THE EVOLUTION OF HORSES - Curated Transcript of BBC In Our Time podcast
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In Our Time is hosted by Melvyn Bragg. Melvyn's guests on this podcast are:

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Christine Janis
Honorary Professor in Palaeobiology at the University of Bristol and Professor Emerita in Ecology and Evolutionary Biology at Brown University

And

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Professor in Evolutionary Biomechanics at the Royal Veterinary College

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[Melvyn Bragg] Hello. The ancestors of horses were as diverse as antelopes are today, roaming in North America for tens of millions of years until becoming wholly extinct there. Some had crossed into Asia and Europe, where they were hunted and faced extinction there too, until humans learned to milk them and then ride them, changing the future of both species immeasurably. One of our contributors has said "the horse is one of the greatest technologies that humans have ever harnessed". From that point, humans have bred horses great and small, while narrowing their genetic diversity. And

while we know more about horse genetics than any other animals, we don't know why the modern horse was the one to survive, whether it was teeth, stamina or speed, or just the one-hoop-toe or just luck. With me to discuss the evolution of horses are Alan Outram
Professor of Archaeological Science at the University of Exeter, Christine Janis Honorary Professor in Palaeobiology at the University of Bristol and Professor Emerita in Ecology and Evolutionary Biology at Brown University, and John Hutchinson Professor in Evolutionary Biomechanics at the Royal Veterinary College.

[Melvyn Bragg] John Hutchinson, what were the earliest ancestors of the modern horse?

[John Hutchinson] Well, there were smallish kind of dog size, maybe around ten kilogram animals back about 55 million years ago or more in North America, and they had four fingers on their front legs and three toes on their back legs. These were animals like things called hyracotherium and eohippus [?]. Already, they had some features that we would call horselike. So their feet were somewhat elongate and their limbs in general were adapted mainly to swing backwards and forwards, not so much mobility side to side. So they were on their way, you could say, to becoming horses, but still very, very different from modern horses.

[Melvyn Bragg] How did they live?

[John Hutchinson] Well, these would have been animals that probably would have mainly browsed, so feeding off of small herbs and bushes and things like that, not grazing because there were no grasslands at the time.

[Melvyn Bragg] 55 million years ago. That's 10 million years after the dinosaurs, et cetera, wiped out. Had it taken those 10 million [for animales] to reassemble themselves as horses?

[John Hutchinson] Well, it's quite possible that improving knowledge of the fossil record might show that they actually extended very, very close to that boundary as mammals just exploded after dinosaurs went extinct. So who knows what the future will bring?

What other animals would have been around them at the time?

[John Hutchinson] Oh, a massive diversity of animals. This was a time when the Earth generally was pretty warm and lots of kind of jungley-type environments. So there were a lot of familiar groups extending back then, even including things like the earliest elephants, although they didn't really overlap with them. Early rhinoceroses were certainly around, and those are close cousins to horses, things called tapirs, which are also close relatives of horses found now in South America - things with a little proboscis or ... extended nose on them. Early primates would have been there. Lots and lots of mammals and diversifying. Birds, of course, no dinosaurs, and reptiles in general had taken a big hit in diversity...

[Melvyn Bragg] Did they have any specific enemies?

[John Hutchinson] Well, there would have been carnivores there, too. A lot of diverse lineages of carnivorous mammals around at the time. ...So early members of what we could consider dog-type lineages, hyena-type lineages, some of which would have overlapped with horse populations, some of which were elsewhere in the world.

[Melvyn Bragg] You talk with authority about something that happened 55 million years ago to sheep-like ...animals. What's your evidence?

[John Hutchinson] Well, the fossil record has been studied for almost 200 years now in quite a bit of detail, and there are places in the world where the fossil record is very, very good, where you can find complete skeletons, in some cases even preserved with soft tissue. So there are windows into that diversity that tell us quite a detailed story, and scientists have gotten very sophisticated in how they study that record. Most of this is happening in the northern part of Americas.

[John Hutchinson] Well, for horses.

[Melvyn Bragg] For horses, yes. And it stays there for a while?

[John Hutchinson] Yeah, until around, what, 23-ish million years ago, or a bit later.

[Melvyn Bragg] Christine Janis, how well adapted were the horses to the area they lived in? Well, adapted enough to last for...more than 20 million years...

[5:11]
[Christine Janis] I think animals are more persistent, always well adapted. ...So earlier, when North America was mainly tropical... forests, as John said, they would have ... looked a little bit more like these sort of big rodents you found in North America with sloping backs... And then as the habitat got more open and grasslands came in, then they became bigger, with longer legs and stiffer backed and better transport across the open habitats.

[Melvyn Bragg] Have we any idea of the numbers? Have we any idea?

