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EQUUS CAPENSIS (MAMMALIA, PERISSODACTYLA) FROM ELANDSFONTEIN

by

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ABSTRACT

The skull and limb bones collected at Elandsfontein, Cape indicate that *E. capensis* was different from a Grevy's zebra. The body proportions were similar to those of an extant draft horse *(E. caballus)* and the skull resembled those of true Cape quaggas and a fossil Algerian plains zebra, *E. mauritanicus*.

KEYWORDS: Pleistocene, Elandsfontein, *Equus capensis*, zebras.

INTRODUCTION

Because *Equus capensis* is a large equid and because the Grevy's zebra is the largest of extant wild equids, it has sometimes been considered that they were conspecific (Churcher & Richardson 1978; Churcher 1986, 1993). This preliminary paper intends to point out some of the general features of *E. capensis* which, as noted by Broom (1913) "was more powerfully built but did not stand so high" as "a modern horse 15 hands in high".

Skull

There is a well preserved skull of *E. capensis* from Elandsfontein (Hendey & Deacon 1977) in the South African Museum Cape Town (E21025). It is very large, but quite unlike a Grevy's zebra skull. Grevy's zebras have very long distances between the posterior border of the palate and the posterior border of the vomer, and their muzzles are narrow (Eisenmann 1980 Plate 1). In the skull of *E. capensis* mentioned above, the muzzle is much wider and the distance between palate and vomer (vomerine length) is relatively short. A scatter diagram of these dimensions in Grevy's zebras, plains zebras, and true Cape quaggas (Figure 1) shows that the *E. capensis* skull has proportions similar to true Cape quaggas although it is larger. On the same diagram, *E. mauritanicus* from Tighenif (Ternifine), Algeria, plots between true quaggas and *E. capensis*.

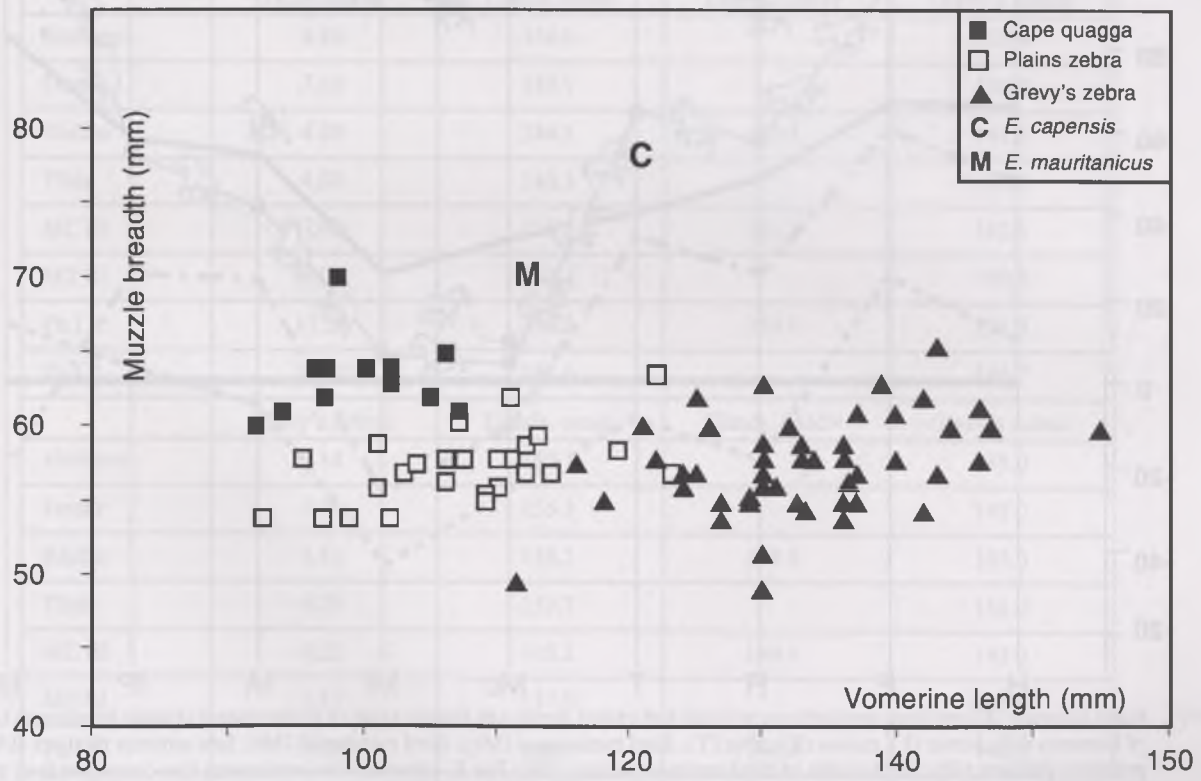

Figure 1. Scatter diagram in millimeters of muzzle breadths versus vomerine lengths in skulls of fossil and extant species of *Equus*.

