PHYLOGENETIC RELATIONSHIPS OF MITOCHONDRIAL DNA UNDER VARIOUS DEMOGRAPHIC MODELS OF SPECIATION[1]

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ABSTRACT

Recent empirical studies have revealed instances in which the maternally-transmitted mitochondrial DNA (mtDNA) genotypes of some populations are more closely related to those of a distinct biological species than to those of other conspecifics. One plausible explanation involves secondary hybridization and introgression. Here we examine whether phylogenetic sorting of matriarchal lineages, independent of any hybridization, can in principle also give rise to discordancies between biological species boundaries and mtDNA genotype.

Computer models are developed to simulate the evolutionary dynamics of matriarchal lineages during formation of daughter species from an ancestral parent population. The relative probabilities of monophyly, paraphyly, and polyphyly of the daughter species (their *phylogenetic status* with respect to mtDNA) are monitored as a function of time since speciation under a variety of demographic scenarios. Major results are as follows: (1) phylogenetic distributions of mtDNA can lack concordance with species boundaries when species are recently separated; (2) the

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phylogenetic status of a given pair of species is itself a dynamic evolutionary characteristic, with a common time-course of changes subsequent to speciation being polyphyly ⟶ paraphyly ⟶ monophyly; (3) the demographic mode of speciation will have a major influence on the developing phylogenetic status of related species.

I. INTRODUCTION

Because mitochondrial DNA (mtDNA) is maternally inherited in higher animals (Avise and Lansman, 1983), its evolutionary dynamics can differ from that of nuclear DNA. In contrast to the nuclear genome, which is transmitted biparentally and is subject to recombination at each generation, a given mitochondrial linaege is apparently isolated from genetic exchange with other such lineages. In effect, recombining nuclear genotypes within a population or species have a reticulate evolutionary history, while mitochondrial genotypes have a linear history.

Recent empirical studies have revealed situations in which the phylogenetic distributions of mtDNA lack concordance with biological species boundaries. Thus the mtDNA genotypes of some populations have appeared to be more closely related to those of a distinct biological species than to those of other conspecifics. For example, Powell (1983) found that *Drosophila pseudoobscura* exhibits a mtDNA often indistinguishable from that of *D. persimilis* where these sibling species are sympatric, although the mtDNA in allopatric populations of *pseudoobscura* differed from that of *persimilis*. Similarly, Ferris *et al.* (1983) found that some European mouse populations, classified by morphology and allozymes as *Mus musculus*, possess a mtDNA genotype normally characteristic of a sibling species, *Mus domesticus*. In both of these instances, results were attributed to past hybridization and introgression of mtDNA between species, with the ultimate fixation of an

"alien" mtDNA genotype. Takahata and Slatkin (1984) have mathematically modeled the effects of low level mitochondrial gene flow between species, and conclude that these scenarios are plausible. Sterility of male hybrids or a selective advantage for the introduced mtDNA genotype can theoretically contribute to the establishment of a foreign mtDNA without appreciable contamination of the nuclear gene pool.

Without necessarily calling into question the interpretations of results of these previous studies, it may nonetheless be worthwhile to consider whether and under what conditions other evolutionary processes, apart from secondary hybridization and introgression, might account for some cases in which the distributions of mtDNA genotypes do not coincide with species boundaries. There is an additional empirical rationale for this concern. Using restriction-site maps of mtDNA, Avise *et al.* (1983) suggested that some populations of the mouse *Peromyscus maniculatus* are genetically closer to a sibling species *P. polionotus* than they are to each other. In this case, the geographic ranges of *maniculatus* and *polionotus* do not overlap, and there is no compelling reason to suppose they have previously hybridized or experienced introgression. In phylogenetic terminology, *maniculatus* appears to be paraphyletic (Wiley, 1981) with respect to *polionotus* in matriarchal ancestry; *polionotus* is monophyletic with respect to *maniculatus,* but constitutes a subclade within the larger *maniculatus-polionotus* assemblage.

