

# Genetic identification of freely traded synanthropic invasive murid rodents in pet shops in Gauteng Province, South Africa

Ndivhuwo Maligana\*, Rolanda S Julius, Tinyiko C Shivambu and Christian T Chimimba

DSI-NRF Centre of Excellence for Invasion Biology and Mammal Research Institute, University of Pretoria, South Africa

\*Correspondence: ndivhuwomaligana@gmail.com

## Abstract

Although synanthropic invasive murid rodents are freely traded in pet shops in South Africa, their taxonomic identities, however, remain largely unknown. Twenty-four murid rodents were sampled from pet shops in four of the five municipalities in Gauteng Province, South Africa for genetic identification using mitochondrial cytochrome *b* (mtDNA) sequence data. Distance-based Neighbour-Joining (NJ), character-based maximum likelihood (ML) and model-based Bayesian inference (BI) were used to infer the relationship between the pet murid rodents. Brown rats (*Rattus norvegicus*) and house mice (*Mus musculus*) were the most dominant species in the pet shops. The results demonstrated that pet shop owners lacked the taxonomic expertise to identify murid rodent species they trade in. For example, the juveniles of brown rats were misidentified as adults of the house mouse. The murid rodents sampled in the current study were genetically affiliated to both wild and laboratory strains of *R. norvegicus* and *M. musculus*. The results of the BI showed that the pet murid rodents were in the terminal clades as those of conspecifics in NCBI GenBank reference sequences. The molecular data used in the current study may be useful for developing national policies and regulations for synanthropic invasive murid rodents in the pet trade industry in South Africa.

**Keywords:** cytochrome b, phylogeny, murids, *Rattus*, *Mus*, pet trade, South Africa

Murid rodents have been introduced worldwide as part of the pet trade industry, aesthetics, food, hunting, commercial enterprises, pest control, and as zoo animals (Long 2003). Globally, the synanthropic invasive brown rats (*Rattus norvegicus* Berkenhout, 1769) are considered to be the most popular as pets and for use in scientific research (Cox and Montrose 2016). Similarly, the black rat (*R. rattus* Linnaeus, 1758) and the Gambian pouched rat (*Cricetomys gambianus* Waterhouse, 1840) are also kept as pets and used for scientific research (Cooper 2008; Driscoll et al. 2009). Rats are also used as food for pet snakes, where they are referred to as feeders (Cooper and Williams 2014). These rodents are also known to damage crops, stored food, household items, cause zoonotic diseases, and have been implicated in the extinction of island birds (Aplin et al. 2003; Witmer and Shiels 2017).

The genus *Rattus* is taxonomically complex (Aplin et al. 2003), with its members showing high degrees of intraspecific morphological variation, such that morphological criteria may

not be appropriate for accurate species identifications (Pagès et al. 2010). For example, the morphologically indistinguishable *R. rattus* and Tanezumi rat (*Rattus tanezumi* Temminck, 1845) that belong to the *R. rattus* species-complex, can only reliably be distinguished using molecular data (Bastos et al. 2011). In addition, different age classes of the relatively large-sized *R. norvegicus* may be mistaken for adult *R. rattus* (Puckett and Munshi-South 2018), and *R. rattus* may also be mistaken for the Polynesian rat (*R. exulans* Peale, 1848) (Motokawa et al. 2001). Furthermore, the juveniles of *R. rattus* may also be mistaken for the adults of the house mouse (*Mus musculus* Linnaeus, 1758) (Reeves and Cobb 2005). These taxonomic complications are exacerbated further by the general tendency for the common terms, mice and rats, to be used interchangeably by the general public (Walsh 2014).

In South Africa, there are ca. 13 rat breeders registered with the South African Rat Breeders Association (SARBU 2017). These rat breeders and the general public may misidentify the rat species that they trade in. Pet rats are generally known by their common names, whose identifications are based on external morphology (Sirois 2015). For example, pet rats with black coat are referred to as black rats, whereas those with white coat and black eyes are called black-eyed white rats (Sirois 2015). Currently, little is known about the identities of pet rats in South Africa and therefore the aim of this study was to identify synanthropic invasive murid rat species freely traded in pet shops in Gauteng Province, South Africa using mitochondrial DNA cytochrome b (mtDNA cyt b) sequence data.

