

CONSERVATION OF ARABIAN GAZELLES

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Foreword by *HRH Prince SAUD AL-FAISAL*

2. Taxonomic Diversity in Arabian Gazelles: The State of the Art

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Abstract: *The discovery that the type of *Gazella arabica* does not correspond to any of the known and authenticated taxa of Arabian gazelles ushered in an era of unfortunate instability in Arabian gazelle taxonomy. This was further compounded by the description of *Gazella bilkis*.*

*Morphologically, *Gazella dorcas* - a largely African species - seems closest not to *G. saudiya* (which has generally been regarded as its Arabian representative) but to *G. gazella cora* and *G. g. muscatensis*. *G. g. gazella* is surely correctly regarded as conspecific with these last two, but at the same time shows approaches to *G. bilkis*, thus completing a confusing ring-species effect.*

*A further complication is the recent resurrection from synonymy with *cora* of *G. g. erlangeri*, a small dark straight-horned subspecies from the south-west of the Arabian peninsula.*

*There are a few problems with *G. subgutturosa* as well: is the Bahrain population different from mainland *G. s. marica*? And are Syrian and Iraqi populations of the species different yet again?*

Skull, horn and pelage characters have commonly been used to differentiate gazelle species and subspecies. In my presentation, I will pay attention to these characters and in addition to certain features of body proportion.

Keywords: gazelle, taxonomy, Arabian peninsula

Introduction

- **Arabian gazelles:** The first description of an Arabian gazelle was that of Buffon (1764), who placed at the head of his thirteen species or varieties of "antilopes" one called simply "the gazelle, found in Syria, Mesopotamia and other provinces of the Levant, as well as in Barbary, and in all the northern parts of Africa". The description specified horns "about a foot in length" (approximately 300 mm), with 12-13 rings; and it was contrasted with a second species, "the kevel", said to be from Senegal, which was smaller, with less rounded, more compressed horns with 14-18 rings. A certain Dr Russel was quoted as saying that in the neighbourhood of Aleppo there were actually two kinds of gazelles, the mountain gazelle, of a deep brown colour, and the gazelle of the plains, much paler and "not so nimble, nor so handsome as the first" (the idmi and the rheem are easily recognizable from these descriptions). Two years later Pallas (1766) gave the name *Antilope gazella* to Buffon's "gazelle", and Neumann (1906) restricted the name, probably correctly in the main (although it was actually somewhat of a composite), to the Palestine mountain gazelle, nowadays generally called *Gazella gazella gazella*.

Lichtenstein (1827) gave the name *Antilope arabica* to some gazelles collected by Hemprich & Ehrenberg: a male from the Farasan Islands and a female and young from Sinai. Brooke (1873) used this name (in the combination *Gazella arabica*) for South Arabian gazelles, and Neumann (1906) restricted the name to the Farasan male; from that date it was customarily used, in the form *Gazella arabica* or *Gazella gazella arabica*, for the common gazelle (idmi) of the Arabian peninsula,

until Groves (1983) re-examined the specimen concerned and showed that it was unlike any other specimen known from that region.

Smith (in Cuvier, 1827) described a new gazelle, *Antilope cora*, based on a pair formerly living in the Tower of London menagerie, "said to have been brought from India, or more properly from the Persian Gulph" (vol. 4), or more definitively from "the shores of the Persian Gulf, eastern Arabia" (vol. 5). Groves (1983) argued that this should be regarded as the earliest name for the idmi of Arabia, which would therefore be known as *Gazella gazella cora*.

Brooke (1873) recognized two species in Arabia: *Gazella dorcas* in the north and *Gazella arabica* in the south. By "North Arabia", however, he meant Sinai, which he called Arabia Petraea; and as far as one can deduce his South Arabian specimens appear to have been restricted to the Farasan specimen in Berlin, and a skull from Mocha in Yemen (now referred to *G. bilkis*), which was the only Arabian peninsular specimen registered in the Natural History Museum, London, by that date. A year later (Brooke, 1874) he added *Gazella muscatensis*, from the Batinah Coast of Oman, to the list; this was based on a pair living in the London Zoo, and his comparative sample of *G. arabica* appears to have been the same as in his earlier paper: this should be borne in mind when reading, for example, his contrasting of the lyrate horns of his new species with the straight horns of *arabica*.

Thomas (1897) described the Arabian sand gazelle, or rheem, as *Gazella marica*. Although Ellerman & Morrison-Scott (1951) associated this with the Saharan *G. leptoceros*, it was later shown (Groves & Harrison, 1967) that its true affinities are with the Central and Western Asian *G. subgutturosa*.

In 1905, Neumann clarified the status of Pallas's *gazella*, as noted above, and observed that the Farasan and Sinai specimens which formed the basis of Lichtenstein's *arabica* were not in fact of the same taxon. Restricting the name *arabica* to Farasan, he described the Sinai specimens as *Gazella arabica rueppelli* (later shown to be synonymous with *G. dorcas isabella* by Groves, 1983), and described a further new subspecies, *G. arabica erlangeri*, from Aden (based on living specimens in the London Zoo).

It was not until well into the present century that the Arabian peninsular afri was described, under the name *Gazella gazella saudiya*, by Carruthers & Schwarz (1935). It was briefly raised to specific rank by Morrison-Scott (1939), then assigned to the African *Gazella dorcas* as an Arabian subspecies by Ellerman & Morrison-Scott (1951).

It was Ellerman and Morrison-Scott (1951) who first brought some semblance of order into the by now rather complicated taxonomy of Arabian gazelles, recognizing three species in the Arabian peninsula: *G. dorcas saudiya* Carruthers and Schwarz, *G. gazella arabica* Hemprich and Ehrenberg (recte Lichtenstein), and *G. leptoceros marica* Thomas. Groves and Harrison (1967) followed this scheme, at least in outline; but they referred the taxon *marica* to the Central Asian *G. subgutturosa* instead of to the Saharan *G. leptoceros*, and revived the name *muscatensis* for the subspecies of *G. gazella* living along the Batinah coast of Oman. Groves (1969) added the Indo-Iranian *bennetti* (and its subspecies) to *G. dorcas*, noting its resemblance to *saudiya*: this was perhaps the ultimate in taxonomic oversimplification applied to the genus.

Since that time, the picture has once more become complicated. Groves (1983) found that the type of *Antilope arabica* Hemprich and Ehrenberg, from the Farasan Islands, is quite unlike the form of *G. gazella* which is widespread in the Arabian peninsula, which therefore takes the next available name, *cora* Smith. The gazelle from the Yemen highlands, placed with some misgivings in

G. gazella as a possible undescribed subspecies by Groves and Harrison (1967), was described as a new species, *G. bilkis*, by Groves and Lay (1985). Groves (1985, 1988) re-established *G. bennetti* as a separate species; he expressed more and more doubt whether the taxon *saudiya* could really be included in *G. dorcas*, and Rebholz *et al.* (1991) confirmed that its karyotype is indeed totally distinct. Thouless and Al Bassri (1991) examined recently taken specimens from the Farasan archipelago, and could not find anything resembling the type of *arabica*; they described the present-day Farasan population as a new subspecies, and thereby left a big question-mark over the whole *arabica* problem. Finally Groves, Thouless and Vassart (in press) recognized yet another subspecies of *G. gazella* on the mainland, for which they revived Neumann's name *erlangeri*.

Table 2.1 Putatively recognized gazelle taxa in the Arabian peninsula.

Species	Arabian subspecies
<i>G. dorcas</i> Linnaeus	<i>isabella</i> Gray
<i>G. saudiya</i> Carruthers and Schwarz	
<i>G. gazella</i> Pallas	<i>gazella</i> Pallas <i>cora</i> Smith <i>erlangeri</i> Neumann <i>farasani</i> Thouless and Al Bassri <i>muscatensis</i> Brooke
<i>G. bilkis</i> Groves and Lay	
<i>G. arabica</i> Hemprich and Ehrenberg	
<i>G. subgutturosa</i> Gldenstdt	<i>marica</i> Thomas

The result of all this is that the putatively recognizable taxa in Arabia are as given in Table 2.1. In this listing, *G. dorcas isabella*, *G. gazella gazella*, *G. g. muscatensis* and *G. bilkis* are not confirmed for Saudi Arabia; all the others - six in all, if the enigmatic *G. arabica* is counted - are known to exist, or have existed until recently, within the borders of the Kingdom.

This paper will examine the interrelationships among these taxa, and outline their differences and recognition features.

The meaning of taxonomic statements

Before reviewing the taxonomy of Arabian gazelles, it is necessary to be explicit about the nature of taxonomic statements: what exactly are species, subspecies, and taxa in general?

Most practising taxonomists, working with what until recently was the only material available for taxonomic study, and is still the most accessible (namely, museum skins and skulls), "know" what species and subspecies are. The working definitions were put succinctly by Deraniyagala (1955):

- A *species* is a community of similar individuals in which each is distinguishable from another of any other community.
- A *subspecies* is one of several populations within a species which differ from one another as a whole but possess types of individuals that are common to some or all of these populations.



Figure 2.1 a



Figure 2.1 b



Figure 2.1c

Figure 2.1 Arabian gazelles formerly in Chester Zoo, U.K. (Adult males): a, b) *Gazella gazella cora*, from Manwakh, Hadhramaut; c) *Gazella bilkis*, from Yemen. Photos: Ken Green.

As a general rule, these characterizations have served as implicit guidelines for museum taxonomists since at least the middle of the century, and probably before (see, for example, Miller, 1934, who classes numerous taxa of colobid monkeys as distinct species, however slight their differences, because "among the 72 specimens... I have found no one that is intermediate or of doubtful status..."). Deraniyagala's description of a species leaves little room for manoeuvre, but how much difference "as a whole" might mean in that of a subspecies is wide open. When it is made explicit, a taxonomist has usually proved to be working with the "Coefficient of Difference" of Mayr *et al.* (1953): when two samples are compared for a given quantitative character, this is the difference between the means divided by the sum of the standard deviations, and a C.D. of >1.27 (joint non-overlap of 90%) is commonly used as rule-of-thumb to indicate subspecies difference.

Historically, the most generally used definition of a species is that of Ernst Mayr (see, for example, Mayr *et al.*, 1953):

A species is a group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.

This is commonly known as the Biological Species Concept (BSC for short). The link with the museum taxonomist's working definition (above), though rarely made explicit, is as follows: reproductive isolation equals genetic discontinuity which in its turn implies absolute morphological separability.

Dissatisfaction with the BSC over the past ten years or so has taken various forms. Most are endoheresies (objections from within), and have to do with the meaning and maintenance of reproductive isolation, or the need to fit nonsexually reproducing organisms into it; but we have now to reckon with an exoheresy, the Phylogenetic Species Concept, which maintains that what species are "about" is not reproductive isolation at all, but something quite different (see below). As Vane-Wright (1992) and Endler (1989) note, species are both the basis for cataloguing the living world and an attempt to describe evolutionary relationships. While "...a lack of certainty should be accepted as inherent to the subject" (Vane-Wright, 1992), especially considering that we are dealing with a dynamic, evolving system not an all-or-nothing static one, there is a practical consideration: species are required by conservation workers, who need the concept to calculate species richness, analyze centres of endemism, communicate to the public about "endangered species" and convince legislators of the need for their protection, and plan protected areas to cover the maximum species diversity (Rojas, 1992). How may all these different interests and concerns best be served?

