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SAPIENT

The Undergraduate Journal of Biological Anthropology

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Sapient is Columbia University's peer-reviewed undergraduate journal of biological anthropology. Founded in 2012 to give undergraduates at Columbia a place to share and reflect upon bioanthropological works of academic and artistic merit, *Sapient* has continued to develop. For questions, comments, or to get involved visit sapientjournal.com.

Editorial Board

Front/Back Cover Art by Anna Oppenheim
Layout and Design by Lily Kuhn and Juliet Azé

Letter from the Editors

Dear Reader,

On behalf of the *Sapient* editorial board, we are proud to share the 10th Volume of *Sapient*, Columbia University's Undergraduate Journal of Biological Anthropology. This year's volume features papers from a wide range of topics in biological anthropology as well as a vast body of visual artwork and poetry. All of these academic and creative works showcase the breadth of students' interests as well as their various talents. We hope that you find the papers and creative works as intriguing and inspiring as we did.

After several years of uncertainty and adjustment due to the Covid-19 pandemic, this year we were able to increase our in-person activities. This year's editorial board expanded, with several new and highly motivated members joining in the fall. We were impressed by the dedication and team spirit that this year's editorial board brought to the journal and are excited to see what the future holds for this growing team. What brought everyone together was our common commitment and motivation to share these works with the wider community and make Volume 10 a rich, stimulating and creative publication.

One of us (Adam) will be continuing this work next year, along with the rest of the editorial board. The other (Juliet) is graduating, but is excited to see where *Sapient* ends up in the years to come. After this year of expansion and great team bonding, we are optimistic that the next year will bring even greater exposure to the journal and lead to further fascinating publications.

To those reading, thank you for making our work worthwhile. We hope that you enjoy reading this volume as much as we enjoyed creating it.

Adam Vogt and Juliet Azé, *Co-Editors-in-Chief.*

Table of Contents

Acknowledgements

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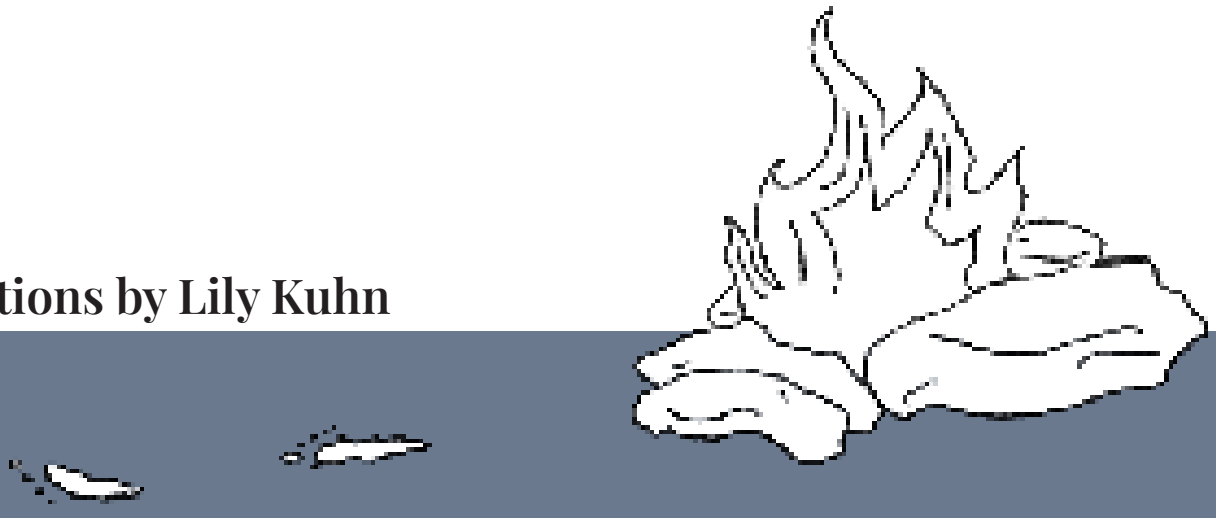
Haiku for *Homo erectus*
By Adam Vogt

Homo erectus
Bringing us fire and fortune
Our worlds at your feet

Illustrations by Lily Kuhn



Energetics and the Evolution of Great Ape Locomotion

Ana Reif, *Columbia University*

Selection for incredibly energy-efficient terrestrial locomotion may have ultimately caused hominins to adopt bipedalism (Pontzer, 2017). The same is not necessarily true for the evolution of the great apes, humans' closest relatives, and their respective locomotor modes. This paper aims to determine the extent to which energetics has been the driving force behind great ape locomotor evolution.

LOCOMOTOR ECONOMY THEORY AND MAMMALIAN TRENDS

There is a finite amount of energy that any given animal will be able to secure during its lifetime. This means that every energy expenditure for a given function represents a cost that will be deducted from the total energy they have to devote to all energetic processes (Hill, 1993). Many of these processes, such as development and reproduction, directly affect individuals' fitness (Hill, 1993). Therefore, it makes sense that natural selection would favor efficient energy expenditure wherever possible to ensure enough is left over for these obligatory processes (Spence *et al.,* 2022). Locomotor capability affects animals' fitness, as it is typically necessary for finding food, avoiding predation, and facilitating social interactions (Reilly *et al.,* 2007). In primates, locomotion's dynamism as part of the energetic budget reflects this relationship with fitness.

Locomotor economy refers to the distance an animal travels per unit of energy, scaled by the animal's mass (kg m J^{-1})(Pontzer, 2017). It is therefore the inverse of the energetic cost of transporting an animal a given distance. Locomotor economy can be measured by proxy using trackers on captive or wild animals that record information about heart rate, oxygen consumption, and or dynamic body acceleration, or it can be modeled using morphological data (Shepard *et al.*, 2013; Spence *et al.,* 2022). Naturally, animals cannot always move with perfect efficiency--locomotion efficiency is subject to several limitations, including behavioral, morphological, and environmental factors (Shepard *et al.,* 2013). Environmental constraints, though generally more static for terrestrial animals as opposed to avian or aquatic animals, can include substrate penetrability and topography, as well as superstrate characteristics (material such as grass that the animal must expend energy to displace before their foot contacts the substrate) (Shepard *et al.*, 2013). Morphology can restrict an animal's range of motion or dexterity, meaning it is not able to take advantage of all strategies and postures that may afford other animals greater efficiency. Finally, behavioral constraints generally relate to animals' gaits, travel speed, route selection, and more (Shepard *et al.*, 2013). These constraints mean that an animal's locomotor economy is a reflection of natural selection for many aspects of its niche, not just maximum efficiency.

Across quadrupedal mammals, locomotor costs scale allometrically with body size (Shepard *et al.,* 2013; Raichlen and Pontzer, 2021; Spence *et al.,* 2022). The cost of transportation of each kilogram of mass for a small animal is much higher than the cost of transporting each kilogram of a larger one (Reilly *et al.,* 2007). At the simplest level, locomotor costs are mainly associated with muscle activation, so animals that use more of their muscles relative to body size in each stride will have larger costs (Kozma *et al.,* 2018; Raichlen and Pontzer, 2021). As a result, body posture is closely related to the cost of locomotion. In animals with crouched body postures (joints remain flexed throughout a movement), muscle mass represents a larger proportion of total body weight than in animals with erect postures (joints largely remain extended) (Raichlen and Pontzer, 2021). This is partly because erect limbs have a greater effective mechanical advantage than flexed limbs, meaning the same limbs can be moved using less relative force depending on their postures. In turn, erect posture is generally

associated with larger-bodied mammals, while crouched posture is associated with small animals (with notable exceptions) (Polk, 2004). According to Reilly *et al.* (2007), body size and posture effectively characterize animals' locomotor costs, and large animals tend to ameliorate the high absolute costs of locomotion with extended postures that confer a mechanical advantage.

GREAT APE BODY POSTURE AND ENERGY EXPENDITURE

Great apes' locomotor capabilities, and therefore costs, are modulated by specific biomechanical features. Great apes, like most other primates, tend to support a relatively large proportion of their body weight with their hind legs, whereas other mammals rely more heavily on their forelimbs (Raichlen and Pontzer, 2021). This trait is likely related to hominoids' drastically increased glenohumeral mobility compared to most monkeys, which is crucial to suspensory locomotion and by extension orthograde posture (Arias-Martorell, 2019). Correspondingly, hominoids have scapulas placed more dorsally rather than laterally, freeing up the shoulder for more dynamic movements (Arias-Martorell, 2019). Additionally, great ape pelves have long ischia which prevent full extension of the hip; this feature represents a contrast between great apes and hylobatids and between great apes and humans (Lewton and Scott, 2017). Together, these features may represent adaptations for arboreal locomotion that constrain great apes' typical ranges of terrestrial hindlimb motion (Kozma *et al.,* 2018).

Analyses of great ape body posture are also necessary to characterize their locomotor efficiency. Great ape locomotion is generally associated with flexed-hip and flexed-knee postures in all locomotor modes, which is incongruous with their large body size (Polk, 2004; Raichlen and Pontzer, 2021). Though great apes are capable of extending both their hips and knees to a degree, they never extend them at the same time during locomotion (Raichlen and Pontzer, 2021). Relevantly, some studies (Sockol *et al.*, 2007; Pontzer *et al.*, 2014) have reported that great apes have higher-than-predicted locomotor costs for their body size when compared to humans, though there is disagreement as to whether these costs are significantly different from those of generalized endotherms (Steudel-Numbers, 2003).

Similar to other mammals, great apes adopt diverse gaits and body postures for different purposes, making it difficult to categorize them definitively by locomotor mode (D'Août *et al.,* 2004; Thorpe and Crompton, 2006; Reilly *et al.,* 2007). In general, knowledge of the locomotion of chimpanzees and bonobos is much more robust compared to gorillas and orangutans (D'Août *et al.*, 2004; Sockol *et al.*, 2007; Pontzer *et al.,* 2014), though all great apes are known to use quadrupedal or quadrumanual gaits habitually (Finestone *et al.*, 2018). Still, broad divisions are possible. Chimpanzees, bonobos, and gorillas all use knuckle-walking as a primary means of locomotion, over 80% of their total locomotor repertoire (Simpson *et al.,* 2018). In contrast, orangutan locomotion is more frequently arboreal (strictly arboreal for some) and is dominated by orthograde suspensory locomotion, particularly clambering and swinging (Cant, 1987; Thorpe and Crompton, 2006; Manduell *et al.,* 2012). Though orangutans are capable of forming knuckle-walking wrist positions, they fist-walk rather than knuckle-walk when moving terrestrially (Cant, 1987; Simpson *et al.,* 2018). All great apes have been observed to use vertical climbing and bipedalism (terrestrial or arboreal) to some degree in addition to their primary locomotor modes (Isler, 2004; Manduell *et al.,* 2012; Simpson *et al.,* 2018). Additionally, the diversity of locomotor profiles may vary significantly within great ape groups based on species and subspecies divisions (Loken *et al.,* 2013; Williams *et al.,* 2023). Understanding the energetic costs of these gaits, and the circumstances that cause hominoids to modulate their gait, is essential to the full picture of great ape locomotor evolution.

These hominoid gaits tend to have similar energetic costs despite major functional and postural differences, though some are more costly than others. Notably, chimpanzees and bonobos, which are the least locomotion-specialized great apes, seem to have relatively large locomotor costs across gaits (Williams *et al.,* 2023). This characteristic is possibly the result of trade-

offs between adaptation for frequent terrestrial walking and arboreal climbing, which are both essential to chimpanzee food allocation (Pontzer and Wrangham, 2004). Other great apes are comparatively better adapted for either terrestrial quadrupedalism or arboreal, suspensory clambering (Williams *et al.,* 2023).

To assess relative gait efficiency, Pontzer *et al.* (2014) investigated the metabolic costs of bipedal and quadrupedal locomotion in captive chimpanzees. In this study, five chimps were trained to walk and run bipedally and quadrupedally on a treadmill while wearing a plastic mask connected to a vacuum air stream, allowing the researchers to calculate oxygen consumption during physical activity as a proxy for metabolic rate. They found that chimps were able to reach similar speeds independent of posture and that most chimps did not show a statistically significant difference between metabolic rate during bipedal and quadrupedal locomotion. In using both of these gaits, the chimpanzees expended 41% more energy than they had predicted based on mammalian energetics trends, confirming the assumption that chimpanzees have a relatively high cost of locomotion in several contexts. The study has its weaknesses; the sample size was quite small (five) and the data showed significant variance, indicating that the results might differ if the study were to be reproduced. Additionally, the chimps were privately owned and had been trained from a young age to act in movies and television, meaning that their physiology and behavior could differ wildly from most captive chimpanzees, let alone chimpanzees in the wild. Though it provides important evidence for the basis of energetic theory in chimpanzees, this study may not be generalizable (Pontzer *et al.,* 2014).

Complementarily, gait selection in chimpanzees may not have a strong relationship with differential locomotor efficiency. Pontzer and Wrangham (2004) suggested that chimpanzees choose gaits independently of their relative energetic costs, indicating that their locomotor adaptations have purposes other than saving energy. They were responding to the contradiction that chimpanzee terrestrial locomotion is thought to be slow and inefficient, but that locomotor efficiency is likely to be a strong selection pressure based on ecological and life history variables (Pontzer and Wrangham, 2004). Resultantly, they predicted that arboreal locomotion would be more efficient than terrestrial locomotion to account for this discrepancy to some extent; it is assumed that any morphologies that may allow efficiency in arboreality do not confer the same advantage in terrestrial locomotion. The new data Pontzer and Wrangham (2004) collected were not entirely consistent with this hypothesis. Any energetic advantage the chimpanzees had in the trees was offset by the much larger (10x) distance they traveled on the ground, resulting in a net cost when compared with the hypothesized energetic expenditure values. Pontzer and Wrangham (2004) therefore concluded that chimpanzees use different forms of locomotion because of factors such as predator avoidance and safety from falls– energetics must be a low priority and likely did not contribute strong selection pressures in chimpanzee locomotor evolution. Otherwise, the costs of terrestrial locomotion would not dwarf the energy saved by arboreal locomotion.

Orangutans, on the other hand, are more highly specialized for arboreal locomotion (Thorpe and Crompton, 2006). It follows that their locomotion should be efficient relative to chimpanzees, as they have made fewer evolutionary trade-offs to be able to succeed terrestrially. In general, orangutans have extremely low daily energy expenditure (DEE) compared to humans and other mammals– three standard deviations below the mean (Pontzer *et al.,* 2010). In a study of orangutan metabolism and energy allocation, locomotion took up around 5-9% of DEE in adult orangutans, which is large relative to the expected 4% based on similarly sized mammals (Pontzer *et al.,* 2010). Pontzer *et al.* (2010) thought that despite being higher than the general mammalian locomotor energy expenditure, these data still reflected high locomotor efficiency because of orangutans' increased physical activity levels in the study population and broadly in the wild. Pontzer *et al.* (2010) also suggested that this low energy throughput is a feature of orangutan metabolism, but they do not connect it to morphological adaptation for locomotor efficiency. Behavioral

factors such as the selection of flexible branches to assist in swaying and limiting height changes may ultimately play a larger role than morphology in the overall efficiency of arboreal locomotion in orangutans (Halsey *et al.*, 2016). Unfortunately, there have not been studies conducted on orangutan metabolism and locomotion directly like there are on chimpanzees (Halsey *et al.*, 2016). There is also not a lot of data comparing the proportion of DEE used for locomotion in orangutans with values in other great apes, so it is tricky to draw conclusions about the role of locomotor economy in the recent evolution of orangutans relative to chimps or gorillas.

The relationship between gorilla locomotion and energetics is a comparatively neglected topic. There have not been many studies relating gorilla metabolism to locomotion in recent years. Though gorillas are terrestrial knuckle-walkers similar to panins, several morphological and behavioral factors should prevent scientists from assuming the groups' energetic similarity, or even from modeling gorilla energetics based on chimp or bonobo data. First, gorillas and panins have divergent behavioral patterns: in general, gorillas are more terrestrial than chimpanzees, though arboreality varies widely between gorilla species, likely in relation to the amount of fruit in their diet (Williams *et al.,* 2023). Additionally, knuckle-walking in panins and gorillas evolved independently after they split from their last common ancestor, and as a result, there are functional differences in their forelimbs and hindlimbs: gorillas use an extended elbow posture whereas chimpanzees keep their elbows flexed while knuckle-walking (Arias-Martorell *et al.,* 2021). Gorillas also have a more human-like, plantigrade heel morphology compared to chimpanzee heels, which tend to contact the ground at the same moment in the stride as the midfoot (Hu *et al.*, 2021; Williams *et al.,* 2023). There is also some evidence that panins and gorillas exhibit functional differences in the kinematics of vertical climbing; Isler (2004) found that bonobos and gorillas have marked differences in speed and joint extension during climbing that cannot be explained by the size differential alone.

