Geographic variation in skulls of the nearly extinct Small Black rhinoceros Diceros bicornis michaeli in northern Tanzania

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Abstract

Skull parameters of Black rhinoceros *Diceros bicornis* (L., 1758) collected in Lake Manyara National Park and in the Ngorongoro Crater, both in northern Tanzania were measured. Statistical analysis showed that they belonged to two morphologically distinct sub-populations with only small overlap. The rhinoceroses from the two areas fall into the subspecies *D. b. michaeli* Zukowsky, 1964. The Ngorongoro area does not form an intergrade zone between the subspecies *michaeli* and *D. b. minor* Drummond, 1876. An analysis of the data published by Groves (1967) and those collected in the present study, shows that the group of skulls delimited as subspecies *minor* appear to be situated within a cline between subspecies *michaeli* and subspecies *D. b. ladoensis* Zukowsky, 1964. Even if the subspecies concept has no strict biological meaning, it has importance for nature conservation, and much effort should be concentrated on saving the Small East African black rhinoceros *D. b. michaeli*, as its numbers in the wild appear to be as low as fifty to one hundred.

Introduction

Until recently, the Black rhinoceros *Diceros bicornis* (L., 1758) was widely distributed in eastern and southern Africa and in the Sahel. At present, its range has been fragmented into small to very small areas (Haltenorth and Diller 1979), and total numbers have declined. For example, in Tsavo National Park, southern Kenya (Fig. 1), the population was estimated at approximately 8000 at the end of the 1960s (Goddard 1969), at 5600 in the mid-70s (Cobb 1976), but at present it has been reduced to a few dozen at most (W. VAN WIJNGAARDEN pers. comm.). A likewise dramatic abatement took place in the Selous Game Reserve, southern Tanzania, where the population in the mid-70s was estimated to be at least 2500 (Douglas-Hamilton 1976), while in 1988 "a few" were left (M. Borner pers. comm.). These extreme declines are due to excessive poaching, just as elsewhere in most parts of Africa, and it is doubtful whether the species will survive in the wild for very long.

The Black rhinoceros as a morphological distinguishable taxon has a long history. It has been recorded in Africa from the Late Pliocene and Early Pleistocene (Guerin 1976; Hooijer 1969, 1976; Leakey et al. 1976; Harris 1983), and only minor evolutionary changes are observable in the fossil material (Harris 1983).

Seven subspecies have been distinguished and described by GROVES (1967) on basis of skulls in museums. Because of the small number of skulls available, the discrimination between the subspecies is on statistical grounds not always very satisfactory. Corbet (1970) stated that "the chief obstacle to determining the pattern of variation in a species is the availability of samples that are sufficiently large and sufficiently random with respect to locality..., to allow the true pattern of variation in nature to be accurately inferred from the pattern of variation seen in the collected sample". As the number of living individuals is dwindling so fast, it is important for the systematics of the Black rhinoceros that as many individual skulls as possible are described before none are available anymore.

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The Small East African black rhinoceros *D. b. michaeli* Zukowsky, 1964, was described by Groves (1967) on basis of twenty-two adults (M₃ in wear), two subadults (M₃ just erupted) and two late juveniles (M₃ unerupted). The type specimen came from "the area between Engaruka and Serengeti" (Fig. 1). The village of Engaruka lies at present in the Tanzania's Eastern Rift Valley (longitude 3°19′ S, latitude 35°58′ E, 800 m above sea level).

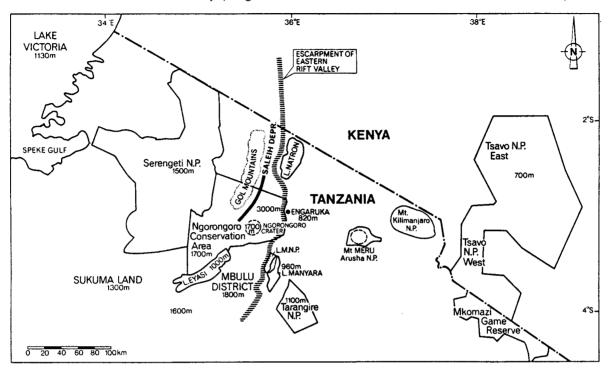


Fig. 1. Location of the study areas and of the geographical names mentioned in the text

