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Chapter 3

SPECIATION OF ARABIAN GAZELLES

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ABSTRACT

Gazelles are distributed across Africa and Asia and are adapted to arid and semi-arid environments. In this chapter, we discuss potential factors promoting the divergence of lineages within this group (*i.e.*, speciation events). The most recent common ancestor of gazelles is thought to have emerged during the Miocene (12-14 Ma) and to have split into the extant genera *Nanger* and *Eudorcas* (both endemic to Africa), *Antilope* (endemic to Asia), and *Gazella* (present in Africa, the Middle East and Asia). Within *Gazella*, two major clades are thought to have evolved allopatrically: (1) a predominantly Asian Clade (*G. bennettii*, *G. subgutturosa*, *G. marica*, *G. leptoceros*, and *G. cuvieri*) and (2) a predominantly African Clade (*G. dorcas*/ *G. saudiya*, *G. spekei*, *G. gazella*, and *G. arabica*). At present, both clades meet in North Africa and, especially, in Arabia. Other splits in this group are better explained by adaptive speciation in response to divergent ecological selection. In both clades, parallel evolution of sister species pairs (a desert-adapted form and a humid mountain-adapted form) can be inferred; desert-dwelling *G. dorcas* in Africa and *G. saudiya* in Arabia have a sister group relationship with mountain-dwelling *G. gazella* in the Levant and *G. arabica* in Arabia. This relationship exists within Africa between the desert-dwelling slender-horned gazelle (*G. leptoceros*) and the mountain-dwelling Cuvier's gazelle (*G. cuvieri*) of the Atlas Mountains. A third species pair occurs in Asia; desert-dwelling goitred gazelle (*G. subgutturosa*) and mountain-dwelling chinkara (*G. bennettii*). These (ecological) speciation events correlate with

ecology and behavior: the mountain forms being browsers, sedentary, territorial, and living in small groups, while the desert forms are grazers, migratory/ nomadic, non-territorial, and living in herds. Furthermore, cryptic sister species (*G. gazella*, *G. arabica*), with strikingly similar phenotypes, exist within presumed '*G. gazella*', alluding to a possible allopatric origin of this divergence following an isolation of humid mountain regions during hyper-arid phases. On the other hand, phenotypes within *G. arabica* tend to be variable, but are difficult or impossible to distinguish genetically.

INTRODUCTION

The earliest known fossil antelope, found in the Baringo Basin, Kenya, is of early Miocene origin (Thomas 1981), but it is uncertain where gazelline antelopes first emerged: in Africa, as proposed by Kingdon (1988), or in Asia, as suggested by Vrba and Schaller (2000). One of the four extant genera (*Antilope*) that evolved from these ancestors is in Asia, two (*Nanger* and *Eudorcas*) are in Africa, and one (*Gazella*) is on both continents as well as on the Arabian Peninsula. To understand the present distribution of gazelles (*i.e.*, *Antilope*, *Gazella*, *Nanger* and *Eudorcas*) it is important to interpret results from phylogenetic analyses in light of the geological and climatological history of the entire historic ranges of these genera.

The Arabian Peninsula is a prime example of a biogeographic transition zone, as it connects the floral and faunal regions of Africa and Asia (Vincent 2008). The present pattern is predominantly the result of the Afro-Eurasian species interchanges following the joining of the northern edge of the Afro-Arabian continent with Eurasia in the mid-Oligocene (ca. 30 Ma; Tchernov 1988; Bosworth et al. 2005; Vincent 2008). At the beginning of the Neogene (23 Ma), the Tethys acted as a substantial geographic barrier between Eurasian and Afro-Arabian faunas (Bernor 1983), leading to great divergence between these two realms and the evolution of two unique biotas (Tchernov 1988). The first major faunal interchange between Eurasia and Africa took place at the Proboscidean Datum Event (ca. 20 Ma; Madden and Van Couvering 1976), when a new land bridge (*i.e.*, the Gomphotherium Land Bridge; Rögl 1999a) connected Africa and Asia, and the Mediterranean Sea was isolated from the Indian Ocean for the first time.

The following faunal exchange was not continuous though, and was intensified during two main dispersal events in the Miocene at ca. 18–19 Ma and ca. 16–17 Ma (Thomas 1985; Rögl 1999b), interrupted by a re-opening of the seaway between Arabia and South Anatolia (Rögl 1999a). Evidence for faunal exchange during the first phase can be found in the Jibal Hadrukh formation in Saudi Arabia (about 19 Ma) which contains fossil representatives of north-Tethyian fauna (Rögl and Steininger 1983). Before the connection to Eurasia was formed, the Arabian Peninsula supported an African fauna. After connection, Palaearctic faunal elements appear in Arabia (Tchernov 1988; Delany 1989). During the early Miocene, extensive rifting of the Rift Valley resulted in a dramatic increase in water depth of the Red Sea, thus separating Arabia from Africa (Bosworth et al. 2005). During this period, savannah and steppe ecosystems expanded, leading to a radiation of grasses (Poaceae) followed by the rise of hypsodont ungulates (Strömberg 2011) and a rapid radiation of several tribes of bovids (Matthee and Robinson 1999). Although Africa became seemingly isolated from the northern hemisphere by the Saharo-Arabian arid belt in the late Miocene, faunal exchange of mammals increased once

savannah- and desert-adapted forms evolved and the arid belt became a less effective barrier to the dispersal of such species (Thomas 1979; Tchernov 1988).

In the late Miocene/ early Pliocene era, the "savannah-mosaic" assemblages of Mesopotamia were already populated with representatives of the tribe Antilopini (*e.g.*, *Gazella deperdita* and *G. rodleri*) and other ungulates (Bernor 1986). The Miocene/ Pliocene boundary was characterized by the onset of the Messinian Salinity Crisis (6 Ma), when the Mediterranean Sea became isolated from the Atlantic ocean and water levels regressed dramatically (Krijgsman et al. 1999). This resulted in an accelerated faunal interchange between Africa and Eurasia (*e.g.*, Agusti et al. 2006), especially of savannah-adapted species (Hassanin and Douzery 1999).

