

The Age of Grasses has Recently Doubled to 113 Million Years

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Three recent studies have discovered grass microfossils from the Cretaceous that have doubled the age of ancestral grasses. The evolutionary development of the grasses is still poorly understood. Grass plant fossilization rates are extremely low. For a geologic time scale of the Cretaceous period and Cenozoic era, see table 1. The oldest unequivocal grass macrofossils are from the Paleocene-Eocene boundary, 56 Ma (million years ago), from the Wilcox Formation in western Tennessee (Kellogg 2001, Poinar 2004, Piperno and Sues 2005). Fossil grass pollen is a little older and relatively more abundant. Grass pollen is distinctive with nearly spherical shape that has a single pore and has minute channels or holes that penetrate the outer wall, but not the inner wall, unfortunately, pollen is only diagnostic to the family level, Poaceae, and the oldest known is from the Paleocene, 66-56 Ma (Kellogg 2001). Before 2005, by default, the origin of grasses had been designated to be no older than the Cenozoic era and no one suspected that herbivorous dinosaurs ate grass. Perplexingly, by the Early Cenozoic the known grasses were relatively well developed and most likely had to have much older ancestors.

Cretaceous Grass Microfossils

During the past two decades, three astonishing paleontological studies have discovered grass microfossils that have doubled the age of fossil grasses, from the Cenozoic, 56 Ma, all the way back to the Cretaceous, 113 Ma. These three groups of resourceful scientists have been able to collect and identify microscopic grass phytoliths and segments of leaf epidermis from Cretaceous deposits.

The first paleontological study was from India, Prasad et al. (2005, 2011), with a group of ten scientists, described grass phytoliths extracted from coprolites (fossilized feces) ascribed to titanosaur sauropods and segments of fossil grass epidermis from related matrix sediments, from the Maastrichtian age, 67-65 Ma, Late Cretaceous, Gondwana, recovered from the Lameta Formation consisting of alluvial to limnic sediments associated with the Deccan Traps (Southern Stairs) Volcanics in central India. Eight new grass species were named from the wide diversity of described diagnostic phytolith morphotypes. For a list of grass subfamilies, see table 2. The authors ascribed four new species to subfamilies as follows: Subfamily Puelioidae, *Pipernoia pearsalla*; Subfamily Oryzoideae, *Matleyite indium*; Subfamily Bambusoideae, *Vonhueneites papillosum*; Subfamily Pooideae, *Chitaleya deccana*; and ascribing subfamily to four of the other new species was ambiguous because the phytolith morphologies overlapped with other more modern subfamilies. Two new grass species were named from epidermal cell structure and 3-D embedded grass silica short cell (GSSC) phytoliths. The authors ascribed these two species to one subfamily as follows: Subfamily Oryzoideae, *Changii indicum*, and *Tateokai deccana*. This study documented that titanosaur sauropods, the prominent terrestrial plant eater in Gondwana, consumed grass as part of their diet. The wide diversity of diagnostic phytoliths in this study represented samples from later diverging poaceae taxa (not primitive enough to be from ancestral taxa) that had emerged and may have spread across Gondwana before 80 Ma, which would be much earlier than previously thought, and the dispersion may have been affected by the interactions of herbivorous dinosaurs.

The second paleontological study was from Myanmar, Poinar (2004, 2011) described a grass spikelet and a leaf fragment with silica bodies (phytoliths) and Poinar et al. (2015), with a group of three scientists, described an ergot sclerotia infecting a grass floret; all three separate specimens were embedded in Burmese amber from a resin-producing araucarian tree growing in a tropical-subtropical forested area from Upper Albian, 110-100 Ma, late Early Cretaceous, on the Burma Plate of Laurasia, occurring in deposits of lignitic seams in sandstone-limestone and mined from the Summit Site in the Hukawng Valley, southwest of Maingkhwan in the state of Kachin, Myanmar. The primitive spikelet was laterally compressed, had two basal sterile glumes, a series of six lemmas and one observed palea, and the remains of three stamen (male parts) and a gynoeccium (female parts). The lemma had several domed papillae (bumps of unpointed prickles). Adjacent to the spikelet were several spherical, monoporate pollen grains, which are diagnostic grass family characteristics. The spikelet was given the new grass name of

Programinis burmitis. The grass leaf fragment epidermis contained stomata with guard cells, rows of long and short cells, and several domed papillae with the same shape and size as those on the spikelet lemma. The leaf fragment was given the new grass name of *Programinis laminates*. The author (2004) suggested that the primitive characteristics of the spikelet and leaf fragment and the occurrence in tropical forested habitat indicated these fossils to be ancient herbaceous bamboo with affinity to the Subfamily Bambusoideae. The second report (2011) restudied the silica bodies (phytoliths) in the leaf fragment in greater detail under 800X magnification. The silica bodies (phytoliths) were located in columns of short epidermal cells. The silica bodies had nine general unspecialized rondel or elongated quadrate morphotypes that were similar to the phytoliths that occur in grasses from the Subfamilies of Bambusoideae, Panicoideae, Arundinoideae, and Chloridoideae.