The Serengeti short grass plain unfolds approximately 40 km due west, at the western side of the Ngorongoro Highlands, but good rhino habitat is not encountered again before the tall grass zone and woodlands some 40 km even further west (pers. obs.). There the Large East and South-East African black rhinoceros D. b. minor (Drummond, 1876) occurs (Groves 1967), although in very reduced numbers (less than 10, T. Caro pers. comm.). Groves (1967) considered the area between Engaruka and Serengeti, thus the Crater Highlands, and the area between Lakes Manyara and Eyasi, immediately south of the Ngorongoro Crater (Fig. 1), as an intergrade zone between the subspecies michaeli and minor.

Black rhinoceros skulls in the Ngorongoro Crater and in Lake Manyara National Park, both in Tanzania, were studied. Nearly all skulls derived from individuals killed by poachers. The objective of the paper is to describe these skulls, and to answer the question whether the rhinoceroses in Manyara and Ngorongoro belong to the same subspecies, and to what subspecies these individuals belong.

Material and methods

Twenty-two rhinoceros skulls were collected in Lake Manyara National Park (long. 3°42′ S., lat. 35°50′ E.), which is situated in the Rift Valley at approximately 1000 m a. s. l. and some 40 km South of Engaruka, and nineteen were collected in the Ngorongoro Crater (long. 3°7′ S., lat. 35°32′ E.), from which the floor is at about 1750 m a. s. l. The linear distance between Manyara and the Crater is

approximately 35 km (Fig. 1). Skulls were collected between 1979 and 1984. Discrimination of the sexes was not possible.

As during the field work we were not acquainted with rhinoceros craniology, we devised our own series of measurements (Fig. 2A and 2B):

- A. Basal length, from the maxillary notch to the foramen magnum ridge between the occipital condyles. This parameter is (nearly) identical to GROVES' (1967) "basal length".
- Snout length, from the maxillary notch to the end of the palate. Basal length minus snout length is identical to "length palatonarial border to occipital condyles" (HARRIS 1983).
- C. Width between the postglenoidal processes. Although this parameter is not equivalent to HARRIS' (1983) "width between occipital condyles", it appears to be roughly the same (Fig. 2B; compare Plate 4.6 in HARRIS 1983).
- D. Squamosal width, measured at the lateral points of the fossae articularis, is apparently equivalent to Groves' (1967) "zygomatic breadth".
- E. Snout width, measured at the most lateral points of the first molar and includes the maxillary bones.
- F. Width foramen magnum, measured at the small caudal ridges of the foramen, is apparently equivalent to HARRIS' (1983) "width foramen magnum".
- G. Height foramen magnum, measured in the medio-sagittal plane, and perhaps equivalent to HARRIS' (1983) "depth foramen magnum"?

 H. Crown height of M₁, at the buccal side of the left and right first molar.
- I. Horn boss diameter, as measured in the transversal plane.

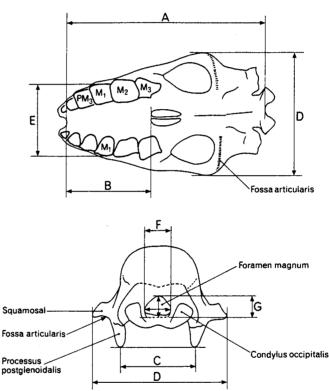


Fig. 2. The skull of a Black rhinoceros viewed from below (A) and from behind (B) to show skull parameters measured (see Methods)

All lengths were measured in mm, and analysed with STATISTIX soft-ware package. Two-tailed probability tests are quoted throughout the paper, and all parameters were tested for normality before choosing the appropriate test.

Coefficients of difference (CD) were calculated following MAYR (1969) as:

$$\frac{mean\ length_b - mean\ length_a}{SD_a + SD_b}\,,$$

in which SD stands for the standard deviation of the sample, and sub-population are denoted with a and b.

