

The Allan Wilson Centre Newsletter

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Inside this issue

Host-parasite Specificity: How Species Specific are Parasitic Trematode Infections? 1

More Realistic Models of Molecular Sequence Evolution 3

Neighbour-Joining Unmasked . 5

AWC Summer Studentships for 2004/2005..... 6

MBE Conference 2005..... 7

Recent Publications 8

Contact Us..... 8

Host-parasite Specificity: How Species Specific are Parasitic Trematode Infections?

Host-parasite evolutionary theory

A popular theory maintains that many hosts and their parasites have evolved in tandem, with the parasite's evolution mirroring the host's evolution. This theory is largely based on studies of host-parasite systems where strong evolutionary links would be expected; e.g. seabirds, which often breed in monospecific (single species) colonies, and their feather lice, which do not survive long away from their seabird host. We are testing this theory of host-parasite evolution in a system where, due to both the host's ecology and the complicated nature of the parasite's life cycle, strong ecological links are not necessarily expected.

The topshell-trematode host-parasite system

Topshells (intertidal snails) were chosen as the host species in this study for several reasons: 1) they are abundant and easy to collect, 2) different species can inhabit the same area, and 3) the snails play host to a parasitic trematode (flatworm) with a complicated life cycle, involving three different host species (Fig. 1). The parasite's complex life cycle, together with different potential host species living in the same area, make topshells and their trematodes an ideal example of a host-parasite system in which strong evolutionary links are not necessarily expected.

Fieldwork study

A field study was undertaken in which >15000 individual topshells from 97 populations (representing 10 different species) were collected from shores in New Zealand and Australia (Fig 2).

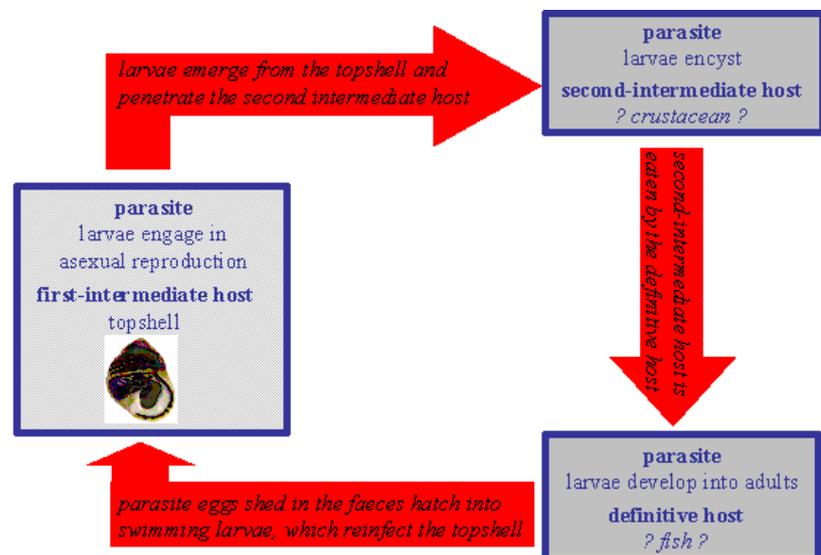


Figure 1: Trematode life cycle





Snails were inspected for parasitic larval infection under the microscope (Fig. 3).

Four New Zealand (*Diloma subrostrata*, *D. nigerrima*, *D. arida* and *Melagraphia aethiops*) and two Australian topshell species (*Austrocochlea constricta* and *A. porcata*) were infected with parasites. The highest level of infection was 17.5% but most topshell populations were either uninfected or infected at low levels. Snails inhabiting soft sediment shores tended to have greater instances and levels of infection, suggesting that infection rates were influenced by host ecology. There were also however several cases where sympatric topshell populations exhibited large differences in infection level, e.g. at Company Bay, near Dunedin, two topshell species were sampled: *D. subrostrata*, exhibited an infection rate of 15%, whereas *M. aethiops* was uninfected. These results imply that both host ecology and host species play a role in determining the level of parasitic infection

