

Horizontal Gene Transfer in Evolution

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Advanced article

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The concept of horizontal or lateral gene transfer (the non-genealogical transmission of genetic material between organisms) was introduced in 1990s to explain the observed incongruence in phylogenetic reconstructions using different genes. Today, horizontal gene transfer is accepted as an important force modulating evolution of Bacteria, Archaea and unicellular eukaryotes, and evidence is rising for their role in the evolution of pluricellular eukaryotes (fungi, plants and animals). The realisation that horizontal gene transfer plays an important role in evolution of both, prokaryotes and eukaryotes, put in question the metaphor of the tree of life and the traditional view of evolution as a slow process. A more pluralistic approach to evolution is emerging that encompasses different evolutionary mechanisms operating at different levels of complexity.

Introduction

The principle of variation by descent has been fundamental to development of evolutionary biology and has accompanied evolutionary thinking during the past 150 years since the original formulation by Charles Darwin.

In the 1930s, the integration of genetic knowledge in the evolutionary theory by the so-called modern synthesis established a strong link between the principle of variation by descent and the vertical inheritance of variation contained in the genetic material of organisms. **See also: [Evolutionary Ideas: The Modern Synthesis](#)**. In addition, the modern synthesis reinforced the idea

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that the acquisition of genetic variation is a gradualist and slow process as proposed by Darwin.

However, in the past years, it is becoming evident that, at least in the prokaryotic world, horizontal or lateral gene transfer (the non-genealogical transmission of genetic material from one organism to another; Goldenfeld and Woese, 2007) is a powerful force in modulating genomes, a source of evolutionary novelties and an interesting mechanism that drives the evolution of prokaryotes and unicellular eukaryotes. In addition, we are only starting to recognise the role of horizontal gene transfer in the evolution of pluricellular eukaryotes but rising evidence suggests that it is not a negligible force in modulating their genomes.

A Brief History of Gene Transfer

Despite that mechanism for genetic exchange between microorganisms has been known since the first days of molecular biology, and the theoretical potential of genetic exchange between organisms as evolutionary mechanism was postulated (Syvanen, 1985), it was only at the beginning of the 1990s when the concept of horizontal gene transfer emerged as an explanation to incongruence in the reconstruction of phylogenetic relationships using different genes (Hilario and Gogarten, 1993). **See also: [History of Molecular Biology](#)**

In 1990, Woese *et al.* proposed, using the sequence of 16S ribonucleic acid (RNA) genes as a promising universal marker that could allow the reconstruction of old phylogenetic relationships, their natural system for the live world encompassing the three Archaea, Bacteria and Eukarya domains. However, it was soon realised that the use of other genes frequently derived different relationships and incongruence, clustering together organisms that are split by other genes or markers, and showing the presence of genes from different origins in the genomes of organisms belonging to the three domains. **See also: [Phylogeny Based on 16S rRNA/DNA](#)**

Horizontal gene transfer emerged in those days as an explanation to these conflictive phylogenies, and with the advent of the 'genomic era' and the completion of the sequences of more

and more genomes, a lot of examples of horizontal gene transfer events have been described.

However, controversy was soon associated with horizontal gene transfer between defenders of its importance as an evolutionary mechanism, challenging the prevailing paradigm in the evolutionary biology, and authors discarding horizontal gene transfer as only playing a minor role in evolution.

How Can Horizontal Gene Transfer Be Detected?

To understand the impact of horizontal gene transfer in evolution, it is necessary to know which and how many genes within a genome have been the product of a horizontal gene transfer event.

Several methods have been proposed (Ragan, 2001) to identify which genes in a genome have been acquired by horizontal gene transfer.

These methods can be classified as surrogate or phylogenetic in function of the used criteria (**Table 1**). Surrogate methods use an indirect approach to identify horizontally transferred genes and phylogenetic methods are more directly focused in the phylogenetic relationships between genes.

Surrogate methods use several criteria as bias in base composition or codon usage between genes in a single genome, or in BLAST proximity and gene distribution in different genomes.

