Linear Enamel Hypoplasia as a Proxy for Environmental Stress in Fossil Apes

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Abstract:

The Anthropocene, our current geological era, is defined by increased anthropogenic environmental alteration that is reducing great ape populations globally. As this occurs, there becomes an increased need to not only understand how great apes are being impacted by the changing environment, but how they will respond to this change. The focus of this research is to use the dental developmental defect Linear Enamel Hypoplasia in the Late-Miocene great ape *Hispanopithecus crusafonti* to reconstruct Late-Miocene seasonality. These patterns are then analyzed in relation to previous research on Late-Miocene climate to understand how *H. crusafonti* responded to increasingly variable seasonality. The Late-Miocene, similarly to the Anthropocene, faced climatic upheaval that resulted in the extinction of many great ape species. Seasonal bouts of physiological stress are expressed through enamel depressions in fossil teeth. Through microscopic analysis and reconstruction of the duration of annual stress intervals, the irregularity of Late-Miocene seasonality is identified. These findings are applied to a comparison with the extant great ape, *Pongo*, who expresses many of the same specialized characteristics as *H. crusafonti*; features like morphology, diet, and ecology are influenced by their similar warm and tropical forest habitats and are therefore reflected in both species. It was determined that the primary factors influencing the decline of both fossil and extant great apes is the frequency of stress events and great ape specialization, which limits adaptability during seasonal and environmental variability. This constrains them and bases their survival on specific environmental conditions that are not conducive to the rapidly changing climate of the Anthropocene. This is likely what led to the extinction of *H. crusafonti* and what is currently severely decreasing orangutan and great ape populations.

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Introduction

In recent decades, the primary focus of conservationists and the greater scientific community has been to predict the course and severity of impact that anthropogenic environmental alteration will have on the planet, as well as how to prevent further damage to already threatened species of flora and fauna. Entire ecosystems are being destroyed in extreme acts of landscape alteration, resulting in significant reductions in population sizes of both marine and land fauna, with the International Union for the Conservation of Nature (IUCN 2020; Smith & Zeder 2013) currently reporting that 10 967 species are currently under increased threat of extinction due to climate change. One such group of fauna, the great apes (including gorillas, chimpanzees, orangutans, and bonobos), have been hit particularly hard in this context (IUCN 2017). Their ranges have greatly been reduced through habitat destruction, encounters with human settlements, and large-scale industrial agriculture, drastically reducing their populations by up to 70% (IUCN) in the wild. All four species of non-human great apes are currently listed as endangered under the IUCN Red List- other than gorillas and orangutans, whom are currently the most predominantly threatened from this group, both being listed as *critically* endangered.

The survival and persistence of great apes is reliant on understanding how populations react to and are influenced by climate change, and more specifically, how they respond to fluctuating environmental conditions and irregular seasonal patterns, as well as both short term and long-term environmental alteration-all developing consequences of current anthropogenic environmental alteration. Ancient extinction events motivated by environmental upheavals act as analogues for current ecosystem loss and may be used to infer how similar extant species may

react to contemporary global climate change. Great apes have a long evolutionary history with fluctuating environmental conditions. A critical area of interest in the study of evolutionary anthropology focuses on assessing the impact of ancient climate change on the evolution of great apes (Eastham 2017; DeMiguel, Alba, & Moyà-Solà 2014). This has been done on a wide variety of ancient great apes, as is seen in a 2017 study concerning *Rudapithecus hungaricus* in ancient Hungary, wherein stable isotope samples were collected from fossil ungulates to reconstruct the paleoecology of European great apes (Eastham 2017). Sharing many morphological and behavioural characteristics, it is also probable that both modern and fossil great ape species would respond and adapt to environmental conditions in similar ways, expressly when using examples who faced many of the same climatic obstacles that modern species do. Extant great apes find themselves subject to many of the more detrimental impacts of anthropogenic environmental alteration due to the specific ecological conditions required to support their unique populations and lifestyles. These requirements, alongside prolonged life histories, contribute to their environmental sensitivity, as will be further clarified through the course of this thesis.

The research presented in this thesis uses the incremental dental developmental defect Linear Enamel Hypoplasia (LEH) to evaluate the impact of Late Miocene climate change on the extinction of the Spanish fossil ape, *Hispanopithecus crusafonti*. Specific objectives of this research include: 1) assessing the periodicity of LEH in *Hispanopithecus crusafonti* for evidence of seasonal bouts of physiological stress (malnutrition/disease) 2), contrasting data derived from dental life history with other paleoenvironmental proxies to examine whether increasing Late Miocene seasonality is likely to have influenced the extinction of fossil apes in this region, 3) utilizing the results of this analysis to infer how living apes might respond to current and

projected climate change. Specifically, the use of the extant *Pongo* as an analogy for *Hispanopithecus* will be carried out, as both *Hispanopithecus* and *Pongo* share similar habitats and, subsequently, similar environmental concerns as generated by fluctuating seasonal conditions. By examining how fossil great apes were impacted by climate change during the Late Miocene, we gain critical insights for understanding how living great apes will respond to climate change in the Anthropocene.

1. The Anthropocene

The term 'Anthropocene' was popularized in 2000 by environmental researchers Paul J. Crutzen and Eugene F. Stoermer (Steffen 2021) to define a new contemporary geological period in our history marked by increased anthropogenic environmental alteration and active human influence over and on the environment. This may be examined in a more general sense, in regards the act of modifying one's environment, or may be interpreted on a higher level, only being applied to highly destructive human activities. These activities constitute habitat destruction, large-scale agriculture, unsustainability, trophy hunting, and many, many more that characterize modern human consumption. These practices have led to a steep increase in global temperatures by approximately 1.2 ˚C on average, what is referred to by the international community as climate change, and a loss of species so severe that it is currently defined as the Sixth Mass Extinction. These events are characterizing features of the Anthropocene, and likely those most instantly recognizable (Trischler 2016;). More aggressive human interaction with the climate has resulted in increasingly exacting reactions from the environment, a transition to erratic weather patterns and events that are threatening all life on this planet, including that of humans. The use of this title has increased in popularity over the decade, along with concerns

over the global climate, yet the estimated onset is still highly contentious (Smith & Zeder 2013). This period is defined by anthropogenic environmental alterations on the environment, but what exactly do these activities entail? At what point do activities become extreme enough to have a significant impact on the landscape, and what constitutes these activities?

To formally define a geological epoch, a GSSP (Global Boundary Stratotype Section and Point) must be identified and established as a marker for the period that took place. A collection of unique fossils or techno fossils (human-fabricated, artificial remains) associated with the era that are found within a continuous layer of the earth's surface act as possible indicators for the boundary of a new geological period (International Commission on Stratigraphy;Trischler 2016), and many anthropogenically associated objects and materials have been excavated and suggested as markers for the Anthropocene. Marking the exact onset of the Anthropocene, however, can prove quite difficult, as the temporal range of said fossils and remains span centuries and are associated with numerous varying stages of human development and culture. Some have proposed an earlier date for the onset of the Anthropocene-a Palaeoanthropocene-corresponding with early human behaviours such as hunting, fire use, and habitat construction (Foley et al. 2013), while later dates have also been suggested, in relation to the development of colonization, and the conception of nuclear energy and weaponry (Smith & Zeder 2013). Cruetzen and Stroemer themselves believed the onset to sit somewhere in the late 18th century, during the early stages of industrialization (Trischler 2016). Human interaction with the environment and climatic patterns will receive principal attention in the final analysis of this paper.