[Christine Janis] Well, there are lots of different genuine species and they're very abundant in the fossil record. So, I mean, I would imagine that if you were to go back about 15, 16 million years ago to North America, they would be as abundant as you would see antelope today in the Serengeti.

[Melvyn Bragg] How well adapted were these first horses to their environment? How specifically well adapted were they?

[Christine Janis] Well, the first horses are clearly adapted to eating browse and eating buds and berries and browse, and then as the habitat changes and the climate changes, they sort-of change with it too. So then you find a little bit later, about 30 million years ago or so, they're probably better at eating leaves rather than buds and berries, and then many of them then get teeth ...and skulls that seem to be better for eating grass. But later on, as the grasslands came in at about 18 million years ago...

[Melvyn Bragg] We have the great business of they became extinct in the Americas. Can you tell us in some detail when and how that happened?

[Christine Janis] Well, ... in the world as a whole, particularly in the higher latitudes, you've got a one way change in climate to becoming cooler and drier, starting at about 14 million years ago ... and then really accelerating at about 2 million years ago. And a lot of mammals are going extinct. I mean, you had a lot of large herbivores such as camels in North America and elephants in North America and Africa and the Old World. You're getting a reduction in all kinds of herbivorous mammals at that time...

[Melvyn Bragg] This is to do with the climate. What's happening, what's the climate doing?

[Christine Janis] ..You're sort of going from a situation where you had a lot of environments like a modern day savannah, where you got a big diversity of things to eat, to [environments which are more] like temperate forest or open grassland, which doesn't support as big a diversity of animals.

[Melvyn Bragg] So over time, the foodstuffs thinned and they became extinct?

[Christine Janis] Yes, more or less.

[Melvyn Bragg] It's a big word, extinct, isn't it? I mean, when do you discover, oh, they're no longer there in North America?

[Christine Janis] Well, obviously, the last ones we find as fossils probably aren't the last ones that ever lived, but we can be pretty sure that by about well, certainly by a million years ago, the modern genus Equus, that is, the horses, asses, and zebras, that was the only one left anywhere.

So the horses come down from various, various different manifestations to being part of the equus. You threw that away, but that's what we're talking about now. From now on. The equus.

[Christine Janis] Well, yes, but the Equus is the modern horses, but there was a whole family of horses. So it'd be almost like thinking, let's say we had all the antelope go extinct, and all we had left was the cow. That's sort of almost like what was happening with the horses. You hadn't lost that big diversity of antelopes, but you did lose that kind of diversity of horses over time. Yes.

[Melvyn Bragg] And so the question is, why did this particular one survive?

[Christine Janis] That's a good question, and it's always hard to know how much how much something is is luck and how much it's, you know, due to adaptation.

[Melvyn Bragg] So there were no more horses in North America until the end of the 15th century, when the Spanish went across with the conquistadors.

[Christine Janis] Yeah, I think the extinction of horses in North America may have been related to humans going over there. Lots of mammals would go extinct at the end of

the Pleistocene. So human hunting may have been part of the problem for horses, for the last of the horses in North America,

[Melvyn Bragg] They cleared out of North America, Alan Outram. They made it across the ice bridge, the famous ice bridge, into Eurasia. Can you tell us about that?

[9:28]
[Alan Outram] Well, it would have been quite a lot earlier, actually. They originally came across and became a hunted quarry of humans. So our first interest in them was very much one of hunting them and using them as a food resource. So Equus in Europe was one of the major species that was hunted alongside things like reindeer, et cetera, and certainly by the Neanderthal period before 40,000 years ago, up to 150,000 years ago, you get some major sites where horses are one of the principal things that are being eaten. So you can take sites like Solutré in France, which has a massive pile of horse bones which have been butchered by Neanderthals. Originally, it was thought that they were horses that had been driven off a big cliff to make such a big pile of dead animals. But now it's thought that, in fact, they were rounded up into a natural cul de sac at the base of the cliff and dispatched, but in large numbers.

[Melvyn Bragg] For food?

[Alan Outram] For food, yes. And actually it created such an abundance of food, it seems that the Neanderthals didn't even fully exploit the carcasses. They'd done a fairly large mass kill and didn't even need to use up all of the food that they got from them.

[Melvyn Bragg] When we talk about southern France, we think of Lascaux Caves. Do they feature in the caves there? Are they part of the art world of the people at that time?

[Alan Outram] They very much are. And of course, that's taken us on a little bit further in time. So that famous artwork is of anatomically modern humans in the Upper Paleolithic - after 40,000 years, but before 10,000 years ago. And there are some very, very beautiful bits of cave art. Lascaux is the is perhaps the most beautiful one in terms of depictions of horses. There's a particularly famous depiction of was probably a mare, maybe even a pregnant mare (because it's quite plump, and some people have speculated that it's a pregnant one). Some very, very beautiful depictions of horses. Humans do appear to have a very particular interest, though, in horses in the artwork. [Even though] the other major quarry was reindeer, ... there are not many depictions of reindeer. [Prehistoric humans] much preferred to paint horses and in fact also make what we call mobiliary art, not just on cave paintings, but carved on things that they would have carried around as well. You see quite a lot of horses.

