



The Polar Bear's Prehistoric Past

Genomic analyses reveal that the polar bear evolved between 4 and 5 million years ago, far earlier than previous studies had estimated.

Ed Yong

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The polar bear has become a symbol for threatened wildlife, and its future in a warming world has created much controversy. The predator's past is equally controversial. The evolutionary history of

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polar bears has been rewritten several times in recent years, complicated by an incomplete fossil record and a history of hybridization with brown bears, and a new study, published today in the *Proceedings of the National Academies of Sciences*, continues the trend.

Researchers from Pennsylvania State University have completed the most extensive genomic study of polar bears to date. By comparing its DNA to that of brown and black bears, the team calculated that polar bears arose between 4 and 5 million years ago, making them far older than anyone had suspected. And their genes carry the imprints of repeated interbreeding with brown bears during much of that history.

The team also started documenting the genetic changes that allowed polar bears to adapt to life in the cold. "Our data gives us ... a first look at what makes a polar bear a polar bear," said co-author Charlotte Lindqvist.

Back in 2010, Lindqvist and her colleagues were telling a different story. Based on an analysis of the

polar bear's mitochondrial DNA, they deduced that the polar bear lineage sat within the brown bear family tree, and established itself between 111,000 and 166,000 years ago. Fossils supported this idea, with the oldest polar bear specimen—a Norwegian jawbone collected in 2008—dating to 110,000–130,000 years ago.

This suggested that polar bears adapted to Arctic life with astonishing speed. But Frank Hailer and Axel Janke from the Biodiversity and Climate Research Center in Frankfurt found evidence of more relaxed evolution. Earlier this year, they analysed 14 sites within the nuclear genome of polar, brown, and black bears, and found that polar and brown bears are sister groups that went their separate ways around 600,000 years ago.

Now, thorough genome sequencing of the nuclear genomes of a polar bear, three brown bears, and an American black bear —covering each letter of DNA between 25 and 100 times— push back that estimate even more, estimating that polar bears and brown bears split some 4 to 5 million years ago, shortly after the brown bears themselves diverged from black bears. Less in-depth sequencing of 22 more living polar bears, and the ancient Norwegian jawbone, also support the estimate.

Janke is not convinced by the new date, however. A split from brown bears that long ago "predates the forming of extensive ice sheets and the Arctic ice cap," he said, meaning the ancestral polar bears would not have had a distinct habitat that kept them separate from the brown bears.

He also added, "The method of estimating this split depends on numerous estimates that one cannot know exactly." These include the size of the ancient bear populations, which can only be inferred from computer simulations, and the rate at which their genes have changed, which the study based upon mutation rates in primates. "Better analyses and models will in the future give a more precise figure," said Janke. But, Lindqvist added, "even if the exact date may change in the future, I believe we are close to the right time frame."

Meanwhile, the new study reveals other facets of the polar bear's past. The team found more than 1,300 sites in its genome that differ from brown bears more than expected, suggesting selection pushed these sites to evolve faster than the rest of the genome. They include genes such as DAG1, which is involved in muscle growth; BTN1A1, which influences the amount of fat in breast milk; and EDNRB and TRPM1, which control the color of mammal skin and hair. Changes in these genes could have helped polar bears to maintain strong muscles in cold conditions, provide their cubs with fatty insulation from the Arctic cold, and evolve white, camouflaged fur.

If Lindqvist's team is right, these changes accrued over a long span of time, featuring several climatic upheavals. By plugging the bears' genomes into computer simulations, the team calculated

that polar bear populations have tracked climate change for millions of years: their numbers dwindled during warmer millennia, but bounced back from small populations that roughed it out within colder refuges. More recently, within the last 500,000 years, the bears have gone through a prolonged and dramatic decline, which may explain why their genetic diversity is so low today. "We cannot look into the future and tell the fate of polar bears," said Lindqvist, "but we hope that getting better insight to their past will inform us in predicting how they might response to future changes."

Warmer climate could bring polar and brown bears into more frequent contact with one another, creating opportunities for them to mate. Indeed, their genomes reveal that such interbreeding was common in the past, for both species contain genes that originated in the other. Some brown bears from southeastern Alaska, for example, have inherited between 5 and 11 percent of their genomes from polar bears, while some polar bears share as much as 20 percent of their genes with brown bears.

The changing evolutionary history of the polar bear mirrors our understanding of our own origins. Until recently, the dominant account of human evolution said that our ancestors swept out of Africa and replaced all other early humans, such as Neanderthals, without mating with them. The Neanderthal mitochondrial genome seemed to confirm that idea, but the full Neanderthal nuclear genome revealed clear signs of interbreeding. We now know that 1 to 4 percent of European and Asian genomes come from Neanderthals.

"This is an exciting time where more and more genomic-scale data will become available for many more species," said Lindqvist. "My guess is that we will see that the process of speciation is much more complex than simple bifurcating splits of ancestral species. Hybridization will play an important role, perhaps as a response to environmental change."

W. Miller et al., "Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change," *Proceedings of the National Academies of Sciences*, doi:10.1073/pnas.1210506109, 2012.

