

The tree of life: introduction to an evolutionary debate

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Abstract The 'Tree of Life' is intended to represent the pattern of evolutionary processes that result in bifurcating species lineages. Often justified in reference to Darwin's discussions of trees, the Tree of Life has run up against numerous challenges especially in regard to prokaryote evolution. This special issue examines scientific, historical and philosophical aspects of debates about the Tree of Life, with the aim of turning these criticisms towards a reconstruction of prokaryote phylogeny and even some aspects of the standard evolutionary understanding of eukaryotes. These discussions have arisen out of a multidisciplinary collaboration of people with an interest in the Tree of Life, and we suggest that this sort of focused engagement enables a practical understanding of the relationships between biology, philosophy and history.

Keywords Tree of life · Prokaryote evolution · Phylogeny · Lateral gene transfer · Multidisciplinarity

Introduction

The term 'Tree of Life' powerfully symbolizes the unity of evolutionary process and pattern. As a concept and graphical entity, its pattern of connected branches represents vertical descent and recurrent species bifurcations. As a comprehensive

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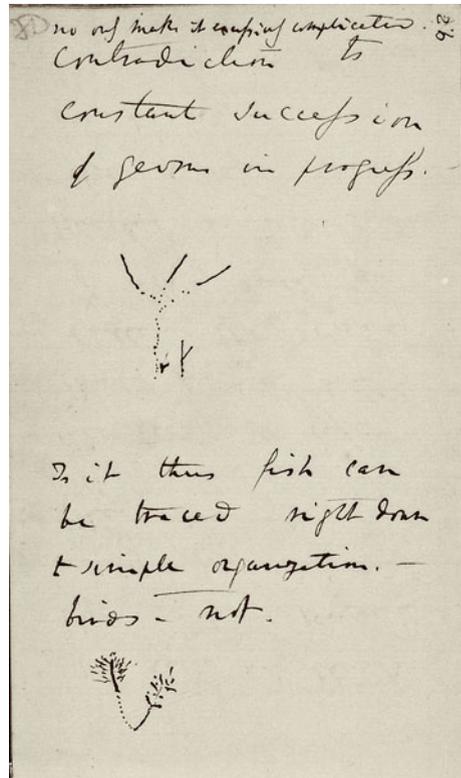
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image, it conveys the grandeur that Darwin envisaged in his evolutionarily linked view of all living things. That a Tree of Life (sometimes capitalized following Darwin's usage, and to indicate its universality) exists in nature is taken for granted and demonstrated by many of today's evolutionary biologists, especially those who work on organisms visible to the naked eye. As evolution has increasingly been understood in terms of the modification and descent of genes, the Tree has been taken to represent the historical channels down which genes have flowed from the distant past to the present. For this very reason, however, once the evolutionary connections among invisible prokaryotes are taken into account, the concept of a Tree of Life is understood to symbolize only a portion of the evolutionary process at best. That is because prokaryotes in nature can—and do—readily acquire genes from various donors, largely without respect for species or other taxonomic boundaries. The realization that this process of lateral gene transfer (LGT; synonymous with horizontal gene transfer or HGT) is quantitatively significant in prokaryote evolution emerged less than 15 years ago, with the dawn of genome sequencing technology. These revelations have forced evolutionary biologists to question the existence of a Tree of Life in the prokaryote world and have made it a deeply contested representation.

Discussed by Darwin as an overarching metaphor of evolutionary history, trees until the molecular era represented only limited clades. These phylogenetic trees, constructed on the basis of morphological and other phenotypic data, seldom spanned phyla let alone kingdoms (notable exceptions are Haeckel 1866, and Whittaker 1969). That changed in the 1970s. With the advent of trees built with molecular data, microbial phylogeny was rapidly able to propose and develop hypothetical scenarios of the early evolution of life up until the present day. These hypotheses were reflected in representations not only of restricted trees of a number of lineages, but also in universal phylogenies of the entirety of evolutionary history. This representation of the universal Tree of Life has spread from molecular microbiology to all phylogeny, and global cooperative efforts to include all organismal lineages within a tree structure have flourished over the last decade (e.g., www.tolweb.org; see O'Malley forthcoming, for statistics).

