

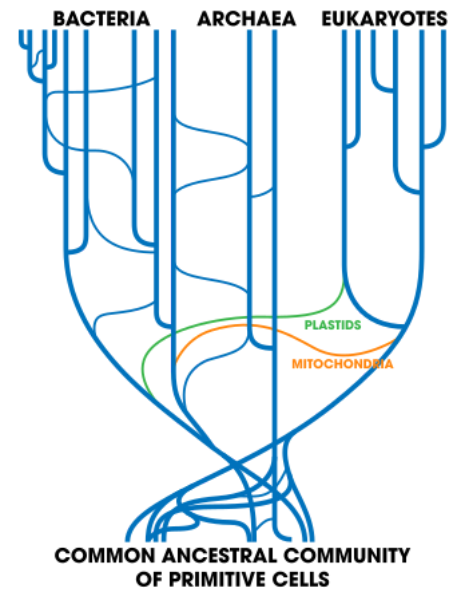
Horizontal gene transfer

Horizontal gene transfer (HGT) or **lateral gene transfer (LGT)**^{[1][2][3]} is the movement of genetic material between unicellular and/or multicellular organisms other than by the ("vertical") transmission of DNA from parent to offspring (reproduction).^[4] HGT is an important factor in the evolution of many organisms.^{[5][6]}

Horizontal gene transfer is the primary mechanism for the spread of antibiotic resistance in bacteria,^{[5][7][8][9][10]} and plays an important role in the evolution of bacteria that can degrade novel compounds such as human-created pesticides^[11] and in the evolution, maintenance, and transmission of virulence.^[12] It often involves temperate bacteriophages and plasmids.^{[13][14][15]} Genes responsible for antibiotic resistance in one species of bacteria can be transferred to another species of bacteria through various mechanisms of HGT such as transformation, transduction and conjugation, subsequently arming the antibiotic resistant genes' recipient against antibiotics. The rapid spread of antibiotic resistance genes in this manner is becoming medically challenging to deal with. Ecological factors may also play a role in the HGT of antibiotic resistant genes.^[16] It is also postulated that HGT promotes the maintenance of a universal life biochemistry and, subsequently, the universality of the genetic code.^[17]

Most thinking in genetics has focused upon vertical transfer, but the importance of horizontal gene transfer among single-cell organisms is beginning to be acknowledged.^{[18][19]}

Gene delivery can be seen as an artificial horizontal gene transfer, and is a form of genetic engineering.



Tree of life showing vertical and horizontal gene transfers

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History

Griffith's experiment, reported in 1928 by [Frederick Griffith](#),^[20] was the first experiment suggesting that bacteria are capable of transferring genetic information through a process known as transformation.^{[21][22]} Griffith's findings were followed by research in the late 1930s and early 40s that isolated [DNA](#) as the material that communicated this genetic information.

Horizontal genetic transfer was then described in Seattle in 1951, in a paper demonstrating that the transfer of a viral gene into *Corynebacterium diphtheriae* created a virulent strain from a non-virulent strain,^[23] also simultaneously solving the riddle of [diphtheria](#) (that patients could be infected with the bacteria but not have any symptoms, and then suddenly convert later or never),^[24] and giving the first example for the relevance of the [lysogenic cycle](#).^[25] Inter-bacterial gene transfer was first described in Japan in a 1959 publication that demonstrated the transfer of antibiotic resistance between different species of [bacteria](#).^{[26][27]} In the mid-1980s, [Syvanen](#)^[28] predicted that lateral gene transfer existed, had biological significance, and was involved in shaping evolutionary history from the beginning of life on Earth.

As [Jian, Rivera and Lake](#) (1999) put it: "Increasingly, studies of genes and genomes are indicating that considerable horizontal transfer has occurred between [prokaryotes](#)"^[29] (see also [Lake and Rivera](#), 2007).^[30] The phenomenon appears to have had some significance for unicellular [eukaryotes](#) as well. As [Baptiste et al.](#) (2005) observe, "additional evidence suggests that gene transfer might also be an important evolutionary mechanism in [protist](#) evolution."^[31]

