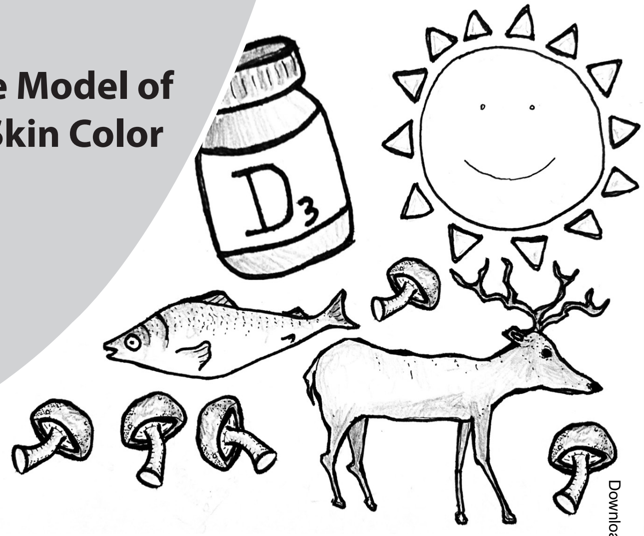
INQUIRY & INVESTIGATION

Teaching a More Accurate Model of the Evolution of Human Skin Color



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Abstract

In popular materials designed to teach American students about the evolution of human skin color, students are guided toward a model in which ancestral latitude predicts levels of skin pigmentation. While this model agrees with data from people whose ancestors practiced intensive agriculture in Europe, Asia, and Africa, this model does not match data from other human populations across the globe, including the predicted skin pigmentation of ancient hunter-gatherer populations who maintained long-term settlements in these same regions. In this review, we discuss findings from ancient genome sequencing and provide guidance on teaching an updated model on the evolution of human skin color. (To increase accessibility for non-specialists, we present here a targeted rationale for updating classroom teaching practices, with a set of frequently asked questions regarding the current state of scientific research on this topic addressed in supplemental material.) With this update, we hope to help students avoid common misconceptions about human evolution—particularly, that the evolutionary pressures encountered by those who adopted a single human culture would apply to all humans, everywhere—and leverage authentic data and argumentation to convey the anti-racist reality that people with a wide range of skin colors thrived in high-latitude regions for many thousands of years, just as students with a wide range of skin colors can thrive in whatever place they currently call home.

Key Words: *human evolution; skin color; modeling instruction; melanin; vitamin D; agriculture; argumentation.*

○ An Introduction to Epidermal Melanin

Well-known and widely used teaching modules on the evolution of human skin color, such as the Illinois Melanin Storyline (ASC, 2021) and HHMI BioInteractive's "Human Skin Color: Evidence for Selection" (HHMI BioInteractive, 2015) typically begin by raising a question: why do people with different ancestries have such different levels of skin pigmentation? Although instructional strategies vary across different lessons on this topic, generally students are next introduced to melanin, a category of biological polymers with appreciable absorption across regions of the UV- and visible spectra (Cao et al., 2021).

Students learn that human skin contains two types of melanin (Thody et al., 1991), and that epidermal eumelanin protects against the damaging effects of ultraviolet radiation (Brenner & Hearing, 2008). Most ancient hominins presumably had lightly pigmented skin beneath dark fur, but approximately one to three million years ago, a lineage arose with less fur; within this lineage, there was such an extreme selective advantage for skin pigmentation that all early *Homo sapiens* had dark pigmented skin with high levels of eumelanin (Jablonski & Chaplin, 2017). When considering human migration out of Africa and the subsequent evolution of local skin color phenotypes, dark skin is the ancestral phenotype, and light skin results from more recent alleles that cause a reduction in eumelanin levels, which we will refer to as "depigmentation."

Students are asked why skin depigmentation was favored in some human populations. The lesson modules offer a potent explanation, informing students that epidermal eumelanin reduces the amount of vitamin D that can be produced by a person's body after a given quantity of sun exposure (Clemens et al., 1982).

In some populations, this resulted in selective pressure promoting the spread of alleles for skin depigmentation. More specifically, populations whose combination of diet, lifestyle, and habitat yielded low amounts of vitamin D—such as the practitioners of intensive agriculture in Europe (continuous cultivation that led to largely grain- and dairy-based diets)—evolved depigmented phenotypes. In these populations, researchers have documented an essentially linear relationship between ancestral latitude and contemporary skin pigmentation (Relethford, 1998). However, this data set, which is a central component of the Illinois Storyline and HHMI BioInteractive materials, is incomplete. The data were collected from only a subset of the Earth's high-latitude regions (Relethford, 1998), and the included data do not match predictions made from genomic data drawn from prehistoric human populations that lived in the included regions (Brace et al., 2019; Bergström et al., 2020; Cerqueira et al., 2012; Dannemann & Kelso, 2017; Ju & Mathieson, 2021; Lalueza-Fox et al., 2007; Lin et al., 2018;

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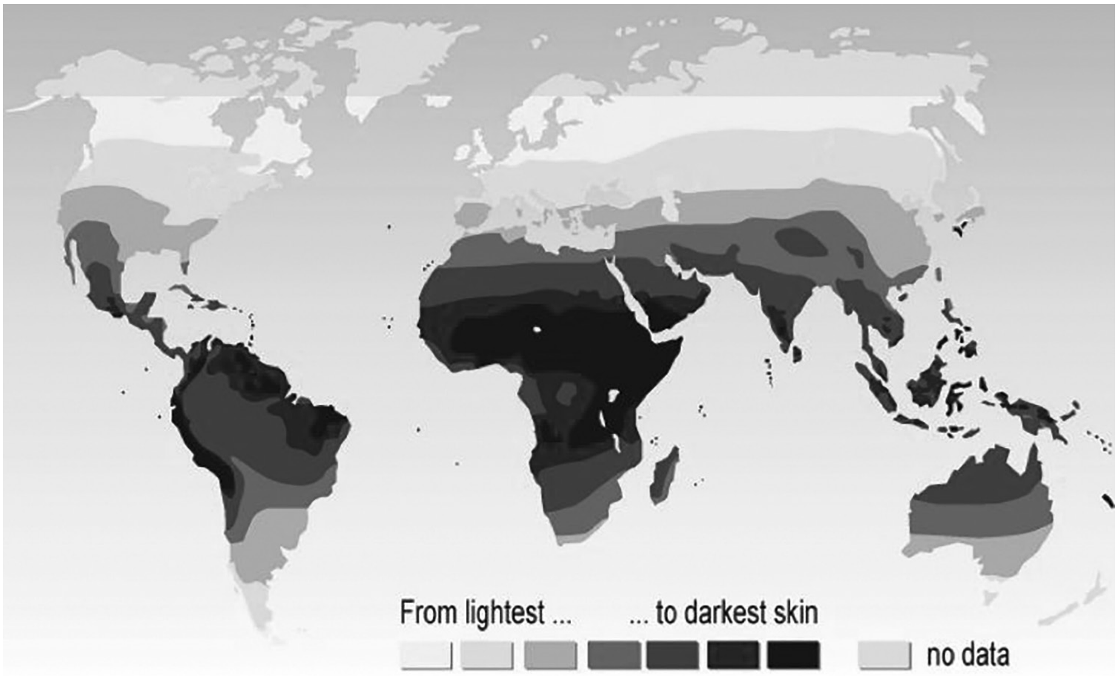

Figure 1. An incomplete model for the evolution of human skin color: note predictions made for populations in North America, South America, South Africa, northern Europe, coastal regions of Asia, and northern Asia. Figure prepared by Bournay, 2009, based on Chaplin, 2004. Equivalent figures appear in many other sources, including Jablonski & Chaplin, 2000, and HHMI BioInteractive's "Human Skin Color: Evidence for Selection."

