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SYSTEMATICS OF THE GENUS *MASTOMYS* (Thomas, 1915) (Rodentia: Muridae)

A REVIEW

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Key words: Mastomys, systematics, chromosomes, species limits.

Abstract. An update of the systematics of the genus *Mastomys* is presented, based on a bibliographical analysis and recent results obtained in various fields. Seven species are considered, namely *M. erythroleucus, M. coucha, M. shortridgei, M. natalensis, M. huberti, M. pernanus* and *M. verheyeni. M. hildebrandtii*, listed by some authors, is considered here as *species inquirenda*, due to insufficient evidence. The main characteristics of these species are described, with special emphasis on the karyotype, which appears to be an especially informative, species-specific character in the genus. The known distribution of each species is mapped, and the various intrageneric phylogenetic hypotheses are presented. The difficulties that remain in this group are listed, together with some directions in which further research should be carried on.

Key words : Mastomys, systematics, chromosomes, species limits.

INTRODUCTION

Distributed throughout Africa south of the Sahara with a relict population in Morocco, the genus *Mastomys* Thomas, 1915 undoubtedly represents one of the major components of the African mammal fauna from various points of view. Except in the primary forest region where it is restricted to human settlements, it is often one of the dominant genera of the small mammal communities. At least two of its species, *M. erythroleucus* and *M. natalensis*, regularly display spectacular population explosions, making them important pests for standing crops and stored foods (Poulet, 1982; Leirs, 1994). Also, some species of the genus are known to be reservoirs for various infectious diseases affecting humans, including bubonic plague and Lassa fever (see Leirs, 1994).

All these characteristics have made *Mastomys* probably the most studied rodent taxon among the indigenous African murids. Nevertheless, it is only recently that its taxonomy has become clearer, and that it has been nearly unanimously recognized as deserving a genus rank. This status was already admitted by ALLEN (1939), after THOMAS (1915) has proposed the taxon *Mastomys,* together with *Praomys* and *Myomys,* as a subgenus of *Epimys* Trouessart, 1881. ELLERMAN (1941) considered all these taxa as subgenera of *Rattus* L., 1758, while MISONNE (1971) placed them within the genus *Praomys,* followed by HONACKI *et al.* (1982). In the meantime, ROSEVEAR (1969) discussed the situation of *Mastomys* as a separate genus, as later did MEESTER *et al.* (1986), and MUSSER & CARLETON (1993). First suggested on morphological grounds, the monophyly of *Mastomys* was subsequently demonstrated via chromosomal analysis (MATTHEY, 1958; LEE & MARTIN, 1980; BRITTON-DAVIDIAN *et al.*, 1995), multivariate analyses of biometrical data (VAN DER STRAETEN, 1979; VAN DER STRAETEN & ROBBINS, 1997) and molecular results (CHEVRET *et al.*, 1994).

Species definition and characterization have also greatly improved since ELLERMAN (1941) who listed 28 forms (except for *M. pernanus)* as subspecies of *Rattus* (*Mastomys*) *coucha*. Here, the use of genetic techniques (*sensu lato*, and especially protein electrophoresis and chromosome analysis), has been of paramount importance in discriminating sibling species (MEESTER, 1988). GREEN *et al.* (1980), HUBERT *et al.* (1983), ROBBINS & VAN DER STRAETEN (1989), LAVRENCHENKO *et al.* (1992), MUSSER & CARLETON (1993) and BRITTON-DAVIDIAN *et al.* (1995) have synthesized the available data and made various propositions regarding the intrageneric taxonomy of *Mastomys.* We here update these data, taking into account the most recent findings that have shed additional light on the systematics of the genus. For the species list, we basically follow MUSSER & CARLETON (1993), with two exceptions:

First, we do not find sufficient data to support *M. hildebrandtii* (Peters, 1878) as presented in MUSSER & CARLETON (1993). QUMSIYEH *et al.* (1990) considered the 2n=32, FN=50-54 *Mastomys* specimens from Kenya as belonging to the same species as those with similar karyotypes found in Somalia by CAPANNA *et al.* (1982) who called them *M. huberti.* But QUMSIYEH *et al.* (1990) then synonymized *M. huberti* and *M. hildebrandtii*, giving priority to the older name *M. hildebrandtii*. MUSSER & CARLETON (1993) followed QUMSIYEH *et al.* (1990), but added that *M. huberti* is the species with 2n=32, and an autosomal fundamental number aFN=44, thus implicitely recognizing a synonymy between two entities with very different fundamental numbers aFN=50-54 and aFN=44, which is very doubtful from a chromosomal point of view. Moreover, this 2n=32, FN=44 karyotype (actually aFN=44-46, see below) has in fact never been found in East Africa, where the type specimen of *M. hildebrandtii* comes from (Kenya). Rather, this karyotype is restricted to West Africa, where it may well correspond to *M. huberti* described from northern Nigeria. That is why we here list *M. huberti* as a more likely valid species, following PETTER (1977), and awaiting comparative studies including karyotyped specimens, the holotype and series from the type locality of *M. huberti*. The existence of an East African species distinct from *M. natalensis,* and that may be *M. hildebrandtii,* is not sufficiently supported to date (see discussion), hence we prefer to consider it as *species inquirenda.*

