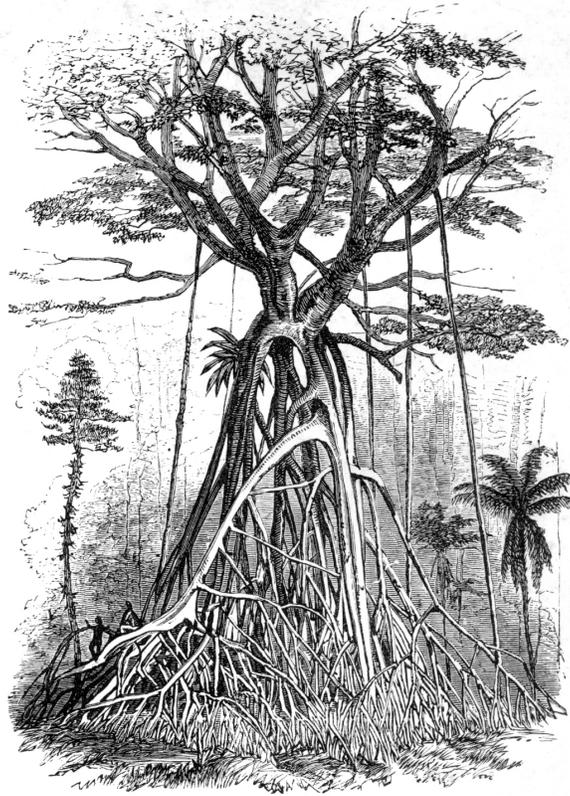


The Leverhulme Trust

Questioning the Tree of Life A Leverhulme Trust Network

Beyond the Tree of Life
London meeting, 2010, July 10th-11th



Alfred Russel Wallace (1869) *Malay Archipelago*

Day 1

Morning: *Insights into the future: An overview of where biology might take tree of life issues*

Chair: Greg Morgan

8.45

Staffan Müller-Wille and Maureen O'Malley (University of Exeter)

Welcome and introduction

9.15

Bill Martin (Heinrich-Heine Universität, Düsseldorf)*The post-arboreal synthesis*

Going beyond the Tree of Life requires a new synthesis of evolution — one we might call the 'post-arboreal synthesis'. My presentation will discuss the various aspects of this synthesis, with particular emphasis on the differences between prokaryote and eukaryote evolution.

9.45

Peter Gogarten (University of Connecticut)*Horizontal gene transfer as a tool in reconstructing the net of life*

Horizontally transferred genes that are maintained in the recipient lineage provide characters useful in phylogenetic reconstruction. These transfer events also can be used to correlate and date evolutionary events that occurred in different parts of the tree/web of life. The choice of reference phylogeny onto which reticulation events can be mapped in reconstructing the reticulate history of life remains an open question. I do not consider the average phylogenetic signal retained in genomes as useful, because it neither reflects organismal evolutionary history, nor does it necessarily reflect the history of any individual gene. Use of the ribosomal phylogeny as backbone appears more appropriate because ribosomal components are only infrequently transferred between divergent organisms. One complication in using the ribosomal phylogeny as backbone is that it cannot be rooted using ancient paralogs. However, the echo from the early expansion of the genetic code that is found in ribosomal proteins can be used to root the ribosomal tree of life directly.

The discussion of gene transfers will include the transfer of a tyrosyl tRNA synthetase (tyrRS) from Haloarchaea to the ancestor of the opisthokonts, and the transfer of over 50 genes from Chlamydia to the ancestor of the archaeplastida (plants, green and red algae, and glaucocystophytes). These transfers reveal that the archaea and bacteria were already diversified into different genera before the major eukaryotic kingdoms and phyla evolved. The transfer of two genes encoding enzymes that allow for the use of acetate as substrate in methanogenesis from cellulolytic clostridia to Methanosarcina suggests that this pathway in Methanosarcinaceae was assembled no earlier than the Mid-Ordovician or about 475 million years ago. One complication in using transfers to correlate the evolution in different parts of the net of life is that many donors of ancient gene transfers belonged to now extinct lineages. Examples include several genes found in Haloarchaea that originated from lineages that branch off before the diversification of bacteria and archaea, respectively.

