

Introduction

The name of this species is derived from its voice, which is a kind of cry somewhat resembling the sounds qua-cha! It is unquestionably best calculated for domestication, both as regards strength and docility . . . we have ourselves been drawn by one in a gig, the animal showing as much temper and delicacy of mouth as any domestic horse . . . It is this species that is reputed to be the boldest of all Equine animals, attacking hyaena and wild dog without hesitation, and therefore not unfrequently domesticated by the Dutch boors for the purpose of protecting their horses at night while both are turned out to grass.

C. Hamilton Smith¹

Such is a thumbnail sketch of an animal the size of a pony that became extinct in the late nineteenth century but whose use in traction and livestock protection might have led to domestication. Quaggas were distinctive in their appearance: they had fewer stripes than other zebras and these were dark reddish-brown or black and a lighter reddish-brown.² Stripes were confined to their faces, necks, manes and forequarters, before becoming irregular and then disappearing altogether at the hindquarters, that were a reddish-brown color. Their unstriped legs were white, as were their underbodies, except for a ventral stripe along their length (Figure 0.1). They seemed to have evolved this distinctive coat coloration from living in an isolated habitat that was colder and drier than the environments of most zebras.

Quaggas lived in a limited area of southern Africa that extended from east of present-day Cape Town across the arid plateau of the Karoo to the grasslands of the high veld – areas that became part of the Cape Colony and the Orange Free State (Figure 0.2). Their preferred food was grass, but they could eat other vegetation. They lived in breeding groups comprising a stallion, one or more mares, and their foals.³ Several groups might join to form a herd and move together looking for water and

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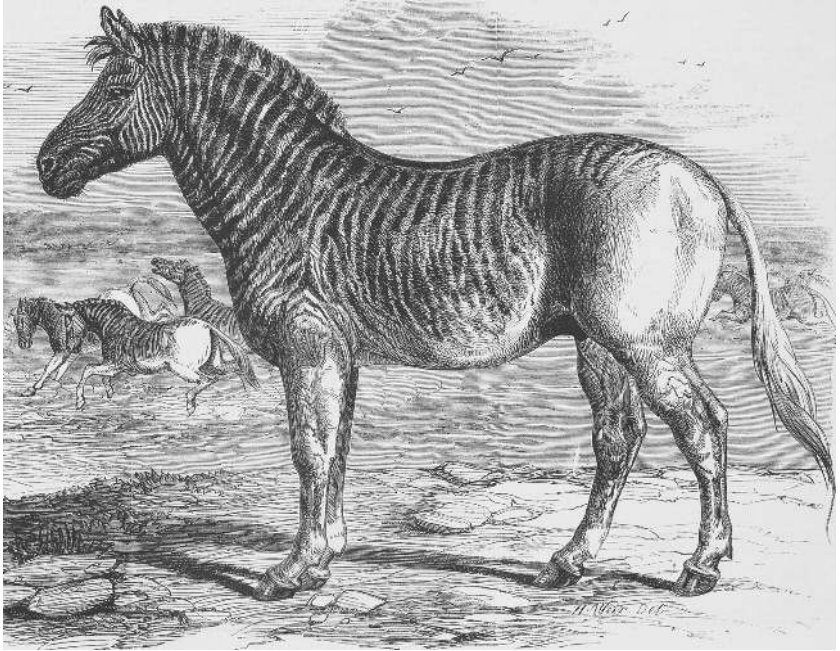


Figure 0.1. *The quagga in the Zoological Society's Gardens, Regent's Park.* From Weir, *The Illustrated London News*, 1858

forage. Sometimes, large numbers congregated: one nineteenth-century account describes “bands of many hundreds” migrating in search of new grazing, and another describes how multitudes of quaggas and other animals picked clean the vegetation in the path of their migration.⁴

Quaggas were not the only zebras in southern Africa: to the north and east were animals that resembled quaggas, but had more stripes and were less brown, and scattered through the west and south-west were mountain zebras, abundantly marked with black and white stripes. Quaggas shared grazing with several species of antelopes, ostriches, and wildebeests (gnus), but it was with the latter two that they formed close bonds that seem to reflect feeding preferences. All these animals faced predation by lions, leopards, hyenas, cheetahs, wild dogs, and humans. The indigenous Khoe-San, who lived alongside quaggas for millennia, immortalized them in paintings and engravings, while also hunting them for meat, hides, and bones.⁶ Lacking firearms and horses, they relied on skill and ingenuity to make and use bows, arrows, spears, poison, and hunting traps. The |Xam (hunter-gatherers of the Karoo) told stories about

