

Koffiefontein quaggas and true Cape quaggas: the importance of basic skull morphology

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Simple morphological characters that distinguish the skulls of horses, asses, mountain zebras, plains zebras and Cape quaggas are described and illustrated. These characters confirm that the alleged 'Quagga' skulls of Koffiefontein actually belong to horse and asses, and that the true Cape quagga skulls have greater resemblance to plains zebra skulls than to mountain zebra skulls. The possible reasons for disagreement in a recent controversy about the relative closeness of the Cape quaggas to the plains and mountain zebras are discussed.

In a recent report¹ a study of five subfossil equid skulls recovered early in the last century from near Koffiefontein, western Free State,² was cited as providing support for a close relationship between the extinct Cape quagga and the living Cape mountain zebra (*E. zebra*). This view was opposed by Eisenmann³ and Rau,⁴ who see a very close relationship (ref. 5, p. 36), or even a specific identity,⁶ between extant plains zebras and the extinct Cape quagga, agreeing with genetic and immunological studies of tissues from Cape quagga skins in museum collections.^{7,8}

The aim of the paper by Klein and Cruz-Uribe,² that stimulated much discussion, was to address the issue concerning the Koffiefontein skulls, and to establish whether they belong to the Cape quagga, by means of discriminant analysis of a number of cranial ratios. It was found that one of the Koffiefontein skulls is that of a horse (*E. caballus*) and that the four others are those of donkeys (*E. asinus*). In the same paper (ref. 2, p. 623), it was stated that 'like the discriminant analysis, the cluster result again implies that quagga and mountain zebra are at least as similar as quagga and plains zebra' and that further genetic studies should be undertaken to determine the position of the quagga relative to plains and mountain zebras.

These are the two independent points that we want to discuss: the identification of the Koffiefontein skulls, and the comparative morphology of the Cape quagga skulls. To address the first point, we examined four of the five Koffiefontein skulls preserved in the McGregor Museum in Kimberley (MMK 4159, 4520, 4521, and 4656) and studied them in the conventional comparative way based on classical and well-documented craniological criteria in equids.⁹⁻¹² We agree with Klein and Cruz-Uribe² that one of the skulls (MMK 4159) belongs to *E. caballus* and the others to *E. asinus*. We do not agree, however, with the conclusions regarding the skull resemblances of the Cape quagga.

In this paper we summarize and illustrate the basic craniological criteria that distinguish Cape quaggas, plains zebras, mountain zebras, asses and horses.

Basic comparative observations may prove more reliable than sophisti-

cated statistical approaches. In our opinion, results do not depend on techniques of comparison as much as on choice of characters.

Figures 1 and 2 show the skulls of A: *E. zebra hartmannae* (Zoologisch Museum 7691, Amsterdam), B: *E. africanus somaliensis* (Laboratoire des Mammifères et Oiseaux du MNHN 1977-65, Paris), C: *E. caballus* (Laboratoire d'Anatomie Comparée du MNHN 1926-301, Paris), D: *E. quagga* (Rijksmuseum van Natuurlijke Historie 18243, Leiden), E: *E. burchelli granti* (National Museums of Kenya 2399, Nairobi) in lateral, ventral and dorsal views. The numbers and letters in the text below refer to measurements or characters illustrated in the figures. The complete set of measurements numbered from 1 to 30 is given in Eisenmann.⁵

Determination of Koffiefontein skulls

Ass skulls (B) can be readily distinguished from horse (C), Cape quagga (D), and plains zebra (E) skulls: in asses, the cranium (24) is long compared to the face (23); the frontal width (13) is large relative to the bizygomatic width (14); the external auditory meatus is very big (20); the distance (3) between the posterior border of the palate (staphylion) and the posterior border of the vomer (hormion) is long compared with the separation (4) of the latter and the basion ($\frac{3}{4}$ is the well-known and useful Franck index). The distinction between ass (B) skulls and mountain zebra (A) skulls is less evident but still apparent. Mountain zebras (like horses, Cape quaggas and plains zebras) have a relatively long face; their choanae are particularly long (9); the muzzle breadth behind the third incisors (17) is much larger than at the level of the diastema (17bis); the suture between the premaxillar and the nasal bones (NPMS) is peculiar. The Koffiefontein skulls MMK 4520, 4521, and 4656 undoubtedly belong to donkeys.

