# Type series of Equus quagga zambeziensis (Mammalia: Perissodactyla: Equidae)\*

T. Mayer<sup>1</sup>, I. Kispál<sup>2</sup>, J. Cuisin<sup>3</sup> & G. Csorba<sup>2</sup>

 <sup>1</sup>Museum of Hungarian Agriculture, H-1146 Budapest, Városliget, Vajdahunyadvár, Hungary. E-mail: mayer.tamas@mmgm.hu
<sup>2</sup>Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13., Hungary. E-mails: kispalistvan71@gmail.com, csorba@nhmus.hu
<sup>3</sup>Muséum national d'Histoire naturelle, 55 rue Buffon, 75231 Paris, France. E-mail: cuisin@mnhn.fr

**Abstract** – The Plains Zebra (*Equus quagga*) is by far the most common species among the four species of zebras. The number of its accepted subspecies (including the extinct Quagga) varies between 6 and 7 although the publications enumerate different names and show different views regarding the synonyms. One of the subspecies with still controversial taxonomic position is *zambeziensis*; the authorship of the name is either attributed to Trouessart or Pražák. In this paper we overview the history of the discovery, description and taxonomic evaluation of the taxon, clarify the authorship and depict the four specimens of the type series. With 5 figures and 1 table.

Key words - African mammals, Plains zebra, subspecies, taxonomy

## INTRODUCTION

Among the four species of zebras (GROVES & GRUBB 2011) by far the most common species is the Plains Zebra (*Equus quagga*). Its original distribution once extended from southern Ethiopia and southern Sudan southward to Cape Province and westward to northern Namibia and southern Angola, but has been considerably reduced since the 18th century. The species was exterminated from many areas and at least one subspecies became extinct (GROVES & GRUBB 2011). The Plains Zebra was subsequently reintroduced to several of its former habitats in South Africa, which means that these areas are now populated by herds derived from other geographic areas (ANSELL 1971). The former species-level separation of the now extinct Quagga (*Equus quagga* Boddaert, 1785) and the Plains Zebra (*Equus burchellii* Gray, 1824) beside the different coat patterns was based on the belief that in the area bordered by the Orange and Vaal Rivers and the

<sup>\*</sup> In memoriam Peter Grubb and Csaba Anghi

Drakensberg Mountains these two animals lived together although in separate herds (HARRIS 1840). Investigations including the study of mitochondrial and nuclear DNA sequences have now firmly established that the Quagga is a subspecies of the Plains Zebra (e.g. RAU 1978, LEONARD *et al.* 2005, LORENZEN *et al.* 2008).

The evaluation of the taxonomic position of the many described varieties, forms and subspecies of the Plains Zebra generated considerable debate among researchers (for overviews see e.g. ST. LEGER 1932, CABRERA 1936, ANSELL 1971, GRUBB 1981, 2005, GROVES & RYDER 2000, GROVES & BELL 2004, GROVES & GRUBB 2011). Although a genetic study of the Plains Zebra populations based on wide geographic and taxonomic representation found very little differentiation (LORENZEN et al. 2008) and the species exhibits a morphological and genetic cline from north to south across its range (GROVES & BELL 2004, LORENZEN et al. 2008), the subspecific separation is still regarded useful from a conservation biological perspective (HACK & LORENZEN 2008). The number of the currently accepted subspecies (including the Quagga) published in comprehensive books varies between 6 and 7 (GRUBB 2005, GROVES & GRUBB 2011, RUBENSTEIN 2011), although they show different names and present different views regarding the synonyms. One taxon with a still controversial taxonomic position is Equus zambeziensis, formally described by TROUESSART (1898) as a subspecies of the Plains Zebra. The present paper overviews the history of the discovery, description and taxonomic evaluation of this taxon, and for the first time depict all specimens of the type series.

### DISCOVERY

Emil Holub Czech physician, ethnographer, cartographer and explorer was inspired to travel to Africa by the travel diary of David Livingstone. He set out for his last expedition in 1883 when he got as far as Barotseland (today Western Zambia) from the south. After an eventful and life threatening journey, he returned to his starting point Colesberg, near the Orange River. After a short rest he went on with his collecting activity (HOLUB 1891) and among others he collected several specimens of a large bodied population of Plains Zebra. Shortly after his return to Europe based on his ethnographical and zoological specimens he organised an ambitious exhibition first in Vienna (1891) and then in Prague (1892). Both events ended up with a huge deficit, therefore he had to sell (and partly donate) significant parts of his collection. He finally shared the results of his journeys among 467 institutes, museums and schools (HALÁSZ 1930: 8).

