takes the resemblances among organisms as epiphenomenal, and regards the fundamental nature of a species to be its exclusive gene pool (Dobzhansky, 1937; Mayr, 1942), within which the evolutionary process known as gene flow unites organisms. Here, a species is considered to be an individual (not a class), composed of parts (not members), each of which stands in a relational context to every other part: the relation is that of reproductive compatibility (Ghiselin, 1975; Hull, 1976; Mayr, 1967; Willmann, 1989).²

This species concept can be extended through time to emphasize the diachronic succession of reproductively compatible populations (Simpson, 1951; Wiley, 1978). Thus, a species defined through genetic isolation could be considered a spatially and temporally localized individual, whose constituent parts are organisms that can reproduce faithfully with one another but not with parts of other species, and who also happen to share many features in common. The process of speciation here involves the formation of reproductive isolating mechanisms, ways in which pop-

²Mayr (1967:154) reviews a number of features by which a species is to be regarded as an individual, as opposed to a class. First, a species is localized in space and time. The same species taxon cannot arise on Earth and also in another galaxy, owing to the genetic historical contingencies of its existence. Second, a species has continuity through time. "For instance, that caterpillar and butterfly are the same individual is inferred not from any similarity in their appearance, but from this continuity. The continuity of different organisms within a species is provided by their historical (common descent) connection." Third, a species is discrete—in spite of its occasionally having a fuzzy boundary, especially at the point of origin, in common with other individuals in nature, from an individual cell to an individual mountain. And fourth, a species has internal cohesion. "Organisms that together form a species have intimate connections with each other . . . due to the fact that they are derived from the joint gene pool of the species, and that they jointly contribute their genotypes to form the gene pool of the next generation."

ulations can become genetically disjunct from one another. Thus a species is defined largely through negation: by being unable to participate in another species' gene pool. Reproductive isolating mechanisms—either prezygotic or postzygotic (depending upon whether an F_1 hybrid zygote can be formed)—are generally taken to be mutually reinforcing, that is, to evolve as group-level adaptations, and to function in differentiating one population (nascent species) from another.

Another biospecies concept, also primarily concerned with gene flow, is Paterson's (1978, 1985) recognition concept. The recognition concept, however, takes reproductive isolation from other species as well as the resemblance among organisms as epiphenomenal. Parts of species look similar, and participate in an exclusive genetic community, but the process of species formation, argues Paterson, involves not isolating one gene pool from another, but rather generating new fertilization systems. That a new fertilization system makes a cluster of organisms reproductively isolated from another cluster of organisms is incidental to what the species are: it is the fertilization system itself—the manner in which a population of individuals identifies potential mates and establishes a genetic succession—that defines a species (Lambert et al., 1987).

A corollary of the recognition concept is that speciation is not an adaptive process. Indeed, whether speciation under the isolation concept (the formation of reproductive isolating mechanisms) is necessarily adaptive had already been questioned on the basis of Sewall Wright's stochastic models of evolution (Carson, 1970, 1975, 1987; Gould, 1980). The recognition concept criticizes the isolation concept for focusing attention on genetic disjunction as though it were actively achieved when genetic disjunction may be only a passive by-product of the breakdown of processes through which genetic continuity is maintained.

By focusing on the maintenance of continuity, the recognition concept inverts the fundamental tenet of the isolation concept. The emphasis is no longer on the origin of reproductive gaps, for which (Paterson [1978, 1985] argues) mechanisms do not exist, but on the breakdown of the processes through which reproductive communities actively maintain their integrity. Thus, if the isolation concept defines a species by negation, the recognition concept defines it by affirmation.

Paterson questions the notion that discontinuities among species evolved in order to separate species. As Vrba (1985:x) summarizes, "... while premating and postmating reproductive isolation exist, these phenomena are never the product of selection for isolation, but are incidental by-products or effects of divergence." Since most speciation occurs in allopatry, the evolution of isolating mechanisms is moot unless and until the populations come into secondary contact (White et al., 1990).

This concept focuses on the manner in which an organism is inclined to reproduce with another organism. Each different species possesses a specific mate recognition system (SMRS), which is a communication mode that functions between organisms of complementary sexes (Tattersall, 1989; White et al., 1990).

In summary, the recognition concept notes a distinction blurred by the isolation species concept: that of the process of speciation and its products, reproductively isolated taxa (or biospecies). Observing that the products of speciation are reproductively isolated taxa may be telling us little or nothing about the process by which species originate (Chandler and Gromko, 1989).

An integrative species concept

A recent advance in species ontology is the cohesion concept of Templeton, being "the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (1989:12). Again a species is defined by affirmation, rather than by negation (i.e., by focusing on mechanisms that make a species a species rather than on mechanisms by which it is not a different species), but, in addition, the cohesion concept is broader than the recognition concept, subsuming both the morphospecies and the biospecies.

This concept acknowledges the similarity of organisms of a single species, the

TABLE 1. Classification of mechanisms of cohesion¹

The genetic similarity (or cohesion) of a species is maintained, and its boundaries are defined, through a variety of factors:	
1.	Factors that influence the spread of genetic variation through gene flow (genetic exchangeability):
A.	Forces promoting gene flow (e.g., male recognition, successful fertilization, successful ontogenetic development)
B.	Forces limiting gene flow (e.g., isolating mechanisms, prezygotic and postzygotic)
2.	Factors that influence the spread of genetic variation through genetic drift and natural selection, and that define a species' fundamental niche (demographic exchangeability):
A.	Forces affecting the action of genetic drift, which increases genetic similarity among members of a population nonadaptively ²
B.	Forces affecting the action of directional and normalizing selection, which increase genetic similarity among members of a population adaptively (e.g., factors influencing the fixation of particular genetic variants, factors constraining the operation of natural selection, including historical, ecological, population genetic, and developmental constraints on the fate of genetic variation)

¹Based on Templeton (1989:13).

transcendental nature of gene pools, and the importance of fertilization mechanisms. However, rather than relying exclusively on how organisms find and attract mates, the cohesion concept stresses the mechanisms that maintain the integrity of the species at all phases of life-history.

According to this species concept, the integrity of a species is maintained in two general ways: participation in a common reproductive community (genetic exchangeability) and ecological equivalence (demographic exchangeability). This further serves to broaden the kinds of evolutionary forces seen to operate in defining a species, from gene flow alone to the inclusion of genetic drift and natural selection, both of which promote genetic identity among descendant organisms. Further, Templeton notes that recognizing a mate is only a part of the defining attribute of a species: there must be a potential for the zygote to develop into a viable and fertile adult as well (Table 1).

THEORIES OF SPECIATION

Morphospeciation and biospeciation

Because species are not simply genetically distinct populations, but morphologically or ecologically distinct populations as well, the process of speciation has two aspects. Not only must the divergence of gene pools be explained, but the emergence of morphological discontinuity out of continuity must also be explained. Studies of "speciation," however, almost invariably are studies of how gene pools diverge. This is "speciation" under the isolation concept. We will call this process biospeciation. The other process we will call morphospeciation: the emergence of diagnostic characters in a population.

When viewed from a distance, that is, from the standpoint of a deep time frame, biospeciation and morphospeciation coincide to a great extent. It is, however, at or around the point of cladogenesis that they can be analytically disjointed. Consequently, in a synchronic context, there will always be "species" that interbred to greater or lesser degrees, and "species" that are diagnosable to greater or lesser degrees, but these may not easily coincide.

All biological evolution is genetic. We will follow Templeton (1989), however, in recognizing two parallel sets of genetical processes involved in speciation: one set involving gene flow and directly affecting the cohesion of the gene pool (direct exchangeability), and one set involving selection and genetic drift, and directly affecting the relationships of the population to its environment and the manner by which parts of the same species self-identity (demographic exchangeability). The ultimate conclusion of a disjunction in the processes of genetic exchangeability is

biospeciation. The ultimate conclusion of a disjunction in the processes of demographic exchangeability is morphospeciation.

Insofar as the relationship between genotype and phenotype is a major unresolved problem in genetics, it is not at all clear that the emergence of new and characteristic phenotypes by which to attract mates or exploit the environment is or should be reducible to the spread of genetic elements affecting the mechanics of reproduction. Morphospeciation has less of a theoretical corpus at present than does biospeciation, possibly because the latter can at least be studied to some extent under a "beanbag" paradigm—that is, as the invasion or spread of discrete genetic elements—while the former is almost invariably epigenetic—that is, involving the expression and interaction of multiple batteries (Waddington, 1957, 1960; Arthur, 1984; Coyne, 1989). Whatever the genetic basis underlying the change in phenotype, it may carry novelties in the signaling mechanisms that hold together organisms in ecological units, and bring them together as potential mates.

Theories of speciation have classically been organized according to geographical criteria. Biologists are generally agreed that the vast majority of speciation events involve some form of spatial disjunction between parent and daughter species (Bush, 1975). But geography is not a mechanism. Allopatry by itself does not result in reproductive isolation. It may be necessary, but is certainly not sufficient. And the fragmentary nature of habitats, coupled with the diversity of habitats within a single range, enables many apparent examples of nonallopatric speciation to be recognized as microallopatric. This being the case, it would seem as though a classification of speciation organized by geography would be less informative than one organized by another criterion, for example, chromosomal, molecular genetic, ecological, or behavioral mechanisms (White, 1978; Templeton, 1981).

Chromosomes and speciation

The hereditary material in a cell is organized into discrete packages called chromosomes, visible as stable structures during cell division. All the chromosomes of a cell define its karyotype, and chromosomal or karyological traits are often diagnostic of species. Gross chromosomal changes have been implicated in the process of species formation in two fundamentally different ways. Richard Goldschmidt, in the 1930s and 1940s, derived a theory of evolution that denied the existence of discrete genes, and saw the processes of heredity to be governed fundamentally by the order and spatial orientation of the genetic material (e.g., Goldschmidt, 1937). While small changes to the organization of the hereditary material would result in what other geneticists were inferring to be point mutations, a large-scale reshuffling or scrambling of the intimate chromosomal architecture, which might occur rarely by chance, will act as a macromutational agent. This means that it will produce, suddenly, a huge effect upon a series of developmental processes, leading at once to a new and stable form, widely diverging from the former (1952:96).

Goldschmidt thus linked morphological change directly to chromosomal change, and these directly to speciation. Stripped of its fallacious assumptions about genetical mechanisms, Goldschmidt's view of speciation by a single macromutational event, a "chromosomal repatterning," was briefly revived by Wilson et al. (1974, 1975), and subsequently by Stanley (1979) and Gould (1980).

The presumption behind "chromosomal repatterning" is that genetic regulation may ultimately be affected by such a mutation. If differences in the protein-coding genes that we can study easily do not seem to correlate with differences in phenotypes (and therefore cannot cause them), then perhaps some other, more cryptic, genetic change does cause them. These genetic changes are presumably regulatory, that is, affecting the timing and expression of other genes (King and Wilson, 1975). The problem with this line of reasoning is the direct link between genotype and phenotype it assumes.

Certainly genetic pathologies are often directly expressed phenotypically. New-

ertheless, the "normal" range of phenotypic expression is hierarchically buffered or canalized (Waddington, 1957) such that it can ordinarily emerge in the presence of considerable genetic or environmental variation. The assumption of a direct and specific link between particular genes and particular phenotypes is the root of "beanbag genetics" (Mayr, 1959), and without the bridging argument from physiological genetics, the assumed direct line from regulatory mutation to new trait is gratuitous. In terms of the processes of evolution, the genome is better conceived as a functional system than as a group of discrete individuated units (Mayr, 1963; Marks, 1969, in press). It is generally taken by evolutionary geneticists that any single mutation with a significant direct effect on the phenotype will have a negligible impact on the evolution of species (Charlesworth et al., 1982; Wright, 1982; Crow, 1986:212).

Though chromosomal differentiation usually accompanies speciation, as does anatomical differentiation, the causal linkage between them is probably spurious. Extensive chromosomal repatterning can occur in the absence of extensive anatomical change, as in the genus *Muricatus* (Artiodactyla: Cervidae, Wurstler and Benirschke, 1970) or the genus *Hylobates* (Stanyon and Chiarelli, 1983; van Tuinen and Ledbetter, 1983; Marks, 1983, 1984, 1987; Cronin et al., 1984). Conversely, notable morphological diversity can be accompanied by little or nothing in the way of chromosomal differentiation, as in the order Cetacea (Arnason, 1972) or in the papionins (Rubio-Goday et al., 1976; Marks, 1983, 1984; Brown et al., 1986; Stanyon et al., 1988).

Thus, chromosomal change is neither necessary nor sufficient for morphological evolution, and cannot be considered to constitute a macromutation. An alternative role for chromosome change in the process of species differentiation was put forth by M.J.D. White (1969, 1978). Here, chromosomes are involved not so much in the direct translation into new organismal morphologies, but simply in the generation of reproductive isolation among populations. An individual heterozygous for a single chromosome rearrangement has no anatomical consequences, and perhaps at worst, minor reproductive consequences. In a structured population (as opposed to a large panmictic one), the spread of such nearly neutral chromosomal rearrangements will be augmented, and the negative effects to fitness compensated for, by genetic drift (White, 1978; Hedrick, 1981; Marks, 1983; Long, 1986; Martin, 1988; Redi and Capanna, 1988; Nachman and Myers, 1989). As these rearrangements are continually arising and reaching fixation in local populations, a threshold may be achieved whereby heterozygosity for several chromosome mutations leads to severe meiotic breakdown, and thus a sterile F₁ hybrid. This is likely, for example, to be the cause of sterility of mules, which can very rarely backcross to a horse or donkey (Rong et al., 1989).