Grafting of one plant to another can transfer [chloroplasts](#) (organelles in plant cells that conduct photosynthesis), [mitochondrial DNA](#), and the entire [cell nucleus](#) containing the genome to potentially make a new species.^[32] Some [Lepidoptera](#) (e.g. [monarch butterflies](#) and [silkworms](#)) have been genetically modified by horizontal gene transfer from the wasp [bracovirus](#).^[33] Bites from insects in

the family Reduviidae (assassin bugs) can, via a parasite, infect humans with the trypanosomal Chagas disease, which can insert its DNA into the human genome.^[34] It has been suggested that lateral gene transfer to humans from bacteria may play a role in cancer.^[35]

Aaron Richardson and Jeffrey D. Palmer state: "Horizontal gene transfer (HGT) has played a major role in bacterial evolution and is fairly common in certain unicellular eukaryotes. However, the prevalence and importance of HGT in the evolution of multicellular eukaryotes remain unclear."^[36]

Due to the increasing amount of evidence suggesting the importance of these phenomena for evolution (see below) molecular biologists such as Peter Gogarten have described horizontal gene transfer as "A New Paradigm for Biology".^[37]

Mechanisms

There are several mechanisms for horizontal gene transfer:^{[5][38][39]}

- Transformation, the genetic alteration of a cell resulting from the introduction, uptake and expression of foreign genetic material (DNA or RNA).^[40] This process is relatively common in bacteria, but less so in eukaryotes.^[41] Transformation is often used in laboratories to insert novel genes into bacteria for experiments or for industrial or medical applications. See also molecular biology and biotechnology.
- Transduction, the process in which bacterial DNA is moved from one bacterium to another by a virus (a bacteriophage, or phage).^[40]
- Bacterial conjugation, a process that involves the transfer of DNA via a plasmid from a donor cell to a recombinant recipient cell during cell-to-cell contact.^[40]
- Gene transfer agents, virus-like elements encoded by the host that are found in the alphaproteobacteria order Rhodobacterales.^[42]

Horizontal transposon transfer

A transposable element (TE) (also called a transposon or jumping gene) is a mobile segment of DNA that can sometimes pick up a resistance gene and insert it into a plasmid or chromosome, thereby inducing horizontal gene transfer of antibiotic resistance.^[40]

Horizontal transposon transfer (HTT) refers to the passage of pieces of DNA that are characterized by their ability to move from one locus to another between genomes by means other than parent-to-offspring inheritance. Horizontal gene transfer has long been thought to be crucial to prokaryotic evolution, but there is a growing amount of data showing that HTT is a common and widespread phenomenon in eukaryote evolution as well.^[43] On the transposable element side, spreading between genomes via horizontal transfer may be viewed as a strategy to escape purging due to purifying selection, mutational decay and/or host defense mechanisms.^[44]

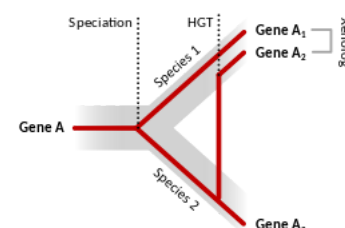
HTT can occur with any type of transposable elements, but DNA transposons and LTR retroelements are more likely to be capable of HTT because both have a stable, double-stranded DNA intermediate that is thought to be sturdier than the single-stranded RNA intermediate of non-LTR retroelements, which can be highly degradable.^[43] Non-autonomous elements may be less likely to transfer horizontally compared to autonomous elements because they do not encode the proteins required for their own mobilization. The structure of these non-autonomous elements generally consists of an intronless gene encoding a transposase protein, and may or may not have a promoter sequence. Those that do not have promoter sequences encoded within the mobile region rely on adjacent host promoters for expression.^[43] Horizontal transfer is thought to play an important role in the TE life cycle.^[43]

HTT has been shown to occur between species and across continents in both plants^[45] and animals (Ivancevic et al. 2013), though some TEs have been shown to more successfully colonize the genomes of certain species over others.^[46] Both spatial and taxonomic proximity of species has been proposed to favor HTTs in plants and animals.^[45] It is unknown how the density of a population may affect the rate of HTT events within a population, but close proximity due to parasitism and cross contamination due to crowding have been proposed to favor HTT in both plants and animals.^[45] Successful transfer of a transposable element requires delivery of DNA from donor to host cell (and to the germ line for multi-cellular organisms), followed by integration into the recipient host genome.^[43] Though the actual mechanism for the transportation of TEs from donor cells to host cells is unknown, it is established that naked DNA and RNA can circulate in bodily fluid.^[43] Many proposed vectors include arthropods, viruses, freshwater snails (Ivancevic et al. 2013), endosymbiotic bacteria,^[44] and intracellular parasitic bacteria.^[43] In some cases, even TEs facilitate transport for other TEs.^[46]