Second, we do not include the species *angolensis* in the taxon *Mastomys*, considering as an important character of the genus the number of mammae of the females, following ELLERMAN (1941, p.168: «mammae usually more than 12, not separated into pectoral and inguinal sets»). In that, we disagree with CRAWFORD-CABRAL (1989), who discarded the mammae count (3-2=10) as a significant character and maintained *angolensis* within *Mastomys* (see ROBBINS & VAN DER STRAETEN (1989), and MUSSER & CARLETON (1993) for further details). We will first characterize as completely as possible the species of the genus, briefly discuss their phylogenetic relationships, then state the problems that remain to be solved, and the subsequent directions of research that we consider as the most important.

SPECIES CHARACTERIZATION

Mastomys erythroleucus (Temminck 1853)

The species was described from Ghana on the basis of a young specimen of unknown sex, the skull of which was in poor condition (ROBBINS & VAN DER STRAETEN, 1989). ROBBINS & VAN DER STRAETEN (1989) questioned the validity of *M. erythroleucus* for animals having a diploid number of 38 chromosomes, a correspondence proposed by PETTER (1957; 1977). We support the now widely admitted view (DUPLANTIER *et al.*, 1990a) that *M. erythroleucus* is a valid species: the name *erythroleucus* refers to a fur color pattern which indeed characterizes individuals with 38 chromosomes. The biometric variability between 2n=38 populations that ROBBINS & VAN DER STRAETEN (1989) mention, is part of the more general problem of intraspecific polymorphism that has been illustrated in *Mastomys* species by various authors (DUPLANTIER, 1988; DIPPENAAR *et al.*, 1993; GRANJON *et al.*, 1996).

The first mention of this karyotype was by MATTHEY (1958, corrected in 1965 and 1966a), based on a specimen from Ivory Coast. The common range of autosomal fundamental number (aFN) recorded so far for this species is 50-56 (DUPLANTIER *et al.*, 1990a). Belonging to this chromosomal form are specimens from Morocco (TRANIER, 1974), Senegal (HUBERT *et al.*, 1983; DUPLANTIER *et al.*, 1990a; BRITTON-DAVIDIAN *et al.*, 1995), Burkina Faso, Mali and Niger (SICARD, pers. comm.; BRITTON-DAVIDIAN *et al.*, unpubl. data), Ivory Coast (MATTHEY, 1958; 1965; 1966a), Benin (CODJIA *et al.*, 1996), Cameroon and East Zaïre (MATTHEY, 1967), and Ethiopia (ORLOV *et al.*, 1989; BASKEVICH & ORLOV, 1993). Specimens with 38 chromosomes have also been found in other localities, but either the aFN was not reported: Sierra Leone and Cameroon (ROBBINS & VAN DER STRAETEN, 1989), Nigeria (DOBROKHOTOV, 1982), Burundi (VERHEYEN, pers. comm. in ROBBINS *et al.*, 1983), or the aFN was outside the range defined above: Central African Republic (aFN=68 or 70, MATTHEY in HUBERT *et al.*, 1983), East Zaïre (aFN=60; KRAL, 1971), Sudan (aFN=40; VIEGAS-PEQUIGNOT *et al.*, 1987).