Molecular genetics and speciation

Other kinds of genomic incompatibilities can lead to reproductive isolation in varying degrees, but their role in speciation is poorly understood. The arguments put forth for their significance in speciation are largely framed as plausibility arguments, and little evidence actually exists for the operation of these factors as primary agents of speciation. Of course, this does not mean the models are false or that they cannot apply to primates. It means only that we know the genome can behave in these manners, but it is difficult to tell whether any of these genomic operations is driving the divergence of populations in any particular case. Kose and Doolittle (1983) and Krieger and Rose (1986) classified these molecular genetic processes into speciation modes.

Genomic disease.

Based on the phenomenon of hybrid dysgenesis in *Drosophila melanogaster*, this mode invokes the invasion of the genome by transposable (or movable) genetic elements. The paradigmatic example involves the fact that strains of *D. melanogaster* collected since the 1960s have bits of genetic information known as "P

elements" in their genomes (and are known as P strains), while those collected before the 1960s and the stocks derived from them lack these elements (and are known as M strains). The P elements code for proteins that permit the elements to be copied and transposed—but they also code for their own repressor. Thus, a P strain is genetically stable, for although P elements are present, the repressor proteins are also present in the cellular cytoplasm. When a sperm from a P strain fertilizes an egg from an M strain, however, the P elements enter cytoplasm that lacks the repressor. Consequently, they transcribe, reinsert themselves, and cause extensive mutational damage—and thereby hybrid sterility (i.e., "dysgenesis") (David and Capy, 1988; Snyer and Doolittle, 1988; Finnegan, 1989). However, whether this system is in fact a precursor to speciation has been disputed (Kidwell and Peterson, 1991).

Genome incompatibility

Here the detectable differences in genome composition between closely related taxa for features such as repetitive DNA are considered to prohibit the genetic system of an F₁ hybrid from functioning properly. As some classes of repetitive DNA are known to evolve "in concert," such that sequences within the same genome become homogeneous, this could provide a mechanism for a large-scale divergence of two gene pools, even if the DNA sequences themselves are not coding, functional genes. Rose and Doolittle (1983) subsume "molecular drive" (Dover, 1982) under this heading.

Genome resetting

Where the two previous models invoked genetic processes causing effects strictly at the genetic level (in terms of crossing-over, pairing, mutagenesis, and linkage relationships), genome resetting seeks to relate genetic processes to presumptive phenotypic consequences. Ultimately, this is based on the early work of Britten and Davidson (1971), wherein the newly discovered repetitive DNA was taken to have a macromutational role in evolution: changes to the genome had direct and dramatic consequences for the phenotype. Regardless of the sophistication with which this approach incorporates genome structure into evolutionary models, it is certainly overly simplistic in inferring once again a direct relationship between genotypic change and phenotypic change. It is a macromutational model based on repetitive DNA.

Genomic turbulence

Additionally, different patterns of interspersion of repetitive DNA elements could create problems in meiotic pairing where both genomes exist in the same individual, i.e., in an F₁ hybrid. The result of such mispairing, coupled with crossing-over, may be aneuploidy in the germ cells of the zygote, and consequent infertility.

These four molecular genetic processes are possible means by which genetic incompatibility between two populations might arise. While the cessation of gene flow might not be complete, as mating and backcrossing may not be wholly eliminated, the operation of these mechanisms may initiate the process of biospeciation.

However, all these genetic models share the assumption that speciation begins with the generation of a genetic incompatibility, and that it is completed by selection against hybridization when the populations come into secondary contact. Morphospeciation would therefore occur as a by-product of selection against hybridization during the phase of secondary contact. These theories, however, do not deal explicitly with the origin of apomorphic characters, and no mature corpus presently exists to explain them, for they relate to the unresolved genotype-phenotype problem.

Ecology, behavior, and speciation

There are other routes by which gene pools may be divided: for example, genetic alterations that ultimately translate into differences in courtship or other behaviors that bring mates together—these may be more directly associated with morphospeciation, particularly in diurnal primates for whom the reproductive community is often defined by visual (morphological) signals. The adaptive diversification of populations to different environments may incidentally carry with it changes in the signals by which group members are recognized. The extraordinarily diverse signals that distinguish primate breeding populations and species may well be examples of this: pelage and vocalizations in arboreal primates; olfactory cues and vocalizations in nocturnal primates; and primarily visual cues (differences in external morphology and behavior) in terrestrial primates (see Pether et al., 1977; Tattersall, 1982, and Jenkins, 1987, on lemurs; Musser and Dagosto, 1987, and Niemitz et al., 1991, on tarsiers; Hershkovitz, 1977, on New World monkeys; Groves, 1984, and Marshall et al., 1984, on gibbons; Kingdon, 1988, on cercopithecines; Jolly, 1991, on papionins).

While these phenotypic alterations do not necessarily lead to an inability of two organisms to form fertile hybrids, they do tend to divorce two gene pools from one another. Thus, they can result directly in biospeciation, though not due to the introduction of some specific molecular or chromosomal device. Here, biospeciation occurs through either: (1) disruption of mating; or (2) impaired development of F₁ hybrids due to selection for different developmental pathways in the different ecological contexts of the parent populations. In the former situation, a healthy hybrid could be produced, but is not; in the latter, a hybrid is produced but is genetically disadvantaged. We emphasize that, just as there is no mature corpus theory in physiological genetics for predicting the phenotypic expression of particular genetic alterations, likewise, there is no such corpus for predicting how any genetic changes at the root of behaviorally or ecologically induced phenotypic differentiation may affect reproductive capabilities.

Patton and Smith (1989) highlight the distinction between genetic isolation (involving the disruption of gene flow) and reproductive isolation (the cessation of mating). In effect, "reproductive isolation" has been loosely applied to a number of technically distinct circumstances. We will organize these situations as follows. (1) Reproductive isolation, narrowly construed, occurs when individuals from different populations do not mate, for whatever reason, including the trivial case of allopatry among potentially interbreeding units. Very similar populations of *Eulemur flavus* live in widely separated regions on either side of the island of Madagascar: such geographic separation is presumed to be a by-product of recent habitat fragmentation. (2) Reproductive incompatibility is narrower than reproductive isolation, and occurs when individuals from different populations cannot mate (due, for example, to differences in the environmental, physiological, or behavioral stimuli that precipitate sexual responses). (3) Genetic isolation is achieved when gene flow does not occur, for whatever reason. (4) Genetic incompatibility is narrower than genetic isolation, and is achieved when gene flow cannot occur (due, for example, to infertility between the two parental populations, impairment of meiosis in F₁ hybrids, or gestational failure). While these have often been conflated in species determinations, it is worthwhile to distinguish them analytically.

Among speciating organisms, there indeed exists a variety of combinations of reproductive isolation, reproductive incompatibility, genetic isolation, and genetic incompatibility (Table 2). Since mating and fertility are not binary variables, a wide variety of gradations between the categories in Table 2 is theoretically possible. Biospeciation is generally regarded as complete when organisms are genetically incompatible, although Paterson (1985) would define it on the basis of reproductively isolated sensu stricto—i.e., whether or not mating occurs. Genetic incompatibility guarantees the integrity of species as individuals, since it is

TABLE 2. States of reproductive isolation

Isolation status	A Two species	B Two species	C Two species?	D Two species?	E One species?	F One species
Reproductive compatibility: Cannot mate (-) or mating possible (+)	-	+	+	+	+	+
Reproductive isolation: In nature mating does not occur (-) or does occur (+)	-	-	-	+	+	+
Genetic compatibility: Gene flow not possible (-) or possible (+)	-	-	+	-	+	+
Genetic isolation: In nature gene flow does not occur (-) or does occur (+)	-	-	-	-	+	+
		Gene flow is prevented by reproductive isolation and hybrid infertility	Gene flow is prevented by behavioral factors only	Gene flow is prevented by hybrid infertility only	Gene flow is not prevented but is limited	Gene flow is not prevented but is limited

A. Populations genetically isolated due to reproductive incompatibility, reproductive isolation, and genetic incompatibility: two good species.

B. Populations reproductively compatible but genetically isolated due to combination of hybrid infertility and normal avoidance of mating in nature.

C. Populations reproductively compatible but genetically isolated due to behavioral factors that prevent mating in nature (caprine hybrids are fertile).

D. Populations reproductively compatible but genetically isolated due to hybrid infertility (individuals readily hybridize in nature but hybrids cannot backcross to either parent species).

E. Populations reproductively compatible but partially genetically isolated due primarily to behavioral factors that limit gene flow: considered members of a single polytypic species or of a syngameon of closely related species, depending on emphasis on gene flow or demographic exchangeability.

F. Freely interbreeding populations: one good species.

through genetic incompatibility that permanent discontinuity of gene pools arises (except under the most unusual circumstances, such as horizontal transmission of viruses [Benveniste, 1985]).

REPRODUCTIVE AND GENETIC ISOLATION IN LIVING PRIMATES

The order Primates contains roughly 200 living "species"—unique clusters of combinations of anatomical, behavioral, chromatic, and/or karyotypic apomorphies in reproductively compatible populations. As such, primate species are essentially statistical phenomena for which some degree of reproductive isolation from closest relatives is often inferred but not known.

Between one biospecies and two

Primates exhibit virtually the entire spectrum of intermediates between complete genetic and reproductive isolation of populations (i.e., multiple biospecies, Table 2, category A) and complete interbreeding (i.e., a single biospecies, Table 2, category F). Some pairs of species, distinct enough to be placed in different genera or subgenera—including *genus* and *mangabeys*, *genus* and *macaques*, and *gibbons* and *siamangs*—hybridize in captivity producing offspring that may have limited (or zero) fertility (Table 2, category B; see Lernould, 1988). Many of these hybridizing species pairs have markedly different anatomical and social structures as well as different karyotypes. Some (for example, *genus* and *mangabeys*) form polyspecific associations in nature and hybridize in captivity, but not in nature (Lernould, 1988). Others (for example, *gibbons* and *siamangs*) tend to avoid contact

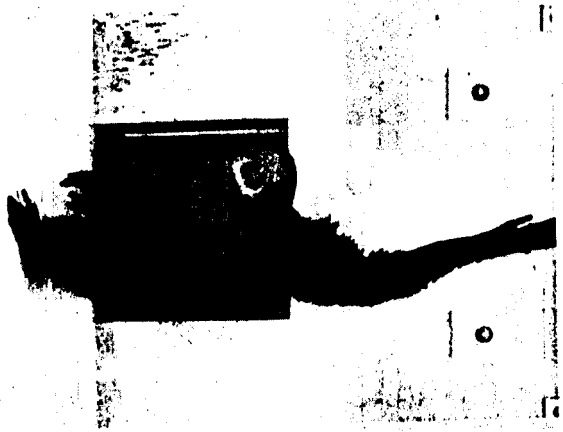


Fig. 2. The aging sole surviving stabon, Shafer-Shawn, was born August 20, 1976. Photograph courtesy of Yerkes Regional Primate Research Center of Emory University.

in the wild (but see MacKinnon and MacKinnon's 1977 documentation of a wild male gibbon and female stamang traveling and chorusing together over a brief period of time).

Gibbon-stamang interbreeding represents an interesting example of captive hybridization among karyologically and phenotypically distinct primates (Shafer et al., 1984). Stamangs weigh about twice as much as gibbons, and they differ in developmental schedule, pelage, vocalizations, chromosome number and banding patterns, hard-tissue anatomy (including skull shape, body proportions, and joint structure), and special adaptations (including interdigital webbing and a specialized throat sac, both present in stamangs but not in gibbons). Yet, in the mid-1970s, two offspring were born to a male gibbon *Hylobates lar muelleri* and a female stamang *Hylobates syndactylus* housed together at the Atlanta zoo (Rummel et al., 1976; Myers and Shafer, 1979; Shafer et al., 1984) (Fig. 2). The "stabon" hybrid inherited full haploid sets of chromosomes from each parent—22 from their father and 25 from their mother—with no obvious autosomal matches, and major differences in heterochromatin and overall DNA content (Pellicciari et al., 1988). Both offspring were anatomical mosaics intermediate in morphology between their parents. Whereas the fertility of the sole surviving stabon remains untested, it seems probable, given the differences between the maternal and paternal chromosomes she carries, that meiotic breakdown would prevent backcrossing (Table 2, category B).

