Evolutionary biologists have sought a correlation between rates of genetic evolution and speciation ever since Mayr (1) proposed his founder-effect model of speciation; indeed this link formed the basis of the theory of punctuated equilibrium. Yet to date few correlations between net rates of speciation (speciation minus extinction) and genetic change have been demonstrated (2, 3), nor has an estimate of the generality of this relationship become available. We compared the net number of speciation events to underlying genetic change using 56 published phylogenies inferred from gene-sequence data (4), and we estimate that the two are correlated in approximately 30 to 50% of cases.

If speciation events and rates of genetic evolution are linked, the total genetic distance from the root of a tree to its tips (“path length,” $x$) will be correlated with the net number of intervening speciation events (“nodes,” $n$). Where many speciation events have occurred, there should be more total genetic change (Fig. 1A). Neither a constant molecular clock nor variable rates of evolution uncorrelated with speciation would show this effect.

We assessed the correlation using all phylogenetic information and controlling for shared ancestry (5). For each tree, we compared the log-likelihood of a model in which the number of speciation events is independent of path length (“random walk” model) with the log-likelihood of an elevated rates (“directional”) model in which path length and number of speciation events are correlated (4, 5).

We found a significant association between speciation events and path length in 28 of the 56 phylogenies (50 ± 7%, Fig. 1B), over a range of taxa (4). Nonrandom sampling of species might bias apparent rates of speciation within a tree, leading to a known artifact of phylogeny reconstruction: that more genetic change will be inferred in regions of the tree in which a greater number of species has been sampled (4). The artifact produces a monotonically increasing and upward-curving relationship for $n$ as a function of $x$. Therefore, it can be assessed by a plot of $n = x^b$, where we expect $b > 1$ when the artifact is present (4). Using a log-likelihood ratio test (4), we found $b$ significantly greater than 1 in 2 of the 28 trees. A more conservative criterion is to exclude from the 28 trees any with $b$ numerically $> 1$. This criterion identified 13 trees, the exclusion of which leaves 43 trees; 15 of these (34.8 ± 7%) show the effect (Fig. 1B). There was no obvious bias in taxa or in tree size (4).

A significant association could arise by chance in any single tree, but can be ruled out for the sample as a whole. Kolmogorov–Smirnov tests of the distribution of likelihood ratio values yielded $P$ values <0.000005 under our most conservative exclusion criterion (4).

Our findings indicate that rapid genetic evolution frequently attends speciation. A punctuated molecular clock is consistent with Mayr’s (1) scenario, although to what degree bouts of rapid genetic evolution could arise from extreme genetic drift during bottlenecks (1) or from adaptive pressures on invasive species (6) remains contentious. Alternatively, the observed correlation could be a consequence of faster-evolving lineages with higher rates of speciation. But lineage-level variation in speciation rates would imply greater species representation in faster lineages, and thus is expected to lead to the phylogeny reconstruction artifact for which we controlled. Therefore, we believe that the results from our filtered data sets in which trees with the artifact were excluded are most likely attributable to a punctuated molecular clock. To the extent that phenotypes and genotypes are coupled, our results provide both a genetic counterpart to and a plausibile link with the observations of punctuated equilibrium of morphological traits reported in the fossil record (7).

**References and Notes**

4. Materials and Methods are available as supporting online material at Science Online.
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**Supporting Online Material**

www.sciencemag.org/cgi/content/full/301/5632/478/DC1
Materials and Methods
Fig. S1
References
Database
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School of Animal and Microbial Sciences, University of Reading, UK.

*Present address: School of Biosciences, University of Birmingham, UK.
†Present address: School of Biological Sciences, Royal Holloway, University of London, UK
‡To whom correspondence should be addressed. E-mail: m.pagel@rdg.ac.uk

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**Fig. 1.** (A) Example tree (8) showing correlation between total path length and net number of speciation events. Numerals, speciation events between root and tips ($n$). Genetic distance is drawn to scale. (B) Log-likelihood of directional model of evolution versus log-likelihood of random walk model for 56 phylogenies. The likelihood ratio statistic $LR = -2\ln\left(\text{likelihood gradual model/likelihood directional model}\right)$ tests whether the directional model provides better description of data from each tree. Where $LR > 3.84$, the directional model of evolution fits significantly better than the gradual model. Points mark phylogenies with $LR < 3.84$ (blue), $LR > 3.84$ and $b > 1$ (yellow), and $LR > 3.84$ and $b < 1$ (red). Thus red points indicate minimum estimate of the number of phylogenies in which rates of speciation and genetic evolution are linked; red plus yellow indicates maximum estimate. Arrow indicates results from phylogeny in [A].