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Material and methods

Karyotypes of six specimens were studied after R-banding (RHG, RBG) and C-banding (CBG) (ISCN, 1978). Metaphases were obtained from fibroblast cultures established from tail biopsies. Two male specimens studied came from Cairo, Egypt (R-banded chromosomes of one specimen were reported previously by VIEGAS-PÉQUIGNOT et al. 1983). Other animals came from: the middle part of the Central African Republic (bank of the Gounda river), one male; from Bamako, Mali, one male; from Oursi, in north Burkina Faso, one male, and from Brançon, Senegal, one male. In order to simplify the description of the karyotypes, we have grouped the animals with identical karyotypes and labelled them as follow: ANI-1 (two specimens from Cairo and one specimen from Senegal), ANI-2 (specimen from Central African Republic) and ANI-3 (specimens from Burkina Faso and Mali).

Results

R-banding, BrdU incorporation

ANI-1: The karyotype is composed of 62 chromosomes. All the autosomes but one pair are acrocentric. The X chromosome, the largest element, is submetacentric, and the Y chromosome is a medium sized submetacentric (see VIEGAS-PÉQUIGNOT et al. 1983).

ANI-2: The diploid number is 58. The first 3 pairs are large meta- or submetacentrics; the next 2 pairs are medium sized metacentrics; pairs 6 to 26 are acrocentric, and pairs 27 and 28 are very small submetacentrics. The X chromosome is a large submetracentric and the Y chromosome is a small metacentric (see VOLOBOUEV et al. 1987).

ANI-3: The karyotype possesses 62 chromosomes. The first 5 pairs are meta- or submetacentric, pairs 6 to 27 are acrocentric, and pairs 28 to 30 are submetacentric. The X and Y chromosomes are large and medium sized submeta- and metacentrics respectively (Fig. 1).

C-banding

ANI-1. All autosomes have a centromeric block of fairly uniform size. The short arms of the X chromosome are stained more intensively in the pericentromeric region, and there is a distinct C-band distally located in the long arms. The proximal part of the long arms of the Y chromosome are stained more intensively in their pericentromeric part.

ANI-2. The first pair is not stained. The second pair is heteromorphic, only one homologue is stained. Among the acrocentrics, 3 pairs are not stained. The proximal part of the long arm of the X chromosome is stained more intensively in the pericentromeric region, and the Y chromosome possesses only a small block intensively stained (see VOLOBOUEV et al. 1987).

ANI-3: C-banding is observed in the pericentromeric regions of the 2 smaller pairs of meta- or submetacentrics and in 10 pairs of acrocentrics. The distribution of C-banding is partially related to the size of the chromosomes since there is no staining of the 3 largest submetacentrics nor of the five largest acrocentrics. The X chromosome possesses a strong

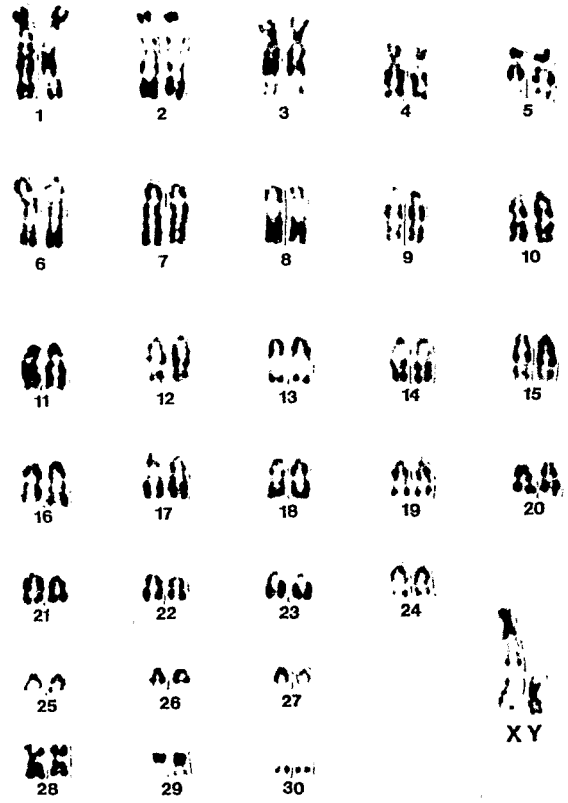

Fig. 1. R-banded (RHG) karyotype of a male *A. niloticus* from Burkina Faso (ANI-3)