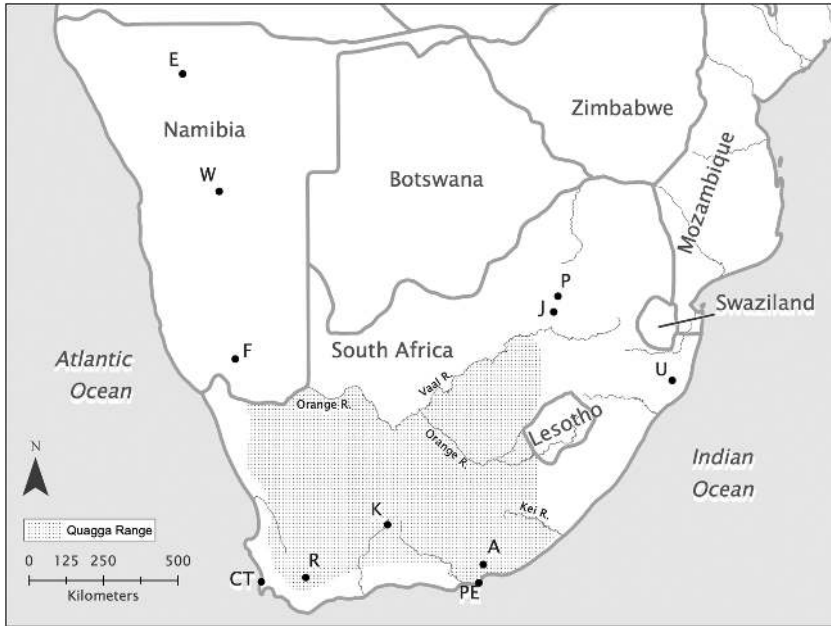


Figure 0.2. Southern Africa, showing locations mentioned in this book. Quaggas lived in areas that are now part of the Western Cape, Eastern Cape, Northern Cape, and the Free State provinces; stippling shows their presumed range in the mid-eighteenth century. The Fish River Canyon, Namibia (F) was a site of unsuccessful searches for quaggas after their extinction. Plains zebras from Umfolozi Game Reserve, South Africa (U) and Etosha National Park, Namibia, (E) were brought to the Vrolijkheid Nature Conservation Station near Robertson (R), the initial location of the Quagga Project, and their offspring now live at several locations, including Addo Elephant National Park (A) and Karoo National Park (K). The map indicates the following cities: Cape Town (CT), Johannesburg (J), Port Elizabeth (PE), Pretoria (P), and Windhoek (W). Swaziland is now Eswatini. This figure by the author was prepared by Bruce Boucek of the Brown University Library (courtesy of Brown University Library); it was originally published in Heywood (2015) and is reprinted courtesy of Kronos⁵

quaggas in which they are not just hunted animals, but also sentient beings living in households with families.⁷

When first encountered, quaggas were wondrously novel to the Dutch at the Cape, who wondered if they might substitute for the domestic equines that they sorely needed. Eventually, they were used to pull wagons and carriages in the Cape Colony and Britain, and some farmers kept quaggas with livestock to protect them against predators by biting and kicking aggressors that came close. Obtained young and

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properly treated, quaggas could have been widely used and probably would have been more resistant to tropical diseases than horses.

Their potential for protection or draft, however, did not prevent quaggas from being killed in large numbers by farmers and hunters in a region engulfed in the eighteenth and nineteenth centuries by the expanding frontier of the Cape Colony. Some people shot quaggas frivolously for “sport”; others killed them to provide meat for servants and laborers and for their hides, which were used to make rough rawhide shoes, leather thongs for binding things together, and cheap bags. Finally, they became the prey of hunters who exported their hides to provide high-quality leather for overseas boot makers. It was all too much: hunted extensively and excluded from water and grazing lands increasingly used to support farm livestock, quaggas that had existed for many millennia became extinct in the wild in the 1870s, leaving the ending – the last of their kind – to die in the Amsterdam Zoo on August 12, 1883.⁸

Some organisms become extinct even before being known to science and the wider world. This was not the case for quaggas: they shaped Charles Darwin’s ideas about mechanisms of inheritance, justified the plot elements of August Strindberg’s play *The Father*, and featured in the stories of the |Xam. Portrayed by unknown rock artists and famous European artists such as Jacques-Laurent Agasse and Nicolas Maréchal, we can envision them today.

