

Karyotypic Megaevolution by Any Other Name: A Response to Marks

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Marks (1983) objected to our (Baker and Bickham, 1980; Haiduk and Baker, 1982) use of the term "karyotypic megaevolution" as a name for the occurrence of a major repatterning of the euchromatic G-band sequences in a karyotype. As an alternative to "karyotypic megaevolution," Marks (1983) proposed the name "chromosomal tachytely." We believe chromosomal tachytely is not an appropriate name for the phenomenon and provide information as to why we chose Simpson's (1944, 1953) abandoned term.

Simpson (1944) proposed two terms to describe relative rates of evolution, "bradytely" which refers to a slower than average rate and "tachytely" to refer to a faster rate. Chromosomal tachytely as proposed by Marks (1983) for an alternative to "karyotypic megaevolution" would perhaps be acceptable, if karyotypic megaevolution were simply a fast rate of chromosomal evolution. As explained below, this is not true. Relatively rapid rates of chromosomal evolution have been demonstrated in a wide variety of mammals, including mice of the genera *Mus* (Capanna, 1982) and *Onychomys* (Baker et al., 1979) and in the examples cited by us in describing "karyotypic megaevolution," as well as examples cited by Marks (1983). All of these different patterns could be included under Marks' usage of the term "chromosomal tachytely." For example, in *Onychomys* (Baker et al., 1979) there has been the addition of many heterochromatic short arms (possibly as many as 32) without altering a single euchromatic linkage group. In *Mus* (Capanna et al., 1977; Capanna, 1982), numerous centric fusions (at least 17) have occurred, yet the internal structure of the euchromatic arms was unaltered. On the contrary, in all examples of

"karyotypic megaevolution" (Baker and Bickham, 1980) many different types of euchromatic rearrangements have become established and most if not all major linkage groups have been altered.

Factors affecting chromosomal evolution were outlined in detail by Lande (1979) who documented that, from a theoretical probability standpoint, certain types of rearrangements (such as heterochromatic additions and centric fusions) are more likely to become established in a species than are other types of rearrangements (such as telomere-centromere translocations and reciprocal translocations). From a theoretical and practical cytogenetic standpoint, it is much easier to explain the evolution of the observed variation in *Mus* and *Onychomys* than it is to explain the observed change in examples of karyotypic megaevolution (Baker and Bickham, 1980).

The types of rearrangements found in *Mus* and *Onychomys* could occur in the heterozygous condition without causing severe problems in fertility. Without severe constraints on fertility, these rearrangements are more likely to become established. On the other hand, many of the rearrangements found in examples of "karyotypic megaevolution" are thought to cause significant meiotic problems and, therefore, should rarely evolve in natural populations (Lande, 1979). Yet, in examples of karyotypic megaevolution, many such rearrangements (minimally 15 to 20) have become established in species since they separated from their nearest relative. Herein lies the significance of karyotypic megaevolution. Based on the assumptions outlined in Lande (1979), karyotypic megaevolution cannot occur in natural populations during a relatively short pe-

riod of time. In this case, the theory (Lande, 1979) is inadequate to explain what is observed in nature.

It is our hypothesis that species that have undergone "karyotypic megaevolution" have either encountered a period of: (1) transposon activity (McClintock, 1978); (2) reduced or no meiotic constraints; and/or (3) some other equally radical change in the factors that normally affect chromosomal evolution in a stabilizing manner (Baker and Bickham, 1980; Bennett, 1982). For *Onychomys* and *Mus*, there are no data to suggest that their extensive chromosomal change has involved any of the above changes. Therefore, it seems to us that, if the term chromosomal tachytely is used, there will have to be some additional adjective to distinguish karyotypic megaevolution from other forms of chromosomal tachytely. Clearly, as originally defined (Baker and Bickham, 1980), karyotypic megaevolution is not "simply an exceedingly rapid rate of karyotypic evolution" as redefined by Marks (1983:209).

As discussed above, we think the factors regulating karyotypic megaevolution are different both from those regulating the typical patterns observed in most species, as well as those regulating certain patterns that would fall under Marks' term, chromosomal tachytely (e.g., *Mus*, *Onychomys*). Other researchers have observed the same pattern that we noted in the description of "karyotypic megaevolution." Baverstock et al. (1983:114) concluded that their example (in the rodent genus *Zyromys*) supports our view that karyotypic megaevolution cannot be explained by theories based on vagility, reproductive patterns, speciation rates, or inbreeding.

We think that "karyotypic megaevolution" is an appropriate name for the phenomenon where there is a relatively rapid and extensive repatterning of euchromatic segments of the genome. However, it is relatively unimportant whether our proposed term or some other is adopted. What is important is how such a significant portion of the euchromatic genome can be altered by numerous chromosomal rearrangements of a nature that should rarely

become fixed in natural populations (Lande, 1979). If it should prove true that species with radically reorganized genomes have encountered a different set of forces or events than those without such reorganization, as in the case of maize (McClintock, 1978), then the potential of this phenomenon must be considered in studies of the genetics of evolution.

Numerous papers in the last 10 years have provided an explanation of differential rates of karyotypic evolution (Wilson et al., 1975; Bush et al., 1977; Bickham and Baker, 1979; Lande, 1979; Bengtsson, 1980; Bickham, 1981; Shields, 1982; Tegestrom et al., 1983). All of these authors discuss their data sets without recourse to special terms such as "chromosomal tachytely" and "chromosomal bradytely." None of these studies, however, documented the unique pattern of variation we call karyotypic megaevolution. It seems reasonable to us to continue to use terms such as rapid karyotypic evolution, karyotypic conservatism, and karyotypic orthoselection, which are well established in the literature. By coining the term "karyotypic megaevolution," we sought to draw attention to a unique process, not merely to add to the already considerable linguistic burden of systematic biology. At this time, karyotypic megaevolution, by any name, is a facet of chromosomal evolution that defies easy explanation.

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A Note on Minimum Length Trees

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In recent years there have been many studies concerned with the properties (such as stability, congruence, etc.) of various methods for constructing classifications from data matrices. Conclusions from these studies have been based on either the inherent properties of the true tree being estimated or else upon the empirical results of sampling experiments (with either actual or artificial data sets). This note is concerned with another aspect—the implications one can draw based on the mathematical properties of the computational methods themselves.

Consider the two artificial data sets (A and B) furnished in Table 1. They differ

only in the state of character 2 for OTU 6. In the first data set OTU 6 is closer to OTU 4, whereas in the second data set it is closer to OTU 5. Figure 1 shows the unique minimum length Wagner trees (Farris, 1970) for these two data sets. They were found by checking all possible trees with David Swofford's program PAUP. The trees as shown are rooted at the midpoint of the longest path (but the question of alternative rootings is not important for the present note). The relationship of OTU 6 with OTUs 4 and 5 are the same in the two trees despite the change in one of OTU 6's characters (implying a degree of stability with respect to the small perturbation