The main problem with methods based on codon usage or base composition is that the foreign genes can be ameliorated after many generations (Marri and Golding, 2008) because, once they are part of the same genome, residents and foreign genes support the same mutational forces. This fact determines that these methods allow the identification of recently transferred genes but have difficulty with identification of gene transfer events that occurred a long time ago.

Surrogate methods based on comparisons of different genomes are very indirect approaches that allow a preliminary identification of possible horizontally transferred genes but they need to be confirmed by others detection methods.

Phylogenetic methods (rooted on the foundations of the horizontal gene transfer concept) are the most efficient in detection of horizontally transferred genes, despite the extensive computing effort required and that, in some cases, it is difficult to distinguish between horizontal gene transfer and gene loss within a determined branch of a phylogenetic tree. The use of different phylogenetic approaches and the application of a test of compatibility between different trees (Gogarten and Townsend, 2005) can be useful in distinction between both possibilities. In addition, the use of probabilistic evolutionary models has been proposed (Cohen and Pupko, 2010) for the inference of gains and losses of gene families in phylogenetic reconstructions.

Horizontal Gene Transfer in Prokaryotic Evolution

Since the initial proposal of horizontal gene transfer as explanation to phylogenetic incongruence, many examples of horizontally transferred genes have been described among prokaryotes. These examples show that the transfer can occur in all possible directions between Bacteria and Archaea (Rest and Mindell, 2003; Gophna *et al.*, 2004). In addition, some genes are acquired from the eukaryotic domain (Guljamow *et al.*, 2007).

But the importance of horizontal gene transfer as evolutionary mechanism driving the evolution of bacteria and archaeans is dependent on the number of genes horizontally transferred and successfully maintained in a prokaryotic genome. It is clear that acquisition of a single gene by a bacteria or an archaea can drive to acquisition of new functions by the recipient that allow to exploit new ecological niches; however, their importance as general evolutionary mechanism is limited if only a few transfer events have taken place during the evolution of a particular lineage.

Initial estimates suggested that 1.6–32.6% of the genes in each prokaryotic genome were horizontally transferred at some moment of their evolutionary history (Koonin *et al.*, 2001). However, Dagan *et al.* (2008) suggest that this percentage rises to $81 \pm 15\%$, taking into account the cumulative impact of horizontal

Table 1 Methods to identify horizontally transferred genes

Criteria	Advantages	Pitfalls
Bias in base composition (G+C content)	Easy detection without comparing different genomes	Only detects recently transferred genes
Bias in codon usage	Easy detection without comparing different genomes	Only detects recently transferred genes
BLAST proximity	Easy comparison of sequences from different organisms	BLAST similarity is not guaranty for the closest phylogenetic relationships
Bias in gene distribution between related organisms	Allow preliminary identification of possible horizontally transferred genes	Misidentification of gene transfer events. Insufficient distinction between gene transfer or gene loss
<i>Phylogenetic incongruence</i>	<i>It is the most accurate method for identify horizontally transferred genes</i>	<i>Computationally extensive. In some cases, insufficient distinction between gene transfer and gene loss</i>

Note: The surrogate methods are in roman font; the phylogenetic methods are in italics font.

gene transfer towards 181 prokaryotic genomes. Other estimates (Bapteste *et al.*, 2008; Lapierre and Gogarten, 2009) are more radical. Bapteste *et al.* (2008) suggest that only 0.7% of prokaryotic genes can be considered as core genes vertically transmitted along the evolutionary history of Archaea and Bacteria. Lapierre and Gogarten (2009) applying the pan-genome concept – a concept initially developed to define the complete set of genes present in a prokaryotic group (Tettelin *et al.*, 2005) – to the complete set of genes present in 573 sequenced bacterial genomes conclude that only 8% of the genes in a particular bacterial genome are present in 99% of the sampled genomes and therefore can be considered as core genes.

