



## Research Article

## Evolution of horn shape and sex dimorphism in subspecies of the dama gazelle (Bovidae: *Nanger dama* (Pallas 1766))

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**Abstract**

The horn shape and its sex dimorphism are compared in museum specimens of all geographical populations of the dama gazelle (*Nanger dama*). Departing from a putatively ancestral morphology prevailing in the west(-central) Sahel zone, a forked cladogenesis is inferred producing the eastern horn type of the red-necked gazelles (*N. d. ruficollis*) in Sudan and the morphotype of the mhorr gazelles (*N. d. mhorr*) in the northwest Sahara. The mhorr-horn type is phylogenetically derived as an autapomorphic novelty evolved by a mechanism driven by female sexual mimicry of the male model. Insufficient museum series from the subspecifically vaguely defined populations in the Sahel belt preclude the recognition of one (or even more?) additional horn morphologies in this intercalating region from Senegal to Niger, but any perhaps possible, further type(s), such as a potential horn morphotype in Damergou, Niger, would be weakly differentiated from the *ruficollis*-horns. Horn morphology suggests moderate subspecies-specific originalities in the fighting behaviours, differing in the intensity of ramming (*N. d. mhorr*) versus sparring (*N. d. ruficollis*). The slightly augmented surface area of the eastern morphotype could facilitate thermoregulation, by horn-mediated export of body heat, in the hyperthermic and hyper-arid desert biotope of *N. d. ruficollis*. Every morphotype is broadly sex-dimorphic, but this dimorphism is reduced in the mhorr gazelles. Andromimicry of female mhorr gazelles, mimicking the sexual phenotype characters of males, is proposed to explain both the diminished sex dimorphism of the horns in this subspecies, and its conspicuously gaudy display and shiny signal coat colours. While the horn ontogeny in female adda gazelles remains unstudied, female mhorr gazelles continued horn length growth during adulthood until old age, but males apparently did not or less so, further raising the complexity of horn shape evolution.

**Introduction**

The horn morphology of the Bovidae is subject to rapid phylogenetic transformation, and it provides excellent characters to infer the evolution and systematics of antelope subspecies, species and genera (e.g., Lydekker, 1914; Herre and Röhrs, 1955; Geist, 1971; Bubenik, 1990). At the same time, horns are of interest to ethologists studying the behaviour of male combat, intrasexual competition, and the releasers of sexual attraction. Functionally integrated into behavioural ecology, horn shapes often mirror adaptive microevolutionary change more finely than many other body traits. As simple structures horns are easy to measure, and they outnumber skulls, skeletons and skins in museum collections. Despite these advantages, the head appendages of antelopes remain underexplored when compared with the better knowledge of cervid antlers (Bubenik and Bubenik, 1990). The dama gazelle is a case in point, because its horn morphology has apparently never been investigated in detail. Taxonomists use to subdivide the dama gazelle into subspecies from skin pigmentation patterns exclusively, but no author has considered the horns (Lydekker, 1914; Andrae and Krumbiegel, 1976; Cano Perez, 1991). A current museum revision of dama gazelle morphology (Schreiber et al., *ongoing study*) is augmenting the hitherto fragmentary database. The present report concerns horn biometry, demonstrating that these head appendages are able to differentiate geographical populations which largely coincide with ac-

cepted subspecies, but partly also certain local populations not generally recognized in mainstream taxonomy.

Another likely function of differentiated horn morphology is the dissipation of excess body heat to the ambient air via the blood circulating in the ossicone (e.g., Taylor, 1966; Geist, 1971; Bubenik, 1990; Hoefs, 2000), without hindrance by an insulating hair coat or a dermal fat layer. The importance of horns in thermoregulation has been confirmed in selected species of the Bovidae (Taylor, 1966; Bubenik, 1990; Hoefs, 2000) but, surprisingly, antelopes from hot deserts have not been studied even though these may profit most from such support mechanisms for stabilizing body energy budgets. One would expect that gazelles from very hot deserts, such as the dama gazelle, which have to cope with a limited supply of drinking water for cooling the body via sweating or panting, might utilize this water-independent mechanism for emitting surplus heat (Taylor, 1972). Horn diameter, correlating with the volume of the ossicone in relation to their heat-dissipating surface area, is one important parameter in this context, and it can be studied easily in museum specimens.

The present contribution characterizes the horn morphology of the dama gazelle in a geographical context. This species is the tallest of all Antilopinae, and prior to widespread anthropogenic extermination it had ranged across North Africa, from the Atlantic coast east to the Nile River (Cano Perez, 1991). The dama gazelle used to roam chiefly in the subdesertic and Sahelian biomes, but it also utilized the true desert at least regionally and at times during migration (Estes, 1991a). In the tropical south, the original range comprised dry savanna biotopes,

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which the species occupied further southwards than is often assumed (Schreiber, 2021). Of the eight described subspecies most current authors recognize three in the absence of a detailed survey of the remaining, neglected ones that had never found the attention of a revisor (Cano Perez, 1991; Groves and Grubb, 2011). The red-necked or addra gazelle (*N. d. ruficollis*) inhabits one of the most severely hyper-arid biotopes of any antelope worldwide, i.e. the northeastern Sahara in Sudan (and prehistorically also in southwest Egypt, see Schreiber and Striedter, 2022) which, in conjunction with adjacent east Libyan deserts, represents the hugest, and one of the most severely arid, expanses of hot desert climate globally (Blümel, 2013). By contrast, the western subspecies *N. d. mhorrr* had lived, prior to its extinction in the wild, in less arid and less hot (sub)deserts in the west Saharan hinterlands of the Atlantic Ocean (in Morocco to Mauretania), where oceanic air masses temper the climate, attenuating the thermal amplitude and preventing hyper-aridity (Blümel, 2013; Médail and Quézel, 2018). The species therefore reflects the west-eastern ecological gradient from the maritime pre-desert to hyper-arid and hyper-thermic desert under a strong continental climate regime.

Previously, only Lange (1971) and Mungall (1980) had referred shortly to the horns of dama gazelles, but without commenting on subspecies. As a purely morphometrical study the present data cannot prove that the observed horn shape evolution is adaptive, but plausible hypotheses for the functional impacts on social and sexual behaviour, and on thermoregulation, can be derived, and these are proposed for subsequent tests by ethologists and physiologists. From a comparison with the closest outgroup species, Soemmerring's gazelle (*N. soemmerringii*), the polarity of the intraspecific character evolution can be inferred, so to reveal additional, and in this species much needed, insights into the species's phylogeny. The Soemmerring's gazelle is the pertinent outgroup, since the only other congeneric species complex, the Grant's gazelles (*N. granti* and relatives), is more distantly related to the dama gazelle (see Discussion). Nevertheless, the chosen outgroup suffers from a very incomplete overview of its geographical variation, *N. soemmerringii* being a polytypic yet taxonomically unrevised species (Matschie, 1912; Groves and Grubb, 2011; Chiozzi et al., 2014; De Francesco et al., 2020).

## Material and Methods

### Material

The study rests on the horns of  $n=256$  dama gazelles, among them  $n=140$  skulls with horns, stuffed skin mounts with horns or trophy horns in museums, and  $n=116$  published literature values. The specimens were measured by the author in the natural history museums at Frankfurt (Forschungsinstitut und Naturmuseum Senckenberg), Berlin (Museum für Naturkunde Berlin – Leibniz Institute for Evolution and Biodiversity Science), Bonn (Zoologisches Forschungsmuseum Alexander Koenig), Stuttgart (Staatliches Museum für Naturkunde), München (both Zoologische Staatssammlung Bayern and Institut der Universität München für Paläoanatomie), and Dresden (Forschungsinstitut und Naturmuseum Senckenberg) in Germany, Vienna (Naturhistorisches Museum) in Austria, Leiden (Museum Naturalis) in the Netherlands, Bruxelles (Musée des Sciences Naturelles) in Belgium, London (Natural History Museum), Birchington (Powell-Cotton Museum), and Tring (Natural History Museum) in the United Kingdom, and Paris (Musée national d'Histoire naturelle) in France. Dr. E. Moreno contributed biometric records from the skeleton collection of the Estación Experimental de Zonas Áridas at Almeria (Spain). Horn data for four specimens had been noted by the late Dr. Peter Grubb (London) at the Institut Fondamental d'Afrique Noire (IFAN) at Dakar (Senegal); these data were ceded to the present author from Grubb's legacy by his literary executor, the late Prof. Dr. Colin Groves (Canberra). Data for another  $n=116$  specimens were taken from the hunting trophy list published by the London-based taxidermy company Rowland Ward, but only records of curvature lengths, horn shaft circumferences, and distances tip-to-tip (Best et al., 1962; Best and Raw, 1973; data update until 2014 by courtesy of G. Damm, pers. comm.). This register rests on horn measurements of trophies of noteworthy quality contributed by

many hunters, implying the risk of methodically heterogeneous, subjective records. Nevertheless, data outliers were not observed in this list, and the circumference and tip-to-tip measures did not deviate in any way from our museum data. Still, the curvature lengths were shifted by 15% towards higher values for the geographically corresponding museum specimens, presumably because Rowland Ward had focused on sizeable hunting trophies and omitted weak ones. Therefore, all statistical analyses were performed twice, with and without the data from Rowland Ward, in order to exclude spurious conclusions due to methodic data heterogeneity; such an influence on biological or evolutionary conclusions was not observed.

Only the horns of adults were considered, which had reached the skull (body) size of full-grown dama gazelles and, if skulls were available, with the posterior molar teeth fully erupted. No measured horn showed traces of the forwardly recurved, crook-like head appendages of adolescents. Accordingly, all measured gazelles should have been at least in their third year of life or older. For many mhorrr gazelles from zoos the exact life ages could be taken from the studbook of this captive population (Domínguez, 2021).

### Nomenclature

The museum sample of *N. d. mhorrr* ( $n=69$ ) comprises individuals collected in Morocco, Mauretania and chiefly the West Sahara (= historical Spanish Sahara, Rio de Oro), and captive specimens bred from mhorrr gazelles imported into zoos from the north of West Sahara. The sample of *N. d. ruficollis* ( $n=59$ ) refers exclusively to horns collected in Sudan, i.e. the federal states of North Kordofan, Northern State, and North Darfur (all of them located west of the Nile valley), in addition to one skull from the Tibesti forelands in northeasternmost Chad. This region is inhabited by a morphologically coherent population which suits the type series of *N. d. ruficollis* from the Nubian desert south of Korti in Sudan (see Kock, 1978) in body pigmentation, skulls and horns (Schreiber, unpubl. data). Several zoological gardens and the ethologist Elizabeth Mungall apply the subspecies name *N. d. ruficollis* also to a breeding lineage in zoological gardens descended from decades-old imports from east-central Chad (Mungall, 2018), but all of those gazelles differ in head pigmentation from the Sudanese population without exception. On account of such differences to the Sudanese *N. d. ruficollis* on a qualitative level the present study — provisionally — does not extend the latter taxon into Chad (except Tibesti), and it omits the very few museum horns available from the Chad-derived zoo herd because of doubts concerning their taxonomic identity after many decades of captive breeding without genetic coordination, and on account of its immense hypervariability that hitherto escapes comprehension (natural hybrid belt of two morphs in Chad or undocumented cross-breeding of subspecies in zoos?). This zoo lineage is looking so extraordinarily variable that in any case the single specimens from it kept in museums would yield utterly incomplete and distorted data distributions failing to represent the real morphological diversity. The present data concerning dama gazelles from Chad therefore refer exclusively to wild-born museum specimens collected in this country (chiefly in the south and central east), and to the Chadian specimens from Rowland Ward's register (most from eastern north-central Chad). This lot is treated as an operational unit "Chad" rather than being assigned to a definite subspecies, which seems premature with present insights. However, the otherwise Sudanese *N. d. ruficollis* has also been collected in the Tibesti forelands of the far northeastern Chad, near the border triangle Chad/Sudan/Libya, and the very small sample from Tibesti is included here in the latter taxon.

