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SECTION A: PEER-REVIEWED PAPERS

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Anatomical comparison between skulls and mandibles of Hartmann's zebra *Equus zebra hartmannae* and Burchell's zebra *E. burchellii antiquorum* in Namibia

HH Berry†

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ABSTRACT

External anatomical features of skulls and mandibles of ten Hartmann's zebras and ten Burchell's zebras in Namibia are described. Out of 44 structural features examined, 13 differ significantly (p=0.001) to the extent that they can be used to unambiguously identify the two species from intact skulls and mandibles. These differences are found in the *foramen magnum*, *processus zygomaticus*, *crista pterygoidea*, *meatus acusticus externus*, *processus mastoideus*, *crista facialis*, *sutura frontonasalis*, *os frontale*, *foramina supraorbitale*, *crista sagittalis externa*, *processus palatini*, *processus retroarticularis* and interalveolar border of the mandible. Using a combination of some or all of these differences enables an observer to identify the skulls of these two species of zebra with relative ease.

Keywords: anatomy; *Equus burchellii antiquorum; Equus zebra hartmannae*; mandible; Namibia; skull; zebra

INTRODUCTION

In Namibia, Hartmann's or mountain zebra *Equus zebra hartmannae* Matschie, 1898 (hereafter ***Ez***) and Burchell's or plains zebra *E. burchellii antiquorum* H. Smith, 1841 (hereafter ***Eb***) intermingle in western Etosha National Park and increasingly so on freehold game farms where introduction of especially ***Eb*** takes place. Following mortalities, carcases are often rapidly reduced to skeletons by scavengers, making identification of which zebra species is involved difficult. Moreover, poaching of these zebra species has legal consequences in which defence lawyers for the accused argue that the State cannot prove whether the skull or mandible of a court exhibit is ***Ez*** or ***Eb***. Consequently, the purpose of my investigation was to examine and quantify differences that may occur in the skulls and mandibles of these species. I based my work on a similar study involving Cape mountain zebra *E. zebra zebra* Linnaeus, 1758 and *E. burchellii antiquorum* by Smuts & Penzhorn (1988).

METHODS AND METHODS

Taxonomy of the two zebra sub-species follows Meester *et al*. (1986). Ten skulls and mandibles (five males, five females) of ***Ez*** were obtained from the Namib-Naukluft Park where zebra were culled as part of management action. Similarly, ten skulls and mandibles of ***Eb*** were obtained from the Etosha Ecological Institute where specimens from natural mortalities in the Etosha National Park are stored. I estimated the age of the specimens, based on tooth development and attrition of ***Ez*** by Joubert (1972) and of ***Eb*** by Smuts (1974). I identified the skull and mandible structures according to an accepted international veterinary anatomical nomenclature (Anonymous 1983), following the procedure and illustrations used by Smuts & Penzhorn (1988). Using a vernier calliper, I measured to the nearest millimetre, the skulls of ***Ez*** from the caudal, lateral, dorsal and basal aspects, to serve as a basis for comparison. Its mandibles are described as a whole. I then compared measurements and morphological aspects of the skulls and mandibles of ***Eb*** to those of ***Ez***. All measurements were analysed, using a statistical package, to establish means, standard deviation (SD), and standard errors of the mean (SE). Using the t-test's paired two sample for means, I tested for significant differences at a probability level of 0.001. Furthermore, if an overlap in the range of any comparative measurements occurred where the means were significantly different, I discarded them as a distinguishing feature between the species. I use the illustrations published by Smuts & Penzhorn (1988) to illustrate the comparison between ***Ez*** and ***Eb***, annotating them with the differences observed in this study. The figures are therefore based on the South African and not the Namibian specimens.

RESULTS

The only marked sexual dimorphism in the skulls and mandibles of ***Ez*** and ***Eb*** are the well-developed canines in males, whilst the females exhibit vestigial canines. Small wolf teeth (*dens premolaris* 1) occurred uni- or bilaterally in three female ***Ez*** and none were observed in ***Eb***. The age classes of the specimens examined were: ***Ez*** 3 years (1 female), 5-6 years (3 males), 7-9 years (1 male), 9-11 years (1 male, 3 females), 11-13 years (1 female) and ***Eb*** 5-6 years (2 males, 3 females), 7-9 years (1 male, 1 female), 9-11 years (2 males, 1 female). The 3 year old specimen of ***Ez*** was sub-adult (permanent molar