Locomotor profiles are not stagnant; recent environmental trends are affecting hominoid locomotion and may have lasting evolutionary effects on their overall locomotor economies (Druelle *et al.,* 2020; Widyatsu *et al.*, 2022). The following studies provide evidence that apes are motivated to consciously modulate their gaits based on non-energetic factors. Druelle *et al.* (2020) discussed the relatively infrequent (though significant) behavior of arboreal leaping in bonobos becoming obligatory as a result of human encroachment. In recent years, bonobos' natural habitats in the Democratic Republic of the Congo have become increasingly fragmented by roads and other human structures, making bonobos' gap-crossing strategies more easily observable. Bonobos generally display the capacity for landing large jumps through the canopy, potentially saving energy when compared to slower terrestrial gap-crossing strategies (Druelle *et al.,* 2020). They are more competent leapers than chimpanzees are, and these abilities may be the cause of some of the anatomical differences between chimpanzees and bonobos. This ability is not uncommon among primates– gibbons are especially adept at leaping across gaps– but it is especially notable in bonobos because larger-bodied primates are at greater risk for serious injury when they fall from trees due to larger impact forces (Druelle *et al.,* 2020). In habitats that are not frequently disturbed by humans, it may ultimately be safer to descend from the trees and cross gaps terrestrially rather than arboreally, however, the risk posed by human traffic on the ground may neutralize the risk of injury from falling (Druelle *et al.,* 2020).

Druelle *et al.* (2020) suggested that bonobos are ultimately opting to take large leaps because they can effectively reduce the total energy expenditure of the action using route selection and posture modulation. They observed that bonobos select branches to leap from based on their flexibility, but do not propel themselves by pumping the branches to increase the recoil energy of the substrate like some monkeys do. They also dissipate kinetic energy on landing by swinging from the branch, preventing injury. A key observation of this study is that these bonobos made their posture pronograde before leaping, presumably to increase drag, giving them greater

control over their landings. Continuation of these conditions may result in bonobos having a heavier reliance on arboreal leaping. This is just one example of primates coping with human-induced selection pressures.

Widyatsu *et al.* (2022) observed similar environmental disturbances and their effects in orangutans. Forest disturbances such as wildfires and human land-use changes in Borneo are causing a great deal of stress on orangutan populations, and to cope they have been spending more time on the ground. This study modeled orangutan habitat loss due to forest fires and the resultant change in energy expenditure orangutan populations would face in order to find food and mates. As previously discussed, orangutans are adapted to arboreal life and their terrestrial locomotion is likely to be relatively inefficient. Habitat fragmentation would probably impact the energetics of orangutans as they would likely have to travel farther on the ground in between forest patches in order to find food. Widyastsu *et al.* (2022)'s models suggested that orangutans in disturbed habitats are more likely to experience an energy deficit as they will be motivated to move inefficiently along the ground more frequently.

CONCLUSIONS

Ultimately, analyses of great ape locomotor energetics are stunted by the lack of evidence pertaining to diverse populations of great ape species. Research in great ape locomotion is frequently tied to the evolution of human bipedalism, which restricts the kinds of conclusions researchers aim to draw from the data they collect (Polk, 2004; Sockol *et al.,* 2007; Pontzer *et al.,* 2014). The overall lack of research on orangutan and gorilla locomotor energetics combined with the subtle, elusive nature of morphological and behavioral differences between subspecies of gorillas and orangutans makes it difficult to draw clear conclusions about the trajectory of great ape locomotor evolution.

Nonetheless, it seems that great apes are morphologically adapted to save more energy during arboreal locomotion than terrestrial locomotion (Finestone *et al.,* 2018; Arias-Martorell, 2019; Arias-Martorell *et al.,* 2021). This is consistent with hypotheses of a predominantly arboreal great ape common ancestor (Kozma *et al.,* 2018). The more recent transition to terrestrial locomotion in some species is reflected in lower energy efficiency during terrestrial locomotion (Pontzer and Wrangham, 2004). Great ape locomotor profiles seem to be influenced mainly by factors independent of energy expenditure, however, when possible they still seem to modulate their behavior to save energy, which demonstrates the continued presence of selection for lowered energy expenditure during locomotion (Thorpe *et al.,* 2007; Druelle *et al.*, 2020; Widyastuti *et al.,* 2022).

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Illustration by Althea Cohen-Porter

The Gibbons' Song
by Ava Rotondo

Pulsing tones, reverb
Piercing through the layers of the jungle
Landing softly on the
        waxy faces of the leaves
        brittle arms of the trees
        damp lungs of the earth.

A warning sign to some
but poetry to me.

An irreproducible duet.
Are we now one?

Painting by Avital Zeldin

Assessing the Role of Major Histocompatibility Complex (MHC) in Human Mate Choice: A Pathogen Driven Preference?

Natalie Sandoval, *Columbia University*

INTRODUCTION

This paper will examine the degree to which sexual selection expresses a Major Histocompatibility Complex (MHC) disassortative preference in humans. Two avenues of research have been studied in this regard: odor and facial attractiveness. Odor preferences have been highlighted as a primary mechanism by which humans recognize MHC genotypes (Yamazaki *et al.*, 1998). In their investigation of facial attractiveness, however, Roberts *et al.* (2005) yielded evidence that suggests an MHC assortative preference. There is speculation that these contrasting forces could work as a "balancing act," resulting in intermediate genetic variability (Nowak *et al.*, 1992; Havlicek and Roberts, 2009). Data collected from varying populations have yielded divergent results in terms of MHC-similarity between partners (Rosenberg *et al.,* 1983; Hedrick and Black, 1997; Ober *et al.*, 1997). Given mixed results from MHC population studies, in combination with the conflicting odor and facial studies, achieving some intermediate diversity is the most plausible conclusion.

Interaction of biological and social factors appears to be responsible for the great variation across populations. Contextual variables, including life history, cultural practices, and hormonal contraceptives create mating patterns that affect the frequency of MHC heterozygosity across populations (Pollack *et al.*, 1982). Adaptive mate choice may be interrupted by beauty products such as perfume that obscure the transmission of genetic information through odor (Havlicek and Roberts, 2009). Health outcomes and degree of susceptibility to infectious disease in MHC homozygotes as compared to heterozygotes is one further application of this research. This includes fertility and pregnancy outcomes, as a growing body of research ties fertility issues with higher rates of allele sharing in couples (Ober *et al.,* 1998; Beydoun and Saftlas, 2005).

BACKROUND

Studies of vertebrates, particularly those conducted with mice and rats, have directed increased attention toward the role of the Major Histocompatibility Complex (MHC) in mate selection. Yamazaki *et al.* (1976) demonstrated that male mice chose MHC dissimilar female mates, using odor cues to guide their choices. Though the precise manner in which MHC molecules influence body odor is an area of debate, Wobst *et al.* (1998) suggested that these molecules are present in human body liquids. These create unique odor profiles, dubbed "odortypes" by Yamazaki *et al.* (1998), capable of communicating individual genetic information to other members of the species. In humans, the MHC is sometimes referred to as the human leukocyte antigen (HLA) system because these histocompatibility antigens were initially discovered and described as utilizing antibodies to attack leukocytes, or white blood cells (Choo, 2007). This paper will evaluate the connection between human mate choice and the MHC, as expressed through various proxies.

Infectious diseases have exerted a strong selective force on human populations, especially since the first epidemiological transition to settled agriculture, shaping allele frequencies (Armelagos *et al.,* 1996). Genetic adaptations such as the sickle-cell allele have been identified as one response to pathogenic infection (Luzzatto, 2012). It follows that the MHC, which plays such a crucial role in pathogen resistance, may contain markers of genetic adaptation to infectious disease. Individuals inherit MHC alleles from both parents, meaning heterozygotes have more antigen diversity than homozygotes (Havlicek and Roberts, 2009). The Pathogen Driven Selection Hypothesis contends that greater antigen diversity gives heterozygotes an immunity advantage, as they are able to recognize and respond to more pathogens (Penn *et al.,* 2002).

The concept of an MHC heterozygote advantage is supported by evidence from Black and Salzano (1981) who noted a significantly higher heterozygote frequency in the Indigenous South American population they studied, departing from the Hardy-Weinberg equilibrium. Results showed there were 39% less people with HLA homozygous haplotypes. In one subpopulation, there were even 56% fewer homozygotes than expected. Given the heterozygote advantage, the hypothesis claims, humans exhibit disassortative mating preference– that is, MHC dissimilar mates are preferred.

BODY

Wedekind *et al.* (1995) conducted the first odor study on MHC in humans. Their method, known colloquially as the "sweaty T-shirt test," has been replicated by many researchers since (Thornhill *et al.,* 2003; Santos *et al.,* 2005; Roberts *et al.,* 2008), making their experimental design significant to the field. They recruited a sample population of 49 heterosexual female and 38 heterosexual male students, noting their HLA–A, HLA–B, and HLA-DR antigens. By sequencing these genes, they were able to identify twelve distinct HLA-A alleles possessed by the subjects. The female and male students did not know each other prior to the study, eliminating the possibility of a preference created by outside data. The males wore a T-shirt for one night, and in order to reduce the confounding variable of perfumes and other odors, were given instructions to ensure 'odor-neutrality' (such as using non-scented detergent and refraining from smoking). The authors' concern with these variables speaks to the impact of modern cultural practices on mate choice. The precise manner in which perfumes and other odor-influencing substances interact with MHC has not been thoroughly examined.

The females were then tasked with rating the odors of the T-shirts. Six T-shirts were presented to each female rater: three worn by males with dissimilar MHCs and three worn by males with similar MHCs. The degree of similarity was determined by the number of shared HLA-antigens between each male and female. The females rated the odor of each shirt for pleasantness on a 1-10 scale. Averaging these ratings, Wedekind *et al.* (1995) found that female raters perceived the odors of MHC-dissimilar males as more pleasant. The female raters were also asked to compare the odors of MHC-similar and MHC-dissimilar males to the raters' own male partners. They reported a likeness between the odors of MHC-dissimilar males and their own partners twice as often as they reported a likeness between the odors of MHC-similar males and their own partners. This implies that MHC, as expressed through body odor, is significant in actual mate choice, with females expressing a disassortative preference.

Hedrick and Loeschcke (1996) criticized the experimental design and data of Wedekind *et al.* (1995) in a short correspondence. They noted that the female raters were sensitized to smell, given nasal sprays and informed on the aims of the study by the researchers. They cite the odor-neutrality instructions given to the males as evidence that the researchers' results have little real-world applicability. In terms of the data, they suggest that due to the slight difference between the pleasantness scores received by MHC similar males and the MHC dissimilar males (about 20%) and the small sample size, the findings of Wedekind *et al.* (1995) are biologically insignificant. Wedekind and Seebeck (1996) defended their study, noting they had attempted to discern if any MHC preference existed, even if it was slight. The elimination of confounding variables, such as smoking, was appropriate in this regard. Havlicek and Roberts (2009) concurred, noting that the effects of sensitizing the female raters to olfactory cues would not explain a systemic preference for MHC dissimilarity. It is possible such methodology could exaggerate this preference among female raters.

The results of other body odor preference studies have yielded similar results, noting a disassortative preference (Wedekind and Füri, 1997; Thornhill *et al.,* 2003). An outlier exists in Jacob *et al.* (2002). Using the odors of T-shirts from six heterosexual males, they asked 49 heterosexual females to rate the pleasantness of the shirts. The highest-rated odors came from males who shared more alleles with the female rater than the lowest-rated odors. On a scale of

0-7, with 7 being the greatest genetic distance, the median match between females and males was 2. The researchers concluded that MHC dissimilarity is only selected to an extent, suggesting a preference for a mate of intermediate genetic distance from oneself. These results have been criticized. Havlicek and Roberts (2009) note that the female raters were Hutterites, an insular religious community where inbreeding occurs. Jacob *et al.* (2002) justified this methodological choice because the Hutterites only have 67 HLA haplotypes, whereas outbred populations have an incredible quantity of HLA haplotypes. This limited number of haplotypes facilitated researchers in identifying whether the HLA-associated odors the Hutterite women chose were based on paternal or maternal alleles (or both). Extensive variation– including age– in the T-shirt-donating males potentially confounds the results of this study as well.

Facial attractiveness is an emerging area of study in regard to MHC-correlated mate preferences. Roberts *et al.* (2005) aimed to determine whether perceived male facial attractiveness, as rated by females, was correlated with the degree of genetic similarity between the participants. In a visual parallel to the Wedekind *et al.* (1995) experiment, heterosexual female participants rated the attractiveness of three photographs of MHC-similar males and three photographs of MHC-dissimilar males on a 1-7 scale. They were asked to rate the attractiveness of these males as mates in a short and long-term context. Examples of a short-term context, as explained to the participants, included a one night stand or affair; examples of a long-term context included a marriage or live-in partnerships. The authors found that females rated MHC-similar males more highly on average, a trend which is exaggerated in the long term context. They offered two explanations for the assortative preference. First, the authors contended that these results could be context-dependent, with females favoring stability and agreeableness in the long term more than attractiveness. They went on to posit that odor and facial preferences could be working in tandem to achieve a sort of genetic equilibrium in a mate. Visual cues may warn against individuals of extremely different genotype, while odor cues may warn against individuals of extremely similar genotype.

Roberts *et al.* (2005) attempted to eliminate confounding variables by using standard lighting, obscuring hairstyle and clothing, excluding males with beards, and directing the male subjects to wear a neutral expression. They also drew from an ethnically homogenous sample population, with both male and female participants being of white and British origin. This methodology was intended to control both degree of allelic diversity among participants and to diminish the impact of divergent cultural preferences in facial features (such as a strong preference for blue eyes that might impact a female participant's ratings).

One last approach to research in MHC-preference studies has been through behavioral evidence, namely collecting population data. These have yielded wildly divergent results. Havlicek and Roberts (2009) claimed this discrepancy is unsurprising, given the MHC contains polymorphic genes, which may require large sample sizes to discover statistical trends. Actual mate choice, they noted, is influenced by a bevy of other psychological, social, and physical traits. As Wedekind and Seebeck (2006) wrote, odor and facial attractiveness experiments only aim to discover if an MHC preference exists in isolation. These population studies may better evidence the degree to which MHC plays a role in mate selection in specific populations.

Ober *et al.* (1997) did find a pattern of divergent HLA haplotypes in Hutterite couples, discovering fewer HLA haplotype matches among spouses than expected. They concluded that within the Hutterite community, haplotype does influence mate choice, with a general disassortative preference. This conclusion complicates Jacob *et al.* (2002), which did not find a disassortative preference among Hutterite participants, but selection for an intermediate degree of genetic distance. Notably, Jacob *et al.* (2002) asked female Hutterites to rate men from outside their community, whereas Ober *et al.* (1997) studied married couples with both spouses of Hutterite origin. This difference in degree of genetic similarity may speak to the divergent results in preference. The results of Ober *et al.* (1997) may also be explained by the Inbreeding Avoidance Hypothesis. This explanation of the

frequency of MHC heterozygosity posits that it was an aftereffect of inbreeding avoidance, which increases average genomic heterozygosity. Given the isolated nature of the Hutterites, perhaps inbreeding avoidance has been an important priority for them, making a disassortative preference especially adaptive. This claim might be disputed by Hedrick and Black's (1997) study of a comparably insular population in South America; The authors found no pattern of HLA divergence among 11 South American Indigenous tribes, indicating no disassortative mating preference.

Chaix *et al.* reported in a 2008 study that heterosexual, European-American couples from Utah tended to choose MHC-dissimilar mates, though no such preference was found among heterosexual, African couples from the Yoruba population in Nigeria. The authors supported the hypothesis that odor cues influence mate choice. The discrepancy between different populations only furthers the uncertainty in this area of research and need for further inquiry. Chaix *et al.* (2008) suggested a variety of factors for the lack of MHC preference in the African couples they sampled: lack of MHC influence on this population, social factors that take priority, or an insufficient sample size. They also considered the idea that mates selected for an optimal, or intermediate, genetic distance. It is possible that MHC preference is regionally specific– that individuals with MHC alleles that offer resistance to the deadliest threats are selected for, not just blanket dissimilarity. This could explain the lack of MHC dissimilarity in the African couples.