Following the Messinian Salinity Crisis the Mediterranean Sea reconnected to the Atlantic Ocean (Hilgen and Langereis 1988). At the same time, there was inflow of marine water into the Red Sea through the Bab el-Mandeb Strait, severing the connection between Arabia and the Horn of Africa (Bosworth et al. 2005). Furthermore, the orogeny of the Zagros Mountains—as part of the Alpine-Himalayan Mountain Belt—hampered biotic exchanges between Arabia and Asia (Tchernov 1988). All these factors led to an increasing isolation of Arabian fauna from Africa and Eurasia.

Moreover, the Afro-Arabian land bridge via the Sinai Peninsula became less permeable to faunal exchange due to a pull-apart basin development along the Aqaba-Levant Transform Fault (Bosworth et al. 2005). It remains uncertain as to whether there was a reconnection of both regions via the Bab el-Mandeb after the Miocene (Wildman et al. 2004; Winney et al. 2004; Fernandes et al. 2006; Bailey et al. 2009; Fernandes 2009). Climatic conditions during this time are thought to have caused a small-scale mosaic of ecosystems in the region (Tchernov 1988). Especially in Africa, faunal and palaeo-climatic records indicate shifts towards increasingly variable (and, on average, drier) conditions during the Plio-/ Pleistocene (2.8 Ma), allowing arid-adapted taxa to become more abundant (Thomas 1979; DeMenocal 2004).

In the Pleistocene the biotic interchange between Arabia and the Sahara was more asymmetric. Asian species, being more adapted to moister (mountainous) conditions, dispersed more easily into Arabia and North Africa along the mountain ridges of Arabia and the Sinai. By contrast, for arid-adapted Saharan species it was more difficult to invade the more humid parts of Asia (Delany 1989). Firstly, Saharan species on their way to Asia needed to cross the Nile Delta, which developed after the Messinian Salinity Crisis (Stanley and Warne 1998). Secondly, only the narrow stretch of sand dunes along the northern Sinai served as a suitable dispersal corridor for species adapted to hyper-arid conditions (Ferguson 1981). In addition, dispersing species would have needed to cross the Aqaba-Levant Transform Fault on their passage from the eastern Mediterranean towards Asia (Tchernov 1988).

The coastal plains of Arabia and the Sinai Peninsula experienced eustatic sea-level fluctuations, and large parts were submerged during inter-glacial periods (Chappell and Shackleton 1986; Shackleton 1987; van Andel 1989; Lambeck and Chappell 2001). During the Holocene (*i.e.*, after the glacial cycles) the geological situation remained more or less stable, and mammalian species in Arabia and surrounding areas—particularly gazelles—were increasingly impaired by human activities. Archeological evidence suggests that hunting by humans in prehistoric times was already having a major impact on populations of gazelles (Legge and Rowley-Conwy 1987; Bar-Oz et al. 2011).

In this section, we have provided a brief overview of the geological and climatological setting in which the evolution of extant gazelle species took place. In the following, we consider

the question of how the above-mentioned factors influenced speciation in this group. We concentrate on possible scenarios for the modes of speciation, and discuss evidence for both allopatric and ecological speciation.

Table 2. List of specimens included in the phylogenetic analyses, their collectors/ accession numbers, and source of sequence. Abbreviations: EEZA – Estación Experimental de Zonas Áridas, Almeria, Spain; KKWRC – King Khalid Wildlife Research Centre; OCE – Office for Conservation of the Environment, Muscat, Oman; WASWC - Wadi Al-Safa Wildlife Centre, Dubai, United Arab Emirates.

Species	Origin	Collector/ accession number	Source	Group
Gazella arabica	Oman, Muscat – Sur	OCE	tissue	African *Gazella*
G. arabica	Farasan Islands, Saudi Arabia	JN410353	GenBank (Lerp et al. 2011)	African *Gazella*
G. arabica	Israel, A'rava Valley	KC188759	GenBank (Lerp et al. 2013)	African *Gazella*
G. bennettii	KKWRC (ancestors from Pakistan)	JN410340	GenBank (Lerp et al. 2011)	Asian *Gazella*
G. bennettii	KKWRC (ancestors from Iran)	JN410341, JN410357	GenBank (Lerp et al. 2011)	Asian *Gazella*
G. bennettii	Pakistan	KKWRC	blood, hairs	Asian *Gazella*
G. cuvieri	EEZA	JN410342, JN410343	GenBank (Lerp et al. 2011)	Asian *Gazella*
G. dorcas	Israel, A'rava Valley	JN410230	GenBank (Lerp et al. 2011)	African *Gazella*
G. dorcas	Chad	JN410237	GenBank (Lerp et al. 2011)	African *Gazella*
G. dorcas	Sudan, Mashail	JN410250	GenBank (Lerp et al. 2011)	African *Gazella*
G. dorcas	Algeria, Hoggar Mountains	JN410252	GenBank (Lerp et al. 2011)	African *Gazella*
G. gazella	Israel, Yehuda Mountains	KC188775	GenBank (Lerp et al. 2013)	African *Gazella*
G. gazella	Israel, Shomeron	KC188774	GenBank (Lerp et al. 2013)	African *Gazella*
G. leptoceros	Hoggar Mountains, Algeria	JN410259	GenBank (Lerp et al. 2011)	Asian *Gazella*
G. leptoceros	Tunisia	JN410345	GenBank (Lerp et al. 2011)	Asian *Gazella*
G. leptoceros	Western Desert, Egypt	JN410346	GenBank (Lerp et al. 2011)	Asian *Gazella*
G. marica	Syria, Dara Region	K. Habibi	hairs	Asian *Gazella*
G. marica	Saudi Arabia, Khunfah	KKWRC	tissue	Asian *Gazella*
G. marica	Saudi Arabia, Uruq Bani ma'Arid	S. Ostrowski	hairs	Asian *Gazella*
G. spekei	WASWC	D. O'Donovan	hairs	African *Gazella*
G. subgutturosa	Mongolia, south	D. Maaz	tissue	Asian *Gazella*
G. subgutturosa	unknown	AF036282	GenBank (Hassanin and Douzery 1999)	Asian *Gazella*
Antilope cervicapra	unknown	AF022058, AF036283	GenBank (Matthee and Robinson 1999; Hassanin and Douzery 1999)	Larger gazelles
Eudorcas thomsoni	unknown	FJ556559	GenBank (Tungsudjai et al. unpublished)	Larger gazelles
E. rufifrons	Sudan	JN632633, JN632634	GenBank (Hassanin et al. 2012)	Larger gazelles
Nanger dama	unknown	AF025 954	GenBank (Matthee and Robinson 1999)	Larger gazelles
N. granti	unknown	AF034723	GenBank (Hassanin et al. 1998)	Larger gazelles
N. soemmerringii	Egypt, Cairo, Giza Zoo	KC188777	GenBank (Lerp et al. 2013)	Larger gazelles
N. soemmerringii	Saudi Arabia, Jenadriyah, private collection	H. Tatwany	blood	Larger gazelles
Litocranius walleri	unknown	AF249974	GenBank (Matthee and Davis 2001)	outgroup
L. walleri	Somalia	JN632653	GenBank (Hassanin et al. 2012)	outgroup
Antidorcas marsupialis	unknown	AF022054, AF036281	GenBank (Matthee and Robinson 1999; Hassanin and Douzery 1999)	outgroup