The purpose of this study is to stimulate thinking about possible mtDNA relationships among closely related species by focusing attention on demographically-influenced patterns of phylogenetic sorting of matriarchal lineages during speciation. Other workers have studied the theory of phylogenetic relationships of DNA sequences among individuals within and between populations (e.g., Hudson, 1983; Tajima, 1983). Here

we employ computer simulations to examine the relative probabilities of monophyly, polyphyly, and paraphyly of matriarchal lineages belonging to species-pairs generated under various speciation scenarios. Speciations can be associated with an immense array of different demographies; we will present outcomes for a few selected examples.

II. MATERIALS AND METHODS

A. General Outline for the Models

Since only female pedigrees are relevant to transmission of mitochondria, mtDNA lineages can be represented as a non-anastomosing tree (Fig. 1). Each node in the tree marks a female individual, and each branch arising from a node traces that female's lineage to her female progeny. At any given time, a species or population can be thought of as a horizontal cross section through the tree. The last common female ancestor shared by two individuals is the point where their respective branches split from a common node. If genetic differentiation is time-dependent, the genetic distance (D) between two individuals can be defined as the time, in generations, since they last shared a common female ancestor.

As shown schematically in Figure 2, a given pair of biological species (A and B) can in principle exhibit one of four patterns of relationship that determines their *phylogenetic status* with respect to mtDNA lineages: I) A and B are both monophyletic in matriarchal ancestry; II) A and B are both polyphyletic; IIIa) A is paraphyletic with respect to B; or IIIb) B is paraphyletic with respect to A. The phylogenetic status of any pair of species can be defined in terms of maximum genetic distances among conspecifics ($\max D_{AA}$, $\max D_{BB}$) and minimum distances between individuals of the two species ($\min D_{AB}$) by the inequalities presented in Table I. For example, when $\max D_{AA} < \min D_{AB}$ and $\max D_{BB}$

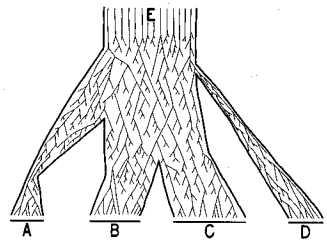

Figure 1. Schematic representation of non-anastomosing mitochondrial lineages, illustrating some possible evolutionary relationships among populations or species A-D. Living members of A trace oldest shared female ancestries to a population bottleneck which postdates the cladogenetic event (separation of A from B). Living members of D trace oldest female ancestries exactly to the separation of D from C. Some living representatives of B and C trace oldest female ancestries to times greatly predating their cladogenetic separation.

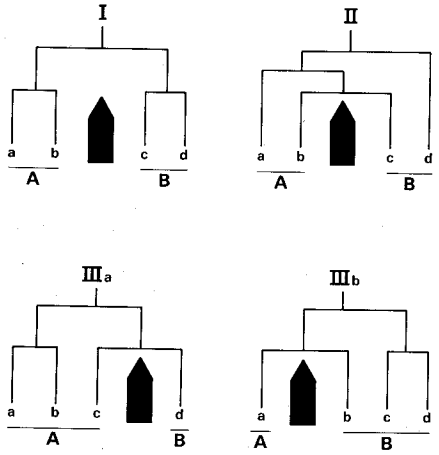

Figure 2. Schematic representations of the *phylogenetic status* of species *A* and *B*. Lower case letters (a-d) are extant mtDNA lineages, each of which can be interpreted to represent an individual animal or an assemblage of related animals sharing a common female ancestor at any time *after* separation from the nearest pictured node. Solid dark arrows indicate onset of reproductive isolation (speciation). See text and Table I for additional explanation.

Table I. Definitions of phylogenetic status in terms of maximum genetic distance within (max D_{AA} or max D_{BB}) versus minimum genetic distance between (min D_{AB}) species A and B. See Figure 2 and text for additional explanation.

