Skin Color, part 2

Hi, I'm Jim, I'm Erik, I'm Jo and this is Speaking of Race.

Jim: It's time to talk more about skin color!

Jo: We're tracing how people have talked about and written about and understood differences in skin color across time, and since we're a podcast about race, we were especially interested in how and when skin color became the sine qua non of race. Last time we started with ancient Egypt (as we often do) and INSANELY kept going until the 20th century.

Erik: We saw how skin color became that signal of race that it so often is today after the mid 1600s. And as an intercontinental slave trade intensified between Europe, Africa, and the Americas --

Jo: -- and as European diseases and policies killed off aboriginal populations from the Caribbean through North and South America --

Erik: -- skin color became a central symbol for an entrenched hierarchy that would last far after intentional genocide and enslavement became outlawed.

Jo: It seems like, last time, we saw a struggle between those natural philosophers who wanted to say that skin color came from something essential, something internal to members of a group and those who insisted it was caused by environmental, external factors.

Jim: And not just scientists! There was the "curse of Ham" stuff taken out of the Bible.

Erik: But it never really resolved. Even in the 20th century, that "inside" versus "outside" or "essence" versus "environment" kept hanging around.

Jo: So I was expecting once we got to the 20th century for us to reveal how genetics solved this problem, but we kept plowing right into the 20th century without even discussing genetics. We actually left off talking about theories--

Erik: --could you quickly remind listeners what those theories are (or were)?

Jo: on the one hand, about why people lost dark skin pigmentation at higher latitudes, and just as a little reminder, the idea there was that people need to have UV exposure in the skin to produce vitamin D, which would mean needing lighter skin at higher latitudes where UV is lower to get enough vitamin D for a healthy skeleton. We had JUUUUUST started to talk a tiny bit about theories for why people retained darker skin pigmentation at lower latitudes, but we didn't really get into it much. We'll talk more about that one today, if I'm not mistaken, right Jim?

Jim: We will! But I need to warn you before we even start: this stuff is a LOT more complicated than anyone—and I'm including us cohosts here—thought. Early skin color geneticists were proposing just a couple of genes that might be involved in skin color. We now know there are way more with incredibly complex interactions.

Genetics

Jo: Ok, Jim, sure it's complicated. But we'll parse through it all, right? I mean, we're smart people. Our listeners are smart people.

Jim: Well, we'll do our best. So, the stuff last episode got us up to the 1970s. And if you haven't already done so, listeners, pause here and listen to that one first. …and as Erik suggested at the end of our last episode, we're gonna start now with a eugenicist.

Erik: Not just ***A*** eugenicist, the Father of American eugenics, Charles Davenport!

Jim: That's right! Surprise, surprise—genetics was immediately part of the eugenics movement.

Jo: As was a consideration of skin color and how it gets passed down, I'm guessing.

Erik: Yeah. This is something we'll have to come back to one day—a thirty-part series on eugenics! I think for now it's enough to say that in the United States, animal and plant breeders in the first decades of the 20th century took those new ideas of genetics and how to segregate and control those unwanted traits in plants and animals....and jumped right on over to humans. So, Davenport, for instance, helped launch the American Breeder's Association from the University of Chicago to study the impact of the new genetic ideas on animal breeding in 1903.

Jim: But he really made a name for himself a decade later as director of the Eugenics Records Office on Long Island, NY.

Jo: OK, we've briefly mentioned Charles Davenport before on this podcast. Since we are talking about skin color here, I'm guessing he had something to say about that specifically, or we wouldn't be talking about him again now?...

Jim: Yep. He proposed one of the first and most influential human skin color hypotheses in his 1913 work, *Heredity of Skin Color in Negro-White Crosses* (Davenport, 1913). He divided the skin color of mixed-race children into five levels, saying that intermediate skin tones were due to environmental variation. He modeled these five levels as coming from two genes with two alleles each using skin color data from Bermuda, Jamaica, and Louisiana. The more black genes—he called this the duplex condition—the individual had, the darker their pigmentation.[1]

Jo: So how influential was this?

Jim: This model was still being seriously considered when I was taking my first anthro classes, just a couple of years later.

Erik: Right—I forgot how venerable you are! You really did live through a lot of this stuff!