The middle Pleistocene (Geraads *et al.* 1986) *E. mauritanicus* is probably a close relative to quaggas and plains zebras (Eisenmann 1979). Not shown on the diagram, horses plot near true quaggas while mountain zebras plot near plains zebras.

General body build

In cursorial animals, the proximal limb bones (humerus, femur, radius, tibia) tend to be relatively short while more distal limb bones, in particular metapodials, tend to be long (Gregory 1912; Osborn 1929).

Simpson's (1941) ratio diagrams of limb bone dimensions make comparisons of sizes and proportions very easy (Table 1). In Figure 2 the onager (*Equus hemionus onager*) – a very cursorial equid – is taken as the reference (horizontal line). Both mountain zebras and plains zebras have longer humeri and femora, but shorter third metacarpals and metatarsals since their body build is less cursorial. The mountain zebras, as usual in climbing animals, have narrower hooves than plains zebras, and even shorter third metapodials relative to the lengths of the tibia and radius. Moreover, mountain zebras and plains zebras have relatively long

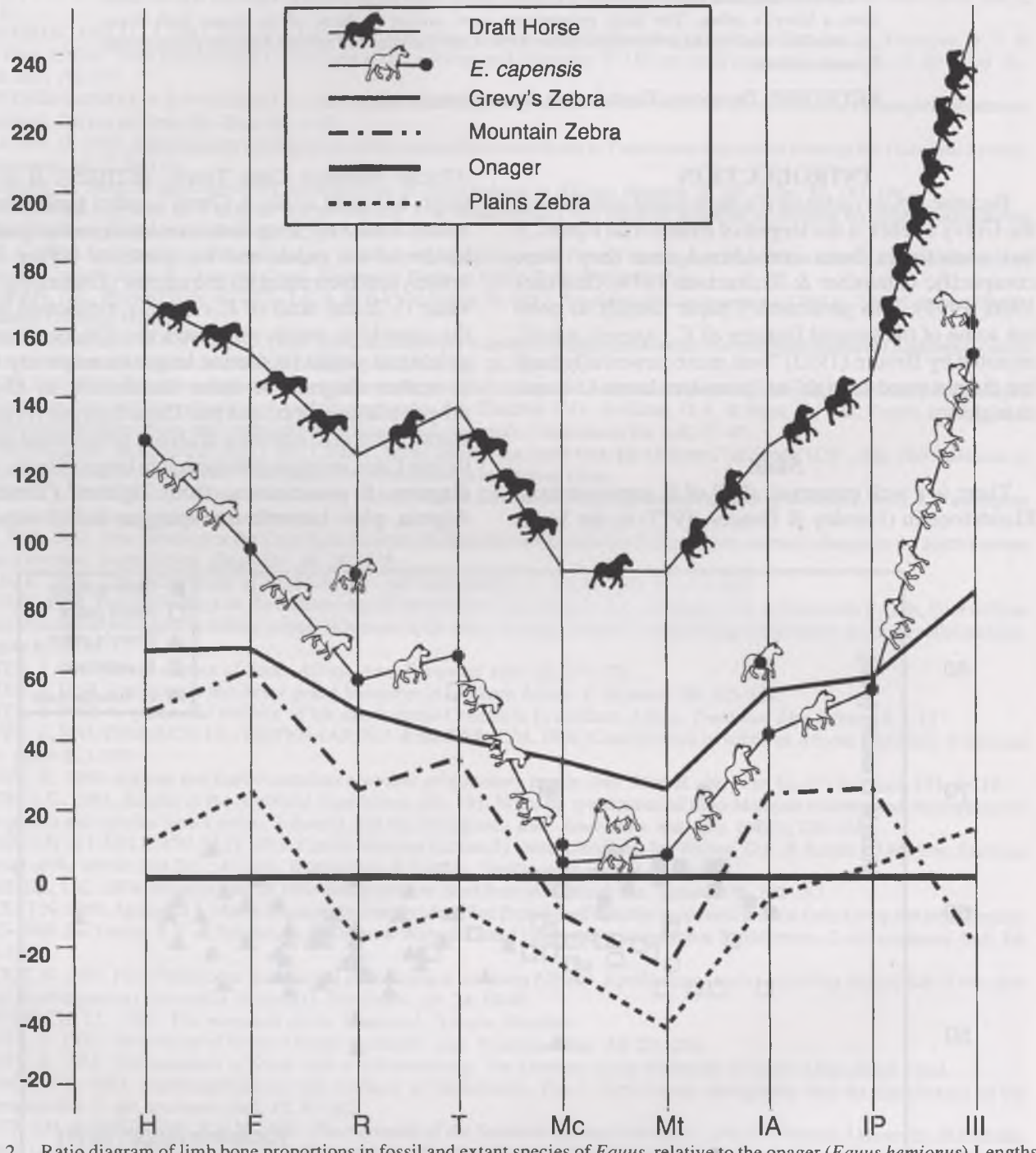

Figure 2. Ratio diagram of limb bone proportions in fossil and extant species of *Equus*, relative to the onager (*Equus hemionus*).Lengths of humerus (H), femur (F), radius (R), tibia (T), third metacarpal (Mc), third metatarsal (Mt), first anterior phalanx (IA), first posterior phalanx (IP), and breadth of third anterior phalanx (III). For *E. capensis*, the continuous line corresponds to average values while the isolated spots correspond to associated bones of a front limb (E 16659).

femora and tibiae. Grevy's zebras appear less cursorial than the onagers but more so than mountain and plains zebras.

An associated front limb of *E. capensis* was found at Elandsfontein (South African Museum, E16659). It has a very long radius relative to the third metacarpal (Table 1). These proportions are unlike those of Grevy's zebras (Figure 2), and quite uncommon in extant equids. Unfortunately, there are not many entire proximal limb bones at Elandsfontein, but the

TABLE 1.

