# Genetic analysis of three South African horse breeds

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## ABSTRACT

Genetic variability at 7 blood-group and 10 biochemical genetic loci was examined in 3 South African horse breeds, the Nooitgedacht, Boerperd and Basuto Pony. Observed heterozygosity for these breeds was intermediate for domestic horses, with the highest heterozygosity in the Boerperd and the lowest in the Basuto Pony. The 3 breeds show greater genetic similarity to each other than to other domestic horse breeds. Compared to other breeds, the South African breeds show greater genetic similarity to breeds such as the Thoroughbred, Holstein, Trakehner and Hanovarian and also to North American breeds such as the Saddlebred, Standardbred and Morgan Horse.

**Key words**: biochemical polymorphisms, blood groups, dendrogram, genetic diversity, South African horse breeds.

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## INTRODUCTION

The horse (*Equus caballus*) was unknown to the inhabitants of the Cape in South Africa before European settlement in the Cape in 1486. The first horses brought to the Cape were Javan ponies from the East Indies that had a strong Oriental influence. Other types of horses that eventually reached the Cape were Persian Arabs, Andalusian stallions from South America, English Thoroughbreds and some Spanish horses[7]. Two importations of horses from the United States of America took place in 1782 and 1808[16].

By 1800 these breeds had been mixed to form what began to be called the Cape Horse. The relative number of each breed in the foundation stock used is not clear. Additional Thoroughbreds were then brought in to improve the Cape Horse. The Cape Horse was highly esteemed for its gentleness, beauty and good service. There was a great demand for these horses and the breed was exported for 130 years, which brought the Cape Horse acclaim as a battle horse from throughout the British Empire. With the Great Trek (1836–1838), the Boers took their horses inland with them, after which these horses were known as the Boerperd[16].

Meanwhile, in the Cape, the Cape Horse continued to be bred true for some time. Later there was importation of Flemish horses to the Cape as well as Hackneys, Norfolk trotters, Morgans and Cleveland Bays to satisfy an increasing demand for coach horses. These breeds certainly must have influenced the development of the Cape Horse.

Another South African breed, the Basuto Pony, was initially the same as the Boerperd, as it was acquired by the Basuto people by trade and by raids on the Boers. The Basuto Ponies were kept in the isolated Mountain Kingdom and as a result of the extreme conditions and poor grazing, only the hardiest were able to survive. This natural selection turned the Basuto Pony into an animal renowned for its hardiness, endurance, intelligence, tractability and remarkably hard hooves[19].

The population size of the Cape Horse was greatly reduced during the Anglo-Boer War of 1899–1902. Because the Boerperd of the Republics had become well adapted to its environment and had established some resistance to the deadly African horsesickness virus, it was a military animal superior to the imported cavalry horses of the British. This resulted in a concerted effort by the British to eliminate the horses[20]. Today only a few stud farms remain that still have horses of old Boerperd origin.

The Nooitgedacht was developed as a breed, starting in 1951, in an attempt to save the Basuto Pony, which was on the verge of extinction owing to popular demand as remounts during the war, the great blizzard of 1902, and the introduction of diseases amongst the highly susceptible ponies. The introduction of Thoroughbreds was also a disaster, as they failed to adapt and initiated a race of clumsy animals, unable to maintain condition at all[19]. There was furthermore a need for a farm and riding horse well-adapted to the rural conditions in South Africa. A search was undertaken for suitable typical Basuto ponies, and horses were found in the Molteno district that were claimed to all be descendants of a stallion bought from Lesotho in 1902.

Others were selected from the Free State. In total, 12 horses were bought and bred at an experimental farm[2]. They were selected very strictly to attain the goal set. In 1977 the herd was sold to private breeders who continued the breeding policy.

The origins of the 3 primary indigenous South African horse breeds (the Boerperd, Nooitgedacht and Basuto Pony) are clearly similar. However, these breeds have had separate histories for some time and different selective procedures and breeding strategies have resulted in horses that have distinctive characteristics and are acknowledged as separate breeds. In this study we examined the genetic similarity of these breeds to each other and other common domestic horse breeds. We also examined current levels of genetic diversity within each breed.

