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Paradigm change in evolutionary microbiology

Maureen A. O'Malley [a], Yan Boucher [b]

[a] Department of Biochemistry and Molecular Biology, Dalhousie University, Halifax, NS, Canada B3H 1X5
[b] Department of Biological Sciences, Macquarie University, NSW 2109, Australia

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Abstract

Thomas Kuhn had little to say about scientific change in biological science, and biologists are ambivalent about how applicable his framework is for their disciplines. We apply Kuhn's account of paradigm change to evolutionary microbiology, where key Darwinian tenets are being challenged by two decades of findings from molecular phylogenetics. The chief culprit is lateral gene transfer, which undermines the role of vertical descent and the representation of evolutionary history as a tree of life. To assess Kuhn's relevance to this controversy, we add a social analysis of the scientists involved to the historical and philosophical debates. We conclude that while Kuhn's account may capture aspects of the *pattern* (or outcome) of an episode of scientific change, he has little to say about how the *process* of generating new understandings is occurring in evolutionary microbiology. Once Kuhn's application is limited to that of an initial investigative probe into how scientific problem-solving occurs, his disciplinary scope becomes broader.

Keywords: Paradigm change; Evolutionary microbiology; Lateral gene transfer

1. Introduction

Thomas Kuhn's *The structure of scientific revolutions* (1970 [1962]) has exercised a considerable influence on philosophical and sociological accounts of scientific

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E-mail addresses: momalley@dal.ca (M.A. O'Malley), yboucher@bio.mq.edu.au (Y. Boucher).

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change. The book's terminology of normal science, paradigm shifts, scientific revolutions, and incommensurability has also slid easily into the parlance of many scientists. The validity of Kuhn's account of scientific change has been much disputed, however, and there is a vast secondary literature on what he really meant at various stages of his career. Significantly, historians of science have shown little inclination to cast their historiographies within Kuhn's framework (Hacking, 1979; Brush, 2000), although this reluctance may be as much due to scepticism about general theories of science as to scepticism regarding Kuhn's in particular (Wade, 1977, p. 145). Sceptics from the scientific side include biologists and ecologists, who harbour a range of doubts about the appropriateness of Kuhn's concepts for the ways their fields are intellectually organized and how their scientific breakthroughs have occurred (e.g., Mayr, 1997, pp. 92–99; Paine, 2002; Wilkins, 1996; Friedberg, 1997; Lederberg, 1987, p. 33). Most of these life scientists, however, take it for granted that Kuhn's framework is perfectly applicable to the physical sciences.[1]

In what follows, our aim is to clarify Kuhn's general usefulness to a historical understanding of how biological science works. More specifically, we intend to gain a better understanding of the process of scientific change currently operating in a particular field of evolutionary biology. The case we will use to work through Kuhn's concepts is evolutionary microbiology, a discipline in which a serious challenge to some key tenets of the dominant Darwinian paradigm is emerging.

2. Kuhn's core concepts

Kuhn set up his developmental account of scientific change[2] as a direct and deliberate challenge to the sort of scientific history that reinterprets the past by present orthodoxies ('Whiggish' historiography)—a practice that results in the overestimation of the cumulativity of scientific knowledge. Kuhn was determined as well to show that the logical empiricists' view of science was unreal and idealistic, because it marginalized the social and practical aspects of science in deference to cognitive values (Hoyningen-Huene, 1992; Kuhn, 1993a). Central to Kuhn's view of science as a social institution was the notion of *paradigm*: the implicit assumptions and explicit claims that guide the research commitments and practices of specific groups of scientists (1970, p. 10). Kuhn postulated that mature paradigmatic science had its normal puzzle-solving activities punctuated and transformed by bouts of anomaly-induced crisis. The new paradigms that resulted from the consequent 'tradition-shattering' revolutions were 'incommensurable' with or fundamentally and irresolvably different from the ones they replaced.

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[1] There are, of course, many biological scientists who do argue for or assume the appropriateness of Kuhn's model and terminology for their particular field and/or biology in general (e.g., Witkowski, 1997; Strohman, 1997; Bard, 1996; Silvestri & Baldassarre, 2000; Wu & Loucks, 1995).

[2] Kuhn himself referred to his framework as consisting of 'developmental stages' (1993a, p. 314) by which he meant the repeating pattern of anomaly–crisis–revolution–normality. Hoyningen-Huene (1993, p. 222) and Bird (2000, p. 130) have pointed out 'the significant parallels' between the way science develops in Kuhn's theory and Hegel's philosophy of history.

Kuhn's pivotal notion of incommensurability changed considerably over four decades from an initial account couched in terms of gestalt switches to one of 'mutually untranslatable linguistic frameworks' (Kuhn, 1993a; 2000a [1982]; 2000b [1990]).[3] He argued that although incommensurable frameworks could be compared at a general level (in terms of values such as simplicity, accuracy, and explanatory power), they could never be closely compared in an exhaustive point-by-point (empirical and theoretical) analysis. Parts of one theory might be translatable into the other, but there would always be losses in that translation or residues of localized incommensurability. Such untranslatability, he held, was due to differences in the 'taxonomic structure' of the interdefined terms of the competing theories (Kuhn, 1989, 1993a, 2000b). As he made this linguistic turn, Kuhn also subordinated his post-*SSR* clarification of paradigms as exemplars or 'model problems and their solutions' (Kuhn, 1970, pp. 42, 175, 187; 1977, pp. 298, 306) to these overarching theoretical lexicons.[4]

Part of Kuhn's success in communicating his account of scientific change lay in how he brought his concepts alive with compelling historical illustrations. Amongst his favourite exemplars of revolutionary or extraordinary science were the shifts from Aristotelian to Newtonian physics, and Ptolemaic to Copernican astronomy. These were far-reaching transformations, which resulted in the reformulation of a whole field's basic concepts, problems, procedures, and data. Kuhn's examples of puzzle-solving science were also taken from physics and chemistry. He declined to discuss a single case of scientific change in biology, claiming the raw youth of its paradigms so far precluded fundamental disagreements (1970, p. 15). He did allow, however, that biology now exhibited 'normal science' characteristics where paradigms had crystallized, and accepted that Darwin's name was attached to a major transformation of biological science (1977, p. xvii).

