

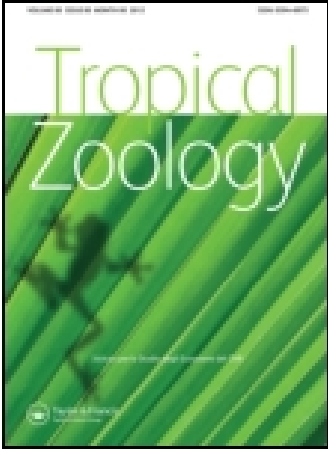
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Tropical Zoology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ttzo20>

A cytotaxonomic approach of the systematics of *Arvicanthis niloticus* (Desmarest 1822) (Mammalia Rodentia)

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Published online: 01 Aug 2012.

To cite this article: E. Capanna & M. V. Civitelli (1988) A cytotaxonomic approach of the systematics of *Arvicanthis niloticus* (Desmarest 1822) (Mammalia Rodentia), *Tropical Zoology*, 1:1, 29-37, DOI: [10.1080/03946975.1988.10539404](https://doi.org/10.1080/03946975.1988.10539404)

To link to this article: <http://dx.doi.org/10.1080/03946975.1988.10539404>

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A cytotaxonomic approach of the systematics of *Arvicanthis niloticus* (Desmarest 1822) (Mammalia Rodentia) *

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Received 8 September 1986, accepted 29 September 1986

Arvicanthis niloticus (Desmarest 1822) (Mammalia Rodentia) exhibits different karyotypes in different populations throughout its wide distribution area, characterized by diploid numbers ranging from $2n = 62$ to 56. A 44 chromosome karyotype is described in one *A. niloticus* from Somalia. The taxonomic and evolutionary inferences are discussed.

KEY WORDS: Rodentia, *Arvicanthis*, systematics, karyotype, Somalia.

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INTRODUCTION

The genus *Arvicanthis* Lesson 1842, includes several taxa of grass rats widely distributed in Africa, from Egypt to Kenya and from Senegal to Ethiopia and Somalia. Like other African myomorph rodents the systematic relationships among and within the genus present unsolved problems. During more than a century of zoological exploration, from 1822 to 1936, 37 taxa belonging to this genus were described, most of them at subspecific level. Only six species were considered in the ALLEN (1939) checklist of African rodents, i.e. *A. niloticus* (Desmarest 1822), *A. lacernatus* Rüppel 1842, *A. abyssinicus* Rüppel 1842, *A. somalicus* Thomas 1902, *A. tenebrosus* Kershaw 1923 and *A. ochropus* (Heuglin 1877).

Subsequent revisions (ELLERMAN 1941, ROSEVEAR 1969, DORST 1972, YALDEN et al. 1976, CORBET & HILL 1980, ROUSSEAU 1983) did not agree with ALLEN's list

* Karyotype of Somalian rodent populations. 5.

(Table 1), particularly concerning the complexes *niloticus* and *abyssinicus* which are very polytypic. The ELLERMAN (1941) checklist includes 12 subspecies of *A. niloticus* and 19 of *A. abyssinicus*. The revision by DORST (1972) is particularly notable; he lists *A. blicki* Frick 1914, as a distinct species from *A. abyssinicus*, and is followed in this opinion by all subsequent authors. The revision by YALDEN et al. (1976), who separate *A. dembeerensis* (Rüppel 1842), (syn. *Pelomys dembeerensis*) from *A. abyssinicus* has been followed by RUPP (1980) only.

A quite different opinion is expressed by MISONNE (1971) who lumps all taxa into the sole species *A. niloticus*. Although we do not agree with this disconcertingly extreme approach, it has to be stressed that all the reviewers of the genus *Arvicanthis* agree that further work is needed to solve the systematic status of the taxa belonging to the genus.

Undoubtedly karyotype analysis is a valuable approach to such a debated taxonomic context, bringing data relevant to a genetic differentiation between populations/species. Nonetheless the karyological data at present available complicate even more the already complex systematic outline of the genus.