Protein electrophoresis has been performed in a number of studies, mainly on hemoglobin, in order to distinguish between sympatric chromosomally differentiated species of *Mastomys*. Such instances where the 2n=38 *Mastomys* analyzed are likely to be *M. erythroleucus* specimens, include the studies of DOBROKHOTOV (1982) in Nigeria, and ROBBINS *et al.* (1983) in Sierra Leone. As stated above, the aFN of these 38-chromosome *Mastomys* individuals was not reported in either cases, nor were those of the 32-chromosome individuals to which they were compared (which could have been either *M. natalensis* or *M. huberti*). It is worth noting, however, that in both studies, the two chromosomal forms were distinguished on the basis of their hemoglobin pattern, and that an important variability was observed within the 38-chromosome form (see LAVRENCHENKO *et al.*, 1992). In a more thorough allozymic analysis, DUPLANTIER *et al.* (1990b) studied a sample of *M. erythroleucus* from Senegal at 20 loci and found not only low levels of interpopulation divergence (a conclusion already suggested by KAMINSKI *et al.*, 1987), but a very slight overall differentiation from *M. huberti* (D_{Nei}=0.118) with no fixed allelic differences between the two species.

From a biometrical and morphological point of view, no single body or skull measurement has been found to unambiguously discriminate between *M. erythroleucus* and *M. huberti* and *M. natalensis* in Senegal (DUPLANTIER, 1988). The same is true for dental patterns and measurements (DENYS *et al.*, unpubl. data). However, the use of multivariate discriminant analyses on cranial and mandibular (DUPLANTIER, 1988) or dental (DENYS *et al.*, unpubl. data) measurements has achieved a nearly complete separation of these three species, at least for specimens from Senegal. Characters that are being more and more used as taxonomic tools are sperm and penis morphology and dimensions. They appear very useful for differentiating *M. erythroleucus* from other species of the genus (BASKEVICH & LAVRENCHENKO, 1995; LAVRENCHENKO & BASKEVICH, 1996).

M. coucha (Smith, 1836)

The species was described from Kuruman, South Africa, and since the synthesis of GREEN *et al.* (1980) who proposed to use this name only for the 2n=36 *Mastomys* from Southern Africa, there has been a general consensus on this point. MATTHEY established the karyotype as early as 1954, and further commented on it in 1958 and 1966(a), reporting the aFN as ranging between 52 and 54. The G-banded pattern is described for specimens from Zimbabwe (LYONS *et al.*, 1977) and South Africa (LEE & MARTIN, 1980) where HALLETT (1979) also mentioned some variability (aFN=54-56). *M. coucha* is only known from Southern Africa, being recorded from South Africa, Zimbabwe and Namibia (see map in SKINNER & SMITHERS, 1990). The individual from Central African Republic with a 2n=36, aFN=56 karyotype described by MATTHEY (1970) may represent another species or an aberrant specimen.

Associated with this karyotype, a specific electrophoretic pattern of hemoglobin («fast») was found (GORDON, 1978; GREEN *et al.*, 1980), consistently different from that of the 32-chromosome *M. natalensis*. Here again, only multivariate discriminant analyses on skull measurements efficiently separated *M. coucha* from *M. natalensis* (DIPPENAAR *et al.*, 1993; NJOBE, unpubl. data). Sperm morphology which appeared very similar between these two species (BREED, 1995), nevertheless allowed *M. coucha* to be distinguished from *M. shortridgei,* a species with a very similar karyotype (GORDON, 1985).

M. shortridgei (St Leger, 1933)

Little has been published on this species which is considered to be restricted to the extreme NE of Namibia and NW of Botswana (see map in SKINNER & SMITHERS, 1990). GORDON (1985) described its mammary formula as being 8:8=16, whereas SKINNER & SMITHERS (1990), following older descriptions, mentioned only 5 pairs of mammae (as in the type-specimen, where the nipples lie in one line, and are not grouped). The karyotype is very similar to that of *M. coucha*, with 2n=36, aFN=50 with an almost complete G-band homology, although the sex chromosomes were found to differ using C-banding. Sperm head shape was also distinctive between these two species (GORDON, 1985).

M. natalensis (Smith, 1834)

The species was described from Durban (South Africa), and as argued by GREEN *et al.* (1980), *M. natalensis* undoubtly represents the valid species name for the 32-chromosome *Mastomys* individuals from Southern Africa. In this region, this diploid number seems to correspond to only one species. The situation is more complicated in other parts of Africa (DUPLANTIER *et al.*, 1990a; BASKEVICH & ORLOV, 1993), where at least two species with 2n=32 are present (*M. natalensis* and *M. huberti* in West Africa, *M. natalensis* and *Mastomys* sp. in East Africa, see discussion). For this reason, DUPLANTIER et al. (1990a) suggested that *M. natalensis* be described by the combination of both its 2n (=32) and aFN (=52-54).