As we have seen, there is no difficulty in distinguishing horse and ass skulls. From mountain zebras, horse skulls differ by having a small external auditory meatus (20), a little-developed supra-occipital crest (16), subequal frontal and bizygomatic widths (13, 14), and a short distance between staphylion and hormion (3). A purely craniological distinction between horse, plains zebras and (especially) Cape quaggas may be more difficult but, in general, horses have shorter choanae (9), less-developed supra-occipital crests (16), wider muzzles at the diastema (17bis), and shorter distances between staphylion and hormion (3). There is no doubt that the Koffiefontein skull MMK 4159 belonged to a horse.

Comparative craniology of the Cape quagga

It has been suggested that skulls of Cape quaggas and of mountain zebras resemble each other more than the former resemble skulls of plains zebras.^{1,2} Before addressing that point, it is useful to emphasize the main craniological differences between plains and mountain zebras.¹³ In mountain zebras (A), the supra-occipital crest is wide (16); the external auditory meatus is large (20); the frontal width (13) is greater than the bizygomatic width (14); the distance between staphylion and hormion is long (3). These are 'ass-like' characters. Indeed, various authors¹⁴⁻¹⁷ have stressed the 'ass-like' exterior and internal anatomy of the mountain zebras as opposed to the 'horse-like' plains zebras. Beside the 'ass-like' skull features, mountain zebras can be distinguished from plains zebras (E) by having long and narrow choanae (9 and 10); shallow infraorbital bars (19); distinctive naso-frontal, inter-palatine, and naso-premaxillar sutures (NPMS); shorter diastemas (6) and longer upper cheek teeth series (8) and several other characters.²⁴

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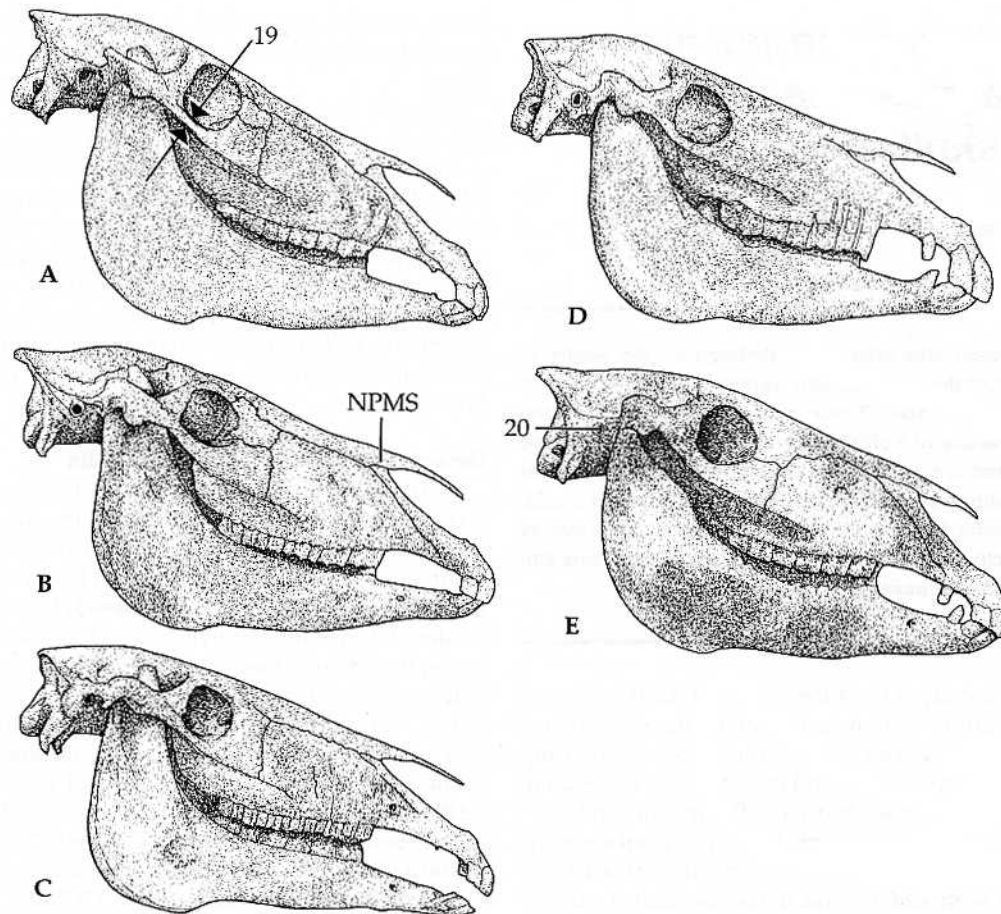