And yet, even as the popular use of this metaphor has flourished, severe conceptual and epistemological faults have been recognized in it (e.g., Martin 1999; Doolittle 1999). Foremost among the challenges of building a universal tree are the implications of LGT, a prominent and ineliminable feature of any adequate representation of prokaryote evolution. Gene transfer between different lineages means that different genes may have very different evolutionary histories, and that the organismal lineages in which the histories of such genes reside cannot be represented by any single tree. The more that has been learned about prokaryote genomes, the greater has grown the need to represent in a more complete and less biased model the way in which prokaryote evolution operates in nature, rather than to force it to fit preconceived arboreal heuristics. This special issue, based on dialogue between biologists, philosophers and historians, examines the viability of the tree metaphor for prokaryote evolutionary biology and beyond it, to the eukaryote world as well.

Fig. 1 Charles Darwin's Transmutation Notebook 'B' (1837–1838), p. 26. Reproduced by kind permission of the Syndics of Cambridge University Library



The Darwinian background

Although the full history of the Tree of Life is still to be written, a number of contributions made recently have brightly illuminated the pre-Darwinian use of trees to represent the history of species (see especially Ragan 2009¹; also Archibald 2009; Barsanti 1992). These discussions make clear, however, that these earlier trees were only sometimes based on notions of species transformation and when they were, almost always assumed in addition the perpetual creation of new species. It is the general metaphor of branching and rebranching that appealed to early tree constructors, and this appeal has persisted into today's phylogenetic practice. For most phylogeneticists, it is only with Darwin that trees and the universal Tree of Life receive the sort of theoretical justification that warrants use of the metaphor. Darwin, as is well known, began discussing and illustrating abstract trees in his 1837 notebooks. As well as the famous 'I think' tree that has saturated Darwinian imagery in 2009 (Darwin 1837–1838, p. 36), two earlier sketches are worth reproducing because of the way in which they track major developments in his understanding of descent with modification (Fig. 1).

¹ This remarkable piece of scholarship traces the history of trees and networks from the eighteenth century to the present day, and provides the original illustrations of the most important of those representations.

Although Darwin seldom drew diagrams, in these pages of his notebook he tries to depict an explanatory account of species, geographical gaps and the generation of life. In the accompanying notes, Darwin says:

‘The tree of life should perhaps be called the coral of life, base of branches dead; so that passages cannot be seen.—this again offers.

contradiction [insert] no only makes it excessively complicated to constant succession of germs in progress.

[Tree sketch]

Is it thus fish can be traced right down to simple organization.—birds—not?

[Tree sketch]

We may fancy according to shortness of life of species that in perfection, the bottom of branches deaden,

so that in Mammalia, birds, it would only appear like circles, & insects amongst articulata.—but in lower classes perhaps a more linear arrangement’ (1837, pp. 25–27).

Immediately after these reflections on animals, Darwin muses on monads, by which he sometimes meant bacteria (as prokaryotes were then known), other times infusoria (generally protists, sometimes more specifically ciliates), and in these passages, an evolving germ of life (‘living atom’) that pulsed polymorphically through lineages. These spontaneously generated living atoms were extinguished most quickly in more sophisticated life forms, along with the lineages they created, because their lifeforce was used up faster in complex organization. Variable extinction rates, due to the differential extinction of lifeforce, explained why gaps between groups were produced, and why some forms—such as infusoria, which attracted Darwin’s attention repeatedly in his writing—appeared to persist unchanged for long periods of geological time.

Monad has not definite existence.—There does appear some connection shortness of existence in perfect species from many ~~therefore~~ changes and base of branches being dead from which they bifurcated.—(Darwin 1837–1838, p. 29e).

These notebook pages and their sketches supply the premises for Darwin’s first unifying theory of evolving life. It involved a theory of uniform generation for all lifeforms, whether sexually or asexually reproducing; species transformism; and a theoretically unifying material entity—the monad—that could take on endless forms as represented by the continuously diverging branches (Hodge 1983; Sloan 1986; Kohn 1980; Kleiner 1981; Oldroyd 1984; Brink-Roby 2009). Beginning just a few pages later, however, with the ‘I think’ tree (p. 36), Darwin’s explanation of these branching patterns was to shift considerably, from the spontaneous generation of monads and their historical achievement of different levels of organizational complexity, to an overarching rationale of genealogical relationships rather than gradational ones (Hodge 1983, p. 87).