In this thesis, three primary effects of the Anthropocene will be examined and analysed in reference to their effects on modern great apes; 1) Climate Change, 2) Increased Seasonality, and 3) Anthropogenic environmental alteration (habitat destruction/displacement, habitat fracturing,

etc.). These factors will be crucial in the comparative observations that are made between this contemporary period and that of the Miocene, an ancient geological time period that reflects the events and effects of the Anthropocene in many noteworthy ways, but also differs in several important respects. Most notably, in the case of this study, both the Anthropocene and the Miocene accounted for erratic seasonal patterns that resulted in similar consequences for the environment and species of their times, and seasonality will be examined in regard to both timeframes. Additional factors unique to both time periods will then be analyzed in relation to the persistence of great ape species, more specifically, for this comparison, those great apes being *H. crusafonti*, an extinct species dating to the Miocene, and the extant orangutan.

2. Fossil Teeth & Evolutionary Anthropology

Teeth are some of the most effective tools in estimating not only physiological development, but environmental conditions (Cuozzo et al. 2012). Many features and attributes of tooth growth have been used in paleontology to reconstruct ancient environments and create timelines of climate events within a given period. Enamel thickness, dental morphology, and chemical composition may all be analysed to understand how exactly individual fauna were impacted by/reacted to the variables in their environment, as well as how they reacted to seasonality on a species-level (Boissoneault 2018; Reid et al. 1998; Dean 1998). A few key features and attributes of dental remains were used in this study as to act as proxies for the Miocene landscape, as well as Miocene climate conditions.

2.1. Dental development

Teeth grow incrementally, with layers of enamel being deposited periodically and at a consistent rate by ameloblasts, our enamel producing cells (McGrath et al. 2018). This growth is expressed through shallow furrows that extend horizontally along the tooth surface called perikymata. Perikymata (PK) represent regular growth increments in the tooth, functioning in a similar manner to tree rings in dendrochronology, acting as a physical record of development. Perikymata are the external appearances of the striae of retzius, internal growth expressions, which are lines that drive up diagonally within the dental matrix and represent long period growth increments, or retzius periodicity (Chollet & Teaford 2010). Both function as temporal markers that are used by researchers to estimate age and growth patterns in an animal, as well as illustrate how different stages of hominid evolution reacted to varying environmental conditions (Modesto-Mata 2020; Dean 1998; Welker et al. 2019).

2.2. Linear Enamel Hypoplasia

Dental development is impacted by a number of factors and may be inhibited by a number of outside influences. A mammal in ideal health will experience regular enamel deposition, driven by regular consumption of resources and lack of environmental stress. However, an animal under increased strain is subject to a disruption in physiological development, which is recorded in the growth of the teeth. When faced with environmental stressors or seasonal variability, enamel growth patterns become intermittent, and create a depression in enamel deposition that is commonly referred to as an enamel hypoplasia (Guatelli, Ferrell, & Spence 2012; Bacon et al. 2020). These enamel hypoplasia may express themselves as deep furrows along the tooth, or through pitting on the surface of the tooth; both expressions may be observed in ancient and modern hominids (Bacon et al.; Towle & Irish 2019). Linear Enamel

Hypoplasia, however, are more frequently seen in dental remains than pitting features, as would be expected in correlation with more uniform ameloblast enamel production and enamel deposition. LEH appearance can be determined by sex, interspecies variation, age related to stress in association with a depression in the weaning period (Bacon et al.; Reid et al. 1998; McGrath et al. 2018), and, most notably, environmental stress. Through many studies conducted on the topic, it has been repeatedly determined that the driving factor in the expression of dental developmental defects in non-human primates is environmental and climate instability. Irregular seasonality has an enormous impact on resource availability and habitat regularity, and over a normally consistent yearly pattern, wherein warm summer and spring months bring seasonal fruits and plants, a slight deviation from these patterns can be destructive to a species (Chollet & Teaford 2010; Marmi et al. 2012; Hassett 2012). Elements like disease stress, although having been cited as having some effect on hypoplasia development, do not hold the same amount of weight as to nutritional stress (Chollet & Teaford 2010). As environmental stress is the leading cause of hypoplastic expression in non-human primates, the presence of LEH on dental remains may be used to represent a timeline of environmental stress events and physiological indicators of stress (Guatelli, Ferell, & Spence 2012). More specifically, and significantly, they function as indicators for how a mammal *reacted to these environmental stressors* (Cuozzo, Ungar, & Sauther 2012). Therefore, in accordance with previously established paleoenvironmental data of the Miocene, results may be compared against these environmental conditions to determine behavioural reactions to the increased seasonality of the Miocene.

3. Great Apes

The family of great apes is a noteworthy and significant group of animals that are intricately tied with the development of our own species. Great apes are a group of hominids belonging to the taxonomic order of Primates and the family Hominidae (discluding gibbons, who belong to the family Hylobatidae, as they are considered *lesser* apes) consisting of gorillas (*Gorilla*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo*), and humans (*Homo sapiens*).

3.1. Characteristics

Great apes possess many of the same features as their prehistoric relatives, however, also differ in many important ways. They belong to the parvorder *Catarrhini*, a specialized group of primates more commonly referred to as old world monkeys, relegated to regions surrounding the equatorial line, in the continents of Africa and Asia (Center for Great Apes 2020; Kuhlwilm et al. 2016). As with most primates, they have opposable thumbs, greater intelligence, and more generalised behaviour than many other mammals. They have complex group structures and social hierarchies, and problem-solving skills that are driven by their increased mental capacities (Martinez et al. 2013).

In terms of morphology, great apes branch off from their catarrhine parvorder in a few recognizable aspects; they possess a reduced vestigial tail bone, a longer torso, and arms than prosimians, dorsally placed scapulae, and a higher EQ (encephalization quotient: brain to body mass) than other primate groups (Martinez et al. 2013; Center for Great Apes 2020). Their long upper limbs and shorter legs correspond with their range of locomotive behaviours, including knuckle walking, brachiation, and, in the case of orangutans, quadrumanous climbing (an

exception to these locomotive patterns are humans, who practice habitual bipedalism) (Andrews 2020).

3.2. Evolutionary History

The evolutionary history of great apes begins with our first common ancestor, *Proconsul*, 28 million years ago during the Neogene (Walker & Teaford 1989). This catarrhine, while retaining many ancestral monkey-like characteristics (smaller body mass, long, curved phalanges, a mobile back, etc.) also exhibits more derived features which are more commonly associated with modern-day great apes (reduced vestigial tail, suspensory adaptations, a strong hallux, and increased EQ) (Michel et al. 2014.; Hawks 2015). As we move into the early Miocene, we see the diversification of great apes through fossil remains (Michel et al. 2014), as adaptive radiation works on apes while they expand into new and untapped environments supported by the Miocene climate. As time progressed, several trends would appear in the evolutionary development of hominids as a group; increased intelligence, social bonds, and lengthened life histories, which enable them to exploit unique habitats today.

While great apes maintain a number of useful and generalised adaptations that help them exploit their respective environments, these characteristics also serve as a detriment to the group in the era of the Anthropocene, as will be expanded upon further in this paper. The time required to develop their specialized characteristics and behaviours comes into direct conflict with an increasing rate of environmental/climate alteration, and upon maturation and complete development of these characteristics, these features prove to be unsuitable for a fractured and highly seasonal environment (Center for Great Apes 2020). The pronounced variation seen between great apes in modern times, enabled by unique specialized behaviours practiced by ape species, is an expression of how specifically designed hominids are for their habitats (DeMiguel

et al. 2014). However, this specialization has led to an increase in life history length, that limits their capacities to adapt to current anthropogenic climate change, which is only increasing in rate.

4. *Pongo*

Orangutans are being used in the comparative portion of this research against *H. crusafonti,* due to their numerous morphological and behavioural similarities. Orangutans (scientific name *Pongo*) are members of the subfamily of great apes known as the pongonins, and part of the genus *Pongo*. As the most specialized of the great apes, there are many features of orangutans that may be examined in correlation with their current conservation status, including their environments, locomotive behaviours, morphology, and life histories.

