

Z. Säugetierkunde 55 (1990) 194–201
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ISSN 0044-3468

GTG-banded karyotype of *Gazella dama mhorri* Bennett, 1833 Cytogenetic relationship with other members of the subgenus *Nanger*

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Receipt of Ms. 15. 11. 1988

Acceptance of Ms. 27. 8. 1989

Abstract

The GTG-banded karyotype of *Gazella dama mhorri* is described, showing an unusual sex-determining mechanism ♂ ($X_1X_2Y_1Y_2$), ♀ ($X_1X_1X_2X_2$) and two variants in the parameter $2n$ (42 individuals possess $2n = 38$, and the rest, 13 individuals, $2n = 39$, due to a structural heteromorphism in pair 1). The comparative study of the karyotypes of *G. dama mhorri*, *G. dama dama*, *G. granti* and *G. soemmerringi* reveals the relationship among these four members of the subgenus *Nanger*.

Introduction

The difficulties concerning a classification of the different species and subspecies of the genus *Gazella* (GROVES 1969) stimulated karyotypical research in this genus (NELSON-REES et al. 1967; WURSTER 1972; WAHRMAN et al. 1973; EFFRON et al. 1976; BENIRSCHKE et al. 1984; FURLEY et al. 1988).

This paper presents a cytogenetic study of *Gazella dama mhorri*, a subspecies not studied in this respect to date. The sample analysed here is relatively large and of well-known and demonstrated origin, preconditions not given in similar studies on other *Gazella* species.

Material and methods

A total of 55 specimens (31 ♀♀ and 24 ♂♂) were examined, all of them belonging to a population developed in the Arid Zones Experimental Station in Almería (Spain) and deriving from 17 *G. dama mhorri* specimens (13 ♀♀ and 4 ♂♂) which had been trapped between 1971 and 1975 in the "Dora-El Gaada" region, in the northern part of the once Spanish colony of Western Sahara, bordering the South-Moroccan area, where the specimens studied by BENNETT have been obtained (CABRERA 1932).

The classification of the specimens of the population under study is based on comparative analyses with *G. dama dama* and *G. dama ruficollis* (CANO 1984). On the other hand, specimens from this geographical area have been classified as *G. dama lozanoi* by MORALES-AGACINO (1949) and EIGENER and SCHLIEMANN (1983).

For the analysis of metaphase plates, chromosome preparations were made from peripheral whole blood, 0,4 ml cultured in 7,5 ml RPMI-1640 medium supplemented by 15 % bovine fetal serum, L-glutamin, antibiotics and Pokeweed mitogen (Flow Laboratories).

The trypsin technique of revealing GTG bands was based on the procedure of SEABRIGHT (1972), with slight modifications (ARROYO and MURCIA 1977).

Results

Chromosome analysis with conventional Giemsa staining showed that of the 55 animals analyzed, 42 (25 ♀♀ and 17 ♂♂) had a karyotype $2n = 38$, and the remaining 13 (6 ♀♀ and 7 ♂♂) $2n = 39$. By means of GTG banding technique, each pair was unequivocally identified. The chromosomes in the karyotypes were grouped morphologically: meta-

submetacentric (1–10) and acrocentric (11–18). Within these groups the chromosomes were ordered according to their length and matched to their respective banding patterns.

