

Zusammenfassung

Adaptive Evolution des Fußes der Equiden

Dieser Artikel diskutiert einige Veränderungen im Bau des Fußes fossiler Equiden während des Übergangs zur Einzebigkeit sowie parallele Anpassungen in einer fortdauernd dreizehigen Gattung.

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Notes on the Gazelles

1. *Gazella rufifrons* and the zoogeography of Central African Bovidae

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Introduction

Taxonomy retains its fundamental importance today as the "donkeywork" end of Systematics, if indeed the two are properly to be distinguished. Systematics may be looked on as the central unifying area in biology: the part without which none of the rest makes sense. While this claim is true in regard to all fields, from palaeontology to molecular biology, from ethology to conservation, its direct impact is perhaps nowhere more obvious than in the field of zoogeography.

An often neglected key paper on the mammalian zoogeography of Africa is ERNST SCHWARZ'S "Huftiere aus West- und Zentralafrika" (1926). Based primarily on the

Duke of Mecklenburg's expedition to the former German possessions of Togo and Kamerun, the paper is an attempt to draw together the threads of ungulate distribution and geographic variation across the African continent north of the forest belt, with the proposal of a major break in morphotypes in the vicinity of Lake Chad, and a pocket of distinctive geographical types in the area to the south of this lake.

MOREAU (1966) has discussed the distribution patterns of Africa's birds, and drawn attention to palaeogeographical findings in as far as they impinge on the situation. Until the end of the Pleistocene the Sudanic grasslands were divided by a major lake, Mega-Chad, of which the present-day Lake Chad is the reduced, seasonally fluctuating remnant. The reticulated, braided pattern of the interlaced rivers south of Lake Chad — the Chari, Logone, Bahr Illi, Bahr Mbassa, Bahr Lairi, Bahr Keita, Batha, Komadugu Gana, and probably the Benue — might be explained as the remains of a delta feeding this major basin. Such a situation would go far to explain and east-west break such as SCHWARZ postulated, and in part also his pocket of special races in the Chari region.

Table 1 lists ten Bovid species claimed by SCHWARZ to show such a pattern of subspeciation. It will be seen that in many, but not all, cases there are different subspecies in the lower (and middle) and upper Chari basins. The Chari forms themselves assort with the eastern subspecies-groups rather than the western; but the latter very often reach into the upper Benue valley and so approach the Chari drainage very closely.

This paper attempts to examine one of SCHWARZ's case studies in some detail, to see whether the evidence for his view stands up to critical analysis. The species examined is *Gazella rufifrons*; the skulls (not the skins, for reasons of time and health) were studied at the Senckenberg Museum, Frankfurt, in the summer of 1973; many thanks are due to Dr. DIETER KOCK for his assistance at this time. Comparative material was seen in the Zoologisches Museum, Berlin, the British Museum (Natural History) and the Powell-Cotton Museum, Birmington, Kent; for assistance in these collections thanks are due to Dr. R. ANGERMANN, Dr. H. HACKERTHAL, Dr. G. B. CORBET, Dr. A. W. GENTRY and Mr. L. BARTON.

Table 1
Subspecies of Bovidae in Central Africa
after SCHWARZ (1926)

	Western form	Eastern forms		
	Nigeria	Lower Chari	Upper Chari	Sudan
<i>Alcelaphus buselaphus</i>	<i>invadens</i>	<i>tschadensis</i>	<i>modestus</i>	<i>lelwel</i>
<i>Damaliscus korrigum</i>	<i>purpurescens</i>	<i>korrigum</i>	<i>lyra</i>	<i>tiang</i>
<i>Sylvicapra grimmia</i>	<i>campbelliae</i>	<i>pallidior</i>	<i>pallidior</i>	<i>lutea</i>
<i>Ourebia ourebi</i>	<i>nigricaudata</i>	<i>splendida</i>	<i>dorcas</i>	<i>goslingi</i>
<i>Kobus ellipsiprymnus</i>	<i>togoensis?</i>	<i>tschadensis</i>	<i>annectens</i> (= <i>schubotzi</i>)	<i>harnieri</i>
<i>Kobus kob</i>	cf. <i>pousarguesi</i>	<i>adolphi</i>	<i>bahrkeetae</i>	<i>leucotis</i>
<i>Gazella rufifrons</i>	<i>hasleri</i>	<i>kanuri</i>	<i>centralis</i>	<i>laevipes</i>
<i>Hippotragus equinus</i>	<i>gambianus</i> (= <i>koba</i>)	<i>scharicus</i>	<i>scharicus</i>	<i>bakeri</i>
<i>Tragelaphus scriptus</i>	<i>scriptus</i>	<i>pictus</i>	<i>signatus</i>	
			<i>punctatus</i>	<i>bor</i>
<i>Syncerus caffer</i>	<i>adamanae</i>	<i>brachyceros</i>	<i>houyi</i>	<i>aequinoctialis</i>