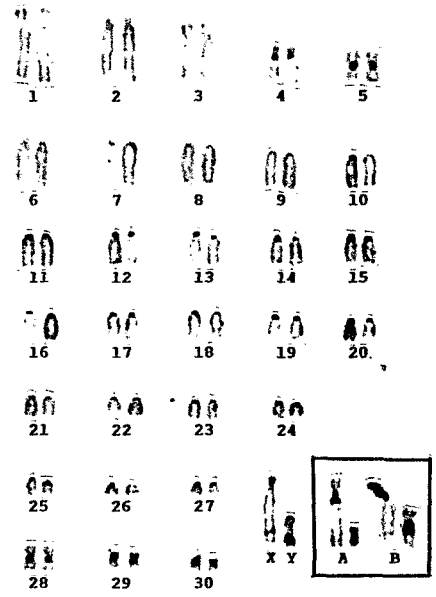

Fig. 2. C-banded (CBG) karyotype of a male *A. niloticus* from Burkina Faso (ANI-3). In the insert, C-banding of the sex chromosomes of ANI-2 (A) and ANI-1 (B)

- Chromosome 6 of ANI-1 corresponds to the short arm of chromosome 2 of ANI-2. It is identical to chromosome 8 of ANI-3.
- Chromosome 3 of ANI-1 corresponds to chromosomes 3 of ANI-2 and ANI-3, respectively. Both chromosomes of ANI-2 and ANI-3 are identical. They differ from chromosome 3 of ANI-1 by a pericentric inversion.
- Chromosome 4 of ANI-1 corresponds to chromosome 7 in ANI-2 and chromosome 9 in ANI-3, respectively but the proximal segment is lacking in these two forms.
- Chromosome 7 of ANI-1 corresponds to the distal segment of chromosome 6 of ANI-3, which corresponds to the short arm of chromosome 1 of ANI-2. The extra material of chromosome 6 of ANI-3, by comparison to chromosome 7 of ANI-1 may well correspond to the missing material of chromosome 9 of ANI-3 by comparison to chromosome 4 of ANI-1. Thus, a reciprocal translocation is likely to have occurred between ANI-1 and ANI-3. Chromosome 7 of ANI-2 is identical to chromosome 9 of ANI-3, and the short arm of chromosome 1 of ANI-2 corresponds to chromosome 6 of ANI-3. Thus, the latter chromosome was involved in a Robertsonian translocation to form

