

The Gazelles of Arabia

Foreword by HRH Prince Saud Al-Faisal

Editors

Khushal Habibi, Abdulaziz H. Abuzinada
and Iyad A. Nader



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2. The Taxonomy of Arabian Gazelles

Colin P. Groves

This chapter will review some recent findings on (1) phylogenetic relationships within the Antilopini, (2) the limits and contents of the genus *Gazella*, and (3) the interrelationships of the Arabian species; and then give brief diagnoses and comments on the species and subspecies in Arabia.

In this chapter, "Arabia" designates all those countries east of the Suez canal where Arab peoples form a significant proportion of the population, and the Arabic language is widely used; that is to say Saudi Arabia, Yemen, Oman, the United Arab Emirates, Qatar, Bahrain, Kuwait, Iraq, Syria, Jordan, Lebanon, Palestine, Israel and the Asian part of Egypt (i.e. the Sinai peninsula). The term "the Arabian Peninsula" here means those countries south of the borders of Saudi Arabia with Iraq, Kuwait and Jordan.

CLADISTIC RELATIONSHIPS OF GAZELLES

The Antilopini

The gazelles are bovid ruminants belonging to the genus *Gazella*, of the tribe Antilopini. Other members of the tribe Antilopini include springbok, blackbuck, gerenuk and dibatag; beyond this there is little consensus on their taxonomy.

The most recent survey of the subfamilies and tribes of the Bovidae is by Gentry (1992). As far as the gazelles and their relatives are concerned, Gentry confirms the usual content of the tribe Antilopini, with the addition of *Saliga* (the saiga antelope of Russia, Kazakhstan and Mongolia), which had previously been included in the Caprini (sheep/goat/chamois group). Gentry defined the newly

expanded Antilopini by the possession of the following derived conditions:

- increased diameter of horn cores
- complicated interfrontal suture
- strong, localized basioccipital anterior tuberosities
- a central cavity on the Mg hypocondylid
- lateral placement of the longitudinal digital flexor ridge on the back of the tibia
- large high position for lateral tubercle of radius.

Not all of these character states, however, are uniquely derived; in particular, some of them recur in the closely allied Neotragini ("dwarf antelopes"). Gentry concludes (1992:29) that the Antilopini and Neotragini together form a subfamily, Antilopinae, one of five which he recognizes within the Bovidae; but he cautions that the Neotragini are probably paraphyletic and some of the genera currently referred to that tribe will probably have to be transferred to the Antilopini.

Recently (but before the publication of Gentry's review), I collected data towards a phylogenetic assessment of the Antilopini, using specimens in the collection of the Natural History Museum, London (formerly the British Museum (Natural History)). The taxa I studied were the following:

Ammodorcas clarkae (the dibatag of Somalia)

Litocranius walleri (the gerenuk of northeast Africa)

Antidorcas marsupialis (the springbok of southern Africa)

Procapra picticaudata and *P. przewalskii* (Tibetan and Przewalski's gazelles, from western China)

Prodorcas gutturosa (the Mongolian gazelle or zeren, from Mongolia and northern China)

Antilope cervicapra (the blackbuck of India and Pakistan)

Gazella (Nanger) granti, *soemmerringii* and *dama* (Grant's, Sommering's and Dama gazelles, large gazelle species from north-east Africa and the Sahara)

Gazella rufifrons and *G. thomsonii* (red-fronted and Thomson's gazelles, from northeast Africa and the Sahel)

Gazella bennetti (Bennett's gazelle or chinkara, from India, Pakistan and Iran)
Gazella subgutturosa (gottered gazelle from the Arabian, Indo-Iranian and Central Asian deserts)
Gazella dorcas and *G. gazella* (dorcas and mountain gazelles, from North Africa and Arabia)

As many specimens as possible were studied for each taxon. Because the study was done prior to Gentry's (1992) publication, *Saiga* and the neotragines were not included. The Caprini (specifically, *Capra* and *Rupicapra*) were used as outgroup.

Fifty characters were used for the analysis. These will be detailed in a future report; briefly, they include 5 characters of the horn sheaths, 4 of horn cores, 13 of the dentition, 22 of the skull, and 6 external.

MacClade, version 2.1 (Maddison and Maddison, 1987) produced five almost equally parsimonious trees of length 225, 226 or 227, and consistency indices of 0.48 or 0.49. These are depicted in Figure 2.1 a-e. There seems no dispute about the initial branching sequence, as follows:

The first branch separates *Procapra* and *Prodorcas* from the rest. There is thus an initial branching into a Central Asian and an essentially Afro-Arabian group. At this point the tribe Antilopini could be split into two subtribes if it were felt desirable.

The second branch separates the only southern African taxon, *Antidorcas* from the rest, and at the third node the two northeast African genera, *Ammodorcas* and *Litocranius* branch off. The sequence of these first three nodes is the same in all the shortest trees, but the sequence of the next two or three branches is in question: the terminal branch consists entirely of the small gazelle species, usually in the sequence *bennetti* (*subgutturosa*, *dorcas*), and it is the relationships between this terminal gazelle group, *G. rufifrons*, the *Nanger* group and *Antilope* that are disputable. These will be discussed in the next section.

