Are mule deer a HYBRID SPECIES?

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White-tailed deer and mule deer come from the same Odocoileus stock that has been in North America for about five million years, but they split from one another during the late Pliocene or early Pleistocene (two to four million years ago). Using fossils to unravel the complete story of deer evolution throughout this period has been hampered by the rarity of deer at that time and repeated glaciations that scoured the landscape for thousands of years, destroying evidence of early North American deer evolution. Even with fossils in hand, white-tailed deer and mule deer are difficult to distinguish. Because body size varies with nutrition, and we are not sure where these species lived during the Pleistocene, most of the past deer fossil identifications are questionable.

There are three main theories that have been proposed to describe how mule deer came to be. All theories are related to different groups of deer being separated for long periods of time and then coming back together. The scenarios proposed are all based on different information and attempt to explain some of the physical or genetic differences. No theory is without contradictions and contrary evidence, which says to me that we are trying to complete a puzzle with a small percentage of the pieces.

MULE DEER DISPERSAL THEORY

Just looking at the physical differences between whitetail, mule deer, and black-tailed deer, ecologists developed a theory that the ancestor of all three types of deer split into a western species (blacktails) and an eastern species (whitetails) more than two million years ago. The original split must have been caused and maintained by some ecological barriers during the periods of glaciation or between them. This theory proposes that as the last ice age glaciers receded, mule deer then split off from the western black-tailed deer and expanded out into the fertile landscape that was either uncovered by the melting glaciers or altered to be very productive. This rapid expansion into fertile, unoccupied habitat is said to have fueled the rapid changes in the mule deer's physical looks as they became much larger than blacktails, with more elaborate antlers and contrasting body markings. Prior to the advent of genetic analysis, this made a lot of sense given what we know about ecological principles of a species expanding into very productive and unoccupied habitat. The more contrasting facial and rump coloration and the larger antlers all make perfect sense for an animal living in the open and using visual communication more than their cousins in the forest.

With the lack of a strong fossil record, science has turned to genetic analysis to investigate the relationships of white-tailed, black-tailed, and mule deer. With more powerful genetic analyses, scientists can tease an amazing amount of information out of the DNA contained in a single cell of a deer's body. Each cell has a nucleus in the center that contains DNA the animal inherits from its mother (50 %) and

father (50 %). This is called nuclear DNA (nDNA) and this is the DNA related to how an animal looks and what traits are passed down from its parents. However, floating around in the cell, outside the nucleus, are little structures called "mitochondria" that help supply energy to the cell and they also carry a small package of DNA. What is unique about mitochondrial DNA (mtDNA) is that it is inherited only from the mother. This means the genetic information from mtDNA is passed down through the female line for generations like last names are usually passed down through generations of male offspring. Analyzing the nuclear DNA tells us about both parents and previous ancestors on both sides of the family. Looking at mtDNA gives us insight into only the ancestors on the mother's side.

Early genetic analyses showed that mtDNA, passed down from mother to daughter, is very similar in mule deer and whitetails, but very different from blacktails! This odd genetic relationship was not expected because mule deer and black-tailed deer are the same species (different subspecies) and they are both very different in many ways from whitetails.

If mule deer simply branched off from blacktails and expanded into vacant habitat when the glaciers receded, how could they have developed completely different mtDNA from their source and end up with similar maternal mtDNA to whitetails? Developing different DNA requires some isolation for a long, long time for two types of deer to drift apart genetically. We know from other genetic work to be discussed below that blacktails originated in the Pacific Northwest and expanded north along the coast when glaciers receded, but mule deer originated in the Southwest and expanded northward. The genetic evidence tells us it is highly unlikely mule deer expanded out of blacktails and so we need a new theory.