Mathieson et al., 2015; Sánchez-Quinto et al., 2012; Skoglund et al., 2014; Wilde et al., 2014).

This limited scope results in a model that has skewed understanding of both evolutionary theory in general and the evolution of human skin color in particular, in ways that are especially harmful given the global legacy of racism against dark-skinned populations. This incomplete model is shown in Figure 1; in the scientific literature, many reviews (e.g., Deng & Xu, 2017; Jablonski, 2012; Jablonski & Chaplin, 2017; Jablonski, 2021; Lucock, 2023; Rocha, 2020; Trivedi & Gandhi, 2017) conclude with variations of this model, and the scientific literature includes no reviews that adequately address the mismatch between this model and real-world skin color data, the central importance of ancestral diet in the evolution of human skin color, or the skin color of ancient human populations in regions of the world that we currently associate with skin depigmentation phenotypes. By including data from more human populations in our instruction, we can help students better understand the evolution of human skin color, and help them avoid harmful misconceptions.

○ Misconceptions Resulting from the Use of an Incomplete Dataset

Teaching modules such as the Illinois Melanin Storyline and HHMI BioInteractive's "Human Skin Color: Evidence for Selection" present students with data relating latitude to the level of skin pigmentation among the practitioners of intensive agriculture in northern Africa and Europe, as shown in Figure 2. Using this data, first published by Relethford (1998), students are encouraged to develop the model shown in Figure 1, predicting that all human populations settling at high latitudes will experience selective pressure for skin depigmentation.

We agree that the quantitative dataset graphed in Figure 2 is an enticing resource for building models and/or making predictions because the skin reflectivity measurements allow for graphical analysis by students, and because the relationship between latitude and skin reflectivity appears so clear and compelling. When using this dataset, students have an opportunity to learn about evolutionary trade-offs: epidermal melanin has many benefits, but epidermal melanin also carried a fitness cost if a population had

1. cultural practices that provided insufficient dietary vitamin D;
2. insufficient UVB exposure for dark-skinned people to produce enough endogenous vitamin D; and
3. sufficient UVB exposure for light-skinned people to produce enough endogenous vitamin D.

This set of preconditions has clearly been met by some populations, which is why we see strong evidence for the positive selection of skin depigmentation alleles among people whose ancestors lived in Europe and non-coastal regions of Asia.

However, the dataset shown in Figure 2 is limited both spatially and temporally: as shown in Figure 3, these data are drawn from only part of the globe, and because these measurements were obtained from contemporary populations, other human populations who lived in these regions previously are excluded.

Whenever students are presented with data derived exclusively from the descendants of a single subpopulation of a species, they are more likely to develop misconceptions (Lederman et al., 2002). In this case, by asking students to focus on quantitative data derived only from the descendants of people who practiced intensive agriculture, with high-latitude data drawn exclusively from a region that was the historical seat of global colonialism, students are likely to assume that these people's culture was "normal," or standard for all ancestral human populations, which is not correct (Graeber & Wengrow, 2021; Scott, 2018). More often, ancient humans seem to have sought habitats where a nearby confluence of biomes could provide a variety of foods to meet their nutritional needs, and, rather than adopting practices that we might recognize as intensive agriculture, instead reshaped their local environments to enrich for desirable plant and animal species.

Through these strategies, many populations of ancient humans were able to meet their nutritional requirements, including the requirement for dark-skinned populations living at high latitudes to consume dietary vitamin D, which can fully substitute for endogenous vitamin D (Wolpowitz & Gilchrest, 2006). As Jablonski writes in a 2021 review, "[t]raditional hunter-gatherer diets centered around coastal marine sources, hunted terrestrial game, and foraged plant foods are rich in vitamin D and make it possible for people to continue to live healthy reproductive lives while maintaining 'dark' and highly tannable skin" (Jablonski, 2021).

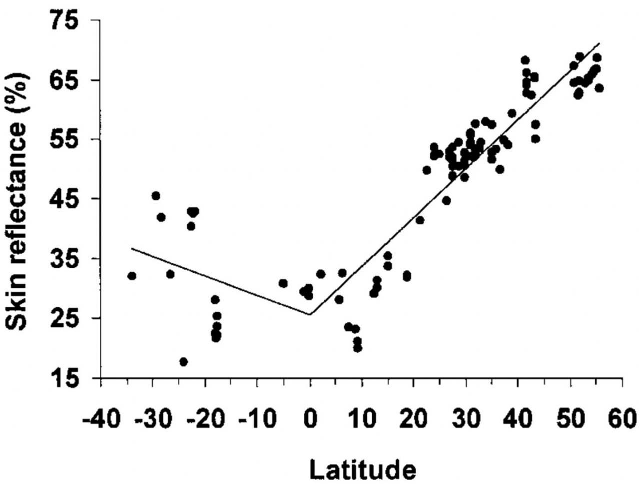

Figure 2. Among the human populations that adopted intensive agriculture in Europe and northern Africa, there is a decisive relationship between latitude and skin color. Reproduced from Relethford, 1998.

Numerous researchers have previously remarked on the coincidence in timing between the arrival of intensive agricultural practices to a region and the local spread of alleles for skin depigmentation (Lin et al., 2018; Lucock, 2023; Wilde et al., 2014). However, these remarks are usually relegated to the discussion sections of research papers, and in the student-facing materials we have reviewed, this dietary dependence is either omitted entirely or brought forth only passingly as evidence to explain the dark skin of people from Greenland, as though this population were a rare exception. In this way, materials aimed at students typically convey the stigmatizing misconceptions that human evolution has routinely selected for depigmented skin at higher latitudes, and that people with dark skin are ill-adapted for these regions. These materials do not expose students to data such as that summarized in Figure 4, which would teach students that there are many human populations outside of Greenland in which dark-skinned phenotypes persisted for thousands of years at high latitudes (or even hundreds of thousands of years, in the case of Neanderthal populations, who are discussed in the FAQ), including many high-latitude regions where such phenotypes have persisted up to the present day.