According to ANGHI (1936) Holub brought seven zebra skins to Europe. Édouard Sicaire Bourdelle of the Muséum national d'Histoire naturelle, Paris, wrote in his two letters sent to Anghi in 1935 that the Paris museum bought an

adult and a juvenile mare in 1894 from Holub determined as Equus Chapmani. Holub also sold an adult stallion to the Naturhistorisches Museum of Vienna as Equus Chapmani, which specimen was subsequently misidentified by Lorenz as Equus burchelli selousi (ANGHI 1936). The Hungarian Natural History Museum acquired an adult mare under the name Equus Böhmi in 1894. In connection with this acquisition there is a list of some of Holub's specimens, dated on 28.10.1894, Vienna ["69 Widmung für öffentliche Anstalten aus den Sammlungen der II. Reise (1883)"]. The 8th item of the 1st part (Zoologie, I. Mammalia) of this list can be translated as: "E. Böhmi. Böhm zebra adult. Found in the woodland situated on the left bank of one of the Zambezi's tributaries Ma-Schupia-Inquisi (West-Ngweze). Ma-Schupia territory, Ma-Rutze (Barotse) Empire, in the southern part of Central Africa". The collecting localities of the Vienna and Paris specimens can also be deducted from the map enclosed to the list. In his letters written in 1934, Jiří Baum (that time the director of the Zoological Department of the National Museum in Prague) sent a photo to Anghi (ANGHI 1936) depicting four zebras brought by Holub from Africa and exhibited in Prague in 1901. On this photo Anghi recognised the Vienna specimen and another zebra, which he thought to belong to the same type as the animals from Paris, Vienna and Budapest. Except for the zebra from Vienna we do not know anything about the further three specimens exhibited in Prague, therefore we are aware of four zebra specimens from Emil Holub's collection in European museums.

### DESCRIPTION

Not only the taxonomic status but even the authorship of the name zambeziensis is controversial. The formal description of the subspecies was given by TROUESSART (1898), who named Pražák as the author of the taxon and referred to his work "The Wild Horses of the Ethiopian Region" thought to be published in London in 1898. In fact, Josef Prokuslav Pražák's book was never published (RZASNICKI 1951, ANSELL 1978, GRUBB pers. comm.) although the manuscript written as a university thesis in the years 1896-1897 is still held in the Special Collections Division of the Edinburgh University Library (Fig. 1). Several authors (e.g. Shortridge 1934, Allen 1939, Antonius 1951, Ansell 1960, Groves & Ryder 2000, Groves 2002, Groves & Bell 2004) attribute the description to Pražák, whereas others (e.g. ANSELL 1978, GRUBB 1981, 2005, RUBENSTEIN 2011) name Trouessart as the author. However, in his work TROUESSART (1898: 63-64) not only named Pražák as the person who is responsible for the name, but when listed the specimens on which the description is based he also explicitly followed the view of Pražák (op. cit.: 65). As it is evident from his work it was, indeed, Pražák himself, who suggested the name and provided a differential

STUDY A ON HORSES WILD THE ETHIOPIAN REGION. 0 F THE A Contribution to the Zoology of Africa and Natural History of Equiade. by J. P. PRAŽÁK, Ph.D., D. iur. . " The au Introduction by Prof. J. C. Ewart, M. D. F.R.S. With 30 Coloured and 10 Plain Plates, several maps and illustrations in the text. Edinburgh. 1897.

Fig. 1. Cover page of J. P. Pražák's thesis held in the Centre for Research Collections, University of Edinburgh

Annls hist.-nat. Mus. natn. hung. 105, 2013

250

diagnosis for this form of zebras (unpublished thesis: 277–278). As defined in the Article 50.1.1. of the Code (ICZN 1999) if it is clear from the contents that a person other than the author of the work is alone responsible both for the name and for satisfying the criteria of availability, then that other person is the author of the name. Accordingly, the authorship of the name *zambeziensis* is correctly assigned to Pražák and the year of description is 1898.