Likewise, subspecies designations are avoided for the populations from the western and central Sahel zone (Senegal, Mali, Algeria, Niger, and Nigeria), intercalating between the ranges of *N. d. mhorrr* and the Sudanese *N. d. ruficollis*. Sometimes merged into a broadly and somewhat vaguely defined subspecies *N. d. dama* despite the absence of a sufficient taxonomic investigation of its variation (e.g. Cano Perez, 1984), various subspecies had been named from this vast area (*N. d. dama*, *N. d. permista*, *N. d. weidholzi*, *N. d. damergouensis*, or even the enigmatic *N. d. reducta*), each of them on the basis of

single or very few museum specimens, and none of them ever revised after their first description. Pending the results of an ongoing study (Schreiber et al., *unpubl. data*) these unrevised stocks are treated here without a subspecies designation, and they are designated provisionally as mere operational population units according to their countries of origin: (i) “Senegal/Mali” (n=9) for origins from north Senegal and south-central Mali; (ii) “Algeria/Niger/northeast Nigeria” (n=9) for gazelles from Bornu Province in Nigeria, central Niger (Damergou, Air), and the Ahaggar Mountains in Algeria; (iii) “Chad” (n=93) for individuals chiefly from east and north-central Chad.

The outgroup specimens of *N. soemmerringii* represent a selection of gazelles chosen to represent most of the range of this species. The eight specimens originated from (i) the Somali region of southeast Ethiopia, chiefly the vicinity of the city of Dire Dawa (n=5), (ii) the Ethiopian Hawash region (or possibly southern Somalia?) (1), (iii) Eritrea (1), and (iv) Sudan (2). Subspecies identifications seem premature in this insufficiently revised species (see Groves and Grubb, 2011; De Francesco et al., 2020).

### Treatment of captive specimens

The population sample of the extinct-in-the wild mhorr gazelles was dominated by animals which had been bred in zoos, in addition to few historical skulls collected in Africa. Since diverse statistical tests failed to distinguish the wild and captive cohorts, all specimens could be analyzed together.

### Measurements

Horn curvature length and horn shaft circumference were determined with measuring tape, and all other records with callipers. Lengths and circumferences represent the arithmetic means from measuring the left and the right horns of the same head whenever both horns were intact. Horn span and tip-to-tip measures refer to faultless, symmetrical horns only, and dysmorphic specimens were omitted. Curvature length specifies the entire course of the horn pedicle including its bends, but neglecting the surface corrugation of the keratinous sheath. The shaft circumference was determined at the base of the horn, where it is thickest. The inside width reflects the interspace between the left and right horn shafts, connecting the closest points of their inner bases. The outer width of horn bases connects the outer faces of the lower pedicles, where these are set most distantly from each other.

### Statistics

The statistical tests were calculated with the IBM SPSS Statistics Software Package in version 23 (International Business Machines Corporation, Armonk, New York, U.S.A.), and Statistica für Windows (Software-System für Datenanalyse), version 8.0 (StatSoft Inc., Tulsa, Oklahoma, U.S.A., 2007). Discriminant function analysis to calculate the percentages of correctly identified individuals to one taxon summed over, on a case-by-case basis, the probability of group adherence of all individuals to one of the compared groups. Factor analysis extracted principal components to confirm the previous results, and to visualize the cohort separation graphically. Factor analysis was performed without mathematical rotation of the dataset. In univariate statistics, Student’s t-tests were used as two-sample location tests of the hypothesis that the means of two population cohorts are unequal. Prior to such tests the normal distribution of data had been tested following Kolmogorov-Smirnov. If sample numbers did not suffice for a t-test, nonparametric U-tests of rank orders after Mann-Whitney or Kruskal-Wallis were employed.

**Index of sex-dimorphism:** The sex-dimorphism was formalized by indices which integrate all six horn shape variables for each individual into one notional value: after standardizing each male data record by subtracting from it the median values of every female horn shape variable (of the same genetic or geographical cohort), the thus standardized male measurements were averaged for individuals or populations, and multiplied by 100 in order to arrive at percentages, using this formula:

$$\text{sex dimorphism index in \%} = \frac{x_{v,t,m} - \bar{x}_{v,t,f}}{\bar{x}_{v,t,f}} \cdot 100,$$

where  $x_{v,t,m}$  are the measured horn shape variables of males from the taxa 1, 2, 3, 4, and 5, and  $\bar{x}_{v,t,f}$  is the median value of females of all data records from the same respective taxonomic cohort.

**Relative surface areas of horns:** To compare the relative horn surfaces of morphotypes (= ratio values of horn surface area  $S$  related to horn volume  $V$ ), a simplified model was employed, treating the horn pedicles as geometrical cylinders. This formula provides the surface-to-volume-ratio:

$$\phi = \frac{S}{V} = \frac{\pi \cdot r \cdot \sqrt{r^2 + h^2}}{\pi \cdot r^2 \cdot h}$$

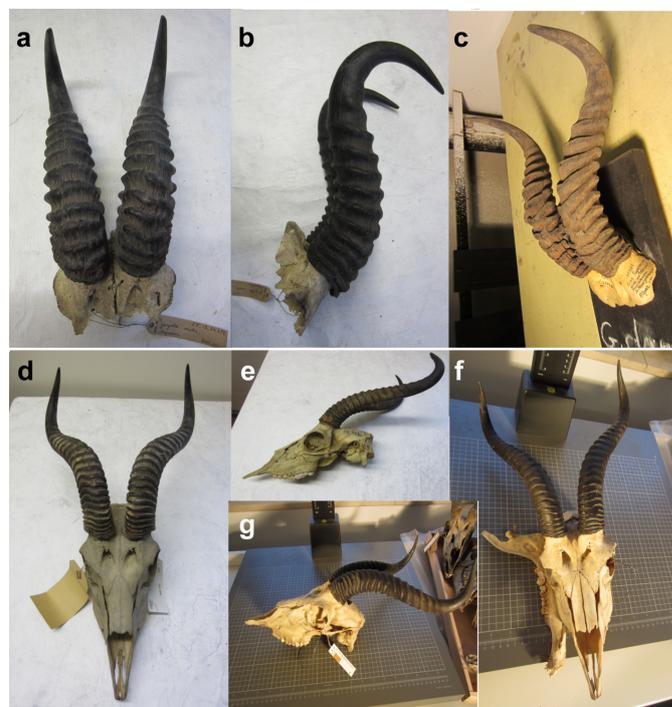
Where  $r$ =the radius of the circular base area of the cylinder (derived from the measured horn shaft circumferences) and  $h$ =the horn curvature length.

## Results

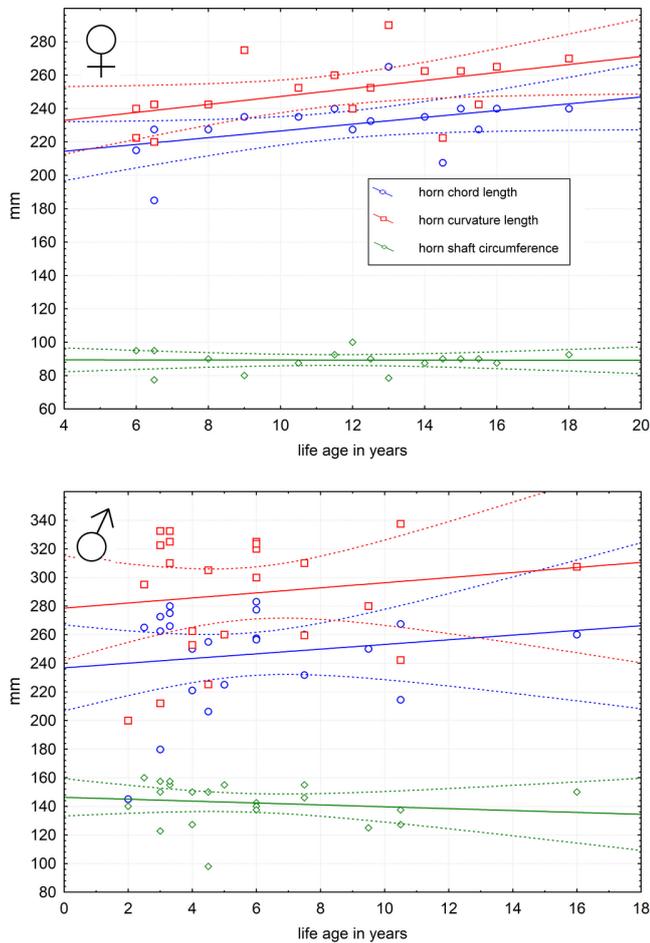
### Species-wide generalities

The horns of adult dama gazelles consist of three segments (Fig. 1): (i) the basal quarter of the pedicle proceeds steeply upward; (ii) the middle intercept turns backward, running almost parallel to the skull roof, likewise protruding sideway; (iii) the apical third is a curved spike with the tip upturned. Up to approximately 20 grooves and ridges cover the basal two thirds of the horn sheath. Horns are roundish oval in cross section, compressed transversely (medio-laterally), with the longer diameter axis aligned in the sagittal body plane.

Immature dama gazelles have differing horns, consisting of rounded hooks bent forward. These crooks correspond to the apical spikes of the adults, which overcome the juvenile stage by preferential intercalary growth of the shaft. Due to a shortage of juvenile museum specimens all following data refer to adults. The life ages of age-dated museum horns from 17 adult female mhorr gazelles from zoo herds indicate continued horn growth in this sex during adulthood, and until



**Figure 1** – Horn morphologies of the dama gazelle (*Nanger dama*). **a** and **b**: Holotype of *N. d. mhorr* (Natural History Museum, London, BM 55.12.20.279) from the basin of the Oued Nun dry river in Morocco. **c**: *N. d. mhorr*, from north of Mbout, Mauretania (Naturkundemuseum Berlin, ZMB-Mam-41201). **d**: and **e**: *N. d. ruficollis* from north Kordofan, Sudan (Natural History Museum, London, BM 58.176). **f** and **g**: Lectotype (Naturmuseum Senckenberg, Frankfurt, SMF 16010) of *N. d. ruficollis*, from Korti (Nubia), Sudan (see Kock, 1978).



**Figure 2** – Growth curves of three horn characters in adult female (upper graphs) and adult male (lower graphs) mhorr gazelles from many museums, whose life ages could be determined from the studbook for the zoo-living herds (Dominguez, 2021). Abscissae: Life age in years, only specimens of the age categories “fully adult” (= older than two years until seven or eight years) and “old adult” (= older than seven/eight years) are shown (for these age categories see Mungall, 2018). The solid lines indicate the linear regression functions of the horn characters, and the dotted lines their respective 95% confidence bands. The increasing increments of chord and curvature lengths during female adulthood are supported by a marginal statistical significance of  $p=0.05$  (Pearson or Spearman correlations), but the regression lines for male gazelles, and the one for the horn circumference also in females, are not significant.

old life ages ( $p=0.05$  for both Pearson and Spearman correlations of horn chord and curvature lengths with life age), but 23 age-dated male mhorr gazelles, also from zoos, did not reveal further horn growth after maturity (Fig. 2).