10.15

Jeffrey Lawrence (University of Pittsburgh)*Remodelling bacterial evolution*

Many papers and meetings have emphasized the lines of evidence and mechanisms by which we believe the tree of life is flawed that any further focus on its inadequacies seems almost gratuitous. Poor suffering thing; we've beat on it so much we should leave it lie there in peace and die. I

propose the construction of frameworks alternative to the ToL wherein bacteria evolution could be understood. The central question I will address is this: how do we reconcile the biological processes we have been inferring with the patterns we see, and thus provide a model for bacterial evolution that is readily grasped by anyone with interests in evolution?

10.45

Coffee break

11.15

Jim Mallet (University College London)

The nature of species: An argument that eukaryotic species are not very different from those in prokaryotes

I have argued elsewhere that species form a continuum with subspecies and other infraspecific categories in eukaryotes, and that this supports the Darwinian argument that speciation is not fundamentally different than intraspecific evolution. But this does not mean that species do not exist: we classify organisms into species by means of observable genetic discontinuities. I will argue here that discontinuities found in nature are indeed evident and can be used to classify species, and that they are of the same type in eukaryotes and prokaryotes. Most 'species concepts' are actually evolutionary explanations of these discontinuities, rather than, as has often been argued, definitions of species *per se*. The relative importance of different processes in generating discontinuities may differ from organism to organism, but the same fundamental processes are involved throughout life.

11.45

Peter Stevens (University of Missouri, St Louis)

Can land plant classifications can be hierarchical – despite species with blurry edges, hybridization and gene duplication?

There is considerable complexity at the intersections between land plant phylogeny, trees, networks, and classifications, and between conventions, standards and ontologies. Even when evolution is tree like, species are constructs with decidedly blurry boundaries, but there is also evidence of quite widespread reticulation (hybridization) and genome duplication, the two perhaps being connected. Less organised lateral transfer may also occur. Aspects of classifications of land plants are conventions, but, properly constructed, such classifications enable communication; I suggest that there is a default understanding of hierarchical classifications (think: noun, adjective) that can be helped or hindered by ideas of rank, yet this understanding is not immutable.

12.15

Dick Burian (Virginia Tech)

Summary and commentary

12.45

General discussion

1.00

Lunch

Afternoon: *Ways forward: An overview of where philosophy and history of biology might take tree of life issues*

Chair: Rob Beiko

2.00

Marc Ereshefsky (University of Calgary)

The future of 'species' in microbiology

A number of biologists and philosophers believe that the notion of species in microbiology is broken. In fact, they believe there is no microbial species category in nature. If this is correct, what is the future of 'species' in microbiology? Some suggest that the word 'species' should disappear from the scientific literature. Others suggest replacement terms. While I agree that we have good reason to doubt the existence of a microbial species category in nature, I don't think we need to banish the word 'species.' Instead we should recognize that 'species' refers to different types of units, some of which may be inconsistent with strongly held beliefs about species. Furthermore, because the word 'species' means different things in different contexts, we should be vigilant in disambiguating what we mean by 'species' in publications and presentations. This proposal has the virtue of accurately tracking theoretical work in microbiology while at the same time being practical.

2.30

Laura Franklin-Hall (New York University)

Prioritizing tree-patterns

This talk draws parallels between dynamic modelling practices in three sciences: that of language evolution, of artefact evolution, and of biological evolution. I suggest that in each case the legitimacy and usefulness of primarily tree-like genealogical representations depends on whether there are complex, interdependent wholes in the domain being modelled. In as much as there do exist wholes—understood as complex systems which regulate the transfer of elements in and out of themselves—tree-like patterns might have some explanatory priority over the otherwise web-like filigree which overlays it. But in as much as there exist no complex systems of this special kind, tree-like patterns should and do fade from view.