[Melvyn Bragg] Why do you think so? Why do you think that is, in preference to the reindeer?

[Alan Outram] Maybe the reindeer was the biggest prey, and maybe that was seen as slightly more normal and perhaps not worth the attention. And then the horse after that was possibly seen as more special. Now, whether that was a religious significance or not, I think is a little bit more difficult to say. There's lots of different interpretations of

rock art at this date as to whether it's shamanic or whatever it is, or whether it's actually to do with providing people with knowledge and passing on information about hunting different animals and their condition and so on and so forth. So there's a whole range of theories. But horses, a lot of attention. Bison, quite a lot of attention. Reindeer, people weren't so interested in.

[Melvyn Bragg] With the hunting and the eating ... was there any fear that the horses might die out in Eurasia as well?

[Alan Outram] I think that is that was a risk. And and I do agree that humans could have contributed to the final loss of horses in the Americas. There are hunted horse remains from the last part of the ice Age in America, when people were finally in North America. So I think they were hunted out in North America. But we do have some evidence that populations were dropping in Eurasia, too. So recent ancient genomic information, and this has only come very recently because we've only really had the technology to sequence very, very large numbers of ancient horses very recently. But information from something called genetic drift has shown that the horse populations were possibly getting more fragmented and dividing up from each other genetically towards the end of the Ice Age. And that certainly continued after the ice Age ended, that populations looked like they were dropping, and humans could have been contributing to that, and you could have been heading towards extinction.

[13:36]
[Melvyn Bragg] John Hutchinson, what was it to equip these surviving horses to survive for speed, first of all?

[John Hutchinson] Well, so even early on in the fossil record, horses are characterized by long limbs. And in many lineages of horses, the limbs, especially the lower limb, like the foot, gets longer and longer and longer and more and more constrained through fusion and loss of bones to only being able to swing forwards and backwards.

[Melvyn Bragg] This is below what we would call the knee, really?

[John Hutchinson] Yeah.

How does that help speed?

[John Hutchinson] Well, that lengthens the stride, mainly - thats's the main benefit. And then also there's reduction of toes. So I mentioned that the earliest things we'd call horses had four toes on the front foot, but several million years into their history, that gets reduced to three toes. And then through the flowering of horse evolution on two different occasions, you get that reduced down to mainly one main middle toe, the third toe.

[Melvyn Bragg] What's significant about that? Did humans have any influence on that? Did the horses do it by themselves?

[John Hutchinson] That's before anything proper human, although I don't think even hominins, the Australopithecus or something like that, would have been around when that was happening. That was considerably earlier. So this is more happening during

the grassland opening that Christine was talking about, that we see the really key features of horse locomotion appearing.

[Melvyn Bragg] So we have this toe, this one toe, which is an enlarged fingernail on which the whole weight of this amazing animal is poised, [and it] stands, runs, jumps, everything.

[John Hutchinson] Yeah. And connecting to that are a series of tendons and ligaments. So a lot of the muscles below the elbow and the knee get reduced to tendons and ligaments. So there's almost no muscle fibers at all below those joints - just a lot of muscle concentrated in the upper limb to generate power. And then these tendons and ligaments transmit that power down the limb to support it and propel it. So that's a really remarkable feature of horses, is this really lightened lower limb that can be swung easily because it doesn't have a lot of inertia. There are other hoofed mammals that are fast. Things like antelope can go extremely fast, faster than a horse. But ... modern horses combine size and speed and economy. That's something that they package together in a pretty amazing way.

[Melvyn Bragg] Can we develop that, then, with you, Christine? We've talked a bit about the speed, but you can take that up more if you want. And then the stamina these two together.

[16:30]
[Christine Janis] Okay, well, I think speed is a little bit of a misnomer because we think of horses being fast because we race horses. But a thoroughbred isn't like what most horses look like. So I think horses are fast, but the thoroughbred has been bred by humans to be especially fast, whereas horses do have, as John said, a lot of stamina and endurance. I think something that's really important in horse evolution, you first see it about 18 million years ago, is not so much the evolution of a single toe ... [but] is the evolution of what's called the "spring foot", where ... now horses are standing up on tippy toe, and the whole leg is a bit like a pogo stick. It's got a lot of elastic energy storage in the ligaments in the leg, and that gives you a lot of economy in terms of locomotion. But that was in ..[hipparions?].. horses that still retained small side toes - they were still technically three toed. And there was a big radiation of these horses and the lineage that led to the modern one-toed horse was only one of them. So in many ways, this is a key thing. It's a spring foot. That means that acts a bit like a pogo stick. And that was, I think, a more important thing than losing the side toes. That was just something that happened in one lineage.

