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The Behemoth of the Last Ice Age: The Evolutionary Saga of the Columbian Mammoth in North America

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The history of Earth is a saga that spans 4.567 billion years. An incomprehensible number compared to the limited time humanity has existed on the planet, which is a meager 300,000 years. Earth is an ever-changing system that underwent significant changes in its geologic and biologic history that is now preserved in the rock record and through fossils of ancient life, which reveal glimpses into the past. However, the pages of the storybook of Earth as presented in these rocks and fossils allows humanity to visualize the ancient Earth, millions of years before the evolution of humans, and it exposes a wonderful diversity of organisms, most of which are now extinct. These long-gone organisms continue to excite the imagination, from the other worldly animals during the Cambrian Period, the giant cockroaches and giant dragonflies which roamed the Carboniferous world, the dinosaurs of the Mesozoic, which have forever influenced many young scientists because of their portrayal in popular culture, all the way to the behemoth mammoths that walked the Earth during the last Ice Age of the Pleistocene. It is no wonder that some scientists devote their time to study these past animals and learn how they survived the ever-changing conditions of Earth. One animal that is worthy of further study is the Columbian Mammoth, *Mammuthus columbi* is its scientific name. The evolution of *M. columbi* can be tracked by following along its classification in the tree of life:

Domain: Eukarya

Kingdom: Animalia

Phylum: Chordata

Class: Mammalia

Order: Proboscidea

Family: Elephantidae

Genus: *Mammuthus*

Species: *Mammuthus columbi*

As the geologic and biologic history of Earth is intertwined, following the divergence in classification of the Columbian mammoth presents the long saga of the dynamic history of Earth, and the evolution of life.

The story of *M. columbi* begins in the domain Eukarya, as its cells contain a nucleus separating the DNA from the rest of the cell. It is placed within the kingdom Animalia and within the phylum Chordata, as it possesses a vertebrate or a backbone, an identifier for an organism's body form. Mammoths gave birth to live young, a keen identifier for placental mammals, thus mammoths are classified to the class Mammalia. Continuing down its classification, *M. columbi* is placed within the order Proboscidea, large mammals that also include the elephant family, and is additionally placed within the family Elephantidae. Finally its genus and species are determined from its scientific name. It is clumped within the genus *Mammuthus*, along with other mammoths, however it is important to note that with slight exceptions, only members of the same species are able to breed and produce fertile offspring, thus the species *M. columbi* is only able to breed with members of the same species, separating it from other mammoth species. As the biological and geologic history of the Earth is intertwined, the study of the evolutionary history of the Columbian mammoth establishes an excellent view of the history of evolution of life on Earth and the geologic events that led to the formation of present-day North America where *M. columbi* fossils are abundant.

To understand the full evolution leading to the Columbian mammoth, it is important to trace back to the root of life itself. The story of the origin of life starts in the Precambrian period, which contains roughly 88% of the Earth's existence (Reis and Evelyn, 2021). Yet, despite the Earth spending much of its history in this time period, there is only a minuscule amount of geologic and fossil evidence preserved for this period of Earth's history. One theory establishes that life evolved during the Archean eon, possibly as early as 3.8 billion years ago, from inorganic material in a process known as abiogenesis, which occurred near hydrothermal vents or submarine volcanoes (Dodd et al., 2017). Hydrothermal vents release nutrients to the oceans which these early life forms could harness for energy. Consequently, in support of this proposed theory, Stanley Miller and Harold Urey conducted an experiment in 1952 that resulted in the creation of amino acids, the building blocks to proteins, in a closed system replicating the primordial conditions of Earth's early atmosphere and oceans (Koppes, 2022). Proteins are central to life, as it is an important component in cells. The first verifiable signs of life however would occur 300 million years later, about 3.5 billion years ago, still in the Archean eon (Prothero, 2021). Another theory, known as Panspemia, theorizes that life was seeded on Earth from meteorites, which carried microscopic biotic material (Prothero, 2021) is still debated, while abiogenesis is more accepted with current scientific thinking. Regardless of where and why life originated, there is a pattern that these early life forms were microscopic and prokaryotic bacteria, meaning single-celled and lacking a nucleus; quite different from the gigantic mammoths and other life forms with many different cells seen later in time. One thing is clear that once life originated, the process of evolution began and has since continued to present time and will continue on into the future as life continues to remain on Earth.