Numerous science commentators have thought the same, and designated the success of Darwin's theory of evolution as a prime example of a scientific revolution (e.g., Cohen, 1985; Ruse, 1979; Thagard, 1992). The triumph of molecular biology is also frequently described as a series of revolutionary achievements (Olby, 1994 [1974]; Olsen, Woese, & Overbeek, 1994; Wilson, 1998, p. 64), a pivotal puzzle-solution of which is considered to be the discovery of DNA's structure by Watson and Crick. Although nobody denies the magnitude of the conceptual and methodological change exhibited in these two general areas, neither example shows much conformity in either mode or tempo to Kuhn's account of scientific revolution (Greene, 1980;

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[3] Kuhn's earlier account, note several commentators, was naturalistic and based on experimental perceptual psychology, whereas his later reformulations were derived from an a priori philosophical (neo-Kantian) stance, with a primary concern for the role of language in science (Bird, 2002; see also Caneva, 2000, p. 114; Hoyningen-Huene, 1993).

[4] Kuhn extracted this much more specific definition of paradigm from his larger sense of paradigm as a disciplinary matrix—a network that included all the scientific values, beliefs, generalizations, models, and techniques of a scientific community (1970, Postscript). For some commentators (e.g., Barnes, 2003; Giere, 1988; Rouse, 2003), the exemplar definition of paradigm leads them to characterize Kuhn as primarily concerned with everyday scientific practice, with theories playing a subordinate role of post-problem-solving justification. This view of Kuhn is clearly at odds with the attention he gave lexical incommensurability, which we hold to dominate his work and to be about the larger theoretical matrix in which exemplars are embedded. See also n. 30 and Bird (2002).

Judson, 1980, 1996, p. 586; Mayr, 1994; Wilkins, 1996).[5] Kuhn appears to work best in biology for very casual and undetailed historical scenarios. Should we conclude that Kuhn was right, and that biological disciplines are too immature to fit his model, or should we consider the alternative interpretation that Kuhn was wrong about how science changes?

Some support for the latter conclusion comes from arguments that it is not just in biology that the 'fit' of Kuhn's framework is questionable. Historians of science[6] are able to point to a multitude of non-biological cases (some presented by Kuhn) that fall in between revolutionary and normal science.[7] These cases fit no clear pattern of continuity or discontinuity (of concepts, methodology, or evidence), since they involve complex interactions between explanatory loss and retention (Bird, 2000; Buchwald & Smith, 2001, p. 463; Caneva, 2000; Laudan, 1977, Laudan, Laudan, & Donovan, 1988; Laudan et al., 1988; McMullin, 1993, p. 59; Nersessian, 2001; Shapere, 1989, 2001). Even the designations of the Copernican, Newtonian, or chemical scientific revolutions as radical discontinuations of orthodoxy have been thoroughly challenged (Barker, 2001; Holmes, 2000; Westman, 1994).[8] For many post-positivist philosophers and historians of science, what matters is the continuous emergence of new research traditions and the modification of older ones.[9] This is the normal and *only* state of science, they claim, and 'revolutions' are just dramatic exaggerations of inevitable rivalries between competing research traditions and the scientific problems they confront and solve or fail to solve (Laudan, 1977, p. 138; 1996, p. 85).

The current state of evolutionary microbiology is an intriguing candidate for a Kuhn-inspired examination, owing to the nature of the problems and solutions presently at play in the field. Anomalies exist that apparently require a solution involving the reconfiguration—but not the destruction—of the discipline's theoretical and methodological matrix. Evolutionary microbiology is all the more interesting as a

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[5] In case these examples are considered to be too broad, there are also fine-grained analyses of more limited explanatory change in biological sub-disciplines that do not bear out Kuhn's dynamic (e.g., Allchin, 1994, 1997). This is work in biochemistry, a field that Kuhn suggested would be atypical because of its hybrid origins (1970, p. 15). The particular case, the oxidative phosphorylation controversy, has often been analysed in Kuhnian terms—although usually very loosely. Unlike Allchin, Matzke & Matzke (1997) find the controversy and its resolution to have happened according to Kuhn's schema, as does Weber (2002), who uses the case to explore a practical definition of incommensurability.

[6] There is also a great deal of philosophical discussion about the analytical validity of Kuhn's framework, especially in relation to incommensurability (see Hoyningen-Huene & Sankey, 2001; Sankey, 1994). Since, however, our real interest is *scientific change* rather than Kuhn's concepts per se, we are taking a historical perspective for our discussion.

[7] Fuller (2003, p. 209) implies that Kuhn took all his examples from pre-1920s physics and pre-1950s chemistry because later science altogether refused to fit the Kuhnian framework.

[8] Furthermore, Sharrock & Read (2002) show how Kuhn's separate historical treatments of the Copernican and quantum revolutions portray them as much more extended and less heroic episodes than *Structure* does.

[9] Hoyningen-Huene (1990, 1993) argues forcefully that Kuhn never endorsed a thesis of radical meaning change and discontinuity between incommensurable theories, but Kuhn's work readily lends itself to such a reading and probably would have had far less impact had this not been the common interpretation.

case study because the balance of old and new has not yet been settled, thereby allowing us to observe scientific history in the making.

3. Evolutionary microbiology

Evolutionary microbiology is concerned with describing and explaining the abundant diversity of microorganisms in the context of their relationship to other organisms.[10] A deep understanding of evolution is dependent on understanding the ancestral relationships of prokaryotes to eukaryotes. The standard account of prokaryotic evolution is usually couched in Darwinian terms of vertical inheritance patterns, which are invariably represented as trees. This Darwinian model superseded an earlier taxonomic approach that sought merely to classify microbes 'rationally' rather than phylogenetically in accordance with their 'natural' evolutionary relationships (Stanier & Van Niel, 1941). The lack of suitable data caused early proponents of bacterial phylogeny to despair of their project (Stanier, Doudoroff, & Adelberg, 1957; Van Niel, 1946), until rescue arrived with the inspiration that molecular sequence data might be able to reconstruct evolutionary history. Zuckerkandl and Pauling articulated this hope most clearly and gave a framework to early sequencing endeavours when they proposed that the trees produced from sequence data would map onto those produced from traditional phenotypic characters, and thus converge upon the truth of macroevolution (Pauling & Zuckerkandl, 1963; Zuckerkandl & Pauling, 1965).