The third report (2015) described a second grass floret with two basal glumes and six lemma that had similar primitive characters as the first grass spikelet named *Programinis burmitis*, however, this infected spikelet did not have enough observable characters to assign a new name. The infecting ergot was erect, protruding from and above the grass floret, with black flattened outgrowths composed of thick, branching, intertwining hyphae in the sclerotium. This fossil fungus was morphologically clearly separate from all extant species of Clavicipitaceae. The ergot was given the new fungal name of *Palaeoclaviceps parasiticus*. This study documented that fungal-grass symbioses was occurring during the late Early Cretaceous of Laurasia.

The third paleontological study was from China, Wu, You, and Li (2018), as a group of three scientists, described two silicified epidermal pieces and three slightly bilobate phytoliths of grass fragments extracted from dentition of two maxillary teeth of a basal (beginning) hadrosauroid, *Equijubus normani* (duck billed dinosaur), from the Albian age, 113-101 Ma, late Early Cretaceous of Laurasia, recovered from the Zhonggou Formation of Gongpoquan Basin, Mazongshan area, Gansu Province in north-western China. The two silicified epidermal pieces showed the presence of short cells intervening between long cells which is a basal characteristics shared by Joinvilleaceae (a grass-like ancestral outgroup family that produced berries) (Blackhall-Miles 2016) and Anomochlooideae (the oldest known basal subfamily of true grass), in addition, the epidermal pieces also had short-cell pairs, which first appeared in Anomochlooideae, which means that the Mazongshan specimens are a synapomorphy (an evolutionary trait shared by several species that can be grouped into a clade) of basalmost (oldest) Poaceae, most likely Anomochlooideae. This study documented that hadrosaur dinosaurs consumed grass as part of their diet. The authors suggested that ancestral grasses must have existed before the early Aptian, 125 Ma, and that deep-diverging grasses could have gained broad distribution across both Laurasian and Gondwanan continents, except for North America, during the Barremian, 129-125 Ma, mid Early Cretaceous.

Grass Phytoliths

All three of these astonishing Cretaceous paleontological studies used grass phytolith microfossils as a significant part of their fossil grass identification. Phytoliths (plant-stones) are rigid, microscopic structures made of silica, located mostly in the epidermal plant tissue (Anonymous 2021c).

Plants absorb silica from soil dissolved in groundwater in the form of monosilicic acid, $\text{Si}(\text{OH})_4$. The rate and quantity of silica uptake is genetically controlled by the plant. Silica uptake requires a small expenditure of energy for metabolic active transport by the xylem sap to the epidermal cells and to be laid down as silicon dioxide, SiO_2 , to form the phytoliths. Silica is not an essential nutrient for plants. The most likely function of silica phytoliths is to provide structural rigidity to plants in order to increase light interception and energy manufacture. The energy cost to the plant to incorporate silica phytoliths is only 3.7% of that to incorporate lignin and only 6.7% of the cost to incorporate structural carbohydrates (Shakoor et al. 2015).

All grasses have some phytoliths, upland grasses have very few, and wet meadow grasses (slough hay) have a huge amount, enough to wear down livestock teeth. Early hypothesis suspected the function of phytoliths was to deter herbivory (grazing). Phytoliths can be detected by insects and small mammals and they can avoid high-silica plants, however, medium to large herbivorous mammals cannot differentiate between plants based on phytolith content (Stromberg et al. 2016).

Silicon phytoliths are nearly indestructible, are resistant to oxidation, and are not subject to decay by microorganisms. Phytoliths can survive for millions of years in fossil coprolites, embedded in amber, stuck on herbivorous dinosaur teeth, and in fossil leaf epidermis fragments in deposits of fossil related sediments. Every

sample of grassland soil contains prodigious quantities of microscopic silica phytoliths. In grasses, living and fossil, the numerous different characteristic shapes and sizes of the silica phytoliths are taxonomically diagnostic to the subfamily, tribe, and sometimes to the genus level. Several comprehensive guides of grass phytoliths have been correlated to grass taxon (Piperno and Pearsall 1998). Research paleontologists can use these reference collections of comparative grass phytoliths to aid in the identification of their collected microscopic fossil grass phytoliths. These silicon phytoliths are the key to identifying all additional Cretaceous fossil grasses.

Cretaceous Age for Ancestral Grasses

The ages of the three recently published Cretaceous grass fossil specimens were used by two large groups of phylogenetic scientists (Consortium 2018, Orton et al. 2021) to perform phylogenomic analysis (Anonymous 2022g) of the subfamily Pooideae that changed the divergence date estimation calibration points with the upper bound set at 110 Ma and the lower bound set to the fossil age. Genetic information from plastomes is maternally inherited and less complicated than that from the nucleus which is a mixture of male and female genetics. The divergence data analysis was run on the Bayesian evolutionary analysis sampling trees (BEAST 1.8 and BEAST 2). Pooideae was selected because it is the largest grass subfamily with nearly 4,000 species with a number of economically significant crop, pasture, and lawn grasses that dominate the northern temperate regions. The ages of the PACMAD clade changed from 41-28 Ma to 95.1-32.2 Ma; the BOP clade changed from 50-41 Ma to 100.1-89.8 Ma; and the APP clade changed to 109.9-105.8 Ma. The adjusted ages for the tribes of the Pooideae subfamily are on table 3.

