

# The Micro-politics of Macromolecules in the Taxonomy and Restoration of Quaggas

PETER HEYWOOD

*Department of Molecular Biology, Cell Biology, and Biochemistry, Brown University*

*Quaggas, partially striped zebras from the Karoo, were a distinctive component of the South African fauna. They had dark stripes on their faces, necks and fore-bodies. Otherwise their bodies were unstriped, and the background colour of both the striped and unstriped upper parts of their bodies was chestnut. They were hunted extensively, and in the nineteenth century were increasingly excluded from grazing land and water. The Game Amendment Act of the Government of the Cape of Good Hope was intended to protect quaggas, as well as other fauna, but by the time of its passage in 1886 they were already extinct. Quaggas were given the binomial name *Equus quagga* in the eighteenth century and many viewed them as a species distinct from plains zebras. However, in 1984 the first DNA sequencing of an extinct organism demonstrated that quaggas were not a separate species but a subspecies of the plains zebra. This revised taxonomy made possible the Quagga Project in which selective breeding from plains zebras has resulted in animals termed 'Rau quaggas' whose bodies have reduced striping but which lack the chestnut background colour that is evident in most paintings of living quaggas. Rau quaggas now live in captivity in several locations in South Africa, and could help restore the ecology of damaged environments where quaggas once roamed. Both quagga DNA and the Quagga Project can be considered as 'boundary objects' that bring together a heterogeneous variety of stakeholders including scientists and hunters, nature lovers and commercial organisations. The successful micro-politics of the Quagga Project in negotiating with different bodies and in obtaining funding from diverse sources provides a model that could be emulated by conservation bodies.*

## Keywords

Boundary objects, *Equus quagga*, macromolecules, selective breeding, Quagga Project, Reinhold Rau

Three types of zebras existed in South Africa in the mid-nineteenth century.<sup>1</sup> In the southwest of the Cape Colony lived Cape mountain zebras. Plains zebras – formerly known as Burchell's zebras – were present in the north and east of the country. South of the Orange and Vaal rivers and especially in the Karoo (Fig. 1) were

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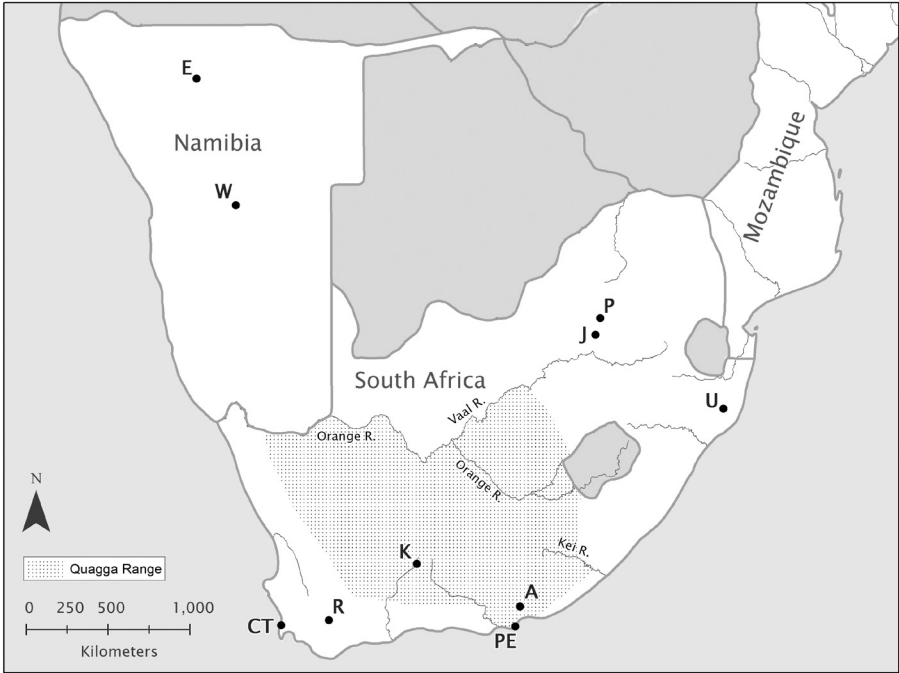


Figure 1: Some of the principal locations described in this paper. Plains zebras from Etosha National Park, Namibia (E), and Umfolozi Game Reserve, KwaZulu-Natal (U) were initially brought to Robertson, Western Cape (R). Rau quaggas are present in several locations, including Karoo National Park (K) and Addo Elephant National Park (A). Cities shown include Cape Town (CT), Johannesburg (J), Port Elizabeth (PE), Pretoria (P) and Windhoek (W). In historical times, quaggas ranged within the area shown shaded that includes parts of the contemporary provinces of the Western Cape, Eastern Cape, Northern Cape and Free State. Sources: L.C. Rookmaaker, *The Zoological Exploration of Southern Africa 1650–1790* (Rotterdam, Netherlands; Brookfield VT: Balkema, 1989), 287; C.J. Skead, *Historical Mammal Incidence in the Cape Province: The Eastern Half of the Cape Province, including the Ciskei, Transkei, and East Griqualand* (Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope, 1987), 568; and A.F. Boshoff and G.L.H. Kerley, 'Historical Mammal Distribution Data: How Reliable Are Written Records?', *South African Journal of Science*, 106, 1–2, 2010, 26–33.

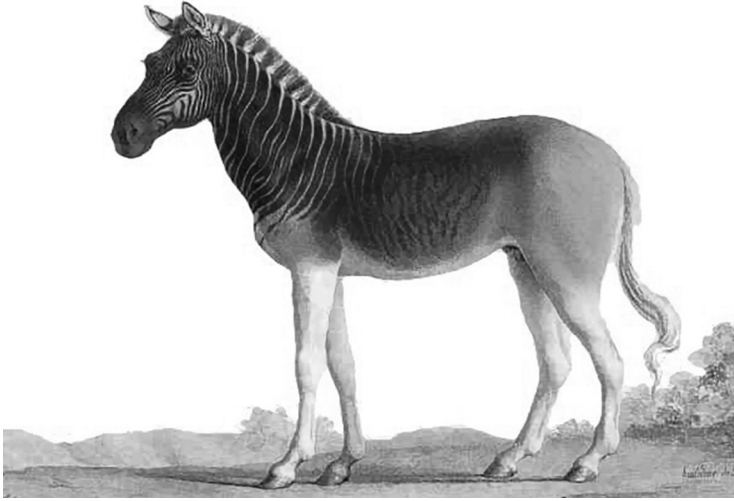


Figure 2: The coat colouration of quaggas is shown in this 1793 painting by Nicolas Marechal of the quagga stallion belonging to King Louis XVI and kept in the menagerie at Versailles, France. Source: Wikipedia Commons

quaggas, whose range overlapped with that of Cape mountain zebras. Mountain zebras and plains zebras survived while quaggas went extinct but have been restored, after a fashion.

In place of black stripes against a white background in most zebras, the face, neck and fore-body of quaggas had dark chestnut stripes against a lighter chestnut background (Fig. 2). Behind the shoulders, the stripes often broke up into spots or blotches and then were lost altogether as the contrast between the stripes and the background colour lessened progressively, giving the upper part of the hind-body a uniform chestnut tone that faded into the white of the unstriped legs and belly.

In 1785 Pieter Boddaert described quaggas and gave them the binomial name *Equus quagga*.<sup>2</sup> In 1788 Friedrich Gmelin also described them and gave them the same name – hence the unusual situation where either Boddaert or Gmelin are cited as the authority for the binomial name.<sup>3</sup> The name quagga and the corresponding Xhosa and Afrikaans names ‘iqwara’ and ‘kwagga’ are onomatopoeic – sounding like the zebra’s cry of ‘kwa-ha!’ Unfortunately, plains zebras have also sometimes been called quaggas, which has at times led to confusion in the historical record.<sup>4</sup>

Descriptions of living quaggas and preserved skins refer to the background colouration as being brown, dark brown, fawn, chestnut, pale red and reddish-brown.<sup>5</sup>

2 <http://www.biodiversitylibrary.org/item/89677#page/206/mode/1up>.

3 <http://babel.hathitrust.org/cgi/pt?id=nyp.33433059147615;view=1up;seq=7>.

4 R.E. Rau, ‘Revised List of the Preserved Material of the Extinct Cape Colony Quagga, *Equus quagga quagga* (Gmelin)’, *Annals of the South African Museum*, 65, 2, 1974, 41–87; C.J. Skead, *Historical Mammal Incidence in the Cape Province: The Eastern Half of the Cape Province, including the Ciskei, Transkei, and East Griqualand* (Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope, 1987), 564.

5 Rau, ‘Revised List’, 41; W.C. Harris, *Narrative of an Expedition into Southern Africa, During the Years 1836 and 1837* (Bombay: American Mission, 1838), 61, 378.

The chestnut background colour was a defining feature of quaggas: it is conspicuous in the quagga painted by Edwards in 1751 that serves as a type specimen (representative example) of quaggas for Gmelin's 1788 description of *Equus quagga*, where his Latin diagnosis refers to the colour as 'castaneus'.<sup>6</sup> The red colour is also visible in paintings by Nicolas Marechal (Fig. 2), Jacques-Laurent Agasse and Samuel Daniell.<sup>7</sup> Although the background red colouration is more muted in Harris's paintings of quaggas,<sup>8</sup> Bryden criticised this representation and noted that quaggas had a 'considerably darker' colour.<sup>9</sup> Photographs of mounted quagga skins from museums show a brownish or reddish-brown background on the upper parts of their bodies. Because taxidermy specimens fade,<sup>10</sup> it is reasonable to believe that the coats of living quaggas were even redder than these museum specimens.