Thirty pet shops in four of the five municipalities in Gauteng Province, South Africa were visited, and only 24 of these were found to trade in pet rats (Figure 1). Pet shops rather than private breeders and hobbyists were chosen, because of their easy accessibility. Ear tissue samples (n = 24) from juvenile and adult rats were obtained between May and July 2017, based on their unique external features, such as body colour patterns (colour patterns indicate a species breed type). A 2 mm tissue sample was obtained by punching one ear from each rat using disposable biopsy punches (Browning Surgical (Pty) Ltd, Cape Town, South Africa), as approved by the Animal Ethics Committee (AEC) of the University of Pretoria (Ethics number: ec010-17). The ear punching process has been reported to have minimal adverse effects on the rodents (Mazlan et al. 2014). Samples were stored individually in 1.5 ml Eppendorf tubes containing 99.9% ethanol.

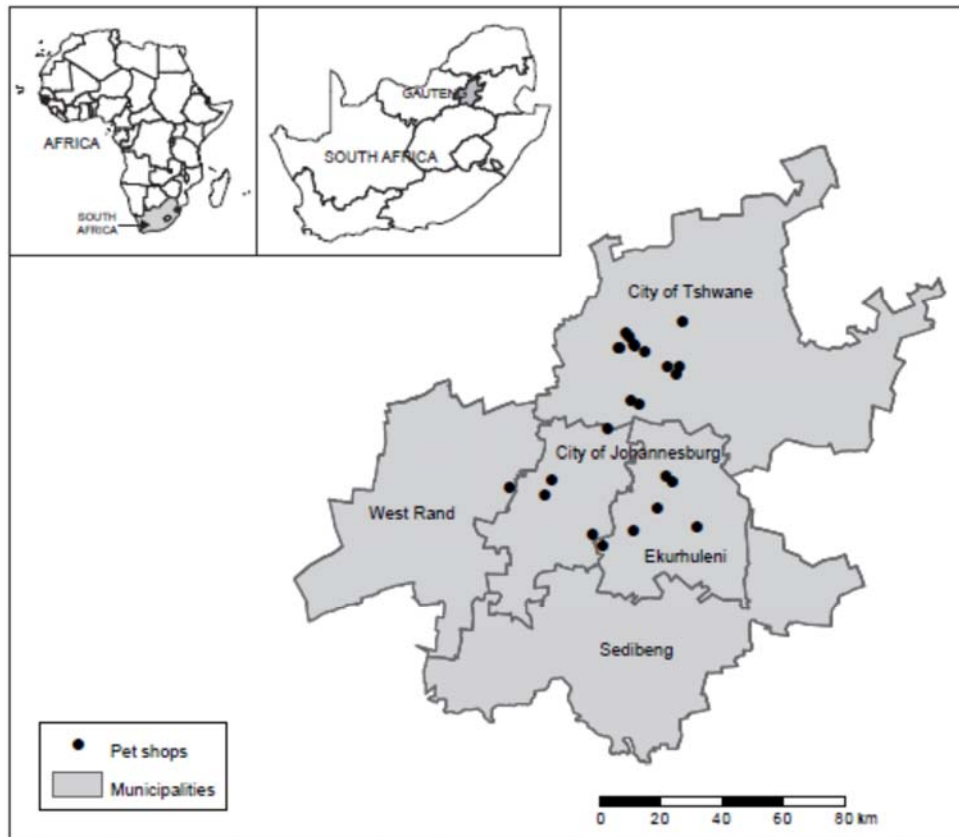


Figure 1: A map of Gauteng Province, South Africa (with inserts of the maps of Africa and South Africa) showing pet shop localities from where pet rodents were sampled

