



Original article

Systematics and evolution of the African pygmy mice, subgenus *Nannomys*: A review

J. Britton-Davidian^{a,*}, T.J. Robinson^b, F. Veyrunes^a

^a Institut des Sciences de l'Evolution, Université Montpellier 2, cc065, Pl. E. Bataillon, 34095 Montpellier cedex 05, France

^b Evolutionary Genomics Group, Department of Botany and Zoology, University of Stellenbosch, Private Bag XI, Matieland 7602, South Africa

ARTICLE INFO

Article history:

Received 9 May 2011

Accepted 3 January 2012

Available online 26 January 2012

Keywords:

Pygmy mouse

Nannomys

Phylogenetics

Chromosomes

Sex chromosomes

Africa

ABSTRACT

African pygmy mice (subgenus *Nannomys*) are a group of small murine rodents that are widespread throughout Sub-Saharan Africa. Although this group has long been recognized for its extensive chromosomal diversity, the highly conserved morphology of its members has made taxonomic assignments problematic. Renewed interest resulting from a series of cytogenetic and molecular investigations has led to the identification of novel patterns of diversification in these rodents that are reviewed herein. These approaches have considerably improved species delimitation and provide tentative diagnostic criteria as well as preliminary phylogenetic relationships that will be refined as more taxa are investigated. Although sparse, ecological data suggest that pygmy mice may exhibit original reproductive traits that deserve further investigation. Chromosomal diversity undoubtedly remains one of the most interesting features of African pygmy mouse biology. They display several karyotypic traits that are rare in mammals: (i) their genomes tolerate the recurrent formation of tandem fusions and sex-autosome translocations, both of which are rare in other mammals due to their highly deleterious effects on fertility; (ii) they exhibit the first case of a whole arm exchange involving an X chromosome, and (iii) two species show novel means of sex chromosome determination – one exhibits XY females, whereas the other harbors populations in which males have no Y chromosome. The diversity of African pygmy mice offers a unique opportunity to study the processes involved in their radiation, and in a broader context, the evolution of sex chromosome determination in mammals.

© 2012 Elsevier Masson SAS. All rights reserved.

In the last decade, African pygmy mice have been the focus of renewed interest driven, to a large extent, by cytogenetic and molecular investigations. These studies have resulted in an improved taxonomy and the identification and description of complex chromosomal patterns that underpin species diversity. This paper reviews the burgeoning literature on these rodents and addresses issues of relevance to their diversification. In addition, we highlight future prospects and suggest new avenues of investigation in this intriguing group of African small mammals.

1. Phylogenetic position of the subgenus *Nannomys*

African pygmy mice are a group of small-sized murine rodents that are widespread throughout Sub-Saharan Africa. They belong to the genus *Mus* and are the only African offshoot of this lineage. Marshall and Sage (1981) were the first to recognize the

morphological distinctiveness of African pygmy mice leading to their inclusion in a single endemic subgenus, *Nannomys*. This classification contributed significantly to clarifying the prevailing taxonomy which had lumped all African and Indian pygmy mice into a single genus, *Leggada*. The taxonomic distinctiveness of the African *Nannomys* from the Indian *Leggada* was later confirmed by allozyme analysis (Bonhomme et al., 1984). *Leggada* is no longer recognized, and recent systematic studies (see for example Suzuki et al., 2004) refer Indian pygmy mice to the subgenus *Mus*.

The genus *Mus* comprises 43 species grouped into four monophyletic subgenera: *Mus*, *Coelomys*, *Nannomys* and *Pyromys* (Shimada et al., 2010). A plethora of molecular studies (allozymes, DNA/DNA hybridization, nuclear and mitochondrial markers) have explored the relationships between these taxa, but there was little consensus among the resulting topologies (Bonhomme et al., 1984, 1986, 1992; Boursot et al., 1993; Catzeflis and Denys, 1992; Chevret et al., 2003, 2005; Jouvin-Marche et al., 1988; Lundrigan et al., 2002; She et al., 1990; Sourrouille et al., 1995; Suzuki et al., 2004; Tucker, 2007; Veyrunes et al., 2005). It is only recently that subgeneric relationships within this genus have been unambiguously

* Corresponding author. Tel.: +33 4 67 14 39 10; fax: +33 4 67 14 36 22.