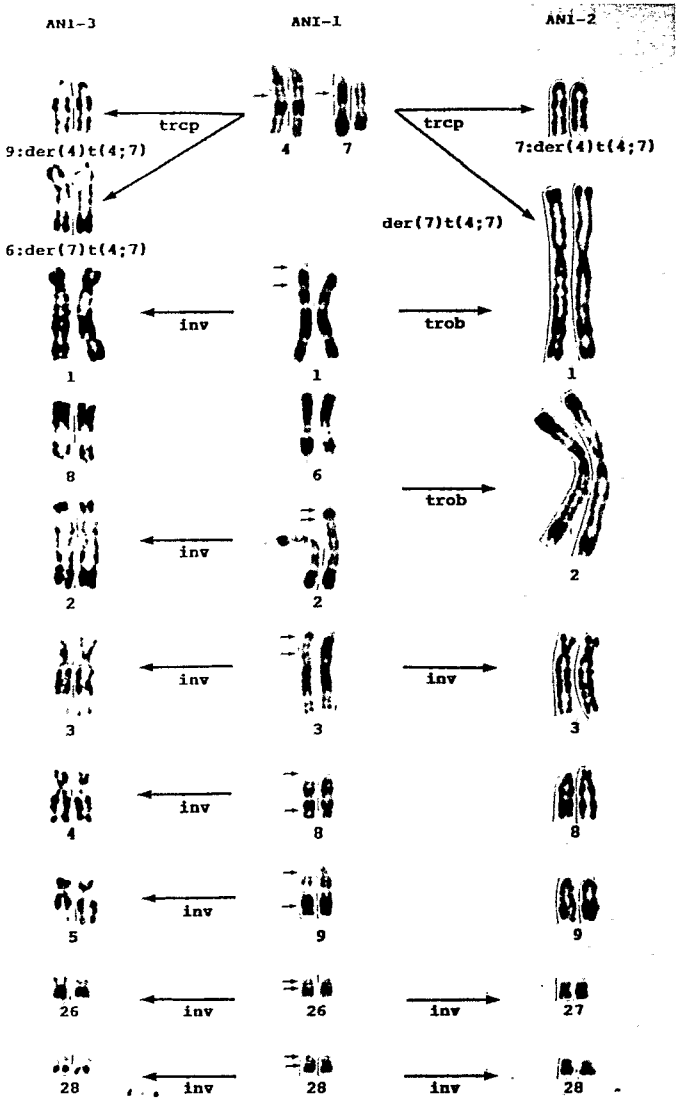

Fig. 3. Comparison of the chromosomes involved in rearrangements separating the karyotypes of ANI-1, ANI-2 and ANI-3 (See text for explanation)

chromosome 1 of ANI-2, indicating that chromosome 6 of ANI-3 is intermediary between chromosome 7 of ANI-1 and chromosome 1 of ANI-2.
- Chromosomes 8 of ANI-1 and ANI-2 are identical. They correspond to chromosome 4 of ANI-3, which differs by a pericentric inversion.
- Chromosomes 9 of ANI-1 and ANI-2 are also identical, and they correspond to chromosome 5 of ANI-3, which differs by a pericentric inversion.
- Chromosomes 26 of ANI-3 and 27 of ANI-2 are identical. They differ from chromosome 26 of ANI-1 by a pericentric inversion.
- Chromosomes 28 of ANI-2 and ANI-3 are identical. They differ from chromosome 28 of ANI-1 by a pericentric inversion.

Chromosome comparison with related genera

In a previous study, VIEGAS-PÉQUIGNOT et al. (1983, 1986) reported a number of karyotypes of African Muridae, including that of ANI-1. They also reconstructed the presumed ancestral karyotype of Muridae and Cricetidae (VIEGAS-PÉQUIGNOT et al. 1985, 1986). These data may be used to infer which of the 3 forms compared here possesses chromosomes most similar to that of the ancestral form. It is most likely that this form is ANI-1 which conserved its chromosomes 1, 2, 3, 4, 6, 7, 9, and perhaps 8, 26 and 28 identical to presumed ancestral chromosomes (see Fig. 12 in VIEGAS-PÉQUIGNOT et al. 1986), whereas the corresponding chromosomes are rearranged in ANI-2 and/or ANI-3.

Proposed chromosomal phylogeny of 3 forms of Arvicanthis niloticus

From the ancestral karyotype of ANI-1, two and perhaps 4 (see below) rearrangements have occurred in a branch common to ANI-2 and ANI-3. These are the reciprocal translocation, affecting chromosomes equivalent of 4 and 7 of ANI-1 and the inversion of