Early molecular work on the phylogenetic relationships between microbes used a variety of amino acid and nucleotide sequences (Schwartz & Dayhoff, 1978) until small subunit ribosomal RNA (SSU rRNA) was settled on as the best 'molecular chromometer' because of its ubiquity, highly conserved structure, functional constancy, predictable rates of variation in different regions, and practical ease of sequencing (Fox, Pechman, & Woese, 1977; Woese, 1987; Woese & Fox, 1977; Woese et al., 1975; Woese, Kandler, & Wheelis, 1990; Olsen & Woese, 1993). Analysing gene sequences from multiple prokaryotes led molecular microbiologist Carl Woese to the discovery that prokaryotes were composed of two major groups: the archaea and the bacteria. This finding in itself brought about an enormous change in the received view of evolution as the old prokaryote–eukaryote dichotomy was replaced by a tripartite division of life. Woese himself saw his interpretation of the rRNA data as paradigm shattering, and any opposition to it as the pre-ordained resistance of those with the most to lose.[11] 'I'd read Thomas Kuhn,' he explained, 'so I knew exactly what was going on' (interviewed by Morell, 1997).

What Woese and fellow molecular phylogeneticists had not anticipated, however, was the possibility of different molecular markers yielding trees that contradicted not only those constructed by 'organismal' biology but also trees constructed from other

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[10] The old axiom—that half the biomass on the planet is prokaryotic—is considered too conservative now that further quantitative analyses have been conducted (Whitman, Coleman, & Wiebe, 1998).

[11] On the other hand, Kuhn is also used to explain why Woese has been so successful (Lyons, 2002).

genes. The first such conflicts between trees built from different genes were noticed in the 1970s, but many tree builders thought that these disagreements were rare and that phylogenetic congruence would be recovered with sufficient sequence data (e.g., Schwartz & Dayhoff, 1978). Many also believed that these problems indicated yet more clearly the inadequacy of morphological and physiological data, and the superiority of SSU rRNA over other genes (Dickerson, 1980; Fox et al., 1977; Woese, Gibson, & Fox, 1980).

3.1. Enter lateral gene transfer

As still more conflicting data accumulated, and perplexed molecular phylogeneticists sought to understand why trees were not 'behaving' as expected, one explanation began to gain increasing support: lateral or horizontal gene transfer.[12] The lateral transfer explanation, simply put, posited that tree anomalies were due to interspecific transfers of genes between organisms—a violation of the Darwinian tenet of intraspecific replicatory inheritance[13] and its outcome of clear lineage genealogies. *Lateral gene transfer* (LGT) is both the process and successful outcome[14] of the transfer of genetic material from one organism to another by conjugation, transduction, transformation, or membrane vesicle transport.[15]

Evidence of transformation had existed since the late 1920s (Griffith, 1928) and it emerged into the scientific limelight in the 1940s (Avery, MacLeod, & McCarthy, 1944).[16] Transformation's status as a strain-specific peculiarity was expanded by

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[12] Horizontal gene transfer (HGT) is both the early and (now) standard term used to describe the outcomes of a range of genetic transfer processes. 'Lateral' is the adjective invoked by Ford Doolittle to capture a more radical understanding of gene transfer (Doolittle, personal communication). We use lateral in this paper because of the paradigm-shifting connotations its users often intend it to have. Horizontal is usually (though not always) used when genetic transfer is incorporated into the old paradigm in which replicatory inheritance dominates (see n. 13).

[13] Here, inheritance of genetic material from a progenitor will be termed *replicatory inheritance* as opposed to the more common term *vertical inheritance*. The latter term dissociates the clonal reproduction of prokaryotes from the vertical descent observed in eukaryotes (involving recombination of genetic material between sexual types), whereas we are counterposing both forms of reproduction to lateral transfer.

[14] For transferred DNA to prevail in an organismal lineage, it must confer selective inheritable advantages to the recipients and their descendants (see Berg & Kurland, 2002, for a discussion of the non-persistence of neutral transfers). These advantages include novel capacities with which to acquire new environments, new metabolic functions, resistance to antibiotics, and increased pathogenic virulence (Feil & Spratt, 2001; Hacker & Carniel, 2001; Lan & Reeves, 1996; Levin & Bergstrom, 2000; Ochman, Lawrence, & Groisman, 2000; Sonea & Mathieu, 2001).

[15] Conjugation is the transfer of DNA that involves cell-to-cell contact between organisms and a mobile genetic element (a conjugative plasmid or transposon); transduction is the carriage of DNA from one organism to another by bacteriophages; transformation is the direct uptake of free environmental DNA by an organism into its genome (Bushman, 2002; Mazodier & Davies, 1991). Membrane vesicle transport, not usually listed as a mechanism deserving of its own category, is the transfer of DNA to a cell by a vesicle released by another cell's membrane (Kolling & Matthews, 1999; Yaron, Kolling, Simon, & Matthews, 2000).

[16] These goundbreaking experiments showing DNA to be the material encoding inheritance further demonstrated the ability of microbes to integrate environmental DNA into their genomes.

studies establishing conjugation and transduction as mechanisms of transfer (Hayes, 1952; Lederberg & Tatum, 1946; Zinder & Lederberg, 1952), and the discoveries that these processes operated over a wide range of bacteria. Gene acquisition was recognized enough by the late 1950s to be blamed for the troubling phenomenon of antibiotic resistance, which—as well as becoming a health concern—became a valuable experimental tool for analysing bacterial characteristics (Davies, 1994; Sonea & Mathieu, 2000; Watanabe, 1963).

As the body of evidence for LGT consolidated, its importance to evolutionary theory started to ratchet up. The endosymbiosis explanation of mitochondria and other organelles was revived (Margulis, 1968, 1970) and became uncontroversial, thereby lending credibility to more extensive accounts of the evolutionary acquisition of genetic material. Commentators with a keen eye for LGT implications began to argue for the extent and adaptive importance of LGT (e.g., Anderson, 1966; Jones & Sneath, 1970; Reanney, 1974; Sonea, 1971). Sonea, for example, claimed very daringly (given the evidence then available) that the frequency of transfer implied a giant database of hereditary information—embodied as 'one immense, non-contiguous, pluricellular entity'—available to local communities of prokaryotes for solving adaptive problems (Sonea, 1971, p. 242; Sonea & Mathieu, 2000). These more general evolutionary accounts added impact to the burgeoning phylogenetic and comparative DNA analyses indicating serious strain in evolutionary molecular microbiology. Most scientists in the field, however, still presumed that more data would repair these cracks and resolve phylogenetic anomalies.

Genomics and the vast bodies of DNA sequence data it generates would seem to be the perfect answer to such hopes. Unfortunately for these expectations, whole genome analysis placed further stress on the vertical evolution paradigm because genome sequences revealed even more atypical DNA that did not match organismal or species patterns. Unlike single genes, genome anomalies could not be explained away as sample bias (due to the selective sequencing of single genes or clusters), and explaining them as non-transfer effects commonly required less parsimonious explanatory strategies (Doolittle, 1999a, 1999b).

