

given in our articles, although as we point out in both articles, and as Self notes, gaps do exist especially with regard to the paucity of recent community-based surveys in the Pacific Region and in some countries of Africa.

Self's comments and the presented data are thus particularly relevant in this context. Indeed, one of the implicit aims of our articles was to elicit responses from those working on filariasis with regard to our estimates and the data on which these are based, since we believe that much pertinent unpublished data may be available with individuals/institutions for many of the under-represented countries in our database. Incidentally, although we worked closely with the Filariasis Control Section of the WHO at Geneva while constructing the database, I am surprised that at no time did we come across the data presented by Self. This suggests that much relevant data

may also be available locally at the various germane WHO Regional Offices.

Whatever the source, I would strongly urge the relevant individuals/institutions to make such data easily available, either by publication or by some other easily accessible form of public dissemination. However, to be truly useful, these reports will crucially require to be accompanied by details (see above), which would allow some independent assessment of the quality of the data collected (this equally applies to the data presented by Self). Such information will also be essential for proper standardization of the data for comparative purposes^{1,2}.

We are currently planning to update and map the distribution of filariasis at various levels from global, regional to within-country. Doubtless, new data on infection and/or disease distribution and the effects of or plans for control at any of these levels, such as those likely to be

available from Self and others, will greatly enhance the utility of this exercise. I look forward to their publication or availability by other forms in the not too distant future.

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Searching for a Tree That Can be Trusted

In his *Comment* 'Can *Trypanosoma* Trees be Trusted?' Noyes¹ discusses possible reasons for a faster evolution in the Salivarian species compared to the remaining trypanosomes and other trypanosomatids, as it appears in the published rRNA phylogenetic trees^{2–5}, and also questions the reliability of such trees. This scepticism is well justified.

It is known that unequal rates of sequence evolution in different lineages may result in the 'branch attraction' artefact⁶. Speaking in terms of the trypanosome trees, accelerated rates of evolution in Salivarian trypanosomes would cause the long branches of an outgroup (the cryptobiid *Trypanoplasma borreli*) and *Trypanosoma brucei* to get together to the exclusion of all other species, thus rendering the entire genus *Trypanosoma* paraphyletic^{2,5}. A known cure to this problem includes finding species which would 'cut' the long branches⁷. We have recently attempted this kind of analysis⁸. Subdivision of the long branches was done by using several other Salivarian species and a reptile trypanosome, as well as two additional bodonids (*Dimastigella*

trypaniformis and *Rhynchobodo* sp.). Additional reduction of the homoplasy (similarity due to reversions or parallelism and not a common origin) was achieved by using only the most conserved sites of the rRNA alignment. Subsequently, we saw a bootstrap support for the monophyly of trypanosomes increasing to 97% and 92% levels for maximum likelihood and maximum parsimony analyses, respectively. This result is in agreement with the protein-based trees^{9,10}. However, the best monophyletic trees were not significantly shorter than the trees in which trypanosomes were 'forced' to be paraphyletic. We interpreted these results as evidence for the victory of the monophyletic model, however, the margin is very narrow.

Returning to the question asked by Noyes, we hope that including additional trypanosome sequences and finding closer bodonid outgroup species would result in the trypanosomatid trees finally become more trustworthy and provide us with a lot of interesting information on 'evolutionary expansion'¹¹ of these rather successful parasites.

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A Key to Understanding *Trypanosoma* Trees

In a recent *Comment* article in *Parasitology Today*, Noyes has raised some fascinating points concerning the increased evolutionary rate in salivarian trypanosomes¹. We were disappointed, however, to see that the article uses the 'usual' limited number of sequences to produce a distance tree which continues to promote the idea that the genus is polyphyletic; this, as the most

recent comprehensive work by Lukeš et al.² illustrates, now appears not to be the case. Moreover, as alluded to by Noyes himself, it is apparent that much (if not all) of the confusion concerning the monophyly (or otherwise) of *Trypanosoma* in early studies was due primarily to insufficient suitable taxa and associated phylogenetic artefacts (see, for examples, Refs 3, 4). As

Maslov and Simpson⁵ and Maslov et al.⁶ have indicated, the key to understanding the evolution of Kinetoplastida may well lie in studying organisms not included in earlier analyses, such as the trypanosomes of fish, amphibians and reptiles. Similarly, we suggest that the small number of *Schizotrypanum* (two *T. cruzi* species) included, compared with the preponderance of salivarian taxa, may be significant in clustering them artificially with other unrelated taxa due to long branch

attraction^{7,8}. Given the imbalanced taxon complement of Noyes' tree, it seems impossible to rule out the influence of such effects and, consequently, any estimate of the degree of relatedness of *T. brucei* and *T. cruzi* derived from it must be similarly affected.