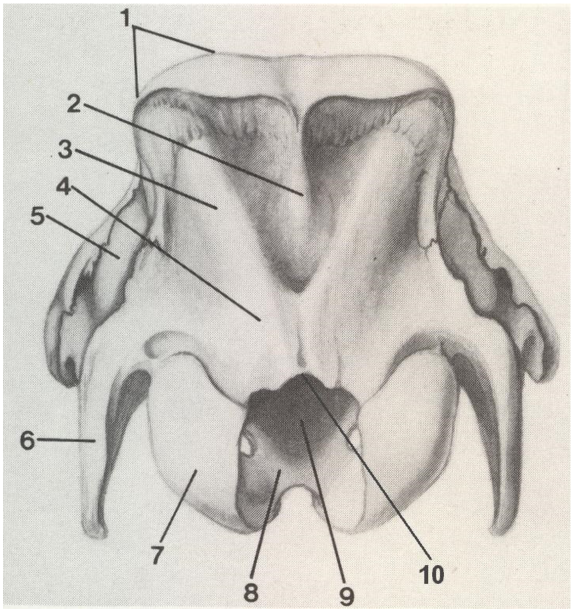


Figure 1: *Skull of* Equus zebra*, caudal aspect, giving the structural components. 1.* Crista nuchae*; 2.* Protuberantia occipitalis externa*; 3. 'Column' in* squama occipitalis*; 4.* Pars lateralis *of occipital bone; 5.* Processus mastoideus *of temporal bone; 6.* Processus paracondylaris*; 7.* Condylus occipitalis*; 8.* Pars basalis *of occipital bone; 9.* Foramen magnum *has median notch (10) in dorsal border. (Source: Smuts & Penzhorn 1988).*

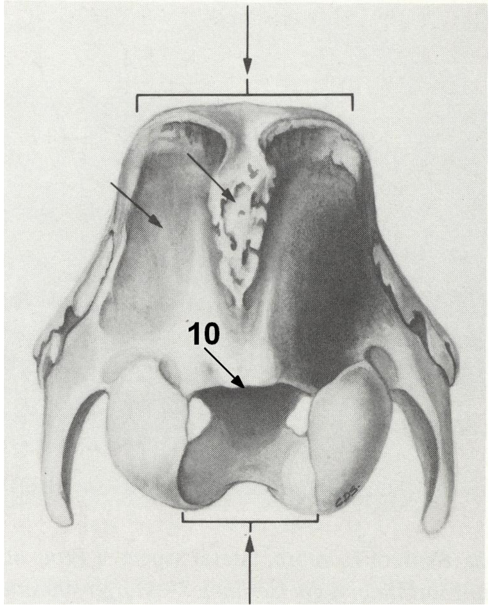


Figure 2: *Skull of* Equus burchellii*, caudal aspect. Unnumbered arrows are differences identified by Smuts & Penzhorn (1988). Numbered arrows are significant differences between* ***Eb*** *and* ***Ez*** *found in the present study: 10. Dorsal border of* foramen magnum *unnotched in* ***Eb****.*

3 erupting); the remaining specimens were all adult with permanent dentition.

When presenting the figures, I use the skull of ***Ez*** as a basis for naming the complete anatomical structure of the caudal, lateral, dorsal and ventral aspects, as provided by Smuts & Penzhorn (1988). I then compare these aspects with the skull of ***Eb***, indicating with arrowed numerals the significant differences that correspond with the structures in ***Ez***. Numbers preceding each anatomical feature in the lists below relate to the number that indicates this feature in the figure.

Caudal (nuchal) aspect (Figures 1 and 2)

10. *Foramen magnum*: The only visible difference is the morphology of the *foramen magnum*. It has a square shape in ***Ez***, with an orifice mean of 29 mm in the vertical and horizontal planes (range 26-31 mm). In ***Eb*** it is rectangular, with a mean of 30 mm (range 28-33 mm) in the vertical and 32 mm (range 30-34 mm) in the horizontal planes. There is overlap in the range of both the vertical and horizontal planes of 15 out of 20 specimens however, and consequently these measurements are not reliable parameters with which to distinguish the two species. The most consistent difference observed is the dorsal border of the *foramen magnum*, which has a distinct median notch in ***Ez***. In ***Eb*** this border forms a more or less straight line.

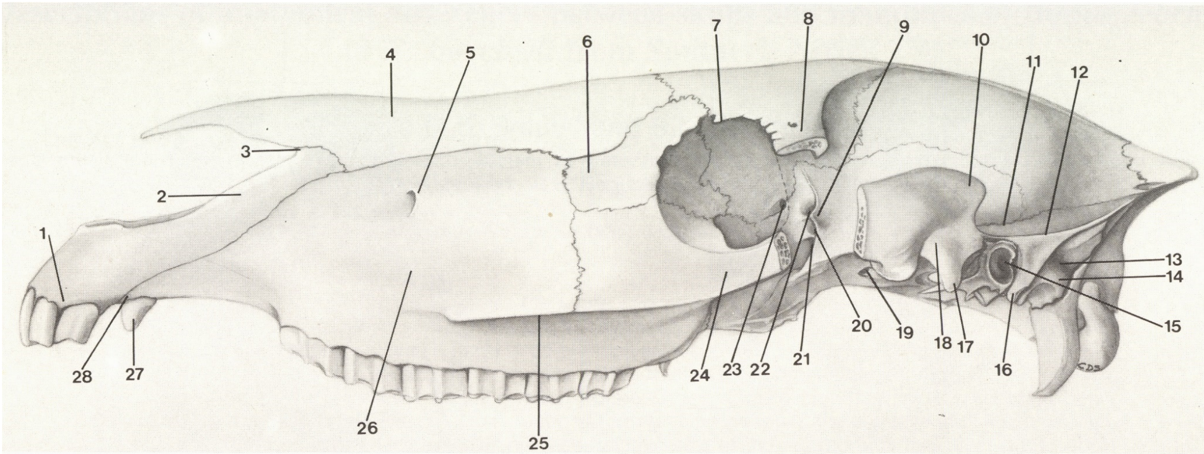
Lateral aspect (Figures 3 and 4)