4.1. Ecology

The orangutan is found in the archipelago of Indonesia, where they reside in the tropical rainforests of Borneo and Sumatra (Center for Great Apes 2020; Felton et al. 2003). The orangutan inhabits a warm and wet tropical forest environment, spending most of their lives in the trees above the forest floors. These rainforests support some of the most varied and wide array of flora and fauna on the planet. Orangutans share this home with fauna such as the Sumatran and Bornean elephants, clouded leopard, the sun bear, and an extensive array of other unique species (most of whom are notably listed as endangered in relation to their population demographics and conservation status) (Dungey 2022). All of these species have developed in accordance with a moist and forested environment, including *Pongo*, and their distinctive characteristics and adaptations reflect this.

4.2. Life History

Life history is defined as the development of an animal throughout the course of it's life (Crespi et al. 2012). The life histories of orangutans have been a subject of interest for many primatologists, as out of all the great apes, their weaning period and adolescence is the longest recorded, with approximately 5-6 years spent under the care of their mothers, with maturation only reached at 11 (Bacon et al. 2020; Smith 2016), as discerned through both observational and skeletal analysis. This, even for a hominid species, is an extensive amount of time, and physiologically expensive for the mothers required to take care of their young (Kennedy 2005). An extended life history may contribute to the high and severe prevalence of LEH found in *Pongo*, with approximately 75-100% of individuals exhibiting some type of hypoplastic deformation (Bacon et al. 2020; Kennedy 2005) the highest expression rate out of all great apes, as compared against a species like gorillas, who express the shallowest LEH features in response to rapid development and a shorter life history (McGrath et al. 2019). Microwear analysis suggests the possibility of stress being associated with the weaning period of the orangutan's development, as well as age distinction, correlated with varying capacities to survive in a given environment and level of developed skills in maturity (Bacon et al. 2020).

4.3. Diet

Diet also plays a significant role in the livelihoods of orangutans. While counting LEH and predicting irregularity/regularity in the presence of these features, factors such as diet are being heavily considered, especially following initial counts. Diet has an enormous impact on an animal's ability to survive in a given environment, and this is true in the case of great apes as well. The orangutan's diet is dictated by its habitat which, as discussed earlier, consists of a humid and tropical forest environment. As they spend the majority of their lives in the forest

canopy, they rarely exhibit terrestrial feeding habits (Dierenfield 1997), primarily exploiting fruit as their favoured source of nutrients. Their dentition reflects this, in their low rounded tooth cusps, ideal for chewing and grinding fruit/plant matter. Although they are largely frugivorous, they have been observed practicing some florivorous and insectivorous feeding habits as a supplement to their mostly fruit-based diets (Dierenfield 1997). The observation of these feeding activities show that diet is a significant factor in the development of adaptive behaviours in orangutans, with groups exhibiting problem-solving skills such as using primitive tools, like sticks, to extract termites from the ground (Harrison & Marshall 2011; Galdikas 1988). Though, orangutans are still primarily reliant on fruit as the core of their diet, which make them increasingly susceptible to a decrease in customary food sources.

It is also important to note, however, that while orangutan dietary specialization puts it at an increased risk as a result of increasingly erratic seasonal patterns, the species has developed some adaptations to help reduce the impact of environmental strain and unfavourable seasonal conditions. Orangutans participate in a practice known as fallback feeding; this refers to the ability to fall back on less favorable food options during periods wherein a regular food source is not readily available. For orangutans, this involves them falling back to harder, more tough foods like nuts and bark when fruits are not plentiful enough to nourish them (Meulman & Schaik 2013; Galdikas 1988). This adaptation is expressed physiologically through a layer of tough, crenulated enamel over the surface of their teeth, which allows them to exploit firmer, less favorable food sources. Adaptations like these are crucial in the species' survival, especially as their environments and food sources are increasingly modified through intensive environmental and climate modification.

4.4. Morphology and Behaviour

The orangutan's morphology, as referred to in earlier sections of this research, is suited to an arboreal lifestyle, that being, a life spent in the trees. Their anatomy is reflective of their use of quadrumanous climbing (Almecija et al. 2007), a form of locomotion that requires one to move (languidly) through the trees with both arms and legs, pulling themselves from tree to tree. Their bulky frames and high body mass do not allow them to commit to the more commonly practised locomotive behaviour of arboreal quadrupedalism, a quicker, and arguably, more effective means of running and climbing through the treetops, as most monkeys exhibit. This is just one example of the specialised nature of many of the behaviours and features of the orangutan, and a reflection of environment, as well as seasonal conditions.

Orangutans are more sensitive than other hominid groups to these types of environmental pressures, as a result of their extremely specialized diets, habitats, and lifestyles. Compared to other primate and great ape species, orangutans live relatively solitary lives, primarily coming together during mating seasons (Mackinnon 1974; Fröhlich et al. 2020). This contributes to the low population sizes and increases the risk of population decline (Carne, Semple, & Lehmann 2015). With lower population sizes to begin with, and their food sources dependent on very regular seasonal and environmental conditions, anthropogenic landscape alteration and climate change are an extreme detriment to the persistence of the species as a whole and will be examined accordingly in the further analysis of climate changes effects on great ape species, in both extinct and existing populations.

5. Environmental proxies

In addition to the identification of LEH features on *H. crusafonti* dental remains, ancient paleoenvironmental data will be used to reconstruct late Miocene environmental and climate conditions, specifically through the collection of environmental proxies. These proxies, in essence, collect environmental data from their surroundings in a specific setting, and may be used as a representative feature for said environment. The most effective proxies are those that maintain their structural integrity over a long period of time, as well as those that are keenly sensitive to their environment. The Miocene period has no shortage of proxies to examine, including various forms of shellfish (You 2010), ice cores, geological deposits, and, in the case of this research, dental remains. A well detailed collection of flora and fauna have been analyzed to build up a forensic portfolio of what we understand were Miocene conditions. Studies performed by Van Dam and Weltje (1999) utilized approximately 44 rodent data compositions, obtained from the same geographical region as where our remains hail from, to formulate a precise timeline of seasonal patterns for the region during the late Miocene, exposing a frequently unintelligible weather and climate pattern. Trace elements have also been used to more concisely reconstruct Miocene landscapes, as detailed in research done using trace element samples and stable isotope examples to deduce the paleoenvironmental conditions of the Miocene (Eastham 2017; Harzhauser et al. 2011; Methner et al. 2020). This exhaustive set of data is crucial in the application and development of this research, creating a basis by which results from analysis may be compared from a full dental analysis of *H. crusafonti.*

6. The Miocene Epoch

The Miocene is a geological epoch in our earth's history that occurred approximately 23-5.3 Ma, and is characterized by it's turbulent climatic and seasonal patterns, brought about by numerous varying factors. Preceding the Miocene was the Oligocene, marked by a global cooling of roughly 3°C which is often attributed by researchers to a drastic decrease in global CO_2 levels which led to the expansion of Antarctic ice sheets, as recorded in early Oligocene isotope samples (Rampino & Haggerty 1995; Harzhauser et al. 2011). The onset of the Miocene saw the collision of continents into their (approximate) modern-day placements, as well as a dramatic rebound in global temperatures. Ocean current fractioning led to a rise of roughly 3-4°C on a planetary scale (Harzhauser et al. 2011), a stark contrast to the cooling of the Oligocene, and the ecology of the planet responded in an equally extreme way. There are two climatic events of note that took place during the course of the Miocene, those being, 1) The Miocene Climactic Optimum (MCO), and 2) The Middle Miocene Disruption (MMD).

