On the Smaller Gazelles of the Genus Gazella de Blainville, 1816

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It has been justly remarked (GROVES and HARRISON, 1967) that the taxonomy of the genus Gazella is one of the most confused in the whole class Mammalia. It is probable that no other genus of large mammals creates such problems in regard to its classification. Ever since first inclusive survey based on modern principles (LYDEKKER and BLAINE, 1914) was published, further surveys have revised the named forms in very diverse ways, with equal justification from the evidence available.

The first attempt to bring order out of the chaos of Lydekker and Blaine's twenty species in their subgenus Gazella was that of Schwarz, 1937. This author recognised just four species of smaller gazelles, which he referred to as G. gazella, dorcas, leptoceros and subgutturosa; the first being a very inclusive species, encompassing the forms recognised by Lydekker and Blaine as the species spekei, bennetti, rufifrons, cuvieri etc. The species marica was placed by Schwarz in G. subgutturosa. The form which had been described a year earlier by Carruthers and Schwarz as G. gazella saudiya was retained in the species gazella although it was already apparent that it is in part sympatric with another race of the same species, G. arabica.

ELLERMAN and MORRISON-SCOTT (1951) reclassified the Palearctic species in quite a different manner. The gazelles of Arabia were reshuffled, marica being placed in the species leptoceros and saudiya in dorcas. The species G. subgutturosa was placed in a new subgenus Trachelocele, thus separating it sharply from marica which Schwarz

had considered conspecific with it.

VON BOETTICHER (1953) described the gazelles keeping exactly to the classification of Lydekker and Blaine, merely arranging their species into Species Groups. No new evidence was presented with regard to their classification; the author appeared to have seen no actual preserved specimens, nor was their any reference to papers written subsequent to Lydekker and Blaine. Many of the Species Groups are entirely artificial (e. g. marica is aligned with arabica and muscatensis); in addition, von Boetticher erected a new subgenus, Rhinodorcas to include Gazella spekei, which Schwarz had placed as a subspecies of G. gazella.

GENTRY (1964) presents a classification which combines the best features of earlier revisers. Like Schwarz, he places G. tilonura in the same species as rufifrons; unlike Schwarzhe makes pelzelni a subspecies of G. dorcas. Since GENTRY's paper is primarily a comparison of four African species (dorcas, spekei, rufifrons and thomsoni) the non-African forms are naturally compared with these four; the forms bennetti and arabica are recognised as being close to dorcas, while marica is re-aligned with subgutturosa. No mention is made of saudiya; were it not for the existence of saudiya, sympatric with arabica in Arabia, there would be no need to question GENTRY's provisional assessment of the latter as the representative of dorcas in Arabia.

GROVES and HARRISON (1967), finding that the chief source of the difficulty is the presence in Arabia of two sympatric species both showing a marked resemblance to dorcas but not to each other, made a special study of the Arabian gazelles. Apart from the definite placement of marica as a subspecies of subgutturosa, it was suggested that, on the basis largely of skull characters, saudiya ranks as a subspecies of dorcas, and that bennetti of India is probably an eastern extension of the same species; while

arabica shows morphological intergradation with gazella of Syria, and the two (together with two other local Arabian variants) formed a species restricted to the Middle East. Ellerman and Morrison-Scott had placed bennetti in gazella, also cuvieri from the Atlas mountains; Gentry, with considerable justification, doubted whether the latter had anything to do with G. gazella.

The present paper represents an attempt to decipher the interrelationships of the small forms of the genus Gazella, basing the assessment partially on new methods in the taxonomy of this group. The large species of the genus stand apart from the smaller ones, being generally placed in a special subgenus Nanger; their classification presents no particular problems, the only difficulty being to decide whether they deserve separate subgeneric status or are more closely related to one or other of the smaller species.

In Groves and Harrison's 1967 paper it was shown that the two supposed species marica and subgutturosa intergrade in the Euphrates region, and are consequently conspecific. In the materials studied for the present paper, three other cases of intergradation were discovered, which enable one to unite certain other supposed species. These three cases are as follows:

1. G. dorcas isabella (Red Sea Hills) with G. pelzelni (Somalia). These two forms are closely similar in nearly all features, but differ in the shape of the horns in the male. In G. d. isabella the horns are curved out and back, then in and forward, i. e. somewhat lyrate; in pelzelni they are nearly straight, but slightly inturned at the tips. Specimens showing an intermediate form of horn are B. M. 36. 5. 20. 18–20, from Danakil country, Ethiopia. The intermediacy can be demonstrated by the following measurements:

	Greatest width across horns	Tip-to-tip width
isabella	140.5 (101—176)	78.0 (23—129) (22)
Danakil	123.0 (99—147)	91.5 (68—115) (2)
pelzelni	114.4 (81—133)	105.2 (76—132) (9)

2. G. rufifrons laevipes (Sudan) and G. tilonura (northern Ethiopia). The situation is closely similar here, except that in addition to a horn difference tilonura is of a smaller size. In laevipes the horns curve backwards, and slightly forwards at the tips; in tilonura there is a marked inturning at the tips giving a hooked appearance. Two specimens in the British Museum — no. 58:193 from Kassala and no 11. 10. 29. 2 from Kituit, Atbara rivers, are intermediate, in the same manner as in case (1).

	Greatest width across horns	Tip-to-tip width
laevipes	130.9 (97—214)	114.0 (66—179) (22)
Kituit and Kassala	135.0 (131—139)	91.0 (74—118) (2)
tilonura	143.5 (119—173)	63.8 (41— 94) (6)

3. G. rufifrons laevipes and G. thomsoni (East Africa). Contrary to the assertions of LÖNNBERG (1914) and BROOKS (1961) the form known as G. thomsoni albonotata is quite intermediate between rufifrons and thomsoni. The main differences between the two supposed species are in horn length, skull shape, naso-premaxillary contact, shape of naso-frontal suture, and the presence in the former of a pale rufous

stripe separating the black flankstripe from the white of the belly. These points will be dealt with one by one.

a. The long horns of typical thomsoni are not found in its race albonotata, in which the horns are as short as in laevipes (Table 4). Both species have very prominent rings round the horns.

b. Both thomsoni thomsoni and t. albonotata have comparatively narrow skulls; but in t. nasalis the skull is proportionally as broad as in laevipes.

c. In G. thomsoni premaxillary-nasal contact is generally longer than maxillary contact. But this is not constant (Table 6) either individually or subspecifically.

d. The shape of the naso-frontal suture is well figured by GENTRY (1964); the forwardly convex shape of the two halves is found in all skulls of *thomsoni*, but it does occur also in *laevipes*, in perhaps 15% of skulls of that form.

e. As recorded by Brooks (1961), one out of four skins in the British Museum of G. t. albonotata possesses a light rufous stripe below the dark flank stripe;

but it is not as pronounced as is usually the case in laevipes.

Until a more adequate picture can be revealed, therefore, we may adopt the following provisional classification for the analysis; it will be modified by the results of the analysis.

Species: rufifrons (includes tilonura and thomsoni)
dorcas (includes pelzelni)
gazella (includes arabica)

bennetti (includes fuscifrons and christii: it will be shown below that these

are valid subspecies) spekei leptoceros

rufina cuvieri

subgutturosa (including marica)

The method of analysis used was multivariate analysis, using the Discriminant Functions (D2) method of Mahalanobis; this is described in Talbot and Mulhall (1962). Briefly, the object of such analysis is to combine all of a series of measurements into a single measurement, the Generalised Distance between pairs of populations (as represented by the samples available). This method was used before by the present author (GROVES, 1967) for a multi-sample problem, and successfully demonstrated the interrelationships between populations of Gorillas. It is another matter, however, to use the method in comparing different species; in general, of course, the mostly closely related forms (i. e. conspecific populations) should cluster together, but the Discriminant Function will not work in cases of sibling species, and will be unsatisfactory in dealing with examples of character displacement. It should also be noted that the Discriminant Function contains an element of discrimination on grounds of Absolute Size alone; while useful in analysing the relations between races, it is Shape which is important in investigating forms which belong to different species. Penrose (1954) managed to separate Size and Shape components of his own statistic; but since only the Mahalanobis statistic successfully takes account of the intercorrelations of measurements, Penrose's method is not much used nowadays.