7. *Aditus orbitae*: The osseous rims of the orbits in ***Ez*** are significantly less rostrocaudally (mean 54 mm, range 51-58 mm) than in ***Eb*** (mean 61 mm, range 57-70 mm). There is an overlap in three of the 40 orbital measurements however, meaning that there is the possibility of ambiguity in this parameter. It is therefore discarded as a distinguishing characteristic. The dorsoventral orbital measurements in ***Ez*** and ***Eb*** are 54 mm (range 48-57 mm) and 56 mm (range 52-69 mm) respectively. This is statistically not significant, with 24 out of 40 range overlaps, and therefore not a distinguishing feature.

8. *Processus zygomaticus*: The zygomatic processes of both frontal bones are significantly broader in ***Ez*** (mean 29 mm, range 26-33 mm) than in ***Eb*** (mean 20 mm, range 14-24 mm). This is a distinguishing feature. Moreover, in ***Ez*** the dorsal edge of the zygomatic arch is directed horizontally at a point caudal to the orbit. In ***Eb*** its direction is dorsocaudal.

9. *Crista pterygoidea*: In ***Ez*** the pterygoid crest has a pronounced triangular shape, whereas in ***Eb*** it is neither triangular nor prominent. This is considered a feature that distinguishes the species.

14. *Processus mastoideus*: The elongated mastoid process of the left and right temporal bones exhibit significant differences, with means of 53 mm (range



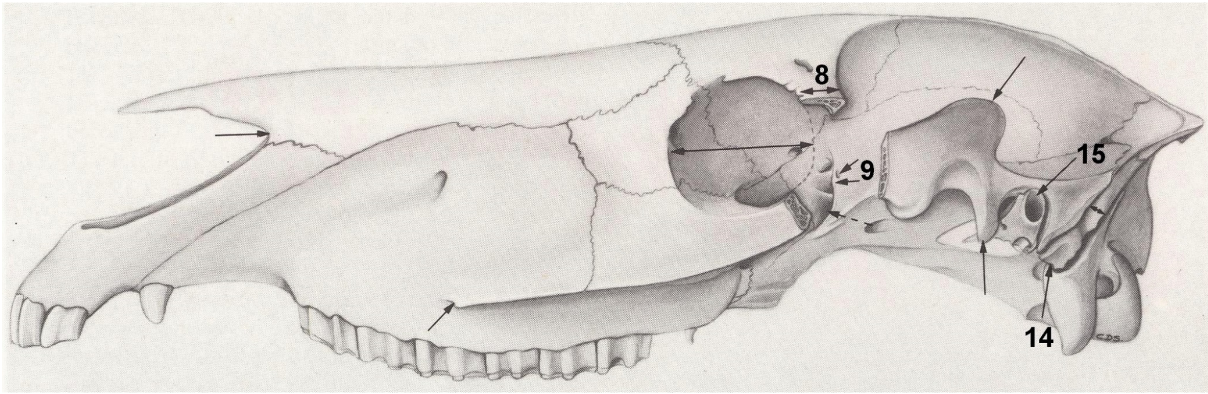


Figure 3 (top): *Skull of* Equus zebra, *lateral aspect, giving the structural components. 1.* Processus alveolaris *of* Os incisivum*; 2.* Processus nasalis*; 3.* Incisura nasoincisiva*; 4.* Os nasale*; 5.* Foramen infraorbitale*; 6.* Os lacrimale*; 7.* Margo supraorbitalis*; 8.* Processus zygomaticus *of frontal bone; 9.* Crista pterygoidea*; 10. Caudal end of* arcus zygomaticus*; 11.* Fossa temporalis*; 12.* Crista temporalis*; 13. Groove for caudal meningeal artery; 14.* Processus mastoideus*; 15.* Meatus acusticus externus*; 16.* Processus retrotympanicus*; 17.* Processus retroarticularis*; 18.* Fossa mandibularis*; 19.* Foramen alare caudale*; 20.* Fissura orbitalis*; 21.* Foramen rotundum*; 22.* Canalis opticus*; 23.* Foramen ethmoidale*; 24.* Processus temporalis *of zygomatic bone; 25.* Crista facialis*; 26.* Maxilla*; 27. Canine tooth; 28. Sutura maxilloincisiva. (Source: Smuts & Penzhorn 1988).*

Figure 4 (bottom): *Skull of* Equus burchellii, *lateral aspect. Unnumbered arrows are differences identified by Smuts & Penzhorn (1988). Numbered arrows are significant differences between* **Eb** *and* **Ez** *found in the present study. In* **Eb***: 8.* Processus zygomaticus *is narrower; 9.* Crista pterygoidea *is not triangulated or prominent; 14.* Processus mastoideus *is shorter; 15.* Meatus acusticus externus *points dorsolaterally at 45°.*

47-59 mm) in ***Ez*** and 19 mm (range 15-22 mm) in ***Eb***. No overlap in the ranges occurs; consequently, this is a distinguishing parameter in the species' skulls.