Two high-impact, genome-based LGT studies led the way in establishing claims for the magnitude of transfer (both the quantity of genes and evolutionary distance of transfer). Analyses of the *Escherichia coli* K12 genome sequence for unusual GC content and codon bias in genes concluded that at least 17–18% of the protein coding DNA (229 genes) had been acquired by LGT over the last 100 million years (Lawrence and Ochman, 1997, 1998). The amount of transfer was no doubt a great deal more, but was undetectable because of amelioration (the gradual homogenization of the acquired DNA's base composition and codon usage biases to those of the host genome), the similarities between acquired and host genome DNA (making the acquisitions undetectable), and post-transfer gene deletion (Lawrence & Ochman, 1997; Martin, 1999). Impressive as this finding was, it was surpassed when the genome of the hyperthermophilic bacteria *Thermotoga maritima* was analysed and investigators claimed that not only were an estimated 24% of its genes the result of transfer, but also that they had been acquired from another domain altogether—that of archaea (Nelson, Clayton, Gill et al., 1999).[17] As a ripple-on effect of these and other rapidly accumulating genomic findings, evaluating the proportion of laterally acquired genes became an important component of the statistical analyses presented with the publication of any newly sequenced genome.[18]

Yet more weight was added to the evolutionary significance of LGT when the phylogenetic effects of homologous recombination[19] began to be reconsidered. Traditionally, population geneticists had thought that clonal replication (with point mutation as the source of divergence) always prevailed over recombination in populations of bacteria. Increasingly sophisticated analyses, however, produced the revised view that recombination is more important than point mutation in creating clonal divergence in numerous genes from a wide range of named bacterial species (Feil, Holmes, Bessen et al., 2001; Gutmann & Dykhuizen, 1994; Guttman, 1997; Denamur, Lecointre, Darth et al., 2000; Lehman, 2003; Maynard Smith, 1999; Spratt et al., 2001).[20] The recombination of gene fragments means there can be large-scale discrepancies between the genes of different isolates of the same species. Consequently, the phylogenetic signal of recombined genes is at best obscured (and often obliterated), and the relationships between major lineages of many bacterial species take the form of webs or networks rather than trees (Awadalla, 2003; Feil et al., 2001; Lawrence, 2002; Maynard Smith, Smith, O'Rourke, & Spratt, 1993; Schierup & Hein, 2000; Holmes, Urwin, & Maiden, 1999).

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[17] If transfers from more closely related organisms (including bacteria from the order Thermotogales) had been added, they would have increased this percentage since transfer is usually more frequent between closely related organisms (see n. 19).

[18] A recent example is the publication of the genome sequence of the methanogenic archaeon *Methanosarcina mazei*, of which 34% of genes were estimated to have a bacterial origin (Deppenmeier, Johann, Hartsch et al., 2002). Even the human genome was released with LGT estimates from bacteria to vertebrates (International Human Genome Sequencing Consortium, 2001), although these estimates were later pruned back severely (Andersson, Doolittle, & Nesbø, 2001; Salzberg, White, Peterson, & Eisen, 2001; Stanhope et al., 2001).

[19] Homologous recombination occurs with the introduction of extra-genomic DNA into a genome by any of the LGT mechanisms listed above (in n. 15). It requires short stretches (~20 bp) of perfect or near perfect identity between the recipient's genome and the acquired DNA, and as a consequence usually occurs between closely related organisms. Because of the small size of the DNA fragments involved, the intraspecific recombinatory distribution of divergent genetic material generally results in the variation of existing genes, rather than the sudden introduction of innovations. Homologous recombination thus plays a bigger role in intraspecies evolutionary change, whereas transfer—with its recourse to other forms of recombination—operates across wider evolutionary distances and has more dramatic effects on phylogenetic reconstruction (Feil & Spratt, 2001; Gogarten, Doolittle, & Lawrence, 2002; Lawrence, 2002; Maynard Smith, Feil, & Smith, 2000; Spratt, Hanage, & Feil, 2001; de Vries & Wackernagel, 2002).

[20] The evolutionary effect of recombination may be strong even in species where recombination rates are as low as or lower than the mutation rate, because recombinant genes that have already passed the test of selection in other organisms are likely to prove more advantageous than unproven mutations (Feil et al., 2001; Levin & Bergstrom, 2000).

4. The 'transfer all the time' paradigm: restructuring the ideas

A useful name for the reconfigured paradigm emphasizing lateral gene transfer might be the *Transfer all The Time* (TTT) paradigm, as opposed to the old 'replicatory inheritance' or *Transfer or Not Transfer* (TNT) paradigm. It requires no stretch of the imagination to describe the emergent understanding of TTT in Kuhnian terms as a paradigm that is competing for dominance in evolutionary microbiology against the forerunner TNT paradigm of replicatory inheritance. In the rival paradigm, fundamental processes of lateral transfer form the *background* of microbe evolution, rather than replicatory inheritance and vertical genealogical patterns. Evolutionary explanation then becomes a matter of discovering the *foreground* pattern of replicatory inheritance against that background of transfer.[21] By reconfiguring LGT as the background instead of the anomaly, the evolutionary picture can be reconstructed *without the abandonment of vertical accounts of evolution*. The 'null' hypothesis is now transfer (with cases of verticality refuting it), whereas, in the old paradigm, the null or default hypothesis was vertical replication or reproduction (Lawrence & Hendrickson, 2003). If the implications of the paradigm are taken far enough, it becomes possible to invert the reasons *against* LGT into reasons *for* it. Take, for example, this claim: 'The congruence between genome content trees and 16S rRNA phylogenies, which has been used to discount the importance of LGT, is in perfect agreement with the theory that prokaryotic taxonomic units exclusively reflect LGT frequencies', due to ribosomal RNAs and genomes being LGT constructions (Olendzenski, Zhaxybayeva, & Gogarten, 2002, p. 427).

Once the balance of assumption is overturned, microbial phylogeny has to be understood as picking its restricted trees out of that extensive background of LGT. What were previously conceived of as clear lines of descent would then be understood as probabilistic signals (sometimes very weak ones) of inheritance against the web-like cacophony of pervasive genetic transfer. Furthermore, tree-like patterns of relationship would no longer be taken automatically to indicate vertical descent. Instead, they would also have to be understood as indicating the frequency of LGT and the intimacy of environmental relationships between organisms and populations (Gogarten et al., 2002; Lawrence & Hendrickson, 2003; Olendzenski et al., 2002).