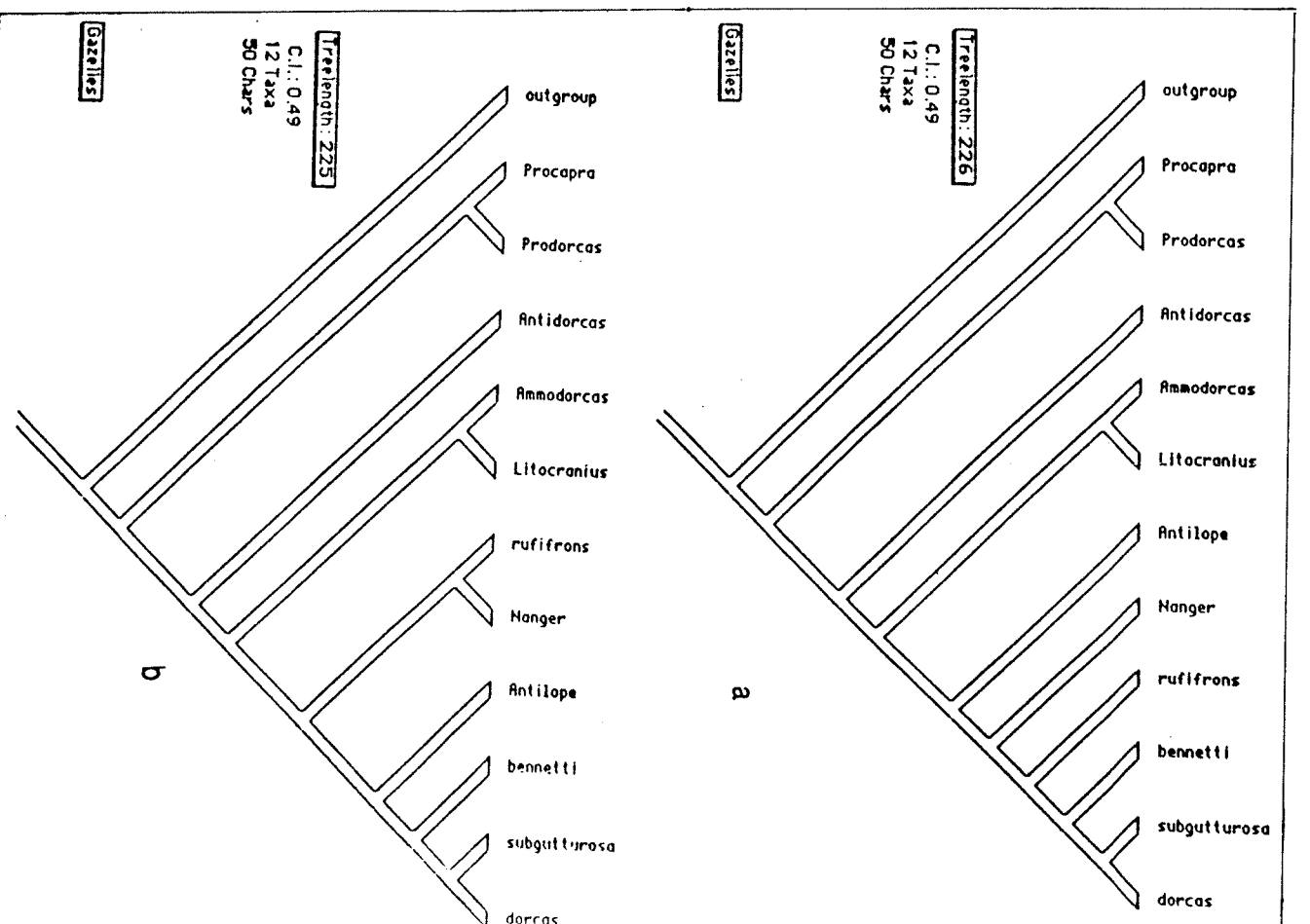


Figure 2.1. a and b

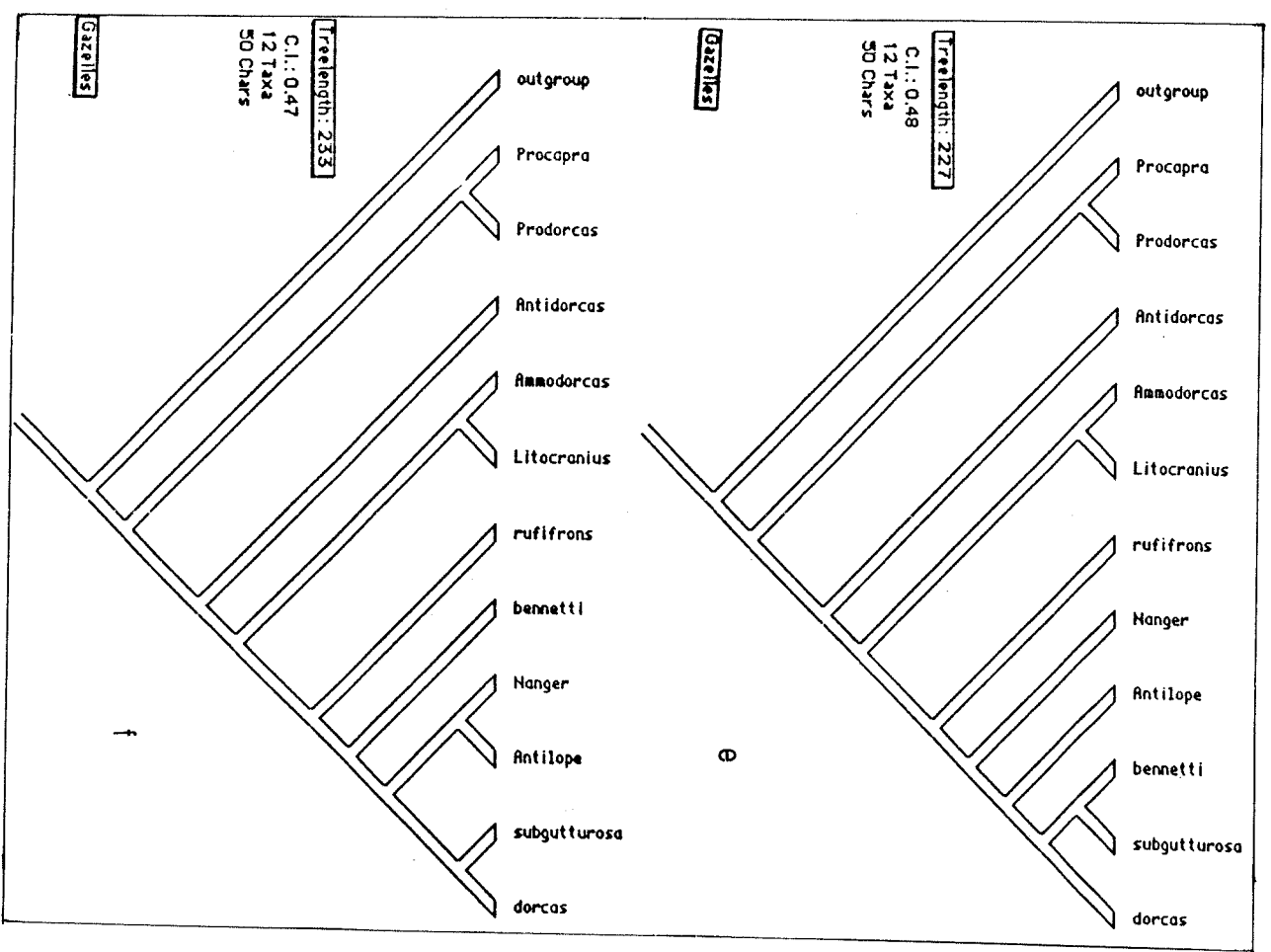
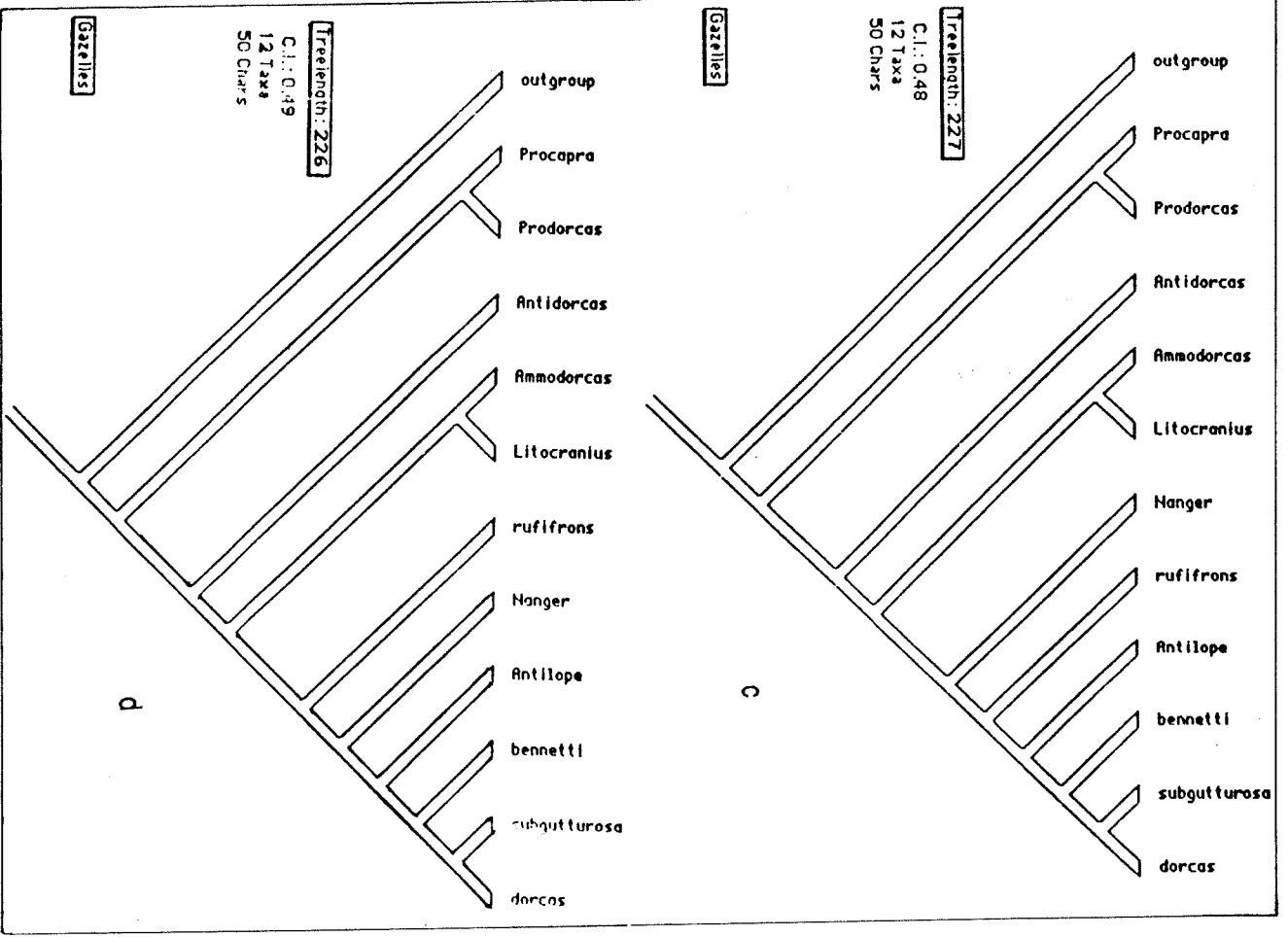