Beyond investigating the existence of MHC preferences in populations, research has been conducted that bears practical and medical significance. Garver-Apgar *et al.* (2006) studied the relation between relationship satisfaction, infidelity, and MHC. They measured how many shared MHC alleles 48 heterosexual couples shared, then asked them to self-report their satisfaction within the relationship. They found that as the number of shared MHC alleles increased, female satisfaction decreased, infidelity increased, and female attraction to males outside of their relationship increased. These findings, albeit yet to be reproduced, suggest MHC could contribute to compatibility and permanence in romantic relationships.

If detecting MHC is an adaptive preference in mate choice, modern cultural practices may interrupt MHC signaling. In Wedekind *et al.*'s (1995) study, for instance, females taking hormonal birth control demonstrated an assortative preference, favoring the odors of MHC-similar males. Roberts *et al.* (2008) similarly demonstrated that among female participants who used the contraceptive pill, preference for the odors of MHC-similar males increased. The consequences of the suppression of an MHC-dissimilarity preference could affect marital relationships. Vollrath and Milinski (1995) note that changes to hormonal birth control use within a relationship, as in the case of couples trying for a pregnancy, could reduce levels of perceived attractiveness between them. Genotype similarity seems to have some bearing on fertility itself. Ober *et al.* (1998) found significantly higher rates of miscarriage in Hutterite couples who shared more HLA alleles. This was significant as the first study to examine pregnancy outcomes and HLA haplotype matching and could have widespread implications in the understanding of fetal loss in the broader population. A review by Beydoun and Saftlas (2004) affirmed this connection, stating that HLA is an integral part of normal fetal development.

SUMMARY AND CONCLUSIONS

Given the robust findings of MHC-driven mate choice in other vertebrates, most often mice, it seems plausible that MHC could influence human sexual selection (Yamazaki *et al.,* 1976; Alberts and Ober, 1993; Brown and Eklund, 1994). The intense selection pressure exerted by pathogens, especially since the advent of agriculture, has changed the human genome in demonstrable instances, such as the maintenance of the Sickle-cell allele in response to malaria (Luzzatto, 2012). The MHC's integral role in recognizing and responding to pathogens indicates that it may contain hints as to the extent to which pathogen driven adaptation has shaped the human genome. The T-shirt experiment conducted by Wedekind *et al.* (1995), the results of which have been successfully

replicated, suggested that odor is a prominent cue in detecting MHC. The authors demonstrated a disassortative mating preference when female subjects were solely prompted by odor. The mixed results of facial attractiveness studies and actual population samples indicate MHC-dissimilar preference is by no means universal. Odor, facial attractiveness, and various cultural factors influence the actual mate choices of individuals. This speaks to the specificity of adaptation– though some adaptations are shared by all humans, others are advantageous only in certain regions or contexts.

In terms of practical applications, public education regarding the influence of perfume and cosmetics on mate choice could affect the purchasing decisions of a mass number of individuals. It is possible that these modern beauty practices are obscuring helpful adaptive signals. General happiness and satisfaction within relationships, if truly impacted by degree of allele sharing, seems another avenue of research. The quality of interpersonal and family relationships is of concern for most individuals, and recognizing the factors at play could result in strategies to mitigate these challenges. There is a growing body of evidence to suggest that pregnancy outcomes are affected by allele sharing, which could potentially be mitigated through preventative care if recognized early. The health of the offspring themselves, provided less natural antigens than their peers, may also be a concern.

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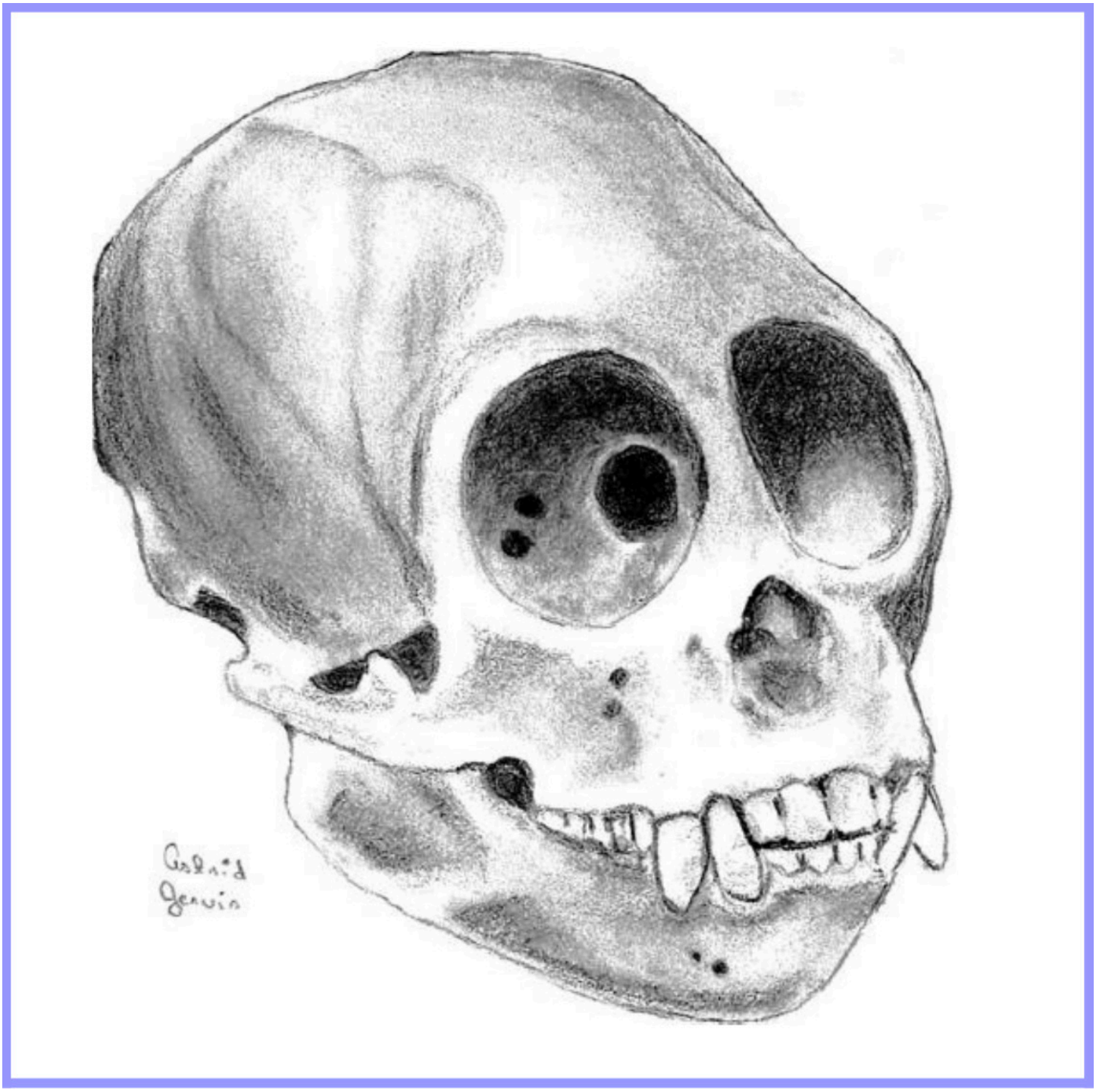
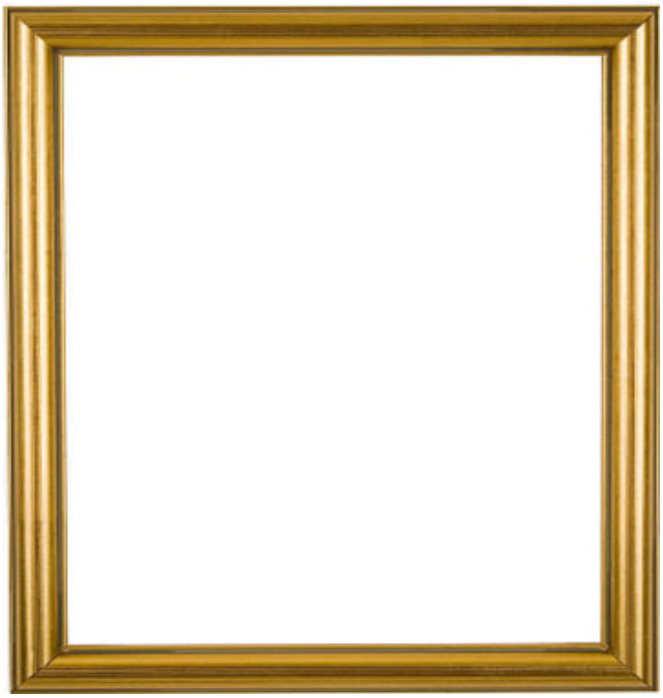


Illustration by Astrid Jervis

The History and Legacy of the Zealy Daguerreotypes

Anna Oppenheim, *Columbia University*



INTRODUCTION

In 1850, Harvard professor and prominent naturalist Louis Agassiz was invited by Dr. Robert Gibbes to study enslaved Africans in Columbia, South Carolina (Gates Jr., 2020). Gibbes commissioned photographer Joseph T. Zealy to create daguerreotypes of the enslaved individuals for Agassiz's analysis of racial difference (Gates Jr., 2020). These daguerreotypes of seven individuals, Alfred, Delia, Drana, Fassena, Jack, Jem, and Renty, are now referred to as the Zealy daguerreotypes (Rogers, 2020). The daguerreotypes were used by Agassiz to support his claims of the separate origins of human species and the innate biological inferiority of African people (Rogers, 2020). After their creation, the daguerreotypes disappeared for over 100 years until their rediscovery in the attic of the Peabody Museum of Archaeology and Ethnology at Harvard University in 1976 (Barbash, 2020). Since their reemergence, the Zealy daguerreotypes have been the subject of extensive scholarly research, artistic appropriation, and heated controversy (Murray, 2013; Smith, 2019; Barbash, 2020; Gates Jr., 2020; *Tamara Lanier v. President and Fellows of Harvard College*, 2022).

This paper will begin with an overview of the history of the Zealy daguerreotypes before discussing what is known about the lives of the seven individuals depicted in them. Next, it will discuss the use and circulation of the daguerreotypes following their rediscovery, focusing on the visual arts and on the *Lanier v. President and Fellows of Harvard College* Supreme Court case. The Zealy daguerreotypes viscerally illustrate the horrors of slavery and the role of the institution in creating harmful conceptions of African people; their ensuing circulation and controversy have transformed these images into icons of the brutality of scientific racism.

LOUIS AGASSIZ AND THE CREATION OF THE ZEALY DAGUERREOTYPES

Louis Agassiz was born in Switzerland in 1807 (Wallis, 1995). As a child, Agassiz developed a keen interest in the natural world, and in 1821, he began his first naturalist work, *Brazilian Fishes* (Rogers, 2010). The work was a comprehensive classification of over 500 species of Brazilian fish, and Agassiz devoted his treatise to famed comparative anatomist Georges Cuvier (Wallis, 1995; Rogers, 2010). Cuvier was one of the leading naturalists and foremost comparative anatomists of Europe (Gossett, 1997). He firmly believed that all species were created independently, and they did not change over geologic time; in other words, he believed in polygenism, or separate origins for each species (Gossett, 1997). Soon after the publication of *Brazilian Fishes*, Cuvier became Agassiz's mentor, and although Agassiz only worked with Cuvier for around a year before

Cuvier's death, his ideas firmly shaped Agassiz's view of the natural world (Rogers, 2010). Like Cuvier, Agassiz believed that all species were independently created; God created each creature specifically for the environment they occupied (Rogers, 2022). Following Cuvier's death, Agassiz moved to Prussia, where he became a professor of natural history (Rogers, 2010).

As Agassiz lectured in Prussia, in the United States, prominent paleontologist, anatomist, and geologist Dr. Samuel Morton was pursuing a different realm of naturalist inquiry: the study of human cranial variation (Gossett, 1997; Rogers, 2010). By the late 1830s, Morton had amassed a gargantuan collection of human skulls from around the world (Lurie, 1954). In 1839, he published *Crania Americana*, a comprehensive analysis of his collection and of human craniometric variation (Lurie, 1954). Notably, Morton used his measurements to classify his collection into five racial categories, and he tentatively claimed that "each Race was adapted from the beginning to its peculiar local destination" (cited in Rogers, 2010, p. 124). Morton would continue to research human racial variation, and he would soon become a prominent figure in the burgeoning debate about human origins in the United States (Gould, 1996).

In 1845, Agassiz published his own comments about the origin of humans, writing that all humans were united; unlike other species, they were created with the ability to occupy various ecological niches (Lurie, 1954). One year later, Agassiz traveled to the United States to lecture about his ideas about the origins of species and to meet with the prominent scientific minds of the Americas (Rogers, 2010). One of his first stops was to Philadelphia to meet with Dr. Morton and to see his collection of human crania (Wallis, 1995). There, Agassiz had his first encounter with people of African descent, and he began to form his initial conceptions of racial difference. About this first encounter, Agassiz stated:

> "I can scarcely express to you the painful impression that I received, especially since the feeling that they inspired in me is contrary to all our ideas about the confraternity of the human type and the unique origin of our species... Nonetheless, it is impossible for me to repress the feeling that they are not of the same blood of us." (Cited in Wallis, 1995, p. 43)

Agassiz's visit to Philadelphia was influential for both scientists; days after Agassiz left, Morton wrote his first explicit statement of his beliefs in separate human origins, and Agassiz's first lectures at Harvard similarly stated that the different races were independently created, contrasting the statements he had made in Prussia (Rogers, 2010).

The burgeoning polygenist views of Morton and Agassiz were one facet of the debate over human origins in the mid-19th century, and Agassiz's arrival in the United States coincided with the rise of its intensity (Gossett, 1997). Morton and Agassiz were two among numerous prominent voices espousing the polygenist view. Others included the physician Joseph R. Nott and Egyptologist George Gliddon, both of whom would go on to create the infamous *Types of Mankind*, a comprehensive analysis of human racial difference widely disseminated to the general public (Gossett, 1997). Morton, and his disciples Nott and Gliddon, argued that all humans were specifically distinct and that miscegenation between different racial types resulted in semi-sterile offspring (Gossett, 1997). The opposing side to polygenism was a belief in monogenism, which stated that all human races were the result of a single creation event and that the existence of miscegenation was proof of the unity of mankind (Gossett, 1997). This view was prominently promoted by religious scholars, most notably the reverend John Bachman (Rogers, 2020). Although polygenist views seemingly provided justification for enslavement, it is critical to note that proslavery sentiments were not confined to either side of the debate (Gould, 1996). Agassiz and Morton considered themselves anti-slavery, while Nott, Gliddon, and Bachman were firmly pro-slavery (Gould, 1996; Gossett, 1997).

Ideas about European supremacy were ingrained in the views of the major proponents on both sides of the debate, but despite their shared beliefs, the debate was vitriolic (Gossett, 1997). It came to a head in 1850 at the American Association for the Advancement of Science (Rogers, 2020). Agassiz, who by this time had achieved immense respect in academic circles

as a naturalist and had been promoted to Harvard professor, dramatically rejected ideas of the unity of mankind (Rogers, 2020). Unlike Agassiz's earlier lectures, this claim was incredibly public, and Agassiz's statements were quickly regurgitated by the press (Rogers, 2020).

Immediately following his declaration, Agassiz visited Dr. Robert W. Gibbes in Columbia, South Carolina, with the express purpose of examining enslaved African people to find support for his views (Rogers, 2020). Gibbes was a fan of Agassiz; he was incredibly well-connected, and he frequently corresponded with Morton (Rogers, 2010). Gibbes first asked Morton to invite Agassiz to the Gibbes household on his behalf in 1847 (Rogers, 2010). Although it is unclear why Agassiz decided to accept the invitation three years later, Gibbes was eager and willing to find enslaved Africans for Agassiz's research (Rogers, 2020). Although Gibbes was a slaveholder, none of the individuals used in Agassiz's research were from his household; instead, he used his status as a physician for enslaved people to find native-born Africans for Agassiz to research (Rogers, 2010).

