Descriptions of anatomical differences between skulls and mandibles of *Equus zebra* and *E. burchelli* from Southern Africa

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The external anatomical differences between the skulls and mandibles of 10 mountain zebras *Equus zebra* and 10 plains zebras *E. burchelli* of both sexes were studied. The nomenclature used conforms to Nomina Anatomica Veterinaria (1983). Eleven structural differences are described for the first time and illustrated, viz., outline of the foramen magnum; length of the alar canal; comparative presence of the *For. alare parvum;* proportions of the mastoid process of the temporal bone; shape and development of the pterygoid crest; notch at the rostral end of the facial crest in *E. burchelli;* different inclination of the caudal end of the zygomatic arch; shape and length of the retroarticular process; relative size of the supraorbital foramina; presence of incisive canals in *E. zebra;* difference in the junction of the interalveolar border of the mandible with the alveolar border of the first cheek tooth. If three or more differences are used for identification, it should be possible to train any worker to distinguish between the skulls of these two species.

Die uitwendige anatomiese verskille tussen die skedels en onderkake van 10 bergkwaggas *Equus zebra* en 10 bontkwaggas *E. burchelli* van beide geslagte is bestudeer. Die nomenklatuur is volgens Nomina Anatomica Veterinaria (1983). Elf strukturele verskille word vir die eerste keer beskryf, naamlik: die vorm van die foramen magnum; die lengte van die alare kanaal; die vergelykende teenwoordigheid van die *For. alare parvum;* die afmetings van die mastoïd-uitsteeksel van die temporale been; die vorm en ontwikkeling van die *Crista pterygoidea;* die insnyding by die rostrale ent van die *Crista facialis* by *E. burchelli;* die verskil in helling van die koudale gedeelte van die *Arcus zygomaticus;* die vorm en lengte van die retroartikulêre uitsteeksel; die relatiewe grootte van die supraorbitale foramina; die teenwoordigheid van *Canales incisivi* by *E. zebra;* die verskil in aansluiting van die interalveolêre rand van die mandibel by die alveolêre rand van die eerste kiestand. As drie of meer verskille vir identifikasiedoeleindes gebruik sou word, sal dit moontlik wees om enige werker op te lei om tussen die skedels van hierdie twee spesies te onderskei.

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Veterinary anatomists studying species other than domestic mammals are often confused by descriptions of anatomical structures by zoologists and paleontologists using a terminology differing from that in current veterinary use. This study was undertaken to describe skulls and mandibles of mountain zebras *Equus zebra* and plains zebras *E. burchelli* from Southern Africa employing terms based on Nomina Anatomica Veterinaria and to define reliable differences between the two species. External surfaces only are described as museum specimens were used which could not be sectioned. We follow the taxonomy of Meester, Rautenbach, Dippenaar & Baker (1986).

Detailed craniometric studies on different equid species were carried out by Eisenmann & Turlot (1978); Piveteau (1979); Bennett (1980); Groves & Willoughby (1981). Specific differences between the skulls of mountain and plains zebras were described by Cooke (1943); Eisenmann & De Giuli (1974); Bennett (1980); Groves & Willoughby (1981). Lundholm (1951) described a skull of the extinct quagga *E. quagga* by comparing its characteristics to known characteristics of *E. zebra* and *E. burchelli.*

Materials and Methods

Ten skulls and mandibles (5 ♂♂; ♀♀) of each species were borrowed from the Transvaal Museum, Pretoria (*E. zebra*: TM 10079, 16414, 25915, 25918, 25919, 25920, 25923, 25926, 25927, 25929; *E. burchelli:* TM 681, 2083, 3501, 10061, 10064, 10072, 13190, 13201, 14171, 35499). The *E. zebra* specimens were all from the Mountain Zebra National Park (32°15'S / 24°41'E); they included two fillies of 7 and 8 months, two colts of ca. 6 and 12 months and six adults. The *E. burchelli* specimens were of adults only and came from various localities in the Transvaal and Botswana.

The skulls of *E. zebra* were described from the following aspects: caudal (nuchal), lateral, dorsal and basal (ventral). The mandibles were described as a whole. The skulls and mandibles of *E. burchelli* were then compared to those of *E. zebra* and notable differences listed. Vernier callipers were used for measuring.

The nomenclature used is based on the third edition of Nomina Anatomica Veterinaria (1983).

Results

Other than well-developed canines in the stallion, no marked sexual dimorphism was observed in the skulls and mandibles. Minor differences are pointed out, but otherwise measurements are lumped. Measurements of adult *E. zebra* skulls only are given. As this study was basically descriptive and not morphometric, an arbitrary decision was made to give ranges of measurements only where there was a reasonable degree of variation; means only are given otherwise.

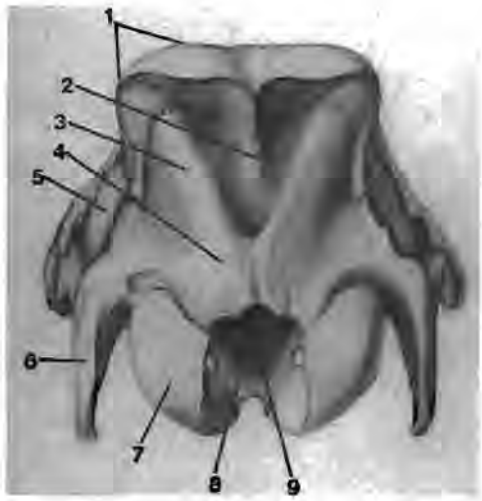

Figure 1a Skull of *E. zebra*, caudal aspect. 1 *Crista nuchae;* 2 *Protuberantia occipitalis externa;* 3 'Column' in *Squama occipitalis;* 4 *Pars lateralis* of occipital bone; 5 *Proc. mastoideus* of temporal bone; 6 *Proc. paracondylaris;* 7 *Condylus occipitalis;* 8 *Pars basalis* of occipital bone; 9 *For. magnum*.