Figure 2.1. The five most parsimonious trees (a-e) depicting interrelationships among the Antilopini (excluding Saiga), and one which, although apparently the most compatible with karyological data, is several steps longer (f).

Figure 2.1. c and d.

LIMITS AND CONTENTS OF THE GENUS GAZELLA

It is clear from the above that the genus *Gazella*, as conventionally defined, forms a clade with the blackbuck, *Antilope*. Within this clade, however, relations are not settled. The four branches, whose relative positions switch around for almost no cost in tree length, are here designated *rufifrons* (which includes the closely related or conspecific *thomsonii*), *Nanger*, *Antilope* and *Gazella* (restricting this name to the *bennethi/subgutturosa/dorcas* group). The shortest tree (length 225) gives the following arrangement:

(*rufifrons*, *Nanger*)/(*Antilope*, *Gazella*)
but two other sequences:

Antilope (*Nanger* (*rufifrons*, *Gazella*))
rufifrons (*Nanger* (*Antilope*, *Gazella*))
require only one more step, and

Nanger (*rufifrons* (*Antilope*, *Gazella*))
is only one step longer again.

The importance of this is that the genus *Gazella*, as conventionally delimited, may well be paraphyletic. The four almost equally parsimonious arrangements described above, and depicted in Figure 2.1, are in fact supported by differing numbers of potential synapomorphies:

(1) There are no character states which unite *rufifrons* with terminal *Gazella* to the exclusion of *Antilope* or *Nanger*. That is to say, although Figure 2.1 a is only one step longer than the most parsimonious solution (Figure 2.1 b), it is not supported by any synapomorphies.

(2) Favouring figures 2.1 b, c or d, *Antilope* alone shares with *Gazella* a total lack of orbital tubularity, the potential occurrence of perforations in the lacrimal, supraorbital foramina that are generally in a deep, wide pit, and an excessively complicated interfrontal suture.

(2i) There is only one character which possibly supports the single most parsimonious solution, figure 1b: lacrimal perforation. It is more likely, however, that this character is a homoplasy between the *Gazella* clade and the *Litocranius/Ammodorcas* clade. In

both *Litocranius* and *Ammodorcas*, the lacrimal is studded with perforations as is the lacrimo-malar suture; in *Gazella* there is at most one fenestra, apparently constant in occurrence in *G. bennethi*, *curvieri*, *subgutturosa*, *leptoceros* and *bilkis*, but only occasional in *dorcas* and *gazella*.

(2ii) In support of figure 2.1c, *Antilope* and *G. rufifrons* share with *Gazella* a tendency for the posterior valley of P₄ to open distally (it is distolingual in *Antilope* and *G. rufifrons*, fully distal in *Gazella*), but it opens lingually in *Nanger*, as in all other *Antilopini*.

(2iii) Supporting figure 2.1d, *Nanger*, *Antilope* and *Gazella* share a large preorbital fossa, extending well into the lacrimal bone (convergent with *Antidorcas*), whereas this does not extend so far in *G. rufifrons*; shortened nasal tips, which often do not extend forward of the lateral nasal prongs; and a rhinarium which extends well along the upper margins of the nostrils.

This distribution of shared derived character states seems, thus, to favour the sequence

rufifrons (*Nanger* (*Antilope*, *Gazella*)).

Interestingly, this result is in reasonable agreement with that of the chromosome banding study by Efron et al. (1976), who found that *Antilope*, *Nanger* and the small *Gazella*, but not *G. thomsonii* (sister species to *G. rufifrons*) share a unique X-autosome translocation; the chromosome workers, on the other hand, tended to favour a link between *Antilope* and *Nanger*, which is not among the most parsimonious solutions morphologically (tree length for this solution is 231: Figure 1f).

All this implies that the taxonomy needs to be revised. There are two possible courses of action: either place all these taxa in one genus, for which *Antilope* Linnaeus, 1758 takes priority over *Gazella* de Blainville, 1816; or else remove the large species (*Nanger*) and the *G. rufifrons* group from the genus *Gazella*. The first alternative, entailing the total loss of the generic name *Gazella*, would result in unspeakable nomenclatural confusion. The second would require some adjustments, but a few authors already do recognize *Nanger* as a full genus (for example Andrae and Krumbiegel, 1976, although they spell the name *Nanguen*). For *G. rufifrons* and *G. thomsonii* the prior

available name would seem to be *Eudorcas Fitzinger*, 1869 (synonym *Kortu Sclater & Thomas*, 1898). The possibility of separating the *ru-fifrons* group generically has been anticipated by Furley et al. (1988).

The small gazelles *G. bennettii*, *G. subgutturosa* and the *G. dorcas/gazella* group are confirmed as forming a monophyletic cluster, for which the prior available generic name is, happily, *Gazella* de Blainville, 1816 (type species, *G. dorcas*). As far as relationships among them go, *G. bennettii* may have branched off before the other two separated: it has primitively prominent horn rings, well-formed even on the posterior surface; the lower molar styliids are exceptionally prominent; the horns are less upright; and the carpal glands are enlarged, and covered with a large "knee" tuft. As far as the karyotype is concerned, *G. bennettii* lacks the extensive fusions characteristic of other small gazelles and shared in part with *Nanger* and *Antelope*; these could be taken to indicate that *G. bennettii* is the sister-group of that entire complex, but the fusions could be homoplasious (and morphologically this solution is unparisimonious: figure 2.1f), and they may even have occurred independently in the *dorcas* group and in *subgutturosa*, as there are similarities between the latter and *G. bennettii* in the Y chromosome (Furley et al., 1988). Possible morphological links between *G. bennettii* and *G. subgutturosa* are the unreduced third lobes of *M₃*, the reduced "goat folds" on the lower molars, and the very thin enamel; the plausibility of such a relationship (only slightly less parsimonious than others: figure 2.1e) will be tested in the next section.