Movement of Tectonic Plates

Plate tectonics changed the environment that affected grass evolution. Gondwana was a large southern continent that included on the west, South America, Africa, and Arabia, and on the east, Madagascar, India, Antarctica, and Australia (Anonymous 2021f). Laurasia was a large northern continent that included North America, Greenland, Europe, Baltica, Siberia, North and South China, and Indochina (Anonymous 2022b). Eastern North America, Spain, and France collided with northeastern Africa around 300 Ma that uplifted the Appalachian and Atlas mountains and folded land in Spain and France (Correia and Murphy 2020). North America and Africa separated in 200 Ma and opened the Central Atlantic Ocean. During most of the Late Cretaceous, North America was divided north to south by the Western Interior Seaway that covered about one third of the continent. The seaway receded following the Laramide orogeny that uplifted the Rocky mountains during a period around 70 Ma. South America and Africa spread from south to north during 190-100 Ma that opened the Southern Atlantic Ocean. Greenland and Norway separated in 57 Ma, which opened the North Atlantic Ocean between Europe and North America (Prothero 2006). Madagascar and India, and Antarctica and Australia separated from Africa around 175 Ma. Australia moving north split from Antarctica moving to the South Pole in 80 Ma. Madagascar and India separated in 68 Ma and caused the eruption of the Deccan basaltic flows that occurred for 800 K years (Anonymous 2022a). India collided with Asia in 50 Ma forming the Himalaya mountains. Western Antarctica separated from southern South America around 33 Ma which opened the Southern Ocean and permitted the cold circumpolar currents to develop causing sea temperature to drop 10°C (18°F) and the global climate became much colder, while Antarctica became frigid and covered with ice. Glacial advances occurred 25-23 Ma on Antarctica (Retallack 2004).

Changes in Cretaceous Vegetation

Vegetation had major changes during the Cretaceous. The flora of early Cretaceous consisted primarily of gymnosperm (naked seed) trees of Cycadaceae (cycad), Ginkgoaceae (ginkgo), Gnetaceae (gnetum), Araucariaceae (araucaria), Podocarpaceae (podocarp), Taxaceae (yew), Cupressaceae (cedar and metasequoia), and ferns Pteridospermales (seed fern), and Polypodioaceae (small understory fern) (Anonymous 2022d, e, f).

Basal angiosperms (flowering plants) originated during the early Jurassic between 198-178 Ma. The evolution of the ancestral line of seed plants and angiosperms is the result of two or three events of whole genome duplication during 319 Ma, 192 Ma, and 160 Ma. The earliest angiosperm macrofossils are from 125 Ma and the oldest reticulated monosulcate (net-veined with one longitudinal groove) pollen are from 140 Ma. During early development, the angiosperms underwent rapid genome downsizing which allowed for faster rates of cell division and smaller cells that facilitated higher rates of leaf gas exchange for photosynthesis and transpiration and faster

rates of growth resulting in a huge competitive advantage (Anonymous 2021d). Rapid diversification and great radiation of angiosperms occurred during mid Cretaceous, 140-100 Ma, coincident with the decline of the previously dominant gymnosperms. Flowering deciduous trees of Lauraceae (laurel and sassafras), Fagaceae (beech and oak), Aceraceae (maple), Magnoliaceae (magnolia), and Moraceae (fig) became dominant along with diversification of Polypodiales (small understory fern).

During the Late Cretaceous most of the earth was warm but only a small part was wet subtropical-tropical rain forests. There were mountains with cooler climates that had light frost. All the continents had northern temperate zones and warm zones with warm temperate between. There were both open and closed habitats. The angiosperm radiation was dominant and moving northward. Dense vegetation of angiosperm trees were along rivers and open habitats of angiosperm shrubs, and herbs with low growing ferns occurring further out. The gymnosperm vegetation had greatly reduced, however, ginkgo and gymnosperm trees persisted in contracting areas along with cycad shrublands. Sequoia, metasequoia, and pinus trees were growing in some northern latitudes (Krassilov 1981, Butler et al. 2009).

Insects diversified during the Cretaceous with early butterflies, moths, wasps, and bees appearing before flowers, grasshoppers appearing before grasslands, ants appearing before picnics, and cockroaches appearing before New York apartments.

Pines Evolve with Fire Regimes

The delayed origin of the *Pinus* genus in the gymnospermae family Pinaceae occurred during the Late Jurassic in 150 Ma. The diversification of the pines overlapped with the evolution and competition of the angiosperms during the Cretaceous and with the change in fire regimes during the Late Cretaceous (Singh et al. 2018).

Deposits of carbon provided evidence of fire as an ecological disturbance driver during the Cretaceous. Fire frequency typically has not been the same for different regions. Fire frequency was determined to be relatively low during the Early Cretaceous when the slow growing gymnosperms were dominant and fire frequency increased during the Late Cretaceous when rapid growing angiosperms were dominant. This change in fire regimes caused the pines to differentiate into two lineages. The fire-adapted pines, subgenus *Diploxylon*, developed in productive environments of temperate and subtropical regions outside of the tropical rain forests and the fire-avoiding pines, subgenus *Haploxylon*, developed in drier and colder regions or other extreme environments with low fire frequency.