Biological Species Concepts

Paterson in particular has objected to defining a species in terms of its external relationships, which as he has argued are a by-product of its species status, not its essence. For him a species is "that most inclusive population of biparental organisms which share a common fertilization system" (Paterson, 1986); this is the Recognition Concept of species. Lack of interbreeding is not part of this definition. The logical domain of this concept, as Templeton (1989) argues, is as unclear as is that of the traditional BSC: not only are nonsexual organisms excluded, but population subdivision (by geographic barriers, for example) and isolation by distance immediately bring their whole basis into question. He proposes instead the Cohesion Concept: the species is "the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms", these being either genetic (interbreeding and so on) or demographic (evolutionary or ecological). Endler (1989) points out, however, that Templeton's new concept is just as hard to make operational as is Paterson's. This drawback to both these new concepts, even though they do manage to a degree to improve on the old BSC, suggests that for sexually reproducing species at least we should return to Reproductive Isolation as a purely practical measure, even though we must continue to enquire into biological mechanisms.

What, then, does Reproductive Isolation of a species imply? Does it mean that the entity under consideration cannot, under any circumstances, interbreed with any other such entity? (Or, if it does, would the resulting hybrids necessarily be sterile?). Or does it mean that it normally does not but may be persuaded to do so under altered circumstances? Or is a certain - even, a considerable - amount of interbreeding permissible, as long as gene-flow from one species to another does not occur? These problems are reviewed by Groves (1989), who notes that in a dynamic, evolving biosphere all stages in the development of reproductive isolation should be expected, and the taxonomist must simply make the strategic decision most appropriate to the occasion.

Endler (1989) and Templeton (1991) suggest that the botanical concept of Sygameon ("the most inclusive unit of interbreeding in a hybridizing species group"), may be relevant to the species concept in mammals. A good example, in the context of this volume, would be that of *Antelope cervicapra* and *Gazella* spp.: all capable of interbreeding, they would form a sygameon, and within it there are subunits which do not form a natural continuum, some at least of which would be species.

Van Valen (1988), indeed, would see species as "fuzzy sets" - sets (as in mathematics) in which for each potential member there is a number which expresses the degree to which it is a member of that set. This is the logical opposite to the essentialist "species as individuals" proposition (Ghiselin, 1974), and hardly more helpful in systematic practice!

Phylogenetic Species Concepts

Nixon & Wheeler (1990) point out that museum taxonomists can observe only pattern, not process: and this of course applies to molecular systematists as well, and even to field biologists in the main (in order to prove that two species do not interbreed, one must see them not interbreeding, which is rather hard to do, though I suppose in principle not impossible). Why not, then, make species definitions depend on observable pattern, and not on this or that hypothesis of how species come to be or are maintained?

The fullest explanation of the Phylogenetic Species Concept (PSC) is that by Cracraft (1989). It emphasizes differentiation; some of this differentiation results in reproductive isolation, some does not. Put simply, populations to qualify as species should be 100% diagnosable - although Cracraft qualifies this by saying that the diagnostic characters may actually be expressed only by one sex or one ontogenetic stage, or indeed they may be obscured by individual variation. The diagnostic character or characters can be morphological, behavioural, chemical - anything, provided a genetic basis can be plausibly inferred; a species is "the smallest exclusive monophyletic group" (Baum, 1992).

It goes without saying that, under the PSC, species should be monophyletic. This is not a requirement of the BSC: cases are known where well-differentiated subspecies have gone on interbreeding (and so, under the BSC, remained conspecific), while a more recently differentiated form has apparently achieved genetic isolation; some of these cases are discussed by Groves (1989).

How the PSC works in practice has recently been exemplified by Cracraft (1992) in his revision of the birds-of-paradise. Some commonly recognized subspecies of these birds are "diagnosably different", so are ranked by Cracraft as full species; others represent mere subdivisions of clines, so are suppressed. The result is that the 40-43 species of earlier revisions become 90 ...and there are no subspecies! The informal category "species group" is used to delimit monophyletic clusters of species within a genus.

Not all PSC supporters necessarily abhor subspecies, as we will see below. All of them, however, would agree to recognize all discretely diagnosable entities as species. Does this sound familiar? It is a return to the museum taxonomist's working definition (e.g. Deraniyagala, 1955; Miller, 1934) above!

Subspecies and the phenotypic plasticity question

There is no doubt but that the phylogenetic taxonomists are right: the subspecies has been all things to all people in the past. As Cracraft (1992) remarks, "degrees of morphological difference among allopatric populations lead the investigator to speculate about the degree of reproductive isolation that might obtain if or when these populations might ever come into contact". In other words, we cannot base a formal taxonomic scheme on mere speculation - let us treat those that are diagnosably different (i.e. discrete) as species, and reject the rest.

Nixon & Wheeler (1990) are not so dismissive. While agreeing that the diagnosable entities are species, it is still worth recognizing groups that are "centric, not monothetic" with subspecific names.

The problem with subspecies has always been that there has been a tendency to reify them, as if they were simply "minor species", with only one or two diagnostic features rather than ten or twenty. They may indeed be population groups in the process of generating the kind of variation that will eventually lead to speciation (Groves, 1989), but if anything they represent the point at which such variation has reached a high enough frequency to attract attention, and do not by any means exhaust the spectrum of intraspecific geographic variation.

This last point is important in present-day conservation contexts, as was forcefully pointed out more than ten years ago by Greig (1979). A case cited by him has since achieved some notoriety: a population of *Capra ibex* successfully translocated to the Tatra Mountains was augmented by well-meaning persons with *C. aegagrus* from Turkey and *C. nubiana* from Sinai, causing the whole hybridized complex to rut earlier, so giving birth in winter, leading to unacceptable infant mortality and eventual extinction. The three species of *Capra* in this case history have at times been treated as subspecies, so the case may be relevant here; but in any case this well-known example has tended to overshadow other cases where some ill-conceived translocation at, or even below, subspecific level had similar unfortunate consequences. Greig (1979) cites the translocation of bighorn sheep, *Ovis canadensis*, from Jasper National Park to Oklahoma, where the species - possibly in a separate subspecies, possibly not - formerly existed; it failed. The addition of red deer, *Cervus elaphus elaphus*, from Germany to a Norwegian population caused the entire indigenous stock to die out. The lesson which he draws from this is that subspecific traits at a morphological level may be in effect the outwardly visible markers of physiological differences; we may go further, and claim that physiological differences may tend to characterize populations not even morphologically separable. This simply reminds us that, ultimately, what we aim to preserve (where we still have the option) is not just species or even subspecies, but gene-pools.

The question which this immediately raises, of course, is: are genes inevitably involved, even where visible differences appear to exist? Or can the appearance of two different taxa be generated by environmental differences alone?

In two groups of artiodactyls, it is well known that there certainly is a remarkable degree of phenotypic plasticity: these are deer and pigs. Hammond (1965) documents the remarkable degree to which domestic pigs may be stunted by undernutrition yet retain their general health and fertility. Huxley (1931) records the evidence for such plasticity in red deer: deer *Cervus elaphus elaphus*, of largely British origin, with a little German admixture, when translocated to optimal-quality habitat in New Zealand grew to sizes "hardly inferior to good Carpathian stags" *Cervus elaphus maral*; and in localities where environmental quality deteriorated, the size declined again. Specifically, the mean body weight of Scottish stags of the heaviest weight class (Huxley, 1931, Table III) is 128.7 kg, and of English (slightly mixed) stags is 169.0 kg, while that of the largest weight-class Carpathian stags is 230.7 kg.; the New Zealand stags would be over 200 kg (one estimated weight of 250 kg is noted). The size of the antlers varies allometrically with body size (Huxley, 1931). Let it be noted, however, that other characters of antlers, and pelage colour, do *not* approach *C. e. maral*, and the differences in colour pattern, pelage disposition, antler type and gross body size between red deer and wapiti *C. e.*

canadensis, likewise introduced to New Zealand (and sometimes hybridizing with red deer), remain fixed. That is to say, environmental plasticity has its limits.

Van Bemmelen (1949) described the rusa deer *Cervus timorensis* of Peucang Island, a small island 500 metres off the coast of the Ujung Kulon peninsula, West Java, as a subspecies (*laronesiotes*) different from that on the mainland (*russa*). The difference resided entirely in the smaller size: condylobasal length of two adult males 282-290 mm, compared to a range of 312-328 mm on the mainland. Hoogerwerf (1970) pointed out that wildlife and much (if not all) of the vegetation of Peucang were almost certainly eliminated by a tidal wave following the colossal eruption of the volcano Krakatao in 1883; thus the deer population must have originated since then, by swimming across from the opposite mainland, and have either become very rapidly genetically dwarfed or, more likely given the New Zealand data, be phenotypically stunted (despite being a healthy, self-perpetuating population). Only breeding experiments can resolve this question. I may note that in 1978 I picked up a wild pig *Sus scrofa vittatus* skull on Peucang, fully mature and perfectly normal but in size way below the range for those from the mainland of Java (Groves, 1981a). Patton & Smith (1989) find much the same phenomenon in pocket gophers *Thomomys bottae*: environmental quality in this species affects size, but not shape parameters.

Developmental plasticity is likely, therefore, to be a very real phenomenon in some groups of ungulates and some other mammals, but its known effects are limited to size and correlated features (such as horn size). This reinforces the commonly-held notion that taxa described on the basis of size alone must always be regarded with some suspicion; on the other hand, since conservation of gene pools is in question, the null hypothesis should be that a described difference - even one of size - is genetically based until proven otherwise. There is clearly a need for breeding experiments along these lines: stocks of a given species from one region would be reared alongside stocks from a different region showing slight phenotypic differences. The identical conditions of rearing would allow determination of what genotypic differences actually do exist.

Material and methods

For taxonomic studies of gazelles going back to Groves (1969), I have studied specimens in museums all over the world, the most important collection being that held at the Natural History Museum, London - formerly the British Museum (Natural History). During my 1992 visit to the Arabian peninsula for the symposium on which this volume is based, I measured skulls of gazelles at the King Khalid Wildlife Research Center, Thumamah, Saudi Arabia, and at the Al-Areen Wildlife Park, Bahrain. I am most grateful to Dr Doug Williamson and Dr Jaime Samour, respectively, for these facilities.

Skin characters were noted (use of colour standards was abandoned as unexpectedly subjective), and skull measurements and observations were made as detailed in Groves (1969). The means, standard deviations and sample sizes of skull and horn measurements are given in Tables 2.2, 2.3 and 2.4.

A series of multivariate analyses, using SPSS Discriminant, was run on different subsets of these measurements. The graphs of first and second Discriminant Functions are shown in Figures 2.3 and 2.5, as follows: Figure 2.3 (a) *G. gazella* group, male cranial variables (variables 1 and 4-13) and (b) female cranial variables (same list), and (c) male horn variables (nos. 1-4); Figure 2.5, *G. saudiya* and *bennetti*, female (a) cranial and (b) horn variables (list numbers as above).

In order to test the PSC (Phylogenetic Species Concept) status of the taxa concerned, 27 skull and horn characters were coded and analyzed cladistically using Hennig86, version 1.5, then examined in detail with branch-swapping using MacClade. At the suggestion of Wilhelmus Rebholz (pers. comm.), *G. d. pelzelni* and other African subspecies of *G. dorcas* were included in the analysis. The characters used, their codes, and the data matrix are given in Table 2.5. The trees generated by this analysis are shown in Figure 2.6.