The black and white stripes present in most zebras may have a selective advantage for social interactions, protection against flies and predators, and thermoregulation.<sup>11</sup> All of these possibilities have been suggested and there is still debate about the nature of the selective advantage, but black and white striping seems to confer some protection against biting flies.<sup>12</sup> The most detailed descriptions of the variety of coat colouration in plains zebras is by Larison and colleagues, who quantified striping in plains zebras and found that striping is correlated with temperature. They noted, however, that temperature itself might be tied to selection in complicated ways.<sup>13</sup>

Conditions in the Karoo, an arid upland region, are different from most zebra habitats. The colder conditions and absence of tsetse flies might have meant that stripes did not have a selective advantage, and so were reduced in quaggas – just as horses are postulated to have lost the stripes of their ancestors.<sup>14</sup> Concurrently, the chestnut basic colour might have provided a better camouflage against predators in the open country of the Karoo than black and white stripes.<sup>15</sup>

While the selective advantage of the coat colouration in quaggas is not certain, their social structure certainly aided survival: quaggas lived in a herd that often grazed with wildebeests (*Connochaetes taurinus*) and ostriches (*Struthio camelus*).<sup>16</sup> An alarm call from one animal would alert the others to danger. In other subspecies of plains zebras, family members will gather around a mare with a young foal to protect

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6 <http://babel.hathitrust.org/cgi/pt?id=nyp.33433059147615;view=1up;seq=7>.

7 [http://en.wikipedia.org/wiki/Quagga#mediaviewer/File:Agasse\\_Quagga.jpg](http://en.wikipedia.org/wiki/Quagga#mediaviewer/File:Agasse_Quagga.jpg). <http://commons.wikimedia.org/wiki/File:Quagga.jpg#mediaviewer/File:Quagga.jpg>. [https://commons.wikimedia.org/wiki/File:Daniell\\_Quagga.jpg](https://commons.wikimedia.org/wiki/File:Daniell_Quagga.jpg).

8 W.C. Harris, *Portraits of the Game & Wild Animals of Southern Africa*, vol 2 (Cape Town: A.A. Balkema, 1969), Plate 2.

9 H.A. Bryden, *Kloof and Karroo: Sport, Legend and Natural History in Cape Colony, with a Notice of the Game Birds, and of the Present Distribution of Antelopes and Larger Game* (London, New York: Longmans, Green, 1889), 401. <https://archive.org/details/travelsininteri00unkngoog>.

10 Elizabeth Nunan, *In Their True Colors: Developing New Methods for Recoloring Faded Taxidermy* in <http://intheirtruecolors.wordpress.com>; D. Barnaby, *Quaggas and Other Zebras* (Plymouth, UK: Basset, 1996), 65.

11 G.D. Ruxton, 'The Possible Fitness Benefits of Striped Coat Coloration for Zebras', *Mammal Review*, 32, 2002, 237–44.

12 A. Egri, M. Blahó, G. Kriska, R. Farkas, M. Gyukovszky, S. Ákesson and G. Horváth, 'Polarotactic Tabanids Find Striped Patterns with Brightness and/or Polarization Modulation Least Attractive: An Advantage of Zebra Stripes', *Journal of Experimental Biology*, 215, 5, 2012, 736–45. T. Caro, A. Izzo, R.C. Reiner Jr, H. Walker and T. Stankowich, 'The Function of Zebra Stripes', *Nature Communications*, 5, 2014, 3535.

13 B. Larison, R.J. Harrigan, H.A. Thomassen, D.I. Rubenstein, A.M. Chan-Golston, E. Li and T.B. Smith, 'How the Zebra Got Its Stripes: A Problem with Too Many Solutions', *Royal Society of Open Science*, 2, January 2015, 140452.

14 C. Darwin, *The Origin of Species* (London: Murray, 1859), 167.

15 Rau, 'Revised List', 41; R.I. Pocock, 'The Coloration of the Quaggas', *Nature*, 68, 1903, 356–7.

16 Harris, *Portraits of the Game*, 10.

them and probably quaggas did likewise.<sup>17</sup> Quaggas vexed by humans kicked and bit them, sometimes mortally, and undoubtedly would do the same with predators that attacked them.<sup>18</sup>

## Extinction

The large scale of hunting wildlife in southern Africa has been well documented.<sup>19</sup> In South Africa populations of zebras suffered terribly from this assault: by the 1930s less than one hundred Cape mountain zebras survived, and plains zebras were extirpated from a long swath of their range. But it was quaggas that suffered most. Nimrods such as Cornwallis Harris shot quaggas<sup>20</sup> and other 'game' in large numbers; sometimes they saved the hides and gave the meat to servants, but often carcasses were left to rot on the veld.

Others in South Africa shot quaggas for their hides, which were made into low-value items such as *veldschoen* (rough shoes) and bags for carrying grain, or were cut into *riempies* (strips) used to bind things together.<sup>21</sup> White South Africans apparently considered zebra meat 'unclean'<sup>22</sup> and gave it instead to Africans (today this cultural taboo against eating zebras seems to have diminished because their meat – praised for its low fat content – is now fashionable for human consumption in South Africa).<sup>23</sup> Clearly, there was little profit in shooting quaggas, 'whose flesh is carrion, and even whose hide is almost useless ... but man, when he has no other motive, delights to destroy for the mere sake of pastime.'<sup>24</sup> Whether the hunting was for meagre profit or sport, a person living near Colesberg in the 1840s, where there were still quaggas, reported that shots were fired almost every daylight hour.<sup>25</sup>

In the mid-nineteenth century farming expanded extensively into areas where quaggas lived;<sup>26</sup> this excluded them from grazing land and water sources, and exposed them to farmers' rifles. Nor did quaggas have any legal protection: between 1866 and 1870 there had been attempts to introduce legislation that would have protected game animals including quaggas, but none passed into law.<sup>27</sup>

The final blow to quaggas began in the 1860s, when their skins and the skins of other game gained the reputation for providing superior leather used in making expensive boots overseas. They became valuable commodities and people, 'at once

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17 R.D. Estes, *The Behaviour Guide to African Mammals* (Los Angeles: University of California Press, 1991), 240.

18 Harris, *Portraits of the Game*, 14.

19 J.M. MacKenzie, *The Empire of Nature: Hunting, Conservation and British Imperialism* (Manchester: Manchester University Press, 1997).

20 Harris, *Narrative of an Expedition*, 308.

21 C.J. Skead, *Historical Mammal Incidence in the Cape Province*, vol 1 (Cape Town: Department of Nature and Environmental Conservation, Cape Provincial Administration, South Africa, 1980), 352.

22 R.J. Gordon, P.E. Raper and M. Boucher. *Robert Jacob Gordon: Cape Travels, 1777 to 1786*, vol 2 (Houghton, South Africa: Brenthurst, 1988), 273.

23 *Independent* (South Africa), 23 July 2014.

24 T. Pringle, *Narrative of a Residence in South Africa* (London: Edward Moxon, 1840), 49.

25 R. Gordon Cumming, *The Lion Hunter in South Africa: Five Years of a Hunter's Life in the Far Interior of South Africa* (London: John Murray, 1855), 68.

26 W. Beinart, 'The Night of the Jackal: Sheep, Pastures and Predators in the Cape,' *Past and Present*, 158, 1998, 172–206.

27 L. van Sittert, 'Bringing in the Wild: The Commodification of Wild Animals in the Cape Colony/Province c. 1850–1950,' *Journal of African History*, 46, 2, 2005, 269–91.

set about the task of exterminating these animals.<sup>28</sup> The *New York Times* commented drolly on the effects of the quagga leather trade: ‘Animals which when dead are exceedingly valuable contract a habit of dying.’<sup>29</sup>

It is not known precisely when quaggas became extinct in the wild, although most authorities consider that this occurred in the 1870s. Their absence, however, caused concern and so (on 6 July 1886) the Government of the Cape of Good Hope passed the Game Amendment Act. Section 4 reads, ‘No person, however, shall be at liberty to pursue, shoot, kill, destroy, or capture any elephant, hippopotamus, buffalo, eland, koodoo, hartebeest, bontebok, blesbok, gemsbok, rietbok, zebra, quagga, Burchell zebra or any gnu or wildebeest of either variety, without having obtained a special permission to that effect from the Governor.’<sup>30</sup> The passage of this Act was too late for quaggas, however, as the last had died in the Amsterdam Zoo on 12 August 1883.

## After Extinction

The realisation that quaggas were extinct caused widespread sadness. Bryden offered one of the earliest statements of regret, ‘That an animal so beautiful, so capable of domestication and of use, and to be found not so long since in so great abundance, should have been allowed to be swept from the face of the earth, is surely a disgrace to our latter-day civilisation.’<sup>31</sup>

What remains of quaggas are 23 mounted skins (only one of which is in South Africa), a mounted head and neck, 7 skeletons and various bones including 13 skulls that were not part of skeletons.<sup>32</sup> It is not certain, however, that all the skulls belong to quaggas, as quagga skins were sometimes mounted on the skeletons of donkeys or horses.<sup>33</sup> Our knowledge of quaggas is based on these artefacts (some of which have provided DNA for analysis), together with paintings and illustrations, several photographs taken of a mare in the London Zoo, and the accounts of people who had observed these animals.