With the above warning, therefore, Table 1 — the result of the Discriminant Function analysis by the Mahalanobis method — may be examined. The groups are numbered as follows:

1. G. r. albonotata (9 skulls).

2. G. r. laevipes from the Nile region (8 skulls).

3. G. g. gazella (5).

4. G. g. arabica from the western seabord of Arabia (9).

Generalised Distances (D2) for Male Skulls, smaller Gazelles

,																	
	15															×	
	14														×	14.00	
	13													×	47.25	39.86	
	12												×	27.92	40.00	36.35	
	11											×	40.55	30.54	62.12	54.17	
	10										×	21.82	31.38	37.61	68.81	64.32	,
	6									×	16.63	30.10	47.25	46.38	91.84	86.13	
	8								×	16.35	17.67	26.21	34.99	31.15	80.81	72.98	
	7							×	13.18	17.10	22.86	32.79	44.91	38.93	66.66	80.66	
	9						×	34.94	19.87	25.93	18.83	29.86	23.61	32.54	44.36	40.33	
	r.					×	14.11	34.79	22.97	26.79	19.22	28.85	20.91	31.98	51.10	43.48	
	4				×	33.20	30.47	43.76	33.97	25.44	24.67	37.78	50.72	60.93	80.28	85.94	
	3			×	26.37	25.95	22.83	54.95	36.29	36.15	24.65	33.53	36.75	41.38	45.97	44.06	
	2		×	39.56	47.02	40.18	33.10	86.96	62.47	67.88	49.53	55.21	48.91	63.34	32.42	38.41	
	1	×	29.05	55.83	65.94	51.08	57.83	110.12	89.50	81.17	58.69	96.89	54.77	77.41	50.64	52.92	
		-	2	3	4	S	9	7	8	6	10	11	12	13	14	15	

- 5. G. b. fuscifrons (8).
- 6. G. b. christii (7).
- 7. G. d. saudiya (7).
- 8. G. dorcas subsp. from Darfur (8).
- 9. G. d. isabella from the Red Sea Hills (15).
- 10. G. d. pelzelni (5).
- 11. G. spekei (7).
- 12. G. leptoceros from Algeria (7).
- 13. G. s. marica (5).
- 14. G. s. subgutturosa from Turkmenistan (12).
- 15. G. s. hillieriana (19).

All the skulls were male. Restricted series only were used, to avoid introducing heterogeneity.

It will be seen at once that size is affecting the results: thus marica it rather further from subgutturosa and hillieriana than would have been expected if skull shape alone were involved. Nonetheles, some interesting results are seen. The clusters are as follows:

- a. Nos. 1 and 2.
- b. Nos. 3-11.
- c. Nos. 12-15.

That numbers 1 and 2 should be close is expected if one accepts that albonotata and laevipes are conspecific. It is interesting that leptoceros (no. 12) is close to subgutturosa; it is difficult to see the former as an African extension of the latter, and possibly the closeness may be due to convergent adaptation to a desert environment. The comparative closeness of the dorcas-gazella group needs to be more fully investigated.

Within cluster (b) there is a circular chain of relationships, thus: gazella-arabica-pelzelni-isabella-dorcas-fuscifrons/christii-gazella, with saudiya being very close to dorcas, and further and further away from

isabella, pelzelni, fuscifrons, arabica and gazella respectively. The whole complex forms a Ring Species. G. fuscifrons and christii are somewhat closer to the dorcas group than to the gazella group; accordingly the suggestion made by GROVES and HARRISON (1967), that bennetti is the Indian representative of dorcas, seems to hold good. The fact that saudiya is not intermediate between dorcas and fuscifrons is best explained by character displacement (BROWN and WILSON, 1956).

The taxonomic handling of a Ring Species is always somewhat arbitrary, not least in this case. Because there appears as yet to be no intergradation involved, however, it is probably safe to maintain a specific distinction between fuscifrons and gazella. No gazelles are recorded of this group from Western Iran by LAY (1967); it would be interesting to know whether the intergradation was with gazella or saudiya. At any rate, it is the latter which extends further northeast in the Arabian region today (see Map 1).

Table 2
Generalised Distances (D2) of Smaller Samples, in the G. Dorcas-Gazella-Rufifrons Group

	1	2	3	4	5	6	7	8	9	10
tilonura (3) rufifrons (1)				37.04 85.67						
rufina (1) cuvieri (2)	57.67	51.12	94.32	104.01	92.34	93.21	180.90	150.48	141.76	131.04
Yemen (2)	44.38			22.28						

No connection is indicated in the Discriminant Function between gazella and rufifrons; Schwarz was certainly mistaken in placing them in the same species. In Tables 2 and 3, smaller samples are compared with the groups they are most likely to be near; the small samples contain anything from 1–4 specimens. It will be noticed (Table 3) that the Kurdistan skull is nicely intermediate between marica and subgutturosa. The small leptoceros sample is of skulls from Egypt; surprisingly, they fall even nearer to marica than to Algerian leptoceros. A glance at the individual measurements (Tables 4, 5) shows that the Egyptian from has a broad palate exactly like G. subgutturoa. However, this author does not feel able at the present time to put leptoceros in the species subgutturosa — especially lacking evidence of the throat swelling and general build of the animal.

The main interest of the other figures is that G. cuvieri comes extremely close to laevipes and albonotata. This is not so surprising as it may seem; in other respects too this form ranks as a North African representative of rufifrons. On the other hand G.

Table 3
Generalised Distances (D2) of Smaller Samples, in G. Leptoceros and G. Subgutturosa

	12	13	14	15	
leptoceros (4)	26.16	19.54	52.15	41.96	
Kurdistan (1)	29.27	10.12	23.98	17.80	
yarkandensis (4)	47.02	61.42	14.77	16.47	

rufina — which was tentatively placed by ELLER-MAN and MORRISON-SCOTT (1951) as a race of rufifrons — is very far from all other samples. It is to be expected that samples of a single skull would be untrustworthy; but the very large distance between rufina and the rufifrons groups is more

Skull Measurements: Male (Means and Standard deviations)