Limb bone dimensions in millimeters (all are maximal lengths except for the third anterior phalanx where the dimension is the maximal width). MC III = third metacarpal; MT III = third metatarsal; Ph I = first phalanx; Ph III = third phalanx; A = anterior; P = posterior. The numbers of specimens on which the means were calculated are in brackets. In the last column are the values concerning associated bones of a front limb (E 16659).

	E. hemionus onager	Grevy's zebra	Plains zebra	Hartmann's zebra	Draft horse	Elandsfontein mean	Elandsfontein 16659
Humerus	241,3 (10)	282 (19)	247 (25)	270 (12)	356 (2)	325 (1)	
Femur	329,7 (10)	385.5 (19)	349.2 (25)	378.4 (12)	467.5 (2)	413 (2)	
Radius	293,5 (10)	329 (20)	280 (25)	312 (12)	387.5 (2)	336 (3)	360
Tibia	313 (10)	342.9 (20)	305.3 (25)	338.9 (12)	425 (2)	363.31 (10)	
MC III	214,1 (10)	232 (21)	201.7 (25)	209 (14)	263 (2)	216.3 (47)	219
Mt III	250,8 (10)	266.5 (21)	226.4 (25)	235.1 (15)	308 (2)	253.9 (64)	
Ph I A	76,3 (10)	86.4 (21)	75.3 (21)	80.6 (13)	101.5 (2)	83.6 (49)	88
Ph I P	71,2 (10)	81.5 (20)	71.3 (21)	75.6 (14)	99 (2)	80.9 (58)	
Ph III A	54 (8)	65.3 (18)	55.6 (13)	51.6 (13)	95 (2)	76.7 (19)	79

TABLE 2.

Estimations of the height at the withers in centimeters in heavy horses and *E. capensis* and in the much more cursorial Grevy's zebra. Withers heights are obtained by multiplying the length of a limb bone (Table 1) by the corresponding 'index'. Indices differ in heavy and cursorial forms.

	Indices	Withers height	Withers height	Withers height
	Draft horses	Elands. mean	Elands. 16659	Grevy's zebras
Humerus	4.80	156.0		135.4
Femur	3.60	148.7		138.8
Radius	4.30	144.5	154.8	141.5
Tibia	4.00	145.3		137.2
MC III	7.00	151.4	153.3	162.4
MT III	6.00	152,3		159.9
Ph I A	17.50	146,3	154.0	151.2
Ph I P	18.00	145,6		146.7
	Grevy's zebras	Elands. mean	Elands. 16659	Grevy's zebras
Humerus	5.14	167.1		145.0
Femur	3.76	155.3		145.0
Radius	4.41	148.2	158.8	145.0
Tibia	4.23	153.7		145.0
MC III	6.25	135.2	136.9	145.0
MT III	5.43	137.9		145.0
Ph I A	16.86	140.9	148,4	145.0
Ph I P	17.68	143.0		145.0

available data (Table 1) indicate that *E.capensis* was rather like a draft horse in its general build, although smaller (Figure 2).

