Why Parsimony?

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particular, the postulated two-fold demographic advantage of parthenogenesis may not be realized. The genetic basis of the transition from sexual to parthenogenetic reproduction receives less attention, presumably because almost nothing is known. In some cases (e.g., some populations of *Solenobia triquetrella*) the transition seems to be straightforward. However, where the necessary changes in meiosis and development have a more complex, polygenic basis (e.g., *Dugesia*), there may be substantial cytological and developmental constraints on the origin of parthenogenesis.

The strength of this book is in its diversity. The authors display an encyclopaedic knowledge of cytological processes and combine this with a broad review of genetic studies. The coverage of the early literature, much of which is still relevant, is particularly valuable. However, it is at times difficult to follow the logical thread connecting observations. There is some repetition between chapters, some observations appear in unlikely places (e.g., cytology of *Phytomyza* in Chapter 7 instead of Chapter 3), and some headings seem inappropriate. A more comprehensive discussion in the introduction of the recent theories on the advantages of sexual reproduction would have provided a clearer context in which to place this wealth of information. For example, what does the diversity of cytological

mechanisms imply for the hypotheses concerning benefits accruing from biochemical functions of meiosis (e.g., DNA repair and methylation)? Do the authors' views on variability and adaptability conflict with theories about the ecological advantages of sex? Thus, most of the recent advantage-of-sex models are still to be properly evaluated against cytological and genetical data. Despite these reservations, this book is a valuable resource for those interested in reproduction and evolution. The cost, however, is likely to be prohibitive to students.

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WHY PARSIMONY?[1]

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For some time now Elliott Sober has been trying to make sense of the use of parsimony in phylogeny reconstruction. What exactly does parsimony assume about the evolutionary process, and under what circumstances is it justified as an inference procedure? Sober demands that these questions be faced head on; as he says, "it is an unsatisfactory mixture of hand waving and numerology to insist without argument that less is better than more" (p. xi). This book is his latest and most comprehensive analysis of the problem. It is an outstanding effort in my estimation and should be read by systematists—other evolutionists and philosophers would benefit as well. The arguments aren't easy, but they are often elegant and always clearly stated.

Sober has had two attitudes to deal with—represented mainly by Steve Farris and Joe Felsenstein—

that have tended to stifle exploration of the issues he wishes to confront. On the one hand, it is said that parsimony assumes nothing at all about evolution. Simplicity is a purely methodological principle that scientists must invoke to connect observations to hypotheses. On the other hand, it is asserted that the use of parsimony assumes a great deal about the evolutionary process. In particular, it must assume that homoplasy (convergence, parallelism, and reversal) is rare. Sober stakes out the middle ground—parsimony certainly makes assumptions, but the rarity of homoplasy isn't necessarily one of them. He hastens to point out that in scrutinizing the claims of Farris and Felsenstein he means no disrespect. Even if their claims have not always been as compelling as we are led to believe, they have at least been useful in illuminating the difficulties. Of course, Sober's evenhandedness won't win many friends. As he notes, "the current biological debate is so polarized that admiring the work of both may place me in a minority of one" (p. 193). As it turns out, he isn't completely alone; for better or worse, I find I'm in the same boat.

Much of the first half of the book is devoted to es-

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tablishing that any appeal to parsimony entails sub-
stantive assumptions about the way the world is—it
cannot be "purely methodological." Here, Sober's most
general arguments rest on the philosophically popular
notion that "confirmation is a three-place relationship"
(p. 59), involving a hypothesis, a set of observations,
and a set of background assumptions. Whether "all
ravens are black" is confirmed or disconfirmed by ob-
serving a black raven or a pair of white shoes (or any
other nonblack nonraven) is seen to depend on what
else one believes. And the appeal to simplicity in this
or any other case is "a surrogate for stating an empirical
background theory" (p. 64). Hume also believed that
there must be an additional assumption behind any
inductive inference, namely the uniformity of nature,
but Sober thinks there need be nothing so universal.
Instead, inductive arguments rest on background as-
sumptions that may vary from one type of inference
problem to the next. Parsimony need not assume a
global simplicity of nature, but in any local application
some assumptions are surely being made. The point is
that these need to be acknowledged and evaluated on
their own merits.

The same basic message emerges in Sober's analysis
of claims by Hans Reichenbach and others to the effect
that common cause explanations (wherein correlated
effects are "screened-off" by an underlying factor) are
unconditionally preferable to those invoking separate
causes. Again, these arguments see too direct a con-
nection between observations and hypotheses and too
little role for background assumptions. The latter spec-
ify, among other things, whether an observed corre-
lation is arbitrary, such as the price of bread in England
and the sea level in Venice.

Turning to systematics, Sober first tackles the view
that phylogeny reconstruction is best interpreted in
Popperian terms, with characters seen as falsifying cla-
distic hypotheses. This, he argues, is simply the wrong
model; once one admits the possibility of homoplasy,
any strictly deductive connection between characters
and cladograms simply vanishes. Sober believes that
the deductive view of the problem may have been
fostered by the stance that cladistic characters are low-
level hypotheses of homology, but surely it is possible
to hold (as I do) the latter view without the former. In
any case, the naive falsificationist position is much
easier to deflate than the position taken by Farris (1983).
Sober agrees with Farris's main point that minimizing
assumptions is not the same as assuming minimality.
However, the fact that the most parsimonious phylo-
genetic hypothesis places no upper bounds on homo-
plasy does not guarantee that the parsimony method
assumes nothing at all about the probability of ho-
moplasy. Sober has identified a technical weakness in
Farris's presentation, but he is careful to point out that
Farris's conclusions may well be right. Indeed, I still
find the form of Farris's argument on the robustness
of parsimony quite attractive.