Cape mountain zebras, *Equus zebra zebra*, almost suffered the fate of quaggas. People continued to hunt them into the twentieth century when fewer than ninety survived.⁹ In 1937, authorities designated a farm containing Cape mountain zebras near Cradock in the Eastern Cape as the Mountain Zebra National Park.¹⁰ In 1950, conservationists moved five stallions and six mares from other locations to the park and a few more animals were added in 1964. Since then, their numbers have steadily increased into the thousands.¹¹

Bonteboks, *Damaliscus pygargus pygargus*, have a similar success story. They, too, like quaggas and Cape mountain zebras, were endemic to South Africa. By 1931, only twenty-two animals remained on a single farm, but conservation has increased their numbers into the thousands, many of which live in the Bontebok National Park.¹² Common to both these accounts is that dedicated people saved a subspecies from extinction by providing the animals with safe, suitable habitats. Initially, this conservation involved neither extensive areas nor major expenditures. Most people take the existence of these animals for granted, not realizing how close they came to extinction.

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Central to the success of conservation in South Africa has been the preservation of habitats such as Mountain Zebra National Park and Kruger National Park, linked to national parks in Mozambique and Zimbabwe to form the Great Limpopo Transfrontier Park.¹³ Some other reserves are also large and provide wildlife corridors that allow migration. Extensive reserves allow sizeable populations of individual species and so reduce the possibility of inbreeding.

To return to quaggas, their story did not end with extinction. Reinhold Rau, a taxidermist at the South African Museum in Cape Town, sent tissue samples from quagga hides to scientists in the United States for analysis in the early 1980s, and these little-known zebras gained the distinction of being the first extinct creatures to have short segments of their DNA sequenced. Quagga DNA sequences proved to be very similar to sequences found in plains zebras, which led to reclassification: quaggas were not a separate species, as some taxonomists had concluded, but were a type of plains zebra that now bore the binomial name, *Equus quagga*.

Rau reasoned that, because quaggas were a subspecies of plains zebras, the genes for their distinctive coat coloration might still exist within populations of plains zebra and be retrievable by selective breeding. He knew that there were populations of plains zebras in both South-West Africa (present-day Namibia, but then under South African administration) and South Africa that resembled quaggas in their reduced striping and coat coloration, and in 1987 he obtained some of these animals as the founder population for the “Quagga Project” – a venture that has received the enthusiastic support of many individuals and organizations.¹⁴ Careful selection of the descendants of these animals by the Quagga Project has yielded zebras with fewer stripes and more brown coloration that now live in the same habitats once occupied by quaggas.

At first sight, this outcome represents an inspiring success story, but it raises the question: to what extent *are* the rebred animals quaggas? Even the brownest of them do not have the chestnut color visible in many paintings, and – importantly – were there genetic, morphological, and behavioral characteristics of quaggas that are not present in Quagga Project zebras?

The opportunity cost of rebreeding is another issue: could the money and resources devoted to the Quagga Project have been used more effectively in conservation projects? South Africa is a country of great biodiversity, but the International Union for Conservation of Nature (IUCN) lists many of its species as endangered. Losing large vertebrate species to hunters may be a thing of the past, but climate change and

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habitat loss all take their toll as the human population expands and as people convert wildlife habitats into housing, farmers' fields, wineries, mines, etc. Might some funding that went to breeding have been used to preserve these habitats? Extinction and breeding raise other important questions. How do humans value species and subspecies? What combinations of circumstances cause anthropogenic extinctions? What organisms can be saved, and how can this best be done? Is breeding extinct animals a worthwhile endeavor in a world of pressing conservation needs?

Whatever the success of breeding, people remember the original quaggas, as they have inspired stories, poems, illustrations, and an animated film. Humans have given their name to other animals and to a range of enterprises. Descriptions from the |Xam, explorers, hunters, scientists, and poets in this book present authentic accounts of these zebras. Their voices will help to tell the story of how quaggas lived, why they were lost, and how people are attempting to breed them. The most prominent presence, nevertheless, should be that of a remarkable animal that was an important part of its environment and whose extinction continues to serve as a warning about the dire effects of human greed and folly on the natural world.

1 • Zebras

I stopped to examine these zebras with my pocket telescope: they were the most beautifully marked animals I had ever seen: their clean sleek limbs glittered in the sun, and the brightness and regularity of their striped coat, presented a picture of extraordinary beauty . . .