Estimation of the height at the withers

The height at the withers of a horse used to be expressed in "hands" (one hand = 4 inches) or in "inches" (one inch = 25,4 millimeters). Thus, a horse "15 hands high" measures 152,4 cm at the withers. The height at the withers can be estimated by multiplying the length of a limb bone by an adequate number. The best known numbers for horses (average and range of variation) are those proposed by Kiesewalter in 1889 ('Kiesewalter's indices' of Gromova, 1949, p.14). However, as already pointed by Gromova and by Mourer-Chauviré (1980), the estimations based on the average indices are often not concordant, while the use of the range of variation makes them so approximate that they become useless. It is indeed natural that numbers adequate for a cursorial form will not give a correct estimation for a draft horse. Using my own data on limb bone lengths of heavy horses, and previously published average heights, I have calculated 'indices' (Table 2) that may reasonably be applied to *E. capensis*. At least, they give relatively concordant indications, whatever the bone used. The estimated heights range between 144 and 156cm, confirming Broom's (1913) opinion: on average, *E. capensis* 'did not stand so high as a modern horse 15 hands high'. The same table shows the indices calculated for Grevy's zebra, assuming an average withers height of 145cm (Kingdon 1979).

If applied to the associated front limb of *E.capensis*, the Grevy's indices would provide estimations of 137cm (using the third metacarpal) to 159cm (using the radius) Conversely, if *E. capensis* indices were applied to the average Grevey's zebra, the estimations would range from 135 to 162cm (Table 2). These discordances are another expression of the fact that *E. capensis* was not a kind of Grevy's zebra.

Estimation of weight

Several ways have been proposed to estimate the body weight of an equid (Alberdi *et al.* 1995). For instance, the occlusal surface of an upper cheek tooth can be taken as a base (Figure 3). Unfortunately, some equids (*E. caballus* in particular) have relatively larger teeth than others. Thus, the occlusal surface of an upper first molar (M1) measures about 500 square millimeters in a horse which weighed about 150 kilos, but about the same surface is the minimum for Grevy's zebras whose minimal weight is about 350 kilos (Kingdon 1979). Obviously, the relationship between tooth surface and body weight is not the same in all equids. It is possible, however, to determine a relationship using regression analyses (Eisenmann & Sondaar 1998): Ln of the weight = -6.388 + 1.873 (Ln surface M1). For *E. capensis* of Elandsfontein, the average upper molar occlusal surface area of M1 is 796 square millimeters (n=50) and the average weight can be estimated at 450 kg.

A better way is to use the product of a limb bone depth (antero-posterior diameter) by its width (transverse diameter). For instance, using the distal end of the third metacarpal, Ln of the weight = -4.525 + 1.434 (Ln of the product of articular width by minimal depth of the medial condyle). In *E. capensis* of Elandsfontein, the average distal depth for 47 third metacarpals is 30.2 (maximum 32mm); the average