Despite this move, Darwin never abandoned his early depiction of endless branching as the pattern of a unified evolutionary history (Hodge 1983; Sloan 1986; Kohn 1980; Oldroyd 1984). As historian Jonathan Hodge observes,

‘For Darwin, late as well as early, there was no full understanding of anything to do with living beings until it was fitted into a hierarchy of analogies among wholes and their parts that extended from living atoms to a tree of life’ (1985: 237).

That core notion of hierarchical branching is now on trial in today’s debates about the tree of life, because the mechanisms of natural variation among prokaryotes produce both arboriform and distinctly non-arboriform patterns. Although Darwin eventually made a pragmatic commitment to trees as tools that would enable natural classification to be derived from the ‘web of affinities’ (1859, p. 434), many phylogeneticists feel stronger epistemic and ontological obligations to the concept of a tree. The following papers explore persisting tensions between different commitments to the Tree of Life, and suggest ways in which to take the debate forward.

Overview of contributions

One of the most direct ways into an understanding of Tree of Life debates is through the many arguments that W. Ford Doolittle has made for the Tree’s demise—or at least its deep destabilization due to what is now known about LGT (Doolittle 1999, 2000, 2009). In this issue’s paper, Doolittle sets out not only the scientific problems of this construction but the philosophical and political failures of efforts to rescue it. He shows how reconceptualizations designed to save the Tree of Life, such as notions of ‘core’ genes (immune to LGT), the ‘Tree of Cells’ and ‘central tendencies’, all have multiple problems. Doolittle suggests that the failure of trees of genomes to track the evolutionary history of organisms compromises both the meaningfulness and the usefulness of the Tree. Phylogeneticists and other evolutionists now need to embrace a range of evolutionary processes and recognise that they produce a range of evolutionary patterns—not all of which will follow the same paths. Although intelligent design enthusiasts argue that reformulation of Darwin’s theory means it must be wrong, Doolittle suggests that pluralistic post-Darwinian biologists can afford to broaden narrow neo-Darwinian tenets, both scientifically and politically. By emphasizing evolutionary science as an explanatory toolkit rather than a unified and fixed meta-theory, Doolittle believes that dialogues both within science and between science and society could be constructively advanced.

Central to the monolithic view that Doolittle opposes is the commitment to understanding phylogeny in terms of bifurcating species lineages. Olivier Rieppel provides an account of the rise of this vision through an investigation of metaphors of order from the *scala naturae* to today’s Tree of Life. He traces the tension between branching diagrams of nested hierarchies and reticulated representations of evolutionary relationships all the way back to the dissolution of the *scala naturae* into reticulated systems, and their subsequent conversion into phylogenetic trees. Cladism’s adherence to strictly bifurcating patterns continues this tension, and means that characters that compromise it will have to be rejected. The clash

between those who prioritize such patterns, and those who emphasize the variable processes that may explain both these and other patterns, underlies disputes about the Tree of Life. Rieppel shows how pattern reconstruction in the form of cladograms trumped process explanations in the form of phylogenies. This is done, however, as much for reasons of epistemic accessibility and 'quasi-Popperian' testability as it is for ontological commitments to evolution being structured by dichotomous splittings. It is the reversal of this cladism-inspired victory that is driving process-based challenges to the Tree of Life. Alongside this reversal comes an emphasis on species as open rather than closed lineages, and species trees as distinct from gene trees.

For many phylogeneticists, the Tree of Life is a tree of species. The species concept and debates about it have been central to a great deal of history and philosophy of biology, and James Mallet's paper takes these debates back to Darwin. Mallet focuses on why and how Theodosius Dobzhansky and Ernst Mayr formulated a concept of species that they argued was more 'real' than Darwin's, and more cohesive. Reproductive isolation becomes, in their formulation, not only an explanation of speciation but also an adaptive trait that ensured ongoing species coherence. Darwin's much misinterpreted account of species instead saw species as not essentially different from varieties, with the former being distinguishable due to gaps in otherwise continuous morphological variation. Modern population genetics, suggests Mallet, allows species to be delimited in ways that accord better with Darwin's vision than with Mayr's and Dobzhansky's. Moreover population genetics, the approach other contributors recommend as the one appropriate for understanding the evolutionary trajectory of prokaryote groups (e.g., Andam et al. 2010; Doolittle and Zhaxybayeva 2009), not only fits well with Darwin's perspective on species, but also supports the possibility that not all speciation may be best captured by bifurcating branches of gene histories.