Results

- **Pelage:** *Gazella bilkis* is the darkest of the Arabian gazelles overall; *G. g. gazella*, *erlangeri* and *muscatensis* are probably equally dark on the dorsum, but are lighter on the face (so that the dark face stripes are conspicuous, which they are not in *G. bilkis*), and become suddenly lighter on the haunches. The white of the underside extends down the hindleg only to the hock in most specimens of *G. gazella*, but to the pasterns in *G. bilkis*. In *G. bilkis* there is a thin red stripe below the dark flank stripe; this does not occur in specimens of *G. gazella* as far as my experience goes.

G. g. cora is much lighter than other subspecies of this group; the haunch transition occurs, but is inconspicuous because of the much lighter overall body tone. It varies considerably in colour, from pale sandy to medium reddish fawn; the darker specimens have a well-marked but thin black flank-stripe, with a zone paler than the body colour just above it, the paler ones lack the light stripe and have the merest trace of a dark one. The forehead and midface are darker fawn to dark chestnut; a smudgy black nose-spot occurs in 11 out of 20 skins in the London collection, and 8 skins have a sprinkling of white hairs on the forehead.

Other members of the *G. gazella* group are darker coloured; dark fawn in *G. g. gazella*, and a very dark grey-brown, sometimes with a silvery sheen, in *erlangeri* and *muscatensis*, and by virtue of the dark hue the transition on the haunch to the fawn tone of the leg is more marked. The black flank-stripe is conspicuous, as is the lighter zone above it; there is a dark pygal band, of which barely a trace exists in *cora*. The face stripes are more clearly expressed than is usual in *cora*; the midface and forehead are dark brown in *gazella*, dark chestnut in the other two, and there is always a well-defined black nose-spot.

G. dorcas is coloured like *G. g. cora*, but the facial markings are clearer and sharper. The Saharan subspecies are often a very pale, sandy colour, but *G. d. isabella*, which is found along the Red Sea coast from Eritrea to the Negev, on the borders of Saudi Arabia, is darker and more reddish and commonly has a nose-spot; many skins of *G. d. isabella* could be mistaken for *G. g. cora*.

G. saudiya averages lighter, more sandy brown, than *G. dorcas*; there is scarcely any trace of a flank stripe, and the face stripes are not sharply differentiated. The white face stripes and the white of the underside are suffused with fawn tones.

The type (and only known) skin of *G. arabica* is medium to dark red-brown, comparable to darker specimens of *G. g. cora*; Neumann (1906) seems to have overdone the "strong red" part of his description, unless the specimen has lost this tone in the meantime. There is a dark grey flank band with a trace of a red-brown stripe beneath it, and the white goes down the inside of the hindleg to the pasterns; in these features it resembles *G. bilkis* but it is by no means as dark or as uniform; most importantly, it has a striking transition between dark dorsal and light limb tones on the haunch.

All subspecies of *G. subgutturosa* are characterized by yellowish body tones without strong markings, and by the invasion of the midfacial region by white with maturity. *G. s. marica* is very pale in colour; *G. subgutturosa* specimens from Iraq, which are as small as *G. s. marica*, are however the same darker, yellow-brown colour as Iranian *G. s. subgutturosa*. It remains to be determined whether the Iraqi populations form a stable race, or are simply intergrades between peninsular and Iranian subspecies.

- **Horns:** Horn shape in the male differs characteristically between taxa. Horns of *G. subgutturosa* and *G. dorcas* bow outward, then turn in (and forward) at the tips; *G. g. cora* and *muscatensis* show the same form to a lesser degree (in Table 2.2, note that the span in the male in *cora* is greater than in *gazella*, but the tip-to-tip distance is less). *G. g. gazella* and *erlangeri*, *G. saudiya*, *G. bilkis* and *G. arabica* males have horns that are straighter, little if at all bowed outward: indeed, those of the type of *G. arabica* are slightly turned out at the tips, and those of *G. bilkis*, shorter than in *G. g. gazella*, are nearly parallel. In the females of *G. g. gazella* and *cora*, the horns tend to be rather short and fragile, easily broken; they are longer in *G. g. erlangeri* and *muscatensis*, and even more so in *G. bilkis*.

Table 2.2 Skull/horn measurements of taxa of the *G. gazella* group.

(1) MALES

Variable	<i>gazella</i> n=23	<i>cora</i> n=20	<i>erlangeri</i> n=4	<i>bilkis</i> n=2	Thumamah n=7
Horn length, straight	243.5	219.3	215.0	229.0	254.9
s.d.	16.23	18.57	18.98	-	18.01
Tip-to-tip (ditto)	91.0	87.7	102.0	69.0	97.7
s.d.	20.06	19.95	16.12	-	15.18
Greatest span across horns (ditto)	120.5	134.4	119.0	94.5	108.4
s.d.	12.81	12.80	16.11	-	14.40
Greatest width across bases of horn	67.2	65.0	60.5	66.5	65.0
s.d.	2.66	2.11	3.87	-	2.16
Width of nasal bones (anterior)	24.3	20.3	22.3	24.0	21.7
s.d.	1.40	1.80	1.26	-	1.11
Width of nasal bones (posterior)	27.7	22.5	24.0	26.0	23.7
s.d.	2.01	1.85	2.83	-	1.80
Greatest length of nasal bones	47.0	46.5	42.5	41.0	46.3
s.d.	4.65	5.15	8.88	-	3.99
Greatest skull length	191.1	184.5	178.5	191.0	190.3
s.d.	5.02	5.99	3.70	-	2.69
Greatest skull breadth (biorbital)	89.9	81.6	81.3	87.0	84.9
s.d.	2.53	2.28	4.92	-	3.13
Preorbital skull length	96.6	95.0	88.0	98.0	96.3
s.d.	2.45	3.97	4.08	-	2.29
Palate width (outside molars)	53.2	45.6	47.5	52.5	52.1
s.d.	2.21	2.14	2.65	-	1.86
Braincase width	61.2	60.1	56.8	63.5	56.9
s.d.	2.42	2.34	4.11	-	1.21
Braincase length (nasion to inion)	111.5	104.3	99.3	110.0	108.4
s.d.	4.21	4.55	4.57	-	3.41

(2) FEMALES

one *G. g.*

s.d.

Variable	<i>gazella</i> n=8	<i>cora</i> n=2	<i>erlangeri</i> n=3	n=	
Horn length, straight	97.1	104.0	125.0	144.5	
s.d.	19.05	-	17.35	7.64	
Greatest width across bases of horn	52.0	51.5	50.3	56.3	
s.d.	1.60	-	1.53	1.53	
Width of nasal bones (anterior)	20.9	19.0	17.3	20.7	
s.d.	2.47	-	0.58	1.15	0.5
Width of nasal bones (posterior)	23.4	21.5	19.0	22.7	20.5
s.d.	2.33	-	1.73	0.58	0.58
Greatest length of nasal bones	46.5	46.5	44.3	48.0	47.0
s.d.	3.96	-	8.50	2.65	5.35
Greatest skull length	181.0	172.0	168.7	188.7	178.5
s.d.	4.41	-	10.02	2.52	5.57
Greatest skull breadth (biorbital)	82.7	77.0	75.7	84.7	78.8
s.d.	3.96	-	2.52	0.58	2.63
Preorbital skull length	93.1	90.0	84.7	99.3	92.5
s.d.	3.56	-	7.64	1.15	3.32
Palate width (outside molars)	52.0	47.0	44.7	51.7	47.5
s.d.	7.17	-	3.21	1.53	1.73
Braincase width	57.5	54.5	55.3	61.0	52.3
s.d.	1.85	-	2.52	2.65	1.50
Braincase length (nasion to inion)	100.9	92.0	93.3	103.3	96.0
s.d.	3.00	-	4.16	1.15	2.94

In the skulls from the Thumamah breeding stock, the horns of the males are on average longer than in any other sample of the *G. gazella* group, and more nearly parallel than any but *G. bilkis*. The horns of females are shorter than in *G. bilkis* but longer than in *G. gazella* except for *erlangeri*.

The distance across the horn bases is broad in *G. g. gazella*, *G. g. cora* and *G. bilkis* (Table 2.2).

G. dorcas isabella has bowed horns remarkably similar to those of *G. g. cora*, but longer in the female. The near identity in horn shape recalls the great external similarity in general (Figure 2.1). In contrast, the horns of *G. saudiya* are very long and straight in both sexes, with very little inturning at the tips; they are not very divergent, resembling in this respect the horns of most subspecies of *G. bennetti* (Table 2.4), but are narrower across the bases.

The horns are closely ringed in the male, with more than 20 rings, in *G. subgutturosa* and *G. saudiya*; in the latter the rings are more prominent than in most Arabian gazelles. The rings are much fewer in number, 12-15, in *G. g. muscatensis*, *G. bilkis* and *G. arabica*, with about 15-20 in the other forms.

Horn shapes in Arabian gazelles are well illustrated in Morrison-Scott (1939, Plate VI); the specimens figured could hardly have been better selected to illustrate the manner in which the range of variation within a taxon, considerable though it may be, does not obliterate the differences between taxa. In this plate are figured three male and one female *G. saudiya* (Figures 1-3 and 10, respectively); one adult and one subadult male *G. s. marica* (Figures 14 and 15 respectively); seven male and one female *G. g. cora* (Figures 4-9 and 13, and 11 respectively, all captioned "*G. arabica*");



Figure 2.2a



Figure 2.2b

Figure 2.2 Naso-frontal suture shapes of **a)** *Gazella dorcas dorcas* (BM 1939.2560, from Aïr, Niger); **b)** *Gazella gazella cora* (BM 40.289, from Dhalm, Saudi Arabia).

two adult male and one adult female *G. g. muscatensis* (Figures 16-17 and 12 respectively); one *G. g. erlangeri* (Figure 18) and one *G. bilkis* (Figure 19). For comparison, two male and two female *G. d. isabella* are figured by Ferguson (1981, Figure 1, though some are incorrectly identified as *G. d. dorcas* or inter-subspecific hybrids).

- **Horn Cores:** The horn cores in males are longitudinally grooved. In *G. dorcas* the 3-4 grooves on the anterior face are short (restricted to the proximal end) and shallow, their edges bevelled; on the posterior face there are one or two deeper, sharp-edged grooves which run for most of the length of the core. In *G. gazella* the anterior grooves are somewhat deeper and broader. In *G. subgutturosa* the anterior grooves are longer, and there is a deep, more sharp-edged groove on the antero-lateral corner; there are two exceedingly deep, sharp-edged grooves on the posterior surface. It was not possible to take off the sheaths of any other species to examine the grooves.

The cores in male *G. subgutturosa* are close together (Figure 2.6). They are also very stout basally, so that their medial edges are even closer together. Other species have more widely spaced horns: width across the bases is relatively greater in *G. gazella* and its relatives than in *G. dorcas* and *G. saudiya* (Figure 2.6).

- **Skull:** Table 2.2 records skull measurements (means and standard deviations) in the *G. gazella* group - *muscatensis* excepted, because despite a fair sample of this taxon most specimens are incomplete, only a single adult male and female skull being available.

G. g. cora differs from *G. g. gazella* in both sexes in that the nasals are much narrower, especially posteriorly, and the skull is shorter, primarily due to the shorter braincase, and narrower; the palate is much narrower.

G. g. erlangeri in the male differs from *gazella* in that the nasals are slightly narrower and much shorter, and the skull is shorter (both pre- and postorbitally) and narrower. Compared to *cora*, the nasals are slightly broader, much shorter; the skull is shorter but no narrower, the palate being actually broader in the male.