Jim: chuckle chuckle, yes, and I barely survived to tell the tale

Jo: Ok, not to rain on the nostalgia parade here, but as you just told us at the beginning of this episode, Jim, one of the trends throughout the 20th century was that we kept finding out that the genetics were much more complicated than anyone suspected. And though skin color genetics isn't exactly my area of expertise, I know for a fact that Davenport's two-gene model is waaaaay too simplistic.

Jim: It is. But it when it comes to skin color, those old justifications for racial hierarchy don't go away easily. So Davenport proposed two genes. And that explanation stuck.

Jo: But then the Holocaust! And the post-World War 2 Civil Rights movements. Didn't all that eugenics stuff get discredited?

Erik: Funnily enough, before the *Brown v. Board* decisions in the mid-1950s a Canadian, Reginald Ruggles Gates, picked up the thread.

Jo: Ruggles Gates! He has a snuggly Teddy Ruxpin sounding name...

Erik: Ya. Funny name, not-funny legacy. He's worth mentioning here, though, because he had a direct connection to Davenport. Gates was actually a botanist who worked with the who's who of early genetics and did his Ph.D. at the University of Chicago while Davenport was running the American Breeders Association and getting American eugenics off the ground.

Jo: I sense a connection. He's one of those plant guys who took the plant breeding stuff and applied it to people, didn't he?

Erik: Ding ding ding! Though his major scientific accomplishments were in botany, he published extensively in anthropology, and hung out with E. A. Hooton in the US during the 1940s and early-50s. In these works, Gates proposed three genes with different values for darkness. AND he maintained that light skin was recessive to dark skin, so in order to have white skin, you need all recessive genes (Gates, 1953).

Jo: WAIT A SECOND—this sounds like that old "one drop rule" that even one drop of Black blood made you Black and, therefore subject to Jim Crow and miscegenation laws!

Erik: And the Nuremberg Codes that sent people with distant Jewish ancestors to the gas chambers.

Jo: The more things change…

Erik: And perhaps it's not surprising to learn that Gates was quite comfortable with fascism during and even after WW2. He received so much resistance from fellow scientists that, as we noted in the third part of our series on Race and Intelligence, with Pioneer Fund support in the early-1960s he was part of the crew that created the journal, Mankind Quarterly, which continued to promote what they called "polygenic inheritance" as the explanation for human races.[2]

Jo: Um, do you mean they were still arguing for polygenism in the 1960s?!?!?

Erik: yep. But Gates really really wanted everyone to know that he wasn't racist. In reaction to the UNESCO documents on race that we discussed in part 3 of Race and Intelligence, he wrote, "To say that all men are equal has not got us very far. It is more accurate to say that all men are different, and then to respect each other's differences" (J. A. F. Roberts, 1964). And he claimed to be surprised when people took statements like that plus all his scientific work purporting to show how interracial breeding was bad to support the notion that racial hierarchies were fine.

Jo: Sounds like a 'non-denial denial' to me. Ok, so we've got Davenport's two genes. We have Teddy Ruxpin's three genes....

Jim: And now, getting back to genetics—as we should: I need to say that it wasn't just these extreme characters who were speculating about skin color and genetics. My first textbook on genetics was Curt Stern's *Principles of Human Genetics*, which he first published in 1949. Stern (1953) also looked at skin color and he published right on the heels of Gates' paper. Stern used skin tone data measured by a spinning color top (BTW, Davenport published a delightful manuscript about how to use this Milton Bradley child's toy to measure skin color in 1926 (Davenport, 1926)). Anyway, Stern found the best fit to be three to five additive genes. In a postscript to his article, Stern specifically criticized the unequal, dominance-based model proposed by Gates noting that it was worse at fitting the distribution of color than any of the models Stern used. He also said the dark/dominant model would produce a distribution of skin colors very different—and very much darker—than that actually found in the U.S.[3]

Jo: So you mean to say that not everyone looking at skin color and genetics around this time was a raving eugenic racist? Ok, ok. Fair. We're still working in the neighborhood of three to five genes here, though, and I know it's more than that...

Jim: Yep, that's true. Even when the measurement of skin color got more scientific, like with the emergence of the reflectance spectrophotometer you mentioned in our last episode, Jo, we stayed in that 3-to-5-genes territory for a while. For instance, one of the first pieces of work to make use of skin color measured this way was by an early influence and acquaintance of mine in grad school, the British human biologist Geoff Harrison. He used a portable spectrophotometer to measure skin color variation in children of European and West African parents in England (Harrison & Owen, 1964). Based on the distribution of the data he argued for four additive genes with no dominance. Then, the American physical anthropologist Frank Livingstone used this four gene model and an innovative FORTRAN program to simulate how long it would take natural selection to produce the north-south variation shown in 14 populations that he had data for (1969, p. 482, figure 1). He said the variation could be accounted for by a small difference in fitness over 800-1500 generations (that is, somewhere between 16 and 30,000 years), well within the recent migratory history of modern humans.