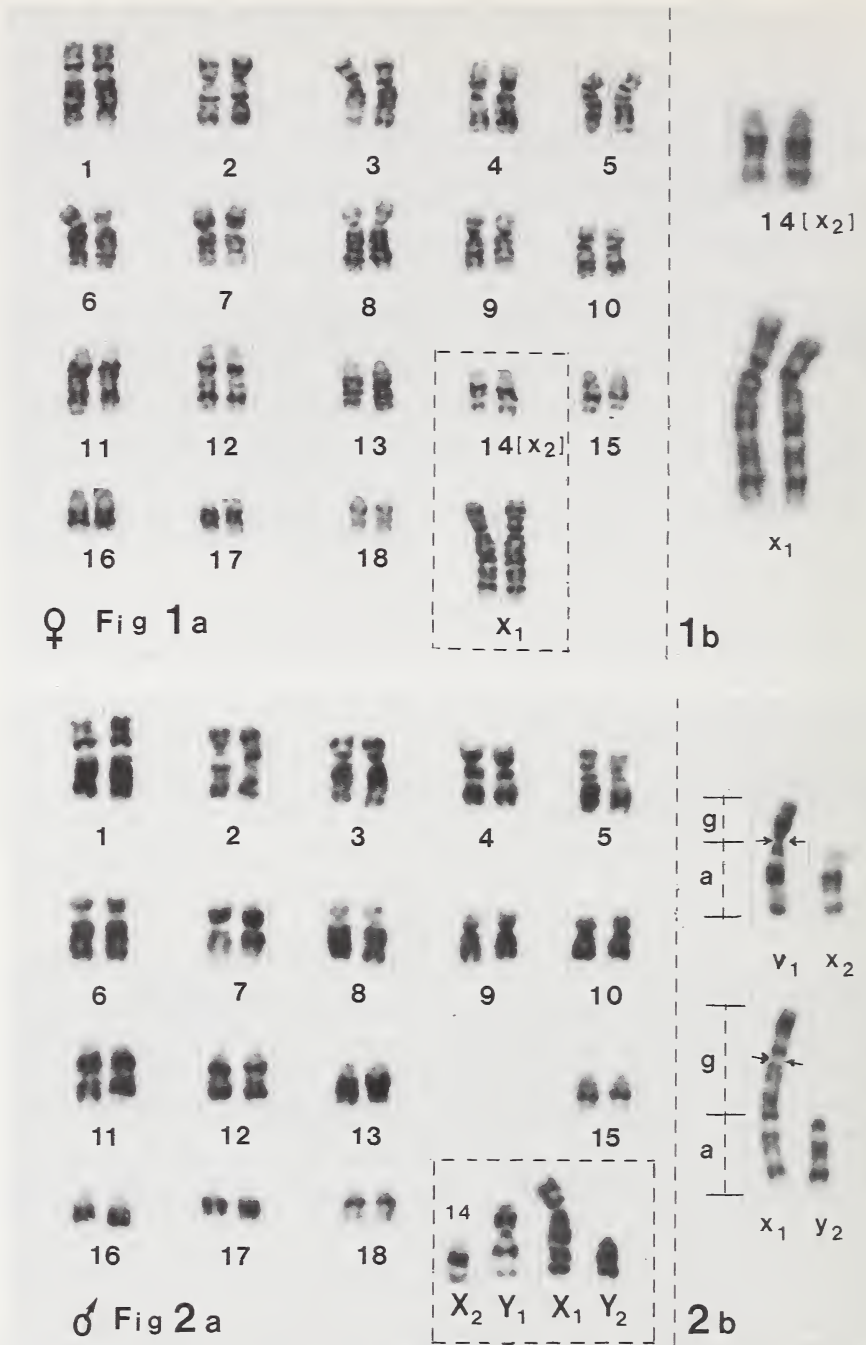
The karyotypes with $2n = 38$ (fig. 1: ♀♀, fig. 2: ♂♂) possess 34 chromosomes (10 meta-submetacentric and 7 acrocentric pairs) identical in both sexes with regard to morphology, relative lengths and banding patterns. The four remaining chromosomes (set off in frames in figs. 1 and 2) differentiate the karyotypes of male and females. In the female (fig. 1) the four chromosomes involved in sex differentiation are paired: two submetacentric ones of maximum length form the gonosomal pair (X_1X_1) and two acrocentric chromosomes form the autosomal pair 14 (X_2X_2). By contrast, in the male the four sex-differentiating chromosomes, (marked out at the end of the karyotype) result unpaired due to their lengths or different banding patterns. The longest of these is identical to the X_1 gonosome, while the acrocentric X_2 when applying the same criteria, appears homologous to the q-arm of the male Y_1 gonosome in the female, the other one is a long submetacentric chromosome, similar in length to that of pair 2, which has been identified as the male Y_1 gonosome. Finally, there are two smaller acrocentric chromosomes Y_2 and X_2 , of similar length, but unpaired among themselves due to their different banding patterns. The Y_2 , by its relative length and banding patterns, turns out to be homologous to the terminal half of the q-arm of the female X_1 gonosome (fig. 2b). Additionally it is identical to pair 14 (X_2) in the female (fig. 1b) in relative length and banding patterns.