E-mail addresses: janice.britton-davidian@univ-montp2.fr (J. Britton-Davidian), tjr@sun.ac.za (T.J. Robinson), frederic.veyrunes@univ-montp2.fr (F. Veyrunes).

resolved – and this through a phylogenomics approach (Veyrunes et al., 2006). These results suggest that the Indian subgenus *Coelomys* is the first lineage to diverge followed by the African *Nannomys* that, in turn, forms a sister group to the Eurasian *Mus-Pyromys* clade. It is thought that the genus *Mus* originated in Asia where the four subgenera diverged virtually contemporaneously (within 1 Myr) approximately 6.7–7.8 Mya (Chevret et al., 2005; Lecompte et al., 2008; Veyrunes et al., 2005), and it is at this time that the African colonization by *Mus* occurred. This is consistent both with the existence of Miocene land-bridges between the two continents which would have favored migrations through the Arabian Peninsula, and with fossil data that place the earliest *Nannomys* remains in East Africa at ~4.5 Mya (Winkler, 2002). Once in Africa, climatic oscillations and habitat modification (known to have occurred 6–3 Mya) may have triggered the radiation observed within *Nannomys* (Chevret et al., 2005; Lecompte et al., 2008; Veyrunes et al., 2005).

2. Phylogenetic relationships within the subgenus *Nannomys*

African pygmy mice represent the most species-rich subgenus (18 recognized species) within *Mus* (see Table 1; Happold and Veyrunes, in press; Musser and Carleton, 2005). The subgenus is noteworthy for its highly conserved morphology which contrasts markedly with its extensive chromosomal diversity. The constrained morphological variation is largely responsible for the absence of useful diagnostic keys, a situation that pervades *Nannomys* taxonomy (see Matthey, 1970a, b). The pioneering karyotypic studies undertaken by the Swiss cytogeneticist Robert Matthey led to a considerable improvement in species delimitation, demonstrating the value of chromosomal characters in resolving nomenclatural issues within these rodents. Matthey's close professional association with the French taxonomist Francis Petter resulted in a remarkable series of papers that combined the respective strengths of the two researchers (see Matthey, 1966b, 1970a,b; Petter, 1969). Matthey's studies were subsequently expanded by

Martine Jotterand-Bellomo whose work further highlighted the fascinating chromosomal variability within *Nannomys* (e.g., Jotterand, 1972; Jotterand-Bellomo, 1984, 1988). Gene-based phylogenetic approaches soon followed. Initially, these were limited to one or two species of *Nannomys* (*Mus minutoides*, *Mus setulosus*; Bonhomme et al., 1992; Boursot et al., 1993; Catzeflis and Denys, 1992; Lundrigan et al., 2002; She et al., 1990; Sourrouille et al., 1995; Suzuki et al., 2004; see Macholan, 2001 for a morphometric analysis), and it is only recently that researchers have expanded taxon sampling thus permitting comprehensive investigations of the evolutionary relationships among pygmy mice (Chevret et al., 2005; Kan Kouassi et al., 2008; Mboumba et al., 2011; Veyrunes et al., 2005). Cytochrome b gene (*Cytb*) sequences are now publicly available for 10 *Nannomys* species as well as for an unidentified taxon from Chad. We build on these studies in the present investigation by constructing a molecular phylogeny that includes published *Cytb* sequences and those of five other *Mus* species (representative of the other subgenera), as well as *Rattus norvegicus* and *Apodemus sylvaticus*, which were used as outgroups in our study. A maximum likelihood (ML) phylogeny was reconstructed from this dataset using PhyML (Guindon and Gascuel, 2003) under a GTR + G + I model of sequence evolution with 100 ML bootstrap replicates to test the support of individual nodes. The resulting molecular phylogeny (Fig. 1) confirms the monophyly of the subgenus *Nannomys*, and provides strong recognition of the monophyly of each species. However, the deeper relationships of species remain mostly unresolved; *M. setulosus*, *Mus baoulei*, and *Mus sorella* occur at the base of the tree, followed by a clade that comprises *Mus haussa*, *Mus mattheyi*, *M. sp.* from Chad, and another one including *Mus indutus* and a strong sister-group association between *Mus musculoides* and *M. minutoides*. The topology presented above is congruent with previous *Cytb* phylogenies, except for *M. setulosus* and *M. baoulei* that formed a monophyletic group when analyzed using a subset of the published *Cytb* sequences (Kan Kouassi et al., 2008; Mboumba et al., 2011). The phylogenetic relationships between the remaining species are well-supported when the sequences of the *IRBP* nuclear gene are included in the analyses (Veyrunes et al., 2005), namely, the sister-species relationship between *M. mattheyi* and *M. haussa*, and the clustering of *M. indutus* at the base of the *M. minutoides*/*M. musculoides* clade. Interestingly, the *Mus bufo* and *Mus tenellus* sequences available in GenBank probably reflect incorrect species assignments since the former nests within the *M. setulosus* clade, and the latter can be convincingly referred to *M. minutoides*. These misidentifications underscore the importance of using molecular and/or chromosomal markers in pygmy mouse species delimitations. With respect to the unknown species from Chad included in our analysis, it is noteworthy that since the specimen shows no close affinity either to *M. haussa*, *M. setulosus*, *M. musculoides* or *M. minutoides* (the only taxa recorded in Chad), it most likely represents an undescribed taxon. In addition, evidence of species heterogeneity is provided by phylogeographic data that show (i) two strongly differentiated genetic groups in *M. setulosus* that segregate geographically (West Africa vs. West Central Africa), (ii) two groups in *M. baoulei* (with specimens from Ivory Coast segregating in both clades suggesting potential reproductive isolation), and (iii) at least three well-supported clades within *M. minutoides*, (West Africa, West Central Africa, and East with South Africa). Regarding the East + South African clade, it includes chromosomally highly divergent populations (Veyrunes et al., 2004, 2010a) and exhibits a more pronounced genetic structure as attested by the deeper terminal branches compared to those of the two chromosomally homogeneous clades (i.e., West Africa and West central Africa; Fig. 1). This concordant pattern of chromosomal and molecular differentiation may suggest that the accumulation of chromosomal