Among primate clades that rapidly accumulate karyological changes (including tarsoids, lemuroids, cercopithecines, and many ceboids, in addition to hylobatids; see Brumback, 1973; Jones et al., 1973; Galbreath, 1983; Hershkovitz, 1983, 1984; Prouty et al., 1983; Marks, 1983, 1984; Rummel et al., 1990; Nimitz et al., 1991), karyological distinctions have, on occasion, been used to help diagnose biospecies or even genera. This is an unreliable criterion, since karyological changes do not

Godfrey and Marks] NATURE AND ORIGINS OF PRIMATE SPECIES 51

always preclude successful hybridization, or may be polytypic in a species (e.g., Nevo, 1982; Nance et al., 1990; Bauchau, 1990, for rodents). Subspecific chromosomal differences are well documented for primates, as well as for other mammals (Rummel and Albignac, 1975; Yunis et al., 1976; Buehner-Janusch and Hamilton, 1979; Mundy, 1990; Couturier and Leronald, 1991).

Indeed, many karyologically diverse primate clades, just as *Hylobates* spp. produce hybrids in captivity and even sometimes in nature (cf. Brockelman and Gittins, 1984, for example, on natural hybrids of the *Hylobates lar* species group; Struhsaker et al., 1988, on natural hybrids of gnomons). Some karyologically distinct species capable of producing fertile hybrids in captivity live in sympatry without mating (Table 2, category C). This is what normally occurs among distantly related gnomons, for example (Struhsaker et al., 1988). Furthermore, the question of genetic isolation in nature is moot when chromosomally distinct sister taxa are allopatric for then they do not even get a chance to hybridize. Nevertheless, large karyological differences are likely to imply genetic incompatibility, and clades that exhibit great chromosomal diversity are likely to comprise numerous genetically isolated species.

All known pairs of primate species that produce hybrids in nature are able to backcross to both parent species. Thus, no primate species are known to belong to category D of Table 2, although such pairs are well documented among pocket gophers and other animals (Barton and Hewitt, 1989; Patton and Smith, 1989; Patton, 1990). In such cases, parent species clearly accept each other as mates, but hybridization is limited to F_1 individuals due to hybrid infertility. Genetic isolation is apparently produced through chromosomal divergence and not through the divergence of specific mate recognition systems. Taxa are therefore genetically but not reproductively isolated.

Kummer et al. (1970; cf. also Nagel 1971; 1973) believed that hamadryas and anubis baboons, which possess striking differences in anatomy, mating behavior, and social organization, produce natural hybrids that backcross to one parent species only. Hybridization was observed in a narrow zone of contact, when male hamadryas abducted female anubis baboons into their own hamadryas groups. Due to the failure of anubis males to herd females, Kummer et al. (1970) believed that gene flow must be unidirectional. However, subsequent study of baboons in the hamadryas-anubis hybrid zone has shown that male hamadryas will join anubis groups and mate with anubis females within them (Sugawara, 1979; Nyström, 1991). The resulting mixed hybrid groups consist largely of anubis baboons, and form reproductive units displaying a variety of gender compositions, including the unimale bisexual units characteristic of hamadryas baboons, the multimale-multifemale units characteristic of anubis baboons, and pair groups characteristic of neither parent. Gene flow among hamadryas and anubis baboons does indeed appear to be bidirectional (cf. also Shotake, 1981). In any case, if there is any bias in the directionality of gene flow among hamadryas and anubis baboons, it is produced through the divergence of social and mating systems rather than through genetic incompatibility.

Many papionins and some cercopithecines clearly belong in category E of Table 2: they breed in captivity, are infertile, and occasionally hybridize in nature (Leronald, 1988; Struhsaker et al., 1988). Particularly among papionins, morphospeciation has outpaced biospeciation. Extant papionin species tend to be genetically compatible but reproductively isolated and morphologically distinct to varying degrees. Natural hybridization of papionins and of cercopithecines occurs most commonly along narrow zones of contact among closely related taxa. Rarely, it also occurs among species that normally live in sympatry without mating—especially under disturbed conditions, or when there is a shortage of appropriate conspecific mates. F_1 hybrids produced by these unions are generally fertile; captive hybrids of congeneric species of *Macaca*, *Cercopithecus* or *Papio*, as well as hybrids of closely related genera such as *Theropithecus* and *Papio*, or *Macaca* and *Cercopithecus*, backcross to parent species. Since most of these animals will hybridize in captivity,

they presumably owe whatever natural genetic isolation they possess to spatial disjunction and to the divergence of their ecological cohesion and mate-signaling processes.

Field studies of macaques demonstrate how variable behaviorally constrained reproductive isolation can be. Natural hybrids occur along some contact zones of contiguous (parapatric) populations belonging to closely related species (cf. Bernstein, 1967; Fooden, 1964, 1971; Southwick and Southwick, 1983, on macaques of the fascicularis group; Groves, 1980, and Supratna et al., 1990, on macaques of the silenus-sylvanus group). More distantly related macaque species normally overlap geographically without hybridizing in nature, yet they readily hybridize in captivity. The likelihood of natural hybridization in macaques tends to increase in rough accord with proximity of relationship, but even closely related, naturally hybridizing species are morphologically distinct (cf., Albrecht, 1978, on macaques of the silenus-sylvanus group).

A parallel situation occurs among savanna baboons, where hybridization has been observed in most, but not all, zones of population overlap (CJ Jolly, 1966, 1967, 1991; Maples, 1972; Jolly and Brett, 1973; Samuels and Altmann, 1986). These animals are treated by some primatologists as a single polytypic biospecies (*Papio cynocephalus*, comprising olive or anubis, yellow, chacma, and Guinea baboons), and by others as several parapatric species. But savanna baboons comprise only part of the natural syngameon (i.e., the largest unit of interbreeding in a group of hybridizing species) of baboons; hybridization with hamadryas has led still other primatologists to synonymize *P. cynocephalus* and *P. hamadryas* (Szalay and Delson, 1979). Here, there would be three species of *Papio*—*P. hamadryas* (savanna and hamadryas baboons), *P. sphinx* (mandrills), and *P. leucophaeus* (drills).

Natural hybridization of anubis and gelada baboons further complicates the picture (Dunbar and Dunbar, 1974). *Theropithecus gelada* differs markedly from both savanna and hamadryas baboons in both soft- and hard-tissue anatomy (Jolly, 1972). Whereas little information is available on the few recorded natural hybrids of gelada and anubis baboons, captive examples prove that crosses of gelada and anubis, as well as of gelada and hamadryas, produce fertile offspring (Dunbar and Dunbar, 1974).

It is possible, of course, that hybrids may be fertile but nevertheless suffer long-term reproductive disadvantage. There is some evidence of reduced fertility among natural hybrids of sympatric, distantly related cercopithecines (*Ceropithecus mitis* × *C. ascotius*; Struhsaker et al., 1988). It seems that none of the few known male F₁ hybrids of blue and reddish monkeys has successfully fathered offspring, and female hybrids have relatively long interbirth intervals, although they successfully backcross to both parent species.

Genetic contact among potentially hybridizing morphospecies

A number of factors may affect gene flow among potentially hybridizing morphospecies. First is the ease with which polyspecific associations form under normal and abnormal conditions, and, once formed, the ease with which they yield successful consorts. Second is the actual degree to which environments are disrupted; interspecific hybridization, especially of more distantly related species, may occur only under environmental perturbation. Third is the social fate of F₁ hybrids and hybrids of subsequent generations.

Mate recognition occurs within the context of broader suites of signals that affect affiliation, bonding, agonism, and indifference during nonmating as well as mating seasons (cf., Tattersall, 1989). In effect, mate recognition can be seen as one aspect of the complex processes that allow species to self-identify (see Swartz, 1983; Yoshikubo, 1985, 1987; Fujita, 1987, 1990). Macaques, for example, appear to have the capacity to discriminate between members of their own and closely related species on the basis of visual cues alone. Some higher primates also appear to be

able to recognize members of another species as belonging to a distinct class (see Fujita and Matsuzawa, 1986, on chimpanzees).

Normally, polyspecific associations differ dramatically in character from conspecific associations. Polyspecific associations are often temporary, passive, and context-specific, and although active interactions occasionally occur, especially among ceboids, they usually do not entail hybridization (see Kummer, 1968, on gelada and hamadryas baboons; Bernstein, 1967, and Bernstein and Gordon, 1979, 1980, on macaques; A. Jolly, 1966, on collared and ring-tailed lemurs; Richard, 1970, on howler and spider monkeys; Mittermeier, 1973, and Maple and Westlund, 1975, on spider and capuchin monkeys; Abordo et al., 1975, on squirrel monkeys and uakaris). Often, the more dominant species simply displaces the other, with little intermingling. Territorial disputes almost always involve members of the same species, rather than members of different species, and polyspecific associations tend to elicit little overt physical contact, particularly among macaques (Bernstein, 1967, 1968; Bernstein and Gordon, 1980). Lone individuals attempting to transfer into social groups of a different species may encounter little resistance, but also little active encouragement, from group residents. Thus, active social bonding may never occur.

This is not always the case, however. Samuels and Altmann (1986) report rapid social assimilation of a male anubis baboon into a cynocephalus group. The new male fathered five of the 12 infants who were conceived in the ensuing 6 months. But only long-term study can reveal the true extent to which such cases of apparent complete social assimilation results in successful consorts. For example, the mixed Awash groups of hamadryas and anubis baboons have only recently begun to reveal differences in the mating successes of hamadryas and anubis males. Hamadryas males living in predominantly anubis groups have relatively low frequencies of consorts with peak estrus anubis females despite their high frequencies of affiliative nonconsort interactions (Nysstrom, 1991).

Many cases of natural hybridization occur along narrow zones of contact with sharp demarcation of ecological boundaries, or in limited localities within large zones of sympatry, and only when the pool of potential conspecific mates has been restricted by historical events (Struhsaker et al., 1988). Those aberrant conditions may well be rare, but normal; that is, they may exist even without human interference. Certainly, natural barriers to hybridization vary greatly and are contingent upon historical circumstances.

The social fates of natural hybrids also vary greatly. In some cases, hybrids form isolated groups (Nagel, 1973; Sugawara, 1979); in others, they become socially integrated into groups of either parent species (Samuels and Altmann, 1986; Struhsaker et al., 1988). While detailed comparisons of the degree of normal social integration among hybrids versus nonhybrids are lacking, there is some evidence, based on research on macaques in captivity, that hybrids may not become fully integrated into social groups of parent species, and that groups composed entirely of hybrids may not form stable social cores (Williams, 1983). On the other hand, Struhsaker et al. (1988) report complete social integration of hybrid blue and reddish monkeys, who behave in territorial disputes as full members of the parent group in which they live.

Mate recognition is sometimes context-dependent; it may involve quantitative preferences rather than absolute binary switches. Captive male macaques have been shown to experience weaker hormonal responses to extra-specific than to conspecific females in estrus, with correspondingly longer latencies prior to overt sexual response (Bernstein and Gordon, 1979). Matings of distantly related macaque species will not ordinarily occur if potential mates are placed in large, mixed-species groups that also include conspecific potential mates (Bernstein and Gordon, 1980).

In summary, what is most striking about hybridization in primates is the extent to which the fertility of hybrids (and the degree of chromosomal divergence within clades) is uncorrelated with the morphological divergence of parent species. Some

phenotypically very different parent species can produce fertile hybrids; others apparently cannot. Thus, morphospeciation is not a direct corollary of biospeciation, and biospeciation is not a direct corollary of morphospeciation. Furthermore, the propensity of two species to hybridize is influenced by the divergence of specific mate recognition systems, and by a variety of social and environmental factors—not solely by their genetic similarity.

PATTERNS OF MORPHOSPECIATION AND BIOSPECIATION AMONG PRIMATES

Patterns of morphospeciation describe the integration and distribution of characteristics by which populations may self-identify, and which serve as differentia from other taxa. These may be adaptive or nonadaptive, and are the result of processes subsumed under "demographic exchangeability" by Templeton (1989). For example, they may entail particular adaptive relationships between anatomical complexes and geographic or ecological variables. They may also entail particular associations among anatomical or behavioral features. Examples will be given below.

Patterns of biospeciation are patterns of continuity and discontinuity in gene flow, leading to the formation of two gene pools from one. They may depend primarily upon population structure and nonadaptive variations of the genome.

The purpose of analytically divorcing morphospeciation from biospeciation is to gain an appreciation of the plurality of processes by which one taxon becomes two. Biospeciation and morphospeciation intersect to bring about the ultimate disjunction of both gene pools and phenotypes—in other words, to create new systems of genetic and demographic exchangeability.

Patterns of ecogeographic variation in primates

Many studies of morphological differentiation among geographically separated sister taxa have focused on univariate comparisons, which often only poorly distinguish closely related taxa. Nevertheless, some multivariate studies do exist (see recent review by Albrecht and Miller, 1992) and even univariate studies have revealed some interesting patterns. Studies of island isolates (Groves, 1970; McGuire, 1974; Poirier, 1977; Tattersall, 1977, 1979; Albrecht, 1980; Sussman and Tattersall, 1981) and populations that have passed through genetic bottlenecks (Poirier, 1977) have demonstrated significant differences between isolate and parent populations. Particularly interesting are studies of isolates whose founding dates are known. St. Kitts vervet monkeys (*Ceropithecus aethiops*) differ from their African counterparts in body size and coat characteristics as well as some dental characteristics after a separation of only several hundred years (Colyer, 1948; Ashton and Zuckerman, 1950, 1951a,b,c; Ashton, 1960; McGuire, 1974). They have also adapted to a variety of habitats that are quite different from those of parent populations (see especially McGuire, 1974; Poirier, 1977).