Ernst Mayr is responsible for popularizing the Biological Species Concept (BSC), which had the drawback of leaving out a great deal of life and evolutionary history. Maureen O'Malley discusses the dichotomization of life that Mayr proposed, between prokaryotes and eukaryotes, in relation to evolutionary processes that produce reticulating patterns: hybridization and lateral gene transfer. Using the tree of life as a guide, she shows the ubiquity of hybridization and lateral gene transfer in all domains of life. Jim Mallet's work on butterfly hybridization, as well as that of many botanists, mycologists, zoologists and protistologists, illustrates how each eukaryote kingdom is prone to evolutionary events that compromise trees of bifurcating branches. Eukaryote evolution appears to be more tree-like because lateral events occur across shorter evolutionary distances or in lower frequencies. The general pervasiveness of lateral processes across all realms of life suggests that instead of the dichotomous view of evolution suggested by Mayr, a continuum with multiple dimensions would be more appropriate. But although the Tree of Life may represent only some parts of evolutionary history, it can still function as a means by which to examine the limitations of standard evolutionary perspectives and to probe the Mayrian inheritance in philosophy of biology.

Despite widespread recognition of the inappropriateness of the BSC for much of life, microbiology still seeks a natural and universally applicable prokaryote species

concept. Marc Ereshefsky discusses the various conceptual alternatives to the BSC in microbiology and why they too fail to do what is asked of them. He examines one by one the main species concepts proposed as natural and pragmatic categories by microbiologists: recombination-based concepts, ecological, phylogenetic and nominalist ‘phylo-phenetic’ operational units. The many flaws of these concepts, conceptual and empirical, make the existence of a universal prokaryote species category a highly doubtful prospect. Additional suggestions, that species are metapopulation lineages or a family resemblance concept, are also problematic in light of prokaryote biology and evolution. If most of life is not covered by such concepts, then their residual applicability is to a very limited corner of biology and evolution.

Taking the species problem even deeper, Jeffrey Lawrence and Adam Retchless indicate a subtle but important further problem with the application of the notions of species and speciation to the prokaryote world. They argue that the Tree of Life hypothesis is profoundly problematized not just by reticulation and the processes that underlie it, but that lineage separation itself is at stake once the processes of genetic divergence and isolation are properly understood. Prokaryote lineages split very gradually, on a gene-by-gene basis. Gene exchange and recombination at different loci will happen because of different events occurring at different times. Because of this very slow and ill-defined process, similar genes in emerging lineages will manifest fragmented genetic relationships. The process of lineage formation results, in fact, in different genes in a genome having different evolutionary histories. As a consequence, argue Lawrence and Retchless, lineage divergence in bacteria cannot produce a tree-like structure, and any inferences made on the basis of such a framework are likely to be incorrect and misleading. Species and ancestral nodes, arguably inferences from tree logic, can be regarded only as theoretical constructs (albeit useful for practical purposes) and not entities to be found in Nature. The Tree of Life has to be understood, therefore, as a fundamentally inappropriate paradigm for bacterial evolution *regardless* of the extent of gene transfer between lineages.

Part of microbiology’s hesitation in taking such insights to heart is the question of what happens to taxonomy if natural species are abandoned. Cheryl Andam, David Williams and Peter Gogarten work from the ‘other’ side of HGT to reveal not its deconstructive power but its creative power of assembling functional traits and creating what appear to be taxonomically recognizable natural groups. HGT does not occur indiscriminately. Preferential modes and pathways of gene sharing may not only create signals that are sometimes confused with those of vertical inheritance: they may thereby constitute the very basis of the relatedness of organisms. Taxonomic categories could, through this reckoning, be a consequence of the frequency with which organisms exchange genes. The Tree of Life does not necessarily contradict the patterns created by gene exchange, but the full array of forces behind that pattern must be incorporated into any explanation of it. Consequently, argue the authors, a broader and more satisfactory account of evolution needs to incorporate not only HGT but other forces of genomic alteration, including neutral ones. To achieve this, they suggest that the methods of population

genetic analysis are applied to prokaryote taxonomy so that the power of HGT in enabling the formation and cohesion of natural groups can be understood.