In *G. bilkis*, compared to *G. g. gazella*, the nasals are slightly less broadened posteriorly, and much shorter; the female, but not the male, is larger. Compared to *cora* the nasals are broader and much shorter, and the skull is much longer (especially postorbitally), and broader. Compared to *erlangeri* the nasals are slightly broader, and the skull is much longer and broader.

Male skulls of the Thumamah "idmi" stock are narrower than *G. g. gazella*, with much narrower nasals, and a slightly shorter, considerably narrower braincase (Table 2.2). The female skulls are slightly shorter than *G. g. gazella*, and have somewhat longer, narrower nasals. They have a broad palate and narrow braincase compared to *cora*, and the nasals are narrower in the female, especially anteriorly. The nasals are much longer and narrower than in *G. bilkis*, and the skull, especially the braincase, is rather narrower.

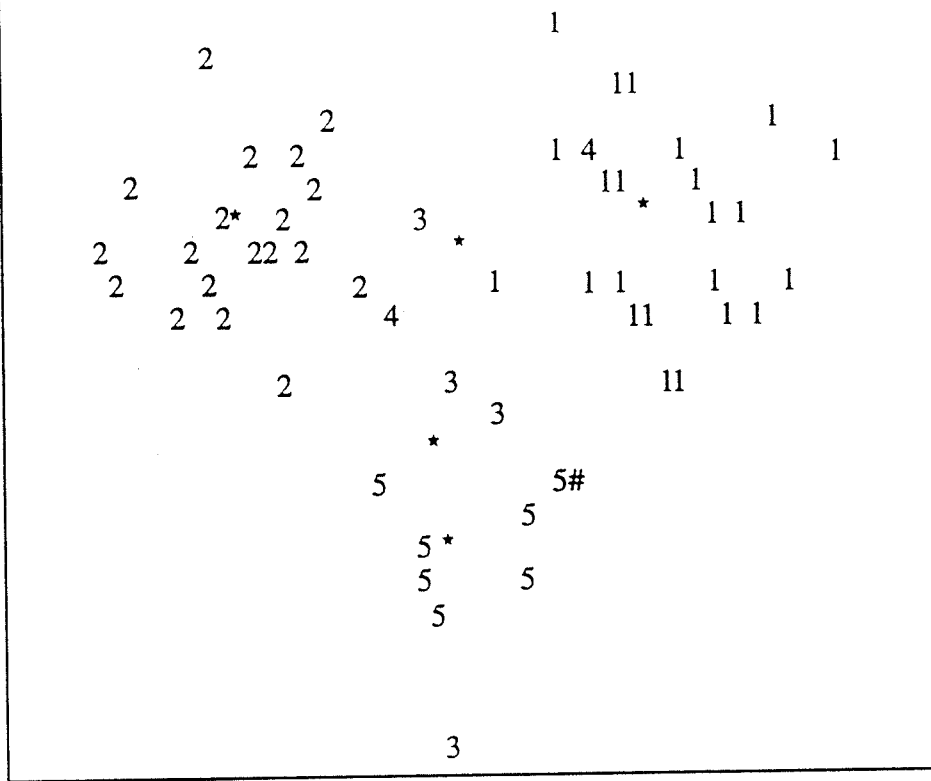


Figure 2.3a

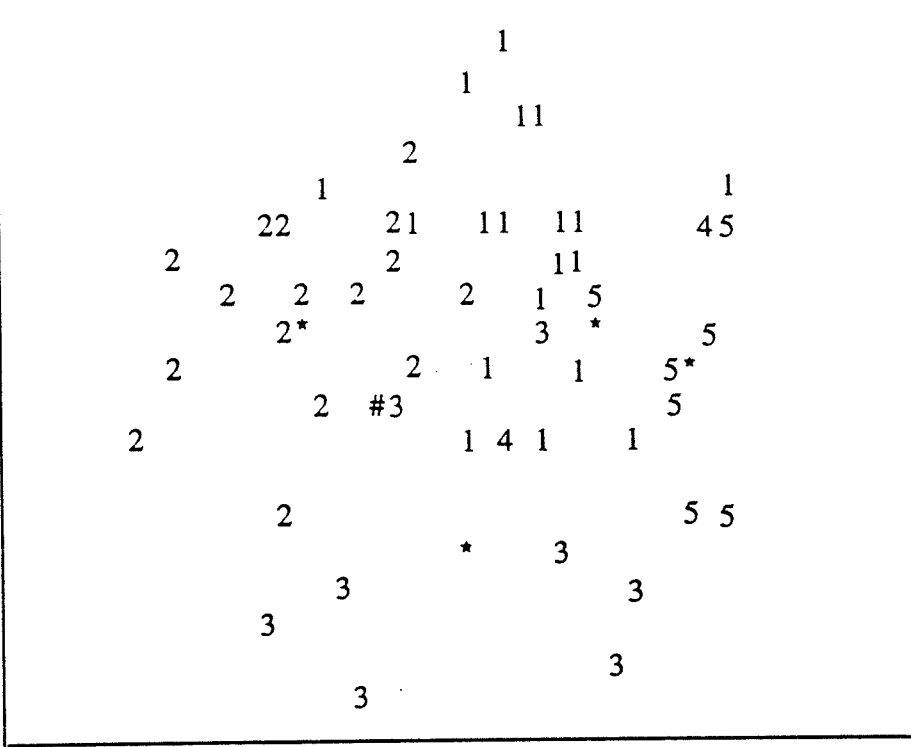


Figure 2.3b

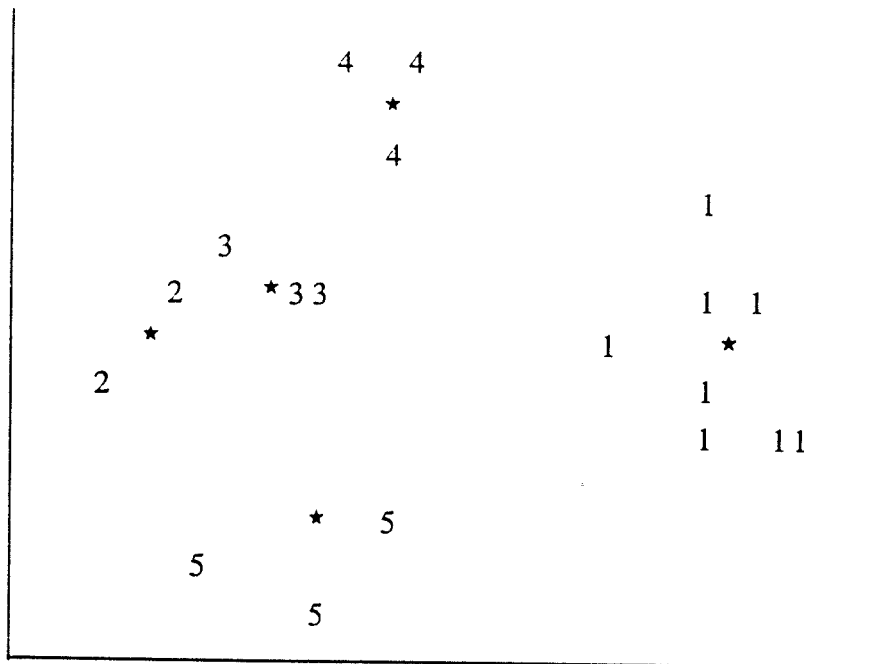


Figure 2.3c

Figure 2.3 Discriminant Function analysis of skull and horn measurements of the *G. gazella* group. In all comparisons, abscissa is Function 1, ordinate is Function 2. a) Skull and b) horn measurements of males; c) skull measurements of females. 1 = *gazella*, 2 = *cora*, 3 = *erlangeri*, 4 = *bilkis*, 5 = *idmi* from KKWRC, Thumamah.

Measurements of *G. dorcas isabella*, a species that may occur within the Kingdom (see below), are given in Table 2.3. The skull is strikingly similar metrically to that of *G. gazella cora*.

Table 2.3 Skull/horn measurements of *G. dorcas isabella*.

Variable	Male n=26		Female n=11	
	Mean	s.d.	Mean	s.d.
Horn length, straight	218.1	16.61	173.1	11.04
Tip-to-tip (ditto)	84.2	25.43	87.4	24.92
Greatest span across horns (ditto)	138.2	19.11	109.4	23.16
Greatest width across bases of horn	61.5	2.30	53.0	1.94
Width of nasal bones (anterior)	20.1	1.69	18.9	1.01
Width of nasal bones (posterior)	20.4	2.34	19.7	1.68
Greatest length of nasal bones	45.2	3.46	45.8	3.73
Greatest skull length	179.7	4.41	173.8	3.90
Greatest skull breadth (biorbital)	80.5	2.53	76.4	1.74
Preorbital skull length	90.3	2.77	89.6	2.35
Palate width (outside molars)	45.9	1.18	44.9	0.93
Braincase width	58.5	2.05	56.0	1.32
Braincase length (nasion to inion)	100.7	3.53	93.2	2.77

G. saudiya is compared in Table 2.4 with two subspecies of *G. bennetti*, both newly described from Iran, including the very small sized *G. b. karamii* from the Bushehr district. The skull is narrower than in any *G. bennetti*, both biorbitally and across the palate but not across the braincase, and very narrow across the nasals which are always narrower posteriorly than anteriorly. Male and female skulls of *G. saudiya* are illustrated in Figure 2.4.

In non-metrical features, there are a few characteristic differences among members of the *G. gazella / dorcas* complex. Most consistent is the shape of the naso-frontal suture, which is arrow-shaped in *G. dorcas* but rounded-arch-shaped in *G. gazella* (Figure 2.2); this is one of the few features in which *G. g. cora* resembles other members of the *G. gazella* group rather than *G. dorcas*. In *G. saudiya* the shape is essentially as in *G. dorcas*; in *G. bennetti* it is similar but somewhat less markedly wedge- or arrow-shaped. Skull differences of *G. bilkis* from *G. gazella* (and *G. dorcas*) are described and figured by Groves & Lay (1985).

G. subgutturosa always has a large long-oval vacuity in the lacrimal bone, of unknown function. It is also consistently present in *G. bennetti*, *G. saudiya* and, unexpectedly, in *G. bilkis* (also in *G. leptoceros* and *G. cuvieri*). The occasional presence of a small vacuity in *G. gazella* is recorded.

Table 2.4 Skull/horn measurements of taxa of the *G. bennetti* group.