Extinction brought value to quaggas. Reports of a quagga’s skull valued at £25,000 in 1952 and a mounted plains zebra head offered for sale as a quagga’s head in 1974 suggests money to be made from quaggas, genuine or not.<sup>34</sup> Reports of quagga sightings into the mid-twentieth century in remote areas of South-West Africa (Namibia) were erroneous, but led to Lutz Heck, director of the Berlin Zoo, receiving an offer in the early 1950s to show him a herd of quaggas for a fee of £70, with all expenses

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28 Bryden, *Kloof and Karroo*, 401.

29 *New York Times*, 9 January 1887.

30 Editor, ‘Act for the Better Preservation of Game’, *African Wildlife*, 37, 4, 1983, 135.

31 Bryden, *Kloof and Karroo*, 402.

32 J. Comrie-Greig, ‘The Quagga and the Taxidermist’s Art’, *African Wildlife*, 37, 4, 1983, 141; Rau, ‘Revised List’, 41; R.E. Rau, ‘Additions to the Revised List of Preserved Material of the Extinct Cape Colony Quagga and Notes on the Relationship and Distribution of Southern Plains Zebras’, *Annals of the South African Museum*, 77, 2, 1978, 27–45.

33 E.H. Harley, C. Lardner, M. Gregor, B. Wooding and M.H. Knight, ‘The Restoration of the Quagga; 24 years of Selective Breeding’ in R. Slomski (ed), *Restoration of Endangered and Extinct Animals* (Poznan, Poland: Poznan University of Life Sciences Press, 2010), 78–87.

34 *Cape Argus* (South Africa), 8 March 1952; Skead, *Historical Mammal Incidence*, 567.



refunded if the quaggas proved not to be genuine.<sup>35</sup> The value accorded to a skull or mounted head might have inspired creative taxidermy, as in this extract from a 1935 letter sent by a London firm of taxidermists describing how they could simulate a quagga skin.

The markings we could reproduce fairly easily with stains and careful scorching. We believe the material to use for this would be the skin of one of your big donkeys... A hot weather coat from a White Donkey (South African) or White Mule, if such a thing exists, would be most suitable, and one might say it was still a South African product.<sup>36</sup>

There are no records of this sleight of hand being put into effect, but it speaks to the importance of South African identity – whether of a quagga or of a faux quagga. Might quaggas be restored by means other than ‘stains and careful scorching’?

### Restoration by Selective Breeding

Humans have used selective breeding for millennia to produce varieties of domestic animals and plants that often differ markedly from their wild relatives. Darwin’s ‘The Variation of Animals and Plants under Domestication’ contains many examples of human selection for particular characteristics, and some of these were achieved within a remarkably short time; for example, it took just five years of selective breeding to obtain an upright comb on a rooster.<sup>37</sup>

The first suggestion that it might be possible to breed animals with the coat colouration of quaggas from plains zebras occurred in a 28 May 1900 letter from J. Cossar Ewart, professor of natural history at Edinburgh University. Writing to Mr Tegetmeier, editor of *The Field*, Ewart commented on a ‘nearly white variety of Burchell’s zebra’ that had well marked stripes on its neck, and suggested, ‘Were a pair of white zebras isolated & protected [bred only with each other] a new quagga might be produced.’<sup>38</sup>

It was plains zebras with a different coat colouration, however, that caught the attention of Lutz Heck. While in Etosha National Park, South-West Africa in the early 1950s he had observed plains zebras with reduced striping and brown shadow stripes and wondered whether quaggas with their reduced striping and chestnut basic colour were also plains zebras.<sup>39</sup> If so, plains zebras similar to those at Etosha might serve as a founder population to obtain, by selective breeding, offspring with quagga-like coats. Lutz Heck was attuned to this possibility because he and his brother Heinz, director of the Hellabrunn Zoo in Munich, had used selective breeding in the 1930s and

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35 L. Heck, *Animal Safari: Big Game in South West Africa* (London: Methuen, 1956), 86.

36 Skead, *Historical Mammal Incidence*, 564.

37 C. Darwin, *The Variation of Animals and Plants under Domestication*, vol 2 (London: John Murray, 1868), 198.

38 D. Barnaby, *Letters to Mr Tegetmeier from J. Cossar Ewart and Others to the Editor of The Field at the Turn of the Nineteenth Century* (Sale, UK: ZSGM, 2004), 26.

39 Heck, *Animal Safari*, 84.

1940s to attempt to breed in Europe animals resembling tarpans (extinct ancestors of horses) and aurochs (extinct wild ancestors of cattle, noted for their large size).<sup>40</sup> The Heck brothers, working independently of each other in separate breeding projects, assembled breeding stocks of cattle types thought to be primitive, selected the most aurochs-like animals, bred them together, and then selected the most aurochs-like offspring for further breeding. Reichsmarschall Hermann Goering took a particular interest in these animals as he wanted aurochs to stock hunting estates in Eastern Europe. Although aurochs were not created, selectively-bred 'Heck cattle' that are said to have some resemblance to aurochs are still maintained.<sup>41</sup> More relevant to the restoration of quaggas was that in 1940 Heinz Heck had bred in Germany from less striped plains zebras a foal lacking stripes on its hind-body. This breeding stock was lost during the Second World War.<sup>42</sup>

For most of human history, selective breeding for particular characteristics was achieved without knowledge of genetics: breeding stock was selected according to its phenotype, usually its visible characteristics. In the mid-nineteenth century Gregor Mendel conducted his famous experiments on inheritance in peas, which demonstrated that traits such as seed colour were under control of genes that existed in alternative versions later termed 'alleles': a seed would have, for example, a yellow seed coat or a green seed coat depending on which alleles for coat colouration were present in the nuclei of its cells.

Selective breeding from plains zebras of animals whose coat colouration resembles that of quaggas could only be effective if the alleles of genes determining coat colouration in quaggas were still present in populations of plains zebras. But if quaggas and plains zebras were separate breeding populations then the alleles governing coat colouration could have been lost with the extinction of quaggas. Consequently the possibility of rebreeding quaggas rested on whether they were a subspecies of plains zebras, and, if this were the case, were the alleles governing coat colouration still present? Darwin, who had seen quaggas when *HMS Beagle* docked in South Africa, grappled with this very question about the status of zebra species, writing enigmatically in his notebook, 'We turn the zebra into the quagga, let them be wild in the same country with their own instincts (even though fertile-hybrids produced when compelled to breed) and then all that I want is granted.'<sup>43</sup> (If mating between closely related animal species occurs it may result in interspecific hybrids, but usually these are sterile – hence the line through 'fertile' in Darwin's notes. This is not always the case, however, and fertile interspecific hybrids of equines are now known to occur).<sup>44</sup>

As Darwin's reflections indicate, it is often difficult to determine what qualifies as a separate species. Early taxonomists recognised four species of zebras. Plains zebras,

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40 H. Heck, 'The Breeding-Back of the Aurochs', *Oryx*, 1, 3, 1951, 117–22.

41 E. Kolbert, 'Recall of the Wild: The Quest to Engineer a World before Humans', *The New Yorker*, 24 December 2012, 50–60.

42 Heck, 'Breeding-Back of the Aurochs', 117; E. Thamm, 'Rebirth of the Quagga', *African Wildlife*, 5, 3, September 1951, 209.

43 C. Darwin, 1838. Notebook C #145, <http://darwin-online.org.uk/content/frameset?keywords=quagga&pageseq=129&itemID=CUL-DAR122.-&viewtype=text>.

44 H. Jónsson, M. Schubert, A. Seguin-Orlando, A. Ginolhac, L. Petersen, M. Furnagalli and A. Albrechtsen, 'Speciation with Gene Flow in Equids Despite Extensive Chromosomal Plasticity', *Proceedings of the National Academy of Sciences*, 111, 52, 2014, 18655–60.



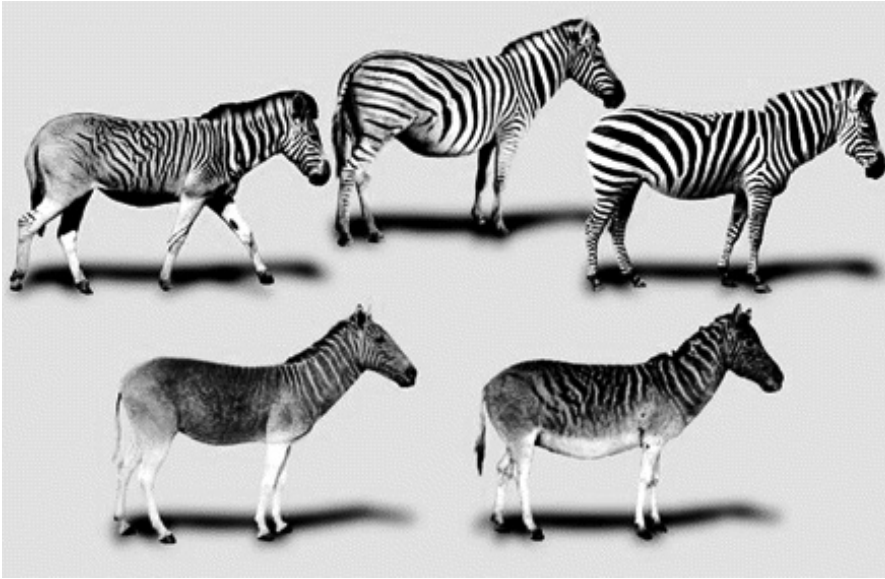


Figure 3: Coat variation in *Equus quagga*. Upper row right is a plains zebra with pronounced striping, including on its legs. Upper row middle is a plains zebra from the Etosha area, Namibia, with reduced striping and brown shadow stripes occurring within the white stripes of its hind body. Upper row left is a second-generation animal from the Quagga Project showing reduced striping on its legs and hind-body. Lower row illustrates variations in striping of quagga skins: at the left is the quagga from the museum in Munich, Germany, and at the right is the more heavily striped quagga from the Tring Museum, UK. Source: Fig. 1 in J.A. Leonard, N. Rohland, S. Glaberman, R.C. Fleischer, A. Caccone, and M. Hofreiter, 'A Rapid Loss of Stripes: The Evolutionary History of the Extinct Quagga', *Biology Letters*, 1, 3, 2005, 291–5. Republished by permission of the Royal Society

