

# CHARLES DARWIN, FOSSIL MAMMALS, AND THE PUZZLE OF EXTINCTION

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## Summary

Geology and fossil-hunting were among Darwin's principal occupations on the Beagle voyage. He collected the first known fossils of several celebrated Late Pleistocene South American megafaunal species. These provided early hints to evolution, and also led Darwin to think deeply about the puzzle of extinction. The discovery of a fossil horse tooth held particular significance, as it was the first evidence that horses had once lived wild in the Americas, before being reintroduced by the Spanish. What had caused the horses to die out? After toying with the idea that species had a finite longevity, he concluded that some environmental change must have been the cause, though he could find no evidence for it. Only later were the major climate and vegetation changes of the Pleistocene understood as likely contributors to extinction, although the relative importance of climate and humans remains as intractable as it was in Darwin's day.

## Samenvatting

**GEOLOGIE EN HET ZOEKEN VAN FOSSIELEN BEHOORDEN TOT DARWINS VOORNAAMSTE BEZIGHEDEN TIJDENS DE REIS MET DE BEAGLE. HIJ VERZAMELDE DE VROEGSTE BEKENDE FOSSIELEN VAN VERSCHILLENDE BEROEMDE PLEISTOCENE SOORTEN UIT DE ZUID-AMERIKAANSE MEGAFUNA. DEZE VORMDEN VROEGE AANWIJZINGEN VOOR EVOLUTIE EN BRACHTEN DARWIN ER OOK TOE DIEP NA TE DENKEN OVER HET RAADSEL VAN UITSTERVING. DE ONTDEKKING VAN EEN FOSSIELE PAARDENTAND WAS VAN BIJZONDERE BETEKENIS, OMDAT HET HET EERSTE BEWIJS WAS DAT PAARDEN OOK IN HET WILD GELEEFD HADDEN IN DE BEIDE AMERIKA'S, VOORDAT ZE DOOR DE SPANJAARDEN OPNIEUW WERDEN GEÏNTRODUCEERD. WAT HAD ERVOOR GEZORGD DAT DE PAARDEN UITSTIERVEN? NA GESPEELD TE HEBBEN MET HET IDEE DAT SOORTEN EEN BEPERKTE LEVENSDUUR HADDEN,**

*Right page. The holotype skull (and a tooth) of *Toxodon platensis*, illustrated in Owen's *Zoology of HMS Beagle* – one of several extinct species (or in this case, an entire Order) discovered by Darwin in South America.*

*Top: paletal view from Owen.  
Bottom: side view as it is today.  
The skull measures 50 cm long.*

*Rechter pagina. Het holotype van de *Toxodon platensis* schedel (en een kies), geïllustreerd in Owen's *Zoology of HMS Beagle* - een van vele uitgestorven soorten (of in dit geval, een hele Orde) door Darwin ontdekt in Zuid-Amerika.*

*Boven: zicht op het verhemelte uit Owen.  
Onder: zijaanzicht van het fossiel vandaag de dag.  
De schedel is 50 cm lang.*



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## DARWIN AND FOSSIL-HUNTING ON THE BEAGLE VOYAGE

From 1831 to 1836, on board the British naval ship HMS Beagle, Charles Darwin completed a voyage around the world. Within months of his return, Darwin was writing his first, feverish notes on evolution that would lead, more than 20 years later, to *The Origin of Species*, one of the most influential books ever published. Later still he wrote: “*The voyage of the Beagle has been by far the most important event in my life and has determined my whole career.*” What he saw on the five-year voyage led him to think deeply about the natural world, and to question received opinion about its origins. He also collected specimens – thousands of them – and these specimens, studied in the field and on his return to England, provided vital evidence in support of his theories.

The Beagle’s main task was to map the coasts of South America for the benefit of naval and commercial shipping, and Darwin, 22 years old at the start of the voyage, was the ship’s naturalist. For two years from 1832-34 the Beagle plied up and down the Atlantic coast of present-day Uruguay and Argentina, from the Plata in the north to Tierra del Fuego in the south, as the officers completed their surveys. Whenever the Beagle was in port, Darwin was off exploring the coast and the interior, on foot or on horseback. On these expeditions he collected plants, insects, fishes, birds and mammals, but by far the largest portion of his time was devoted to geology: observing and recording rocks and understanding the formation of the lands he was visiting. Together with the rocks came fossils, from countless shells to petrified trees and the remains of giant mammals.