Genomic DNA was extracted using Roche High Pure PCR Template Preparation Kit (Roche Diagnostics, Randburg, South Africa) following the manufacturer protocol and stored at  $-20^{\circ}\text{C}$ . Primers, L14724 (Irwin 1991) and H15915 (Russo et al. 2006) were used to amplify the mtDNA *cyt b* gene. Polymerase Chain Reaction (PCR) products were purified using the Roche PCR Product Purification Kit and cycle sequenced on a quarter reaction using BigDye terminator chemistry (Applied Biosystems, Foster City, USA). Nucleotide sequencing resulted in a partial fragment of 1 135 bp of the *cyt b* gene generated for each of the 24 pet rodent samples. Sequences were edited and aligned in Mega 7 (Kumar et al. 2016), and species with the highest sequence similarity were identified in a BLAST search in the NCBI GenBank database ([www.ncbi.nlm.nih.gov/blast](http://www.ncbi.nlm.nih.gov/blast)). The sequences generated in the current study were deposited into the GenBank reference database under accession numbers MK482341- MK521426.

For phylogenetic analysis, non-unique sequence representatives were removed and the 24 sequences were therefore reduced to a dataset of four taxa. The four unique sequences were combined with five *R. norvegicus* and eight *M. musculus* reference sequences obtained from the NCBI GenBank database and *Mastomys natalensis* sequence was

included as an outgroup. The reference sequences were chosen based on maximum identity (100%), high query coverage percentage (99–100%); and if published. JModeltest v.0.1 was used to select the best-fit model of sequence evolution and the parameters were identified under the Akaike Information Criterion (AIC) (Posada 2008). Phylogenies were inferred using model-based Bayesian inference (BI) (MrBayes v.2.1.3; Huelsenbeck and Ronquist 2001) where four Markov Monte Carlo chains (MCMC) were run for 20 000 000 generations. Markov Monte Carlo chains were sampled for every 100th generation and the default heating and swap settings were used. The resultant BI phylogeny and posterior probabilities were displayed in FigTree (FigTree v 1.4.3; Rambaut 2016) where 25% of the trees were discarded as ‘burn-in’. The character-based Maximum Likelihood (ML) and the distance-based Neighbour-Joining (NJ) phylogenetic analyses were computed in Mega 7 (Kumar et al. 2016), where 10 000 non-parametric bootstrap replications were run. Percentages were used to indicate the nodal support for NJ and ML, whereas posterior probability was used to indicate nodal support for BI.

Sequence results showed that four rodent species labelled as small rats were in fact strains of *M. musculus* and 20 different rat varieties were all identified as *R. norvegicus* (Table 1). GTR + I + G model with Gamma-distributed sites were selected as the best fit in JModeltest v.0.1. Tree topologies generated by NJ, ML and BI were similar, and as a result, only the NJ tree was illustrated in the current study, but includes nodal support values for all the three phylogenetic analyses (Figure 2). This tree topology showed that the four genotypes belonged to two major clusters of *M. musculus* and *R. norvegicus* each having two different strains (Figure 2). The *M. musculus* group was well supported with small white rat having different genotypes, from small Russian champagne, small grey and small American cinnamon rat (Table 1; Figure 2). The *R. norvegicus* group was also well supported with adult white rat, adult hairless naked rat, beige rat and juvenile black rat sharing the same genotype, whereas juvenile white rat and the other 15 rat varieties (Table 1; Figure 2) share the same genotype. *Mus musculus* identified in the current study were related to several laboratory strains from Sanger Institute and CLEA Japan, Inc., but also to a wild type from Turkey, Altindere (Table 1; Figure 2). Similarly, *R. norvegicus* identified in the current study was also related to common laboratory strains, including Sprague Dawley strain, but also to a wild strain from Tokyo, Japan (Table 1; Figure 2).