Category	Phylogenetic Status	Genetic Distance Relationship
I	A and B monophyletic	max D_{AA} < min D_{AB} and max D_{BB} < min D_{AB}
II	A and B polyphyletic	max D_{AA} > min D_{AB} and max D_{BB} > min D_{AB}
IIIa	A paraphyletic with respect to B	max D_{AA} > min D_{AB} and max D_{BB} < min D_{AB}
IIIb	B paraphyletic with respect to A	max D_{AA} < min D_{AB} and max D_{BB} > min D_{AB}

< min D_{AB}, A and B by definition are monophyletic with respect to each other (phylogenetic status I); conversely, when max D_{AA} > min D_{AB} and max D_{BB} > min D_{AB}, A and B by definition are polyphyletic (status II).

When speciation occurs, individuals from a parental stock become the founders of two or more daughter species. We can envision a continuum of possibilities about how this may occur, but for purposes of tractability in the simulations we will consider two general *modes*: (1) the founders of each daughter species are a random sample of individuals in the parent species; or (2) the parent species may be structured in some way (e.g., geographically) so that individuals that become founders of new species are more likely to share a recent common ancestor than individuals drawn at random. The position of an individual along the parental lineage tree would then correspond to its geographic location. This latter possibility will in turn be considered in two submodes: 2a) individuals founding each

daughter species are drawn at random from the tree but are grouped so that they come from opposite sides of the tree; or 2b) individuals founding each daughter species are drawn from end-points of the parental lineage tree, corresponding to extreme geographic regions.

B. Computer Simulations

Our simulations involve the tracing of mtDNA lineages through the process of speciation. To determine the phylogenetic status of a pair of species (with respect to mtDNA) under various speciation modes, it is necessary and sufficient to know: (1) the distribution of genetic distances among the lineages in the parental generation which supplied founders for the daughter species; and (2) the founder lineages which have survived in the daughter species to the time of interest. Space does not permit a complete listing of the computer programs written to provide this information, but the entire programs and all supporting documentation are available from JEN upon request. Programs were written in FORTRAN, and were run on the Digital PDP-11/34 computer. The following is a brief outline of the three major routines.

1. PARDIS

This program (PARent DIStances) generates a vector of mtDNA genetic distances (D) for the individuals in the parental population. A tree represents the development of the population which is assumed to exhibit density regulated growth and a Poisson distribution of female offspring per mother. The mean of the Poisson distribution (AVPROG) is determined by the population size (NPOP) and the carrying capacity (K) with the formula AVPROG = EXP((K-NPOP)/K). The program's inputs are the number of founders for the tree (NFND), the length (in G generations)

of the tree, the carrying capacity of the population (K), and two random number seeds. In practice, we used K = NFND = 2500 and let 4K generations pass to generate a vector of distances. In every case the maximum D in the vector was less than $4K$. The program's output (stored in a file named "DIST.DAT") consists of the number of values in the vector of genetic distances and the vector itself.

The most significant feature of this program is its efficient (time-saving) mode of generating and retaining distance information. It is not necessary to generate distances between all possible pairs of extant individuals for a given generation; all relevant information can be summarized in a set of values that specifies the distances (from common female parent) between pairs of adjacent individuals in the tree as it is being developed. The required number of values which need be retained is thus only one less than NPOP (see Fig. 3 for a pictorial representation of the procedure).

2. EXTANT

EXTANT simulates the random extinction of founder lineages through time in the daughter species. As before, each population is assumed to exhibit density regulated growth, with a Poisson distribution of offspring and mean number of female progeny determined by AVPROG = EXP((K-SUM)/K), where in this case SUM and K refer to the population size and carrying capacity of a particular daughter species. The program's inputs are the initial number of lineages founding the daughter species (NLIN1, NLIN2), the carrying capacities (K1,K2) of the respective species, the total