MATTHEY (1959) first reported the karyotype of *Arvicanthis abyssinicus* which is characterized by $2n = 62$. All autosomes are acrocentrics, whereas the X sex chromosome is a large submetacentric. MATTHEY (1965) analyzed the karyotype of *Arvicanthis niloticus* using specimens coming from Bangui, Central African Republic. The diploid number is 56 and three pairs of banded chromosomes were observed, namely two pairs of large metacentrics and one pair of medium subtelocentrics. Accordingly, the karyotypes of two species become reciprocally congruent by speculating Robertsonian translocations.

Very recently VOLOBOUEV et al. (1986) presented the karyological data concerning specimens of *Arvicanthis niloticus* from three separate African regions, i.e. Egypt, Burkina-Faso and Central African Republic. The karyotypes show relevant diversities due to numerous chromosomal rearrangements, such as pericentric inversions, reciprocal translocations, Robertsonian fusions as well as differences in the pattern of constitutive heterochromatine.

The Egyptian *A. niloticus* shows a 62 all-acrocentric chromosome complement; the same diploid number characterizes the karyotype of the Burkina-Faso animals, which, however possess five pairs of submetacentric chromosomes originated by pericentric inversion from the acrocentrics of the Egypt karyotype. More relevant are the differences showed by the karyotype of the Central African animals: the diploid number is reduced to $2n = 58$ as a consequence of Robertsonian fusions which gave rise to two pairs of large metacentrics; one reciprocal translocation and one pericentric inversion are also seen in comparing the Central African karyotype to the Egyptian one.

Summarizing the karyological situation described at present for *A. niloticus*, four karyotype were identified, namely:

- $2n = 62$ all acrocentrics in Egypt,
- $2n = 62$ five submetacentric pairs in Burkina-Faso,
- $2n = 58$ two pairs of Rb-metacentrics in Central Africa,
- $2n = 56$ three pairs of Rb-metacentrics in Central Africa.

These findings of karyotype variability within *A. niloticus* prompted us to publish the datum concerning one specimen of this species from Somalia, the karyo-

type of which was analyzed by our group in 1978, and is characterized by an extreme reduction in diploid number. This finding now fits well with the outline of Robertsonian variability in the *Arvicanthis niloticus* karyotype.

MATERIAL AND METHODS

Two species of *Arvicanthis* (Mammalia Rodentia) are found in Somalia, i.e. *A. niloticus* (Desmarest 1822) and *A. somalicus* Thomas 1902. The presence of two distinct but sympatric species has been clearly recognized (SIMONETTA et al. 1978) but it is difficult to understand the nature of the different ecological needs which allow the maintenance of such sympatry. The main structural difference between the two species concerns the size, larger in *niloticus* and smaller in *somalicus*; the tooth row is, consequently, shorter in *somalicus* than in *niloticus*. Because *Arvicanthis* is essentially a grass-loving species, the different size of the molar-row could entrain selective differences in the size of the seeds, leaves and grass shoots composing the diet of the two species.

The specimens used in the present research was an adult female, trapped by A.M. Simonetta in June 1978 near Afgoi, southern Somalia (Somali Democratic Republic). The large size of this specimen (HB 140 mm; T 125 mm; weight 84 g) clearly attributes it to *Arvicanthis niloticus*. Indeed the body measures of the two species present in this part of the East Africa ranges — according to the data collected by SIMONETTA et al. (1978) on Somalian material — as follows:

- A. niloticus*, HB 115-160 mm, T 115-135 mm;
- A. somalicus*, HB 80-120 mm, T 80-115 mm.

The detailed analysis of the skull morphology (Fig. 1) fully supports this taxonomic attribution. In Table 2 the cranial measures of our specimen are compared with the range of variability of those of *niloticus* and of *somalicus* according to the data of ROUSSEAU (1983) based on an extensive biometrical study carried out on the relevant collections of the Muséum National d'Histoire Naturelle of Paris.