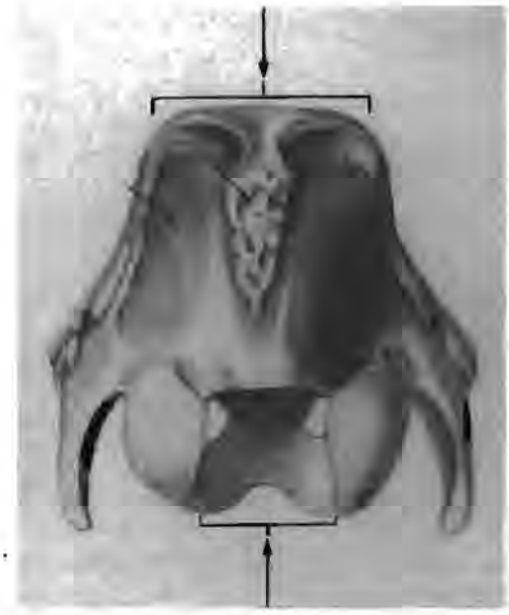

Figure 1b Skull of *E. burchelli*, caudal aspect. Arrows indicate the differences between *E. burchelli* and *E. zebra*.

Caudal (nuchal) aspect

E. zebra (Figure 1a)

The external laminae of the squamous and lateral parts of the occipital bone (*Os occipitale)* form the nuchal surface. The nuchal crest (*Crista nuchalis*) separates this surface from the roof of the skull. The nuchal crest is directed caudodorsally. The width of the nuchal crest (from side to side) is greater in mares (71–75 mm) than in stallions (66–68 mm) when measured at a level directly dorsal to the mastoid process of the left and right temporal bones. The squamous part of the occipital bone is quadrilateral in outline. The external occipital protuberance (*Protuberantia occipitalis externa*) is situated in the midline, directly ventrally to the nuchal crest. In the immature skull it consists of a prominent crest and is flanked by two deep, clearly demarcated depressions. In adults the crest is prominent in 3/6 specimens, while in the remainder it is represented by a slightly raised median ridge which is surrounded laterally and ventrally by a triangular, rough depression with its apex towards the foramen magnum. This depression is flanked by prominent columns forming a V which reaches to the level of the nuchal crest dorsally. The foramen magnum is ca. 30 mm wide; in all but one specimen a median notch is present in the dorsal border.

The occipital condyles (*Condyli occipitales*) flank the foramen magnum in such a way that the lateral borders of the foramen are vertical. The paracondylar processes (*Procc. paracondylares*) are directed ventrally, with convex lateral and concave medial surfaces. The rostral edge is always sharper than the caudal. The length varies: in immature skulls the paracondylar processes do not reach the level of the condyles while in adults they always end ca. 6 mm beyond the latter.

E. burchelli (Figure 1b)

The differences are the following:

(i) The width of the nuchal crest does not differ markedly in stallions (66–70 mm) and mares (69–70 mm).

(ii) The outline of the squamous part of the occipital bone presents a rounded border dorsally, compared to the quadrilateral shape of *E. zebra.*

(iii) The V-shaped columns, well-developed in *E. zebra,* are poorly defined and do not extend dorsally beyond the ventral border of the external occipital protuberance.

(iv) The external occipital protuberance is represented by a sharp vertical crest in 3/10 specimens, while in the remainder it consists of a rough, raised area which is surrounded by a V-shaped depression.

The *Foramen magnum* presents the most striking difference. It appears as a rectangular opening with its long axis in the horizontal plane. The latter measures ca. 36 mm between the occipital condyles while the dorsoventral measurement (taken from the dorsal border to the free end of the occipital condyle) is ca. 28 mm. The dorsal border forms a more or less straight line.

The paracondylar processses do not present notable differences.

Lateral aspect

E. zebra (Figure 2a)

The incisive bone (*Os incisivum*) contains three incisors in its alveolar process. The dorsocaudally directed nasal process forms an acute angle with the nasal bone (*Os nasale*) presenting a true nasoincisive notch (*Incisura nasoincisiva*). Along the dorsal border of the nasal bone a slight depression is evident midway along its length in all specimens. The canine tooth is placed directly caudal