MAJOR CLADES OF GAZELLES

Gazelles are members of the tribe Antilopini. Although the other members of this tribe are not part of this review, they are worth mentioning since they are considered to represent highly derived descendants of gazelle-like ancestors (Gentry 1992). Today the tribe Antilopini comprises as many as 13 genera (*Raphiceros*, *Ourebia*, *Madoqua*, *Dorcatragus*, *Saiga*, *Litocranius*, *Ammodorcas*, *Antidorcas*, *Procapra*, *Eudorcas*, *Nanger*, *Antilope* and *Gazella*; Effron et al. 1976; Gentry 1992; Rebholz and Harley 1999; Groves 2000; Grubb 2005; Groves and Grubb 2011; Hassanin et al. 2012), four of which are traditionally labeled 'true gazelles', *i.e.*, the genera *Gazella*, *Antilope*, *Nanger*, and *Eudorcas* (von Boetticher 1953; Groves 1985, 1988, 2000; Groves and Grubb, 2011).

To infer the phylogeny of gazelles, we investigated sequence variation of the mitochondrial cytochrome *b* gene of 17 taxa (including newly sequenced and already published data, see Table 2) covering all four gazelle genera, as well as the genera *Antidorcas* (springbok) and *Litocranius* (gerenuk). Bayesian analysis was performed in BEAST 1.5.2 (Drummond and Rambaut, 2007); no outgroup was defined beforehand. We used molecular clock data estimates inferred for *Gazella dorcas*. For methodological details see Lerp et al. (2011). jModelTest 0.1.1 (Posada 2008) uncovered HKY + Γ as the best fitting substitution model. We ran a Metropolis coupled Monte Carlo Markov chain (MC3) for 15 million generations with a burn-in phase of 1.5 million generations.

The phylogenetic tree inferred from this analysis is shown in Figure 8. High statistical support [*i.e.*, posterior probability (PP) greater than 0.9] was found for the monophyly of gazelles (*i.e.*, the genera *Antilope*, *Eudorcas*, *Gazella* and *Nanger*), but our analysis could not unambiguously resolve whether *Antidorcas* or *Litocranius* is the extant sister genus to the gazelles. Our findings are congruent with the results from a recent phylogenetic investigation of the order Cetartiodactyla by Hassanin et al. (2012), who analyzed the complete mitochondrial DNA sequence information, but included fewer gazelle taxa. Within the gazelles, all four genera were well supported as forming monophyletic clades, although the exact relationship among those genera could not be resolved. Time estimates for the first emergence of gazelles (95% credibility interval: 10.5–6.3 Ma), based on a molecular clock, were statistically not well supported (PP = 0.68), but are comparable to those provided by Hassanin et al. (2012), who estimated 8.5 ± 1.3 Ma (mean ± SD) for the corresponding phylogenetic split. During this time (*i.e.*, in the late Miocene) savannah and steppe ecosystems with xerophytic shrub-land expanded into eastern and northern Africa and onto Arabia (Pound et al. 2011). This expansion of grasslands, together with the subsequent diversification of grasses (Strömberg 2011), probably facilitated the remarkable diversification (*i.e.*, radiation) of antelopes at this time.

In contrast to paleontological studies describing the earliest fossil Antilopini from the middle Miocene in Africa (14 Ma; Vrba 1985) our molecular estimates for the first appearance of gazelles are considerable younger (10.5–6.3 Ma). How can these contrasting findings be reconciled? First of all, phylogenetic analyses through the analysis of sequence variation are based on extant taxa only, so extinct clades typically go undetected unless analyses of ancient DNA are feasible. Also, inference of time estimates from molecular phylogenetic approaches—as was done in this study—depend on the settings (*i.e.*, substitution model and rates) for the

molecular clock. Here, we used no fossil calibration points as constraints for our analysis (see below), but found similar time estimates as described by Hassanin et al. (2012), who used six calibration points from the fossil record for estimating the diversification of the entire order Cetartiodactyla. We are, therefore, confident that the settings of the molecular clock used in this study were realistic. Secondly, the classification of fossils is based on morphological measurements, especially with respect to skull and horn morphology. Gazelles show character state combinations that are likely plesiomorphic for the entire subfamily Antilopinae or, perhaps, even for the entire family Bovidae, which first appeared in the early Miocene (Gentry 1992; Vrba and Schaller 2000). Such morphological parallelisms and the incomplete fossil record render taxonomy within the Bovidae difficult (Vrba 1985; Gentry 1992). In addition, some bovid fossils showing this plesiomorphic character state combination are likely misclassified and falsely described as belonging in the vicinity of the genus *Gazella*.

The divergence of gazelles (PP = 1; 95% credibility interval: 8.0–4.8 Ma)—ultimately leading to the four extant genera in a relatively short period of time (Fig. 8)—could have been promoted by climate change following the Messinian Salinity Crisis (~6 Ma). Conditions were generally dryer (DeMenocal 2004), and new and larger areas became inhabitable for arid-adapted antelopes. The ancestors of the genus *Antilope* seem to have reached Asia by this time (Khan et al. 2006). The occurrence of blackbuck (*Antilope cervicapra*)—the only extant species of this genus—is still restricted to the Indian subcontinent and might be a descendant of this first expansion wave. Today, the descendants of *Eudorcas* and *Nanger* occur exclusively in Africa, and it remains doubtful if these genera ever occurred outside Africa.