William John Burchell¹

Plains zebras, mountain zebras, and quaggas were important members of the southern African biota: they interacted with other grazing animals and, together with them, were prey for predators. Collectively, these animals influenced the nature of several biomes.

Zebras and quaggas were well known to indigenous people: they provided them with necessities, such as hides and meat, and featured in their art and stories. Indigenous people distinguished between quaggas and mountain zebras. To the |Xam, the first known inhabitants of the Karoo, they were “||ǃkhwī” and “||kabba,” respectively.² People who spoke the Xhosa language seem to have differentiated between them by their calls: they called quaggas with their barking neigh “iqwarha,” and knew Cape mountain zebras as “idawuwa.”³ The other indigenous people of the region, the Khoekhoe, named both mountain zebras and quaggas “quacha” (sometimes rendered as “qua-cha” or “quakka”).⁴ “Iqwarha” and “quacha” – like the Dutch and English names of “kwagga” and “quagga” – are onomatopoeic, suggesting the animal’s barking cry of “kwa-haa, kwa-haa,” which was often repeated in rapid succession.

After the European colonists introduced horses, which in Xhosa were “ihashe,” to the region, the Xhosa incorporated a reference to the equine family into their name for the barking zebras: “iqwarhashe.”⁵ By differentiating local animals and connecting them to a global family, those names – iqwarha and iqwarhashe – represent the project of taxonomy well, but writ small. Globally, there were several horse-like animals, some striped, some not, and clear names are necessary to catalog the set.

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Equines

Carl Linnaeus (1707–1778) developed the modern system of classification that uses a hierarchy of categories to construct closer and more distant affinities. Species are grouped most closely within a genus; the binomial name of genus and species provides a signifier that is unique to the organism. Because many reports of animals came to Linnaeus from all over the world, he had a bigger challenge than Xhosa speakers did with their handful of local species. Linnaeus had to sort out several types of horse-like creatures. Recognizing the similarity between horses, zebras, and asses (wild donkeys), he placed them in the same genus, which he called *Equus*, using the Latin name for horse. Collectively, these animals are referred to as equines. The genus *Equus* is grouped with extinct equids into the family Equidae.⁶

The ancestors of the Equidae can be traced back over 50 million years to animals less than twenty inches (508 mm) tall and with three toes on their hind feet and four toes on their fore feet. The earliest equids browsed on various plants but, with the creation of vast grasslands, their descendants evolved into larger grass-eating animals. The fossil record shows that there were many such species, most of which are now extinct. Equines, animals clearly belonging to the *Equus* lineage, were present in North America about 4 million years ago and their descendants living there died out about 10,000 years ago. Beginning about 3 million years ago, equines spread into South America and, via the land bridge of Beringia, into Eurasia and Africa where their descendants became horses, asses, and zebras.⁷

Equines use their incisors to crop vegetation and their premolars and molars to grind it; their digestive systems enable them to live by eating large amounts of food having a low nutrient content. Their eyes on the sides of their heads afford vision over a wide arc to detect predators, and their senses of hearing and smell provide additional warning of dangers.⁸ Speed to avoid predators comes from highly specialized legs whose digits are reduced to just the middle toe of each foot, which is thickened and greatly elongated; their long legs end in hard, impact-absorbing hooves.⁹ Zebras can run at speeds up to 55 kilometers per hour (34 miles per hour) and horses are even faster.¹⁰ As well as providing speed, strong legs can deliver a powerful kick to a predator or competitor.

DNA evidence reveals the evolutionary history of horses, asses, and zebras. The sequence of four nucleotides, chemical groups that are linked end-to-end to form DNA molecules present in nuclei and mitochondria,

provides key information. Collectively, the DNA of an organism is called its genome and its study is termed genomics. The technique of DNA sequencing enables scientists to compare the order of nucleotides between the genomes of different organisms: an identical or similar sequence of nucleotides argues that two organisms are closely related, or even belong to the same species. Scientists study genomes from both extant (present-day) equines and from preserved material including ancient horse bones preserved in permafrost for over 500,000 years and quagga hides and bones.¹¹ Genomes evolve over time and so the degree of difference between nucleotide sequences of species can help determine the time when they diverged from a common ancestor.