[Melvyn Bragg] And what did the spring foot give precisely?

[Christine Janis] It gives you more elastic energy recovery. So modern horses can recover up to about 40% of the energy expenditure when they trot and gallop by that elastic energy recovery. So it means that if you're going a long distance, either at a slow gait or a fast gait, you expend less energy per unit traveled.

[Melvyn Bragg] Is that linked to their ... stamina?

[Christine Janis] I think so, yes.

[Melvyn Bragg] And were they outstanding in that regard, the speed and stamina combination?

[Christine Janis] In North America, they were. North America is sort-of the home of most horse evolution, although camels were there as well, and camels were pretty good as well. And then, of course, you have the antelope in Africa and Eurasia. So I think lots of animals were sort of doing this at the same time. It's just that horses were the ones that we ended up using for our own use for transport and racing and everything else.

[Melvyn Bragg] So that takes me to you, Alan Outram. So when did the humans start to domesticate animals and ride them and bring them into the ken of many people listening to this [and] become the horse that we, ... our ancestors, have known for millions of years?...

[18:58]
[Alan Outram] Well, horses actually have been very troublesome in this because unlike a lot of other animals like cattle, sheep and goats and so on, they don't have a very obvious immediate change. So those [other] animals were domesticated in the Near East around 8000 years ago ... whereas horses didn't show any clear evidence for quite a long time. And, in fact, for a long time, archaeologists were relying upon the first depictions of people on the back of horses to really show that they were domesticated. And that was around 4000 years ago in the Bronze Age. But zooarchaeologists, people that study animal bones in archaeology, thought that [domestication] must be a lot earlier than that and we began to focus on other potential evidence. And around between sort of 5-6000 years ago, we do see a number of archaeological sites in the plains of Eastern Europe and across in the steppe of Central Asia, where people begin to focus on doing things with horses in much larger numbers. You get archaeological sites with very large numbers of horses on them. And that interest actually may have been more to do with food. And the culture that has provided the best evidence for early horse husbandry so far is a site called Botai, and a culture called Botai Culture, which is in northern Kazakhstan, just south of Russia ... in an area of forest steppe - so we're talking about relatively lush step with grasslands and trees and you get sudden absolute focus on horses. So ...the site of Botai itself, has 99.9% horse bones on it, but suddenly they're settled in villages. Before that, these people were hunter gatherers, hunting all sorts of different animals and highly mobile. And all of a sudden you get really quite sizable villages that are at least semi-sedentary - people staying there for long periods of time and exploiting just the horse. ... So we started to investigate that in more detail and a few lines of evidence begin to suggest that these were horses that were under control. The first one is, as I said earlier, that we now know that horse populations were crashing. If horse populations were crashing, then how on earth could you, as a hunter gatherer, suddenly settle down and exploit only the species that was crashing unless you were actually husbanding it in some way? So that's the first line of evidence, a sort of contextual line of evidence. Then we have the line of evidence that almost all of the horse skeleton is present on the site. And that's unusual with hunting, because if you hunt an animal out away from your site, which you will do as a normal hunter, you've got a large animal. Usually there's a selection of animal bones that brought back to the site and some that are left. And in this case, it shows that the animals are all killed on the site, which is unusual for hunting. It demonstrates some sort of control. Then we got into some really interesting new techniques that

showed that the horses might have been milked. Now, this may come as a surprise to some people who are not familiar with horse milk, but in Central Asia today, this is a normal practice - that horses are milked. And a technique was developed that could identify the residues of fats in pottery and tell whether it was from horse or other animals, and also tell it was horse meat or horse milk. And we were able to demonstrate that, in fact, there was apparently some horse milk in the pots of the Botai people, which is a fairly clear indication, I think, that there is at least a degree of control of these animals, as I don't think you would want to particularly milk a totally wild horse.

[Melvyn Bragg] John Hutchinson, is this ... the time when humans were changing the ways that horses move?

[22:50]
[John Hutchinson] I don't think we really know. Well, I would guess ... it's a very recent phenomenon, the way we've bred horses for particular gaits.

[Melvyn Bragg] What's recent? We're talking to people like you recently could mean 2 million years ago. What does it mean?

[John Hutchinson] A couple hundred years or so? I think, .. 19th century, 18th century ...would be my my guess. It's not my not my specific expertise. Maybe Alan can comment?

[Alan Outram] I don't think we don't really have much very early evidence for them changing sort of the way in fact, they might move as animals at this point. But one of the first things we do see which might indicate a degree of selection is changes in coat color. So the ancient genomics that's been done recently shows that when humans start interacting with animals, we can identify that coat colors began to expand from a very limited range of brown in most wild ones, and you begin to see more unusual mixtures of coat colors expanding at this very early period, showing that there must be some selection going on.