MULE DEER AS A HYBRID THEORY

This early genetic evidence spawned an alternative theory proposed by Valerius Geist that blacktails and whitetails did, indeed, split two to three million years ago, but that mule deer are a relatively "new" species, resulting from the later hybridization of female whitetails and male blacktails. He proposed that after the retreat of the last glaciers starting about 14,000 years ago at the close of the Pleistocene, whitetails and blacktails again came into contact with one another and interbred. Dr. Geist based this theory on the fact that if mule deer were running around with very similar mtDNA as whitetails, then they must be the product of male blacktails mating with female whitetails so that all offspring had mtDNA from their whitetail mothers. The beauty of this theory is that it explains the very confusing situation of why mule deer and whitetails have similar maternally inherited mtDNA. Although this theory is consistent with the genetic relationships, it is also burdened with many reasons that make it implausible.

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The current geographic distribution of mule deer and white-tailed deer overlap in no less than 21 Mexican and U.S. States and Canadian Provinces. This overlap represents a secondary contact between the two species that evolved separately as evidenced by nDNA as well as physical and behavioral differences. Where they occur together, hybridization has been documented, but occurs at a low rate in the wild. Even in captivity when given unlimited food, water, and protection from predators, hybrid fawns have a very low survival. Dr. Geist acknowledged the weakness of his theory, but thought perhaps the Pleistocene extinction of predators allowed these hybrids to survive. The difficulty of this explanation is that deer at the time probably faced the same predators they currently have. The universally low survival of hybrid fawns from this mismatch of parents erodes support for the theory that this type of mating resulted in a new hybrid species with enough competitive advantage to dominate western North America.

It is thought that most hybridization between these two species that have been documented occur from the more-aggressive male whitetails breeding

The theory that mule deer are a hybrid species relies on a scenario of blacktail bucks breeding whitetail does, but hybridization is rare and when it occurs, it is more commonly in the opposite direction. Hybrid fawns are most often seen with mule deer does. Photo: Reavis

passive female black-tailed or mule deer. Therefore, hybrids often have mule deer or blacktail mothers (and their mtDNA). Hybrid offspring in larger female mule deer groups might experience higher survival than if they were in smaller whitetail groups. Mule deer females are also more aggressive in protecting their fawns which would favor survival. The hybrid mule deer theory relies on hybridization occurring in the opposite direction we commonly see in nature and in a situation that makes it harder for the hybrids to survive.

To look at the genetic relationships closer, I collaborated with Dr. Emily Latch, at University of Wisconsin – Milwaukee, on a continent-wide genetic analysis of black-tailed and mule deer. We looked at nuclear DNA (nDNA) a deer receives from both parents and showed that mule deer and blacktails are very similar subspecies and clearly different from whitetails. This conflicts with the mtDNA interpretation that mule deer are intermediate forms of whitetails and blacktails.

If mule deer are hybrids of whitetails and blacktails, then nDNA inherited from both parents should be well represented in mule deer. Instead, black-tailed and mule deer are closely related subspecies and different than whitetails. How could whitetails and blacktails come together and produce hybrid offspring that breed with each other and yet lose all nDNA from their blacktail fathers? Nuclear DNA is mostly what determines physical appearance, but mule deer do not look like a cross between a blacktail and a whitetail. In fact, curiously enough, blacktails look very much like verified whitetail X mule deer hybrids. They are not, however, because this conflicts with the genetic and geographic evidence.

To be derived from blacktail fathers and whitetail mothers, mule deer would have to also be separated from breeding with both parent species for a long time to develop into a new type of deer without blending back into one or the other species. That would require widespread and very common hybridization between only blacktail bucks and whitetail does, followed by reproductive isolation of this new hybrid species so it bred only with itself, followed by expansion throughout western North America with only negligible hybridization of this intermediate form with its parent species after that. After a flurry of Pleistocene whitetail X blacktail hybridization to create mule deer,

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wouldn't we expect to find at least some mule deer away from blacktail range that ended up with blacktail instead of whitetail mtDNA? How could that have been 100% one-sided?