The skulls and bones of extinct mammals were among the most significant of all Darwin’s discoveries in South America. His finds included five genera of ground sloth (four of them new to science), glyptodonts, giant rodents, and the first recorded finds of two endemic (and now extinct) orders of South American mammals – the litopterns (*Macrauchenia*) and notoungulates (*Toxodon*). As his diaries and letters of the time make clear, these fossils made a huge impression on Darwin and led to some of his earliest inklings about evolution, as he recognised the connection between the animals he was finding as fossils, and those he saw living in the same regions, such as sloths, armadillos and capybaras.

## THE PUZZLE OF THE SOUTH AMERICAN HORSE

Of almost equal significance to Darwin, but less amenable to a solution, was the question of extinction. Even in *The Origin of Species*, after 20 years of puzzling over the issue, he considered it ‘the most gratuitous mystery’. It was the extinction of the large mammals, whose remains he had unearthed during the voyage, that lay at the root of his puzzlement. As he wrote in his *Journal of Researches*: “*It is impossible to reflect without the deepest astonishment, on the changed state of this continent. Formerly it must have swarmed with great monsters, like the southern parts of Africa, but now we find only the tapir, guanaco, armadillo, and capybara; mere pigmies compared to the antecedent races. ... What then has exterminated so many living creatures?*” (Fig. 1).





For Darwin, nothing exemplified this problem more clearly than a humble horse's tooth he discovered in a stream bed at Bajada de Santa Fe (now the city of Paraná) in northern Argentina in October 1833. Here, in a deposit of red clay, Darwin found fossils of glyptodon, gomphothere and *Toxodon*, as he had at many other places. Among the remains, however, was a single molar of a horse – a find that, unlike many of the others, he could immediately identify with certainty (Fig. 2). It appeared to be embedded in the same layer as the remains of extinct fauna, but since fossil horses were at that time unknown in South America, Darwin doubted the evidence of his eyes. Might it have been washed down from close to, or even on, the modern land surface, muddy sediment then hardening around it? Was it, in other words, the worthless tooth of a domestic horse post-dating the Spanish conquest? After careful scrutiny, Darwin satisfied himself that the tooth had indeed originated within the same ancient layer as the extinct beasts. Its state of preservation was identical to a *Toxodon* tooth found nearby – both were similarly corroded and stained red. To strengthen his argument further, Darwin noted that the surrounding country was uninhabited and without fresh water, so modern domestic animals were unlikely. He need not have worried; it later emerged that a similar horse tooth, albeit somewhat less well preserved, lay embedded in a sediment block he had collected two months earlier alongside bones of giant sloths and *Toxodon* at Punta Alta, 800 km to the south.

Darwin marvelled at the finds, discussing them at length in his notebooks, in the *Journal of Researches*, and even in *The Origin of Species* published a quarter of a century after the discovery. With characteristic English understatement, the great anatomist Richard Owen described the finding of the horse teeth as “not one of the least interesting fruits of Mr. Darwin's palaeontological discoveries”; but celebrated US palaeontologist George Simpson later called it “the most important single result of Darwin's collections of fossil mammals during the voyage of the *Beagle*”. The cause for Darwin's astonishment lay not only in the co-existence of extinct species with those still alive, for this had already been demonstrated in the bone caves of Europe, but in the revelation that horses had once lived wild in South America, and the puzzle it posed about the causes of extinction. It was well known that the Spanish had found no horses when they arrived in the Americas at the turn of the 16th century; yet, as Darwin emphasized, once introduced and escaping into the wild, horses had multiplied in huge numbers and were clearly well adapted to the Pampas environment. So if they had previously existed there as native animals, why had they gone extinct?

Figure 1 (left page). Late Pleistocene megafauna in Patagonia. In the foreground, the sabre-toothed cat *Smilodon* and litoptern *Macrauchenia*; middle distance, a glyptodont, ground sloth *Megatherium*, and horses *Equus*; background, the gomphothere *Notiomastodon*.

(linker pagina) Laat-pleistocene megafauna in Patagonië. Op de voorgrond de sabeltandkat *Smilodon* en de litoptern *Macrauchenia*; in het midden een glyptodont, een grondluiaard *Megatherium* en paarden *Equus*; op de achtergrond de tot de gomphoteriën behorende *Notiomastodon*.



Figure 2. The upper molar of a horse found by Darwin at Bajada de Santa Fe – the first recorded evidence of ancient horses in South America, that led Darwin to ponder the question of extinction. The molar is approximately 3 cm wide and has been sectioned to show the enamel pattern.

De bovenkaakse kies van een paard gevonden door Darwin in Bajada de Santa Fe – het eerste vastgelegde bewijs van oorspronkelijke paarden in Zuid-Amerika, dat Darwin aan het denken zette over het vraagstuk van uitsterving. De kies is ongeveer 3 cm breed en is doorgezaagd om het emailpatroon te laten zien.