15. *Meatus acusticus externus*: In all specimens of ***Ez*** the external acoustic meatus is placed horizontally and faces laterally. In ***Eb*** it points dorsolaterally at an angle of about 45° in all specimens. This is a distinguishing feature.

17. *Processus retroarticularis*: Although the retroarticular process is, on average, significantly longer in ***Ez*** (mean 26 mm, range 21-30 mm) than in ***Eb*** (mean 19 mm, range 17-27 mm), 19 of the 40 measurements overlapped in their range. It is therefore not a reliably distinguishable feature.

19. *Foramen alare caudale*: Although the lengths of both left and right alar canals were significantly different for ***Ez*** (mean 24 mm, range 20-28 mm) and ***Eb*** (mean 20 mm, range 17-25 mm), 19 out of 40 measurements overlapped in their range. It is thus not a distinguishing feature.

Dorsal aspect (Figures 5 and 6)

2. *Crista nuchae*: The width of the nuchal crest in ***Ez*** is significantly greater (mean 71 mm, range 64-77 mm) than in ***Eb*** (mean 63 mm, range 57-70 mm). The overlap in eight of the 20 measurements makes it necessary to disregard this feature for identification purposes.

4. *Crista sagittalis externa*: The length of the external sagittal crest is significantly shorter (mean 81 mm, range 72-88 mm) in ***Ez*** than in ***Eb*** (mean 102 mm,

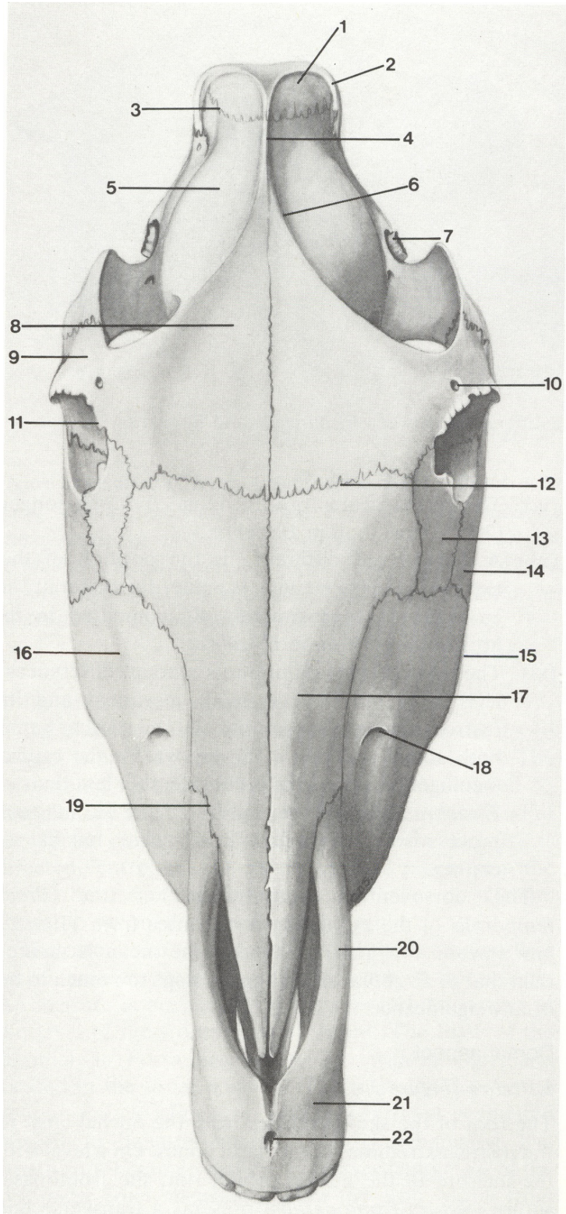


Figure 5: *Skull of* Equus zebra, *dorsal aspect, giving the structural components. 1.* Squama occipitalis*; 2.* Crista nuchae*; 3.* Sutura squamosoparietales*; 4.* Crista sagittalis externa*; 5.* Os parietale*; 6.* Linea temporalis*; 7.* Meatus acusticus externus*; 8.* Os frontale*; 9.* Processus zygomaticus *of frontal bone; 10.* Foramen supraorbitale*; 11.* Margo supraorbitalis*; 12.* Sutura frontonasalis*; 13.* Os Iacrimale*; 14.* Os zygomaticum*; 15.* Crista facialis*; 16.* Maxilla*; 17.* Os nasale*; 18.* Foramen infraorbitale*; 19.* Sutura nasoincisiva*; 20.* Processus nasalis ossis incisivi*; 21.* Corpus ossis incisivi*; 22.* Canalis interincisivus. *(Source: Smuts & Penzhorn 1988).*