THE INTERRELATIONSHIPS OF THE ARABIAN SPECIES

The relationships depicted in figure 2.1a-e show some slight inconsistency; a more detailed study is needed, bringing in the other taxa of the genus *Gazella* as now restricted. This study is being published in a different context (Groves, 1996). Briefly, using mainly specimens in the Natural History Museum (London), 27 skull and horn characters (some of them derived from gap-coding of measurements) were coded and analysed using Hennig 86, version 1.5 (Farris, 1988), then examined using MacClade. In that study, the interrela-

tionships of the *dorcas/gazella* group was the focus; as reported in Groves (1996), of several nearly equally parsimonious solutions, one was favoured (figure 2.2 a) because it corresponded with "biological species" limits. Relationships among taxa are very close, however, and a number of almost equally parsimonious solutions are possible; unlike the large-scale relationships cladograms (previous section), the alternative placements concern almost all the taxa. In addition to the taxa analysed as above, the relationships of those outside the *dorcas/gazella* group are of interest, and a new cladogram, as parsimonious as the previously "most-favoured" one, is presented here (figure 2.2 b).

The taxa analysed were as follows:

- *G. subgutturosa*: this sample was a mixture of Arabian peninsular *G. s. murica* (n=12) and Iranian *G. s. subgutturosa* (n=26).
- *G. bennettii*: a sample of this species, mainly from Iran (n=22), was utilised mainly as context for Arabian taxa.
- *G. saudiya* (16): the *afri* of Saudi Arabia, formerly classified as a subspecies of *G. dorcas* but shown by Reholz et al. (1991) to be a distinct species.
- *G. dorcas*: the *dorcas* gazelle of North Africa. The subspecies analysed separately were *G. d. dorcas* (Western Desert of Egypt) (n=26), *G. d. ostris* (Sahara, mainly utilising a sample from Tadmert) (n=61), *G. d. isabella* (Red Sea Hills of Sudan) (n=36) and the distinctive *G. d. pelzelni* (n=19) from northern Somalia.
- *G. arabica*: the single known specimen, supposedly from Farasan.
- *G. bilkis* (n=5): the Queen of Sheba's Gazelle, from the Yemen highlands.
- *G. gazella*: the "common Arabian" or "Mountain" Gazelle, the *idmi* (Arabic) of Saudi Arabia, including the following samples, analysed separately: *G. g. erlangeri* (Yemen, and Thuwal, north of Jeddah) (n=10); *G. g. cora* (southwestern Arabian peninsula, both Saudi Arabia and Oman) (n=30); *G. g. muscatensis* (northeastern Oman) (n=19); *G. g. gazella* (Israel) (n=64); and a sample from the King Khalid Wildlife Research Centre, identified *faut de mieux* as *G. g. gazella* (n=13). I have not seen the type series of *G. g. farasani*, so this taxon is for the moment omitted.

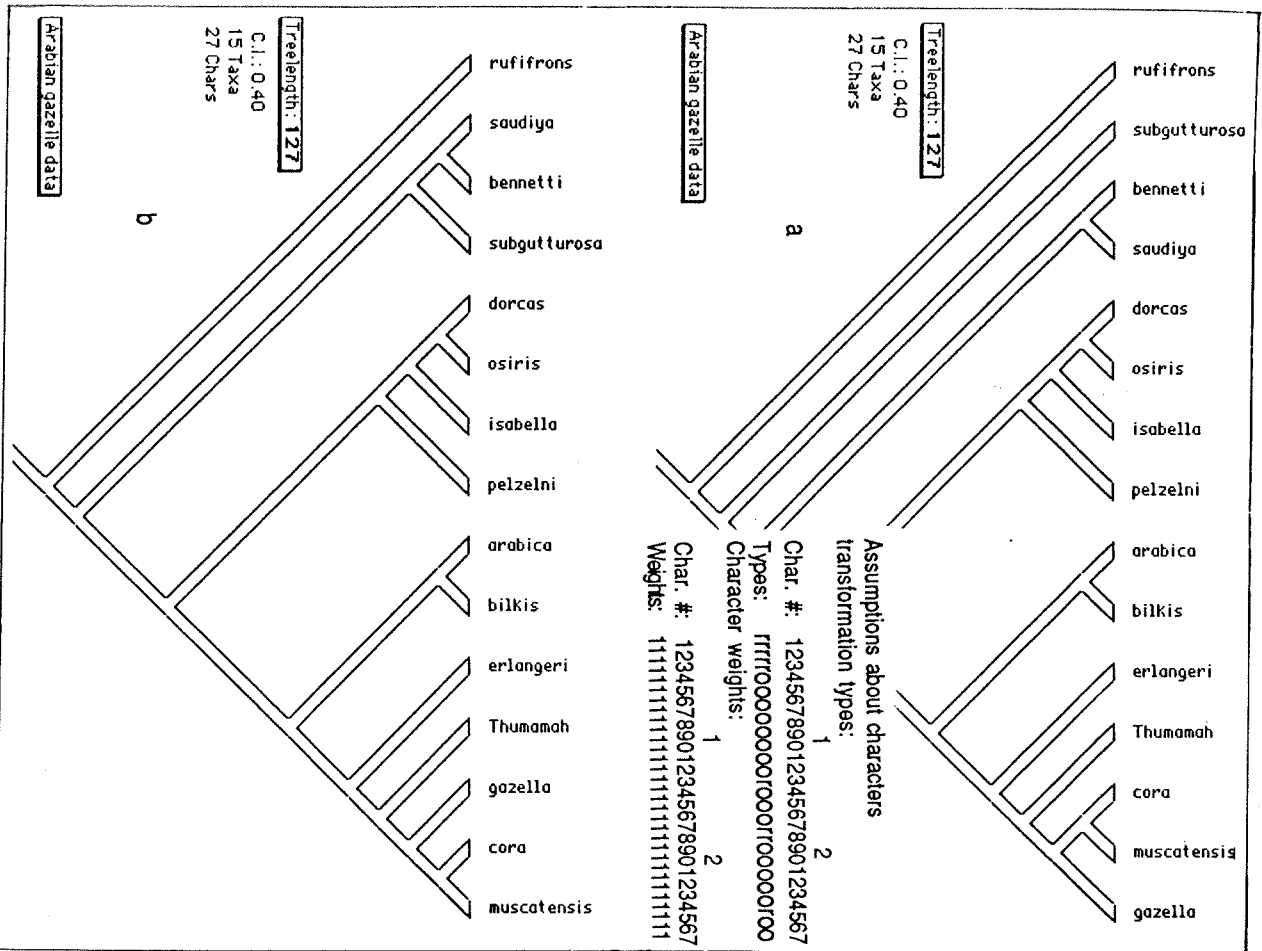


Figure 2.2. The two equally parsimonious cladograms depicting the interrelationships of *G. subgutturosa*, *bennettii* and *saudiya*. As discussed in Groves (1966), other branch patterns of the *G. dorcas/gazella* clade are slightly (up to 3 steps) shorter than the "preferred" interpretation shown here.