3.00

Maureen O'Malley (University of Exeter)

Tree preservation

I will discuss the idea of the tree of life as a heuristic, and whether this is a valuable way of thinking about how the tree has been used in the past and how it might be used in the future. Doing this will involve an analysis of what heuristics are, compared to theories, models, metaphors, idealizations, frameworks and so on. In addition, examining the various ways in which the tree of life has been used might give us ways to distinguish between different types of heuristics and how they are used in biology.

3.30

Coffee break

4.00

Staffan Müller-Wille (University of Exeter)*From maps to trees: Early taxonomic diagrams*

The first graphical representations of taxonomic affinities date back to the second half of the eighteenth century and were produced in a conscious attempt to overcome the age-old tradition of representing relationships among organisms within the framework of a linear scale of nature. I will provide a detailed analysis of one of the first of these representations, the 'Genealogical-geographical table of plant affinities (*Tabula genealogico-geographica affinitatum plantarum*)' published by Paul D. Gisecke in 1792, but based on lectures given by the famous naturalist Carl Linnaeus (1707–1778). My aim in this analysis will be twofold: First, to relate this graphical representation to the practices of morphological comparison that Linnaeus and his students employed in order to establish 'natural' affinities. And second, to understand why map-like and reticulate representations of the 'natural system' of organisms preceded the aboreal representations of the nineteenth century.

4.30

François-Joseph Lapointe (Université de Montréal)*Summary and commentary**Tree dynamics: Dissecting trees in bits and pieces as a means of identifying common historical traces*

Phylogenetic trees are deemed to depict the dynamics of evolution, yet it is generally assumed that such trees are fixed. Namely, when several gene trees disagree with each other, LGT, gene duplication and/or recombination have to be postulated in order to reconcile them with a unique species tree. Whereas different trees may support incompatible partitions, some parts of trees are usually more stable than others. Phylogenies need to be assessed, not only by looking at whole trees, but by dissecting them into bits and pieces which may trace back distinct signals, vertical as well as non-vertical. I will argue that new types of questions can be addressed by taking trees as dynamical entities characterized by statistical parameters that are allowed to change in time and from branch to branch. I will discuss the implications of this framework for the TOL hypothesis, with respect to the different opinions expressed at this meeting.

5.00

General discussion

5.15

Break for drinks and dinner

6.30

Main dinner at Acorn House

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Day 2

Morning: *An overview of new methods, approaches, bodies of evidence and theories and how they open up future understandings of microbial evolution*

Chair: Marc Ereshefsky

8.45

Eugene Koonin (National Center for Biotechnology Information)

Discerning vertical and horizontal trends in the phylogenetic jungle

I will discuss ways to detect a consistent vertical signal in the compendium of phylogenetic trees for prokaryotic genes but also, within the same analytical framework, detecting 'highways' of horizontal transfer. I will further present new analysis addressing the question of whether or not a gradient of horizontal transfer rate might mimic a vertical phylogenetic signal.

9.15

Rob Beiko (Dalhousie University)

It's a phylogenetic network and everyone's invited!!!!

We can all agree that the bacterial phylogenetic tree on the inside of your microbiology textbook is at best misleading, and in some cases completely false. In generalizing a tree to a network, we can accommodate reticulated relationships and make room for uncertainty too. However, an important consequence of reticulate evolution is that no bacterial genome can stand for another: two genomes with identical 16S rDNA sequences can have very distinct sets of genes, and different implied sharing partners in the network. Consequently, when we build networks we need to consider all available data, and even account for unsampled and extinct lineages whenever possible. Of course, with 1000+ bacterial genomes this is not a trivial exercise. Customary tools of phylogenetic network inference and recovery of putative pathways of gene sharing do not scale well with increasing amounts of data. As if choosing and interpreting an appropriate network structure wasn't difficult enough, we also need to serve them up a huge amount of data.