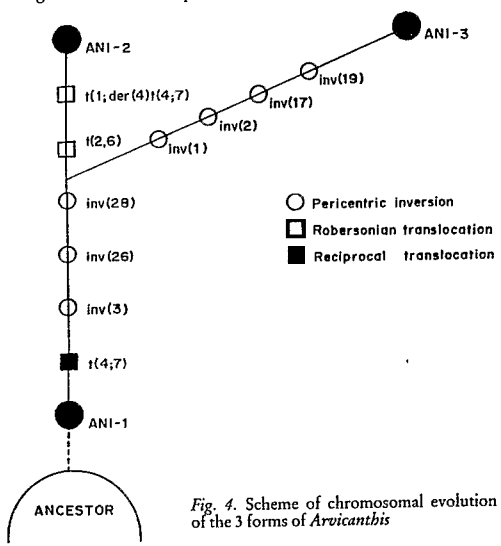

Fig. 4. Scheme of chromosomal evolution of the 3 forms of *Arvicanthis*

chromosome 3. The two other rearrangements are pericentric inversions affecting chromosomes 26 and 28 of ANI-1. Since these chromosomes are very small, they could not be accurately identified in the ancestral karyotype, making the identification of their inversions uncertain. However, the metacentric form of these chromosomes does not exist in species from other genera, making more likely the interpretation that the acrocentric form is ancestral.

The form ANI-2 has acquired two further rearrangements, i.e. two Robertsonian translocations. In one of these translocations a chromosome is involved which can be derived from the reciprocal translocation which had occurred in the common branch. The form ANI-3 has acquired 4 rearrangements, all pericentric inversions making submetacentrics from ancestral acrocentrics. Among them, the inversion affecting chromosome 8 of ANI-1 is not certain since this chromosome was not clearly identified in the ancestral karyotype of Muridae.

Discussion

Chromosomal evidences that Arvicanthis niloticus is a polytypic species

The chromosomal comparisons performed between 3 forms of *A. niloticus* lead to several conclusions. Ten structural rearrangements involving euchromatin have occurred: one reciprocal translocation, two Robertsonian translocations and 7 pericentric inversions. Four of these rearrangements can be found in two forms (ANI-2 and ANI-3), making the existence of a single ancestral lineage for them very likely. The 3 karyotypic forms differ from each other by 6 to 8 rearrangements, and moreover variations of heterochromatin exist both at the intra- and interform level: there is a progressive decrease of the total amount of heterochromatin from ANI-1 to ANI-2 and ANI-3.

Although no studies exist on hybridization between forms with different karyotypes, it seems very likely that the observed chromosomal modifications should establish a very efficient gametic barrier, including or strengthening the isolation of the three chromosomal forms. Thus, it is very likely that *A. niloticus* (*sensu* auctorum) is composed of three different species at least. One, ANI-1, possesses a karyotype ancestral for the two others, which are equally distant from it. It is also likely that other species are included in *A. niloticus* since Matthey (1956) described a form with 56 and Capanna et al. (1983) a form with 46 chromosomes.

Finally, chromosomal data suggest first, that the genus *Arvicanthis* is polytypic, as proposed also by morphological data by Rousseau (1982) and Nowak and Paradiso (1983) in contrast with the earlier opinion of Misonne (1974) and Honacki et al. (1982). Secondly, *A. niloticus* should be regarded no longer as a single species but as a cluster of several true species.

Biochemical evidence

There is strong biochemical evidence supporting the conclusion made on the basis of chromosomal data. Electrophoretical analyses of blood proteins of three samples of *Arvicanthis* from Egypt, Cairo (corresponding to ANI-1 in our study), Burkina Faso,

Morphological and eco-ethological evidence

In a detailed study of various populations from Senegal, Egypt, Burkina Faso and Central African Republic, Rousseau (1982) clearly distinguished various morphological forms. These results are in good agreement with the biochemical data. They also fit the chromosomal data excepted that karyology failed to show any significant difference between specimens from Egypt and Senegal. Finally these data are not inconsistent with eco-ethological information reported by Nowak and Paradiso (1983) who noticed a large habitat and comportement variation in *A. niloticus*.