also known as 'Burchell's zebras' and so given the binomial name *Equus burchelli*, are the most numerous and consequently are sometimes called 'common zebras'. Quaggas held the status of a separate species and were given the binomial name *Equus quagga*. The third species, *Equus zebra*, has two subspecies, Cape mountain zebras in South Africa and Hartmann's mountain zebras in Namibia. Grévy's zebra, *Equus grevyi*, is restricted to Ethiopia and Kenya and is the largest and most striped species. In spite of a difference in chromosome number between *Equus grevyi* and *Equus quagga*, the two species are able to mate and produce fertile offspring.<sup>45</sup>

Most definitions of species include the criteria that they are natural populations of organisms able to interbreed to produce fertile offspring,<sup>46</sup> but these criteria are not useful in this instance as there are neither records of quaggas and plains zebras breeding, nor records of them failing to breed. Without these data, could comparative morphology answer the questions about species status? The most striking morphological characteristic was, of course, coat colouration. Based on this feature, both Boddart

45 J.E. Cordingley, S.R. Sundaresan, I.R. Fischhoff, B. Shapiro, J. Ruskey and D.I. Rubenstein, 'Is the Endangered Grevy's Zebra Threatened by Hybridization?', *Animal Conservation*, 12, 6, 2009, 505–13.

46 E. Mayr, 'What Is a Species, and What Is Not?', *Philosophy of Science*, 63, June 1996, 262–77.

and Gmelin recognised quaggas as a species separate from the plains zebras,<sup>47</sup> and this view persisted among some biologists until late in the twentieth century.

Others, notably Rau, a taxidermist at the South African Museum, and Selous, a hunter and naturalist, argued that quaggas were not a separate species but the most southern form of plains zebras.<sup>48</sup> They observed that over their vast range from Ethiopia through Central Africa to South Africa, plains zebras show a gradual transition, or cline, in coat colouration, with quaggas having been the most southerly form:

Burchell's zebras [plains zebras] ... appear to have attained their maximum of striping in the well-watered, forest-clad portions of Central and Eastern Africa, and to have become less richly marked as they extended southwards and westwards into countries where the forests grew scarcer and the climate drier, culminating in the poorly striped quagga of the Cape Colony, which appears to me to be the extreme southerly form of the various races of Burchell's zebra [plains zebras].<sup>49</sup>

The most heavily striped plains zebras occur near the northern end of their range and have distinct black stripes on a white background over their entire bodies,<sup>50</sup> as in the zebra at the upper right of Fig. 3. Progressing in a southern direction over the length of the cline, stripes become fewer, browner, and thinner; concurrently, brown 'shadow stripes' become conspicuous in the white background,<sup>51</sup> as in the zebra in the middle of the upper row of Fig. 3. In some plains zebras, brown shadow stripes occur against a background that is light brown rather than white. Quaggas can be seen as the extreme southern form of coat colouration in which the stripes were browner and absent from the legs and hind-body. At the same time, the white between the dark stripes was lost as the brown of the shadow stripes became redder and occupied all the spaces between the dark stripes. Behind the shoulders the stripes were lost altogether as the contrast between the stripes and the background colouration gave way to a uniform chestnut colouration of the hind-body.<sup>52</sup>

Clearly, there were very different views of coat colouration and so this feature could not resolve whether quaggas were a separate species or merely the least-striped plains zebras. Might other morphological studies resolve this issue? Careful comparative studies of skull morphology, however, yielded conflicting conclusions. Analysing 23 cranial dimensions from four quagga skulls of undoubted provenance, and comparing these dimensions with those from skulls of various *Equus* species, Klein and Cruz-Uribe determined that plains zebras and quaggas differed to approximately the

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47 <http://www.biodiversitylibrary.org/item/89677#page/206/mode/1up>; <http://babel.hathitrust.org/cgi/pt?id=nyp.33433059147615;view=1up;seq=7>.

48 F.C. Selous, 'Burchell's Zebra' in HA Bryden (ed), *Great and Small Game of Africa: An Account of the Distribution, Habits, and Natural History of the Sporting Mammals, with Personal Hunting Experiences* (London: Rowland Ward, 1899), 79–84; Rau, 'Revised List', 41.

49 Selous, 'Burchell's Zebra', 79

50 Rau, 'Revised List', 41, Larison et al, 'How the Zebra Got Its Stripes', 140452.

51 Ibid.

52 Rau, 'Revised List', 41.

same degree as plains zebras and mountain zebras.<sup>53</sup> As the latter two are regarded as separate species, these findings argue that quaggas might be a different species from plains zebras. This conclusion was in contrast to measurements showing a closer resemblance between quagga skulls and plains zebra skulls than between quagga skulls and mountain zebra skulls.<sup>54</sup> Studies of dentition provided starkly different conclusions even when conducted by the same scientist: in 1988 Thackeray concluded that quaggas may have been a subspecies of the plains zebra, whereas in 1997 he determined that mountain zebras and plains zebras were more similar to each other than either was to quaggas.<sup>55</sup> It is noteworthy that four morphological studies with different conclusions were published after the molecular studies described below that, for most scientists, decisively answered the question of quagga taxonomy.

## Taxonomy Revised

Reinhold E. Rau at the South African Museum in Cape Town (now the Iziko South African Museum) provided the means to resolve the impasse about species status. Rau (1932–2006) was a taxidermist born near Frankfurt-am-Main, Germany. His childhood fascination with nature led to training as a taxidermist and employment at the South African Museum in Cape Town beginning in 1951 where, among other accomplishments, he rediscovered a species of tortoise thought to be extinct which led to the establishment of a reserve for it. Rau was described as ‘a scientific educator, whose aim was to involve people in the joys of scientific exploration and discovery’, and it was observed that he ‘was responsible for the appointment and training of taxidermists from disadvantaged backgrounds’.<sup>56</sup>

As a schoolboy, Rau saw one of Heck’s cattle and was impressed with the idea that selective breeding might be used to restore extinct animals. As a taxidermist, he remounted the skin of a quagga foal at the South African Museum and the skins of three quaggas exhibited at the Natural History Museum in Mainz, Germany. He became passionately interested in quaggas, and pondered both their fate and the possibilities of restoring them, ‘The quagga became extinct through man’s ignorance and greed. It wasn’t a natural occurrence. It is our moral duty to rectify that mistake.’<sup>57</sup>

Much of what follows derives from Rau’s unpublished account of his attempts to gather support from people and organisations to restore quaggas from plains zebras.<sup>58</sup> (I use the term ‘restoring’ as the one used by Eric Harley of the Quagga Project.<sup>59</sup>

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53 R.G. Klein and K. Cruz-Uribe, ‘Craniometry of the Genus *Equus* and the Taxonomic Affinities of the Extinct South African Quagga’, *South African Journal of Science*, 95, 2, 1999, 81–6.

54 V. Eisenmann and J.S. Brink, ‘Koffiefontein Quaggas and True Cape Quaggas: The Importance of Basic Skull Morphology’, *South African Journal of Science*, 96, 9/10, 2000, 529–33.

55 J.F. Thackeray, ‘Zebras from Wonderwerk Cave, Northern Cape Province, South Africa: Attempts to Distinguish *Equus burchelli* and *E. quagga*’, *South African Journal of Science*, 84, 2, February 1988, 99–101; J.F. Thackeray, ‘Morphometric, Palaeoecological and Taxonomic Considerations of Southern African Zebras: Attempts to Distinguish the Quagga’, *South African Journal of Science*, 93, 2, February 1997, 89–93.

56 *Cape Towner*, 2 March 2006.

57 *Los Angeles Times*, 30 August 1998.

58 R. Rau, ‘Rough Road Towards Re-Breeding the Quagga: How It Came About’ (Unpublished manuscript, 1999, indexed as z.30.9.65, Iziko South African Museum Library, 1999).