## MATERIALS AND METHODS

Blood samples were collected by jugular venipuncture in acetate dextrose (7 mℓ). Boerperd samples (*n* = 34) were taken from horses on different stud farms in Mpumalanga in conjunction with breed registry regulations requiring blood typing. Nooitgedacht (*n* = 21) samples were collected from stud farms in Gauteng and Mpumalanga. Basuto ponies (*n* = 34) were sampled on a farm in the Mulimo Ntuse district in Lesotho. These horses were not registered in a studbook as were the other 2 breeds.

Standard immunological procedures involving haemagglutination and complement-mediated haemolysis[17,18] were used to detect variation of red-cell allo-antigens at 7 blood-group loci.

Starch and polyacrylamide gel electrophoresis and isoelectric focusing were used to detect variation at 10 serum and rbc lysate protein loci[5,6,9,10,13,15].

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The loci examined were the *A, C, K, P, Q,* and *U* horse blood-group loci and the biochemical protein loci were alpha-I beta glycoprotein (*A1B*), albumin (*Al*), serum esterase (*Est*), vitamin D binding protein (*Gc*), glucosephosphate isomerase (*GPI*), alpha-haemoglobin (*Hb*), 6-phosphogluconate dehydrogenase (*6-PGD*), phosphoglucomutase (*PGM*), protease inhibitor (*Pi*) and transferrin (*Trf*). Nomenclature for variants at all 17 loci was in accord with internationally standardised usage for horses[3,4], except for variants at some loci that have not yet received international recognition.

Gene frequencies for biochemical loci were calculated by direct count. Frequencies of alleles at blood-group loci were calculated by the allocation method[1]. Genetic variation was measured as observed heterozygosity (*Ho*), Hardy-Weinberg expected heterozygosity (*He*), unbiased expected heterozygosity (*Hu*)[11], effective number of alleles (*Ae*), and the total number of variants found in each population (*Na*). *Ho* was calculated for biochemical loci only on account of the presence of recessive alleles and/or ambiguous genotypes at blood-group loci. Therefore, for direct comparison, *He* and *Hu* were calculated for biochemical loci only (in an ideal population, *He* (*Hu*) should equal *Ho*), for blood-group loci, and for all 17 loci. In addition, population inbreeding level was estimated by Wright's $Fis = 1(Ho/He)$. Values of genetic variation of the South African breeds were compared to those of domestic horse populations that have been tested at the University of Kentucky. These were not South African breeds but they are regarded as international breeds and not country-based. Genetic relationships of the South African breeds to the other domestic breeds were investigated using Rogers'[14] genetic similarity coefficient (*S*) and Nei's modified distance (*Da*)[12]. Restricted maximum likelihood (*RML*) analysis[8] was used to construct the dendograms in Figs 1 and 2.

## RESULTS

Allele frequencies for the 3 South African horse breeds are shown in Table 1. Measures of genetic variability are given in Table 2. Variability values for 9 other domestic horse breeds and the means of these measures based on data from 99 domestic horse breeds examined at the University of Kentucky also are shown in Table 2. The 9 breeds were selected to demonstrate the range of variability in domestic breeds.

Values of Rogers' *S* and Nei's *Da* for comparisons of the 3 South African breeds with 55 breeds of domestic horses are

Table 1: **Allele frequencies for 17 genetic loci examined in South African horse breeds.** HBG = horse blood group. See text for additional information about the loci.