6.1. Miocene Climactic Optimum

The Miocene Climactic Optimum (17.5-14 MA) made up the majority of what can be termed the 'optimal' period of the Miocene, in relation to climate and seasonal conditions. Seasonal patterns were regular and consistent, which benefited the sustainability of the planet's ecology, as recorded in *Crassostrea* (shellfish) isotopes from Miocene-dated oyster samples of the Western Tethyan, which illustrate optimal growth rates during this period (Harzhauser et al. 2011). Uncomplicated seasonality resulted in a boom in biodiversity, which in turn led to the increase and diversification of mammalian species, as well as the movement of these species into new and untapped regions that were previously inhospitable to them. Notably, in the case of this research, the planet saw a, 'Golden Age,' of great apes, with over 100 species of great apes

found globally (Begun & Gurche 2006). These species varied dramatically in both morphology and behaviour, exploiting all manner of environmental niches through rapid adaptive radiation. In Europe, we saw species such as *Oreopithecus bambolii,* (DeMiguel, Alba, & Moya-Sola 2014) (it's interesting to note, however, that *Oreopithecus* lived from 8.3-6.7 ma, *after* the approximated extinction of *H. crusafonti*, which was likely due to the species being geographically cut off the mainland and subsequent environmental deterioration during the end of the Miocene), while in Vietnam, there lived the infamous *Gigantopithecus blacki*, the largest species of great ape that has ever existed in the history of the planet, measuring roughly 10 feet (3 meters) in height (Welker et al. 2019), displaying impressive physiological diversity not seen to the same extent in modern great apes. Much of the Northern Hemisphere was covered in temperate forests, which further benefitted the expansion of great ape species, who often favoured these types of environments. Once again, the significance of this period in relation to this research is not necessarily the temperature itself, but how it impacted seasonal patterns. Seasons fluctuated between warm/wet and cool/dry conditions (Harzhauser et al. 2011), and these shifts were steady and reliable, bringing with them a consistent supply of alimentary resources and environmental habits, in turn, attributing to the ecological prosperity brought on by the MCO.

6.2. Middle Miocene Disruption

14 million years ago, the planet saw a sudden return to global cooling, a period referred to as the Middle Miocene Disruption. A drop in global CO2 levels and expansion of Eastern Antarctic ice sheets contributed to a decrease of approximately 8˚C, which transformed the landscape of the planet (Methner et al. 2020). Seasonality of the Miocene became erratic and rapidly changing weather patterns turned a warm-cool binary seasonal pattern into a wet-dry one

(Harzhauser et al. 2011). Extended dryer and cooler seasonal periods led to a decrease in temperate forested environments, which were subsequently replaced by grasslands, savannahs, and prairies, which were far more suited to these climatic conditions. Resources that many mammals had come to rely on to survive were rapidly depleting, and species that had become accustomed to regular seasonal cycles slowly decreased, up until their total extinctions towards the end of the MMD (Van Dam & Weltje 1999). Forest-adapted fauna were hit the hardest, as many frugivorous fauna lost their primary food source when fruit-bearing trees and plants began to disappear from the Miocene landscape. The MMD is notable for being a significant extinction event for many species prior to the Pleistocene and Quaternary extinction (Sandom et al. 2014). This applied to many of the late Miocene great ape species as well, especially those of European origin. Dietary proxies obtained from ungulate mesowear indicate a transition from browsing activities to grazing activities in Western Europe, demonstrating a marked shift from the forested environments of the MCO to the more fragmented and open environments of the MMD and late Miocene (Merceron et al. 2010).

In examining the initial and subsequent transitioning periods of the Miocene paleoclimate, several important trends and features may be identified; A rise and fall of CO_2 concentrations, an initial environment, climate, and seasonality suitable to an increase in biodiversity of great apes, a sudden global cooling akin to that of the Oligocene, an increased seasonality and fragmentation of the Miocene landscape, and a resulting decline and eventual extinction of European ape species. What's significant to note in this analysis of Miocene paleoenvironmental conditions is not the global temperature, but how it impacted seasonality and unpredictability in the global climate. Early Miocene conditions resulted in regular seasonal patterns that were conducive to the subsistence and diversification of great ape species, however,

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the MMD introduced far more erratic seasonal patterns that were inconsistent and non-conducive to the persistence of these mammals. Great apes, once prolific throughout the Miocene landscape, were succinctly removed from the record of biodiversity on the planet, highlighting the relationship between the environment, seasonality, and great ape adaptability.

7. Vallès Penedès, Catalonia

The site from which the dental samples were collected is found in the Vallès Penedès Basin of Catalonia, in the Northeast region of Spain. This site is well-regarded for its extensive fossil record which includes samples ranging from 20-7 Ma in age, encompassing the majority of the Miocene period (Casanovas-Villar 2016). These samples consist of large mammalian fauna, small fauna, plant material, and geological deposits, providing a wealth of biological evidence pertaining to this period (Reinhardt et al. 2018). Biological remains such as soil samples and both macro and micro botanicals function to recreate this ancient ecosystem and give insight as to how the environment was structured and what features of the environment were most prevalent in making up the specific biome (Reinhardt et al. 2018). Skeletal remains of fauna from the region may be analysed to reconstruct the niches of individuals and determine how they fit in/reacted to their environments based on small details in their physiologies, which may be used to inform us on what conditions and patterns were affecting these individuals in their correlated time periods. Alongside the numerous floral and faunal remains found at the basin since it's discovery in the early 1900s (Casanovas-Villar 2016), the site has also provided researchers with the most complete *Hispanopithecus* fossil on record in 2001, consisting of both cranial and post cranial remains, yielding a great deal of information relating to both the morphology and lifestyle of this hominid (Alba et al. 2012). Although there are questions

surrounding the effective use of these proxies in the recreation of palaeoenvironments, the science and research behind it is significant enough, along with the vast amount of remains and data, to be used in creating a full picture of ancient ecosystems and climate conditions (You 2010; Merceron et al. 2010). Through the subsequent research and analyses of peers in the field, a biochronology may be constructed, as well as a representation of the environment that was used to build our own research upon.

Proxies excavated from the Can Feu site show that the Vallès-Penedès basin was a warm and tropical forested ecosystem through the Late Miocene (11.6-5.3ma) (Marmi et al. 2012; Casanovas-Vilar et al. 2012) and this assessment applies to most of Western Europe as well. As stated in the previous section concerning the Miocene, the movement of continents to their modern geographical positions on the globe had an enormous impact on the planet's climate, which in turn, led to the expansion of these warm and humid forest biomes throughout the continent (Marmi et al. 2012). Europe saw explosive biodiversity throughout the Miocene, brought about by the exploitation of these rich environments by a wide range of mammalian species. The Vallès-Penedès basin hosted riparian environments, dominated by evergreen trees and a marshy terrain, with associated warm and cool seasonal shifts (Marmi et al. 2012; Casanovas-Vilar et al. 2016).

8. *Hispanopithecus crusafonti*

As the rapidly evolving Miocene landscape changed seasonal patterns and the respective habitat of this *H. crusafonti*, the following behavioural patterns and adaptive efforts that were required had an enormous impact on its survival and persistence through the period.

8.1. Morphology

Much of the data collected to reconstruct the morphology of *Hispanopithecus* has come from partial skeletal remains obtained from the Can feu Industrial Park in Catalonia, Spain (Alba et al. 2012). A substantial number of both cranial and post-cranial fragments have allowed researchers to recreate a relative framework of the great ape, and evaluate physiological features such as body mass, locomotive behaviours, and physical similarities to modern great apes.

Hispanopithecus retains both primitive features of ancient great ape species and more derived adaptations akin to those of extant great apes. Vertebral remains obtained from the Can Llobateres site point to the retention of a stiff lumbar region, indicative of an orthograde body plan (Susanna et al. 2014). Other features observed from partial skeletons, like a flexible joint at the olecranon process, and strongly curved phalanges, indicate a combination of both suspensory behaviors and arboreal quadrupedalism (Alba et al. 2007; Pina et al. 2012). a unique locomotive form likely adopted for a heavily forested environment. The morphological adaptations seen in *Hispanopithecus* are strongly similar to those observed in modern orangutans (Alba et al. 2007). It is probable these similarities are due to both species being highly arboreal, especially in comparison to other great apes. A highly specialized body plan suited to a forested environment likely contributed to the decline of *Hispanopithecus* as a species, as forests were slowly replaced with more heterogeneous landscapes, suited for more varied locomotive behaviours and terrestrial movement.