The homologies of these two acrocentric and unpaired chromosomes support the assumption that the present morphology of the sex chromosomes X_1 and Y_1 are apomorphies originated by the respective translocations of ancestral X and Y gonosomes with two acrocentric autosomes (Y_2 and X_2) of different pairs. The translocation between the ancestral X and the autosomal Y_2 would be of the tandem type, by fusion of the telomeric region of the ancestral X with the paracentromeric region of the autosome. This chromosome would then inactivate or lose its centromere and incorporate its genetic material to the neo-X (X_1), thus lengthening its q-arm. On the other hand, the translocation between the ancestral Y, which is short and acrocentric, and the autosome X_2 would have to be Robertsonian – centric fusion – and generating the long submetacentric male Y_1 gonosome. Both gonosomes in their present morphology, thus possess two regions: one which corresponds to the ancestral sexual chromosomes – gonosomal region g – and another one corresponding to the translocated autosome – region a – (fig. 2b).

Thus, the actual karyotype, ♂ $2n = 38 (X_1X_2Y_1Y_2)$, ♀ $2n = 38 (X_1X_1X_2X_2)$ – according to the notation proposed by FREGDA (1970) and HSU (1979) – preserve the ancestral genetic material and are balanced as regards both sexes. In the females the autosomal designate Y_2 pair would be incorporated in the terminal segment of both X_1 gonosomes (double apomorphy), whereas the X_2 pair would make up pair 14 (X_2) (double plesiomorphy). In the males, however, the Y_2 pair would have a chromosome incorporated in the female gonosome (simple apomorphy) and the other Y_2 would be free and acrocentric (simple plesiomorphy). Pair 14 (X_2) would possess a chromosome from this pair, incorporated in the male Y_1 (male-specific sex chromosome) forming its q-arm (simple apomorphy), and the other acrocentric free X_2 (14) simple plesiomorphy. The Y_2 acrocentric free chromosome is present only in males.

The karyotypes with $2n = 39$ only differ from the type with 38 chromosomes in the autosomal pair 1, which present structural heteromorphism – due to Robertsonian translocation (one submetacentric chromosome and two acrocentric chromosomes which are homologous to the arms p and q of the submetacentric) – (fig. 3). The rest of the pairs, including the gonosomal ones, are identical for both variants.

In the analyzed population no $2n = 40$ specimens were identified. Theoretically these variants are likely to appear in offspring of inbreeding between $2n = 39$ specimens.



Figs. 1 and 2. 1a: GTG banded female karyotype of *G. dama mborr* $2n = 38$ (animal n° 258). The four chromosomes involved in sex differentiation are framed out; *1b:* Detail of the sex-differentiating chromosomes from another metaphase. *2a:* Male karyotype of *G. dama mborr* $2n = 38$ (animal n° 370). At the end of the karyotype the four chromosomes involved in sex differentiation are framed out. The free acrocentric autosomes X₂ (14) and Y₂ are paired and aligned with the respective homologous segments in the neogonosomes Y₁ and X₁; *2b:* Detail of the male sex-differentiating chromosomes, marking the gonosomal region g and the autosomal region a

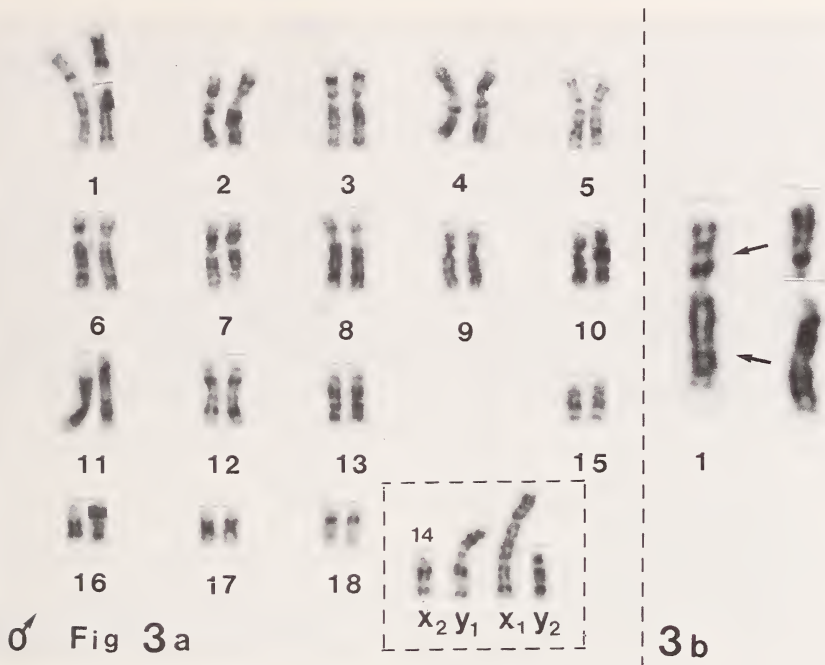


Fig. 3. a: Male karyotypes of the *G. dama mhorri* $2n = 39$ (animal n° 284). Structural heteromorphism in pair 1: one submetacentric and two acrocentric chromosomes, these latter homologous with the p and q arm of the submetacentric; b: Detail of pair 1