	Horn length	Base br.	Skull 1	Skull br.	Preorb. 1	Postorb 1	Palate br.
massaesyla	226.0	58.0	161.5	77.8 ± 1.0	80.5	88.5	45.3 ± 1.0 .
dorcas	234.3 ± 24.1	56.6±3.0	165.8 ± 2.6	77.2 ± 2.2	83.0 ± 1.6	92.0 ± 3.5	45.2 ± 1.7
saudiya	275.0 ± 18.9	56.4 ± 1.9	$\frac{(3)}{172.8 \pm 2.8}$	77.8 ± 1.5	86.5±1.0	97.9 ± 2.8	44.7±1.4
osiris	235.0 ± 16.3	58.5 ± 2.2	(6) 174.2 ± 4.7 (75)	79.3 ± 3.1	(6) 87.9±3.3	95.4 ± 2.4	46.0±1.7
isabella	221.9 ± 13.9	(44) 61.3 ± 2.2	(52) 180.1 ± 4.2	79.7 ± 2.1	90.7 ± 3.3	(50) 101.4 \pm 3.3	46.1 ± 1.6
pelzelni	255.7 ± 21.1	(0.4 ± 2.1)	183.0 ± 3.6	82.4 ± 1.9	93.0±1.9	103.5 ± 2.5	46.7 ± 1.5
fuscifrons	247.7 ± 26.3	(0.9 ± 2.5)	186.9 ± 5.2	83.4 ± 1.7	95.1 ± 3.6	99.1 ± 5.1	48.9±1.2
christii	(10) 258.5 ± 18.1	(3.7 ± 2.4)	190.7 ± 2.1	85.7 ± 3.4	97.3 ± 1.8	103.3 ± 3.1	48.9 ± 2.1
Salt Range	293.6 ± 17.8	(5.2 ± 2.2)	202.5	87.5 ± 2.5	101.4 ± 4.6	106.6±4.1	51.7 ± 1.4
bennetti	254.7 ± 13.3 (7)	(4.5 ± 3.3) (11)	180.8 ± 4.6 (5)	84.5 ± 3.1 (11)	90.8 ± 3.1 (6)	100.2 ± 3.5 (9)	48.0 ± 2.6 (8)
gazella	238.9 ± 17.0	67.7 ± 3.2	187.3 ± 4.8	88.8 ± 2.2	95.8 ± 2.5	107.8 ± 2.6	51.8 ± 1.0
Yemen	229.0	(/)	(†) 191.0 (2)	(6) 87.0 (3)	98.5	110.0	52.5
arabica	223.1 ± 15.5	(4.5 ± 2.3)	186.7 ± 4.5	80.5 ± 2.7	95.8 ± 2.5	105.1 ± 2.7	45.3 ± 2.4
muscatensis	190.0 ± 14.0	61.6 ± 1.7 (3)	172.0 (1)	78.0 ± 3.5 (3)	87 (1)	102.6 ± 2.5 (3)	$(\frac{-2}{2})$ (44.3 ± 1.4) (3)
spekei	236.7 ± 15.7 (12)	58.7 ± 2.8 (13)	180.0±5.7 (7)	83.1 ± 2.2 (13)	90.2 ± 4.1 (7)	98.9 ± 3.8 (13)	49.5 ± 2.8 (13)

Table 4, continued

	Horn length	Base br.	Skull I	Skull br.	Preorb. 1	Postorb. 1	Palate br.
leptoceros	337.3 ± 28.3	58.7 ± 1.0	178.0	84.0±1.9	90.5	97.7 ± 4.9	51.8±1.9
loderi	297.5 ± 15.8	57.3 ± 2.2 (8)	187.0 ± 5.8 (8)	83.9 ± 3.6 (8)	97.6 ± 3.8 (8)	102.0 ± 5.0 (8)	50.0 ± 2.2 (8)
rufina	287.0	76.0	213.0	97.0	124.0	109.0	58.0
cuvieri	309.7 ± 21.1	71.7 ± 2.5	215.5	94.3 ± 1.9	117.0	116.3 ± 1.0	55.7 ± 1.0
rufifrons	257.0	(5)	222.0	100.0	121.0	(5)	(c) 54.0 (1)
laevipes	258.2 + 20.1	(8.3 + 2.7)	212.7 + 5.8	93.5 + 3.2	113.9 + 3.8	115.4 + 5.9	53.7 + 2.2
tilonura	211.3 ± 7.8	61.8 ± 1.8	203.5	90.0±1.4	110.7 ± 1.1	115.5	53.3 ± 1.2
albonotata	247.3 ± 16.2	(5) 64.0 ± 2.1	209.8 ± 4.9	86.6±1.8	113.9 ± 2.2	114.6 ± 5.2	54.4±2.5
thomsoni	307.7	(e)	209.1 ± 5.5	88.0±2.4	103.4 ± 4.1	120.0 ± 3.8	2
nasalis	(21) 308.3 (68)] {	195.4 ± 4.4	86.1 ± 2.5	98.7 ± 5.3	(20) (113.7 ± 4.1) (67)	
marica	271.5 ± 21.9	56.7 ± 2.5	178.8 ± 5.3	84.0±2.2	91.2 ± 2.5	99.4±3.8	51.4 ± 2.5
Kurdistan	267.0 ± 20.3	59.0 ± 1.4	(e)	85.0 ± 1.0	<u> </u>	101.0 ± 3.8	52.0 ± 1.3
Mahammerah	274.6 ± 12.4	60.4 ± 1.9	185.5	89.2 ± 1.7	92.5	108.0	53.0
subgutturosa	$318.0^{(5)}_{-23}$	(5.2 ± 2.5)	203.9 ± 4.1	95.9 ± 1.9	110.0 ± 3.1	112.1 ± 3.3	57.1 ± 2.4
billieriana	256.9 ± 12.5	63.6 ± 2.5	202.2 ± 4.2	95.9 ± 2.4	105.2 ± 3.4	106.8 ± 3.4	59.2 ± 2.1
yarkandensis	303.4 ± 14.9	66.8 ± 2.3	215.0 ± 4.2	96.8 ± 2.0	(29) (111.5 ± 1.7) (4)	114.5 ± 4.2	60.3 ± 3.4
Kelat (Baluchistan)	244.0	58.0	E11	88.0		104.0	53.0

Skull Measurements: Female (Means and Standard Deviations)

	Horn length	Base breadth	Skull 1	Skull br.	Preorb. 1	Postorb. 1	Palate br.
dorcas	187.7 ± 20.9	50.6 ± 1.4 (7)	162.7 ± 4.1 (6)	74.7 ± 1.0 (7)	82.0 ± 3.3 (6)	88.1 ± 2.3 (7)	. 44.4±1.1 (7)
saudiya	211.1 ± 19.9 (9)	47.6 ± 1.8 (9)	164.8 ± 3.4 (5)	71.0 ± 1.1 (9)	85.4 ± 2.7 (5)	90.9 ± 2.5 (9)	43.3 ± 1.6 (9)
osiris	180.7 ± 19.0 (14)	50.8 ± 1.8 (16)	162.6 ± 2.6 (8)	74.8 ± 1.7 (16)	82.9 ± 1.6 (8)	89.0 ± 1.7 (16)	44.3 ± 1.1 (15)
isabella	165.1 ± 18.8 (9)	51.5 ± 1.8 (11)	169.8 ± 4.9 (3)	74.5 ± 2.1 (9)	88.0 ± 2.9 (5)	93.8 ± 2.1 (8)	43.1 ± 1.5 (10)
pelzelni	177.3 ± 12.5	53.0±0.7 (5)	178.8 ± 1.4 (5)	77.6 ± 1.0 (5)	94.3 ± 2.2 (5)	97.0 ± 1.4 (5)	45.2 ± 1.8 (5)
fuscifrons	173.8 ± 33.8 (6)	53.3 ± 2.7 (5)	178.3 ± 4.0 (4)	82.7 ± 3.2 (5)	91.5 ± 2.7 (4)	94.9 ± 3.9 (5)	49.3 ± 1.6 (5)
christii	118.0 ± 19.2	50.3 ± 1.5	184.0	81.0 ± 2.0 (4)	95.5	96.0 ± 0.8 (4)	47.8 ± 1.5 (4)
Salt Range	127.8 ± 25.2 (4)	51.2 ± 1.3 (5)	189.3 ± 3.7 (4)	81.2 ± 2.8 (5)	101.0 ± 2.5 (4)	100.0 ± 3.0 (5)	49.0 ± 2.2 (4)
bennetti	120.2 + 18.0 (5)	51.1+1.1 (7)	178.8+7.6 (5)	80.3 + 2.3 (7)	92.5 + 4.5 (6)	97.0+5.6 (6)	46.6+1.6 (7)
gazella	113.5	52.0	174.0	79.5	92.5	100.0 (1)	55.5
Yemen	144.5 ± 5.4 (4)	54.8±3.4 (4)	186.5 ± 4.8 (4)	82.5 ± 4.4 (4)	97.8 ± 3.3 (4)	102.0 ± 2.8 (4)	50.5 ± 2.0 (4)
arabica	111.5 ± 4.8 (5)	52.0 ± 2.4 (5)	167.5 ± 5.1 (4)	75.4 ± 3.4 (5)	85.2 ± 5.3 (4)	92.0 ± 3.2 (5)	44.0 ± 7.6 (5)
muscatensis	120.5 ± 25.5 (2)	52.5 ± 1.1 (2)	1 1	73.2 ± 2.1 (5)	1 1	91.0 ± 1.6 (5)	43.0 ± 5.2 (5)