It is clearly not just evolutionary microbiology that has to adjust itself in light of LGT but also the conceptual fabric of Darwinian evolutionary theory, which was historically modelled on what was understood of eukaryotic reproduction and evolution. Another way to describe the reconfiguration is that the evolution of prokaryotes is being given equality with the evolution of eukaryotes, rather than being unquestioningly subordinated to it. The basic assumptions of TTT and how they affect theoretical understandings of microbial evolution and general Darwinian thinking can be compressed into a number of interconnected claims.

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[21] This visual image is also suggested in microbial population genetics by Maynard Smith et al.'s diagram (2000, p. 1117), which foregrounds relatively enduring clonal complexes against a background of free recombination.

1. *All genes can be transferred*. All genes can be transferred or recombined, in whole or in part, and have been at some point in their histories (Brown, 2001; Martin, 1999). There may be different propensities for transfer exhibited by different genes, but at least some level of homologous recombination can be detected for any given gene within certain populations of closely related organisms.
2. *Transfer is always active in prokaryotes* through the coupling of transfer processes operating over great phylogenetic distances (e.g., as accomplished by broad-host-range plasmids) and those that operate on a more restricted scale (e.g., homologous recombination).[22] LGT is an ongoing process, and it is unlikely to have radically diminished after the 'Darwinian threshold', which saw the emergence of microbial species from a soup of lateral transfer and cellular simplicity (Jain, Rivera, & Lake, 1999; Woese, 1998, 2002).
3. *Far more LGT is happening than has been detected*. Current methods of detection are inadequate for estimating the extent of LGT. Any given method is only valid for detecting transfer at a given phylogenetic level. For example, methods for detecting interspecific transfer tend to be inadequate for establishing recombination between closely related organisms (Posada & Crandall, 2001). Considering *all* phylogenetic levels would substantially increase estimates of the fraction of genes suspected to have been introduced in an organism (or its ancestor) by LGT. In addition, most methods exclude a subset of genes from testing for transfer because of their tendencies to distort phylogenies, owing to factors such as low conservation, limited distribution, or a high amount of paralogy. These excluded genes, specifically because of these properties, are likely to be more frequently transferred than the genes commonly included in the analyses.
4. *Evolutionary divergence is driven by recombination as well as mutation*, and evolutionary success for prokaryotes *depends* on their ability to obtain, integrate, and express genetic material from a broad range of other species or populations (Levin & Bergstrom, 2000). There are clearly many fitness advantages to evolutionary changes that are 'modular' (i.e., more than one mutation at a time) and that have run the selection gauntlet elsewhere. What is not being challenged, however, is that *natural selection is still the 'final arbiter*' of transferred as well as mutated material (Lawrence, 2001, p. 487), and so we are looking at the same metaprocess of Darwinian selection.[23]
5. '*Species*' *is a practical pluralistic term used in a purely conventional sense for classifying prokaryotes*. Defining a phylogenetic group of microorganisms can be done in two ways at the molecular (genomic) level. Either a group is made up of individuals whose genes diverge little from one another in nucleotide sequence, or of

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[22] This claim of 'always active' is reinforced by the intimate involvement of recombination with the replication process (see Cox, 2001). Such intimacy implies that wherever there is replicating DNA, the potential for recombination exists.

[23] We are emphasizing this point because of the tendency of anti-evolutionist 'intelligent design' proponents to seize upon LGT as evidence against Darwinian evolution and support for supernatural design (e.g., Brewer, 2003; Nelson-Alonso, 2003; Renick, 2003).

individuals whose genomes have similar gene contents. The problem with these definitions is that some ecological groups of microbes will be mostly determined by similar gene content, whereas others will be defined by the similarity of their genome sequences. It is therefore impossible to affix invariable characteristics to a unit of prokaryotic evolution (Maynard Smith et al., 2000). Species can only be thought of as populations of closely (but not exclusively) related individuals inhabiting a specifiable ecological niche (Lawrence, 1999, 2001). At best, any prokaryotic 'species' boundary will be fuzzy and much ink will be spent insulating the word with inverted commas (though perhaps less ink than has been spilt already over the viability of the concept).

6. *Time contractions and space expansions*. With as much or more lateral transfer driving divergence and adaptation as advantageous mutations, 'the evolutionary time-scale may have been telescoped into a shorter span' (Anderson, 1966). Major leaps in prokaryote and unicellular eukaryote evolution are probably produced by transfer events (De la Cruz & Davies, 2000), since they allow organisms to move into or acquire wholly new environments, and not just to expand their niches gradually (Gogarten et al., 2002; Lawrence, 1999, 2001).
7. *The evolutionary role of reproductive isolation is diminished* in the transfer paradigm (Syvanen, 1985, 1994) and environmental proximity becomes a key factor (Olendzenski et al., 2002). Lineages of prokaryotes may experience frequent transfer because of sharing an environment, with the consequence of sharing similarities that have little to do with organismal genealogy (Doolittle, 1999c; Nesbø, Boucher, & Doolittle, 2001a, Nesbø, L'Haridon, Stetter, & Doolittle, 2001b; Zhaxybayeva & Gogarten, 2002).
8. *Evolutionary lineages of microbes form networks. There is no universal molecular tree of life*. Trees that do exist are local, highlighted genealogies of particular amounts of DNA over restricted time-frames, found within a context of networks. Contemporary LGT events affecting complex eukaryotes such as animals are probably rare, so evolutionary depictions of animal speciations would continue to be represented by tree-like depictions. Over the entirety of evolutionary history, however, ancestral gene transfers effectively destroy all hopes of a single molecular tree mapping on to an organismal tree of life. Such an outcome need not be perceived as a tragedy.[24] Rather, it is an opportunity for more effective classification in which all modes of inheritance are properly investigated. If conventional phylogenies are inaccurate and inadequate representations of evolutionary history, then their loss should be welcomed.
9. *Understanding the role of genetic transfer in prokaryotic evolution has implications for eukaryotic evolution*. Although eukaryotes have separate somatic and germ lines and cannot participate in transfer to the same extent that prokaryotes do, their evolution is nonetheless affected by both deep ancestral acquisitions and more recent transfers (Brown, 2003; De la Cruz & Davies, 2000; Hartman,

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[24] Logsdon and Faguy's dismay that 'Prokaryote phylogeny (evolutionary history) is in serious danger of becoming *mere* taxonomy (similarity grouping)' is an example of such a perception (1999, p. R750—emphasis added).

2002; Koonin, Makarova, & Aravind, 2001; Krassilov, 2002; López-García & Moreira, 1999; Martin, 1999; Smith, Feng, & Doolittle, 1992). A full understanding of eukaryotic evolution has, therefore, to take all the implications of prokaryotic evolution into account.