Despite that, in some cases, methods used to detect horizontally transferred genes are not optimal and studies using phylogenetic approaches lower these estimates (Chan *et al.*, 2009), these works underline the importance of horizontal gene transfer in prokaryotic evolution.

An important question regarding the importance of horizontal gene transfer in microbial evolution is if it has been equally prevalent throughout the evolutionary time, or conversely, is it more prevalent between closely related organism than between those distantly related?

Taking into account that the products of genes transferred between organisms that diverged a long time ago will need to integrate into a very different regulatory network, and that this is an important determinant of the maintenance of transferred genes (Lercher and Pál, 2008), evolutionary distance between organisms can be an important constraint to transfer and maintenance of genes in the prokaryotic world.

Several studies suggest that gene transfer could effectively be more frequent between recently separated organisms than between organisms separated a long time ago. For example, Wagner and De la Chaux (2008) analysed the evolution of 2091 insertion sequences in 438 prokaryotic genomes finding only 30 cases that correspond to presumptive transfer events between distantly related clades.

However, the presence of genes with a bacterial origin have been found in Archaea, and conversely, genes with an Archaeal origin have been found in Bacteria (Rest and Mindell, 2003; Gophna *et al.*, 2004), showing that horizontal gene transfer is not limited to recently diverged organisms. The more difficult detection of ancient gene transfer events because of the amelioration process discussed in the preceding text (Marri and Golding, 2008) makes it difficult to evaluate the real contribution of ancient gene exchange to evolutionary history of bacteria and archaeans.

Nevertheless, several studies start to give us certain cues about this topic. For example, a study by Kanhere and Vingron (2009) shows an interesting trend within the interdomain gene transfer events: that the majority of the transfers between Bacteria and Archaea seem to have taken place from Bacteria to Archaea. In this sense, a recent study reveals the role of horizontal gene transfer from Bacteria to Archaea in the origin of the major Archaea clades (Nelson-Satho *et al.*, 2015)

Others studies (Zhaxybayeva *et al.*, 2006, 2009; Boussau *et al.*, 2008) show that the intraphylum *versus* interphylum gene transfer in Bacteria is different among different lineages. For instance, in Cyanobacteria, intraphylum transfer is dominant

over interphylum exchange. By the contrary, in Thermotogales, interphylum transfer seems to be dominant over intraphylum exchange. Another instance of interphylum dominance could be the multiple gene exchange between ϵ -Proteobacteria and Aquificales. Moreover, interphylum gene transfer could be more prevalent than previously thought, favoured by shared physiological and ecological factors (Caro-Quintero and Konstantinidis 2015). In this sense, shared habitats emerged in the past years as an important factor that favours the gene exchange between prokaryotes. We can conclude from these studies that despite that horizontal gene transfer seems to occur more easily between recently diverged organisms, it also occurs between both prokaryotic domains, and between phyla inside particular domains, playing an important role in the evolution of Bacteria and Archaea.

Another question linked to the horizontal gene transfer process is to whether different types of genes show different susceptibility to transfer (and maintenance) between organisms.

Jain *et al.* proposed in 1999 the complexity hypothesis, suggesting that the so-called informational genes (whose products are involved in replication, transcription and translation processes and participate in multiple molecular interactions) are less prone to horizontal gene transfer than operational genes (whose products have few interactions with other molecules and are involved in cell maintenance).

Although several studies seem to confirm this general trend (Nakamura *et al.*, 2004), it has been shown that there are no a priori absolute barriers to the cloning of any gene in *Escherichia coli*, and consequently, no barriers to the transfer of any gene to *E. coli* (Sorek *et al.*, 2007).

These results, along with evidences emerging from the study of bacterial pan-genome discussed in the preceding text (Lapierre and Gogarten, 2009) suggest that the functional split-up of genes into informational and operational is not absolutely predictive in establishing what type of genes are transferred and maintained between prokaryotes. Conversely, the number of interactions (molecular complexity) in which their products participate can be a more important constraint to transfer and maintenance of genes in the prokaryotic world (Cohen *et al.*, 2011).

