Review of: "Hippotherium Datum implies Miocene palaeoecological pattern"

Lawrence Flynn[1]

1 Harvard University

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DISPERSAL DATUMS

This important study[1] presents a crucial analysis of well-preserved fossils of early modern equids from Linxia Basin, Gansu Province, China. The material includes excellent skulls and much of the postcranial skeleton of late Miocene age horses that were previously known from only a few dental fossils that left much of the anatomy of these classical ungulates to the imagination. Equids had a long evolutionary history with deep roots in North America. The new fossils represent early evidence of an iconic animal that spread throughout the Old World after late Miocene entry into eastern Asia. The Linxia equid had running adaptations, but retained three toes in contrast to the single-toed cursorial modern horse. These particular fossilized limb bones are slender, and the authors build a convincing case that they represent a grazing cursor of open habitat, in contrast to heavier-limbed late Miocene relatives of Europe and North Africa that suggest browsing in more closed habitat.

This is just the sort of study needed to evaluate factors bearing on the conquest of Old World landscapes by ungulates that came to dominate as large-bodied herbivores. The Family Equidae had flowered in North America as several lineages, one known by the familiar term ‘hipparions’. The hipparion group invaded the Old World at the beginning of the late Miocene via the Beringian land connection and Siberia as one or more species. Later, at the end of the Pliocene, the modern horse *Equus* followed almost the same path into Asia[2]. What better strategy to analyze the Miocene equid immigration – and date it – than to study the oldest fossil population that can be found in the eastern part of the landmass, in this case, Gansu, China? The middle to late Miocene Dongxiang Formation of the Linxia Basin has produced an exceptional sample of early hipparions. The present authors reanalyze and affirm that the Linxia horse shows natural variation that distinguishes its single species, *Hippotherium weihoense*. It was a slender-limbed open habitat grazer and cursor.

The Old World invasion event by hipparions has been named the Hipparion Datum. Exactly how and when did these equids disperse to northern Eurasia? Closely related predecessors are recorded earlier in North America. Hipparions entered Eurasia in the Late Miocene, but dating that event precisely has been elusive. Several studies [3,4, 5] on fossils from the Iberian Peninsula and eastern Europe put the datum in excess of 11 Ma. Bou Hanifia in North Africa[6] is of similar vintage on the present time scale. The Linxia work[1] proposes the datum uncritically as 11.5 Ma. At the risk of appearing to quibble over a trivial few hundred thousand years, I point out that the true first appearance in Linxia Basin remains imprecisely documented. The “Guonigou fauna” containing *Hippotherium* is posited as ranging from 11.5 to 9.8 Ma based

on a paleomagnetic study[7] in Linxia Basin, but individual species ranges remain to be analyzed. Faunal components of paleocommunities do not turn over simultaneously; *Hippotherium* did not necessarily appear precisely at 11.5 Ma. While the Guonigou fauna contains one species of *Hippotherium*, fossils from elsewhere suggest that another horse species may have immigrated at about the same time as *Hippotherium*. *Cormohipparion sinapensis* represents a slender-limbed equid in the early late Miocene of Turkey. While it could be a second immigrant, alternatively it may have been the first, because nothing precludes it[8] from immediate ancestry of *Hippotherium*.

Questions relating to the Hipparion Datum, confirmation of age and the number of immigrants, find parallels in datums of other exotic long-distance immigrants. The Leporid Datum concerned the invasion by modern rabbits from North America into Eurasia, but later in the late Miocene than the equids[9]. Modern leporines spread throughout the Old World about 8 Ma, replacing archaic genera and filling empty niches, but possibly two leporid genera, *Alilepus* and *Hypolagus,* invaded at the same time. Both the dating and the number of species participating will be tested by the accumulating fossil record.

The yet earlier Proboscidean Datum is a bit different, but also problematic. It refers to the late early Miocene dispersal to Eurasia by elephant relatives from Africa. As the African continental landmass moved northward proboscideans spread into territory devoid of the group. They dispersed to the east[10] and north by multiple routes at different times. Pascal Tassy opined appropriately[11]: How many proboscideans and how many events? There was more than one dispersal of different ages, probably of multiple forms.

The Linxia Basin study takes great strides toward defining the *Hippotherium* Datum. Its timing and its participants are better understood. It shows especially that the single Linxia species was adapted for open habitat grazing and hypothesizes such a lifestyle as the pattern for early late Miocene equids across Asia, in contrast to a closed habitat browsing ecomorphology at the same time in Europe and North Africa. Isotopic study of molar enamel (oxygen and carbon stable isotopes) might be applied as an approach to test the paleoecological pattern. As with most studies and accumulating complementary data, the new work on the *Hippotherium* Datum stimulates new questions and the need for more fossils.

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