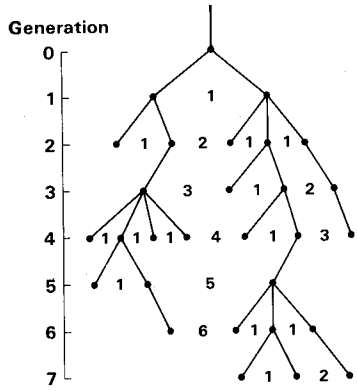

Figure 3. Pictorial representation of the "bookkeeping" involved in the computer program PARDIS. In each generation of the developing computer tree, a vector of distance values is updated as follows: multiple progeny from a given female receive a new distance value of 1; progeny from different but adjacent mothers in the tree receive a distance value one unit greater than the *largest* distance in the line of values between their mothers. The number of distance values which must be retained is thus one less than NPOP. The distance between any non-adjacent individuals in a given generation of the tree is simply the largest distance value between them.

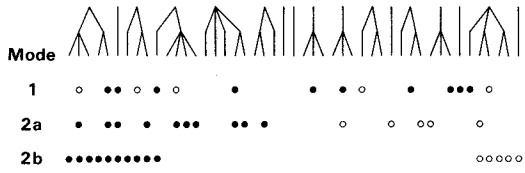

Figure 4. Pictorial representation of alternative speciation modes utilized by the program STATUS for choosing founders for two daughter species. The tree represents the last two generations of a parent population before speciation. In mode 1, founders for daughter species A and B (shown by closed and open circles, respectively) are chosen at random from the parental species. In mode 2a, individuals are chosen at random from separate parts of the parent species tree; and in mode 2b, founders are taken from endpoints of the parent tree. In the simulations, numbers of founders for the daughter species can be varied.

duration (LRUN) of the run in generations, the interval (IVAL) in generations at which the program will output data, the number of desired replicates, and two random number seeds. The program's output (stored in a file named "NLIN.DAT") contains the numbers of original founder lineages still surviving (represented by one or more extant individuals) at each output interval. This program is only a slight modification of one which we used earlier (Avise *et al.*, 1984) to study mtDNA lineage survivorship patterns within a population.

3. STATUS

STATUS selects two sets of lineages from a parent population represented by a vector of genetic distances, and determines the "phylogenetic status" of the two daughter species (Table 1; Fig. 2). The manner in which these lineages are chosen from the parent population can be altered in the program to reflect the *mode* of speciation, as discussed above and pictured in Figure 4. The program's inputs are the vectors of distances for the parent population, which are taken from the file DIST.DAT previously generated by PARDIS, and the number of surviving lineages in each daughter species, which is taken from the file NLIN.DAT previously generated by EXTANT. The output consists of the phylogenetic status of the daughter species at various time intervals after speciation.

III. RESULTS

A. Parent Population

An example of distances in a parent population (consisting in this case of 2458 lineages) is presented in Figure 5. In this figure, each vertical line is the distance (D) to the most recent common ancestor for pairs of *adjacent* individuals along the vector of the final tree. Most such distances (> 96 percent) are less than 50; that is, adjacent

individuals have usually shared a common female ancestor within the past 50 generations. Nonetheless, some distances are much larger, and reflect the chance evolutionary retention of separate lineages for long periods of

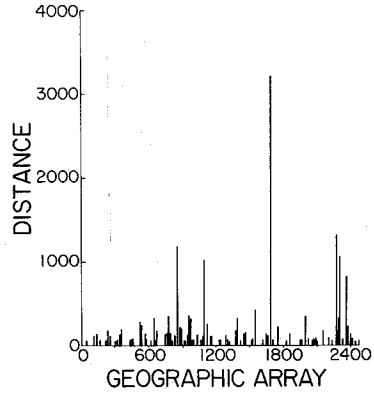

Figure 5. Example of a plotted "DIST.DAT" output, consisting of distances (measured in generations since last shared node) between geographically *adjacent* lineages in a parental population prior to speciation. This population has 2458 extant elements. Distances less than 50 do not stand out above the abscissa.