The situation within genus *Gazella*, however, is more complex, because extant species occur both in Africa and Asia, as well as in Arabia (Kingdon 1988; Gentry 1992). Two major clades, with a well-supported monophyly, are inferred by our present study; their split is estimated at 3.9–2.3 Ma, *i.e.*, in the Pliocene (Fig. 8). The 'African Clade', comprises more species, endemic to Africa, whereas the 'Asian Clade' is predominantly in Asia. Both clades, however, comprise taxa that occur on the "opposite" continent (Fig. 8).

The African Clade contains Speke's gazelle (*G. spekei*), which is endemic to the Horn of Africa in Somalia (East 1999), dorcas (*G. dorcas*), mountain (*G. gazella*) and Arabian gazelles (*G. arabica*; Effron et al. 1976; Rebholz and Harley 1999; Wronski et al. 2010; Bärmann et al. 2012; this study). The diversification of the African Clade started 2.8–1.6 Ma ago (early Pleistocene; Fig. 8). By far the widest distribution range within this clade is that of *G. dorcas*, which includes large parts of northern Africa and, once, much of Arabia (where described as Saudi gazelle *G. saudiya;* Carruthers and Schwarz 1935; Rebholz et al. 1991; Rebholz and Harley 1997; Hammond et al. 2001). Together with *G. gazella* and *G. arabica*—which also inhabit the Arabian Peninsula—this is the most eastern extent of the range of the African Clade. We hypothesize that *G. dorcas* represents the ancestral character state combination of the African Clade because cytogenetic and morphological data showed *G. dorcas* to be basal to several species within *Gazella* (Lowenstein 1986; Gentry 1992; Vassart et al. 1995b). Moreover, it is suggested that the Antilopini evolved as grazers in the open, semi-desert and desert habitats of Africa (Kingdon 1988; Hassanin et al. 2012) and that the dispersal into mountainous and more humid habitats represents a shift associated with speciation events. At the edges of its distribution range, *G. dorcas* seems to have split rapidly into *G. spekei* and *G. gazella*, leaving sister group relations of these three species unresolved. This diversification was probably the result of 'ecological speciation' (see below). Lerp et al. (2011) found support for the idea that *G. dorcas* colonized Arabia via the Sinai and not via the Bab el-Mandeb. Thus,

great distance and the Red Seas likely separated the ancestors of today's *G. arabica*, *G. gazella* and '*G. saudiya*' of Arabia from Africa's *G. spekei* and *G. dorcas*.
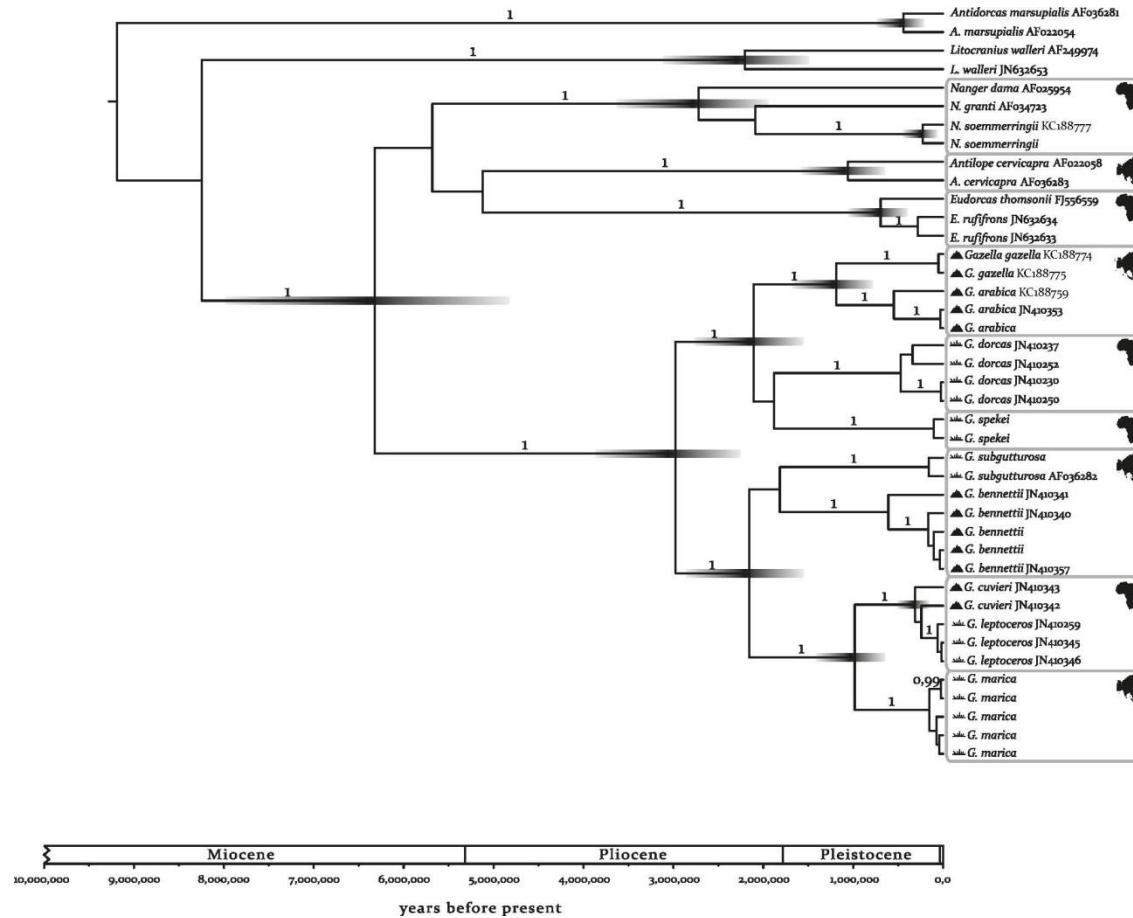
Figure 8. Phylogeny based on the alignment of the complete sequences of the cytochrome *b* gene. Bayesian analysis was performed with 41 sequences with the HKY + Γ substitution model. Only posterior probability values larger than 0.9 are reported. Node bars represent the 95% credibility intervals of the divergence times of statistically supported phylogenetic splits. Symbols of Africa and Asia indicate the occurrence of single species on that continent. Within the genus *Gazella,* a mountain symbol indicates a more humid and/or mountainous habitat, whereas a grass symbol indicates open savannah/ desert habitat.