TROUESSART (1898) defined the type locality of *E. zambeziensis* as "Mushupia, vallée de l'Ingwisi", which is in the lower drainage of the Ngwezi River most likely between the Ngwezi-Zambesi and Machili-Zambesi confluences, Southern Province, Zambia (ANSELL 1978, GRUBB 1981). In the description he used the width of the black and white stripes, the number of stripes extending downwards to the belly, the stripe-pattern of the legs, the colours of the fetlocks and the tail (including the final hair tuft) as distinguishing characters. He provided mensural data of the adult Paris specimen (body length from the base of tail to the anteriormost part of the mane 163 cm; shoulder height 138 cm) and noted that these values exceed those of *chapmanni* and *E. zebra*. He further mentioned that there are no shadow stripes in the fully grown specimen (in contrast with the Chapmann's Zebra) but they are present in the young individual, which is generally more slender than a Chapmann's Zebra foal of the same age.

Trouessart compared *zambeziensis* (in a tabular form) with the geographically closest two other Plains Zebra subspecies, namely *selousi* and *crawshaii*. This comparison supplemented by us with the externally most similar subspecies *boehmi*, is given herewith in the form of a character matrix (Table 1).

Beside the two Paris specimens TROUESSART (1898) mentioned the Vienna and Budapest specimens as other representatives of the taxon *zambeziensis* investigated by Pražák and emphasised their common origin. In the absence of holotype designation, based on Article 72.4. of the Code (ICZN 1999) the specimens listed below are regarded as syntypes (Figs 2–5).

- MNHN ZM-MO 1894–208, adult female, full mount and skull, Muséum national d'Histoire naturelle, Paris (Fig. 2).
- MNHN ZM-MO 1894–96, young subadult female, full mount, Muséum national d'Histoire naturelle, Paris (Fig. 3).
- HNHM 1915.8, adult female, full mount, Hungarian Natural History Museum, Budapest (Fig. 4).
- NMW ST341, adult male, full mount, Naturhistorisches Museum, Wien (Fig. 5).\*

<sup>\*</sup> A skull with full dentition (NMW ST382) thought by ANTONIUS (1951) as belonging to this specimen is of unsure origin and as the front teeth and at least part of the skull are present in the NMW ST341 mounted specimen the NMW ST382 skull is not regarded as part of the type material (B. Herzig pers. comm.).

#### DEBATE

Early authors (ST. LEGER 1932, SHORTRIDGE 1934) accepted the character combination described by TROUESSART (1898) as typical for the Upper Zambezi population of the Plains Zebra and regarded zambeziensis as valid subspecies. However, in his meticulous work CABRERA (1936) does not accept zambeziensis as separate subspecies but put it into the synonymy of *boehmi* Matschie, 1892, the Grant's Zebra. He noted that Trouessart did not compare zambeziensis with boeh*mi* and emphasised the fact that the two taxa could not be distinguished from each other by colour patterns. Following his work several subsequent authors (ALLEN 1939, ANTONIUS 1951, ANSELL 1960) regarded zambeziensis as a mere synonym of the Grant's Zebra. However, some researchers (ANGHI 1936, RZASNICKI 1951) still regarded zambeziensis as evidently separable from the other subspecies by its medium wide stripes, the usually absent shadow stripes and large body measurements. AZZAROLI (1966) investigating a series of skulls thought that zambeziensis might be differentiated by the elongated braincase. His results were used by GRUBB (1981) to support the subspecific distinctness of zambeziensis, although with a reservation that the cranial evidence was based only on six skulls. It is worth noting that two of the most influential ungulate systematists, Peter Grubb and Colin Groves have changed their opinions in the course of time. After his 1981 publication, in the latest taxonomic reference work of all the mammalian species GRUBB (2005) synonymised zambeziensis with boehmi. Strangely enough, in the web-based version of the very same book (WILSON & READER 2005) zambeziensis has been listed among the accepted subspecies. Groves in some of his earlier works (GROVES 1974, GROVES & RYDER 2000) regarded zambeziensis as valid subspecies, while later (GROVES & BELL 2004, GROVES & GRUBB 2011) synonymised it with boehmi. In this latter publication they characterised boehmi as the smallest subspecies which seems to be contradictory to their taxonomic action as the Upper Zambezi Zebra is one of the biggest forms of the Plains Zebra. Citing LORENZEN et al. (2008) RUBENSTEIN (2011) also did not regard zambeziensis as a valid taxon. However, according to the mtDNA investigations of LORENZEN et al. (2008) the Upper Zambezi Zebra is closer to the more southern populations than to the northern subspecies *boehmi* which contradicts the morphology-based conclusions of GROVES & BELL (2004) and GROVES & GRUBB (2011).