Even more informative have been studies of ecogeographic variation of major primate taxa (that is, phenotypic variation within its ecological and geographic context). Studying morphological variation within an ecogeographic framework allows us to address two questions that bear directly on processes of speciation: (1) how are the patterns of morphological differentiation distributed with respect to geographic and ecological variables? and (2) are the patterns of morphological differentiation concordant across levels of taxonomic rank? If intraspecific patterns duplicate interspecific patterns, this would suggest that the processes leading to local differentiation are also involved in producing between-species differences (Albrecht et al., 1990; Albrecht and Miller, 1991).

For example, while patterns of body size variation have been described in primates, they differ in clade-specific ways that are not yet understood. As is true of mammals in general, patterns of ecogeographic body size variation among primates fall into two general categories: (1) ecocline and (2) latitudinal. Ecocline patterns hold for lemurs and baboons (Godfrey and Petto, 1981; Popp, 1983; Vitz-

thum, 1986; Godfrey et al., 1990; Albrecht et al., 1990). Latitudinal clines generally hold for macaques (Albrecht, 1980). Other primate species show patterns of body size differentiation that fit neatly into neither ecocline nor latitudinal expectations, apparently responding to temperature gradients and to variation in habitat in a more complex, multifactorial fashion (Albrecht et al., 1990).

Ecogeographic size variation among lemurs contrasts sharply with that of macaques. Lemur taxa from arid southern Madagascar tend to be smaller in body size than closely related taxa from the dry west, which are in turn smaller than sister taxa from the humid eastern rain forest, in turn smaller than sister taxa from the mosaic central highlands. This pattern of body size variation holds for intraspecific as well as interspecific comparisons, and for extinct as well as extant taxa (that is, for animals varying in body size over a range equal to that of all living primates outside of Madagascar). In contrast, macaque body size does not bear any relationship to variations in rainfall or resource productivity. Some species (such as *Macaca sinica*, the toque macaque) live in habitats as diverse as those of all of Madagascar, ranging from arid to dry deciduous forest to moist evergreen forest, without showing ecocline influence on body size differentiation. Instead, increases with increasing latitude and decreasing temperature. This pattern is evident interspecifically for several superspecies groups of macaques (including the *sinica* and *fascicularis* groups) and intraspecifically for several geographically widespread species, with minor exceptions (Albrecht et al., 1990).

Clearly, understanding differences in patterns of morphological differentiation such as those manifested by lemurs and macaques requires careful measurement of both the patterns themselves and of the variables that might influence them, such as life histories, resource utilization, and energy expenditure of the organisms involved. It seems likely, for example, that niche breadth will influence how finely body size tracks resource availability, at least among organisms that are resource- or energy-limited. But niche breadth is only one variable in a complex set of interactions.

The intersection of morphospeciation and biospeciation in primates

Where morphological divergence occurs in the absence of chromosomal divergence (as in the papionins), the morphospecies that comprise such clades may achieve genetic isolation through the emergence of new reproductive and demographic cohesion mechanisms. Because such morphospecies are not insulated in any absolute sense from the invasion of foreign genes, biospeciation is not guaranteed. Yet, given sufficient *de facto* reproductive isolation (without incompatibility) over sufficiently long periods of time, anatomical and behavioral changes that reduce their probability of natural hybridization may accumulate. When the probability of natural hybridization becomes effectively zero, the morphospecies will have become true biospecies. In such clades, the acquisition of genetic incompatibility is incidental to the process whereby reproductive (and therefore genetic) isolation arises. Prezygotic barriers here precede postzygotic barriers, and are not necessarily connected to them.

In other clades (such as hylobatids, lemurs, some ceboids, and to some extent, cercopithecids, with strikingly variable karyotypes), rapid chromosomal diversification accompanies varying degrees of morphological or behavioral diversification. Here, genetic isolation can precede, and can occur largely in the absence of, the evolution of morphological and behavioral diversification. Postzygotic barriers can begin and effectively complete the process of biospeciation, without a necessary connection to morphospeciation. In many cases, it must be noted, karyological differentiation is accompanied by variation in superficial phenotypic traits, such as external coat characteristics, olfactory signals, or vocalizations. To that extent, morphospeciation parallels biospeciation, but would go undetected by a paleontologist or skeletal anatomist. Furthermore, these species identifiers may not track environmental parameters in any apparent way.

Patterns of biospeciation may be affected by demographic and socioecological characteristics of clades (Wilson et al., 1975; Templeton, 1980b; Cronin et al., 1984; Marks, 1983, 1987). The probability of fixation of adaptively neutral chromosomal rearrangements is largely set by the social and ecological dynamics of the breeding population. Clades whose species are highly territorial, not very vagile, divide into small structured reproductive units (especially, monogamous breeding pairs), live on fairly discontinuous substrates (such as tree canopies), and have small effective breeding populations with relatively large amounts of inbreeding, should tend to exhibit high rates of fixation of new chromosomal variants, and thus have a relatively high probability of chromosomal speciation. Genetic drift will maximize the extent of between-group genetic variation, and selection against hybrids may contribute to the process through which biospeciation is achieved.

On the other hand, clades of organisms that are not territorial, have high vagility, live on generally continuous substrates, and have large effective breeding populations (such as papiomins), tend not to exhibit chromosomal speciation. Gene flow maximizes the homogeneity of the groups (Melnick and Kidd, 1983; Melnick, 1988; Marks, 1987). For such clades, biospeciation will depend more on behaviorally induced reproductive isolation arising in allopatry than on chromosomally induced genetic incompatibility. Where genetic incompatibilities ultimately arise, they may do so as incidental byproducts of adaptive morphospeciation, and the sources of such incompatibilities may involve other (nonchromosomal) genomic features. In such cases, the importance of selection against natural hybrids may be trivial.

In summary, clade-specific patterns of morphological, behavioral, and chromosomal divergence exist among primates. Primatologists need to quantify these patterns, as well as possible explanatory variables, in order to understand the plurality of processes of speciation that affect primates. While it is clear that there is no necessary short-term relationship between morphospeciation and biospeciation, there may be an indirect relationship between the two. Both may be predictable as complex functions of population genetic and socioecological variables that characterize particular clades.

FOSSIL PRIMATES

Paleospecies diagnosis

Over 100 extinct primate genera are currently recognized, comprising well over 100 paleospecies (Szalay and Delson, 1979). Paleospecies are, operationally, fossil morphospecies, for which information on phenotypic variation not preserved in hard-tissue anatomy is absent. From the pattern of hard-tissue discontinuity and trait distribution in the fossil record, we may be able to infer that cladogenesis has occurred.

However, paleospecies are not species in the sense that they are verifiably reproduced or genetically isolated (Templeton, 1982; Cracraft, 1983, 1987; Tattersall, 1986, 1991). Given what we know of pattern and process among extant species, we can anticipate that some diagnosable morphospecies will belong to syntaxons that include other morphospecies with which they occasionally share genes. We can also anticipate that, to the extent that biospecies originate through chromosomal mechanisms, they may be difficult to diagnose morphologically, especially when those markers must be skeletal. If one is interested in the problem of extracting processual information from the pattern and tempo of morphological transformation in the fossil record, then understanding the limits of paleospecies diagnosis becomes extremely important.

Identifying paleospecies requires assessing patterns of discontinuity as well as continuity in hard-part morphology. The common procedure is to find unique clusters of apomorphies that distinguish groups of individuals (Eldredge and Tattersall, 1975; Cracraft, 1983, 1987; but see Gingerich, 1976, 1979; Rose and Bown, 1986). There is some question as to how well such clusters generally correspond to neontological morphospecies or biospecies. Tattersall (1986, 1991) has defended the

view that paleontologically diagnosable mammalian morphospecies underestimate the number of biospecies they actually represent, whereas Templeton (1982) has defended the opposite view. In part, such divergent views highlight the lack of necessary correspondence between morphospeciation and biospeciation: some morphospecies before they effectively biospeciate, while others morphospeciate before they effectively biospeciate. In other words, both Tattersall and Templeton may be right, but for different taxonomic groups.

Since the discrimination of biospecies from the fossil record is an intractable problem, the goal of paleospecies diagnosis should be to approximate neontological morphospecies as closely as possible. Ideally, reconstructed groups of synchronous paleospecies should exhibit patterns of intraspecific and interspecific variation similar to those exhibited by modern taxa (Simons and Pilbeam, 1965:101). Being able to diagnose species at any time horizon is prerequisite to exploring diachronic patterns of species origination, transformation, and extinction (cf. Eldredge, 1971; and Simons, 1980; Rose and Bown, 1986; Tattersall, 1986; Levinton, 1989) as well as sequences of evolutionary change.

Analytical concerns

Largely because of the fragmentary nature of fossil remains and small sample sizes, most investigators have relied on univariate tools, such as the coefficient of variation (CV, standard deviation/mean, usually expressed as a percentage), maximum/minimum ratios, and range/mean ratios, for taxonomic discrimination (Walker and Teaford, 1991), as well as probabilistic models (Lieberman et al., 1988). These are essentially univariate, in that they do not address possible differences in the covariance structure of different taxa.

The most commonly employed univariate statistics, such as CVs, are all scale-free measures of relative dispersion. If they are effective as diagnostic tools, it is because mixed-species samples tend to exhibit greater relative dispersion than do single-species samples (Simpson et al., 1960; Gingerich, 1974; Gingerich and Schoeninger, 1979; Kay, 1982; Kay and Simons, 1983). Kay (1982) and Kay and Simons (1983) argued that, in principle, samples of extinct species from single assemblages should be no more variable in any particular character than samples of their closest living relatives. For any character, then, the maximum interspecific variation exhibited by related extant species could provide an upper limit for the variation expected of an extinct sister species. In the past decade, measures of dispersion have been increasingly applied in just this manner to problems of taxonomic discrimination among primates (for example, Blumenberg, 1985; Wood, 1985; Stringer, 1986; Groves, 1989), with somewhat mixed results (Plavcan, 1989, 1991; Miller, 1989, 1991).

Unfortunately, even the best of these tools, the CV, is effective only under rare circumstances, and all are problematic. Maximum/minimum ratios allow no correction for differences in absolute scale: a range of 10 mm can yield an infinite number of maximum/minimum ratios, depending on where the sample is centered. Maximum/minimum ratios are mathematically appropriate only in comparisons of samples centered at approximately the same mean. Maximum/minimum ratios are also strongly influenced by variation in sample size, and small samples are notorious for underestimating true population ranges (Pearson, 1932; Simpson et al., 1960).

Both the range/mean statistic and the CV compare a measure of absolute variation to a measure of absolute size, but they are, like maximum/minimum ratios, strongly influenced by sample size. Sokal and Rohlf (1980) published a correction for small sample size and the procedure for calculating associated confidence limits (see also Lewontin, 1966). When applied (e.g., Miller, 1991), these confidence limits may reveal how poor a taxonomic discriminator the CV can be. Simpson et al. (1960) found that linear dimensions measured for samples of single species generally have CVs lower than 10%. Accordingly, assemblages

TABLE 3. Comparison of coefficients of variation (CV) for mixed species and single species assemblages for area and linear dimensions and for sexually dimorphic cercopithecoidea (Papio) and monomorphic lemurus (Propithecus Indri, and Megaladapis)

Species	N	CVs for humeral		CVs for square root humeral output area	
		Caput area	19.9	4.9	5.4
<i>Propithecus diademata</i>	5	9.9	19.9	4.9	9.8
<i>Propithecus verreauxi</i>	10	10.9	9.9	5.4	5.0
<i>Indri indri</i>	10	9.9	9.9	5.0	5.0
<i>Papio hamadryas</i>	14	24.5	24.4	12.9	12.7
<i>Papio leucophaeus</i>	3	26.0		13.7	
<i>Papio sphinx</i>	3	25.1		13.2	
<i>Megaladapis edwardsi</i>	14	7.9	18.4	4.0	9.5
<i>Megaladapis madagascariensis</i>	5	6.5		3.2	
<i>Megaladapis grandidieri</i>	4	15.9		7.8	

whose values for individual variates are higher than 10% have sometimes been interpreted as comprising several species (Wood, 1985; Stringer, 1986; Groves, 1989). This is problematic when applied to nonlinear dimensions (Lande, 1977; Miller, 1991), or to linear dimensions among sexually dimorphic species (Gingerich, 1974; Kay, 1982) (see Table 3). It is worth noting that Simpson et al. (1960) derived most of their low CV values from intraspecific samples of adult males. High CV values do occur intraspecifically, for example, characters that reach maturity relatively late in ontogeny may have exceptionally high CVs (Yablokov, 1974; Gingerich, 1974; Lande, 1977; Gingerich and Schoeninger, 1979). High CV values do not necessarily signify multiple taxa.