Fig. 1. Skulls of (A) *Equus zebra hartmannae*, (B) *E. africanus somaliensis*, (C) *E. caballus*, (D) *E. quagga* and (E) *E. burchelli granti* in lateral view. Measurements 19 and 20 are defined in Tables 1 and 2.

Far from having an 'ass-like' appearance (like mountain zebras), Cape quaggas are said to be very 'horse-like', more so even than plains zebras.¹⁸ The similarities extend to the skulls.¹⁹ Indeed, Cape quaggas' skulls (D) often have even shorter distances between staphylion and hormion (3), even smaller auditory orifices (20), and even narrower supra-occipital crests (16) than plains zebras. To these clearly cabaloid features may be added other characters often, although not exclusively, present in horses: shallow faces and crania, shallow infraorbital bars, and big teeth; moreover, cups are present, at least on lower I/1 and often also on lower I/2. One character seems very specific of Cape quaggas: the remarkable size of the incisors (17), still more emphasized by the narrowness of the muzzle at the diastema (17bis).

Why ~~are~~ Cape quagga skulls considered to be more similar to mountain zebras than to plains zebras?² To address this question, we must examine a number of possibly interrelated causes: sample composition, personal bias in the measurements, techniques of elaboration of the data, and choice of variables.

Klein and Cruz-Urbe² used for their study three Cape quagga skulls preserved in the British Museum (London), the Peabody Museum (Yale), and the Academy of Sciences (Philadelphia). Our observations include also the specimens preserved in Paris, Leiden, Amsterdam, London (University College), Berlin, Stuttgart, Turin, and Basel. Since doubt has been expressed regarding their validity,^{2,20} we stress that the specimens were accepted as belonging to the Cape quagga after careful considerations of museum data (6 and 21, in particular) and of the material itself. Our sample (Tables 1 and 2) is composed of 12 complete

adult skulls (it does not include the nearly mature skull of Stuttgart).

What variation can be expected when the same specimens are measured by different people? The three skulls of Cape quagga studied both by us and by Klein and Cruz-Urbe² afford the opportunity for such a comparison (Table 3). For the median of the basilar length, the relative difference is 2%. For the medians of 11 ratios, the difference ranges between 0 and 5%. The biggest differences are for the height of the face behind M3 (8%) and the cranial breadth (14%), clearly indicating a difference in the techniques of measurement. For these two variables, the comparison of data is not reliable.

Sample size and composition also influence the consistency of measurements, especially when the samples are small. Comparison of the samples of three skulls and 12 skulls (both measured by one of us) shows percentage differences between 0 and 5% for the medians of the basilar length and of 12 ratios (Table 3). The biggest differences are for the muzzle breadths (11%: the ratio is smaller, even more 'quagga-like', in the larger sample) and for the thickness of the infraorbital bar (12%: the ratio is larger).