| Locus | Allele | Nooitgedacht | Boerperd | Basuto Pony |
|---|---|---|---|---|
| Trf | D | 0.024 | 0.396 | 0.147 |
| | D2 | 0.000 | 0.000 | 0.059 |
| | E | 0.000 | 0.015 | 0.029 |
| | F1 | 0.333 | 0.015 | 0.074 |
| | F2 | 0.357 | 0.250 | 0.427 |
| | F3 | 0.024 | 0.074 | 0.088 |
| | H2 | 0.095 | 0.059 | 0.103 |
| | O | 0.071 | 0.015 | 0.029 |
| | R | 0.096 | 0.176 | 0.044 |
| A1B | F | 0.000 | 0.015 | 0.000 |
| | K | 1.000 | 0.985 | 0.985 |
| | S | 0.000 | 0.000 | 0.015 |
| Est | F | 0.118 | 0.044 | 0.029 |
| | G | 0.000 | 0.015 | 0.044 |
| | H | 0.000 | 0.015 | 0.015 |
| | I | 0.810 | 0.867 | 0.883 |
| | R | 0.024 | 0.000 | 0.000 |
| | S | 0.048 | 0.059 | 0.029 |
| A1 | A | 0.548 | 0.618 | 0.368 |
| | B | 0.452 | 0.382 | 0.632 |
| Gc | F | 0.952 | 0.985 | 0.956 |
| | S | 0.048 | 0.015 | 0.044 |
| 6-PGD | F | 0.952 | 0.956 | 0.824 |
| | S | 0.048 | 0.044 | 0.176 |
| PGM | F | 0.071 | 0.132 | 0.044 |
| | S | 0.929 | 0.824 | 0.956 |
| | V | 0.000 | 0.044 | 0.000 |
| GPI | F | 0.286 | 0.162 | 0.059 |
| | I | 0.714 | 0.794 | 0.883 |
| Hb | AII | 0.000 | 0.044 | 0.000 |
| | BI | 0.143 | 0.618 | 0.559 |
| | BII | 0.857 | 0.338 | 0.441 |
| Pi | F | 0.238 | 0.250 | 0.176 |
| | G | 0.048 | 0.250 | 0.044 |
| | I | 0.000 | 0.132 | 0.015 |
| | J | 0.000 | 0.015 | 0.000 |
| | L | 0.381 | 0.103 | 0.323 |
| | L2 | 0.000 | 0.000 | 0.015 |
| | N | 0.000 | 0.044 | 0.059 |
| | O | 0.214 | 0.000 | 0.015 |
| | Q | 0.000 | 0.015 | 0.000 |
| | R | 0.000 | 0.044 | 0.074 |
| | S | 0.024 | 0.000 | 0.132 |
| | T | 0.000 | 0.044 | 0.000 |
| | U | 0.095 | 0.059 | 0.088 |
| | Z | 0.000 | 0.044 | 0.029 |
| A HBG | adf | 0.399 | 0.611 | 0.508 |
| | adg | 0.130 | 0.000 | 0.030 |
| | b | 0.058 | 0.048 | 0.117 |
| | c | 0.211 | 0.000 | 0.034 |
| | e | 0.027 | 0.000 | 0.000 |
| | bc | 0.000 | 0.032 | 0.026 |
| | bce | 0.050 | 0.031 | 0.000 |
| | – | 0.125 | 0.278 | 0.285 |
| C HGB | a | 0.622 | 0.827 | 0.616 |
| | – | 0.378 | 0.173 | 0.384 |
| D HBG | ad | 0.132 | 0.073 | 0.029 |
| | dn | 0.059 | 0.000 | 0.126 |
| | dk | 0.310 | 0.293 | 0.167 |
| | dghm | 0.190 | 0.074 | 0.210 |
| | de | 0.000 | 0.024 | 0.064 |
| | deo | 0.143 | 0.270 | 0.138 |
| | dfk | 0.000 | 0.060 | 0.015 |
| | bcm | 0.095 | 0.118 | 0.118 |
| | cgm | 0.071 | 0.059 | 0.118 |
| | cegimn | 0.000 | 0.029 | 0.015 |
| K HBG | a | 0.383 | 0.126 | 0.143 |
| | – | 0.617 | 0.874 | 0.857 |
| P HBG | ac | 0.075 | 0.110 | 0.112 |
| | ad | 0.053 | 0.032 | 0.191 |
| | b | 0.100 | 0.000 | 0.000 |
| | bd | 0.000 | 0.045 | 0.030 |
| | d | 0.000 | 0.150 | 0.350 |
| | – | 0.772 | 0.663 | 0.317 |
| Q HBG | abc | 0.000 | 0.126 | 0.076 |
| | b | 0.101 | 0.071 | 0.119 |
| | c | 0.049 | 0.108 | 0.101 |
| | – | 0.850 | 0.695 | 0.704 |
| U HBG | a | 0.100 | 0.406 | 0.196 |
| | – | 0.900 | 0.594 | 0.804 |