4.1. Resistance to TTT

As Kuhn might have predicted, however, the TTT reconstruction is not proceeding without strong opposition. TNT-ers are trying to hold on to the general notions of the dominance of replicatory inheritance and the viability of phylogeny by marshalling a number of methodological and epistemological arguments against the TTT paradigm. LGT's role in evolutionary history is exaggerated, claim TTT critics, because it has been conflated with the inadequacies of methods for inferring it (Eisen, 2000; Glansdorff, 2000; Kurland, Canback, & Berg, 2003; Penny & Poole, 2003).

Methods for the detection of transfer fall into two categories: comparative and phylogenetic (Karlin, Campbell, & Mrázek, 1998; Koonin et al., 2001). Comparative methods used without phylogenetic analysis are problematic in that their ahistorical approaches easily misidentify evolutionary transfers (Sicheritz-Pontén & Andersson, 2001; Stanhope et al., 2001), and also because different comparative methods often identify a completely different set of putatively transferred genes (Ragan, 2001). Phylogenetic analysis itself, however, may also mislead microbiologists because of its general uncertainty, beset as the field is by problems of unequal rates of evolutionary change, data ambiguities, low signal-to-noise ratios, and methodological misuses and sloppiness (Brocchieri, 2001; Daubin, Moran, & Ochman, 2003; Forterre & Phillippe, 1999; Logsdon & Faguy, 1999; Stiller & Hall, 1999a). TNT-ers also find it contradictory for TTT-ers to detect transfer by phylogenetic methods and yet claim to be unravelling the very rationale for phylogeny.[25]

For many TNT-ers, 'ordinary' events such as gene loss, rate variation, and poor sampling are *better explanations* of phylogenetic anomalies than extraordinary events such as LGT (Salzberg et al., 2001, p. 1906). Implicit in this objection is the claim that LGT is not the most parsimonious explanation for cases of incongruous or atypical sequence data (Glansdorff, 2000). 'Most of the data' can supposedly

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[25] TTT-ers are trying to devise better methods to capture and represent microbial evolutionary history, on the basis of multiple network methods that compare molecular sequences and incorporate population as well as species level data without making assumptions about vertical descent being dominant (Bryant & Moulton, 2004; Huson, 1998; Posada & Crandall, 2001). These methods are good for detecting conflicting phylogenetic information, whether it comes from transfer events or the accumulation of mutations, but only indicate how tree-like the data actually are rather than 'forcing' trees to appear (Bandelt & Dress, 1992; Feil & Spratt, 2001). There is still more work to be done, however, to develop such methods and make them more user-friendly, easy to interpret, and better known. Recent advances in methods for detecting patterns of descent in recombining populations (Feil, Li, Aanensen, Hanage, & Spratt, 2004) greatly assist such development.

be accounted for without requiring an overhaul of the vertical paradigm, meaning that LGT should be *explained away* wherever possible. Moreover, say critics such as Stiller and Hall (1999b), accepting widespread transfer leads into even more dangerous epistemological territory because it means adopting an *unfalsifiable* hypothesis. In the TTT paradigm, any phylogenetic pattern could be attributed to a mix of intraspecies recombination and interorganismal gene transfer. In other words, transfer would explain everything. 'Thus, unless more reliable evidence is uncovered, the scientific method requires that we invoke the idea of ubiquitous LGT only as a last resort' (Stiller & Hall, 1999b, p. 1443a).

Both sides can agree, it seems, that the TTT premisses are not cosmetic changes: they require major reconstruction of general assumptions, specific theories, and methodology. But does the struggle for theoretical supremacy fit the Kuhnian account of paradigms and *how* they change?

5. A continuum of positions on transfer: restructuring the scientists

To work out whether an episode of scientific change is revolutionary or normal, says Kuhn (2000c [1970], p. 146), the historical analyst has to determine 'the nature and structure of group commitments before and after the change', by examining each of those groups for the degree of change in their positions. Everyone agrees that LGT became widely accepted by *all* evolutionary microbiologists as the evidence mounted over the 1990s. The way in which individuals accepted LGT and its implications took a number of forms, however, and rather than lumping all opposition to gene transfer into one category, a more nuanced categorization seems necessary. One suggestion for how to understand the field is proposed by Ford Doolittle (2005), an evolutionary microbiologist and strong LGT proponent, who sets out four 'schools of thought' on how LGT is understood and dealt with methodologically in microbial phylogenetics.

The first group consists of the *strongest rejecters* of LGT, who conceive of transfer as an occasional irritant within a fundamentally unaltered model of coherent replicatory inheritance. These conservatives insist that species and the universal tree are theoretically indispensable for Darwinists (e.g., Kurland, 2000). From their point of view, LGT may occasionally blur vertical patterns (the tree-like structure), but its extent has been exaggerated and sensationalized (Kurland et al., 2003; Logsdon & Faguy, 1999). Phylogeneticists simply need to fine-tune their methods to screen out the LGT disruptions.

The second group consists of *moderate rejecters* of LGT, who believe that the tree analogy still holds for a discernible minority of genes that are much less frequently transferred than others—the 'core' or 'backbone' arguments (Daubin, Gouy, & Perrière, 2001, 2003; Makarova et al., 1999; Sicheritz-Pontén & Andersson, 2001; Woese, 1998, 2002). This core of genes—usually genes coding for components of the 'informational' part of the cellular machinery (i.e., DNA replication, transcription, and RNA translation)—is meant to be unaffected by the lateral transfer swirling around it as a 'variable shell' throughout evolutionary history.[26] They take the fact that gene content or genome trees generally correspond with rRNA trees as evidence for a genuine and detectable vertical pattern that is conserved over deep evolutionary time (Fitz-Gibbon & House, 1999; Fraser, Eisen, & Salzberg, 2000; Kunin & Ouzounis, 2003; Snel, Bork, & Huynen, 1999, 2002; Tekaia, Laziano, & Dujon, 1999)—enough so that 'prokaryote species are easily recognized by both phenotypes and gene pool' (Lan & Reeves, 2000, p. 399). The core, therefore, is the true genealogy indicator, and gene transfer is something to be overcome by good evolutionary analysis.