In summary, we can conclude that horizontal gene transfer is a widespread phenomenon among prokaryotes that modulates evolution of Bacteria and Archaea. Despite particular trends, gene transfer is observed between different domains and it affects different types of genes.

Horizontal Gene Transfer in Eukaryotes

Even though the impact of horizontal gene transfer in eukaryotic evolution has been considered minor in comparison to its effect in prokaryotic evolution (except for the case of gene transfer from mitochondrial and plastid precursors to nuclear genomes; see also: **Mitochondria: Origin**), an increasing number of sequenced eukaryotic genomes and transcriptomic analyses are permitting us to determine the real impact of horizontal gene transfer in eukaryotic evolution. Today, it is widely accepted that horizontal gene transfer is an important force in the evolution

of unicellular eukaryotes (Keeling and Palmer, 2008) in which the absence of a germ line favours the transgenerational maintenance of the transferred genes. In addition, studies published in the past 5 years have revealed different examples of adaptive horizontally transferred genes to fungi, plants and metazoan genomes which suggest that horizontal gene transfer is underscored in eukaryotic genome evolution.

Genes of prokaryotic origins associated to fungal pathogenicity and other adaptive traits have been found in fungal genomes (Gladieux *et al.*, 2014). Furthermore, many genes, which provide adaptive traits, from different origins (bacteria, fungi or other plants), including those involved in plant colonisation of land have been found in mitochondrial, plastid and nuclear plant genomes (Gao *et al.*, 2014). Moreover, an increasing number of examples of genes related to adaptive traits from different origins have been identified in metazoans (Boto, 2014) including genes involved in plant parasitism in nematodes and insects, genes involved in carotenoid biosynthesis in arthropods and genes involved in biomineralisation processes in sponges or genes involved in a number of different metabolic pathways in Cnidarians to cite just a few examples.

An exceptional case is the extensive horizontal transfer detected in genomes of bdelloid rotifers (Gladyshev *et al.*, 2008; Flot *et al.*, 2013). Genomes of these invertebrates harbour up to approximately 10% of genes of foreign origin (bacteria, fungi or plants) and it has been suggested that this extensive transfer provides additional genetic variability that probably compensates for the unisexual reproductive mode of these animals, thereby allowing for the adaptation to desiccation periods during their life cycles.

However, other potential interesting cases, such as the horizontal gene transfer from the alga *Vaucheria litorea* to the sea slug *Elysia chlorotica* of genes involved in photosynthesis have been questioned in the past years (see Boto, 2014, for a discussion, but see also Schwartz *et al.*, 2014).

Together, these studies suggest that despite the fact that the extent of horizontal gene transfer among eukaryotes can be lesser relative to prokaryotes; it could be not a negligible force in modulating eukaryotic genomes, contributing consequently to eukaryotic evolution. In this sense, a recent study (Crisp *et al.*, 2015) analysing the transcriptomes from 12 insect, 4 nematode and 10 primate species suggest that animal genomes harbour a greater number of genes of foreign origin than had been initially suspected.

However, unlike the well-known conjugation, transformation and transduction processes that allow horizontal gene transfer in prokaryotes, the mechanisms involved in eukaryotic gene acquisition are poorly known (Boto, 2014).

The importance of horizontal gene transfer in eukaryotic evolution could be even higher if we consider animal and plant hybridisation as a massive transfer of genes or the outstanding evidences for the importance of horizontally transferred transposable elements in eukaryotes (Oliver and Greene, 2009). **See also: Hybrid Speciation; Transposable Element-driven Duplications during Hominoid Genome Evolution**

How Does Horizontal Gene Transfer Fit in the Evolutionary Thinking?