Jo: But does that really work to account for the distribution we see of skin color?

Jim: No, but that's what I was taught—I did better than that in our race class, didn't I?

Jo: Snark

Jo: So we've done 2 genes, 3 genes, 3 to 5 genes, and now 4 genes. Let me guess—it gets messier as we began to get more of these measurements from different populations.

Jim: Yep. I'll say it again: it's freaking complicated. And in a way, that's kind of the point—just like race, skin color isn't one thing that can be easily identified in the genes, as we'll see once we start digging into the more contemporary stuff on skin color and genetics. But! —the reflectometry stuff was an important turning point, because it allowed for much more exact, reliable, and replicable measurements of skin color to serve as the basis for genetic modeling.

More Data!

Jo: So, throughout the 60s to the 90s, this reflectometry data is accumulating, and that should have provided a much better understanding of skin color distribution than the Biasutti map we talked about in our last episode. Remember, this was the one made with the ceramic tiles that faded in the sun, and where he just filled in holes in the map with guesses?

Jim: You know, I was actually a part of a group that helped accumulate this global skin color data at Penn State. it was called the Human Adaptability section of the International Biological Program. The research programs under this umbrella started in the late 1960s and involved scientists in 40 nations completing 230 different studies of populations all over the globe. Many of these studies included reflectance spectrophotometry to explore skin color as a climatic adaptation (Little, 1982, pp. 412-414).

Erik: Whoa, you're up close and personal with this stuff, Jim! So what did they find?

Jim: Well, one of the earliest analyses showed that even after adjusting for temperature and humidity, latitude was most strongly associated with skin color (D. F. Roberts & Kahlon, 1976). Higher the latitude, lighter the skin color.

Jo: Didn't we already know that—for several centuries? Even Biasutti's map, for all its flaws, shows this pretty clearly.

Jim: Intuitively, of course, but it wasn't scientifically measured and demonstrated until the 1970s. Since the British geneticists analyzing the measurements had controlled for temperature, they assumed that ultraviolet radiation was responsible for the association (D. F. Roberts & Kahlon, 1976).[4]

Erik: OK, so then how did they explain that association?

Jim: They didn't. They merely reported on the latitude, temperature, and humidity associations with reflectance.

Jo: Say what? How do you do a global analysis like that and not at least mention Vitamin D?

Jim: Derek Roberts, the first author, was a no-nonsense British scientist type, so you shouldn't be surprised by the absence of a just-so model in the paper. So even though this sounds like a "so-what" moment, studies like Roberts's were laying the foundation to redraw the old Biasutti map using better measurements of skin color and providing a better understanding of just how complicated the genetics were.

More Genetics, More Data, More Just-So Stories

Jo: Wait, you mean, it's complicated?

Erik: hahaha joke blah

Jim: For many years, I used a 1981 article by a fellow physical anthropologist, Pam Byard, in my class on human adaptation at the University of Alabama. She used a state-of-the-then-art quantitative genetic technique to suggest a six gene system, but she also acknowledged the extreme complexity of skin color in humans, anticipating some discoveries to come (Byard, 1981).[5]

Jo: I hate to keep harping on this Biasutti thing, but why the heck has his map continued to be used so long after its deficiencies were known??

Erik: Did you see the graphic accompanying this episode? Now compare that to some of the colorized versions of Biasutti's map and you begin to see why it has such staying power! It's just nice and simple looking.

Jo: Where did that ridiculous skin color map with this episode come from?

Jim: It was drawn by a team using a program developed at Oregon State, just up the road from you, Jo, in 1978. The map for this episode comes from a 1985 research conclusion piece in *Current Anthropology* based on 86 populations and it was one of the first attempts at global mapping of reflectance data (Tasa, Murray, & Boughton, 1985).

Erik: It's not very pretty!

Jo: No, but maybe it's an indication that things were changing—it's certainly a lot messier looking than the Biasutti one, maybe reflecting some of that complexity we keep foreshadowing?......