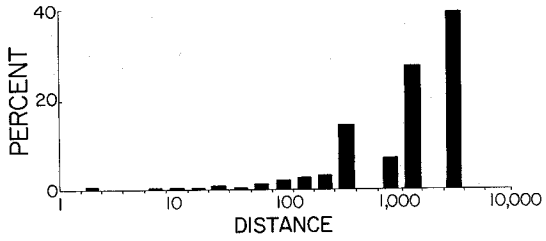

Figure 6. Example of frequency distribution of distances (measured in generations since last shared node) between 1000 *randomly selected* pairs of lineages in a parental population prior to speciation.

Table II. Demographic conditions utilized in the computer simulations. For each of the seven conditions, speciations were allowed to occur by any of the modes pictured in Figure 4.

Simulation file name	Daughter Species: # of founders Species A	# of founders Species B	Carrying capacity Species A	Carrying capacity Species B	Replicate runs
DAT1	3	2	100	100	400
DAT2	30	20	100	100	400
DAT3	300	200	1000	1000	100
DAT4	300	200	300	200	400
DAT5	300	20	300	200	100
DAT6	300	20	300	20	200
DAT7	300	2	300	200	400

time. For example, two lineages near position 1800 in the array last shared a common female ancestor 3294 generations ago.

The structure of a parent population can also be expressed by distances between *randomly selected* pairs of lineages from the tree. An example is given in Figure 6. The distance categories in the figure were chosen to provide a log scale that covers the observed range with 20 intervals. Note the multi-modal character of this distance distribution, reflecting the major divisions in the parent tree. The multiple-modes also exemplify how random extinction processes can generate discrete clusters of lineages.

B. Daughter Species

The demographic conditions accompanying the simulated speciations are listed in Table II. For each of the seven conditions, speciations were allowed to occur by any of the three modes pictured in Figure 4. Thus a total of 21 simulations (each replicated 100-400 times) was conducted.

In our simulations, all speciations via mode 2b in Figure 4 (in which the founders of the daughter species are selected from the extreme ends

of the parent species tree) resulted in monophyletic daughter species (case I, Table I and Fig. 2). However, speciations via modes 1 and 2a (Fig. 4) yielded varied outcomes of monophyly, polyphyly, and paraphyly. The general pattern of the phylogenetic status curves proved to be similar in all cases; computer outputs for eight of the twenty-one sets of simulations are shown in Figures 7-9.

To exemplify the interpretation of these curves, we will describe Figure 7 in some detail. This set of simulations was run with the demographic conditions (DAT4) specified in Table II -- daughter species A and B were initiated with 300 and 200 founders, respectively, and were subsequently maintained at these same carrying capacities. Speciation

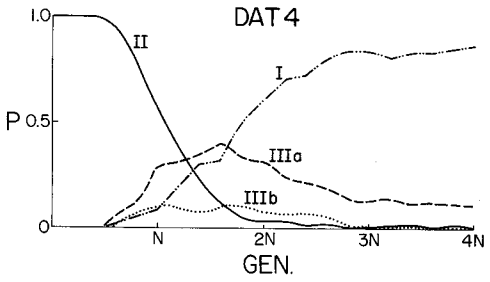

Figure 7. Probability (P) of a given phylogenetic status for two species GEN. generations following simulated speciation. Status I, both species monophyletic; status II, both species polyphyletic; status IIIa, species A paraphyletic with respect to species B; status IIIb, species B paraphyletic with respect to A. Speciation was via mode 1 (see Fig. 4) with demographic parameters DAT4 (see Table II). N is the carrying capacity of the larger daughter species.

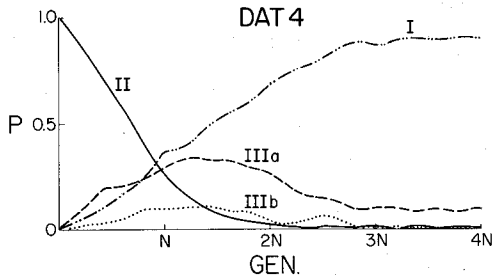

Figure 8. Probability (P) of a given phylogenetic status for two species GEN. generations following simulated speciation. Symbols as in legend to Figure 7. Speciation was via mode 2a (see Fig. 4) with demographic parameters DAT4 (see Table II).