Agassiz spent eight days in South Carolina, and he examined at least the seven individuals in the daguerreotypes, possibly more (Gates Jr., 2020). When Agassiz returned to Harvard, Gibbes commissioned the popular local daguerreotypist Joseph T. Zealy to photograph the enslaved individuals for Agassiz's continued morphological analysis and comparison (Gates Jr., 2020). It is crucial to note that the intent of Gibbes and Agassiz was not to photograph the individual; Delia, Jack, Renty, Drana, Jem, Alfred, and Fassena were seen as representatives of Agassiz's racial types (Rogers, 2006). Later that year, Agassiz published his findings about human variation in the July issue of the *Christian Examiner*; the article was titled "The diversity of origins of the human races." This was his first published statement on human origins, and it revealed both Agassiz's thoughts on the question of the unity of mankind as well as some of the specifics of his visit to Columbia (Lurie, 1954).

In his article, Agassiz reiterated the statements he made at the American Association for the Advancement of Science (Agassiz, 1850). He plainly states that the different races are physically and behaviorally distinct, and that they had separate origins. He also states that polygenist beliefs are not incompatible with religious beliefs, and that the theory should be separated from questions about the morality of slavery. Agassiz (1850, p.17) makes only one reference to his time in South Carolina, stating:

> "The writer has of late devoted special attention to this subject, and has examined closely many native Africans belonging to different tribes, and has learned readily to distinguish their nations, without being told whence they came; and even when they attempted to deceive him, he could determine their origin from their physical features."

Although it is not descriptive, it is clear that Agassiz analyzed the physical features of each individual, and that he spoke with them about their place of origin. At this point, Agassiz was certain that each broad race was a distinct species, but his visit to Columbia allowed him to make more distinctions within broad racial categories (Rogers, 2020). To Agassiz, the different tribes that he identified were all indicative of a separate origin (Rogers, 2010). There were not just five races, as Morton had previously identified, there were an indefinite number of races, and the daguerreotypes provided Agassiz with visual evidence of his claims (Rogers, 2010; Rogers, 2020). Additionally, Agassiz implies that he ignored the individual's assertions about their native nation, instead prioritizing his morphological assessment over the knowledge of the individual about their own history and heritage (Rogers, 2020). Following his publication of "The diversity of origin of the human races," Agassiz presented the daguerreotypes to members of the Cambridge Scientific Club (Rogers, 2020). He used the images as proof of the innate difference between Africans and Europeans and between different groups of Africans (Rogers, 2010). Agassiz never publicly displayed the images again (Rogers, 2020).

After the publication of Darwin's *On the Origin of Species*, evolution became the leading scientific view, and debates about origins faded (Gossett, 1997). However, Agassiz continued to espouse polygenist theory using the same

methods he had used in 1850 (Rogers, 2006). In 1865, Agassiz visited Brazil to photograph the racial morphology of Brazilians and provide more evidence for his ideas about the origin of mankind (Rogers, 2006; Isaac, 2015). Despite Agassiz's persistence, polygenist theory faded from discussions of natural science and racial difference (Gossett, 1997). Agassiz died in 1873; it is unclear if he gifted his collection, including the daguerreotypes, to Harvard during his life or if they were donated by his son in the early 1930s (Murray, 2013). Regardless, the daguerreotypes remained hidden in the attic of the Peabody Museum until they were rediscovered in 1976 (Murray, 2013).

Agassiz was one of the last vestiges of the once fervid debate over origins in the United States; however, Agassiz's views on race did not die with him (Murray, 2013). The daguerreotypes are a reminder of the horrid history and lasting legacy of this debate and of ideas of the innate inferiority of African people.

THE DAGUERREOTYPES AND THE PEOPLE THEY DEPICTED

Each of the Zealy daguerreotypes depicts the individual fully naked or in a state of partial undress (Gates Jr., 2020). Zealy took frontal, lateral, and rear views of the seven individuals, and although it is unclear how many daguerreotypes he originally took, fifteen remain (Rogers, 2010; Gates Jr., 2020). Robert Gibbes labeled each of the daguerreotypes with the first name of the individual, their occupation, relationships, information about their "owners," and their origin, as identified by Agassiz (Rogers, 2010). Jack, a driver, was thought to be from Guinea, and his daughter, Drana, was born in the United States (Rogers, 2010). Renty was from the Congo, and his daughter Delia was born in the United States (Rogers, 2010). Fassena was from the Mandika tribe, Alfred was from Foulah, and Jem was Gullah (Gates Jr., 2020).

Wills, probate and church records give some limited insights into the lives of Jack, Drana, Renty, Delia, Fassena, Jem, and Alfred (Hecimovich, 2020). Renty and Delia have the most extensive records. According to probate records, Renty and Delia worked at Benjamin F. Taylor's Grub Field Plantation until 1852, when they were sold with the plantation to Benjamin's sister-in-law Sarah C. Taylor (Hecimovich, 2020). At the time of the sale, Renty was valued at an unusually low amount, indicating that he may have been sick; in the daguerreotypes, he appears to have a tumor on his neck (Rogers, 2010). According to the descendants of Renty, he was known as Papa, and he taught himself and others to read the Bible (Tamara Lanier vs. President and fellows of Harvard College, 2022). He was married to an enslaved woman named Eady, and they had four children: Hector, Caesar, Molly, July, and Delia (Hecimovich, 2020). The family was intact while enslaved by Benjamin F. Taylor, but by 1852, Eady, Hector, Caesar, and July are absent in the probate records; it is not known what happened to them (Hecimovich, 2020).

Jack is a more common name than Delia or Renty, and thus it is more difficult for scholars to discern information from the probate records (Hecimovich, 2020). Church records suggest that both Jack and Renty were baptized at the First Baptist Church in Columbia (Gates Jr., 2020). There is little information about Drana (Hecimovich, 2020). Drana was not sold with Jack when the Grub Field Plantation was purchased in 1852; there is no Jack and Drana pair in Sarah C. Taylor's slave inventories (Hecimovich, 2020). She either passed away, was sold, or she ran away prior to the sale (Rogers, 2010).

Jem worked as a mechanic and an artisan for the building projects of Frederick W. Green. He was 60 years old in 1850 when the daguerreotypes were made (Hecimovich, 2020). It is likely that he worked in the city rather than on a plantation (Rogers, 2010). Alfred was a slave of John Lomas, a livestock owner with a small corn field. Alfred was one of nine individuals who worked on the field (Hecimovich, 2020). Fassena worked on the Woodlands plantation, owned by the prominent Hampton family (Hecimovich, 2020). He likely worked on the plantation until it was burned down in 1865 by the Union general William Sherman (Hecimovich, 2020). After the plantation burned down, he moved to Lower Richland County, South Carolina (Rogers, 2010).

The records of the lives of the seven

individuals is frustratingly sparse; for most of the individuals, scholars know very little about their relationships or their lives after the Civil War (Hecimovich, 2020). Unfortunately, most available records only describe the lives of the individual in relation to their enslaver (Rogers, 2010; Hecimovich, 2020). Following the rediscovery of the Zealy daguerreotypes, artists attempted to fill the gaps and give a voice to the individual.This incited a debate about the ethics of appropriating their images (Smith, 2019; Barbash, 2020).

THE DAGUERREOTYPES IN ART

In the 1990s, American artist Carrie Mae Weems visited the archives of the Peabody Museum of Archaeology and Ethnology to view the Zealy daguerreotypes (Barbash, 2020; Murray, 2013). Weems signed a contract promising not to use the images without the permission of the museum; despite this, she photographed the daguerreotypes and broke her contract with Harvard (Murray, 2013). The photographs that Weems took were used in her 1995 exhibition, *From Here I Saw What Happened and I Cried*. Weems modified images of Delia, Renty, Jack, and Drana with a red tint and a text overlay (Barbash, 2020). The text on the images reads: "You became a scientific profile/ a negroid type/ an anthropological debate/ & a photographic subject" (Murray, 2013, p.4). Harvard University threatened to sue Weems for breaking her contract, but they never followed through with the threat (Murray, 2013).

Weems's work attacks the role of the institution in perpetuating ideas of inferiority and giving scientific support to racism. In the text overlay, she directly states the role that Agassiz and other naturalists had in designating the African people as the racial other (Murray, 2013). In this respect, Weems arguably granted a voice to Delia, Renty, Jack, and Drana by transforming them into actors in her institutional critique (Barbash, 2020).

Although the response to the work was primarily positive (Murray, 2013; Raymond, 2015; Barbash, 2020), Weems was also criticized over the ethics of her use of the Zealy daguerreotypes. The daguerreotypes are fundamentally violent images; Alfred, Delia, Drana, Fassena, Jack, Jem, and Renty were stripped of their right to their own image and body, and Agassiz used their bodies to support theories that provided scientific justification for slavery (Lurie, 1954). Agassiz transformed the individual into an object for scientific analysis (Rogers, 2006). An argument has been made that each time these images are recirculated, each time they are published, and each time they are plastered to the walls of an art museum, the autonomy of the subjects is once again stripped (Raymond, 2015; Smith, 2019). Recontextualizing the images does not remove their history; as art history professor Cherise Smith (2019, p. 50) states:

> "Delia's and Drana's breasts are still exposed to viewers against their will... Moreover, the women's breasts...will always be available for inspection, for fetishization, and as illustrations, among other uses, regardless of the new context that Weems and/or I provide."

Carrie Mae Weems is not the only visual artist who incorporated and appropriated the daguerreotypes in their work. Other examples include Heidi Fancer's For Delia, which is a replica of Delia's daguerreotypes with the artist as the subject, and Sasha Huber's project known as Rentyhorn, which features a portrait of Agassiz made with metal staples (Barbash, 2020). Notably, both works critique the legacy of Agassiz and invoke the image of the Zealy daguerreotypes without directly appropriating the images. There is no clear answer to how viewers and artists should engage with images like the daguerreotypes, or whether it is ethical to appropriate and circulate them at all. This same debate and controversy over the Zealy daguerreotypes extends into the legal sphere (*Tamara Lanier vs. President and fellows of Harvard College*, 2022).

LANIER v. HARVARD UNIVERSITY

In 2019, Tamara Lanier sued Harvard University for emotional distress and for unauthorized use of the image of Renty (*Tamara Lanier vs. President and fellows of Harvard College*, 2022). Lanier had grown up with stories of African-born Papa Renty, and while documenting the oral history of her family, she

came across his daguerreotype (Vartanian, 2022). According to Lanier, her family's oral history of Renty and his descendents lined up with what information is known about Renty and his children (Vartanian, 2022). After acquiring this documentation, she contacted the Peabody Museum multiple times asking to be informed about research into the daguerreotypes; Harvard never responded (*Tamara Lanier vs. President and fellows of Harvard College*, 2022). In 2017, Lanier requested that Harvard give her Renty and Delia's daguerreotypes, but the institution did not acknowledge her request. Two years later, Lanier sued the university for emotional distress and ownership of the physical daguerreotypes (*Tamara Lanier vs. President and fellows of Harvard*, 2022). About her lawsuit, Lanier stated that she "as their lineal descendent...not only have standing to bring to claim, but also have a right to generational inheritance." (Cited in Vartanian, 2022, [Internet]).

The case was initially dismissed by the Superior Court of Massachusetts, and Lanier filed an appeal with the Massachusetts Supreme Judicial Court (*Tamara Lanier vs. President and fellows of Harvard College*, 2022). The Supreme Court ruled that Lanier had no rights to control the distribution of Renty's image, since there is both federal and state precedence that photographs are the property of the photographer, not the subject (*Tamara Lanier vs. President and fellows of Harvard College,* 2022). The photographs were commissioned by Gibbes, who gave the images to Agassiz; Agassiz or his family then gave those images to Harvard. Thus, they are the legal property of Harvard (*Tamara Lanier vs. President and fellows of Harvard College*, 2022). However, the court ruled that Lanier had sufficient grounds in her claim of emotional distress, since the daguerreotypes were the result of atrocities perpetrated against her ancestors, and Harvard's continued use of these images perpetuated this violence (*Tamara Lanier vs. President and fellows of Harvard College*, 2022). Since one claim was overruled, the case is still ongoing (Brockell, 2022).

As with the controversy surrounding the appropriation of the Zealy daguerreotypes in art, the question of who has the right to use and to own images of brutality like the Zealy daguerreotypes is not easily resolved. One argument is that any distribution of the daguerreotypes is unethical; the daguerreotypes were taken without the subjects' consent. Thus, Harvard has an ethical obligation to return the images when possible and avoid distributing them. The distribution of the images violates the individuals' right to privacy, and invokes the cruel history of their creation (Murray, 2013). The opposing argument is that these images are important historical works, thus no one person or institution can claim ownership (Gates Jr., 2020). As representatives of the broader history of scientific racism, the daguerreotypes need to be studied (Gates Jr., 2020). An alternative view is the strictly legal one; Zealy created the images for Agassiz, Agassiz's son or Agassiz himself gave the images to Harvard, and thus they are the property of Harvard (Murray, 2013; *Tamara Lanier vs. President and fellows of Harvard College,* 2022). Ultimately, there is no definitive answer. The Lanier case has the potential to set a precedent of compensation for emotional distress over the use of images of violence, but the question of property rights still poses an ethical dilemma.

CONCLUSION

The Zealy daguerreotypes are reflective of a history of brutality justified by science. They are a visceral reminder of the role that science has played in creating conceptions of the African people as a racial other. The daguerreotypes represent the broader debate over origins in the mid-19th century, in which naturalists and scholars like Agassiz provided scientific support for slavery by asserting that Africans were specifically distinct and separately created. Each photograph is a reminder of the cruelty perpetrated against Alfred, Fassena, Jem, Renty, Delia, Jack, and Drana; one can simply look at Delia's watery and glassy eyes and understand some fraction of her pain. Since they were rediscovered, the Zealy daguerreotypes have been transformed into covers of books, works of art, and subjects of lawsuits; they have been viewed by more people today and are arguably more popular today than they ever were during Agassiz's time. This invites questions about the

ethics of publicizing the photos of victimized people and invites questions about who owns the rights to images taken through acts of violence. Although these questions have no resolute answer, this paper has opted not to include images of the daguerreotypes to avoid further dehumanization and revictimization of Renty, Delia, Jack, Drana, Alfred, Jem, and Fassena.

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Watson Frank: The Tarsier Inside All of Us

Population Genetics of Lynch Syndrome and Hereditary Nonpolyposis Colorectal Cancer as an Autosomal Dominant-Activating Germline Mutation

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INTRODUCTION

Little is known about how a multitude of cancers and other incurable diseases have emerged as some of the most fatal unsolved modern medical problems plaguing the 21st century. They are the sixth leading cause of global fatality (Mármol *et al.,* 2017), despite numerous advances in science and technology. Researchers are determined to find a way to halt this impassable and complex wall of mutations in cell DNA as well as their uncontrollable replication and cell growth. What makes this global health issue even more daunting is that it can be more easily inherited as an autosomal dominant-activating mutation requiring only one copy of the mutated gene in subsequent generations, such as with the third most prominent cancer for both men and women, known as hereditary nonpolyposis colorectal cancer (HNCC) (Peltomäki *et al.*, 2020). This incurable, yet treatable, disease caused by a germline gene change in the body's reproductive cells is initiated by Lynch syndrome, a hereditary and often cancer-causing condition. It increases the risk of many cancers and diseases, notably colorectal cancer (Mármol *et al.,* 2017). Through its high-probability of inheritance and high-risk health factors, it has adverse effects on the genetic composition of the global population.

This paper will detail the attributes of Lynch syndrome as a heritable disease that causes many health complications, including its most common and fatal: metastatic colorectal carcinoma. It will discuss the extent of HNCC, an autosomal dominant variant, on population genetics, its effects through generational inheritance and affected and related genetic communities. Finally, it will describe current and past research done on Lynch syndrome and what can be done in the future to help negate the effects of the disease and its associated health risks and treat the symptoms ensued by the mutated Lynch syndrome gene. Many scientists (Ramos *et al.*, 2015; Loewe and Hill, 2010) researching population genetics in response to genetic diseases such as hereditary nonpolyposis colorectal cancer wonder whether HNCC affects genotypic and phenotypic frequencies and the subsequent inheritance patterns in a population. Scientists (Hamilton, 2021; Greenstein, 2018) have also been studying how we can neutralize these effects, provide adequate treatment and prevention for the disease and its symptoms. This paper strives to answer these questions and to bring clarity to the increased generational inheritance, high-risk health factors, and reverberations of hereditary nonpolyposis colorectal cancer.

BACKGROUND

Lynch syndrome is an inherited disease that increases the risk of many types of cancer, especially cancers of the colon, large intestine, and rectum, collectively referred to as colorectal carcinoma (Chen *et al.,* 2018). People with Lynch syndrome also have an increased risk of cancers of the stomach, small intestine, liver, gallbladder ducts, urinary tract, brain, and skin (Chen *et al.,* 2018). In addition, women with this disorder have a high risk of ovarian and endometrial cancers (Chen *et al.*, 2018). Therefore, women with Lynch syndrome have a higher overall risk of developing cancer than men with the condition (Chen *et al.*, 2018).