Table 2: **Estimates of genetic variability for South African and selected other domestic horse breeds**. The means of the genetic variation measures were based on data from 99 domestic horse populations. *Ho, He* and the unbiased estimator of *He (Heub)* were calculated from the 10 biochemical loci only; *Heb* was from the 7 blood-group loci, and *TtlHe* was from all 17 loci.

| Breed | n | Ho | He | Heub | Fis | Heb | TtlHe | NA | Ae |
|---|---|---|---|---|---|---|---|---|---|
| Nooitgedacht | 21 | 0.357 | 0.329 | 0.337 | −0.100 | 0.477 | 0.390 | 59 | 2.289 |
| Boerperd | 34 | 0.385 | 0.358 | 0.363 | −0.077 | 0.478 | 0.407 | 70 | 2.352 |
| Basuto Pony | 34 | 0.347 | 0.336 | 0.341 | −0.032 | 0.534 | 0.418 | 70 | 2.607 |
| American Saddlebred | 259 | 0.404 | 0.409 | 0.410 | 0.013 | 0.470 | 0.435 | 96 | 2.625 |
| Arabian | 117 | 0.307 | 0.327 | 0.328 | 0.061 | 0.448 | 0.376 | 67 | 2.132 |
| Bedouin Arabian | 213 | 0.209 | 0.224 | 0.225 | 0.066 | 0.418 | 0.304 | 52 | 1.890 |
| Chilean Criollo | 173 | 0.375 | 0.383 | 0.384 | 0.022 | 0.564 | 0.457 | 86 | 2.919 |
| Friesian | 314 | 0.307 | 0.306 | 0.307 | −0.003 | 0.407 | 0.348 | 54 | 1.901 |
| Peruvian Paso | 141 | 0.451 | 0.445 | 0.446 | −0.014 | 0.503 | 0.469 | 77 | 2.761 |
| Quarter Horse | 168 | 0.396 | 0.393 | 0.394 | −0.007 | 0.508 | 0.440 | 87 | 2.653 |
| Standardbred Pacer | 341 | 0.401 | 0.395 | 0.395 | −0.016 | 0.441 | 0.414 | 85 | 2.142 |
| Thoroughbred | 265 | 0.294 | 0.288 | 0.289 | −0.019 | 0.376 | 0.325 | 64 | 2.009 |
| | | | | | | | | | |
| Domestic horse mean | 99 | 0.377 | 0.364 | 0.371 | −0.034 | 0.486 | 0.413 | 64.7 | 2.393 |
| Standard deviation | | 0.051 | 0.044 | 0.045 | 0.066 | 0.054 | 0.039 | 11.2 | 0.250 |

shown in Tables 3 and 4, respectively. The breeds in Tables 3 and 4 are grouped based on relationship to each other (see Fig. 1) and mean values of *S* and *Da* for each group also are given. Fig. 1 shows the majority rule, strict consensus tree based on 20 *RML* trees for the 3 South African breeds, 51 other domestic breeds and the Przewalski horse (used as an outgroup). Because the 3 South African breeds formed a separate cluster, each was examined separately as shown in partial consensus trees (Fig. 2).