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Reply

We agree with the correspondents (above) that increasing the number of taxa included in phylogenies of the genus *Trypanosoma* will increase the confidence that we may have in these trees. However, insufficient data is a perennial problem, and one objective of the paper¹ was to highlight the dangers of accepting gene phylogenies too uncritically, particularly when they are so grossly inconsistent with what else is known of the organisms in question.

The reason why insufficient taxa has caused particular problems in the genus *Trypanosoma* is that the faster evolution of the salivarian trypanosomes has led to an exceptionally strong systematic error. This was demonstrated by a maximum likelihood and parsimony analysis, by Andrew Rambaut, of the alignment used to prepare the Kimura distance-based tree presented in the original paper. Both methods found the genus *Trypanosoma* to be monophyletic with 100% bootstrap

support despite the fact that the distance matrix based tree had found the genus to be paraphyletic also with 100% bootstrap support. This result was robust to the model of substitution used in the maximum likelihood analysis. We suggest that this high level of support (100%) for the 'wrong' tree when using the distance method was a consequence of an increase in the rate of evolution in the *Salivaria* by a factor of eight. Both maximum likelihood and parsimony obtain the branching pattern by considering the nucleotide pattern at each site. The sequences from a fast evolving clade will show considerable divergence from those from a sister clade and therefore may be treated as outgroups under a distance-based method.

This confirms that the placement of *T. brucei* at the root of many earlier trees of the Trypanosomatidae is a consequence of systematic error, this is one of the clearest examples of this effect. Such a large increase in evolutionary rate is very unusual and may have important consequences for the development of methods of treatment

and control. Furthermore, it may provide valuable opportunities for studying the mechanisms of rate changes. Increasing the density of taxa in a tree is always desirable but critical evaluation of preliminary gene trees using the available non-molecular data can provide guidance on when it is essential. Denser trees of the genus *Trypanosoma* are clearly needed and should prove more robust than those published to date, but investigators should also be wary of unequal rate effects. We look forward to those more reliable *Trypanosoma* trees.

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Book Reviews

Vertical Food Web Interactions: Evolutionary Patterns and Driving Forces

edited by K. Dettner, G. Bauer and W. Völkl, *Ecological Studies Vol. 130*, Springer-Verlag, 1997. £76.00 (xxi + 390 pages) ISBN 3 540 62561 5

The editors of this collection of 19 invited papers have aimed to bring together two aspects of ecology that have received considerable attention in recent years; the evolution of life history strategies, and the structure and function of food webs. The subject matter is therefore very wide-ranging, and in a compendium of this type, authors inevitably interpret their brief in diverse ways, some contributing literature reviews and others original data. The result is, at times, hard-going on the reader, who is one minute learning about community structure of ticks on an African antelope (Petney and Horak), and the next about the way that pycnogonids protect themselves from crabs by excreting large

quantities of moulting hormone (Tomaschko). In fact the subjects covered range even more widely than this, from sympatric speciation and host race formation (Bush and Smith, Romstöck-Völkl) through epidemiology of diseases of *Daphnia* (Ebert, Payne and Weisser) to biodiversity in a vineyard agro-ecosystem (Boller, Gut and Remund). However, ecology is all about making links, and the editors provide an all-embracing synopsis in the final chapter, which makes the whole book worthwhile.

The underlying theme of the book is that the ways in which organisms interact depend particularly on their respective life history strategies. In order to put at least

some limit on the field, only vertical food web interactions are considered, but this still represents an immensely complex interplay of trophic relationships. The type of food and mode of feeding define the symmetry of the impact between resource and consumer, and hence the way in which an interactive system evolves. Relationships between generation times of resource and consumer, and the degree to which their phenology is synchronized, have important influences on the mode and intensity of interactions. Body-size relationships might be expected to have fairly predictable effects on trophic interactions, but these become more complicated when the host provides not only the food, but also the habitat for the parasite.

A minority of relationships are non-interactive, the consumer having no influence on its resource, which therefore does not need to evolve defence mechanisms. Some of the best-studied insect-plant relationships of this kind are between tephritid fruit-flies and their hosts.