The propensity to develop colorectal cancer is dependent on different factors including age. Those who develop cancer from Lynch syndrome are most often 50 years or older when cancer occurs, although it can still affect teenage patients (Chen *et al.*, 2018). In individuals aged 40-59, colorectal cancer (CRC) rates have increased exponentially since the 1990s and even more dramatically since the 1980s in the 20-39 age cohort (Chen *et al.,* 2018). In addition, from 2018 to 2022, the incidence of colorectal cancer increased by 1.5% per year in those younger than 50, and more advanced colorectal cancer cases were

diagnosed in the younger population (Sinicrope, 2022). The American Cancer Society estimates that in 2023, the number of colorectal cancers in the U.S. will rise more than 3.2% for colon cancer and 2.4% for rectal cancer (Stintzing, 2014). In addition to cancerous growth in the colon, people with HNCC may occasionally have non-cancerous, or benign growths in the colon, called colon polyps (Chen *et al.*, 2018). In individuals with this disorder, colon polyps occur at a younger age but not in greater numbers than they do in the general population (Chen *et al.,* 2018).

Most cases of colorectal cancers are instigated by growth polyps on the inner lining of the colon or rectum (Mármol *et al.,* 2017). Some types of polyps can change into cancer over time, however not all do (Mármol *et al.,* 2017). Adenomatous polyps, or adenomas, sometimes change into cancer and are described as precancerous conditions (Mármol *et al.,* 2017). Hyperplastic polyps and inflammatory polyps are more common but they are usually not precancerous unless they are extremely large (Greenstein, 2018). Sessile serrated polyps and traditional serrated adenomas are often treated like adenomas because they have a higher risk of changing into colorectal cancer (Mármol *et al.,* 2017). A polyp is more likely to become cancerous if it is larger than 1 cm, there are more than three polyps, or if it is dysplastic (Mármol *et al.,* 2017). Dysplasia is another precancerous condition where there's an area in a polyp or in the lining of the colon or rectum where the cell growth is abnormal and contains a spongy white mass, but it hasn't yet become cancerous (Lindor *et al.,* 2006).

After colorectal cancer onset, it can spread when a polyp grows into the wall of the colon or rectum over time (Mármol *et al.,* 2017). The wall of the colon and rectum is made up of many layers. Colorectal cancer is established in the innermost layer (mucosa) and can grow outward through one or many of the other surfaces. When cancer cells are in the wall, they can then grow into blood or lymph vessels that carry away waste and fluid (Mármol *et al.,* 2017). From there, they can travel to nearby lymph nodes or distant parts of the body (Mármol *et al.*, 2017). The stage of colorectal cancer depends on how deeply it grows into the wall and if it has spread outside the colon or rectum (Mármol *et al.,* 2017). Of colorectal cancers, 99% are adenocarcinomas that start in cells that make mucus to lubricate the inside of the colon and rectum. Some subtypes of adenocarcinoma, such as signet ring and mucinous, may have a worse prognosis than other subtypes of adenocarcinoma. The other 1% includes carcinoid tumors that start from special hormone-making cells in the intestine, gastrointestinal stromal tumors that start from special cells in the wall of the colon called the interstitial cells of Cajal which are sometimes benign, lymphomas that are cancers of immune system cells in the lymph nodes and colon, and sarcomas that start in blood vessels, muscle layers, or other connective tissues in the walls of the large intestines (Mármol *et al.,* 2017). In hereditary nonpolyposis colorectal cancer, nonpolyposis designates how colorectal carcinoma can occur when only a small number of polyps are present or even not at all. In families that have HNCC, cancer usually occurs on the right side of the colon, which can prove useful as a diagnostic tool for CRC patients (Chen *et al.,* 2018).

The most prominent symptoms of Lynch syndrome include abdominal pain, continued cramps, change in bowel habits, blood in stool, diarrhea, constipation, internal gut bleeding, reduced availability to absorb nutrients from foods, glioblastoma, lethargy, nausea, vomiting, and unexplained weight loss (Lindor *et al.*, 2006). Lynch syndrome, as an autosomal dominant predisposition, causes predominantly colorectal carcinoma that is diagnosed in 1 out of every 18 people in the U.S., where a third of these colon cancer cases are directly due to familial hereditary predisposition, including from Lynch syndrome (Jasperson *et al.,* 2010).

POPULATION GENETICS OF LYNCH SYNDROME AND HNCC

HNCC was first recognized by the University of Michigan pathologist Aldred Warthin in 1913, who looked at the history of a family with many cases of cancer, constructed a pedigree, and proposed a familial genetic explanation for this "cancerous fraternity" (Boland and Lynch, 2013, p. 148). Others (Kluge, 1964; Glidzic and Petrovic,

1968) followed his work and found numerous similar families in many different communities and countries. The coordinated identification of rigorously defined families then led to the linkage of the cancer-prone phenotype to a single locus on chromosome 2p in 1993 (Boland and Lynch, 2013). An accidental experiment allowed the investigators to recognize that some familial colorectal cancers (CRCs) were associated with a new cancer pathway that had already been independently discovered without the knowledge that there might be a hereditary form of this pathway. A race then quickly led to the discovery of the 5 genes responsible for Lynch Syndrome (Boland and Lynch, 2013). Now, scientists have a lot of useful information and knowledge of the genetic basis of the disease and validation of two powerful clinical identifiers, microsatellite instability (MSI) and immunohistochemistry (IHC), of Lynch syndrome that they can use to advance diagnosis and treatment of the disease (Boland and Lynch, 2013).

Hereditary nonpolyposis colorectal cancer is caused by mutations in the MLH1, MSH2, MSH6, PMS2, or EPCAM genes (Peltomäki *et al.,* 2020). It is the result of locus heterogeneity potentially caused by mutations in multiple different genes and involves a defect in a tumor-suppressor gene (a gene that prevents cancer, where a loss-of-function mutation can allow cancerous growth) (Peltomäki *et al.*, 2020). The MLH1, MSH2, MSH6, and PMS2 genes are involved in repairing errors that occur when DNA is copied in preparation for cell division during the process of DNA replication (Peltomäki *et al.,* 2020). Since these genes work together to fix DNA errors, they are known as mismatch repair or MMR genes (Peltomäki *et al.*, 2020). Mutations that happen in any of them can prevent the necessary repair of DNA replication errors (Peltomäki *et al.,* 2020). As the abnormal cells continue to divide, the accumulated errors can lead to uncontrolled cell growth and possibly cancer (Peltomäki *et al.,* 2020). Variants in the MLH1 or MSH2 gene tend to lead to a higher risk (70 to 80 percent) of developing cancer in a person's lifetime, while variants in the MSH6 or PMS2 gene result in a lower risk (25 to 60 percent) of cancer development (Peltomäki *et al.*, 2020). Thus, the MLH1 and MSH2 mutations contrute more than the MSH6 and PMS2 variants to the overall risk of cancer with Lynch syndrome. Mutations in the EPCAM regulatory gene (which encodes for carcinoma-associated antigens and the protein known as epithelial cell adhesion molecule) also lead to hindered DNA repair, even though this gene is not a part of this process itself (Peltomäki *et al.,* 2020). The EPCAM gene lies next to the MSH2 gene on chromosome 2 and specific EPCAM gene variants cause the MSH2 gene to be inactivated (Peltomäki *et al.*, 2020). As a result, the MSH2 gene's role in DNA repair is hindered, which can lead to accumulated DNA errors and cancer development (Peltomäki *et al.,* 2020). Although variants in these genes predispose individuals to cancer, not all people with the variants develop cancerous tumors (Peltomäki *et al.,* 2020). Lynch-like syndrome has almost identical gene mutations, except it is defined as a CRC case with microsatellite instability, (MSI) and loss of expression of MLH1, MSH2, MSH6, or PMS2 (Peltomäki *et al.,* 2020). This loss by immunohistochemistry (IHC) happens in the absence of a germline mutation in these genes that cannot be explained by BRAF mutation or MLH1 hypermethylation (Carethers, 2014).

Every person has two copies of each of the genes involved in Lynch syndrome, one inherited maternally and the other paternally. If a person inherits a mutation in a Lynch syndrome gene, they will have an increased risk of cancer due to only having one normal copy of the gene from the other parent (Barrow *et al.,* 2013). Cancer can then occur when a second mutation affects the normal working copy of the gene so that the person no longer has a copy of the gene that works properly. Unlike the inherited HNCC mutation, the second mutation would not be present throughout the person's body, but only in the cancer tissue (Barrow *et al.,* 2013).

As hereditary nonpolyposis colorectal cancer is an autosomal dominant-activating germline mutation, it can be more easily inherited than other cancers since, if one parent has the mutated gene, the children have a 50% chance of inheriting the cancer-causing mutation; only one copy will cause the genetic condition. Most affected individuals will be heterozygotes unless both parents have the mutated gene, in which case the offspring with the condition will

be homozygous (Greenstein, 2018). HNCC also results from haploinsufficiency where a person has only a single functional copy of the gene and that single functional copy does not produce a normal phenotype (Ryan *et al.,* 2021). In these disorders, 50% of the functional protein is not sufficient to produce a normal phenotype (Ryan *et al.,* 2021). Haploinsufficiency shows a dominant pattern of inheritance because a heterozygote (with one functional allele and one inactive allele) has the disease (Ryan *et al.,* 2021). HNCC is due to a germline mutation, which becomes incorporated into the DNA of every cell in the body of the offspring. These mutations are passed from parents to offspring (Ryan *et al.,* 2021). Hereditary breast and ovarian cancer, prostate cancer, and hereditary diffuse gastric cancer are also similar to HNCC as they are caused by an autosomal dominant inheritance and are also germline mutations in the BRCA1 and BRCA2 or HDGC and CDH1 genes (Ford *et al.,* 1998).

Hereditary nonpolyposis colorectal cancer has major effects on the genetic composition of populations, including distributions and changes in genotypic and phenotypic frequency in response to evolutionary processes over many generations, as it results from autosomal dominant inheritance patterns that allow the mutated cancer-causing gene and genetic condition to be inherited in a dominant pattern (Mankaney *et al.,* 2017). Many populations of familial relation in most predominantly Hungary, Norway, the Netherlands, and Denmark carry the Lynch syndrome gene and have the highest incidence of CRC (Mankaney *et al.*, 2017). Ashkenazi Jews also have the highest incidence rate of CRC and expression of the MMR variant of any ethnic group (Mankaney *et al.,* 2017). Populations with severe sedentary lifestyles and rising rates of obesity, tobacco, and alcohol consumption also have a higher risk of developing CRC (Mankaney *et al.,* 2017). In addition, microevolution and the changes in a population's gene pool from each generation involving the actions of evolutionary mechanisms that alter the prevalence of a given allele or genotype in a group have the potential to promote widespread genetic changes over time (Hamilton, 2021). A parent with the variant MLH1, MSH2, MSH6, PMS2, or EPCAM genes has a 50% probability of passing on the condition to their offspring and future generation (Peltomäki *et al.,* 2020). This generation's children then also have a 50% chance of inheriting the mutation and exponentially increasing the abundance of the variant gene and its health complications and increased risk of cancer in the genetic composition of the local population. The gene coding for Lynch syndrome becomes more abundant and heritable within the affected populace, and its distribution affects linked communities and other groups, further increasing the dominant trait in every generation and connected populations (Ford *et al.,* 1998). In addition, the effects on population genetics include changes in the genotypic frequency of dominant genes expressed in exponentially more affected populations as well as the phenotypic frequency of HNCC symptoms, cancerous diseases, and life expectancy (Burt *et al.,* 1992). Furthermore, the probability of developing colorectal cancer from Lynch syndrome is up to 80% for men and 60% for women who also have up to a 60% chance of developing endometrial cancer (Greenstein, 2018). Both men and women have up to a 20% chance of developing uterine and gastric cancer (Greenstein, 2018). To further add on to the health and medical crisis, with an often late onset of metastatic colorectal carcinoma in the patient's 50s or 60s, the affected individual will have likely already reproduced without knowing the repercussions and consequences of passing on the mutation, which emphasizes the need for effective early screening and preventions made for hereditary nonpolyposis colorectal cancer and treatments for later in the individual's life if or when they develop the cancerous disease (Greenstein, 2018).

TREATMENTS AND PREVENTIONS FOR HNCC AND LYNCH SYNDROME

Due to changes in the local and global gene pools, as well as increased genetic variation over many generations favoring the dominating HNCC mutation and greater risk of colorectal cancer, steps must be taken to prevent, treat, and diagnose Lynch syndrome. This is especially important for families with a history of HNCC and colorectal carcinoma in order to lessen the effects on population genetics and the increased health

impact of the autosomal dominant-activating germline mutation.

Although there is no Lynch syndrome prevention, individuals with HNNC can undergo lifelong cancer screenings to detect early signs of cancer. Screening and multigene panel genetic testing can be done to diagnose HNNC in individuals, especially when a family member has colorectal cancer or Lynch syndrome, as their immediate relatives including parents, children, and siblings will have a 50% chance of also having the mutated gene coding for CRC (Hamilton, 2021). Tumor screening using Immunohistochemistry (IHC) to test for the presence or absence of the proteins synthesized by the Lynch syndrome genes: MLH1, PMS2, MSH2, MSH6, or EPCAM can result in an effective diagnosis of HNCC (Cohen *et al.,* 2019). This method uses antibodies linked to enzymes to check for certain antigen markers in colon and rectum tissue samples (Cohen *et al.,* 2019). Genetic testing using Microsatellite Instability (MSI) also screens for microsatellites and pieces of DNA that can show if the mismatch repair process is not working well, which is an indication of Lynch syndrome (Cohen *et al.,* 2019). MSI indicates if there is a change in the cancer cells in which the number of repeated DNA regions in a microsatellite differs from when it was inherited (Cohen *et al.,* 2019). In addition, advances in next-generation sequencing technologies allow rapid and scalable somatic and germline sequencing and determination of nucleotide order in entire genomes and targeted regions of DNA or RNA (Cohen *et al.,* 2019). This promises to help identify Lynch syndrome in individuals who otherwise lack classic phenotypes. Geneticists can also identify mutant genes that cause cancer by using family pedigrees and localizing a disease-causing allele to a small region on a chromosome that is distinguished by its haplotype (Cohen *et al.,* 2019). By comparing the transmission patterns of many molecular markers with the occurrence of an inherited disease, special markers, closely linked to the disease-causing mutant allele, can be distinguished (Cohen *et al.,* 2019).

Besides genetic testing and cancer screenings, the most common treatment for HNCC includes using immune checkpoint inhibitors to block checkpoint proteins from binding with their partner proteins which prevent the "off" signal from being sent, allowing the T immune cells to kill cancer cells (Yurgelun and Hampel, 2018). This immunotherapy drug acts against a specific checkpoint protein called CTLA-4 (Yurgelun and Hampel, 2018). Immune checkpoint inhibitors are shown to be very effective among patients with metastatic colorectal cancer harboring high microsatellite instability and/or mismatch repair deficiency (Yurgelun and Hampel, 2018).

In addition to treatments for hereditary nonpolyposis colorectal cancer, preventions for colon cancer include regular cancer screening to detect any kind of cancer early, preventative surgery to reduce the risk of developing cancers, daily doses of 600 mg of aspirin per day to reduce cancer risk (two years of ingestion can reduce the cancer burden by 63%) (Burn *et al.*, 2012), high-definition colonoscopies, prophylactic colectomies which remove the colon, chemopreventive compounds that reduce recurrent colorectal adenomas and/or cancer including selenium, calcium carbonate, hormone replacement therapy, and nonsteroidal anti-inflammatory drugs (Hawk and Levin, 2005). The mechanisms of action of nonsteroidal anti-inflammatory drugs include inhibition of the cyclooxygenase, or COX-2, system as well as cyclooxygenase-independent effects. COX-2 is the key enzyme of prostaglandin E2 that induces cancer stem cell-like activity, and promotes the development, proliferation, apoptotic resistance, angiogenesis, invasion, and metastasis of cancer cells (Hawk and Levin, 2005). Daily exercise, alimentary habits, wearing sunscreen, reducing exposure to environmental toxins, and low alcohol and tobacco consumption are also effective natural preventions that lead to staying healthy and lowering the risk of colorectal cancer and other fatal diseases (Greenstein, 2018).