Because the evolution of human skin color was a response not just to ground-level UVB photon flux but also to cultural practices such as diet, and because we now have ample genomic evidence demonstrating that people with dark skin flourished at high latitudes all over the world for many thousands of years (Brace et al., 2019; Carratto et al., 2020; Lin et al., 2018; Skoglund et al., 2014;

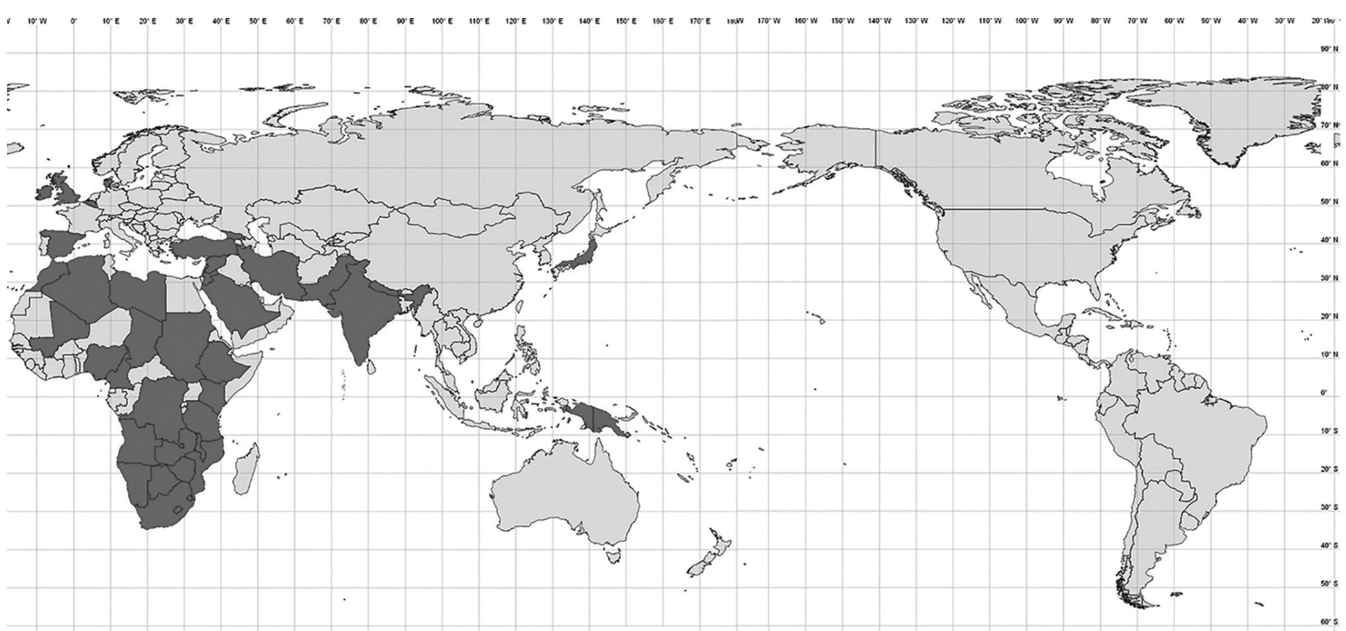

Figure 3. The skin color data used to create Figure 2 were collected from contemporary populations living in the regions indicated in red (online version of article) or darker gray (print version of article). Human populations with ancestors who lived in regions shown in light gray were not included, nor were human populations that lived in Europe between the end of the last glacial maximum and the arrival of intensive agriculture—a time period lasting approximately 10,000 years. Data drawn from Rethelford, 1998.

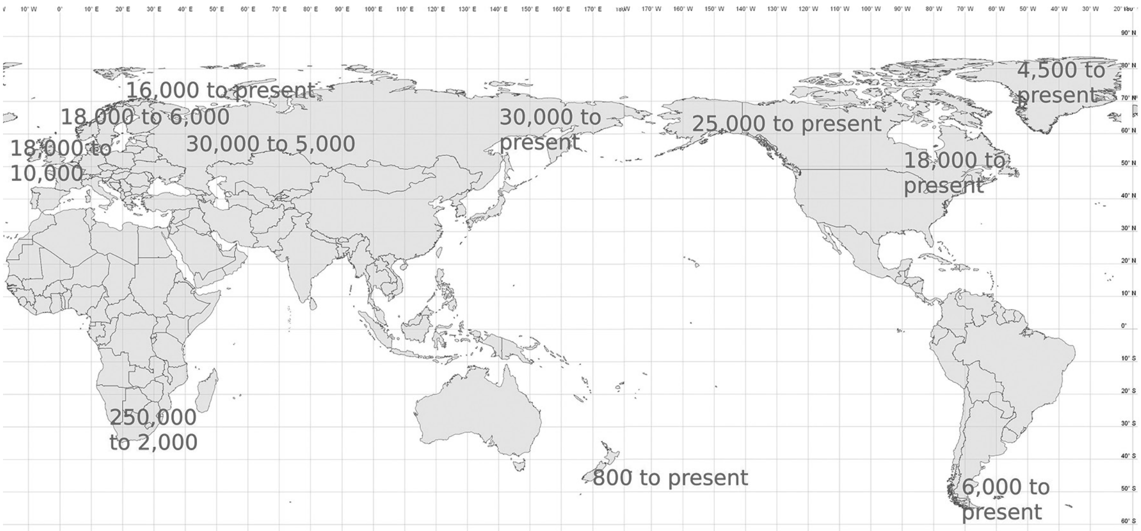

Figure 4. Time ranges during which dark-skinned human phenotypes persisted, based on predictions made from ancient genomics, for high-latitude populations across the globe. For regions in which Indigenous populations with dark-skinned phenotypes still reside, the latter time boundary is marked as "the present." The data in this figure were drawn from Brace et al., 2019; and Carratto et al., 2020; Forsius et al., 2012; Lin et al., 2018; Mathieson et al., 2015; Skoglund et al., 2014; Wilde et al., 2014.

Wilde et al., 2014), biology educators have an opportunity to make instruction about this topic more accurate while simultaneously helping students of color feel confident that someone who looks like them belongs in whatever place they currently call home. Students bring their whole selves to the classroom, and presenting an incomplete model that is racially stigmatizing is especially harmful given that many teachers, students, and communities still experience racism based on the color of their skin (Allchin, 2021; Fuchs & Tan, 2022; Hodson, 2013; Mackenzie, 2020). Furthermore, by framing our understanding of the evolution of human skin color in this way, we can help students realize that if they have adopted cultural practices that limit endogenous vitamin D production—as many educators and our students have, since we tend to be indoors during the hours of peak UVB photon flux on weekdays throughout the school year—they should be mindful of their dietary intake of vitamin D.

○ Incorporating Data from Geographically and Temporally Diverse Human Populations into Cycles of Model Development

To determine whether sufficient time elapsed for a local phenotype to arise, it is essential to know when humans first arrived in a region. As shown in Figure 4, there are many instances of humans migrating to high latitudes without experiencing significant selective pressure for skin depigmentation. Additionally, ancient genomics data have revealed that dark-skinned populations long resided in regions of the globe that we now associate with people with depigmented skin, such as Northern Europe and Asia. These data are in stark contrast with the predictions made by the incomplete model shown in Figure 1.

In fact, in every high-latitude region that has been investigated to date, researchers have found that the alleles for skin depigmentation spread rapidly only after the introduction of intensive agricultural practices. As shown in Figure 5, the timeline for the adoption of intensive agriculture and the cessation of foraging coincides well with the timeline for the selection of depigmentation alleles in human populations across the globe, including those featured in widely used instructional materials, such as the ancient peoples of Africa and Europe (Stephens et al., 2019).

Unfortunately, a search of the scientific literature does not identify a collection of quantitative skin reflectivity data that includes people whose ancestors lived as hunter-gatherers at high latitudes in northern Europe, North America, South America, or northeastern Asia to complement the data set that is graphed in Figure 2 and highlighted by the HHMI BioInteractive and Illinois Storyline materials. Also, because skin color is such a highly polygenic trait, with dozens of genes contributing to each person's resulting skin color phenotype, it is not possible to quantitatively predict a person's skin reflectivity based on their genome, and so it is not possible to combine data from ancient genome sequencing with a contemporary quantitative dataset.