Taxonomy is, of course, essential to any understanding of biodiversity, and microbial biodiversity measures have proved elusive despite major technological advances. Greg Morgan takes a philosophical notion of biodiversity and tests it against microbial biodiversity, in which he includes viral biodiversity. Viruses, often included in the general messy category of 'microbes', are highly diverse and powerfully evolvable. Although they are seldom recognized in any efforts to reconstruct the Tree of Life (e.g., Moreira and López-García 2009; plus replies), the deep involvement of viruses in biogeochemistry, the evolutionary history of organismal life, and all organismal physiology means that no account of life, evolution and biodiversity can be complete without them. Morgan specifically examines microbial biodiversity in light of James Maclaurin and Kim Sterelny's (2008) conception of biodiversity, which divides living things into units (most often species) and then quantifies the differences between such units. Morgan shows how a formulation based on species does not work in regard to entities that engage extensively in LGT, and he argues that a phenetic approach based on David Raup's morphospaces is a better way in which to understand biodiversity—whether it is for viruses, other microbes or multicellular organisms. He cautions, however, that consideration of microbial biodiversity exacerbates rather than resolves existing problems in conceptualizing units and differences in biodiversity analyses, and that a single measure of biodiversity is not a likely outcome of more inclusive analyses.

Once concepts of species and biodiversity have been challenged, the door is wide open to reconceptualizations of other entities often taken for granted in evolutionary biology. Frédéric Bouchard focuses on the implications of processes such as LGT for the functional properties of lineages and individuals. Based on the idea of 'lateral function transfer' (LFT, which could also be called 'horizontal adaptation transfer'), Bouchard explores the superorganismal world and how considerations of symbiotic associations of organisms, the way in which most of life is organized, not only destabilize the spatial and temporal boundaries of organisms and lineages, but also draw attention to the importance of functional and adaptationist thinking for understanding lineages of any sort of biological individual. However, adaptation needs to be understood as a potentially ephemeral state of affairs, achieved in multiple ways by different combinations of adapting entities. Rather than thinking solely about a single all-encompassing Tree of Life built on the continuity of genes and their bearers, suggests Bouchard, we should be thinking of multiple 'saplings' of life that sprout in the shadow of a more conventional tree. These saplings represent the ways in which biological individuals, understood largely as superorganismally organized, come into and pass out of evolutionary existence.

Such reflections and reconceptualizations do not stop at the boundary between evolving life and the 'protoliving systems' that must have preceded it. Christophe Malaterre goes below the cellular trunk of the tree of life and presents a case for how minimally alive entities might constitute its very roots. These proto-living roots should be conceived multidimensionally, and Malaterre introduces a novel notion of 'liveness signatures' to encompass the various factors that together constitute being alive in the full sense. Different transitional states between life and non-life can be

assessed along these dimensions of life-associated functions, and empirical examples can be precisely explored with the aim of scoring their performance on these various dimensions. Through such assessments of liveness signatures, different definitions of life can be reconciled and the transitional state between life and non-life can be modeled multidimensionally. The resultant model, according to Malaterre, does not show a single clear root but an entangled and rapidly fluctuating system of many roots. And, most radically, he suggests that we should also consider whether the above-ground tree of organismal lineages (represented mostly by gene histories) should be supplemented by currently existing more-or-less-alive systems that might embellish the Tree's branches in an ongoing and evolutionarily significant way.