With the early prokaryotic life forms present in the Archean eon, the next step of the evolutionary chain toward the evolution of *M. columbi* is the split of the domains of life. Every organism with a nucleus regardless of being single or multi-celled belongs in the domain Eukarya. The appearance of the green algae fossil *Grypania* in the Paleoproterozoic, about 2.1 billion years ago, provides evidence for early eukaryotes (Prothero, 2021). *Grypania* fossils also reveal much of the environmental conditions of Earth during the Paleoproterozoic as it establishes the understanding for the photosynthesis release of oxygen into the early atmosphere (Sharma and Shukla, 2009). This was a step that environmental conditions in the early Earth were slowly becoming tolerable for the evolution of oxygen-breathing organisms. The next step in evolutionary innovation in the history of life didn't occur until the near-end of the Neoproterozoic during the Ediacaran period, where the first evidence of metazoans, comprising the kingdom Animalia, appears in the rock record roughly 635 million to 541 million years ago (Prothero, 2021). Notice that the time when life is thought to originate is about 3.8 billion to 3.5 billion years; that is over 3 billion years of Earth history that had since passed before the first verifiable appearance of animal life. The fossils of the Ediacaran fauna were first cataloged on the continent of Australia and within them included *Dickinsonia,* fossils which paleontologists described as mobile, marine, benthic animals (Ivantsov and Zakrevskaya, 2023). Indicating the appearance of the first animals moving around on the seafloor.

The Precambrian transitioned to the Paleozoic era, with the first division of time called the Cambrian period. During the Cambrian period, at roughly 541 million years ago, a revolution was underway that forever changed the lackluster variety of life in the Precambrian and kickstarted the rapid evolutionary arms race between predator and prey. The transition from the Precambrian to the Paleozoic era started with an explosion, an explosion in the variety of life that occurred in a short time frame in terms of geologic time, within a few million years. This involves the appearance of hard body parts in animals, which allows for better preservation. The further one goes back in time, the sparser the record, because life was all soft-bodied and fewer fossiliferous units are preserved (Schopft, 2021). The Cambrian period marks a time for the evolutionary radiation of nearly every Phyla of life in existence today, except for the invertebrate Bryozoans which occurred in the Ordovician (Prothero, 2021). As the Columbian mammoth is a vertebrate, its vertebrate origins can be traced back to the Cambrian with a tiny organism known as *Pikaia*, which was fund in the Burgess Shale lagerstätten within the Canadian Rockies in British Columbia, Canada (Prothero, 2021). The *Pikaia* fossils are of great importance as it noticeable exhibits the development of a notochord (Morris and Caron, 2012). A notochord was an evolutionary precursor to a vertebrate backbone, and signifies the beginnings of the phylum Chordata. The chordates continued to evolve later in the Paleozoic, with the appearance of the agnathans or jawless fish in the Ordovician around 485 million years ago (Prothero, 2021). These jawless fish were precursors of jawed vertebrates (Gai, et al., 2011) as jawed fish would appear one geologic time period later, in the Silurian about 445 million years ago (Prothero, 2021). It is worth noting that these jawless fish still survive today, represented by lampreys and hagfish found in the northern Atlantic Ocean and the northern Pacific Ocean respectively. Transitioning into the Devonian which spans roughly 60 million years from 419 to 358 million years ago, and is known as the Age of Fishes, the next evolutionary marvel occurred, with the appearance of the Osteichthyans, better known as bony fish. Through the modification of gill arches, fishes evolved the ability to have hinged jaws for opening and closing of the mouth later followed by equipping those jaws with teeth (Doeland et al., 2019). Teeth assisted in hunting prey and digesting food, an advantageous evolutionary development (Prothero, 2021). A group of bony fish, known as the Sarcopterygians, or lobe-finned fish, had club-shaped fins similar to modern arm bones. This lineage would later give rise to the tetrapods, or four-footed animals, that would rise from the sea and walk on land (Prothero, 2021).

