SECTION I, THEORY: WHAT "STORY OF EVOLUTION" ARE WE SUBSCRIBING TO?

It is important to first chronicle a story of the planet's evolution in the Pre-Cambrian so that we have an understanding of the theory which underlies the simulation we are trying to create. There are many important pieces of information which must be considered, and there are several viewpoints on the causes of, nature of, and implications of various important events in our planet's history. Here is a rough outline of Earth's chronology with which the Thrive team is using to create our personal narrative of evolution.

I would like to note that I may "anthropomorphize evolution" from time to time - make it seem like evolution has an underlying plan or otherwise suggest that evolution is an intelligent being strategizing adaptations like a game of Risk. This is done in the context of Thrive itself, as the player is an intelligent designer creating their lifeform. So it can make things easier to translate to in-game visions and mechanisms.

The Beginning

Life started relatively early on Earth - perhaps anywhere from 4.2 billion years ago to 3.8 billion years ago, when the oceans were still much warmer than the modern day, meteoric bombardments were common, and volcanic activity was constant. The first cells likely emerged either near alkaline hydrothermal vents or shallow, sun-exposed pools of water, utilizing consistent sources of energy and natural gradients to create primitive metabolisms, and thus, replicate material. The first lifeforms were likely thermophilic, and although the oceans were warm, their cooling would mean that much of life would initially inhabit what we now consider extreme environments. Eventually, life would spread across the oceans, utilizing a large pool of pre-formed natural organic material to fuel themselves.

As these organics were consumed however, and even before then, life increasingly found a need to diversify in metabolic strategies. Various bizarre sources of food/growth/respiration, such as nitrogen fixation, hydrogen sulfide, rustic iron, and intracellular fermentation evolved as prokaryotes began forming the root of our current ecosystems. One incredibly important metabolic strategy involved the advent of photosynthesis - using the sun to generate glucose. Initially anoxygenic, cyanobacteria (perhaps evolving as early as 3.5 billion years ago) would eventually evolve the ability to split water in the process of photosynthesis, creating free-floating oxygen. And although the long-lasting implications of free-floating oxygen wouldn't manifest itself just yet, cyanobacteria already began to oxygenate the immediate surfaces of the ocean, resulting in the arrival of aerobic respiration. Various important geological phenomena, such as prominent tectonic plate activity and the depletion of natural chemical reservoirs, hadn't fully matured yet, meaning that the various chemical processes cells would utilize could have resulted in dramatic localized changes. However, the metabolic pathways evolved during this time would be world-shaping, eventually forming an incredibly important part of the complex biogeochemical processes we see on Earth, such as the sulfur, iron, oxygen, and carbon cycle.

The Prokaryotic Paradox

Bacterial evolution had transformative effects on the planet's atmosphere, paving a road for complex lifeforms in the distant future. However, bacterial evolution appears to be rather "limited". Bacteria are the essence of an efficient lifeform: they are small, infinitely populous, rapidly reproducing, and everywhere. Their simple genome and structure allows them the luxury of something as impressive as "genetic lateral transfer", where bacteria can literally integrate a completely distinct piece of genetic information into their own genome and rapidly pivot ecological strategies. This allows very closely related species of bacteria to demonstrate dramatically different metabolisms, for example; one species could respire oxygen, another could perform nitrification, and another could be methanogenic, which absolutely is a level of dramatic diversity not seen even when comparing eukaryotes at two different ends of their kingdom.

However, this simplicity comes with its own detriments. Unlike eukaryotes, prokaryotes are unable to make huge leaps in size and morphological complexity - in fact, bacteria are evolutionarily-pressured to remain both miniscule and simple. There are two forms of bacterial competition: a "scramble" and a "contest". Scramble competition involves strategies which seek to uptake a resource as rapidly as possible: for example, increasing the intake of compounds means you can take up more resources more quickly, and increasing rate of reproduction means you can more rapidly conquer a specific resource. Contest competition is much more antagonistic, where bacteria attempt to somehow inhibit another organism from gathering resources. This oftentimes takes the form of ejecting toxins which either somehow reduces another species' uptake of resources (slowing down metabolism or membrane intake) or outright poisons another cell.

