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Rapid acquisition of microorganisms and microbial genes can help explain punctuated evolution

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The punctuated mode of evolution posits that evolution occurs in rare bursts of rapid evolutionary change followed by long periods of genetic stability (stasis). The accepted cause for the rapid changes in punctuated evolution is special ecological circumstances – selection forces brought about by changes in the environment. This article presents a complementary explanation for punctuated evolution by the rapid formation of genetic variants in animals and plants by the acquisition of microorganisms from the environment into microbiomes and microbial genes into host genomes by horizontal gene transfer. Several examples of major evolutionary events driven by microorganisms are discussed, including the formation of the first eukaryotic cell, the ability of some animals to digest cellulose and other plant cell-wall complex polysaccharides, dynamics of root system architecture, and the formation of placental mammals. These changes by cooperation were quantum leaps in the evolutionary development of complex biological systems and can contribute to an understanding of the mechanisms underlying punctuated evolution.

KEYWORDS

holobiont, punctuated evolution, horizontal gene transfer, gene variation, placental mammals, hologenomes, microbiome

Introduction

The punctuated equilibrium mode of evolution, although first introduced by Simpson (1944), is generally attributed to the paleontologists Eldredge and Gould (Eldredge, 1971; Eldredge and Gould, 1972; Gould and Eldredge, 1977). Punctuated evolution posits genetic stability followed by rare bursts of rapid evolutionary change. Once a species appears in the fossil record, the population will become stable, showing little evolutionary change for most of its geological history. This state of little or no morphological change is called stasis. In contrast, phyletic gradualism is a more gradual, continuous model of evolution that occurs uniformly by the steady and slow transformation of whole lineages. Eldredge and Gould argued that the degree of gradualism, commonly attributed to Charles Darwin (Rhodes, 1983), is virtually nonexistent in the fossil record and that stasis dominates the history of most fossil

species. According to [Gould and Eldredge \(2016\)](#), “Phyletic gradualism was an *a priori* assertion from the start—it was never “seen” in the rocks; it expressed the cultural and political biases of 19th-century liberalism.” More studies that are recent have provided support for the theory of punctuated evolution ([Erwin and Anstey, 1995](#); [Palmer et al., 2012](#); [Cross et al., 2016](#); [Gemmell et al., 2019](#); [Schmidt and Wolf, 2021](#)).

What is the accepted explanation for the bursts of rapid evolutionary change? The most common cause designated to the rapid changes in punctuated evolution is special ecological circumstances, which select specific genetic variants in the population ([Rhodes, 1983](#)). For example, when a species acquires a gene that allows it to exploit some feature of the changed or changing environment, such as a new environmental niche, the species may then show rapid changes in other traits as it adapts to this new niche ([Milligan, 1986](#)). Another example is extreme events, such as volcanism and asteroid impacts, which can be major drivers of evolutionary change by providing new niches ([Grant et al., 2017](#)).

This article presents complementary mechanisms for the understanding of punctuated evolution, derived from a consideration of the role of microorganisms in the evolution of animals and plants ([Margulis, 1999](#); [Margulis and Sagan, 2003](#); [Rosenberg and Zilber-Rosenberg, 2018](#)). Although never specifically referring to punctuated evolution, the symbiogenesis theory of Margulis posits that organisms come about primarily through the merger of separate organisms.

Punctuated evolution driven by acquisition of microorganisms

One of the most profound evolutionary events was the formation of the eukaryotic cell by the acquisition of one bacterium by another. Mitochondria and chloroplasts were probably formed by the acquisition of Alphaproteobacteria ([Roger et al., 2017](#)) and cyanobacteria ([Ponce-Toledo et al., 2017](#)), respectively. The nucleus of eukaryotic cells was possibly generated by the acquisition of an Archaea ([Williams et al., 2020](#)) or a virus ([Takemura, 2020](#)). Thus, it is generally accepted that eukaryotes were not formed by the slow process of mutation but, rather, by endosymbiosis, followed by the gradual conversion of the endosymbiont into an organelle. After the eukaryotic cell was formed, the acquisition of bacteria and viruses has continued to play a fundamental role in the evolution of eukaryotes to this day. Today, all eukaryotes (plants and animals) are not individuals but complex systems referred to as holobionts, composed of the host and myriad microorganisms living on or in them.

Prokaryotes were on this planet for 2.1 billion years before there were any animals or plants ([Mikhailovsky and Gordon, 2021](#)). During this time, they evolved enormous biochemical diversity and split into two domains: Bacteria and Archaea.