59 Harley et al, ‘Restoration of the Quagga’, 78.

Other terms used include 'rebreeding', 'breeding back', 'back breeding', 'retrieving' and 'recreating'.) Beginning in 1975, Rau wrote to scientists and administrators advocating restoring quaggas from plains zebras that most resembled quaggas. In order to obtain permission and funding for this venture, however, he had to demonstrate that the two zebras were conspecific, that is, that they were the same species. Rau, who had obtained quagga tissue while remounting a museum specimen, in 1979 contacted an authority on zebras, W.F.A. Ansell of the National Parks and Wildlife Service in Chilanga, Zambia, to enquire whether tests on this preserved tissue would determine whether quaggas were conspecific with plains zebras. Ansell's response was not encouraging, 'Unfortunately, as I suspected would be the case, there does not seem to be any meaningful cytological tests that could be carried out on such long dead material.'<sup>60</sup>

An opportunity presented itself from California in 1981 when Oliver Ryder of the San Diego Zoo contacted Rau with a request for blood and other tissues from zebras. Rau sent him tissue from the quagga specimen in the Mainz museum which Ryder divided between Jerold Lowenstein at the University of California, San Francisco (who analysed its proteins) and Russell Higuchi and colleagues at the University of California, Berkeley (who analysed its DNA). Lowenstein and Ryder determined that proteins from quagga tissue more closely resembled those of the plains zebra than those of the mountain zebra (*E. zebra*) or of Grévy's zebra (*E. grevyi*).<sup>61</sup>

Higuchi and his colleagues extracted DNA from mitochondria occurring in muscle tissue removed from a quagga skin. Mitochondria are small cellular structures that generate most of an animal's energy, and contain multiple copies of a DNA molecule. Mitochondrial DNA mutates at a higher rate than nuclear DNA and this creates changes in the order (sequence) of four chemical groups termed 'bases' that occur along the length of DNA molecules. Comparison of the sequence of bases in the corresponding portions of DNA of different organisms that arose from a common ancestor can be used as a measure of similarity or difference between those organisms. Higuchi and colleagues analysed the sequence of bases in two short lengths of mitochondrial DNA of a quagga, and then compared this with the base sequences from corresponding parts of the mitochondrial DNA of plains zebras. This molecular comparison showed a close relationship between quaggas and plains zebras.<sup>62</sup>

Some queried whether this short segment of mitochondrial DNA could permit this conclusion about a close relationship between quaggas and plains zebras.<sup>63</sup> While the 229 bases of DNA sequenced in quaggas was only a small part of the total mitochondrial DNA, which is approximately 16,600 bases long in zebras,<sup>64</sup> it is

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60 Rau, 'Rough Road', 2.

61 J.M. Lowenstein and O.A. Ryder, 'Immunological Systematics of the Extinct Quagga (Equidae)', *Cellular and Molecular Life Sciences*, 41, 9, 1985, 1192-3.

62 R. Higuchi, B. Bowman, M. Freiberger, O.A. Ryder and A.C. Wilson, 'DNA Sequences from the Quagga, an Extinct Member of the Horse Family', *Nature*, 312, 15 November 1984, 282-4; R.G. Higuchi, L.A. Wrischnik, E. Oakes, M. George, B. Tong and A.C. Wilson, 'Mitochondrial DNA of the Extinct Quagga: Relatedness and Extent of Postmortem Change', *Journal of Molecular Evolution*, 25, 4, 1987, 283-7.

63 Klein and Cruz-Urbe, 'Craniometry', 81.

64 M. George, and O.A. Ryder, 'Mitochondrial DNA Evolution in the Genus Equus', *Molecular Biology and Evolution*, 3, 6, 1986, 535-46.

significant that over this length it differed from plains zebra DNA by only two bases, whereas it differed from *Equus zebra* DNA by 12. Even this two-base difference may have originated due to postmortem changes in DNA and, if this were the case, then the 229 bases of DNA would be identical between quaggas and plains zebras.<sup>65</sup> A later study that examined longer sequences of mitochondrial DNA extracted from 13 quagga museum specimens – mainly skins but also from a bone fragment and a tooth – confirmed the similarity between mitochondrial DNA from quaggas and plains zebras.<sup>66</sup>

The mitochondrial DNA of an organism is termed its mitochondrial genome. This is the smaller of two genomes in animal cells, the larger being the nuclear genome which contains almost all the genes of an animal. Modern technologies have provided DNA sequence data for mitochondrial and nuclear genomes of all extant (living) *Equus* species and quaggas. These studies indicate that there is little difference between the DNA of quaggas and plains zebras, hence confirming that they are conspecific.<sup>67</sup>

DNA sequencing convinced taxonomists that quaggas and plains zebras belong to the same species, *Equus quagga*. In these circumstances, the International Code of Zoological Nomenclature can be used to make corrections to taxonomy using priority as a guiding principle. Because Boddaert and Gmelin had given valid descriptions and a binomial name for quaggas before plains zebras were given their binomial name in 1824,<sup>68</sup> the name *Equus quagga* had priority and, as a result of these DNA studies, is now accepted as the binomial name for all plains zebras, including the lesser striped subspecies of the Karoo<sup>69</sup> (the other species of zebras, *Equus grevyi* and *Equus zebra*, are unaffected by this reclassification).

Taxonomists have provided ways to acknowledge the variation within plains zebras. Extinct quaggas as a subspecies of the plains zebra are given the trinomial designation of *Equus quagga quagga*. Five extant subspecies of *Equus quagga* are recognised: *Equus quagga boehmi* (Boehm's zebra or Grant's zebra), *Equus quagga borensis* (half-maned zebra), *Equus quagga chapmani* (Chapman's zebra), *Equus quagga crawshayi* (Crawshay's zebra) and *Equus quagga burchelli* (Burchell's zebra).<sup>70</sup> (With the recognition that *Equus burchelli* is no longer a valid name for the plains zebra, 'Burchell's zebra' should not be used to designate the species, and should only be applied to the subspecies *Equus quagga burchelli*). *Equus quagga burchelli*, which occurs at the southern end of the plains zebra's range, declined in numbers during the nineteenth century but still exists in Namibia and KwaZulu-Natal; it is the subspecies

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65 Higuchi et al, 'Mitochondrial DNA', 283.

66 J.A. Leonard, N. Rohland, S. Glaberman, R.C. Fleischer, A. Caccone and M. Hofreiter, 'A Rapid Loss of Stripes: The Evolutionary History of the Extinct Quagga', *Biology Letters*, 1, 3, 2005, 291–5.

67 Jónsson et al, 'Speciation', 18655.

68 <http://www.biodiversitylibrary.org/item/89677#page/206/mode/1up>; <http://babel.hathitrust.org/cgi/pt?id=nyp.33433059147615;view=1up;seq=7>.

69 C.P. Groves and C.H. Bell, 'New Investigations on the Taxonomy of the Zebras Genus *Equus*, Subgenus *Hippotigris*', *Mammalian Biology*, 69, 2004, 182–96.

70 Groves and Bell, 'New Investigations', 2004.

that, with its reduced striping and brown shadow stripes, most closely resembles *Equus quagga quagga*.<sup>71</sup>

The experiments by Higuchi and his co-authors had a significance which went far beyond quaggas. The demonstration that intact DNA could be obtained from tissue that had been dried and stored at room temperature for more than one hundred years showed that DNA has a remarkable resistance to harsh treatment and could be recovered from very old specimens; for example, DNA from a horse bone that was 560,000 to 780,000 years old and that had been preserved in permafrost has been sequenced.<sup>72</sup> By the late twentieth century, research in molecular biology was increasing at the very time that research in taxonomy, already an old discipline when Linnaeus transformed it in the eighteenth century, was declining. Now the old and new sciences were brought together: the science of paleogenomics was born, and a new term, aDNA, for ancient DNA, was coined.

Base sequences from ancient DNA can be compared with DNA base sequences from living organisms to throw light on evolutionary history. Such studies have shown that plains zebras originated about 1.1 million years ago, and that quaggas diverged from other plains zebras as little as 233,000 to 356,000 years ago.<sup>73</sup> During this period the climate of the Karoo underwent major changes,<sup>74</sup> which would have altered its environments and might have selected for the coat characteristics of quaggas.

## The Politics of Restoration

The demonstration that quaggas are a subspecies of plains zebras meant that their restoration should be possible, but it left open the question of whether there was reason to pursue this venture, and opinions on this matter were divided. In 1975 the Natal Parks Board replied to Rau's ideas for quagga restoration: 'The answer is that we consider the proposal to breed a quagga-like animal to be merely an academic exercise of very dubious conservation value'.<sup>75</sup> In contrast, however, Rau received encouraging letters from three biologists to whom he had explained his ideas for restoration, G.L. ('Butch') Smuts and Banie L. Penzhorn (authorities on zebras) and Uys de V. Pienaar (described by Rau as 'a well known South African zoologist'). The latter wrote in 1977, 'we should be successful in breeding back a true likeness of the extinct quagga in a relatively short space of time. A project of this nature could have tremendous prestige value not only for the Parks Board but also for the country'.<sup>76</sup> But in 1981 Pienaar's suggestion to the Parks Board 'to selectively breed plains zebras to produce an animal resembling the extinct quaggas' was rejected. Likewise, the National Zoological Gardens of South Africa in 1982 and the Endangered Wildlife

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71 Rau, 'Revised List', 41; Rau, 'Additions to the Revised List', 27; Rau, 'Rough Road', 2.

72 L. Orlando, A. Ginolhac, G. Zhang, D. Froese, A. Albechtsen, M. Stiller and M. Schubert, 2013, 'Recalibrating *Equus* Evolution Using the Genome Sequence of an Early Middle Pleistocene Horse', *Nature*, 499, 7456, 2013, 74–8.

73 Jónsson et al, 'Speciation', 18655.

74 M.E. Meadows and M.K. Watkeys, 'Paleoenvironments' in W.R.J. Dean and S. Milton (eds), *The Karoo: Ecological Patterns and Processes* (Cambridge: Cambridge University Press, 1999), 35.

75 Rau, 'Rough Road', 2.

76 Ibid.



Trust in 1983 both rejected Rau's restoration proposal. These organisations cited lack of funds as their reasons, rather than reservations about the restoration project itself.