While "contest" competition is utilized by bacteria - prokaryotes have "mastered" the use of toxins - "scramble" competition is absolutely the most important factor in bacterial competition. And more specifically, reproduction rates are absolutely the most viable weapon in the "scramble" competition toolkit. **Reproductive cost** is an incredibly important determinant for bacterial success, and an incredibly decisive strategy behind prokaryotic evolution is reducing said reproductive cost. This has various implications…

1. Bacteria do not like size. Volume increases much more rapidly than surface area does as a lifeform grows, and since volume does not intake resources from the environment, an increase in volume does not necessarily mean an increase in energy. As a result, too much size means diminishing returns on energy (ATP generation), which is needed to successfully reproduce and thus increases reproductive cost.
2. Bacteria do not like complexity. Complexity, even that which results from more efficient methods of energy generation, results in a bigger genome, which means more genetic material needs to be processed, which means a higher reproductive cost. Unless an adaptation results in an astronomically high amount of net-energy produced - which is unlikely given evolution's iterative nature - a bacteria likely wouldn't risk evolving a complex morphology and getting beat out by a competitor who reproduces fast.

As such, prokaryotic evolution inherently favors - in fact, perfected - simplicity, but it rarely evolves complexity unless a very good reason is present. Of course, evolutionary success isn't necessarily defined by population numbers, but a larger population indicates a much greater degree of genetic diversity, even in asexual cells. As such, bacteria would universally heavily value reduced reproductive rates, and thus, very simplified genetic material. And this is the reason why, despite perhaps 4 billion years of evolutionary history and an unfathomable diversity of species, the vast majority of prokaryotes look incredibly similar. As a result, interspecific prokaryotic interactions are rather indirect and simple. The concept of a predator, prey, grazer, etc. became much more prominent with eukaryotes. In nature, prokaryotic competition is essentially rapidly taking advantage of the presence of an important resource *before* your competition can.

Endosymbiosis and Its Fallout

Eventually however, the "prokaryote rule of simplicity" was broken. Remember implication #2 from above, mentioning a theoretical yet highly improbable adaptation which generates enough energy to warrant increased reproductive costs? That adaptation was endosymbiosis - more specifically, the evolution of a fully-integrated mitochondria. Certain prokaryotes eventually evolved relatively complex membranes which allowed for the phagocytosis of other cells. Endosymbiosis likely advented as an error at first, but as it became slightly more common in the few species of prokaryotes which used it, certain prey items began actively adapting to take advantage of it. Just as parasitic animals are incredibly simple because of a more stable environment (the host's insides), an "endosymbiont" (the integrated cell) would be incredibly simple, as no environment is as hospitable for a cell as the inside of another cell. In the pursuit of reduced reproductive costs, endosymbionts would discard all unnecessary genetic material, coding for complex equilibrium-balancing membranes, now unnecessary regulatory proteins, and the other “expenses” which follows a cell. What would be left after a while is, essentially, the energy-production of a cell without any of the energy costs, and with an incredibly small amount of genetic material.

This relationship would eventually evolve from commensalism to mutualism. For the endosymbiont, the death of the host cell would absolutely mean horrible things - the loss of a safe environment, and exposure to an absolutely hostile environment which would likely result in very rapid death. As such, these endosymbionts actually benefited from sharing their incredibly potent energy generation potential with the host. Lateral genetic transfer occurred rapidly between the host and the endosymbiont due to the endosymbiont’s intimate connection within the larger cell, and full reproductive-integration occurred. Hence, the birth of the mitochondria - an entire cell’s worth of energy with barely a fraction of an entire cell’s added genetic material. The added energy was so tremendous in scale, that it absolutely shattered the size and complexity constraints which prokaryotes faced.

In addition, during the transfer of genetic material between the endosymbiont and the host, an additional organelle with transformative implications emerged. In a few cases, the endosymbiont would transfer instructions for producing lipid membranes to the host, potentially resulting in the creation of lipid membranes within the host cell itself. While surely catastrophic for the structural integrity of some cells, for others, this membrane would go on to surround the genetic material of the entire host, protecting from potential genetic parasites and other undesirable illnesses. And while this made lateral genetic transfer as seen in prokaryotes harder to achieve, this added layer of security minimized the risk of intrusion from an external virus, allowing genomes to increase in size without an added risk of being hijacked. This lipid membrane would eventually evolve into the nucleus - and hence, the birth of eukaryotes, perhaps somewhere as early as around 2.7 billion years ago.