The tree of life metaphor has been synonymous with the evolutionary biology since Darwin first proposed the connexion of all of the living organisms with an ancient ancestor, and it encouraged the founding of several research programs focused on establishing the real tree of life (*Tree of Life web project*, <http://tolweb.org> or *Assembling the Tree of Life project*, <http://www.mcz.harvard.edu/initiatives/atol.html>). **See also: Universal Tree of Life.** However, the realisation of the importance of horizontal gene transfer in evolution, particularly among bacteria and archaeans, entails a philosophical challenge to the reliability of the reconstruction of phylogenetic relationships, and subsequently, the recovery of a proper tree of life.

Despite this, some authors sustain the idea of a core of genes, never transferred and maintaining a phylogenetic signal that enables the reconstruction of a prokaryotic phylogenetic tree (Gribaldo and Brochier, 2009). After the analysis of multiple gene trees from published bacterial genomes, other authors suggest the existence of an underlying trend in bacterial evolution that could allow for the reconstruction of phylogenetic relationships among prokaryotes (Puigbó *et al.*, 2010). However, evidences discussed in the preceding sections to this article show that the proposed core encompasses a small number of genes (Baptiste *et al.*, 2008; Dagan *et al.*, 2008; Lapierre and Gogarten, 2009), making the idea to depict life evolution such as a tree problematic.

In this sense, some authors (Doolittle, 1999; Doolittle and Baptiste, 2007) point out that it is definitively impossible to reconstruct the tree of life taking into consideration the pervasiveness of horizontal gene transfer, and they propose new metaphors to represent evolution, such as the web or net of life (Doolittle, 1999) and the ring of life (Rivera and Lake, 2004) (**Figure 1**) among other less accepted metaphors.

The net of life (**Figure 1a**) proposes to depict the evolution like a tree with many interbranch connections, meanwhile the ring of life (**Figure 1b**) depicts the evolution of the three domains of life as connected in a ring, considering that the eukaryotic domain has been originated from a hybridisation event involving representatives from both Bacteria and Archaea domains.

However, defenders of the reliability of a true tree of life propose the use of several statistic tools to deal with horizontal gene transfer in phylogenetic reconstructions (networks, supermatrices, supertrees or stochastic models) (Galtier and Daubin, 2008; Baptiste *et al.*, 2013). The problem is that these tools are not always free of criticisms (Rannala and Yang, 2008).

Nevertheless, in some cases, the use of ancient horizontal gene transfer events as synapomorphies aiding to solve problematic phylogenetic relationships is possible (Huang and Gogarten, 2006).

It has been proposed that evolution of prokaryotes and pluricellular eukaryotes could be mediated by radically different processes of acquisition of genetic variability (Baptiste *et al.*, 2009). In this view, evolution in Bacteria and Archaea (and probably in unicellular eukaryotes) could be modulated by horizontal