The arrival of a new TE in a host genome can have detrimental consequences because TE mobility may induce mutation. However, HTT can also be beneficial by introducing new genetic material into a genome and promoting the shuffling of genes and TE domains among hosts, which can be co-opted by the host genome to perform new functions.^[46] Moreover, transposition activity increases the TE copy number and generates chromosomal rearrangement hotspots.^[47] HTT detection is a difficult task because it is an ongoing phenomenon that is constantly changing in frequency of occurrence and composition of TEs inside host genomes. Furthermore, few species have been analyzed for HTT, making it difficult to establish patterns of HTT events between species. These issues can lead to the underestimation or overestimation of HTT events between ancestral and current eukaryotic species.^[47]

Methods of detection

Horizontal gene transfer is typically inferred using bioinformatics methods, either by identifying atypical sequence signatures ("parametric" methods) or by identifying strong discrepancies between the evolutionary history of particular sequences compared to that of their hosts. The transferred gene (xenolog) found in the receiving species is more closely related to the genes of the donor species than would be expected.



A speciation event produces orthologs of a gene in the two daughter species. A horizontal gene transfer event from one species to another adds a xenolog of the gene to the receiving genome.

Viruses

The virus called Mimivirus infects amoebae. Another virus, called Sputnik, also infects amoebae, but it cannot reproduce unless mimivirus has already infected the same cell.^[48] "Sputnik's genome reveals further insight into its biology.

Although 13 of its genes show little similarity to any other known genes, three are closely related to mimivirus and mamavirus genes, perhaps cannibalized by the tiny virus as it packaged up particles sometime in its history. This suggests that the satellite virus could perform horizontal gene transfer between viruses, paralleling the way that bacteriophages ferry genes between bacteria."^[49] Horizontal transfer is also seen between geminiviruses and tobacco plants.^[50]

Prokaryotes

Horizontal gene transfer is common among bacteria, even among very distantly related ones. This process is thought to be a significant cause of increased drug resistance^{[51][51]} when one bacterial cell acquires resistance, and the resistance genes are transferred to other species.^{[52][53]} Transposition

and horizontal gene transfer, along with strong natural selective forces have led to multi-drug resistant strains of *S. aureus* and many other pathogenic bacteria.^[40] Horizontal gene transfer also plays a role in the spread of virulence factors, such as exotoxins and exoenzymes, amongst bacteria.^[5] A prime example concerning the spread of exotoxins is the adaptive evolution of Shiga toxins in *E. coli* through horizontal gene transfer via transduction with *Shigella* species of bacteria.^[54] Strategies to combat certain bacterial infections by targeting these specific virulence factors and mobile genetic elements have been proposed.^[12] For example, horizontally transferred genetic elements play important roles in the virulence of *E. coli*, *Salmonella*, *Streptococcus* and *Clostridium perfringens*.^[5]

In prokaryotes, restriction-modification systems are known to provide immunity against horizontal gene transfer and in stabilizing mobile genetic elements. Genes encoding restriction modification systems have been reported to move between prokaryotic genomes within mobile genetic elements (MGE) such as plasmids, prophages, insertion sequences/transposons, integrative conjugative elements (ICE),^[55] and integrons. Still, they are more frequently a chromosomal-encoded barrier to MGE than an MGE-encoded tool for cell infection.^[56]

Lateral gene transfer via a mobile genetic element, namely the integrated conjugative element (ICE) *Bs1* has been reported for its role in the global DNA damage SOS response of the gram positive *Bacillus subtilis*.^[57] Furthermore it has been linked with the radiation and desiccation resistance of *Bacillus pumilus* SAFR-032 spores,^[58] isolated from spacecraft cleanroom facilities.^{[59][60][61]}

Transposon insertion elements have been reported to increase the fitness of gram-negative *E. coli* strains through either major transpositions or genome rearrangements, and increasing mutation rates.^{[62][63]} In a study on the effects of long-term exposure of simulated microgravity on non-pathogenic *E. coli*, the results showed transposon insertions occur at loci, linked to SOS stress response.^[64] When the same *E. coli* strain was exposed to a combination of simulated microgravity and trace (background) levels of (the broad spectrum) antibiotic (chloramphenicol), the results showed transposon-mediated rearrangements (TMRs), disrupting genes involved in bacterial adhesion, and deleting an entire segment of several genes involved with motility and chemotaxis.^[65] Both these studies have implications for microbial growth, adaptation to and antibiotic resistance in real time space conditions.