The transition of the marine-based vertebrates to land tetrapods, also occurs in the Devonian with the fossils of a transitional species known as *Tiktaalik*, showing noticeable forelimbs, primitive fingers, wrist bones, and shoulder bones (Prothero, 2021). *Tiktaalik* was found in rocks on Ellesmere Island in Nunavut, Canada and it was clear that this animal had adapted to live moving around on land as well as in water, showcasing similar characteristics to modern amphibians (Carlton, 2019). Tetrapods would later diverge into amphibians and amniotes in the Carboniferous (Prothero, 2021). Amniotes are animals that lay eggs on land; the eggs form a hard outside layer during their development, which was significant for vertebrates to escape them being bounded within the confines of water (Sander, 2012). In addition, amniotes exhibit parental care behavior (Botha-Brink, 2007), nurturing their young to improve their chances of survival as seen in extant groups including all mammals and crocodiles. These organisms are now able to traverse and exploit niches in dry land as seen within the Carboniferous fossil record, the time period ranging from 359 to 299 million years ago. Amniotes are further divided into two categories, both of which are still extant today, the synapsids and the diapsids (Prothero, 2021). Among these, the Columbian mammoth would arise from the synapsid line which would later give rise to the proto-mammals and then later again to true mammals. Synapsids are identified by having one skull opening behind the eye socket, called a temporal fenestra (Prothero, 2021). Interestingly, humans are also descended from the synapsids. As the looming threat of Earth's greatest mass extinction threatened the Paleozoic fauna at the end of the Permian, 252 million years ago, the synapsids continued to dominate the landscape (Prothero, 2021). Pelycosaurs, which are often mistaken for dinosaurs, roamed the land at this time with their distinctive finback sails. Before their impending doom during the mass extinction event, pelycosaur groups were experimenting with different lifestyles are some of these these lizard-like animals were seemingly arboreal (Spindler et al., 2018), this adaptation would again arise in later mammalian radiations in the Cenozoic. From the pelycosaurs came the therapsids that would evolve in the Permian and see its descendants survive the end Permian extinction and push forward into the Triassic but not without a price. The end of the Permian witnessed the greatest mass extinction recorded in Earth's history wiping out 75% of the land vertebrates including the once dominant synapsids, relegating them in the ecological minority and creating new niches that would be occupied in the Mesozoic Era by the mighty dinosaurs. The main driver of this extinction was associated with a pulse of global warming (Cui and Kamp, 2015). Warming was due to the volcanic outgassing of carbon dioxide and other greenhouse gases from the flood basalt event of the Siberian Traps, which encompassed over 7 million km^2 or 3 million square miles in the Siberian region of Russia (Prothero, 2021). The price the therapsids had to pay for surviving the greatest mass extinction recorded on Earth was a reduction in body size which imparts a strong influence on ecological, physiological, and the life history of the surviving therapsids (Huttenlocker, 2014). The phenomena known as Lilliput effect, arises when resources are limited and a sign that life was slowly recovering after an extinction event.

The small surviving therapsids of the Triassic period, which ranged from 252 to 201 million years ago, are best represented by the disaster taxa *Lystrosaurus* and then spread out across the unified landmass Pangaea where their fossil evidence is present in Africa, India, and