Mutation and evolution in prokaryotes is much faster than in eukaryotes because they are haploid single cells, they multiply rapidly, and they readily exchange genetic information ([Pepper, 2014](#)). Animals and plants come into random contact with billions of microorganisms during their lifetime *via* air, water, and through interaction with organic and inorganic surfaces. Occasionally, some of these microbes find a niche and, under appropriate conditions, amplify on or in the host and affect the phenotype of the holobiont. Unlike mutation, which causes changes in existing genomes, the acquisition of a microbe introduces thousands of new genes into the holobiont. This way, rather than reinventing the wheel, animals and plants can acquire pre-evolved genetic information in the form of microbes. It is likely that, after the microbe is acquired, mutations and selection occur in both the microbe and host to optimize the interaction.

A major evolutionary event driven by the acquisition of microbes was the ability of some animals to digest cellulose and other plant cell-wall-complex polysaccharides. With few exceptions ([Sharma et al., 2016](#)), animal genomes do not code for the synthesis of cellulose-degrading enzymes. Instead, animals such as ruminants and termites rely totally on anaerobic cellulolytic microorganisms that are present in the internal space of their digestive tract. How did they gain access to these specialized microbes? It seems likely that at least some of the cellulose-degrading bacteria in ruminants originated from the consumption of grass, straw, and foliage that contained these bacteria on their surfaces ([Sari et al., 2017](#)). [Gilbert \(2020\)](#) discusses the ability of symbionts to promote development supporting the evolution of herbivory. It has been suggested that the first ruminant evolved in Southeast Asia about 50 million years ago from a small forest-dwelling omnivore, and, later, ruminants evolved from this original taxon ([Hackmann and Spain, 2010](#)).

Following the original acquisition of an anaerobic cellulose-degrading bacterium by a mammal, and, along the way, additional ones, there would be a strong selection for optimizing the interaction between the bacterium and the host, including changes in the host size, shape, internal organs, and teeth. These new adaptations helped ruminants leave more descendants and become one of the most widespread groups of large mammals they are today. A key point is that the evolution of ruminants was driven initially by the acquisition of cellulose-degrading bacteria. Large amounts of cellulose were already available in the environment as a selective force ([Sarkar et al., 2009](#)). The higher ruminants (Pecorans) are believed to have rapidly evolved in the Mid-Eocene, giving rise to five distinct extant families: Antilocapridae, Giraffidae, Moschidae, Cervidae, and Bovidae ([Decker et al., 2009](#)). The acquisition of cellulose-degrading bacteria made this rapid radiation possible.

Another example of how the acquisition of a microbial symbiont can lead to rapid evolution is the evolution and expansion of shallow-water scleractinian corals, following

the uptake of dinoflagellates roughly 240 million years ago (Frankowiak et al., 2016). The coral-dinoflagellate photosymbiosis allowed for growth in a nutrient-poor, low-productivity marine environment. Isotopic data support the role of photosymbiosis during the sudden Triassic expansion of coral reefs (Stanley, 2003). At present, we are living through a punctuated evolution event in the opposite direction. Global warming is causing disruption of coral symbioses, loss of coral reefs, and changed distributions of corals (Loya et al., 2001).

The acquisition of microorganisms not only played a crucial role in the emergence of chloroplasts, as discussed above but also in the continuing evolution of plants (Cordovez et al., 2019). One of the interesting contributions of microbiota to plants is the synthesis of the hormone auxin, indole-3-acetic acid. Auxin underpins plant development and growth (Frick and Strader, 2018). Bacteria and filamentous fungi, attached to roots in the rhizosphere, synthesize auxin (Wagi and Ahmed, 2019), which initiates several growth and developmental processes in plants, such as root hair and tip growth, formation of lateral roots, and the dynamics of root system architecture (Zamioudis et al., 2013). These auxin-producing microorganisms were, and probably still are, the driving force behind the evolution of plant synapses and other interactive behaviors of higher plants.

In conclusion, this section demonstrated that acquired beneficial microbes have the potential to be amplified and to spread rapidly to other holobionts in a manner similar to pathogen epidemics. This could accelerate the rate of adaptation and evolution of whole groups of holobionts. Such evolutionary changes by cooperation sometimes brought about quantum leaps in the development of biological complex systems. Gilbert (2019) has recently reviewed some of the literature on evolution by symbiosis but does not relate them to punctuated evolution.