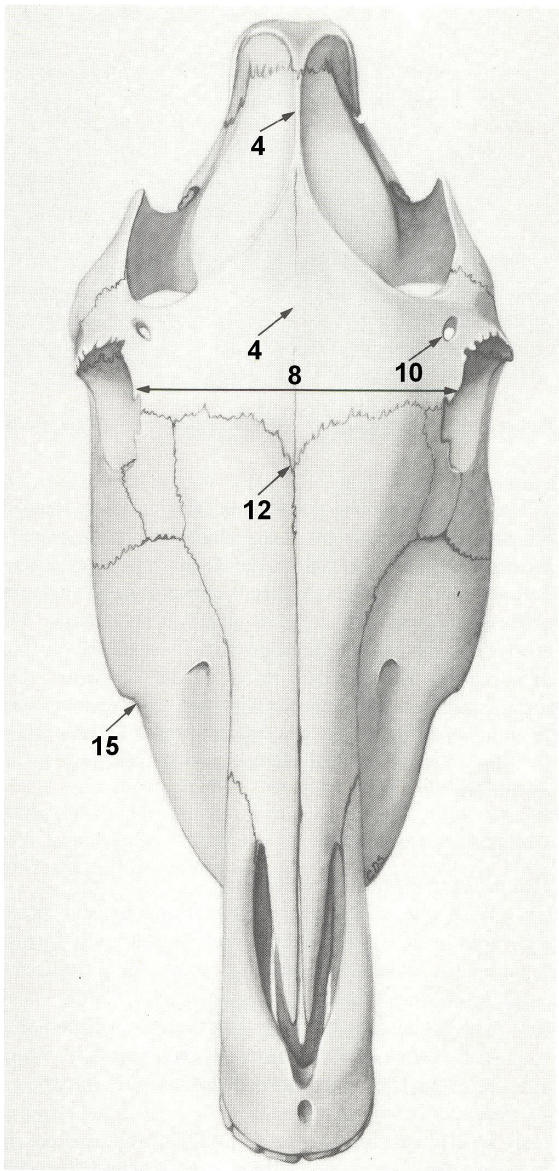


Figure 6: *Skull of* Equus burchellii, *dorsal aspect. Numbered arrows are differences between* **Eb** *and* **Ez** *identified by Smuts & Penzhorn (1988) and found to be significantly different in the present study. In* **Eb***: 4.* Crista sagittalis externa *is longer; 8.* Os frontale *is narrower; 10. The major* foramen supraorbitale *diameters are twice as large; 12.* Sutura frontonasalis *has a rostrally directed median angle; 15.* Crista facialis *is notched rostrally.*

range 92-112 mm), with no overlap. This feature distinguishes the two species.

8. *Os frontale*: In ***Ez*** the mean width of the frontal bones is 152 mm (range 142-165 mm). In ***Eb*** it is 130 mm (range 125-136 mm). This difference is significant, with no overlap between the ranges. It is a feature that distinguishes the species.

9. *Processus zygomaticus*: In ***Ez*** the outside width of the paired zygomatic processes of the lateral frontal bones, measured across the skull, is significantly greater (mean 188 mm, range 180-192 mm) than in ***Eb*** (mean 172 mm, range 166-180 mm). There is an overlap in one out of 20 measurements, thereby invalidating this as a distinguishing parameter.