8.2. Diet/Ecology

Microwear analysis alongside analysis of microbotanicals and associated plant matter on dental remains suggest that *Hispanopithecus* specialised in the consumption of soft fruits and

leaves found in trees, with a primary emphasis on frugivory (DeMiguel , Alba, & Moya-Sola 2014; Alba et al. 2012). Low and rounded tooth cusps are indicative of this manner of diet, while also indicating some manner of fallback feeding associated with microwear on the tooth surface (DeMiguel et al. 2014). These nutrient sources were easily exploited within *H. crusafontis* humid and forested habitat. Their consumption of these foods allowed *Hispanopithecus* and other mid to late Miocene apes to expand and radiate into most of western Eurasia.

Other Miocene great apes, who had lived in drier and more fragmented environments contemporarily to *Hispanopithecus* (Andrews 2020) following the movement and subsequent collision of continents, were exploiting far different and more varied sources of food. Alongside fruits, leaves, and less frequently, meat, these apes also practised sclerocarpus feeding (a diet consisting of the specific species of herb/flowering plant sclerocarpus) (DeMiguel et al. 2014). Diet, alongside increasing seasonal instability and environmental change, likely played a leading role in the downfall of Eurasian apes, including *Hispanopithecus*, and therefore serves as a subject of interest in the analysis of its extinction. It's initial exploitation of forest fruits and leaves to survive and expand into a new environment had, over a few million years, turned into a reliance. *Hispanopithecus* was dependant on specific and regular seasonal patterns to deliver it fixed nourishment and being contingent on very specific and consistent environmental conditions only made it more subject to climate variability. As the Miocene climate once again saw sudden and rapid global change-this following the MMD and MMTD-seasonal patterns became erratic, weather became inconsistent, and the earth's landscape was radically transformed. Abundant food sources were significantly depleted, this being the case for the once favoured fruit reserves of the subtropical forests of Eurasia. Animals generalised enough to adapt to the changing circumstances of the period began to favour long grasses that dominated the globe with the

increasing expansion of open-plain environments, as seen in the fossil record pertaining to grazing species like horses, and in paleodiet samples obtained from various other ungulate species in relation to a transition from browsing to grazing practices (Merceron et al. 2010). However, the highly specialised feeding behaviours of forest adapted fauna like *Hispanopithecus* were not suited to this new environment, and this emphasis on diet is often cited as being one of the leading factors in the extinction of the Eurasian great apes (DeMiguel, Alba, & Moya-Sola 2014; Marmi et al. 2012). Once again, it is the rapid environmental change of the late Miocene that provoked many Vallesian extinctions, especially in the case of mammals living in warm forest environments.

9. Variability selection

Environmental variability is a dynamic force that is influenced by a number of factors including both natural processes and recently increased anthropogenic environmental alteration (You 2010). These environmental forces shape species in similarly dynamic ways. Many faunal remains from the Miocene show evidence of this (Cano et al. 2014; Eastham 2017; Harzhauser et al. 2011). Rodent assemblages from southeast Europe show specialized adaptations to specific environmental niches and were used in assessing various climate intervals during the Miocene, depending on the richness of assemblages found (Cano et al. 2014), as both adaptive behaviours and physical features are indicative of seasonal reactions. Many species are now accounting for the unpredictable climate that anthropogenic environmental alteration has influenced by assuming more generalized characteristics, an evolutionary effect known as Variability Selection (Potts 1998). As opposed to Natural Selection, wherein traits are passed down generationally based on their utility in a specific environment/niche, Variability Selection selects for traits that

allow animals to adapt to environmental instability more easily, impacted by unpredictable seasonal patterns (Skinner 2012; Potts 1998)

9.1. Variability Selection in Great Apes

This research presented in this thesis evaluated the role of Variability Selection in allowing ancient and modern apes to adapt to rapidly fluctuating seasonal patterns. Variability Selection not only applies to physiological characteristics, but behavioural ones as well, particularly in the case of great apes (Kalan et al. 2020). A study conducted in 2021 found that chimpanzees in Caiquène–Cadique, Cantanhez National Park, had developed specific methods of risk mitigation in response to the human settlements that were progressively encroaching on their habitat (Bersacola, Hill, & Hockings 2021). In the thoroughly studied Fongoli chimpanzees, through residing in the harsh, dry, environment of the Fongoli desert, in correlation with LEH expression (Skinner & Preutz 2012), it is observed that they have developed methods for exploiting the most from their ecosystem, through techniques like digging deep wells to gain access to water reserves (Kalan et al. 2020). Mosaic-like environments with unpredictable seasonality produce more variable behavioural patterns in these chimpanzees than seen in populations living in stable environments.

9.2. Generalization vs Specialization

In understanding the concept of Variability Selection, it's first important to consider the differences between specialization and generalization. Specialization refers to the adoption of specialized behaviours/characteristics in response to a unique/specific set of environmental conditions, or to exploit a specific niche of resources. A giraffe's long neck is an apt example of this, as it extends high to allow giraffes to surf the tops of trees for leaves, a resource

unattainable for most other animals. Specialization is a major part of adaptive theory and has been a driving force in millions of years of evolution on this planet. Adopting characteristics to allow an individual to exploit its environment to the fullest ensures success in said environment.

As opposed to specialization, generalization refers to the suite of varying and generalised characteristics (Prange 2003). Though not suited to a specific kind of environment, these characteristics allow the behaviour and physiology of an animal to be plastic and adaptable to a wide range of environments. A raccoon, for example, is not a highly specialized animal; its more generalised, and can exploit many different habitat types, including rural forests, towns, and even urban cities (Prange 2003; Driscoll et al. 2009). The racoon is able to move between these environments with ease due to a suite of generalised characteristics (i.e. opposable thumbs, effective dexterity, superior problem-solving skills) that don't relegate it to a single niche. Though not necessarily sitting at the top of the food web in its characteristic habitat, the adaptability of generalised fauna is important to note, especially when viewing species survival through a lens of increased seasonality and unstable ecosystems during a period of climate change (Cano et al. 2014). The concepts of specialization and generalization are playing an increasingly significant part in the survival of species on this planet. They are both adaptive methods for species to exploit their environments, but how exactly will they be influenced during the Anthropocene?

Variability Selection is a key concept in understanding the persistence and eventual decline of ancient and modern great ape populations (Kalan et al. 2020). The evolutionary success of humans as a species is often attributed directly to this theory, as the adoption of both behavioural and morphological adaptations such as an orthograde stance, increased cranial capacity, and bipedalism enabled *Homo sapiens* to take advantage of a fractured and

heterogeneous landscape (Potts 1998; Ko 2015). Did an ability to adapt to variable environments impact the ability of *H. crusafonti* to survive in the shifting Miocene landscape? Might this play a part in modern apes' ability to adapt to climate change in the environment?

10. Methods and Analysis

10.1. Microscopy

Initial phases of analysis were conducted using a Scanning Electron Microscope (SEM), to produce images of the teeth that could then be analyzed to identify LEH. Analysis of the enamel hypoplasia will be conducted using a scanning electron microscope (SEM). This microscope functions in a unique way in comparison to many conventional models (McMullan 1995). This starts at the preparation stage of the samples being examined. Specimens must be prepared in a special resin to allow for proper observation by the machine. Once placed within the device, examination may begin. A monitor is attached to the microscope and enables you to see a live feed from inside the machine. The mechanism proceeds to shoot a beam of electrons at the subject placed within the microscope (Vernon-Parry 2000). Upon hitting the subject, these electrons may reflect, scatter, or go directly through the matter, and are referred to as secondary electrons. A secondary electron detector then uses these electrons to create a 3D image of the object, which can be further magnified on the monitor on the computer. Photos acquired through use of the SEM in Saint Mary's Microscopy lab were then manually stitched together in a photomontage in order to facilitate surface analysis. The microscope provides a more precise and accurate representation of features on the surface which can be used to compile a complete data set by which we may determine environmental variables and conditions of the time. It also

happens to be non-destructive/invasive, preserving the integrity of the fossils. However, upon completion of SEM use and the retrieval of tooth images, it was determined that the photos were not high resolution enough to use in analysis. Stitching of the images yielded incomplete and overlapping tooth photos that were not magnified to a level which would be conducive with LEH identification. The stitching software Image Pro Plus was ineffective at making the tooth surface detailed, and a second means of microscopic analysis had to be conducted.