The horns of the dama gazelle are broadly sex-dimorphic, and the 193 males and 63 females require separate statistics. Species-wide (Fig. 3), the horn shafts of males are thicker by 153.6% compared with females, more widely protruding sideways by 138.4%, longer by 124.7% in curvature length, and the left and right pedicle tips are further aloof by 132%; the outer horn base width is augmented in males by 123.4%. Only the inside width between the left and the right horn shaft falls behind in males by 22.9%, since the thicker male beams approach each other. In return the female horns are shorter, thinner and less divergent. All these sex differences are highly significant with  $p<0.0001$  for every single character (t-tests). The shorter curvature length of females, their reduced lateral span and their smaller distance tip-to-tip overlap marginally with a few exceptionally small males; the sex-wise tip-to-tip distances overlap slightly more. The horn diameters and the widths between the outer horn flanks are very far out from any overlap, female values being lower on a qualitative scale.

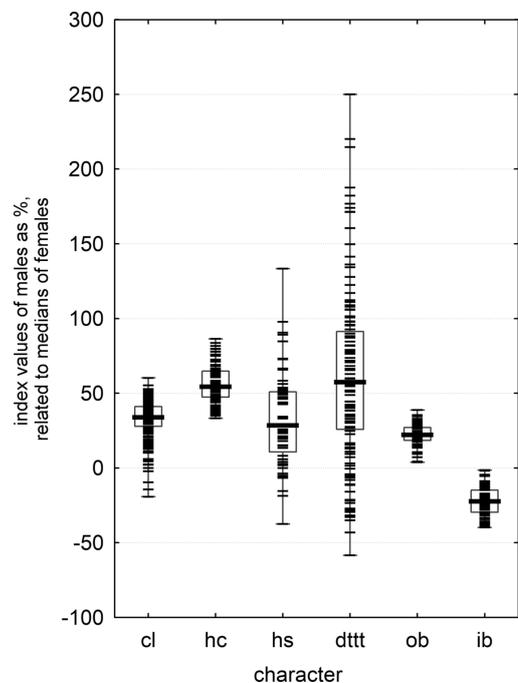
### Two horn morphotypes of *N. d. mhorr* and *N. d. ruficollis*

Two horn morphologies (Fig. 1, 4), henceforth designated as *mhorr*- and *ruficollis*-morphotypes, differentiate the two eponymous subspecies (Fig. 1, 4). The *mhorr*-morphotype is thoroughly diagnostic for the

subspecies *N. d. mhorr* in Morocco, Western Sahara, and Mauritania. The *ruficollis*-type is centered on *N. d. ruficollis* in northwest Sudan, where it reaches a high proportion in the population, but it also spreads proportionately westwards, into populations from adjacent Chad (which however differ from *N. d. ruficollis* by displaying a complex head pigmentation). Those few *N. d. ruficollis* which do not display the full *ruficollis*-horn type do not necessarily approach or even match the *mhorr*-phenotype, but partly deviate in other directions.

In males both morphotypes differ significantly in each measurement recorded (Tab. 1) except the outer horn width. Neither differed the beam flexure calculated from the raw measurements (= quotient resulting from curvature length and straight chord length). Discriminant function analysis (Fig. 5) separates the two types completely and reveals a diagnosability of the *mhorr*-phenotype of 95.6% (in  $n=23$  male *N. d. mhorr* with complete measurements) or 88.6% (in  $n=43$  specimens with a few data gaps), against a diagnosability of the *ruficollis*-phenotype of 77.8% (in  $n=9$  male *N. d. ruficollis* with complete data) or 76.9% (in  $n=52$  specimens with single gaps in their data records). The *mhorr*-phenotype is thus better defined, presumably on account of a higher horn shape variability of *N. d. ruficollis*. Factor analysis (Fig. 6) confirms this separation, albeit with a minor overlap: three principal components, explaining 39.7% (PC 1), 28.0% (PC 2), and 16.7% (PC 3) of the male shape variance, were determined chiefly by horn span, tip-to-tip distance and curvature length (PC 1), horn circumference and the outer width of the horn shafts (PC 2), and the distance tip-to-tip (PC 3). All PCs contribute to the separation, and most horn measures load significantly on the PCs, indicating that both morphs are broadly based.

The horns of females mirror the male pattern with only few differences in detail. 91.4% of  $n=35$  female *mhorr*- and 70.0% of  $n=10$  female *ruficollis*-phenotypes are diagnosable by discriminant functions (Fig. 5). The averaged female diagnosability (86.7%) moderately supersedes the separation observed in all males, and again the *mhorr*-phenotype is better defined. Factor analysis produced two principal components, explaining 46.2% (PC 1) and 26.1% (PC 2) of the female variance (Fig. 6), PC 1 being determined chiefly by curvature length, horn span and the distance tip-to-tip, while tip-to-tip distance and outer horn base width impact on PC 2. Both PCs cooperate concordantly in

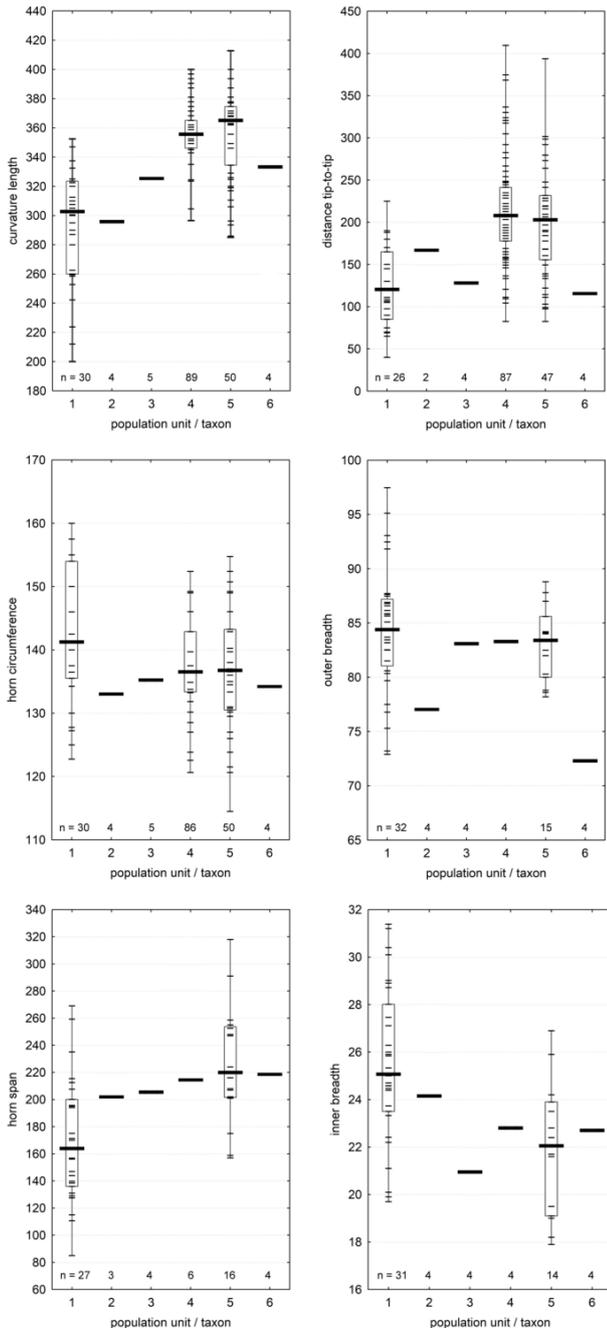


**Figure 3** – Sex-dimorphism in the horns of the dama gazelle (*Nanger dama*). Axis of abscissae: Horn measurements. Cl: curvature length. hc: horn shaft circumference. hs: lateral horn span. dttt: distance tip-to-tip. ob: width between the outer lateral flanks of horn shafts. ib: inside width between left and right horn shafts. Ordinate: Percentage values showing how much the various horn measurements of males supersede (positive values) or fall short of (negative values) the median of the respective character in females. In this plot, the dama gazelles from all subspecies or regional cohorts are combined.

**Table 1** – Differentiation of the horns of the *mhorr*- (n=35) and the *ruficollis*-morphotypes (n=52) in male dama gazelles.

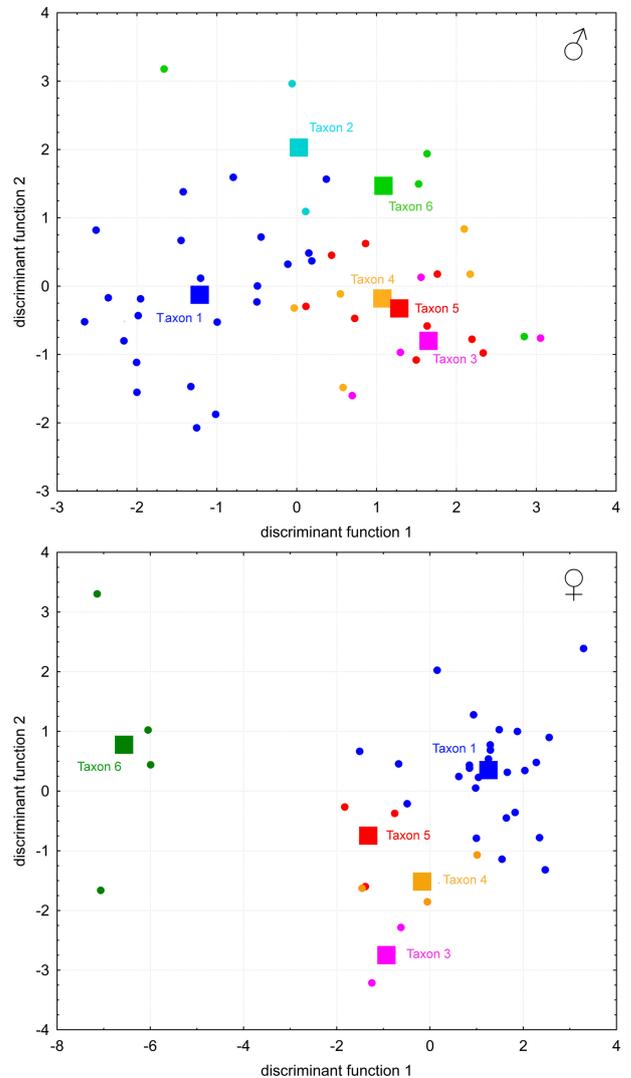
	<i>mhorr</i> -phenotype (medians in mm)	<i>ruficollis</i> -phenotype (medians in mm)	differences (as percentage)	t-test
lateral horn span	167.9	226.2	-25.8 %	$p < 0.0001$
horn shaft circumference	142.8	136.9	4.0 %	$p < 0.01$
curvature length <sup>a</sup>	290.8	324.7	-11.7 %	$p < 0.00001$
inside shaft width	25.5	21.9	16.3 %	$p < 0.001$
distance tip-to-tip	128.2	199.7	35.8 %	$p < 0.00001$

<sup>a</sup> The difference of the curvature lengths rises to -21.9 % (354.5 mm in *ruficollis* versus 290.8 mm in *mhorr*) if the heads of trophy quality supplied by Rowland Ward (Best et al., 1962; Best and Raw, 1973) are included (see Methods section).