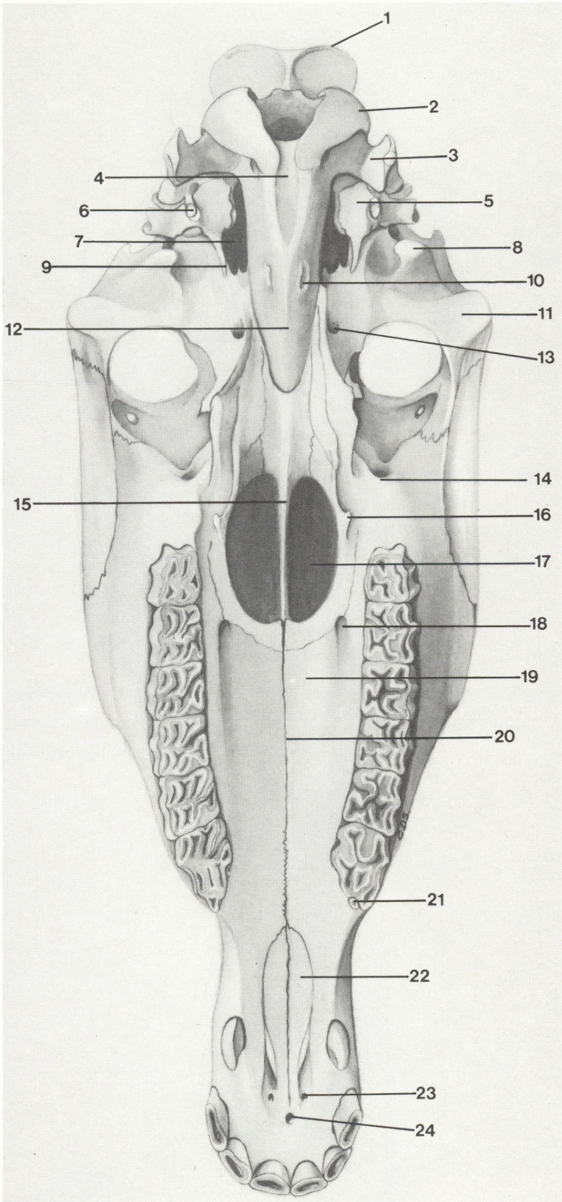


Figure 7: *Skull of* Equus zebra*, basal (ventral) aspect, giving the structural components. 1.* Crista nuchae*; 2.* Condylus occipitalis*; 3.* Fossa condylaris ventralis*; 4.* Pars basilaris *of occipital bone; 5.* Bulla tympanica*; 6.* Processus styloideus*; 7.* Foramen lacerum*; 8.* Processus retroarticularis*; 9.* Processus muscularis*; 10.* Tuberculum musculare*; 11. Articular surface of* fossa mandibularis*; 12.* Os basisphenoidale*; 13.* Foramen alare caudale*; 14.* Tuber maxillae*; 15.* Vomer*; 16.* Hamulus *of pterygoid bone; 17.* Choana*; 18.* Sulcus palatinus*; 19.* Processus palatinus *of maxilla; 20.* Sutura palatina mediana*; 21. Wolf tooth (PM 1); 22.* Processus palatinus *of incisive bone; 23. Opening of incisive canal; 24.* Canalis interincisivus*. (Source: Smuts & Penzhorn 1988)*

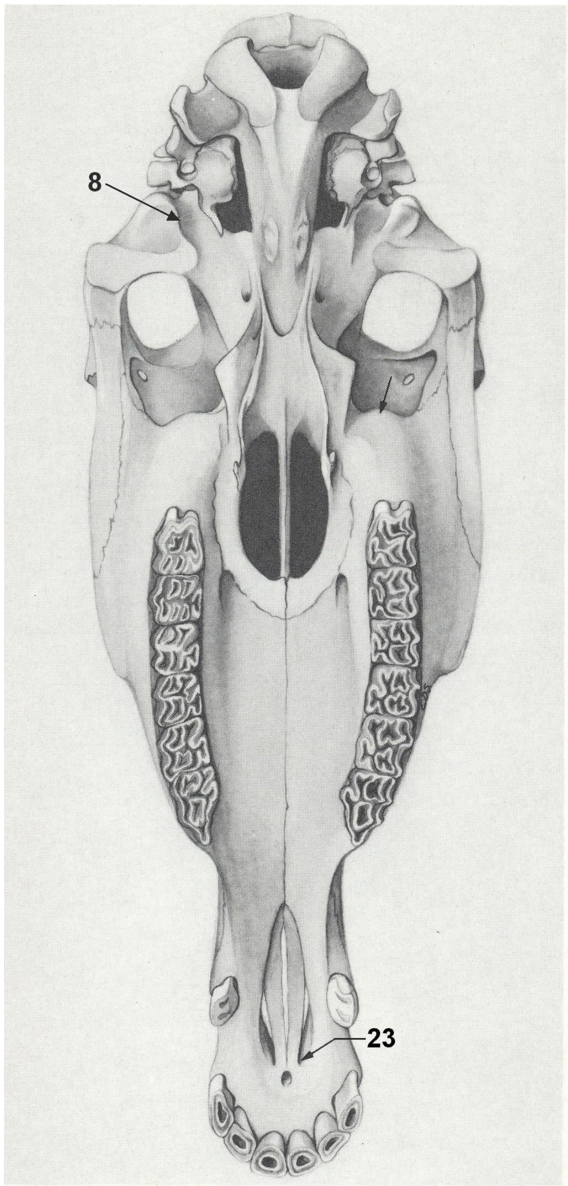


Figure 8: *Skull of* Equus burchellii*, basal (ventral) aspect. Numbered arrows are significant differences between* **Eb** *and* **Ez** *found in the present study. In* **Eb***: 8.* Processus retroarticularis *medial border is not notched; 22.* Processus palatinus foramina *are absent.*

10. *Foramina supraorbitale*: The supraorbital foramina in each frontal bone vary in number from 1-3 in ***Ez***. In ***Eb*** they are 1-2 in number, the minor foramen always being minute, and the diameter in the major foramen is twice that (5 mm) of ***Ez***. With experience, an observer will be able to distinguish the species using this parameter.