Imaging was subsequently done with the use of a digital microscope (Keyence VHX-7000), in Dr. Erin Cameron's lab in the Environmental Science Department at Saint Mary's University. Functioning in a similar way as a standard microscope, the utility of the microscope is elevated through the automation of many features, including the stitching process, which eliminated any potential overlap or blurring of images. Features such as glare removal and auto-focus also enabled the enhancement of images and subsequent identification of hypoplastic defects on the tooth surface.

10.2. Hypoplasia and Perikymata Counts

Hypoplasia were evaluated following an initial count of perikymata (PK), regular growth markers on the teeth. There are several things that were considered in this analysis; PK count between the start of one LEH feature and the start of the next (periodicity) the PK count in between the end of one LEH feature and the beginning of the next (interval) and the number of PK found within an LEH feature (duration). The periodicity is necessary in determining the temporal pattern of seasonal/climate events, as they demarcate the beginning of one event and the beginning of the following event. The intervals will enable one to understand seasonal patterns as well, in that they reveal the exact length of time that existed between climate events, outside of less then ideal seasonal conditions. The final factor examined, the duration, illustrates

the overall length in which the environmental conditions that instigated the LEH formation persisted. These factors, in combination, enable the effective cyclical reconstruction of late Miocene seasonal patterns, as well as provides a number of timeframes of which to compare against one another. More consistent and regular numbers that are received indicate adoption of effective responses to variable seasonal conditions, while irregular and highly varying counts point to a failure to adopt means of survival to erratic climate conditions. Upon the grouping of the collected numbers, estimated periodicity (not to be confused with periodicity in counts) were multiplied by counts of PK to determine the amount of time that passed between each period of environmental oscillation. Periodicity, in this case, refers to the amount of time that is represented between each PK expression. It varies depending on species, sex, and life history length, but tends to represent approximately a week in most great apes. In the case of *Hispanopithecus*, it represents about the same amount, approximately 7 days (Kelly et al. 2001). Therefore, PK counts were multiplied by seven in order to determine how many months were separating LEH expressions and subsequent environmental stress events.

Crown formation time (CFT) is defined as the amount of time taken for complete tooth development. It can be used to reconstruct the life history of an individual, because in calculating total growth time alongside LEH expression on the tooth, periods of stress can be identified in relation to growth and development. CFT is an important element of analysis and was calculated by first multiplying PK counts by the Retzius periodicity (7 days), to determine total number of days, and then divided by 375 to translate that number into years. The total dental developmental time is critical in understanding how developmental patterns/weaning periods in *Hispanopithecus* may contribute to variation in LEH frequency/expression. In addition to a primary comparison against *Pongo*, CFT was also examined in relation to *Pan* (chimpanzees).

Interobserver error was calculated prior to timeline reconstruction, and was determined to be 3 PK, which translates to 21 days.

11. Analysis

11.1. Sample and Imaging Procedure

There are four teeth that were analyzed for this research: upper buccal premolar 3 (P3), premolar 4 (P4), molar 1 (M1), and molar 2 (M2). All specimens are associated with the upper left palate of *H. crusafonti*. The specimen number from the IPC (Catalan Institute of Paleontology) is 1798.

All images were taken at 100x magnification, and glare caused by coating was removed using reduction software for the microscope. Stitching was also an automatic process, with multiple photos at 100x being taken and sutured together using additional software on the computer.

All hypoplasia are marked by green brackets (figures 1, 2, 3, and 4), and perikymata (short growth interval markers) are marked by small red lines (figures 1, 2, 3, an 4). As will be visible in the following tooth images, as well as in their associated tables, LEH expressions begin to decrease in frequency towards the occlusal surface of the tooth. This is because that section of the tooth surface is in most contact with food during the mastication process. This creates significant abrasion near the bottom of the teeth but remains an important factor to keep in mind during the analysis. Stacking of PK lines also occurs towards the tooth cervix, that being the medial surface of the tooth, and as a result, makes hypoplasia appear closer in distance to each other than they are, another dental feature that will be taken into account during analysis.

11.2. Tables and Images

See following pages →

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Above- Figure 1: Premolar 3

Below- Table 1

	LEH	PK	Days	Months	Mean PK	Mean Months
Periodicity	1-2	24	168	5.5	20.25	4.7
	2-3	17	119	3.9		
	3-4	17	119	3.9		
	4-5	23	161	5.3		
Duration	1	18	126	4.1	10.4	2.7
	2	7	49	1.6		
	3	10	70	2.3		
	4	15	105	3.4		
	5	10	70	2.3		
Interval	1-2	6	42	1.4	7.75	1.8
	2-3	10	70	2.3		
	3-4	7	49	1.6		
	4-5	8	56	1.8		

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P3: Observations

P3 has approximately 142 PK markers, which translates to a CFT of 2.7 years. There are 5 identifiable LEH expressions, with LEH 1 and 4 representing major stress events. LEH 1 is significant due to it being present on both P3 and P4 (figures 1 and 2), likely associated with the same stress event overlapping in expression between the two. The first major event, LEH 1, occurs 6.5 months after PK 1, with the actual duration of the event being about 4.5 months. The following year, from PK 50-100, there are 3 LEH expressions, albeit far shorter than LEH 1. The total period of stress over the year amounts to 7.3 months, while non-stressed time amounts to 5.2. While stressed time accounts for longer in this year than the proceeding, its important to note the difference in frequency and length between the LEH features, seeing as these 3 hypoplasia (LEH 2, 3, and 4) represent 3 different stress events separated by non-stressed intervals, while LEH 1 extends for 4 months with no pause. The last LEH feature, LEH 5, is at the 2 year marker towards the cervix of the tooth. This appears near the end of crown formation.
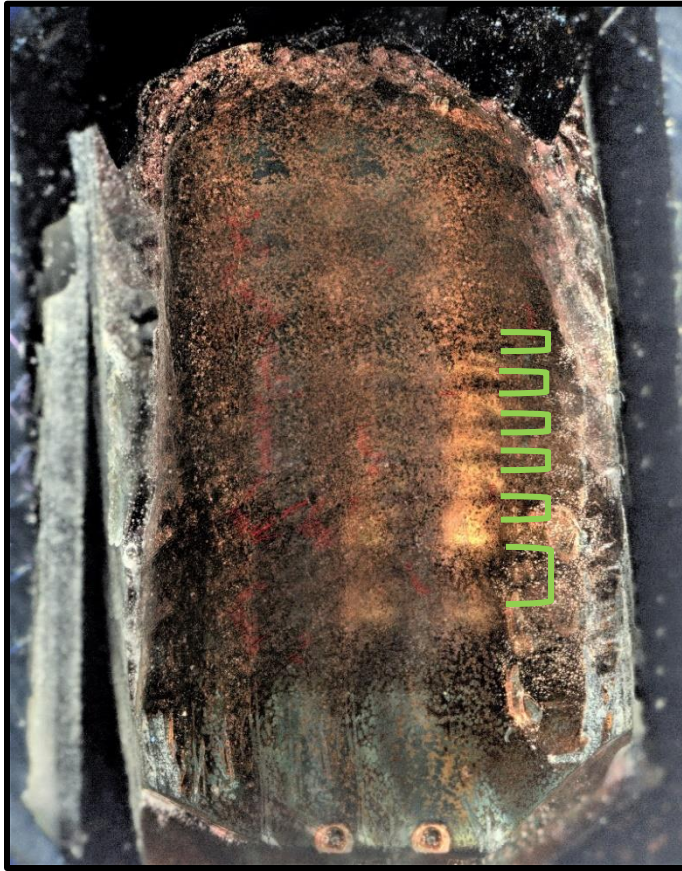
Above: Figure 2: Premolar 4