Although mtDNA and microsatellite sequences indicate no subspecific differences between populations of the Plains Zebra, in our opinion – based on external (body size and striping pattern) and cranial (skull size and shape) features – *zambeziensis* is a clearly distinguishable taxonomic unit, which has an evolutionary meaning and therefore represents a separate entity for conservation management as well. Further research is definitely needed to resolve the conflicting morphological and genetic results using the combined sets of evidence.

	Table 1. Con	nparison of four subspecies o	of Equus quagga	
character	E. q. selousi	E. q. crawshaii	E. q. zambeziensis	E. q. boehmi
body stripe width	black stripes much broader than light interspaces	stripes and interspaces strikingly narrow and numerous	stripes medium broad and of nearly the same breadth or broader than light interspaces	stripes and interspaces few and broad
number of stripes meeting median ventral line between elbow and "saddle" stripe	3 or 4	at least 5 (often 6–8)	only 3 or 4	only 3 or 4
shadow stripes	narrow, but always distinguishable	ио	vary from fairly prominent to absent, but usually absent	poor or absent
fetlock colour	white	black	black	black
leg stripes	incomplete	complete to hoofs	usually complete or nearly so	always complete to hoofs
inner surface of legs above knee	not striped	striped	striped	striped
tail and tuft colour	tail striped, tuft partly white	tail blotched, tuft black	tail striped, tuft black	tail striped, tuft black.
body size	large	large	large	small
body colour	nearly white or pale fawn	white or off-white	varies from ochre through off- white to white	generally pure white

Type series of Equus quagga zambeziensis (Mammalia: Perissodactyla: Equidae) 253

T. Mayer, I. Kispál, J. Cuisin & G. Csorba



Figs 2–3. Type series of *Equus quagga zambeziensis*. 2 = MNHN ZM-MO 1894-208, 3 = MNHN ZM-MO 1894-96



Figs 4–5. Type series of *Equus quagga zambeziensis*. 4 = HNHM 1915.8, 5 = NMW ST341

Acknowledgements – We are very grateful to F. Zachos and B. Herzig of the NMW for providing information on the *zambeziensis* syntype specimen stored in Vienna, and to C. Groves and A. Demeter for their advice. We are indebted to Gy. Szél for translating Trouessart's original description, to Z. Soltész and L. Csorba for their help with the photographs and to D. Anderson of the Centre for Research Collections, University of Edinburgh for her kind help in locating Pražák's manuscript. GC is specially grateful for M. Motokawa of the Kyoto University Museum for providing ideal working conditions to work on the manuscript, while staying there under the visiting professorship programme.

### REFERENCES

- ALLEN G. M. 1939: A checklist of African mammals. Bulletin of the Museum of Comparative Zoology 83: 1–763.
- ANGHI Cs. G. 1936: A zambezi-tigrisló Európa múzeumaiban. [Zambesi zebra specimens in European museums.] Állattani Közlemények 33(3–4): 173–180.

ANSELL W. F. H. 1960: Mammals of Northern Rhodesia. - The Government Printer, Lusaka, 155 pp.

- ANSELL W. F. H. 1971: Order Perissodactyla. In: MEESTER J. & SETZER H.W. (eds): The mammals of Africa. An identification manual. Part 14. Smithsonian Institution Press, Washington D. C., pp. 1–14.
- ANSELL W. F. H. 1978: *The mammals of Zambia*. The National Parks and Wildlife Service, Chilanga, 126 pp.

ANTONIUS O. 1951: Die Tigerpferde. Die Zebras. – Monographien der Wildsäugetiere 11: 148 pp.

