# On the origins of the Exmoor pony: did the wild horse survive in Britain?

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**Abstract:** The Exmoor pony is considered the most primitive horse breed of Great Britain, but not a type of wild horse. In this article we draw upon historical descriptions, the literature on anatomical and morphological characteristics and on evidence based on mitochondrial DNA (mtDNA) and combine this with original analysis of the jaws and teeth of Exmoor ponies. Unlike elsewhere this wild pony type did not mix with other horse types on Exmoor. This leads us to argue that the Exmoor pony is not a 'man-made' breed, but a wild horse type with a separate history that has been uninfluenced by domestic horses.

## Introduction

During the 1950s and 1960s, Speed (1951a, 1951b, 1956), Speed and Etherington (1952a, 1952b) and Ebhardt (1962) compared the bones and teeth of Pleistocene pony fossils with those of modern horse breeds and Exmoor ponies. They concluded that the modern Exmoor pony directly descends from the smaller Northern horse that lived in France and Britain during the Late Pleistocene. Unfortunately, these findings went relatively unnoticed by zoologists at the time. According to Groves (1986) British wild horses became extinct after the Pleistocene and Exmoor ponies descend from escaped domestic horses. Mohr (1971), on the other hand, argues that Exmoor ponies are partly descended from wild ponies that lived in Britain during the Late Pleistocene and partly from later imported breeds. The earliest discovered definitively British wild horse remains are estimated to date back to 8411 BC (Sommer et al. 2011).

In recent years the Exmoor pony has generally been described as the most primitive man made horse breed found in Britain (e.g. Aberle & Distl 2004, Cieslak et al. 2010) and the wild ancestors of domestic horses are regarded as being extinct (Warmuth et al. 2011). However, recent mitochondrial DNA (mtDNA) studies on the origin of horses have revealed new insights, particularly on the geographical distribution of different wild horse populations (Jansen et al. 2002, Cieslak et al. 2010). We argue in this paper that the Exmoor pony may directly descend from a wild type of pony population that lived in north-west Europe during the Late Pleistocene. The aim of this paper is to reconsider the true origin of the Exmoor pony, by focussing on specific anatomical, morphological and genetic characteristics, such as the jaws and teeth, coat colour, manes and mtDNA of Exmoor ponies and other horse types.

## The recent history of the Exmoor pony

The presence of free ranging Exmoor ponies on Exmoor, England, was first described

in 1086 by tax inspectors of King William 1 (Morris et al. 1985). They reported that, besides their pack horses, some farmers around Exmoor owned 'unbroken horses' or '*Equi silvatici*' (the modern differentiation between the words 'pony' and 'horse' have no taxonomic relevance). Subsequent historical manuscripts (after 1617) refer to the Exmoor ponies as 'horse beasts', and describe how Exmoor pony foals were annually caught on Exmoor and sold into domestic service. In 1818 several local families started to breed 'pure bred' Exmoor ponies on small areas of moorland on the fringes of the old Royal Forest. Their herds were established with Exmoor ponies that were caught on Exmoor, and records show that the breeding of pure bred Exmoor ponies has continued right up until the present day (Baker 2008).

## Anatomy: jaws and teeth

As far as we know Speed (1951a, 1951b), Speed & Etherington (1952a, 1952b) and Ebhardt (1962) are the only studies that analyse the bones and teeth of both Late Pleistocene and modern horse populations. These authors compared the bones and teeth of modern Exmoor ponies, Przewalski's horses, modern European horse breeds, fossils of Late Pleistocene north-western European ponies (up to approximately 102,000 to 6,500 years old) and ponies from Celtic graves (of ca. 2,250 years of age). They examined X-rays of lower jaws, molars and premolars and distinguished two horse types from north-western Europe in the Late Pleistocene. One was the larger Northern horse, which was (more or less) similar to Przewalski's horse. The larger Northern horse was adapted to a cold climate, whose optimal habitat is thought to be the steppe. Most of the Pleistocene horse remains from Britain and France were of this type. They also identified the smaller Northern horse. Remains of this smaller type were found in 21 excavation sites in the Mendip Hills, several other English and Scottish sites, in the Dordogne (France) and in Alaska (Speed & Etherington 1952a). According to Speed and Etherington (1952a) the smaller Northern horse probably migrated from America to Siberia during the Pleistocene and then subsequently it came to central and northern Europe via Asia Minor. It is presumed that it was once widely distributed and was well adapted to cold climates.