The combination of personal bias and sample size results in the following differences between the medians (Table 3). In our sample of 12 Cape quagga skulls, the ratio of the thickness of the infraorbital bar is larger by 13%, and the ratio of hormion to basion distance is larger by 6% than in the sample of three skulls.² Moreover, according to our data,⁵ the means of the latter ratio vary little among modern species of *Equus* other than the domestic horse: from 0.245 in Grevy's zebras to 0.249 in hemionides. In ref. 2, the ratios are in general about 4% smaller than ours, but

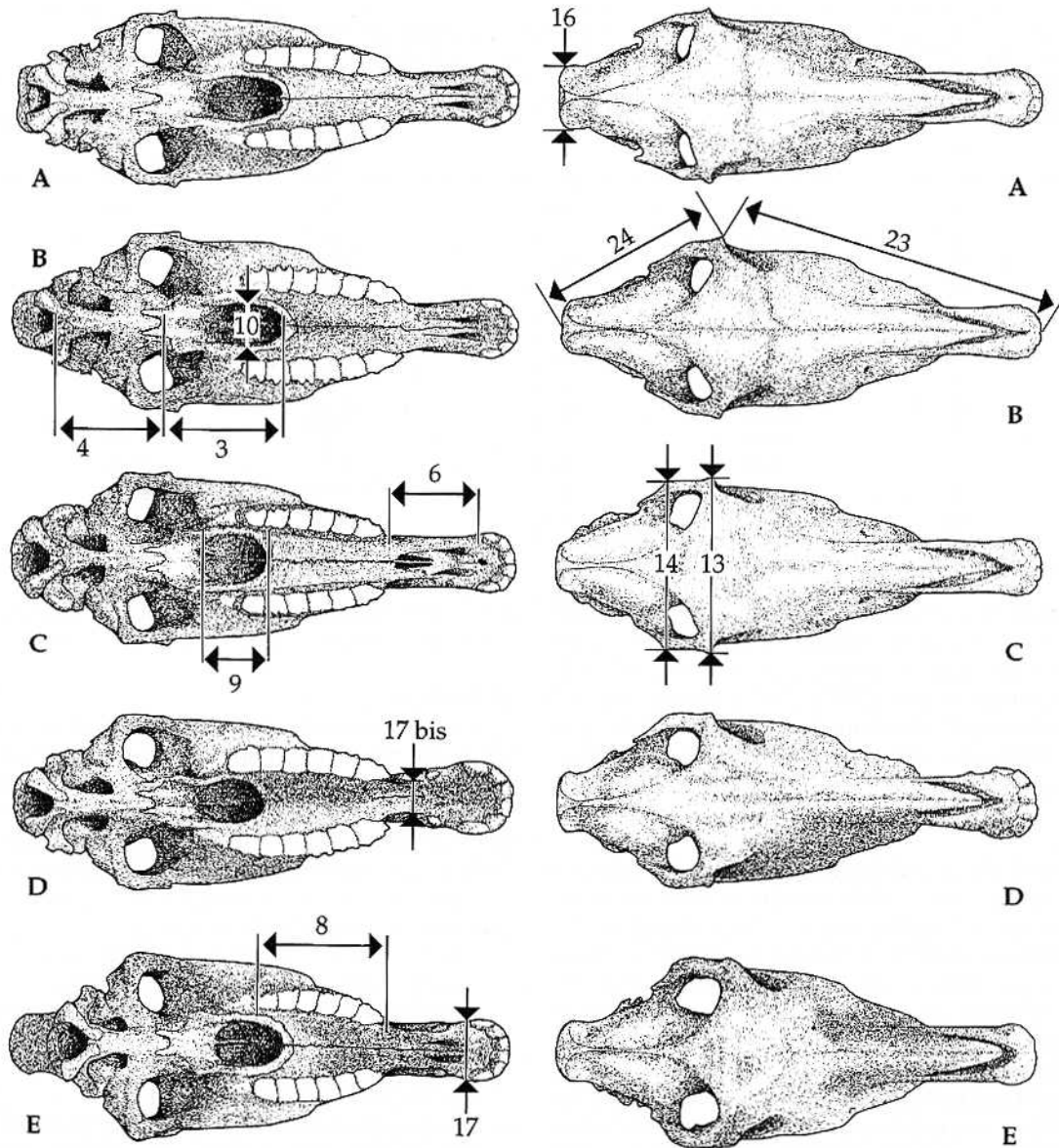


Fig. 2. Skulls of (A) *Equus zebra hartmannae*, (B) *E. africanus somaliensis*, (C) *E. caballus*, (D) *E. quagga* and (E) *E. burchelli granti* in ventral and dorsal views. Measurements are defined in Tables 1 and 2.

that should not affect the general pattern. What is surprising is the ratio for the donkeys, for which the difference is nearly double.