As well as preventing colorectal cancer, treatments are effective for cancer already diagnosed. Treatments for colorectal carcinoma include lymphadenectomy or lymph node dissection that is immediately after the bifurcation of the left colic artery and surgically removes groups of lymph nodes and halts the superior

lymphatic spread along the inferior mesenteric artery (the main metastatic route) (Burn *et al.,* 2012). Chemotherapy also uses a drug treatment with powerful chemicals to kill fast-growing cells in the body, prolong life, and reduce symptoms (Wolpin and Mayer, 2008). Chemotherapy protective drugs, such as amifostine which helps protect the kidneys, mesna which helps protect the bladder, and dexrazoxane which helps reduce heart damage, are used to reduce the side effects of chemotherapy treatment (Wolpin and Mayer, 2008). Fluorouracil-based chemotherapy with the inclusion of oxaliplatin is best used for later stages of colorectal cancer that is lymph node-positive (Wolpin and Mayer, 2008). Furthermore, current research and clinical trials are being done on Aflibercept therapy, an intravenously administered anti-VEGF and anti-placental growth factor agent, in combination with 5-fluorouracil, leucovorin, and irinotecan, as an effective treatment of patients with metastatic colorectal cancer (Ciombor *et al.,* 2013).

CONCLUSION

Hereditary nonpolyposis colorectal cancer is an incurable, yet treatable disease, caused by a germline gene change in the body's reproductive cells and an autosomal dominant-activating mutation that increases the risk of many cancers, most predominantly metastatic colorectal carcinoma. Through its high-probability inheritance and high-risk health factors, it has major effects on the global population and genetic composition. HNCC is caused by mutations in the MLH1, MSH2, MSH6, PMS2, or EPCAM genes that affect DNA mismatch repair (Peltomäki *et al.*, 2020). It is the result of locus heterogeneity which is caused by mutations in multiple different genes and involves a defect in a tumor-suppressor gene and a loss-of-function mutation that allows for the occurrence of cancerous growth (Peltomäki *et al.*, 2020). Cancer is a disease caused by an uncontrolled abnormal division of cells that invade nearby tissues and exponentially replicate in the body (Greenstein, 2018). Carcinoma cells, unlike normal cells, hide from the body's immune system and trick it into protecting cancer cells and tumors, helping them thrive and grow instead of attacking them. Cancer is one of the most serious and fatal global health illnesses, and colorectal cancer is especially daunting due to its dominant 50% inheritance rate abundant through many generations and its up to 80% probability of developing colorectal cancer and numerous other dangerous diseases (Greenstein, 2018). HNNC has effects on population genetics through generational inheritance and health risks for local and global gene pools (Ryan *et al.*, 2021). It also involves changes in the genotypic frequency of more dominant genes and leads to certain populations being exponentially more affected, increases in the phenotypic frequency of HNCC symptoms and cancerous diseases, and decreases in life expectancy. Although Lynch syndrome cannot be prevented, there are many treatments available including multigene panel genetic testing, immunohistochemistry, microsatellite instability, and immune checkpoint inhibitors, as well as many preventative means available including colonoscopies, prophylactic colectomy, chemopreventive compounds, lymphadenectomy, chemotherapy, and Aflibercept therapy (Cohen *et al.,* 2019). As new cancer research is developing and progressing each year, many scientists, researchers, and medical practitioners (Hong *et al.,* 2020; Zheng and Fang, 2022) are working tirelessly and determinedly, so that one day these cancerous obstacles will be overcome, and already, there has been incredible and influential progress that is racing forward.

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Henry Fairfield Osborn and the Construction of Natural History

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Visions of disappearing wildlife joined forces with fears of a declining racial stock to produce the mindset that would govern Henry Fairfield Osborn's twenty-five-year tenure at the American Museum of Natural History (AMNH) from 1908 to 1933. Born to the president of the Illinois Central Railroad Company in 1857, an early, pre-mortem biography describes young Osborn as slated for a career in finance (Fuller, 193?). After being sent to Princeton for an education, however, he fell in love with the natural sciences: first embryology, and then paleontology (Fuller, 193?). Reluctantly, his father, William Osborn, allowed him to study for a year longer in England and—after some heavy foot-dragging on the younger Osborn's part—released him from obligations to pursue a career in business (Regal, 2002). Although he may have harbored skepticism for his son's scientific abilities, William never wavered in his support—even paying Henry Fairfield's Princeton salary when the school could not afford to do so (Regal, 2002). At a time when there was no public funding for science, wealth was a prerequisite to becoming a scientist. It was through the financial help of his father that Osborn was able to accept an assistant professorship at Princeton in 1881 and begin to make a name for himself (Regal, 2002).

Osborn sought to transform biology, a fledgling discipline, at his alma mater. He worked with the school's president, James McCosh, to make the natural sciences a cornerstone of the curriculum (Regal, 2002) and later with his former schoolmate William "Wick" Scott to develop the department of vertebrate paleontology (Rainger, 1991). In a letter dated May 13, 1881, Osborn wrote to a colleague requesting lecture and laboratory space at the School of Science for a proposed science course (Osborn, 1891): "The President is fully alive to the importance of the proposed Laboratory," he explains, "and it is indeed high time that Princeton should adopt a course which has been so successfully inaugurated at Harvard and the Johns Hopkins" (Osborn 1891, p.1). His work definitively pivoted from embryology to paleontology in 1885, and he would spend the late 1880s collaborating with Wick Scott on questions of fossil mammals and evolution (Regal, 2002).

Despite his interventions, Princeton never became the powerhouse Osborn dreamed it could be. In 1891, he was offered positions at both Columbia College and the American Museum of Natural History—a scheme devised by Seth Low, then president of Columbia College (Sloan, 1980).[1] Low had been in contact with Osborn about a job at Columbia since early 1890 (Sloan, 1980). The school wanted to establish itself as a research university on par with Johns Hopkins and Harvard, but it had no biology department (Sloan, 1980). The biological sciences were becoming extremely important in the second half of the nineteenth century thanks to the doctrine of evolution, and Columbia's lack of advanced instruction meant it was lagging behind (Sloan, 1980). Low reached out to Osborn, and also to AMNH president Morris K. Jesup, about developing a biology department at Columbia (Sloan, 1980). Hoping to foster closer ties with AMNH, Low proposed that they offer Osborn a joint appointment as chair of the department and curator of mammalian paleontology at the museum (Sloan, 1980). Jesup was on board, and Osborn readily accepted (Sloan, 1980).

Osborn's pedigree and political connections made him quite the catch. Osborn biographer Brian Regal contends that the "tribal elders of New York society" were happy to see someone in charge with "higher ideals" (Regal, 2002, p.71). They imagined he would teach the people of New York moral lessons, in addition to scientific ones, and promote social order and stability. But the pull of Osborn's scientific acumen should not be discounted. Fossils were all the rage, and the museum was eager to put its newly expanded Department of Mammalian Paleontology to use (Sloan, 1980). Columbia, in turn, got a first-rate biology department, in no small part due to their partnership with AMNH. The alliance between AMNH and Columbia would

prove fruitful to both institutions. For Osborn, it meant the backing power and resources of both. It was at this point in his career that Osborn was able to ensconce himself in the political and academic circles of New York and emerge as a force to be reckoned with.

Osborn quickly settled into New York City life. He wrote to his longtime friend Edward Poulton in 1896 that his work at the museum was progressing well. "The great Hall in the Museum will be opened before long," he boasted, "and by the time you get here I hope all the various innovations which I have introduced to the exhibition of the paleontological collection will be completed so that you can see what the fossils are, biologically considered" (Osborn, 1896, p.1). He appears equally satisfied, albeit stressed, with his work at Columbia, writing to Poulton about the classes he was teaching on comparative vertebrate zoology, organ development, and mammalian paleontology. "[M]y brain is a whirl," he writes, "and the only way to straighten out the tangles and snarls is a good long run on a bicycle, and New York affords most wonderful opportunities for this sport..." (Osborn, 1896, p.1-2).

In 1908, Osborn was elected president of AMNH by the museum's board of trustees (Museum News ... 1908). In its news section, the American Museum Journal counts his development of the museum's Department of Vertebrate Paleontology among his chief accomplishments as a staff member (Museum News ... 1908). Biographer Ronald Rainger considers Osborn's presidency a rather foregone conclusion in An Agenda for Antiquity (1991). Jesup, the outgoing president, had brought him into the museum administration in the first place, recognizing his talent as a curator (Rainger, 1991). Osborn shined in this administrative role, instilling confidence in Jesup of his capacity to lead the museum. His role as president would magnify his power in both social and academic spheres, allowing him to further shape museum priorities, channeling time, energy, and resources towards specimens and their exhibition.

New work in the biological and geological sciences relied increasingly on experimental biology (Rainger, 1991). Experimental biology can be understood as that biology which occurs in laboratories and concerns subjects such as genetics, biochemistry, and physiology (Rainger 1991, p.7). Henry Fairfield Osborn would resist this type of research, advocating instead for fieldwork and the study of large specimen collections ("naked-eye science") (Rainger, 1991, p.8). As President of the AMNH, he attached much value to the physical specimens and displays that the museum had to offer. For him, they were visible facts, testifying to the greatness of nature, science, and God (Rainger, 1991). He advocated for the educational and transformational power of seeing objects and insisted on fieldwork as the basis of scientific knowledge. Taking interest in various scientific disciplines, Osborn was what one might have called a "dabbler." Still, he was instrumental in reinvigorating and keeping alive what Rainger terms the then "peripheral" field of vertebrate paleontology, creating breathtaking displays and transforming dinosaurs into the iconic fixtures they are at museums of natural history (Rainger, 1991, p.19).

In Osborn's estimation, New York City offered few opportunities to experience nature up close. He linked the degradation and disappearance of nature from New Yorkers' lives with the social and spiritual degeneration of the city at large and saw the American Museum of Natural History as an antidote. People from all walks of life could come, observe, and leave transformed. In his book Creative Education in School, College, University, and the Museum, Osborn writes that the function of the American Museum is to "restore the vision and inspiration of nature" (1927, p.120). To "restore the vision" of nature, Osborn would invest heavily in visual display. He and the museum's new director, Frederic A. Lucas, hired an increasing number of artists and taxidermists in the early 1910s (Cain, 2011). New taxidermical techniques allowed for more detailed sculpting of specimens. At the same time, murals and background paintings were becoming increasingly central to museum exhibits. The museum's attention to visual detail paid off, as AMNH's annual income increased from $446,000 in 1910, to $946,000 in 1920, and finally to $1,827,000 in 1930 (Cain, 2011).

Osborn's legacy as an innovative and successful museum president cannot

be separated from his identity as an anti-immigrant eugenicist (Figures 1 and 2). In a 1934 autobiographical essay, Osborn described himself as having "a double heritage of self-made New Englanders" (1934, p.1). He drew upon his family's purported hardworking identity and long-term residence in the U.S. to fashion himself as an authority on immigration and a champion of American values. "Since 1637 my family has been working for the public welfare," he wrote to New York senator Royal S. Copeland in 1935 (Osborn, 1935, p.1). "[M]y immediate ancestors, one and all, have been helping the great city of New York, its hospitals, its museums, its churches, its universities and its schools" (Osborn, 1935, p.1). Osborn shared the same xenophobic and racist attitudes as thinkers like Madison Grant, though they sometimes expressed these attitudes in different ways (Chase, 1976). Regal asserts that Osborn had a more "paternalistic" view towards the downtrodden and, at times, appeared somewhat sympathetic to their struggle (2002, p.129). For instance, in a 1912 letter to Jacob H. Schiff,[2] Osborn cited concern for the working class as justification for his anti-immigrant views. "I have myself become a restrictionist," he wrote, "because I believe nothing would so greatly help our working class as to decrease the competition of labor for awhile" (Osborn, 1912, p.2). Nevertheless, it should be underscored that the harm wrought by these vitriolic positions towards immigrants and non-white persons was commensurate. Grant and Osborn both served on the Immigration Restriction League, the International Eugenics Society, and other such organizations (Chase, 1976).

Fig. 1. Marble bust of Henry Fairfield Osborn previously located in the Teddy Roosevelt Memorial Hall, 2008. Source: Gobetz W. 2008. NYC - AMNH: Henry Fairfield Osborn bust. [December 6, 2008]. [Photo]. [accessed 2023 Apr 5]. Available from:. https://www.flickr.com/photos/wallyg/3097038814/.

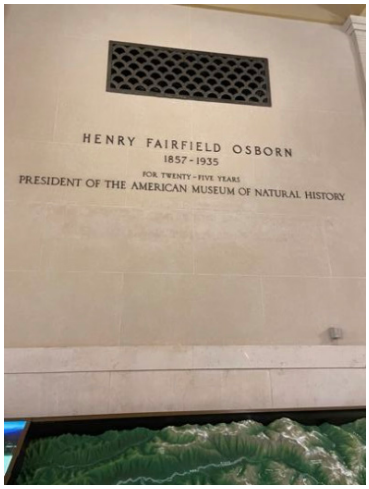

Fig. 2. Former site of HFO bust, as seen on 3/24/23. The bust and some text has been removed. Source: Author.

Osborn's restrictionist views went hand-in-hand with his commitment to eugenics. Patriotism, to Osborn, meant "the conservation and multiplication for our country of the best spiritual, moral, intellectual and physical forces of heredity..." (1916, p.viii). He feared the replacement of "that race which has given us the true spirit of Americanism" (meaning the 'Nordic race') and saw their replacement (by immigration or outbreeding) as "the greatest danger which threatens the American republic to-day..." (Osborn, 1916, p.ix). The Osborn Papers at the New-York Historical Society contain memorabilia attesting

to his active membership and leadership in such organizations as the Aryan Society, the Galton Society (which he co-founded), and the Eugenics Society (Cutler, 1930). In 1921, he hosted the Second International Congress of Eugenics at the American Museum, calling it "[p]erhaps the most important scientific meeting ever held in the Museum" (Announcement ... 192?). His scientific racism colored many of his contributions to the museum, including the infamous Hall of the Age of Man which presented racial hierarchy as fact (Figure 3). In this way, Donna Haraway argues in "Teddy Bear Patriarchy" that Osborn was one of the leading figures to so effectively link eugenics and conservation at the museum (Haraway, 1989). His scientific background, powerful political connections, and position as museum president helped legitimize and advance eugenics.

Fig. 3. The Ancestry of Man display in the Hall of the Age of Man, 1929. The human skulls on the left are meant to suggest that different races are different species, with 'Nordic Whites' occupying the most evolved position (Regal, 2002). Source: Kirschner, Julius. The Ancestry of Man, Age of Man Hall, 1929. June 1929. Photo. AMNH Digital Collections. https://digitalcollections.amnh.org/CS.aspx?VP3=DamView&VBID=2URMLBED-PCLB&SMLS=1&RW=1104&RH=822#/Dam-View&VBID=2URMLBEDPRUO&PN=1&WS=-SearchResults.

We should not take for granted that so many prominent AMNH personnel were directly involved in the eugenics movement. While Osborn was raving about 'race plasm' and the dangers of miscegenation, anthropologist Franz Boas was pioneering his relativist approach to the study of human culture (Regal, 2002). He butted heads with Osborn from 1895 until 1905, when Boas left for Columbia (Regal, 2002). William K. Gregory, a student and later associate of Osborn's, is another prominent museum figure who condemned Osborn's social and political views—largely because he saw them as foregrounding his theory of evolution (Rainger, 1991). He quit Osborn's Galton Society in 1935 due to its overtly political and racial agenda (Rainger, 1991).

Osborn's desire to combat forces of decadence and social degradation and, thereby, preserve the 'great race' accompanied his desire to preserve nature. He saw the perceived degeneration of race, class, and nature as interlinked and fashioned his concern into an ideology, which he in turn promoted at the American Museum (Rainger, 1991). The goal of museum education, per Osborn, was "to restore to the human mind the direct vision and inspiration of nature as it exists in all parts of the world..." (Cited in Rainger, 1991, p.120). The exhibits Osborn promoted sought to both preserve and to communicate the importance of that preservation. To do so, they relied on taxidermied specimens and the creation of hyperreal, naturalistic settings in which to place them. It was hoped that these exhibits would generate appreciation and concern for the natural world and teach individuals more than they could learn from books alone.