## DISCUSSION

Levels of individual genetic variation within the 3 South African breeds was intermediate for a domestic horse breed, with the highest *Ho* in the Boerperd and the lowest in the Basuto Pony. Only the Boerperd had an *Ho* greater than the domestic horse mean (Table 2). *He* showed a similar pattern. For all 3 breeds *Ho* exceeded *He,* resulting in negative *Fis* values; however, the excess was not statistically significant. For all 3 breeds, *He* was below the mean for domestic horse breeds. Blood-group expected heterozygosity (*Heb*) was highest in the Basuto Pony with a value of 0.534, which was well above the domestic horse mean, as was total expected heterozygosity (*Ttl He*) and *Ae.*

In the case of the Boerperd, there has been some controversy. As a result of the small gene pool, some breeders crossbred their horses with overseas breeds, especially the American Saddlebred, Arab, Thoroughbred and Hackney, which led to a split in the Society, as other breeders were strongly opposed to these actions. The former group of crossbred horses now numbers about 800 breeding



Fig. 1: **Majority rule, strict consensus tree from 20 *RML* trees of the 3 South African breeds with 52 other horse breeds.**

Table 3: **Rogers' genetic similarity for 3 South African horse breeds compared to other domestic horse breeds, and mean values for groups of domestic horse breeds**.

| Saddle and harness light horses | TB | SF | QH | HN | HO | TK | Mean | s.d. | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nooitgedacht | 0.805 | 0.811 | 0.807 | 0.807 | 0.803 | 0.801 | 0.805 | 0.003 | | | | | |
| Boerperd | 0.797 | 0.819 | 0.855 | 0.825 | 0.810 | 0.838 | 0.819 | 0.030 | | | | | |
| Basuto Pony | 0.814 | 0.882 | 0.892 | 0.862 | 0.834 | 0.882 | 0.861 | 0.031 | | | | | |
| **Gaited North American breeds** | PA | TR | MH | RM | SB | Mean | s.d. | | | | | | |
| Nooitgedacht | 0.824 | 0.790 | 0.804 | 0.803 | 0.773 | 0.801 | 0.015 | | | | | | |
| Boerperd | 0.817 | 0.818 | 0.848 | 0.845 | 0.859 | 0.837 | 0.019 | | | | | | |
| Basuto Pony | 0.828 | 0.819 | 0.868 | 0.833 | 0.867 | 0.843 | 0.023 | | | | | | |
| **Arabian type breeds** | AR | SA | TU | AT | KU | CS | KA | BS | YA | Mean | s.d. | | |
| Nooitgedacht | 0.773 | 0.770 | 0.802 | 0.800 | 0.776 | 0.754 | 0.778 | 0.778 | 0.794 | 0.781 | 0.016 | | |
| Boerperd | 0.841 | 0.821 | 0.858 | 0.816 | 0.875 | 0.831 | 0.841 | 0.813 | 0.857 | 0.839 | 0.021 | | |
| Basuto Pony | 0.859 | 0.833 | 0.876 | 0.828 | 0.851 | 0.808 | 0.847 | 0.868 | 0.858 | 0.847 | 0.021 | | |
| **Heavy draft horses** | CD | BE | BR | PC | SH | SU | CL | HF | NK | PH | Mean | s.d. | |
| Nooitgedacht | 0.719 | 0.791 | 0.736 | 0.781 | 0.725 | 0.741 | 0.697 | 0.774 | 0.755 | 0.747 | 0.747 | 0.029 | |
| Boerperd | 0.788 | 0.799 | 0.788 | 0.806 | 0.776 | 0.764 | 0.754 | 0.796 | 0.800 | 0.800 | 0.787 | 0.017 | |
| Basuto Pony | 0.792 | 0.835 | 0.803 | 0.831 | 0.809 | 0.777 | 0.751 | 0.804 | 0.814 | 0.819 | 0.804 | 0.025 | |
| **Pony breeds** | WP | HP | SP | MN | DL | NF | IC | EX | Mean | s.d. | | | |
| Nooitgedacht | 0.791 | 0.759 | 0.719 | 0.757 | 0.761 | 0.753 | 0.685 | 0.721 | 0.744 | 0.031 | | | |
| Boerperd | 0.828 | 0.790 | 0.744 | 0.797 | 0.787 | 0.827 | 0.740 | 0.770 | 0.785 | 0.031 | | | |
| Basuto Pony | 0.876 | 0.814 | 0.779 | 0.841 | 0.785 | 0.815 | 0.754 | 0.767 | 0.802 | 0.038 | | | |
| **Iberian Peninsula-derived breeds** | AN | LU | PP | CP | CC | RP | PF | MM | MA | BZ | AC | GR | Mean | s.d. |
| Nooitgedacht | 0.741 | 0.767 | 0.773 | 0.772 | 0.797 | 0.790 | 0.774 | 0.787 | 0.752 | 0.768 | 0.781 | 0.778 | 0.773 | 0.016 |
| Boerperd | 0.818 | 0.825 | 0.816 | 0.815 | 0.844 | 0.839 | 0.817 | 0.838 | 0.809 | 0.823 | 0.806 | 0.850 | 0.825 | 0.014 |
| Basuto Pony | 0.803 | 0.834 | 0.845 | 0.823 | 0.864 | 0.860 | 0.841 | 0.831 | 0.778 | 0.831 | 0.810 | 0.869 | 0.832 | 0.027 |
| **South African breeds** | NO | BP | BU | | | | | | | | | | | |
| Nooitgedacht | — | 0.821 | 0.839 | | | | | | | | | | | |
| Boerperd | 0.821 | — | 0.861 | | | | | | | | | | | |
| Basuto Pony | 0.839 | 0.861 | — | | | | | | | | | | | |