[Melvyn Bragg] So ... humans have been in contact with [horses], riding ... horses, the horses been pulling their chariots and being useful for travel and being used in warfare and so on but the human interaction, you say, only happened about it began probably about a couple of hundred years ago?

[John Hutchinson] In terms of the wide panonopoly of gaits that horses use today, which are mainly used for our own enjoyment.

The gaits mean?

[John Hutchinson] Visual appearance [of movement], so emphasizing pacing or dressage type, fancy gaits or the toelting gait, which is kind of a running walk that Icelandic ponies use. These are probably much more modern phenomena that use the plasticity of horses in many ways to our own advantage for aesthetic purposes largely.

[Christine Janis] ...What's interesting, though, is that although the running walk gait seems to be a modern event in horses, a single gene, we have evidence that some of the three-toed horses, the Hipparions, also used a running walk gait from trackways in

Africa, in Laetoli, the same trackways in Tanzania that produced those footprints of Australopithecus, ...about 4 million years old. We have a three-toed horse there doing a running walk gait.

[Melvyn Bragg] So are you saying until about a couple of hundred years ago, horses had not changed much, and then they changed an awful lot in the last 200 years?

[25:34]
[John Hutchinson] I would say the major changes are non-locomotor. So other changes that humans were harnessing in terms of the genetic plasticity of horses, horses equuids- the whole group, including asses and zebras and so forth - horses are tremendously plastic in terms of how many chromosomes they can have. They can go from 16 to 33 sets of chromosomes in zebras to wild horses, for example. And then there's plasticity in their muscle, how much myostatin, a certain protein they have that relates to endurance or sprinting ability. So that could have been harnessed, stamina could have been harnessed and cold or hot adaptiveness - so horses have certain genes related to like, water conservation that have been shown to have a lot of selection on them that humans probably harnessed, especially once they brought horses around the world.

[Alan Outram] It's quite correct that many of the modern things are actually very recent. So if you think about major developments - by 4100 years ago ... we know that they are pulling chariots and involved in warfare. So the first culture we know that's doing that is also in that same area of the northern step in Russia and northern Kazakhstan, called the Sintashta culture about 4100 years ago. And you get burials with chariots and warriors. So they're definitely doing things very early on and actually that culture is the very first time that you see the modern clade of domestic horses come in, because we actually find that those early Botai horses are not the ones that led to the modern domesticates, but those Sintashta ones do lead to the modern domesticates.

[Melvyn Bragg] ...They must be changing the way people travel. Are people riding them to go longer distances? Are they pulling things? Because one thing I said in the introduction, and all of you say in your pieces is [that horses] change things - they massively change travel, change warfare, change agriculture. So I'm trying to get to grips with that. So if you could give me a hand, that would be much appreciated....

[Alan Outram] So that very first interaction, I think, was more about food and using them as a food animal. That's first specialization. But by the time you're getting to the middle Bronze Age period around that 4000 years ago, it's quite clear they've been used in a much more equestrian way. And that's when the modern type of horse appears. And around that time you do see huge amounts of migration going on. So there's a culture called the Yamnaya culture around that time that has spread out all the way across Europe, and it *might* have been horse aided. But certainly by this time you're getting a major interaction with horses. They're beginning to be used as a high-status animal. They're appearing in graves with rich people, with warriors and so on and so forth. So they are having a major effect on our ability to move, trade, conduct different types of warfare.

[Melvyn Bragg] John Hutchinson, can we talk about the Przewalski horse and how does that fit into what's going on?

[28:52]
[John Hutchinson] ... So that's a wild horse that has some differences from the domestic horse, as Alan was saying. ...The Przewalski's horse seems to date back earlier, is a proper wild horse with some interesting characteristics. If we looked at it, we would say, "oh, that's a different kind of horse". It's got some stripy legs, it's got a kind of a big, robust muzle that's adapted to its harsh climate.

[Melvyn Bragg] Where is it found? Is that found back in the steppes?

[John Hutchinson] Yeah. So it's back in the Eurasian environment that modern equuids evolve from, but it's not exactly that stock.

[Alan Outram] So there's a difficult finding we've [got] at the moment because it's always been regarded that the Przewalski horse is the only true wild horse

[Melvyn Bragg] And it's still there now?

[Alan Outram] And it's still there now, although it was reintroduced, it really survived in New York Zoo and was reintroduced into Mongolia. But the difficulty we now have is that some of these horses that are some of the earliest, we think, that had husbandry at Botai appear to have be direct ancestors of these Przewalskis. Which raises the question (and I always say raises the question because we need to do a lot more work) as to whether that population is still a true wild one, or actually a long time feral one, one that went back into the wild. And we don't know the answer absolutely yet, we need more work, but there are hints at that.