The outgroup was the red-fronted gazelle: as we must now call it, *Eudorcas rufifrons*.

Several points need to be made about Figure 2.2 a:

First, disagreeing alike with the results on the generic-scale characters (above) and with the chromosomal data, *Gazella subgutturosa* is sister-group to all other *Gazella*. The shortest tree of all (length 124) placed *G. bennettii* as sister, with *G. subgutturosa* linked with *G. saudiya* on the next line to split off, but no very short tree would accept

(*bennettii*, *saudiya*)/(*subgutturosa*, others)

as a viable option. The alternative that did, however, prove as short as Figure 2.2 a is presented in Figure 2.2 b:

(*bennettii*, *saudiya*)/(*subgutturosa*)/others).

A link between the three non-*dorcas/gazella* group is in fact supported by just two derived character states:

- 1) fenestra in lacrimal bone large, constant in occurrence (convergent with *G. bilkis*)
- 2) lacrimal bone not extending far into preorbital fossa (convergent with *G. arabica* and *bilkis*)

- while *G. bennettii* and *saudiya* are linked with the *dorcas/gazella* group, to the exclusion of *G. subgutturosa*, equally by two derived conditions:

- 1) preorbital fossa reduced in depth
- 2) tips of premaxillae more pointed, not broad and shovel-shaped (this is reversed in *G. bilkis/arabica* and *G. g. gazella*).

One concludes that, whichever link is the correct one, any common stem was short, and little different from a trifurcation.

The *dorcas/gazella* group is defined by the following derived conditions: rings on male's horns reduced in prominence, rings angled (somewhat convergent with *G. subgutturosa*), preorbital fossa reduced in depth (again convergent with *G. subgutturosa*), nasals short (usually <25% of skull length). Within this group, the *G. gazella/arabica* group has the following derived states: nasofrontal suture arch-shaped, horns of female short (less than 80% of skull length), preorbital fossa still less deep, nasals broadened posteriorly.

In the final section, a list of the species and subspecies of Arabian gazelles will be presented, with notes on their affinities.

SPECIES AND SUBSPECIES OF GAZELLE IN ARABIA

There are six species of *Gazella* in the Arabian region, as follows:

1) *Gazella subgutturosa*.

A species with noticeable sexual dimorphism (female skull length about 95% that of male).

Skull: Broad, its breadth across the lower orbital rims about 47% of its length. Preorbital length at least 90% of postorbital. Braincase breadth >60% of its length. Palate broad, the toothrows strongly curved. Nasal bones long (>27% of skull length), only half as broad posteriorly as long, wedging into frontals. A large fenestra in lacrimal bone; lacrimal bone does not extend far into preorbital fossa; preorbital fossa deep. Ethmoid fissure broad, triangular. Premaxilla makes a long suture with nasals; its anterior tip broad, shovel-like; strongly ridged on palatal surface. Supraorbital foramina multiple.

Horns: In male, long (>150% of skull length), lyrate, with numerous (>20) prominent, slightly angulated rings, equally well expressed on posterior and anterior surfaces; span wide, >70% of horn length. In female either long (>130% of skull length) or absent. Horn bases close together.

Pelage: Pale brown to creamy; face stripes poorly marked, obliterated with age by invasion of white on midfacial region; flank stripes poorly marked.

Glands: Preorbital glands enormously developed in male, everted during rut. Knee-brushes not prominent.

Geographic variation: Peninsular subspecies, *Gazella subgutturosa marica* (Arabian sand gazelle or *rheem* [Arabic]). Compared to Iranian, Central Asian and Mongolian forms, this is small in size, pale in colour (creamy in winter, more yellow in summer), female always horned; distribution includes Arabian Peninsula, Bahrain, Jordan (specimens from Kubla Monastery and Mafrak, Tel Aviv

University Zoology Museum), probably Syria, apparently southeastern Turkey (old mounted skin in Leiden Museum). Specimens from east of the Tigris/Euphrates but west of the Zagros Range (eastern Iraq, and Khuzestan Province, Iran) are darker, like *G. s. subgutturosa* from Iran and Azerbaijan, but tend to be small like *G. s. marica*, and females are usually horned; because of the variability in this region, these specimens surely represent secondary intergradation rather than a stabilised intermediate subspecies.

Relationships: Closest relatives in *Gazella* are *G. leptoceros* (Slender-horned, Loder's or Saharan dune gazelle), restricted to erg regions west of the Nile; and *G. cuvieri* (Cuvier's or Atlas gazelle), from Atlas mountains and foothills. The two North African species form a group relative to *G. subgutturosa*.

2) *Gazella scudtitya*.

The smallest Arabian species, with noticeable sexual dimorphism in cranial dimensions (female skull length about 95% of male).

Skull: In general, lacks the idiosyncratic shape of *G. subgutturosa*. Nasals fairly short (24-25% of skull length), narrow (combined width about 40% of length), wedge deeply into frontals; widen forward, so that their anterior width exceeds their posterior. A large fenestra in lacrimal bone; preorbital fossa not as deep as in *G. subgutturosa*. Ethmoid fissure usually broad, triangular. Premaxilla forms a substantial suture with nasals; premaxillary tip narrow, round-pointed. Supraorbital foramen single.

Horns: In male, extremely long (>150% of skull length), rather straight, their span less than half their length; 25 prominent rings (as prominent posteriorly as anteriorly), strongly angulated on posterior surface but not anteriorly. In female, well-formed, well-ringed, long, >125% of skull length.

Pelage: Light sandy-brown above; white of ventral surface yellowed. Facial markings poorly expressed; flank stripe virtually absent.

Glands: Carpal glands apparently large; knee-brushes well-developed.

Distribution: Formerly, known from the western part of the Arabian Peninsula (east of the mountainous zone); Kuwait; Iraq (Abu al Jir: Harrison, 1968:358).

Relationships: After 40 years of being classed as a subspecies of *G. dorcas*, if with misgivings, this species was finally shown by Rebholz et al. (1991) to be quite distinct. Its nearest relative is Indo-Iranian *G. bennetti* (the Chinkara or Jebeer), which however is generally larger, often with multiple supraorbital foramina, shorter but stouter less-ringed horns in the male, horns especially shorter in the female, longer broader differently shaped nasals, larger teeth, and even more poorly expressed colour contrasts.

G. saudiya is almost certainly extinct in the wild. Only two captive colonies are known to exist: one in Al Ain Zoo, United Arab Emirates, the other at Al-Areen, Bahrain. Representatives of both stocks are now living at the KKWRRC. A skull of one of the Bahraini stock is unusually large, but otherwise typical for this species (Groves, in press).

3) *Gazella dorcas*

A small species, but most populations somewhat larger than *G. saudiya* (only *G. d. dorcas* from western Egypt and Libya is smaller); sexual dimorphism is less (female skull about 97% of male in length). Skull: Nasals form a wedge into frontals much as in *G. saudiya*, but less narrowed posteriorly so that anterior width is only slightly more than posterior. There is no lacrimal fenestra. Ethmoid fissure broad, block-shaped. Premaxillae narrow; ridges on palatal surface poorly expressed.