Rau had examined the coat colouration of many of the quagga specimens in museums and had noted the similarity between these and the plains zebras in Etosha National Park, Namibia, and KwaZulu-Natal.<sup>77</sup> Consequently, he determined to use animals from these locations as a founder population for restoration of quaggas. In 1985, however, the authorities in Namibia rebuffed his request for animals: 'This Directorate regards your proposed project on the extinct quagga as academic and of little importance to conservation ... we regret to inform you that we cannot make any Burchell's zebra available to you.'<sup>78</sup>

The tide turned, however, when it became known that DNA and protein analysis of quagga tissue indicated that quaggas were conspecific with plains zebras. Additionally, J.F. Warning, a retired veterinarian from Somerset West who was knowledgeable about horse breeding, rallied support for Rau's cause. This led to a meeting in 1985 between Rau, scientists from the University of Cape Town and officials of Nature Conservation, who were encouraging about Rau's proposals to restore quaggas and even offered accommodation for the zebras at the Vrolijkheid Nature Conservation Station belonging to the Cape Department of Nature and Environmental Conservation near Robertson, Western Cape. Further success followed on 20 March 1986 when Rau and five others met with M.A. Cluver, director of the South African Museum, when it was agreed that the South African Museum would support 'The Quagga Breeding Programme', later named the 'Quagga Project'.<sup>79</sup> The seven people present at the 20 March 1986 meeting constituted – together with Warning and Harley, who were not at the meeting – the 'Quagga Experimental Breeding Committee'.

## The Quagga Project

In March 1987, Rau and a capture team from the Department of Nature Conservation and Tourism of Namibia sought plains zebras with reduced striping and conspicuous brown shadow stripes at Etosha National Park, Namibia. This exercise proved to be stressful for all involved: an unspecified number of zebras died after capture, Rau was unimpressed with the colouration of zebras that had already been captured for him, and 'The capture team became disenchanted with me not liking most of the animals which were pointed out to me as "good."<sup>80</sup> Nine captured zebras were brought from Etosha to the Vrolijkheid Nature Conservation Station. The cost of the animals and their transport was borne by the South African Nature Foundation. These animals were joined by plains zebras from the Umfolozi Game Reserve in KwaZulu-Natal to form a founder population of 18 animals for the selective breeding programme. In 1993 zebras were moved away from Vrolijkheid to other locations that provided better

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77 Rau, 'Revised List', 41; Rau, 'Additions to the Revised List', 27; Rau, 'Rough Road', 2.

78 Ibid, 5.

79 <http://www.quaggaproject.org>.

80 Rau, 'Rough Road', 9.



Figure 4: Undated photograph of a fifth-generation Rau quagga from the Quagga Project born on 10 December 2013. This photograph is the property of and copyright to the Quagga Project Association, and is reproduced with their permission

grazing, including land in Cape Town overlooking Groote Schuur Hospital. In 1998, 14 Quagga Project zebras were donated to the South African National Parks Board and were resettled in the Karoo National Park.<sup>81</sup>

In 1868 Darwin had summarised the approach of breeders whose work had given rise to many of the varieties of domestic plants and animals: ‘Methodical selection is that which guides a man who systematically endeavours to modify a breed according to some predetermined standard.’<sup>82</sup> The ‘predetermined standard’ defining the ‘Quagga Project Management/Action Plan’ of January 2005 calls for ‘selectively breeding zebra with quagga-like characteristics’ and then features a list of six: ‘Decreased body stripes; Body stripes not extending to the ventral midline; A chestnut basic colour on unstriped, upper parts of the body; Unstriped legs; Unstriped tail; Reddish muzzle.’<sup>83</sup> The latter characteristic, which does not appear to be mentioned elsewhere, is puzzling because Cornwallis Harris in his detailed description of quaggas described their muzzles as being black.<sup>84</sup>

Beginning with animals chosen for their reduced striping, selecting the least-striped of their offspring for further breeding, and repeating this selection in subsequent generations has led to fourth-generation progeny with reduced striping of the legs and hind-bodies when compared to the founder population,<sup>85</sup> but with no significant reduction in striping of the necks and fore-bodies. A fifth generation foal was born on 10 December 2013 (Fig. 4), but it is too soon to know if coat colouration in the fifth generation will differ significantly from that in the fourth generation.

81 D. Barnaby, ‘The Karoo Receives Plains Zebras from the Quagga Project’, *International Zoo News*, 46, 2, 1999, 94–8.

82 Darwin, *Variation*, 163.

83 <http://www.quaggaproject.org/quagga-coordination.htm>. Although this plan is labelled ‘draft’, there is no other version on the Quagga Project website.

84 Harris, *Narrative of an Expedition*, 378.

85 Harley et al, ‘Restoration of the Quagga’, 78; R. Parsons, C. Aldous-Mycock and M.R. Perrin, ‘A Genetic Index for Stripe-Pattern Reduction in the Zebra: The Quagga Project’, *South African Journal of Wildlife Research*, 37, 2, 2007, 105–116; <http://www.quaggaproject.org/Quagga-Graphic-Elements/PhotoGallery/PhotoGallery/slide.html>.

As of February 2015, the Quagga Project listed 119 animals at ten locations. The Quagga Project, which has been a Section 21 non-profit company since 2008, registered the name 'quagga' as a trade and certification mark to prevent others from profiting by producing quaggas.<sup>86</sup> The Quagga Project now refers to restored quaggas as 'Rau quaggas'. This name acknowledges Rau's central role in the restoration of the animal and also serves to distinguish the animals from extinct quaggas. This is important, because populations of Rau quaggas have some different characteristics from populations of extinct quaggas; for example, the dimensions of cranial bones differed between extinct quaggas and extant plains zebras.<sup>87</sup> In the absence of selection for cranial bone dimensions, it is reasonable to assume that the dimensions of these bones in Rau quaggas will resemble those of the plains zebras from which they were derived, and will differ from those of extinct quaggas.

Other differences probably existed between Rau quaggas and extinct quaggas. Quaggas evolved in the arid conditions of the Karoo for at least 233,000 years<sup>88</sup> and so may well have evolved adaptations that differed from those in the plains zebra. This possibility had been suggested in 1951 by B. Lundholm, who observed that restored quaggas would be similar only in coat colour, not in physiology.<sup>89</sup> The point was later made more dramatically: 'Just because a man may look like Napoleon, that does not make him Napoleon.'<sup>90</sup> The Quagga Project, however, counters this criticism by noting that, 'since extant Plains Zebras occupy habitats of similar degree of aridity to those of the Quagga, there is no sound reason for proposing significant adaptive features of the Quagga to its original habitat'. There was not, however, a single 'original habitat': the Karoo occupies more than one quarter the area of South Africa and over its extent it varies in both topography and climate with annual rainfall decreasing from approximately 500mm in the eastern Karoo to below 100mm in the west.<sup>91</sup> Even more significantly, these habitats have varied over time: there were periods when the whole region was drier and colder than at present. For example, about 21,000 to 16,000 years ago which corresponded with maximum glaciation in Europe, temperatures were 5 to 6 degrees Celsius cooler in the Karoo than at present, while from 7000 to 6500 years ago temperatures may have exceeded those of the present. Precipitation varied too, with heavier rainfall from 16,000 to 13,000 years ago causing a lake to form east of Kimberley.<sup>92</sup> Recent evolution of animals has occurred in environments that have always been changing,<sup>93</sup> and this is certainly true for quaggas of the Karoo. It is possible that quaggas evolved adaptations to these former conditions and so had selection for alleles that are not present, or only at low frequencies, in other subspecies of plains zebras.

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86 *Farmer's Weekly* (South Africa), 21 March 2014.

87 Klein and Cruz-Urbe, 'Craniometry', 81.

88 Jónsson et al, 'Speciation', 18655.

89 B. Lundholm, 'Is Rebirth of the Quagga Possible?', *African Wildlife*, 5, 3, September 1951, 209–12; Thamm, 'Rebirth of the Quagga', 209.

90 Peter van Bree, quoted in *New York Times Magazine*, 1 January, 2006.

91 W.R. Siegfried, 'Human Impacts' in Dean and Milton (eds), *Karoo*, 239–41.

92 Meadows and Watkeys, 'Paleoenvironments', 36, 37.

93 H. Ritvo, *Noble Cows and Hybrid Zebras: Essays on Animals and History* (Charlottesville: University of Virginia Press, 2010), 207.