Jim: Not long afterwards, the South African clinical pharmacologist, Ashley Robins, published the definitive human biology work on skin color, in 1991. I used his book as a guide in my classes on human adaptation for many years (Robins, 1991). As you might imagine for a pharmacologist, his summary of genetics was not terribly enlightening, but he brought up most of the characters we've talked about!

Erik: So what did he know about?

Jim: He knew the history! He dredged up all the previous ideas about what selective factors were driving skin color variation and gave them critical reviews, and then he pushed some of his own notions.

Jo: Like what?

Jim: Well, for depigmentation, he favored a model based on cold injury (i.e., frost bite) selecting for less melanin.

Erik: That seems kind of random. Where did that come from?

Jim: Anecdotal reports and epidemiological analysis of frost bite from World Wars I and II, and the Korean War showing Black GIs were more susceptible than White GIs (Post, Daniels, & Binford, 1975).[6]

Jo: Why haven't I ever heard of this?

Jim: Because I refuse to perpetuate bad anthropology if I can help it.

Jo: Har. Fair enough. But this does remind me: I mentioned at the beginning of the episode that we were going to get more into the theories for darker skin color, and here we are, still talking about why lighter skin might have evolved. Last episode we had this vitamin D theory for *lighter* skin color, which was initially proposed in the 1930s by a physician by the name of Murray. As far as I know, that one is now pretty well accepted. But what about *darker* skin color?

Jim: You're right, Jo, that the vitamin D hypothesis is pretty taken for granted at this point. As for models of darker skin color, at the veeerrrrryyy end of the last episode, we mentioned the one proposed by Branda and Eaton in 1978 that darker skin would have been maintained in high-UV environments to protect folic acid. A number of circulating molecules in the blood, including folic acid, can break down with UV exposure to the skin (a process called photolysis). Severe folic acid deficiency can affect normal fetal development, so the idea is that in high-UV environments selection would favor highly melanized skin to prevent the photolysis—assuming the deficiency couldn't be made up in the diet.

Jo: Ya, and that makes sense, cause if you didn't have enough folic acid, it's going to pretty immediately have serious consequences for reproduction—babies born with debilitating or even deadly conditions like spina bifida or anencephaly, for instance. So people without enough folic acid would not have survived well.

Erik: Ya, oh ya. That sounds logical, and it kind of goes nicely with the vitamin D at higher latitudes argument; it's like the converse.

Jim: Well, I hate to disappoint you both, but Robins says of the Branda and Eaton paper (1978), "the hypothesis is insufficiently structured and the data provided are unconvincing."[7] As he points out, folic acid deficiency is not a huge problem for light skinned denizens of the tropics.

Erik: Robins of the frostbite. Ok, then, so what selective factor does he zero in on for darker skin in high UV areas?

Jim: Sunburn.

Jo: Come on!

Jim: No, really. He says the most profound impact on selection would be through sunburn causing impaired sweating in light skinned individuals, which would then lead to hyperthermia and death (Robins, 1991, p. 191).[8]

Erik: Well, both those explanations for darker skin color—the sunburn one and the folic acid one—seem a little more likely than Phaethon losing control of the sun god's chariot. But I thought Vitamin D and folic acid are the current consensuses, right?

Jim: Among those seeking simple answers,

Jo: Like me.

Jim: But…there are a numerous considerations that complicate things. First, none of the genetic models we've talked about so far are actually in the ball park of how complex skin color genetics are. Secondly, the selection pressures for dark and light skin are nowhere near as simple as the one you just mentioned, Jo—that is, Murray's (1934) vitamin D or Branda and Eaton's (1978) folic acid.

Jo: SIGH. It's never as simple as I would like it to be. It's actually the simplicity of those two models that makes them so satisfying to teach. But alas.

Erik: Wait, do you mean to say.....IT'S MORE COMPLICATED THAN WE THOUGHT?! (hahaha, we all laugh because by this point it's a super-funny-but-true running joke, …..right?)

Jim: Take this as an example. The same year Robins' book came out, the Stanford anthropologist, William Durham, wrote Coevolution (Durham, 1991), and one of his chapters is about milk drinking.

Jo: Wait a minute, wait a minute—we've already done the milk thing!

Erik: Right, Jim—remember when I opened our series on race and health with that white supremacist poem about non-milk drinkers having to go back to Africa?

Jo: And we asked you to never bring it up again!