Generic and specific names have been altered to accord with modern usage; sub-specific names according to Schwarz (1926) except for *Kobus kob adolphi* Lydekker and Blaine, 1914, which has been substituted for *Adenota kob adolfriederici* Schwarz, 1914 (preoccupied if the species is transferred to the genus *Kobus*).

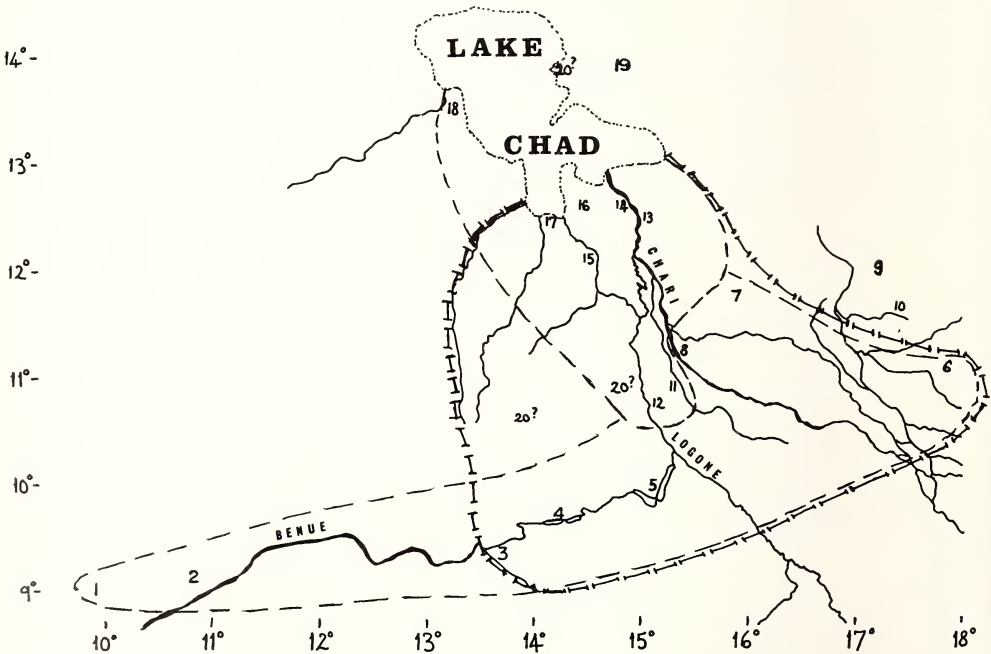
Central African gazelles

Only one species of gazelle occurs in the Sudanic grasslands and extends to the south of Lake Chad: *Gazella rufifrons* Gray, 1846, the Red-fronted Gazelle. By the present author (GROVES 1969) this species was united with the East African *G. thomsonii* Günther, 1884, an attitude maintained in this paper (despite the remonstrances of LANGE 1972) on the grounds of (1) basic similarity, (2) the existence of the morphologically bridging and geographically intervening race *albonatata*; and with the North African *G. cuvieri* Ogilby, 1840, a union which will not be proceeded with in this paper since the similarity, while real enough, is less close than with *thomsonii* and there are no intermediate forms.