Antarctica (Prothero, 2021). Today, these continents are noticeably disconnected from each other, so the fossil remains of *Lystrosaurus* have served as evidence used to reconstruct the long past supercontinent of Pangaea. By the Late Triassic, true mammals had evolved, around 210 million years ago, however unlike any mammals today, the mammals of the Triassic laid eggs and are known as the monotremes (Prothero, 2021). This lineage is still extant today, with the platypus and echidna serving as examples of egg-laying mammals. Monotremes are a step to the evolution of ecological adaptations (Zhou et al., 2021) that would ultimately result in the evolution of the Columbian mammoth millions of years after the monotremes' first appearance. Popular culture portrays the Jurassic Period as dominated by the dinosaurs, but the Jurassic also witnessed an important evolutionary development of mammals. This critical event in mammalian history (Luo et al., 2011) is when mammals split into the lineages of the placentals, or mammals with a placenta which birth live young, which includes mammoths as well as humans, and the marsupials, or pouched mammals (Luo et al., 2011). Fossils of *Juramaia* reinforce this concept as *Juramaia* is thought to be the earliest ancestor of true placental mammals (Wang et al., 2022). Mammal evolution during the Jurassic remained as small-bodied forms in order to remain hidden from the large and abundant carnivorous dinosaurs looking for their next meal Due to these ground-dwelling adaptations, mammals evolved improved jaws, teeth, and ears in order to adapt to the changing environments of the Jurassic (Prothero, 2021). Again, *Juramaia* serves as an indicator of this environmental pressure as placentals experienced very high rates of evolutionary radiations (King and Beck, 2020). This would make sense as the egg-laying monotremes would be vulnerable compared to the placentals which gave live birth, eliminating the egg stage in the life cycle in favor a live young ensured better chances of survival and subsequently, an increase in the chance to maturity into adulthood allowing the placentals to reproduce and propagate the next generation.

The dinosaurs went out with a bang, as an asteroid impact resulted in an extinction event known as the K-Pg extinction that wiped out the non-avian dinosaurs 66 million years ago, leaving behind the remnants of a hidden crater near the Gulf of Mexico, known as the Chicxulub Crater. The 160 million year dominance of the dinosaur had come to an end, leaving many new niches in the environment now open. The small mammals found themselves in a world of little to no predators. Throughout the Cenozoic era, which spans the time from 66 million years ago to the present-day, mammals would evolve to exploit new niches, resulting in the adaptive radiation of many new mammalian groups (Prothero, 2021). While most remained on land, some returned to the oceans, and some developed flight and took to the skies. The reign of the mammals had begun. As the Columbian mammoth nears its entrance in the story of life, its ancestral lineage can now be traced back in order Proboscidea which evolved during the the early Eocene epoch about 55 million years ago (Liu et al., 2008). Proboscideans became keystone megaherbivores in the Cenozoic terrestrial ecosystems and became some of the largest species of mammals to exist so far in Earth's history (Cantalapiedra et al., 2021). One key characteristic of the Proboscideans is their increase in size, which is a similar evolutionary trend that occurred for the sauropod dinosaurs during the Jurassic. Gigantism of animals occurs as a response to the environmental pressures as is an ecologically important trait associated with competitive superiority (Vermeij, 2016) an example of how a mammal has overtaken a niche which the long-necked dinosaurs previously dominated. Though most Proboscideans have a noticeable increase in size, there are exceptions to this rule as there is evidence of dwarfism in the fossil record of mammoths on isolated islands, exemplified by the Pygmy mammoth fossils found in the Channel Islands off the coast of California (Agenbroad, 2012). The Proboscideans that remained isolated on an island may have suffered from insular dwarfism, a reduction in the size of large animals due to being confined in a small environment with limited resources forcing the larger-bodied mammals to adapt (Htun, 2020), similar to the Lilliput effect observed during the recovery after a mass extinction. Going forward into the Cenozoic, a further split occurred resulting in the Family Elephantidae to have evolved by the Late Miocene 9-10 million years ago (Prothero, 2021). The earliest Elephantidae fossils found in Nakalia, Kenya contain shared derived features with later elephantids (Saegusa et al., 2014) with teeth fossils tracking evolutionary changes within the genera and species (Baigusheva et al., 2016) as it serves as proxy to the type of diet the animals followed and the paleoenvironment of the Neogene. The genus *Mammuthus* likely diverged during the Late Miocene, about 6 million years ago represented by the African fossils *Mammuthus subplanifrons*. *M. subplanifrons* were considered generalists as they spent more time in open habitats and were dietary flexible (Groenewald, 2020) allowing *M. subplanifrons* to survive in diverse environmental conditions and disperse from the African continent and diversify throughout Europe and Asia (Prothero, 2021).