Conversely, low CV values are not diagnostic of single taxa (Playcan, 1991). When the means for two species are similar and the distributions overlap considerably, the standard deviations for the pooled and single species samples may be virtually the same. Dental data for two species of sifaka, *Propithecus diademata* and *P. verreauxi*, as well as two closely related but allopatric fossil lemurs, *Archaeolemur edwardsi*, and *A. majori*, demonstrate this point (Table 4). These taxa would appear to be ideally suited for discrimination using the CV, since they exhibit limited or no sexual dimorphism (Kappeler, 1990; Jenkins and Albrecht, 1991; Godfrey et al., 1991), and significant congenic differences in body size. Coefficients of variation are only potentially useful as taxonomic discriminators if the two species being compared (or at least the particular variables being compared) differ extremely in absolute size. They are not useful if the taxa differ in relatively minor aspects of size or shape, as is quite common for closely related species. Just as high CVs do not always permit diagnosis of several species, low CVs do not permit diagnosis of only one. The use of CVs as diagnostic tools for assessing the number of fossil hominid species is probably inappropriate.

The real problem with using the CV as a taxonomic discriminator is simply that it is a univariate tool, and univariate dimensions are likely to display considerable overlap among closely related species. Species are normally distinguishable not by the central values and spreads of single variables, but by the central values, spreads, and relationships among sets of variables. In other words, morphospecies differ not solely in their variance structure but, more importantly, in their covariance structure. The reason multivariate tools are better than univariate tools is that they focus on the nature as well as the degree of variation, and they allow the cumulative summation of many variables that, taken individually, are not sufficient to discriminate two or more species. In other words, based on the covariance structure of the data, multivariate techniques allow weighted linear combinations (or summations) of variables to be constructed that optimally discriminate among closely related taxa (e.g., Cramer, 1977; Albrecht, 1978; Thorington, 1985; Shea and Coolidge, 1988; Cheverud and Moore, 1990; Froehlich et al., 1991; Albrecht and Miller, 1991). This can be accomplished using only hard-tissue traits

TABLE 4. Comparison of dental coefficients of variation for single species and for congeneric species pairs

Variable	<i>P. verreauxi</i>		<i>P. diademata</i>		All <i>Propithecus</i>		<i>A. majori</i>		<i>A. edwardsi</i>		All <i>Archaeolemur</i>	
	\bar{x}	CV	\bar{x}	CV	\bar{x}	CV	\bar{x}	CV	\bar{x}	CV	\bar{x}	CV
M ¹ and	6.1	8.2	6.0	8.2	6.1	8.2	9.5	8.9	10.2	8.1	5.9	9.1
P ¹ bl	3.6	10.4	3.8	9.0	3.7	10.2	8.3	8.1	9.0	9.7	8.7	9.8
P ¹ nd	5.2	8.4	5.1	7.7	5.2	8.1	7.5	6.4	8.23	8.2	8.0	9.0
P ² bl	4.2	10.2	4.8	5.1	4.4	10.9	10.8	6.5	12.0	6.6	11.4	8.4
M ¹ nd	6.8	6.7	7.3	6.5	7.0	7.6	7.8	6.7	8.6	4.5	8.2	7.3
M ² bl	6.1	6.3	6.8	5.8	6.4	8.4	9.6	6.0	10.7	4.3	10.1	7.5
M ² nd	6.5	5.9	7.2	6.4	7.0	7.9	6.7	7.5	7.8	5.3	10.1	8.9
M ³ bl	6.4	6.9	7.2	6.5	6.7	8.9	8.6	6.7	9.8	5.2	7.2	8.9
M ³ nd	4.2	10.1	5.2	7.0	4.6	13.3	3.8	6.7	6.6	9.0	6.2	8.6
M ³ bl	4.8	7.0	5.8	5.2	5.2	11.1	7.0	7.1	7.9	6.2	10.2	10.6

Sample means and coefficients of variation for two species of the genus *Propithecus* and two morphospecies of the extinct hominid genus *Archaeolemur*. Note that the coefficients of variation for mixed species samples of *Propithecus* are often not higher than those for single species. Furthermore, sifaka natural samples of *Archaeolemur* morphospecies have higher CVs than do unimixed samples; the difference is not great enough to provide any sort of reliable indication that the samples are indeed mixed. Variables: P = premolar; M = molar; superscript indicates maxillary tooth number; bl = buccolingual diameter; nd = mediolateral length. N = sample size; \bar{x} = mean (in mm); CV = coefficient of variation (standard deviation \times 100/mean). CVs are dimensionless.

that are also available in fossils—that is, without any reference to reproductive behavior, genetics, or external morphology.

For example, it takes only a half-dozen craniodental traits to discriminate virtually perfectly skulls on *Propithecus diademata* and *P. verreauxi*, using a linear discriminant function. Diademated sifakas are slightly larger and have relatively smaller premolar series and wider palates than Verreaux's sifakas. A discriminant function based on palate breadth, postorbital constriction, orbital width, skull length, molar series length, and premolar series length separates them. However, any single one of these variables, taken alone, would be a poor discriminator. Occasionally, only one or two variables are sufficient to perfectly discriminate between two allopatric fossil populations, but this depends on either a fortuitous choice of discriminator variable, or large differences in body size between members of the two populations. Maximum skull length alone does a credible job of separating *Archaeolemur edwardsi* and *A. majori*, which differ, on average, by about 10 kg. Yet, as we have seen, even with this great a difference in body size, dental CVs fail to verify a mixed-species assemblage.

It is also possible to ascertain, using discriminant function techniques, that the two sifaka species differ in craniodental shape more than do the two species of *Archaeolemur*, which are essentially scaled versions of one another, almost identical in craniodental shape. Macaque morphospecies exhibit similar patterns: some differ in craniodental shape, while others are virtually scaled versions of each other (Albrecht, 1978).

One can use distance statistics to quantify the degree of morphological difference between two or more forms given any set of parameters, and to characterize their interspecific as well as intraspecific variability. Thus, it is possible to measure the nature and degree of morphological difference between sister taxa. Ideally, one can apply these same tools directly to the fossil record. Some studies of pattern and process in the fossil record have attempted to do so (Cheetham, 1986, 1987; Stanley and Yang, 1987; Jackson and Cheetham, 1990).

It is not, however, always a simple matter to apply multivariate tools to the fossil record. The fragmentary nature of the fossil record sometimes constrains the set of variables that can be analyzed, and poor sample sizes will constrain their discriminatory power. Furthermore, tools appropriate for finding clusters of individuals in a fossil assemblage (clustering tools) are different from those that allow discrim-

ination between a priori groups (canonical variates or discriminant function tools). The optimal canonical discriminator between two species will be a weighted linear combination of the n dimensions measured for both species. The weights will be driven primarily by the particular idiosyncratic differences that distinguish groups. Canonical variates analysis is a powerful tool that helps one to ascertain those variables that contribute most to group separation. But it cannot be applied unless group membership is already known.

The problem for fossil species diagnosis is one of finding discriminators between groups when group membership is missing. The clustering techniques that accomplish this will not replicate differences that are maximized by discriminant function analysis. In cluster analytic techniques, each variable is given equal weight, or assigned a weight by the investigator based on some external criterion. Unless the differences between morphospecies (or between clusters of individuals sampled from different geographic areas) are sufficient to yield clear group separation, there may continue to be acrimonious disagreement in the literature concerning species boundaries, and patterns of morphological transformation, in the fossil record.

CONCLUSIONS

"Speciation" among primate taxa probably subsumes a very heterogeneous set of processes (cf. Kimbel and Martin, 1991). Given taxa and gaps between them, traditional theory has focused upon how the gaps are generated, and has only recently begun to turn the question around to how the taxa between the gaps are generated. The evolution of genetic discontinuity, or biospeciation, may involve chromosomal mechanisms, repetitive genomic mechanisms, or more simply, the gradual accumulation of point mutations; nevertheless, it is invisible in the fossil record, and is only directly amenable to study in a strictly synchronic context. The evolution of phenotypic discontinuity is at least partially visible in the fossil record, in a diachronic context.

The evolution of "reproductive isolation" has been used very loosely, and subsumes four inferences: strict reproductive isolation (failure to mate), reproductive incompatibility (breakdown of mating), genetic isolation (absence of genetic inflow), and genetic incompatibility (impossibility of genetic inflow). Biospeciation is generally judged to be complete when populations are genetically incompatible. However, biospeciation is neither necessary nor sufficient for morphospeciation, the evolution of apomorphies, which, though often correlated with biospeciation, can be studied in its own right. The evolution of new macroevolutionary units, which we call species, involves both sets of processes. Socioecological characteristics of organisms themselves may contribute significantly to patterns of morphological and chromosomal diversification, and account for some of their observed clade-specificity.

The discrimination of biospecies from the fossil record is an intractable problem. We can hope to retrieve biospecies from fossil assemblages only to the extent that morphospecies and biospecies coincide. Since it is possible to identify neontological morphospecies from those hard tissues that are often preserved in the fossil record (teeth, skulls, long bones), paleontologists may be able to apply tools that work for neontological species diagnosis to the problem of interpreting the patterns of variation in the fossil record. The goal of fossil species diagnosis should be to approximate neontological morphospecies. Such diagnosis must precede attempts to describe the spatiotemporal boundaries of paleontological species, which alone allows us to understand diachronic patterns of morphospecies origination, transformation, and extinction, and ultimately, the relationship between morphological transformation and morphospeciation.

ACKNOWLEDGMENTS

We thank Emke J.E. Scahnamary for the invitation to write this review, and for her comments on it; and Gene Albrecht and three anonymous reviewers for their

comments. We also thank the following for discussions of some of the ideas presented here: Eric Delson, Rob DeSalle, Jeff Froehlich, Joe Miller, Andrew Petto, David Povinelli, Mike Sutherland, Lynn Watson, and Annie Williams. Ronald Nadelor of Yerkes Regional Primate Center kindly provided Figure 2, Tables 3 and 4 are based on unpublished data collected by L. Godfrey. This work was supported in part by a grant from the National Science Foundation (BNS-8911315 to L.G and BNS-8919047 to J.M.).

GLOSSARY

- allopatric*—two populations having nonoverlapping geographic ranges.
aneuploidy—any deviation from the normal amount of chromosomal material for a species.
apomorphy—a derived character, an evolutionary novelty; if found in a single taxon it is an autapomorphy, if shared by more than one taxon, it is a synapomorphy.
backcross—a mating between an organism with a hybrid genotype and an organism with one of the parental genotypes.
biospecies—broadly applied here to mean any species concept that uses continuity or discontinuity of gene flow as its primary defining criterion. Thus, we use "biospeciation" to refer to the rearing of gene pools, the cessation of genetic contact between two populations.
canalization—the conservative property of a phenotype to be expressed under different environmental circumstances, or in spite of genetic variability.
canonical variates analysis—multiple discriminant function analysis; a statistical procedure that renders the differences between more than two groups discrete by finding the orthogonal linear combinations of variables that maximize group separation.
clade—a cluster of lineages descended from a single common ancestor, including all the descendants of that ancestor.
cladogenesis—the branching of a single lineage to form two lineages; contrasted with anagenesis, evolution within a single lineage, and stasigenesis, or stability.
class—a group of items linked by the possession of a common property.
cluster analysis—any of a series of statistical techniques that link individuals or objects based on some criterion of relative similarity.
coefficient of variation (CV)—a measure of relative "variability," designed to allow comparison of samples with radically different means or units of measure by expressing the standard deviation as a percentage of the mean; because the standard deviation and the mean always have the same dimensions, this ratio is dimensionless.
conspecifics—of the same species.
covariance—a measure of the linear relationship between the dispersions of two variables; the "standardized" covariance is the coefficient of correlation.
discriminant function—a statistical procedure that assigns group membership to individuals based on a trial set of attributes of individuals of known group membership.
ecocline—any ecological gradient along a geographic transect.
F₁ hybrid—a first-generation cross between two different hereditary lineages. The mating of an F₁ hybrid and a representative of either parental strain is a backcross, and can result in the introgression of genetic information from one line into the other. Traditionally, failure to backcross defines species as different.
founder effect—a situation in which descendants of a colonization are not genetically representative of the parental population.
genotype—hereditary composition of an organism.
heterochromatin—darkly staining material visible on chromosomes, usually considered genetically inert.

individual—an entity localized in time and space (in biology, attendant properties include discreteness, replicative continuity, and internal cohesion).

karyotype—the metaphase chromosomes from a representative cell, often characteristic of a species.

macroevolution—hereditary change directly causing a major effect on the phenotype. Though evident as pathologies, these are not regarded as significant factors in evolution.

morphospecies—broadly applied here to mean any species concept that uses the distribution of characters (chromatic, behavioral, structural) as a primary defining criterion. Thus, we use "morphospeciation" to refer to the emergence of ecological or phenotypic discontinuities between populations, involving natural selection and genetic drift.

multivariate statistics—statistical procedures that are designed to treat simultaneously (and to assess relationships among) several variables per object, including data description and reduction techniques (such as multiple correlation, multiple regression, factor analysis) and comparisons of multiple samples (such as multiple analysis of variance, discriminant function, canonical variates).

neontology—the study of contemporary biota (the living world; contrasted with paleontology).

palaeospecies—a fossil species, possessing time depth, and generally recognized by morphological criteria.

panmictic population—one in which genotypes associate at random, i.e., with equal probabilities. Genetic drift, related to population structure, is here minimized.

parapatry—having geographic ranges that border extensively on one another.

paraphyly—relationship of descent, including close relatives, but excluding a divergent one; the exclusion may confound phylogenetic reconstructions (see clade).

phenotype—outward characteristics of an organism.

poly-specific—involving more than one species.

postzygotic—under the isolation concept of species, a reproductive isolating mechanism that precludes the ability of an F₁ hybrid to survive or reproduce.

przygot—under the isolation concept of species, a reproductive isolating mechanism that precludes the formation of an F₁ hybrid.

repetitive DNA—hereditary material that may vary greatly among closely related species, and consists of DNA segments of varying lengths copied many times, distributed either in tandem or dispersed, and constituting the bulk of the DNA in a cell, though of generally unknown function.

repressor—a substance that impedes the normal functioning of a gene.

specific male recognition system (SMRS)—the system of signals (chemical, olfactory, vocal, visual) that bring together potential mates.

structured population—breeding situation in which genotypes come together with unequal probabilities, not at random, due to factors that include population subdivision, mating preferences, dispersal patterns, etc.

sympatry—having overlapping geographic ranges.

syngameon—an assemblage of partially hybridizing species in sympatry.

transferable elements—bits of DNA that can alter their linkage relationships, moving to another locus in the genome.

univariate statistics—statistical procedures designed to treat a single variable per object, including simple descriptive statistics (such as the mean, standard deviation, variance) and inferential comparisons of multiple samples (*t* tests, analysis of variance).

variance—moving freely and broadly.

variance—a widely employed measure of the dispersion in the values of a single variable (the square of the standard deviation); cf., covariance; coefficient of variation.

weighted linear combination—a mathematically constructed variable, defined as the sum of the values of differently weighted existing variables.