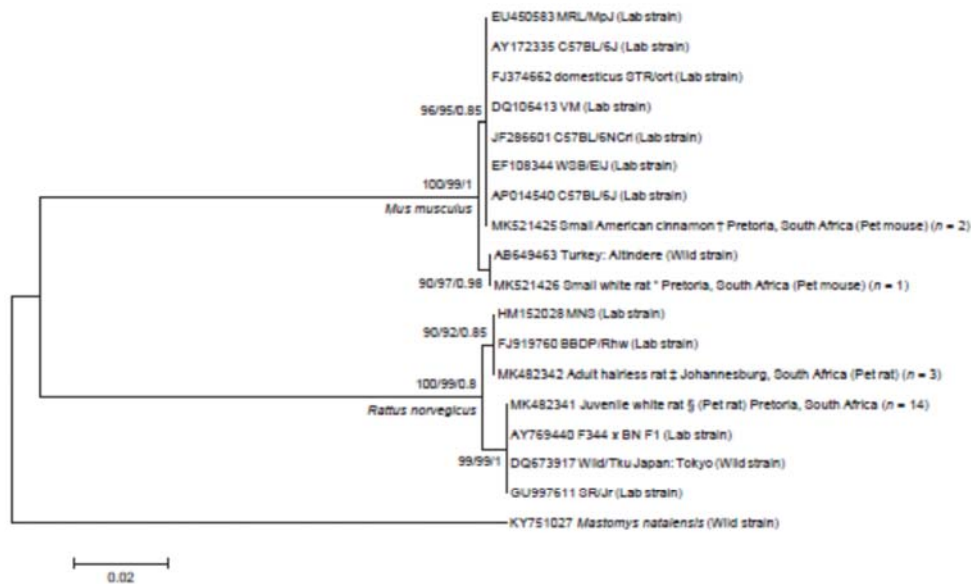
The current study demonstrated that there is confusion in the identification and differentiation between young rats and mice in pet shops in Gauteng Province, South Africa. It is possible that both young rats and mice may have similar coat colours and fur type (N Maligana pers. obs.), and that rats and mice sampled in the current study were not referred to by their scientific names. Similarly, in the USA, Reeves and Cobb (2005) reported that some mice sampled from pet shops in South Carolina were not *M. musculus*, but *R. rattus*, whereas Lankau et al. (2017) reported that rodents, such as *R. norvegicus* and *M. musculus*, that were sold online were described by their common names only.

**Table 1:** A summary of the sequences of the mitochondrial cytochrome *b* (*cyt b*) gene region generated in the current study, based on a fragment size of 1 135 nucleotides for rodents sampled in pet shops in four of the five municipalities in Gauteng Province, South Africa, supplemented by reference sequences obtained from the NCBI GenBank database