Fig. 1. — Skull of the specimen studied: dorsal (A) and ventral (B) view.

Table 2.
Body and cranial measures.

	Present specimen (mm)	Range of variability according to ROUSSEAU (1983)	
		<i>A. niloticus</i> (mm)	<i>A. somalicus</i> (mm)
HB	140	130-140	120-134
T	125	112-153	94-108
UL	33.6	31.9-33.7	22.0-29.8
ZB	17.3	14.9-17.0	13.8-16.0
NL	12.1	9.8-11.3	7.1- 9.8
IO	4.6	4.5- 5.3	3.6- 4.7
IF	5.6	6.1- 6.5	4.2- 6.2
TB	6.2		
LD	8.5		

HB, head and body length; T, tail length; UL, upper length; ZB, zygomatic breadth; NL, nasal length; IO, interorbital constriction; IF, length of the anterior incisive foramen; TB, greater longitudinal diameter of tympanic bullae; LD, length of diastema.

Our specimen has been deposited with the collections of the Muséum National d'Histoire Naturelle of Paris (no. 1983-840).

Somatic metaphases were prepared by the usual air-drying method from bone marrow. Velban was used as cytostatic and 0.075 M potassium chloride for hypotonic treatment. Slides were stained with 4% Giemsa in pH7 buffer. C-bands were obtained according to the SUMNER (1972) technique.

RESULTS AND DISCUSSION

The karyotype of this Somalian *Arvicanthis niloticus* is composed of 44 chromosomes, most of them biarmed: seven pairs are metacentrics (nos 1, 2, 6, 8, 9, 10 and 11) and five pairs are subtelocentrics (nos 3, 4, 5, 7 and 12). Two pairs are small metacentrics (nos 13 and 14). The remaining eight pairs are acrocentrics, the largest of them measures 2.4 μm and the smallest 0.6 μm . Because of the feminine sex of the specimen investigated the sex chromosomes have not been identified.

C-band staining (Fig. 2) reveals sharp heterochromatic masses in the centromeric regions of all chromosomes in the karyotype, both acrocentrics and metacentrics. The presence of centromeric constitutive heterochromatine was shown also by VOLOBOUEV et al. (1986) in the all-acrocentrics 62 chromosomes karyotypes of Egypt *A. niloticus* as well as in the Burkina-Faso and Central Africa ones. It is interesting to underline such a cytochemical character of the *Arvicanthis* chromosomes; in fact the presence of centromeric highly repetitive DNA sequences characterizes the genoma structure of other rodent species, like *Mus domesticus* RUTTY 1772, involved in an extensive process of chromosomal rearrangements (CAPANNA et al. 1985), so that REDI & CAPANNA (in press) proposed a molecular model of Robertsonian fusion based on the presence of terminal satellite DNA sequences.

Two lines of thought could be promoted by this evidence of wide chromosomal variability among the *Arvicanthis niloticus* populations in Africa: the first, more