## THEORIES OF EXTINCTION

Darwin first dismissed the then prevalent view of ‘catastrophism’ – promoted by Cuvier and passed on to him by his Cambridge tutors, that species only became extinct en masse, during cataclysmic events that brought each geological period to a close. He had noted that his extinct mammals occurred in beds filled with mollusc species that had survived to the present day; hence, as pioneering geologist Charles Lyell had pointed out before him, not all species had died out at the same time. Equally important against catastrophism, the geological context of his finds suggested that they had been deposited under normal, relatively calm conditions, not during a time of major environmental upheaval. Early in his collecting, at Punta Alta on the coast of Argentina, he had concluded that the beds, horizontally aligned with pebbles, shells and bones, were not the relic of a sudden catastrophe but had formed in a normal river or estuarine environment. In a later essay, Darwin enlarged on the idea - if there had been a major debacle, chaotic deposits, with the inclusion of rocks and trees, would be expected; instead, the beds were the result of gradual deposition and the bones testified to “a succession of deaths, after the ordinary course of nature”. These conclusions strongly supported the ‘uniformitarian’ views of Lyell, whose *Principles of Geology* had been Darwin’s key text on the Beagle voyage. Darwin also pointed to his discovery of complete fossil skeletons in the case of *Macrauchenia* and the ground sloth *Scelidotherium*, which seemed to be lying at or close to the place they had died; a great upheaval would surely have broken them up and dispersed the bones.

These observations, however, compounded Darwin’s puzzlement as to the cause of extinction of the giant mammals. If their remains were geologically extremely recent, there had scarcely been time for, nor was there any evidence for, a great upheaval subsequent to the deposition of the bones. Therefore their extinction must have resulted from a much less dramatic cause, but what could that be? For Lyell, the answer seemed straightforward – since individual species are adapted to certain environments, and since we know that the Earth has undergone constant change, then those changes will periodically cause the extinction of species, and new species, better adapted to the changed circumstances, will take their place. Darwin’s South American exemplar made it difficult for him to accept this simple solution. He believed that the deposits within which the bones occurred indicated little if any difference in the past environment compared to that of today. Moreover, it seemed unlikely that the gravel-strewn plains of Patagonia could ever have supported a more luxuriant vegetation than the present sparse scrubland. Even if there had been a certain change of climate, it cannot have been substantial – witness the unchanged composition of the marine fauna.

Darwin’s conclusion that the past environment of Patagonia was as poorly vegetated as that of today brought fresh problems – how had large numbers of huge mammals managed to subsist there? The apparent solution came in June 1836 when the Beagle stopped off in South Africa for 18 days. There Darwin met with two local naturalists who described the abundance of large mammals living in

relatively impoverished environments of the region. His notebook reads: “*Elephant lives on very wretched countries thinly covered by vegetation. Rhinoceros quite in deserts*”. “*That large animals require a luxuriant vegetation, has been a general assumption*”, noted Darwin; “*I do not hesitate, however, to say that it is completely false.*”

While these conclusions explained the former existence of large mammals in Patagonia, they made their extinction through changed environments even harder to accept. There was also the unique issue of his fossil horse teeth – since reintroduced horses thrived so well in the present-day habitat, why did they go extinct in the first place? Finally, by this time it was becoming known that megafauna had died out, recently by geological standards, in many parts of the world – mammoths in Europe and Siberia, kangaroos in Australia, mastodons in North America. Darwin exclaimed in his notebook: “*It is a wonderful fact, horse, elephant and mastodon dying out about same time in such different quarters. Will Mr. Lyell say that some circumstance killed it over a tract from Spain to South America? Never.*”

The only serious contender for a global event sufficient to have exterminated megafauna worldwide was Louis Agassiz’s glacial hypothesis, first revealed in 1837. It had been proposed in catastrophist vein, a global glaciation wiping out all life on Earth. This was certainly too much for Lyell, who refuted it with examples where bones of megafauna had been found above supposedly glacial deposits. Darwin agreed that the large mammals had survived the glacial period, citing the lateness of his South American fossils. He added, presumably based on the hardiness of the beast: “*Horse at least has not perished because too cold.*”

Largely by default, Darwin turned to the idea proposed by Italian geologist Giovanni Brocchi that species, like individuals, had a finite lifetime; as summarized by Lyell (who roundly rejected the idea), Brocchi proposed that the longevity of a species “*depends on a certain force of vitality, which, after a period, grows weaker and weaker...*”. In an essay of February 1835, seeing no environmental cause for the extinction of the South American megafauna, Darwin flirted with the Brocchian concept, and even in an 1837 notebook after his return, wrote: “*Tempted to believe animals created for a definite time – not extinguished by change of circumstances.*”