Pearson's coefficient of racial likeness (CRL) was calculated as given by SOKAL and SNEATH (1963).

Three dimensional figures were prepared to show differences between the two sub-populations. In these figures, the axes stand for one skull parameter, and the sum of the three axes equal 100 % because each parameter is expressed as a percentage of the sum of the three linear values.

Differences between ratio's were t-tested after arcsine transformations. Not all measurements could be taken from each specimen for many were damaged, hence there is variation in sample size.

Results

For the Ngorongoro and Manyara material a distinction was made between adults (M₃ in wear), intermediates between adult and sub-adult stages (M3 not fully in wear) and sub-adults (M3 erupted). Only one skull of a juvenile rhino was found, which clearly confirms the notion that most of the skulls came from individuals killed for their horns. Many skulls had bullet holes, or showed traces of horn removal. Differences between the three age categories, or between adults and the combined other two categories, were not significant for the craniological parameters. Hence, in the analyses no further distinction was made between adult or subadult. As an additional measure of age, M₁ crown height was taken. Because of tooth wear, it is likely that older animals have shorter cheek teeth than younger ones. Table 1 shows that the skull parameters were not dependent on crown height within the data set of sub-adult and adult individuals. Although there are some exceptions (squamosal width for the Ngorongoro skulls and horn boss diameter for the Manyara skulls), the finding that the relations for the two localities were not both significant makes it safer not to reject the hypothesis that there is no effect of crown height, thus age, on the skull parameters.

The variation of the different characters is virtually independent of one

By using the negative values of crown heights, an indirect effect of inferred age on the skull parameters can be investigated. No consistent significant effect of age could be demonstrated within the data sets that comprised adult and northern Tanzania and the negative value of M1 crown Because of tooth abrasion, individual rhino with the lowest crowns are thought to be oldest. parameters for two areas in Table 1. Linear correlations between Black rhinoceros skull

	sub-adult individuals	•
Skull parameters	Linear correlations with "age" Manyara	ith "age" Ngorongoro
Basal length Snout length Postglenoid width Squamosal width Snout width Foramen magnum width Foramen magnum height Horn boss diameter Snout length as % of basal length Postglenoid width as % of squamosal width Horn diameter as % of squamosal width	r = 0.407, $R^2 = 16.6\%$, n = 17; N.S. r = 0.232, $R^2 = 5.4\%$, n = 17; N.S. r = 0.256, $R^2 = 6.6\%$, n = 17; N.S. r = -0.403, $R^2 = 16.2\%$, n = 17; N.S. r = -0.322, $R^2 = 10.3\%$, n = 17; N.S. r = 0.067, $R^2 = 0.4\%$, n = 17; N.S. r = 0.402, $R^2 = 16.2\%$, n = 17; N.S. r = -0.403, $R^2 = 4.2\%$, n = 17; N.S. r = -0.205, $R^2 = 4.2\%$, n = 17; N.S. r = -0.014, $R^2 = 4.2\%$, n = 17; N.S.	r = 0.040, R ² = 1.6 %, n = 16; N.S. r = 0.139, R ² = 1.9 %, n = 18; N.S. r = 0.297, R ² = 8.8 %, n = 20; N.S. r = 0.580, R ² = 33.6 %, n = 19; P<0.02 r = 0.216, R ² = 4.6 %, n = 15; N.S. r = 0.220, R ² = 4.8 %, n = 17; N.S. r = 0.230, R ² = 5.9 %, n = 6; N.S. r = -0.179, R ² = 5.9 %, n = 16; N.S. r = -0.179, R ² = 5.2 %, n = 16; N.S.
TIOILI MAINCEL AS /0 OI SHOUL WILLI	I = 0.077, IN = 40.0 / 0, II = 12; I < 0.02	r = -0.633, $R = 40.3%$, $n = 4$; IN.5.