According to Speed (1951a, 1951b), Speed & Etherington (1952a, 1952b) and Ebhardt (1962), larger and smaller Northern horses, Przewalski's horses and Exmoor ponies have deep lower jaws with deeply rooted molars and premolars, set in a radial pattern (like the spokes of a wheel, see figure 1a). As these authors could not distinguish the bones, lower jaws, premolars and molars of the smaller Northern horse from those of modern Exmoor ponies, they concluded that the Exmoor pony was its only pure survivor in Britain.

In addition, Speed (1951a, 1951b), Speed & Etherington (1952a, 1952b, 1953) and Ebhardt (1962) argued that most of the modern north European horse breeds are partly descended from mares of the smaller Northern horse type, that were 'improved' by introducing Arabian and other types of stallions into the herds to replace the native stallions. According to them the Arabian horse was a type of wild horse, which no longer exists in its pure form in the present Arabian horses. This horse type had small premolars and molars in a shallow, lower jaw (Speed 1951a, 1951b). Figure 1b shows an X-ray of a lower jaw from a horse found in a Celtic grave from around 250 BC; its shallow jaw and small molars and premolars are, according to Speed (1951a, 1951b) and Ebhardt (1962), typical for Arabian horses. The presence of such a horse in a Celtic grave indicates that at this time the Celts already had horses whose appearance was very different from that of modern Exmoor ponies. Speed (1951a, 1951b), Speed & Etherington (1952a, 1952b, 1953) and Ebhardt (1962) concluded that, except for the Exmoor

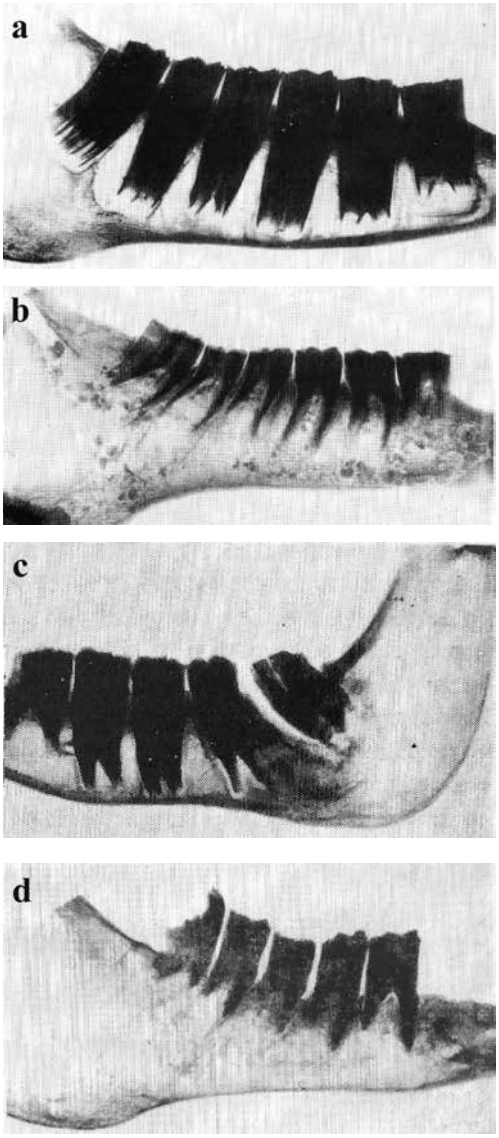


Figure 1. X-rays of a lower jaw of: a. a 4.5 year old Exmoor pony mare showing a deep lower jaw with deeply rooted molars and premolars, set in a radial pattern; b. an aged Arab-type stallion from a Celtic grave from around 250 BC, showing small premolars and molars in a shallow lower jaw; c. a Shetland pony, showing a short lower jaw with impaction of the 3rd and 2nd molars and; d. an aged 'Celtic' pony mare from Iceland, showing large teeth in a shallow jaw. The first two X-rays are taken from Speed & Etherington (1952b), the second two from Speed (1951a).

pony and the Przewalski's horse, all modern horse breeds are a mixture of original wild types. As a result the proportion of premolars and molars is often out of order to the available depth and length of lower jaws in modern breeds. This results in abnormalities, such as the impaction of the second and third molars (figure 1c) or large teeth in a shallow jaw (figure 1d). Such abnormalities are not found among Exmoor ponies or Przewalski's horses.

