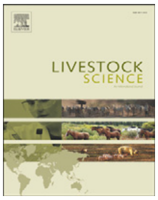
Livestock Science 143 (2012) 105–115

Contents lists available at SciVerse ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci



Review article

Discordances between morphological systematics and molecular taxonomy in the stem line of equids: A review of the case of taxonomy of genus *Equus*

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ARTICLE INFO

Article history:
Received 3 June 2011
Received in revised form 10 August 2011
Accepted 21 September 2011

Keywords:
Evolutionary history
Phylogenetic relationship
Speciation order
Equus

ABSTRACT

This paper revises the evolutionary history of the stem root of the genus *Equus* from Eocene period (54 million years before present, MYBP) to present. It also assesses molecular taxonomy and evolutionary relationships of this line since the first appearance of fossil records in terrestrial deposits. Combining these two lines of evidences, we outline a more informative and consensus phylogeny in a more understandable context. We also compare and contrast evolutionary histories and phylogenetic relationships of equids inferred from paleontological as well as varieties of molecular data and their implications. Using pair-wise coalescence time estimates, we draw a consensus speciation order in the stem root of the genus *Equus*. With the help of molecular data, we suggest the reasons for enigmatic speciation events between asses and zebras as well as the backgrounds for genetic dissimilarities between hemiones of Asia and asses of Africa regardless their phenotypic similarities. Based on the evidences from molecular data and review of late Pleistocene megafauna extinction in the Americas, we believe that horses were certainly domesticated in the Eurasian Steppe or elsewhere that survived late Pleistocene megafauna's extinction than in the Americas. We discuss the true wild horse that was involved in horse domestication processes in line with recent evidences that unraveled multi-geographic origins and multi-maternal lineages in the present day domestic horses.

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doi:10.1016/j.livsci.2011.09.017

1. Introduction

Member of the family Equidae comprises a single genus, *Equus* that represents a group of seven closely related species (George and Ryder, 1986; Oakenfull et al., 2000) notable for their rapid rate of chromosomal evolution and recent speciation (Bush et al., 1977; Ryder et al., 1978). The living member of the genus *Equus* include caballines or true horses (*E. caballus* and *E. przewalskii*) and non-caballines: hemionids (*E. hemiones onager* and *E. hemiones kulan* for Persian and Turkmenian wild asses, respectively), African wild asses (*E. africanus africanus* and *E. africanus somaliensis* for the Nubian and Somali wild asses, respectively) and zebras (*E. greyvi*, *E. burchelli antiquorum* and *E. zebra hartmannae* for Greyvi's zebra, plain zebra and Damara/mount zebra, respectively) (Oakenfull et al., 2000; Orlando et al., 2009). Other subspecies of hemiones (*E. hemiones Kiang* (Tibetan wild ass) and *E. hemiones kuur* (Indian wild ass)) are absent from the literature and molecular studies, and this posed difficulties to equine taxonomists to put the valid number of *Equus* species survived into historical times. One of the members of the genus *Equus*, *E. gagga guagga*, became extinct in the wild in the late 1870 (Groves and Ryder, 2000; Higuchi et al., 1984). Excluding *E. quagga quagga*, currently, there are six universally recognized members of the genus *Equus*. Yet, no consensus has been reached on the valid number of species belonging to the genus *Equus*.

The rich fossil records and widespread biogeographical distribution of the horse over the past 55 million years made it an icon and one of the most frequently cited examples to elucidate the patterns and processes of macroevolution (MacFadden, 1988; Orlando et al., 2009; Weinstock et al., 2005). On the contrary, studies argued that, though the overall picture of the evolution of the family Equidae is well known, the details and their phylogenetic relationships are poorly understood (George and Ryder, 1986; Groves and Ryder, 2000; Oakenfull et al., 2000; Orlando et al., 2009; Weinstock et al., 2005). Oakenfull et al. (2000) also reported that though data from many morphological, protein and modern DNA studies were examined to discern the taxonomy and evolutionary relationships among extant species, taxonomists failed to finalize the order of speciation events and taxonomic relationships in the genus *Equus*. Much of the controversy of the phylogenetic relationships of the genus *Equus* centers on implications drawn from morphological studies of dental, cranial and postcranial specimens (George and Ryder, 1986), perhaps from the target DNA used for the analysis and methods used to outline taxonomic classifications.

Moreover, there are apparent differences between the paleontological and molecular taxonomy in the genus *Equus*. For instances, based on morphological grounds, Weinstock et al. (2005) reported that more than 50 Pleistocene equids were named in the Americas, most of them during the 19th and 20th century. However, molecular characterization using ancient DNA (aDNA) drastically reduced all the named and extinct 50 Pleistocene equids into four major classes (Orlando et al., 2009; Weinstock et al., 2005). This invoked the idea to carry out major revisions of equid taxonomy. Thus, Orlando et al. (2009) carried out major revision of the recent evolutionary history of the genus *Equus* at generic, sub-generic and species levels and found out unique evolutionary history and taxonomy of the genus *Equus* than previously thought.

Another point of long-standing debate was that two subspecies of wild horses namely, *E. ferus ferus* (the Tarpan) and *E. ferus przewalskii* (Przewalskii's horses) of Mongolian Steppe survived in historic times. There had been arguments on whether the Tarpans or Przewalskii's horses were the true wild ancestor of domestic horses. Our review work thus summarizes and pinpoints the true wild ancestor involved in horse domestication. Thirdly, there had been thoughts that domestic horses had restricted origination events (limited to Eurasian Steppe) and other strains have been emerged through selective breeding. By reviewing recent genetic evidences, we present the true wild ancestor contributed to domestic horses, its multi-geographic origins and multi-maternal genetic signatures in domestic horses. Moreover, based on molecular coalescence/divergence time estimates, we attempt to outline the most problematic speciation order in the genus *Equus* and reconstruct phylogenetic tree based on the wide and reliable evidences on molecular taxonomy than those based on incomplete archaeological records.

2. Evolutionary history and taxonomy of the stem group of the genus *Equus*

2.1. Paleontological taxonomy

The widely used evolutionary timescale in the study of equids (a stem group of horses and its close relatives) evolution and genera emerged at different evolutionary time periods are presented in Table 1 and Fig. 1. Most of the evidences from archaeological remains suggest that the majority of extinct and extant forms of the genus *Equus* were emerged during Pliocene period from the stem line *Dinohippus* (Hunt, 1995).