Is one toe really better than three? How horse' legs evolved for travel rather than speed

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Palaeobiologists from the University of Bristol and Howard University have uncovered new evidence that suggests that horses' legs have adapted over time to be optimised for endurance travel, rather than speed.

The ancestors of horses (including asses and zebras) had three toes on each foot. Because only single-toed (monodactyl) forms survive today this anatomy has been perceived as a superior evolutionary outcome, enabling horses to outrun predators.

But our interpretation of equine evolution may be biased by our own history with horses: performance at the racetrack has been less important for human history than the endurance of horses at slower speeds, and such endurance may have been the critical factor in horse evolution.

The research team combined evidence from the fossil record with existing studies on horse locomotion and propose that the adaptive significance of single-toed limbs was for trotting during roaming for food and water, rather than for galloping to avoid carnivores.

The real evolutionary 'step forward' in horse foot anatomy was not the loss of additional toes, but the evolution of the 'spring foot'.

This pogo-stick type of foot anatomy evolved in the three-toed distant ancestors of modern horses, which sported an enlarged central toe but retained small 'side toes', which likely prevented the foot from over-extending during extreme locomotor performance.

The 'spring foot' enables the storage of elastic energy in the limb tendons during locomotion, and its evolution coincided with the spread of grasslands around 20 million years ago in North America (the original home of horse evolution).

The spring-footed horses radiated extensively and were as diverse during their time as antelopes in Africa today.

By around 11-million-years ago they also spread into Eurasia and Africa, where they eventually included forms larger than a modern horse. But

only the lineage leading to modern horses, one amongst many, showed any tendency to reduce the number of toes.

If being single-toed was evolutionary advantageous, why did the majority of horses retain the three-toed condition for most of their evolutionary history?

Professor Christine Janis, lead author from the University of Bristol's School of Earth Sciences (and also affiliated with Brown University, USA) said: "Early members of the single-toed horse lineage were not only losing their side toes, but the bones of the remaining central toe showed evidence of the boosting-up of the 'spring foot' apparatus, implying that these horses were becoming more reliant on energy-efficient locomotion.

"But at the same time these horses' backs were becoming shorter and stiffer, contraindicative of adaptation for the back-flexing fast galloping gait. Rather, the preferred locomotion was more likely the medium-speed trot."

The authors propose that the early single-toed horses were changing their daily foraging behaviour to roam more widely in search of food, promoting energy-saving adaptations in their feet.

The loss of the side toes may simply have been a consequence of upgrading the anatomy of the main, central toe, and with the boosted-up ligament system their original function was no longer necessary.

Single-toed horses appeared in North America around 12-million-years ago. Over the next few million years they radiated alongside three-toed horses but remained pony-sized and were neither diverse nor numerous.

But at this time the climate in northern latitudes was becoming cooler

and drier. An increase in roaming behaviour would promote selection for the energy-efficient single-toed foot.

At the time, the foraging behaviour of the single-toed horses would have been one adaptive strategy among an equine diversity, much as different kinds of antelope have different modes of foraging today.

But by around five million years ago the cooling and drying trend became more intense worldwide; the former great diversity of three-toed horses had dwindled, and the direct ancestor of modern horses (early species of the genus Equus) appeared. By a million years ago all lineages of three-toed horses were extinct.

Why were single-toed horses the only equine lineage to survive to the present day? It is unlikely that competition was involved between the differently-adapted equines, as the Old World three-toed horses started their decline several million years before Equus emigrated from North America to join them 2.5 million years ago. More likely, the climatic changes of the late Cenozoic favoured the evolutionary strategy of the single-toed horses.

Professor Ray Bernor, the co-author of the paper, from Howard University's College of Medicine, notes that the single-toed horses really just got a lucky break due to changing climates.

He added: "The three-toed horses, especially the Old World hipparions, were an incredibly successful radiation, and their skeletons showed adaptations for leaping and springing as well as running. But they evolved for a world that was warmer and wetter than that of today, and like many other large mammals did not survive to the present day"

Single-toed horses became the dominant equines across the world in the past couple of million years, and only went extinct in the Americas at the

end of the Pleistocene, around 12,000 years ago.

Professor Janis added: "However, nobody could have foreseen this eventual success ten million years ago, when single-toed horses were merely a minor lineage among equines, confined to North America.

"Their foot anatomy was ultimately important for finding food, rather than for avoiding becoming food themselves."

More information: Christine M. Janis et al. The Evolution of Equid Monodactyly: A Review Including a New Hypothesis, *Frontiers in Ecology and Evolution* (2019). DOI: 10.3389/fevo.2019.00119

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