Molecular analysis

As all the trematode larvae looked identical, we needed to use molecular

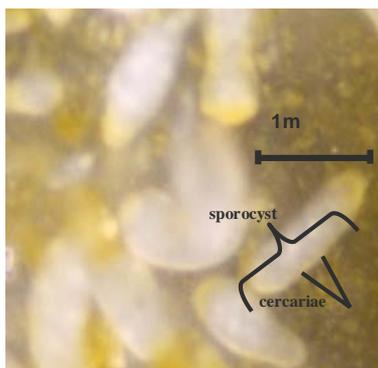


Figure 3: Parasitic trematode larvae dissected from their topshell host

techniques to determine if the single larval morphotype actually consisted of distinct genetic groups. Portions of two genes, one mitochondrial (16S) and one nuclear (ITS2), were sequenced and a phylogenetic tree was constructed from the sequence data (Fig. 4). At the molecular level, parasite larvae,

which look identical, can be separated into three, possibly four, groups, with parasites in each group exhibiting differing degrees of host specificity. Parasites belonging to the group 1 infect two Australian topshell species, *A. constricta* and *A. porcata*: two species that are ecologically and genetically very similar. Parasites from group 3b infect three New Zealand topshell species: *M. aethiops*, *D. nigerrima* and *D. arida*. These three topshell species are not particularly closely related, they are morphologically distinct, and their habitat preferences do not overlap greatly (*D. nigerrima*, for example, lives on decaying kelp cast high on exposed rocky shores, whereas *M. aethiops* occurs on mid-tidal rocks). In contrast to these two cases of host sharing, trematodes infecting *D. subrostrata* do appear to be host specific. Trematodes in groups 2 and 3a infect only *D. subrostrata*, even

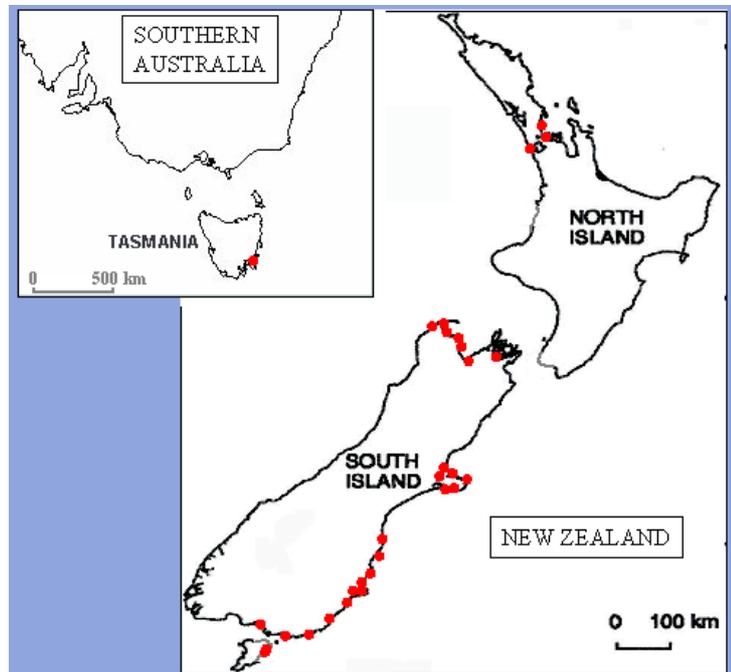
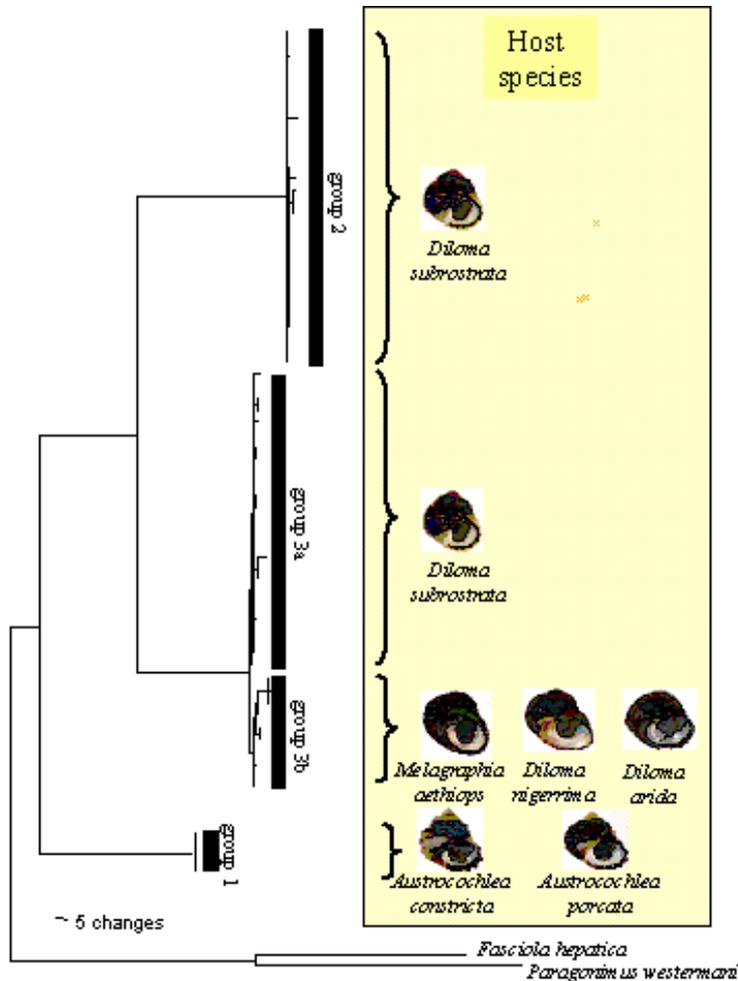