SCHWARZ (1914) and LYDEKKER and BLAINE (1914) divided this species' exclusive of the *thomsonii* group and the Ethiopian *tilonura*) into five subspecies as follows:

1. *rufifrons* Gray, 1846: Senegal
2. *hasleri* Pocock, 1912: Nigeria (Kano)
3. *kanuri* Schwarz, 1914: Lower Chari
4. *centralis* Schwarz, 1914: Upper Chari
5. *laevipes* Sundevall, 1847: Sudan

SCHWARZ (1914, elaborated in 1926) distinguished the two Central African races thus: *kanuri* is cinnamon in colour with the flank-stripe brown-black, 20–30 mm broad; pygal stripe not well expressed; skull small and narrow with a long narrow



Localities for *Gazella rufifrons* in Central Africa — 1 = Wase; 2 = Muri, Adamawa; 3 = Bey; 4 = Lere; 5 = Fianga; 6 = Magretta, Melfi; 7 = Deridja; 8 = Madubu; 9 = Bokoro-Erla road; 10 = Erla-Bedanga road; 11 = Diao; 12 = Duguia; 13 = Gulfei (Goulfey); 14 = Gulfei Gana; 15 = Between Koda and Kalim Mud'i; 16 = Mafate; 17 = Wulgo; S. shore of Lake Chad; 18 = Yo; 19 = Ira; 20 = Mugur (Mougour) — The dashed lines indicate the boundaries of *kanuri* (northern) and of *centralis* (southern) as recognised by SCHWARZ. The ticked dashed line (—|) indicates the approximate boundary of *kanuri* as recognised in this paper.

rostrum, orbits almost unprotuberant, short premaxilla making a long suture with the nasal. Horns are fairly long, diverging towards the tips. By contrast *centralis* is a darker cinnamon, with the flank stripe deep black, 30–40 mm broad; pygal stripe clear but narrow. Skull larger and heavier with orbits strongly protuberant, a short narrow rostrum, longer premaxillae. The horns diverge more abruptly at the tips.

The other subspecies were more briefly described in his 1926 paper. The Nigerian race *hasleri* was said to be near *kanuri* but rather more wine-red in colour; there was no indication that any specimen but the type was available to SCHWARZ, as other Nigerian specimens (from Wase and Bida) were compared more closely with *centralis*. The nominate *rufifrons* was livid brown with a darker forehead (this latter feature not seen in other races except, slightly developed, in the type of *kanuri*), the white face-stripe rather narrow, the skull large with a short rostrum. Finally the eastern *laevipes* is said to be lighter, less red (orange-ochre to cinnamon), with the horns diverging from the very base.

Table 2a

Skull measurements of Central African *Gazella rufifrons* (males)

	Horn length	Horns, tip-to-tip	Horns, greatest span	Greatest skull length	Biorbital breadth	Preorbital length of skull
1. Specimens assigned by SCHWARZ (1926)						
<i>G. r. centralis</i>						
6437. Magretta (Type)	252	110	136	204	97	109
6428. Deridja	233	121	138	207	91	111
6438. Mugur	237	132	136	216	100	115
6430. Muri (young)	—	—	—	195	89	102
<i>G. r. kanuri</i>						
6440. S. shore L. Chad	197	63	86	201	88	106
6439. Gulfei (subad.)	265	82	103	194	88	102
6451. Gulfei	235	110	131	203	91	99
6441. locality?	212	111	118	201	91	106
6454. Gulfei (Type)						
(subad.)	264	93	110	199	86	105
6445. Gulfei	206	78	98	200	92	109
2. Other specimens from within the same area						
<i>G. r. centralis</i>						
P-C. Cam. II. 90. Bey (9.20 N, 13.40 E)	187	100	110	199	88	109
B. M. 5.5 10.4. Wase, N. Nigeria. Mentioned by SCHWARZ and assigned by him to <i>centralis</i>	190	100	109	211	93	116
<i>G. r. kanuri</i>						
P-C. NN. 4. Between Koda and Kalim Mud'i (12.07 N, 14.35 E)	231	104	121	205	87	105
B. M. 7.7.8.210. Yo, L. Chad. Mentioned by SCHWARZ and assigned by him to <i>kanuri</i>	251	97	111	211	96	115
3. Specimens from just outside the area						
P-C. NN. 21. Near Ira (13.55 N, 14.50 E)	239	133	148	212	92	113
P-C. NN. 88. Erla-Bedanga road (11.38 N, 17.26 E)	272	114	142	214	94	114

Listing (Table 2a) some skull measurements of the specimens referred by SCHWARZ to the two Chari valley races appears at first sight to confirm his allocation of them to two separate subspecies: notwithstanding that the range of variation for many measurements is very wide in *centralis*. (This applies in the case of males only: measurements of the females are not listed because they not only overlap, but the range of *kanuri* in every case encompasses that of *centralis*). These skulls, it should be emphasised, are the only adult males in the Frankfurt series: some of them, indeed, are not fully mature but except in the case of no. 6430, from Muri (Adamawa) it is likely that all are fully grown.