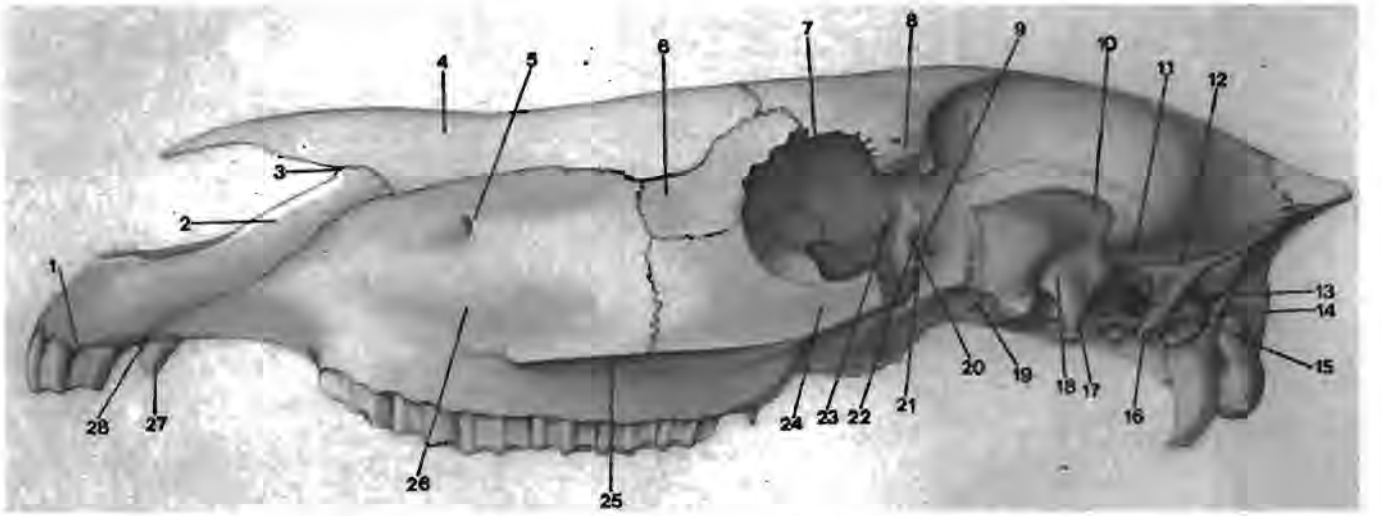

Figure 2a Skull of *E. zebra*, lateral aspect. 1 *Proc. alveolaris* of *Os incisivum;* 2 *Proc. nasalis;* 3 *Incisura nasoincisiva;* 4 *Os nasale;* 5 *For. infraorbitale;* 6 *Os lacrimale;* 7 *Margo supraorbitalis;* 8 *Proc. zygomaticus* of frontal bone; 9 *Crista pterygoidea;* 10 Caudal end of *Arcus zygomaticus;* 11 *Fossa temporalis;* 12 *Crista temporalis;* 13 Groove for caudal meningeal artery; 14 *Proc. mastoideus;* 15 *Meatus acusticus externus;* 16 *Proc. retrotympanicus;* 17 *Proc. retroarticularis;* 18 *Fossa mandibularis;* 19 *For. alare caudale;* 20 Fissura orbitalis; 21 *For. rotundum;* 22 *Can. opticus;* 23*For. ethmoidale;* 24 *Proc. temporalis* of zygomatic bone; 25*Crista facialis;* 26 *Maxilla;* 27 Canine tooth; 28 *Sutura maxilloincisiva.*

to the maxilloincisive suture.

The *Maxilla* forms the largest surface of the facial region. It narrows rostrally to the first cheek tooth. The infraorbital foramen (*For. infraorbitale*) is situated 55 mm dorsally and ca. 6 mm rostrally to the rostral end of the facial crest. The facial crest (*Crista facialis*) is directed ventrolaterally. A vertical line taken from the caudal border of the last molar tooth lies ca. 20 mm rostral to the medial margin of the orbit.

The osseus rim (*Aditus orbitae*) of the orbit measures ca. 60 mm dorsoventrally and ca. 55 mm rostrocaudally. An incisure is present along the supraorbital border at the level of the frontolacrimal suture. The fossa of the lacrimal sac (*Fossa sacci lacrimalis*) is wide and deep and located in the usual position. The fossa for the ventral oblique muscle (*Fossa m. obliqui ventralis*) is situated caudally to the latter and is not clearly demarcated. The dorsoventral diameter of the *Processes temporalis* of the zygomatic bone, measured below the orbit, varies from 10 to 15 mm (mean: 12,6 mm).

The *Proc. zygomaticus* of the frontal bone forms the caudal border of the orbit. It measures 26–29 mm in width (mean: 26,4 mm).

The flat, smooth medial surface of the orbit is formed by the orbital aspect (*Facies orbitalis*) of the lacrimal and frontal bones. Ventrally, where the orbital aspect of the frontal bone joins the perpendicular part of the palatine bone, a slight ridge is formed, demarcating the dorsal border of the pterygopalatine fossa (*Fossa pterygopalatina*). The latter has a smooth surface. It presents the round, large (mean diameter: 7 mm) sphenopalatine foramen (*For. sphenopalatinum*) rostrally. Rostrolaterally to the latter, the maxillary foramen (*For. maxillare*) is situated. A bar of bone ca. 5 mm wide separates the two foramina. The caudal palatine foramen (*For. palatinum caudale*) is located ca. 5 mm below the sphenopalatine foramen with a groove leading to it.

The ethmoid foramen (*For. ethmoidale*) is situated at the rostroventral border of the sphenoid incisure of the orbital part of the frontal bone. Caudally and ventrally to the ethmoid foramen are in dorsoventral sequence the optic canal (*Can. opticus*), the orbital fissure (*Fissura orbitalis*) and the round foramen (*For. rotundum*). They are separated by thin bony plates and are overlapped by the prominent pterygoid crest (*Crista pterygoidea*) of the pterygoid process of the basisphenoid. It is thin and triangular with a pointed rostral angle. The alar canal (*Can. alaris*) passes through the base of the pterygoid process of the sphenoid bone to end at the rostral alar foramen within the round foramen. It varies in length from 25 to 34 mm (mean: 28,3 mm). The caudal alar foramen is situated at the level of the rostral border of the articular surface of the mandibular fossa. The *For. alare parvum* is present in 5/10 specimens. The temporal fossa (*Fossa temporalis*) is limited laterally by the zygomatic arch (*Arcus zygomaticus*) and caudally by the temporal crest (*Crista temporalis*) which connects the sharp dorsal edge of the zygomatic arch with the nuchal crest. Caudally to the orbit the dorsal edge of the zygomatic arch is convex. Its caudal end is rounded and turns down almost perpendicularly before joining the temporal crest. Several accessory canals of the temporal meatus open rostrally to the crest.

The retroarticular process (*Proc. retroarticularis*) is slightly flattened rostrocaudally, but its borders are rounded. It is ca. 22 mm long. The tympanic incisure is bordered caudally by the retrotympanic process (*Proc. retrotympanicus*) which extends ventrally to approximately the same level as the free end of the retroarticular process. The external acoustic meatus (*Meatus acusticus externus*) is placed horizontally and faces laterally.

Figure 2b Skull of *E. burchelli*, lateral aspect. Arrows indicate the differences between *E. burchelli* and *E. zebra*.

The elongated mastoid process (*Proc. mastoideus*) of the temporal bone is situated behind the retrotympanic process. Its rostral and caudal borders are clearly defined and diverge slightly ventrally. The mastoid process is ca. 45 mm long in all adult specimens. The groove for the caudal meningeal artery is clearly visible, demarcating the ventral third of the process. The rostrocaudal measurement taken above the groove is ca. 12 mm, while it widens slightly below the groove to ca. 14 mm. The free ventral border is notched in all specimens.

E. burchelli (Figure 2b)

The differences are the following:

(i) With one exception, the nasal and incisive bones join in such a way that the notch is actually formed by the nasal bone so that a typical nasoincisive notch does not exist.

(ii) The facial crest is more horizontally inclined than in *E. zebra*, and the notch formed rostrally, where it joins the alveolar process of the maxilla, is deeper.

(iii) In 9/10 specimens, the diameter of the osseous rim of the orbit is greater rostrocaudally than dorsoventrally. The mean measurements are 60 mm × 56 mm.

(iv) The zygomatic process of the frontal bone is ca. 5 mm narrower than in *E. zebra*. It varies from 18 to 30 mm (mean: 21,8 mm) in width.

(v) Caudally to the orbit the dorsal edge of the zygomatic arch is directed dorsocaudally in contrast to its horizontal position in *E. zebra*.