Horns: In Arabian subspecies, males' horns less lyrate than in *G. subguthurosa*, but curved out and back, the tips forward and in, so that distance between tips is about 75% of span across horns; 17-20 rings, close together and less prominent than in *G. saudiya* and angulated; posteriorly rings fade. Length in males about 120-125% of skull length; in females about equal to skull length.

Pelage: Arabian subspecies is brown-grey with reddish tones. Face stripes well-marked, white bordered by dark brown; a dark nose-spot

in most individuals. Flank stripe generally poorly marked, a darker tint of the general body tone.

Distribution in Arabia: Well known from the Negev, southern Israel; occurs in Jordan (photos sent courtesy Maher Abu Jafar, Royal Society for the Conservation of Nature, Jordan, 10/12/87). Specimens apparently of this species, stated to have been captured in western Saudi Arabia, are in Al Wabbara, Qatar, and a "red gazelle" is stated to exist in some areas. There is a need for caution because of the great external similarity between this species and *G. gazella cora*. Subspecies: Groves (1981), basing himself on abundant skull, horn and pelage data of both sexes, recognised six subspecies in North Africa, as follows: *G. d. dorcas* (Western Desert of Egypt, to Libya); *G. d. massaesyla* (Maghreb); *G. d. osiris* (synonym *neglecta*; Sahara and Sahel, west of the Nile); *G. d. isabella* (synonym *littoralis*; northern Eritrea and Sudan, east of the Nile); *G. d. beccarii* (Eritrean highlands); and *G. d. pelzelni* (southern Eritrea and northern Somalia).

Ferguson (1981) hypothesised that the gazelles of northern Sinai are *G. d. dorcas*, those of southern Sinai are *G. d. isabella*, and those of central Sinai and Israel are a mixture. Study of specimens in the Museum of the Department of Zoology, Tel-Aviv University, suggests that in fact in both Sinai and Israel the subspecies is *G. d. isabella*; merely, there are slight differences in the expression of the nose-spot and flank-stripe (Table 2.1).

Table 2.1. Expression of nose-spot and flank-stripe in *Gazella dorcas* from Sinai and Israel.

	Nose-spot	dark	trace	absent
N. Sinai	0	1	3	
S. Sinai	1	3	1	
Israel	5	4	5	
Flank-stripe	dark	medium	light	
N. Sinai	0	1	3	
S. Sinai	0	2	3	
Israel	5	6	3	

Compared to specimens from Sudan, *G. d. isabellia* from Sinai and Israel have horns that are very slightly less spread in the male (horn span averages 131.7mm, against 142.2 in Sudan), and the braincase is slightly shorter and narrower.

4) *Gazella arabica*

I have taken the step of uniting *G. bilkis* and *G. arabica* into one species, for reasons given below. In what follows, therefore, references to sexual and individual variation are based on the Yemen Highlands sample, hereinafter *Gazella arabica bilkis*.

The largest species in Arabia, with very little sexual dimorphism. Skull: Nasal bones short, about 20% of skull length in males, somewhat more (25%) in females; broad compared to length (>60%, in males). Naso-frontal suture arch-shaped. Ascending process of premaxilla does not reach nasal, or only just; palatal process broad, shovel-shaped. Preorbital fossa shallow; lacrimal extends very little into fossa. Ethmoid fissure elongated.

Horns: Short, stout, straight (tips not inturred), with only 12-15 rings, well-spaced and almost unangulated, in male; on posterior surface, rings are faint. Unlike other gazelles, there are not the thin longitudinal ridges connecting the transverse horn rings. In female, relatively long, about three-quarters length of skull, well-formed, with noticeable rings.

Pelage: Facial markings well expressed; the lateral black stripes almost lost in the dark tone of the cheeks. There is a thin red stripe below the black flank-band; the white runs down the inner side of the hindleg to the fetlock, whereas it stops at or above the hock in other species.

Distribution: High mountains of Yemen (if it still exists); formerly, reputedly on the Farasan Islands.

Subspecies: This study confirms the conclusions of Groves (1996) that *G. bilkis* is very similar to (the type and only known specimen of) *G. arabica*, and that the two are best regarded as conspecific. They resemble the *G. gazella* group in a number of features (see above), but share the following derived conditions not seen in the latter: preorbital fossa shallower; lacrimal bone short so that it does not extend

far into preorbital fossa; horn rings reduced in number (convergent with *G. gazella*); no longitudinal ridges between transverse horn rings; very short and broad nasals (convergent with *G. g. muscatensis*); premaxilla tips broad. The female (known only in *G. a. bilkis*) is virtually as large as male; there is thus less sexual dimorphism than in any other Arabian gazelle.

The two subspecies differ as follows:

G. a. arabica (known from a single [adult male] specimen, the type): Deep sooty grey with a tinge of red; the horns are very long, 140% of the skull length; there is no lacrimal fenestra; there are several supraorbital foramina on each side; the nasal bones are extremely short and broad, and broader anteriorly than posteriorly, and the median nasal tips extend forward of the lateral prongs; the skull is narrower and the braincase longer. The evidence would seem clear-cut, that Hemprich and Ehrenberg collected the specimen on "Farsan Island" (Groves, 1983), but no such gazelle occurs there today. Dr K. Habibi (*in litt.*, 9th March, 1984) reminds me that trade in live animals between private collections has been going on for centuries, so that Hemprich & Ehrenberg's gazelle collected on Farasan need not have been indigenous; moreover, the Farasan Islands formerly belonged to Yemen. The present day Farasan gazelles, *G. gazella farsani*, are small in size, as indeed one would expect for an insular population of a large mammal; the type of *G. arabica* is very large, contrary to what one might expect.

G. a. bilkis (known from two adult males, three adult females and a juvenile): Deep black-brown, so dark that the lateral black face-stripe is lost in the dark tone of the cheek; the horns of the male average 120% of skull length, those of the female 77% of skull length; a lacrimal fenestra is present; there is only one supraorbital foramen on each side; the nasal bones are somewhat less shortened, narrower anteriorly, and the median nasal tips are about level with the lateral prongs; the skull is less narrow, the braincase shorter. Apart from a skull labelled "Mocha", the known specimens were field-collected at high altitudes (>2000m.) in the vicinity of Ta'izz, Yemen. The type of *G. arabica* (see above) does fall outside the known variation of *bilkis*, but the number of specimens of the latter is very small, and it re-

mains possible that future specimens could bridge the gap. Taken in conjunction with the question-mark over the locality of the type of *arabica*, this leaves a very real possibility that the description of *Gazella bilkis* (Groves & Lay, 1985) in effect signaled a rediscovery of *G. arabica*.

5) *Gazella erlangeri*.

A small species, only a little larger than *G. saudiyana*, and with a similar degree of sexual dimorphism.

Skull: As in *G. gazella* the nasofrontal suture is arched, the lacrimal extends well into the preorbital fossa, and the nasals are relatively long and less narrowed anteriorly; but differs in the longer ethmoid fissure and the longer suture of the premaxilla with the nasals; the lacrimal is more rounded, less angular than in *G. gazella*; the supraorbital foramina are sunk into deep triangular depressions. The median nasal tips extend forward of the lateral prongs.

Horns: Differs from *G. gazella* in that the female's horns are less reduced (length 75% of the skull length), the tips are less inturned than most *G. gazella* populations (tip-to-tip distance 85% of span in the male) and the posterior horn rings of the male are only slightly angulated. The number of horn rings averages more (often >20).