Discussion

The comparison of the karyotypes of *G. dama mhorri* and *G. dama dama* Pallas, 1766, (EFFRON et al. 1976) allows the following conclusions:

1. Female karyotypes with $2n = 38$ are identical in both subspecies (10 meta-submetacentric pairs, 8 acrocentric pairs plus 2 female gonosomes of maximum length with translocations between X and autosomal Y_2).
2. Male karyotypes in turn, are differentiated: a. by karyological parameter $2n$ (39 in *dama*, 38 in *mhorri*, disregarding at the moment the Robertsonian polymorphism of autosome 1); b. by the morphology and size of the male gonosome (small acrocentric Y_1 in *dama*, and long submetacentric Y_1 in *mhorri*) and c. by the presence of two free autosomes of pair 14 in *dama* and only one free autosome of this pair in *mhorri*.

These three features distinguish the male karyotypes of both subspecies, and are the results of one single chromosomal rearrangement (Robertsonian translocation, centric fusion) between the short acrocentric Y_1 male specific sex chromosome and an autosome of pair 14 in *dama*, which would result in forming the long submetacentric Y_1 gonosome, leaving the other autosome of pair 14 (X_2) free, in subspecies *mhorri* and reducing the diploid set to $2n = 38$. This rearrangement likewise determines the evolution of male $2n = 40$ karyotypes in *dama* towards the $2n = 39$ in *mhorri*, which presents structural heteromorphism in both subspecies (due to Robertsonian translocation) in pair 1 (fig. 3). One single evolutionary novelty, the submetacentric apomorphy of the Y_1 gonosome, differentiates the karyotypes of both subspecies.

The comparison of the karyotypes of *mhorri* with *G. soemmeringi* Cretzschmar, 1826, (BENIRSCHKE et al. 1984) permits to establish the following relationships:

1. Both gonosomes have the same morphology and banding pattern in both members of the *Nanger* subgenus (long submetacentric male gonosome with autosomal translocation Y/X₂ in *mborr*, X/17 in *soemmeringi*), and the maximum length submetacentric female chromosome X/Y₂ in *mborr*, X/14 in *soemmeringi*.
2. The meta-submetacentric autosomes (1–10) in *mborr* are identical to the meta-submetacentric ones in *soemmeringi* (16/11; 1–9).
3. The acrocentric pairs (11–18) in *mborr* correspond to the acrocentric pairs (10–20) in *soemmeringi* (the numbering is influenced by the inclusion of the Y₂ and X₂ autosomes), although some individuals of these species are affected by Robertsonian translocations, 13/12 and 18/10.

With regard to the sexual chromosomes of both species, we agree with BENIRSCHKE et al. (1984), in assigning the autosomal region of the female X gonosome to the terminal half of the q-arm. We are, however, in disagreement with these authors regarding the identification of the autosomal region of the male Y₁ gonosome. Whereas they assign it to the short arm in *soemmeringi*, we identify it with the long q-arm in *mborr*.

Finally comparison between the karyotypes of *mborr* and *G. granti* (EFFRON et al. 1976) allows the establishment of the following relationships:

1. The meta-submetacentric pairs in *mborr* (1–10) are identical to pairs (3, 5, 4, 8, 10, 6, 9, 12, 13 and 14) in *granti*.
2. The acrocentric pairs (11–18) of *mborr*, by means of four Robertsonian translocations, are incorporated in the submetacentric chromosomes 1, 2, 3 and 11 of *granti*.
3. The female sex chromosomes are identical in both species; the male gonosome, however, is small and acrocentric and hence identical to *dama*, both being different from the long submetacentric Y₁ in *mborr*.

Table 1 provides a synthetic view of the homoeologies that are assumed to exist among the chromosomes of the karyotypes of *G. dama dama*, *G. granti*, *G. dama mborr* and *G. soemmeringi*, preserving the nomenclature and numbering of the respective authors.