Adding other specimens, however, from other collections, the skull differences break down. Two skulls (Table 2a) are from within the distribution of *centralis*; two from within the distribution of *kanuri*; two from the near vicinity. The skull from Bey is much smaller than any adult *centralis* skull in Frankfurt, and fits into the middle of the range of *kanuri*; one from "between Koda and Kalim Mud'i", in the middle of the area of *kanuri*, is slightly larger than any Frankfurt skull of this race, and falls into the bottom end of the *centralis* range. In fact, turning to the Frankfurt skulls individually, it appears that only the skull from Mugur, assigned to *centralis*, really brings up the average for this race: but for this skull, the two Chari races would be much the same size.

Unfortunately the exact location of Mugur is in doubt; the U.S. Board of Geographic Names Gazetteer lists Mougou at 10.54 N, 14.54 E and at 13.53 N, 14.15 E; and Mouhour at 10.37 N, 13.52 E. The third is perhaps more likely phonologically, but none of the three falls exactly inside the boundaries of *centralis* as drawn on the evidence of other specimens.

Nor can it be said that the other skull differences cited by SCHWARZ stand up to critical examination. Orbital protrusion, as estimated from the biorbital breadth of the skull, overlaps, as does rostral (preorbital) length: the latter only marginally so, but more decisively when the non-Frankfurt specimens are included. The length of the nasopremaxillary suture (Table 2b) is not different: indeed, the length of this suture was mentioned under *kanuri*, but "type d" (in which the naso-premaxillary suture is longer than the naso-maxillary) is slightly more frequent in *centralis*.

It is difficult to judge the value of the colour differences assigned to the two forms. Colour differences, though average rather than absolute, do exist in the species: *G. r. rufifrons* tends to be redder than *laevipes*, with often considerable blackening on the forehead, but this feature is clinal, being bridged by some Nigerian skins (such as the type of *hasleri*). Moreover SCHWARZ states that the skins of specimens from Diau and Musgum (the latter, from which no skulls are available, being on the Logone at 10.59 N, 15.00 E, and so well into putative *kanuri* country) are

intermediate between *kanuri* and *centralis*, while a skin from Bida, in the British Museum, is darker than most of the latter. So colour differences within the Chari district would seem likewise to be clinal, from a dark cinnamon on the upper courses of the Chari and Logone to a lighter tone, not different from the usual Nigerian

Table 2b

Premaxilla types of Central African *Gazella rufifrons*

	Type		
	b	c	d
" <i>centralis</i> "	—	4	6
" <i>kanuri</i> "	1	7	4
b: premaxilla makes point contact with nasal			
c: premaxilla makes long contact with nasal			
d: premaxilla makes longer contact with nasal than does maxilla			

type, towards Lake Chad; and again, these would be on average rather than absolute differences.

The conclusion is that, while there may be weakly marked clines involved, basically the two Chari subspecies are the same: the names *centralis* and *kanuri* are synonyms. It remains to compare the general Chari population with populations of the species from elsewhere within its range.

Subspeciation in *Gazella rufifrons*

Table 3a gives skull measurements of all specimens of *G. rufifrons* available to the author, exclusive of *thomsonii*, *nasalis* and *tilonura* (concerning which there is nothing to add to the author's 1969 paper). Many additional skulls of *rufifrons* and *albonotata* were measured in Berlin; and the measurements of still further skulls of the nominate race, housed in the Institut Fondamental de l'Afrique Noire at Dakar, were kindly made available to me by Dr. PETER GRUBB.

The whole aspect of the nominate race, *Gazella rufifrons rufifrons* Gray, 1846, is completely altered by the new material. In the previous paper (GROVES 1969) it was characterised as "the largest race" — primarily on the basis of a single skull, B.M. 9. 11. 2. 31 from Longol, Senegal, measuring 222 mm in greatest length. This skull is now seen to be a quite exceptional specimen, an outsize example of a race which averages smaller than the Nigerian and Sudan representatives of the species! The standard deviations of the skull measurements of the race are very large in the males: in the basic dimensions (greatest length, greatest [biorbital] breadth, preorbital length) far greater than for other populations. For this reason the males' measurements of the skull of *rufifrons* fail to reach the traditional 75% limits when compared to those from Nigeria or Sudan, whereas the females' reach and well surpass these limits. This curious situation may be recognised by maintaining the separation of *rufifrons* and *laevipes*, but on a provisional basis only.