(1) MALES

Variables	<i>G. b. shikarii</i> n=5	<i>G. b. karamii</i> n=1	<i>G. saudiya</i> n=6/8
Horn length, straight	255.8	228	268.8
s.d.	28.26	-	18.35 (6)
Tip-to-tip (ditto)	141.3	190	101.8
s.d.	31.50	-	24.29 (6)
Greatest span across horns (ditto)	156.2	210	115.0
s.d.	27.08	-	21.19 (6)
Greatest width across bases of horn	63.0	58	56.3
s.d.	3.08	-	2.14 (7)
Width of nasal bones (anterior)	22.9	21	18.6
s.d.	1.25	-	0.98 (7)
Width of nasal bones (posterior)	24.4	22	17.6
s.d.	1.80	-	0.79 (7)
Greatest length of nasal bones	54.8	41	42.4
s.d.	3.40	-	3.89 (8)
Greatest skull length	192.4	173	172.8
s.d.	2.88	-	3.06 (6)
Greatest skull breadth (biorbital)	85.7	84	77.8
s.d.	2.08	-	1.68 (7)
Preorbital skull length	97.0	-	86.5
s.d.	3.26	-	1.05 (6)
Palate width (outside molars)	49.8	49	44.6
s.d.	1.30	-	1.27 (7)
Braincase width	63.7	58	57.5
s.d.	2.59	-	1.60 (8)
Braincase length (nasion to inion)	103.4	98	97.6
s.d.	5.04	-	3.15 (7)

(2) FEMALES

Variable	<i>G. bennetti</i> (mixed) n=7(horns)/10(crania)	<i>G. saudiya</i> n=6	Bahrain n=1
Horn length, straight s.d.	165.9 38.12	209.7 21.75	238
Tip-to-tip (ditto) s.d.	66.1 15.71	73.0 34.51	102
Greatest span across horns (ditto) s.d.	80.6 13.87	85.8 28.94	114
Greatest width across bases of horn s.d.	52.3 2.21	48.7 2.16	49
Width of nasal bones (anterior) s.d.	21.0 1.76	17.8 0.75	21
Width of nasal bones (posterior) s.d.	21.9 2.02	15.8 0.41	20.5
Greatest length of nasal bones s.d.	49.2 5.65	40.3 3.67	50
Greatest skull length s.d.	179.7 6.11	164.0 3.95	174
Greatest skull breadth (biorbital) s.d.	81.2 2.70	70.8 1.33	81
Preorbital skull length s.d.	92.6 3.66	85.2 2.71	88
Palate width (outside molars) s.d.	48.3 1.70	43.0 2.00	46
Braincase width s.d.	59.5 2.55	52.5 3.15	55
Braincase length (nasion to inion) s.d.	95.5 3.06	91.5 2.74	91

The premaxilla always ascends the margin of the nasal aperture to some degree, and may actually reach and suture with the nasal. It usually fails to meet the nasal in *G. g. gazella*, *muscatensis* and *bilkis*, and in the skull of *arabica*, but usually does meet the nasal in other taxa.

The anterior ends of the nasals are abruptly truncated in the genus *Gazella* (and in *Antilope*), and have lateral flanges. The median tips are recessed to or behind a line joining the tips of the lateral flanges in most Arabian taxa and some others, but not usually in *G. g. gazella* or *erlangeri*, and not in the type skull of *G. arabica*. This is perhaps connected with the puffy dorsal inflatability of the nasal cavity, which is so noteworthy in the north-east African *G. spekei* but can be detected in some other taxa as well.

The supraorbital foramina, generally sunk into triangular pits at the bases of the horns, are commonly multiple in *G. subgutturosa*, also in *G. arabica* and some non-Arabian species such as *G. bennetti*, but not, as far as the data go, in other Arabian taxa.

Canonical analyses of skull and horn measurements in Arabian gazelles were depicted in Groves (1989), and new analyses, designed to examine the affinities of the KKWRC "idmi" group and of the Al-Areen breeding group assigned to *G. saudiya*, are shown in Figures 2.3 and 2.5. Briefly, *G. g. gazella* and *cora* are well-distinguished, with *erlangeri* somewhat intermediate but (especially as far as the females are concerned) closer to *cora*; *G. bilkis* is close to *G. g. gazella* in the male, rather separate in the female; and the KKWRC specimens segregate independently, overlapping

(in the males) with *erlangeri*. The reputed *saudiya* of Al-Areen does indeed assort with *G. saudiya*, not with *G. bennetti*.

The cladistic analysis generated a single most parsimonious tree, of length 124 and consistency index 41, but there proved to be trees of almost equal length when this was modified using MacClade (Figure 2.6). In the first of the cladograms generated by Hennig86 (Figure 2.6a), in some agreement with the descriptive observations above, a comb-like tree is produced, with *dorcas*, *osiris*, *isabella* and *pelzelni* branching successively off the main stem leading to the *G. gazella* group. In this tree, the similarities between *isabella* and *cora* are evidently to be interpreted as plesiomorphic. The Thumamah taxon branches off next; but this may be an artefact of its incomplete data set. The terminus of the branch is a bifurcation between *bilkis* and *arabica*. The initial split is between *bennetti* on the one hand, and the *subgutturosa / saudiya* and *gazella / dorcas* groups on the other.

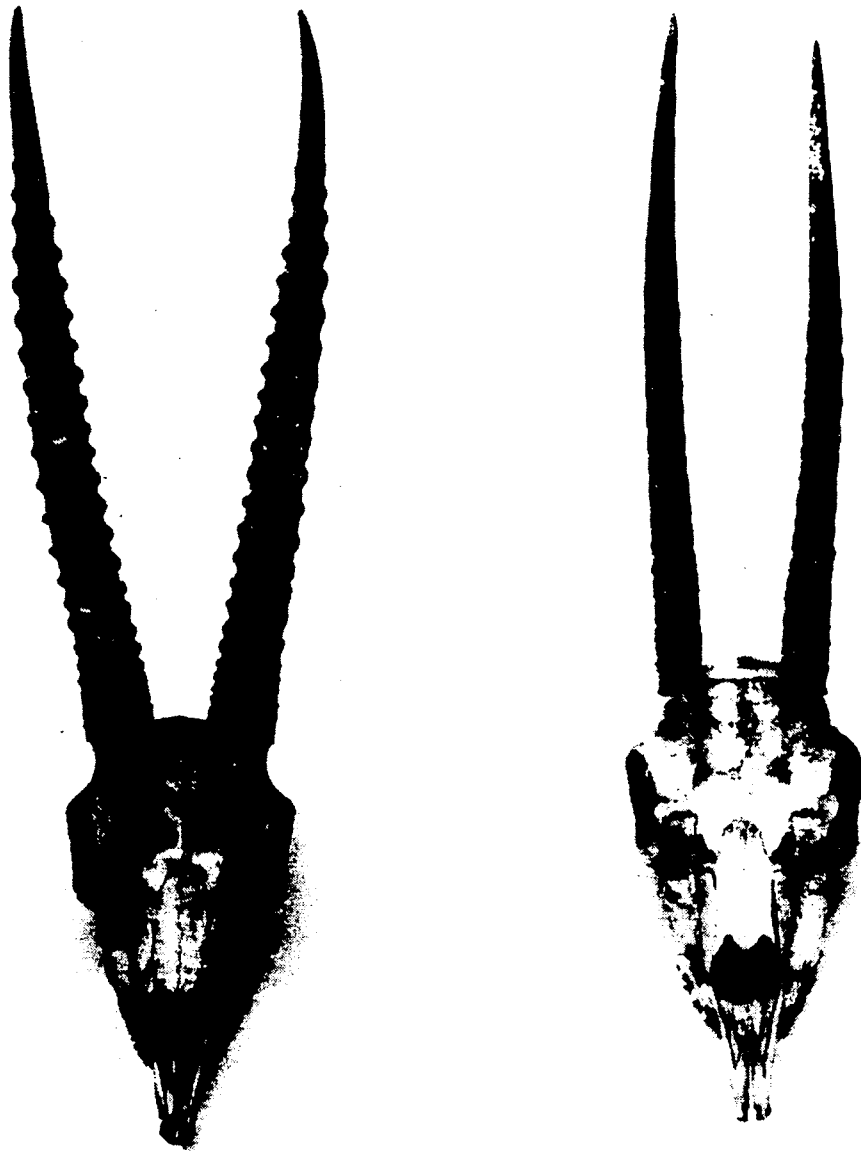


Figure 2.4 Skulls of *Gazella saudiya* (left) male, BM 40.303, from Wadi Markha and (right) female, BM 40.305, from Arq Abu Da'ir.

In the two other equally parsimonious trees, the subspecies of *G. dorcas* except for *pelzelni* are on a single branch together, thus dissolving the peculiar *isabella / cora* affiliation; one (Figure 2.6b) retains the comb-like asymmetry of *pelzelni* plus the *gazella* group; the other (Figure 2.6c) places *gazella* and *muscatensis* in a branch of their own.

Table 2.5 Data set for cladistic analysis of Arabian gazelles.

(a) Character description

0 - nasofrontal suture:	0 - wedge, 1 - arch
1 - lacrimal fenestra:	0 - usually no, 1 - yes
2 - premaxilla:	0 - usually contacts nasal, 1 - usually not
3 - median nasal tip:	0 - longer than lateral flanges, 1 - shorter
4 - supraorbital foramen:	0 - single, 1 - multiple
5 - horn rings:	0 - less than 15, *1 - 16-20, 2 - more than 20
6 - female horn length:	0 - >skull length, *1 - 85-100%, 2 - 70-85%, 3 - <70%
7 - (male) horn span:	0 - <50% of horn length, *1 - 50-60%, 2 - 60-70%, 3 - >70%
8 - (male) horn tip-to-tip distance:	0 - >85% of span, 1 - 65-85%, 2 - <65%
9 - nasal length:	0 - >27% of skull length, 1 - 22-27%, 2 - <22%
10 - nasal width (posterior):	0 - <45% of nasal length; *1 - 45-53%, 2 - 53-60%, 3 - >60%
11 - anterior nasal width:	0 - <90% of posterior width, 1 - 90-100%, 2 - >posterior width
12 - preorbital length:	0 - >98% as long as postorbital, 1 - 90-98%, 2 - <90%
13 - braincase width:	0 - >58% of braincase length, 1 - <58%
14 - palate breadth:	0 - <50% of preorbital length, 1 - 50-55%, 2 >55%
15 - horn ring prominence on anterior surface	0 - very prominent, 1 - prominent, well-spaced, 2 - closer together, 3 - poorly expressed, close together
16 - longitudinal ridges between horn rings	0 - none, 1 - barely visible, 2 - fairly well-marked
17 - anterior angulation of horn rings:	0 - absent (rings circular), 1 - slight
18 - posterior prominence of rings:	0 - just as prominent as on anterior surface, 1 - less so
19 - posterior angulation of rings:	0 - absent, 1 - slight, 2 - strongly expressed
20 - preorbital fossa:	0 - deep, 1 - less so, 2 - shallow
21 - lacrimal bone:	0 - not, or hardly, extending into preorbital fossa, 1 - extends into about one-quarter of fossa, 2 - about one-half
22 - ethmoid fissure:	0 - long, slit-like, 1 - broader, 2 - triangular or block-like
23 - ventral premaxillary ridges:	0 - strongly raised, crest-like, 1 - simple, ridge-like, 2 - very weak, not extending to level of premolars
24 - premaxillary tips:	0 - broad, shovel-like, 1 - rounded-pointed
25 - female skull length:	0 - >97.5% of male, 1 - 95-97%, 2 - <95%
26 - male horn length:	0 - >140% of skull length, 1 - 130-140%, 2 - 125-130%, 3 - <125%

* indicates primitive state; otherwise, 0 is primitive.