Table 1

List of tentative diagnostic characters for the 18 species of African pygmy mice. Species distributions, body dimensions, ventral pelage color and number of mammae are compiled from Happold and Veyrunes (in press). Three size categories were arbitrarily determined from the range of mean head and body lengths: pygmy (48–55 mm), small (59–69 mm), large (75–89 mm). Tail% is the tail length relative to head and body length (the two extremes are in bold). 2n/G refers to diploid number and the existence of G-banded karyotypes (see Table 3). *Cytb* = cytochrome b sequences available in Genbank. n.d. = not determined.

	<i>Mus</i>	HB size	Tail%	2n/G	<i>Cytb</i>	Belly color	N° nipples
West Africa	<i>baoulei</i>	Small	65	2n	✓	White	n.d.
	<i>haussa</i>	Pygmy	75	2n	✓	White	8
	<i>mattheyi</i>	Pygmy	70	2n	✓	White	8
	<i>musculoides</i>	Small	72	2n	✓	White	8
West Central Africa	<i>setulosus</i>	Large	68	2n	✓	White	n.d.
Central Africa	<i>callewaerti</i>	Large	50	n.d.	n.d.	Greyish	n.d.
	<i>goundae</i>	Small	55	2n/G	n.d.	White	8
	<i>oubanguii</i>	Small	61	2n/G	n.d.	White	10
	<i>sorella</i>	Small	65	n.d.	✓	White	8
Eastern Africa	<i>bufo</i> ^b	Small	97	2n	✓	Greyish	8
	<i>mahomet</i> ^b	Small	74	2n	n.d.	Greyish	10
	<i>tenellus</i> ^a	Pygmy	70	n.d.	n.d.	White	8
South-Eastern Africa	<i>indutus</i>	Pygmy	80	2n	✓	White	8
	<i>neavei</i>	Large	43	n.d.	n.d.	White	n.d.
	<i>orangiae</i>	Small	63	n.d.	n.d.	White	8
	<i>setzeri</i>	Small	59	n.d.	n.d.	White	n.d.
	<i>triton</i> ^b	Large	70	2n/G	n.d.	Greyish	n.d.
Sub-Saharan Africa	<i>minutoides</i>	Pygmy	75	2n/G	✓	White	10

^a Distinctive sub- and post-auricular white spots.

^b These species occur at altitudes >1000 m for *M. triton*, and >1500 m for *M. bufo* and *M. mahomet*.

Download English Version:

<https://daneshyari.com/en/article/4381305>

Download Persian Version:

<https://daneshyari.com/article/4381305>

[Daneshyari.com](https://daneshyari.com)