

ANCIENT DNA FROM FOSSIL EQUIDS: A MILESTONE IN PALAEOGENETICS

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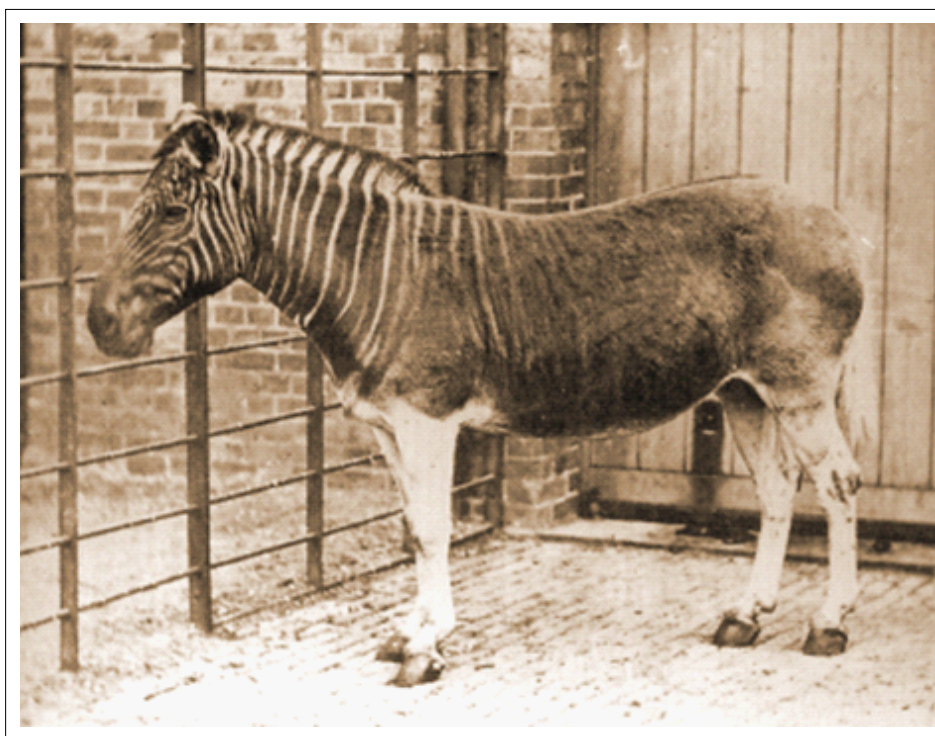
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The family Equidae includes a diversity of extant species in the single genus *Equus*, notably horses (*E. caballus* and *E. przewalskii*) and a group called the non-caballines (which includes both Asian and African asses, as well as African zebras). The fossil record, however, shows even more remarkable diversity: within the past 5 million years at least 12 equid genera have been documented, including *Hipparion*, which is known from Plio-Pleistocene deposits in the Cradle of Humankind World Heritage Site in South Africa. A linear evolutionary sequence from a hyracotherian ancestor was proposed by Othaniel Marsh and championed by Thomas Huxley, but the evolution of equids within the past 55 million years is now recognized as being much more complex. Palaeontologists such as Basil Cooke, Rufus Churcher, Vera Eisenmann and Alan Gentry have generally relied on morphology and measurements for purposes of addressing the taxonomy of southern African Equidae, as others have done for equids from other areas. More recently the potential of genetic data has been demonstrated, most remarkably in a study published in December by Orlando et al.¹

In the 1980s, Higuchi et al.^{2,3} succeeded in isolating mitochondrial DNA from the tissue of a museum specimen of the partially striped South African Cape 'quagga', which became extinct in the 19th century. The genetic results stimulated a great deal of discussion as to whether the Cape quagga was distinct at the species level from the more completely striped Burchell's zebra.^{4,5}

Genetic techniques to analyse modern and ancient DNA have improved dramatically within the past 25 years. A striking demonstration of this was Orlando et al.'s successful recovery of a DNA from 22 of 35 teeth of *Equus*, dating to the Late Pleistocene or Holocene. Four of the teeth which were successfully analysed for ancient DNA were attributed to *E. capensis*, a species which has been thought to have become extinct in South Africa in the Late Quaternary. Other fossil equid specimens in the analysis were from sites in Europe, Asia and the American continents.

