## This Week's Citation Classic®

CC/NUMBER 27 JULY 6, 1987

Fitch W M. Toward defining the course of evolution: minimum change for a specific tree topology. Syst. Zool. 20:406-16, 1971.

[Department of Physiological Chemistry, University of Wisconsin, Madison, WI]

The paper solved the following problem: given a suite of characters for a set of species, how many changes are minimally required for a specific tree that might reflect their evolutionary relationship? [The SCI® and the SSCI® indicate that this paper has been cited in over 130 publications.]

Walter M. Fitch
Department of Biological Sciences
University of Southern California
Los Angeles, CA 90089-1481

March 23, 1987

Evolution is descent with change. Any genetic change in a species' character will be passed on to its descendants and hence all of that species' descendants can be identified by that mark (for example, all vertebrates descended from a species that acquired vertebrae). To place two different vertebrate taxa into two remotely related groups is to require that vertebrae arose independently on two separate occasions. Of course any given character may indeed arise independently more than once, but it seems clear that the fewer multiple independent events an evolutionary relationship (tree) demands, the more likely that tree is to be the correct evolutionary relationship. This fewer-changes-is-better philosophy is the parsimony principle and is in the spirit of Occam's razor.

The paper took many years to write because, due to my lack of mathematical expertise, I could not prove correct my algorithm for determining the minimal number of changes required for a specific tree (for a given suite of characters for a set of species) that reflected their evolutionary relationship. I could only try to devise examples on which the algorithm might fail. After failing for four years to find a counterexample (and hence suspecting possible success), the manuscript, containing what would have been described as a mathematical conjecture had I been mathematically knowledgeable, was sent off. It was a good thing I had waited no longer. Shortly thereafter, John Hartigan of Yale proved my conjecture correct.<sup>1</sup>

Finding the minimum number of changes for a given proposed evolutionary tree was the simplest part. Finding the particular tree that is most parsimonious from among all possible trees is still unsolved. Indeed, William Day of Newfoundland has proven that it is what mathematicians call hard, viz. NP-complete.<sup>2</sup>

The procedure is related to cladistic methods that are also parsimonious but that limit how characters can change. In molecular evolution one usually assumes that any nucleotide can change to any other and that that change is reversible.

The procedure is widely employed today, and I expect that only a minority of those who use parsimony know who designed the method. But it is more important, perhaps, that many also do not know, as Joe Felsenstein of the University of Washington has shown, that while parsimony is the method of choice sometimes, there are cases where parsimony is almost certain to get the wrong answer.<sup>3</sup> How to identify either case separately is one of many exciting questions the field of evolutionary reconstruction is currently addressing.

<sup>1.</sup> Hartigan J. Minimum mutation fits to a given tree. Biometrics 29:53-65, 1973.

<sup>2.</sup> Day W H E. Computationally difficult parsimony problems in phylogenetic systematics. J. Theor. Biol. 103:429-38, 1983.

Felsenstein J. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27:401-10, 1978. (Cited 80 times.)