It has been asserted that ‘The only characters that have been used to identify the quagga are its coat-pattern characteristics. Therefore, if within successive generations of selective breeding, animals with these characteristics are obtained, they will, by implication, be quaggas, as they will possess the same assemblage of coat-pattern genes as the original quagga.’<sup>94</sup> This claim does not acknowledge that coat colouration could not determine the quagga’s specific status: based on coat colouration, Boddaert, Gmelin and many others into the twentieth century drew now-outdated taxonomic conclusions.<sup>95</sup> Molecular information was key to the inception of the Quagga Project: it was only when non-coat characteristics (proteins and DNA) were analysed that quagga were shown to be a subspecies of the plains zebra. This anonymous author also overlooks the range of striping and coat coloration that occurred within quagga populations: there was not an ‘original quagga’ but a variable population of quaggas whose coat colouration varied:<sup>96</sup> the specimen in the Munich Museum has stripes confined to its head and neck, whereas the specimen in the Tring Museum has stripes over its head, neck and much of its body (Fig. 3), as does the type specimen for *Equus quagga*.<sup>97</sup> As the Quagga Project Committee noted, ‘It is evident from the 23 preserved skins of the extinct quagga, that the former population displayed great individual variation.’<sup>98</sup>

The Quagga Project has addressed the question of how closely Rau quaggas resemble extinct quaggas,

It has been argued that there might have been other non-morphological, genetically-coded features (such as habitat adaptations) unique to the Quagga and that therefore, any animal produced by a selective breeding programme would not be a genuine Quagga. Since there is no direct evidence for such characters and since it would be impossible now to demonstrate such characters were they to exist, this argument has limited value. The definition of the Quagga can only rest on its well-described morphological characteristics and, if an animal is obtained that possesses these characters, then it is fair to claim that it is a representative of, at least, the visible Quagga phenotype.<sup>99</sup>

This statement is now out of date because sequencing of the entire genome of quaggas means that genetically coded features can now be investigated; in fact, selection for a particular nuclear gene has already been demonstrated in quaggas.<sup>100</sup> And the ‘morphological characteristics’ used to define quaggas are confined to coat

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94 Anon, ‘Update on the quagga project’, *African Wildlife*, 52, 2, 1998, 9.

95 <http://www.biodiversitylibrary.org/item/89677#page/206/mode/1up>; <http://babel.hathitrust.org/cgi/pt?id=nyp.33433059147615;view=1up;seq=7>.

96 Rau, ‘Revised List’, 41; Rau, ‘Additions to the Revised List’, 27.

97 <http://www.biodiversitylibrary.org/item/89677#page/206/mode/1up>.

98 Quagga Project Committee, ‘Quagga Breeding Project: The Aim’, *Mane*, 4, March 1997, 2.

99 <http://www.quaggaproject.org/quagga-criticism.htm>.

100 Jónsson et al, ‘Speciation’, 18655.

colouration: ‘since the coat-pattern characteristics are the only criteria by which the Quagga is identified, re-bred animals that demonstrate these coat-pattern characteristics could justifiably be called Quaggas.’<sup>101</sup>

Yet ‘a chestnut basic colour on unstriped, upper parts of the body’ has not been achieved, and this was one of the most characteristic features of quaggas. As the Quagga Project website notes, ‘Background colour estimates have so far shown no progressive change over time.’<sup>102</sup> However, an anonymous reviewer of an earlier draft of this text observed in 2015, ‘we have, with the appearance of Rau quaggas, noticed an increase in the background brown colour such that this is similar to the least brown of the museum quagga skin specimens; it is as if the pigment in the stripes has smeared out to give a uniform brown colour.’

Is it accurate, then, to state that Rau quaggas have the coat-pattern characteristics of extinct quaggas? Evidently, this question has been considered because the Quagga Project website in referring to a photograph of ‘one of our better third generation animals’ notes, ‘The background brown colour is not so well developed as in either museum example [these examples were the mounted quagga skins at the museums in Munich and Tring, featured in Fig. 3], but this is such a variable feature in the museum specimens (of which there are 24 in all), that this is only a secondary concern for the project.’<sup>103</sup> This wording is a noteworthy shift from a ‘chestnut basic colour’ being a ‘quagga characteristic’ in the 2005 Quagga Project Management/Action Plan to the statement that a ‘brown colour’ is ‘only a secondary concern for the project.’ The issue of background colour is addressed in a somewhat different way in a recent paper: ‘The background colour, being so difficult to quantify in both museum quaggas as well as living project animals, will not be a defining criterion for the term “Rau quagga”, but will continue to be an objective in the breeding process, and animals with the darkest background colouration will claim priority in the ranking of Rau quaggas.’<sup>104</sup> This is a reasonable conclusion, and it is to be hoped that the attractive chestnut coat colouration can be achieved in future Rau quaggas.

Changes in coat colouration could have conferred an adaptive advantage on quaggas, as discussed earlier, or they may have occurred as a result of random genetic drift – a process that has been postulated to drive some evolutionary change<sup>105</sup> – or through a combination of the two.<sup>106</sup> Common to all these possibilities are the requirements for alleles that will confer a chestnut colour to the body.

The assumption behind the selective breeding of Rau quaggas from plains zebras with pronounced brown shadow stripes appears to be that the alleles producing shadow striping are the same as those that produced the chestnut background colour of quaggas. But suppose that this is not the case. If a mutation in an ancestral population of quaggas gave rise to the chestnut background colour of their bodies, then alleles

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101 <http://www.quaggaproject.org/quagga-objectives.htm>.

102 <http://www.quaggaproject.org/what-is-quagga.htm>.

103 <http://www.quaggaproject.org/what-is-quagga.htm>.

104 Harley et al, ‘Restoration of the Quagga’, 80.

105 M. Kimura, *The Neutral Theory of Molecular Evolution* (Cambridge: Cambridge University Press, 1983).

106 Gisella Caccone, <http://news.yale.edu/2005/09/26/how-zebra-lost-its-stripes-rapid-evolution-quagga>.

for the chestnut background coat colour will not be present in extant plains zebras unless this mutation has also occurred in them, or unless there was interbreeding between ancestral populations of quaggas and other southern populations of plains zebras. The possibility of such interbreeding has been suggested: colder conditions in the past that led to expansion of grassland communities would have affected the distribution of ancestral populations of zebras – possibly resulting in quaggas occurring in the same habitats as other plains zebras.<sup>107</sup> Such intermingling could have allowed the differentiating populations of plains zebras to interbreed, resulting in gene flow between ancestral populations of quaggas and other subspecies of plains zebras.<sup>108</sup> This possibility was also suggested by Rau, who observed that, ‘It is likely that the quagga population was not totally isolated from adjoining plains zebra populations, and that some quagga genes are still present ... though diluted and dispersed.’<sup>109</sup> Another possibility is that alleles for the chestnut colour do occur at low frequencies in plains zebra populations as suggested by Rau, but were not present in animals of the founder population; if so, they could not be recovered by selective breeding and would not be present in Rau quaggas. Klein and Cruz-Uribe observe, ‘It would be comforting to think that its [the quagga’s] essence lives on in the plains zebra, but our craniometric study suggests that something more unique may have been lost.’<sup>110</sup> What was true for cranial structure may also be true for coat colouration.

We may learn more about this in future. Svante Pääbo, a leader in the field of paleogenomics, observed that it should be possible to identify the gene for the coat colouration of quaggas.<sup>111</sup> This prediction, made long before the genomes of quaggas and all extant equines had been completely sequenced, could be tested by comparing the nuclear genomes of quaggas with those of plains zebras which have distinct black and white stripes over their whole bodies and which lack any brown colour. The alleles controlling chestnut coat colouration might then be apparent. Nuclear genomics of quaggas might also settle the question of whether quaggas had physiological adaptations to Karoo environments. A gene that helps plains zebras respond to unfavorable conditions has been identified;<sup>112</sup> this or similar genes may well have been important for quaggas in the Karoo.

### **The Quagga Project as a Boundary Object**

The Quagga Project has brought together, among others, lovers of nature and equines, conservation and commercial organisations, scientists and hunters. The concerns and goals of these heterogeneous stakeholders differ, but all overlap in the restoration of quaggas. Consequently the Quagga Project can be understood as a ‘boundary object’ – a term originally applied by Star and Griesemer to museum artefacts that are

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107 Thackeray, ‘Morphometric’, 89.

108 Ibid.

109 *Weekend Argus* (South Africa), 12 February 1994.

110 Klein and Cruz-Uribe, ‘Craniometry’, 81.

111 *New York Times*, 25 June 1991.

112 Jónsson et al, ‘Speciation’, 18655.



viewed differently by, among others, the scholars who study them, the museum staff who attend to them, and the public who gaze upon them.<sup>113</sup>

Central to the Quagga Project was the vision of Reinhold Rau. He recruited support from others who had different views of the enterprise. First, there were molecular biologists for whom quagga DNA provided proof of concept that DNA of extinct animals could be sequenced. Quagga DNA, in turn, provided data necessary for taxonomists to reclassify zebras. This was particularly appropriate since Bowker and Star view classificatory schemes as boundary objects because of their ambiguity and flexibility.<sup>114</sup> Revised taxonomy demonstrated that quaggas were conspecific with plains zebras, which was information essential for restoring quaggas. Rau then set about gaining the approval of various organisations, raising funds and initiating the Quagga Project.

The expenses of the Quagga Project are substantial: by 1993 with more than twenty zebras in the Quagga Project, annual costs had increased to about R70,000.<sup>115</sup> There have been many donors and for each the Quagga Project may carry different meanings. The South African Nature Foundation paid for the purchase of the initial nine zebras caught at Etosha, Namibia, and their transport to the Nature Conservation Station, Vrolijkheid, where a fencing company had built an enclosure at discounted cost. Additional zebras, fodder, and accommodation were donated by other organisations, while some fodder came from the proceeds of selling a Quagga Project zebra to a vineyard in Stellenbosch.<sup>116</sup>

Since 1998 South African National Parks has provided significant support, as when they funded the transport of Quagga Project zebras to the Karoo National Park and to Addo Elephant National Park, both locations where quaggas formerly occurred.<sup>117</sup> On 29 June 2000 representatives of the Quagga Project Association and the South African National Parks signed a co-operation agreement that provides the Quagga Project with both finances and plains zebras that have quagga-like coat colouration.<sup>118</sup>

Early financial support also came from Chasa, the Confederation of Hunters Association of South Africa. In presenting the first cheque from this body, Darmehl Vosloo of Chasa observed, 'Because the hunters were blamed for the fact that the quagga became extinct, we decided to support this venture.'<sup>119</sup> This support, which parallels the cooperation of hunters and conservationists in other ventures, was vital: Rau noted that without it the project would have collapsed.<sup>120</sup> Other hunting and conservation groups have also donated funds. The position of Chasa in seeking to make amends for extinction echoes the same moral duty expressed by Rau.<sup>121</sup> This is

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113 S.L. Star, and J.R. Griesemer, 'Institutional Ecology, Translations and Boundary Objects: Amateurs and Professionals in Berkeley's Museum of Vertebrate Zoology, 1907-39', *Social Studies of Science*, 19, 3, 1989, 387-420.