Jim: Ok, but this is different. One of the things that Durham points out is how lactose might enhance calcium absorption, reducing the need for vitamin D synthesis among milk drinkers. And SURPRISE SURPRISE—it turns out that the lactose-calcium absorption connection in humans is way more complicated than Durham thought—likely involving the prebiotic effects of lactose on the gut microbiome (Ilesanmi-Oyelere & Kruger, 2020).

Jo: Jim, I feel like you just keep saying that: the connection is much more complicated than so and so suggested....

Erik: OK that's now officially now the theme of these episodes: 18th century: It's much more complicated than we thought! 19th century: It's much more complicated than we thought! Annnddddd 20th century!....

Jim: Guilty as charged! That's because it always is! ...But my point here is that Murray was on to something back in 1934 when he pointed out that a diet high in fish and organ meats is likely to provide substantial vitamin D. The fact that Durham sees a link to milk consumption doesn't disprove that; it actually further supports it. Similarly, folic acid is present in a lot of foods available in the tropics. What this means is that groups of people can be living in exactly the same UV environment, but depending upon their upper Pleistocene diet, they would be under very different selective pressures to increase or decrease pigmentation.

Erik: OK, can we say *anything* definitive about the evolution of skin color at this point?

Jim: Well, we can say it's kept a lot of anthropologists occupied for a long time. As happened several times over the last 150 years or so, there was a resurgence of interest in skin color in the in the 1990s—signaled, perhaps, by Robins book coming out in 1991, and this resurgence included the compilation of skin color measurements and the discovery of an important gene implicated in skin color.

Jo: I know one of those databases was the one put together by Nina Jablonski who we interviewed way back in September of 2017?[9] Anyway, she and George Chaplin tied global UV data to population skin color measurements (Chaplin, 2004; Chaplin & Jablonski, 2009; Jablonski, 2004, 2008, 2012, 2021; Jablonski & Chaplin, 2000, 2010, 2017; Yuen & Jablonski, 2010).

Erik: Right—they made a case for the relationship of UV to skin color relying on the vitamin D and folic acid models—kind of.

Jo:...which is part of why I like to teach them.

Jim: Their maps are the best counterpoint to Biasutti, for sure. The other skin color analysis hasn't received as much fanfare, but an oversimplified graph from that study has been paired with Biasutti's skin color map and is becoming somewhat of a meme. John Relethford put together a database and regressed skin color values against latitude, showing different relationships in the northern and southern hemispheres (Relethford, 1997, p. 453, figures 3 and 4). This has shown up paired with Biasutti's map multiple times in the last two decades (Barsh, 2003; Deng & Xu, 2018).

Jo: What do you mean an oversimplified graph?

Jim: Well, John presented a scatter plot with the regression trendlines, but the scatterplot was removed and just the trendlines appear as if they're some sort of reified fact of nature when they're paired with Biasutti. Relethford also demonstrated that skin color variation is greater within sub-Saharan African populations than in other areas (Relethford, 2000) and that the apportionment of skin color variation is very different than for other phenotypic or genetic characteristics (Relethford, 2002).

Jo: If I'm not mistaken here, what you're saying with all that fancy verbiage is that skin color is actually a very bad marker for race. No?

Jim: Yes. It's pretty astonishing, actually, how much that's the case, but it is. If more skin color variation is found just within Africa as opposed to any other region, and most Americans think of Africa as a place of black people, that tells us something about how both skin color and race aren't actually reflective of reality, but of stereotypes.

Erik: That's pretty cool—too bad about being paired up with Biasutti, though. You said there was a significant genetic development, too?

Jim: Yep, that's figuring out some of the genes behind skin color variation like the melanocortin 1 receptor or MC1R (Rana et al., 1999). A lot of work was done figuring out how different mutations to the gene for MC1R might influence skin color, including an analysis of a Neanderthal MC1R suggesting light skin and red hair (Lalueza-Fox et al., 2007).

Erik: I remember news items about that, where they were all like, "Surprise, cavemen were gingers!" and then everybody started drawing them that way.

Jim: It turns out that MC1R is influential primarily in populations with red hair and light skin, but it plays a limited role in global variation.

Jo: But the basic idea that selection works to favor dark skin near the equator and lighter skin tones at higher latitudes is correct! Right?!!!......

Jim: Sort of, but…this stuff gets really messy.

Jo: There's our theme again.