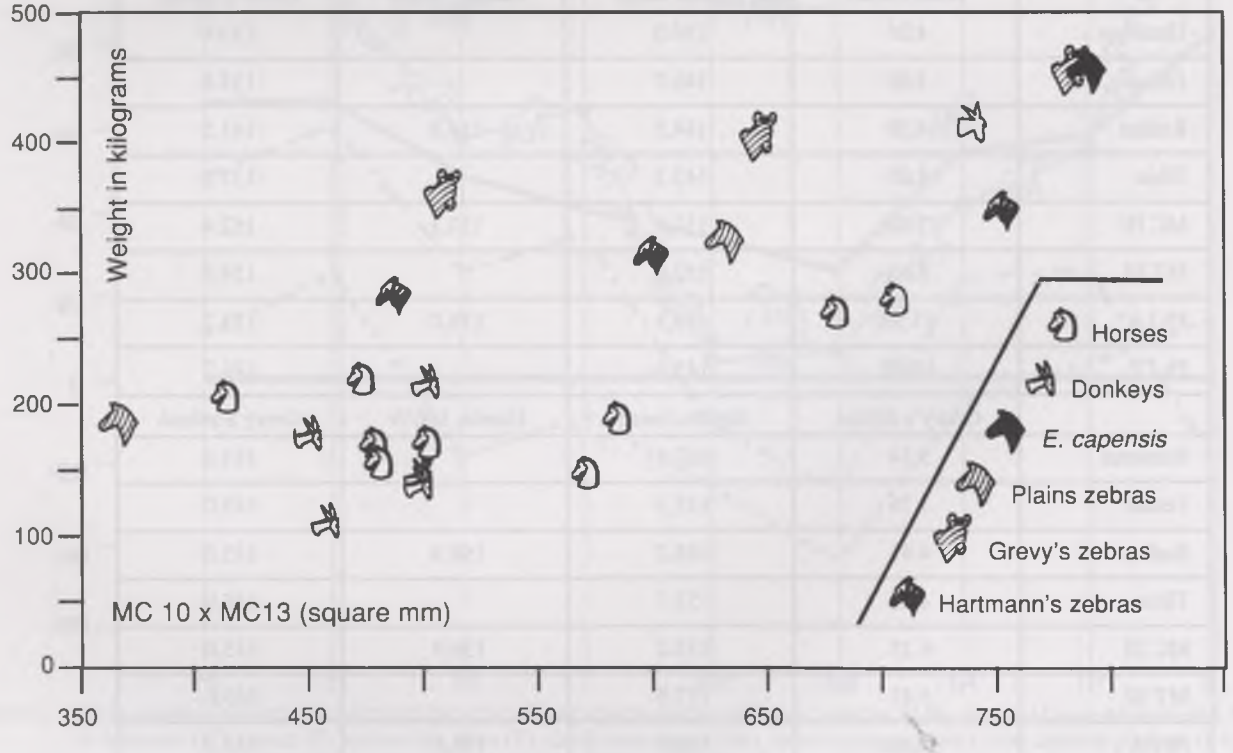

Figure 3. Scatter diagram of weights versus occlusal surfaces of upper M1 of extant *Equus*. The weight of *E. capensis* was calculated according to the regression: Ln of the weight = -6.388 + 1.873 (Ln product occlusal length by occlusal width of M1).

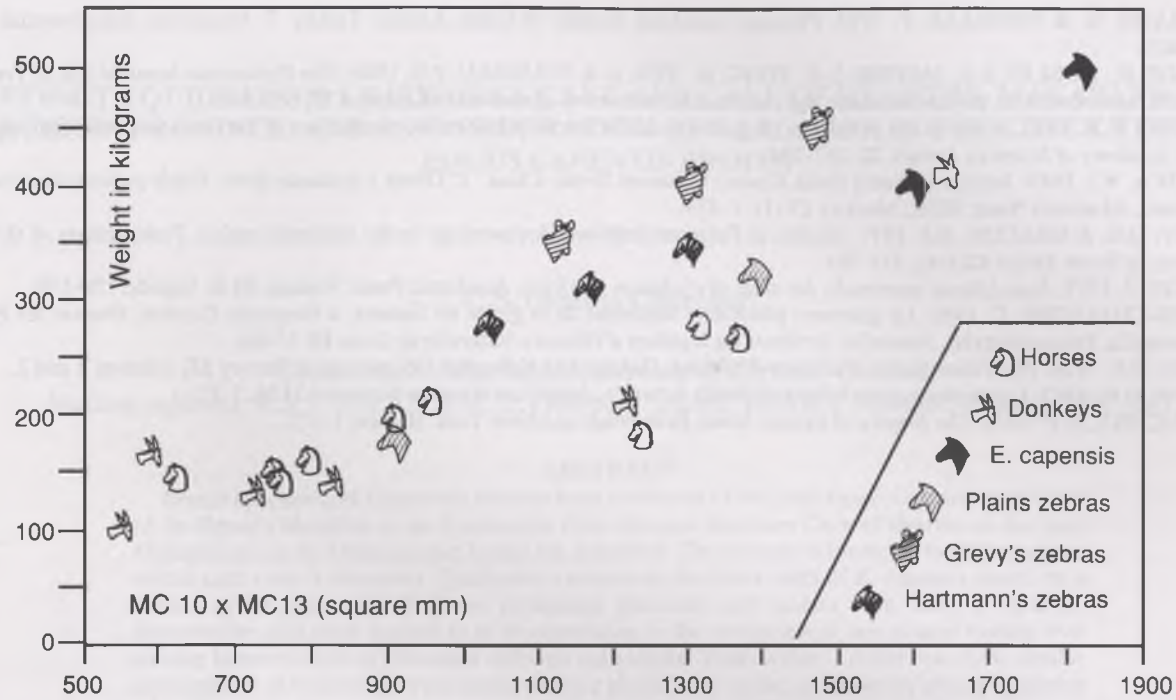

Figure 4. Scatter diagram of weights versus sections of third metacarpals of extant *Equus*. The average and maximal weights of *E. capensis* were calculated according to the regression: Ln of the weight = -4.525 + 1.434 (Ln product of articular width by minimal depth of the medial condyle).