114 G. Bowker, and S.L. Star, *Sorting Things Out: Classification and Its Consequences* (Cambridge MA: MIT, 1999).

115 *Argus* (South Africa), 27 July 1993.

116 *Argus Northern* (South Africa), 25 March 1998.

117 Barnaby, 'Karoo', 94; *Star* (South Africa), 3 July 2000.

118 *Ibid.*

119 *Argus*, 17 September 1987.

120 *Sunday Times* (South Africa), 26 September 1993.

121 *Los Angeles Times*, 30 August 1998.

presumably true for some other supporters of the Quagga Project, though for others it may also grade into broader issues of prestige for the organisations involved, and for South Africa itself: as Pienaar observed, 'A project of this nature could have tremendous prestige value not only for the Parks Board but also for the country.'<sup>122</sup>

Attempts to restore quaggas have been widely covered in the South African press. The usual tone of the reports is inspirational but occasionally exaggerated, as when animals in the Quagga Project were said to represent 'a scientific miracle.'<sup>123</sup> A more measured description came from Harley of the Quagga Project: 'It is quite a classic experiment in selective breeding.'<sup>124</sup> Quaggas occurred only in South Africa and their extinction has weighed heavily on some of its people.<sup>125</sup> Consequently, the sentiment of C. S. Lardner, head co-ordinator of the Quagga Project, is probably shared by many: 'it's good to know they're back and we haven't lost this animal that is thoroughly South African.'<sup>126</sup> Social scientists and cultural studies scholars have written about the Quagga Project in academic journals,<sup>127</sup> but missing from most accounts is discussion of the opportunity costs: could the funds needed for restoration achieve more for the biota of South Africa if spent on conservation of endangered organisms, not just animals but also plants such as fynbos and succulents, many of which – as quaggas did – occur only in South Africa?

Association with the Quagga Project may provide additional recognition for some enterprises, for example, the Wedderwill Wine Estate claimed bragging rights on its website: 'The owners of the Wedderwill Game Reserve are part of the quest of bringing back the Quagga.'<sup>128</sup> And reality connects with the silver screen in the 2013 animated film *Khumba*, which features the eponymous quagga-like zebra: the film is dedicated to Rau, a Rau quagga foal was named Khumba, and Triggerfish Animation Studios, the movie makers, donated artwork for a noticeboard of the Quagga Project.<sup>129</sup> Questions of identity – both his own as a white South African and of Khumba, whose lack of some stripes sets him apart from other zebras – helped the director, Anthony Silverston, formulate the film's concept.<sup>130</sup> Identity also features in the similarities noted between the restoration of quaggas and the resurgence of South African culture.<sup>131</sup> In both these instances, quaggas – virtual or living – serve as boundary objects in a more symbolic way to examine questions of personal or national identity.

The founder of the Quagga Project is usually described as a taxidermist, but – as also noted by Swart<sup>132</sup> – Rau was much more. The art of the taxidermist is to make

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122 Rau, 'Rough Road', 2.

123 E. Levitz, 'Who Cares?: He Does', *Publico*, 14, 1, February 1994, 7–9.

124 *Argus*, 17 September 1987.

125 Skead, 'Historical Mammal Incidence', 563.

126 *Farmer's Weekly* (South Africa), 21 March 2014.

127 R. de Vos, 'Stripes Faded, Barking Silenced: Remembering Quagga', *Animal Studies Journal*, 3, 1, 2014, 29–45; C. Freeman, 'Ending Extinction: The Quagga, the Thylacine and the "Smart Human"' in C. Gigliotti (ed), *Leonardo's Choice: Genetic Technologies and Animals* (New York: Springer, 2009), 235–56; S. Swart, 'Frankenzebra: Dangerous Knowledge and the Narrative Construction of Monsters', *Journal of Literary Studies*, 30, 4, 2014, 45–70.

128 <http://wedderwill.co.za/category/blog/>.

129 <http://www.quaggaproject.org/index.htm>, February 2014 co-ordinator's report.

130 <http://www.iol.co.za/tonight/movies/stars-and-stripes-by-sa-animators-1.1554879#VOnMBGTF-Uc>.

131 M. Clasquin, *Quagga Kultuur: Reflections on South African Popular Culture* (Pretoria: Aurora, 2003).

132 Swart, 'Frankenzebra', 45.

dead animals look as lifelike as possible; incorporated into a diorama, these animals can help to represent habitats. The vision of Rau was to restore extinct animals; incorporated into their habitats, these animals can help to restore environments where the reduction of native grazing animals has resulted in indigenous vegetation being replaced by introduced plants.<sup>133</sup> Appropriate degrees of grazing are often required for indigenous plants to survive: as John Comrie-Greig notes, quaggas were ‘an important component of the karoo environment’<sup>134</sup> and their extinction ‘heralded major ecological changes to that environment.’ Consequently, ‘rewilding’<sup>135</sup> of the Karoo with Rau quaggas as an integral component of the environment would be important. Of course, the introduction of plains zebra would serve the same purpose, but would not have the same symbolic significance.

Several factors are involved in the environmental degradation of the Karoo including climate change, overgrazing and human activities such as mining.<sup>136</sup> Although Don Borroughs was being overly optimistic with his pronouncement that ‘The last, best hope for the fragile Karoo may be that one day it will be known as the place where the quagga was exterminated, only to rise again,’<sup>137</sup> Rau quaggas can be one part of environmental restoration.

An important lesson of this account is that the Quagga Project can serve as a model for ways to bring together heterogeneous players to achieve a common goal. While Rau was pivotal, many other people and organisations were also involved. Moral duty, prestige, and making amends were among the various and overlapping reasons for giving support in cash and kind, and media attention throughout served to keep restoration of quaggas in people’s minds. In short: the Quagga Project succeeded because it was a boundary object. Each of the stakeholders and parties involved had their own interests and perspectives, but all overlapped at the common goal, of restoring quaggas. The same model could be applied successfully to conservation projects.

A counter example stands out. In Mozambique the Selous zebra, a ‘rare, morphologically unique population’<sup>138</sup> of the plains zebra, has suffered a precipitous drop in numbers: an estimated population of over 20,000 in 1970 had declined to fewer than fifty animals in 2000,<sup>139</sup> although their numbers have now risen slightly. This tragic situation appears to have gone largely unnoticed. Suppose that someone had advocated to rescue Selous’ zebras, and with the 1992 end of the civil war a small population had been saved in Mozambique or outside the country. If someone with Rau’s vision and determination had enlisted support from a heterogeneous array of people

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133 A.V. Milewski, ‘Dwarf Ebonies and Mega-herbivores: The Low Vegetation of the South-Western Cape Cannot Be Preserved Without Emulating the Large Herbivores that Kept It Treeless’, *Veld Flora*, 86, 2000, 33–5.

134 J. Comrie-Greig, ‘The Lesson of the Quagga’, *African Wildlife*, 37, 4, 134–5.

135 Kolbert, ‘Recall of the Wild’, 50.

136 M.L. Masubelele, M.T. Hoffman, W. Bond and P. Burdett, ‘Vegetation Change (1988–2010) in Camdeboo National Park (South Africa), Using Fixed-point Photo Monitoring: The Role of Herbivory and Climate’, *Koedoe*, 55, 1, 2013, 1–16.

137 D. Borroughs, ‘Stripes and Shadows’, *Timbila: Spirit of Africa*, 2, 1, 2000, 42–9.

138 R.D. Beilfuss, C.M. Bento, M. Haldane and M. Ribaue, ‘Status and Distribution of Large Herbivores in the Marromeu Complex of the Zambezi Delta, Mozambique’ (Unpublished report, World Wide Fund for Nature, Maputo, Mozambique, 2010).

139 P. Dutton and S. Dutton, ‘Tragedy in the Making’, *African Wildlife*, 54, 3, 2000, 27.

and organisations – biologists, conservationists, tourist bodies, and well-wishers of Mozambique – then the Selous' zebra might not now be critically endangered.

What distinguishes the critically endangered Selous' zebras from quaggas, which are restored? The reworking of the taxonomic status of quaggas from a species to a subspecies was essential to the success of the Quagga Project. Taxonomic reform and political transformation created an opportunity that was taken up by well-developed scientific governmental and private institutions able to support the creation of a national symbol. Quaggas, with their history of victimisation and loss, provided the new South Africa with a symbol of restoration in the environmental realm. Sadly for Selous' zebras, postwar Mozambique has had no similar moment of reconstruction, and has fewer resources and weaker institutions. Not least, denied the status of a subspecies,<sup>140</sup> Selous' zebras have no taxonomic standing to rally people around their conservation. In contrast, taxonomy based on macromolecules catalysed the restoration of quaggas.

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140 Beilfuss et al, 'Status and Distribution', 47.