The fire-adapted pines, *Diploxylon*, formed three different sets of traits. The fire-tolerator pines have thick bark that protects the cambium from extreme heat, the trees have a tall height and self prune dead branches to reduce crown fires, large quantities of seeds are produced that germinate better in bare soil after a surface fire, seedlings have a long juvenile stage when deep roots are produced and long needles protect the apical buds against fire. The fire-embracing pines retain dead wood of lower branches that promote crown fire that intensify the temperature enough to consume and decimate competing plants which advances postfire regeneration by their serotinous seeds that are delayed because the cones do not open until after a fire. The fire-refugia pines have thick bark that protects the cambium, however, they retain dead branches in the crown and they lack cone serotiny, their stressed environment is fire-prone with relatively high fire frequency, except the fine fuel load is low.

The fire-avoiding pines, *Haploxylon*, occur in stressful environments prone to drought and low available nutrients, they can close stomata at relatively higher water potential and are capable of hydrolytic lift, they have lower nutrient requirements than competing plants, pine needle litter buildup modifies soil by changing the pH, increasing nutrient availability and have allelopathic effects, they produce high quantities of seeds with relatively high germination rates for vigorous regeneration, and they have well developed ectomycorrhizal association that produce enzymes which enable access to organic nitrogen and that transport soil water (Singh et al. 2018).

Stages of Grass Evolution

Evolution of grasses has occurred over an extremely long time. The flowers of grasses evolved by reduction in several steps from plants that had showy flowers and were insect pollinated. Typical grass florets (flowers) are wind pollinated and are composed of reduced structures of an androecium (male parts) of three

stamens each with an anther and filament, and a gynoecium (female parts) of a single chambered ovary with two stigmas at the top for pollen reception, and a pair of lodicules at the base. The androecium and gynoecium organs are covered and protected by hardened internally located palea and an externally located lemma (Anonymous 2021b). At anthesis, the lodicules become turgid (swollen) and force the floret open. If pollen reaches the stigma, each floret has the potential to produce a single fruit which is uniquely a caryopsis (grain). One or more florets are attached to a rachilla (stalk) that is subtended by a pair of glumes (bracts) comprising a spikelet, and one or more spikelets comprise an inflorescence (Stanley 1999, Kellogg 2001).

Reductions of Grass Flowers

All grass relatives are wind pollinated which would mean that insect pollination and sticky pollen were lost before ancestral grasses evolved. Wind pollination of grasses has several problems; wind moves pollen for relatively short distances, the florets are open for a few hours, and the pollen is viable for only a short period. Grass ancestors had six stamens, ovaries of three fused carpels, and a large perianth of petals and sepals. As grass ancestors evolved through numerous steps of reduction, three of the stamens were lost, two of the ovules aborted, and the perianth was greatly reduced with two modified petals becoming the lodicules, and two modified sepals becoming the palea and lemma (Stanley 1999, Kellogg 2001).

Grazing Defense Mechanisms

Two of the three astonishing Cretaceous paleontological studies documented that herbivorous dinosaurs, titanosaurs and hadrosaurs, ate grass plants as part of their diet. These two scientific data points will completely change the previous concepts of how grass evolution occurred. These new data have doubled the grass evolutionary time line back to 110 Ma and placed ancestral grasses at the beginning of the Late Cretaceous when other major changes were occurring world wide. The angiosperms were rapidly developing and radiating.

The extent and abundance of ancestral grasses during the Cretaceous will probably not be known for some time. Coincidental with the rapid radiation of angiosperms and an improvement in available forage quantity and quality during the mid Cretaceous, there was an extensive explosion of new herbivorous dinosaurs. Grasses were most likely not a major portion of the dinosaurs diet during the early stages, but a result of curiosity feeding. Even so, herbivorous dinosaur grazing was an important driver that influenced the development of ancestral grass growth mechanisms. The ancestral grasses would have been subjected to intensified curiosity feeding which would have forced grasses to develop grazing defensive mechanisms. Modern perennial grasses with both C₃ and C₄ photosynthesis in several subfamilies from two clades possess the same four primary defoliation resistance mechanisms. These four mechanisms of improved water use efficiency, compensatory physiological processes, vegetative reproduction by tillering, and nutrient resource uptake competitiveness are activated by partial defoliation by grazing. The development of these resistance mechanisms must have occurred at an early stage of ancestral grass during the association with Cretaceous herbivorous dinosaurs.

The grazing pressure from herbivorous dinosaurs would require ancestral grasses to produce a low growing point below grazing height, to produce double the herbage biomass greater than the leaf area needed for photosynthesis, to develop the structures and hormone systems in order to greatly improve water use efficiency, to develop a complex system for compensatory physiological growth of replacement tissue from basal and intercalary meristem and rejuvenated meristematic tissue that can rapidly assimilate newly fixed carbon and microbial mineral nitrogen into new leaf and stem structures, to develop a highly competitive belowground system with symbiotic endomycorrhizal and ectomycorrhizal fungi for uptake of soil water and nutrients, to produce axillary buds consisting of meristematic tissue and a controlling hormone feedback system for vegetative reproduction of tillers that maintain active growth for two growing seasons with a juvenile vegetative stage and a mature stage for sexual reproduction, and to shed the ability to produce antiherbivory toxic substances (Manske 2018).