12. *Sutura frontonasalis*: The frontonasal suture is a more or less straight line in ***Ez***, while in ***Eb*** it forms

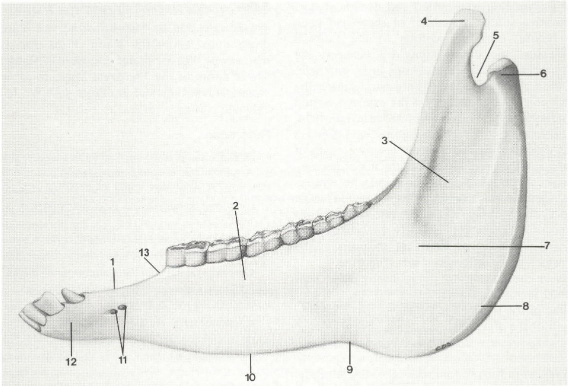


Figure 9: Mandible of Equus zebra*, left lateral aspect, giving the structural components. 1.* Margo interalveolaris*; 2.* Pars molaris *of* Corpus mandibulae*; 3.* Fossa masseterica*; 4.* Processus coronoideus*; 5.* Incisura mandibulae*; 6.* Processus condylaris*; 7.* Ramus mandibulae*: 8.* Angulus mandibulae; *9.* Incisura vasorum facialium*; 10.* Margo ventralis*; 11.* Foramen mantale *(paired); 12.* Pars incisiva *of* corpus mandibulae*; 13. Interalveolar border. (Source: Smuts & Penzhorn 1988).*

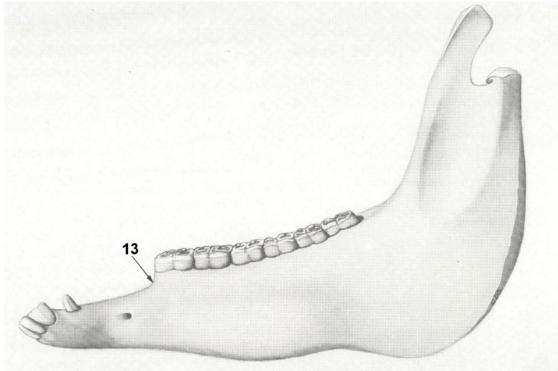


Figure 10: Mandible of Equus burchellii*, left lateral aspect. Arrow 13 is the significant difference between* **Eb** *and* **Ez** *identified by Smuts & Penzhorn (1988) and the present study, i.e. the interalveolar border has an angle of almost 90° in* **Eb**.

an angle, meeting rostrally in the median plane. This feature is diagnostic.

15. *Crista facialis*: In ***Ez*** there is no notch at the rostral end of the facial crest where it joins the alveolar process of the maxilla. In ***Eb*** there is a pronounced notch at this junction, when viewed from the dorsal aspect. An experienced observer will be able to use this to distinguish between the species.

Ventral (basal) aspect (Figures 7 and 8)

8. *Processus retroarticularis*: The medial border of the retroarticular process is notched in ***Ez***, whereas it is straight in ***Eb***. This difference is distinctive.

23. *Processus palatini*: There are paired foramina at the rostral end of the palatine fissure in all ten specimens of ***Ez***, forming a triangle with the *canalis interincisivus* at its apex rostrally. In ***Eb*** the paired foramina are absent in all ten specimens, with only the intercisive canal present at the rostral end of the median palatine suture. This is a distinguishing feature.

Mandible (lateral aspect) (Figures 9 and 10)

12. *Pars incisiva*: In ***Ez*** the width of the incisive plate between the base of incisors 3, measured at their lateral edge, is significantly less (mean 54 mm, range 48-57 mm) than in ***Eb*** (mean 58 mm, range 57-63 mm). There are three out of 20 measurements that overlap in their range, making this parameter unreliable.

13. Interalveolar border: In ***Ez*** there is no acute angle at the junction of this border with the border of the first premolar. In ***Eb*** they join in such a way that the junction forms an angle of almost 90°. This distinguishes the two species.

DISCUSSION AND CONCLUSIONS

Smuts & Penzhorn (1988) describe at least 17 anatomical differences between the skulls and mandibles of ten *E. z. zebra*, taken from South Africa's Mountain Zebra National Park, and ten *E. b. antiquorum* from various localities in South Africa's Transvaal Province and neighbouring Botswana. They found ambiguity in some of the parameters because of exceptions and overlap in measurements. Their data give means, providing ranges of measurements only where a degree of variation occurred, and no statistical analyses were presented. My investigation, based also on a small sample size, shows similar ambiguity in several parameters and I decided to discard the parameters with overlapping measurements, notwithstanding the fact that the means were statistically significantly different. Thereby the number of apparent differences in the specimens I examined is reduced from 18 to 13, which are mutually exclusive. Considerable variation exists in the range of measurements done on the 20 specimens I examined, and it is possible that with a larger sample, overlap of some parameters will occur, which were not recorded in this study.

The five parameters whose means are significantly different, but where overlap in their ranges occurs are: length of the alar canal, rostrocaudal diameter of the orbit, length of the retroarticular process, width of the nuchal crest, and width of the mandible's incisive plate.

Thirteen parameters are identified where the measurements or the morphology are mutually exclusive to either ***Ez*** or ***Eb***. These are:

Caudal

10. *Foramen magnum*: Presence of a median notch in the dorsal border in ***Ez***. Absence of this notch in ***Eb***.