Within the Asian Clade the majority of species are distributed on the Asian continent. The divergence time of this clade is estimated as 2.9–1.6 Ma ago and is comparable with the diversification of the African Clade of the genus *Gazella*. Therefore, the early Pleistocene is when most of today's species of *Gazella* emerged. We hypothesize that the diversification of the Asian Clade occurred in central Asia after the first (smaller) gazelles appeared, probably in the late Pliocene. The Asian Clade consists of *G. subgutturosa* and *G. bennettii*, both forming a reciprocally monophyletic clade in our present phylogeny. Both species occur in central Asia and India. Other members of the Asian Clade include *G. marica* and the African *G. cuvieri* and *G. leptoceros*, which together form a highly supported monophylum (Hammond et al. 2001; Wacher et al. 2010; Fig. 8). Changing climatic and geological conditions at the beginning of the Pleistocene could have enabled the ancestors of *G. marica* to cross the Zagros Mountains and invade the Middle East, where they occurred sympatrically with gazelles from the African Clade. Pliocene and early Pleistocene fossils of gazelles found in Turkey support this hypothesis, because they are distinct from fossils of *G. gazella* from the same period (Sickenberg 1975). Later (1.4–0.7 Ma ago) members of the Asian Clade crossed the Sinai Peninsula and Nile River to enter Africa and evolve into *G. leptoceros* which, today, occupies a habitat type similar to that of *G. marica* (*i.e.*, the sand dunes and gravel plains of northern Africa; Harrison 1968; Devillers et al. 2005).

EXTANT SPECIES OF SMALLER GAZELLES

Before we elaborate on the mechanisms of speciation within the group of smaller gazelles (genus *Gazella*), we provide a brief overview of the historical and current distribution patterns as well as the current threats to the survival of the nine extant species in this group.

Dorcas gazelles (*G. dorcas*) were originally distributed from Morocco and Mauretania eastwards to the Horn of Africa, Sinai Peninsula, the Levant (Yom-Tov et al. 1995; East 1999; Hammond et al. 2001) to east of the Hejaz and Asir Mountains of western Arabia. This species was extirpated from Arabia about 30-40 years ago (Vesey-Fitzgerald 1952; Thouless et al. 1991; Habibi and Williamson 1997). With the exception of Israel and Ethiopia, numbers are decreasing rapidly and populations are increasingly fragmented (Smith 1999; Mallon and Kingswood 2001; Lafontaine et al. 2005). This decline is estimated at >30% over three generations, with less than 25% of the remaining animals living in protected areas, resulting in the IUCN status 'Vulnerable' (Mallon and Kingswood 2001; IUCN/SSC Antelope Specialist Group 2008a).

Mountain gazelles (*G. gazella*) are distributed from the eastern Turkey and Lebanon, through Palestine, Golan and western Jordan. Previously lumped with the Arabian gazelle (which we refer to as *G. arabica*—see below), which ranged over the Arava Valley in southern Israel, western Saudi Arabia, Yemen, Oman and United Arab Emirates. The number of *G. arabica* has declined dramatically during the past 50 years (Thouless and Al Bassri 1991; Magin and Greth, 1994; Mallon and Kingswood, 2001). Extensive hunting, habitat loss, and population fragmentation are principal causes of decline (Thouless et al., 1991; Magin and Greth 1994; Mallon and Kingswood 2001). The IUCN category is 'Vulnerable' based on *G. gazella* plus *G. arabica* (Mallon and Kingswood 2001; IUCN/SSC Antelope Specialist Group

2008b). The situation for *G. gazella* from northern and central Israel is less critical (Clark and Frankenberg 2001).

Speke's gazelle (*G. spekei*) is endemic to the Horn of Africa, occurring in Somalia from the Indian Ocean westwards to the Gulis Range (Heckel et al. 2008). Although traditionally not hunted by people, numbers have collapsed over the last 20 years due to uncontrolled hunting by soldiers (Heckel et al. 2008). Probably the species is extirpated from Ethiopia. No effective protection is in place for *G. spekei*. The IUCN status is 'Endangered' (Heckel et al. 2008).

Goitred gazelle (*G. subgutturosa*) occurs east of the Tigris/ Euphrates Basin, north into the Caucasus and across Iran into Turkmenistan. Following the steppes of central Asia, *G. subgutturosa* inhabits the Takla Makan, Tarim Basin and Sianking of China and extends farther eastwards to central Mongolia, where it is replaced by the Mongolian gazelle (*Procapra gutturosa;* Groves 1985; Kingswood and Blank 1996; Mallon and Kingswood 2001; Zachos et al. 2010). Large populations occurred over a vast area until recently with ca. 100,000 individuals in the early 1990's (Mallon and Kingswood 2001). Hunting and habitat loss have caused a decline of >30% over the last ten years in many populations, resulting in the IUCN status 'vulnerable' (Mallon 2008a). The example of Mongolia should be highlighted, since a substantial proportion of the global population of *G. subgutturosa* once lived there, but heavy poaching, following collapse of the communist regime, has eliminated most of the large herds, resulting in a population decline >50% (Mallon 2008a).

The chinkara (*G. bennettii*) occurs in western and central India (especially in the Thar Desert), in the arid regions of Baluchistan and Sindh Provinces in Pakistan, south-western Afghanistan and north-central Iran (Rahmani 1990, 2001; Habibi 2001; Karami et al. 2002; Mallon 2008b). Scattered populations are also found in the sub-mountainous tracts of Punjab (Roberts 1977; Habibi 2001). Although numbers in Pakistan and Iran are decreasing due to overhunting (Mallon 2008b), the population in India is >100,000 (Rahmani 2001). Despite the large number of people in India, antelope populations there are relatively stable. This is mainly the result of an extensive network of protected areas coupled with low hunting pressure (Mallon and Kingswood 2001). *G. bennettii*, in particular, is secure in the Thar Desert with 80,000 individuals (Rahmani 2001) and, furthermore, is protected in reserves or by local people (Mallon and Kingswood 2001). For these reasons, *G. bennettii* is the only *Gazella* sp. that is not threatened (IUCN status 'least concern'; Mallon 2008b).