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another. For example, basal length is not related to squamosal width (Manyara: $R^2 = 0.32$, n = 15, N. S.; Ngorongoro: $R^2 = 0.34$, n = 19, N. S.), neither is postglenoid width related to basal length (Manyara: $R^2 = 0.14$, n = 19, N. S.; Ngorongoro: $R^2 = 0.13$, n = 17, N. S.), nor is snout width significantly correlated with snout length (Manyara: $R^2 = 0.32$, n = 16, N. S.; Ngorongoro: $R^2 = 0.07$, n = 19, N. S.). However, for Manyara rhino postglenoid width is 0.286 * squamosal width + 16 mm ($R^2 = 0.29$, n = 18, P < 0.05) and for Ngorongoro rhino postglenoid width is 0.323 * squamosal width + 13 mm ($R^2 = 0.43$, $R^2 = 0.43$, $R^2 = 0.01$). It appears that, even if the correlations are significantly deviating from zero, the correlations are weak because the explained variance (R^2) is low.

The average values for the craniological parameters for the two sub-populations of Manyara and Ngorongoro are very similar but for a number of parameters (Table 2). Basal

Table 2. Mean value and SD (in mm) for skull parameters for Manyara and Ngorongoro rhino Differences between the two sub-populations are tested with t-test for equal variance or unequal variance where relevant

Skull parameters	Manyara	Ngorongoro	Equal variance?	Difference
Basal length	$503 \pm 20 (N = 19)$	$500 \pm 22 (N = 17)$	yes	N.S.
Snout length	$211 \pm 10 (N = 19)$	$201 \pm 10 (N = 19)$	yes	P < 0.01
Postglenoidal width	$107 \pm 7 (N = 19)$	$115 \pm 9 (N = 21)$	yes	P < 0.005
Squamosal width	$319 \pm 14 (N = 19)$	$317 \pm 17 (N = 20)$	yes	N.S.
Snout width	$165 \pm 6 (N = 15)$	$160 \pm 9 (N = 15)$	P < 0.1	P = 0.1
Foramen magnum width	$55 \pm 4 (N = 19)$	$55 \pm 5 (N = 18)$	yes	N.S.
Foramen magnum height	$48 \pm 4 (N = 19)$	$53 \pm 4 (N = 18)$	yes	P < 0.001
Crown height	$34 \pm 10 \ (N = 17)$		P < 0.05	P < 0.0001
Horn boss diameter	$129 \pm 13 (N = 16)$	$140 \pm 4 (N = 7)$	P < 0.01	P < 0.01

length, squamosal width, and foramen magnum width do not differ significantly. The Manyara rhinoceroses have a significantly longer snout length (10 mm), perhaps a wider snout width (5 mm; this is only significant at P=0.1), a narrower postglenoid width (6 mm), a substantially smaller height of the foramen magnum (7 mm), and a smaller horn boss diameter (11 mm) than the Ngorongoro rhinoceroses. Moreover, the crown height of the first molar of the Manyara rhino is substantially lower than that of the Ngorongoro individuals (14 mm). Snout length as percentage of basal length is not related to presumed age, nor is postglenoid width as percentage of squamosal width, or horn boss diameter as percentage of snout width (Table 1).

Coefficients of variation are small, except for crown height (Table 3). Excluding this last

Table 3. Coefficients of variation (%) for skull parameters for the two sub-populations of Black rhinoceros, and MAYR's coefficient of difference (see Methods)

Skull parameters	Coefficient of variation (%)		Coefficient of difference	
•	Manyara	Ngorongoro	for Manyara and Ngorongoro	
Basal length	4.0	4.4	0.071	
Snout length	4.7	5.0	0.500	
Posglenoidal width	6.5	7.8	0.500	
Squamosal width	4.4	5.4	0.065	
Snout width	3.6	5.6	0.333	
Foramen magnum width	7.3	9.1	0.000	
Foramen magnum height	8.3	<i>7</i> .5	0.625	
Crown height	29.4	14.6	0.824	
Horn boss diameter	10.1	2.9	0.647	

parameter, the average coefficient of variation for the Manyara sub-population is 6.1 %, and for the Ngorongoro sub-population 6.0 %. MAYR's (1969) coefficient of difference is low for all parameters (ranging between 0 and 0.824) (Table 3).