Moderate accepters of LGT make up the third level, and they tend not to quibble too much with the extent and significance of LGT. Their phylogenetic justification implicitly draws an analogy between genomes and how ropes are constituted by a large number of individual threads being twisted into one coherent form. Moderate transferists think that if enough genes and genomes are used (in the form of gene content or genome trees, as well as combined phylogenies called 'supertrees'), they will all eventually form a universally coherent evolutionary story—even if no single gene or group of genes tells the same story as another. The resultant tree is *not* a species tree (they admit that such a thing does not exist), but it is a 'central trend in the rich patchwork of evolutionary history, replete with gene loss and horizontal transfer events' (Wolf, Rogozin, Grishin, & Koonin, 2002, p. 477). Tapping into 'some underlying history' is a good enough project for these very pragmatic phylogeneticists (Olsen, 2001).

Finally, at the far end of the continuum is a vocal group of *strong supporters* of LGT (quintessential TTT-ers), who argue most radically that LGT is so extensive that no single tree of life will ever be possible. Limited stretches of tree-like evolution can be found in the molecular annals, but evolutionary relationships are more accurately seen as webs than trees (e.g., Doolittle et al., 2003; Gogarten et al., 2002; Nesbø et al., 2001a, 2001b).

Radical LGT supporters do not accept the core argument for both empirical and epistemological reasons. First of all, they point to a growing body of evidence identifying the transfer of informational genes—the usual candidates for the core (e.g., Asai, Zaporojets, Squires, & Squires, 1999; Brochier, Phillipe, & Moreira, 2000; Makarova, Ponamarev, & Koonin, 2001; Wang & Zhang, 2000; Yap, Zhang, & Wang, 1999). Secondly, TTT-ers see the core notion as a paradigm-saving strategy that raises very troublesome epistemological questions. The size of the core (probably less than 10% of the genome), its taxonomic level, and the extent to which transfer is 'allowed' to affect it are all problematic issues for radical LGT supporters. They do not find it scientifically legitimate to say (as do core supporters such as Daubin et al. (2003, p. 831)) that 'LGT is concentrated in a class of genes that are not candidates for phylogenetic analysis.' Nor does the overall 'treeing tendency' of genomes

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[26] Sometimes the core is separated into a 'hard' core (never transferred) and a 'soft' core (rarely transferred) (Phillippe & Douady, 2003).

persuade TTT-ers of the renewed viability of the universal tree concept, because no unique or unambiguous tree (with gene-to-gene congruence) is really anticipated from these approaches (Doolittle, 2005). Consequently, the paradigm is not saved, but merely given a soft landing as it crashes.

These groups of response to LGT are not discrete categories, but clusters on a position continuum that is built from theoretical assumptions and philosophical tenets as much as practical confrontations with evidence. Aside from using the same data, there is a common body of technology, methodology, and epistemology drawn on by all positions and comprehensible from one end of the continuum to the other. Because the differences in interpretation form a continuum, individuals can slide along it with no major justification—just a series of minor adjustments—as the cumulative effects of evidence and theory modification move the general paradigm into a new configuration.

That movement appears to be primarily towards greater appreciation of transfer, especially when early evolutionary history is being considered. The 1990s saw many strong rejecters become core supporters (moderate LGT rejecters), without any subsequent retreat. Core believers have already shifted from 'most genes in the genome will share a common history' (Olsen & Woese, 1993), to just a few 'genealogy-defining' genes being enough to constitute a core (Woese, 2000, 2002). From the end of the 1990s until now, the general movement has been towards the moderate acceptance of TTT. This is where the new tree-building techniques are concentrated, and the concept of a tree is being fundamentally transformed. Core and rope positions are being made 'compatible' as the notion of a core is weakened to mean an overall tendency (Wolf et al., 2002). From a Kuhnian perspective of theoretical change, it should be impossible for scientists to slide back and forth between these last two positions because of the huge conceptual fissure that exists between 'cores are true trees' (moderate rejecters) and 'genome phylogenies produce overall appearances of trees' (moderate accepters). Despite Kuhn's strictures, the bridges over the supposed chasm are bearing a lot of scientific traffic as evolutionary microbiologists continue to work on the problem of LGT.

6. Paradigm change: pattern versus process

Much of the explanatory transformation that we trace above can be set out so it fits the general characteristics of an imminent Kuhnian paradigm shift. By moving gene transfer to the *background* and replicatory (vertical) inheritance to the *foreground*, the epistemological importance of LGT changes from anomaly to guiding principle. Either the Darwinian paradigm has to be rent into two complementary sub-paradigms (prokaryotic and eukaryotic), or the conceptual effects of the transfer model pervade the whole evolutionary model. Whichever solution prevails, the general Darwinian understanding will be transformed. Despite the significance of the changes, however, the groups involved do not seem to show the bifurcated thinking Kuhn espoused, but far more connected and fluid differences of understanding.

Rather than trying to describe the situation in Kuhn's normal–revolutionary categories, we find it more useful to say that transfer and replicatory inheritance accounts of prokaryote evolution are teetering on the fulcrum of an explanatory balance. When the balance changes and tips an earlier paradigm over to a new configuration of theory and evidence, there is an apparently 'revolutionary' scientific shift. Because accumulated evidence is organized around such explanatory fulcrums, scientific change can have a ragged tempo rather than a gradual one. We would not want, however, to think of scientific change as 'discontinuous' but as a steadier and much messier process of practical problem-solving punctuated by ongoing paradigm-tipping episodes—a process that is supported by the way scientists are grouped in the field.

Fully accepting the emerging transfer paradigm would not, therefore, be a matter of holistic conversion from one position to another that is incommensurable with it.[27] Paradigm change in evolutionary microbiology appears to be an ongoing process of bit-by-bit substitution, as new evidence (often brought in by radically new technologies)[28] replaces older information, and new sub-paradigm explanations and methods piece the data back together. Multiple small elements in the overarching story have already been relinquished or converted without too great a sense of loss in order to obtain a greater explanatory reach, until a recognizably new story has formed that could allow the major paradigm-defining loss of the universal tree. The reconfiguration of evolutionary microbiology also appears to involve a very subtle conversion process, in which many opponents of the significance of LGT for evolutionary reconstruction have gradually moved into a way of thinking from which their original (much stronger) opposition is not even recalled, involving a 'What's all the fuss about?' mode of reflection. There is still some distance to be covered, however, before the loss of the universal tree can be countenanced by more scientists than those at the far end of the LGT continuum.

Kuhn's account of scientific change is in many ways a poor fit for the situation in evolutionary microbiology. It may not, however, be straightforwardly wrong. His interest lay in describing the *structure* of scientific change, or the *pattern of its out-*

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[27] Lawrence and Hendrickson (2003, p. 9) argue for a 'holistic change in mindset amongst microbiologists' in relation to transfer and recombination, but this refers to an attitude change rather than a holistic paradigm shift of the kind for which Kuhn argues.

