

Hobgoblin of phylogenetics?

SIR — The exchange between Stewart^{1,2} and Sidow³ on the use of parsimony versus model-based methods for phylogenetic inference highlights a surprisingly underappreciated consideration in the choice of methods: the tradeoff between consistency⁴ and efficiency (or power⁵). Although Sidow correctly notes that distance methods need not equate raw similarity with closeness of relationship, his argument for the superiority of model-based methods deserves closer scrutiny. Specifically, knowing that a method will correctly reconstruct the phylogeny given an infinite amount of data (= consistency) does not necessarily lead to preference for that method when only a finite amount of data are available. If the method is inefficient, requiring large amounts of data before converging on the true tree, attaching too much importance to consistency may be misguided.

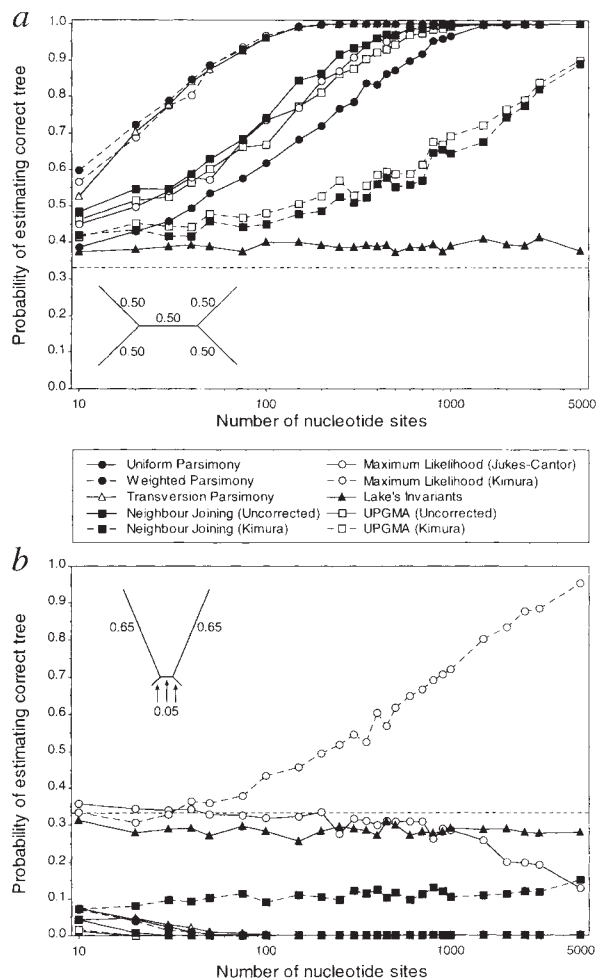
We illustrate this point with the computer simulation results shown in the figure. Most, if not all, phylogenetic methods make a consistent estimate of the phylogeny under the conditions of the first simulation (*a* in the figure), a Kimura 2-parameter model of evolution⁶ with equal probabilities of change in all branches (and a relatively strong transition bias). However, many of these methods become inconsistent when certain branch-length inequalities are introduced (*b* in the figure). Unfortunately, the price of consistency throughout the parameter space of the Kimura model can be high. For the first simulation, the neighbour-joining method⁷ using Kimura distances (corrected according to the same model used to generate the data) requires 5,000 nucleotides to reach the same level of accuracy in reconstructing the true evolutionary tree (90%) that standard parsimony achieves with only 600 nucleotides. Furthermore, parsimony analysis with transversions weighted more heavily than transitions reaches essentially 100% accuracy at only 300 nucleotides whether the transversion:transition weight is set to 2:1, 5:1, 10:1, or infinity (= transversion parsimony). Neighbour-joining with Kimura distances requires more than 50,000 nucleotides to achieve even 99% accuracy. Note also that the expected (average)

number of substitutions per site for the full tree is 5.2, exposing the common misconception that parsimony analysis "requires that each nucleotide has a negligible probability of having changed more than once" (ref. 3).

The simulation in *b* compares the performance of methods when some are known to be inconsistent. Neighbour-joining with uncorrected or Jukes-Cantor⁸ distances, UPGMA, and all parsimony variants quickly converge on the wrong tree. Neighbour-joining with Kimura distances is consistent, but less effective than randomly choosing a tree (= 33% accuracy) for up to about 10,000 nucleotides. Lake's method of invariants⁹, although also consistent under the Kimura model, seems to have little to recommend it in this case; by the time its performance exceeds that of choosing a random tree (at about 100,000,000 nucleotides), neighbour-joining with Kimura distances and maximum likelihood (under the Kimura model) find the correct answer 50 and 100% of the time, respectively. Given the considerably poorer performance of neighbour-joining with Kimura distances under conditions where there is a reasonable chance of reconstructing the correct tree (simulation 1), we question the desirability of choosing it to achieve consistency under other conditions (simulation 2) for which it works barely half of the time even when available sequence length exceeds the genome size of many organisms.