Jim: If you look for signatures of selection based on specific genes, you have to consider a whole bunch of genes—like the study that examined 81 candidate skin color genes in 2006 (Izagirre, García, Junquera, de la Rúa, & Alonso, 2006).

Jo: Whoa, so we're now up to 81 genes?! Is that because they're looking for these kinds of "signatures" in genomes that would allow them to at least theoretically impute how selection might have favored particular mutations?

Jim: Yes—and when you're doing that, you want to cast the net as far and wide as possib;e. That study with the 81 genes found signs of selection for light skin in European populations and dark skin in African groups. Maybe their most interesting result was that the genes in Africans were involved in DNA repair and cancer prevention, lending some credibility to Robins' ideas about selection for dark skin being related to skin cancer prevention.

Erik: Ok, so we're, like, back to the drawing board in a sense here. What other explanations are at play nowadays?

Jim: One of the more interesting ones revolves around Darwin's sexual selection argument from *The Descent of Man. T*he Japanese biologist Aoki disdained the Vitamin D just-so story and favored an analysis of the Human Relations Area Files that argued for a mate preference for lighter skin in 47 of 51 societies (2002). He used this to revive Darwin's argument, saying that when selection is relaxed for dark skin, sexual selection may be enough to account for the reduction in pigmentation.[10]

Jo: So this guy is saying that instead of concerns about not having enough vitamin D, or folic acid, or worries about sunburn and cancer, maybe skin differs at least in part because we're supposed to prefer mates with lighter skin than we have?

Jim: That's what he's saying.

Erik: Snarky comment about Darwin and sexual selection.

Jim: As genetic data on African populations has grown, we're also getting a better appreciation of how complicated the skin color situation is there, with populations showing both more phenotypic and genotypic variability than in other parts of the globe (Crawford et al., 2017; Lin et al., 2018; Tang & Barsh, 2017)! This includes mutations and selection going back at least a half-million years and recent admixture in the last few thousands of years.

Jo: OK, so Africa remains the most variable part of our global distribution. Kind of an echo of what Relethford was saying, right?

Jim: Right, although it took a long time to even begin to figure out what kinds of mechanisms might be underpinning that variability. The genetics of skin color variation in Africa are much more variable than for Eurasian populations (Quillen et al., 2019). We also have clear cut evidence of epistasis or the interaction between genes affecting skin color and GWASes are turning up additional regions of our genome that play a role (Huang, Wang, Jin, & He, 2021).

Erik: So yeah. Complicated AF. What do we do about this? Should we continue to teach about skin color as an example of selection with vitamin D and folic acid as the prime movers, when there's obviously still so much uncertainty in the literature?

Jim: If you only have 15 minutes to talk about genes, culture, and race, I'd do a cut-down version of sickle cell instead. But as an historian, Erik, I know you'll be comfortable with telling students how complicated the skin color situation is.

Jo: We teach that humans first evolved dark skin 1-2 million years ago after our early ancestors lost most of their body hair, and that's where the folic acid story comes in.

Erik: Right, although that one is obviously much more complicated, in the sense that there are other explanations out there for what motivated that change.

Jo: Then once our species began our last worldwide migration out of Africa some 60-70,000 years ago we gradually lost much of that pigmentation through natural selection to facilitate vitamin D synthesis as we moved farther from the equator.

Erik: Yep, that's the one. Also, again, other potential explanations, though this one might be a little less wishy-washy....

Jim: Unfortunately, most of our students come away thinking that it worked just like that—

Jo: —kind of like the sickle cell gene we've talked about before in the podcast—

Jim: —but the incredibly complex genetics of skin color doesn't make for the same kind of simplistic evolutionary scenario. It's important to point out that vitamin D synthesis in the skin—or drinking milk or eating fish organs—are not the only ways to adapt to low levels of UV radiation (Hanel & Carlberg, 2020b).

Jo: So you're saying it's quite plausible that vitamin D played a role, but other stuff did too.

Jim: Yes. Also, this isn't something that would have just progressed in a linear fashion as we moved to higher and higher latitudes.

Jo: So it wouldn't have just happened in a neat and tidy fashion, because humans didn't actually move very linearly during global migration.