Bacterial transformation

Natural transformation is a bacterial adaptation for DNA transfer (HGT) that depends on the expression of numerous bacterial genes whose products are responsible for this process.^{[66][67]} In general, transformation is a complex, energy-requiring developmental process. In order for a bacterium to bind, take up and recombine exogenous DNA into its chromosome, it must become competent, that is, enter a special physiological state. Competence development in *Bacillus subtilis* requires expression of about 40 genes.^[68] The DNA integrated into the host chromosome is usually (but with infrequent exceptions) derived from another bacterium of the same species, and is thus homologous to the resident chromosome. The capacity for natural transformation occurs in at least 67 prokaryotic species.^[67] Competence for transformation is typically induced by high cell density and/or nutritional limitation, conditions associated with the stationary phase of bacterial growth. Competence appears to be an adaptation for DNA repair.^[69] Transformation in bacteria can be viewed as a primitive sexual process, since it involves interaction of homologous DNA from two individuals to form recombinant DNA that is passed on to succeeding generations. Although transduction is the form of HGT most commonly associated with bacteriophages, certain phages may also be able to promote transformation.^[70]

Bacterial conjugation

Conjugation in *Mycobacterium smegmatis*, like conjugation in *E. coli*, requires stable and extended contact between a donor and a recipient strain, is DNase resistant, and the transferred DNA is incorporated into the recipient chromosome by homologous recombination. However, unlike *E. coli* high frequency of recombination conjugation (Hfr), mycobacterial conjugation is a type of HGT that is chromosome rather than plasmid based.^[71] Furthermore, in contrast to *E. coli* (Hfr) conjugation, in *M. smegmatis* all regions of the chromosome are transferred with comparable efficiencies. Substantial blending of the parental genomes was found as a result of conjugation, and this blending was regarded as reminiscent of that seen in the meiotic products of sexual reproduction.^{[71][72]}

Archaeal DNA transfer

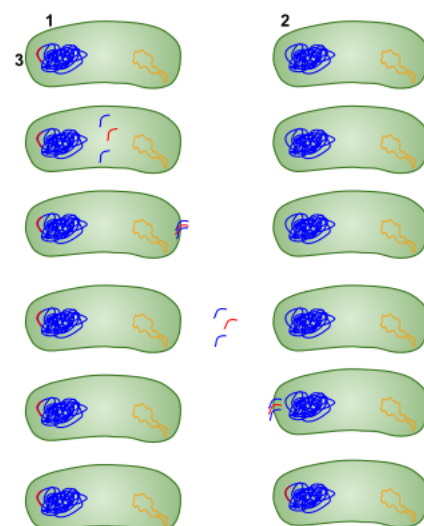
The archaeon *Sulfolobus solfataricus*, when UV irradiated, strongly induces the formation of type IV pili which then facilitates cellular aggregation.^{[73][74]} Exposure to chemical agents that cause DNA damage also induces cellular aggregation.^[73] Other physical stressors, such as temperature shift or pH, do not induce aggregation, suggesting that DNA damage is a specific inducer of cellular aggregation.

UV-induced cellular aggregation mediates intercellular chromosomal HGT marker exchange with high frequency,^[75] and UV-induced cultures display recombination rates that exceed those of uninduced cultures by as much as three orders of magnitude. *S. solfataricus* cells aggregate preferentially with other cells of their own species.^[75] Frols et al.^{[73][76]} and Ajon et al.^[75] suggested that UV-inducible DNA transfer is likely an important mechanism for providing increased repair of damaged DNA via homologous recombination. This process can be regarded as a simple form of sexual interaction.