Finally, after roughly 4.4 billion years since the formation of the Earth, the Columbian mammoth, the behemoths of the last ice age, enters the story of life around 1.5 million years ago arriving in North America by crossing the Beringia land bridge, which was an area of land that connected Siberia to Alaska when sea level was much lower during the ice ages of the Pleistocene and dispersed throughout North America (Prothero, 2021). Arriving from Eurasia, the prevailing view of these early American mammoths were of primitive morphology (Lister and Sher, 2015) still adapting to the environmental conditions of North America during the Pleistocene ice age. Dispersal of *M. columbi* would eventually lead to its geographic occurrence extending south of Mexico, and the northernmost limit aligning parallel somewhere between the present-day United States-Canada border. An unfortunate fate awaits the Columbian mammoth, as the species would become extinct by 12,000 years ago, joining 99.9% of all species that have existed within Earth in extinction (Walther et al., 2015). It is exciting to know that the Columbian mammoths existed at the same time as humans, however this timely coincidence may have contributed to its decline and resulted in its extinction due to extensive hunting (Klapman and Capaldi, 2019). While the cause of the extinction is an ongoing debate, factors including environmental change and human activity likely contribute to the demise of the species. The Columbian mammoth serves as an example of the perils of life and the indifference of evolution, favoring the survival of organisms that are best adapted to its environment. With the mammoths long gone, it is now memorialized as grand displays in museums leaving humanity in awe of the marvel of the evolution of life.

As the biological and geologic histories are intertwined, the North American continent had to be assembled before the Columbian mammoth's arrival. Tracing back again all the way to the Archean where the Earth's crustal material begins to be preserved and plate tectonics, the movement of the continents is widely considered to have emerged (Brown et al., 2020). Three- to four-billion year old Archean rocks make up the core of North America, and are some of the oldest rocks preserved on the planet.These assemblages are found through central to eastern Canada in the United States, with the Acasta Gneiss found in the Northwest Territories of Canada (Prothero, 2021). The Columbian mammoth is mostly a western North American species, therefore the geologic history of the West is brought into focus. Western exposures of Precambrian rocks, which also consists the North American core, are few, but there are some exposed along the East Humboldt Range in Nevada (Lush et al., 1998). Western North American rocks are mostly younger, being deposited during the Paleozoic, when the area along the western margin of the core was covered by oceans and experiencing sedimentation, with intervening mountain building events that attach crustal material onto the North American core. The first period of the Paleozoic, the Cambrian preserves the Sauk transgression, which was a period of heightened sea levels that surged waters onto the North American core. These rocks are represented by what is referred to as "the carbonate factory" which are characteristic carbonate deposits formed in shallow tropical oceans, similar to the Caribbean Sea today (Prothero, 2021). Shallow ocean conditions persisted through the Ordovician and Silurian, roughly 200 million years of time, which resulted in the thick limestone deposits that are now exposed at the peaks of most mountain ranges throughout Nevada. This lengthy residence time for an ocean covering the West is due to a passive margin, a region of tectonic quiescence (Howley et al., 2010). This was a vastly different view from the active margin present in the West today, where the North American plate meets the Pacific plate resulting in subduction and volcanism. Tectonic quiescence persisted up until the Late Devonian when mountain building began and Paleozoic sediments were uplifted, folded, and faulted (Donkervoot, 2023), signifying the start of the Antler orogeny which continued during the Mississippian. The Antler orogeny was a widespread orogenic event, where crustal material spanning southwest Canada, eastern Idaho, central Nevada, and into eastern California was tacked onto the North American craton (Duncan, 2022). The Antler orogeny was followed by another pulse of uplift, called the Sonoma orogeny which took place during the Permian period, and marked by more crustal material sutured to North America along with volcanism. The building of the mountains and the draining of the ocean resulted in erosional unconformities, periods of missing time, in the late Paleozoic rock record evident throughout the Nevadan basins (Leary et al., 2021).