This karyotype was first found by MATTHEY (1955) in Ivory Coast, then in Central African Republic, Congo (MATTHEY, 1966a) and Chad (MATTHEY, 1966b). In these regions, the Y chromosome was described as submetacentric whereas it was scored as an acrocentric chromosome in specimens from all other areas. In West Africa, *M. natalensis* is also known from Senegal (DUPLANTIER et al., 1990a), Benin (CODJIA *et al.*, 1996), Burkina Faso, Mali and Niger (HUBERT *et al.*, 1983; SICARD, pers. comm.; BRITTON-DAVIDIAN *et al.*, unpubl. data). The same karyotype was described from Somalia (CAPANNA *et al.*, 1982), Ethiopia (ORLOV *et al.*, 1989; BASKEVICH & ORLOV, 1993) and Tanzania (LEIRS, 1994). HUBERT *et al.* (1983), citing DOBROKHOTOV *et al.*, mentioned this karyotype in Nigeria, although DOBROKHOTOV (1982) did not report the aFN of the 32-chromosome *Mastomys* individuals he studied in this country. In Southern Africa, the presence of *M. natalensis* was confirmed in South Africa and Namibia (HALLETT, 1979) and Zimbabwe (LYONS *et al.*, 1980). Finally, 32-chromosome *Mastomys* individuals were mentioned from Sierra Leone and Burundi (ROBBINS *et al.*, 1983), but the aFN was not reported. The conspecificity of *M. natalensis* from Senegal and South Africa (i.e. the two extremes of the species range) has recently been definitely proven by GRANJON *et al.* (1996), which probably makes this species the most widely distributed mammal of Africa.

Protein electrophoresis studies on *M. natalensis* have mainly focused on the study of hemoglobin patterns: in Southern Africa (South Africa, Zimbabwe, Namibia), GORDON (1978) and GREEN *et al.* (1980) have shown that a «slow» Hb allele was associated with the 32-karyotype. The same type of study was performed on 32-chromosome *Mastomys* from Sierra Leone (ROBBINS *et al.*, 1983) and Nigeria (DOBROKHOTOV, 1982), but without specifying their aFN (see above). The analysis at 20 loci of a sample of *M. natalensis* from Senegal by DUPLANTIER *et al.* (1990b), showed a rather low genetic variability in this species when compared to *M. erythroleucus* and *M. huberti*, and no diagnostic loci between these 3 species. MILISHNIKOV *et al.* (1992) also found low levels of diversity in a sample of what they called *M. huberti*, but which more likely represents *M. natalensis.*

Morphological and biometrical studies on *M. natalensis* have been performed on specimens from Senegal (DUPLANTIER, 1988; DENYS *et al.*, unpubl. data) and South Africa

(DIPPENAAR *et al.*, 1993). Only discriminant analysis on skull and dental measurements enabled the complete or nearly complete characterization of *M. natalensis*. The sperm morphology of *M. natalensis* was very similar to that of *M. coucha* (BREED, 1995; BASKEVICH & LAVRENCHENKO, 1995), whereas the penis and bacculum morphology of *M. natalensis* was distinct from that of *M. erythroleucus* and *Mastomys* sp. from Ethiopia (LAVRENCHENKO & BASKEVICH, 1996).

M. huberti (Wroughton, 1908)

To this species described from Northern Nigeria, PETTER (1977) referred the specimens with 32 chromosomes from Western and Central Africa. Since then, the situation has proven to be more complicated, two species with this 2n (but with different aFN) having been characterized in this region (or at least part of it – DUPLANTIER *et al.*, 1990a). One of them is *M. natalensis*, as stated above, and the specimens with the other aFN probably belong to *M. huberti*. The standard karyotype of this species has been presented by HUBERT *et al.* (1983), the G-banded one by VIEGAS-PEQUIGNOT *et al.* (1983). DUPLANTIER *et al.* (1990a) and BRITTON-DAVIDIAN *et al.* (1995), working on a larger sample, identified its chromosomal variability: 2n=32, aFN=44-46. This chromosomal form, which for a long time was known only from Senegal, has been recently confirmed in Mauritania (GRANJON *et al.*, 1997), Mali and Burkina-Faso (SICARD, pers. comm.). This last finding supports the belonging of these specimens to *M. huberti*, a decision which will be definitely validated when specimens from the type region are studied. Unless there is a spectacular range extension of this form towards East Africa, we see no reason to refer it to *M. hildebrandtii*, the type specimen of which was described from Kenya.