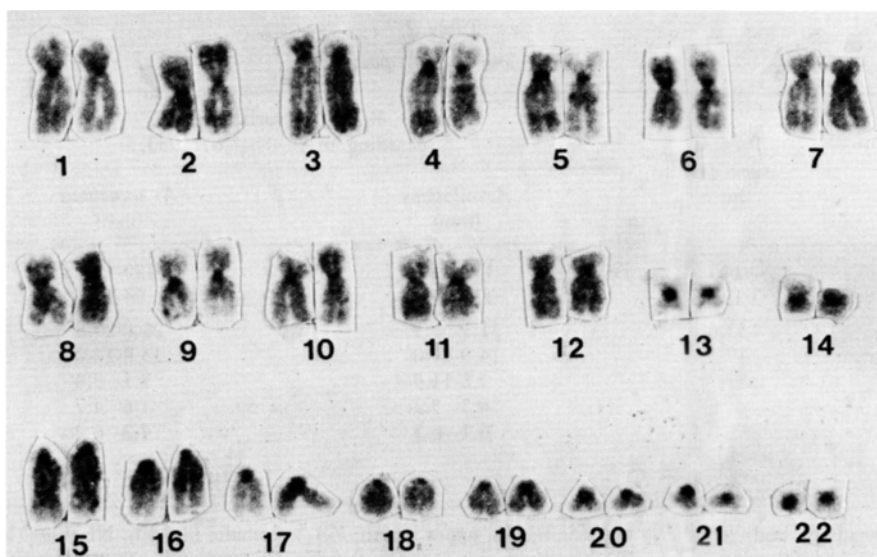


Fig. 2. — C-banded karyotype of the *Arvicanthis niloticus* from Somalia analyzed in the present study. Notice the 12 large biarmed chromosomes and the heterochromatic masses in the centromeric region of all chromosomes.

obvious, concerning taxonomy, the second concerning the evolutionary meaning of the chromosomal reordering in speciation.

There are no doubts that the different karyotype morphology shown by the different *A. niloticus* populations reveals the existence of a great genetic differentiation and the impossibility of any gene flow between populations. Consequently, according to an evolutionary criterion of species, each karyotypically differentiated population has to be considered a separate species. Some uncertainty can surround the two chromosome forms of Central Africa, showing $2n=56$ (MATTHEY 1965) and $2n=58$ (VOLOBOUEV et al. 1986). This phenomenon could be interpreted as the maintenance of an intermediate evolutionary stage of balanced chromosomal polymorphism of two Robertsonian variants. Nonetheless only the presence of hybrids between the two karyological forms — and such a hybrid has not yet been found — would be essential to support this hypothesis.

This evidence for separate chromosomal species does not agree with the apparent morphological similarity. Although classical univariate analysis is unable to phenetically discriminate the *A. niloticus* populations throughout its wide distribution area, multivariate analysis, such as the one performed by ROUSSEAU (1983), has been revealed as a very sensitive method for enhancing differentiations in skeletal structure between *A. niloticus* populations. The correspondence analysis performed by the above author clearly discriminates phenetic groups within *A. niloticus* identified under subspecific name, such as *A. n. centralis* Dollman 1911, from Central African Republic and *A. n. solatus* Thomas 1925, from the mountain of Niger. Moreover the multivariate approach clearly divides the population from Senegal from any other *A. niloticus* population, as well as from any other *Arvicanthis* species. The Senegal

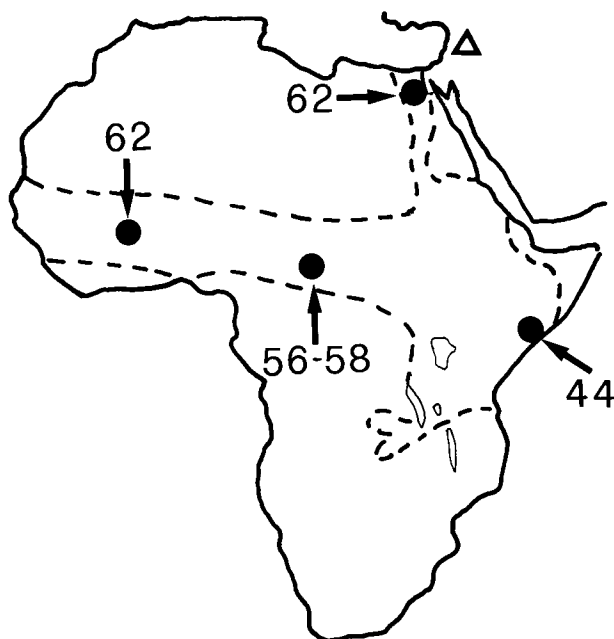


Fig. 3. — The area of distribution of *Arvicanthis niloticus* is enclosed by dotted lines; black circles indicate the localities from which the samples were taken and figures indicate the respective diploid numbers. The triangle shows the location at which the subfossil *Arvicanthis* was found.

population inhabits the extreme end of the *Arvicanthis* distribution area and no subspecific name was previously attributed to it in literature.