The two populations can be fairly well separated by using three significantly differing parameters, for example, snout length, postglenoid width and crown height (Fig. 3 a), or snout length, postglenoid width, and foramen magnum height (Fig. 3 b). Because molars are subjective to wear from abrasive food, crown height is a less attractive parameter to include in the distinction of the two sub-populations. The Manyara rhinoceroses have a longer snout in relation to basal length than those of the Ngorongoro Crater (t-test after arcsine transformation: $t_{34} = 4.866$, P < 0.005), they also have a narrower postglenoid width in relation to the squamosal width ($t_{37} = 4.581$, P < 0.005), and their horn boss diameter may be narrower ($t_{14} = 1.843$, P < 0.1).

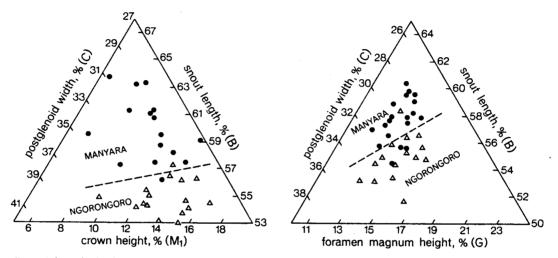


Fig. 3. The Black rhinoceros skulls from Lake Manyara National Park and from the Ngorongoro Crater fall into two distinct groups, although there is some small overlap. This indicates that the rhino from Manyara and those from the Ngorongoro Crater constitute two distinct sub-populations, and only rarely individuals move from one area into the other (see Discussion)

Discussion

As shown in Table 3, the coefficient of difference for all skull parameters is low and on average as small as 0.396. This value is much lower than the critical value of 1.28 needed if one is to speak of two different subspecies (MAYR 1969): the Black rhinoceroses of Manyara and Ngorongoro therefore clearly belong to the same subspecies. By the same token, the coefficient of racial likeness is only 0.313 (excluding crown height; if this parameter is included the CRL is 0.428). In terms of PEARSON (1928), these two groups are "very intimate associated". It is likely that the number of characters studied is small in view of the genetic information contained in the genome and also that inclusion of more characters might change the similarity coefficient (SOKAL and SNEATH 1963, p. 110 et seq.). Nevertheless, the differences between the skull characteristics are large enough to make it likely that the rhinoceroses from Manyara and those from the Ngorongoro do represent two different sub-populations (Fig. 3 a and b). Manyara rhino have a relative longer snout and more space between the postglenoid and the outside of the squamosal, hence more space for jaw muscles. At present, rhino from the Ngorongoro Crater select herbs from between grasses, while those from Manyara typically browse from shrubs. It is possible that these different feeding habits have been selected for, together with small changes in

skull morphology. Because herbs are softer than twigs, this difference in diet could also explain the significant difference in tooth wear between Manyara and Ngorongoro rhino (Table 2).

However, the sub-populations are not totally isolated. Figures 3a and b show that some of the skulls from Manyara fall into the Ngorongoro group, and vice versa. The absence of a strict separation is confirmed by observations of rhino moving from the Ngorongoro into Manyara in 1968 (WARDENS REPORTS 1968) and in 1983 (a female with her calf: pers. obs.). The Mbulu District, between the Ngorongoro Crater and Lake Manyara, although at present densely settled by humans, used to provide excellent rhino habitat (BAUMANN 1894), and even in the 1960s hundreds of rhino were killed in this area (WARDENS REPORTS 1959–1973).

A comparison with the data provided by GROVES (1967) (Tables 4 and 5), clearly shows that both the Manyara and the Ngorongoro rhino fall in the subspecies *michaeli*, as described by him. As cited above, the type specimen of this subspecies came from the area between Engaruka and Serengeti. By my reckoning it is highly likely that this statement refers to the Ngorongoro area, as it lies between Engaruka and the Serengeti. The conclusion that the skulls of Ngorongoro Crater rhino clearly fall into those of the *michaeli* subspecies group, confirms this notion. Hence, GROVES' (1967) remark that the area between Engaruka and Serengeti falls into the intergrade zone between subspecies *michaeli* and subspecies *minor* ist not born out by the data. Apparently, the very dry Salei Depression, bordering the Ngorongoro Highlands to the northwest (Fig. 1), acted as an ecological barrier for rhino between the moist Ngorongoro area and the Serengeti woodlands. However, the Mbulu District in the direction of Lake Eyasi may have been an intergrade zone between the two named subspecies (Table 4). If this is true, rhino from the