However, it is possible to make reasonably accurate qualitative predictions about the level of skin pigmentation based on genomic data. After they have analyzed the Relethford 1997 data, students can be shown Figure 3 to appreciate this data set's limited scope, then Figures 4 and 5 to introduce them to data on the skin color of people from other high-latitude regions of the world, as well as data from ancient humans whose ancestors had lived at high latitudes for thousands of years. (When sharing data from ancient populations, it is important to note to students that the data includes only individuals whose ancestors had lived in a particular region for thousands of years; otherwise, these individuals might not have a genotype that underwent selection within the context of that environment and their particular cultural practices.)

In our experience, the qualitative data shown above are sufficient for students to recognize that their initial model predicting skin color based on latitude might be incorrect. The addition of these data allows students to build a more accurate conceptual

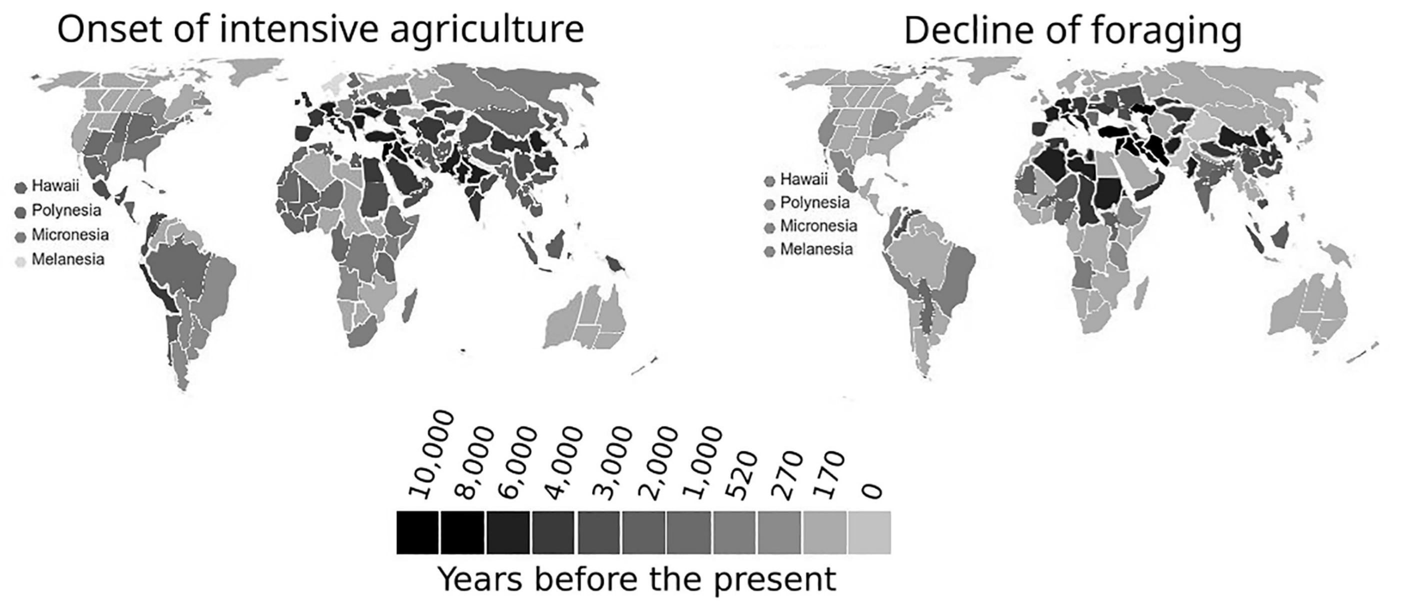

Figure 5. The earliest time at which intensive agriculture was commonly practiced in a region, and the earliest time at which foraging was no longer commonly practiced in a region, as measured in thousands of years before the present. Note that these changes closely parallel timelines for the increase in allele frequency for skin depigmentation in high-latitude regions shown in Figure 4. Figure adapted from Stephens et al., 2019. (Full color version of this figure is available with the online version of the article.)

model (Fuchs et al., 2021; Sadler & Sonnert, 2016), recognizing the importance of cultural practices in human evolution and engaging in argumentation to describe why and how they are refining their initial models. At this point, students may wish to discuss other instances of cultural practice influencing human evolution, such as the use of fire, language, clothing, or other technologies (Herculano-Houzel, 2018; Watanabe et al., 2021). From here, more advanced students can analyze data on when various alleles for skin depigmentation spread among the relevant populations, or dive more deeply into the temporal data from an archaeological assessment of land use from Stephens and colleagues (2019).

Because most people alive today have adopted cultural practices associated with intensive agriculture—and because most people in positions of power are descended from people who have practiced intensive agriculture for thousands of years—it is easy to slip into the misconception that this particular set of practices constitutes a "normal" culture for humans (Graeber & Wengrow, 2021; Scott, 2018). However, this misconception not only leads students astray scientifically—students may overestimate the explanatory reach of models or theories trained on data derived from a single culture—but also, this can be seen as a hurtful act of erasure against the myriad other cultural adaptations employed by humans all over the world, including the very recent ancestors of many people still living today.

We exercise not only our scientific reasoning but also our empathy as fellow humans when we recognize that the ancient humans who settled at extreme latitudes may have developed intentional cultural practices in order to survive there. Harvesting marine resources (Alexandra & Barbara, 2013); utilizing the entire bodies of game animals they killed (Alexandra & Barbara, 2013); sun-drying their food, which increases its vitamin D content (Cardwell, 2018; Larson-Meyer, 2017; Nölle, 2017; Steenbock, 1928); long-distance seasonal travel (Sánchez-Quinto et al., 2012): these are some of the strategies that high-latitude populations of ancient people may have used, which would have led them to experience different selective pressures from the people who practiced intensive agriculture at similar latitudes.

Finally, we note to students that, across the contemporary world, dietary supplementation of vitamin D is such a low-cost intervention that people who adopt nearly any culture, anywhere, can obtain a diet with sufficient vitamin D. But this has not always been the case: indeed, a relevant example from recent history illustrates the harms that can arise when scientific findings are employed inequitably. In the 1920s, biochemist Harry Steenbock from Wisconsin discovered that the vitamin D content of foods could be increased by treating the foods with UV radiation. This process was patented, and the patent was licensed to many food producers. However, to protect Wisconsin's dairy industry, use of the patented technology was denied to margarine producers. Many poor families used margarine instead of butter because it was cheaper; poor families were also more likely to suffer from vitamin D insufficiency. By selectively ensuring that a food often consumed by poor people was not fortified with vitamin D, this needlessly perpetuated the correlation between poverty, race, and vitamin D insufficiency (Zaitchik, 2022).

○ CONCLUSION

As educators, we often present students with simplified models, with the understanding that a topic can be revisited later to be explored in greater depth or complexity. All models are incorrect; many are still useful. The evolution of skin color among people who practiced intensive agriculture is a compelling story, and would seem to provide the basis for an excellent lesson: the topic is engaging, the data are clear, and the model is good—for the descendants of particular populations of intensive agriculturalists from whom data was collected to create Figure 2. Updating this lesson series to include another round of model development that draws from the

Table 1. Frequently asked questions addressed in the supplemental material accompanying the online version of this article.