These simulations and many others we have performed (refs. 10–11 and our unpublished data) show the fallacy of Sidow's claim that "statistical methods" (lumping maximum likelihood with neighbour joining and invariant analysis) have all the "powers" of parsimony without its "pitfalls". Parsimony's performance is considerably enhanced when events that

have a higher frequency of occurrence (for example, transitions) are given less weight. Conditions do exist where parsimony will fail with certainty, but under these same conditions most "statistical methods" will also fail more often than not for sequences of even thousands of bases. Among statistical methods, maximum likelihood (which performed well in both simulations) is clearly preferable as a



Efficiency of various methods of phylogenetic inference for a four-taxon tree evolving under the Kimura model of evolution⁶ with transitions ten times more likely than transversions and equal base frequencies. *a*, With all branches $P = 0.5$ in length, where P is the probability that a difference will be observed in a site at the two ends of the branch (tree shown in lower left). *b*, With two opposing peripheral branches of $P = 0.65$, and $P = 0.05$ for the remaining three branches (tree shown in upper left). All points are based on 1,000 simulated trees. Parsimony methods include transversion:transition weights of 1:1 (uniform parsimony), 10:1 (weighted parsimony), and infinity (transversion parsimony). The results for transversion:transition weights of 5:1 and 2:1 are not shown because of excessive overlap, but differ from results shown for 10:1 weighting by no more than 6% up to 200 nucleotides and are indistinguishable for longer sequences. Neighbour-joining (NJ) with Kimura distances requires 50,000 nucleotides (off scale shown) to achieve 99% accuracy under the conditions simulated in *a*. Lake's method of invariants is consistent under the conditions simulated in *a*, but has only a 94% chance of finding the correct tree at 100,000,000 nucleotide sites (off scale shown). The horizontal dashed lines indicate the probability of selecting a correct tree at random.

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4. Felsenstein, J. *Syst. Zool.* **27**, 401–410 (1978).
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9. Lake, J. A. *J. molec. Evol.* **4**, 167–191 (1987).
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11. Hillis, D. M. *et al. Science* (in the press).

criterion, but it is vastly more computationally intensive. Consequently, discovery of the optimal tree(s) is less likely due to the necessity of using more approximate tree searches. We agree with Sidow's desire for increased acceptance of model-based methods, but there are significant tradeoffs to be considered. The choice between these tradeoffs is, unfortunately, much more complicated than Sidow's "brief statistical guide".

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Holocene mammoth dates

SIR — The reported persistence of dwarf mammoths well into the Holocene on Wrangel Island (S. Vartanyan, V. E. Garutt and A. V. Sher, *Nature* **362**, 337–340; 1993) has been called into question by some people who doubt the validity of the dates obtained in two Russian laboratories by conventional ¹⁴C dating. We have now submitted two previously dated dwarf teeth from Wrangel to the accelerator mass spectrometry (AMS) dating facility at the University of Arizona. Here are the uncalibrated results based on the 5568-year half-life from the paper by Vartanyan *et al.*:

Sample	Conventional date and lab no.	AMS date and lab no.
GUS-9	6,260 ± 5; (LU-2799)	6,360 ± 60 (AA-11529)
PIK-1	7,250 ± 60 (LU-2809)	7,295 ± 95 (AA-11530)

The extremely close correspondence of the dates corroborates both the veracity of the Russian results and the Holocene survival of the mammoths.

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Mammoths in ancient Egypt?

SIR — Lister in News and Views¹ described new work² on the genus *Mammuthus* and its allies, suggesting that dwarf mammoths may have survived in northeast Siberia to coexist with the Egyptian pharaohs, and that dwarfed-mammoth populations and other dwarf

trunk is more like a reconstruction of a living mammoth than an immature elephant. The beast is probably unrelated to the modern mini-elephant reported from central Africa^{6,7}. It looks different and no direct contact (transport of live animals) between that part of Africa and ancient Egypt has ever been documented. Both now and in the Pleistocene, miniature elephantids tended to segregate into miniature forms, which further suggests that the figure does depict a mature



elephantids survived on Mediterranean islands well into the Pleistocene. The figure, reproduced from a scene painted in a pharonic tomb³, is about the ivory trade, and raises the possibility that the elephantid represents a dwarf mammoth.

Egyptian artists could reproduce in colour two-dimensional identifying marks of living biological specimens very much like those in field-identifying manuals today. Thus specimens such as fish⁴ and birds⁵ can be placed into the modern frame of genus and species.

The figure represents tribute brought to Egypt and a parade of exotic animals. The bear is probably a sub-species of *Ursus arctos*, *U. arctos syriacus* or *U. arctos arctos*⁴. As native bears and modern man did not co-exist in Egypt^{4,5}, the first bear seen would be as exotic to the Egyptians as the dwarf mammoth. This picture demonstrates the artist's ability to draw a creature alien to him. Similar bears existed in Asia (Palestine to Asia Minor), on some Mediterranean islands, south Europe and northwest Africa⁴.

The elephantid depicted here is not an immature elephant because of its large tusks. Its skull is domed, similar to a mammoth or possibly an Asian elephant. Its stance and the position of the tusks and

elephantid. Nevertheless, the man in the figure leading the animal is carrying two elephant tusks on his shoulder, and it is possible that the animal could be an elephant symbolic of the ivory's source rather than intended to be an accurate representation of its size.

If the elephantid, the tusks, the bear and the ingot (in the figure) came from the same source, one could speculate that they had a common origin.

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