That is a lot to wrap our minds around and there is so much we don't yet know. Some version of this theory, yet to be refined with further study, might make sense in the future, but given what we know now it is difficult to see how hybridization could have produced mule deer.

ICE AGE REFUGEES HYPOTHESIS

It is well known that many species and subspecies differences we see today are because populations of animals were separated by glaciers or isolated from each other because of dramatic habitat changes that kept them apart. The large-scale changes in the distribution of forests, shrublands, and grasslands occurred through the many glacial/interglacial changes in the last few million years. Physical isolation for long periods of time is the most likely cause for the differences between a mule deer/blacktail-type deer and white-tailed deer. We can find evidence of what the vegetation looked like during the most recent ice age, but there were others before it and it is difficult to reconstruct what North America looked like more than 100,000 years ago. Any one of several glacial cycles over the last few million years (each lasting 10,000 – 100,000 years) could be enough to isolate and differentiate eastern whitetail and the western mule deer/blacktail type. The last Pleistocene glaciation peaked in North America (19,000 – 26,000 years ago) and probably resulted in the less obvious divergence of mule deer subspecies and ecotypes.

Looking at the patterns of genetic diversity across black-tailed and mule deer populations throughout North America can reveal the areas animals occupied during the last ice age before expanding out with the retreating glaciers. Our North American genetic work, published in the scientific journal Molecular Ecology, indicated mule deer waited out the maximum extent of the glaciers in several areas of southwestern United States and Mexico. Looking at the pattern of genetic diversity, we found high diversity in the Southwest and then a more uniform pattern among mule deer populations throughout the West, indicating they expanded rapidly out of these southwestern refugees after the glaciers melted.

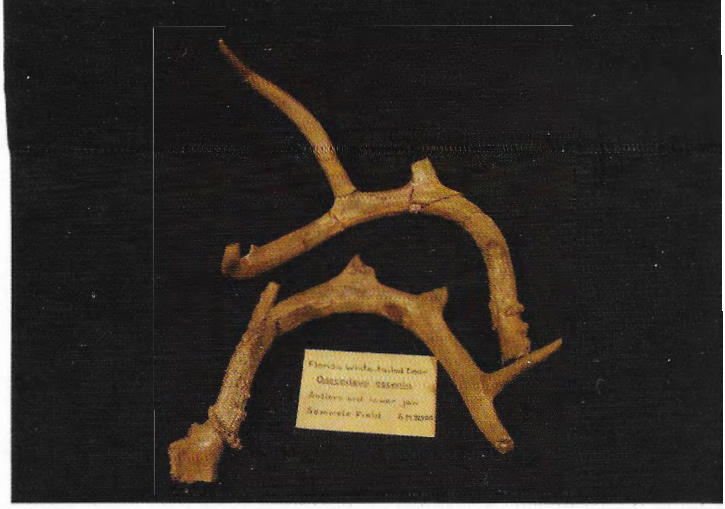
The genetic patterns revealed that blacktails were trapped along the ice-free coastal areas in Washington and Oregon and expanded, mostly northward, from there after the glaciers melted. Black-tailed and mule deer then came into contact once again along the crest of the Cascade Range and other points of contact in the Pacific Northwest. We know that scattered pacific coastal areas from Alaska to California did serve as ice-free refuges that held populations of early western deer through many repeated glaciations and subsequent warm periods. Perhaps blacktails were trapped and retrapped in glacial refuges repeatedly.

Support for this theory hinges on whether this isolation (or repeated isolation) of blacktails in relatively small, fragmented populations along the coast and on islands of the Pacific Northwest would have created the large difference in mtDNA between blacktails and mule deer. We know that large genetic changes can occur rapidly through what geneticists call genetic drift, founder effect, and lineage sorting. This kind of repeated isolation in small coastal areas could account for these large genetic differences in mtDNA. In fact, it may be the reason that Sitka blacktails today are the most genetically distinct of all the mule deer subspecies.