- AZZAROLI A. 1966: Pleistocene and living horses of the Old World. *Palaeontographica Italica* 61: 1–15.
- CABRERA A. 1936: Subspecific and individual variation in the Burchell zebras. Journal of Mammalogy 17(2): 89-112.
- GROVES C. P. 1974: Horses, asses and zebras in the wild. David & Charles, Newton Abbott and London, 192 pp.
- GROVES C. P. 2002: Taxonomy of living Equidae. In: MOEHLMAN P. D. (ed.): *Equids: zebras, asses and horses.* – IUCN, Gland, Switzerland and Cambrige, UK, pp. 94–107.
- GROVES C. P. & BELL C. H. 2004: New investigations on the taxonomy of the zebras genus Equus, subgenus Hippotigris. *Mammalian Biology* 69(3): 182–196.
- GROVES C. P. & GRUBB P. 2011: Ungulate taxonomy. The Johns Hopkins University Press, Baltimore, 317 pp.
- GROVES C. P. & RYDER O. A. 2000: Systematics and phylogeny of the horses. In: BOWLING A. T. & RUVINSKY A. (eds): *The genetics of the horse.* Wallingford, Oxon, CAB International, pp. 1–24.
- GRUBB P. 1981: Equus burchelli. Mammalian Species 157: 1–9.
- GRUBB P. 2005: Order Perissodactyla. In: WILSON D. E. & REEDER D. M. (eds): *Mammal species of the World: A taxonomic and geographic reference. 3 ed.* – The Johns Hopkins University Press, Baltimore, pp. 629–636.
- HACK M. A. & LORENZEN E. 2008: Equus quagga. In: IUCN 2012: *IUCN red list of threatened* species. Version 2012.2. http://www.iucnredlist.org [Accessed: 26 December 2012.]
- HALÁSZ GY. 1930: [Translator's note.] In: HOLUB E.: Tizenegy év Dél-Afrikában. [Eleven years in South Africa.] Franklin-Társulat, Budapest, 140 pp.

- HARRIS W. C. 1840: Portraits of the game and wild animals of southern Africa. W. Pickering, London, 144 pp.
- HOLUB E. 1891. A Fokvárostól a masukulumbék országába 1883–1887. II. kötet. [From Cape Town to the country of the Masukulumbe 1883–1887. Vol II.] Ráth Mór, Budapest, 515 pp.
- ICZN 1999: International Code of Zoological Nomenclature. 4th edition. The International Trust for Zoological Nomenclature, London, 155 pp.
- LEONARD J. A., ROHLAND N., GLABERMAN S., FLEISCHER R. C., CACCONE A. & HOFREITER M. 2005: A rapid loss of stripes: the evolutionary history of the extinct quagga. *Biology Letters* 1(3): 291–295.
- LORENZEN E. D., ARCTANDER P. & SIEGISMUND H. R. 2008: High variation and very low differentiation in wide ranging plains zebra (Equus quagga): insights from mtDNA and microsatellites. – *Molecular Ecology* 17(12): 2812–2824.
- 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. – *Annals of the South African Museum* 77(2): 27–45.
- RUBENSTEIN D. 2011: Family Equidae (Horses and relatives). In: WILSON D. E. & MITTERMEIER R. A. (eds): *Handbook of the mammals of the World. Vol. 2. Hoofed Mammals.* – Lynx Edicions, Barcelona, pp. 106–143.

RZASNICKI A. 1951: Zebras and quaggas. – Annales Musei Zoologici Polonici 14(16): 203–251.

- SHORTRIDGE G. C. 1934: The mammals of South West Africa. W. Heinemann, Ltd., London, 779 pp. ST LEGER J. 1932: On Equus quagga of southwestern and eastern Africa. – The Annals and Magazine of Natural History, Ser. 10, 10: 587–593.
- TROUESSART E. 1898: Sur une varieté nouvelle du zébre de Burchell (Equus burchelli subsp. zambeziensis, Prazak). Bulletin du Muséum d'histoire Naturelle Paris 4(1): 63–67.
- WILSON D. E. & REEDER D. M. (eds) 2005: Mammals species of the World. 3rd edition. http:// www.vertebrates.si.edu/msw/mswcfapp/msw/index.cfm [Accessed: 30 December 2012.]