Klein and Cruz-Uribe² used cranial ratios (mostly on the basilar lengths) to distinguish horses, donkeys, plains zebras, and mountain zebras, by way of box plots for univariate comparisons and by way of discriminant analyses for multivariate comparisons. The same ratios are at the base of the tree resulting from their cluster analysis of all modern *Equus* species. They argue that the use of ratios is to be recommended because of the large variation of absolute measurements. We agree with this statement, but remark that the correspondence and discriminant analyses previously used by one of us²² neutralized the absolute size of raw measurements. The tree produced by the hierarchical ascendant classifications was naturally also based on 'size independent' variables. Thus, we think that the diverging interpretations are not the result of different techniques.

In the craniometrical system initially proposed by one of us,⁵ Klein and Cruz-Uribe² chose 21 variables which they have combined in 15 ratios. The box plots illustrated by them show that,

among the 15 ratios, three are irrelevant for distinguishing among Cape quaggas, plains zebras, and mountain zebras, i.e. those dealing with the hornion-basion distance, the breadth of the brain case, and the facial breadth. Three characters tend to group Cape quagga skulls with plains rather than with mountain zebras: the relative lengths of face and cranium, the ratio between muzzle widths, and the ratio between orbital diameters. One ratio at least is clearly 'horse-like': the maximum skull length versus the basilar length. For five ratios (diastema/premolars; premolars/molars; diameter of the foramen magnum; thickness of the infraorbital bar; frontal width/bizygomatic width) the Cape quagga is intermediate between plains zebras and mountain zebras. For three ratios, it is closer to the mountain zebra (relative length of cheek teeth; shallowness of the face and of the cranium).

We have noted that several of these 'mountain zebra-like' characters may also be found in horses (big cheek teeth, shallow infraorbital bars, shallow faces and crania). Indeed, one of our discriminant analyses²² assigned 8 out of 9 skulls of supposed quaggas to horses, although not one has ever been assigned to

Table 1. Adult Cape quagga skulls. n = number of specimens; \bar{x} = mean; min = minimum observed value; max = maximum observed value; s.d. = standard deviation; C.V. = variation coefficient (100s.d./ \bar{x}). 16: breadth of the supra-occipital crest; 23: anterior ocular line; 3: distance from palate to hornion; 4: distance from hornion to basion; 2–5: palatal length *sensu stricto*; 5: muzzle length; 17: muzzle breadth at the posterior borders of I3; 17bis: least muzzle breadth between the interalveolar borders; 13: frontal breadth; 10: greatest choanal breadth; 25: facial height in front of P2; 28: cranial height behind the orbits; 9: choanal length; 20: height of the external auditory meatus.

	n	\bar{x}	min	max	s.d.	C.V.
16	12	62.0	56.5	66.0	3.24	5.23
23	12	347.6	327.0	365.0	11.24	3.23
3	12	100.2	92.0	107.0	4.43	4.42
4	12	112.5	104.0	128.0	7.74	6.88
2–5	12	116.2	107.0	129.0	7.16	6.16
5	12	125.3	115.0	134.0	5.69	4.54
17	12	63.6	60.0	70.0	2.50	3.93
17bis	12	36.3	31.0	42.5	3.12	8.60
13	12	185.9	180.0	204.0	6.56	3.53
10	12	44.8	41.7	49.0	2.03	4.53
25	12	93.2	78.0	104.0	8.08	8.67
28	12	91.8	84.0	100.0	4.59	5.00
9	10	63.2	56.0	67.0	3.22	5.09
20	12	13.7	12.0	16.0	1.13	8.25

mountain zebras. We emphasize here that we have used variables missing in the study of Klein and Cruz-Uribe.² They correspond to conspicuous characters: measurements 16, 3, 9, 20 are larger in the mountain zebra (A) than in the Cape quagga (D). These are variables which also distinguish plains and mountain zebras.¹³ They augment the number of 'plains zebra-like' characters of the Cape quagga.