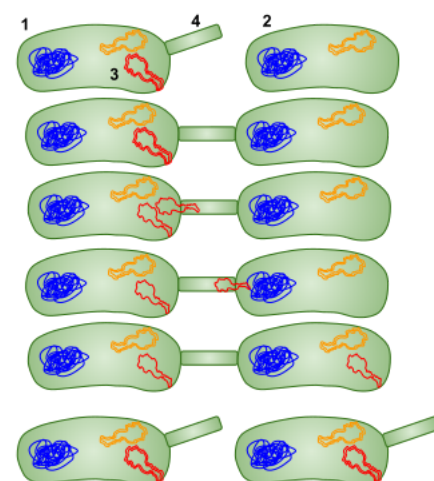
Another thermophilic species, *Sulfolobus acidocaldarius*, is able to undergo HGT. *S. acidocaldarius* can exchange and recombine chromosomal markers at temperatures up to 84 °C.^[77] UV exposure induces pili formation and cellular aggregation.^[75] Cells with the ability to aggregate have greater survival than mutants lacking pili that are unable to aggregate. The frequency of recombination is increased by DNA damage induced by UV-irradiation^[78] and by DNA damaging chemicals.^[79]

The *ups* operon, containing five genes, is highly induced by UV irradiation. The proteins encoded by the *ups* operon are employed in UV-induced pili assembly and cellular aggregation leading to intercellular DNA exchange and homologous recombination.^[80] Since this system increases the fitness of *S. acidocaldarius* cells after UV exposure, Wolferen et al.^{[80][81]} considered that transfer of DNA likely takes place in order to repair UV-induced DNA damages by homologous recombination.

Eukaryotes



1: Donor bacteria 2: Bacteria who will receive the gene 3: The red portion represents the gene that will be transferred. Transformation in bacteria happens in a certain environment.



1: Donor bacteria cell (F+ cell) 2: Bacteria that receives the plasmid (F- cell) 3: Plasmid that will be moved to the other bacteria 4: Pilus. Conjugation in bacteria using a sex pilus; then the bacteria that received the plasmid can go give it to other bacteria as well.

"Sequence comparisons suggest recent horizontal transfer of many genes among diverse species including across the boundaries of phylogenetic 'domains'. Thus determining the phylogenetic history of a species can not be done conclusively by determining evolutionary trees for single genes."^[82]

Organelle to nuclear genome

- Analysis of DNA sequences suggests that horizontal gene transfer has occurred within eukaryotes from the chloroplast and mitochondrial genomes to the nuclear genome. As stated in the endosymbiotic theory, chloroplasts and mitochondria probably originated as bacterial endosymbionts of a progenitor to the eukaryotic cell.^[83]

Organelle to organelle

- Mitochondrial genes moved to parasites of the Rafflesiaceae plant family from their hosts^{[84][85]} and from chloroplasts of a still-unidentified plant to the mitochondria of the bean Phaseolus.^[86]

Viruses to plants

- Plants are capable of receiving genetic information from viruses by horizontal gene transfer.^[50]

Bacteria to fungi

- Horizontal transfer occurs from bacteria to some fungi, such as the yeast Saccharomyces cerevisiae.^[87]

Bacteria to plants

- Agrobacterium, a pathogenic bacterium that causes cells to proliferate as crown galls and proliferating roots is an example of a bacterium that can transfer genes to plants and this plays an important role in plant evolution.^[88]

Bacteria to insects

- HhMAN1 is a gene in the genome of the coffee borer beetle (*Hypothenemus hampei*) that resembles bacterial genes, and is thought to be transferred from bacteria in the beetle's gut.^{[89][90]}

Bacteria to animals

- Bdelloid rotifers currently hold the 'record' for HGT in animals with ~8% of their genes from bacterial origins.^[91] Tardigrades were thought to break the record with 17.5% HGT, but that finding was an artifact of bacterial contamination.^[92]
- A study found the genomes of 40 animals (including 10 primates, four Caenorhabditis worms, and 12 Drosophila insects) contained genes which the researchers concluded had been transferred from bacteria and fungi by horizontal gene transfer.^[93] The researchers estimated that for some nematodes and Drosophila insects these genes had been acquired relatively recently.^[94]
- A bacteriophage-mediated mechanism transfers genes between prokaryotes and eukaryotes. Nuclear localization signals in bacteriophage terminal proteins (TP) prime DNA replication and become covalently linked to the viral genome. The role of virus and bacteriophages in HGT in

bacteria, suggests that TP-containing genomes could be a vehicle of inter-kingdom genetic information transference all throughout evolution.^[95]