Table 5, continued

	Horn length	Base breadth	Skull 1	Skull br.	Preorb. 1	Postorb. 1	Palate br.
spekei	210.0 ± 15.6 (3)	51.3 ± 2.1 (3)	175.0	81.0 ± 3.0 (3)	89.0	97.0 ± 4.7 (3)	48.7 ± 1.0 (3)
leptoceros	273.0	49.0	183.0	79.0	96.0	93.0	50.5 (2)
loderi	248.4 ± 19.0 (5)	49.2 ± 1.4 (6)	181.8 ± 3.2 (5)	81.2 ± 2.1 (6)	95.0 ± 3.1 (5)	95.7 ± 2.8 (6)	49.1±1.7 (7)
cuvieri	204.2 ± 22.8 (6)	57.4 ± 2.3 (8)	198.4 ± 7.3 (5)	87.3 ± 3.8 (5)	106.0 ± 6.2 (6)	105.8 ± 4.3 (8)	51.3 ± 3.7 (7)
rufifrons	147.0	53.0 ± 2.0 (3)	194.0	81.3 ± 1.0 (3)	106.0 ± 1.0 (2)	113.0	49.7 ± 1.0 (3)
laevipes	187.9 ± 16.0	56.1 ± 3.0	207.4 ± 3.6 (7)	88.3 ± 2.6 (9)	111.7 ± 5.0 (7)	108.2 ± 3.4 (9)	54.2 ± 3.5 (11)
tilonura	144.0	58.0	195.0	85.0	107.0	105.0	49.0 (1)
albonotata	124.0	53.0	206.3 ± 5.2	85.0 ± 2.7 (4)	112.7 ± 1.5 (3)	105.5	55.3 ± 2.2 (4)
thomsoni	120.0	Ĵ.	198.6 ± 6.3	82.9 ± 2.4	105.7 ± 5.7 (10)	110.3 ± 4.2	
nasalis	9.66		184.4 ± 5.3	80.4 ± 2.2	95.9 ± 5.0	104.0 ± 4.2	
marica	226.0	47.0	169.0	80.0	85.0	93.0	50.0
Kurdistan	Ξ	Ē	(1) (1) $(161.0 \pm 1.6$ (3)	75.7 ± 1.6	83.3 ± 1.6	87.7±1.9 (3)	47.0±1.0 (3)
Mahammerah			174.5	80.0±1.8	90.06	92.8±4.2 (6)	47.8±1.7 (6)
subgutturosa			(2) (2) (3) (8)	88.0±1.2 (8)	103.5 ± 0.2	(5) (5) (8)	56.0±1.0 (8)
billieriana			(9) 193.0 (1)	88.0	103.0	100.0	58.0

Table 6
Frequencies of types of naso-premaxillary contact

	a	ь	c	d	Number
dorcas saudiya osiris isabella pelzelni	6.9 30.3	22.2 5.9 69.0 57.6 75.0	77.8 94.1 24.1 12.1 25.0		9 -17 29 33 16
bennetti etc.		11.8	82.3	5.9	51
gazella Yemen arabica muscatensis	100.0 50.0 31.6 81.8	50.0 57.9 18.2	10.5		5 6 38 11
spekei	50.0	37.5	12.5		16
leptoceros subspp.			50.0	50.0	10
rufina		' .	100.0		1
cuvieri rufifrons laevipes tilonura albonotata nasalis thomsoni		22.0 28.6	66.7 50.0 61.0 71.4 4.6 22.1	33.3 50.0 17.0 100.0 95.4 73.5	3 4 41 7 6 131 68
subgutturosa subspp.		2.8	91.7	5.5	36

Type A = nasal branch of premaxilla not reaching nasal bones; Type B = premaxillae just in contact with nasals; Type C = premaxilla in contact with nasals; Type D = premaxillary-nasal contact longer than maxillary-nasal contact.

than one should expect by chance. Accordingly it is best to continue to recognise this form as a distinct species; on the other hand there is nothing against uniting the species cuvieri and rufifrons, in which case the species would be known by the earlier name, Gazella cuvieri Ogilby, 1841. It is clear that cuvieri bears no relation at all to G. gazella. This view of the two Algerian species corresponds with that of HEIM DE BALSAC, 1936, who also states that the two are (or were) sympatric in certain areas.

The following classification of the smaller gazelles is therefore proposed:

Subgenus Trachelocele Ellerman and Morrison-Scott, 1951

I. Gazella (Trachelocele) subgutturosa Güldenstaedt, 1780 Goitred gazelle

Large gazelles, of robust build; a small swelling on throat of male. Horns of male lyrate, of circular cross-section at base, with 20–27 rings. Horns of female absent in most races, but when present often well-developed, incipiently lyrate (and may be present on one side only). Occipito-parietal suture angular; premaxillae nearly straight; fronto-nasal suture somewhat V-shaped; medial and lateral nasal flanges approximately equal in length; palato-maxillary suture V-shaped; anterior basioccipital tuberosities of types 4–5 (GENTRY, 1964: 362); premaxillary-nasal contact nor-

Table 7Mean values of certain indices in Gazelle skulls

	Nasal index (Mean anterior- posterior nasal %)	Horn length index (female as % of male)	Skull length index (female as % of male)	Preorbital + postorbital - Skull length
massaesyla dorcas, osiris saudiya isabella pelzelni fuscifrons christii Salt Range bennetti	102.8 97.4 107.7 94.8 91.0 96.3	76.1 76.8 74.4 69.3 70.2 45.6 43.5 47.3	94.5 95.4 94.3 97.7 95.4 96.0	7.5 9.2 11.6 12.0 13.0 7.7
gazella Yemen arabica muscatensis	91.0 91.7 89.3 89.7	47.1 63.1 51.7 69.4	92.9 97.6 89.7	17.4 15.4 11.5 13.0
speki	90.4	88.7	97.2	10.0
leptoceros loderi	90.4 98.9	78.0 83.5	102.8 97.2	8.1 10.8
rufina	90.0	_	_	20.0
cuvieri rufifrons laevipes tilonura albonotata nasalis	94.5 83.3 85.0 85.0 82.1	67.9 57.2 72.0 70.7 50.2 39.0	92.1 87.4 93.3 95.8 98.3 94.4	15.6 21.0 14.6 19.9 15.3 16.3
thomsoni marica subgutturosa (others)	102.0 95.0	32.2 83.2	95.0 94.5 95.1	15.5 10.4 12.2

mally of type c; auditory bulla large; preorbital fossa comparatively small, its lower edge horizontal; ethmoid fissure comparatively wide; supraorbital pits rather small; nasals nearly or quite as wide anteriorly as posteriorly (nasal index, table 7); skull not excessively flexed (Preorb.-postorb.-index, table 7). Face stripes never very strongly expressed, become obliterated with age leaving the face white; flank band indistinct; pygal band present (usually) but indistinct; nose spot absent.