(vi) The pterygoid crest is always less prominent and never has the pronounced triangular shape that is evident in *E. zebra*.

(vii) The alar canal is 5–7 mm shorter than in *E. zebra* – a difference that can easily be detected by an observant eye, as the caudal alar foramen is placed rostrally to the level of the articular surface of the mandibular fossa.

(viii) The *For. alare parvum* is present in 8/10 specimens.

(ix) The retroarticular process is ca. 3–5 mm longer (25–27 mm) than in *E. zebra*.

(x) A pronounced difference is the position of the external acoustic meatus. It points dorsolaterally at an angle of approximately 40° compared to its horizontal position in *E. zebra*.

(xi) The mastoid process presents marked differences: it is > 10 mm longer in all specimens and its rostrocaudal borders are parallel, measuring 8 mm both above and below the groove for the caudal meningeal artery. This is considerably less than in *E. zebra*. The free ventral border of the mastoid process is not concave as in *E. zebra*, but flat or convex.

The dorsoventral measurement of the *Proc. temporalis* of the zygomatic bone varies from 11 to 19 mm (mean: 14,4 mm). Although the mean is greater than that of *E. zebra*, the range overlaps too much to be of any significance.

Dorsal aspect

E. zebra (Figure 3a)

The roof of the skull stretches from the nuchal crest to the rostral extremities of the nasal bones. On a level with the incisure in the medial orbital rim, the frontonasal suture (*Sutura frontonasalis*) presents a transverse line which varies from straight to slightly convex rostrally.

The width of the frontal bones (*Ossa frontalia*), measured directly caudally to the incisures in the supraorbital rim (*Margo supraorbitalis*), is ca. 150 mm in all adult skulls. There is a depression in the frontal bone, midway between the zygomatic processes, in 8/10 specimens, while the surface is flat in the remainder. In juvenile skulls the depression extends rostrally to the frontonasal suture. The supraorbital foramen (*For. supraorbitale*), lodged in the base of the zygomatic process of the frontal bone, is single in 5/10 specimens and double in the remainder. The mean diameter is 2,4 mm.

The external sagittal crest (*Crista sagittalis externa*), measured from the caudal border of the nuchal crest to where it diverges into the temporal lines (*Linear*

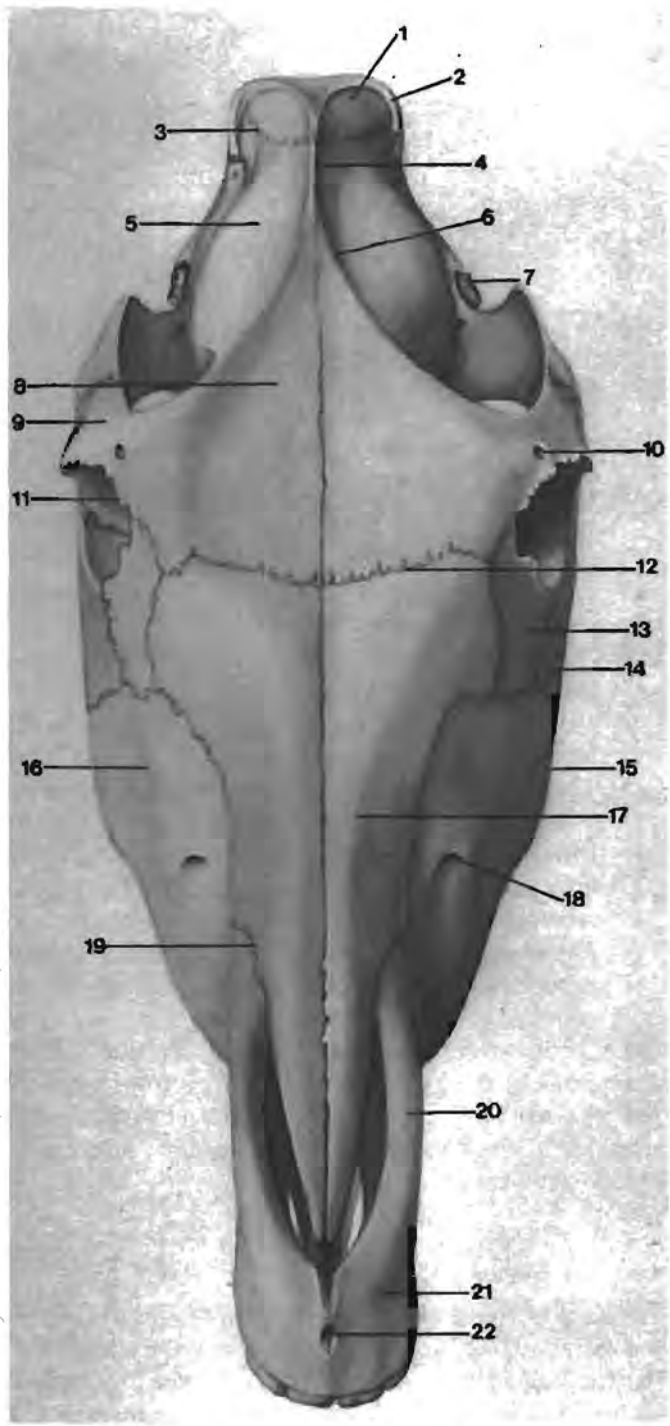

Figure 3a Skull of *E. zebra*, dorsal aspect. 1 *Squama occipitalis*; 2 *Crista nuchae*; 3 *Sutura squamosoparietales*; 4 *Crista sagittalis externa*; 5 *Os parietale*; 6 *Linea temporalis*; 7 *Meatus acusticus externus*; 8 *Os frontale*; 9 *Proc. zygomaticus* of frontal bone; 10 *For. supraorbitale*; 11 *Margo supraorbitalis*; 12 *Sutura frontonasalis*; 13 *Os lacrimale*; 14 *Os zygomaticum*; 15 *Crista facialis*; 16 *Maxilla*; 17 *Os nasale*; 18 *For. infraorbitale*; 19 *Sutura nasoincisiva*; 20 *Proc. nasalis ossis incisivi*; 21 *Corpus ossis incisivi*; 22 *Canalis interincisivus*.