Figure 2: Sampling sites of infected topshell populations

when other topshell species are present at the same location. *D. subrostrata* can harbour two genetically distinct groups of parasites and in several populations, both groups of parasites are present. Thus, in spite of the substantial degree of host sympatry, the tremendous potential for host sharing amongst trematodes is not always realised.

Final word

Although host ecology does play a role in host-parasite interactions, the molecular techniques applied in this study have shown that variability in the infection rate among co-existing snail species is also due to the single parasite morphotype consisting of several genetically distinct groups (which almost certainly comprise separate biological species), with different groups exhibiting differing degrees of host specificity.



More Realistic Models of Molecular Sequence Evolution

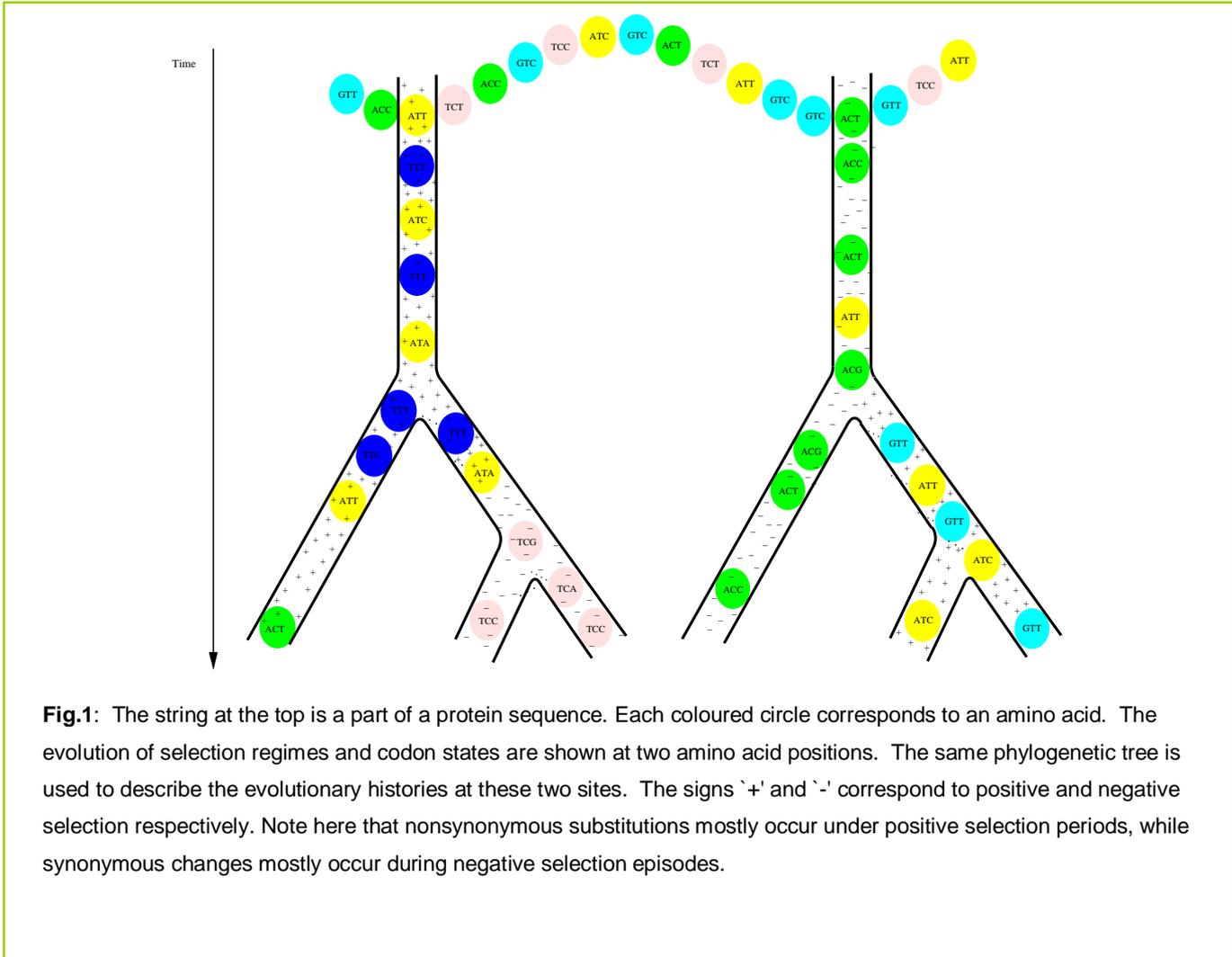
AWC investigators Stephane Guindon and Allen Rodrigo, together with researchers in the USA have developed a promising new model of sequence evolution that allows selection to vary within sites. The model has been applied to HIV evolution and was published in August 2004, in Proceedings of the National Academy of Sciences, U.S.A.

The model extends an earlier approach by Rasmus Nielsen and Ziheng Yang from 1998 in their paper in Genetics where they allow (and average over) different selection values across sites. Together with John Huelsenbeck (UC San Diego) and Kelly Dyer (U. Rochester), Guindon and Rodrigo have taken a further step by allowing the selection regime at a site to vary through time (see Figure 1).

The aim in their analysis is not to estimate the most likely history of switches between selection regimes during the course of evolution, but rather to integrate (average) over the different scenarios. Therefore, Guindon *et al.* modelled switches between selection regimes as a stochastic process, mediated presumably by external forces. By doing so, substitution events are no longer non-synonymous or synonymous changes only: switches between selection regimes are now explicit

Figure 4 Molecular phylogeny of parasitic trematodes is based on portions of two genes, 16S and ITS2

Our finding of morphological similarity masking substantial genetic differences among parasites calls into question the interpretation of studies that rely on parasite morphology alone to assign the degree of host specificity (if we had done this, we would have concluded that one trematode species infected six snail species in two countries).



parameters of the model. This model is very similar in its structure to the covarion model proposed by Chris Tuffley and Mike Steel in 1998 to describe the sites specific variation of substitution rates.