The Mesozoic was a time marked by continued subduction along western North America. The Sonoma orogeny concluded by the Early Triassic, and the oceans drained away, never the cover the West again (Price et al., 1999). During the Jurassic, sand was deposited in a massive sand desert known as an erg that stretched across the West, from Nevada up to Montana. The sand was supplied to this part of the continent from the erosion of the Appalachian highlands in the east. These sandstone formations are geologically known as the Aztec Sandstone and make up the brilliant red sandstones at Valley of Fire State Park (Price et al., 1999). All the while, subduction continues along the western margin and the Late Jurassic would mark the beginning of another mountain building event, the Nevadan orogeny, this one is credited with the formation of the ancestral Sierra Nevada Range. The Laramide orogeny would follow in the Cretaceous, forming the ancestral Rocky Mountains. It was through this series of mountain building events that the North American West formed.

While the Paleozoic and Mesozoic eras were building the West. The geologic history of the Cenozoic era is dominated by pulling it apart. Extensional stress caused the stretching of the crust and faulted it apart to produce the Basin and Range topography with highlands or horst and grabens or valleys littering the landscape (Price et al., 1999). The transition from subduction to extension was accomplished as the Farallon Pacific plate began sliding past the western margin of North America, forming the San Andreas fault line. This change in motion was what initiated the stretching of the Basin and Range roughly 17 million years ago. Subduction beneath the continent reduced to just the Pacific Northwest, up through Canada, and Alaska, which is responsible for earthquakes and volcanism along that margin. During the Pleistocene, roughly 2 million years ago, was the time of the last ice ages, mountain glaciers covered the caps of northern Nevada's mountains, while southern rangers were covered in thick deposits of snow.

The copious amount of precipitation during the last Ice Age and the melting of the snow and ice accumulated into vast lake systems within the basins of the Basin and Range. One example is Lake Bonneville, a large lake system that stretched across much of the state of Utah, whose remnants are now concentrated into what is today the Great Salt Lake. With ice covering much of land, the ocean levels lowered, forming corridors of land connections and allowing life to pass through. To the north, the Beringia land bridge was exposed connecting Siberia to Alaska (Prothero, 2021) and facilitating the faunal exchange resulting in the evolutionary precursors of the Columbian mammoth crossing the continents and evolving in North America.

The proboscidea lineage evolved in Africa, including the precursor species of the Columbian mammoth. This ancestral form dispersed out of Africa. Some species remained in Africa as evident by the modern African elephant that lives there today. The lineage that migrated away found their way into Europe and Asia, the latter is where some remained, as evident by the modern Asian elephant. During the last ice age, lowered sea level exposed a large area of the crust (Prothero, 2021), the Beringia land bridge where megafauna such as an ancestor mammoth species, called *Mammuthus subplanifrons*, was able to cross the Asian continent and migrate to North America. As ice sheets melted and sea level increased, the Beingia land bridge retreated under the sea, and has been lost to time. Upon arriving in North America, *M. subplanifrons*, diverged into two separate species: the wooly mammoth, *Mammuthus primigenius*, which inhabited the northern latitudes of North America, and the Columbian mammoth, *M. columbi*, which would reside in the southern latitude of North America. *M. columbi* continued to disperse to the south, all the way down to central Mexico. Areas such as Tule Springs in the Las Vegas Valley, were prime environmental habitats for Columbian mammoths to thrive during the last ice age (Springer et al., 2018). The marshy wetland setting and lush vegetation was a draw for the Columbian mammoth and they gathered by the herds as they continued their migration throughout the North American West. Today, Columbian mammoth fossils are found in abundance at Tule Springs Fossil Beds. The Pleistocene landscape has considerably changed as time progressed into the Holocene. The climate warmed, the snow melted, the water dried up, and the Columbian mammoth was no more (Prothero, 2021).

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