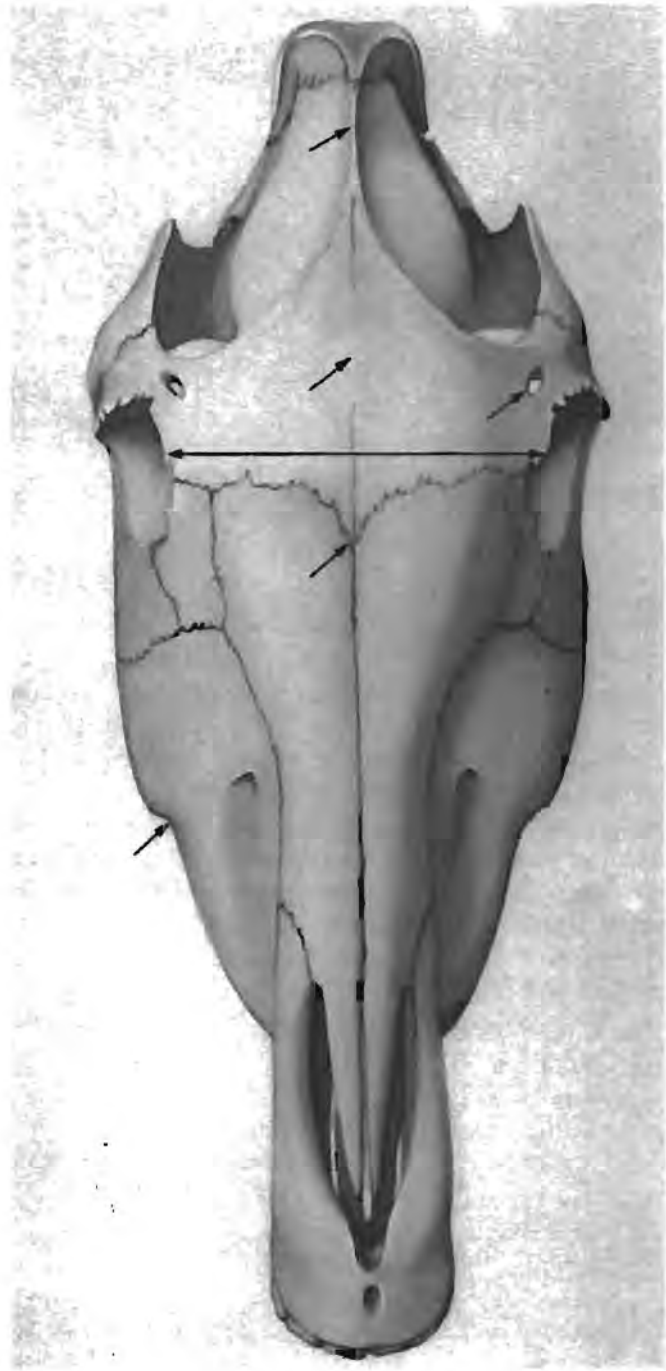

Figure 3b Skull of *E. burchelli*, dorsal aspect. Arrows indicate the differences between *E. burchelli* and *E. zebra*.

temporales), is ca. 89 mm long in all adult skulls.

The nuchal crest is in the horizontal plane in most specimens, while there is an upward tilt in two females and one male.

The parietal bones (*Ossa parietalia*), together with the frontal bones, form the roof of the cranium. In juvenile specimens ≤ 7 months of age an interparietal bone (*Os interparietale*) is clearly visible caudally in the midline. It is situated between the caudal third of the parietal bones and joins the squamous part of the occipital bone caudally.

E. burchelli (Figure 3b)

The differences are the following:

(i) The frontonasal sutures always meet at an angle rostrally in the median plane.

(ii) The width of the frontal bones ranges from 130 to 150 mm. The mean of 140 mm is 10 mm less that in

E. zebra. There is a slight but marked convexity between the roots of the zygomatic processes.

(iii) The supraorbital foramina are single in 9/10 specimens and ca. 5 mm in diameter, more than twice that of *E. zebra*.

(iv) The length of the external sagittal crest varies from 83 to 108 mm, with a mean of 97 mm. This is ca. 8 mm longer than in *E. zebra*.

The nuchal crest is horizontally placed in 3/10 specimens and tilted dorsally in 7/10. This difference is disregarded for identification purposes.

The notch where the rostral end of the facial crest joins the alveolar process of the maxilla is pronounced from this view.

Basal (ventral) aspect

E. zebra (Figure 4a)

The occipital condyles are wider caudally than rostrally. The convex surfaces of the major part of each condyle become flattened at its rostral end to form a slightly concave lip where it joins the basal part of the occipital bone. The ventral condylar fossa (*Fossa condylaris ventralis*) is deep. A single *Canalis n. hypoglossi* is present on each side.

The *Foramen lacerum* separates the base of the occipital bone from the petrous part of the temporal bone (*Os temporale*). The *Bulla tympanica* is not prominent and is flanked laterally by the styloid process (*Proc. styloideus*). The muscular process (*Proc. muscularis*) of the tympanic part of the temporal bone is pointed and measures from 12 to 18 mm. The muscular tubercle (*Tuberculum musculare*) at the occipitosphenoidal junction is paired and varies in prominence.

The articular surface of the mandibular fossa (*Fossa mandibularis*)is an elongated area, convex rostrocaudally and wider towards its lateral end. The medial border of the retroarticular process is concave. The hamulus of the pterygoid bone (*Os pterygoideum*) is broken off in the majority of specimens, but where present it has a pointed end, directed ventrally.

The choanae are oval in shape and separated by the vomer. The horizontal part of the palatine bone (*Os palatinum*) forms the lateral and rostral borders of the choana. In 9/10 specimens a well developed caudal nasal spine (*Spina nasalis caudalis*) is present. The length of its suture with the contralateral bone varies from 13 to 18 mm. The hard palate is 130–135 mm long.

The maxillary tuberosity (*Tuber maxillae*) projects ca. 40 mm caudally to the last molar tooth at a level which does not obstruct the entrance to the sphenopalatine and maxillary foramina. The palatine process (*Processus palatinus*) of the maxilla forms most of the hard palate and is slightly concave.

The palatine groove (*Sulcus palatinus*) is ca. 10 mm medially to the cheek teeth. At the level of the third premolar it becomes indistinct. The midline suture (*Sutura palatina mediana*) between the palatine processes of the maxilla forms an almost straight line caudally. In the rostral third the suture is characterized by a zig-zag pattern.