[30:26]
[Melvyn Bragg] Christine, how do feral horses then differ...from domesticated horses?

[Christine Janis] I think it's interesting... that all feral horses tend to revert back to being a rather similar kind of horse. Think of the mustang in North America, the brumbie in Australia, even the native ponies, they are all the sort of the size of a stocky, large pony. That seems to be a basic sort of horse morph that they revert back to. So you see things like thoroughbreds or [sire?] horses being feral horses, anything like the horses that came in North America, that came from the conquistadores. They're all sort-of stocky, large pony kind of horses. That seems to be the optimum kind of body shape and size for a horse.

[Melvyn Bragg] I might be restricting myself unnecessarily by talking about the "horse". [There are] various different sorts of horses moving along different tracks, is that right? Big horses, small horses, cart horses, speed horses, war horses...?

[Christine Janis] Well, I'm talking about when you get feral horses and horses go back to the wild today, they tend to converge on a certain kind of body form.

[Melvyn Bragg] Alan, when did the idea of intensive breeding of horses set in? It's now a part of the world economy, but when did it set in?

[Alan Outram] Well, you mentioned war horses earlier, and actually, I think some of it is to do with war horses. I think the earliest evidence we have for intensive breeding programs ([people were] certainly selecting horses earlier on) ... might come in the medieval period. The first hints of it in the genetics are in the early medieval period, around the 8th, 9th centuries.

[Melvyn Bragg] Whereabouts?

[Alan Outram] ...Within in Europe in general, but it seems to relate partly to the Islamic conquest of Spain, and actually ...a little bit later, our crusades in contact with Arabian stocks.

[Melvyn Bragg] I was wondering where the Arabian horses fitted in. They come in here, do they?

[Alan Outram] Yes. So in this medieval period, you begin to see the proportion of Arabian stock rise, and that seems to be quite deliberate.

[Melvyn Bragg] What was so good about Arabian stock?

[Alan Outram] Well, possibly some traits to do with speed, possibly related to that. We see some of those coming up in the genetics, too, at this time, beginning to increase in frequency - to do with speed. So that is the period, and at the same time, we know that people were setting up proper studs. That's when the first studs were happening, and largely to do with things like war horses. So royal studs were being set up in deer parks in England to provide high quality horses for warfare. And we've got a new project, actually at the moment, which is looking at the medieval war horse and looking at all of the documentary information, all the armor, measuring it all, trying to work out what these horses looked like and how this breeding worked and tying that into the genetics to understand how this is going on. And that intensified into the later medieval period and into the last few hundred years, as John said earlier, when you really see the modern breeds come out. But I think the start of that intensive breeding is the medieval period.

[Melvyn Bragg] So can I come back to you, John? This breeding - has it introduced weaknesses as well as strengths?

[33:39]
[John Hutchinson] Certainly - the breeding combined with the bottlenecks, or genetic drift, that horses have experienced throughout their history...

[Melvyn Bragg] What does that mean? Bottlenecks of genetic drift?

[John Hutchinson] Oh, reduction of genetic variability overall or genetic diversity. [This] has caused problems for horses in breeding ... especially the male lineage of horses. The Y chromosome has very, very low genetic diversity today, suggesting that domestic horses descend from a pretty restricted number of stallions used to breed with, whereas the female stock seems to have been larger, from what I understand. But also there are advantages there that humans have used in terms of the genetic flexibility of horses that I mentioned before in terms of chromosome counts of different

horse species or breeds that humans have bred. [It's possible to] use those chromosome counts to breed hybrids that are sterile, like horse-donkey hybrids (mules) using the advantages of both species in order to produce a breed that has compliance and endurance and other characteristics that we desire. So that's an advantage, through that plasticity provided by the genetics and chromosome count.

[Melvyn Bragg] There's an enormous number of science, biology, money and hope going into trying to improve the breed of horses. Is there a sense in which ...racing horses [are] reaching a peak of perfection, or near perfection, and it'll blow up like in Cope's law?...

[35:30]
[Alan Outram] I suppose it depends what you take as a peak of perfection. I mean, maybe a peak of perfection in terms of the way they perform for how they're being bred. But of course, they do carry quite a high, what we call, "deleterious load" in genetics... sort-of caused by inbreeding and not having the natural selection to take out various genes that are not healthy. On the one hand, they're very good at performing, but they're not necessarily healthy. And if you look at genetics over time, the deleterious load has gone up. Up until that medieval period where people started breeding intensively, the deleterious load was very low. So domestication had existed for thousands of years without really doing that, and then all of a sudden the deleterious load goes up... and until now all domestic horses have a much higher deleterious load than the ones we look at in the premedieval period, and actually even the poor Przewalskis have a high deleterious load because they were bottlenecked in New York Zoo, and so there's not actually a horse that we haven't messed up genetically at this point.