The skull from Labbezanga, Niger (Chicago no. 42757), included in *laevipes* in the 1969 paper, now clearly fits much better into the nominate race (greatest length 183 mm.: not fully grown, however). Other specimens of the nominate race are from both Senegal and Mauretania.

In *laevipes* are included specimens from Nigeria; these differ, as can be seen from Table 3a, hardly at all from those from the Sudan, except in their rather shorter nasal bones. Specimens from localities around Lake Chad, exclusive of the Chari valley (Yo, Ira, Erla-Bedanga road, Mugur: males; Ira, Bokoro-Erla road: females) are kept separate from the Nigerian series, but do not in fact differ from the latter, except in the slightly narrower braincase. Within the Sudan group, skulls from Darfur have been kept separate from those from the White Nile itself, and they do differ slightly as can be seen; three female skulls from the Nuba Mountains also show trifling differences from the Nile valley series. It is uncertain whether any of the latter are from the Nile's east bank: localities like Paloich (Chicago Museum) suggest that this might be so, but field observations are lacking.

G. r. albonotata is included in the Table both to take advantage of rather larger samples than were available previously, and to reiterate the conclusion reached in the author's 1969 paper that it is very close to (not specifically distinct from) *laevipes*, as well as *thomsonii*. It is similar in size to *laevipes* but with a narrower skull, and is slightly longer in the rostrum. None of these differences are particularly great.

In the Table, the designation *kanuri* incorporates all Chari valley skulls, since it was found above that no valid differences exist between true *kanuri* and SCHWARZ's

Skull measurements of subspecies and local populations of *Gazella rufifrons*

	Greatest skull length			Biorbital breadth			Preorbital length			Nasal length			Braincase breadth		
	Mean	s. d.	n	Mean	s. d.	n	Mean	s. d.	n	Mean	s. d.	n	Mean	s. d.	n
<i>rufifrons</i>	204.7	9.16	7	87.7	5.14	11	Males								
<i>kanuri</i>	201.6	3.81	9	90.1	3.33	9	108.1	6.49	7	49.9	5.51	9	63.1	4.04	9
<i>laevipes</i>							105.8	3.70	9	48.3	3.97	9	62.3	2.83	9
Nigeria	212.3	1.50	4	94.2	3.97	6	113.0	2.92	5	52.3	5.97	4	70.0	4.32	7
Yo. Ira	213.3	2.25	4	95.5	3.50	4	114.3	1.00	4	57.0	5.96	4	67.5	4.25	4
Darfur	220.0	—	2	95.0	—	2	117.0	—	2	54.0	—	2	74.0	—	2
White Nile	212.2	6.55	9	92.9	2.77	10	113.4	4.93	9	58.8	5.78	9	70.6	1.57	11
<i>albonotata</i>	212.1	5.33	9	88.2	4.00	11	114.6	2.96	9	52.9	6.45	9	65.3	3.20	11
							Females								
<i>rufifrons</i>	187.1	5.79	7	79.8	2.49	9	100.8	5.09	8	44.5	2.67	8	57.3	3.69	8
<i>kanuri</i>	194.3	5.06	8	85.6	3.50	9	104.8	4.17	8	48.8	5.93	9	58.0	2.06	9
<i>laevipes</i>															
Nigeria	—	—	—	89.7	4.73	3	—	—	—	—	—	—	64.3	5.03	3
Ira etc.	212.5	—	2	92.5	—	2	118.5	—	2	53.5	—	2	62.0	—	2
Darfur	205.0	—	2	89.5	—	2	112.0	—	2	57.0	—	2	65.0	—	2
Nuba Mts.	205.0	3.00	3	90.0	1.00	3	110.0	1.73	3	51.7	5.77	3	64.0	4.00	3
White Nile	202.5	4.99	10	86.3	3.06	10	109.9	4.18	10	53.1	4.84	10	63.3	4.52	10
<i>albonotata</i>	202.3	5.25	4	83.8	2.49	5	112.0	1.83	4	45.0	—	2	61.6	5.32	5

centralis. To combine all measurements into one series and calculate means and standard deviations is, in a sense, to "invent" a population, so that what are being compared are figments of the imagination rather than any reality. However in the absence of workable samples from restricted localities, this is all that can be done; it is

necessary in order to get some idea of how one race differs from another, on the understanding that selection pressures will doubtless differ slightly from place to place within the boundaries of a single subspecies so that the "average *kanuri*" parameters could not be expected to correspond to any one population existing on the ground.