Jim: Yes again. A case in point is the famous 10,000 year old British fossil, Cheddar Man. The DNA from this fossil has alleles that suggest he was very dark skinned. In fact, Europeans were heavily pigmented for most of the 30-40,000 years they lived in the area. It wasn't until the last 5-10,000 years that Europeans evolved lighter skin tones, at least in part as a result of migration from the southeast and east and admixture with extant populations—in other words, not just because selection favored lighter skin for vitamin D synthesis (Hanel & Carlberg, 2020a, 2020b).

Jo: It's good to remind students that all of Eurasia was home to relatively dark-skinned peoples until recently—although I don't think it will gain much purchase with the folks who douse themselves in milk.

Erik: You mean Richard Spencer and his white supremacist buddies!

Jo: Yah.

Jim: So, we started with a two gene, two allele model. At this point, can we agree to say that in conclusion, it's complicated.

Jo: You weren't kidding when you said that right off the bat Jim. But actually, as I mentioned a bit ago, I think the complication is where the insight arises. We spend a lot of time showing how race is an oversimplified way of trying to sort out human diversity. The buckets we use for skin color are just the same—the variation underlying what we might see in a particular culture as "white" skin or "black" skin is remarkably complex. And there are multiple ways, genetically, that you could arrive at lighter or darker skin, so even if people look kind of the same, that doesn't mean they have the same genetic profile underlying it.

Jim: Erik, we haven't given you a quote yet. How about taking us out on this quote from a paper published late last year?

Erik [Getting into quote mode]: It seems now clear that the genetic basis of skin color is less simple than previously thought and that the geographic variation in skin pigmentation is not exclusively driven by hard selective sweeps in a few key genes. The recent increase in the number of populations studied for pigmentation variation, including African groups from a wide range of geographic origins, has revealed that the complexity of skin color can vary across populations and that the evolutionary history of pigmentation involved adaptations achieved by the concerted action of different types of selection. (Rocha, 2020, p. 84).[11]

Jo: So, IT'S COMPLICATED!

Jim: And that's putting it simply. I'm Jim, the physical anthropologist…

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Notes

[1] On the foregoing hypothesis we may look for five conditions of skin color, as follows : (1) no factor for black-the Caucasian condition; (2) no B factor, the A factor simplex-the light-colored; (3) either no B factor and the A factor duplex or both A and B factors simplex-the medium-colored, or mulatto; (4) one factor duplex and the other simplex-the dark-colored skin; (5) both factors duplex-the black skin. It is evident, moreover, that these five grades do not correspond to sharp percentages of black, and, indeed, it was not to be expected that they would. Every character is subject to fluctuations due to variations in conditions during development, effects of sunlight, etc. (Davenport, 1913, p. 13)
The following hypothesis is supported by the facts: That there are two (double) factors *(A* and *B)* for black pigmentation in the full-blooded negro of the west coast of Africa. There is no sex-linkage in skin pigmentation of man. Colored persons tend to select as consorts persons of about their own grade of skin color. The yellow element in the skin color of light-colored persons and those with Chinese blood is frequently high (about 25 per cent). This excessive yellow element, obscured in full blacks, is revealed in diluted black. The tradition that a person with negro blood who passes for white may have, by a white consort, a child with a black skin color probably depends on the observation that two "light-colored persons" may have a medium-colored child. (Davenport, 1913, p. 47)
[2] http://speakingofrace.ua.edu/podcast/race-and-intelligence-part-3

[3] After the manuscript had gone to press R . R. Gates has elaborated on his model [1949] of three pairs of genes for pigmentation differences of Negroes and Whites (Studies of Interracial Crossing, II : A new theory of skin color inheritance. Intern. Anthrop. and Linguist. Review 1 : 15-67, 1953). Gates proposes, on the basis of "many observations" of individual pedigrees "some of which are detailed in the present contribution" that the three pairs of genes "are weighted for pigmentation, as follows: R = 6, S = 2, T = 1," where RRSSTT = 18 produces the darkest and rrsstt = 0 the lightest color. When Gates' model is used to compute the distribution frequencies of color types in the American Negro striking deviations from the observed distribution become apparent. There is (1) an even larger deficiency of expected lighter types than was found to exist for the best fitting models discussed above, (2) a very great surplus of expected individuals of the darkest group, and (3) a bimodality of expectation in which the second darkest class is only slightly more than half as frequent as the next lighter class and somewhat less than one third as frequent as the darkest class. These deviations make it unlikely that the new model with its assumed considerable inequality of genic actions is close to reality[.] If, as seems a priori likely, some inequality of action exists of the different pairs of genes concerned with pigmentation differences, it is probably only of minor extent. The population-genetic analysis of Gates' model illustrates the need for simultaneous use of pedigree and population data. (Stern, 1953, p. 296)