[Melvyn Bragg] Can you tell us about looking at the horses now and take a few steps back [to compare them with] their ancestors? Can you tell the listeners what are the chief differences?

[36:46]
[Christine Janis] Well, we do have horses. The horses that are around today all have a single toe, as do zebras and donkeys. ...I think what's really going on with that, compared to their three toed cousins who were around until a couple of million years ago, it's not just having a single toe, they're also more stiff backed and they also have a less flexible knee and they seem to be more endurance animals in general. So I think what's going on with a single toe is they are getting sort-of a beefed up, pogo stick kind of foot, more elastic energy storage, better endurance locomotion than their three-toed cousins. But that comes at an expense, ... they're ... less agile. And if you think about a modern horse ... compared to their three-toed cousins, it'd be a bit like comparing a cow to a deer. ...They wouldn't have been as agile, they wouldn't have been as flexible, but they would have had an advantage in the very cold, arid wild of the past couple of million years when they had to traverse long distances per day to get food. So that may have been why they survived.

[Melvyn Bragg] John, I believe it was you who said in your notes that horse is one of the greatest technologies that humans have harnessed. Would you like to develop that?

[38:04]
[John Hutchinson] I find it fascinating that humans are, ironically, are both the cause of horses demise to a certain degree, that we had a big impact on horse extinctions early on, but also were the salvation of horses. ...We are the reason why horses, to a large degree, are still around and are so, in a way, diverse. Although they're also inbred so they're not diverse, that's a contradiction of sorts, but they have helped us tremendously culturally, technologically, through means that we've discussed - transportation, agriculture, warfare, et cetera, enjoyment, leisure, and we have helped them by preserving them and hopefully they're enjoying some of that as well.

[Melvyn Bragg] It depends - not if you're Black Beauty, for instance, but still. Where do you think the horse is now? Do you think it's towards the end of a magnificent flourish of life or do you think there's more development to come?

[Christine Janis] I think most mammals are towards the end of a magnificent flourishing of life. I think we have got a lot of things going extinct right now. It's very, very worrying.

[Melvyn Bragg] Do you think the horse is only kept alive because of the human attention thats paid to it?

[Christine Janis] Equus in general, probably not. But horses, they are not a species that are wild anymore, really. Particularly now we found out that the Przewalski's horse is probably a feral horse. So, no, that species wouldn't be here at all except for humans, I don't think

[Alan Outram] John was absolutely right when he said that we caused potentially both the demise (because we could have easily hunted horses out completely) but actually we saved them through domestication. But just imagine a world just imagine a world where we weren't able to travel faster than our own walking pace, and horses gave us the fastest form of land transport for thousands of years until you got the steam train, but then that wasn't available to everybody, until the motor car became common. Think about the change in the way that people would have fought each other, how migrations would have happened, how trade would have happened. The whole world would have looked completely different if you hadn't have had that ability to move at high speed over all those thousands of years.

[John Hutchinson] I mean, dogs, of course, they're a major success story and similar parallels with genetic plasticity and how we've used that to produce all sorts of dog breeds. But dogs weren't really on their way out. Dogs were probably doing okay. Canid species in general, compared to equuids - horses are big, yummy animals that are great for paleolithic hunters to make extinct, to hunt down. They're easier prey, bigger animals are easier to take out. And with climate change, bigger animals are more susceptible to extinction, they evolve more slowly, broadly speaking. So horses are fascinating, the fact that they're still around, that they've survived despite all the odds, think about all the big mammals that went extinct in the Ice Ages. Horses just sneaked by.

[Melvyn Bragg] We're all rather pleased about that, I hope? Yes....Thank you very much. Christine Janis, Alan Outram and John Hutchinson.

And the In Our Time podcast gets some extra time now with a few minutes of bonus material from Melvyn and his guests.