Punctuated evolution driven by horizontal gene transfer

Horizontal gene transfer (HGT), also known as lateral gene transfer, refers to the movement of genetic material, and together with it genetic information across normal mating barriers, between more or less distantly related organisms. Thus, it differs from the standard vertical transmission of genes from parent to offspring. HGT enables the acquisition of novel traits *via* non-Mendelian inheritance of genetic material. HGT is generally associated with gene transfer between different types of bacteria and is a well-known and ubiquitous evolutionary mechanism in prokaryotes (Soucy et al., 2015; Kloub et al., 2021). An average of 81% of the genes in 181 sequenced prokaryotic genomes has been subject to HGT during the long history of prokaryotic evolution (Dagan et al., 2008). It was observed that HGT is more frequent than mutation in *E. coli* colonizing the mammalian gut (Frazão et al., 2019). Most prokaryotes possess different classes of mobile genetic elements that allow for the acquisition, loss,

or rearrangement of sometimes large regions of their genome. Transposons, plasmids, genomic islands, and viruses, including bacteriophages, mediate HGT. One of the best-studied examples of HGT in bacteria is the evolution of antibiotic resistance (Maclean and San Millan, 2019). I would like to suggest that HGT could play a vital role in the genetic adaptation that is suggested to occur during punctuated evolution as a result of environmental changes. This can be achieved first by HGT between microorganisms within holobionts and, second, by HGT between these microorganisms and their host.

HGT between bacteria that are part of plant, animal, and human holobionts can bring about evolutionary change. For example, the ability of Far East Asian people to break down agar (an abundant ingredient in their diet since antiquity) originated from HGT between bacteria in their gut. Agar-decomposing genes, present in a marine bacterium, were transferred to a human gut bacterium, *Bacteroides plebeius*, by HGT as a result of eating food that contained raw seaweed (Hehemann et al., 2010). Although HGT usually occurs between bacteria in the same ecological niche, apparently the marine bacterium was present in the gut long enough to have some of its genes transferred to the resident gut bacterium. These genes code for the porphyranases that degrade the polysaccharide agarose of agar (Li et al., 2014). Westerners lack these enzymes and, therefore, cannot digest agar. The bacteria with the transferred genes spread throughout the Far East Asian population by vertical and horizontal transmission (Hehemann et al., 2012; Porter and Martens, 2017). This is an interesting example of a very fast, but minor, metabolic evolutionary change that could not be observed in fossil records.

The recent availability of a large number of high-quality sequences of fungus, plant, and animal genomes has led to the conclusion that HGT in these organisms has been more frequent events than observed previously (Li et al., 2018). It should be noted that the observable HGT events are probably only those occurring relatively late in evolutionary time scales since early ones are already masked by many genetic mutation events (Nielsen et al., 2014). Sixty sequenced fungal genomes contained 713 horizontally transferred genes from bacteria (Naranjo-Ortiz and Gabaldón, 2020). Invertebrate genomes contain numerous bacterial, fungal, and viral genes (reviewed by Drezen et al., 2017). For example, the genomes of 12 *Drosophila* species showed, on average, 40 foreign genes that had been horizontally transferred from bacteria and fungi (Crisp et al., 2015). When the *Drosophila* species were placed on a phylogenetic tree, there was a correspondence between the number of HGT events and the length of each branch, suggesting that HGT has occurred throughout *Drosophila* evolution and is likely to be ongoing (Serrato-Capuchina and Matute, 2018).

The evolutionary significance of HGT in plants has been reviewed by Wickell and Li (2020). Analysis of the 13.7-megabase genome of the extremophile red alga *Galdieria sulphuraria* indicated that 5% of its protein-coding genes were

acquired by HGT from bacteria and archaea (Schönknecht et al., 2013). Genomic data have uncovered that 57 gene families in the moss *Physcomitrella patens* genome were derived from prokaryotes, fungi, or viruses by HGT (Yue et al., 2012). Many of these genes are involved in essential or plant-specific activities, such as xylem formation, plant defense, nitrogen recycling, and the biosynthesis of starch, polyamines, hormones, and glutathione. Clearly, HGT has played an important role in the direction and the rate of evolution in plants (Ma et al., 2022).

Horizontally transferred genes can also be found in vertebrates (Dunning Hotopp, 2018). It was estimated that the human genome contains 1,467 HGT regions, involving 642 known genes (Huang et al., 2017). However, it is not clear when these HGT events took place. In one study, Crisp et al. (2015) reported that 145 human genes, which are not present in other primates, were probably attributed to HGT. The majority of the 145 genes identified in the study came from bacteria, but some originated from viruses and yeasts. Popov et al. (2019) have suggested that viruses and intracellular microbial pathogens were the modes of acquisition of bacterial genes into the human genome.