What the papers above are all suggesting, both ontologically and conceptually, is a far more complex understanding of the Tree of Life. Any revised Tree concept would have to draw on a much richer cast of entities and processes, and could not be represented in any simple way. Deeply interwoven into those ontological issues, and constituting major practical concerns for phylogeny, are a number of epistemic issues. For many evolutionary microbiologists and phylogeneticists, the existence of lateral gene transfer implies the necessity of using network methods to reconstruct evolutionary relationships. Rob Beiko reflects on the tensions between methods used to recover signals of vertical inheritance and those that trace horizontal relationships. He frames his paper with the suggestion that the question, 'Is there a tree of life?' is in fact a red herring, and argues that instead, genome data have to be meaningfully interrogated by the question, 'To what extent can the organismal tree be recovered from the available data?' The enterprise of quantifying the roles of vertical and lateral inheritance, at various phylogenetic depths, is one in which units of measurement are controversial and interpretations often fiercely debated. Beiko reminds us that although cellular inheritance or vertical descent is an essential contributor to the tracing of evolutionary history, indeed to the very notion of evolving populations and species, many of the strategies used to filter or average out vertical signals from genome data are problematic. Despite such difficulties, Beiko cautions against abandoning the quest for the reconstruction of vertical relationships of cellular entities. After all, DNA replication produces vertical inheritance patterns, whereas gene acquisitions, as captured by networks but not by trees, produce the lateral patterns. Because networks on their own do not distinguish vertical from lateral inheritance, they can be profitably combined with tree methods. Such combinations may allow more refined accounts of the relationships between vertical and horizontal inheritance processes, Beiko concludes, and lead to a sophisticated and conceptually clarifying framework of evolutionary history.

Methods for distinguishing vertical and horizontal inheritance are further explored in Joel Velasco and Elliott Sober's contribution. However, rather than settling for a combination of a tree method to reveal the tree-like part of an evolutionary history, and a network method to reveal the lateral transfers, Velasco and Sober argue for a single method that infers the total history of a dataset. To do this they propose an approach that treats strictly vertical trees as more parsimonious than networks inferring lateral as well as vertical events. They show how the Akaike Information Criterion allows the comparison of tree and network models. Adding

extra lateral branches is penalized by this criterion, and the advantages of improved fit to data have to be higher than this penalty for the addition to be approved. By carrying out such evaluations, say Velasco and Sober, not only are alleged lateral branches more rigorously assessed, but the vertical history is simultaneously revealed.

The many efforts to revise concepts of the Tree of Life and the methods by which it can be reconstructed lead Laura Franklin-Hall to examine the good and bad reasons for abandoning such a programme. She analyses a range of responses to 'refined' tree concepts (trees of cellular lineages). Rejections of these trees are sometimes made on the grounds of essentialism or problems of lineage identity, but Franklin-Hall shows how these do not find their mark. Other criticisms of refined trees have demanded the total representation of evolutionary patterns, but she argues these criticisms also fail because they are an oversimplified view of what scientific representation is doing. But although refined trees may escape these criticisms, they still suffer from other failures, most notably in regard to the explanatory purposes they are meant to serve in systematics and dynamic modelling. In the first case, a Tree of Cells does not serve its intended purpose of explaining the hierarchical nature of classifications. But in the second case, Franklin-Hall suggests that a Tree of Cells might have some claim to being the Tree of Life if cell lineages were to exert a special control over their lineage components, particularly in relation to the addition of new components (i.e., laterally transferred genes). This would be analogous to the way in which a language exerts control over incorporations of words from other languages. Only if such control can be demonstrated, she concludes, could the refined Tree of Cells be a useful explanatory construct. This is the key question that must be asked in relation to whether a Tree of Cells can be equated with the Tree of Life.

The final paper reinforces the difficulties inherent in refined conceptualizations of the Tree. Taking a perspective they call 'integrative phylogenomics', Eric Baptiste and Richard Burian argue that distinguishing between LGT and vertical events needs to be part of a much broader effort to understand in an unbiased way the evolutionary processes that have shaped lineages and gene complexes. Reflecting on the extent and impact of LGT, within and without cellular genetic systems, the authors stress that an adequate epistemology of trees must be able to recognize the depth and breadth of interactions between vertical and lateral processes over evolutionary time. Shared sequence networks offer one solution to the methodological aspect of this problem, but conceptual innovations are also needed, they argue. They outline three categories of entity that form the basis for an integrative phylogenomic approach to evolution: functional genetic units (exchangeable genetic units with phenotypic properties), interacting genetic partners (the entities that participate in genetic sharing), and emergent genetic associations (persisting communities of genetic partners). New tools with which to analyse the upward and downward causal pathways of these entities have yet to be devised, but a comprehension of such units enables the appropriate tools to be developed. Baptiste and Burian thereby unite this issue's two foci, of ontological and epistemic questions about the Tree of Life, as they provide a constructive departure point for

future scientific and philosophical developments. This is also, we hope, the overall achievement of this special issue.