Table 4. Skull characteristics of three subspecies of Black rhinoceros and of two sub-populations from northern Tanzania

All data, except from Manyara and Ngorongoro, from GROVES (1967). Rhino from Lake Manyara National Park and from the Ngorongoro Crater are considered to belong to the *michaelis* group, but those from the Mbulu District and the vicinity of Lake Eyasi are intergrades between *michaelis* and *minor* (see Discussion)

	Basal length	Zygomatic breadth	Occipital breadth	Sample size
Lake Manyara and Ngorongoro Crater	501.4 ± 20.8	317.7 ± 15.8	-	38
subspec. <i>michaeli</i>	514.2 ± 14.2	326.8 ± 9.8	186.2 ± 10.1	22
Lake Eyasi and Mbulu District	525.8 ± 14.8	327.0 ± 12.8	187.7 ± 12.6	12
subspec. minor	545.5 ± 16.9	330.4 ± 10.5	188.2 ± 12.1	23
subspec. ladoensis	557.5 ± 14.2	347.7 ± 11.2	210.2 ± 6.3	6

subspecies *minor* must once have been living in Sukumaland (on the west side of Lake Eyasi) as they still do in the western Serengeti. The chance to confirm this hypothesis is remote, as it is extremely unlikely that rhino still live in Sukumaland.

North of the Serengeti (Fig. 1), between the White Nile and Lake Naivasha, Kenya, another subspecies of the Black rhinoceros occurs, D. b. ladoensis Zukowsky, 1964. This subspecies is even larger than minor (GROVES 1964; Table 4). The rhino from Ngorongoro and Manyara, and the michaeli group are clearly distinct from ladoensis, and the coefficient of difference is (nearly) as high as advocated by MAYR (1969) to distinguish subspecies (Table 5). However, the value of this coefficient is not high enough to distinguish between minor and ladoensis (pace GROVES 1967).

Based on data from GROVES (1967), i.e. greatest skull length, basal length, zygomatic

breadth, and occipital breadth, but excluding teeth row length (as this parameter is subjective to shortening in older age because of teeth wear), coefficients of racial likeness (CRL) values have been calculated for *michaeli*, *minor*, and *ladoensis*. This value is highest for *michaeli* and *ladoensis* (CRL = 5.789), so these two subspecies are least alike. It is lowest for *ladoensis* and *minor* (CRL = 3.296), and intermediate for *minor* and *michaeli* (CRL = 4.630; all values with standard error of 0.477 and in the class "moderate" association' of Pearson 1928). Together with the data presented in Table 5, the conclusion is that the subspecies *minor* ist not clearly distinct from either *michaeli* or *ladoensis*.

Table 5. Coefficients for basal length (B) and zygomatic breadth (Z) for different pairs of groups of Black rhinoceros (upper right values), and average coefficients of difference for the same pairs (lower left values)

Only the rhinoceroses from Manyara and Ngorongoro, and perhaps those from the *michaelis* group, differ enough from the *ladoensis* group to warrant subspecific distinction

	Manyara and Ngorongoro	Subspec. michaeli	Lake Eyasi and Mbulu District	Subspec. minor	Subspec. ladoensis
Manyara and Ngorongoro	-	B=0.366 Z=0.355	B=0.685 Z=0.325	B=1.170 Z=0.483	B=1.603 Z=1.111
Subspec. michaeli	0.361	-	B=0.400 Z=0.009	B=1.106 Z=0.177	B=1.525 Z=0.995
Lake Eyasi and Mbulu District	0.505	0.205	-	B=0.621 Z=0.146	B=1.093 Z=0.863
Subspec. minor	0.827	0.642	0.384	_	B=0.386 Z=0.797
Subspec. ladoensis	1.357	1.260	0.978	0.592	-