Pelage: Colour of body is very dark, a dark grey-brown even tending towards blackish in some individuals; but there is the same sharp transition to ochery buff on the haunch. The dark flank band and the face pattern are well marked; there is a lighter, pinky-grey zone above the flank-band, and there is always a large black nose-spot. The forehead and midface are dull buffy-brown.

Distribution: Well known from the southwest of the peninsula, especially in Yemen, but there are populations sporadically as far north as Thuwal, on the coast north of Jeddah (Figure 2.3). (Specimens from Thuwal are in the Natural History Museum, London; a specimen from the Najran district was received by M. Vassart (pers. comm.)). It is this apparent interdigitation of the range with *G. gazella cora* that makes it necessary to give this taxon specific rank; morphologically, it differs little or no more from subspecies of *G. gazella* than these do

from each other, indeed the pelage characters are identical to *G. g. muscatensis* (Groves, 1966).

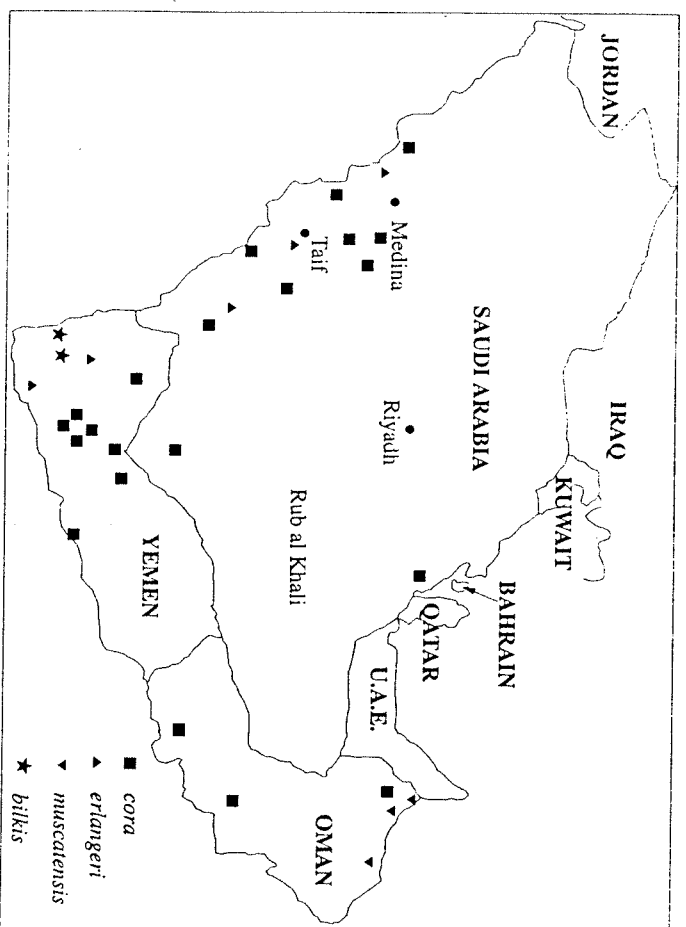


Figure 2.3. Map of recorded localities of *G. gazella* group in the Arabian Peninsula. Note that the taxon *erlangeri* is sympatric with both *G. g. cora* and *G. arabica bilkis*, and consequently must be regarded as specifically distinct from both. The Farasan Islands gazelle (*G. gazella farasani* and perhaps *G. arabica arabica*) have not been included. Locality records are given in Groves (1966).

6) *Gazella gazella*.

A medium-sized species, with more sexual dimorphism than any others in the region, expressed both in body size and in the peculiarly small, fragile horns of the female which in most subspecies are smooth, unringed.

Skull: Like *G. arabica* and *G. erlangeri*, the nasofrontal suture is arch-shaped, not greatly indenting into the frontals. The nasals are broad, especially posteriorly, and very short. There is only rarely a

lacrimal fenestra; the supraorbital foramen is single on each side; the braincase is narrow; the preorbital fossa is shallow, the lacrimal extending well into it.

Horns: These are sturdy in the male, and broad across the base, generally with intumed tips and a reduced number of rings (usually about 15-18). In the female they are short, averaging 50-66% of the male's in length in different subspecies; usually unringed, and straight, but so thin that they regularly break or become deformed.

Pelage: The colour is very variable, nearly always some shade of buff, and always with a noticeably sharp transition from darker upper parts to buffy legs on the upper haunch. Face-markings and flank stripe are generally well expressed; there is generally a broad, smudgy black nose-spot.

Distribution: All over the peninsula, north west as far as Syria; in the northeast it apparently does not cross the Tigris/Euphrates, though there is an isolated population on Fortur Island, in Iran; and in the east it does not enter Sinai.

Subspecies: There is considerable variation across the geographic range of this species, such that it is uncertain whether some of the subspecies would not be better ranked as full species, as has proved necessary for *G. erlangeri* (above). Currently the following are included in the species:

Gazella gazella gazella: Known primarily from northern Israel (from Galilee to somewhat south of Jerusalem) and Israeli-occupied territories (Golan; Dead Sea valley); formerly known from southern Lebanon, and presumably occurred in Syria. The largest subspecies; female's horns very reduced, barely 50% of skull length; male's horns not bowed outward to any extent, but tips tend to turn in. Skull noteworthy in that ascending branch of premaxilla almost never reaches nasal, and nasal tips protrude further forward than lateral prongs.

Gazella gazella subsp. (1): The very rare "Acacia Gazelle", now restricted to the vicinity of Yotvata, in the southern Arava Valley of Israel; possibly could occur on the Jordanian side of the border. As

this subspecies is currently under description (Mendelssohn et al., in press), little will be said of it here, beyond that it is a large but slenderly built form, in many respects close to *G. g. cora*.

Gazella gazella cora: Formerly could have been described as "the Common Arabian Gazelle", and still apparently occurring sporadically in the Asir Mountains and parts of the desert regions of Saudi Arabia, and in southern Oman. Smaller than the two previous subspecies; horns in male shorter, more outbowed, the tips turning in; premaxilla nearly always meets nasal; nasal tips short, do not protrude forward of lateral prongs; nasals narrower than *G. g. gazella*, facial part of skull narrower, braincase shorter and broader. There is a wide range of colour hues, some individuals being a pale sandy tone with little trace of a flank-stripe, most being a medium fawn with varying amounts of reddish. Groves (in press) stresses how strikingly similar many examples are, externally, to *Gazella dorcas isabellae*; this could perhaps be the explanation for the reputed presence of the latter in Saudi Arabia.

Gazella gazella muscatensis: A very small subspecies, restricted to the Batinah Coast of Oman; very dark (pelage indistinguishable from *G. erlangeri*, except that the forehead and midface are more chestnut, and the nose-spot is smaller and less conspicuous); horns more outbowed, tips more intumed, than any other subspecies (tip-to-tip distance only 60% of span); premaxilla does not usually extend to nasal; nasal tips short; nasals exceptionally short, broad posteriorly, and narrowed anteriorly; skull broad, both facial skeleton and braincase.

Gazella gazella farasani: a small, rather dark population from the Farasan archipelago. I have not seen skulls of this subspecies. This subspecies must still be regarded as provisional, as the stock may actually be of mixed origin (pers. comm. from A. Greth, I. Nader and others); even if this is so, of course, it is still likely that the basis of the Farasan gene-pool is an indigenous population.