1.	Where did populations of humans maintain a dark-skinned phenotype despite living at high latitudes for long periods of time?
2.	When did alleles for skin depigmentation spread through Northern Europe?
3.	Could ancient humans get all the vitamin D they needed from food alone?
4.	Do we have evidence that contemporary dark-skinned people living at high latitudes are at increased risk for vitamin D deficiency?
5.	Have researchers rejected the hypothesis that dark skin arose in part due to the selective pressure to protect people from skin cancer?
6.	The Neanderthal lived at high latitude; what skin color did they have?
7.	If agricultural diets were unhealthy, why did people adopt and then continue to practice agriculture?

data shown in Figures 4 and 5 allows teachers to highlight the iterative nature of scientific discovery and support students as they build a more comprehensive, rigorous model of skin color diversity and its origins. For those interested in learning more, the questions in Table 1 are addressed in the supplemental material accompanying the online version of this article.

Many of the students in our classes have a teleological view of the history of technology, in which innovations such as agriculture are seen as "better" than the cultural practices that had been adopted earlier. But students should be encouraged to question: better in what ways, and for whom? Human populations that maintained their pigmented skin were those that adopted cultural practices that fulfilled each individual's need for dietary vitamin D; in other words, these populations adopted cultural practices that allowed people to thrive regardless of their skin color. By way of contrast, in the populations that experienced strong selective pressure for skin depigmentation (who had adopted cultural practices that students may be inclined to view as "more advanced"), no one consumed as much dietary vitamin D as they needed; this lack of dietary vitamin D was the source of selective pressure for increased endogenous production, even at the cost of losing the protective benefits of epidermal melanin.

Depigmented skin is not necessary for humans to thrive at extreme latitudes. Instead, we need the right cultural practices. Presenting students with more complete datasets allows them to discover this, simultaneously pushing back against both racial prejudice and scientific misconceptions about human evolution while highlighting the breadth of biological data that can be applied to exploring high-interest topics in the classroom.

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SUPPLEMENTAL MATERIAL for "Teaching a more accurate model of the evolution of human skin color":

FREQUENTLY ASKED QUESTIONS

1) Where did populations of humans maintain a dark-skinned phenotype despite living at high latitudes for long periods of time? 2) When did alleles for skin depigmentation spread through Northern Europe? 3) Could ancient humans get all the vitamin D they needed from food alone? 4) Do we have evidence that contemporary dark-skinned people living at high latitudes are at increased risk for vitamin D deficiency? 5) Have researchers rejected the hypothesis that dark skin arose in part due to the selective pressure to protect people from skin cancer? 6) The Neanderthal lived at high latitude; what skin color did they have? 7) If agricultural diets were unhealthy, why did people adopt and then continue to practice agriculture?

Questions addressed in this supplement.

1) Where did populations of humans maintain a dark-skinned phenotype despite living at high latitudes for long periods of time?

In Northern Europe, Northern Asia, North America, Greenland, South Africa, South America, and New Zealand, distinct populations of humans settled at high latitudes yet maintained dark-skinned phenotypes. It is, of course, possible that these groups of people also encountered selection pressure that would have favored depigmented skin. There are many reasons why a favorable phenotype might fail to develop even under selective pressure: for instance, the necessary genetic variation might be absent; the population size might be too small for the influence of selection to overcome the effects of genetic drift; genetic flux from other regions might prevent the emergence of a local phenotype; etc.

However, given the population sizes involved in these migrations and the wide variety of genetic variants that seem to influence human skin color that were already present at low or moderate levels in these populations for long periods of time (Crawford et al., 2017), it seems more likely that highly depigmented skin was not significantly favored in these environments, *unless* a population adopted a lifestyle that was particularly low in vitamin D.

In several of these regions, populations with relatively dark-skinned phenotypes have persisted up to the present day. Please note that when the following summaries include "the present," we are referring to contemporary people whose ancestors settled in these regions long ago, rather than more recent migrants. Also, all present-day people are likely to have some degree of genetic admixture from people whose ancestors lived elsewhere (Gopalan *et al.*, 2022; Witt *et al.*, 2023). This makes it difficult to assess ancestral skin color phenotypes based on contemporary data, which is why qualitative predictions from ancient DNA sequencing are so valuable for this lesson.

NORTHERN EUROPE: Dark-skinned people lived throughout Europe from about 16,000 years ago until about 6,000 years ago, by which time most European hunter-gatherer populations had been displaced by incoming agrarians. Because skin reflectivity data from northern Europe forms the basis of many existing modules intended to teach students about the evolution of human skin color, we will discuss the skin color phenotypes of European populations in more detail below, including a discussion of the European populations in which dark-skinned phenotypes have persisted to the present day.

NORTHERN ASIA: Dark-skinned people lived in Northern Asia from about 30,000 years ago until about 5,000 years ago, at which time agrarian cultural practices were introduced to the region and genes for skin depigmentation spread rapidly (Wilde *et al*., 2014). Even after the introduction of intensive agricultural practices, diets that included marine resources may have reduced the selective pressure for skin depigmentation. Populations in East Asian regions like Japan or Korea, where many people continued to consume ample quantities of marine resources even after the introduction of rice as a culinary staple, are less depigmented than the model shown in Figure 1 predicts (Jablonski & Chaplin, 2000). All data from Japan fall below the regression line in the Relethford 1998 dataset, as would data from Korea, had the latter been included (Bazarragchaa *et al.*, 2020; Seo *et al.*, 2022).

NORTH AMERICA (TURTLE ISLAND): Dark-skinned people have lived in North America (Turtle Island) from about 25,000 years ago until the present. Many of the people living in North America maintained hunter-gatherer lifestyles with some measure of communal agricultural production until approximately 300 years ago (Carratto *et al*., 2020). Although there are no published skin reflectivity data for this entire region, we have qualitative evidence that predictions made by the incomplete model shown as Figure 1 are incorrect: contemporary people whose ancestors lived in regions comprising many parts of present-day Canada are still sufficiently dark-skinned that many have experienced significant impediments from skin-pigmentation-based racism (MacKinnon, 2017). Populations that had been living at high latitude in North America for over 20,000 years were ancestral to the people of Greenland, where dark-skinned people have been living from about 4,500 years ago until the present (Kromann *et al.*, 1983), although present-day populations in Greenland have significant genetic admixture from European populations (Moltke *et al.*, 2015).

SOUTH AFRICA: Dark-skinned people lived in South Africa from about 250,000 years ago (Grün *et al*., 2020) until about 2,000 years ago without experiencing selection for genes related to skin depigmentation; after this time, incoming agrarians displaced the hunter-gatherers from many of the most productive regions, including those with access to a variety of biomes. Researchers believe that in a process beginning either approximately 2,000 years ago or approximately 500 years ago, genes for skin depigmentation spread rapidly among the surviving hunter-gatherers, whose diets had presumably become worse after having been displaced from their ancestral lands (Lin *et al.*, 2018).