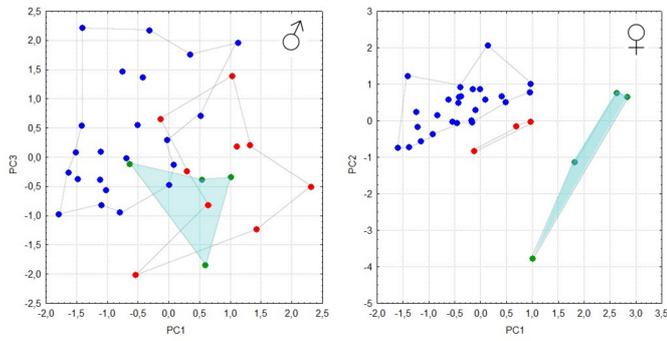


**Figure 4** – Horn shape in geographical/taxonomic groups male dama gazelles (population units 1–5) and Soemmerring's gazelles (population unit 6). Black horizontal bars denote median values, boxes comprise the central 50% of values and the attached whiskers the 25% of the largest and smallest values respectively. Boxplots are shown only if the sample size exceeds n=10 specimens per cohort. Population units/taxa: 1 *N. d. mhorr*, Morocco/West Sahara/Mauretania. 2 Senegal/Mali. 3 southeast Algeria/Niger/northeast Nigeria. 4 Chad. 5 *N. d. ruficollis*, Sudan. 6 *N. soemmerringii*. The numerals at the bottom of the plots represent the specimen numbers measured per population unit.

grouping the female morphotypes, which also rest on a broad character set. The sorting characters are similar in both sexes, but horn thickness is less important in female gazelles. Three characters, i.e. curvature length (248.8 mm in the *mhorr* — versus 259.8 mm in the *ruficollis* — phenotype;  $p=0.067$ ), horn circumference (88.5 mm versus 84.5 mm;  $p=0.1$ ), and tip-to-tip distance (106.4 mm versus 129.0 mm;  $p=0.17$ ), failed to differentiate the female morphotypes in t-tests, against only one in males (outer width). By contrast horn span (140.7 mm versus



**Figure 5** – Canonical discriminant function analyses of six horn shape variables in male (upper plot) and female dama gazelles (lower plot). Plotted are the scores of the first two discriminant functions for 46 individual gazelles representing the taxonomic/population units numbered as explained in the caption of Fig. 4. The numerals 1–5 and the corresponding coloured symbols denote population units of the dama gazelle, and 6 and the green symbols the Soemmerring's gazelle as an outgroup species. The small dots represent individual animals, the large squares are the group centroids of the six cohorts. In males the two plotted functions explain 89.7% of the total data variance, and in females 98.9% of it.



**Figure 6** – Factor analysis of six horn shape characters in male (left) and female (right) dama gazelles, showing two principal components (PC) for each sex. Blue dots denote *Nanger dama mhorri*, red dots *N. d. ruficollis*, and green dots *N. soemmerringii*. The factor space of the latter species is emphasized by shading in light blue. For explanations, see text.

164.8 mm;  $p=0.03$ ), inside width between the horns (31.7 mm versus 29.9 mm;  $p=0.02$ ), and outside width between the external horn flanks (70.2 mm versus 65.6 mm;  $p<0.0001$ ) support the female morphotypes significantly, the last measure in contrast to the males.

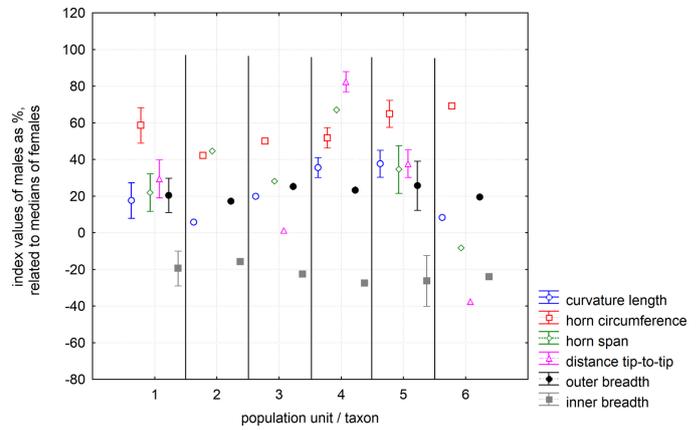
The two horn morphotypes correlate with craniometric subspecies differences, of which only a few with direct relevance for the frontal appendages are provided here: *N. d. ruficollis* has a reduced length of the skull roof (distance nasion toinion;  $p<0.0001$ ; only males testable due to insufficient female samples) and minor measures of braincase breadth ( $p=0.02$ ), biorbital breadth ( $p=0.005$ ), and zygomatic breadth ( $p=0.0001$ ) (t-tests throughout), so that the longer horns of the eastern subspecies rest on a shorter, narrower and less voluminous braincase. Total skull length, basal length or condylobasal length of the two subspecies do not differ in males (t-tests of males; females untestable due to insufficient specimens). Neither is there a significant correlation of horn lengths with crude estimates for shoulder heights (length of forelegs plus body height up to the withers measured in flat museum skins) or published values for the body weights of the two concerned subspecies (see Discussion).

### Morphotype-wise sex dimorphism

The two referred subspecific horn types differ in the intensity of their sex-dimorphism, regardless of whether the horn characters are tested individually or all of them combined. Fig. 7–8 visualize the combined sexual differentiation per population unit/taxon, indicating that male *ruficollis*-morphotypes outperform their female counterparts more than do horns of the male *mhorri*-type their respective females. This difference is statistically significant at  $p<0.0001$  (Mann-Whitney U-test, Kruskal-Wallis). The elevated sex-dimorphism in *N. d. ruficollis* is evident in each horn shape variable separately, but is particularly prominent in horn curvature length and horn span.

### Horn surface areas relative to horn volumes

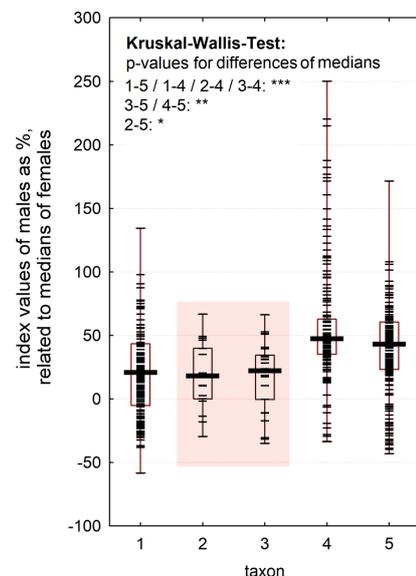
Assuming a crudely approximative model of the horn pedicles as ideal geometrical cylinders, males of the *mhorri*-morphotype have a lower cylinder volume (4857.8 mL), lessened by 12.9%, with a decreased horn surface area (42.8 cm<sup>2</sup>) lessened by 14%, compared with values of 5485.9 mL and 49.9 cm<sup>2</sup> in the *ruficollis*-morphotype. The longer and thinner horns of the latter have a relative surface area increased by 3.2% over the horns of the western subspecies. Female *N. d. mhorri* have a larger model horn volume (1551.2 mL), increased by 5%, and a weakly augmented surface area (22.02 cm<sup>2</sup>), increased by 0.3%, compared with 1475.9 mL and 21.95 cm<sup>2</sup> in the female *ruficollis*-phenotype. Females of the eastern subspecies, therefore, have their relative horn surface augmented by 4.7% over female *mhorri* gazelles. One may hypothesize a moderately increased heat dissipation via horns in addra gazelles over *mhorri* gazelles in both sexes. Moreover, a weakly raised relative horn surface area of females over males is observed in each subspecies.



**Figure 7** – Plot to illustrate the population- or taxon-wise sex dimorphism in the dama gazelle. The coloured symbols depict the median index values of male horn measurements (as explained at the right margin) in relation to the medians of the respective female cohort from the same population unit. Positive index values indicate that males have horn variables larger than females, and negative indices that male values fall short of those in females. The colour symbols indicate the median values, and their whiskers the 95%-confidence interval, if specimen numbers supersede  $n>10$  for a respective cohort. The population units are numbered in the axis of abscissae as explained in Fig. 4, i.e. 1-5 represent five taxonomic/regional subgroups of the dama gazelle, and 6 denotes the outgroup species, Soemmerring's gazelle.

### Additional horn morphotypes in dama gazelles from the Sahel zone?

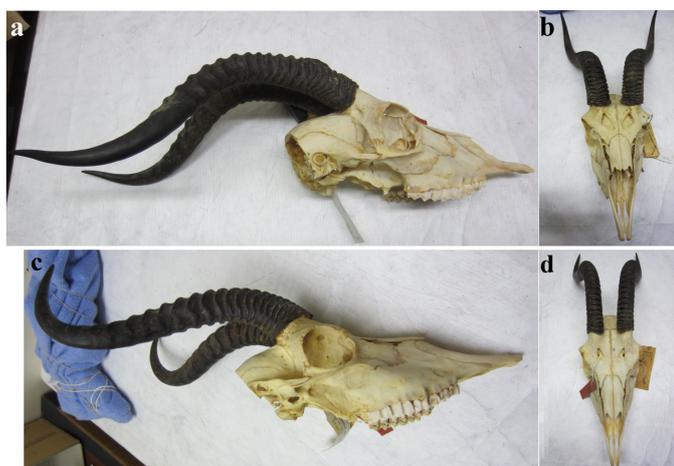
The paucity of study samples from the west and central Sahel zones (often combined in recent literature into one broadly conceived and vaguely defined *N. d. dama*, see Cano Perez, 1991) precludes most statistics of their subspecies assignment, which must be left unresolved. Therefore, the gazelles from this geographical vastness (“*N. d. dama* sensu lato”, op. cit.) are grouped provisionally into operational population units (see Methods), i.e. (i) Senegal and Mali, (ii) east Algeria, central Niger and the Bornu Province of adjacent Nigeria, and (iii) Chad (except Tibesti). The horns of all these units approach the *ruficollis*-morphotype more or less in both sexes, despite minor local



**Figure 8** – Degrees of sex-dimorphism of horn shape in five geographical populations of the dama gazelle. Axis of abscissae: same subspecies or population units (1–5) as explicated in Fig. 4. The two cohorts shaded in the pink field rest on few specimens, so that their data appear less well supported. Ordinate: index values expressing the horn parameters in males (averaged over all six horn characters) relative to the combined median values of females from the same regional cohort. The boxes comprise the central 50% of measured animals for each cohort, and the peripheral whiskers the 25% upper and the 25% lower range records. Broad crossbars amidst the boxes indicate the median values, and the many fine bars are records of individuals. The different median values of the five cohorts are authenticated by Kruskal-Wallis tests, whose significance levels are as follows: \*\*\*:  $p\leq 0.001$ ; \*\*:  $0.001 < p\leq 0.01$ ; \*:  $0.01 < p\leq 0.05$ .

deviations (Fig. 4–9). This intra-Sahelian microheterogeneity, usually evident best from sensitive multivariate statistics rather than by macroscopic, visual inspection of the specimens, may possibly be explicable by the chance preponderance of single, slightly deviant individuals in the invariably small population samples, but it could just as well reflect a degree of regional stock differentiation. A continent-wide, west-eastern morphocline is not observed, but possibly a limited degree of local horn shape peculiarity in each of the Sahelian population units. In Chad, 50 % of the males and one third of the females assigned to their own regional (Chadian) unit, while the important remainders grouped with the *ruficollis*-type from Sudan. This westward introgression of *ruficollis*-horns from their areal center in Sudan into Chad seems to terminate somewhere near the western boundary of Chad to Niger (or within Niger?). The unit “east Algeria, Niger, Nigeria” contains the most distinctive of the Sahelian cohorts, classifying as a local cluster of itself in all females, whereas 25–50 % of the regional males are not grouped safely by discriminant functions to their own, on account of a, albeit weak, similarity to the *ruficollis*-type.