LITERATURE CITED

- Ahobilo Ed, Zimmerer RA, Lee J, and Mason P (1975). Social grooming between squirrel monkeys and humans in a seminatural environment. *Primates* 16:217-222.
- Albrecht GH (1978) The Craniofacial Morphology of the Sulawesi Macaque: Multivariate Approaches to Biological Problems. Contributions to Primatology, Volume 13. Basel: S. Karger.
- Albrecht GH (1980) Latitudinal, taxonomic, sexual, and insular determinants of size variation in pitfall mammals. *Mozzica nemertaria*. Int. J. Primatol. 1:141-152.
- Albrecht GH, and Miller JA (1991) Geographic variation in primates: A review with implications for interpreting fossils. In WH Kimbel and LB Martin (eds.): Species, Species Concepts, and Primate Evolution. New York: Plenum Press (in press).
- Albrecht GH, Jenkins PD, and Godfrey LR (1990) Ecogeographic size variation among the living and subfossil primates of Madagascar. *Am. J. Primatol.* 22:1-50.
- Arnason U (1972) The role of chromosomal rearrangement in mammalian speciation with special reference to Cetacea and Pinnipedia. *Hereditas* 70:113-118.
- Arthur W (1984) Mechanisms of Morphological Evolution: A Combined Genetic, Developmental, and Ecological Approach. Chichester: John Wiley & Sons.
- Ashton E (1980) The influence of geographic isolation on the skull of the green monkey (*Cercopithecus aethiops sabaeus*). V. The degree of differentiation in the dimensions of the St. Kitts green monkey. *Proc. R. Soc. Lond.* 137:583-585.
- Ashton E and Zuckerman S (1950) The influence of geographic isolation on the skull of the green monkey (*Cercopithecus aethiops sabaeus*). I. A comparison between the teeth of the St. Kitts and African green monkey. *Proc. R. Soc. Lond.* 137:212-238.
- Ashton E and Zuckerman S (1951a) The influence of geographic isolation on the skull of the green monkey (*Cercopithecus aethiops sabaeus*). II. The cranial dimensions of the St. Kitts and African green monkey. *Proc. R. Soc. Lond.* 138:204-213.
- Ashton E and Zuckerman S (1951b) The influence of geographic isolation on the skull of the green monkey (*Cercopithecus aethiops sabaeus*). III. The developmental stability of the skull and teeth of the St. Kitts and African green monkey. *Proc. R. Soc. Lond.* 138:213-218.
- Ashton E and Zuckerman S (1961c) The influence of geographic isolation on the skull of the green monkey (*Cercopithecus aethiops sabaeus*). IV. The degree and speed of dental differentiation in the St. Kitts green monkey. *Proc. R. Soc. Lond.* 138:354-374.
- Barton NH and Hewitt GM (1989) Adaptation, speciation, and hybrid zones. *Nature* 341:497-503.
- Bautuan V (1990) Phylogenetic analysis of the distribution of chromosomal races of *Mus musculus musculus* Ratty in Europe. *Biol. J. Linn. Soc.* 41:171-192.
- Benveniste R (1986) The contributions of retrovi-
- ruses to the study of mammalian evolution. In RJ Mauthner (ed.): Molecular Evolutionary Genetics. New York: Plenum Press, pp. 359-418.
- Berruetein IS (1967) Intraspecific interactions in a Malaysian primate community. *Folia Primatol.* (Basel) 7:198-207.
- Berruetein IS (1968) Social status of two hybrids in a wild troop of *Macaca urus*. *Primates* 6:217-228.
- Berruetein IS and Gordon TP (1979) Inter- and intraspecific sexual behavior in two species of macaques: A possible behavioral barrier to gene flow. *Behavioral Processes* 4:265-272.
- Berruetein IS and Gordon TP (1980) Mixed taxa introductions, hybrids and taxonomic systematics. In D. Lindburg (ed.): The Macaques: Studies in Ecology, Behavior and Evolution. New York: Van Nostrand Reinhold Company, pp. 125-147.
- Bumenberg B (1985) Biometrical studies upon hominoid teeth: The coefficient of variation, sexual dimorphism, and questions of phylogenetic relationship. *Bioevolution* 1:8149-184.
- Britten RJ and Davidson EH (1971) Repetitive and non-repetitive DNA sequences and a speculation on the origins of evolutionary novelty. *Q. Rev. Biol.* 46:111-138.
- Broekelmann WY and Gittins SP (1984) Natural hybridization in the *Hylobates lar* species group: Implications for speciation in gibbons. In H Puschendorf, DJ Chivers, WY Broekelmann, and N Creel (eds.): The Lesser Apes: Evolutionary and Behavioral Biology. Edinburgh: Edinburgh University Press, pp. 498-532.
- Brown CJ, Dunbar VG, and Shafer DM (1986) A comparison of the karyotypes of six species of the genus *Macaca* and a species of the genus *Cercopithecus*. *Folia Primatol.* (Basel) 46:164-172.
- Brumback RA (1973) Two distinctive types of owl monkeys (*Aotus*). *J. Med. Primatol.* 2:284-289.
- Buettner-Janusch J and Hamilton AE (1979) Chromosomes of *Leontideus coludris*. *Am. J. Phys. Anthropol.* 57:363-366.
- Bunn GT (1978) Modes of animal speciation. *Annu. Rev. Ecol. Syst.* 6:339-364.
- Carson HL (1970) Chromosome tracers of the origin of species. *Science* 169:1414-1418.
- Carson HL (1978) The genetics of speciation at the diploid level. *Am. Nat.* 109:83-97.
- Carson HL (1987) The genetic system, the deme, and the origin of species. *Annu. Rev. Genet.* 21:405-423.
- Chandler CR and Gromko MH (1989) On the relationship between species concepts and speciation processes. *Syst. Zool.* 38:116-125.
- Charleworth B, Lander R, and Selkin M (1982) A neo-Darwinian commentary on macroevolution. *Evolution* 36:474-498.
- Chesham AH (1986) Tempo of evolution in a Neogene bryozoa: Rates of morphologic change within and across species boundaries. *Paleobiology* 12:190-202.
- Chesham AH (1987) Trends of evolution in a Neogene bryozoa: Are trends in single morphologic characters misleading? *Paleobiology* 13:286-296.
- Chervad JM and Moore AJ (1990) Subspecific morphological variation in the saddle-back tam-