Conclusions

The differences between the findings published by Klein and Cruz-Uribe² and ourselves probably result not from a different choice of statistical methods but from a different choice of variables. Why did Klein and Cruz-Uribe not use all measurement criteria of our initial system,⁵ and in particular the four (3, 9, 16, 20) which show similarities between Cape quaggas and plains zebras? A possible answer is that these measurements are relatively imprecise and not easy to take. We believe, however, that characters should not be chosen for their precision but for the possibility that they may express a pattern. Most diagnostic measurements describe, even imprecisely, a difference that can be seen. In general, statistical treatments of measurements provide

only a confirmation of what is evident; they are rarely more important than basic observations.

Addendum

After this manuscript was submitted for publication in 1998, Klein and Cruz-Uribe reported²³ on multivariate analyses of separate contributions of size and shape on slightly different sets of measurements and samples. The results 'suggest that the quagga differed from the plains zebra about as much as the plains zebra differs from the mountain zebra' (ref. 23, abstract p. 81), and that 'the quagga may... have been specifically distinct'. Our comments on this paper are the following.

1. It is not true that 'Eisenmann found no meaningful difference between *E. quagga* and *E. burchelli*' (ref. 23, p. 85). Actually, in the paper quoted by Klein and Cruz-Uribe, it was stated that discriminant analyses provide evidence in favour of a specific distinction between *E. quagga* and *E. burchelli* (ref. 5, p. 36). We are still of this opinion.
2. The quagga sample analysed by Klein and Cruz-Uribe²³ now includes four skulls instead of three. We agree that the fourth specimen belongs also to a true quagga (it is the cast of a skull

Table 2. Basilar skull length and Klein and Cruz-Uribe² indices for the sample of 12 adult Cape quagga skulls. 1: basilar length; 6 = diastema; 7: length of P2/P3/P4; 7b: length of M1/M2/M3; 8: length of P2/ to M3; 29: breadth of the occipital condyles; 18: vertex length; 27: facial height behind M3; 21: antero-posterior diameter of the orbit; 22: dorsoventral diameter of the orbit; 19: infraorbital height; 24: posterior ocular line; 11: facial breadth; 14: bizygomatic breadth; 15: cranial breadth; n = number of specimens; other measurements and abbreviations as in Table 1.

	n	Median	\bar{x}	s.d.	Min	Max
1	12	44.3	44.9	1.28	43.0	47.2
17b/17	12	0.550	0.571	0.059	0.492	0.696
6/7	11	1.076	1.041	0.124	0.845	1.223
8/1	11	0.347	0.341	0.015	0.311	0.360
7/7b	11	1.191	1.178	0.046	1.101	1.233
29/1	12	0.163	0.164	0.010	0.151	0.183
4/1	12	0.248	0.251	0.012	0.234	0.273
18/1	12	1.108	1.107	0.015	1.085	1.135
27/1	12	0.284	0.278	0.024	0.218	0.306
28/1	12	0.205	0.204	0.010	0.190	0.222
22/21	12	0.961	0.949	0.043	0.871	1.018
19/1	12	0.026	0.026	0.004	0.020	0.031
23/24	12	1.946	1.930	0.060	1.835	2.005
11/1	12	0.318	0.318	0.013	0.302	0.342
13/14	12	1.012	1.008	0.008	0.967	1.039
15/1	12	0.211	0.209	0.008	0.195	0.226

Table 3. Comparison of the basilar lengths and skulls indices calculated for three Cape quagga skulls by Klein and Cruz-Urbe² (K3), on the same Cape quagga skulls by the present authors (V3), and on a sample of 12 Cape quagga skulls (V12).