The sand gazelle (*G. marica*) is found in open habitats of the Middle East from the Tigris/ Euphrates Basin in Iraq, through Jordan and Syria into southern Turkey, and southwards through much of Arabia (Wacher et al. 2010). Current distribution is limited to a few (protected) areas in the United Arab Emirates, Oman, Syria, Turkey, probably in Jordan and perhaps western Iraq (Kasparek 1986; Mallon and Kingswood 2001; Massolo et al. 2008). In Saudi Arabia, *G. marica* is probably extinct outside of two protected areas Mahazat as-Sayd and Uruq Bani Ma'arid, both of which harbor reintroduced populations (Cunningham and Wacher 2009). There are probably <10,000 mature individuals and the population trend is downwards (IUCN/SSC Antelope Specialist Group 2008c). A good number of *G. marica* occur in captivity and are available for re-introductions (Cunningham and Wacher 2009). The current IUCN status is 'Vulnerable' (IUCN/SSC Antelope Specialist Group 2008c).

Slender-horned gazelle (*G. leptoceros*) is endemic to the sand dunes (ergs) of the Sahara, west of the Nile River (Devillers et al. 2005). Until recently, two subspecies were distinguished, *i.e.*, *G. l. loderi* from the sand deserts of Tunisia, Algeria and Libya, and *G. l. leptoceros* from the Western Desert in Egypt (Devillers et al. 2005). However, phylogeographic analyses for

validating these subspecies are lacking (Mallon et al. 2008). Numbers of *G. leptoceros* have decreased severely in the past decade due to hunting, especially in Egypt (Saleh 1987; Mostafa 2005), but also to habitat loss (Devillers et al. 2005). The conservation status of *G. leptoceros* in Mali, Niger, Chad and Libya is not known, but numbers are probably low (Devillers et al. 1999, 2005). All known populations are small to very small. The IUCN degree of threat status is 'Endangered' (Mallon et al. 2008).

Finally, Cuvier's gazelle (*G. cuvieri*) is endemic to the Atlas Mountains and neighboring ranges in Morocco (including the lowlands in the west), Algeria and Tunisia (Lafontaine et al. 1999; Beudels-Jamar et al., 2005). As for most *Gazella* spp., hunting is the major threat to the species and has caused a sharp population decline since the 1930's (Lafontaine et al. 1999; Beudels-Jamar et al. 2005). Habitat loss and degradation have also contributed to this decline (Sellami et al. 1990; de Smet 1991, 1994; Beudels-Jamar et al. 2005). There are currently ca. 2,500 individuals in several fragmented populations. The IUCN status is 'Endangered' (Mallon and Cuzin 2008). Some populations recently reported to be stable or even increasing (Mallon and Kingswood 2001; Mallon and Cuzin 2008).

PARALLEL, ADAPTIVE SPECIATION OF SPECIES PAIRS

Within both clades of genus *Gazella*, species pairs exist that exhibit parallel specializations in trophic ecology and social organization: On-the-one-hand, there are species more adapted to open, hot dry deserts. These species likely represent the ancestral character state combination. These species tend to be grazers, form herds and migrate. On-the-other-hand, species adapted to a more humid climate, are browsers that live in small groups and are sedentary and territorial. Our phylogenetic analysis infers three such species pairs (*i.e.*, *G. dorcas* vs. *G. gazella* plus *G. arabica*; *G. subgutturosa* vs. *G. bennettii*, and *G. leptoceros* vs. *G. cuvieri*), where three lineages of desert-adapted forms independently diverged into a browsing, mountain-dwelling form, and a grazing, desert- or savannah-dwelling form. Even though we lack a plausible explanation as to how adaptation to different habitat types promoted reproductive isolation in gazelles, we argue that these three splits represent ecological speciation events.

Schluter and Nagel (1995) presented three—rather strict—prerequisites for parallel ecological speciation to occur; "(1) separate populations in similar environments must be phylogenetically independent […], (2) ancestral and descendant populations […] must be reproductively isolated, and (3) separate descendant populations inhabiting similar environments must not be reproductively isolated from one another". This concept is particularly useful when considering contemporary parallel speciation within the same species, as indicated by the third criterion. When trying to apply the concept of parallel speciation to the phylogeny of gazelles it needs to be interpreted in a slightly broader sense. Point (3) of Schluter and Nagel's (1995) definition is not met, as speciation in response to adaptation to a more humid climate occurred, independently, three times, and at different times, in different geographical regions, and from different ancestral species.

The oldest split of an ecologically divergent species pair inferred from our phylogenetic analysis is between *G. dorcas* and *G. gazella/ G. arabica*. This split occurred 2.8–1.6 Ma (late Pliocene; Fig. 8). *G. dorcas* are grazers that inhabit Sahelian savannahs as well as semi-arid gravel and sand deserts, while avoiding hyper-arid areas and the upper elevations of the central-

Saharan massifs (Yom-Tov et al. 1995; Wacher et al. 2004). This species usually forms small family groups of 5–12 individuals (Yom-Tov et al. 1995), but during migration form herds of more than 100 individuals (Haltenorth and Diller 1977). *G. gazella* and *G. arabica*, by contrast, are sedentary, live in very small groups (two to maximal 20 individuals), live in upland areas of broken terrain on the Arabian Peninsula and the Levant, and adult males defend territories (Walther et al. 1983; Mendelssohn et al. 1995; Martin 2000; Wronski and Plath 2010). *G. dorcas* can cope without surface water by relying on hygroscopic food and respiratory water (Yom-Tov et al. 1995), whereas *G. gazella* and *G. arabica* prefer to drink on a regular basis (Mendelssohn et al. 1995). *G. dorcas* are reproductively isolated from *G. gazella*, and their hybrids are sterile or at least sub-fertile (Mendelssohn et al. 1995).

The second ecologically diverged species pair is *G. subgutturosa* and *G. bennettii*. Divergence probably occurred ca. 2.4–1.3 Ma ago (late Pliocene/ early Pleistocene) but statistical support for this date is weak (PP=0.89). *G. bennettii* are adapted to sand dune areas, regolith plains and hilly regions up to 1,500 m above sea level. This species avoids flat and steep terrain, and is typically on the edge of deserts (Roberts 1977; Sharma 1977; Rahmani 1990; Karami et al. 2002). *G. bennettii* are sedentary and live in groups of one to three individuals, but sometimes in larger herds (Rahmani 1990; Bagchi et al. 2008). Males form territories that they defend vigorously (Walther et al. 1983). The species is typically a browser, but during the rainy season they also graze (Sharma 1977; Habibi 2001). Compared to *G. subgutturosa*—which meet their water needs entirely from hygroscopic food plants—*G. bennettii* are independent of surface water only in winter. In the hotter months, when temperatures are >40°C, they have to drink regularly (Habibi 2001). *G. subgutturosa* are grazers that can also browse on xerophytic bushes (Roberts 1977; Kingswood and Blank 1996; Karami et al. 2002). This species is semi-nomadic with males forming territories only during the rut (*i.e.*, October-December; Kingswood and Blank 1996; Blank 1998; Bekenov et al. 2001).