Although there is a lack of quantitative analysis in the work of Speed (1951a, 1951b) and Ebhardt (1962) these researchers mention having examined 'numerous horse skulls' (Speed 1951a) and 'a range of Celtic pony skulls, ancient and modern, from Iceland, Shetland, the mainland and Java' (Speed & Etherington 1952a). Boessneck et al. (1959) referred to Ebhardt's study material of horses and horse fossils as: 'an extensive collection of bones and X-rays of horse heads'. However, since there were only 50 Exmoor ponies extant in the world in 1945, the authors probably only examined a limited number of Exmoor ponies. In order to verify the lack of jaw abnormalities in Exmoor ponies, as mentioned by Speed (1951a, 1951b) and Ebhardt (1962), we dissected the lower jaws of 16 (four foals and twelve (sub) adults) deceased Exmoor ponies that were registered in the studbook of the 'Samenwerkingsverband Exmoorpony' (The Dutch Exmoor Pony Association). The molars and premolars in all the lower jaws were set in a regular radial pattern (figure 2) and all the (sub) adult Exmoor ponies had deep lower jaws (the lower jaws of foals become deep during the first year). The abnormalities that Speed (1951a) found in modern horse breeds were not present in any of the 16 lower jaws that we dissected. Two individuals had (pre) molars that were a little less deep rooted, similar to the X-ray of a lower jaw of a 2 ½ -year old Exmoor pony mare described by Speed (1951a). We believe that this may be a minor abnormality that sometimes occurs in natural populations.

Figure 2. Partly dissected lower jaw of a deceased adult Exmoor pony in 2012, showing a deep lower jaw with deeply rooted molars and premolars set in a radial pattern.

## Morphology: coat colours and manes

DNA studies on coat colour variation in ancient, wild horse types show that most Siberian and European Pleistocene wild ponies were bay coloured, and probably dun, while a minority was spotted (Ludwig et al. 2009, Pruvost et al. 2011). This is consistent with Pleistocene drawings of wild horses in the caves at Lascaux and Chauvet, France: most of the horses in these drawings are bay dun (Pruvost et al. 2011). Colour mutations (chestnut, tobiano, sabino, buckskin and blacksilver) first occurred in Siberia and eastern Europe around 3000 BC, and strongly indicate horse domestication (Ludwig et al. 2009, Pruvost et al. 2011). Unlike most primitive European horse breeds (such as Shetland pony, Dartmoor pony, Icelandic horse and konik) Exmoor ponies lack these colour variations. They show a clear uniformity in coat colour, that is (dark) bay dun (figure 3a and b), similar to their free ranging ancestors in the early C19th (Baker 2008). Przewalski's horses are the only other remaining wild horse population that, to this day, have a uniform coat colour that is also bay dun (Pruvost et al. 2011).

Unlike Przewalski's horses, zebras and wild asses, Exmoor ponies have long pendulous manes (figures 3a and b). In Europe which has a predominant oceanic climate, pendulous manes might be advantageous as they allow rain drops to slide more easily down the coat. The recovery of a horse carcass from Yukon, Canada, estimated to be 26,000 years old, demonstrates that horses with long hanging manes already existed at the end of the Pleistocene (Harington & Eggleston-Stott 1996).

## Genetics: mitochondrial DNA (mtDNA)

Recent mtDNA studies have revealed considerable new information on the maternal phylogeny of horses. Modern horse breeds appear to have maternally descended from a mixture of pre-domestic horse populations (e.g. Jansen et al. 2002). Aberle et al. (2007) showed that the mtDNA types of seven Exmoor ponies cluster almost entirely in one robust clade,

Figure 3. Exmoor ponies in a nature reserve in the Netherlands: a. Three year old Exmoor ponies in winter coat and; b. Three year old stallion, showing a deep lower jaw.

with low variability. Similar results were found by Vilà et al. (2001) and Jansen et al. (2002), who both found a low variation in the mtDNA sequences of Late Pleistocene Alaskan horses. They suggested this might be a feature of natural populations. The low level of diversity among Exmoor ponies may be due to a direct maternal link with a North-European wild pony type, but might also be due to a population bottleneck.