Adaptive Mechanisms to Dry Open Conditions

Ancestral grasses to the PACMAD clade and the Pooideae subfamily shifted from relatively wet environments with no water stress to drier open habitats with variable degrees of water stress. This shift to open habitats required the development of deep branching fibrous roots with a symbiotic relationship of arbuscular mycorrhizal fungi to absorb water and nutrients from the soil and the mechanisms to control the rate of water loss in

order to prevent cellular dehydration and for the control of gas exchange. These grasses needed to develop an elaborate vascular tissue system, complex leaves with waterproof cuticles, and complex stomata with dumbbell shaped guard cells and lateral subsidiary cells. The grasses developed bulliform cells to roll or fold the leaf to reduce water loss. These improved structures provided fast action response to environmental changes in water balance resulting in improved water use efficiency permitting grasses to live in open, water deficient environments and still maintain significant biomass production. These grasses also developed mechanisms and phytohormones to repair and recover from the tissue damage caused by water deficient conditions (Wang and Chen 2020).

Cold Tolerance Mechanisms

The average temperature during the Cretaceous was warmer than the present. The mountains had cool temperatures where a few lineages in the Pooideae subfamily developed adaptations to cold temperatures. However, all the rest of the ancestral grass lineages did not develop cold tolerance mechanisms during the Cretaceous.

Grasses that moved to the temperate zones had to develop mechanisms for cold tolerance and to survive winter dormancy periods. The earth experienced cooling events during the late Eocene and Oligocene, 47.5-26 Ma. Grasses share a common ancestral trait to prevent cellular dehydration which is also beneficial in the development of cold acclimation responses. Enhancement of freezing tolerance was provided by a genetically controlled Poaceae specific inhibitor of ice recrystallization by production of a protein (IRIP) which helps prevent cell rupture by ice crystal development. Grasses developed a seasonal phenology cycle with vernalization responsiveness that allows synchronization of flowering with favorable conditions of spring and activation of autumnal senescence for termination of growth activity before damaging freezing temperatures and for the translocation of synthesized compounds from cells downwards to the crown for respiration during the winter period to maintain life in crown cells and meristematic tissue (Preston and Sandve 2013, Korner 2016).

Surviving Drought and Fire

Perennial grasses living in temperate zones are known to have high survival rates during environmental stressful conditions of drought and fire. However, perennial grasses have no measurable mechanisms activated by either drought or fire events. The high survival rates during drought or fire conditions are attributed to the grass mechanisms that have evolved for adaptation to grazing defoliation, shifting to open habitats, and cold temperature tolerance.

Intensified Grazing Pressure from Herbivorous Dinosaurs

The increase in angiosperm development and radiation also occurred in North America, however, fossil Cretaceous grasses have not been found yet. The huge increase in new herbivorous dinosaurs did occur (table 4).

The Thyreophoras and Nodosaurids were heavy set critters fully covered with armor. They had small heads with small leaf shaped teeth for grinding leaves picked from low lying plants in open habitats. The Hadrosaurs, Pachycephalosaurs, Neornithischians, and Ceratopsians were Ornithopods (bird foot) that had comparatively small replaceable teeth for grinding leaves grazed from plants close to the ground or browsed from low plant branches and they had cheeks that kept the food in their mouths while chewing. The Hadrosaurs (duck billed) and Ceratopsians (horn faced) were large quadrupeds that lived in open habitats and traveled in large herds with young and old individuals. The Pachycephalosaurs (thick dome heads) and Neornithischians (wondrous lizard) were moderate sized bipeds that lived in open habitats and may have traveled in small groups. The last large long necked sauropod roaming in western North America was one of the giant Titanosaurs; Alamosaurus was one of the largest, with an adult estimated to be 98 feet long, 25 feet tall, and at a weight of 70-80 tons. This large animal lived near tall trees and had a relatively small head with rod shaped teeth for stripping the leaves from branches, it had no large teeth for oral processing of the leaves, instead, it had a large muscular gizzard containing stones to mechanically breakdown the food (Barrett et al. 2006, Mallon et al. 2013, MacLaren et al. 2017, Takahashi 2019).

Mass Extinction by Asteroid

At the end of the Cretaceous, a massive asteroid 6 miles wide impacted the earth at Chicxulub Mexico on the coast of the Yucatan Peninsula in 66.043 Ma (Anonymous 2021a). The asteroid created a 112 mile wide crater

that ejected vaporized granite rocks into the atmosphere that formed into minute spherules of crystallized droplets of molten rock which fell back to earth. The impact set off a global firestorm that denuded the land and put 16.5 billion tons of soot into the atmosphere which blocked sunlight from reaching the earth for 1 to 2 years. The temperature of the ocean dropped 20° F and on land it dropped 50° F. Freezing temperatures at the middle latitudes lasted for 3 to 4 years (Bardeen et al. 2017, Anonymous 2022h).

This asteroid impact caused the Cretaceous-Paleogene (K-Pg) mass extinction event. All of the non-avian dinosaurs plus the mosasaurs, plesiosaurs, and pterosaurs became extinct (Anonymous 2021a). The shallow sea coral, belemnoids, and ammonoids also became extinct. Surprisingly, many ocean animals survived, 90% of the boney fish, 66% of the sharks, and 69% of the skates and rays.