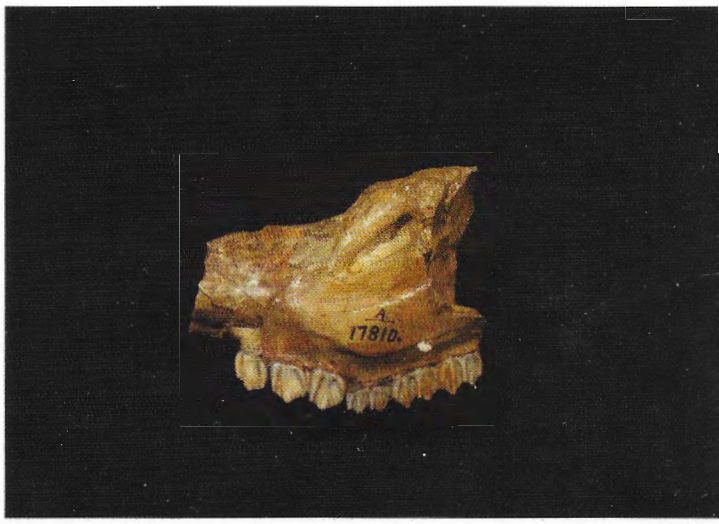
Our research did not include whitetails, but fossil evidence in unglaciated areas indicates they apparently didn't change much through time. Florida is

well-known for its Pleistocene whitetail fossils that are indistinguishable from today's whitetail antlers, skulls, and skeletons. White-tailed deer most likely spent the last Ice Age in the unglaciated areas of southeastern United States, Mexico, and down through Central and South America where they provided ancestral stock for all South American deer species. The same changes in habitat conditions at the end of the last ice age undoubtedly also brought whitetails back in contact with mule deer.

A problem with this theory is that whitetail and mule deer mtDNA has remained remarkably similar for a very long time; more than one might expect. One possibility to explain this pattern is "lineage sorting" whereby different species end up with very similar mtDNA through chance over long periods of time. In other words, when whitetail and the ancestor of all mule deer/blacktails split, they all had a variety of mtDNA (more than today) and by chance a very divergent blacktail mtDNA became dominant in the small isolated coastal populations while the more common mtDNA variations were retained in mule deer and whitetails. In any event, despite having different mtDNA, blacktails and mule deer are genetically close to each other, and a different species from whitetails.



Using fossils to unravel the complete story of Odocoileus in North America has been hampered by the rarity of deer at that time and repeated glaciations that destroyed most of the evidence. Photo: Jim Heffelfinger.



Most fossil identifications of mule deer, blacktails, or whitetails are questionable because researchers simply guessed based on what species occupied the area currently. Photo: Jim Heffelfinger.

MORE QUESTIONS THAN ANSWERS

The glaciers that covered the northern part of North America only came as far south as the Canada-U.S. border in the West and covered the Great Lakes and northeastern states in the East. All these deer types were south of the glaciers, except perhaps the blacktails as they were trapped in refuge areas along the coast by alpine glaciers extending down the Cascade Range through the middle of northern California, Oregon, Washington, and southern British Columbia (precisely where blacktails are separated from mule deer today).

People tend to like nice, neat stories with no loose ends or confusing facts. The reality here is that any simple straightforward story confidently explaining where mule deer and black-tailed deer came from has ignored a lot of contradictory evidence. There is no way to reconstruct deer distributions in all the various ice advances and retreats in the last five million years that whitetail, blacktail, and mule deer ancestors have been around. We must think in more general terms in our search for a reasonable theory that is consistent with the most physical, genetic, and geographic information at hand.

Hopefully future researchers will hand us more puzzle pieces to continue to build a more complete picture. Thoughtful discussions like this should spark a deeper consideration of these relationships and the available information to keep us all learning together. It matters little from whence they came, I am just glad they are here.