Sober is at his best in analyzing arguments that relate
parsimony and maximum likelihood. Felsenstein (1973)
reached the conclusion that parsimony and maximum
likelihood coincide only when change is assumed to be
rare. Sober shows that although this is part of a suffi-
cient condition it may not be necessary. High proba-
bilities of change "*can* lead parsimony and likelihood
to part ways," but "this does not mean that parsimony

and likelihood *must* fail to coincide if change is not
assumed to be rare" (p. 166). Sober also teases apart
likelihood and statistical consistency, showing that the
latter is at the heart of Felsenstein's important paper
of 1978. Felsenstein shows that parsimony can fail to
be consistent under a simplified process model, and
believes that it may also fail under more realistic cir-
cumstances. Farris argues, in contrast, that parsimo-
ny's performance in the context of a manifestly un-
realistic model has no bearing on how it would fare in
more realistic situations. Rather than pursue this ar-
gument, Sober instead questions the view that statis-
tical consistency is a necessary or desirable criterion.
He demonstrates that likelihood can be justified as a
rule of evaluation by virtue of choosing better-sup-
ported hypotheses, even if it fails to converge on the
truth in the limit. Perhaps we should prefer methods
of inference that best reflect the finite data at hand,
rather than worrying so much about their asymptotic
behavior. The upshot is that Felsenstein has overstated
the case that parsimony assumes low rates of change;
at least, he has not provided a general proof of this
assertion (also see Felsenstein and Sober, 1986 p. 624).

Having shown that it is still unclear exactly what
parsimony assumes about evolution, Sober outlines
what he believes is a step in the right direction. In
particular, he explores the implications of a simple
model of evolution for overall similarity and "cladistic
parsimony," where the latter is equated with the view
that shared ancestral states (symplesiomorphies) are
evidentially meaningless and should be given zero
weight. It emerges that shared derived characters pro-
vide evidence of relationship regardless of the level of
homoplasy, and they provide better evidence than do
symplesiomorphies except when the ancestral state is
rare. Rarity of the ancestral state will obtain given cer-
tain transition probabilities and enough time, but un-
der these same conditions outgroup polarity assess-
ment (using, unfortunately, only a single outgroup)
ensures that one is still better off weighting synapo-
morphies. So Hennig and Farris appear to be vindi-
cated. However, Sober is quick to point out that these
results may not obtain under a different model of evo-
lution. In this regard the assumption of uniform rates
of change is especially troublesome; if branches can
vary in their associated transition probabilities (as we
assume they can), it is unclear what conclusions will
be reached. In fact, these are the very circumstances
that Felsenstein and others have pointed to as posi-
tively misleading parsimony.

The problem Sober chooses to address with his mod-
el helped focus a nagging difficulty I had with the entire
presentation. It seems to me that two questions are
conflated in his view of "cladistic parsimony"—wheth-
er the number of state changes should be minimized
and whether only derived characters are evidentially
meaningful. In part, I think this confusion arises nat-
urally from Sober's having focused throughout on
problems involving only three taxa, because in such
cases incompatibilities of binary characters can result
only from having established character polarities or
the position of the root. In considering more complex
problems, involving four or more taxa, one finds that
character incompatibilities can arise solely by virtue
of conflicts in the distribution of states among the taxa,
independent of directionality (e.g., Meacham, 1984).

That there are really two issues here is also evident in considering how cladists deal with the more complicated problems they are forced to tackle; in fact, they don't ignore the plesiomorphies, as Sober implies they do. Indeed, it happens not infrequently that a clade is actually united by a state scored as plesiomorphic at the outset, simply because a parsimonious interpretation of all of the data indicates a reversal. In other words, it might emerge in the course of an analysis that some of the 0s in a matrix end up performing the same work as the 1s in establishing which groups are monophyletic, and for this reason the 0s aren't dismissed at the outset. It may be that Sober's three-taxon portrayal is fully compatible with the view that arises through consideration of more complex cases, and in fairness to Sober I should note that he leaves this question open (see p. 235). However, I worry that his premise that "cladistic parsimony accords zero weight to symplesiomorphies" (p. 201), and his conclusion that "parsimony's absolute dismissal of symplesiomorphies as evidentially meaningless is not sustained within the model investigated here" (p. 220), may promote an overly simplistic view of phylogenetic analysis.

We should be very grateful to Elliott Sober for investing so much of his energy in this project. His book is especially valuable, I think, in exposing just how much we still don't know about the use of parsimony in phylogeny reconstruction. Let's hope there will be more attention paid to this issue and that a much clearer picture will emerge. In the meantime, there are new approaches that require the same attention; one wonders, for example, about the assumptions underlying Lake's method of invariants ("evolutionary parsimony"; Lake, 1987). In the end, Sober's book leaves me optimistic. My hunch is that parsimony will turn out to be a robust and even statistically consistent inference procedure over a wide range of evolutionary circumstances. Furthermore, I suspect that systematists, by virtue of their role in selecting characters, are helping to ensure that their data sets reside in that sizeable portion of the universe where parsimony is justified.

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