- arin (*Saginus faeccolis*). *Am. J. Primatol.* 2: 1-15.
- Colver JF (1948) Variations in the teeth of the green monkey in St. Kitts. *Proc. R. Soc. Med. Lond.* 41:945-948.
- Courcier J and Lemonn J-M (1991) Karyotypic study of four gibbon forms provisionally considered as subspecies of *Hylobates (Nomascus) entellus* (Primate, Hylobatidae). *Folia Primatol. (Basel)* 56:95-104.
- Coyne JA (1983) Genetics of sexual isolation between two sibling species, *Drosophila simulans* and *Drosophila mauritiana*. *Proc. Natl. Acad. Sci. USA* 80:5464-5468.
- Crawcraft J (1983) Species concepts and classification analysis. In RF Johnston (ed.), *Current Ornithology*, Volume 1. New York: Plenum Press, pp. 159-187.
- Crawcraft J (1987) Species concepts and the ontology of evolution. *Biology and Philosophy* 2:329-358.
- Crawcraft J (1989) Speciation and its Ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In D Otis and JA Eder (eds), *Speciation and Its Consequences*. Sunderland MA: Sinauer Associates, pp. 28-59.
- Cramer DL (1977) Craniofacial Morphology of *Parapithecus*. Contributions to Primatology. Volume 10. Basel: Karger.
- Cronin JE, Scarth VM, and Byler O (1984) Molecular evolution and speciation in the lesser apes. In H Frenschler, DJ Chivers, WY Brockelmann, and N Creel (eds.), *The Lesser Apes: Evolutionary and Behavioral Biology*. Edinburgh: Edinburgh University Press, pp. 467-485.
- Crow JF (1986) Basic Concepts in Population, Quantitative, and Evolutionary Genetics. New York: W. H. Freeman.
- David JR and Cappy P (1989) Genetic variation of *Drosophila melanogaster* natural populations. *Trends Genet. Evol.* 4:106-111.
- Dobzhansky T (1987) Genetics and the Origin of Species. New York: Columbia University Press.
- Dover G (1982) Molecular drive: A cohesive mode of species evolution. *Nature* 299:111-117.
- Dumbar KIM and Dumbar EF (1974) On hybridization between *Theropithecus gelada* and *Protopithecus* in the wild. *J. Hum. Evol.* 3:187-192.
- Eldredge N (1971) The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* 25:156-167.
- Eldredge N and Gould SJ (1972) Punctuated equilibria: An alternative to phyletic gradualism. In TDM Schopf (ed.), *Models in Paleobiology*. San Francisco: Freeman, Cooper and Co., pp. 82-115.
- Eldredge N and Stebbins SN (1984) Hierarchy and evolution. In R Dawkins and M Ridley (eds.), *One New Surveys in Evolutionary Biology*, Volume 1. New York: Oxford University Press, pp. 194-206.
- Eldredge N and Tattersall I (1975) Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. In F Szalay (ed.), *Approaches to Primate Paleobiology*. Basel: S. Karger, pp. 218-242.
- Finnegan D (1989) Epiallopatric transposable elements and genome evolution. *Trends Genet.* 5:103-107.
- Footen J (1964) - Rhesus and crab-eating macaques: Intergradation in Thailand. *Science* 143:363-365.
- Footen J (1971) Report on primates: Collected in western Thailand, January-April, 1967. *Fieldiana, Zool.* 59:1-62.
- Froehlich JW, Supriana J, and Froehlich PH (1991) Morphometric analysis of *Ateles*: Systematic and biogeographic implications. *Am. J. Primatol.* 25:1-25.
- Fujita K (1987) Species recognition by five macaque monkeys. *Primates* 28:353-366.
- Fujita K (1990) Species preference by infant macaques with controlled social experience. *Int. J. Primatol.* 11:553-513.
- Fujita K and Matsuzawa T (1986) A new procedure to study the perceptual world of animals with sensory reinforcement: Recognition of humans by a chimpanzee. *Primates* 27:283-291.
- Galbreath GJ (1983) Karyotypic evolution in *Aotus*. *Am. J. Primatol.* 4:245-251.
- Glendon MT (1966) On psychobiology in the logic of taxonomic controversies. *Syst. Zool.* 26:207-215.
- Glendon MT (1975) A radical solution to the species problem. *Syst. Zool.* 23:536-544.
- Glendon MT (1981) Categories, life, and thinking. *Behavioral and Brain Sciences* 4:269-313.
- Glendon MT (1986) Species individuality has no necessary connection with evolutionary gradualism. *Syst. Zool.* 37:66-68.
- Gingrich PD (1974) Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *J. Paleontology* 48:895-903.
- Gingrich PD (1976) Paleontology and phylogeny: Patterns of evolution at the species level in early Tertiary mammals. *Am. J. Sci.* 276:1-28.
- Gingrich PD (1979) The stratophenic approach to phylogeny reconstruction in vertebrate paleontology. In J Crawcraft and N Eldredge (eds.), *Phylogenetic Analysis and Paleontology*. New York: Columbia University Press, pp. 41-71.
- Gingrich PD and Schoeninger M (1979) Patterns of tooth size variability in the dentitions of primates. *Am. J. Phys. Anthropol.* 51:457-461.
- Godfrey LR and Perto AJ (1981) Clinal size variation in *Archaeolemur* spp. on Madagascar. In B Charnelli and RL Corruccini (eds.), *Primate Evolutionary Biology*. New York: Springer-Verlag, pp. 14-34.
- Godfrey LR, Sutherland MR, Perto AJ, and Boy DS (1990) Size, space, and adaptation in some subfossil lemurs from Madagascar. *Am. J. Phys. Anthropol.* 81:45-66.
- Godfrey LR, Lyon S, and Sutherland MR (1991) Sexual dimorphism in large-bodied mammals: The case of the subfossil lemurs (in preparation).
- Goldschmidt R (1971) Spontaneous chromatin rearrangements and the theory of the gene. *Proc. Natl. Acad. Sci. USA* 23:621-623.
- Goldschmidt R (1982) Evolution, as viewed by one scientist. *Am. Sci.* 40:84-96, 135.
- Gould SJ (1980) Is new and general theory of evolution emerging? *Paleobiology* 6:119-130.
- Gould SJ and Eldredge N (1977) Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology* 3:115-151.
- Groves CP (1970) The forgotten leaf-eaters, and the phylogeny of the Colobinae. In JF Napier and PH Napier (eds.), *Old World Monkeys: Evolution, Systematics, and Behavior*. New York: Academic Press, pp. 555-587.
- Groves CP (1980) Speciation in *Macaca*: The view from Sulawesi. In D Lindburg (ed.), *The*
- Macaques: Studies in Ecology, Behavior and Evolution. New York: Van Nostrand Reinhold Company, pp. 84-124.
- Groves CP (1984) A new look at the taxonomy and phylogeny of the gibbon. In H Frenschler, DJ Chivers, WY Brockelmann, and N Creel (eds.), *The Lesser Apes: Evolutionary and Behavioral Biology*. Edinburgh: Edinburgh University Press, pp. 542-561.
- Groves CP (1989) A Theory of Primate and Human Evolution. Oxford: Clarendon Press.
- Hedrick PW (1981) The establishment of chromosomal variants. *Evolution* 35:322-332.
- Hershkovitz P (1977) *Living New World Monkeys (Platyrrhini) with an Introduction to Primates*, Volume 1. Chicago: University of Chicago Press.
- Hershkovitz P (1983) Two new species of night monkeys, genus *Aotus* (Cebidae, Platyrrhini): A preliminary report on *Aotus* taxonomy. *Am. J. Primatol.* 4:209-243.
- Hershkovitz P (1984) Taxonomy of squirrel monkeys *Saimiri* (Cebidae, Platyrrhini): A preliminary report with description of a hitherto unnamed form. *Am. J. Primatol.* 6:257-312.
- Hull D (1976) Are species really individuals? *Syst. Zool.* 25:174-191.
- Hull D (1980) Individuality and selection. *Annu. Rev. Ecol. Syst.* 11:311-332.
- Jackson JBC and Cheetham AH (1980) Evolutionary significance of morphospecies: A test with chelonoid Bryozoa. *Science* 246:579-583.
- Jankins PD (1987) Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles. Part IV: Suborder Strepsirhini, including the subfossil Madagascar lemurs and family Tarsiidae. British Museum (Natural History), London.
- Jankins PD and Altheide GH (1991) Sexual dimorphism and sex ratios in Madagascar primates. *Am. J. Primatol.* 24:1-14.
- Jolly A (1966) *Chimpanzee Behavior: A Madagascar Field Study*. Chicago: The University of Chicago Press.
- Jolly CJ (1966) Introduction to the Cercopithecoidea, with notes on their use as laboratory animals. *Symp. Zool. Soc. Lond.* 17:427-467.
- Jolly CJ (1967) The evolution of the baboons. In H Vargborg (ed.), *The Baboon in Medical Research*, Volume 2. Austin: University of Texas Press, pp. 23-50.
- Jolly CJ (1972) The classification and natural history of *Theropithecus* (*Stenopithecus*) (Andrews, 1916), baboons of the African Pilo-Pleiolestes. *Bull. Br. Mus. (Nat. Hist., Geol.)* 22:1-122.
- Jolly CJ (1991) Species definitions and variation in extant *Papio*. *Am. J. Phys. Anthropol.* [Suppl.] 22:100.
- Jolly CJ and Brett FL (1973) Genetic markers and baboon biology. *J. Med. Primatol.* 2:85-99.
- Jones TC, Thomington RW, Hu MM, Adams E, and Cooper RW (1973) Karyotypes of squirrel monkeys (*Saimiri sciureus*) from different geographic regions. *Am. J. Phys. Anthropol.* 38:269-278.
- Kappeler PM (1990) The evolution of sexual size dimorphism in primate primates. *Am. J. Primatol.* 21:201-214.
- Key RF (1982) *Stenopithecus simonsi*, a new species of Miocene hominoid, with comments on the phylogenetic status of the Ramapithecinae. *Int. J. Primatol.* 3:113-173.
- Key RF and Simons EL (1983) A reassessment of the relationship between later Miocene and subsequent Hominoida. In RL Coobson and RF Corriveau (eds.), *New Interpretations of Ape and Human Ancestry*. New York: Plenum Press, pp. 577-624.
- Kidwell MG and Peterson KR (1991) Evolution of transposable elements in *Drosophila*. In L Warren and H Kopyovskii (eds.), *New Perspectives on Evolution*. New York: Wiley-Liss, pp. 139-154.
- Kimble WH and Martin JB (1991) Species, Species Concepts and Primate Evolution. New York: Plenum Press (in press).
- King MC and Wilson AC (1975) Evolution at two levels in humans and chimpanzees. *Science* 186:107-118.
- Kingdon J (1989) What are face patterns and do they contribute to reproductive isolation in gnomons? In A Gaudier-Hion, F Bouvillier, and J-P Gauthier (eds.), *African Radiation: Evolutionary Biology of the African Genus*. Cambridge: Cambridge University Press, pp. 227-245.
- Klug AG (1990) Species as historical individuals. *Biology and Philosophy* 5:417-432.
- Krieger M and Rose MR (1986) Molecular aspects of the species barrier. *Annu. Rev. Ecol. Syst.* 17:463-483.
- Kroeber AL and Klutchnik C (1982) Culture: A critical review of concepts and definitions. *Pap. Peabody Mus. Arch. Ethnol.*, Volume 47.
- Kummer H (1968) Social Organization of Hamadryas Baboons: A Field Study. Chicago: University of Chicago Press.
- Kummer H, Goetz W, and Angst W (1970) Cross-species modifications of social behavior in baboons. In JF Napier and PH Napier (eds.), *Old World Monkeys: Evolution, Systematics, and Behavior*. New York: Academic Press, pp. 351-383.
- Lambert DM, Michaux B, White CS (1987) *Alece species self-defining?* *Syst. Zool.* 36:196-206.
- Lande R (1977) On comparing coefficients of variation. *Syst. Zool.* 26:214-217.
- Lernould J-M (1989) Classification and geographical distribution of genuses: A review. In A Gaudier-Hion, F Bouvillier, and J-P Gauthier (eds.), *African Radiation: Evolutionary Biology of the African Genus*. Cambridge: Cambridge University Press, pp. 54-78.
- Lewontin JC (1989) Genetics, Paleontology, and Macroevolution. Cambridge: Cambridge University Press.
- Lewontin JS and Simon CM (1980) A critique of the punctuated equilibria model and implications for the detection of speciation in the fossil record. *Syst. Zool.* 29:130-142.
- Lewontin RC (1966) On the measurement of relative variability. *Syst. Zool.* 15:141-142.
- Leiberman DE, Pilbeam DR, and Wood BA (1989) A probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: A comparison of KNM-ER 1470 and KNM-ER 1813. *J. Hum. Evol.* 17:503-511.
- Long SE (1989) Segregation patterns and fertility of domestic mammals with chromosomal translocations. In A Daniel (ed.), *The Cytogenetics of Mammalian Autosomal Rearrangements*. New York: Alan R. Liss, Inc., pp. 383-396.
- MacKinnon J and MacKinnon K (1977) The formation of a new gibbon group. *Primates* 18:701-708.
- Maple T and Westlund B (1975) The integration of social interactions between cebus and spider