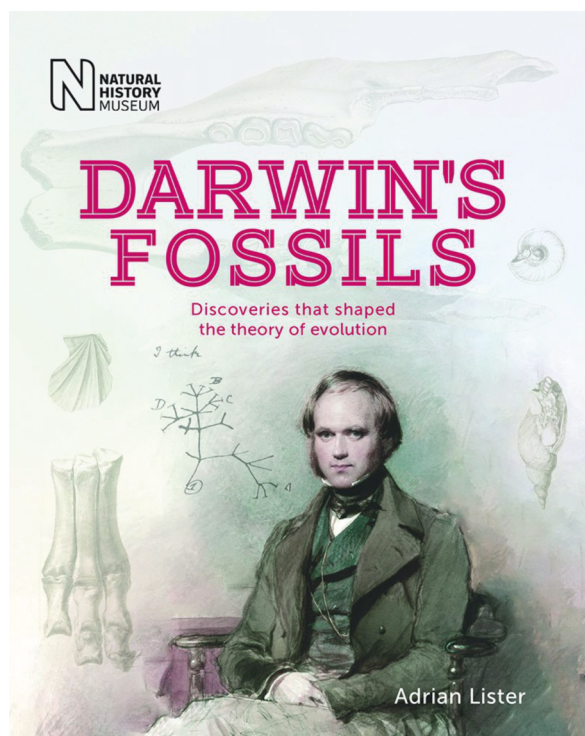
Soon after, however, Darwin recognized that such an idea was not biologically sustainable, accepting that in a general sense extinction must be “*a consequence ... of non-adaptation of circumstances*”; this was, indeed, almost implied by his theory of evolution by natural selection. Thus, “*extinction ... will take place when conditions are unfavourable to numbers of animals, as in changing from warm to cold, damp to dry*”. As far as the South American megafauna were concerned, he could only reflect on how little we understand the precise ecological conditions that determine the success, or otherwise, even of species alive today; hence we can “*argue with still less safety about either the life or death of any extinct kind*”.

That humans might have played a part in the megafaunal extinctions appears not to have been considered by Darwin. Both Lyell and Owen had rejected evidence that humans had coexisted with the megafauna, arguing that people had appeared on Earth after their extinction. Lyell dramatically changed his mind in his 1863 book *Geological Evidences of the Antiquity of Man*, and while still emphasizing environmental causes, admitted that “*the growing power of man may have lent its aid as the destroying cause of many Post-Pliocene species*”.

As for competition between species, Darwin’s early writings doubted it as a plausible explanation: “*Will it be supposed that the armadillos have eaten out the Megatherium, the guanaco the camel?*” [the latter referring to *Macrauchenia*]. In his mature view, however, expressed in *The Origin of Species*, Darwin came to see competition between species as a major driving force of extinction. Since natural selection is constantly producing better-adapted species, “*the consequent extinction of less-favoured forms almost inevitably follows*”. He acknowledged that environmental change could also play its part; for example, the preferential extinction of larger species among the mammals might be due to their requiring a greater amount of food.

## THE DEBATE CONTINUES

Today, the causes of extinction are still debated, in much the same terms as those considered by Darwin and his contemporaries. In general, through geological time, environmental change is seen as the dominant factor, with direct competition playing a significant but lesser role. In the particular case of recent megafaunal extinctions, the principal contenders are ice-age climate change and hunting by people. We now know that these climate changes were highly complex, and not limited to times of actual glaciation, so Lyell’s observation that many extinct megafauna survived beyond the glacial episode was correct. In South America, some 66 species of large mammal died out, mostly between about 15,000 and 8,000 years ago. Climate changes around this time led to the spread of forest and to changes in grassland habitats, which would have impacted the large herbivores. At the same time, humans had arrived in South America by at least 15,000 years ago, and there is clear archaeological evidence that they utilized species such as sloths and gomphotheres for products such as meat, skin, bone and tendon. Evidence for butchery, however, such as cut marks on bones, does not distinguish between hunting the living animal and scavenging a carcass, and only a very few finds clearly indicate actual hunting. The relative contributions of hunting and climate change to the extinction of the megafauna, as in Darwin’s day, remain to be determined, but a synergistic effect of the two seems increasingly likely.



This article has been adapted from:

A.M. LISTER, 2018  
**DARWIN'S FOSSILS. DISCOVERIES THAT SHAPED THE THEORY OF EVOLUTION**

Paperback: 232 pages  
 Publisher: Natural History Museum, London  
 Language: English  
 ISBN: 9780565093921

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## PRINCIPAL SOURCES

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