(b) Character state matrix

<i>*ruffrons</i>	00000111001000001100000000
<i>subgutturosa</i>	010112032012101111010121013
<i>bennetti</i>	010011120002101100021102102
<i>saudiya</i>	01010200010320110002112?113
<i>isabella</i>	000101122112201311111221110
<i>gazella</i>	101000311120212221112221021
<i>cora</i>	100101322111110311112221120
<i>erlangeri</i>	100001210121212311002211111
<i>muscatensis</i>	101101332230201221002221120
<i>bilkis</i>	111100201231211201112111000
<i>arabica</i>	101010?002332112011121110?2
Thumamah	100001300111211?????????22

* outgroup

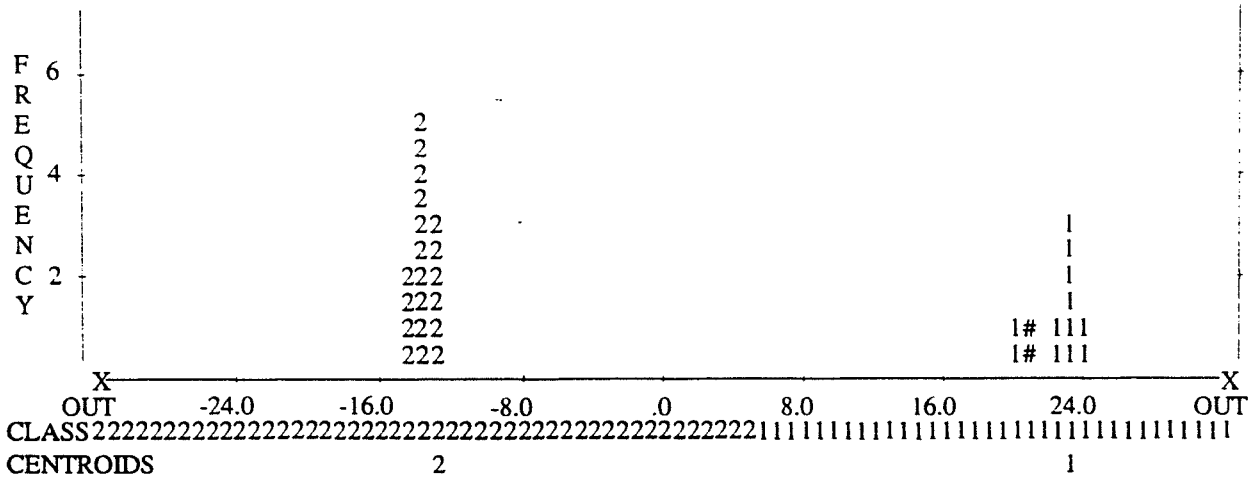


Figure 2.5a

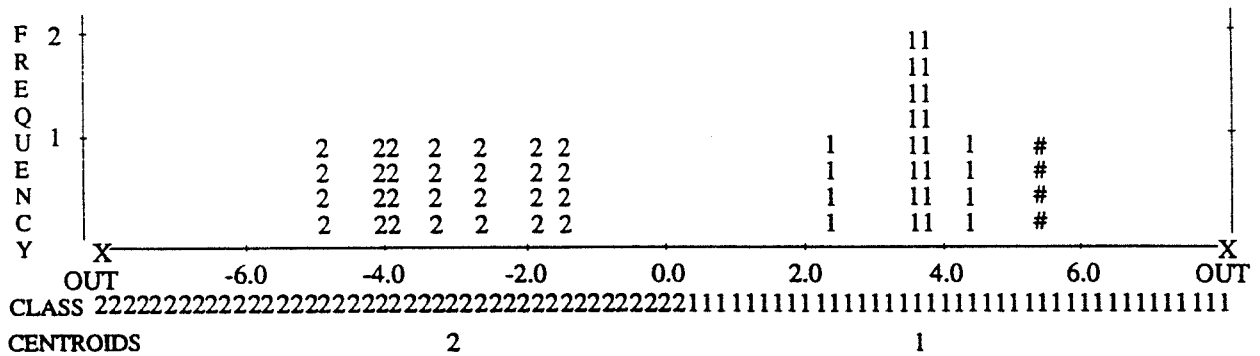
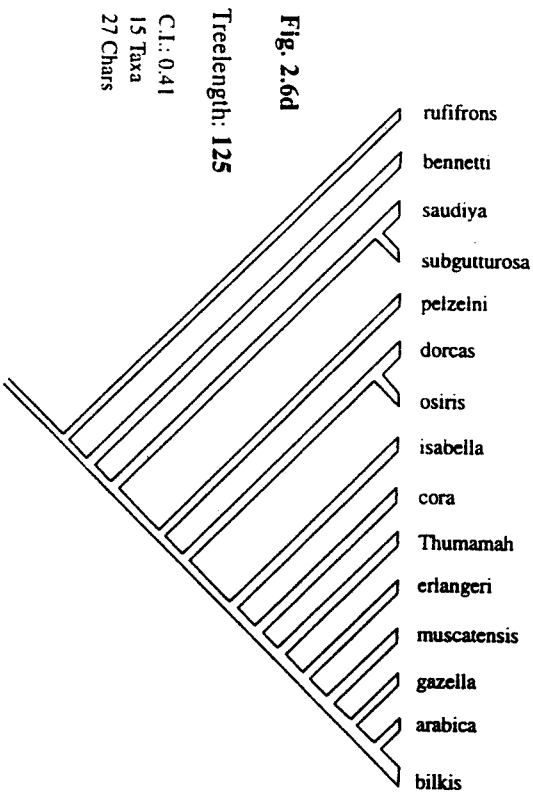
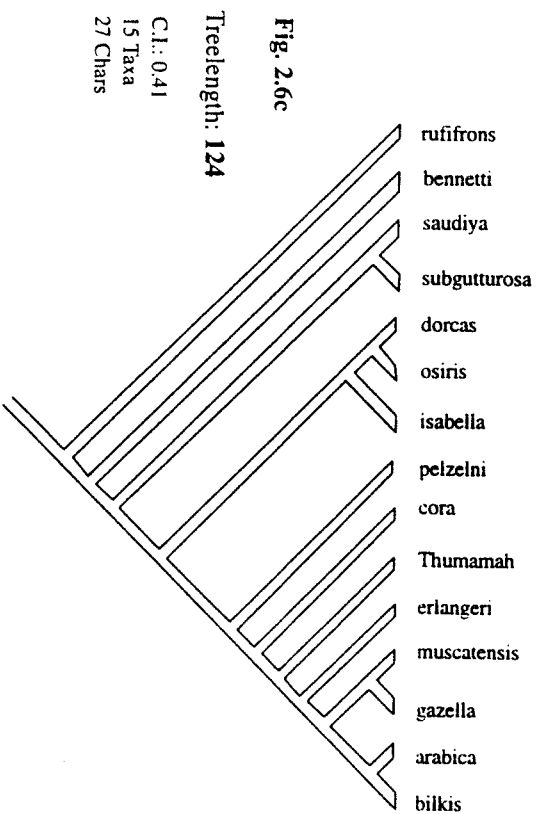
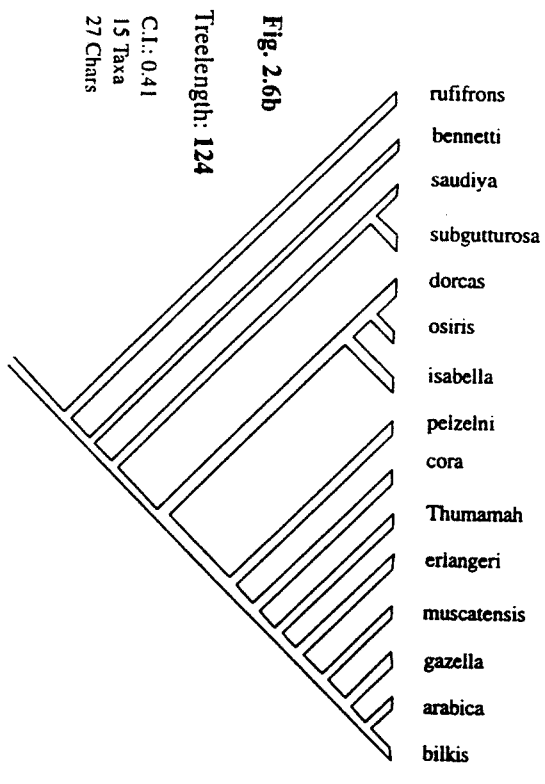
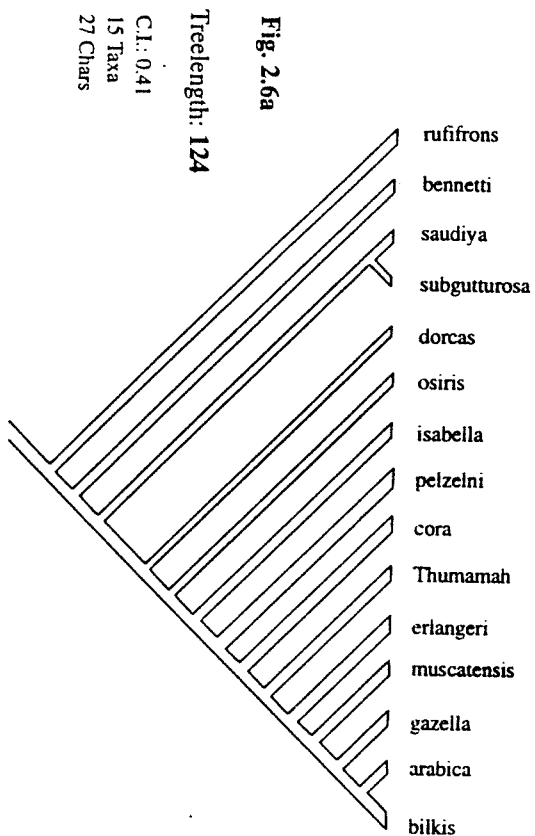


Figure 2.5b

Figure 2.5 Discriminant Function analysis of *Gazella saudiya* and *G. bennetti* female a) skulls and b) horns. 1 = *saudiya*, 2 = *bennetti*, # = skull from Al-Areen, Bahrain



ASSUMPTIONS ABOUT CHARACTERS
TRANSFORMATION TYPES:
Char #: 1234567890 1234567890 1234567
Types: rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr

ASSUMPTIONS ABOUT CHARACTERS
TRANSFORMATION TYPES:
Char #: 1234567890 1234567890 1234567
Types: rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr

Figure 2.6a-d

By branch-swapping, using MacClade, three trees were found with a length of 125, one step longer than the first three, but with the same consistency index. The first of these (Figure 2.6d) retains the asymmetry of the shorter trees, but returns *isabella* to the stem leading to the *gazella* group, and makes *pelzelni* the sister taxon to the entire *dorcas* / *gazella* clade. The second (Figure 2.6e) places the *bilkis* / *arabica* branch as sister-group to all the *G. gazella* group except *erlangeri*, and unites *cora* with *muscatensis*, *gazella* with the Thumamah taxon. The third (Figure 2.6f) puts *erlangeri* on the *bilkis* / *arabica* stem.

To reunite *pelzelni* with other subspecies of *G. dorcas* requires an increased tree length of 126, and a slightly lower consistency index. When this is done, either *cora* is the sister species to the rest of the *gazella* group, and *G. g. gazella* is part of the *bilkis* / *arabica* cluster (Figure 2.6g), or it falls within the *G. dorcas* cluster, as sister group to *isabella* (Figure 2.6h). In either case, Thumamah can be added to the *gazella* / *bilkis* / *arabica* cluster at no extra cost.

Interestingly, *G. subgutturosa*, with a low chromosome number like *G. dorcas* and *G. gazella*, cannot be added to their branch with a tree length below 127. Placing *G. bennetti* and *G. saudiya* on a branch together requires a tree length of at least 128, though the consistency index is still 40.

- **Body Build:** *G. bilkis* appears more sturdily built than other Arabian gazelles, and *G. g. cora* more slenderly; but in the absence of extensive external measurements it is difficult to quantify this. Harrison and Bates (1991) and Mendelssohn and Yom-Tov (1987) give some measurement data (Table 2.6). For their size *G. saudiya*, and to a lesser extent *G. s. marica*, clearly have extremely large ears; they appear to be short-legged, but the above measurements suggest that the difference is in the hind limbs, which are elongated in *G. gazella* (as represented by *G. g. muscatensis*) but not in the other two species. *G. s. marica* also has a relatively longer tail.