SOUTH AMERICA: Dark-skinned people have lived in South America from about 11,000 years ago until the present, with distinct populations establishing long-term settlements in high-latitude regions approximately 6,000 years ago (Piana *et al*., 1992; Carratto *et al.*, 2020), including the Indigenous Yahgan people (whose last native speaker died in 2022 (Araya & Saez, 2022)). Several other groups of Indigenous people with dark-skinned phenotypes lived at the extreme latitudes of present-day Argentina and Chile until very recently, when many were killed by either infectious diseases from Europe or intentional genocide (Garcia-Bour *et al.*, 2004). Archaeological evidence suggests that these populations maintained diets rich in vitamin D, with the vast majority of their caloric intake consisting of animal proteins and fat, including ample marine resources. However, people descended from these high-latitude populations were not included in studies on the evolution of skin color in the Americas (Adhikari *et al*., 2019); there are no published data on skin reflectivity for these populations.

NEW ZEALAND (AOTEAROA): Dark-skinned people have lived in New Zealand (Aotearoa) from about 800 years ago until the present (Nessvi *et al*., 2011; Bunbury *et al.*, 2022). Based on the time typically required for new alleles to arise and then spread among a population, most researchers would assume that the people living in New Zealand would not yet have developed phenotypes that match the environment and culture of their new communities. Because these people lived as hunter-gatherers with appreciable use of marine resources, however, we would not expect for there to have been significant selective pressure for skin depigmentation.

2) When did alleles for skin depigmentation spread through Northern Europe?

Because vitamin D deficiency reduces bone density and causes skeletal abnormalities, the archaeological record can preserve evidence of a mismatch between an ancient person's requirement for and access to vitamin D. Although bone abnormalities that we might presume to be indicative of vitamin D deficiency can also be caused by lack of calcium (Pettifor, 2004), preventing a definitive diagnosis from fossil evidence, the absence of these diagnostic bone abnormalities indicates that an ancient person had sufficient access to both calcium and vitamin D, whether from dietary sources or endogenous production (Meyer, 2016). In Europe, the first case of rickets that has been found in the archaeological record dates to approximately 5,300 years ago in Scotland (Armit, 2015). This time is shortly after neolithic farmers displaced the hunter-gatherers who had been previously inhabiting this region, a process that began approximately 6,000 years ago (Brace *et al*., 2019). The archaeological record suggests that bone abnormalities symptomatic of rickets continued at a frequency of approximately 1% to 3% after the neolithic transition to agriculture in this region (Littleton, 1991), a rate that is presumed to be sufficient for a selective effect (Chaplin & Jablonski, 2009). By way of contrast, in high-latitude regions where populations did not transition to intensive agriculture, such as North and South America, rickets is largely absent from the archaeological record (Wells, 1975).

Within the past decade, researchers have been able to utilize small amounts of ancient bones to sequence the genomes of ancient hunter-gatherers who lived in Northern Europe before the arrival of the neolithic farmers. These hunter-gatherers, such as "Cheddar Man," found approximately 50 degrees north of the Equator, "likely had blue/green eyes, dark brown possibly black hair, and dark or dark to black skin" (Brace *et al*., 2019). Cheddar Man lived perhaps 10,000 years ago, indicating that the dark-skinned phenotype had persisted in this region for at least 8,000 years, ever since *Homo sapiens* expanded into this territory after the last glacial maximum. An Early Neolithic individual from the same region, who lived approximately 6,000 years ago, was found to have alleles predicting “dark to intermediate skin.” Similarly, 5,000-year-old Scandinavian hunter gatherers from the “pitted ware culture,” found approximately 60 degrees north of the equator, still had ancestral alleles for skin-color genes SLC45A2 and SLC24A5, suggesting that they had darkly pigmented skin, while contemporaneous nearby people who practiced intensive agriculture had alleles for depigmented skin (Skoglund *et al*., 2014).

Ancient DNA sequencing has found that many alleles for skin depigmentation were present at low to moderate frequencies among the various hunter-gatherer populations of Northern Europe – such as a skin depigmentation allele with a frequency of about 25% among 8,000-year-old hunter-gatherers at Motala, 58 degrees north of the equator (Mathieson *et al.*, 2015) -- but appeared not to have been significantly favored, as such alleles would be soon after agrarians settled in the region.

Some populations living in northwestern Europe, such as the Sámi of Finland, maintained a diet more similar to ancient hunter-gatherers until nearly contemporary times; these populations experienced significantly less selective pressure for skin depigmentation (Forsius *et al*., 2012), and many present-day people with this ancestry have relatively dark skin despite recent genetic admixture with people whose ancestors practiced intensive agriculture.

3) Could ancient humans get all the vitamin D they needed from food alone?

As Jablonski notes in a 2021 review, a typical hunter-gatherer diet would often provide ample vitamin D (Jablonski, 2021). Twenty grams or less of many types of fish provide a sufficient daily allotment; mushrooms have a moderate amount; wild animal butchery that utilizes the whole body produces several cuts with plentiful vitamin D (Alexandra & Barbara, 2013).

Even foods that are not significant sources of vitamin D when eaten fresh can be enriched in vitamin D by exposing them to sunlight; this technique dramatically increases the vitamin D content of meats, dairy products, and plant-based foods (Steenbock, 1928; Larson-Meyer, 2017; Nölle, 2017; Cardwell, 2018). We do not know for certain how ancient people preserved food for winter months or for travel, but sun-drying is a technique commonly used by contemporary Indigenous communities. With this method, ancient humans may have (perhaps inadvertently) bolstered their dietary vitamin D intake. We can also surmise that cultural practices to preserve food would have been more common among ancient peoples living at extreme latitudes, where there is a significant reduction in the amount of available vegetation during winter months.

That the entire allotment of vitamin D required by a human body can be supplied by diet was essential for ancient humans' survival in places such as Scotland, where Jablonski and Chaplin write that "there are only 3-4 months during the year during which sufficient UVB is present in sunlight to initiate cutaneous production of [vitamin D] even for people with maximally depigmented skin" (Chaplin & Jablonski, 2013). The seasonal window of time in which a person with depigmented skin can produce more endogenous vitamin D than a person with dark skin is even more brief at higher latitudes (Robins, 2009).

SUPPLEMENTAL MATERIAL for Human Skin Color

4) Do we have evidence that contemporary dark-skinned people living at high latitudes are at increased risk for vitamin D deficiency?

Some educational materials ask students to analyze data from Saintonge *et al*. (2009), leading to the conclusion that people with dark skin are at an increased risk for vitamin D deficiency compared to people with depigmented skin. For example, in the HHMI BioInteractive and the Illinois Storyline materials, students are shown Figure 6.