Guindon *et al.* analysed eight HIV-1 env homologous sequence data sets. These data sets are derived from samples that were collected in eight individuals at different stages of the infection. The results indicate that the fit to the data of their new model is significantly better than those obtained with models that

ignore switches between selection regimes. Hence, the time dependant variation of selection process is likely to be a strong evolutionary feature here. The investigators also show that ignoring this feature might affect the quality of the estimation of other evolutionary parameters of the model, such as the frequencies of negative or positive selection.

One interesting feature of the model remains to be explored. In theory, the approach allows to identify the positions

in the phylogeny of site specific switches between selection patterns. Future work will concentrate on using this feature to find cases where switches are correlated with important changes at the phenotypic level.

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Neighbour-Joining Unmasked

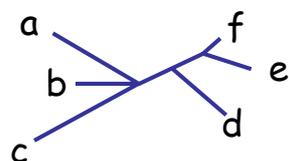
Today the most widely used method for constructing evolutionary trees from distance data is 'Neighbor-Joining' (NJ). The method is fast, and seems to perform well, but there has been some mystery and debate as to what the method aims to achieve. Unlike other (slower) methods, NJ does not globally optimize any particular quantity, rather it proceeds in a step-wise fashion selecting pairs of taxa as 'sister taxa' according to a somewhat complicated recipe.

Recent work by AWC investigators has help unravel the mystery of what NJ is actually optimizing at each stage of building a tree. This theoretical work by

Charles Semple and Mike Steel – published this year in *Advances in Applied Mathematics* - was motivated by an earlier result published four years ago by French biologist Yves Pauplin in *Molecular Biology and Evolution*. Pauplin found a new, elegant and compact way to compute the 'total evolutionary history' in a phylogenetic tree in terms of the evolutionary distances between pairs of species. What was most remarkable about this formula was that no-one had discovered it until four years ago!

Pauplin's proof was somewhat obscure -- it relied on the mathematical technique of 'induction' which often fails to show why a result is true. Semple

and Steel presented an explicit and constructive proof that also provided a more general result – unlike Pauplin's original statement, the theorem allows for the tree to be non-binary (i.e. only partially resolved), as illustrated in Fig. 1. This extension turned out to be the crucial ingredient for another French researcher – in this case a mathematician, Olivier Gascuel – to provide the first rigorous explanation of what the neighbor-joining algorithm is optimizing. The extension of the Pauplin formula implies that at each stage NJ selects a pair of sister taxa to minimize the global 'balanced minimum evolution' score of the resulting tree. The theory behind the extension of Pauplin's formula, based 'on circular orderings' of trees, has also received another application – it provide a way to answer questions like 'how much error can certain tree reconstruction methods tolerate and yet still be accurate?'



$$l = \frac{1}{3}d(a,b) + \frac{1}{6}d(a,d) + \frac{1}{2}d(e,f) + \dots$$

Fig. 1: The extension of Pauplin's formula to non-binary tree. The sum of the branch lengths (l) is a weighted sum of the inter-species distances. The weight of $d(x,y)$ is 1 divided by the product of the number of 'outgoing' arcs encountered at the nodes on the directed path from x to y . For example, the weight for the pair (a,d) is $1/(3 \times 2) = 1/6$.



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Summer Studentships at AWC 2004-2005

This year there is a total of 24 summer studentships offered by the Allan Wilson Centre. The studentships enable students to undertake a project for eleven weeks (including a break over Christmas), in the fields of molecular ecology and evolution. Not all positions were filled.