Table 2.6 Body build measurements for Arabian gazelles (data for both sexes combined).
Data from Harrison and Bates (1991) and Mendelssohn and Yom-Tov (1987).

	Head+Body length	Tail length	Hindfoot length	Ear length	Shoulder height
<i>gazella</i> (19-20)	1016.5	105	.*	117.5	-
<i>cora</i> (1)	1041	-	-	120	610
<i>muscatensis</i> (2)	943.5	105.5	276.5	114.1	559
<i>saudiya</i> (1)	928	90	255	123	600
<i>marica</i> (1-2)	966.5	152	272	125	-

* Note: hindfoot lengths given by Mendelssohn and Yom-Tov are not comparable to those given by Harrison and Bates.

Skeletal postcranial measurements are available only for *G. g. gazella*, *G. dorcas isabella*, *G. s. subgutturosa* and a single reputed *G. saudiya* (author's data). The last of these is in the collection of Al-Areen Wildlife Park, Bahrain. These data are given in Table 2.7 (sexes combined). As far as these measurements can be extended to the Arabian peninsula representatives of their respective groups, this appears to confirm that *G. gazella* have elongated hindlimbs compared to forelimbs, but shorter distal segments; *G. saudiya* is generally short-legged; *G. subgutturosa* has elongated metapodials but not an elongated tibia.

Table 2.7 Skeletal postcranial measurements for certain Arabian gazelles
(data from both sexes combined).

	Humerus length	Foreleg: hindleg	Tibia: femur	Metatarsal: femur	Hindleg: skull
<i>gazella</i> (20)	125	78	127	100	302
<i>dorcas</i> (11)	119	81	133	111	314
<i>saudiya</i> (1)	116	80	130	109	298
<i>subgutturosa</i> (10)	125	81	127	109	290

Discussion

It is probable that, according to a Phylogenetic Species Concept, all the following taxa would be regarded as separate species: *saudiya*, *arabica*, *bilkis*, *erlangeri*, *gazella*, *muscatensis*, and *cora*. The status of *marica* vis-à-vis *G. subgutturosa* was not tested, but both morphologically (Groves & Harrison, 1967) and genetically (Kingswood *et al.*, this volume) there is ample reason to regard it as part of the same species. Similarly, there seems little doubt that *isabella* and other forms of *G. dorcas* are conspecific (Groves, 1981b). As little other than metrical data was collected on the Thumamah crania, the position of this quasi-taxon on the cladogram remains somewhat hypothetical. The status of the other taxa will be discussed in turn.

- **Status of *Gazella saudiya*:** That *Gazella saudiya* is totally distinct from *G. dorcas* is confirmed; as Rebholz *et al.* (this volume) have concluded, it is much closer to *G. bennetti*. It would be difficult to propose uniting them specifically, however. Metrically, *G. saudiya* falls outside the range of variation of *G. bennetti*, and the skull is a different shape from the similarly small-sized *G. b. karamii* (Table 2.4). In addition it shares some derived states with *G. subgutturosa* which are not seen in *G. bennetti* (Figure 2.6): nasal tip shortening, ethmoid fissure shape, greater sexual size difference, horn length in both sexes, more horn rings. Unless the polarities of these characters are incorrect, or there is an unsuspected degree of homoplasy, this does imply that *G. bennetti* and *G. saudiya* may not be sister species.

A question that must be asked is whether the Al-Areen (Bahrain) breeding group, phenetically resembling *G. saudiya*, is pure-bred or has been mixed with *G. bennetti* (see Rebholz *et al.*, this volume, for discussion). The only detailed evidence is the morphology (mainly craniometry) of a female specimen made available courtesy of Dr Jaime Samour, formerly of the Al-Areen Wildlife Park. This specimen (Table 2.4) is considerably larger than wild-collected *G. saudiya* in the Natural History Museum, London (the only existing study sample), but is in proportion; compared to *G. bennetti*, it has a narrow skull, especially the braincase and across the horn bases, and the nasals are narrower posteriorly than anteriorly. The horns are extremely long, like *G. saudiya*, and spread more widely than either (on average), though they would be easily within the 2-standard-deviation limits of *G. saudiya*; but it must be borne in mind that the female of *G. bennetti karamii*, whose horns are exceptionally widely flared for that species, is unknown. In Figure 2.5 this skull, entered as an unknown in a Discriminant Analysis comparing *G. bennetti* and *G. saudiya*, falls within the range of the latter, confirming its identity in shape.

There is consequently only one character in which the Al-Areen specimen falls outside the expected range of *G. saudiya*: absolute size. It is possible that this is an effect of captivity (see the discussion above on subspecies and phenotypic plasticity); it is also possible that it derives from a population outside the known area of distribution of *G. saudiya* (Appendix 2.1).

On my first visit to Al-Areen, in 1987, the breeding group now called *G. saudiya* were listed as "Qatari *subgutturosa*". This implies that they had originated from Qatar, but no-one at Al-Areen had any record of their date of arrival or their origin. Dr Faris Al-Timimi (Doha, Qatar) informed the group visiting him (Drs Rebholz and Sayeed, Mr Kitchenside and myself) in November, 1992 that there are gazelles, of unknown species and origin, in a free-ranging government-owned facility in the north of Qatar, and that gazelles reputed "Qatari" in other countries are likely to be from there. If this is the case for the Al-Areen group, it re-opens the possibility that some of them may be of mixed stock. There is an urgent need to study this stock intensively; all skeletal remains should be saved, and breeding records should be kept so as to see whether matings between animals of different karyotypes (see Rebholz *et al.*, this volume) are associated with reduced fertility.

- *Gazella arabica* and *Gazella bilkis*: These two species are very close (Groves, 1987: Figures 1, 2; this paper, Figure 2.6), though not identical; they are not dissimilar in pelage characters either. The cladistic analysis always links them. A case could be made for uniting them conspecifically.

- Is *Gazella "gazella" cora* related to *Gazella dorcas*? The "spoilers" in many of the cladograms, rendering *Gazella gazella* polyphyletic, are *G. dorcas isabella* and *pelzelni*, one or other of which often emerge as the sister-group to *G. gazella*, especially *G. g. cora*. The similarity of *isabella* and *cora* in pelage characters and horn shape was noted above; they are, in fact, exceedingly easy to confuse when alive. Most of their skull codes are identical, in view of which their potential cladistic closeness is perhaps little surprise. In fact, the shape of the naso-frontal suture (Figure 2.2) is the only strikingly different aspect of skull morphology. The possibility that this relationship is real, an alternative to the general association of *cora* and *gazella* in the same species, was raised previously (Groves, 1989).

It is difficult to see *cora* as close to *G. g. gazella*. In discriminant analysis of cranial variables both sexes separate completely (Figures 2.3 a,b; Groves, 1989: Figures 1,2); on horn characters, they separate almost completely (Figure 2.3c). The only form of *G. gazella* with which it is sometimes linked in the shortest trees (Figure 2.6) is *muscatensis*.

In the light of the conclusions of Rebholz *et al.* (this volume) and Vassart *et al.* (this volume), these findings must be regarded as unexpected. One possible explanation could be that there has been simple misidentification of some reddish-toned *cora* as *dorcas*, and that specimens identified as *cora* for genetic study were actually something else. Alternatively, gross morphological characters are so replete with homoplasy as to cause a spurious linkage on some of the cladistic analyses and in the discriminant analysis; it is less plausible that the DNA segments sequenced by Rebholz *et al.* (this volume) or the blood protein loci analyzed by Vassart *et al.* (this volume) might be subject to extreme homoplasy. The problem is difficult but not intractable. For the moment it does seem better to adopt the conservative course and retain *cora* in *G. gazella*, but this option must be tested and re-tested in the future.

- **The status of *Gazella "gazella" erlangeri***: Though formerly confused with *G. g. cora* (for example, Groves & Lay, 1985), and only recently identified as a separate taxon (Groves *et al.*, in press), this form turns out to be thoroughly distinct both metrically (Figures 2.3 a,b,c: but note small

sample sizes) and cladistically (Figure 2.6). It is also readily distinguished in the flesh. The map (Figure 2.7; see also localities listed in Appendix 2.1) shows a striking anomaly: undoubted *erlangeri* are known from coastal localities north of Jeddah, as well as from Yemen; yet *cora* is known from the coastal plain as well, in intervening localities. There is no evidence of gene exchange. Under such circumstances it would seem perverse to retain the two taxa in the same species.

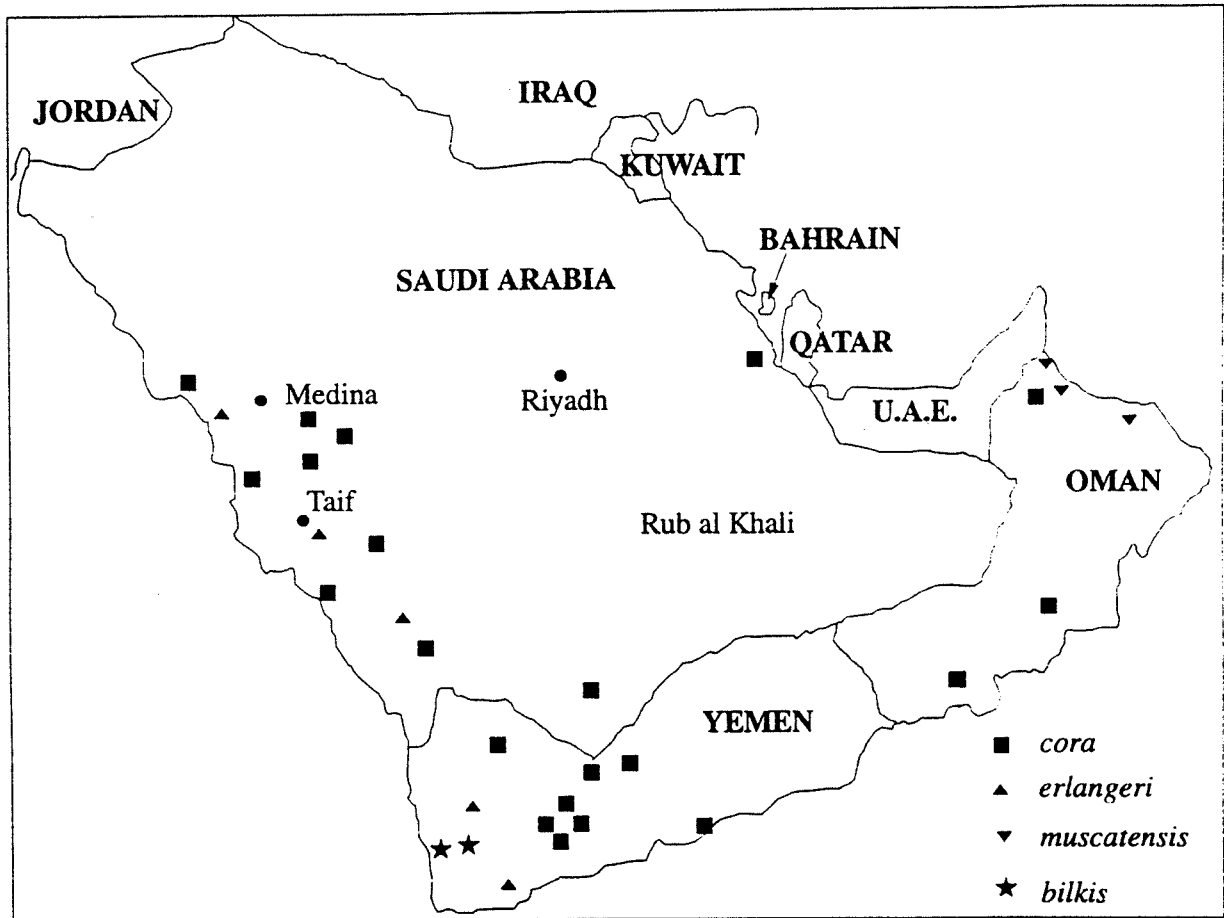


Figure 2.7 Distribution map of taxa assigned to, or related to, *Gazella gazella* in the Arabian peninsula.