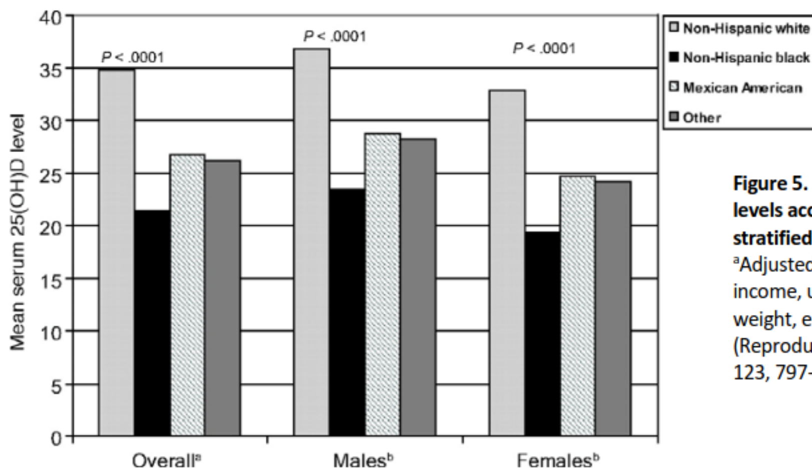

Figure 5. Adjusted mean serum 25(OH)D levels according to race/ethnicity and stratified according to gender (n = 2629). [a]Adjusted for gender, age, weight, education, income, urban, region; [b] adjusted for age, weight, education, income, urban, region. (Reproduced with permission from *Pediatrics* 123, 797-803, Copyright© 2009 by the AAP.)

FIGURE 6: *Reproduction of a figure from Saintonge et al. (2009) including in the instructional materials under discussion.*

However, these data were collected in a way that artificially magnifies the apparent racial differences in serum blood levels. Blood samples from middle- and high-school-aged young people in the United States were collected and analyzed for the level of serum vitamin D. From young people living in the northeastern U.S., blood samples were collected during summer. From young people living in the southern U.S., blood samples were collected during winter.

Because most middle- and high-school-aged young people spend the hours of potential peak sun exposure indoors at school during winter months, most would have little or no endogenous vitamin D production in winter, no matter the pigmentation level of their skin. Only 25% of the white participants in this study had their blood drawn during winter; 60% of the Black participants had their blood drawn during winter (Looker *et al*., 2002). In the text, the researchers state that having blood drawn during winter was correlated with low levels of vitamin D, regardless of ethnicity. If all samples had been collected during the same time of year, the apparent racial difference would be much smaller, if not absent.

Circulating blood levels are also reduced by a person's percentage of body fat, with people classified as obese at a significantly higher risk of vitamin D deficiency (Wortsman *et al*., 2000). Because cultural factors in the United States like systemic racism, chronic stress, and food deserts have created an environment where Black children are more likely to be diagnosed with obesity than white children (Petersen *et al*., 2019), this could offer an additional explanation for any disparities. Even if a future study were to find differences between racial groups whose blood samples had all been collected at the same time of year; a disparity would not necessarily indicate any difference in endogenous vitamin D production. While we feel that an extended discussion about either systemic racism or scientific publishing bias are beyond the scope of a lesson about the evolution of human skin color, educators should certainly be aware of both the non-standardized methodology and alternate explanations for this commonly cited figure. This is not to criticize the authors of the aforementioned study: their aim was simply to raise awareness about vitamin D insufficiency among contemporary people living in the United States, and these data are sufficient for that purpose (Saintonge *et al*., 2009). But these data should not be included in a lesson on human evolution.

That said, appropriately designed studies have shown a difference between different bodies' ability to synthesize endogenous vitamin D. Below a certain threshold of UVB photon flux, no endogenous vitamin D can be produced, and epidermal melanin raises this threshold, such that a person with dark skin might require a five-fold higher photon flux than a person with depigmented skin in order to produce any vitamin D (Clemens *et al.*, 1982).

Cultural adaptations like wearing clothing, wearing sunscreen, and spending the hours of potential peak sun exposure indoors also reduce a person's ability to produce endogenous vitamin D. This is a benefit of teaching students about the cultural adaptations that allowed various human populations to maintain a dark-skinned phenotype despite settling at high latitudes: students may realize that they too should adopt a cultural practice like increasing their dietary intake of vitamin D.

Additionally, students should keep in mind that the production of endogenous vitamin D levels off quickly, as illustrated by Gilchrest (2008), whose figure is reproduced in Figure 7.

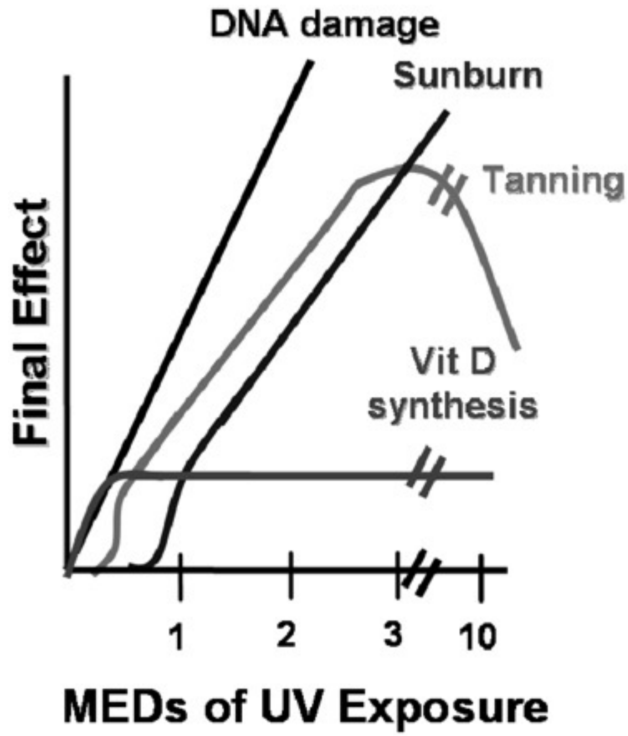

FIGURE 7: *Figure reproduced from Gilchrest (2008).*

When there is enough UV exposure for both people with dark skin and people with depigmented skin to produce the amount of endogenous vitamin D that they need (which may even be zero, depending on diet), there is no selective benefit for depigmented skin.

This is true on summer days even at high latitude; a controlled trial has shown that UVB exposure equivalent to approximately 30 minutes of summer sun in Denmark, 56° N latitude, results in the same increase in vitamin D levels in people with either dark skin or depigmented skin (Bogh *et al.*, 2010).

Similarly, there is no selective benefit for depigmented skin if there is insufficient UV exposure for people with depigmented skin to produce the vitamin D they need. This is true during winter at high latitude, and for school-aged and college students in cultures like our own, where the majority (or even the entirety) of peak sun hours are spent indoors during the school year. There is only a selective benefit for depigmented skin within a relatively narrow regime of UV flux, presumably occurring during windows of time in the spring and fall at high latitude, and only for people with low dietary vitamin D. In populations with high levels of facultative pigmentation – increased melanogenesis in response to sun exposure, or tanning – this may be reduced further, to a window of time only during the spring. Facultative pigmentation occurs over several time scales (Eller & Gilchrest, 2000), but the "delayed tanning" response, which is photoprotective against the UVB radiation required for endogenous vitamin D synthesis, persists for weeks or months (Brenner & Hearing, 2008).

5) Have researchers rejected the hypothesis that dark skin arose in part due to the selective pressure to protect people from skin cancer?

When a trait has many benefits, it is difficult to know which benefit was most significant over evolutionary time. For example, we know that language is very helpful for our species, but researchers still debate whether the initial impetus for the evolution of humans' capacity for speech was to communicate while hunting, to share gossip, or to bond with infants and young children.