With this proviso, then, it is valid to compare *kanuri* with other races and local populations of the species. The sample as a whole is about the same size as the nominate subspecies — males a little smaller, females a little larger — with more protrusive orbits (Table 3a), and shorter horns in the males, which diverge much less. Compared to *laevipes* the sample is a good deal smaller in both sexes (above the 75% level for Greatest Length, Preorbital length and Braincase Breadth in males), and the horns differ in a similar manner as from the nominate race.

In the premaxillary-nasal contact types, *rufifrons* is predominantly of type d (very long contact), with the Labbezanga specimen being of this type as well; *kanuri* is of both d and c, with a single instance (among 20 skulls) of type b (point contact) which *rufifrons* does not show; while *laevipes* is mostly type c with a fair representation of type b.

The somewhat unlooked-for conclusion, therefore, is that *kanuri* is intermediate between *rufifrons* and *laevipes*. In colour it resembles the latter, as in its protuberant orbits; in size, and in its short nasals, it resembles the former. It is intermediate in its premaxillary disposition, and different from either in its horns. The surprising part about this is that its range is encompassed to the north, east and west by that of *laevipes*: Nigerian specimens ("*hasleri*") from Wase, Zaria, Kalani, Bida, Fakai, Kano and Argungu are all clearly representative of *laevipes* (contra SCHWARZ 1926, who pointed out a colour resemblance between the Wase skin and his "*centralis*"); specimens from the Chad region (Yo, Ira etc.) which about on the range of *kanuri* differ just as sharply, so that the transition between *kanuri* and *laevipes* seems to be quite narrow; and the nearest *rufifrons* locality is at Labbezanga, on the Niger River exactly on the border between Mali and Niger (15.02 N, 0.48 E), separated from *kanuri* by the whole breadth of Nigeria.

Table 3b
Premaxilla types in *Gazella rufifrons*

	b %	c %	d %	n
<i>rufifrons</i>	—	30	70	10
Niger	—	—	100	1
<i>kanuri</i>	5	50	45	20
<i>laevipes</i>				
Nigeria	29	57	14	7
Sudan	27	55	18	49

The pattern of subspeciation in Central Africa

The other instances of Central African subspeciation noted by SCHWARZ will now be briefly described, to see whether any light can be shed on the gazelle situation.

1. *Alcelaphus buselaphus*. To the west of Lake Chad occurs the *major* group; to the east of it, the *lelwel* group. South of the lake, SCHWARZ distinguishes *tshadensis* in the

Table 3c
Horn measurements in *Gazella rufifrons*

	Horn length	Tip-to-tip interval	Greatest span
	Males		
<i>rufifrons</i> (n = 10)	260.0,	s. d. 39.49	126.4,
<i>laevipes</i> Sudan (10)	264.0	21.86	129.9
<i>kanuri</i> Nigeria (6)	242.2	26.82	102.5
	239.8	22.50	101.1
			s. d. 25.25
			27.20
			11.40
			15.24
			140.7,
			147.3
			125.5
			119.4
			s. d. 26.62
			25.94
			12.38
			15.00
	Females		
<i>rufifrons</i> (4)	161.3	26.54	60.7
<i>kanuri</i> Sudan (9)	189.2	11.70	60.9
<i>laevipes</i> (8)	162.1	15.91	54.0
			23.03
			16.59
			10.66
			79.6
			74.2
			71.4
			13.32
			10.92
			21.23

lower and middle Chari valley, and *modestus* in the upper. From the measurements he gives, *tschadensis* falls in the range of *lelwel* while *modestus* is smaller: but the same situation may obtain as was found above with the gazelles. It seems probable that (1) there is a valid race in the Chari drainage, perhaps not exactly as defined by SCHWARZ, (2) the border between the two semispecies (*major* and *lelwel*) really is Lake Chad, with the western representative *invadens* (of the *major* group) coming right up the Benue valley (type locality is Garua, 9.17 N, 13.22 E) to abut closely on the range of the *lelwel*-like Chari valley race.