Externally, it is very close to *muscatensis*, as noted above; but skull characters and horn shape distinguish them (see above, and Figure 2.6). The cladistic analysis never associates them; indeed, as noted above, it refuses to associate *erlangeri* with any other member of the *G. gazella* group except, in one tree (Figure 2.6f) *G. bilkis* and *arabica*.

- **What are the Thumamah idmi?** The large, very dark, straight-horned idmi, identified as *Gazella gazella* cf. *gazella*, in the breeding pens at the King Khalid Wildlife Research Center, Thumamah, Saudi Arabia, together with the rheem (*G. subgutturosa marica*) held at the same Center, were the subjects of a thorough behavioural study by Habibi (1991). They closely resemble *G. g. gazella* externally, but differ craniometrically (see above), especially in their straighter horns, narrower nasals and overall narrower skulls. The horns of the females are longer. The ascending

branch of the premaxilla generally touches the nasals, unlike *G. g. gazella* and many *G. g. cora*. Discriminant analysis of both male and female crania separates them completely from both *gazella* and *cora*; that of horns nearly separates them. The cladograms (Figure 2.6) tend to separate the Thumamah gazelle as the sister-group to most other members of the *G. gazella* group; but this is likely to be a spurious effect of the incomplete data set.

Conclusions

- **Relationships of Arabian Gazelles:** The interrelationships of Arabian gazelles are complex. The *G. gazella* group has produced compactly built, dark representatives with stout, straight horns in more mesic highland regions (*G. g. gazella* in the Levant, *G. bilkis* in Yemen) and small, dark forms in coastal zones (*G. g. erlangeri* along the Red Sea coast, *G. g. muscatensis* along the Batinah coast). The pale desert form, *G. g. cora*, is strikingly like *G. dorcas*. If the desert morphology is primitive, then the highland and coastal forms have converged; if the remarkable resemblance between *G. g. gazella* and *G. bilkis* is due to retention of primitive features, then the convergence of *G. g. cora* on *G. dorcas* is extraordinary. Either way, it seems that these gazelles exhibit an ability to adapt genetically to a wide range of environments.

The affinities of *G. saudiya* are puzzling. Cranially the species in many respects recalls *G. dorcas*, with which indeed it has generally been considered conspecific. Chromosomally, however, it resembles *G. bennetti* much more; and its suppressed colour contrasts increase this resemblance. The most westerly subspecies of *G. bennetti* lives in the region of Bushehr, on the Gulf shores of Iran; this is also the smallest subspecies. Skull measurements of the single available skull, compared to males of *G. saudiya* (n=6), are given in Table 2.4. Skull size, as measured by the greatest length, is exactly equal to that of *G. saudiya*. However, it has the typical broad nasal bones of *G. bennetti*, wider posteriorly than anteriorly; the skull is broader, the teeth are larger, the horns are shorter but very widely bowed outwards. In other words, the two may be sister species, but *G. saudiya* is not simply a westward extension of *G. bennetti*.

I have considered whether the type skull of *G. arabica* might actually be a misplaced specimen of *G. bilkis* (in which case, of course, the prior available name would be *arabica*). While Hemprich and Ehrenberg obtained the specimen on Farasan (Groves, 1983), it is possible that they did not themselves shoot it but that it was brought there, alive or dead, from the mainland. The skin is redder and less dark than of *G. bilkis*; the skull is narrower, and has a longer braincase and very short nasal bones. Cladistic analysis (Figure 2.6) always associates them. It seems likely that they are subspecies of the same species. Though generally associated with *G. gazella* in the cladograms, this is not obligatory (Figure 2.6f), and they are not clearly part of that species.

While the evidence is not complete, it seems likely that *cora* is a subspecies of *G. gazella*, as are *muscatensis* and the Thumamah taxon. Efforts to identify the origin of this apparently subspecifically distinct form need to be intensified. But *erlangeri* is surely not part of the same species. Cladistically it always appears as the sister-group to the rest of the species *G. gazella* (unless it is the sister-group to *G. arabica / bilkis*). Moreover its distribution would seem to overlap or interdigitate with that of *G. g. cora* (see above), without any indication of gene flow between them.

The position of *G. subgutturosa* is unclear. It is the most readily differentiated of the Arabian species, but this may be simply a matter of adaptation to a different environmental setting. There is also the matter of the number of subspecies to be considered: those of Iraq and, perhaps,

Syria, are small like *G. s. marica* but like *G. s. subgutturosa* in colour and in the females being normally hornless - are they simply intergrades, or a stable subspecies? Are the representatives on Bahrain Island different from those on the mainland?

I propose the following classification of Arabian gazelles:

G. subgutturosa marica

G. saudiya

G. dorcas isabella (in Israel and Sinai, and perhaps extending into Saudi Arabia, on the evidence of Bedouin suppliers of specimens to Al Wabra)

G. erlangeri

G. arabica arabica

G. arabica bilkis

G. gazella gazella

G. gazella (Thumamah subspecies)

G. gazella cora

G. gazella muscatensis

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Appendix 2.1 Gazelle specimens and localities from the Arabian peninsula. Unless otherwise stated, all specimens are in the Natural History Museum (London).

Gazella gazella cora

- Ain al Rizat (3 skins, 1 skull).
- Arq Abu Da'ir, 4,000 feet: 16°40'N, 45°15'E (1 skin, 1 skull).
- 15 miles north of Ashiera: 22°00'N, 41°00'E (1 skull).
- Buraiman, coastal plain: 21°38'N, 39°13'E (1 skin).
- Buraimi: 24°15'N, 55°45'E (2 skulls).
- Dhalm: 22°50'N, 41°40'E (1 skull).
- ?Garshaw'r (Qilwah) area (light red-brown gazelles, photos 4a and b of NCWCD Protected Area Report no. 18).
- Hadhramaut: ± 15°50'N, 48°50'E (1 skin).
- Wadi Hammam: 14°50'N, 46°36'E (1 skin, 1 skull).
- Hanum, N.edge of Jebel Garra: ± 25°27'N, 49°42'E (1 skin).
- Haraj plain: 14°50'N, 46°40'E (1 skin, 1 skull).
- Hudhaiyab al Aranib, 3,300 feet: 20°30'N, 42°40'E (1 skin, 1 skull).
- Jurbaib: 17°00'N, 54°10'E (1 skin, 1 skull).
- Manwakh: 16°57'N, 48°06'E (Figures 2.1a, b, this article).
- Wadi Markha: 14°57'N, 46°35'E (1 skin, 1 skull).
- Mughshin: 19°28'N, 54°57'E (2 skulls).
- Qunfida: 19°00'N, 41°00'E (1 skin, 1 skull).
- Rabigh Qasr: 22°50'N, 39°02'E (1 headskin, 1 skull).
- Raqba plain: 22°30'N, 41°40'E (2 skins, 9 skulls).
- South Arabian coast at 49°50'E (4 skulls).
- Sudaihat, 3,000 feet: 16°00'N, 45°50'E (1 skin, 1 skull).
- Taraf Al Ain, 2,500 feet: 15°50'N, 47°40'E (1 skin, 1 skull).
- Uqla-Jifr plain, 3,000 feet: 15°25'N, 46°50'E (1 skin, 2 skulls).
- Plain between Uqla and Wadi Mudhaib al Jifr (1 skin).

Gazella gazella erlangeri

Aden: 12°50'N, 45°03'E (4 skins, 2 frontlets; also one skull in Paris Museum).
Ma'bar, 7,400 feet: 14°46'N, 44°21'E (2 skins and skull, one a fawn, Field Museum, Chicago).
Najran Emirate: 17°30'N, 44°20'E (NWRC, Taif).
Taif district: 21°10'N, 40°45'E (1 skin of a fawn).
Thuwal, Hejaz Tihama: ± 22°30'N, 30°00'E (3 skulls, 3 skins and 2 head-skins).

Gazella gazella muscatensis

Abieat, north of Muscat (Harrison Museum, Sevenoaks, Kent, U.K.).
Baikit et Maze, Oman (1 skin and skull).
Khode: 23°37'N, 58°08'E (2 skins, 2 skulls).
Muscat: 23°37'N, 58°38'E (1 skull, 2 skins; also one skull in Booth Museum, Brighton, U.K., and one skull in Harrison Museum).
Saham: 24°10'N, 56°53'E (2 skulls, Harrison Museum).
Sohar area: 24°23'N, 56°45'E (11 skulls, Harrison Museum).

Gazella bilkis

Mocha: 13°15'N, 43°15'E (1 skull).
El Hauban, Wadi Maleh, 5 miles east of Ta'izz: 13°36'N, 44°07'E (1 skin, 1 skull, Field Museum, Chicago).
Ta'izz, 4,100 feet: 13°35'N, 44°02'E (1 skin, 1 skull, same).
Usaifira, 4,000 feet: 13°36'N, 44°00'E (1 skin, 1 skull, same).
Jebel Zarba, 7,000 feet, east of Ta'izz: 13°30'N, 44°03'E (1 skin, 1 skull, same).

Gazella saudiya

"Arabia" (2 skulls).
Alam Abyadh: 16°00'N, 45°42'E (1 skin and skull).
Arq Abu Da'ir: 16°40'N, 45°15'E (1 skin and skull).
Dhalm: 22°50'N, 41°40'E (7 skins and skulls).
Kuwait: ± 29°N, 48°E (1 skin and skull).
Wadi Markha: 14°57'N, 46°35'E (1 skin and skull).
Wadi Naq'a: 15°30'N, 47°15'E (1 skin and skull).
Ruwaik tract: 15°55'N, 46°10'E (1 skin and skull).
Sirr al Yamani: 16°20'N, 46°50'E (1 skin and skull).
Taraf al Ain: 15°50'N, 47°40'E (1 skin and skull).

Gazella subgutturosa marica

Arabia, 29°15'N, 47°E (1 skin and skull).
Arabia, 29°45'N, 40°28'E (1 skin and skull).
Arabia, 29°46'N, 40°56'E (1 skin and skull).
"Arabia" (2 skins and skulls).
Afalil: 46°30'N, 15°45'E (1 skin and skull).
Bisaita plain.
Jebel Dhalm, between Alif and Khuna: 22°50'N, 41°40'E (1 skin and skull).
Dibdibbah, 60 miles south-west of Kuwait: 29°10'N, 46°50'E (1 skin and skull).
Harrath al Arrat, Saudi/Jordan border: ± 30°N, 38°E (NWRC, Taif).
Kuwait.
Ibri, Nejd: 23°15'N, 56°35'E (2 skins and skulls).
Es Taisiya Nejd, 27°30'N, 44°20'E (2 skins and skulls).
Safala plain, 27°N, 39°E (1 skin and skull).