To understand the history of the American Museum of Natural History is to understand a number of interrelated ideologies and fears associated with post-Civil War urban America, best embodied by Henry Fairfield Osborn. Osborn represented a specific breed of scientist that would soon go extinct. Devoted to "naked-eye science" and the transformative power of seeing, he invested time and energy into creating the American Museum of Natural History we know today. At the same time, Osborn injected his troubling thinking into various aspects of the institution, implicitly and explicitly using his platform as president to advance scientific racism, eugenics, and anti-immigrant legislation, ideals espoused by a fair share of his naturalist contemporaries. Their attitudes may seem outdated. Regardless, when examining the

representations of nature that proliferated at the American Museum in the early twentieth century, it is interesting to consider what has remained. We still find habitat dioramas in natural history museums today. In this way, early twentieth-century constructions of nature, far from being outdated, continue to inform our understanding of the natural world today.

NOTES

[1]This was before Columbia attained university status. During the 1880s, faculty debated whether the school should remain a college with loose attachments to different professional schools or become a university focusing on graduate-level research and teaching. President Low wanted Columbia to become a university. In 1893, after some hefty reorganizing, Columbia University was born (Sloan, 1980).

[2]Jacob H. Schiff was a prominent Jewish philanthropist. NYZS records at the New-York Historical Society indicate that he was a prominent donor (Cohen, 1999).

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Ode to *Gorilla gorilla gorilla*
By Juliet Azé

Gorilla gorilla gorilla, what a lovely name.
You roam on the western lowland forest floor
And through the years rose to fame
As the largest primate no one can ignore.

Your sagittal crest, robust bones, chewing teeth and more
Make all others salute as the most special primate
Motivating humans to travel and explore
The wonders of your habits of highest rate.

Your size and magnificient presence was noticed before,
But less is well known about your mellow demeanor devoid of hate
In the trees, on your knuckles on the ground, you are never a bore
The friendly and formidable giant we all adore.

Illustration by Nicole Bonaccorsi

5 REASONS WHY I, BRONAGH DOUGHTY, CONSIDER *PROPITHECUS VERREAUXI* TO BE THE BEST TAXON, PRESENTED IN NO PARTICULAR ORDER:

A FORMAL DEFENSE.

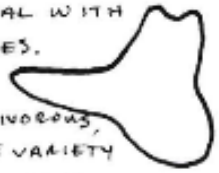
II. UTTERLY FASCINATING ASPECTS OF THE SKULL AND DENTITION

A. THE TOOTH COMB

AS OPPOSED TO OTHER STREPSIRRHINES, THE TOOTH COMB OF *P. VERREAUXI* IS ONLY MADE UP OF 4 TEETH. THIS HAS LED TO SIGNIFICANT DEBATE ABOUT WHETHER OR NOT THEY HAVE A PERMANENT MANDIBULAR CANINE. SOME ARGUE THAT THE DENTAL FORMULA IS $\frac{2,1,2,3}{2,0,2,3}$, SOME ARGUE IT IS $\frac{2,1,2,3}{1,1,3,3}$.

B. THE LARGE ANGULAR PROCESS

THE MANDIBLE OF *P. VERREAUXI* IS CHARACTERIZED BY A HIGH ASCENDING RAMUS AND A GONIAL ANGLE THAT PROTRUDES TO SUCH AN EXTENT THAT IT BECOMES AN ANGULAR PROCESS, NECESSARY FOR CHEWING TOUGH FIBROUS MATERIAL WITH LARGE MASTICATORY MUSCLES.



C. THE COMPLEX DIET

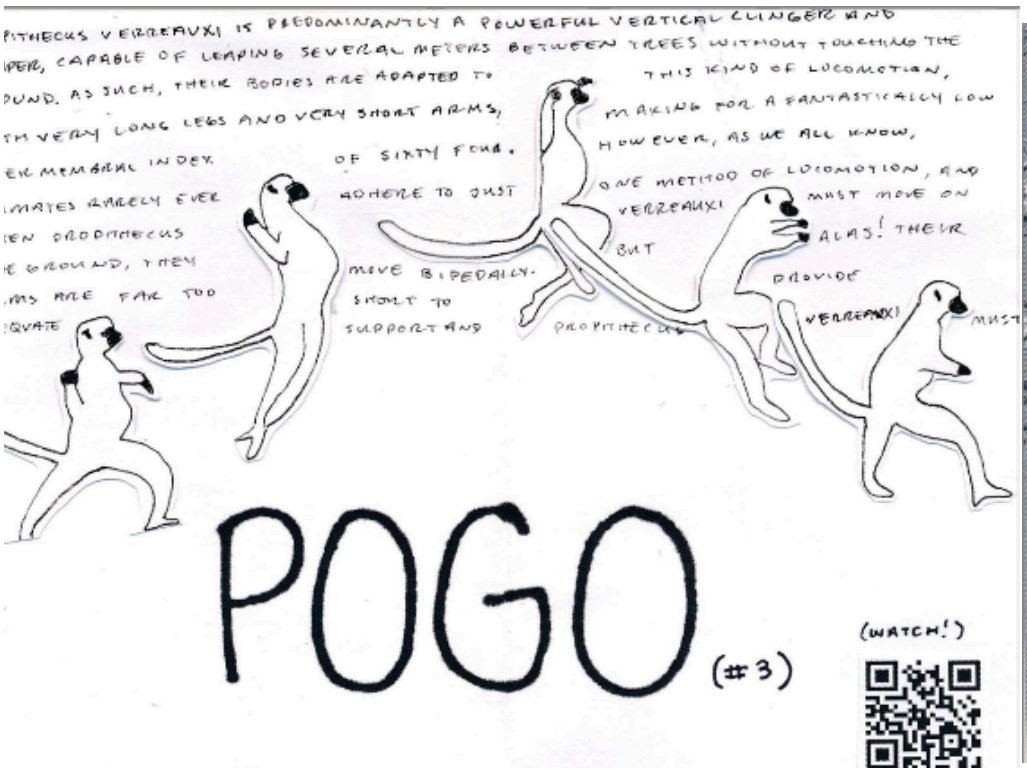
P. VERREAUXI IS MAINLY FOLIVOROUS, BUT WILL EAT A VERY WIDE VARIETY OF PLANTS, INCLUDING BOTH YOUNG AND MATURE LEAVES, AS WELL AS BARK AND DEAD WOOD — LEADING TO COMPLICATED MOLAR CUSPS AND LARGE, STRONG CHEWING APPARATUSES AND A DIGESTIVE TRACT 14 TIMES LONGER THAN THEIR BODIES.

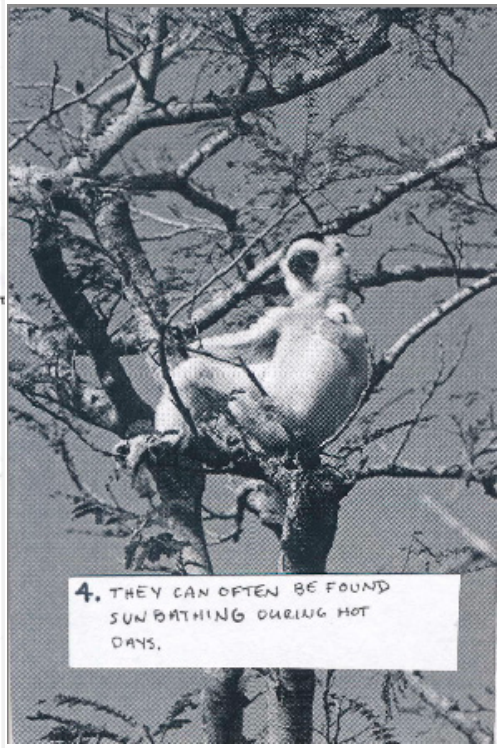
(1) *PROPITHECUS VERREAUXI* IS ALSO KNOWN AS VERREAUX'S SIFAKA, AND IS ONE OF SEVERAL SPECIES OF SIFAKA. WHY ARE THEY CALLED SIFAKA, YOU ASK?

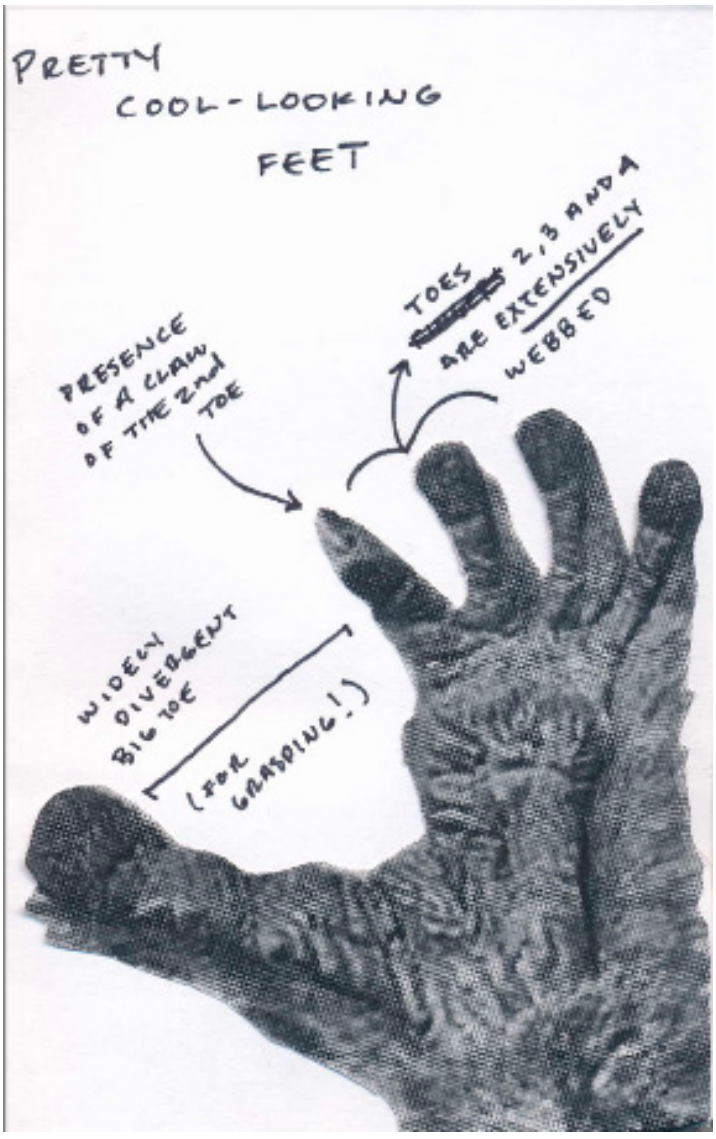
SHEE-FAUK!

THIS ONOMATOPOEIA SOUNDS LIKE A CAMERA SHUTTER, AND IS OFTEN USED AS AN ALARM CALL.

(LISTEN!)







PROPITHECUS VERREAUXI IS LISTED AS CRITICALLY ENDANGERED BY THE IUCN REDLIST.

FOR MORE INFORMATION, VISIT THEIR PAGE HERE:

Booklet by Bronagh Doughty

Marks of Ecological Stress on Dental Surfaces of Anthropoids

Juliet Azé, *Columbia University*

INTRODUCTION

Dental surfaces are treasure troves of information. Looking at the overall shape of each tooth, researchers can infer dietary habits of various species exhibiting distinct topographies and wear patterns visible with the naked eye (Evans *et al.,* 2007; Boyer, 2008; Bunn *et al.*, 2011; DeSantis *et al.,* 2018). Taking a closer look at dental microstructure, scientists are also able to discern patterns of dental development, and potentially trace back certain growth disturbances or traumatic experiences of one's life using dental markings (Boyde, 1990). Using high-resolution visualization tools, such as the scanning electron microscope (SEM), researchers are able to uncover these patterns and work to reconstruct extant and extinct primate dietary, life history and overall behavioral patterns using dental remains (Kay, 1975; Rosenberger and Kinzey, 1976; Walker *et al.,* 1978; Covert and Kay, 1981; Goodman and Rose, 1990; Anapol and Lee, 1994; Hillson and Bond, 1997; Ungar, 2019).

One of the ways that teeth can be useful in reconstructing primate life histories is through their use as biomarkers of ecological stress (Boyde, 1990; Goodman and Rose, 1990). Stress here is broadly defined as "physiological change caused by strain on an organism from environmental, nutritional or other pressures" (Reitsema and McIlvaine, 2014, p.181). Some of these stressors include malnutrition, illness, trauma, social group size and structure (Chollet and Teaford, 2010). Stress is a reliable proxy for individual health, and therefore using teeth to uncover stress patterns can be useful in discerning overall health of extant and extinct primate forms (Reitsema and McIlvaine, 2014). This paper will look more closely at the types of ecological stress-related dental defects that exist and are manifested in human and non-human primates, and the variations in their prevalence within and between primate species. To tackle this topic, I will start by exploring the ways in which dental surface markers can be used to trace different life history stages as well as the types of stresses that can be visible on dental surfaces. Then, I will compare the presence and prevalence of a specific type of dental developmental defect (i.e., linear enamel hypoplasia) in several non-human primates.

LIFE HISTORY AND DENTAL STRESS MARKERS

Through analysis of dental microstructure (i.e., the structure of teeth at the microscopic level) it is possible to uncover indicators of ecological stress throughout the lifetime of individuals (Dean, 2006; Newell *et al.*, 2006). It is useful to discuss how dental microstructure can be an overall indicator of life history stages in different primate species, and then delve deeper into the question of how dental microstructure exhibits indicators of disturbances during the individual's life history. Through analysis of dental microstructure, scientists have been able to uncover patterns in growth and development of the dental tissues which can be correlated to timescales and help reconstruct individual life-histories (Boyde, 1990; Dean, 2006). The timing and sequence of the eruption of permanent dentition is often a reliable indicator of age of the specimen (Swindler, 2002; Dean, 2006; Hogg and Walker, 2011). Although this timing varies for different primate species, it is a useful proxy for growth and development stages (Hogg and Walker, 2011). Through using information about the sequence of dental eruption, as well as dental microstructure information uncovered in fossil remains, researchers have also been able to reconstruct parts of the life histories of hominins (Boyde, 1990; Dean, 2006; Newell *et al.*, 2006). This supports the idea that careful analysis of teeth can be used to uncover the mysteries of extant and extinct primate populations.

Markings formed during dental development due to various stressors can sometimes be indicative of life history stages and

the variations in their timing between different species (Austin *et al.,* 2016; Cerrito *et al.,* 2020). Teeth exhibit visible indicators of stressors that occur in the normal process of growth and development stages, such as birth and weaning (Cerrito *et al.,* 2020). The rate of tooth development has also been associated with the degree of maternal investment, meaning that infants with invested mothers tend to have slower dental growth than those with less invested mothers (Hogg and Walker, 2011). Teeth develop incrementally (these increments being marked by ridges called perikymata), and the different layers correspond to physiological cycles that can be traced back chronologically (Boyde, 1990; Cerrito *et al.,* 2020). Angles of enamel formation have also been linked to the pace of growth and development of several different non-human primate species, suggesting that smaller enamel formation angles may be associated with faster dental development (Guatelli-Steinberg *et al.,* 2018).

In addition to predicting early life history stages like birth and weaning (that occur while the teeth are still developing), teeth can also show signs of childbirth and menopause (Cerrito *et al*., 2020). Cerrito *et al*. (2020) investigated the changes in cementum microstructure of human teeth. They found that it was possible to notice markings of microstructural changes in the cementum that correlated with childbirth and menopause and attributed these changes to hormonal variation. This is important evidence as it shows that not only can we glean information about pre-maturity life history stages by looking at dental developmental defects in enamel and dentin in primates, but cementum microstructure is a useful tool to uncover later life history stages that happen during maturity (Austin *et al.,* 2016; Cerrito *et al.,* 2020).

More specifically, primate dental microstructure changes have also been linked to exposure to health stressors (Austin *et al.,* 2016). Early stages of life are critical, as pressures during this window of time are often visible on the microsurfaces of teeth (Boyde, 1990; Austin *et al.,* 2016). With the use of high-quality microscopes, it is possible to uncover indicators of illness, malnutrition, injuries, and social trauma (Guatelli-Steinberg and Benderlioglu, 2006; Austin *et al.,* 2016). The chemical composition of teeth has also been shown to be a reliable indicator of exposure to certain elements, such as metals, organic compounds, or even dietary elements, all of which are useful when reconstructing the behavioral ecology of non-human primates (Austin *et al.,* 2016).