Chromosomally characterized *M. huberti* have been studied by protein electrophoresis (DUPLANTIER *et al.*, 1990b) and biometrical analyses (DUPLANTIER, 1988; DENYS *et al.*, unpubl. data). None of these methods led to the finding of any clear diagnostic character for distinguishing *M. huberti* from its sympatric congeneric species (*M. erythroleucus* and *M. natalensis*).

M. pernanus (Kershaw, 1921)

This species, characterized by its small size, is only known from a few specimens and raptor pellet remains from N.W. Tanzania, S.W. Kenya and Rwanda (MISONNE & VERSCHUREN, 1964). The latter authors proposed to maintain this species within *Mastomys*, but this decision was questioned by ROBBINS & VAN DER STRAETEN (1989) who stated that it may belong to the taxon *Myomys*.

M. verheyeni (Robbins & Van der Straeten, 1989)

This recently described species is still only known from the «Nigeria and Cameroon savanna immediately surrounding the Southern part of Lake Chad» (by ROBBINS & VAN DER STRAETEN, 1989). At present, it has only been studied morphologically and biometrically, and is mainly characterized by its large size.

DISCUSSION

Some authors have made an attempt to elucidate phylogenetic relationships within *Mastomys*, but in no instance have all the species cited above been taken into account. A preliminary analysis by Gordon (1985), based on chromosomal data, distinguished two groups: one with *M. coucha* and *M. shortridgei* (i.e. the species with 2n=36), with *M. erythroleucus* (2n=38) as the sister species, and the other with *M. natalensis* and *M. huberti* (i.e. the species with 2n=32). Later, Chevret *et al.* (1994) using DNA/DNA hybridization were not able to resolve the relationships between *M. huberti*, *M. erythroleucus* and *M. natalensis*, *M. coucha* representing a possible sister species of the three others. They proposed a date of divergence of 0.3 Myr for the first three species, whereas *M. coucha* could have diverged 1.0 Myr ago. Finally, Britton-Davidian *et al.* (1995) performed a phylogenetic analysis of chromosomal characters based on parsimony on the same 4 species, using *Myomys daltoni* (Thomas, 1892) and *Praomys tullbergi* (Thomas, 1894) as outgroups. They suggested that *M. natalensis* and *M. huberti* were the most derived taxa, from a chromosomal point of view. According to this analysis, chromosomal evolution in the genus would have proceeded by i) changes in diploid number by fusion-fission events, and ii) modification of aFN mainly through pericentric inversions. The phylogenetic relationships inferred from these 3 studies are represented on Fig. 1.

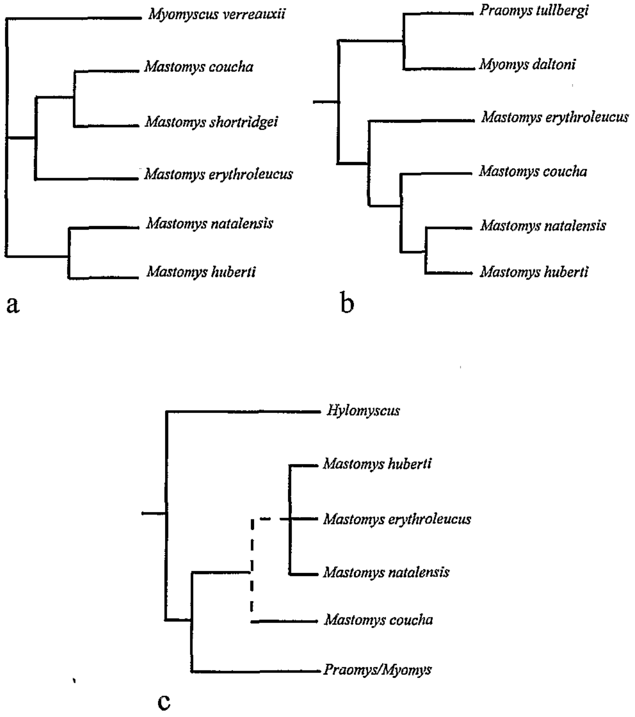


Fig. 1. – Phylogenetic relationships in *Mastomys* and related genera, according to a) Gordon (1985); b) Britton-Davidian *et al.* (1995); c) Chevret *et al.* (1994).