[28] Evolutionary microbiology could only really begin to deal with its problems of natural classification when molecular technologies began to produce entirely new forms of phylogenetic evidence. The subsequent interaction of high-throughput genome sequencing with new phylogenetic and statistical computation packages (plus a massive increase in DNA-related experimental capacity) generated the data and interpretations that have led to TTT conclusions. The next technology leap would appear to be happening in environmental genomics, where novel (or newly applied) technologies are producing huge amounts of data that have yet to be theoretically assimilated (e.g., Venter et al., 2004). The technological history of the fields involved in our case has still to be written in any detail and was greatly encouraged by one of our reviewers as a source of further insight into paradigm change. We predict that any such history will show a complex interweaving of technological, methodological and theoretical change, rather than revolutionary discontinuities between theory-shaping technologies.

come. Commentators such as ourselves and some of the post-positivist historical philosophers we mentioned above are more focused on the *process* and *how that outcome is reached*.[29] Kuhn's model of bifurcating lineages of theory (due to lexical differentiation within a common pool of language shared by a speech community), was primarily concerned with the outcome of distinct and separate 'species' (taxonomic linguistic categories) whose vehicles (scientific groups) occupied increasingly narrow knowledge niches and lost the capacity to cross-communicate (2000b, p. 98; 1993a, pp. 329, 339; Hoyningen-Huene, 1998). His 'evolutionary tree' of scientific speciation was constructed by designating criteria that allowed the observer to separate two theories taxonomically (1970, p. 205). He based it on similarity–dissimilarity relations that were driven by a developmental–differentiation dynamic (1993a, p. 336).

Although described as a 'dynamic' theory of change (Hoyningen-Huene, 1993), Kuhn's evolutionary explanation is clearly just a schema of developmental stages meant to explain taxonomic differentiation between categories. A truly evolutionary historical approach might have led him to emphasize more process and continuity in scientific change, rather than discontinuous categories.[30] The extent of LGT in microbiological evolution has made the bifurcating tree pattern questionable, and since scientific theories and practices show every sign of being even more transferable than microbial DNA, it seems highly unlikely that paradigms form definitively tree-like patterns in their 'speciation' (or that bifurcating categories can capture the conceptual, practical, and social change in scientific paradigms).

7. Conclusion

Taking it for granted that Kuhn is right and that paradigm shifts must conform to his structural taxonomic approach is probably the least useful way to use his

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[29] As well as historical accounts of the microprocesses of scientific change, there are Kuhn-based analyses of the cognitive processes involved (e.g., Nersessian, 1998, 2001; Nickles, 1998). Nickles (p. 81), for example, provides cognitive reasons for the inevitability of paradigm change by equating paradigms with schemas that function to reduce the 'cognitive overload of an infinitely complex world to manageable levels'. While these are flexible and efficient heuristic compromises, they end up failing because they blur and lump together phenomena. The practices of science eventually demand more precision and division and thus a new paradigm develops.

[30] As Kuhn himself noted (1993b, p. xii), his later concerns were almost exclusively philosophical and his 'concern with history [was] gradually transmuted to a concern with developmental or evolutionary processes in general', in order to explain the generation of new categories. He recognized the conflict in his approach between its philosophy (espousing discontinuity) and its history (of continuity) but never managed to resolve it (see Caneva, 2000, pp. 95–96; Hacking, 1979, pp. 233, 236; Sankey, 1993). So, although some commentators try to reconstruct Kuhn as deeply concerned with everyday scientific practice (e.g., Barnes, 2003; Giere, 1988; Rouse, 2003), such a reconstruction does not capture the mode or focus of analysis that Kuhn increasingly emphasized. It should be obvious by now, however, that a practical problem-solving approach must shape how Kuhn is reconstructed if his ideas are to be helpful for understanding scientific change.

ideas—whether in biology or other disciplines. While it is true that Kuhn's work shook up the history of science by making it highly suspect to tell complacent accumulationist stories of scientific change, his preoccupation with the *structure of changed science* meant he had little to say about paradigm *restructuring of current science*. Kuhn's notion of paradigm is too taxonomically static to explain the rapid and sometimes extensive proliferation of methods and approaches (often involving entirely new forms of data) that bring about a flow of far-reaching conceptual adjustments and social reorganization.[31] 'Incommensurability' and 'revolution' are too distant from scientific activity to model the mode of reconfiguration involved in the case of evolutionary microbiology,[32] and we think it unlikely any area of science will prove a better fit.

The paradigm reconfiguration in evolutionary microbial biology is far from over, and tracking it throughout its twists and turns promises to be a valuable exercise. Rather than the scientists involved continuing to move towards the far end of the LGT spectrum, it may well happen that new methods preserve the tree (in a practical rather than an ontological sense) and that lateral transfer networks have to be subordinated to it. Whatever solutions are settled on for the problem of LGT, historians can anticipate the question of whether subsequent changes in the paradigm will lead to further reconstruction of the history we have outlined above, or whether the future will just need to be added on to this account of the recent past. We would think that it would have to be the former—for Kuhn as much as anyone—an answer that indicates the importance of paying attention to the process of restructuring as opposed to the supposed outcome.

Although Kuhn can be of only the most general heuristic help in understanding ongoing processes of scientific problem-solving, his ideas appear to prompt valuable lines of inquiry. In other words, Kuhn is best used as a probe that can ask broad questions of specific cases of scientific change, and not as a framework able to supply answers about how that change is actually happening. Conversely, while Kuhn may appear on the surface to have less to say to biology than to his favoured disciplines, we find he has more to offer than he intended. As soon as radical bifurcation is not the criterion of Kuhn's applicability, his account can range more broadly over scientific change and legitimately encompass biology.

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[31] We have not, in our discussion, attempted a re-analysis of the term 'paradigm' and its appropriateness for evolutionary microbiology or any other field. Implied in what we have said, however, is that paradigms are complex and fluid interactions of ideas, technologies, evidence, argument, and communication strategies. While their boundaries are loose and permeable, scientists and historians (if they negotiate on a case-by-case basis) are generally able to come to practical agreement about where paradigms exist and what problem-solving areas they cover.

[32] As one of our reviewers noted, the evolutionary microbiology story could be just at its beginning and on its way to a more revolutionary outcome, after which historians could conclude that 'webs and trees are incommensurable and the revolutionary web account triumphed'. We believe that the more interesting and historically accurate story, however, lies in the details of how any such resolution happens—for which (as we have shown) the standard Kuhnian framework is inadequate.

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