Below: Table 2

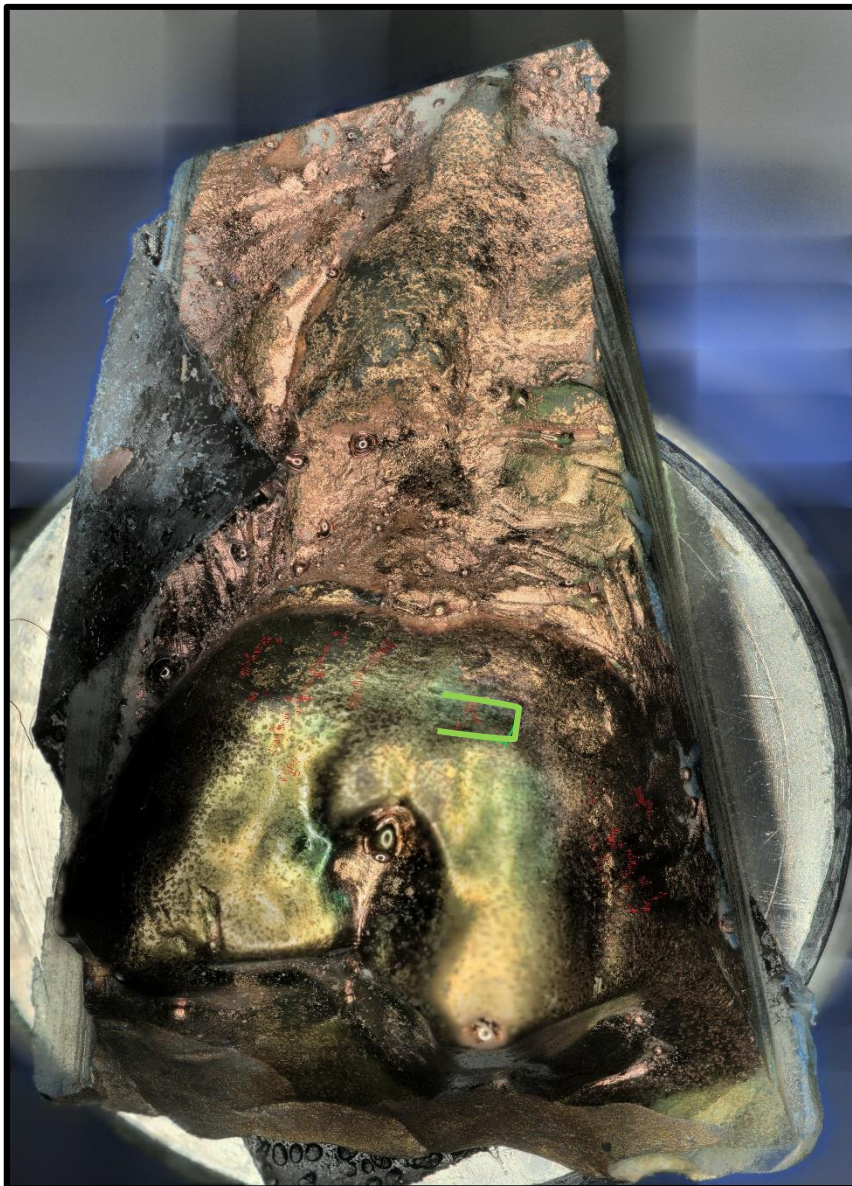|	LEH	PK	Days	Months	Mean PK	Mean Months
Periodicity	1-2	21	147	4.8	17.4	4
	2-3	15	105	3.4		
	3-4	17	119	3.9		
	4-5	18	126	4.1		
	5-6	16	112	3.7		
Duration	1	18	126	4.2	9.3	2.15
	2	7	49	1.6		
	3	7	49	1.6		
	4	10	70	2.3		
	5	6	42	1.4		
	6	8	56	1.8		
Interval	1-2	13	91	2.9	9.8	2.2
	2-3	8	56	1.8		
	3-4	10	70	2.3		
	4-5	8	56	1.8		
	5-6	10	70	2.3		

P4: Observations

CFT in P4 is approximately 3 years, with a count of 155 PK. 6 LEH expressions are observable, notably with LEH 1 representing a major stress event at the occlusal surface. The hypoplasia themselves are separated into three years; LEH 1 occurs in year one, LEH 2, 3, and 4 occur in year two, and LEH 5 and 6 occur in year 3 (it should be noted that LEH 2 and 2 occur right on the cusp of yearly transition). LEH 1 lasts for approximately 4.2 months- similar to that of LEH 1 in P3 (figure 1)- while the non-stressed portion of the year accounts for 6.9 months before it. The 3 hypoplasia in year two add up to 7 months of stress, while the rest is composed of unstressed intervals. Once again, it's noted that these hypoplasia, unlike LEH 1, are separated from each other by periods of non-stress. LEH 5 and 6 combine for 3.1 months of stress (with an interval of 2.3 months), and the other 9.4 months are unstressed. LEH 1 in P4 overlaps with that of P3, signifying a major overarching stress event near the beginning of tooth development. We see, like P3, that there are a similar amount of hypoplasia in each represented year, with only one extra seen in P4. These varying numbers of expressions in each year highlight an inconsistency in seasonal stress events, likely not

Figure 3 : Molar 1

M1: Observations

Although there are no observable LEH expressions on M1, CFT may be calculated using PK counts and month calculations. 104 PK were counted on the tooth surface, approximate to 2 years. It could be argued that a hypoplastic defect may express itself towards the upper cervix of the tooth, at a similar point to LEH 1 on M1 (figure 3), perhaps signifying the same stress event. However, there are no indicators evident enough to warrant the identification of a LEH expression.

Above: Figure 4 : Molar 2

Below: Table 3

	LEH	PK	Days	Months	Mean PK	Mean Months
Duration	1	21	147	4.8	21	4.8

M2: Observations

M2 shares a similar lack of visible LEH expressions as M1, though the one recognizable hypoplasia on the tooth represents a similar monthly amount as both P3 and P4, approximately 4 months. It does appear later and further up towards the tooth cervix; however, it's possible it could correlate with LEH 4 on P3 (figure 1), and perhaps the expression is on slightly different spots on the teeth. This major stress event, uninterrupted by breaks, represents a period of prolonged seasonal stress that takes up about ¼ of the year illustrated from PK 100-140, and it's also interesting to note that this event comes towards the end of the CFT; approximately 2 years into crown formation, out of the average 2.7 years for total development. This may indicate that there was likely a period of stress associated with the end of the weaning period. Having to transition to adulthood and self-sufficiency during periods of environmental alteration would only exacerbate the physiological stress an individual faces, which is visible in the hypoplasia that appear on the tooth surface.

12. Results and Discussion

Monthly intervals calculated through the application of periodicity estimates on PK appear slightly irregular, and defects vary quite substantially from year to year, as seen in P4, with one year exhibiting one hypoplasia, and the subsequent years having 3 and 2 hypoplasia respectively (figure 1), though with deviations from this pattern appearing M1 and M2 which show little or no LEH expressions (figures 3 and 4). This yearly irregularity in seasonal stress events is, as noted with P4, not correlated with an annual seasonal cycle, which would appear consistently on the enamel surface. Instead, we see sporadic and inconsistent hypoplastic defects, a reflection of an increased seasonality characteristic of the Late Miocene. It is also the case that both P3 and P4 exhibited a hypoplastic defect (LEH 1 in both specimens) that was significantly longer than the following hypoplasia, representing the same major stress event, extending for a prolonged period of time during the year (Hubbard et al. 2009). It can be observed that the first discernable LEH feature on both teeth exhibit an increased length compared to the following hypoplasia. This may point to an environmental event that differed considerably from subsequent periods and resulted in resource scarcity that acted as an intensified pressure on *H. crusafonti*.