[4] Overall, for both sites and all wavelengths, these results indicate a remarkably close relationship of mean pigmentation with environmental variables. In particular, there is a dominating association of pigmentation with latitude, in that latitude accounts for a very great proportion of the total variance in the reflectance means observed in human populations. It is reasonable to argue therefore that some factor associated with latitude has a strong biological influence. Of the environmental variables associated with latitude, the amount of ultra-violet radiation received at the earth's surface varies inversely with latitude (Kendrew, 1938), while temperature is also strongly associated with latitude; the effect of both at a given locality is, of course, modified by other variables such as cloudiness or altitude. Temperature is already taken into account in the analysis, and the latitude association of reflectance values is independent of it, as the partial correlation coefficients show (table 4). It seems most likely, therefore, that ultra-violet radiation is the factor responsible for the latitudinal association of pigmentation. (D. F. Roberts & Kahlon, 1976, pp. 19-20)

[5] The complexity of the pigmentation system and the evidence for endocrine interaction lead to the expectation that the inheritance of skin color is rather complex, yet studies in this area have almost unanimously agreed on a model of from three to five additive loci. It seems improbable that all of the variation in human skin color can be attributed to these few factors. Studies so far have concentrated on the major differences between “racial” groups (particularly blacks and whites), and have oversimplified the range of variation found within groups and in intermediate groups. That very few alleles can cause large differences in pigmentation is shown by the simple inheritance of albinism, but melanization has a more complex basis than simple presence of absence of tyrosinase. (Byard, 1981, p. 136)

[6] The observation that Blacks are apparently more susceptible to cold injury than Whites, goes back to World War I, when Senegalese troops were found to have a higher attack rate of "frozen-feet" than French troops (Mignon, 1926-27). Similar observations concerning frostbite or trenchfoot have since been made on Ethiopian troops during the Korean War (Schuman, 1953), and on American troops during World War II (Whayne, 1950), the Korean War during the winters of 1950-51 (Orr and Fainer, 1952), and 1951-52 (Schuman, 1953, 1954), and near Fairbanks, Alaska during the winters of 1959-60 and 1960-61 (Miller and Bjornson, 1962). (Post et al., 1975, p. 66)

[7] He goes on: “There is no evidence, for instance, that Caucasoids or albinos in tropical regions are more folate-deficient than Negroids; on the contrary, frank folate deficiency is so prevalent—for example, among South African Negroids (Van der Westhuyzen et al., 1986; Baynes et al., 1986)—that it is difficult to credit a dark skin with any protective function against such deficiency. (Robins, 1991, p. 210)

[8] Sunburn would probably have its most profound impact on survival by its interference with sweating. UV produces a diminution in the sweating rate of Caucasoid, but not Negroid, skin by blockage of sweat gland ducts (due to epidermal damage) and by a possible reduction of the sweat secretion itself (Thomson, 1951). The failure of a light skinned person with sunburn to sweat efficiently under a solar heat load and during physical exertion would lead to hyperthermia and death. (Robins, 1991, p. 191)

[9] http://speakingofrace.ua.edu/podcast/a-conversation-about-race-and-skin-color-with-nina-jablonski

[10] In this review I have argued that, where natural selection for dark skin is sufficiently weak, a sexual preference for lighter-than-average skin colour could have driven the evolution of light skin. Although no quantitative estimates of the strength of sexual preference are available, sexual selection is potentially powerful enough to have effected a major phenotypic change, even within the past 10,000 years. It is not necessary under these circumstances for light skin to be favoured by natural selection. Nor need light skin be an indicator of fitness—a handicap that signals ‘good genes’. Rather, the preference may be arbitrary or the result of a pre-evolved sensory bias. (Aoki, 2002, p. 603)

[11] It seems now clear that the genetic basis of skin color is less simple than previously thought and that the geographic variation in skin pigmentation is not exclusively driven by hard selective sweeps in a few key genes. The recent increase in the number of populations studied for pigmentation variation, including African groups from a wide range of geographic origins, has revealed that the complexity of skin color can vary across populations and that the evolutionary history of pigmentation involved adaptations achieved by the concerted action of different types of selection. (Rocha, 2020, p. 84)