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Paleovirology reveals the macroevolution of complex retroviruses

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Endogenous retroviruses (ERVs) result from permanent germline insertion of exogenous retroviruses within host genomes, and are abundant within mammalian genomes. The overwhelming majority of ERVs possess a relatively simple genomic organisation, lacking many of the accessory genes found in the more complex retroviruses. Furthermore, insertions prior to the radiation of mammalian orders lack closely related present day circulating exogenous counterparts. Foamy viruses (also termed Spumaviruses) are a superfamily of complex retroviruses that possess distinctive replication features, and are of great interest as both biological markers of zoonotic exposure risk and as candidate vectors for stem cell gene therapy. Despite a long evolutionary association with mammals, endogenous counterparts of infectious foamy viruses have been notably absent from mammalian genomes. We have discovered the first endogenous foamy virus (SloEFV) in the genomes of sloths (superorder: Xenarthra). SloEFV represents the first complex retrovirus to be described from the basal Xenarthran mammalian group. By determining the taxonomic distribution of related viruses in other Xenarthrans, and using bioinformatic approaches, we establish that SloEFV invaded sloth genomes prior to the colonization of continental South America by Boreoeutherian mammals. This observation, combined with exact congruence of branching order and statistically significant association of divergence between foamy virus and mammalian phylogenies, supports an extended cospeciation scenario under which foamy viruses remarkably similar to contemporary strains circulated in ancestral mammals >100 million years ago and diverged in

concert with their hosts throughout the Cenozoic Era. Our discovery provides the first direct evidence for ancient and mammalian-wide origins of complex retroviruses, highlighting the role of evolutionary constraint in maintaining viral genome structure. We propose that the evolution of retroviral accessory genes and mammalian mechanisms of innate immunity are the products of a macroevolutionary conflict played out over a geological timescale. Furthermore, the extended coevolutionary relationship revealed by our analysis has implications for models of viral cross-species transmission and emergence.