Based on the hypothesized homoeologies outlined in Table 1, assuming the ancestral nature of the acrocentric morphologies and selecting a minimum number of evolutionary steps (CAMIN and SOKAL 1965), it is possible to establish a hypothetical evolutionary scheme or cladogram (fig. 4) which would relate the four *Nanger* members cytogenetically by means of Robertsonian translocations, (centric fusion). Assuming these criteria as a working hypothesis, the *G. dama* karyotype would then correspond to the ancestral type among the members of the *Nanger* subgenus. Two different branches could have derived from the *dama* karyotype: one which would preserve the morphology of the *dama* sex chromosomes and giving rise to *granti*, whereas the other, by means of morphological modification of the male gonosome could have developed to *mborr* and *soemmeringi*.

In one of the branches *dama* and *granti* share the morphology of the sex chromosomes and the meta-submetacentric autosomes of *dama*. Four Robertsonian translocations of the acrocentric pairs 13-12, 17-11, 15-14 and 18-16 in *dama*, would yield four submetacentric apomorphies (1, 2, 8 and 11) in *granti*. The diploid set is thus reduced to $2n = 31$ and all chromosomes are meta-submetacentric.

For the other branch, Robertsonian translocation between the Y (small acrocentric) and the autosome of pair 14 in *dama* would generate the submetacentric male Y₁ gonosome in *mborr*, (the only evolutionary novelty which differentiates both subspecies) whereas they share the morphology and structure of the other chromosomes, and the diploid set in *mborr* is reduced to $2n = 38$. Finally and starting from the *mborr* karyotype, two Robertsonian translocations involving pairs 13-12 and 17-11 would give rise to the *G. soemmeringi* karyotypes $2n = 34-39$. With respect to *dama*, *mborr* and *soemmeringi* as a common synapomorphy share the submetacentric neomorphism of the male gonosome.

In the light of the cytogenetic relationships described above and ignoring the possibilities of hybridization among the different members of subgenus *Nanger* it is legitimate

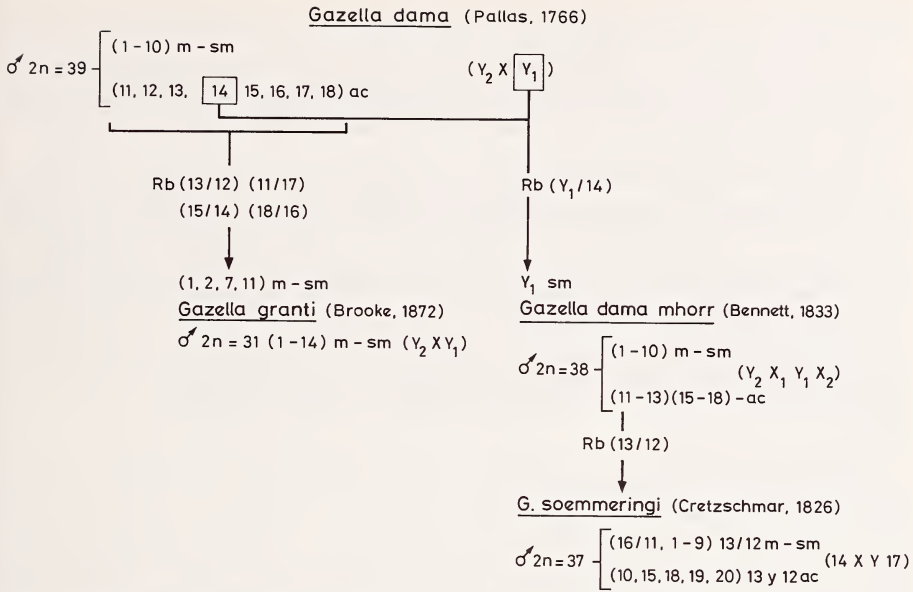


Fig. 4. Hypothetical evolutionary scheme

Table 1. Presumptive chromosome homologies between *G. dama mhorr*, *G. dama*, *G. granti* and *G. soemmerringi*