A major event in the evolution of mammals, the formation of placental mammals, which includes humans, was driven by the acquisition of the gene coding for the protein syncytin from a retrovirus by HGT (Dupressoir et al., 2012). It is assumed that the ancestor of placental mammals was solitary, seasonally breeding, insectivorous, and likely nocturnal (Wu et al., 2017). The original function of syncytin in such an ancestor was to allow retroviruses to fuse host cells so that they could move from one cell to another. Now, syncytin is necessary for the development of the placental syncytium, an essential part of the mother-fetus barrier. Endogenous retroviruses have been shown to be involved in placentation in various mammalian species Nakaya and Miyazawa, 2015; Hao et al., 2020, demonstrating that this event occurred a number of times during evolution. Moreover, recent molecular dating estimates for placental mammals echo fossil inferences for an explosive diversification about 76 million years ago (Halliday et al., 2015; Phillips and Fruciano, 2018). These data are consistent with the punctuated theory of evolution.

Discussion

Evolution depends both on a selective force and variants in the population that can benefit from this selected force. With regard to punctuated evolution, the rare bursts of rapid evolutionary change are generally attributed to extreme environmental events, such as large changes in temperature, and mass extinctions caused by volcanism or asteroid impact (Marshall, 2015; Grant et al., 2017). These extreme events set up strong selection pressures on organisms and are analogs of the dramatic changes documented in the fossil record.

When an organism acquires a genetic variation that allows it to exploit some feature of the changed environment—a new environmental niche—the species may then show rapid changes in other traits as it adapts to this new niche (Milligan and Wood, 1986).

This article presents data demonstrating that the rate of formation of variants in the population can also help explain punctuated evolution. According to neo-Darwinian theory, formulated in the 1940s, genetic variation is ultimately generated by mutation (Hershberg, 2015; Ibraimov, 2020). However, evolving a novel function by mutation is a very slow process. For example, it was reported that laboratory adaptive evolution of *E. coli* to grow on a novel substrate, 1,2-propanediol, took ~700 generations (Lee and Palsson, 2010), and the ability to grow on citrate required ~31,000 generations (Lenski, 2017). One would expect that evolution by mutation in animals and plants would be much slower than in bacteria (Weller and Wu, 2015).

Acquisition of microorganisms from the environment and horizontal gene transfer bring forth underappreciated rapid modes of genetic variation (Zilber-Rosenberg and Rosenberg, 2021). Rather than “reinvent the wheel,” holobionts have the ability to acquire genes and clusters of genes in a single step that initially evolved in microorganisms. If the acquisition provides a selective advantage to the holobiont, then it will multiply in the population by vertical and horizontal transfer and lead to the evolution of new species. Furthermore, changes in the composition of the microbiome have been shown to drive speciation in *Nasonia* wasps (Brucker and Bordenstein, 2013) and two house mice subspecies (Wang et al., 2015).

What is often not appreciated is that acquisition of microbiota can not only affect the metabolism of animals and plants but also their morphology. Examples include the hindgut of termites (Brune, 2014), rumen (Jami and Mizrahi, 2012), the squid eye organ (Nyholm and McFall-Ngai, 2004), and the nodule of legumes (Velázquez et al., 2017). In each of these examples, the morphology of the holobiont has undergone an evolutionary change while optimizing the interaction of the host with its microbiota for the benefit of the holobiont.

Cooperation is a fundamental property of all biological systems, from genes and cells to animals and societies. Evolutionary history can be viewed as a series of major transitions in which replicating units came together and formed new, more complex levels of biological organization (West et al., 2015). As examples, in this article, I discussed how eukaryotic cells were formed from the union of archaea and eubacteria, the formation of ruminants by the acquisition of cellulose-decomposing bacteria, the emergence of coral reefs by acquiring endosymbiotic algae, and the evolution of placental mammals by acquiring a viral gene. All of these examples would be expected to give rise to rapid evolution (punctuated evolution), even if they might not be observed directly in the fossil record.

In conclusion, the evidence described in this paper that the acquisition of microorganisms and microbial genes played an important role in the rapid evolution of animals and plants may contribute to a better understanding of the mechanisms underlying punctuated evolution. Finally, it should be noted that there are other mechanisms that have been suggested to play a role in punctuated evolution, including (i) regulatory gene evolution (Davidson, 2006; Tomoyasu et al., 2009), (ii) developmental plasticity wherein genes follow phenotypes (West-Eberhard, 2005; Standen et al., 2014), and (iii) stress-induced activation of cryptic genetic pathways (Love and Wagner, 2022). These mechanisms clearly contribute to specific examples of punctuated evolution. However, the major evolutionary events discussed in this article, the formation of eukaryotes, the ability of some animals to digest cellulose, and the formation of placental mammals are more readily understood by the acquisition of microbes and microbial genes.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

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Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

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