1. G. s. subgutturosa (Güldenstaedt, 1780) Persian gazelle

- 1780: Antilope subgutturosa Güldenstaedt, Acta Ac. Sci. Pterop. 1778, 1, 251. LYDEKKER and BLAINE (1913) give "Persia; probably the Bussora district" as type locality; but it is clear from the original description (p. 253) that the actual type locality is Tiflis (now Tbilisi) in the Caucasus.
- 1843: Antilope dorcas var. persica Gray, List Mamm. B. M. 160. nom. nud.
- 1900: Gazella subgutturosa typica Lydekker, Great and Small Game of India, 180.
- 1910: Gazella seistanica Lydekker. Nature, 83, 202 Seistan, eastern Persia.

1956: Gazella subgutturosa gracilicornis Stroganov, Zap.-Sib. philial (Ak. nauk. SSSR), 1, 17. Bakhshan valley, Tadjikistan.

Distribution: Caucasus; Iran east of Zagros range; Russian Central Asia along the west flank of the mountains as far as the Sayan range, Altai system.

A large race, with long horns in the male which are absent or poorly developed in the female.

2. G. s. marica Thomas, 1897 Rhim, or Arabian Sand Gazelle

1897: Gazella marica Thomas, Ann. Mag. N. H. 19, 162. Ibri, Nejd desert, Saudi Arabia.

Distribution: Sand areas in Arabia as far east as Kuwait and as far north as Palmyra. Size small: horns relatively as long as in last race, and present in female, in which they are well-developed, 80% as long as the males. Colour very pale, nearly white; face is white throughout adult life.

3. G. s. yarkandensis Blanford, 1875 Saikik or Yarkand gazelle

1875: Gazella subgutturosa var. yarkandensis Blanford, J. Asiat. Soc. Bengal, 44, 2, 112. Plains of Yarkand.

Distribution: flanks of the mountains bordering the Takla Makan desert, Sinkiang. The largest race, with horns relatively shorter than in typical race. Colouration more intense sandy-yellowish, with less of a reddish hue than Persian race.

4. G. s. hillieriana Heude, 1894 Mongolian gazelle

1894: Gazella hillieriana Heude, Mém. H. N. Emp. Chin. 2, 245. Gobi, Mongolia.

1894: Gazella mongolica Heude, loc. cit. Mongolia.

1900: Gazella subgutturosa sairensis Lydekker, Great & Small Game of India, 184. Saiar Mountains, Dzungaria.

1931: Gazella subgutturosa reginae Adlerberg, C. R. Acad. Sci. URSS, 327. Northwest Tsaidam, Tibet. This race appears to have been named without knowledge of Heude's names, as the Mongolian gazelles are included by ADLERBERG within reginae.

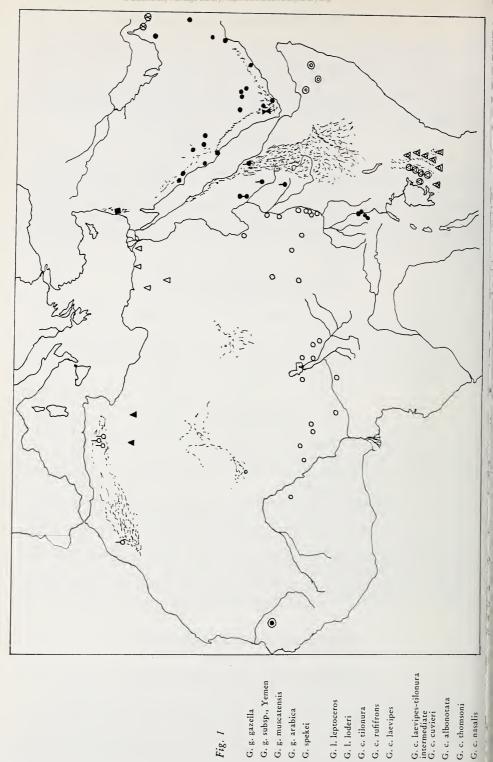
Distribution: Gobi region, west in Dzungaria and east as far as the Hwang-Ho (localities Paotow and Ninghsia); south into Tsaidam.

Similar in size to typical race, but horns of male much shorter. No horned females appear to be known. Colour less greyish; very pale sandy.

Subgenus Gazella de Blainville, 1816

II. Gazella (Gazella) dorcas Linnaeus, 1758 Dorcas gazelle

A small, slenderly built species, with no throat swelling. Horns of males usually lyrate, somewhat compressed at base, with 17–25 rings. Horns of females about 43–77% of length of males'; often somewhat lyrate. Premaxillae very concave on upper surface; fronto-nasal suture narrow, generally in form of a V; medial and lateral nasal flanges approximately equal in length; palato-maxillary suture on palate V-shaped; anterior



G. g. gazella

Fig. 1

G. g. subsp., Yemen G. g. muscatensis

G. spekei

G. g. arabica

G. c. rufifrons G. c. tilonura

G. c. laevipes

G. l. leptoceros

G. I. loderi

 $\triangleleft \Diamond$

G. c. albonotata

G. c. thomsoni

G. c. nasalis

basioccipital tuberosities of GENTRY's types 3—6, premaxillary-nasal contact mostly of types b or c; auditory bulla rather large; preorbital fossa small, with lower edge nearly horizontal; ethmoid fissure wide; supraorbital pits small. Palate distinctly narrower than in subgenus *Trachelocele*. Nasals often as broad at anterior as at posterior ends. Skull not very flexed. Face stripes strongly marked; flank band fawn to reddish, not generally very marked; pygal band indistinct; nose spot usually present.

1. G. d. dorcas (Linnaeus, 1758) Egyptian dorcas gazelle

1758: Capra dorcas Linnaeus, Syst. Nat. ed. 10, 1, 69. Lower Egypt. 1766: Antilope kevella and corinna Pallas, Misc. Zool. 7. No localities.

1869: Gazella dorcas sundervalli Fitzinger, S. B. Akad. Wiss. Wien, 59, 1: 159. N. Africa. (Based on Antilope dorcas var. y of Sundevall). This name might as well be fixed as a synonym of the present race.

Distribution: western desert of Egypt, into Libya.

A small race with rather short horns; horn length of female over 70% of length in male. Naso-premaxillary contact usually of type c.

2. G. d. massaesyla Cabrera, 1928

1816: Cemas maculata Oken, Lehrb. Naturgesch. 3: 738. Senegal.

1847: Antilope kevella Sundevall, K. Svenska Vet.-Ak. Handl. 1845: 268. Morocco. Not of Pallas, 1766.

1928: Gazella dorcas massaesyla Cabrera, J. Mamm., 9: 242. Rif plateau, between Taza and Gaurirt. Morocco.

1929: Gazella dorcas cabrerai Joleaud, Bull. Soc. Zool. de France, 54: 440. Substitue for massaesyla, thought to be preoccupied by massaesilia Pomel, 1894 (fossil species).

Distribution: Rif plateau, Morocco, down west coast through Rio de Oro to Senegal. The smallest race, slightly smaller than nominate race. Horns less distinctly lyrate. Colour comparatively dark.

3. G. d. osiris Blaine, 1913

1913: Gazella littoralis osiris Blaine, Ann. Mag. N. H. 11: 295. Nakheila, near junction of Nile and Atbara rivers, Sudan.

1926: Gazella dorcas neglecta Lavauden, Bull. Soc. H. N. Afr. du Nord, 17: 16.

Plateau du Tadmeit, Algerian Sahara.

Distribution: Sahara; known from Tadmeit, Air, Ahaggar, Lake Chad region, Darfur, and the west bank of the Nile. It is uncertain whether the type specimen came from the east or west banks of the Nile; consequently the boundary between this race and the next cannot as yet be drawn accurately.