Lateral

8. *Processus zygomaticus*: The zygomatic process of the frontal bone is broader in ***Ez***.

9. *Crista pterygoidea*: The pterygoid crest has a pronounced triangular shape and is prominent in ***Ez***. It has neither of these attributes in ***Eb***.

14. *Processus mastoideus*: The mastoid process of the temporal bones is longer in ***Ez***.

15. *Meatus acusticus externus*: The external acoustic meatus is placed horizontally and faces laterally in ***Ez***. It is directed dorsolaterally in ***Eb***.

Dorsal

4. *Crista sagittalis externa*: The length of the external sagittal crest is shorter in ***Ez*** than in ***Eb***.

8. *Os frontale*: The frontal bones are broader in ***Ez*** than in ***Eb***.

10. *Foramina supraorbitale*: The diameter of the major supraorbital foramen in each frontal bone is twice as large in ***Eb*** than it is in ***Ez***.

12. *Sutura frontonasalis*: The frontonasal suture forms a more or less straight line in ***Ez***. It has a rostrally directed angle in the median plane in ***Eb***.

15. *Crista facialis*: There is no notch at the rostral end of the facial crest in ***Ez***, whereas a pronounced notch occurs in ***Eb***.

Ventral

8. *Processus retroarticularis*: The medial border of the retroarticular process is notched in ***Ez***, whereas it is straight in ***Eb***.

23. *Processus palatini*: There are paired foramina at the rostral end of the palatine fissure in ***Ez***, which are absent in ***Eb***.

Mandible

13. Interalveolar border: There is no acute angle at the junction with the border of the first premolar in ***Ez***, compared to the angle of almost 90° in ***Eb***.

ACKNOWLEDGEMENTS

Profs. Malie Smuts and Banie Penzhorn (Faculty of Veterinary Science, Onderstepoort, South Africa) permitted me to use their illustrations of zebra skulls as a basis for reference. Prof. Alan Hodgson, Scientific Editor of the South African Journal of Zoology (now African Zoology), which holds the copyright, gave permission to reproduce these illustrations. I appreciate their helpfulness. I thank Chief Warden Wilferd Versfeld for access to skulls housed at the Etosha Ecological Institute. Likewise, Senior Warden Peter Bridgeford provided skulls from the Namib–Naukluft Park. My wife Conny checked all measurements and my son Paul modified the original figures of zebra skulls by computer.

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Postscript by editor:

Dr. Hu Berry was a renowned and respected Namibian scientist, serving in the Ministry of Environment and Tourism. At one time he was called upon to testify in a court case where poachers claimed that the evidence, zebra skulls, were from plains zebras and not from mountain zebras, which carried different penalties. After researching the differences between zebra skulls, he was able to convince the court that the skulls indeed belonged to mountain zebras (P. Bridgeford, pers. comm.).

The current paper deals with that work on zebra skulls. It was first submitted to Cimbebasia, the former journal of the National Museum of Namibia, in September 2003. At the time A. Kirk-Spriggs (pers. comm.) was editing Cimbebasia as a mostly unpaid volunteer. Dr. Berry's manuscript was peer-reviewed and accepted for publication in what would have been Cimbebasia volume 20. That volume, as well as Cimbebasia Memoir 10 (Advances in Afrotropical Arachnology, co-editor T. Bird) and Cimbebasia Memoir 11 (Lepidoptera of the Brandberg, co-editor W. Mey) were all in various stages of completion with manuscripts ranging from still under review to print-ready when Dr. Kirk-Spriggs left the museum in July 2004. None of these volumes were ever published (A. Kirk-Spriggs, T. Bird, and W. Mey, respectively, pers. comm.), nor did any other issues of Cimbebasia ever appear.

During recent clean-up operations at the National Museum all the comprising manuscripts of these volumes were found. They lack any indication of editorial activity subsequent to July 2004 although, somewhat bizarrely, literature (Suhling & Martens 2007; Kipping 2010) indicates that other papers were later accepted for a different 'Cimbebasia Memoir 10' that was also never published.

Most of the authors involved in all the abandoned volumes eventually published elsewhere, sometimes with great difficulty due to having to recreate original illustrations they could no longer access (K. Vohland, pers. comm.). Dr. Berry had not yet followed suit when he passed away in 2011, and his is today the only remaining unpublished manuscript from that time. The conservation law-enforcement aspects of the paper remain as relevant now as they were then, and NJE is honoured to publish it. The text has been left mostly unchanged, minor anachronisms and all.

Paul Berry is gratefully acknowledged for assistance and permission to publish his father's paper posthumously. Dr. Conrad Brain kindly agreed to check the content for currency. Former Naukluft warden Peter Bridgeford, Walfish Bay; former Cimbebasia editor Dr. Ashley Kirk-Spriggs, London; arachnologist Dr. Tharina Bird, Pretoria; lepidopterist Dr. Wolfram Mey, Berlin; and myriapodist Dr. Katrin Vohland, Berlin, are all thanked for providing contextual information.

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