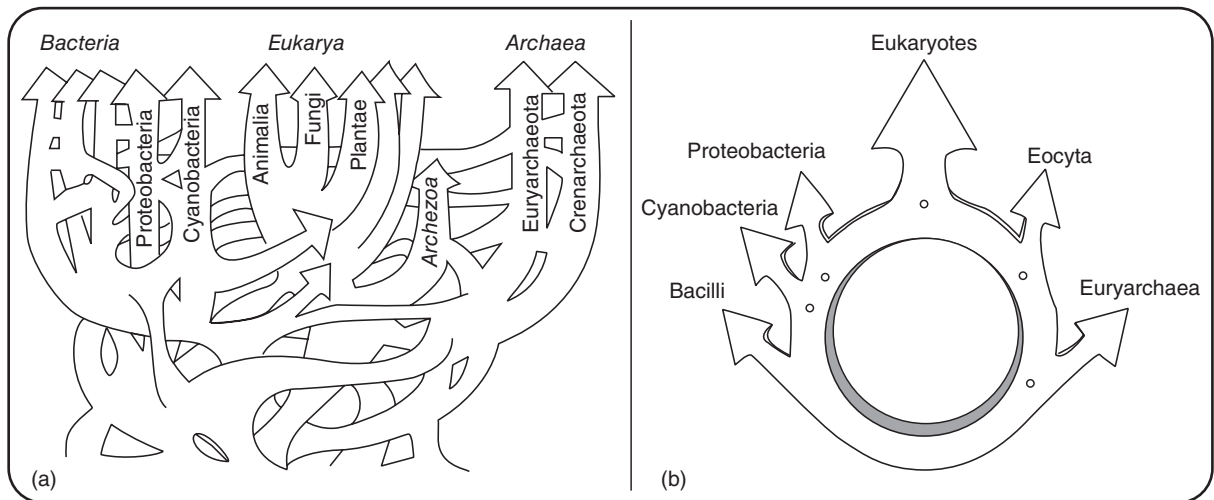


Figure 1 New metaphors of evolution taking into consideration the role of horizontal gene transfer. (a) The web of life (Reproduced with permission from Doolittle WF (1999) © The American Association for the Advancement of Science). (b) The ring of life. (Reproduced with permission from Rivera and Lake (2004) Nature Publishing Group)

processes of acquisition of variability; meanwhile, evolution in metazoan eukaryotes has been preferentially modulated by mutation, gene duplication and vertical inheritance. In this sense, though depicting the evolution of prokaryotic (and unicellular eukaryotes) world like a tree makes little sense, a metazoan eukaryotes tree of life could be a real goal for evolutionary biologists.

However, if we consider introgressive hybridisation and cases of hybrid speciation described in animals and plants as massive horizontal gene transfer events, the pattern of evolution in eukaryotes could seem more to be a reticulated one than the traditional tree-like pattern. In addition, horizontal gene transfer challenges, in some sense, the traditional view of evolution as a slow and gradual process. Horizontal gene transfer is a fast process of acquisition of variability and this variability could be fixed, in some cases, in a very short number of generations (Lovell *et al.*, 2009).

Taking into consideration this Lamarckian taste coming from horizontal gene transfer, it has been proposed that Darwinian and Lamarckian modes of evolution could reflect 'different aspects of the interaction between populations and environment' (Koonin and Wolf, 2009) and both modulate the evolution of the living world. In this sense, a pluralistic approach to evolution is becoming more widely accepted. This pluralistic approach contemplates horizontal or vertical evolution operating at different levels of complexity (**Table 2**): prokaryotes and unicellular eukaryotes evolution *versus* that of pluricellular eukaryotes, genome *versus* gene evolution, genome *versus* cell evolution or genetic *versus* cytoplasmic evolution.

At these different levels, horizontal or vertical transmission can modulate evolution in a different degree, in such a way that it is necessary to consider the different levels of evolution to obtain a complete picture of the evolutionary process.

Table 2 Proposed evolutionary modes at different levels of complexity

	Evolutionary level
Gene	Vertical
Genome	Vertical and horizontal
Cell	Vertical
Prokaryotes	<i>Horizontal</i> and vertical
Unicellular eukaryotes	<i>Horizontal</i> and vertical
Pluricellular eukaryotes	Vertical and horizontal
Genetic	Vertical and horizontal
Cytoplasmic	Vertical
Organismal	Horizontal and vertical. Modulated by the evolution at different levels

Note: Preferential modes of evolution suggested are in italics.

Concluding Remarks

Horizontal gene transfer is a widespread mechanism for acquisition of genetic variability that has modulated the evolution of Bacteria and Archaea domains and also the evolution of unicellular eukaryotes. However, we are only starting to recognise their real impact on the evolution of pluricellular eukaryotes. Consideration of hybridisation processes occurring in plants and animals as massive horizontal gene transfer events or the recent paper by Crisp *et al.* (2015) increases the importance of reticulated evolution among eukaryotes.

Realisation of the important role of horizontal gene transfer in evolution (at least in prokaryotic evolution) challenges both the reliability of recovery of a universal tree of life and the traditional view of evolution as a slow process.

A pluralistic approach to evolution, considering vertical and horizontal transfer processes of acquisition of variability and

character transmission operating at different complexity levels, can provide a more realistic picture of the evolutionary process that modulates the current biodiversity in the earth.

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