In my presentation I will talk about some of the big conceptual decisions that need to be made in order to build a meaningful phylogenetic network, and identify the problems that are (i) solved, (ii) amenable to cutting corners, and (iii) still terrifying to contemplate in a 10,000-genome world. I will highlight recent advances in these areas, particularly our recent progress in topological comparison algorithms, and identify some promising future directions.

9.45

Yan Boucher (MIT/University of Alberta)

Gene ecology and epidemiology

Almost all virulence genes that make organisms pathogenic are found on mobile genetic elements. Using *Vibrio cholerae* and a few other pathogens as examples, I will make a case that epidemiologists are better off tracking genes than tracking organisms, as has been done in the past (and of course it follows that other microbiological disciplines would also benefit from this approach). This recognition heralds a new facet of metagenomics, which we can call 'gene ecology'. In this paradigm, trees still have their place, but they are trees of genes. Microbiologists will begin to track genes in patients and

environments to predict disease and the spread of antibiotic resistance, and monitoring programs will be set up in various environments.

10.15

Coffee break

10.45

Nick Lane (University College London)

Eukaryote evolution and the evolutionary necessity of endosymbiosis

I will focus on the bioenergetics of why endosymbiosis was necessary for the evolution of the eukaryotic cell, and by the same token, why it is borderline impossible for complex cells to have arisen by point mutations in a prokaryotic population. I have some new data on this that I would like to share.

11.15

James McInerney (National University of Ireland, Maynooth)

Moving on from observation to prediction: What hope do we have for the future?

The Tree of Life with its vertical pattern of inheritance was a comforting idea. It had a solid predictive essence. Given a human genome and some idea of how recently humans and chimps shared a common ancestor, we could make some nice predictions about, say, the chimpanzee genome - it would have genes for vision, it would have genes for an adaptive immune system, it would have genes for sarcasm. We might not be completely accurate in our predictions, but we were likely to be moderately successful. Any confusion could generally be traced to confounding events like gene duplications and losses, some of whom were hidden. However, all told, the Tree of Life offered predictive power. Given that we now know that we don't have a Tree of Life, do we have to abandon hope or do we now have a new set of predictions?

We certainly have to have new methods of analysis. In this talk I will present two things. First a method for identifying genes that are sparsely distributed and whose distribution is 'weird' as a consequence of HGT and secondly I will describe what I think a HGT model predicts and what lies ahead for the bright future of microbiology with a solid HGT-encompassing model of evolution.

11.45

Eric Bapteste (Université Pierre et Marie Curie, Paris)

What's next for microbial evolution?

I agree with Bill Martin that a post-arboreal synthesis of evolution is welcome, and with Jeffrey Lawrence that we need a better model for bacterial evolution. I will make some propositions regarding the kinds of evolutionary objects and the kinds of relationships that such an updated model of evolution could consider and should explain. I will also introduce a few methods with the potential to improve analyses of the evolutionary — yet not strictly genealogical — signals present in massive molecular datasets (such as genomic and metagenomic data).

12.15

Joel Velasco (Stanford University)

Summary and commentary

1.45

General discussion

1.00

Lunch**Afternoon:** *Philosophical and historical perspectives on microbial evolution*

Chair: Dick Burian

2.00

John Dupré (University of Exeter)*Microbes and the unit of selection*

Microbes function as community units with complex evolutionary histories and pluralistic ecologies. Moreover, traditionally multicellular eukaryotes are actually parts of highly mutualistic systems involving embedded or surrounding prokaryote communities. I will examine the implications of such communities for concepts of the unit of selection.

2.30

Thomas Pradeu (Paris-Sorbonne University)*At home in the organism: Immunity and the tolerance of symbiotic microorganisms*

All organisms host commensal or symbiotic microorganisms. In many instances, these microorganisms play key roles in the host, including for digestion, development or metabolism. I am interested in determining how the host immune system actively tolerates these microorganisms, and what the evolutionary interplay between the host and these microorganisms is. I will try to show that the old immunological self-nonself theory is of no use to understand these phenomena, and to present new theoretical perspectives that may help to shed light on them.