It is worth noting the opinion expressed by ROUSSEAU (1983) concerning the *A. niloticus* of Central Africa: «S'il se vérifie que la formule chromosomique de cette population de R.C.A. diffère de celle de l'ensemble des autres *Arvicanthis niloticus*, ces spécimens pourraient être les représentants d'une espèce distincte: *Arvicanthis centralis*, décrite du Bahr-el-Ghazal». The karyotype is different indeed, but what is the chromosome complement of *Arvicanthis niloticus*? Is it $2n=62$ as in Egypt or $2n=44$ as in Somalia? Actually there is no an «ensemble» of *Arvicanthis niloticus* but a complex of separate population-species. It is clear that such a systematic context is extremely entangled and will be solved when a complex of integrate multivariate morphological, karyological and biochemical studies characterize each geographical population throughout the wide distribution areas of the genus.

A further consideration can be made concerning the spatial placing of the different karyotypically characterized populations of *A. niloticus* throughout its distribution area (Fig. 3). It is noteworthy that the diploid number decreases from North to South, i.e. from 62 in Egypt, to 44 in Somalia. A similar geographically ordered distribution of karyological variants was described in other polykaryotypic species complexes in rodents. For example in *Spalax ehrenbergi* Nehring 1898 the diploid number decreases from the North to the South of Palestine, i.e. from humid to arid

regions. This fact was interpreted by NEVO (1983) as evidence of a selective value of the chromosomal reordering itself, in other words, of an adaptive meaning of the chromosomal configuration of the genoma. On the other hand a model of «adaptive» chromosomal evolution was suggested by BICKHAM & BAKER (1979) which implies that the karyotype morphology is a significant aspect of the adaptive strategy of an organism. In this hypothesis for each «adaptive zone» there is an optimum karyotype that can be evolved by chromosome rearrangement.

A similar hypothesis could fit the spatial distribution of the *Arvicantis niloticus* cytotypes. Nonetheless the vastness of the African area inhabited by the *A. niloticus* complex and the substantial climatic uniformity of the grassland and savanna habitats do not fully agree to the «adaptive» hypothesis which needs evidence of sharp climatic diversities in close spaces.

More probably the gradient in karyological distribution can be related to progressive chromosomal changes which occurred during the colonization of Africa by *Arvicantis*. The presence of subfossil *Arvicantis* in Palestine (KINGDOM 1974) demonstrates that such a colonization began from Egypt and spread toward the South and South-West. Consequently the Egyptian population can be considered ancestral and $2n = 62$ the basic karyotype; on the other hand the diploid number 62 is shared by *A. abyssinicus* to. In our alternative hypothesis, progressive fusions occurred during the North-South expansion of the *Arvicantis*, creating a chain of semispecies karyotypically differentiated; some of them extinguished and some gave rise to the chromosomal species of the *A. niloticus* complex.

A detailed karyological recognition of several *A. niloticus* populations along the North South and North South-West axes could reveal the presence of such hypothetical intermediary karyotypes.

Once more studies of the karyotype of African rodents reveal surprising data and enhance the importance of such an analysis in taxonomy and systematic.

ACKNOWLEDGEMENTS

We thank our colleague, and friend, Prof. Alberto M. Simonetta (University of Camerino), who provided us with this interesting Somalian specimen of *Arvicantis* and Prof. Francis Petter (Muséum National d'Histoire Naturelle of Paris) who checked the taxonomic attribution of the specimen. This work has been supported by grants of the Italian Ministry of Education (Ministero della Pubblica Istruzione 40%) and of the National Research Council (Consiglio Nazionale delle Ricerche 83.02003.04).

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