The genus *Arvicanthis* is distributed in savanas of South Sahara, from Senegal to Ethiopia. Studies on population dynamics in Senegal have shown that *A. niloticus* is affected by intensive cyclic pullulation and that it may disappear almost completely in a given locality as a result of a consecutive series of the dry years (Poulet 1982). This relationship with humidity may well explain its extension in Sahara, during wet periods during Quaternary (Rousseau 1982). The present distribution of *A. niloticus* in Africa is well known, from Dakar (Senegal) to Omo valley (Ethiopia) and Alexandria (Egypt). The fact that similar karyotypes and fertile hybrids exist between animals from Dakar and Omo (Petter et al. 1969) and from Senegal and Alexandria (Rousseau 1982) suggest that the corresponding populations have not diverged much. The distinct karyological forms from Burkina Faso and Central African Republic seem to correspond to residual populations isolated from the rest of the population by dry areas which developed since the last wet period.

Proposition for a taxonomic revision

Since many discrepancies exist in the systematics of the whole genus *Arvicanthis*, which seems to be composed of 1 to 6 species, the systematics of each of the presumed species remains even more uncertain. This is the case for *A. niloticus* in particular. Our own results show that at least 3 forms exist. They are quite distinct, since their karyotypes differ by 6 to 8 structural rearrangements. These results are in agreement with those of Rousseau (1982) and Kaminski et al. (1984, 1987) who even proposed a forth form since they differentiated some populations from Senegal and Egypt. Neglecting *Arvicanthis* from other regions, for which other chromosomal modifications may exist (Matthey 1965; Capanna et al. 1985), it seems reasonable to propose that at least 3 or perhaps 4 species exist. We propose to relate them to the previously described forms with close geographical distribution, until there is a more complete study to establish the distribution limits:

ANI-1 = *A. niloticus* Desmarest, 1822 described from Egypt and Senegal, and possibly also from Omo valley, Ethiopia.

ANI-2 = *A. centralis* Dollman, 1911 described from Bahr el Gazal (Sudan), and that which we obtained from the Central African Republic.

ANI-3 = *A. solatus* Thomas, 1925 described from Aïr, and that which we obtained from Burkina Faso and Mali.

Finally, since many difficulties remain especially for the group *A. niloticus* sensu auctorum, it seems necessary to continue chromosomal and biochemical studies before prop-

ANI-2 et ANI-3 se différencient entre elles par 6 à 8 remanienents de structure: translocation réciproque, translocations Robertsoniennes et inversions pericentriques. En outre, il existe des différence dans la quantité d'hétérochromatine. Les données obtenues montrent que ces formes, isolées cytogénétiquement, représentent trois espèces différentes, et que la révision taxonomique approfondie du genre *Arvicanthis* est nécessaire.

Zusammenfassung

Cytotaxonomische Beweise für eine polytypische Zusammensetzung von Arvicanthis niloticus (Rodentia, Muridae)

Eine Analyse der Chromosomen von *Arvicanthis niloticus* nach R- und C-Banding-Färbung zeigt in Stichproben von fünf Standorten in Afrika (Ägypten, Senegal, Burkina-Faso, Mali und Zentralafrikanische Republik), daß es drei verschiedene Karyotypen gibt, die in der vorliegenden Arbeit mit ANI-1, ANI-2 und ANI-3 bezeichnet werden. Die Karyotypen unterscheiden sich voneinander durch 6 bis 8 Chromosomen-Dislokationen, wie reziproke und Robertsonsche Translokationen und perizentrische Inversionen. Außerdem ist die Zahl der C-Heterochromatin-positiven Stellen unterschiedlich. Die Ergebnisse lassen erkennen, daß die drei verschiedenen Chromosomen-Rassen distinkten Arten entsprechen, die voneinander cytogenetisch isoliert sind, und daß weitere taxonomische Analysen für die Gattung *Arvicanthis* notwendig sind.

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