2. *Damaliscus korrigum*. BLAINE (1914) draws attention to the existence of a cline of increasing purplish suffusion in the colour of this species from west to east: from *korrigum* in Senegal via *purpurescens* in Nigeria to *tiang* in the Sudan, and so into East Africa. SCHWARZ (1926) puts a different interpretation onto it, pointing out that the type locality of the nominate race *korrigum* is not Senegal but Bornu (to the southwest of Lake Chad), and proposing that this species like the last is divided into two segments meeting at Lake Chad: a western group (only one race, *purpurescens*) without much purplish bloom, with horns very little curved, very strongly bent back basally, and short, thick, little curved tips; and an eastern group (*korrigum* — Bornu and lower Chari; *lyra* — upper Chari; *tiang* — Sudan; etc.) with more purplish bloom, more curved horns and longer tips. From the description, as well as the measurements in his table, *lyra* does not seem to differ much from *korrigum*; but what is more important is that in this instance, while the western type as before comes up the Benue as far as Ibi (8. 11 N, 9.44 E) and so approaches the Chari race, the latter is said to extend west to Bornu, so that the final divide is not east-west but north-south and Lake Chad is only the barrier in a rather general way.

3. *Sylvicapra grimmia*. In this case there is not said to be more than one race in the Chari valley. Provisionally, the author's conclusions from the British Museum and Powell-Cotton Museum material confirm SCHWARZ's view that there is a Chari valley race *pallidior* different from both the Sudan form (*lutea*?) and the Nigerian (*campbelliae*). The western type — a single subspecies, *coronata* — is in this case restricted to the same sort of range as *Gazella rufifrons rufifrons*, from Senegal to Togo; it is remarkably different from other races, and the Chari valley race has nothing to do with it.

4. *Ourebia ourebi*. Again there are said by SCHWARZ to be two Chari races: *splendida* in the lower Chari valley and *dorcas* in the upper. To judge from his descriptions and measurements, they do not differ much from each other or from *goslingi* (Uele), and together with the Sudan races they differ from the western group of forms (*quadriscopa*, *nigricaudata*) by their large size. However there is some indication that *oribi* in Nigeria may belong to the eastern rather than the western group.

5. *Kobus ellipsiprymnus* (*defassa* section). Again we are said to have two separate races in the Chari valley, but this time no sharp separation of general eastern and western semispecies. There is little in the description of *tschadensis* (from Mafaling, southern shore of L. Chad) to distinguish it from either the Sudan or western races of the species, but *annectens* of the lower Shari (with which *schubotzi* of the Libenge region is synonymised in SCHWARZ's 1926 paper) represents a strikingly different animal. Specimens said to be intermediate between *annectens* and *tschadensis* were recorded by SCHWARZ from the upper Logone and upper Benue.

6. *Kobus kob*. Again we are said to have a basic division into eastern and western types: a big eastern group of forms and a small type west of Lake Chad. While *adolphi* (lower Chari and Lake Chad) is close to the Sudan races, to the south occur *bahrkeetae* (upper Chari), *ubangiensis* (Libenge) and *pousarguesi* (Sanaga River) forming a group intermediate in size but with shorter horns than either.

7. *Hippotragus equinus*. In this species (for which SCHWARZ employed the invalid generic name *Egocerus*) as in *Sylvicapra grimmia* there is only one subspecies described for the Chari valley, *scharicus*, which stands between the western *gambianus* (earlier name, *koba*) and the Sudan *bakeri*, but nearer the latter.

8. *Tragelaphus scriptus*. As in the case of the Waterbuck and Kob, three subspecies have been described by SCHWARZ for the Chari valley but LYDEKKER and BLAINE (1914) considered two of them, *signatus* from the Gribingi region and *punctatus* from the Libenge, to be synonymous, while SCHWARZ himself (1926) inclined to this opinion, keeping *pictus* (lower Chari) distinct. The taxonomy of bushbuck is in such chaos, with sex and age characters being used to separate putative subspecies, that pending a continuing study of the species by GRUBB, it is impossible to make much sense of the Central African situation.