History, philosophy, phylogeny, and science

All of these contributions were developed within the context of an interdisciplinary discussion between biologists investigating microbial evolution while concerned with its philosophy and history, and philosophers and historians with broad interests in evolution and phylogeny, specifically as applied to microbes. Each participant brought different perspectives to a network that has so far produced two profitable meetings and this special issue. Our aim in all this dialogue was to encourage the hybridization or the transfer and integration of ideas and ways of thinking. Biologists were able to share a great many observations, interpretations, problems and research agendas with the humanities scholars, all of whom gained a far deeper appreciation of the issues associated with microbial evolution and the lateral processes in eukaryotes.

Philosophers and historians are not, in the usual institutionalized way of thinking about the academic division of labour, doing the science. However, deeper engagement with any scientific area inevitably leads to different ways of thinking about it. One outcome of such engagement is that philosophers and historians make contributions to collaborative discourse by broadening the scope of the scientific material under discussion, and providing extra context and additional perspectives in the process. Rather than prematurely narrowing the conclusions, these contributions tend to make discussions more general—something that may be especially useful in the case of scientific programmes with contested alternatives. Very often, highly specific expertise in a particular scientific programme, such as the Tree of Life, the origin of eukaryotes, or the origins of life, may artificially narrow the approaches to the topic and restrict its conclusions. Indeed it is often argued that such narrowing of focus is an inevitable risk of the depth of focus demanded by contemporary cutting-edge scientific work. With additional, extra-disciplinary insight, the implications and assumptions of particular ways of thinking may be recognized more fully. While this may not make the science easier or faster, it can allow collaborative ‘taking-stock’ to occur—something that is valuable for a field where disputes have a long and complex history.

Another way of thinking about philosophical and historical contributions to scientific discussion is that these disciplines train their academics in how to pull apart scientific (and other) discourses and interrogate them for consistency, coherence, epistemic commitments, ontological assumptions and the like. These lines of interrogation find multiple points of purchase in the Tree of Life debate, which—as the summary of contributions shows—lends itself to numerous angles of philosophical inquiry. While scientists often have to maintain certain commitments in order to be productive and maintain research programmes, philosophers and historians have the freedom to interact with such programmes by questioning these obligations and drawing different (although not necessarily practical) conclusions.

For example, there are many background factors guiding research programmes that attempt to represent evolution both before and after the origin of eukaryotes, which is where a major innovation in evolutionary mechanisms occurs (Baptiste et al. 2009). Because looking so far back in time through the spyglass of gene sequence comparisons allows observers to see only darkly, the knowledge generated is highly inferential and the margins of uncertainty poorly defined. Where data is limited and its interpretations open, training in abstract and logical thinking can be useful for evaluating the assumptions and theoretical frameworks being used to structure the knowledge produced. Historical analysis may reveal crucial contextual influences on interpretation that are—as we write—shaping it along particular lines of inquiry. Sociological examination of debates (something this particular collaboration needs more of) may lead to a closer appreciation of how they are structured by membership in particular communities or institutions, or even—as the Doolittle paper points out—by responses to far broader social forces.

But being able to contribute in such ways, whether historically, philosophically or sociologically, requires considerable involvement with the science—its current disputes, their history, the alternatives that have been discarded, and the reasons why particular alternatives have been favoured. This involvement leads to the final point, that many of the people engaged in this sort of collaboration share an interest simply in better understanding, from a variety of complementary perspectives, the nature of scientific practice.

Conclusion

These two-way benefits are all motivations for bringing together the disciplines involved in this network, and for producing the papers that are the early products of ongoing multidisciplinary engagement. We envision there will be many more such outcomes, some of them more tangible than others. We expect to see further collaborative engagement in which the cross-fertilization of perspectives manifest in this special issue is developed and refined. Rather than reaching a final verdict about any solitary Tree of Life, and the degree to which it is symbolic or real, a fuller understanding of the history of our microbial ancestors and kin will unfold, and a plurality of perspectives will flourish.

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