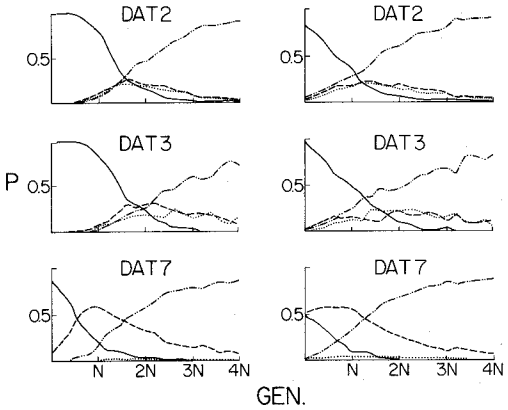

Figure 9. Probability (P) of a given phylogenetic status for two species GEN. generations following simulated speciation. Symbols and line designations as in Figure 7 and its legend. The indicated demographic parameters (e.g., DAT2) are given in Table II. The three graphs on the left are for speciation via mode 1; the graphs on the right are for speciation via mode 2a (Fig. 4). In all cases, N is the carrying capacity of the larger daughter species.

was via mode 1 (foundresses chosen at random from the parental population). The solid line in Figure 7 plots the probability of polyphyly (case II, Table I and Fig. 2) for the daughter species at various times subsequent to speciation. These times are measured in N generations, where N is the carrying capacity of the larger daughter species. The other lines in Figure 7 plot the probabilities of monophyly and of paraphyly (Table I, Fig. 2) of these daughter species. The simulations shown in Figure 8 were conducted under conditions identical to those in Figure 7, but in this case speciation was via mode 2a (Figure 4).

Throughout our simulations, daughter species generated via speciation modes 1 and 2a were polyphyletic, with high probability, for at least N generations following speciation. At intermediate (N - 4N) times after speciation, probabilities of paraphyly typically rise and then fall. In most cases, only after about 4N generations is it highly probable that both daughter species will appear monophyletic. The evolutionary change to monophyly is of course attributable to the random extinction of lineages through time in the simulations. In general, probabilities of polyphyly remain high for longer times under speciation mode 1, where foundresses are chosen at random, than under speciation mode 2a, where foundresses are chosen in part by location in the tree (compare Figs. 7 and 8, and the left- versus right-hand columns of Figure 9).

IV. DISCUSSION

Our simulations trace the evolutionary histories of non-recombining, asexually-transmitted genomes (such as mtDNA) across speciation events in sexually reproducing organisms. We assume that mtDNA genome differentiation is strictly time-dependent, so that knowledge of the times of separation of female lineages in a non-anastomosing evolutionary tree

is sufficient to specify the phylogenetic status of species-pairs with respect to mtDNA. The particular simulations shown in Figures 7-9 are, of course, far from exhaustive of the possible demographies of speciation, but they do allow several qualitative conclusions about general patterns of distribution of mtDNA sequences among closely related species.

1) *Phylogenetic distributions of mtDNA can lack concordance with species boundaries.* When the time since separation of two biological species is relative short (e.g., less than about $N-4N$ generations), the probability is high that some mtDNA lineages from one species are more closely related to those from another species than they are to other mtDNA lineages from the same species. Thus in an empirical study, an observed discordance between species affiliation and mtDNA genotype does not necessarily signal effects of secondary introgression, particularly if there is evidence that the species involved could have shared a common ancestor less than about $4N$ generations earlier. This counter-intuitive result is not an artifact of sampling error in choice of individuals or in number of mtDNA genetic characters assayed. It is a biologically meaningful phenomenon attributable to potentially realistic patterns of lineage survivorship across speciation events. However, the probability of such phylogenetically-generated discordancies between species boundaries and mtDNA genotype decreases greatly for species-pairs that have been separated for longer periods of time. Using a somewhat different, mathematical approach, Tajima (1983) obtained these same results and concluded that for recently separated species relationships of particular DNA sequences can differ from the species phylogeny.