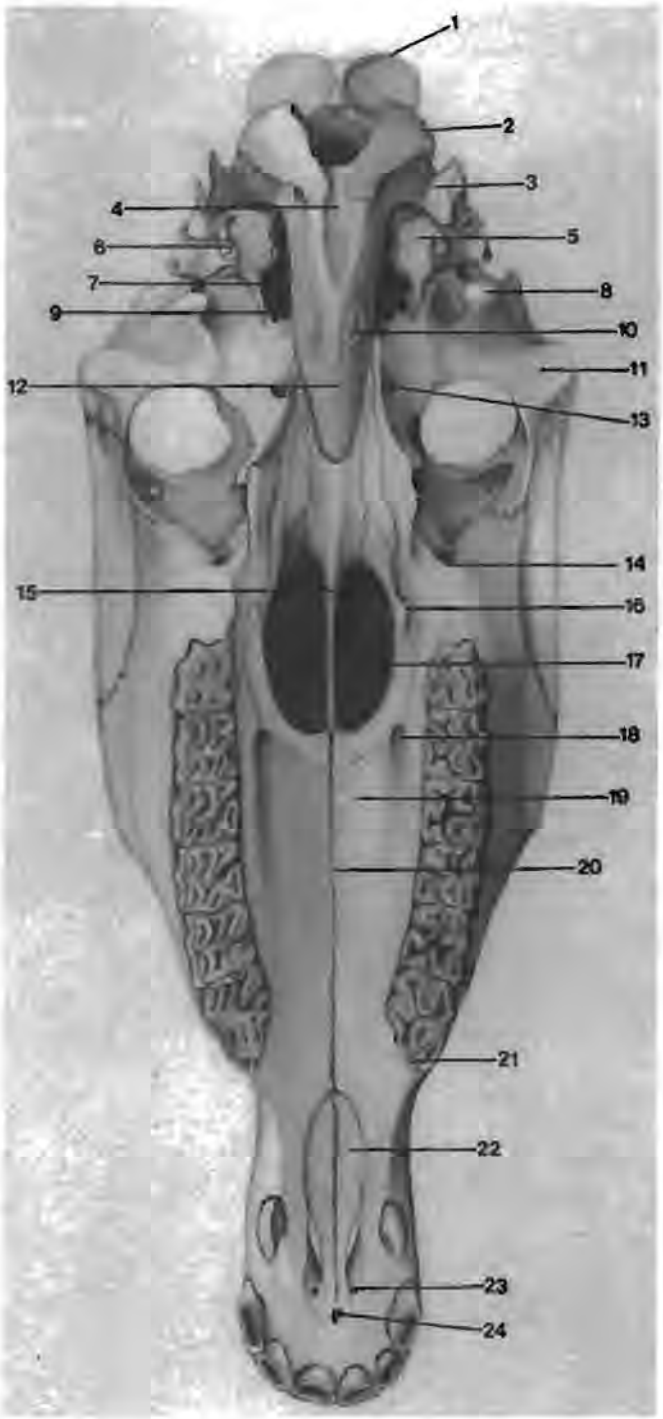

Figure 4a Skull of *E. zebra*, basal (ventral) aspect. 1 *Crista nuchae;* 2 *Condylus occipitalis;* 3 *Fossa condylaris ventralis;* 4 *Pars basilaris* of occipital bone; 5 *Bulla tympanica;* 6 *Proc. styloideus;* 7 *For. lacerum;* 8 *Proc. retroarticularis;* 9 *Proc. muscularis;* 10 *Tuberculum musculare;* 11 Articular surface of *Fossa mandibularis;* 12 *Os basisphenoidale;* 13 *or. alare caudale;* 14 *Tuber maxillae;* 15 *Vomer;* 16 *Hamulus* of pterygoid bone; 17 *Choana;* 18 *Sulcus platinus;* 19 *Proc. palatinus* of maxilla; 20 *Sutura palatina mediana;* 21 Wolf tooth (PM 1); 22 *Proc. palatinus* of incisive bone; 23 Opening of incisive canal; 24 *Can. interincisivus.*

The palatine processes (*Processus palatini*) of the incisive bone project caudally in the palatine fissure (*Fissura palatina*) attaching variably to the borders of the