The minute museum series from the Damergou district in Niger, home to a population once proposed as the subspecies *Gazella dama damergouensis* Rothschild 1921, consisted of 2–3 males (Fig. 9a, b) with longer and more profoundly curved horns (mean chord length 282 mm, curvature length 347 mm) than observed in eight bucks (chord 253 mm, curvature 319 mm) from surrounding populations sampled at distances of a few to several hundreds of kilometers around. The male horns from Damergou also protruded further sideways (horn span 231 mm versus 195 mm) and their shafts were set more distinctly parallel to each other than in surrounding populations, although even so the tip-to-tip measure was augmented (196 mm versus 146 mm). The single female pair of horns of the Damergou-series (Fig. 9c, d) was likewise elongated (chord length of 278 mm, compared with 248 mm in seven females from surrounding regions), and more profoundly curved (curvature length 321 mm against 273 mm). The geographically closest museum specimen to Damergou, from Zinder in Niger (ZMB-Mam-49101; museum at Berlin), is a juvenile without yet the adult horn morphology, while several more skulls from a few hundred kilometers or more farther off (Air Mountains in Niger, Bornu Province in Nigeria, Lake Chad, east-central Algeria) consistently have shorter and thinner horns. Insufficient samples preclude most statistical tests, but in discriminant function analysis all specimens from Damergou were separated from every horn specimen from the Air Mountains (n=5–6), the Bornu Province of Nigeria (n=4), the western shores of Lake Chad (n=7), and from the Ahaggar Mountains (n=2) in Algeria.



**Figure 9** – Horns of the type specimens of “*Gazella dama damergouensis* Rothschild 1921” from the Damergou district in Niger, stored at the Natural History Museum, London. **a, b:** The male type skull (BM 39.2538) in lateral and frontal views. **c, d:** Female syntype (BM 28.2539) in similar perspectives. These types have thicker horns which are also longer in proportion than in dama gazelles from surrounding areas, and their shafts are set rather parallel with less lateral protrusion. The validity of this subspecies, also proposed for differences in skin pigmentation (Rothschild, 1921), seems possible, but cannot be confirmed by the very few samples known so far.

The population unit “Senegal/Mali” proved somewhat distinctive from all others too; it exhibited no influence any more from the eastern *ruficollis*-phenotype, but a subordinate affinity to the *mhorr*-phenotype in males (whereas none assigned to this phenotype in females), which cannot be quantitated in the minute sample series. Apparently, the *mhorr*-morphotype has expanded but little into the populations of Senegal and Mali, but it is largely restricted to the range of *N. d. mhorr* (Morocco, Western Sahara, Mauretania) itself.

### Comparing intra- and interspecific differentiation

The overriding phenetic divide within the dama gazelles separates the horns of *N. d. mhorr* from those of all other populations/subspecies. However, discriminatory analysis reveals a second, albeit more weakly expressed division, because the population unit “east Algeria/Niger/Nigeria” is completely free of any influence of the *mhorr*-, and predominantly devoid of an influence of the *ruficollis*-clade. This central Sahelian population unit thus intercalates, as a centrally located hinge, between the two bidirectionally radiating clades, whose terminal morphologies are fully attained only in Morocco or in Sudan respectively. The intensity of sex-dimorphism (Fig. 7) reflects the same central separation hinge, and confirms it, with a salutation in this additional character discernible between the unit “east Algeria/Niger/Nigeria” and “Chad”; all these population differences of the sex-dimorphism are statistically significant (Fig. 8).

Four male and four female *N. soemmerringii* are correctly identified as the outgroup species in multivariate comparisons (Fig. 5–6), but more so in females (Fig. 5), while in the male sex the species differences do not notably transcend the distinction between the intraspecific dama gazelle morphotypes (Fig. 5). Discriminant functions show perfect species diagnosability of 100 % in females but of only 50 % in males, with just one out of two male Soemmerring’s gazelles diagnosable to the proper species but the others assigned to dama gazelles from “Senegal/Mali” and “east Algeria/Niger/Nigeria”. This trans-specific similarity of males identifies the intraspecific differentiation of the male *mhorr*- from the male *ruficollis*-morphotype as being quite substantial in relation to the barely better distinction of the sister species. Overall, the horns of Soemmerring’s gazelles resemble more the *ruficollis*- rather than the *mhorr*-morphotype (Fig. 5), the latter being more distinct in all aspects. The horns of the west Sahelian dama gazelles (population unit “Senegal/Mali”) were the most similar ones to the sister species, rather than those of *N. d. ruficollis* which is the geographically closest subspecies living next to *N. soemmerringii*. Horns of male Soemmerring’s gazelles even intercalate between the *mhorr*- and the *ruficollis*-phenotypes in factor analysis, adjoining the dama gazelles from Senegal/Mali and Niger (Fig. 6), on the basis of chiefly horn span, tip-to-tip distance and curvature length (PC 1 explaining 39.7 % of the variance). These results are consistent with a (west, west-central) Sahelian center of intraspecific horn shape evolution in the dama gazelles, and with two bidirectionally divergent clades of derived horn shapes radiating from a plesiomorphic character state found in the Sahel, evolving from there towards the northwestern and the eastern species range boundaries.

## Discussion

### No allometric covariation of horn size

The horn length of antelopes correlates with their body size according to Popp (1985), and therefore the longer-horned *ruficollis*-morphotype could indicate nothing more than a passive allometric relationship. Prior to any functional interpretation of the different horn shapes in dama gazelles, it is therefore reasonable to evaluate if horn size and body size correlate. However, Popp’s (1985) proxy for body size were shoulder height estimations taken from scattered literature, measured by field biologists or hunters with unspecified methods and in unknown specimen numbers, and probably many of the body size data rested on very few individuals. As such, Popp (1985) allometry function can only be tentative, and perhaps it is inappropriately crude for subtle, intraspecific comparisons. The shoulder heights of the dama gazelle subspecies

are unknown, but flat museum skins assessed in our museum study can yield approximations: such shoulder height estimates from flat skins for *N. d. mhorrr* did not differ from those for *N. d. ruficollis*, arguing against an allometric correlation of horn size with shoulder height. However, most museum skins of *N. d. mhorrr* were tanned recently from contemporary zoo specimens, and typically consisted of soft, flexible buckskin leather, whereas all measured skins of *N. d. ruficollis* were historically old, dried or salted and often hardened specimens; deformation by taxidermy may thus bias the derived shoulder height estimates. Body weights might be more pertinent to test the allometry, because the body masses of two bucks clashing during a fight are the paramount determinants of the mechanical stress affecting the horns (Kitchener, 1985). Body weights of 65 kg for male and 60 kg for female *mhorrr* gazelles were reported for a captive herd (Barbosa and Espeso, 2005), and of 55.8 kg in male and 40.9 kg in female eastern dama gazelles from Chad, which had been raised on a ranch in Texas (Mungall, 2018). These data suggest a weightier western subspecies, contradicting a suspected allometry of horn length and body sizes. However, body mass data for captive specimens do not necessarily refer to wild dama gazelles which are not fed ad libitum with a nutrient-rich diet. In the present case, therefore, certain craniometric measurements emerge as the most pertinent proxies for body size. Craniometry (Schreiber, *unpubl. data*) reveals a significantly shorter length of the skull roof and shorter braincase breadth, biorbital breadth, and zygomatic breadth in *N. d. ruficollis* than in *N. d. mhorrr*, so that the longer horns of the former rest on a reduced cranial fundament, i.e. a shorter, narrower and in general less voluminous posterior skull. Additional length data such as total skull length, basal length and condylobasal length are statistically equivalent in males of both subspecies (t-tests; females untestable due to insufficient specimens), but all of these cephalic lengths are numerically (albeit not significantly) smaller in *N. d. ruficollis* than in *N. d. mhorrr*, rather than larger as would be expected in the case of allometric covariation with horn size. Obviously, the two described morphotypes are not merely passive, allometric correlates of head or body sizes, but they are uncorrelated designs sui generis. This makes a discussion worthwhile of possibly adaptive, functional differentiation of the subspecific horn shapes.

### Functional implications: fighting behaviour

A broad consensus allocates the main functions of antelope horns to their roles in intraspecific combats among male rivals and in intimidation displays. Additional functions, like the use of horns in defense against predators or as tools to manipulate food objects or to poke the soil, have been confirmed occasionally, but are of secondary importance (Geist, 1966a; Schaffer, 1968; Walther, 1968; Leuthold, 1977; Estes, 1991a, 1999; Lundigran, 1996; Caro et al., 2003).

Horns serve primarily as sparring tools in fights between males competing for territories or females, or other resources. Different horn morphologies therefore propose, first and foremost, different fighting techniques among the subspecies. There are three overriding functions of horns in this context: (i) to deal out blows versus the adversary, and to absorb his blows without a mechanical damage to the recipient; (ii) to serve as sparring gear, for example when the opponents gauge their strength by wrestling or pushing with the horns mutually interlocked; (iii) to warrant safety during interlocking by preventing slippage of the opponent's spikes towards one's own body, with all the risk of trauma implied (Walther, 1968, 1979). Horn shapes must be adapted to all these roles by design and robustness, not least in order to guarantee mechanical stability and prevent rupture. A biomechanical analysis of fighting in dama gazelles would be desirable to interpret the subspecific horn morphotypes. Such biomechanical studies are unavailable, and they are rare even for all Antilopinae and Bovidae. Kitchener (1985) estimated the liability of many bovid horns to breakage during fights, including dama gazelles of unspecified subspecies: he found this species to rank in a group of bovids having horns with a low resistance to bending stress, lower than in many other antelopes. According to this author, the diameter of the horn base is crucial for protection against bending and shearing stress.

The concrete vital parameter is the second moment of area of the horn base, a value calculated as a fourth power function of the horn base radius, because this value determines the resistance of a beam against deformation and rupture. The two horn morphotypes of the dama gazelle differ primarily just in this key factor, i.e. basal horn shaft diameter, as plausible evidence that their robustness might differ. There is the visual impression that the stouter, more parallel horn shafts of the *mhorrr*-phenotype resemble a thrust weapon able to exert effective strokes or, in passive fights, serve as a battering ram able to absorb massive blows by the adversary. If the limited body weight data available for dama gazelles (see above) are correct, the *mhorrr* gazelles are (potentially considerably?) weightier, supplying them with more thrust to deal out powerful blows than occurs in the (potentially much less?) less weighty *N. d. ruficollis*. On the contrary, the thinner pedicles and the augmented tip-to-tip distance of the more lyrate and presumably more fragile *ruficollis*-phenotype appear to be inferior tools to exert or to absorb blows, but at the same time two facing fighters might interlock such horns more efficiently with the opposing structure of the adversary, in order to fix the position of the two fighters during sparring (limiting the risk of injury by horn slippage).

These ideas propose that *mhorrr* bucks could be preferentially fighters of the ramming type, and addra gazelle bucks rather wrestlers, sparring with the horns mutually interlocked. This interpretation implies an analogy of the two dama gazelle subspecies with the relation found among several (sub)species of Alcelaphinae or Caprinae, where for example the impressive impact weapons of lelwel hartebeests (*Alcelaphus buselaphus lelwel*) or bighorn sheep (*Ovis canadensis*) diverge as evident mechanical adaptations for powerful ramming from the thinner and lyrate hooks of Swayne's hartebeests (*A. b. swaynei*) or urials (e.g. *Ovis cycloceros*). If these comparisons are pertinent, the *mhorrr*-morphotype of the dama gazelle would be unusual among the Antilopinae, in which no other examples of horns specialized for battering seem to be known. One must appreciate, however, that the horn designs of dama gazelles diverge less than the more impressively specialized alcelaphine and caprine examples. We conclude differences likely on a certain quantitative rather than on a qualitative level between the fighting behaviours of the two subspecies of *N. dama*; this hypothesis should be tested by quantitative studies counting the frequencies of the likely many kinds of combative actions observed in either taxon.