Many land animals survived, 80% of the turtles, most of the snakes, lizards, crocodiles, birds, and the mammals smaller than the size of a racoon. Almost all of the plants in the southern hemisphere survived. In North America, 43% of all terrestrial plants survived (Anonymous 2022h). All of the plants that survived this asteroid impact were polyploidy, containing more than two sets of chromosomes (Lohaus and Van de Peer 2016). Angiosperms, Poaceae, and Pinus emerged from the Cretaceous as the dominant plant forms.

Saprotrophic fungi became the dominant living organisms because they can live on dead organic material without sunlight. When the sunlight returned, two species of ferns recolonized the entire planet and were dominant for 1,000 years. How or where the terrestrial plants and animals survived two years without sunlight and four years of extreme cold is not explained in the literature.

Survival After Mass Extinction

Ancestral grasses from twelve subfamilies survived the K-Pg extinction event, 66 Ma. The number of grass subfamilies that did not survive extinction is not known. Evidence of grasses remained obscure for 10 million years after the K-Pg boundary. Nevertheless, by Early Eocene, 56-46 Ma, grass fossils had nearly a world wide distribution (Stromberg 2011). Following the K-Pg extinction, North American vegetation was dominated by evergreen gymnosperm and deciduous dicotyledonous trees with an abundant understory of palms and bamboo grass (Stromberg 2011). Some regions increased in aridity causing large openings to occur in the forest canopy permitting “desert” (arid) bunch grasslands to form during the Late Eocene-Early Oligocene, 33 Ma (Retallack 2004). These grasses were identified by their phytoliths as stipoid poidids and PACMAD clade grasses (Stromberg 2005). Areas of open grass dominated habitats appeared and started to be used as forage by large and medium sized herbivorous mammals during the Late Oligocene to Early Miocene, 25-19 Ma (Stebbins 1981, Semprebon et al. 2019). Open grasslands of C₃ poidids and PACMAD formed into wide savanna woodlands following the reduction of trees during Early Miocene, 19-15.5 Ma (Retallack 2004, Stromberg 2005, 2011). Open grasslands with C₃ grasses increased rapidly during the Middle to Late Miocene, 15-5 Ma (Stromberg 2005, 2011). There is no known fossil charcoal to indicate fire occurrence during the long period of grassland development in North America (Retallack 2004, Stromberg 2011).

C₃ and C₄ Photosynthetic Pathways

The C₃ photosynthetic pathway converts carbon dioxide and water into complex molecules by using the Calvin-Benson cycle which is the most primitive photosynthetic process in terrestrial plants. The C₃ photosynthesis process originated 2500 Ma when the atmosphere had very high CO₂ levels and much lower O₂ content. The product is a three carbon sugar (C₃), for every three molecules of CO₂ fixed, six 3C sugars are produced. However, in an atmosphere with higher levels of O₂, the process is disadvantaged because the high levels of oxygen expose some of the product to photorespiration which reduces the concentration of CO₂ that decreases the potential photosynthetic rate by up to 30%-40% (Tipple and Pagani 2007).

The C₄ photosynthetic pathway has increased effectiveness by adding a series of preliminary biochemical reactions that concentrate the CO₂ into a four carbon acid (C₄) in the leaf mesophyll cells that is then moved into nearby large bundle sheath cells resulting in a much higher rate of carbon assimilation during the Calvin-Benson cycle (Tipple and Pagani 2007).

The earliest C₄ grasses evolved during the early Oligocene, 32-30 Ma, when atmospheric CO₂ concentrations dropped to low levels (Stromberg and McInerney 2011, Christin et al. 2014). The oldest C₄ grass macrofossils date to 12.5 Ma in the Middle Miocene (Kellogg 2001). The C₄ photosynthetic trait has evolved from C₃ grasses 22 to 24 times, but this has only occurred in four subfamilies that are in the PACMAD clade, Chloridoideae, Panicoideae, Aristidoideae, and Micrairoideae. The C₃ plants that have evolved into C₄ plants had to have a specific arrangement of suitable leaf anatomy with greater than 15% proportion of vascular bundle sheath tissue and with only a very short distance to the large bundle sheath cells (Christin et al. 2013).

Grassland Development

Grasslands dominated with C₄ grasses primarily from the Chloridoideae subfamily expanded during the period of Late Miocene to Early Pliocene, 7-4 Ma (Tippie and Pagani 2007, Osborne 2008, Stromberg and McInerney 2011, Christin et al. 2013, Fox et al. 2018, Kirshner and Hoorn 2020). The late Miocene grasslands in North America, Africa, Argentina, Ukraine, China, and Pakistan were extensive enough to sequester sufficient quantities of carbon dioxide to reduce the Cenozoic greenhouse conditions and cool the global temperature (Prothero 2006). Continuation of the North American expansion during the Early Pliocene, 5 Ma, created an extensive treeless grassland between the Rocky Mountains and the Appalachian Mountains (Holliday 1987, Fredlund and Tieszen 1997, Dyke 2005).