Considerably larger than previous two races. Naso-premaxillary contact more usually of type b. Colour a rather pale brownish-fawn.

4. G. d. isabella Gray, 1846 Eritrean gazelle

1846: Gazella isabella Gray, Ann. Mag. N. H. 18, 214. "Abyssinia".

1847: Antilope isidis Sundevall, K. Svenska Vet.-Ak. Handl. 1845, 267. Sennaar.

1913: Gazella littoralis Blaine, Ann. Mag. N. H. 11, 295. Khorasot, Nubian desert, at base of Red Sea Hills.

1931: Gazella isabella beccarii de Beaux, Ann. Mus. Civ. Stor. Nat., Genova, 55, 210. Barka, Dancalia.

Distribution: Red Sea Hills, extending into Eritrea, and onto outposts of the Ethiopian highlands as far as Kassala. The type of *littoralis*, from Khorasot, seems to represent an intergrade between this race and the last; but is closer to the present race.

Larger than previous races, with shorter, thicker horns and greater width across their

bases. Colour darker, distinctly more reddish.

5. G. d. pelzelni Kohl, 1886 Pelzeln's gazelle

1886: Gazella pelzelni Kohl, S. B. k. k. Zool.-Bot. Ges. Wien, 36, 4. Berbera. Distribution: northern Somalia; intergrades with the last in Danakil country. Slightly larger than the last, with a broader skull; horns longer, straighter, more slender, narrower across the bases. Colour similar.

6. G. d. saudiya Carruther and Schwarz, 1935

1935: Gazella gazella saudiya Carruthers and Schwarz, P. Z. S. 155. Dhalm, 150 mi. N. E. of Mecca.

Distribution: whole Arabian peninsula. Recorded as far north as Abu al Jir, south of Rutba-Ramadi road, Iraq (specimen in D. L. HARRISON'S private collection).

Size a little less than osiris; horns much longer, straighter and more slender than the latter; postorbital region of skull longer. Anterior end of nasals invariably at least as broad as posterior. Colour similar to osiris.

The type of Neumann's Gazella arabica rueppeli (probably in the Berlin museum) needs to be examined with relation to this form, as do topotypes of G. arabica.

7. G. d. fuscifrons Blanford, 1873

1873: Gazella fuscifrons Blanford, P. Z. S. 317. Jalk, Seistan desert.

1908: Gazella yarkandensis kennioni Lydekker, Field, 111, 499. Kain, Iran-Afghan border.

1911: Gazella hayi Lydekker, P. Z. S. 961. "Africa": actually Seistan.

Distribution: Seistan and the Mekran region, W. Pakistan; it is uncertain whether the boundary of this race is the Indus river, or the edge of the Iranian plateau.

Similar to *pelzelni* but somewhat larger, with horn-tips turned less inward; postor-bital region of skull shorter. Hair longish, especially in winter, rather greyish sandy; flank-band almost absolete.

8. G. d. christii Blyth, 1842

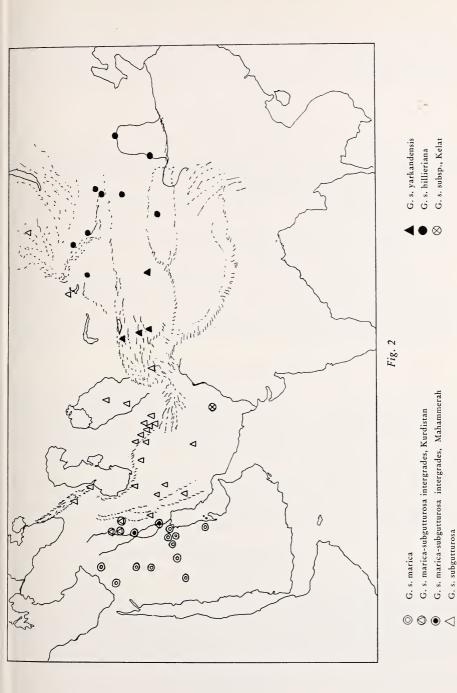
1842: Gazella christii Blyth, J. Asiat. Soc. Bengal, 11, 452. Thar desert, India.

Distribution: Cutch and Kathiawar, north to Khairpur and Bikaner.

Slightly larger than the last race, but horns of female only half the length of those of male instead of 70%; hair very short, with little seasonal variation; colour very pale, almost silvery drab brown.

9. G. d. subsp. (Salt Range gazelle)

Distribution: Salt Range, Punjab, south and east to Sira, Bhattu, Gwalior and Jhansi. This appears to be the largest, longest-horned race of the present species, but females are more distinctly smaller than males than is usually the case. A single skin is rich tobacco-brown.



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Although 11 males skulls and 5 females of this race are available in collections, it would appear to be unadvisable to name the race at the present time because of the damaged condition of most of the skulls. It will be noticed that only two male skulls are sufficiently complete to enable the greatest length measurement to be taken. Equally it would be advisable to study more than a single skin, since colouration on the whole forms a better guide to geographic variation than skulls among Indian gazelles.

10. G. d. bennetti (Sykes, 1831) -Indian gazelle

1831: Antilope bennetti Sykes, P. Z. S. 1830-1, 104. Deccan, Hyderabad.

1843: Antilope hazenna I. Geoffroy in JAQUEMONT, Voy. Inde, 4, 74. Malwa, C. India. Distribution: Deccan, north to Ganges valley, upstream as far as Rohtak and Gourgaon, downstream as far as Palamau and Jagodih.

The smallest Indian race, about the size of G. d. isabella but with a distinctly broader skull; horns comparable in size with those of christii. Length of hair distinctly longer in winter than in summer; darker and less drab than in christii with distinct contrasts: middle of back reddish brown or tawny, and the same on lower part of flanks, with a dull-coloured zone between.

In all, the Indian gazelles form three (probably four) well-marked races, distinguished by size, length of horns in male and in female, skull proportions and skin characters (for measurements, see Tables 4 und 5). Skin comparisons are based on 9 fuscifrons, 10 christii, 1 Salt Range, and 5 bennetti.

It is noteworthy that the most westerly - fuscifrons - is the most like African dorcas, e. g. in colour and in length of horns in the female.

III. Gazella (Gazella) gazella Pallas, 1766

Often difficult to distinguish from dorcas; closely approached by some of the Indian and North-east African races of the latter. Horns tend to be shorter, thicker, often lyrate, more compressed at base, with only 10—15 rings; horn of female 47—63% of length of that of male; premaxilla more nearly straight; fronto-nasal suture in form of a U; palato-maxillary suture straighter; anterior basioccipital tuberosities of types 5—6; naso-premaxillary contact of types a or b; auditory bulla commonly bigger than dorcas, but very variable; posterior end of nasals always considerably wider than anterior; skull rather more flexed. P4 may sometimes be three-lobed, instead of having only 2 lobes as in all other gazelles. Flank and pygal bands often more distinct than in dorcas, sometimes blackish-brown.

1. G. g. gazella (Pallas, 1766) Palestine gazelle

1766: Antilope gazella Pallas, Misc. Zool. 7. Syria.

1904: Gazella merrilli Thomas, P. Z. S. 2, 347. Hizmeh, north of Jerusalem.

Distribution: restricted to the mountains of Palestine.

Size large, skull comparatively broad. Horns thick, fairly straight in front view with little trace of lyration. Hair longish, colour rather dark grey-brown.

2. G. g. subsp. (Yemen gazelle)

Distribution: mountains of Yemen around 7,000 feet. Localities: "Mocha", Jebel Zarba (near Ta'iz), Wadi Maleh (5 mi. E. of Ta'iz). A skull labelled "Ta'iz, 4100 feet"

(Chicago Mus. no. 77736) belongs to the next race; altitudinal replacement is consequently very clear.