More detailed predictions of form-function relations are difficult: Mungall (2018) reported several body positions of fighting dama gazelles, but the implied biomechanics has not been studied. However, many elaborate descriptions of fighting styles in other gazelles permit broad generalizations for the Antilopinae (Walther, 1964, 1965, 1966, 1968, 1979, 1995; Walther et al., 1983; Estes, 1991a, 1999; Leuthold, 1977). According to this evidence, fighting in gazelles is not narrowly specialized, but employs a range of body positions, and the horns of gazelles must be prepared to sustain mechanical stress from many angles and directions. Not surprisingly, therefore, their horn bases are roundish in cross-section, even though they are not ideally circular at the base but flattened, elliptical cylinders whose longer axis aligns with the sagittal body plane. This orientation suggests mechanical stress prominently in the sagittal plane, according to force loads either from the front or the rear. Both directions correlate with two common fighting positions of male gazelles: either the opponents oppose each other with their heads and horn tips vis-à-vis, dealing blows against the horn front of the opponent, stressing the pedicles backward, or the opponents face each other with lowered heads, repelling each other with the horns anchored and interlocked amidst the adversaries. In this case the horns take a horizontal position almost parallel to the substratum, being employed to lever out the opponent's horns from bottom up, in order to overthrow him. In this bottom-up posture the horns of the subordinate male are stressed in forward direction from behind. Not rarely, two opponents may also collocate side by side in parallel, lumping together their necks and horns sideways and interlocking them in collateral stance; in this case the lateral flanks of the horn shafts are stressed. Frequently, different fighting modes will crop up in combination. Variable fighting styles, comprising also additional modalities not recoun-

ted here, are so characteristic of all investigated gazelles that likely the same multitude might equally apply to the less-studied dama gazelle. The more robust horns of *N. d. mhorri* are compatible with a higher intensity of combat in all these techniques, because their roundish-oval horn shafts are stronger, predisposing against rupture in most conceivable contingencies.

Horns play another, important function in social behaviour, namely as visual cues and releasers of behaviour responses, being symbols for the proud display of male rank and fitness to a rival or to females (Geist, 1966a; Walther, 1968, 1979, 1984). This symbolic function is well confirmed in very many antelopes, chiefly in threat, dominance and intimidation displays, which usually imply head-high postures with the horns turned towards the challenger (Walther, 1968, 1984; Leuthold, 1977). Gazelles carry their neck and head in a more steeply upraised position than do many other antelopes (Walther, 1968), wherefore their horns may be particularly conspicuous visual releasers. Mungall (2018) exemplified the “head flagging” of male dama gazelles in this context, which may be homologous to a similar “head-high posture” in the Grant’s gazelle (Walther, 1965, 1995; Estes, 1991a, 1999), whose bucks try to impress their adversaries by turning their head and horns in a raised posture offensively towards them; in *N. granti* this display was found as common as were real combats (Walther, 1965, 1968). Head-flagging ostensibly displays the front body pole with the horns and the neck which, remarkably, in *N. d. ruficollis* is emphasized by darkened brownish pigmentation in contrast to the otherwise whitish body, instead of that in *N. granti* by anatomical thickening of the neck (Estes, 1991a), or in lieu thereof in the male gerenuk (*Litocranius walleri*) by facultative thickening of the neck (by an unknown mechanism of apparent “neck inflation”) visible during the mating displays only (Ullrich, 1963). When driving the wooed female, courting males of many gazelles display ostensive head postures too (Walther, 1968; Estes, 1991a), particularly so the males of the dama gazelle (Mungall, 1980). Even less than in the case of fighting techniques is there any sound evidence to claim or to doubt intraspecific differences in the role of horns as optical releasers, and either of the two morphotypes of the dama gazelle horns may be a “better” releaser in various contexts of animal psychology: however, despite such uncertainties we have to come back to this putative signal function when discussing a bearing of the theory of andromimicry evolution for horn morphology.

### Functional implications: thermo-physiology

A thermoregulatory role of horns has been demonstrated for selected bovid species and may be a vital adaptation in many more, despite limited research on tropical antelopes. The pioneer study by Taylor (1966) on the domesticated goat was arguably the first to confirm the important role of the horn blood circulation in the meshwork of fine blood vessels on the ossicone, derived from the Arteria temporalis, whose blood stream can be regulated depending on the ambient air temperature: vasoconstriction of the horn vessels conserves body heat, but vasodilatation dissipates surplus heat via the horn surface if the temperature of the horn supersedes the air temperature. The ossicone vessels are not insulated from the environment by layers of subcutaneous fat or a hair coat, but merely by thin fibrous tissue and by the keratin layer of the horn sheath, facilitating the export of heat. Taylor (1966) measured that a goat emits 3 % of its metabolic heat via the horns at an ambient heat of 30 °C with wind (which increases heat export via the horns), this amount rising to 8 % under exercise. Geist (1971) reported rather warm horns in heavily exercised bighorn sheep. Taylor (1966) extrapolated, by calculating the horn surface areas for additional species, that most Bovidae should radiate 3–7(–14)% of their body heat via the horns. Geist (1971), Hoefs (2000) and Bubenik (1990) correlated the ossicone volume or the relative surface areas of horns with the ambient climate, chiefly in cold-adapted Caprinae from temperate, boreal and arctic zones, which tend to have shortened, but thick (= more voluminous) ossicones with accordingly reduced radiating surfaces, other than their thin-horned tropical sister taxa. The aoudad (*Ammotragus lervia*), a Saharan caprine sharing biotopes with the dama gazelle, has a longer and bulkier ossicone than have caprines from cooler climate

zones, due to the presence of extended hollow cavities separated by only paper-thin bone lamellae, which provide a voluminous reservoir for warm blood assembling here close to the radiating surface (Duerst, 1926). This species sometimes covers its horns with moist sand or mud on hot days (Ogren, 1965). The oryxes in the subfamily Hippotraginae (Bubenik, 1990), including the scimitar-horned oryx (*Oryx dammah*) that is sympatric with the dama gazelle in the hottest and driest parts of the Sahara, have extraordinarily elongated ossicones (presumably the relatively longest of any antelope), reaching up to the tip of the keratinous horn sheath, and filling the entire horn with blood-supplied bone of a finely porous structure reminiscent of pumice stone (A. Schreiber, pers. obs.). Moreover, in some bovid species the blood cooled down in the horns is refrigerating the blood stream circulating from the body to the cerebrum, by means of a cooling collar formed by a capillary plexus of veins arriving from the horns which wraps the artery to the brain, and which functions as a counter-current heat exchanger. Taylor (1972) confirmed a cooling collar near the external carotid artery of the congeneric Grant’s gazelle. It consists of a rete mirabile of many ramifying arterial capillaries running in parallel, which are embedded into a cooling envelope (sinus cavernosus) fed with cool blood from the air-exposed nasal mucosae. An additional vein supply from the horns to this sinus cavernosus, in addition to the supply from the nose, has not been studied in this and in any other gazelle species.

Heat export via the horns could plausibly prove of particular impact in the dama gazelle in its sometimes extraordinarily hot desert climate, because it does not consume water, as alternative cooling methods like sweating or panting would. However, the presence or the efficiency of this capillary mechanism in the horns has never been investigated in any gazelle or in further antelopes from hot deserts. Unfortunately, only very few museum specimens of the dama gazelle permitted the present author to remove the horn sheaths for a direct study of the Os cornu, precluding comparisons of the length and the volume of the ossicone among the subspecies. In the dama gazelle, the ossicone fills only the proximal portion of the horn sheath but not its tip, limiting the segment with potential heat dissipation. The ossicone surface is dotted with many fine pores, arguably minute fenestrae through which thin blood vessels leave the bone core to ramify on its surface, reminiscent of the superficial vessel meshwork spread out on the goat ossicone as a heat radiator (Taylor, 1966). Clearly, experimental physiology is overdue in desert-dwelling gazelles, which are among the most heat-resistant bovinds

Our crude, approximative estimation of the relative horn surface proposes that *N. d. ruficollis* has a slightly increased relative horn surface in relation to horn volume, compared with *N. d. mhorri*. Our estimation of the relative horn surface is not precise, since it was assessed from the oversimplified assumption that the horn pedicles were ideal cylinders which, of course, they are not: (i) they are rather irregularly shaped, because the cross-section of the horn base (but not so the horn tips) resembles a compressed ellipse more than a circular cylinder; (ii) the course of the pedicle is not a straightly uniform cylinder, but it tapers towards the horn tips, although not with a steady incline, so that the horns are not ideal cones either; (iii) the horn surface is not smooth like in a true cylinder, but is corrugated by transverse grooves, ridges, wrinkles and fissures of the sheath. These falsifications of our cylinder model should result in an overestimated ossicone volume and an underestimated horn surface, and thus it should underestimate the relative horn surface. However, both the *mhorri*- and the *ruficollis*-horn morphotypes have fundamentally the same geometrical design and the same surface corrugation of the beams, so that the falsifications should affect them in parallel manner alike, and the subspecies comparison be unaffected by these errors. We conclude as a supported hypothesis that the horns of *N. d. ruficollis*, on account of a moderately increased relative horn surface, can potentially serve as somewhat superior radiators of excess body heat. This conclusion refers to the subspecies inhabiting the most severe climate zone of all dama gazelles, since its haunts in the north-west Sudan represent one of the most severely hyper-arid deserts worldwide (Blümel, 2013): typical for this region is a harsh, continental regime with notable circadian and seasonal temperature amplitudes (min-

ima of  $-7^{\circ}\text{C}$  in cold nights and up to more than  $50^{\circ}\text{C}$  on hot days), and extremely low rainfall of (5–)10 mm annually in long-term recording, and not rarely consecutive years without any precipitation (Blümel, 2013). Frequent episodes of heat stress and hyperthermia while suffering from a severe lack of water for evaporative cooling seem guaranteed in these habitats. The mhorrr gazelles, on the other hand, ranged in the western peripheral Sahara, in (sub)deserts within the reach of maritime Atlantic westerlies which dampen this regionally oceanic climate, with less extreme thermal amplitudes, and aridity but not hyper-aridity (Blümel, 2013; Médail and Quézel, 2018). The numerical difference of the volume-to-surface ratios in the two morphotypes is quite limited, 3.2% in males and 4.7% in females of increased horn surface in *N. d. ruficollis*, but such a simple numerical comparison may be deceptive: a dehydrated *N. granti* was observed to survive periods of extreme heat of  $45^{\circ}\text{C}$  air temperature by a water-saving physiology based on intended hyperthermia, by raising the body temperature up to  $46^{\circ}\text{C}$ , so to avoid water loss by evaporative cooling even under such stressful ambient heat (Taylor, 1972). How long a *Nanger* gazelle can survive a body temperature of  $46^{\circ}\text{C}$  without irreversible damage to vital organ functions is unknown, but such extraordinary hyperthermia might be close to the tolerable maximum, and any auxiliary heat-dissipating mechanism — even if not large in absolute terms — could make a difference.

The increased horn surfaces of females over males are expected from their thinner horns with necessarily larger surfaces, since the horns of females need no hardening to guarantee horn robustness during combats, as is obligatory in the male sex. Thus, mechanical selection criteria have less relevance in females, and horn thickness may be kept in limits to enhance thermoregulation.