Global cooling began when Antarctica moved over the south pole and the Southern Ocean had unhindered circulation around the continent about 33 Ma, causing decreases in forest density (Retallack 2004). A global ice age intensified during late Pliocene, 3.5 Ma, with the formation of multiple continental glaciers. The largest glacier was on North America, which experienced at least 20 discrete glacial-interglacial cycles. The greatest advance occurred about 2.4 Ma in North America covering nearly all of Canada and most of the northern tier of states west of the Great Lakes, extending south along the Mississippi River to the confluence of the Ohio River, and extending east to Long Island. The land ahead of advancing glaciers and adjacent to receding glaciers was a herb tundra with sedges, grasses, and shrub willow and in some places permafrost developed. A white spruce savanna extended about 200 km (124 mi) out from the glacier with open woodlands of aspen, ash, and birch forming along lake margins and grasses covered upland areas (Holliday 1987, Fredlund and Tieszen 1997).

The old literature based on palynological studies described a spruce forest that covered the United States south of glacial margins during the Pleistocene ice age (Holliday 1987). Identification of ancient biomes from pollen analysis is hugely biased towards trees and against grasses and sedges. Trees produce much greater quantities of pollen, tree pollen moves further by wind, tree pollen has greater preservation, and tree pollen can be identified down to the genus level and be an indication of environmental conditions (Holliday 1987). Grass pollen is cosmopolitan and present at relatively low percentages in virtually all pollen samples. Grass pollen can only be identified to the family level and thus does not indicate environmental conditions. Graminoid dominated ecosystems can not be identified by pollen analysis. Phytoliths have better resolution than pollen for graminoid taxa. Phytoliths accumulate over more local areas and are remarkably durable in dry acidic conditions and can be used to identify graminoid communities (Anonymous 2021c).

The central portion of the United States south of the glacial margins was actually a grass dominated community with scattered spruce and aspen that was highly variable during the changeable conditions of the Pleistocene Epoch (Fredlund and Tieszen 1997, Dyke 2005). This age of megamammals included large quantities of mammoths, horses, zebras, asses, camels, llamas, pronghorns, oxen, and bison that depended on grasses for forage and grasslands for habitat and their predators of wolves, bears, and cats (table 5).

The last glacier melted around 11,500 years ago. The areas that had been glaciated had the previous vegetation completely destroyed and were revegetated by migrating plants from the south that developed dynamic communities in place. The current North American biomes have existed for only the last 5000 years. No new plant species have originated in the previously glaciated regions.

Synopsis of Cretaceous age ancestral grasses

The age of ancestral grasses has recently been doubled and moved back to the Cretaceous, 113 Ma, by three astonishing paleontological studies that used grass silica short cell phytoliths to identify Cretaceous ancestral

grass microfossils. This was possible because grass phytoliths are nearly indestructible and they have unique morphotypes that are taxonomically diagnostic to subfamily, tribe, and to some genera. This major scientific advancement opens the path for future studies to use grass phytolith microfossils to help explain grass species evolution in greater detail and to describe the historical development of grasslands more precisely.

Pushing the age of ancestral grasses back to the Cretaceous implicates herbivorous dinosaurs as the driving force for the development of the same four grazing defense mechanisms in most temperate perennial grasses. Today, grasslands are the primary forage source for the livestock production industry because of what grazing herbivorous dinosaurs did to ancestral grasses one hundred million years ago.

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Table 1. Geologic Time Scale of the Grasses during the Cretaceous and Cenozoic.

Epoch	Age	Ma	Epoch	Age	Ma
Cenozoic Era			Cretaceous Period		
		now			66
Holocene		0.012		Maastrichtian	
Pleistocene	Calabrian	1.8			
	Gelasian	2.6		Campanian	72
Pliocene	Piacenzian	3.6			
	Zanclean	5.3			
Miocene	Messinian	7.2	Late		84
	Tortonian			Santonian	86
		12		Coniacian	90
	Serravalloian	14		Turonian	94
	Langhian	16		Cenomanian	
	Burdigalian				
		20			100
Oligocene	Aquitanian	23		Albian	
	Chattian				
		28			
		34			113
Eocene	Priabonian			Aptian	
		38			
	Bartonian				
		41			
			Early		125
				Barremian	
		48			129
				Hauterivian	133
				Valanginian	
		56			
Paleocene	Thanetian	59			139
	Selandian	62		Berriasian	
	Danian	66			145

Data from the Geological Society of America, V.5.0. 2018.

Table 2. Classification of the worldwide family Poaceae (Gramineae), the Grasses.

Clade	Subfamily	Tribe	Genera	Species
	Chloridoideae	5	124	1602
	Danthonioideae	1	19	292
	Micrairoideae	3	8	184
PACMAD				
	Arundinoideae	2	14	40
	Panicoideae	13	247	3241
	Aristidoideae	1	3	367
	Pooideae	15	202	3968
BOP	Bambusoideae	3	125	1670
	Oryzoideae	4	19	115
	Puelioideae	2	2	11
APP	Pharoideae	1	3	12
	Anomochlooideae	2	2	4
3	12	52	768	11,506

Data from Soreng et al. 2017. Oldest to Youngest, Bottom to Top.

Table 3. Adjusted ages of grass tribes in subfamily Pooideae using calibration points of fossils from three new Cretaceous studies.