3.00

Davide Vecchi (Independent scholar)*Microbial evolution and the challenge to neo-Darwinism.*

What does abandoning the Tree of Life metaphor entail for neo-Darwinian evolutionary biology? In this talk I will try to evaluate aspects of this complex issue by focusing on the evolutionary relevance of two domain-general features of life on this planet. The first feature concerns sharing resources. Recent biological research is increasingly stressing the fundamental role of processes of cooperation and sharing between different and distantly related life forms. Processes of lateral gene transfer and evolution by association potentially affect all levels of biological organisation and integrate all life domains. Resource-flow mediated by so-called 'selfish' replicons is ubiquitous. It could be argued, for instance, that major biological innovations are more a collective effort than the result of random exploration within a lineage. The other feature of life that I would like to emphasise is modularity. The property of the concept that I would like to stress is associated with the repetitive nature of the modules. In this sense modules can be seen as reusable resources that can potentially be mobilised within and across

species, taxa and domains. Modules become fundamental units of evolution as they allow the emergence of compositional processes. Evolutionary novelty achieved through reshuffling and recombining modular units provides a powerful and alternative process to blind variation and selective retention. The picture of evolution emerging from contemporary biology seems to me radically different from the neo-Darwinian one. Compositional processes operating on mobile elements make evolutionary change richer and render the Darwinian jingle of *numerous, successive and slight modifications* anachronistic. I speculate that future evolutionary biology will be more about tinkering and integration and less about adaptation.

3.30

Coffee break

4.00

Greg Morgan (Stevens Institute of Technology, NJ)

The ethics of science popularization

The tree of life debates raise questions of whether scientific popularizers face particular moral constraints. What values should govern how the idea that evolution is not tree-like is conveyed to the public? I will draw from philosopher Heather Douglas's recent work on the whether science and science policy are value free and I might collaborate with my colleague here at Stevens, John Horgan, who is a science writer of some note.

4.30

Ulrich Kutschera (Universität Kassel)

Summary and commentary

Symbiogenesis, directional selection, and the dynamic Earth: A synthesis

In an article signed 11. January 1909, the Russian biologist Constantin S. Mereschkowsky (1855–1921) introduced the symbiogenesis theory for the origin of chloroplasts from ancient cyanobacteria which was later supplemented by Ivan E. Wallin's (1883–1969) proposal that mitochondria evolved from once free-living bacteria. Today, this Mereschkowsky-Wallin principle of symbiogenesis, which is also known as the serial primary endosymbiosis theory, explains the evolutionary origin of eukaryotic cells and hence the emergence of all eukaryotes (protists, fungi, animalia and plants). On July 1, 1858, the concept of natural selection was published independently by Charles Darwin (1809–1882) and Alfred R. Wallace (1823–1913). In the same year, the French geographer Antonio Snider-Pellegrini (1802–1885) proposed the idea of shifting continents, which was later expanded by the German scientist Alfred Wegener (1880–1930), who published the final version of his theory of continental drift in 1929. Today, directional natural selection is accepted as the major cause of adaptive evolution within populations of micro- and macro-organisms and the theory of the dynamic Earth (plate tectonics) is well supported. In this contribution, I combine the processes and principles of symbiogenesis, natural selection and the dynamic Earth and propose an integrative 'synade-model' of macroevolution which takes into account organisms from all five Kingdoms of life. In addition, I discuss these findings with respect to the Tree of Life Project, a collaborative effort of biologists from around the world that goes back to a metaphorical

sentence in Darwin's *Origin of Species* (1859), wherein he proposed that all organisms on Earth may be related to each other.

5.00

General discussion and conclusion: Where to now? A group discussion with an eye to the future

5.30

Close of meeting

6.00

Drinks then dinner at St Pancras Grand