- monkeys in captivity. *Appl. Anim. Ethol.* 1:305-308.
- Maples W (1972) Systematic reconsideration and a revision of the nomenclature of Kenya baboons. *Am. J. Phys. Anthropol.* 36:9-20.
- Marks J (1983) Homoid cyogenetics and evolutionary theory. In Ed Devor (ed.): *Molecular Evolutionary Theory*. In Ed Devor (ed.): *Molecular Evolutionary Theory*. New York: Academic Press.
- Marshall JT, Sugarliff J, and Markaya M (1984) Gibbons of the far group: Relationships based on voice. In H Prenschoff, DJ Chivers, WY Brockelmann, and N Oresel (eds.): *The Lesser Apes: Evolutionary and Behavioral Biology*. Edinburgh: Edinburgh University Press, pp. 383-541.
- Martin RH (1988) Abnormal spermatozoa in human translocation and inversion carriers. In A Daniel (ed.): *The Cytogenetics of Mammalian Autosomal Rearrangements*. New York: Alan R. Liss, Inc., pp. 397-417.
- Mayer E (1942) Systematics and the Origin of Species. New York: Columbia University Press.
- Mayer E (1950) *Where are we?* Cold Spring Harbor, N.Y.: Quant. Biol. 24:1-9.
- Mayer E (1953) *Animal Species and Evolution*. Cambridge, Mass.: Harvard University Press.
- Mayer E (1970) *Populations, Species and Evolution*. Cambridge, Mass.: Harvard University Press.
- Mayer E (1987) The ontological status of species: Scientific progress and philosophical terminology. *Biology and Philosophy* 2:145-168.
- McGuire MT (1974) *The St. Kitts Vervet: Contributions to Primatology*. Volume 1. Basel: S. Karger.
- Melnick DJ (1988) The genetic structure of a primate species: rhesus macaques and other central and southern monkeys. In J. Primatol. 9:185-231.
- Melnick DJ and Kidd KK (1983) The genetic consequences of social group fission in a wild population of rhesus monkeys (*Macaca mulatta*). *Behavioural Ecology and Sociobiology* 12:299-306.
- Miller JA (1989) *Homo habilis* and endocranial volumes: The use and abuse of coefficients of variation. *Am. J. Phys. Anthropol.* 78:289.
- Miller JA (1991) Does brain size variability provide evidence of multiple species in *Homo habilis*? *Am. J. Phys. Anthropol.* 4:389-398.
- Mittermeier RA (1973) Group activity and population dynamics of the howler monkey on Barro Colorado Island. *Primates* 14:1-19.
- Mundy MD (1990) Cyogenetic variability within and across populations of *Cebus apella* in Argentina. *Folia Primatol. (Basel)* 54:206-216.
- Musser GG and Dagosto M (1987) The identity of *Taruius puntila*, a hybrid species endemic to the montane mossy forests of central Sulawesi. *American Museum Novitates* 2867:1-53.
- Myers RH and Shaker DA (1978) Hybrid ape offspring of a mating of the gibbon and orangutan. *Science* 205:308-310.
- Nachman MW and Myers P (1989) Exceptional chromosomal mutations in a rodent population are not strongly underdominant. *Proc. Natl. Acad. Sci. USA* 86:6666-6670.
- Nagel U (1971) Social organization in a baboon hybrid zone. In H Kummer (ed.): *Proceedings of the Third International Congress of Primatology*, Zurich, 1970. *Behaviour*. Vol. 3. S. Karger, Basel, pp. 48-57.
- Nagel U (1973) A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatol. (Basel)* 19:104-165.
- Nance V, Vanleberghpe F, Nielsen JT, Bonhomme P, and Britton-Davarian J (1990) Chromosomal introgression in house mice from the hybrid zone between *M. m. domesticus* and *M. m. musculus* in Denmark. *Biol. J. Linn. Soc.* 41:215-227.
- Nelson G (1989) Species and taxa: Systematics and evolution. In D Oresel and JA Emler (eds.): *Speciation and Its Consequences*. Sunderland, Mass.: Sinauer Associates, pp. 60-81.
- Nesvo E (1982) Speciation in subterranean mammals. In C Bergquist (ed.): *Mechanisms of Speciation*. New York: Alan R. Liss, Inc., pp. 191-218.
- Nienitz C, Nierisch A, Warter S, and Rumpel Y (1991) *Taruius danau*: A new primate species from central Sulawesi (Indonesia). *Folia Primatol. (Basel)* 56:105-116.
- Nixon KC and Wheeler QD (1990) An amplification of the phylogenetic species concept. *Cladistics* 6:211-223.
- Novkoff AB (1985) The concept of integrative levels and biology. *Science* 101:209-215.
- Nyström P (1991) Mating success of hamadryas anubis and hybrid male baboons in a "mixed" social group in the Awash National Park, Ethiopia. *Am. J. Phys. Anthropol. (Suppl.)* 12:138.
- Paterson HEH (1978) More evidence against speciation by reinforcement. *S. Afr. J. Sci.* 74:369-371.
- Paterson HEH (1988) The recognition concept of species. In ES Voss (ed.): *Species and Speciation*. Transvaal Museum, Pretoria: Transvaal Museum Monograph no. 4, pp. 21-23.
- Patton JL (1990) Geovoid evolution: The historical, selective, and random basis for divergence patterns within and among species. In E Nervo and OA Reig (eds.): *Evolution of Subterranean Mammals at the Organismal and Molecular Levels*. New York: Alan R. Liss, Inc., pp. 49-69.
- Patton JL and Smith MF (1988) Population structure and the genetic and morphologic divergence among pocket gopher species (*Geomys thomomys*). In D Oresel and JA Emler (eds.): *Speciation and Its Consequences*. Sunderland, Mass.: Sinauer Associates, pp. 284-304.
- Pearson E (1982) The percentage limits for the distribution of range in samples from a normal population. *Biometrika* 24:404-417.
- Pellucari C, Formand D, Zucotti M, Sanyon R, and Manfredi Romanini MG (1988) Genome size and constitutive heterochromatin in *Hylobates muselleri* and *Symphalangus syndactylus* and in their viable hybrid. *Cytogenet. Cell Genet.* 47:1-4.
- Petter J-J, Albignac R, and Rumpel Y (1977) *Mammifères Lemnuriens (Primates Prosimians)*. Faune de Madagascar 44:1-513.
- Piavvan JM (1989) The coefficient of variation as an indicator of interspecific variability in fossil assemblages. *Am. J. Phys. Anthropol.* 78:236.
- Piavvan JM (1991) Catastrophe variability and species concepts in fossil samples. *Am. J. Phys. Anthropol. (Suppl.)* 12:144.
- Poirier FE (1977) The human influence on genetic and behavioral differentiation among three non-human primate populations. *Yrbk. Phys. Anthropol.* 1976, 20:234-241.
- Popp JL (1983) Ecological determinism in the life histories of baboons. *Primates* 24:198-216.
- Proby LA, Buchanan PD, Pollitzer WS, and Mootnick AR (1983) *Biopopuliferus*: A genus-level taxon for the Hooleck Gibbon (*Hylobates hooleck*). *Am. J. Primatol.* 5:83-87.
- Raff CA and Gagnana E (1988) Robertsonian heterozygotes in the house mouse and the fate of their germ cells. In A Daniel (ed.): *The Cytogenetics of Mammalian Autosomal Rearrangements*. New York: Alan R. Liss, Inc., pp. 315-359.
- Richard A (1970) A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Alouatta geoffroyi*. *Folia Primatol. (Basel)* 12:241-263.
- Rong R, Charadley AC, Song J, McBeath S, Tan PP, Bai Q, and Speed RB (1988) A fertile male and binary in China. *Cytogenet. Cell Genet.* 47:134-139.
- Rose KD and Bown TM (1986) Gradual evolution and species discrimination in the fossil record. In K Flanagan and JA Lilljgraven (eds.): *Vertebrates, Phylogeny, and Paleontology*. Contributions to Geology, University of Wyoming Special Paper no. 3. Laramie, WY, pp. 119-130.
- Rose MR and Doolittle WF (1983) Molecular biological models of speciation. *Science* 220:157-162.
- Rubio-Godoy A, Caballin MR, Garcia Caldes M, and Egroze J (1976) Comparative study of the banding patterns of Cercopithecidae. *Folia Primatol. (Basel)* 26:306-309.
- Rumbaugh DM, Wolkin JR, Wilkerson BJ, and Myers RH (1976) A hybrid ape (*Hylobates lar moloch* x *Symphalangus syndactylus*). *Lab. Primate Newslett.* 15:32.
- Rumpel Y and Albignac R (1975) Intraspecific chromosome variability in a lemur from the north of Madagascar: *Lepidoteur septentrionalis*, species nova. *Am. J. Phys. Anthropol.* 42:425-430.
- Rumpel Y, Warter S, Rabetrivola C, Petter J, and Durillur B (1990) Chromosomal evolution of Malagasy lemurs. XII. Chromosomal banding study of *Awohi langger occidentalis* (Syn. *Lichanotus langger occidentalis*) and cytogenetic data in favour of its classification in a species apart—*Awohi occidentalis*. *Am. J. Primatol.* 21:307-316.
- Samuels A and Altman J (1986) Immigration of a *Papio anubis* male into a group of *Papio cynocephalus* baboons and evidence for an anubis-cynocephalus hybrid zone in Amboseli, Kenya. *Int. J. Primatol.* 7:131-138.
- Shaker DA, Myers RH, and Saltzman D (1984) Biogenetics of the sabon (gibbon-stanung hybrid). In H Prenschoff, DJ Chivers, WY Brockelmann, and N Oresel (eds.): *The Lesser Apes: Evolutionary and Behavioral Biology*. Edinburgh: Edinburgh University Press, pp. 486-497.
- Shes BT and Coolidge HJ Jr (1988) Craniometric differentiation and systematics in the genus *Pan*. *J. Hum. Evol.* 17:671-683.
- Shostak J (1981) Population genetical study of natural hybridization between *Papio anubis* and *P. hamadryas*. *Primates* 22:285-308.
- Simons EL and Pilbeam DR (1985) Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). *Folia Primatol. (Basel)* 3:81-152.
- Simpson GG (1991) The species concept. *Evolution* 5:285-298.
- Simpson GG (1961) *Principles of Animal Taxonomy*. New York: Columbia University Press.
- Simpson GG, Roe A, and Lewontin RC (1960) *Quantitative Zoology* (revised edition). New York: Harcourt, Brace and Company.
- Snyder M and Doolittle WF (1988) P elements in *Drosophila*: Selection at many levels. *Trends Genet.* 4:147-149.
- Sokal RR and Braumann CA (1980) Significance tests for coefficients of variation and variability profiles. *Syst. Zool.* 29:50-66.
- Sokal RR and Sneath PHA (1963) *The Principles of Numerical Taxonomy*. San Francisco: W.H. Freeman.
- Southwick CH and Southwick KL (1983) Polyploid groups of macaques on the Kowloon Peninsula, New Territories, Hong Kong. *Am. J. Primatol.* 5:17-24.
- Stanley SM (1979) Macroevolution: Pattern and Process. San Francisco: W.H. Freeman.
- Stanley SM and Yang X (1987) Approximate evolutionary status for bivariate morphology over millions of years: A multivariate multivariate study. *Paleobiology* 13:113-139.
- Stanyon R and Charvillat B (1983) Mode and tempo in primate chromosome evolution: Implications for hybrid and phylogeny. *J. Hum. Evol.* 12:305-315.
- Stanyon R, Fanfani C, Campetero-Ciani A, Charvillat B, and Ardito G (1988) Banded karyotypes of 20 Papiionini species reveal no necessary correlation with speciation. *Am. J. Primatol.* 16:3-17.
- Stebbins GL (1987) *Species concepts: Semantics and actual situations*. *Biology and Philosophy* 2:198-203.
- Stringer CB (1986) *The credibility of Homo habilis*. In B Wood, L Martin, and P Andrews (eds.): *Major Topics in Primate and Human Evolution*. Cambridge: Cambridge University Press, pp. 266-294.
- Stricker TT, Butynski TM, and Lwanga JS (1988) Hybridization between redtail (*Crotophaga occidens acridalis*) and blue (*C. minor submerens*) monkeys in the Kibale Forest, Uganda. In A Gauster-Hon, P Bourriere, and J.P. Gauster (eds.): *A Primate Radiation: Evolutionary Biology of the African Guinea*. Cambridge: Cambridge University Press, pp. 477-497.
- Sugawara K (1979) Sociological study of a wild group of hybrid baboons in the Awash valley, Ethiopia. *Primates* 20:21-56.
- Suvarata J, Freshfield JW, Corbin C, and Erwin J (1990) Secondary intergradation between *Macaca maura* and *Macaca tonkeana* in Sulawesi. *Selam*. *Am. J. Primatol.* 20:236.
- Susunan RW and Tattersall I (1981) *The ecology and behavior of Macaca fascicularis in Mauritius*. *Primates* 22:192-205.
- Swartz KB (1983) Species discrimination in infant

- pitral macaques with pictorial stimuli. *Dev. Psychobiol.* 16:219-231.
- Sealy FS and Delson E (1979) *Evolutionary History of the Primates*. New York: Academic Press.
- Tattersall I (1977) Ecology and behavior of *Leurus fulvus moyotensis* (Primates, Lemniformes). *Anthropol. Papers Am. Mus. Nat. Hist.* 54:421-482.
- Tattersall I (1979) Patterns of activity in the Mayotte lemur, *Leurus fulvus moyotensis*. *J. Mammal.* 60:314-323.
- Tattersall I (1982) The primates of Madagascar. New York: Columbia University Press.
- Tattersall I (1986) Species recognition in human paleontology. *J. Hum. Evol.* 15:165-175.
- Tattersall I (1989) The roles of ecological and behavioral observation in species recognition among primates. *Hum. Evol.* 4:117-124.
- Tattersall I (1991) What was the human revolution? *J. Hum. Evol.* 20:77-83.
- Templeton AR (1980a) Modes of speciation and inferences based on genetic distances. *Evolution* 34:719-729.
- Templeton AR (1980b) The theory of speciation via the founder principle. *Genetics* 94:1011-1038.
- Templeton AR (1981) Mechanisms of speciation—a population genetic approach. *Annu. Rev. Ecol. Syst.* 12:23-48.
- Templeton AR (1982) Genetic architectures of speciation. In C. Barigazzi (ed.): *Mechanisms of Speciation*. New York: Alan R. Liss, Inc., pp. 105-121.
- Templeton AR (1989) The meaning of species and speciation: A genetic perspective. In D. Otte and JA. Endler (eds.): *Speciation and Its Consequences*. Sunderland, Mass.: Sinauer Associates, pp. 3-27.
- Thornington RW Jr (1985) The taxonomy and distribution of squirrel monkeys (*Saimiri*). In LA Rosenblum and CL Coe (eds.): *Handbook of Squirrel Monkey Research*. New York: Plenum Press, pp. 1-33.
- van Tuinen P and Ledbetter DH (1983) Cytogenetic comparison and phylogeny of three species of Hylobatidae. *Am. J. Phys. Anthropol.* 61:453-466.
- Vitzthum VI (1986) The Role of Ecological Factors in Ontogenetic Variability and Its Implication for Body Size Adaptations in The Cercopithecoidea. Ph.D. thesis, University of Michigan, Ann Arbor.
- Vrba ES (1986) Introduction. In ES Vrba (ed.): *Species and Speciation*. Transvaal Museum Monograph #4, Pretoria, South Africa: Transvaal Museum, pp. ix-xviii.
- Vrba ES and Eldredge N (1984) Individuals, hierarchies and processes: Towards a more complete evolutionary theory. *Paleobiology* 10:146-171.
- Waddington C (1957) *The Strategy of the Genes*. London: George Allen and Unwin.
- Waddington C (1960) Evolutionary adaptation. In S Tax (ed.): *Evolution After Darwin*, Vol. 1. Chicago: University of Chicago Press, pp. 381-402.
- Walker A and Teaford MF (1991) Species discrimination in *Proconsul* from Ruweng and Mgorano Islands, Kenya. *Am. J. Phys. Anthropol. Suppl.* 12: 179-179.
- White CS, Macaux B, and Lambert DM (1990) White CS, Macaux B, and Lambert DM (1990) 413. Species and neo-Darwinism. *Syst. Zool.* 39:399-413.
- White MJD (1969) Chromosomal rearrangements and speciation in animals. *Annu. Rev. Genet.* 3:75-96.
- White MJD (1978) Chain processes in chromosomal speciation. *Syst. Zool.* 27:285-298.
- Wiley EO (1978) The evolutionary species concept reconsidered. *Syst. Zool.* 27:17-26.
- Williams LE (1983) Sociality among captive hybrid macaques. *Behavioural Processes* 8:177-187.
- Williamson R (1989) Evolutionary or biological species. *Abh. naturwiss. Ver. Hamburg* 26:95-110.
- Wilson AC, Sarich VM, and Maxson LR (1974) The importance of gene rearrangement in evolution: Evidence from studies on rates of chromosomal protein and anatomical evolution. *Proc. Natl. Acad. Sci. USA* 71:3028-3030.
- Wilson AC, Bush GL, Case SM, and King MC (1975) Social structuring of mammalian populations and rate of chromosomal evolution. *Proc. Natl. Acad. Sci. USA* 72:5061-5065.
- Wood BA (1985) Early *Homo* in Kenya, and its systematic relationships. In E Delson (ed.): *Antecenters: The Hard Evidence*. New York: Alan R. Liss, Inc., pp. 206-214.
- Wright S (1982) Character change, speciation, and the higher taxa. *Evolution* 36:427-443.
- Wurster DH and Benschke K (1970) Indian Mungac, *Muntiacus muntjak*: A deer with a low diploid chromosome number. *Science* 169:1364-1366.
- Yablouk AV (1974) *Variability in Mammals*. New Delhi: Amerind Publishing Co.
- Yoshikubo S (1985) Species discrimination and concept formation by rhesus monkeys (*Macaca mulatta*). *Primates* 26:285-299.
- Yoshikubo S (1987) A possible reproductive isolation through a species discrimination learning in genus *Macaca*. *Primate Res.* 3:43-47.
- Yunis EJ, Torres de Caballero DM, Ramirez C, and Ramirez ZE (1976) Chromosomal variations in the primate *Alouatta seniculus seniculus*. *Folia Primatol. (Basel)* 25:215-224.