The genus *Equus* diverged into evolutionary lineages leading to asses, zebras, and horses (Figure 1.1). One horse, *Equus ferus caballus*, was

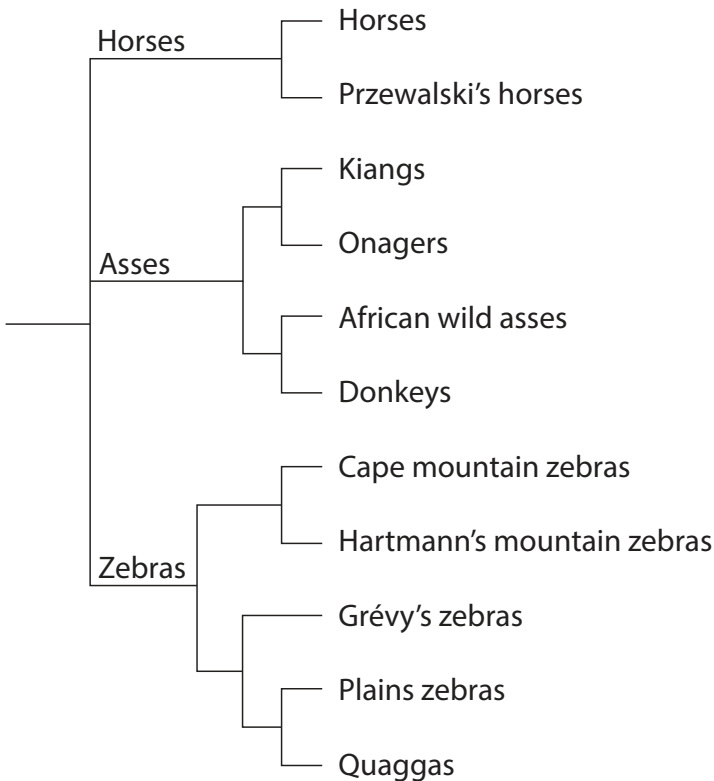


Figure 1.1. Evolutionary relationships between equines showing the divergence of lines leading to horses, asses, and zebras. This figure by the author was prepared by Camille Tullos¹²

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domesticated about 5,000–6,000 years ago and another, Przewalski's horse, *Equus ferus przewalskii*, remains wild and endangered. Asses exist in Asia as *Equus kiang* (kiangs) and *Equus hemionus* (Asian wild asses or onagers) and in Africa as wild asses (*Equus africanus*) whose domestication gave rise to donkeys (*Equus africanus asinus*).

Hippotigris¹³

Linnaeus took the common name *zebra* – derived from a Portuguese word meaning “wild ass” – and used it as the species name for the striped equine that lived in mountainous areas of southern Africa, *Equus zebra*. Boddaert and Gmelin distinguished this species from the partially striped equine of the plains, which they named *Equus quagga* – basing the name on the animal's barking call.¹⁴

Hippotigris, the name Romans gave to zebras, is used to denote a subgenus of *Equus* containing the three zebra species.¹⁵ It is thought that the ancestors of zebras diverged from the ancestors of asses approximately 1.7 to 2.0 million years ago and that the common ancestor of all Hippotigris species separated between 1.28 to 1.59 million years ago into the evolutionary lines leading to the currently recognized species: mountain zebras (*Equus zebra*), plains zebras, which includes quaggas (*Equus quagga*), and Grévy's zebras (*Equus grévyi*).¹⁶

Zebras occur from Ethiopia to South Africa in a variety of habitats from treeless grassland to savanna to open woodlands. They show a slight sexual dimorphism in body size, with stallions usually being a little longer, taller, and heavier than mares. Stallions have thicker necks and possess canine teeth that are used to bite predators and other stallions when fighting; canine teeth are reduced or absent in mares.

Zebras have a black dorsal stripe running from the mane to the tail and a black ventral stripe. Grévy's zebras and mountain zebras have black and white stripes over most of their bodies, although they are broader and fewer in the latter (Figure 1.2). Plains zebras have the fewest stripes, and these are variable in distribution and appearance. Striping characteristics are prominent in the criteria used to identify zebra species, and each animal has distinctive striping that enables even humans to recognize individual zebras. Striped, upright manes and a long tail that terminates in a brush of long hairs are other characteristic features.¹⁷

Zebras prefer to eat grass but will also browse some herbaceous plants and even parts of woody plants and geophytes (rhizomes and corms) if food is scarce. Their incisors crop vegetation and their high crowned premolar and molar teeth have hard surfaces to chew tough plant