According Corbet (1970), "the concept of subspecies is meaningless unless it is restricted to discrete segments of a species. A distinction should be drawn between 'definite subspecies' that have been convincingly shown to be discrete entities in nature and 'provisional subspecies' that are based on discretely definable samples that are too small or non-random to indicate with a high degree of probability whether the populations from which they were drawn are or are not discrete entities". It appears that the forms described as michaeli, minor, and ladoensis may well represent clinal variation, with minor being the intermediate. If this is true, then minor should not be considered a "definite subspecies" (sensu Corbet 1970).

Although the difference between ladoensis and michaeli is not very large either, the fact that the fossil material from the Lake Turkana area, northern Kenya, from the Early Pleistocene yielded a rhino skull that would fall into the present-day small subspecies group (Harris 1983) increases the likelihood of a real distinction between a small and a large Black rhinoceros in East Africa. Added to this is that, as least in the border area between Tanzania and Kenya, there appears to be an ecological barrier between the two forms ladoensis and michaeli in the arid Salei Depression. This would counter the critique of Corbet (1970) that many subspecies have been described and subspecific boundaries drawn with little regard to the probability of either the range or the variation being continuous or discontinuous.

Several authors have suggested that the designation of subspecies would be helpful for the study of geographic variation but for the lack of a good biological definition of the subspecies (Johnson 1982; Storer 1982; Zusi 1982). Eldredge and Cracraft (1980) do not even mention the subspecies, the species being considered the "minimal phylogenetic group" or the "taxon of the lowest categorical rank within the Linnaean hierarchy".

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However, if by multi-variate statistical procedures groups of individuals can be distinguished, it could be possible that there are barriers in the gene flow between these groups or populations. "A name for such a population may be defensible on the grounds that it signals phenotypic divergence and a reduction of gene flow; in other words, the populations might be incipient phylogenetic species" (McKitrick and Zink 1988).

Whether or not the subspecies is a valid category in systematics, it is of value in nature conservation. Perhaps the observed degree of non-homogeneity within a species, such as in the Black rhinoceros, could result in new species in the future. Nature conservation is not only about maintaining what exists and has evolved, but should also concentrate on keeping open avenues for future evolution.

The situation for the Small black East African rhinoceros is very grim at present, and without very firm conservation measures it is doubtful whether the subspecies will survive another five or ten years. The range has been extremely fragmented, with perhaps a dozen or so still alive in Tsavo N.P., less than ten on Mts Kilimanjaro and Meru, thirty at the most in Tarangire N.P., perhaps ten or twenty in Manyara, and twenty in the Ngorongoro. The total population is therefore between 50 and 100, with the largest populations in the Tarangire-Manyara – Ngorongoro area. If subspecies *michaeli* is to be saved it should be by concentrating much of the conservation measures on this area, for example through extending Lake Manyara National Park (Prins 1987), by international financing of salaries of park rangers, and by education of the people living around the protected areas.

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Zusammenfassung

Geographische Variation der Schädel beim bedrohten Spitzmaulnashorn Diceros bicornis michaeli in Nordtansania

Schädelparameter des Spitzmaulnashorns Diceros bicornis (L., 1758), aus dem Lake Manyara Nationalpark und dem Ngorongoro-Krater – beide Lokalitäten liegen in Nordtansania – wurden vermessen. Die statistische Analyse zeigte, daß die Schädel zu zwei morphologisch unterscheidbaren Subpopulationen mit nur schmaler Überlappungszone gehören. Die Nashörner beider Gebiete werden der Unterart D. b. michaeli Zukowsky, 1964, zugeordnet. Das Ngorongoro-Gebiet stellt keine Übergangszone zwischen den Unterarten michaeli und D. b. minor Drummond, 1876, dar. Eine Analyse der Daten von Groves (1967) und jener, die für diese Studie gesammelt wurden, zeigt, daß Schädel, die zur Unterart minor gehören, zwischen den Unterarten michaeli und D. b. ladoensis Zukowsky, 1964, eingeordnet werden müssen. Selbst wenn man dem Konzept der Unterarten keine entscheidende biologische Bedeutung beimißt, ist es im Zusammenhang mit dem Naturschutz wichtig. Große Anstrengungen sollten zur Rettung des Spitzmaulnashorns D. b. michaeli gemacht werden, da in der freien Natur nur noch zwischen 50 und 100 Tiere leben.