<i>G. granti</i> (EFFRON et al. 1976) ♂ 2n=31 (Y ₂ X Y ₁)	<i>G. dama</i> (EFFRON et al. 1976) ♂ 2n=39 (Y ₂ X Y ₁)	<i>G. dama mhorr</i> (ARROYO et al. 1988) ♂ 2n=38 (Y ₂ X ₁ Y ₁ X ₂)	<i>G. soemmerringi</i> (BENIRSCHKE et al. 1984) ♂ 2n=37 (14 X Y 17)
3-sm	1-sm	1-sm	16/11-sm
5-sm	2-sm	2-sm	1-sm
4-sm	3-sm	3-sm	4-sm
8-sm	4-sm	4-sm	5-sm
10-sm	5-sm	5-sm	3-sm
6-sm	6-sm	6-sm	2-sm
9-m	7-m	7-m	7-m
12-sm	8-sm	8-sm	6-sm
13-sm	9-sm	9-sm	8-sm
14-sm	10-sm	10-sm	9-sm
2q-sm	11-ac	11-ac	10-ac
1q-m	12-ac	12-ac	12-ac 13/12-sm
1p-m	13-ac	13-ac	13-ac 13-12-a
7q-m	14-ac	X ₂ -ac(14 ♀)	17-ac
7p-m	15-ac	15-ac	19-ac
11q-m	16-ac	16-ac	15-ac
2p-sm	17-ac	17-ac	18-ac
11p-m	18-ac	18-ac	20-ac
Y ₂ -ac	Y ₂ -ac	Y ₂ -ac	14
X(X/Y ₂)-sm	X(X/Y ₂)-sm	X ₁ (X/Y ₂)-sm	X(X/14)-sm
Y-ac	Y-ac	Y ₁ (Y/X ₂)-sm	Y(Y/17)-sm

m = metacentric, sm = submetacentric, ac = acrocentric, p = short arm, q = long arm,
Homoeology = partial or residual homology

to raise the question whether its four members actually are differentiated species or simply four karyotypic races of *G. dama*.

On the other hand, it would be interesting to know, whether the cytogenetically most closely related *Nanger* members occupy adjacent geographical areas. The lack of data about the geographical origin of the experimental animals, however, makes it impossible to correlate both variables.

The anomalies encountered in the sexual chromosomes of *G. dama mhorri*, especially in male specimens, with two free autosomes in different pairs homoeologous with the autosomal regions of both sex chromosomes, X_1Y_1 , allow the assumption that a quadrivalent complex is generated during gametogenesis, consisting of four morphologically differentiated elements: the two sexual chromosomes and the autosomes X_2 and Y_2 . This quadrivalent is likely to cause segregational problems during the first meiotic division with the consequential effects on fertility and the viability of descendants. As a matter of fact, the populations under study present reproduction problems together with considerable perinatal mortality. Hence a meiotic study would constitute a compulsory task for the future.

Mating has been performed randomly to date. Yet, since the karyotypes of the 55 experimental animals are now known, future matings will be guided, in order to match 38×38 , 38×39 and 39×39 . We are especially interested in inbreeding between hybrids with $2n = 39$, i.e. with a heteromorphous pair 1, consisting of a submetacentric chromosome and two acrocentrics. The descendants thus inbred in theory could yield individuals with $2n = 40$, e.i. specimens in which the submetacentric pair 1 of $2n = 38$ individuals would be represented by two acrocentric pairs.

Zusammenfassung

GTG-Banden-Karyotyp von *Gazella dama mhorri* Bennett, 1833. Zytogenetische Beziehungen zu anderen Vertretern der Untergattung *Nanger*

Der GTG-Banden-Karyotyp von *G. dama mhorri* wird beschrieben. Er zeigt einen ungewöhnlichen geschlechtsbestimmenden Mechanismus ($\sigma\sigma = X_1X_2Y_1Y_2$ und $\sigma\sigma = X_1X_1X_2X_2$) und zwei Varianten des Parameters $2n$ (42 Exemplare haben $2n = 38$ und die übrigen 13 Tiere zeigen Heteromorphismus im Paar 1, also $2n = 39$). Aus der vergleichenden Gegenüberstellung dieser Karyotypen mit denen von *G. dama dama*, *G. granti* und *G. soemmeringi* wird das zytogenetische Verhältnis abgeleitet, das für diese vier Vertreter der Untergattung *Nanger* besteht.

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 1990

Band/Volume: [55](#)

Autor(en)/Author(s): Nombela J. J. Arroyo, Murcia C. Rodriguez, Abaigar T., Vericad J.

Artikel/Article: [GTG-banded karyotype of Gazella dama mhorh Bennett, 1833 Cytogenetic relationship with other members of the subgenus Nanger 194-201](#)