These data highlight the fact that, as in many other African rodent genera (MEESTER, 1988), species diversification in *Mastomys* has occurred recently (i.e. within the last million of years or so), and has been accompanied by extensive chromosomal rearrangements. The morphological and genetic divergence between the species is relatively small which explains the difficulties in recognition and characterization of the different species. Karyological studies appear as an especially informative method for species identification, and have yielded clear diagnoses of species such as *M. erythroleucus*, *M. coucha*, *M. nata-*

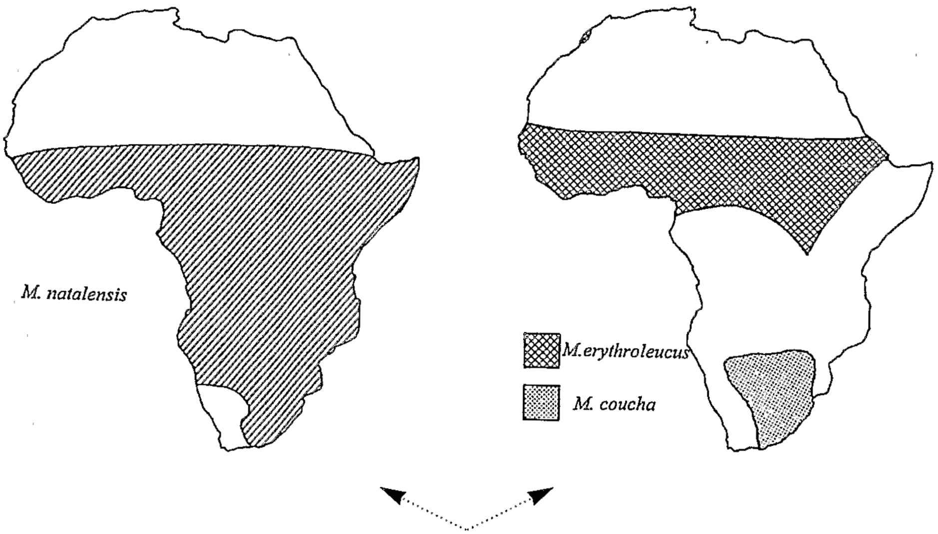
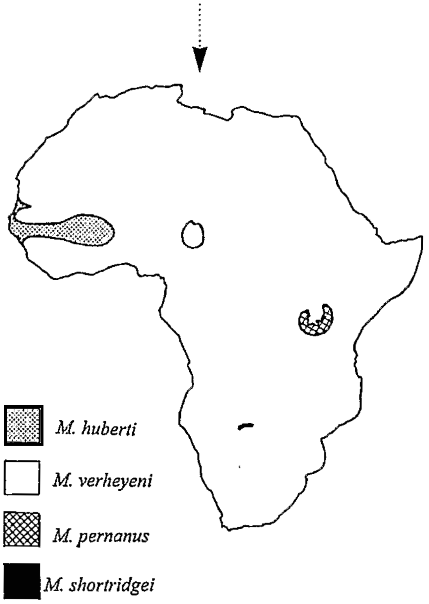


Fig. 2. – Distribution maps
of the different species of *Mastomys*



lensis and *M. huberti*. The precise status of *M. shortridgei* still needs to be ascertained and will require other types of analysis (protein electrophoresis, DNA sequencing...) as its karyotype is closely related to that of *M. coucha*. A combination of various techniques will also be necessary to further define the status of *M. verheyeni* and *M. pernanus*, and of *Myomys* (?) *angolensis*, as well as to identify additional cryptic species in the genus, among which some of the chromosomal variants with 38 or 36 chromosomes (see above) are good candidates. Another problem concerns the confirmation of an East African species which may be *M. hildebrandtii*. QUMSIYEH *et al.* (1990) presented a karyotype for Kenyan specimens with 2n=32, aFN=50-54, that they consider different from *M. natalensis*. Similarly, LAVRENCHENKO *et al.* (1992), BASKEVICH & ORLOV (1993) and LAVRENCHENKO & BASKEVICH (1996) have described specimens of *Mastomys* sp. from Ethiopia, also carrying 32 chromosomes, but that they consider as belonging to a species distinct from *M. natalensis*. However, the evidence is still not convincing, and further studies should try to definitely characterize and name this species, and more precisely to define its species limits when compared to true *M. natalensis* (as was done in West Africa between *M. huberti* and *M. natalensis*, as described above).

Finally, the distribution of all these species has to be precisely determined, the maps given in Fig. 2 representing only preliminary attempts based on the data available to date. Only in a few cases (DUPLANTIER & GRANJON, 1988, for Senegal; SKINNER & SMITHERS, 1990, for Southern Africa) have the distribution areas of the *Mastomys* species been mapped on a larger scale. These biogeographical aspects will represent one important by-product of the development of new methods of species discrimination, and of the application of genetic (and especially chromosomal) techniques on specimens from throughout the genus range.

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