**Key to breed abbreviations used in Tables 3 and 4**

TB = Thoroughbred; SF = Sella Français; QH = Quarter Horse; HN = Hanovarian; HO = Holstein; TK = Trakehner; PA = Standardbred Pacer; TR = Standardbred Trotter; MH = Morgan Horse; RM = Rocky Mountain Horse; SB = American Saddlebred; AR = Arabian; SA = Shagya Arabian; TU = Turkoman; AT = Akhal Teke; KU = Kurd; CS = Caspian Pony; KA = Khuzestan Arabian; BS = Bedouin Arabian (Blue Star); YA = Yabou; CD = American Cream Draft; BE = Belgian Draft; BR = Breton; PC = Percheron; SH = Shire; SU = Suffolk Punch; CL = Clydesdale; HF = Haflinger; PH = Polish Heavy Horse; NK = Noriker; WP = Welch Pony; HP = Hackney Pony; SP = Shetland Pony; MN = Miniature Horse; DL = Dales Pony; NF = Norwegian Fjord; IC = Icelandic Horse; EX = Exmoor Pony; AN = Andalusian; LU = Lusitano; PP = Peruvian Paso; CP = Campolina; CC = Chilean Criollo; BZ = Brazilian Criollo; AC = Argentine Criollo; RP = Puerto Rican Paso Fino; PF = American Paso Fino; GR = Garrano; MM = Mangalarga Marchador; MA = Mangalarga; NO = Nooitgedacht; BP = Boerperd; BU = Basuto Pony.

horses (Cape Boerperd), whereas the latter have about 1400 breeding animals (Historical Boerperd). For these non-crossbred horses there is a strict breeding programme, where animals are selected at 2½ years of age as potential breeders. No foreign breeds are used. The samples analysed here were from the purebred group.

The Nooitgedachts number about 3000 breeding animals. Since the beginning of 1998 they have been acknowledged as a developed breed. A strict selection programme is also followed. In the past, Arabs and Boerperd were used to counteract inbreeding. At present there are no height restrictions and breeders are now selecting for larger animals.

In Lesotho there is a campaign at present, with Irish assistance, to save the Basuto Pony. A herd is kept that is bred to approved stallions (Basuto Pony, Connemara and Arab) and their selected offspring are available to farmers. There are, however, a number of ungelded horses in a country where no fences exist. The government herd consists of 30 horses, and 5 stallions are used. The horses in Lesotho number 200 540.