Despite being heavily outpaced in reproduction rate by simple prokaryotes, due to increased size and morphological complexity, eukaryotes immediately benefited from their complexity enough to stake out a unique niche in the environment. While prokaryotes were bound to simple networks of interspecific competition and nutrient uptake, eukaryotes were able to completely shift the balance of power in their local food webs, having the size and ability to uptake large concentrations of resources, and even other cells. As eukaryotes diversified and filled out this role further, additional layers in the food chain began to be filled; the predators had predators, and those predators had predators. It would take a while for eukaryotes to become prominent. Initial populations were low, as it is likely that the pre-mitochondrian prokaryote had larger reproductive costs and the fact that all eukaryotes emerge from a single common ancestor points to an initially small population.

Oxygenation and Other Inflection Points

In the meantime, Earth's larger biogeochemical phenomena were beginning to fully establish themselves around 3 billion years ago. The nitrogen cycle, heavily mediated by microbes, formed as a result of the shifting supply of freely accessible nitrogen in cellular environments, and the sulfur cycle was one of the first to begin its process of maturation. Tectonic plates began to assume some semblance of significance sometime around 3 billion years ago, resulting in a proliferation of geological processes. This geological activity would become essential to the build up of substantial oxygen in the atmosphere. As natural reservoirs of materials which reacted with oxygen, such as surface-level iron deposits, began to be used up, and as the planet's crust would begin to recycle itself through plate tectonics, conditions were ripe for massive atmospheric change. Somewhere around 2.2 billion years ago, oxygen produced from photosynthesis began to build up enough to start showing in the fossil record. Although still present at an insignificant level compared to the modern atmosphere (around 2% of the atmosphere), this development had massive implications for metabolic strategies on Earth. When utilized properly, oxygen essentially can result in a controlled combustion of food items, and thus, huge amounts of energy. Once aerobic respiration evolved, organisms supercharged their metabolisms, which played especially in the hand for eukaryotes.

Around the same time, the first (as far as we know) of a unique total-planet glaciation period known as "snowball Earth" occurred. Although causality has not effectively been proven, glaciation periods appear to correspond with the various significant oxygenation events in Earth's history - it is theorized that the presence of oxygen might push out greenhouse gases, such as methane. Regardless, anywhere from 2.4 billion to 2.1 billion years ago, the Earth's surface was either completely or almost completely covered with ice. These periods of time would last for a relatively short amount of geological time, potentially around 50 million years for the all-encompassing ice sheets to melt. In the wake of each period of heavy glaciation, heavy runoffs from land supplied high amounts of phosphate and accessible nitrogen to life. This, coupled with newly open ecological space, allowed for the rapid restructuring of ecosystems, and provided new opportunities for life.

The Prelude to Complexity

The period of time from 2 billion years ago to 1 billion years ago is oftentimes referred to as the “Boring Billion” due to geological stability and a relatively low rate of evolution. Looking deeper however, it is around this time that eukaryotes began to solidify themselves as potent evolutionary competitors. Although oxygen still wasn’t very present in the atmosphere - perhaps even dipping a bit - enough was present to allow the advent of more complex organelles. In fact, various experiments with multicellularity originated at this point of history, with incredibly dubious fossil remains dating from 2 billion years ago - the Francevillian biota - representing a very surprising debut of multicellular life. Although these biota likely died out, and although complex multicellular life wouldn’t really take off until atleast around 700 million years ago, rising oxygen levels resulted in a proliferation of eukaryotic capabilities. Multicellularity has been theorized to originate from multiple sources - in other words, multicellular organisms don’t all come from the same multicellular ancestor.

Regardless, Earth’s systems, and life, began to mature around 1.5 billion years ago. And as oxygen levels rose throughout the next billion years, complex life began to take shape.

A Question: How Close to Earth Should the Average Thrivian Planet Be?

An important question to address is how similar we want the average playthrough’s history to be to Earth’s evolutionary history. There are two prominent sides to this question…

1. Earth’s evolutionary history is, definitively, Thrive’s standard for scientific-accuracy. Our entire understanding of evolution is based on what we observe on Earth, so straying from what we see on Earth can carry with it risks of Thrive becoming a bit less accurate than what is hoped for.
2. Alien evolution is, ultimately, alien, and it can be somewhat arrogant of us to assume that all potential alien life would have an evolutionary story similar to that of Earth. By being too prudish and conservative in the leeway we give ourselves by straying away from Earth’s chronology, we could potentially be limiting creativity and replayability.

What evolutionary traits and stories will we assume to be universal in Thrive?