The largest race; horns shorter and thicker than the last in males, but longer in

females; skull comparatively narrower.

Although specimens in the British Museum labelled "Aden" belong to the following race, it would be advisable to examine the type skulls of *erlangeri* Neumann before stating definitely that that name does not apply to this race.

3. G. g. arabica (Lichtenstein, 1827) Arabian gazelle

1827: Antilope arabica Lichtenstein, Darstellung Säugeth. pl. 6. Farsan I., Red Sea.

1827: Antilope cora H. Smith, Griffith's Cuv. Anim. Kingd., 4, 216. Arabian coast of Persian Gulf. This name might as well be fixed as a synonym of this race.

(?) 1906: Gazella arabica erlangeri Neumann, S. B. Ges. Naturf. Fr. Berlin, 244. Lahej, Aden.

(?) 1906: Gazella arabica rueppelli Neumann, loc. zit. Sinai. It is possible that this name refers to a form of dorcas (see above, under G. d. saudiya).

1910: Gazella arabica typica Ward, Rec. Big Game, ed. 6, 251.

1927: Gazella arabica hanishi Dollman, P. Z. S. 1005. Gt. Hanish I., Red Sea.

Distribution: Arabian peninsular, mainly the coastal regions.

Horns more lyrate than previous races, and narrower across the base. Rather smaller than nominate race, and skull markedly narrower. Colour very variable: usually a light sandy brown; flank band broader than in most *dorcas*, but sometimes little if at all darker.

4. G. g. muscatensis Brooke, 1874

1874: Gazella muscatensis Brooke, P. Z. S. 142. Muscat, Oman.

Distribution: coastal region of Oman.

Much smaller and darker than previous race; horns shorter in male (not in female), even more lyrate. Horns of female 70% of length of those of male; the only race of this species in which there is a trace of the shape of the male's horns.

IV. Gazella (Gazella) spekei Blyth, 1863 Speke's gazelle

1863: Gazella spekei Blyth, Cat. Mamm. Mus. Asiat. Soc. Bengal, 172. Interior of Somaliland.

1868: Gazella naso Sclater, P. Z. S. 504. Somaliland.

Distribution: Ogaden and Somalia; except the coast of northern Somalia, where G. d. pelzelni is found.

Very similar to G. dorcas and G. gazella. Horns sigmoid in shape from the side in both sexes; horns of females 88. 7% of those of males in length; compressed at base; 12–15 rings in male. Premaxillae very concave; fronto-nasal suture U-shaped, occasionally bracket-shaped like certain forms of G. cuvieri; palato-maxillary suture V-shaped; anterior basioccipital tuberosities of type 5; nasal index as in G. gazella; skull not very flexed. Externally very distinctive; has a black flank-band, but pygal band indistinct; a puffy elevation on nose in both sexes, of unknown use (? to provide a greater moistening surface for dry desert air).

V. Gazella (Gazella) rufina Thomas, 1894 Red gazelle; le gazelle rouge

1894: Gazella rufina Thomas, P. Z. S. 467. Skin and skull bought in Algiers.

1895: Antilope (Dorcas) pallaryi Pomel, Paléontologie – Les Antilopes Pallas, 9. Skin

and skull bought in Oran.

Distribution: unknown! All known specimens have been purchased in markets in either Algiers or Oran. Heim de Balsac (1936) has suggested that it existed in the same regions of the Tell as G. cuvieri; "D'apres les reseignements que nous avons pu recueillir", there are severals mall herds of this form in the mountainous districts and the deep valley of the Chelif river. Gazella rufina bears a close relationship to the fossil G. oranensis of Pomel (Heim de Balsac, p. 89). Lavauden (1930) suggests that this species is a gazelle of brush or forest; a very unlikely habitat for a gazelle. Both Lavauden and Heim de Balsac deny that this species has any relationship with rufifrons of subsaharan Africa.

VI. Gazella (Gazella?) leptoceros F. Cuvier, 1842 Algerian sand gazelle; Rhim

It is possible that this species belongs to the subgenus Trachelocele; certainly it shows many resemblances. These are: the multi-annulated horns (24–30 rings), nearly straight premaxillae, naso-premaxillary contact of types c or d; very large auditory bullae; small, horizontal preorbital fossa; small supraorbital pits; obliterated face stripes and obsolete flank-band; very pale colour and somewhat elongated hoofs. However these features either are not peculiar to these two forms, or else are explainable by convergent adaptation to a common environment, as may be the closeness in the generalised distance analysis. It would be necessary to know also whether the bodily build of the two is similar, and whether the male has a throat swelling. The horn shape is entirely different: the horns are virtually straight, though nearly circular at the base, and evenly divergent. The female has horns 80% of those of the male in length. The occipitoparietal suture is unique in the genus in being rounded, instead of angular. Other features tend to be more like dorcas; it is not difficult to see this species as an extreme desert-living version of the latter.

1. G. l. leptoceros (F. Cuvier, 1842)

1842: Antilope leptoceros F. Cuvier, in Geoffroy and Cuvier, H. N. Mamm., 4, 72. "Sennaar": probably between Giza and Wadi Natron (Flower).

1869: Leptoceros abu harab Fitzinger, S. B. Akad. Wiss. Wien, 59, 1, 160, Libyan desert.

1869: Leptoceros cuvieri Fitzinger, loc. cit.; renaming of A. leptoceros. Not OGILBY, 1841.

1898: Gazella leptoceros typica Sclater & Thomas, Book of Antelopes, 3, 149.

Distribution: western desert of Egypt.

Size comparatively small, but horns very long; palate relatively broad, as in G. subgutturosa.

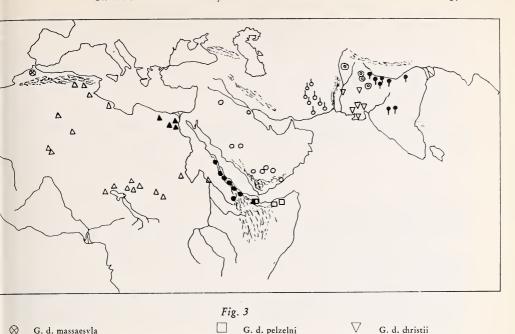
2. G. l. loderi Thomas, 1894

1894: Gazella loderi Thomas, Ann. Mag. N. H. 13, 452. Oued Souef, 100 mi. S. of Biskra.

Distribution: ergs of eastern Algeria and the Tunisian border area. Larger, with narrower skull and shorter horns.

G. d. subsp., Salt Ra.

G. d. bennetti



VII. Gazella (Gazella) cuvieri Ogilby, 1841 Cuvier's gazelle; Red-fronted gazelle; Thomson's gazelle, etc.

G. d. dorcas

G. d. saudiya

G. d. fuscifrons

Λ

G. d. osiris

G. d. isabella

G. d. isabella-pelzelni intermediate

This species is different in many respects from those preceding. It is larger than any of the others excepting rufina and some races of subgutturosa. Characteristic of this species, and distinguishing it from all others including rufina, are: (1) the very strongly expressed horn-rings of the male, which are extremely prominent on the front of the horn and quite clearly expressed even on its posterior surface; (2) the almost completely straight premaxillae; (3) the very long medial flange of the nasals, which greatly exceeds the lateral flange in length; (4) the anterior basioccipital tuberosities, which are of GENTRY's types 1 or 2, rarely of type 3; (5) the small auditory bulla; (6) the very large preorbital fossa, which has an oblique lower edge; (7) the generally very narrow ethmoid fissure; (8) the large supraorbital pits; (9) the very broad hinder end of the nasals compared to the anterior end (correlated in part with no. (7), nasal index 82-94; (10) the highly flexed skull. The posterior ends of the nasals, where they make suture with the frontals, have a U-shaped or bracket-shaped margin. The face stripes and lateral and pygal bands are very wellmarked, though the light face-stripes may become obliterated on the muzzle. A nose spot is usually present. The colouration is sharply contrasting.

