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Museum specimens tell the history of rhinoceroses

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Rhinoceroses are facing an uncertain future due to human-induced population-size reductions. In this issue of *Cell*, Liu et al. analyze rhinoceros genomes to study their past and find support for an early divergence between African and Asian species, signatures of past hybridization, and evidence of loss of genetic diversity.

Few groups of animals are more emblematic of the currently ongoing mass extinction (Ceballos et al., 2017) than rhinoceroses. Of the five living rhinoceros species, three (the African black rhinoceros, the Sumatran rhinoceros, and the Javan rhinoceros) are classified as “critically endangered,” one as “vulnerable” (the Asian greater one-horned rhinoceros), and one as “near threatened” (the African white rhinoceros) (IUCN 2021). Both the Sumatran and the Javan rhinoceros have no more than 50–80 individuals living in isolated pockets of Indonesia, which form a tiny fraction of their former distributions that once reached the foothills of the Himalayas (Pusparini et al., 2015). The whole species of the Javan rhinoceros now survives in a single national park, the Ujung Kulon National Park at the western tip of Java, after a second subspecies, which had been rediscovered in Vietnam only in 1988, was extinguished by hunters in 2010 (Brook et al., 2012). In Africa, the formerly widespread western subspecies of the black rhinoceros suffered the same fate around 2006 (Lagrot et al., 2007). Tragically, the next subspecies extinction is waiting to happen, as the last male northern white rhinoceros died in 2018, and the subspecies now consists of only two females.

In contrast to the threats faced by many other endangered species, the public is very aware of the risk of rhinoceros extinction. But despite the public attention that they receive, we still know surprisingly little about some of the species of this characteristic group, due to their rarity and vulnerability. The Javan rhinoceroses, for example, are so elusive in the dense jungle of the Ujung Kulon National Park that few people living today have ever seen one. Until a 2014 expedition into this jungle, not even high-definition

images of live Javan rhinoceroses existed. Consequently, most of our limited knowledge of their ecology and behavior comes from anecdotal accounts from the 18th and 19th centuries, when the species was still far more widespread than today (Fernando et al., 2006).

However, another source of information has recently begun to provide knowledge about rhinoceroses and is tapped in great volume by Liu et al. (2021) in this issue of *Cell*. The authors applied ancient DNA technology to sequence the genome of a Javan rhinoceros specimen that was obtained by the Natural History Museum, Oslo in 1838 (Figure 1) and analyzed this genome together with additional genomes of a total of eight rhinoceros species. These included previously published genomes of the white, the black, and the Sumatran rhinoceros, as well as other newly sequenced genomes of the greater one-horned rhinoceros and three species that went extinct in the Pleistocene: the woolly rhinoceros, Merck’s rhinoceros, and the so-called Siberian unicorn. Like for the Javan rhinoceros specimen, ancient DNA technology was applied to extract and sequence DNA from bones of the latter three species, which had all been collected in Siberia.

The analyzed genomes turned out to be a molecular treasure trove of information. While earlier, smaller molecular datasets had been unable to fully resolve the relationships of rhinoceros species (Fernando et al., 2006; Willerslev et al., 2009; Kosintsev et al., 2019; Margaryan et al., 2020), the new genomic dataset strongly supports a single species tree of rhinoceroses. In this species tree, the two African species are most closely related to each other, as are the Javan and the greater one-horned rhinoceros. The Sumatran

rhinoceros is closest to the extinct woolly and Merck’s rhinoceroses, and the group combining these three is placed next to the Javan and the greater one-horned rhinoceros. Thus, the major division among the living rhinoceros species lies between the two African and the three Asian species, in line with their geographical separation.

In combination with the fossil record of rhinoceroses, their genomes also inform about the time of the divergence between African and Asian species, placing this event around 16 million years ago, after the formation of a land bridge between the two continents. Furthermore, the genomic data show that rhinoceroses diverged from tapirs, their closest living relatives, around 61 million years ago; that the two African rhinoceros species diverged around 7 million years ago; and that the divergence between the Javan and the greater one-horned rhinoceros occurred about 4 million years ago. Additionally, the Sumatran rhinoceros, now critically endangered with no more than 80 living individuals, seems to be the last survivor of a 15-million-year-old lineage that was once diverse and species-rich. Interestingly, all sampled members of this old lineage (the Sumatran rhinoceros and the extinct woolly and Merck’s rhinoceroses) carry signatures of past hybridization in their genomes, which might have been enabled by formerly overlapping geographic distributions with other rhinoceros species.

Besides informing about their relationships, divergence times, and species interactions, the rhinoceros genomes also tell us about their past and present genetic diversity, a critical factor for their conservation. We learn from these genomes that rhinoceroses generally seem to be





Figure 1. Skull of a rare Javan rhinoceros used for genome sequencing

This skull of a Javan rhinoceros (NHM-DMA-26801/1-O) was collected in Java in 1838 and is housed at the Natural History Museum, Oslo. The specimen was used to sequence the genome of the Javan rhinoceros through ancient DNA technology. The analysis of this genome together with four other newly sequenced and three previously published rhinoceros genomes helped to resolve the species tree of rhinoceroses, demonstrated the occurrence of past hybridization between rhinoceros species, and supported a loss of genetic diversity through reduced population sizes. Photograph by Lars Erik Johannessen, Natural History Museum, Oslo.

characterized by low genetic diversity compared to other mammals, as might be expected for large-bodied animals with solitary lifestyles. However, the genetic diversity is still lower in the recent specimens compared to the Pleistocene ones, indicating that human-induced population-size reductions have led to a further decline even from these low levels. On the other hand, the recent specimens do not carry greater numbers of loss-of-function mutations, suggesting that their fitness may not be immediately affected by the low genetic diversity. This is good

news for the conservation of the living rhinoceros species, as it implies that the current populations still have the potential to re-expand and stabilize. It is now up to us to restore the conditions that would allow rhinoceroses to realize this potential.

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