Endosymbiont to insects and nematodes

- The adzuki bean beetle has acquired genetic material from its (non-beneficial) endosymbiont Wolbachia.^[96] New examples have recently been reported demonstrating that Wolbachia bacteria represent an important potential source of genetic material in arthropods and filarial nematodes.^[97]

Plant to plant

- Striga hermonthica, a parasitic eudicot, has received a gene from sorghum (Sorghum bicolor) to its nuclear genome.^[98] The gene's functionality is unknown.
- A gene that allowed ferns to survive in dark forests came from the hornwort, which grows in mats on streambanks or trees. The neochrome gene arrived about 180 million years ago.^[99]

Plants to animals

- The eastern emerald sea slug Elysia chlorotica has been suggested by fluorescence in situ hybridization (FISH) analysis to contain photosynthesis-supporting genes obtained from an algae (Vaucheria litorea) in their diet.^[100] LGT in Sacoglossa is now thought to be an artifact^[101] and no trace of LGT was found upon sequencing the genome of Elysia chlorotica.^[102]

Plant to fungus

- Gene transfer between plants and fungi has been posited for a number of cases, including rice (Oryza sativa).

Fungi to insects

- Pea aphids (Acyrtosiphon pisum) contain multiple genes from fungi.^{[103][104]} Plants, fungi, and microorganisms can synthesize carotenoids, but torulene made by pea aphids is the only carotenoid known to be synthesized by an organism in the animal kingdom.^[103]

Animals to animals

- Smelt fish received antifreeze protein (AFP) gene from herring through a direct horizontal transfer.^[105]

Human to protozoan

- The malaria pathogen Plasmodium vivax acquired genetic material from humans that might help facilitate its long stay in the body.^[106]

Human genome

- One study identified approximately 100 of humans' approximately 20,000 total genes which likely resulted from horizontal gene transfer,^[107] but this number has been challenged by several

researchers arguing these candidate genes for HGT are more likely the result of gene loss combined with differences in the rate of evolution.^[108]

Artificial horizontal gene transfer

Genetic engineering is essentially horizontal gene transfer, albeit with synthetic expression cassettes. The Sleeping Beauty transposon system^[109] (SB) was developed as a synthetic gene transfer agent that was based on the known abilities of Tc1/mariner transposons to invade genomes of extremely diverse species.^[110] The SB system has been used to introduce genetic sequences into a wide variety of animal genomes.^{[111][112]} (See also Gene therapy.)

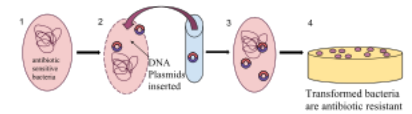
Importance in evolution

Horizontal gene transfer is a potential confounding factor in inferring phylogenetic trees based on the sequence of one gene.^[113] For example, given two distantly related bacteria that have exchanged a gene a phylogenetic tree including those species will show them to be closely related because that gene is the same even though most other genes are dissimilar. For this reason, it is often ideal to use other information to infer robust phylogenies such as the presence or absence of genes or, more commonly, to include as wide a range of genes for phylogenetic analysis as possible.

For example, the most common gene to be used for constructing phylogenetic relationships in prokaryotes is the 16S ribosomal RNA gene since its sequences tend to be conserved among members with close phylogenetic distances, but variable enough that differences can be measured. However, in recent years it has also been argued that 16s rRNA genes can also be horizontally transferred. Although this may be infrequent, the validity of 16s rRNA-constructed phylogenetic trees must be reevaluated.^[114]

Biologist Johann Peter Gogarten suggests "the original metaphor of a tree no longer fits the data from recent genome research" therefore "biologists should use the metaphor of a mosaic to describe the different histories combined in individual genomes and use the metaphor of a net to visualize the rich exchange and cooperative effects of HGT among microbes".^[37] There exist several methods to infer such phylogenetic networks.