[41:33]
[John Hutchinson] ...you mentioned Cope's Law, and horses are such a pivotal discussion point on that topic. I think that one would be fun to cover. So, Edward Drinker Cope was a paleontologist in America back in the 1800s - a very, very influential paleontologist and with quite a personality. He had a big fight with a guy named Marsh over various fossil dig sites, and kind of an arms race for digging up fossils. But anyway, he's credited for coming up with an idea called Cope's Rule, or Cope's Law, depending on who you ask (sometimes it's given other names). He didn't really call it anything like that, he used one term called the Law of the Unspecialized. But anyway, the point was that as animals evolve, they tend to get more specialized or get bigger or both. And horses, if you look at their fossil record, they start small, and then today we have big horses. So if you connect the dots, which is misleading, as I'll get to, it seems like there's a linear trend for horses to get bigger through time. And Cope and other people, especially after him, especially in the early 20th century, linked this idea of what we today would call Cope's Rule to another evolutionary phenomenon called orthogenesis or straight-line evolution, which is that organismal lineages, or even societies (they often made an analogy there), will change in certain directions until they get too specialized, and then they'll get decrepit and go extinct. They'll collapse, ...like the Roman Empire or something like that. Things are going great and then, oh, you're debauched and things go horrible, because you've just kind of boxed yourself into too specialized of a space - being too big, too big to change or something like that. So horses were long ... thought to be an example of ...Cope's Rule. However, more recently people have looked at this more carefully through a better fossil record, better techniques and realized, well, that's way overly simplistic - that horses had a very bushy family tree and evolved into diverse sizes throughout their evolution. It just so happens that the survivors of the horse family tree today, or recently, are relatively large or among the largest. There were some other large ones as well. There were some size reductions as well, that are kind-of swept under the carpet by Cope's Rule. So that sort of orthogenesis or Cope's Rule doesn't really apply well to horses, instead, it seems to be more like a drunken walk of size through various sizes and then ultimately with a big chopping block that gets rid of everything except for the big horse, and almost the big horse too.

[4:39]
[Christine Janis] There's also this sort-of idea of progression in evolution that somehow things that were around today... must be must be the best because they've been ...[around] the longest. And you had that classical sort of scenario of human evolution starting off with a chimpanzees and a person sort of crawling upright. And it's easy with hindsight to draw that kind of line if you actually look at the details of what happened. For example, part of the reason why the early horses were smaller is because at that point the whole northern hemisphere was covered by forests, and so animals who live in the forest today tend to be smaller, and then they got larger when the grasslands came in. So some of that change in size is driven not by some sort of evolutionary rule but by change in climate and habitat. And, as John said, it's been quite variable. You've had decreases in size and you've had increases in size in other lineages.

[John Hutchinson] And also many lineages tend to start small anyway. You have to start somewhere, and you're probably going to start small if you're going to diversify. So in a way, the only way to go is up to a certain degree or to diversify in terms of let's have more small, medium and large things instead of just small things, you can't get much smaller from small.

[Alan Outram] I think one thing, you were talking about making assumptions from the present to a certain extent there, and I think there is a problem in my field of people making assumptions from what is here in the present day. And when you start looking at the fossil record, the archaeological record, and now we're getting all of the next generation sequencing genetics out of all of this material, we see that the past is a very different place indeed. And there's all sorts of things we didn't know existed and don't exist at all in the present day. So, for instance, we had no idea that the Botai horses were going to turn out to be Przewalski's... And as we do this ancient genetic work, we're beginning to find lots and lots and lots of lost lineages that aren't actually detectable in the bone record. Przewalski's and modern domesticates, you can't actually tell apart easily from the bones - they overlap. Whereas if you do it genetically, you can see these at completely different clades. And as well as seeing that relationship that we didn't see before about that type of horse in the modern day, we're seeing a whole pile of other types that are now completely extinct and we see domestic types that have disappeared. We see a very large range of wild types that have disappeared. So the horses that are depicted in the Ice Age caves that we were talking about in Lascaux - they're gone. And for a long time people thought they were Przewalskis, because the depictions in the caves look like Przewalskis, they've got manes that stand up like a brush. And now we know they're not Przewalskis. We find out that the earliest domestic horses that we thought were the ancestors of our modern ones are Przewalskis. So there's a big revolution happening at the moment and it's all very, very recent indeed. It's only the last ten, five years that such techniques have been possible. ...

[47:47]
[Christine Janis] I want to take us back again to earlier history, and we think about horse evolution happening in North America and then horses getting over to the Old World about 2 million years ago. They were the third migration over. You had a migration over at about 18 million years of things called [Anchitheriinae?] that were big browsers, and they were around till about 5 million years ago. And then you had the Hipparions, the three toed cousins of modern horses, and they got to the Old World and were very successful not only in Europe, but also in Africa until about 1 million years ago. And so you had all these different lineages of Equuates basically, going over from North America to the Old World and being very successful in the Old World. And modern horses are a recent migration over there, really, compared to the history of horse evolution.

[John Hutchinson] I think the Copes Rule and the problem of drawing lines between two points is a good example, though, of science as progress. That, of course as science goes along, we're going to start with two data points and draw a line between them, because that's all we have. But then we're going to get a third data point and it probably isn't going to fit on that line. So we're going to realize, "oh, it's not straight, linear change, it's not simple, it's complicated". But I find that reassuring to find that

things aren't simple because nature isn't simple. And so we should, I think, be pleased to see that science is revealing a richer, more diverse portrait of the change of the world through time, especially very complicated changes through very deep time. We should expect surprises.

In our time with Melvyn Bragg is produced by Simon Tillotson.