The late Reinhold Rau, taxidermist at the South African Museum (now part of the Iziko Museums of Cape Town), was delighted by the initial mitochondrial DNA analyses because he had observed a gradation in the degree of striping from north to south, which suggested clinal variation without a clear boundary between two taxa.^{6,7} Similar sentiments were expressed by Thackeray^{4,5} on the basis of variation in the entoflexid of a lower premolar (P₄). He used modern museum specimens of equids from the Transvaal Museum (Northern Flagship Institution), the Natural History Museum (London) and the American Museum of Natural History (New York) for comparative purposes, as well as fossil equid specimens from Wonderwerk Cave, near Kuruman in the Northern Cape Province of South Africa, which has a long Quaternary sequence. Wonderwerk is particularly interesting, as it is situated at the northern limit of the distribution of the partially striped 'quagga' and close to the southern limit



Source: Photograph taken by Frederick York and Frank Haes. Downloaded from <http://en.wikipedia.org/wiki/Quagga>
A partially striped quagga (*Equus quagga quagga*) photographed alive in 1870 in the Regent's Park Zoo in London

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of that of the plains zebra. The latter was formerly classified as *E. burchelli*, but was reclassified as *E. q. burchelli*, distinct at a subspecies level from the historically extinct *E. q. quagga* on the basis of mitochondrial DNA analyses by Higuchi et al.^{2,3}

The extraordinary ancient DNA results by Orlando et al.¹ were published in a recent issue of the *Proceedings of the National Academy of Sciences*. They were obtained from two separate laboratories: one in Lyon in France under Ludovic Orlando himself and the other, at Adelaide at the Australian Centre for Ancient DNA, under the direction of Alan Cooper. The paper was co-authored by a team of 21 other researchers from many parts of the world.

After checking and controlling for contamination, the team used the DNA results to explore phylogenetic relationships. The DNA clearly separated Old World non-caballine equids from caballine and New World horses. In the case of Africa, the four specimens attributed to *E. capensis* (three from Wonderwerk Cave, and one from Glen Craig Shelter near Port Elizabeth) grouped closely with specimens attributed to *E. q. burchelli* and *E. q. quagga*. Specimens of the latter taxon were obtained from the Iziko Museums (South Africa), the Yale Peabody Museum (New Haven, USA), as well as the Darmstadt and Berlin museums in Germany.

The authors noted that the results suggested 'limited reproductive isolation (if any) amongst Cape quaggas and plains zebras'.¹ This view, based on a limited sample of 'Cape quaggas', is not in conflict with the opinion of a north-south clinal variation expressed by Rau^{6,7} and Thackeray^{4,5}. However, the genetic data do not support Churcher's⁸ view that *E. capensis* and *E. greyvi* (from East Africa) were conspecific. *Equus capensis* is believed to have, instead, 'formed part of the same diverse taxonomic group as plains zebras and quaggas', and 'possessed a marked plasticity' in terms of morphology and size.¹

Equus greyvi from Ethiopia and Kenya appears to group more closely with Asian asses than with the South African zebras. The mountain zebra (*E. hartmannae*) does not group with *E. q. quagga* or *E. q. burchelli*. Instead, the latter two taxa are more closely related to each other than either is to the mountain zebra, *E. hartmannae*.

These exciting results constitute an important milestone in the growing understanding of equid phylogeny, not only in terms of African zebras, but also in relation to Late Quaternary equids from Europe, Asia and the Americas. The study adds credibility to ancient DNA studies, given appropriate sampling and preparation techniques.

Sites such as Wonderwerk Cave in South Africa have excellent preservation. This cave has yielded extinct ungulate horn samples with keratin believed to be as old as 500,000 years BP, if not older.⁹ Keratin samples are currently being acquired for DNA analyses to supplement existing results obtained from this site. Wonderwerk is believed to have a cave sequence extending back 2 million years. At Wonderwerk, preservation is such that nitrogen, as well as carbon stable isotopes, can be measured in equid teeth.¹⁰ Orlando et al.¹ have set the stage for exciting new developments in palaeogenetics, with special reference to South African fossils. ■

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