Tribe	Age Ma (mega-annum)		Geologic Age
	Range	Mean	
Brachyelytreae	93.2-76.3	84.8 ²	Turonian
Nardeae	69.4-55.4	62.4 ¹	Maastrichtian
Lygeae			
Duthieae	64.4-50.3	57.3 ¹	Danian
Phaenospermateae	81.7-38.3	60.0 ²	Campanian
Brylkinieae	61.3-47.2	54.3 ¹	Selandian
Meliceae			
Ampelodesmeae	62.8-48.7	55.9 ¹	Danian
Stipeae			
Diarrheneae	57.6-43.5	50.6 ¹	Thanetian
Brachypodieae	55.6-41.6	48.4 ¹	Ypresian
Poeae	62.4-47.8	55.1 ²	Danian
Littledaleae	52.4-38.8	45.5 ¹	Ypresian
Bromeae			
Triticeae			

Data determined by BEAST v 1.8¹ or BEAST 2²
 Data from Consortium 2018 and Orton et al. 2021.

Table 4. Herbivorous Dinosaurs Living in Western North America during the Late Cretaceous, 100-66 Ma.

Thyreophora	Hadrosaurs	Ceratopsian	Sauropoda Titanosaur
Ankylosaurus	Augustynolophus	Achelousaurus	
Borealopelta	Brachylophosaurus	Anchiceratops	Alamosaurus
Euoplocephalus	Corythosaurus	Arrhinoceratops	
Zuul	Edmontosaurus	Avaceratops	
	Gryposaurus	Brachyceratops	
Nodosaurid	Hypacrosaurus	Bravoceratops	
	Kritosaurus	Centrosaurus	
Denversaurus	Lambeosaurus	Chasmosaurus	
Edmontonia	Maiasaura	Coronosaurus	
Glyptodontopelta	Parasaurolophus	Crittendenceratops	
Nodosaurus	Prosaurolophus	Diabloceratops	
Panoplosaurus	Saurolophus	Einiosaurus	
		Eotriceratops	
		Judiceratops	
	Pachycephalosauria	Kosmoceratops	
		Leptoceratops	
	Acrotholus	Machairoceratops	
	Pachycephalosaurus	Medusaceratops	
	Sphaerolitholus	Mercuriceratops	
		Montanoceratops	
		Nasutoceratops	
	Neornithischian	Pachyrhinosaurus	
		Pentaceratops	
	Parksosaurus	Regaliceratops	
	Thescelosaurus	Styracosaurus	
		Terminocavus	
		Torosaurus	
		Triceratops	
		Utahceratops	
		Vagaceratops	
		Wendiceratops	
		Xenoceratops	

Data from Anonymous 2021 g, h, i; 2022 i, j, k, l, m, n, o, p.

Table 5. Pleistocene Grassland Megafauna Herbivores and Predators in North America, 1.9-0.011 Ma.

Grassland Herbivores	
Mammuthus	Mammoth
<i>M. imperator</i>	Imperial mammoth
<i>M. columbi</i>	Columbian mammoth
<i>M. jeffersonii</i>	Jefferson's mammoth
<i>M. primigenius</i>	Woolly mammoth
Equus	Horse
<i>E. conversidens</i>	Mexican horse
<i>E. giganteus</i>	Giant horse
<i>E. niobrarensis</i>	Niobrara horse
<i>E. occidentalis</i>	Western horse
<i>E. scottii</i>	Scott's horse
<i>E. (Asinus) calobatus</i>	Stilt legged onager/ass
<i>E. (Plesippus) simplicidens</i>	American Plains zebra
Camelidae	Camel/Llama
<i>Camelops hesternus</i>	Western camel
<i>C. minidakae</i>	Minidak camel
<i>Titanotylopus spatula</i>	Giant camel
<i>Hemiauchenia macrocephala</i>	Long legged llama
Bison	Bison
<i>B. latifrons</i>	Giant bison
<i>B. alaskensis</i>	Alaska bison
<i>B. alleni</i>	Long horn bison
<i>B. antiquus</i>	Ancient bison
<i>B. occidentalis</i>	Western bison
<i>B. bison bison</i>	Plains bison (extant)
Bos	Oxen
<i>Euceratherium collinum</i>	Shrub oxen
Antilocapridae	Pronghorn
<i>Capromerix minor</i>	Small four horned pronghorn
<i>Tetramerix irvingtonensis</i>	Large four horned pronghorn
<i>T. shuleri</i>	Four horned pronghorn
<i>Antilocapra americana</i>	American pronghorn (extant)

Table 5 (cont). Pleistocene Grassland Megafauna Herbivores and Predators in North America, 1.9-0.011 Ma.

Platygonus	Peccary
P. compressus	LeContes peccary
P. vetus	Flat head peccary
Tapirus	Tapir
T. haysii	Giant Hays tapir
Grassland Predators	
Canis	Wolf
C. edwardii	Edward's wolf
C. armbrusteri	Armbruster's wolf
C. dirus	Dire wolf
C. lupus	Gray wolf (extant)
C. latrans	Coyote (extant)
Ursidae	Bear
Arctodus pristinus	Lesser short faced bear
A. simus	Giant short faced bear
Ursus arctos	Grizzly bear (extant)
Felidae	Cat
Smilodon gracilis	Saber toothed cat
S. populator	Saber toothed cat
Homotherium serum	Scimitar toothed cat
Miracinonyx trumani	American cheetah
Panthera atrox	American lion
P. onca	Jaguar (extant)
Felis cancolor	Puma (extant)

Data from Hibbard 1958, Bell et al. 2004, Dyke 2005.

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