Genetic variability within these 3 South African breeds has been influenced by both small population size and outcrossing. It is possible that both past bottlenecks and recent small population sizes have counteracted the crossbreeding to keep variation relatively low. However, it is worth noting that the least outbred (in recent years) breed, the Boerperd, has the highest *Ho*. Genetic similarity and distance values show that the 3 South African breeds are genetically most similar to the light riding horses, as would be expected (Tables 3, 4), and show least relationship to the heavy draft horses and ponies. Both the Nooitgedacht and Basuto Pony have the closest relationship to those breeds with a strong English Thoroughbred influence, while the Boerperd shares the highest mean values with gaited North American breeds, which also have some (but more distant) English Thoroughbred ancestry. Among the 3 breeds, the Boerperd and Basuto Pony shared the greatest resemblance.

The dendrograms of Figs 1 and 2 support the relationships indicated by the similarity and distance values. Fig. 1 indicates that the 3 breeds are more closely related to each other than to any other breed analysed. This is consistent with the known histories of the South African breeds. The position of the South African horses is between the Thoroughbred-related breeds and the gaited North American breeds.

It is surmised that the influence of the 2 USA imports to the Cape (1782 and 1808) had a strong influence on the creation of the foundation stock, causing the Boerperd to be closer to the gaited North American Breeds. Although in later years upgrading was performed by a few breeders, these herds were not included in the sampled group.

The Arab was a foundation breed and regularly contributed to the Nooitgedacht as well as the Basuto Pony. The Thoroughbred, apart from being foundation stock breed through the Boerperd, was also used extensively by the Basutos for cross-breeding. It was, however, never

Table 4: **Nei's modified genetic distance for 3 South African horse breeds compared to other domestic horse breeds, and mean values for groups of domestic horse breeds.**

| Saddle and harness light horses | TB[a] | SF | QH | HN | HO | TK | Mean | s.d. |
|---|---|---|---|---|---|---|---|---|
| Nooitgedacht | 0.109 | 0.100 | 0.085 | 0.113 | 0.115 | 0.087 | 0.102 | 0.013 |
| Boerperd | 0.103 | 0.080 | 0.055 | 0.092 | 0.101 | 0.070 | 0.083 | 0.019 |
| Basuto Pony | 0.085 | 0.047 | 0.039 | 0.072 | 0.079 | 0.047 | 0.062 | 0.019 |

| Gaited North American breeds | PA | TR | MH | RM | SB | Mean | s.d. |
|---|---|---|---|---|---|---|---|
| Nooitgedacht | 0.105 | 0.124 | 0.104 | 0.105 | 0.101 | 0.108 | 0.009 |
| Boerperd | 0.091 | 0.106 | 0.073 | 0.074 | 0.063 | 0.081 | 0.017 |
| Basuto Pony | 0.084 | 0.085 | 0.070 | 0.071 | 0.065 | 0.077 | 0.012 |

| Arabian type breeds | AR | SA | TU | AT | KU | CS | KA | BS | YA | Mean | s.d. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Nooitgedacht | 0.114 | 0.125 | 0.106 | 0.131 | 0.129 | 0.145 | 0.110 | 0.122 | 0.120 | 0.122 | 0.012 |
| Boerperd | 0.080 | 0.090 | 0.073 | 0.116 | 0.085 | 0.100 | 0.086 | 0.110 | 0.097 | 0.092 | 0.014 |
| Basuto Pony | 0.060 | 0.080 | 0.063 | 0.090 | 0.073 | 0.094 | 0.083 | 0.083 | 0.082 | 0.077 | 0.011 |

| Heavy draft horses | CD | BE | BR | PC | SH | SU | CL | HF | NK | PH | Mean | s.d. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nooitgedacht | 0.163 | 0.124 | 0.151 | 0.118 | 0.169 | 0.153 | 0.199 | 0.127 | 0.150 | 0.134 | 0.145 | 0.025 |
| Boerperd | 0.116 | 0.110 | 0.118 | 0.105 | 0.146 | 0.136 | 0.178 | 0.101 | 0.106 | 0.102 | 0.122 | 0.025 |
| Basuto Pony | 0.120 | 0.085 | 0.114 | 0.072 | 0.110 | 0.120 | 0.145 | 0.086 | 0.106 | 0.084 | 0.104 | 0.022 |