> 1. G. c. cuvieri (Ogilby, 1841) Cuvier's or Mountain gazelle; Edmi

1804: Antilope corinna Lacépede Cuvier, Ménag. Mus. H. N. Paris. Not of Pallas, 1766. Constantine, Algeria.

1841: Antilope cuvieri Ogilby, P. Z. S. 1840, 35. Mogador, Morocco.

1850: Gazella vera Gray, Gleanings Menag. Knowsley Hall, pl. 3. No. locality.

1853: Gazella cineracens Temminck, Esquis. Zool. sur la Cote de Guiné, 193.

1860: Gazella kevella Tristram, Great Sahara, 387. Not of Pallas. Atlas mountains, south of Teniet el Haad, Western Algeria.

1895: Dorcas subkevella and setifensis Pomel, Paléont., Les Antilopes Pallas.

Distribution: Atlas Moutains.

Colour a dark grey-brown, with lateral band not completely black. Horns rather long, width at base comparatively great. Nasal index 94.5 — higher than in other races. Nose-spot large; knee-tufts present; forehead dark brown.

2. G. c. rufifrons Gray, 1846 Red-fronted or Korin gazelle

1846: Gazella rufifrons Gray, Ann. Mag. N. H. 18: 214. Senegal.

1869: Eudorcas laevipes senegalensis Fitzinger, S. B. k. k. Akad. Wiss. Wien, 59, 1, 159. (Based on Antilope laevipes, var. B, Sundevall). Senegal.

1910: Gazella rufifrons typica Ward, Records Big Game, ed. 6, 262.

Distribution: Senegal.

The largest race, with broad skull but rather narrow palate. Nasal index around 85, as in al subsequent races. Colour sandy rufous; nose-spot slightly marked; knee-tufts absent; a clear reddish-fawn band between black lateral flank-band and white of belly.

3. G. c. laevipes (Sundevall, 1847)

1847: Antilope laevipes Sundevall, K. Svenska Vet.-Ak. Handl., 1845, 266. Sennaar.

1906: Gazella salmi Lorenz, S. B. Akad. Wiss. Wien, 115, 1, 21. Fashoda, Sudan.

1912: Gazella rufifrons hasleri Pocock, P. Z. S. 5. Kano, northern Nigeria.

1914: Gazella rufifrons centralis Schwarz, Ann. Mag. N. H. 13, 40. Magretta, near Melfi, Bagirmi, Oubangui-Shari district.

1914: Gazella rufifrons kanuri Schwarz, loc. cit. Gulfei, lower Shari, Northern Cameroun.

Distribution: northern Nigeria via Lake Chad district to the west bank of the Nile. The farthest west locality is Labbezanga, Niger colony (now Niger Republic).

Skull smaller and much narrower than previous race; nose-spot absent, knee-tufts small, color less reddish than previous race. There may be a few white hairs on fore-head. Study of further specimens of *rufifrons* may reveal that the present race is identical with the last.

4. G. c. tilonura (Heuglin, 1869) Heuglin's gazelle

1863: Antilope melanura Heuglin, Nova Acta Ac. Caes. Léop.-Car. 30, 2, 6. Bogosland, Eritrea, Ethiopia. Not of Bechstein, 1799 (= Ourebia ourebi).

1889: Antilope tilonura Heuglin, Reise Weiss. Nil, 315. Replacement.

Distribution: northern flank of the Ethiopian highlands; known from the Setit, Atbara and Bogos rivers. A specimen from Kituit, lower Atbara (and another from Kassala prov.) is an intergrade between this race and the last, but closer to this race.

Much smaller than the last race, but with as long a postorbital region; horns rather short, suddenly hooked in near their tips. Colour more rufous; nose-spot absent, but knee-brushes larger than in last race; light lateral face-strips nearly obsolete except in region of eyes. Pygal band completely absent.

5. G. c. albonotata Rothschild, 1903 Mongalla gazelle

1903: Gazella albonotata Rothschild, Novit. Zool. 10, 480. 40 mi, N. of Kero, Mongalla.

Distribution: both sides of the upper Nile, south of the Sudd and north of the Uganda border.

Similar to *laevipes* but narrower across the horn-bases and in orbital region. Horns of females only 50% of length of males'. Nose-spot usually present; knee-tufts large; forehead often entirely white, a condition foreshadowed by *laevipes* and seen commonly in G. c. nasalis; lateral band broader, and only rarely with a light rufous stripe beneath it. Pygal band present.

The remaining two races, G. c. thomsoni and G. c. nasalis, have been well described and compared by Brooks (1961). It need only to be reiterated that they continue the gradation begun with laevipes and continued with albonotata, nasalis being the more

albonotata-like of the two except for its small size.

There are several gaps in the above scheme — notably the mention of two new forms without sufficient material to name them; also further information would be most desirable about *G. rufina*, *G. leptoceros*, *G. cuvieri rufifrons*, and the forms from Sinai and Aden described by Neumann. It is considered, nonetheless, that the scheme outlined above best fits the interrelationships of the smaller living gazelles.

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Summary

The systematics of the living small gazelles is reviewed; seven Species are recognised, falling into two subgenera, Gazella and Trachelocele. The Ring-species relationship of Gazella dorcas and Gazella gazella is demonstrated. Of the two Algerian gazelles, it is G. cuvieri and not, as usually thought, G. rufina, which bears a conspecific relationshiß to G. rufifrons of subsaharan Africa. The geographic variability of each of the species is described and the subspecies mapped, with synonymy. The Mahalanobis Generalised Distance statistic is applied to skull measurements.

Zusammenfassung

Die Systematik der kleineren Gazellen wurde revidiert; sieben Arten in zwei Untergattungen: Gazella und Trachelocele sind unterscheidbar. Die Gazella dorcas/G. gazella-Verwandtschaft wird als Ring-Species beschrieben. Algerien wird von 2 verschiedenen Arten bewohnt. G. cuvieri — und nicht G. rufina, wie gewöhnlich angenommen wurde — ist mit der subsaharischen G. rufifrons conspezifisch. Für alle Arten werden Verbreitungskarte, Beschreibung und Synonymie gegeben. Die verallgemeinerte Abstands-Statistik von Mahalanobis wurde auf die Schädelmaße angewandt.

C. P. Groves

Appendix

The Discriminant Functions analysis was based on a simultaneous examination of eleven variables, as follows:

1. Breadth across horn-cores at base.

Breadth of nasals, at widest point anteriorly.
 Breadth of nasals, at widest point posteriorly.

4. Length of nasals, along median line.

5. Greatest length of skull, from tip of premaxillae to occipital protuberance.

6. Greatest breadth of skull, on posterior borders of orbits.

7. Preorbital breadth; from tip of premaxillae to anterior border of orbit.
8. Postorbital breadth; from fronto-parietal suture to occipital protuberance.

9. Breadth across braincase, at supramastoid crests.

10. Length of toothrow, from P² to M³.
11. Breadth across palate, outside M².

In addition to these measurements, three horn measurements (not used in the D² analysis) have been cited from time to time during this paper:

1. Greatest horn length, in a straight line on front of horn from base to tip (or most distal point of this is not the tip, e. g. usually in G. c. tilonura).

Tip-to-tip distance.

3. Greatest breadth across the horns, taken on the outside.

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