Use of commensal rats as markers of human mobility in Near and/or Remote Oceania

Supervisor: Dr Lisa Matisoo-Smith, University of Auckland
Students: Lauren Craig; Kasey Robb

Scientific Programming and DNA Sequences

Supervisors: Prof David Penny and Dr Michael Woodhams, Massey University, Palmerston North
Student: Michael Newton

Bioinformatics Supercomputing

Supervisors: Prof Mike Hendy and Dr Barbara Holland, Massey University, Palmerston North
Student: Glenn Connor

DNA in the South Pacific

Supervisors: Drs Peter Lockhart and Craig Morley (University of the South Pacific) Massey University, Palmerston North
Student: Tamara Osborne

Secondary structure modelling of the RNAs that initiate bacteriophage replication

Supervisor: Dr Lesley Collins, Massey University, Palmerston North
Student: Martin Peak

Conservation genetics of New Zealand grasshoppers

Supervisor: Dr Steve Trewick, Massey University, Palmerston North
Student: Rachael Carter

Diversity in New Caledonian *Placostylus* snails

Supervisor: Dr Steve Trewick, Massey University, Palmerston North
Student: Corina Jordan

Molecular studies of the origin of introduced invasive terrestrial animals on Macquarie Island

Supervisor: Dr Mark Stevens, Massey University, Palmerston North
Student: Angela McGaughan

Phylogeography of alpine *Ourisia/Ranunculus*.

Supervisor: A/Prof Peter Lockhart, Massey University, Palmerston North
Student: Lisa Schafer

MHC Variation in tuatara

Supervisors: Prof Charles Daugherty and Dr Hilary Miller, Victoria University of Wellington
Student: Michael Green

Mate choice and territoriality in tuatara

Supervisors: Prof Charles Daugherty and Dr Nicky Nelson, Victoria University of Wellington
Student: Jennifer Moore

Immune function in tuatara

Supervisors: Prof Charles Daugherty and Dr Hilary Miller, Victoria University of Wellington
Student: Shay O'Neill

Frozen tissue collection database management

Supervisors: Prof Charles Daugherty and Susan Keall, Victoria University of Wellington
Student: Karen Britton

Cataloguing collections

Supervisor: Prof David Lambert, Massey University, Albany campus
Student: Margaret Heaslop

"Barcoding" birds

Supervisor: Prof David Lambert, Massey University, Albany campus
Student: Tamara Brown

Molecular Ecology

Supervisor: Prof David Lambert, Massey University, Albany campus
Student: Shih-Chen Yeh



Molecular Biology and Evolution Conference 2005

19 - 23 June 2005

On behalf of the MBE 2005 Organising Committee we invite you to participate in the 2005 meeting. The conference theme will reflect the valuable contribution which Allan Wilson had in the fields of molecular ecology and evolution.

Conference Location and Venue

The conference venue for is the Aotea Centre which forms part of The Edge® in central Auckland.

Social program

A conference is not complete without the opportunity to socialise and network. An opening reception and a conference banquet will be the main social functions.

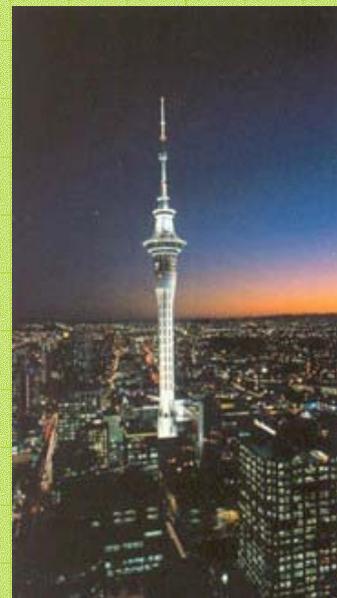
Abstract Submission

Abstract submission is to be sent by 15 March 2005 as a single email attachment, saved as a Microsoft Word document, to email address: e.k.low@massey.ac.nz

Further information

All enquiries should be directed to the conference organisers:

Allan Wilson Centre
Massey University
Private Bag 11-222
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New Zealand
Tel: ++64 6 350 5448
Fax: ++64 6 350 5626
Email: j.r.wood@massey.ac.nz
Conference website: www.mbe05.com





Recent Publications

Asmussen, M.A., Cartwright, R.A. and Spencer, H.G. (2004). Frequency-dependent selection with dominance: A window onto the behavior of the mean fitness. *Genetics* 167: 499-512.

Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., Foley, R.A., Gluckman, P., Godfrey, K., Kirkwood, T., Mirazón Lahr, M., Macnamara, J., Metcalfe, N.B., Monaghan, P., Spencer, H.G. and Sultan, S.E. (2004). Developmental plasticity and human health. *Nature* 430: 419-421.

Bashford, J.D., Jarvis, P.D., Sumner, J. and Steel, M. (2004). $U(1) \times U(1) \times U(1)$ symmetry of the Kimura 3ST model and phylogenetic branching processes. *J. Phys. A: Math. Gen.* 37: L81-L89.

Esser, C., Ahmadinejad, N., Wiegand, C., Rotte, C., Sebastiani, F., Gelius-Dietrich, G., Henze, K., Kretschmann, E., Richly, E., Leister, D., Bryant, D., Steel, M., Lockhart, P.J., Penny, D. and Martin, W. (2004). A genome phylogeny for mitochondria among α -proteobacteria and a predominantly eubacterial ancestry of yeast nuclear genes. *Molecular Biology and Evolution*. 21(9): 1643-1660.

Guindon, S., Rodrigo, A.G., Dyer, K.A., and Huelsenbeck, J.P. (2004). Modeling the site-specific variation of selection patterns along lineages. *PNAS* 101: 12957-12962.

Hordijk, W. and Steel, M. (2004). Detecting autocatalytic, self-sustaining sets in chemical reaction systems. *Journal of Theoretical Biology* 227(4): 451-461.

Huson, D.H. and Steel, M. (2004). Distances that perfectly mislead. *Systematic Biology* 53(2): 327-332.

Matisoo-Smith, E. and Robins, J.H. (2004). Origins and Dispersals of Pacific peoples: Evidence from mtDNA phylogenies of the Pacific rat. *PNAS* 101 (24): 9167-9172.

Miller, H.C and Lambert, D.M (2004) Gene duplication and gene conversion in class II MHC genes of New Zealand robins (Petroicidae). *Immunogenetics* 56: 178-191

Morgan-Richards, M., Trewick, S. A., Chapman, H. M. (2004). Evidence of hybridisation among *Hieracium* species in New Zealand from flow cytometry. *Heredity*. (Published on line 12 May 2004)

Mossel, E. and Steel, M. (2004). A phase transition for a random cluster model on phylogenetic trees. *Mathematical Biosciences*. 187: 189-203.

Penny, D. and Phillips, M. J. (2004). The rise of birds and mammals: are microevolutionary processes sufficient for macroevolution?. *Trends in Ecology and Evolution*. 19(10):516-522

Phillips, M. J., Delsuc, F. and Penny, D. (2004). Genome-Scale Phylogeny and the Detection of Systematic Biases. *Molecular Biology and Evolution*. 21(7):1455-1458.

Ritchie, P.A., Millar, C.D., Gibb, G. Baroni, C. and Lambert, D.M. (2004). Ancient DNA enables timing of the Pleistocene origin and Holocene expansion of two Adélie penguin lineages in Antarctica. *Molecular Biology and Evolution* 21(2): 240-248

Semple, C. and Steel, M. (2004). Cyclic permutations and evolutionary trees. *Advances in Applied Mathematics* 32(4): 669-680.

Spencer, H.G., Feldman, M.W., Clark A.G. and Weisstein, A.E. (2004). The effect of genetic conflict on genomic imprinting and modification of expression at a sex-linked locus. *Genetics* 166: 565-579.

Steel, M. and Penny, D. (2004). Two further links between MP and ML under the Poisson Model. *Applied Mathematics Letters* 17(7): 785-790.

Woodhams, M.D. and Hendy, M.D. (2004). Reconstructing phylogeny by Quadratically Approximated Maximum Likelihood. *Bioinformatics* 20(1): i348-i354

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