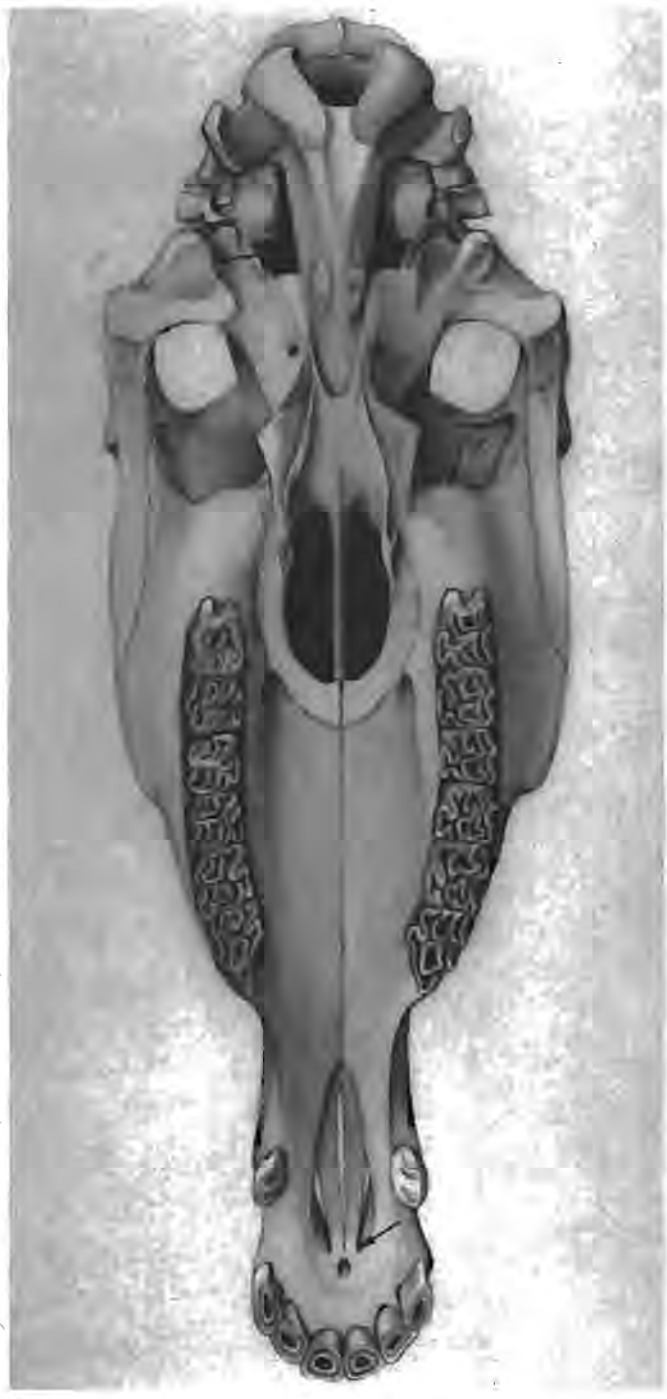

Figure 4b *E. burchelli*, basal (ventral) aspect. Arrows indicate the differences between *E. burchelli* and *E. zebra*.

fissure. A pair of foramina is present at the rostral end of the palatine fissure. Each foramen leads to a canal which traverses the substance of the incisive bone to open in the nasal cavity, thus connecting the oral and nasal cavities as incisive canals. The large interincisive canal (*Canalis interincisivus*) occurs in the midline, rostrally to the latter.

Well-developed canines are present in all the male specimens. In females they are rudimentary.

Small wolf teeth (*Dens premolaris I*) occur in 7/10 specimens uni- or bilaterally. They are situated either at the mediorostral aspect of PM 2, or rostrally to the latter.

E. burchelli (Figure 4b)

The differences are the following:

(i) The medial border of the retroarticular process is straight and not notched as in *E. zebra*.

(ii) The maxillary tuberosity extends ca. 50 mm caudally to the last molar tooth, overlapping the entrance to the sphenopalatine and maxillary foramina.

(iii) Incisive canals at the rostral end of the palatine fissure are absent in all specimens.

The sutures of the hard palate: the length of the suture between the horizontal parts of the palatine bones appear to be longer, but here are too many variations in both species to rely on this point. The suture between the palatine processes of the maxillae are straighter in all specimens. The length of the hard palate does not differ markedly.

Mandible

E. zebra (Figure 5a)

The two halves of the mandible are fused in all the specimens, including the 6-month-old foal.

The *Ramus mandibulae* is tall with the caudal border slightly convex and almost vertical, while the straight rostral border is inclined dorsocaudally. The coronoid process (*Proc. coronoideus*) is flattened and directed dorsocaudally in the sagittal plane. The distance between the free ends of the coronoid processes varies from 120 to 130 mm. It projects ca. 35 mm beyond the level of the condylar process (*Processus condylaris*). The head of the condylar process (*Caput mandibulae*) is convex and its long axis is in the transverse plane. Medially it ends in a caudally directed projection.

The mandibular notch (*Incisura mandibulae*) is open and rounded. The most prominent depression of the masseteric fossa (*Fossa masseterica*) occupies the rostral two thirds of the lateral surface of the ramus. The mandibular angle (*Angulus mandibulae*) is thickened.

The mandibular foramen (*For. mandibulae*) occurs rostrally to the pronounced pterygoid fossa (*Fossa pterygoidea*) on the medial surface of the ramus, in line with the cheek teeth.

The ventral border of the molar part of the body (*Corpus mandibulae*) is gently convex rostrally to the vascular incisure of the face (*Inc. vasorum facialium*), but as its junction with the incisive part there is a concavity. The alveolar border contains six alveoli for the cheek teeth.

On a level with the middle of the interalveolar border a single or double mental foramen (*For. mentale*) occurs.

The interalveolar border is straight. On lateral view it is directed at a slight dorsocaudal angle to join the alveolar border at the base of the first cheek tooth. The incisive part contains three alveoli for the incisor teeth, with the alveolus for the canine tooth behind them. The angle of divergence (*Angulus mentalis*) is reasonably sharp, with ca. 70 mm between the caudal aspects of the last cheek teeth.