### Phylogeny of horn shape

The Soemmerring's gazelle is the sister species of *N. dama* according to evidence from crania, skin pigmentation, the sequences of four mitochondrial and five nuclear genes, and a combined data matrix of body size, horn shape and aspects of social ecology (Knottnerus-Meyer, 1934; von Boetticher, 1953; Bärmann et al., 2013; Bärmann, 2014). This makes it the suitable outgroup to root the evolutionary polarity of the dama gazelle morphotypes. The only other conceivable outgroup taxon, the Grant's gazelle species complex (*N. granti* and relatives), is not compared in detail, since it is more distantly related to dama gazelles (von Boetticher, 1953; Lange, 1971), to the extent to have been removed generically as the, however hardly accepted, genus *Matschiea* (Knottnerus-Meyer, 1907, 1934). The (sub)species of the diverse *N. granti*-species group exhibit substantial internal differences of horn shape, and their obviously autapomorphic horn morphologies differ conspicuously from the head appendages of *N. dama*/*N. soemmerringii*. Perhaps the horns of three to four years old, just matured male Grant's gazelles approach the morphology of male *N. dama*/*N. soemmerringii*, but this intermediate ontogenetic stage is soon overcome by the terminal addition of the more deviant, laterally twisted and quite elongated horns of the older bucks (Walther, 1965). One must conclude a mosaic of primitive and derived features in the horn shapes of all the *Nanger* gazelles, just as in further morphological character complexes of gazelles in general (Lange, 1971). Such a mosaic quality of evolution demands to be cautious when concluding taxon phylogenies from a few single characters, like horns only. Therefore, an extrapolation from the inferred character evolution of horn shape to the phylogeny of the dama gazelle subspecies as such (phylogeny of the taxa) is postponed until more organ systems will have been evaluated too (Schreiber et al., *ongoing study*). Even only the inferred pathway of the horns' mere character phylogeny (see below) rests on fairly few samples from Senegal, Mali or Niger only, whose plesiomorphic position in the variability span of the dama gazelles therefore may be questioned for this reason. Nevertheless, one may safely conclude that the *mhorrr*-morphotype cannot be plesiomorphic but is the most highly derived character state of all, and with somewhat less certainty the fully-developed *ruficollis*-type from Sudan should not qualify for an ancestral position either. The conclusion of a Sahelian center of intraspecific

horn shape evolution appears supported despite the relatively few specimens investigated from this zone, wherever exactly within the Sahel belt it may have been located.

The horns of the *N. soemmerringii*-outgroup assign preferentially to dama gazelles from Senegal and Mali, identifying, while having in mind the preceding reserve, their horn morphology as presumably plesiomorphic for the dama gazelle, and the western or central Sahel zone as the center of evolutionary origin of the species's horn characters. This assignment proposes two diverging, intraspecific morphoclines spreading out from this center eastwards (*ruficollis*-morphotype) and northwestwards (*mhorrr*-type). This divergent cladogenesis is unequal in phenetic transformation, because the evolution of the *mhorrr*-phenotype implies more prominent anagenetic change. Previous authors did not comment on the phylogenetic polarity, but Lydekker (1914) observed that the dama gazelles from Senegal had less impressive horns than seen in *N. d. mhorrr*. Krumbiegel (1960) considered the “desert-coat” of *N. d. ruficollis* as phylogenetically derived, which undoubtedly it is.

Difficulties of proving this phylogenetic polarity arise from our ignorance of the geographical variation in the outgroup: the evidently polytypic composition of *N. soemmerringii* remains incompletely known and its microtaxonomy is unrevised (Matschie, 1912; Groves and Grubb, 2011; Chiozzi et al., 2014; De Francesco et al., 2020), so that the number and the distribution ranges of the approximately half a dozen proposed albeit untested subspecies cannot be evaluated. Neither can the chosen outgroup specimens used in this study be assigned to subspecies. In this situation, widely scattered origins from across the species's distribution range (see Methods section) were included in the outgroup panel, so that it comprises up to three possible subspecies. Nevertheless, the recorded horn characters of this geographically diverse panel yielded a fairly contiguous morphospace in multivariate statistics, suggesting that the horn morphology of *N. soemmerringii* has been represented well by our specimen panel. Most variation contained in this species seems to refer to tones and patterns of skin colours anyway, with horn morphology presumably providing additional, but less important subspecies characters (Matschie, 1912). One may conclude that the chosen panel of *soemmerringii*-horns might suit the present purpose of phylogenetic polarity rooting in the dama gazelle. Nevertheless, the eight chosen Soemmerring's gazelles need not necessarily comprise the complete morpho-variation contained in the species, and neither with certainty the most plesiomorphic horn character states found in it. Nevertheless, one can tentatively conclude that the most plesiomorphic horn shapes of all dama gazelles might be found in the (west or west-central) Sahel zone.

### Bearings for subspecies taxonomy

The subspecies classification of dama gazelles continues to rest predominantly on the most eye-catching character, i.e. the extension of the brown saddle patch of the dorsal skin, whereas additional traits, and even the equally eye-catching complex patterns of head pigmentation, have been underrated traditionally; the horns have been ignored altogether (Lydekker, 1914; Andreae and Krumbiegel, 1976; Cano Perez, 1984, 1991). Horn morphology supports at least the subspecies *N. d. mhorrr* and *N. d. ruficollis*, although Best et al. (1962) and Best and Raw (1973) claimed homogeneous horn shape in all dama gazelles, with subspecies allegedly differing but insignificantly. This erroneous conclusion might rest on the narrow limitation of the investigated dama gazelles exclusively to origins from parts of Chad, which these authors extrapolated imprudently to the entire, truly pluritypic species. Since coat colour patterns alone already separate practically 100% of all individuals of *N. d. mhorrr* and *N. d. ruficollis*, not counting additional markers from crania or chromosomes, horn shape only adds a further argument in favour of already established subspecies. The high diagnosability of their horn shape alone justifies the validity of *N. d. mhorrr*, even without the various additional characters in its favour. The lower diagnosability of *N. d. ruficollis* from horns alone just narrowly matches the conventional taxonomic rule that subspecies should be differentiable at a level where three quarters of its individuals can

be identified (Amadon, 1949; Patten, 2015). The lowered diagnosability of the *ruficollis*-morphotype rests on intrapopular shape variation which reduces its distinctiveness but does not necessarily approach it to *N. d. mhorrr*.

The present data call to check the validity of further potential horn morphotypes, if not perhaps even subspecies, within a widely conceived nominate subspecies *N. d. dama*, which among other authors (Cano Perez, 1991) thought to range throughout the whole Sahel belt from Senegal to Chad, across an enormous west-easterly distance of 4300 km. This broadly conceived nominate subspecies remains vaguely defined (and poorly studied) and it is better conceived as a negatively defined remnant group which neither qualifies as *N. d. mhorrr* nor *N. d. ruficollis*. Unfortunately, these Sahelian populations are difficult to revise because of insufficient museum samples. A *damergouensis*-morphotype from central Niger may perhaps be justified, the more so since its possibly distinctive horn shape is accompanied by a peculiar skin pigmentation (Schreiber et al., *ongoing study*). Rothschild (1921) had advocated his new subspecies *Gazella dama damergouensis* on the narrow basis of only two type specimens, arguing that it differed by a rusty suffusion of the underbelly skin which is whitish (olive buff) in all other dama gazelles, and by horns reported as thick as in *mhorrr* gazelles, but longer in proportion. By now the present author could identify, in addition to the two syntypes, only two more, probably relevant specimens, both in the natural history museum at London too: one of them apparently also originates from Damergou (inventory number BM 28.7.24.3), and another one (BM 73.822), although lacking origin data on the museum label, had been donated by the same donor Walter Rothschild who had donated the syntypes too. The limited study material precludes a statistical validation of this putative horn morphotype, since the few specimens could also represent individual variants rather than a homogeneously deviant population, but just as possible *N. d. damergouensis* from south-central Niger could be valid, being perhaps diagnosable by horn and skin characters alike; further discussion is postponed until the respective skulls and skins will have been assessed. It is likewise too early to establish a relationship of a putative *damergouensis*-horn type and the still hypothetical center of phylogenetic origin of the dama gazelles in the Sahel zone (see above). Clearly, however, the Sahelian stocks are of chief interest for taxonomy and phylogeny.

Further local microvariants in the western and central Sahel belt, for which the enigmatic and hardly investigated subspecies names *N. d. permista*, *N. d. weidholzi* and perhaps also the obscure *N. d. reducta* have been proposed, in addition to *N. d. dama*, are even more difficult to evaluate. Perhaps one will never know how many subspecies had ranged in the Sahel zone, chiefly on account of the regionally uneven collection intensity of museum samples: most dama gazelle specimens preserved in natural history museums were obtained in the late 19<sup>th</sup> and the early 20<sup>th</sup> centuries, when the African range countries were administered by European colonial powers, i.e. France, Britain, Italy, and Spain. None of them conducted a systematic and comprehensive zoological inventory, but the higher significance and appreciation of natural history in the United Kingdom led to the gradual haphazard collection of more than just single dama gazelles in museums, imported from the British-controlled territories of Sudan and Nigeria, where private hunters or colonial officers sometimes donated stuffed heads or skins to the national science collection. The other European powers operating in the Sahara were far more indifferent towards zoology, unfortunately also the nation of France and the French civil society, who controlled most of west and north-central Africa, and by far most of the range of the dama gazelle. Whereas the historical Afrique Équatoriale Française, in what is today the Republic of Chad, was a prime continent-wide stronghold of big game hunting, hardly any of the masses of dama gazelles shot in the French colonies have arrived in French scientific collections, and the information about the origin and the identity of the very few specimens stored in the Musée national d'Histoire naturelle at Paris, as the central museum for the fauna of the French colonies during the heyday of large mammal collecting for taxonomy, is, as a rule, missing or incomplete; smaller museums

in France mostly preserve no materials at all. The relative French indifference with respect to colonial zoology, and to mammal subspecies taxonomy in general, is the decisive reason for our very limited insights into the mammalogy of wider Sahel belt, including the region's dama gazelle, and only the fortuitous visits by a few British, German or Austrian collectors to these French colonies, and the imports of single West African dama gazelles to zoos in Central Europe, provided at least a minimum of evidence for extensive parts of West Africa. In this situation, the future discovery of significant, complementary clues to the taxonomy of the Sahelian population is unlikely, which implies that perhaps forever the now largely or completely extinct regional populations from Senegal, Mali, Niger, and Algeria cannot any longer be properly revised, and those from Chad insufficiently, despite the masses of gazelles killed in the latter area for the mere pleasure, personal honour and prestige of trophy hunters. The author suspects that the currently prevailing concept of an all-embracing taxon *N. d. dama* (Cano Perez, 1991) for the entire Sahel belt may rest on this reduced museum collecting in West Africa, which prevents regional variants to be recognized: intriguingly, the widely conceived *N. d. dama* occupies a range that embraces perhaps some 90 % of the entire historical species range, and its assumed range is closely equivalent to the arid portions of the combined former French territories Afrique-Occidentale Française and Afrique Équatoriale Française, hardly transcending these politically defined territories. It does not fit any of the North African ecoregions or centers of regional endemism. By contrast, the more adequately explored subspecies *N. d. mhorrr* and *N. d. ruficollis* are from spatially comparatively restricted areas which had happened to become the colonial possessions of Spain (Rio de Oro) and Britain (Sudan). Despite our distorted and regionally uneven insight, in any case the various proposed subspecies from the francophone Sahel belt are, if valid taxa at all, more discrete in skin pigmentation than in horn morphology which, taken in isolation, hardly justifies additional taxa beyond perhaps in the Damergou district of Niger.