DENTAL MICROSTRUCTURE AND ECOLOGICAL STRESS: AN EXPLORATION OF LINEAR ENAMEL HYPOPLASIA

More specific indicators of life history variables in primate species relate to marks on dental surfaces that are indicative of physiological and environmental stress. These include enamel hypoplasias (EH), the most common being linear enamel hypoplasia (LEH) which is defined by Chollet and Teaford (2010, p.1) as "a nonspecific indicator of physiological stress" manifested by "localized thinning of tooth enamel" which are not always, but often in the form of "a thin linear depression." LEH is a developmental defect, and therefore it is a biomarker of stresses experienced during tooth development (see Fig. 1) (Goodman and Rose, 1990; Newell *et al.,* 2006; O'Hara, 2017). The perikymata spacing and size are linked to how LEH manifests on the surface of the tooth (Hillson and Bond, 1997; Hannibal and Guatelli-Steinberg, 2005). Generally, LEH results from physiological stress like trauma, malnutrition, illness, and genetic defects, but it is not easy to establish a causative link between one type of stressor and the form of LEH (e.g., is the depression deep, is it across several teeth or just one etc.) (Guatelli-Steinberg and Benderlioglu, 2006; Chollet and Teaford, 2010; O'Hara, 2017).

Different species of primates have varied LEH expressions, with certain taxa being more prone to developing it than others. LEH is most prevalent among great apes, and least among strepsirrhines (Guatelli-Steinberg and Skinner, 2000; Newell *et al*., 2006; Skinner, 2023). It should be noted, however, that the lack of evidence for LEH in strepsirrhines and non-hominoid anthropoids may be due to the placement of the LEH, rather than its actual presence (Hillson and Bond, 1997; Newell *et al.,* 2006). In other words, sometimes the LEH markers may be on the

occlusal surfaces of the teeth, and therefore more difficult to distinguish than if found on the lingual or buccal surfaces (Newell *et al.*, 2006). Generally, LEH is present on the mandibular canines and maxillary incisors of monkeys and apes, although there is variation and LEH can appear on other teeth of these species (Chollet and Teaford, 2010). Studies (Hillson and Bond, 1997; Guatelli-Steinberg and Skinner, 2000; Chollet and Teaford, 2010) have explored the links between various physiological stressors, such as illness or malnutritional, and the prevalence of LEH among study populations. There is, however, a more limited body of research exploring the impact of environmental or ecological stressors on the prevalence of LEH.

Fig. 1. From Guatelli-Steinberg *et al.,* 2012. Linear enamel hypoplasias marked by arrows from *Pongo pygmaeus*.

Environmental temperatures and their fluctuations have been associated with higher or lower LEH prevalence among certain primate populations (Chollet and Teaford, 2006; Skinner, 2021). When looking at *Cebus* (capuchin monkey) groups living in different environmental conditions in Brazil, Chollet and Teaford (2010) found significant differences in LEH prevalence, with populations living in colder climates exhibiting it more frequently. Analysis of additional variables such as precipitation and wind speed yielded similar patterns when looking at African ape samples (chimpanzees and bonobos) who exhibit LEH during the colder and wetter times of the year (Skinner, 2021). Another study (Guatelli-Steinberg and Skinner, 2000) looking at Afro-Eurasian monkeys and apes found greater LEH prevalence to be linked with populations living in environments in which temperatures fluctuated. Taken together, these findings suggest temperature, seasonality and broad environmental conditions may impact the prevalence of LEH in developing anthropoids.

Other ecological factors linked with LEH patterns include dietary habits and social structure. Greater LEH prevalence has been associated with groups that consumed abrasive foods, as well as species of non-human primates that rely primarily on seasonal foods, such as fruit that are scarce, seasonal, and spread in patches so not always easily accessible (Hannibal and Guatelli-Steinberg, 2005; Chollet and Teaford, 2010; Skinner, 2023). Undernourished non-human primate populations also tend to exhibit greater LEH frequencies (Guatelli-Steinberg and Skinner, 2000; Guatelli-Steinberg and Benderlioglu, 2006). This was first illustrated in the Cayo Santiago rhesus macaques (Guatelli-Steinberg and Benderlioglu, 2006). Although the association was not very strong, the researchers found that LEH was prevalent (mostly in females) in the group that, until provisioning, was generally malnourished (Guatelli-Steinberg and Benderlioglu, 2006). This finding was important, as it was the first evidence to suggest that LEH could be a biomarker of malnutrition in non-human primates (Guatelli-Steinberg and Benderlioglu, 2006). LEH was also more prevalent in populations that lived in large social groups, suggesting that in addition to being tied to nutritional stress, it may result from social stress (Guatelli-Steinberg and Skinner, 2000; Benderlioglu and Guatelli-Steinberg, 2019). Although when studying this macaque population, Benderlioglu and Guatelli-Steinberg (2019) found that there may be a possibility for differences in LEH manifestations between varying social ranks, these results were not significant. More than simply being caused by social ranking, other confounding factors linked to social rank, like illness, injuries and malnutrition may also be linked to variations in LEH among different individuals within the social hierarchy of a group.

There are other dental anomalies associated with ecological factors, such as wear,

caries, dental breakage, and general enamel defects (Lucas, 2004; Hannibal, 2017; Towle *et al.*, 2022). Dental wear is caused by attrition and abrasion during the lifetime of an individual (Lucas, 2004). Patterns of dental wear can be linked to dietary habits, illustrating the dietary and by extension behavioral patterns of individuals (Kay, 1975; Rosenberger and Kinzey, 1976; Bunn *et al.,* 2011). Breakage can also be linked to highly abrasive diets which put a lot of stress on the teeth (Hannibal, 2017; Benderlioglu and Guatelli-Steinberg, 2019). Related to dietary habits and food preferences, caries are lesions in the teeth that lead to tooth decay (Towle *et al.,* 2022). Caries are quite rare among non-human primate species, but their presence can be indicative of localized stress (e.g., attrition) on the decayed tooth (Towle *et al.,* 2022). These other dental anomalies should not be confused with LEH, although its presence has been found to potentially increase the risk for dental caries (Hannibal, 2017). Hannibal (2017, p.3) uncovered the presence of another, non-LEH enamel defect which he named "maxillary lateral incisor defect" (MLID). This was only found in upper second incisors of great apes (Hannibal, 2017). Due to its specificity to one type of tooth, it is distinct from LEH and has been linked to systemic stressors (Hannibal, 2017). Overall, this shows that there are several other, visible, dental anomalies that can be exhibited on dental surfaces and indicative of various ecological stresses.

REGIONAL, INTRA-, AND INTER-SPECIFIC DIFFERENCES IN LEH IN CATARRHINES

Regional variation

Great apes have been found to have a greater prevalence of LEH relative to lesser apes and monkeys, but the specificities and variation between great ape species may be linked to their location (Hannibal and Guatelli-Steinberg, 2005; Skinner, 2023). Of the great apes, gorilla subspecies have the lowest frequencies of LEH compared to orangutans and chimpanzees (Goodman and Rose, 1990; Hannibal and Guatelli-Steinberg, 2005). When looking more closely at great ape taxa, an interesting contrast was found: mountain gorillas had an extremely low prevalence of LEH relative to lowland gorillas, chimpanzees, and orangutans (Hannibal and Guatelli-Steinberg, 2005). Based on the taxa involved and their known dietary habits (frugivory for chimpanzees, orangutans, and lowland gorillas, folivory for mountain gorillas), the authors argue that it is likely that these patterns are related to their dietary differences (Hannibal and Guatalli-Steinberg, 2005). This comparative study looking at variation in LEH prevalence among great ape populations living in different regions also found there to be a difference in LEH frequencies of gorilla and chimpanzee populations from Gabon and from Cameroon (Hannibal and Guatelli-Steinberg, 2005). These results suggest that in addition to the variation between species, there is variation of LEH frequencies within species living in different regions, which could potentially be explained by dietary differences, variation in exposure to certain illnesses as well as varying stressors and proximity to humans (Hannibal and Guatelli-Steinberg, 2005).

Intra- and inter-specific variation

There are also sex differences in dental development which can then influence the prevalence of certain dental defects (Guatelli-Steinberg *et al.,* 2009). These differences are relevant when looking at sexually dimorphic species, and the development of these dimorphic traits varies among species (Guatelli-Steinberg *et al.,* 2009; McGrath *et al.,* 2019). For example, in catarrhines, male canine development is prolonged, resulting in their larger teeth (Guatelli-Steinberg *et al.,* 2009). This longer period of canine development in sexually dimorphic male catarrhines suggests that they experience an extended period of susceptibility to dental developmental defects, suggesting that rates of LEH may be greater than in females (Guatelli-Steinberg and Lukacs, 1999; Guatelli Steinberg *et al.,* 2009; McGrath *et al.,* 2019). Generally, when examining the presence of enamel hypoplasias in human and non-human great apes, scientists found that there was a tendency for EH to be more prevalent among male specimens (Guatelli-Steinberg and Lukacs, 1999). Human males have also been found to exhibit greater rates of EH from fetal development stress, but these trends were not seen in other non-human great apes

(Guatelli-Steinberg and Lukacs, 1999).

Further studies (Guatelli-Steinberg and Benderlioglu, 2006; O'Hara and Guatelli-Steinberg, 2020), however, found opposite patterns suggesting that females experience higher rates of LEH relative to males. In a study of LEH prevalence in malnourished rhesus macaques on Cayo Santiago (Guatelli-Steinberg and Benderlioglu, 2006), scientists found irregularly provisioned females to be most affected. The sex differences in LEH in this sample were likely due to males experiencing greater dental wear, potentially erasing the effects of LEH on dental surfaces (Guatelli-Steinberg and Benderlioglu, 2006). A similar result was found when looking at samples of *Macaca fascicularis* and *Trachypithecus cristatus* where females exhibited greater enamel defects than males (O'Hara and Guatelli-Steinberg, 2020). Again, this may be due to variations in wear in males and females, potentially hiding enamel defect markers (McGrath, 2019).

The manifestation of enamel defects on dental surfaces may also differ between species who experience varying processes of enamel formation and aging (Goodman and Rose, 1990; Guatelli-Steinberg and Skinner, 2000; Hannibal and Guatelli-Steinberg, 2005; O'Hara and Guatelli-Steinberg, 2020; Skinner 2023). Apes have greater LEH frequencies than monkeys, which has been linked to their longer period of dental development (Guatelli-Steinberg and Skinner, 2000; Skinner, 2023). Taking a broad inter-specific approach, Guatelli-Steinberg and Skinner (2000) compared LEH frequencies in sympatric monkey and ape populations, finding that there was a much higher frequency and severity of LEH in the great ape population compared to the lesser ape and monkey samples. They did, however, find that there was more variation in the prevalence of LEH within cercopithecoid populations (Guatelli-Steinberg and Skinner, 2000). More specifically, they uncovered differences among colobines and other cercopithecines, with colobines experiencing faster extension rates, which the researchers link to having fewer noticeable enamel defects compared to taxa with slower extension rates (O'Hara and Guatelli-Steinberg, 2020). Although LEH has been found to be a reliable indicator of physiological and envionrmental stress, it should be noted that other factors may play a role in influencing its prevalence (Guatelli-Steinberg *et al.,* 2012). When testing the association between social rank and LEH, Benderlioglu and Guatelli-Steinberg (2019) found age to be a more important factor in influencing observed LEH prevalence, with older individuals exhibiting less LEH. This may have been due to the erasing of the visual manifestation of these defects with increased wear.

CONCLUSIONS

This paper has provided an overview of some of the research on dental markers of ecological stress in primates, all finding interesting links between dental marks of growth, development, and ecological stress. Intriguing interspecific and intraspecific comparative patterns and contrasts have been found. More specifically, LEH seems to be a valuable biomarker of stress experienced by primates. It is worth bearing in mind, however, that data collected on LEH may be susceptible to error, with its frequency and distribution being subject to natural aging and wear processes that confound results (Guatelli-Steinberg *et al.,* 2012; Benderlioglu and Guatelli-Steinberg, 2019). Given this, there is clearly a need for more studies to be done, as there is more potential for analyses of dental biomarkers to be invaluable resources as scientists reconstruct the life histories of extant and extinct primates.

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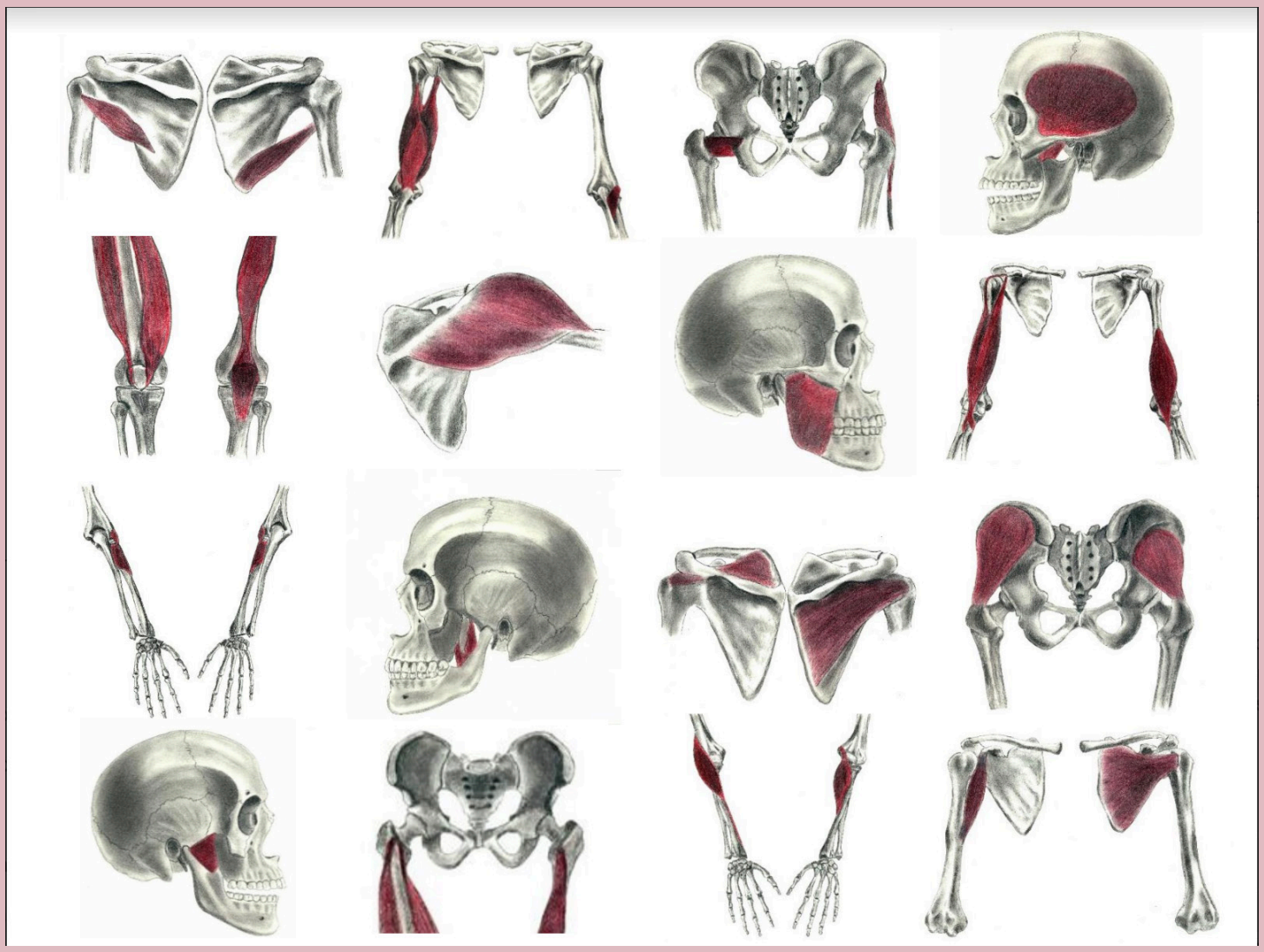

Illustration by Astrid Jervis

Bonobos: a poem
By Charla Teves

These are the bonobos
Though they go by *Pan paniscus*.
They live in the Democratic River of the Congo
And they sometimes eat flowers, though not often the hibiscus.

They are anthropoids with their increased relative brain size
They also have a thick supraorbital torus across the orbits of the eyes.
They are catarrhines with their "tube-like" ears
And with their large canines, there is nothing that they fear.

Their molars are so unique
They have a Y-5 pattern and a crista oblique.
Like chimpanzees, they have thin molar enamel
But don't get them confused, they are their own animal.

They have broad and shallow ribcages
And they can be quadrupeds throughout many of life's stages.
I think they're the best species
So let's get them off the endangered list please!

SAPIENT

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