The youngest split of an ecologically divergent species pair is between *G. leptoceros* and *G. cuvieri* and dates to 420,000–110,000 years ago (middle Pleistocene). The young age of this split (*i.e.*, the small genetic divergence between them) raises doubt concerning their species status (Hassanin et al. 2012). Nonetheless, both species are morphologically readily distinguished (Gentry 1964; Groves 1969; Groves and Grubb 2011). *G. leptoceros* are desert-dwelling grazers (Louys et al. 2011; Smith et al. 2001), that occasionally browse on *Acacia* (Saleh 2001). The species is nomadic, crossing vast areas of flat, open desert in search of sparse, ephemeral grasses (Kingdon 1997; Saleh 2001; Smith et al. 2001). The typical group size is <15 individuals (Smith et al. 2001). In contrast, *G. cuvieri* inhabit dry forests and maquis of the semi-arid Mediterranean type (Sellami and Bouredjli 1991; Beudels-Jamar et al. 2005), browse on acorns and young leaves of legumes, but also graze (Kingdon 1997; Smith et al. 2001). They live up to 2,600 m above sea level where they are limited by snow in winter (Aulagnier et al. 2001; Beudels-Jamar et al. 2005). *G. cuvieri* need to drink on a regular basis (Smith et al. 2001; Beudels-Jamar et al. 2005). This species lives in groups of 5-8 individuals, but solitary individuals are common (Sellami and Bouredjli 1991; Kingdon 1997; Beudels-Jamar et al. 2005). Males are territorial during the rut (in winter; Sellami and Bouredjli 1991; Kingdon 1997; Smith et al. 2001).

A TAXONOMIC REVIEW OF THE GENUS *GAZELLA*

It has been repeatedly emphasized that the taxonomy of gazelles is one of the least resolved among mammals (Groves and Harrison 1967; Groves, 1969). No other genus of large mammals creates such problems with regards to its classification based on skull morphometry, phenotypic appearance and genetic information, as does *Gazella*. As such, many taxonomic revisions of this genus have been put forth (Lydekker and Blaine 1914; Ellerman and Morrison-Scott 1951; von Boetticher 1953; Gentry 1964; Groves and Harrison 1967; Groves 1969, 1985, 1988; Lange 1972; Rostron 1972).

While the taxonomy of *Antilope* and *Nanger* has not changed substantially in recent decades (von Boetticher 1953; Gentry 1964; Lange 1972; Groves and Grubb 2011) the taxonomy within *Eudorcas* and *Gazella* remains uncertain, and with recent molecular findings casting doubt on earlier classifications that are based on morphological and cytogenetic traits. Our phylogenetic analysis of *Gazella* supports the existence of nine species (G. g*azella*, *G. arabica*, *G. dorcas*, *G. spekei*, *G. bennettii*, *G. subgutturosa*, *G. marica*, *G. leptoceros* and *G. cuvieri*), most of which require further taxonomic clarification.

Gazella marica (Thomas 1897), was subsumed within *Gazella leptoceros* by Ellerman and Morrison-Scott (1951). Subsequently, *G. marica* was considered a subspecies of *G. subgutturosa* based on morphological and karyological similarity (Groves and Harrison 1967; Kingswood et al. 1996, 1997). In more recent studies the phylogenetic relationships between *G. subgutturosa* from east of the Euphrates/ Tigris Basin and from the Arabia (*G. marica*) were reanalyzed based on molecular genetic information (Hammond et al. 2001; Wacher et al. 2010) and supported *G. marica* as a species. This conflicted with the grouping pattern inferred from skull structure and horn conformation (Groves and Harrison 1967). *G. marica* appears to be most closely related to the North African species *G. leptoceros* and *G. cuvieri* (Hammond et al. 2001; Wacher et al. 2010; see above).

In case of *G. subgutturosa*, Vassart et al. (1995b) state that *Gazella* will be paraphyletic when this species is included, because *G. subgutturosa* could be a sister taxon of *Antilope*. Both taxa share two unique centric fusions in their chromosomes causing the need to revive the genus *Trachelocele* (Ellerman and Morrison-Scott 1951; Groves 1969). Other studies investigating morphology or mitochondrial sequence variation placed *G. subgutturosa* within *Gazella* and refute *Trachelocele* (Grubb 2005; Groves and Grubb 2011; Hassanin et al. 2012; this study). Due to morphological variation within *G. subgutturosa*, up to three species are proposed by Groves and Grubb (2011), but there are no empirical data to support this position.

Early classifications place *G. bennettii* as either a subspecies of *G. gazella* (Haltenorth and Diller 1977; Roberts 1977) or as a subspecies of *G. dorcas* (Gentry 1964; Groves 1969; Lange 1972). Karyological data, however, found *G. bennettii* to be unrelated to *G. gazella* (Furley et al. 1988; Kumamoto et al. 1995). Within *G. bennettii*, up to six species are proposed on the basis of morphological divergence (Hemami and Groves 2001; Groves and Grubb 2011), but, again, evidence justifying this division is lacking. In this study—where two of the proposed *G. bennettii* taxa were included—there was no indication of more than one species. Nevertheless, a phylogeographic study with individuals from the entire distribution range is highly warranted.

In the cases of *G. cuvieri* and *G. leptoceros* the taxonomic classification remains confusing. Lange (1972) classified *G. cuvieri* under *G. gazella*, while *G. leptoceros* was considered a subspecies of *G. subgutturosa*. Later, a karyological study showed that *G. cuvieri* is unrelated

to *G. gazella* (Kumamoto and Bogart 1984). Furthermore, a division of *G. leptoceros* into two subspecies (*G. l. loderi* and *G. l. leptoceros*) was suggested based on differences in distribution ranges and ecology (Devillers et al. 2005). In contrast, *G. marica* and *G. leptoceros* are recently proposed to be subspecies of *G. cuvieri* because of their relatively low mitochondrial sequence divergence (Hassanin et al. 2012).