	K3	V3	V12	K3-V3	%	V3-V12	%	K3-V12	%
1	456.0	445.0	443.5	11.0	2	1.5	0	12.5	3
17b/17	0.576	0.616	0.55	-0.040	-7	0.066	11	0.026	5
6/7	1.063	1.142	1.076	-0.079	-7	0.066	6	-0.013	-1
8/1	0.340	0.347	0.347	-0.001	-2	0.000	0	-0.007	-2
7/7b	1.194	1.142	1.191	0.052	5	-0.049	-4	0.003	0
29/1	0.164	0.170	0.163	-0.006	-4	0.007	4	0.001	1
4/1	0.234	0.243	0.248	-0.009	-4	-0.005	-2	-0.014	-6
18/1	1.086	1.112	1.108	-0.026	-2	0.004	0	-0.022	-2
27/1	0.259	0.281	0.284	-0.022	-d	-0.003	-1	-0.025	-10
28/1	0.206	0.200	0.205	0.006	3	-0.005	-3	0.001	0
22/21	0.915	0.964	0.961	-0.049	-5	0.003	0	-0.046	-5
19/1	0.023	0.023	0.026	0.000	0	-0.003	-12	-0.003	-13
23/24	1.876	1.949	1.946	-0.073	-4	0.003	0	-0.070	-4
11/1	0.328	0.318	0.318	0.010	3	0.000	0	0.010	3
13/14	1.000	1.038	1.012	-0.038	-4	0.026	3	-0.012	-1
15/1	0.232	0.204	0.211	0.028	14	-0.007	-3	0.021	10

preserved in Leiden, the original of which was, from the beginning, included in our sample and is illustrated both in ref. 5 and in this paper). But we do not agree that this sample of four skulls is 'at least as likely... to reflect the real craniometrical affinities of the quagga' as our sample of carefully checked 12 skulls. We do not see which, among the skulls studied in Paris, Amsterdam, London (University College), Berlin, Stuttgart, Turin, and Basel, 'may come from *E. burchelli*' (ref. 23, p. 85).

3. The set of measurements analysed in the new paper does not include several of the dimensions best discriminating quaggas and mountain zebras: diameter of the external auditory orifice, length of choanae, distance between vomer and hornion. Even if some of these measurements are lacking in the Koffiefontein material, they could be used to compare the four quagga skulls (in which they are present) and probably most of the 63 skulls of *E. zebra*.

4. We agree that it would be interesting to perform biomolecular studies on quagga skins, as well as other equid skins, and if possible bones, in order to gather more information about the relationship of these taxa.

5. We also agree with one of the referees that quaggas, plains zebras, and mountain zebras 'share some relationships with ancestral African equid populations' and that 'boundaries between taxa are not always distinct'.

The illustrations were prepared by H. Lavina from photographs taken by D. Serrette and one of the authors in the collections of the Zoologisch Museum, Amsterdam; Laboratoire des Mammifères et Oiseaux du MNHN, and Laboratoire d'Anatomie Comparée du MNHN, Paris, France; Rijksmuseum van Natuurlijke Historie, Leiden; National Museums of Kenya, Nairobi. Thanks are due to all the curators who welcomed us and helped by giving access to their collections, in particular to Peter Beaumont, the curator of the Koffiefontein skulls. Thanks are also due to the referees, whose suggestions improved our manuscript. This work was partly supported by the GDR 983 of the CNRS.

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1. Skinner J. (1996). Further light on speciation in the quagga. *S. Afr. J. Sci.* 92, 301-302.
 2. Klein R.G. and Cruz-Urbe K. (1996). The identification of *Equus* skulls to species, with particular reference to the craniometric and systematic affinities of the extinct South African quagga. In *Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals: Tributes to the Career of C.S. Churcher*, eds K.M. Stewart and K.L. Seymour, 589-629. University of Toronto Press, Toronto.