## Andromimicry in the dama gazelle?

The horns of female *N. d. mhorrr* resemble their male counterparts more than those of female *N. d. ruficollis* resemble their consubspecific males. The subspecies-wise varied sex dimorphism poses intriguing questions concerning the underlying evolutionary mechanism. Horned females of the Antilopinae generally have horns smaller than conspecific males by 10–60 % (Estes, 1991a), and so the sex dimorphism in the dama gazelle, with the female horns shortened by 20 % (averaged over all subspecies), is relatively weak. This dimorphism falls short of the sexual differentiation in the majority of antelopes, the dama gazelle ranking in the second-lowest of the four sex dimorphism classes defined by Estes (1991a) for African Bovidae, together with topi, hartebeest and wildebeest, and with only the oryxes and the addax being less sex-dimorphic. Horned females evolved independently in several bovid clades, presumably to improve the female ability to defend themselves in conflict: the classical view was that horned females can keep off predators from themselves or their offspring (Packer, 1983; Stankowich and Caro, 2009), but Roberts (1996) proposed that horned females compete more efficiently with conspecifics for food. The elaborated sexual mimicry theory of Estes (1991b, 2000, 2014) complements these traditional explanations: it postulates female mimicry of male sexual characters, chiefly horns, so that a mother conceals the sex identity of her male offspring by looking similar to him, even after a son has started to grow horns. By growing horns (or longer horns), mothers diminish their releaser function for male aggression, thus buffering an adolescent son against the despotic aggression of dominant or territorial males, who drive off each competitor identified as equal-sexed. Untimely, forced dispersal by despotic dominant master bucks could be avoided if a son does not identify himself as an obvious male, but resembles the horned females. Despotic aggression by dominant bucks against youngsters has often been observed in many bovids, and it may well prove fatal to the evicted son if forced too early to cope outside the natal group (Estes, 1991a). The death of a son lowers the lifetime reproductive success of his mother more profoundly than the reproduction

of the expelling male (who eventually is the father of the expelled juvenile but cannot be certain of this paternity), and therefore the fitness of females, more than of adult males, profits from tempering despotic aggression. An adaptive female andromimicry strategy would ensue, i.e. mothers to acquire horns up to a size which equals the growth stage of their sons' horns at the very life age when sons can be evicted without running a risk to perish. Horned females may result from this mimicry. Here the story does not end, however, since dominant males should try to evade this andromimicry: females copying "male" sexual traits diminish the phenotypic singularity of master bucks, for example his capacity to announce superior strength or to look sexually attractive, or his ability to recognize rivalling peers unambiguously. This conflict causes non-identical sexual strategies, with the males replying to the female mimicry by developing themselves ever more impressive horns, hurrying away phenotypically from the mimicking females, and the latter in turn continue tracking this male upgrade to keep the sex dimorphism small. These two interdependent strategies are analogous to an "arms race", which results in rapid directional evolution ("runaway evolution") towards hypermorphic males, and towards females trailing the male prototype during its ever-rising progression. Estes (2014) exemplified this theory with examples from the oryxes, whose various drab-coloured, small-bodied and sex-dimorphic tropical (sub)species contrast with the larger-bodied, subtropical gemsbok (*Oryx gazella*), which has stronger and more robust horns in both sexes, coupled with a showy display pigmentation of its skin, and a reduced sex dimorphism of all bodily characters ("gaudy, hyper-attractive unisex population"). Another example are the various subspecies of the sable antelope (*Hippotragus niger*), which display various grades of morphological sex dimorphism (Estes, 2000). The mhorrr gazelles, also an extratropical descendant from (peripheral-)tropical ancestors, offer a striking analogy of these examples, because *N. d. mhorrr* has a comparable combination of more robust horns of suggestive preeminence in combat strength, coupled with reduced gender differences in horn shape and, most conspicuously, very showy, gaudy body colours, with both males and females concomitantly brightened by the brilliant contrast between the shining, red-brown dorsal saddle field and the glossy whitish (pale olive buff) ventral skin. Mhorrr gazelles exhibit one of the gaudiest phenotypes of all gazelles (or even antelopes) indeed, appearing even more signalling than are gemsboks, and thereby they differ considerably from the drab *N. d. ruficollis*, whose skin colours propose the opposite function of camouflage in the surrounding biotope ("desert coat"). In fact, the skin pigmentation of the addra gazelle is far from being a visual cue, instead it converges in colouration, even in the fine details of the only two represented pigments, on the equally cryptic phenotypes of the sympatric scimitar-horned oryx or the Sahelian giraffe (*Giraffa camelopardalis peralta*), each of them camouflaged in the same-coloured arid landscape. Contrary to the disguise phenotype of the addra gazelle, mhorrr gazelles maximize their visual conspicuousness, and do so in both sexes alike. If mhorrr gazelles really attain larger body weights (see above), this would be another analogy with Estes's (2000) gemsbok example. All of these striking characters of the mhorrr gazelle are intraspecific autapomorphies of this subspecies, derived apparently rapidly (by intraspecific evolution) from a less conspicuous ancestral pattern, as is exemplified by the phenotypes of all other subspecies of the dama gazelle and of the other congeneric *Nanger* species. The andromimicry theory is able to explain the otherwise unintelligible combination of all of these attributes of the mhorrr gazelle, each single one of which would be remarkable already, as one coadapted complex of functionally interrelated characters, which may have been co-selected as a syndrome of adaptive female mimicry of an ever-increasingly hypermorphic male prototype.

The andromimicry concept is admittedly theory-loaded, but it can be tested empirically, although this remains to be done in gazelles. Behaviour studies can verify that despotism directed against young gazelles exists, that horns are a visual releaser of such aggression, and that despotism starts or increases when young males are developing horns which look more impressive than the horns of females. Also testable is the prediction that the lifetime reproductive success of a single female

is lower than that of a dominant male. The dispersal age of young male mhorrr gazelles is poorly known, since this subspecies, extinct in the wild, can only be studied in captivity where dispersal depends on human intervention. However, Mungall (2018) observed adult male herd masters of eastern dama gazelles driving off their sons as subadults 13–20 months of age, and chasing adolescents (4–)6–13 months of age, verifying male despotism against young offspring, and referring it to the age period of six months to approximately two years. Because the spatial restrictions of captivity could plausibly lead to earlier despotism by crowding, data from free-ranging herds would be desirable. By the age of four months, when the earliest chasing of sons was observed, young dama gazelles have largely acquired the contrasted skin pigmentation pattern of adults. The lyrate adult horn morphology ("S-shape") is developing during the subadult stage at 20–24 months, and it is this life period when eviction is finalized. The andromimicry theory can apply earliest in this same subadult stage, since previously the adolescents carry the hook-shaped crooks of juveniles bent to the front, which identify them readily as immatures. Of interest therefore, eviction seems to be completed (according to present insights from captivity) just when the juvenile horns are being replaced by the adult morph. The available observations therefore are compatible with the andromimicry theory, although data concerning forced dispersal in free-ranging gazelles are needed.

Walther (1995) noted that young gazelles do not form kindergarten groups and so have to endure the full male despotism as single, exposed individuals without the protection of a group, if not supported by the mother. Walther (1995) also noted that gazelle mothers tend to protect their offspring when molested or chased by territorial males, and they do not only interfere directly with male despotism, but may even accompany evicted sons into their new haunt in order to ease their familiarization in a bachelor group. Young Thomson's gazelles (*Eudorcas thomsoni*) have to endure aggressive behaviour from the territorial male from their seventh month of life age (Walther, 1995), and Estes (1999) observed territorial bucks of this gazelle expelling their sons within the first six months of age. This is a younger age than proposed by the observation of Mungall (2018) for the dama gazelle, where eviction awaits the formation of the adult horn morphology, which is in compliance with the andromimicry theory for mhorrr gazelles.

If Estes's (2000) hypothesis of female andromimicry can be substantiated for the mhorrr gazelle by additional behaviour data, it would be the second case of enhanced runaway evolution in the Antilopinae, after Schreiber et al. (1997) had concluded another case to explain the highly autapomorphic body and horn morphology of the blackbuck (*Antelope cervicapra*). This species is, despite its deviant phenotype, a late phylogenetic descendant from the crown-group gazelles (Bärmann et al., 2013), which has rapidly acquired a novel morphology setting it apart from its morphologically more conservative relatives to the extent to represent a novel genus. The behavioural ecology of the mating system was held responsible for this enhanced evolutionary rate, by intensified sexual selection and strong genetic drift due to mate election in a display arena (lekking), where very few stringently selected males reproduce with numerous females. This highly selective mate choice should result in runaway evolution of sexually attractive traits which are rewarded and multiplied by females in disposition to mate by copulating exclusively with the dominant lek buck(s). However, other than in the mhorrr gazelle, the morphological sex dimorphism is most pronounced in blackbuck, and much increased over other Antilopinae, proposing, in the terms of Estes's (2000) andromimicry hypothesis, that female blackbucks are mimicking their male counterparts to a lesser degree (or that the selection for male secondary characters is more intense in this species). On the contrary, the raised conspicuousness of the gaudily painted mhorrr gazelle, in its contrast to the other dama gazelle subspecies, is found in both sexes, and it is coupled with reduced sex dimorphism of the horns. This "mhorrr-syndrome" is not easily interpreted without invoking the sexual mimicry hypothesis. Molecular clock studies would be interesting to find out the time frame of the autapomorphic transformation of the *mhorrr*-clade, so to estimate how much the phenotype evolution of this clade was enhanced in relation to

the *ruficollis*-clade. Not unlikely because following putatively a simple trajectory of sexual selection, this transformation evolved fairly rapidly, so that the overall genomic distance (in socially unselected genes) between *N. d. mhorrr* and the other subspecies could be smaller than expected from the phenotypic change of the signalling characters. Of interest, the inferred runaway evolution in blackbuck has presumably eroded its genetic variability as a corollary of an intense one-sided selection (Schreiber et al., 1997). In this context, assessing the molecular heterozygosity of the *mhorrr*-clade is worthwhile, in order to test if its putative runaway evolution had eroded its genetic variation too. To this aim, several museum specimens collected in Africa, prior to the extinction of the *mhorrr* gazelle in the wild, are available in museums, for a genetic analysis of the original state, and prior to the variance-depleting bottleneck of founding the surviving zoo herd of this subspecies from very few individuals. The superior morphological diagnosability of the *mhorrr*-horn morphotype in comparison to the *ruficollis*-phenotype (see Results) is in agreement with a lowered genetic variation of *mhorrr* gazelles, as is their uniform external appearance, whose homogeneity is not confined to the bottle-necked zoo stock, but is also observed in the (few) historical museum specimens collected in Africa. Not unlikely, therefore, *N. d. mhorrr* and *N. d. ruficollis* exhibit different levels of genomic variation resulting from diverging evolutionary strategies. In this context, the immense hyper-variability of the Chad-derived zoo lineage (see Methods section) comes to mind, but its interpretation would be premature since this strange phenomenon remains unexplained (natural hybridization of adjacent morph populations in Chad? Undocumented hybridization in zoos?).

The present data suggest that female but not male *mhorrr* gazelles continue their horn length growth even as adults, progressively reducing the sex differentiation female-male until old age. Unfortunately, no age-dated horns of *N. d. ruficollis* were available to see if the same continued growth holds true for adults of this subspecies too. Lifelong horn growth in adult bovids has been investigated and demonstrated in few species only, for example in male bighorn sheep (*Ovis canadensis*), where dominant adult bucks continue to acquire and augment master trophies by sustained horn growth until progressed life ages (Geist, 1971). To the knowledge of the present author such a sustained ontogenetic growth has never been investigated in gazelles. Clearly, the horn growth in adult gazelles from other species deserves greater attention. Since our observation refers to one narrowly founded breeding lineage in zoos only, because exact age data are confined to these captive *mhorrr* gazelles contained in the zoo studbook (Domínguez, 2021), some hesitation is reasonable before interpreting the present sex-specific growth curves too far. Nevertheless, it is tempting to interpret this detail of ontogeny as a strategy of females adjusting with increasing age — i.e. with a prolonged reproductive period — their horn size ever more to the male archetype, being perhaps another co-selected adaptation under a scenario of female sexual mimicry of the male model. If so, older females and thus presumably mothers with a long-standing reproductive career will resemble the male phenotype more closely than young females with yet less reproductive output. ☞

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