Nonetheless, the expected times to monophyly in our simulations are probably very conservative. Particularly under speciation modes 1 and 2a, any factor inhibiting lineage extinction should further extend the times

for which daughter species appear poly- or paraphyletic. For example, population growth following speciation extends the expected absolute time to monophyly by temporarily dampening extinction of lineages (compare DAT3 and DAT4 in Figures 7-9). Another very important factor (not modeled here) likely to inhibit lineage extinction in nature is density regulation in subdivided populations (Avise *et al.*, 1984). Thus the results presented in this report may in reality represent *minimal* expected times to monophyly.

In an empirical study of mtDNA within and between populations or species, there will of course be sampling errors associated with estimating sequence divergence from a finite number of bases or restriction sites, and from limitations in the number of sampled extant lineages. The former source of sampling error might also account for some situations in which species truly monophyletic in matriarchal genealogy appear at face value polyphyletic, or vice versa. The latter source of sampling error would be more likely to leave unrecognized some true cases of poly- or paraphyly.

2) *The phylogenetic status of species is itself dynamic.* For a given pair of species, phylogenetic relationship is not necessarily fixed at time of speciation, but rather will itself change through time. Thus the time after speciation at which a pair of species is observed will usually be an important factor influencing phylogenetic status. The usual order of status following speciation will be polyphyly ⟶ paraphyly ⟶ monophyly, although the polyphyly or polyphyly + paraphyly stages may be bypassed. Once lineage sorting reaches a stage where species are monophyletic, reestablishment of a poly- or paraphyletic appearance can only be achieved through secondary gene exchange, most likely mediated by hybridization and introgression.

3. *Mode of speciation influences the phylogenetic status of related species.* Time (in generations) to expected monophyly for daughter species is clearly strongly influenced by population sizes at and subsequent to the speciation event. It is also strongly influenced by the geographic distributions of lineages among the founders. When founders of daughter species arise from geographically distinct portions of the parent species range (modes 2a and 2b), initial probabilities of monophyly are enhanced relative to the situation in which founders are chosen at random (mode 1). In effect, in geographic speciations much of the lineage sorting eventually leading to monophyly may already have been achieved prior to the actual speciation.

Speciations can certainly be associated with a wide variety of demographic conditions (Powell, 1982). For example, Dobzhansky (1970) summarized a model of speciation involving large, allopatric populations; Mayr (1954) emphasized speciation by founder effect in small peripheral isolates; and Carson (1968) emphasized founder events following by rapid population flushes (expansions) and contractions. Templeton's (1980) model of speciation via founder event from a large panmictic ancestral population would appear to have genetic consequences similar to our "mode 1" speciation (Fig. 4). Results of the models presented in this paper demonstrate that demographies of speciation can have considerable influence on expected relationships of mtDNA genotypes within versus between species.

We have explicitly focused on the evolutionary dynamics of mtDNA across speciations because of empirically motivated concerns about the pattern of mtDNA genetic variation among related species (see Introduction), and because the linear mtDNA transmission simplifies the modeling process. Nonetheless, the results should apply equally well to the distribution of mtDNA within and among conspecific populations. For

example, Cann *et al.* (1982) and Nei (1982) showed that the distribution of assayed mtDNA genotypes in humans does not always accord with racial (e.g., white, Orientals, American blacks) designation. The exceptions might be attributable to interracial gene exchange, but the possibility should also be considered that some or all exceptions might be due to phylogenetic sorting independent of introgression. Some portions of the nuclear genome may also exhibit for varying times a linear evolutionary history, unaffected by processes such as interallelic recombination or gene conversion (examples may include the DNA within chromosomal inversions in *Drosophila*--Anderson and Aquadro, personal communication). The principles elucidated by our models may also apply to expected patterns of distribution of such nuclear DNA sequences within and among population or species.

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