Gazella gazella subsp. (2): The Iranian population described by Kararni & Groves (1992). Close, but not identical, to *G. g. muscatensis*.

Gazella gazella subsp. (3): There has been for many years a breeding group of *G. gazella* at the KKWRRC, Thumamah, which is traditionally identified as *Gazella gazella gazella* but is decidedly not; externally it certainly closely resembles *G. g. gazella* but, as shown by Groves (in press), its skull characters forbid this identification. Nor is it a hybrid: many of its skull and horn measurements are extreme for the species. Thus, though it is almost as large as *G. g. gazella*, the horns are longer, indeed in the female they are longer than any other population of the species; they are also exceptionally straight and nearly parallel (tip-to-tip distance 90% of span). The nasals are very narrow, especially anteriorly; the skull is very narrow across the orbits and the braincase.

The origin of the Thumamah group is quite unknown, though one could speculate that this might be the "tdm" of Al-Harrath. In the present parlous condition of wild gazelle populations in most Arabian countries it would be unthinkable to collect fresh specimens; but as this mystery taxon is readily recognisable from its skull and horns, pick-up material would be perfectly adequate. In fact, the need for pick-up collections of all gazelles, to document remnant distributions taxon by taxon, is urgent.

Among the three described subspecies (and excluding *G. g. farasani*), skull size in both sexes decreases in the series *gazella-cora-muscatensis*, with *G. erlangeri* about the same size as *muscatensis* or slightly larger; horn size follows the same sequence in males, but in females it is exactly reversed.

BODY BUILD AND PROPORTIONS IN ARABIAN GAZELLES

Skull measurements for all Arabian taxa are given in Groves (1996). Postcranial and external body measurements given in that paper are now augmented, so a new survey is given here (Tables 2.2, 2.3).

Table 2.2 Body measurements in Arabian gazelles.

	H + B	Tail	Hf	Ear	Weight
Males					
<i>gazella</i>	102-114	9-13	33-36	11-12.5	22.5-28
"Acacia"	100	15.5	34	13.5	16
<i>cora</i>	104-124	17-17	-	12	19.8-23.4
<i>muscatensis</i>	99	10.8	28.6	11.9	-
<i>erlangeri</i>	98-103	11-13	-	-	16.4-18.4
<i>dorcas</i> ssp.	91-111	11.5-19	27-32	13-18.1	14-20
<i>marica</i>	113-122	16.5-20	-	-	17.7-23.8
Females					
<i>gazella</i>	91-101	9.5-13	31-33	10-12.5	14.5-17.2
<i>cora</i>	113-118	15.5-20	-	-	12.7-15.6
<i>muscatensis</i>	89.5	10.8	26.7	10.9	-
<i>erlangeri</i>	94-100	11-11.5	-	-	10.6-12.3
<i>saudiya</i>	92.8	9	25.5	12.3	-
<i>dorcas</i> sp.	88.5-114	10.4-17	27-32.5	14-16	9.2-18
<i>marica</i>	99-116	14-18.4	30	-	15.3-18.4

(Source: museum labels; Harrison, 1968; Groves, in press; A. Greth, pers. comm.).

Linear measurements in cm., weight in kg.

n for linear measurements: *gazella* male 9, female 5; *cora* (H+B, Tail and Wt) male 3, female 5; *erlangeri* (H+B, Tail and Wt) male 2, female 2; *osiris* male 9; *isabella* (H+B, Tail and Wt) male 6, female 13, (Hf and Ear) male 5, female 9; *marica* (H+B, Tail and Wt) male 3, female 4. For the rest, *n*=1.

Putting these data together:

Within *G. gazella* we can note the great variations between subspecies: the desert forms "Acacia" and *cora* are lightly built with long extremities (tail, limbs, ears in the case of the "acacia gazelle"), and the "acacia gazelle" has especially marked distal limb elongation. The cooler climate, more mesic-habitat *gazella* and *muscatensis* have a more compact build. Compared to other species (except *G.*

erlangeri, whose skeleton is not known) all members of this species tend to have rather long hindlegs compared to the forelegs.

G. erlangeri is lightly built like *G. gazella cora*, but short-tailed like *G. g. gazella* and *muscatensis*.

Table 2.3. Body proportions in Arabian gazelles.

	(a) External measurements			
	Tail as % H + B	Hf as % H+B	Ears as % H+B	3 rd weight as % H + B
<i>gazella</i>	8.1-14.0	28.8-34.4	10.2-13.4	2.56-2.92
Acacia	15.5	34.0	13.5	2.52
<i>cora</i>	13.7-20	-	11.5	2.06-2.36
<i>muscatensis</i>	10.9-12.1	28.8-29.8	12.0-12.2	-
<i>erlangeri</i>	10.6-13.3	-	-	2.20-2.56
<i>saudiya</i>	9.7	27.5	13.3	-
<i>dorcas</i> ssp.	11.4-17.2	28.7-37.6	14.0-18.1	2.12-2.79
<i>marica</i>	13.5-16.7	30.3	-	2.21-2.62

(b) Limb proportions

	Foreleg as % hind	Tibia as % femur	Metatarsal as % femur	Hindleg % skull
<i>gazella</i>	77-80	124-128	96-106	288-312
Acacia	79	136	115	307
<i>cora</i>	79	125	105	318
<i>saudiya</i>	80	130	109	298
<i>dorcas</i> ssp.	79-83	133-139	114-117	306-323
<i>marica</i>	80-83	127-131	109-115	283-293

Numbers are as follows: *gazella* 22, *Acacia* 1, *cora* 1, *dorcas* 7, *marica* 4.

G. saudiya is extremely short-tailed and short-legged, and has very long ears. Although overall short-legged, the tibia is somewhat elongated, but the metatarsal is short.

G. dorcas is rather variable, but never as extremely short-tailed as *G. saudiya*; the ears are even longer than in the latter. The limbs of some individuals are more elongated than in any other species, and the distal limb segments are differentially elongated compared to the femur.

Finally *G. subgutturosa marica* is a rather lightly-built, long-tailed gazelle; its limb proportions are unusual, the metatarsal being elongated but not the tibia. Data from non-Arabian representative of the species show similar proportions.

CONCLUSIONS AND SUMMARY

The genus *Gazella*, as hitherto generally recognised, is polyphyletic. Unless the entire group is placed in Antelope, several species normally included in the genus must be separated generically from it as *Eudorcas* and *Nanger*.

Arabia is the centre of diversity of the genus *Gazella* as now restricted. Here two species, *G. gazella* and *G. subgutturosa*, are widely sympatric; a third species, *G. saudiya* (now extinct in the wild), was formerly sympatric with them in restricted areas; a fourth, *G. erlangeri*, is sympatric with *G. gazella* along the Red Sea coast and mountains; a fifth, *G. arabica* (possibly now totally extinct), was sympatric at high altitudes with *G. erlangeri*; and a sixth, *G. dorcas*, certainly extends into Jordan and may also occur in the Peninsula, although this may be a misapprehension due to its close external similarity to the now rare (and consequently unfamiliar) *G. gazella cora*.

Relationships between these species are not as formerly depicted. In particular *G. saudiya* is not, as has generally been thought, the local representative of *G. dorcas* but instead seems likely to belong in a loose-knit group with *G. subgutturosa* and *G. bennettii*. *G. erlangeri* is closely allied to *G. gazella*; indeed it differs very little more from it than the subspecies of *G. gazella* differ from each other.