Cieslak et al. (2010) analysed mtDNA sequences from 207 ancient horse remains and 1754 modern horses, from Alaska to north eastern Siberia and Europe. Some mtDNA haplotypes were already widely distributed over Asia, Europe and Alaska, before the horse was domesticated. Other haplotypes were restricted to a geographic region before domestication, and their presence in a wild horse population indicates a period of isolation. The presence of some unique haplotypes in remains of Iberian Pleistocene horse indicates that the Iberian Peninsula was an ice-free refuge during the Pleistocene (Cieslak et al. 2010). In addition, Cieslak et al. (2010) found exclusive mtDNA haplotypes in remains of pre-domestic northern European horses (which they named B1 and F), that are still present in primitive European breeds, such as the Icelandic horse and Norwegian Fjord, but most frequently in the Exmoor pony (in 11 out of 17 samples; M. Cieslak, personal communication). One Exmoor pony sample (out of 17) had a haplotype (which they named X3) that probably was of a pre-domestic western European lineage as well, given the X3c2-sample from Shandon, Ireland from around ca. 25,624 BC (Cieslak et al. 2010). The presence of 11 (and probably 12) unique pre-domestic northern European haplotypes among 17 Exmoor pony samples, indicates that most Exmoor ponies are maternally linked to a wild north European pony type.

The five remaining Exmoor pony samples had haplotypes named I and D2e (Cieslak et al. 2010). Since the authors analysed relatively few ancient European horse samples, and the oldest horse remains with haplotypes I and D2e had a northern European origin, it is likely that these haplotypes also have a pre-domestic European origin. In summary, the mtDNA data indicate a separate history and a lack of influence of domestic horses in the maternal line of Exmoor ponies.

## Discussion

During the Pleistocene, horses from colder climates inhabited the steppes and tundras of North Europe, Asia and Alaska, whereas horses from warmer climates inhabited the Iberian peninsula, and other ice-free refuges (Cieslak et al. 2010). The rising of the temperature after the Pleistocene could have created the conditions under which horse populations

from ice-free refuges moved northwards. However, this was probably not enough to enable them to make contact with the north European horse population, since at the same time the central European steppe gradually changed to forest vegetation, a biotope not liked by horses (Zeiler & Kooistra 1998, Birks 2005). Although horses were very rare in central Europe between 7,100 and 5,500 BC, remains of ancient wild horses indicate that wild horses were present in north western Europe and Iberia during this period (Sommer et al. 2011).

Even in the absence of a geographic barrier, such as a dense forest, other mechanisms, such as sexual imprinting (Irwin & Price 1999) are also likely to have prevented the fusion of colder and warmer horse types after the Pleistocene. In Mongolia, for example, Przewalski's horses and free ranging domestic horses remained different types (Orlando et al. 2013), in spite of them spending thousands of years in the same area. In and around the Hustai National Park owners of domestic horses often let them range freely (often not seeing them for several months (Hovens & Tungalaktuja 2005), but these horses have never formed or joined a harem group with the Przewalski's horses that were reintroduced in 1994 (N. Bandi, personal communication, director of Hustai National Park; J.P.M. Hovens, personal observations between 1994 – 2007).

Since the Pleistocene, Britain has always had open areas, which are a suitable horse habitat (Whitehouse & Smith 2010). The country was also connected to the North-European mainland until 7,000 BC (Sturt et al. 2013). Since wild horses inhabited the northern European mainland (northern France, Belgium, southern Sweden and northern Germany) during the 1,000 years before Britain was separated from the European mainland (Sommer et al. 2011), it is arguable that part of a Nordic population of wild horses lived and survived in Britain.

It is certain that horses of various types were crossbred by man during the period of domestication that started approximately 5,500 years ago (Cieslak et al. 2010). The British wild horse population, however, cannot have been mixed with other horse types until the Bronze period (2,000 BC), since Neolithic boats were not able to transport a living (wild) horse (Dent & Goodall 1962). Exmoor was relatively isolated until the C19th and wild horses were already recorded as being present on Exmoor as early as 1086. These two facts indicate that the Exmoor pony has remained largely separated from domestic horses and has retained its primitive features.

In view of the evidence (from different disciplines) that we have collected together here we conclude that the Exmoor pony is not a 'man-made' breed, but a wild horse type with a separate history that has been uninfluenced by domestic horses.

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## Samenvatting

### De herkomst van de Exmoorpony: Overleefde het wilde paard in Groot-Brittannië?

De Exmoorpony wordt doorgaans beschouwd als het primitiefste ponyras van Groot-Brittannië, maar niet als een ondersoort van het wilde paard. Op basis van historische bronnen, literatuur over anatomische en morfologische kenmerken, literatuur over mtDNA en eigen onderzoek aan kaken en tanden, blijkt echter dat de Exmoorpony een wild type paard is en geen door de mens gecreeerd ras. In tegenstelling tot elders in Europa, is deze ondersoort van het wilde paard in het Engelse Exmoor niet met andere paardentypen gekruist.

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