9. *Syncerus caffer*. An interim report on this species by GRUBB (1972) has begun to shed light in this extremely dark corner of taxonomy. It is becoming clear that, after early attempts to split the species into some 50 subspecies, the pendulum swung back too far and modern arrangements are over-lumped. As far as the Central African region is concerned we have not only an east-west division but also intergradation between forest and savannah buffaloes to contend with. In its main outline, however the problem seems to be clear enough: GRUBB finds that buffaloes south and west of the Chari are assignable to the western savannah subspecies *brachyceros*, while those north and east of it belong to the Sudan *aequinoctialis*. There is evidently no trace of a special race in the Chari valley, specimens from the valley itself being satisfactorily accounted for as intergrades between the western and eastern races. Interestingly in this species the western race appears to advance further east than in any other Bovid, reaching to 22° E along the Ubangui river. This is a region which, at least in Waterbuck and Kob, is inhabited by the Chari (or upper Chari) subspecies, so that the western savannah buffalo is in effect ranging eastwards to compensate for the absence of such a race.

Conclusions

It does seem that the Sudanic Bovids are in most cases divisible into an eastern and a western type. Lake Chad is often the approximate boundary between them, but sometimes (*Gazella rufifrons*, *Sylvicapra grimmia*) this boundary is shifted far westwards, to about the Niger. Even this might be consistent with the „Mega-Chad“ theory, as the enlarged lake extended this far west and received the waters of the upper Niger. On the other hand some western races (*Alcelaphus buselaphus*, *Damaliscus korrigum*) extend into the upper Benue valley and abut on the range of an eastern-type subspecies.

The second conclusion is that, in almost every case, there is evidence for a special subspecies in the Chari region: but the evidence for two such subspecies — one in the upper valley, one in the lower — is unsatisfactory. The Lower Chari race in *Gazella rufifrons* turns out to be a construct of specimens correctly assigned and of some better placed with the Nigerian race, and the same may be true of the Upper Chari race; with the extraneous specimens weeded out, the two turn out to be taxonomically identical. It may be suspected that a similar process in other cases may yield a similar result.

The Chari race of a given species may be (a) firmly of eastern type (most cases), (b) indistinguishable from the western type (buffalo), or (c) intermediate between the two (*Gazella rufifrons*, *Hippotragus equinus*). The latter case is unstudied, but in the gazelle example the intermediacy is puzzling because the Chari race borders

only on the range of the eastern form *laevipes* and nowhere meets that of the nominate, western race. It may be hypothesised that with the eastward shrinkage of Lake Mega-Chad the range of *G. r. rufifrons* expanded eastwards, initiating gene-flow into an eastern-type Chari population, but that since then the eastern race *laevipes* has expanded its range at the expense of the western. A similar westward expansion, into northeastern Nigeria, has occurred in some other species, e. g. *Damaliscus korrigum*.

Summary

Study of Central African *Gazella rufifrons* confirms the validity of the subspecies *kanuri* (*centralis* a synonym). It is a sharply-bordered race, unexpectedly intermediate in some respects between Sudan/Nigeria *laevipes* and the Senegal/Mauretania *rufifrons*. As SCHWARZ postulated, Lake Chad forms an approximate boundary between semispecies of a given species, and in most cases there is a special Chari valley subspecies showing predominately eastern affinities. This is consistent with the geological findings of a greatly expanded Lake Chad in the Upper Pleistocene.

Zusammenfassung

Notizen über die Gazellen. 1. Gazella rufifrons und die Zoogeographie der zentralafrikanischen Boviden

Ein Studium der zentralafrikanischen Art *Gazella rufifrons* bestätigt die Gültigkeit der Unterart *kanuri* (mit Synonym *centralis*). Es ist eine scharf abgegrenzte Rasse, die unerwarteterweise in mancher Hinsicht zwischen *laevipes* (Sudan/Nigeria) und *rufifrons* (Senegal/Mauretanien) liegt. Wie SCHWARZ ausführt, bildet der Tschadsee eine ungefähre Grenze zwischen Semispecies einer bestimmten Art. In den meisten Fällen gibt es eine spezielle Unterart im Scharibecken, welche hauptsächlich nähere Verwandtschaft nach Osten zeigt. Dieses stimmt mit den geologischen Entdeckungen eines viel weiter ausgebreiteten Tschadsees im Hochpleistozän überein.

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