Within *G. dorcas,* several subspecies are described on the basis of phenotypic variation, such as coat coloration and horn shape and length (Groves 1969, 1981; Alados 1987; Yom-Tov et al. 1995; Groves and Grubb 2011). A phylogeographic study based on sequence variation of the mitochondrial cytochrome *b* gene and control region recently indicates that *G. dorcas*—including '*G. saudiya*' and '*G. pelzelni*'—represent a reciprocally monophyletic group with a sister-group relationship to *G. gazella* and *G. arabica* (Lerp et al. 2011). No statistically significant support was found for any geographic structure within the distribution range of *G. dorcas*. Nevertheless, keeping *G. dorcas,* '*G. saudiya*' and '*G. pelzelni*' separated at captive breeding centers is warranted as low genetic divergence at neutral markers does not preclude the potential existence of local adaptations (Hammond et al. 2001; Lerp et al. 2011).

Confusion over taxonomy and nomenclature at the species level has reached a maximum in *G. gazella* and *G. arabica* (Groves and Harrison 1967; Harrison 1968; Groves 1969, 1983, 1989, 1996, 1997; Lange 1972; Groves and Lay 1985; Vassart et al. 1995a; Greth et al. 1996; Vassart et al. 1996; Kingswood et al. 1997; Rebholz and Harley 1999; Wronski et al. 2010). At least four species (*G. gazella*, *G. bilkis*, *G. arabica*, and *G. erlangeri*) and eight subspecies have been named (Groves 1996, 1997; Grubb 2005; Groves and Grubb 2011). Based on the analysis of cytochrome *b* sequences of five *G. gazella* in the context of a phylogeny of the Antilopinae, Rebholz and Harley (1999) suggested that two genetically distinct lineages might exist: one from the Levant (Galilee to Turkey) and one from Negev and Arabia. Those findings have been confirmed in an analysis comprising more individuals from a larger area and more mitochondrial and microsatellite markers (Wronski et al. 2010; Lerp et al. 2013). This supports recognition of two 'cryptic' species in this clade, which may have evolved due to prolonged isolation or local adaptations to divergent environments (Wronski et al., 2010; Lerp et al. 2013). The nominate *G. gazella* was originally described as *Antilope gazella* (Buffon 1764) from the Levant. This raises the question of which species name to assign to the populations in Arabia. Recent molecular analyses of the cytochrome *b* gene from the type *G. arabica* (described as *Antilope arabica* Lichtenstein 1827) indicate that this taxon is invalid, because skin and skull of the type specimen of *G. arabica* did not form a separate lineage, but clustered with *G. gazella* (skin) and with *G. arabica* (skull; Bärmann et al. 2012). Following the rules of precedence (priority rule, International Code of Zoological Nomenclature, ICZN) the name *G. arabica* is available for gazelles in Arabia.

Within *G. arabica*, however, much taxonomic uncertainty remains. One of the most challenging questions is the status of *G. erlangeri*. Neumann (1906) described specimens from Lahadsch (Lahej), north of Aden, as a greyer form of *G. arabica*. He introduced a new subspecies name to account for this difference and cited the illustration labeled *G. arabica* in Sclater and Thomas (1898) as an accurate representation of what he was describing. Due to its putative sympatric distribution with *G. arabica*, Groves (1996) suggested full species status for *G. erlangeri*. Gazelles currently kept in captivity at King Khalid Wildlife Research Centre in Saudi Arabia and at Al Wabra Wildlife Preservation in Qatar show the described combination of diagnostic features and thus, were considered to represent *G. erlangeri* (Groves 1996)—even though the provenance of these gazelles is not known. Phylogenetic studies (using

mitochondrial markers) on these putative *G. erlangeri* cluster them amongst other *G. arabica* from all over Arabia (Hammond et al. 2000; Blacket et al. 2001; Hundertmark and Omer 2004; Wronski et al. 2010). In summary, it remains unsolved whether Neumann's (1906) *G. erlangeri* is a distinct taxon and how it relates to other gazelles.

Finally, the most enigmatic gazelle described from Arabia should be mentioned: the Queen of Sheba's gazelle (*Gazella bilkis*). Specimens shot in the Taizz Mountains of southern Yemen in 1951 (now stored at Chicago FMNH) were originally identified as *G. arabica erlangeri* by the collector Hoogstraal. They were, however, re-evaluated retrospectively based on skull morphology and described as *Gazella bilkis* (Groves and Lay 1985; Groves and Grubb 2011). Even though the taxonomic status of these gazelles remains unclear, there is no doubt that *G. bilkis* is extinct (Mallon and Al-Safadi 2001).

CONCLUSION

Gazelles comprise four monophyletic genera (*Antilope*, *Nanger*, *Eudorcas* and *Gazella*) and emerged in the early Miocene (10.5–6.3 Ma). While three genera are restricted to the continent on which they probably evolved (*Antilope* to Asia, *Nanger* and *Eudorcas* to Africa), the situation in *Gazella* is more complex, with extant species in Africa, the Middle East, and Asia. Different modes of speciation are apparent within *Gazella*: (1) allopatric speciation in two major clades, with one predominantly Asian Clade and the other a predominantly African Clade; (2) parallel, adaptive speciation of three species pairs in parapatry, with one representative being a grazing, desert- or savannah-dwelling, (semi-)nomadic form, and the other being a browsing, mountain-dwelling and mostly sedentary form; and (3) cryptic speciation following phases of geographic isolation, where two genetically distinct forms with similar phenotypes can be seen (*G. gazella* and *G. arabica*). In general, gazelles are characterized by pronounced phenotypic variability that is not always mirrored by molecular sequence divergence, and a part of this variation may be due to phenotypic plasticity. This led to taxonomical incongruence plainest expressed in the number of described species that reached a maximum in a recent book by Groves and Grubb (2011), with 36 extant gazelle species (including 1 species in the genus *Antilope*, 5 in *Nanger*, 6 in *Eudorcas* and even 24 in *Gazella*) being listed. In terms of conservation this situation is unfortunate. The taxonomical incongruence hampers conservation efforts regarding captive breeding or re-introduction programs, as it remains confusing which gazelles should be bred separately to preserve natural biodiversity. Further investigations using nuclear DNA markers of the extant taxa will be helpful to clarify the situation for critical taxa.

ACKNOWLEDGMENTS

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