Literature

BAUMANN, O. (1894): Durch Masailand zur Nilquelle. Reisen und Forschungen der Masai-Expedition des deutschen Antisklaverei-Komite in den Jahren 1891–1893. Berlin: Reimer.

COBB, S. (1976): The distribution and the abundance of the large herbivores of Tsavo National Park, Kenya. D. Phil. Thesis, Oxford University.

Douglas-Hamilton, I. (1976): Selous elephant and wildlife survey. Typescript, 70 pp.

ELDREDGE, N.; CRACRAFT, J. (1980): Phylogenetic patterns and the evolutionary process - methods and theory in comparative biology. New York: Columbia Univ. Press.

GODDARD, J. (1969): Aerial census of black rhinoceros using stratified random sampling. E. Afr.

Wildl. J. 7, 105-114. GROVES, C. P. (1967): Geographic variation in the Black rhinoceros *Diceros bicornis* (L., 1758). Z. Säugetierkunde 32, 267-276.

GUERIN, C. (1976): Rhinocerotidae and Chalicotheriidae (Mammalia, Perissodactyla) from the Shungura Formation. In: Earliest man and environments in the Lake Rudulf Basin. Ed. by Y. COPPENS, F. C. HOWELL, G. L. ISAAC, and R. E. LEAKEY. Chicago: Chicago University Press. 214-221.

HALTENORTH, TH.; DILLER, H. (1979): (revised and enlarged by Smeenk, C.): Elsevier gids van de Afrikaanse zoogdieren. Amsterdam: Elsevier.

HARRIS, J. M. (1983): Family Rhinocerotidae. In: Koobi Fora Research Project. The Fossil ungulates: Proboscidea, Perissodactyla, and Suidae. Ed. by J. M. HARRIS. Oxford: Clarendon Press. Vol. 2,

HOOIJER, D. A. (1969): Pleistocene East African rhinoceroses. Fossil vertebrates Afr. 1, 71-98.

HOOIJER, D. A. (1976): Evolution of the Perissodactyla in the Omo Group Deposits. In: Earliest man and environments in the Lake Rudolf Basin. Ed. by Y. COPPENS, F. C. HOWELL, G. L. ISAAC, and R. E. LEAKEY. Chicago: Chicago University Press. 209-213.

JOHNSON, N. K. (1982): Retain subspecies - at least for the time being. Auk 99, 605-606.

Leakey, M. D.; Hay, R. L.; Curtis, G. H.; Drake, R. E.; Jackes, M. K.; White, T. D. (1976): Fossil hominids from the Laetolil Beds. Nature 262, 460-466.

MAYR, E. (1969): Principles of systematic zoology. New York: McGraw-Hill Book Co.

McKitrick, M. C.; Zink, R. M. (1988): Species concepts in ornithology. The Condor 90, 1-14.

Pearson, K. (1928). On the coefficient of racial likeness. Biometrika 18, 105-117.
Prins, H. H. T. (1987): Nature conservation as an integral part of optimal land use in East Africa: the case of the Masai Ecosystem of northern Tanzania. Biological Conservation 40, 141-161.

SOKAL, R. R.; SNEATH, P. H. A. (1963): Principles of numerical taxonomy. San Francisco: W. H. Freeman and Co.

STORER, R. W. (1982): Subspecies and the study of geographic variation. Auk 99, 599-601.

WARDEN'S REPORTS (1959-1973): Unpubl. monthly reports by respective wardens of the Lake Manyara Game Reserve/Lake Manyara National Park to the Director of Tanganyika/Tanzania National Parks. Arusha.

Zusi, R. L. (1982): Intraspecific geographic variation and the subspecies concept. Auk 99, 606-608.

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