Using single genes as phylogenetic markers, it is difficult to trace organismal phylogeny in the presence of horizontal gene transfer. Combining the simple coalescence model of cladogenesis with rare HGT horizontal gene transfer events suggest there was no single most recent common ancestor that contained all of the genes ancestral to those shared among the three domains of life. Each contemporary molecule has its own history and traces back to an individual molecule cenancestor. However, these molecular ancestors were likely to be present in different organisms at different times."^[115]



Before it is transformed, a bacterium is susceptible to antibiotics. A plasmid can be inserted when the bacteria is under stress, and be incorporated into the bacterial DNA creating antibiotic resistance. When the plasmids are prepared they are inserted into the bacterial cell by either making pores in the plasma membrane with temperature extremes and chemical treatments, or making it semi permeable through the process of electrophoresis, in which electric currents create the holes in the membrane. After conditions return to normal the holes in the membrane close and the plasmids are trapped inside the bacteria where they become part of the genetic material and their genes are expressed by the bacteria.

Challenge to the tree of life

Horizontal gene transfer poses a possible challenge to the concept of the last universal common ancestor (LUCA) at the root of the tree of life first formulated by Carl Woese, which led him to propose the Archaea as a third domain of life.^[116] Indeed, it was while examining the new three-domain view of life that horizontal gene transfer arose as a complicating issue: *Archaeoglobus fulgidus* was seen as an anomaly with respect to a phylogenetic tree based upon the encoding for the enzyme HMGCoA reductase—the organism in question is a definite Archaeon, with all the cell lipids and transcription machinery that are expected of an Archaeon, but whose HMGCoA genes are of bacterial origin.^[116] Scientists are broadly agreed on symbiogenesis, that mitochondria in eukaryotes derived from alpha-proteobacterial cells and that chloroplasts came from ingested cyanobacteria, and other gene transfers may have affected early eukaryotes. (In contrast, multicellular eukaryotes have mechanisms to prevent horizontal gene transfer, including separated germ cells.) If there had been continued and extensive gene transfer, there would be a complex network with many ancestors, instead of a tree of life with sharply delineated lineages leading back to a LUCA.^{[116][117]} However, a LUCA can be identified, so horizontal transfers must have been relatively limited.^[118]

Phylogenetic information in HGT

It has been remarked that, despite the complications, the detection of horizontal gene transfers brings valuable phylogenetic and dating information.^[119]

The potential of HGT to be used for dating phylogenies has recently been confirmed.^{[120][121]}

The chromosomal organization of horizontal gene transfer

The acquisition of new genes has the potential to disorganize the other genetic elements and hinder the function of the bacterial cell, thus affecting the competitiveness of bacteria. Consequently, bacterial adaptation lies in a conflict between the advantages of acquiring beneficial genes, and the need to maintain the organization of the rest of its genome. Horizontally transferred genes are typically concentrated in only ~1% of the chromosome (in regions called hotspots). This concentration increases with genome size and with the rate of transfer. Hotspots diversify by rapid gene turnover; their chromosomal distribution depends on local contexts (neighboring core genes), and content in mobile genetic elements. Hotspots concentrate most changes in gene repertoires, reduce the trade-off between genome diversification and organization, and should be treasure troves of strain-specific adaptive genes. Most mobile genetic elements and antibiotic resistance genes are in hotspots, but many hotspots lack recognizable mobile genetic elements and exhibit frequent homologous recombination at flanking core genes. Overrepresentation of hotspots with fewer mobile genetic elements in naturally transformable bacteria suggests that homologous recombination and horizontal gene transfer are tightly linked in genome evolution.^[122]

Genes

There is evidence for historical horizontal transfer of the following genes:

- Lycopene cyclase for carotenoid biosynthesis, between Chlorobi and Cyanobacteria.^[123]
- TetO gene conferring resistance to tetracycline, between *Campylobacter jejuni*.^[124]
- Neochrome, a gene in some ferns that enhances their ability to survive in dim light. Believed to have been acquired from algae sometime during the Cretaceous.^{[125][126]}
- Transfer of a cysteine synthase from a bacterium into phytophagous mites and Lepidoptera allowing the detoxification of cyanogenic glucosides produced by host plants.^[127]
- The LINE1 sequence has transferred from humans to the gonorrhea bacteria.^[128]

See also

- Agrobacterium, a bacterium well known for its ability to transfer DNA between itself and plants.
- Endogenous retrovirus
- Genetically modified organism
- Inferring horizontal gene transfer
- Integron
- Mobile genetic elements
- Phylogenetic network
- Phylogenetic tree
- Provirus
- Reassortment
- Retrotransposon
- Symbiogenesis
- Tree of life (biology)
- Xenobiology

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