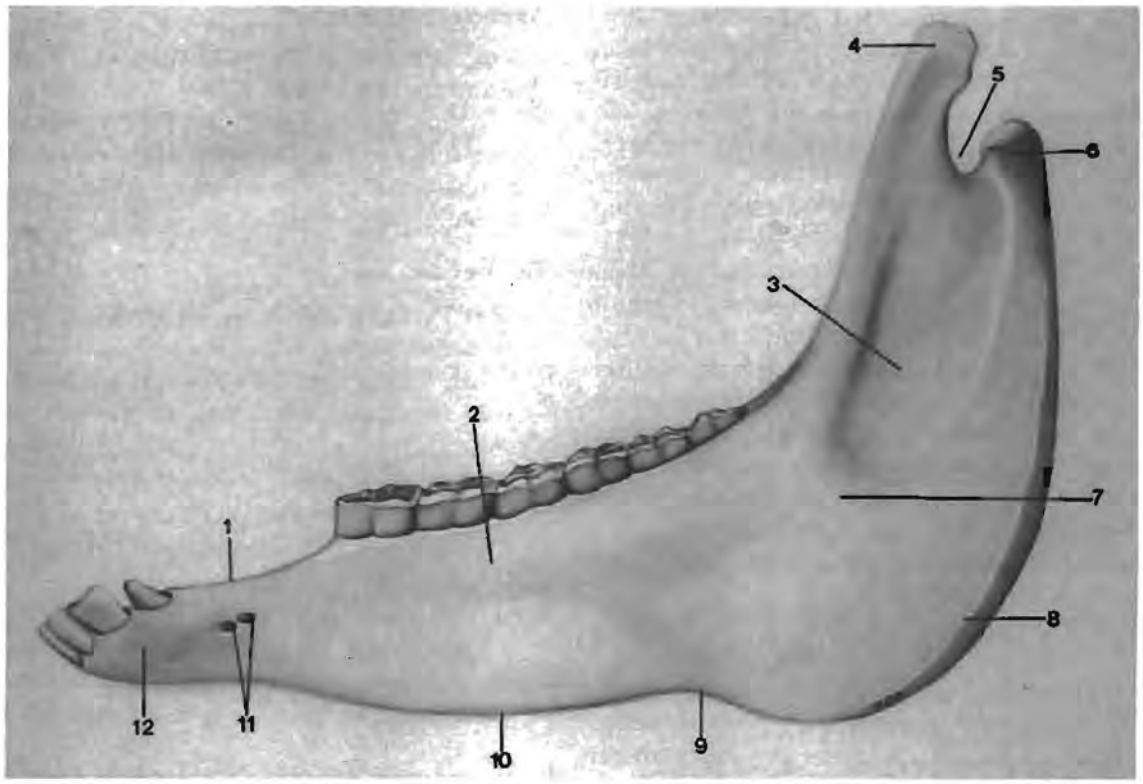

Figure 5a Mandible of *E. zebra*, left lateral aspect. 1 *Margo interalveolaris;* 2 *Pars molaris* of *Corpus mandibulae;* 3 *Fossa masseterica;* 4 *Proc. coronoideus;* 5 *Incisura mandibulae;* 6 *Proc. condylaris;* 7 *Ramus mandibulae;* 8 *Angulus mandibulae;* 9 *Incisura vasorum facialium;* 10 *Margo ventralis;* 11 *For. mantale* (paired); 12 *Pars incisiva* of *Corpus mandibulae.*

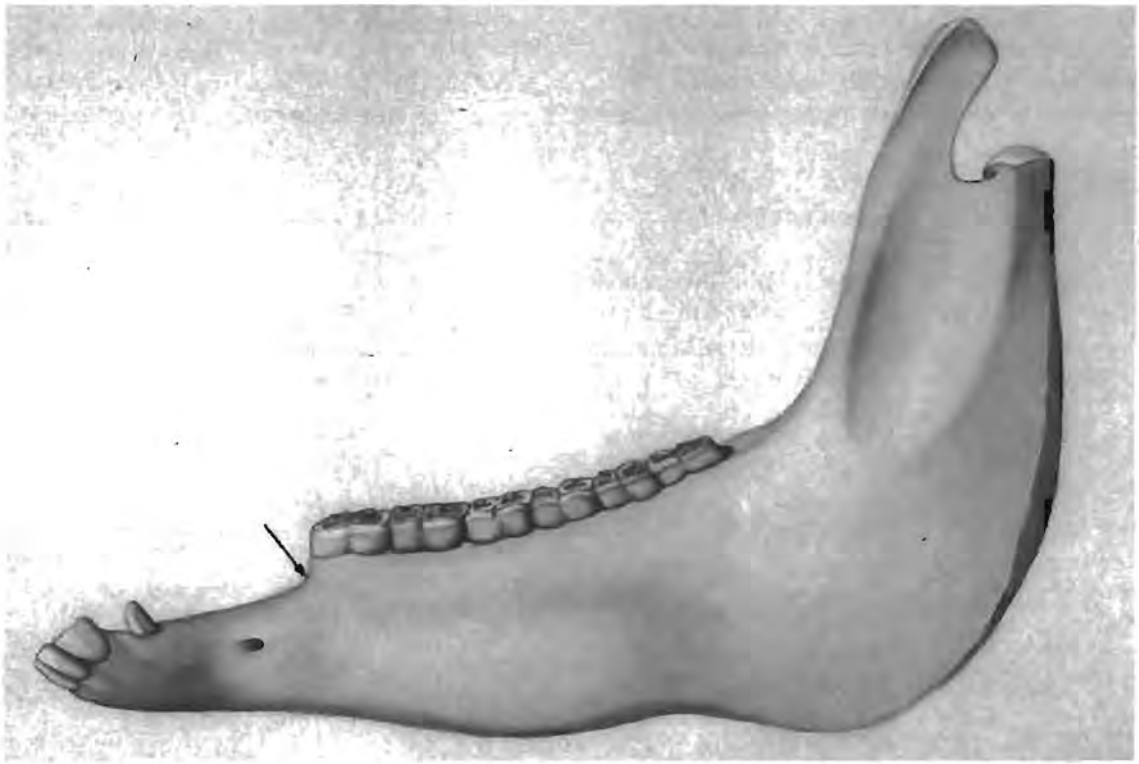

Figure 5b Mandible of *E. burchelli*, left lateral aspect. Arrow indicates main difference between *E. burchelli* and *E. zebra.*

E. burchelli (Figure 5b)

The only reliable difference was the following:
The interalveolar border joins the alveolar border of the first cheek tooth in such a way that it forms an angle of almost 90° at this level.

Discussion

Several anatomical differences between the skulls of *E.*

zebra and *E. burchelli* were noted and documented in this comparative study. A number of them had been described before, e.g. the position of the external acoustic meatus, the dorsal convexity between the zygomatic processes of the frontal bone in *E. burchelli,* the shape of the orbital rim, the fronto-nasal suture, the nasoincisive notch and the length of the external sagittal crest (Lundholm 1951; Eisenmann & de Giuli 1974; Piveteau 1979; and Groves & Willoughby 1981). Certain differences described before, i.e. the relative length of the diastema and the premolar row of the upper jaw, the difference in shape of the choanae and the sutures rostrally to them as well as their reference to the length of the vomer, do not appear as reliable differences in this study. A possible reason could be that specimens from populations sampled by us were not included in the studies in which these differences were reported.

As far as we could ascertain, the following differences are described for the first time:

(i) Outline of the foramen magnum.
(ii) Length of the alar canal.
(iii) Constant presence of the *For. alare parvum* in *E. burchelli,* with a 50% occurrence only in *E. zebra.*
(iv) Differences in the mastoid process of the temporal bone.
(v) Shape and extent of the pterygoid crest.
(vi) Notch at the rostral end of the facial crest in *E. burchelli.*
(vii) Different inclination of the caudal end of the zygomatic arch.
(viii) Shape and length of the retroarticular process.
(ix) Relative size of the supraorbital foramina.
(x) Presence of incisive canals in *E. zebra* and their absence in *E. burchelli.*
(xi) Junction of the interalveolar border of the mandible with the alveolar border of the first cheek tooth.

We believe that if three or more of the differences described are used in identifying the skulls of these two species, any worker can be trained to distinguish accurately between *E. zebra* and *E. burchelli.*

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