distal width is 51.4 (maximum 57mm); the product of average distal depth by distal width is 1552.3 (maximum 1824). These parameters indicate (Figure 4) an average weight of about 400 kg, and a maximum weight of about 500 kg.

CONCLUSIONS

On the basis of fossils of *E. capensis* collected at Elandsfontein, one can conclude that this species resembled, in its general body build, a heavy horse (*E. caballus*) more than any other extant equid. By comparison with extant heavy horses, the height at the withers of *E. capensis* can be estimated at about 150cm, which is in accordance with Broom's estimation. Judging by the width and depth of its third metacarpals, the average weight would have been about 400 kg. Skull proportions resemble true Cape quaggas more than any other extant species, and also *E. mauritanicus*, a probable relative of plains zebras, represented in the Middle Pleistocene of Tighenif, Algeria.

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REFERENCES

ALBERDI, M.T., PRADO, J.L. & ORTIZ-JAUREGUIZAR, E. 1995. Patterns of body size changes in fossil and living Equini (Perissodactyla). *Biological Journal of the Linnean Society* **54,** 349-370.

BROOM, R. 1913. Note on *Equus capensis* Broom. Bulletin of the American Museum of Natural History **32** (25), 437-439.

CHURCHER, C.S. & RICHARDSON, M.L.1978. Equidae. **In:** Maglio, V.J. & Cooke, H.B.S. Eds, *Evolution of African Mammals*, Cambridge, Harvard University Press, 379-422.

CHURCHER, C.S. 1986. The extinct Cape zebra. *Sagittarius* **1**(4), 4-5.

CHURCHER, C.S.,1993. *Equus grevyi. Mammalian Species* **453,** 1-9.

EISENMANN, V. 1979. Caractères évolutifs et phylogénie du genre *Equus* (Mammalia, Perissodactyla). *Comptes Rendus de l'Académie des Sciences, Paris*, serie D **288,** 497-500.

EISENMANN, V. 1980. Les Chevaux (*Equus* sensu lato) fossiles et actuels: cranes et dents jugales supérieures. *Paris, Cahiers de Paléontologie* 1-186.

EISENMANN, V. & SONDAAR, P. 1998. Pliocene vertebrate locality of Çalta, Ankara, Turkey. 7. *Hipparion. Géodiversitas* **20**(3), 409-439.

GERAADS, D., HUBLIN, J.-J., JAEGER, J.-J., TONG, H., SEN, S. & TOUREAU, P.H. 1986. The Pleistocene hominid site of Ternifine, Algeria: new results on the environment, age, and human industries. *Quaternary Research* **25,** 380-386.

GREGORY, W.K. 1912. Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. *New York Academy of Sciences Annals* **22,** 267-294.

GROMOVA, V.I. 1949. Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 1. Obzor i opisanie form. *Trudy paleontologicheskovo Instituta,* Akademii Nauk SSSR, Moskva **17** (1), 1-373.

HENDEY, Q.B. & DEACON, H.J. 1977. Studies in Palaeontology and Archaeology in the Saldanha region. *Transactions of the Royal Society of South Africa* **42**(3-4), 371-381.

KINGDON, J. 1979. *East African mammals. An atlas of evolution in Africa.* Academic Press, Volume III B. Equids, 120-179.

MOURER-CHAUVIRE, C. 1980. Le gisement pléistocène supérieur de la grotte de Jaurens, à Nespouls, Corrèze, France: les Equidés (Mammalia, Perissodactyla). *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* **18,** 17-60.

OSBORN, H.F. 1929. *The Titanotheres of ancient Wyoming, Dakota and Nebraska.* US geological Survey **55,** volumes 1 and 2.

SIMPSON, G.G. 1941. Large pleistocene felines of North America. *American Museum Novitates* **1136,** 1-27.

WILLOUGHBY, D.P. 1974. *The Empire of* Equus. South Brunswick and New York. Barnes, 1-475.