Also of note is the frequency of LEH features on the teeth. Each period of seasonal stress, has an accompanied depression of enamel, denoting the negative physiological effects that were experienced by *H. crusafonti* (Cuozzo, Ungar, & Sauther 2012; Hubbard 2009). We see *frequent* seasonal irregularities illustrated through these markers, also exhibiting a lack of adaptive variability expressed by *H. crusafonti* in response to these conditions.

Tooth	Great ape	CFT (Days)	CFT (Years)
P3	*H. crusafonti*	994	2.7
	Chimpanzee	803	2.2
	Orangutan	_____	_____
P4	*H. crusafonti*	1120	3
	Chimpanzee	1401	2.2
	Orangutan	_____	_____
M1	*H. crusafonti*	728	2
	Chimpanzee	867	2.5
	Orangutan	1204	2.9
M2	*H. crusafonti*	980	2.7
	Chimpanzee	1084	3
	Orangutan	1200	3.3

Table 4: Great ape CFTs (Bonis, Koufos, and Andrews 2001; Smith et al. 2015) M1-Molar 1, M2-Molar 2, P3-Premolar 3, P4-Premolar 4

Results appear concordant with prior estimates of CFT, and there was a notable similarity between CFTs estimated for *H. crusafonti* and those already established for *Pan troglodytes* (table 4). It's observed in table 4 that *Pan* has an increased CFT for both premolars, while *H. crusafonti* has increased molar CFTs. P3 and P4 orangutan estimates were not available. It's important to note that these numbers *can* vary, however, the ones displayed would normally be the benchmark for evaluations.

CFTs in the three great apes can be compared against one another to help illustrate lengths in life histories (primarily through the analysis of *Molar 1*) and examining hypoplastic defects following the complete collection of CFTs can enable us to better understand how length of physiological development influences how outside stressors impact an individual (Birch &

Dean 2014). CFTs calculated for *H. crusafonti* were 2.7 years (P3) compared to 2.2 years in *Pan*, 3 years (P4) compared against 2.2 years in *Pan*, 2 years (M1) compared with 2.5 years in *Pan* and 2.9 years in *Pongo*, and 2.7 years (M2) compared against 3 years in *Pan* and 3.3 years in *Pongo*. It is observed with both M1 and M2 that the CFTs for *H. crusafonti* are distinctly reduced in comparison to *Pan* and *Pongo* (a common developmental trend as we retreat back through our evolutionary timeline). The great ape with the second lowest CFT is *Pan* (as CFT in M1 is the primary indicator of life history length), though only slightly. *Pan* is recognized as having one of the shorter CFTs among modern great apes, alongside Gorillas (McGrath et al. 2018; Guatelli-Steinberg et al. 2012). After *Pan* comes *Pongo,* exhibiting the highest CFT estimates seen among the hominid subjects (Smith et al. 2015). Orangs sit as the individuals with the highest CFT among the great apes. As we revisit our evolutionary history, our hominid ancestors begin to have increasingly reduced CFTs, and alongside that, briefer life histories. This is the commonly accepted understanding of how CFTs function evolutionarily in great apes, as CFTs are an expression of the development an animal goes through during it's growth, or, in other words, act as proxies for reconstructing life histories. CFT lengths are indicative of an animal's development. so, it's no coincidence that the great ape with the highest CFT count (among living hominids, *Pongo*), has the most prolonged weaning period and life history (Grehan & Schwartz 2009).

Considering the lifestyle and habitat similarities between *H. crusafonti* and *Pongo*, it's significant that there is a marked divergence in CFT, and therefore a difference in weaning periods and life histories between the two. Extended weaning periods are generally correlated with the necessary development of more skills that are needed in adulthood, and therefore, life history is also extended (Kennedy 2005), and the compulsory acquirement of more skills during

development is commonly associated adaptation to a specific niche or habitat (Carne, Semple, and Lehmann 2015). Orangutans can live under the care of their mother for up to 8 years (Kennedy 2005) to develop the proficiencies needed to properly exploit their ecosystem. Among great apes, this is timeframe is known as the weaning period. This causes them to be especially vulnerable to seasonal variability, variability that disrupts the behaviours that have been developed over their entire lives. In a tropical forested environment, *H. crusafonti* and *Pongo* exhibit many specialized traits that enable them to thrive under very specific and consistent environmental circumstances (Grehan & Shwartz 2005; Carne, Semple, & Lehmann 2015); however, it's clear through the analysis of LEH frequency/stress event lengths on dental surface remains that this, in an unstable environment, acts more as a detriment rather than a benefit. It is understood in Primatology circles that orangutans exhibit the most hypoplastic defects of all the great apes (Skinner 2014), and through analyzing previous research, as well as our own fossil teeth, *H. crusafonti* also faced many environmental stressors as it's ecosystem faced intensive environmental alteration during the MMD.

Frequent expressions of hypoplasia correlated with consistent enamel defects suggests that environmental stress events were undeniably having noticeable physiological effects on *H. crusafonti* (Guatelli-Steinberg et al. 2012; Chollet & Teaford 2010). On P4, we see as many as 6 hypoplasia expressed on the enamel surface, a marked indicator of the stress induced through increased environmental variability and seasonality. As emphasized throughout this research, *H. crusafontis* decline towards the end of the Miocene had much to do with the dramatic seasonal fluctuations of the time, provoked by the MMD (Methner et al. 2020), but more importantly, it was exacerbated by their high levels of specialization which would lead to increased environmental sensitivity. Hypoplastic defects reflect this increased seasonality, as well as how it

inhibited the development and persistence of *H. crusafonti* and other great apes of the Late Miocene. These observations and subsequent interpretations lead to significant conclusions on the similarly precarious situation of great apes in the age of the Anthropocene. Orangutans are facing extinction as a result of increasingly erratic seasonal patterns and habitat deterioration (Felton et al. 2003; Carne, Semple, & Lehmann 2015). Although orangutans posses useful adaptive traits that allow them to withstand some level of environmental variability (eg. fallback feeding), they, like *H. crusafonti*, face unique environmental pressures as a result of its specialized behaviours suited to a uniquely warm and tropical-forested environment. Subsequently, the orangutan is currently one of, if not the most, severely impacted great ape species as a result of climate change (Felton et al. 2003; Carne et al. 2015).

There is one additional factor that concerns not the similarities between *Pongo* and *H. crusafonti*, but a key difference that will allow for complete interpretation of modern great ape survival and responses to the Anthropocene. Anthropogenic environmental alteration was not a factor in the Late Miocene, as *Homo sapiens* were still millions of years away from making their evolutionary debut. Compared against ancient climate fluctuations, current anthropogenic climate trends exhibit an accelerated degree of speed, even when compared against some of the most intense climate upheavals in prehistory. The rate at which the global climate is changing remains a significant factor in the increasing rate of ecosystem deterioration. Primates, and more specifically, great apes, cannot keep up. If proper conservation efforts are to be adopted moving forward, these findings must be taken into consideration. At the rate that anthropogenic environmental alteration is destroying the planet's ecosystems and biodiversity, it's highly likely that orangutans will face an eventual extinction. The incredibly varied and extraordinary family of great apes has lived on our earth for millions of years, radiating and diversifying onto all

corners of the globe. Now, their specializations have virtually trapped them where they are, relegating all to regions bordering on the equator. But through the study of both modern and ancient climate events, as well as past and current great apes' responses to environmental alteration, one group of great apes, *Homo sapiens*-our own species- might be able to use that knowledge to formulate plans to limit the impact of climate change and protect great apes like orangutans from the environmental upheavals of the Anthropocene.

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