Jablonski has argued that skin cancer, which typically does not result in debilitation or death until after a person's reproductive years, could not have contributed to the evolution of dark skin (Jablonski, 2021). However, ancient humans lived in communities, with human babies and children typically being so helpless that they relied upon provisioning, protection, and care from many adults in order to survive. During evolutionary periods of time when child mortality was high – among contemporary hunter-gatherer populations, 40% of all children die before reaching reproductive age (Gurven & Kaplan, 2007), and there may have been eras of human evolution when childhood mortality was even higher – additional provisioning or care from grandparents or community elders may have been crucial for childhood survival. Some studies of contemporary populations have found a 70% increased rate of survival for children with surviving maternal grandmothers (Sear & Mace, 2008). Based on our species' extended lifespan, including the significant length of female humans' post-fertile lives, we can assume that traits that increased the likelihood of children having a surviving grandmother were selected for during human evolution (Hawkes *et al*., 1998). This reasoning suggests that protection from skin cancer could be an evolutionary driver for dark skin.

In some instructional materials, such as the educator materials for HHMI BioInteractive "The Biology of Skin Color," these considerations are stressed; in others, such as the materials for HHMI BioInteractive "Human Skin Color: Evidence for Selection," these considerations are rejected, which is incorrect.

Both sets of HHMI BioInteractive teaching materials promote a theory that either the major or the only source of selective pressure for dark skin was to protect folate, an essential nutrient implicated in birth defects and reduced spermatogenesis. However, the sort of birth defect caused by low folate is relatively rare, certainly compared to the total mortality rate of children younger than reproductive age. For example, a study from South Africa in the 1970s and 1980s found that these birth defects occurred at a rate of about 1 per 1,000 among people with dark skin, and about 3 per 1,000 among people with depigmented skin (Buccimazza *et al*., 1994). Worldwide, before efforts were made to supplement women's intake of folic acid, the rate of these birth defects was approximately 2 per 1,000 (Botto *et al.*, 1999). These numbers are also sensitive to cultural practices: clothing is protective, and these birth defects cycle seasonally, as one would expect given their link to UVB exposure. One of the best protective measures is to increase dietary intake of folic acid – this is the protective measure recommended by healthcare providers today – and hunter-gatherer diets typically have much more folic acid than unfortified grain-based diets (Metz *et al*., 1971). Although neural tube defects have accounted for as much as 10% of all post-perinatal mortality in the worst-affected contemporary populations, they were unlikely to account for more than 0.5% of pre-reproductive deaths among ancient peoples (assuming a mortality rate of 2:1000 due to neural tube defects, out of a total mortality of 400:1000 children who died before reaching reproductive age). It is more difficult to make quantitative predictions about the effect of reduced spermatogenesis on reproductive success, because we have little data on the relationship structures of very ancient human populations; if they were sexually monogamous, sperm competition may have had little influence on an individual's reproductive success (van der Horst & Maree, 2014).

This is not to argue that folate played no role in the evolution of human skin color; there is no reason to doubt that this was a contributing factor. But it is inappropriate to teach students that folate was the *only* factor. Indeed, considering the magnitudes of the risk of neural tube defects compared to the reduction in childhood mortality in families with a surviving maternal grandmother, it is unlikely that the role of melanin in protecting folate was more important than preventing skin cancer.

Humans are a social species. As in eusocial insects and mammals, in which the phenotypes of nonbreeding members can have a dramatic impact on the reproductive success of the colony as a whole, the phenotypes of humans past their reproductive age can have a major impact on the reproductive success of their entire communities, through mechanisms like increased provisioning, watchful care, and intergenerational knowledge transfer.

6) The Neanderthal lived at high latitude; what skin color did they have?

We can make predictions about Neanderthal skin color based on genetic evidence: a 2012 study by Cerqueira and colleagues looked at the genomes of three Neanderthal individuals who lived approximately 40,000 years ago and whose bones were found at a latitude of 46° N and, based on the number of alleles that each individual had that are correlated with dark or light skin among contemporary people, concluded that all three individuals probably had dark skin (2012). However, these are difficult predictions to make. Skin color is such a complex, polygenic trait that it is difficult to use genetic markers to predict exact skin color phenotypes, even when using dozens of genetic markers to predict the skin color of contemporary people (Chen *et al*., 2021).

Another form of evidence is to look at the contribution of Neanderthal alleles to contemporary people's phenotypes. In a 2017 study, Dannemann and Kelso found that some Neanderthal alleles seem to cause lighter skin tones, while other Neanderthal alleles seem to cause darker skin tones (Dannemann & Kelso, 2017). These authors concluded that there was probably a range of skin tones present among the Neanderthal; some may have had light skin and others dark skin.

A 2007 study by Lalueza-Fox and colleagues found that some Neanderthals had a MC1R allele that probably caused depigmentation (2007). In this study, the researchers estimated that approximately 1 in 100 individuals among the population of Neanderthals would have been homozygous for this gene, and so would probably have had skin as pale as people from contemporary Ireland. (By way of contrast, nearly all *Homo sapiens* living in Ireland 500 years ago were homozygous for similar alleles. Within each local population of Neanderthals, there was probably a much greater range of skin tones present than among the people living in Europe 500 years ago.)

When archaeologists have sorted through Neanderthal trash heaps, they have found evidence that Neanderthals consumed a wide variety of foods, similar to ancient *Homo sapiens.* Of particular relevance is the finding that Neanderthals consumed many types of invertebrates, fish, marine mammals, and wild game (Zilhao *et al.*, 2020), which is a type of diet that has provided sufficient vitamin D for many human populations living at high latitudes. Because they lived in Northern latitudes through several ice ages, times when it may have been more difficult to find food in wintertime, it is possible that Neanderthals also practiced the vitamin-D-enriching food preservation technique of sun-drying.

Based on the evidence we have from *Homo sapiens* hunter-gatherers living at similar latitudes, we predict that it was unlikely that the Neanderthal experienced significant selective pressure for skin depigmentation. This may be why the MC1R alleles associated with skin depigmentation did not become fixed among the Neanderthal during the nearly 400,000 years that they lived in Europe, even though similar alleles often became fixed among *Homo sapiens* who practiced intensive agriculture within a few thousand years of settling at high latitudes.

7) If agricultural diets were unhealthy, why did people adopt and then continue to practice agriculture?

As Scott discusses in *Against the Grain*, the individual people who practiced agriculture were often less healthy than the individual people who adopted hunter-gatherer cultures. “Evidence for the relative restriction and impoverishment of early farmers’ diets comes largely from comparisons of skeletal remains of farmers with those of hunter-gatherers living nearby at the same time. The hunter-gatherers were several inches taller on average. This presumably reflected their more varied and abundant diet” (Scott, 2018).

For thousands of years after the rise of agriculture, humans often had to be coerced into abandoning hunter-gatherer cultures: Scott documents many occasions during which people intentionally fled civilizations that practiced intensive agriculture in order to pursue other modes of subsistence (Scott, 2018). This may have resulted in improved nutrition for the individuals involved.

However, humans are social species. The story of human evolution often reflects the successes and failures of entire communities, not individuals. The practice of intensive agriculture allowed for higher population densities (Bergstrom *et al.*, 2020); even though each individual might have been less healthy than an individual hunter-gatherer, in conflicts over land usage, the more numerous practitioners of agriculture were likely to prevail.

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