| Pony breeds | WP | HP | SP | MN | DL | NF | IC | EX | Mean | s.d. |
|---|---|---|---|---|---|---|---|---|---|---|
| Nooitgedacht | 0.101 | 0.139 | 0.195 | 0.140 | 0.157 | 0.139 | 0.194 | 0.154 | 0.153 | 0.029 |
| Boerperd | 0.079 | 0.104 | 0.147 | 0.104 | 0.144 | 0.083 | 0.138 | 0.133 | 0.117 | 0.026 |
| Basuto Pony | 0.054 | 0.094 | 0.135 | 0.082 | 0.118 | 0.078 | 0.133 | 0.118 | 0.103 | 0.028 |

| Iberian Peninsula-derived breeds | AN | LU | PP | CP | CC | RP | PF | MM | MA | BZ | AC | GR | Mean | s.d. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nooitgedacht | 0.159 | 0.139 | 0.120 | 0.123 | 0.096 | 0.117 | 0.116 | 0.122 | 0.170 | 0.140 | 0.150 | 0.126 | 0.132 | 0.021 |
| Boerperd | 0.113 | 0.092 | 0.098 | 0.106 | 0.079 | 0.090 | 0.089 | 0.099 | 0.118 | 0.100 | 0.132 | 0.070 | 0.099 | 0.017 |
| Basuto Pony | 0.097 | 0.088 | 0.072 | 0.089 | 0.057 | 0.071 | 0.071 | 0.088 | 0.123 | 0.093 | 0.111 | 0.050 | 0.085 | 0.020 |

| Other breeds | NO | BP | BU |
|---|---|---|---|
| Nooitgedacht | — | 0.095 | 0.071 |
| Boerperd | 0.095 | — | 0.049 |
| Basuto Pony | 0.071 | 0.049 | — |

[a]Horse breed abbreviations are defined in Table 3.

used in the Nooitgedacht, as such, for upgrading.

Individually, the Nooitgedacht and Basuto Pony fit into the Thoroughbred-related breeds cluster. Both breeds occupy a position near the outside of the cluster between the Sella Français and American Quarter Horse. The Boerperd falls in the centre of the gaited North American Breeds cluster. It is slightly closer to the American Saddlebred and the Rocky Mountain Horse (a light riding horse with origins similar to the American Saddlebred). A study of the 2 Cape horse populations, the Cape Boerperd and the Historical Boerperd, is required to clarify the exact source of American influence.
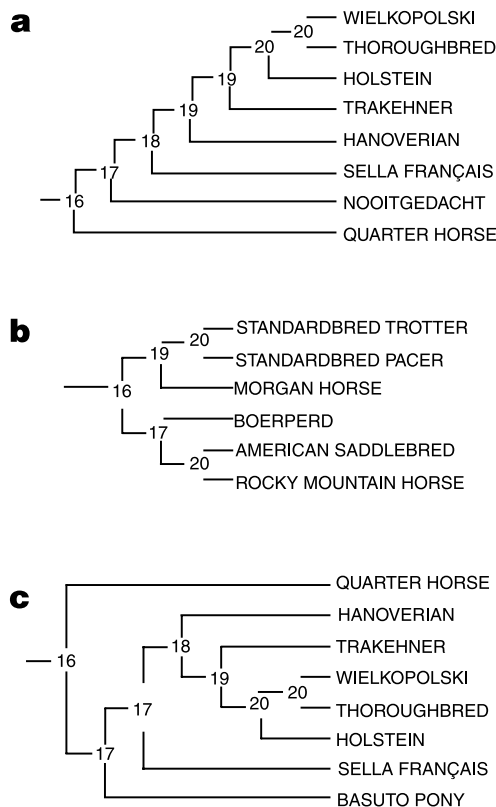
## ACKNOWLEDGEMENTS

Fig. 2: **Partial consensus trees for each South African breed, each from 20 *RML* trees for the same set of breeds as in Fig. 1. The rest of the trees, not shown, were the same as in Fig. 1. a = Nooitgedacht; b = Boerperd; c = Basuto Pony.**

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