3. Eisenmann V. (1997). Does the taxonomy of the quagga really need to be reconsidered? *S. Afr. J. Sci.* 93, 66-67.
 4. Rau R. (1997). Does the taxonomy of the quagga really need to be reconsidered? *S. Afr. J. Sci.*, 93, 67-68.
 5. Eisenmann V. (1980). Les Chevaux (*Equus sensu lato*) fossiles et actuels: crânes et dents jugales supérieures. Cah. Paléont., 186 pp. CNRS, Paris
 6. Rau R.E. (1978). 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. *Ann. S. Afr. Mus.* 77, 27-45.
 7. Higuchi R.G., Wrischnik L. A., Oakes E., Matthew G., Benton Tong and Wilson A.C. (1987). Mitochondrial DNA of the extinct quagga: relatedness and extent of postmortem change. *J. molec. Evol.* 25, 283-287.
 8. Lowenstein J.M. and Ryder O.A. (1985). Immunological systematics of the extinct quagga (Equidae). *Experientia* 41, 1192-1193.
 9. Franck L. (1875). Ein Beitrag zur Rassenkunde unserer Pferde. *Landwirtschaftliche Jahrbücher* 4, 33-51.
 10. Branco W. (1883). Über eine fossile Säugethier Fauna von Punin bei Riobamba in Ecuador. *Paläont. Abhandlungen* 1(2), 57-204. Dames und Kayser, Berlin.
 11. Nehring A. (1884). Fossile Pferde aus deutschen Diluvial-Ablagerungen und ihre Beziehungen zu den lebenden Pferden. Ein Beitrag zur Geschichte des Hauspferdes. *Landwirtschaftliche Jahrbücher* 13, 81-160. Dames und Kayser, Berlin.
 12. Tscherski J. (1893). Beschreibung der Sammlung posttertiärer Säugethiere, Wissenssch. Resultate d. Neusibirischen Exp. i.d. J. 1885 u. 1886. 23. *Equus caballus*. *Mémoires de l'Académie Impériale des Sciences de Saint-Petersbourg*, 7ème série, Tome 40, 1, 257-383.
 13. Eisenmann V. and De Giuli C. (1974). Caractères distinctifs entre vrais Zèbres (*Equus zebra*) et Zèbres de Chapman (*Equus burchelli antiquorum*) d'après l'étude de 60 têtes osseuses. *Mammalia* 38, 509-543.
 14. Pocock R.I. (1902). A new arrangement of the existing species of Equidae with the description of a new subspecies of 'Zebra'. *Ann. Mag. Natural History*, ser. 7, 10(43), 304-308.
 15. Bourdelle E. (1934). Notes anatomiques et considérations zoologiques sur les Zèbres. *C.R. Congr. Soc. Sav.* 67: 99-112.
 16. Bourdelle E. (1936). Quelques caractères anatomiques du Zèbre de Hartmann (*E. zebra hartmannae* Matschie). *Bull. Mus. natn. Hist. nat. Paris* 2ème série, 8, 473-477.
 17. Groves C.P. and Willoughby D.P. (1981). Studies on the taxonomy and phylogeny of the genus *Equus*. *Mammalia* 45, 321-354.
 18. Bourdelle E. (1944). Chevaux, Anes et Zèbres. *Bull. Soc. natn. Acclimat. Fr.* 91, 49-71.
 19. Cabrera A. (1936). Subspecific and individual variation in the Burchell zebras. *J. Mammal.* 17, 89-112.
 20. Thackeray F. (1988). Zebras from Wonderwerk cave, northern Cape Province, South Africa: attempts to distinguish *Equus burchelli* and *Equus quagga*. *S. Afr. J. Sci.* 84, 99-101.
 21. Rau R. (1974). Revised list of the preserved material of the extinct Cape Colony quagga, *Equus quagga quagga* (Gmelin). *Ann. S. Afr. Mus.* 65, 41-87.
 22. Eisenmann V. and Turlot J.C. (1978). Sur la taxinomie du genre *Equus* (Equidés). *Les Cahiers de l'Analyse des Données*, vol.III (2), 179-201.
 23. Klein R.G. and Cruz-Urbe K. (1999). Craniometry of the genus *Equus* and the taxonomic affinities of the extinct South African quagga. *S. Afr. J. Sci.* 95, 81-86.
 24. Smuts M.M.S. and Penzhorn B.L. (1988). Descriptions of anatomical differences between skulls and mandibles of *Equus zebra* and *E. burchelli* from Southern Africa. *S. Afr. J. Zool.* 23, 328-336.