Species description	Cyt <i>b</i> (% Identity)	GenBank Accession number	Locality	Reference
Small white rat *	<i>Mus musculus</i> (100)	MK521426	Pretoria, South Africa	This study
Small Russian champagne rat †	<i>Mus musculus</i> (100)	–	Pretoria, South Africa	This study
Small grey rat †	<i>Mus musculus</i> (100)	–	Pretoria, South Africa	This study
Small American cinnamon†	<i>Mus musculus</i> (100)	MK521425	Pretoria, South Africa	This study
Adult white rat ‡	<i>Rattus norvegicus</i> (100)	–	Johannesburg, South Africa	This study
Adult hairless rat ‡	<i>Rattus norvegicus</i> (100)	MK482342	Johannesburg, South Africa	This study
Beige rat ‡	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Juvenile black rat ‡	<i>Rattus norvegicus</i> (100)	–	Johannesburg, South Africa	This study
Juvenile white rat ‡	<i>Rattus norvegicus</i> (100)	MK482341	Pretoria, South Africa	This study
Adult champagne blazed hooded rat §	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Adult black rat §	<i>Rattus norvegicus</i> (100)	–	Johannesburg, South Africa	This study
Black blazed variegated hooded rat §	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Juvenile champagne blazed hooded rat§	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Black and white rat§	<i>Rattus norvegicus</i> (100)	–	Johannesburg, South Africa	This study
Adult female weaners rat§	<i>Rattus norvegicus</i> (100)	–	Johannesburg, South Africa	This study
Dumbo grey and white rat§	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Dumbo black rat§	<i>Rattus norvegicus</i> (100)	–	Johannesburg, South Africa	This study
Adult male weaners rat§	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Dumbo white rat§	<i>Rattus norvegicus</i> (100)	–	Johannesburg, South Africa	This study
Chocolate brown rat§	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Juvenile hairless naked rat§	<i>Rattus norvegicus</i> (100)	–	Gauteng Province pet shop	This study
Medium weaners rat§	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
Dumbo Grey rat§	<i>Rattus norvegicus</i> (100)	–	Pretoria, South Africa	This study
<i>Mus musculus</i> strain MRL/MpJ	–	EU450583	Jackson Laboratory	Sachadyn et al. 2008
<i>Mus musculus</i> strain C57BL/6J	–	AY172335	Sanger Institute	Bayona-Bafaluy et al. 2003
<i>Mus musculus domesticus</i> strain STR/ort	–	FJ374662	Jackson Laboratory	Yu et al. 2009
<i>Mus musculus</i> strain VM	–	DQ106413	University of Edinburgh and Jackson Laboratory	Kiebish and Seyfried 2005
<i>Mus musculus</i> strain C57BL/6NCrl	–	JF286801	Charles River Laboratories	Stewart et al. 2008
<i>Mus musculus domesticus</i> strain WSB/EiJ	–	EF108344	Jackson Laboratory	Goios et al. 2007
<i>Mus musculus</i> strain C57BL/6J	–	AP014540	CLEA Japan, Inc.	Shimizu et al. 2014
<i>Mus musculus domesticus</i> isolate IZEA6068	–	AB649463	Turkey, Altindere	Suzuki et al. 2013
<i>Rattus norvegicus</i> strain MNS	–	HM152028	University of Toledo College of Medicine and Life Sciences	Rowe et al. 2008
<i>Rattus norvegicus</i> strain BBDP/Rhw	–	FJ919760	Temasek Life Sciences Laboratory, Singapore	Abhyankar et al. 2009
<i>Rattus norvegicus</i> strain F344 x BN F1	–	AY769440	National Institute on Aging colony (Indianapolis, USA)	Pak et al. 2005
<i>Rattus norvegicus</i> strain Wild/Tku	–	DQ673917	Japan, Tokyo	Schlick et al. 2006
<i>Rattus norvegicus</i> SR/Jr	–	GU997611	University of Toledo College Of Medicine	Kumarasamy et al. 2010

\*,†,‡,§ indicates the different genotypes

Molecular analysis in the current study revealed that pet shops visited in Gauteng Province were dominated by *R. norvegicus* and *M. musculus*, which were mostly affiliated to laboratory strains. This may not be surprising, because most pet rats originate from laboratory-bred stocks (Carbone et al. 2016) rather than tamed wild rats. In addition, mice are often adopted after the completion of research projects (Baumans et al. 2007). Two rodents of the 24 sampled rodents were affiliated to wild strains, suggesting that they were potentially released into the wild and also sourced from the wild.



**Figure 2:** Neighbour-Joining (NJ) tree representing the phylogeny of murid rodents sampled from four of the five municipalities in pet shops in Gauteng Province, South Africa. Nodal support values (>70%) from NJ and maximum likelihood (ML) analysis and posterior probability (>0.75) from Bayesian inference (BI) are indicated by the following order: NJ/ML/BI. Genotypes sampled in the current study are indicated by symbols and the number of identical taxa is indicated in parentheses. GenBank accession numbers are included in both reference sequences and samples from the current study

*Rattus norvegicus* and *M. musculus* are listed in the NEMBA Act in Category 1b for offshore islands (NEMBA 2016). For mainland South Africa, however, the two species are not listed and consequently their moving around, breeding, and selling is not prohibited or even monitored. This may result in further introductions through the pet trade industry and this may be followed by successful introduction and spread. It is therefore recommended that trade in species that are already invasive should be regularly monitored to prevent reintroductions. In addition, alien rats and mice should also be routinely sampled from sources, such as breeders and hobbyists, in order to genetically identify the founder populations of kept, bred and sold rats and mice in South Africa. Such data may be useful for developing national policies and regulations on the rodent pet trade in South Africa.

### Acknowledgments

We gratefully acknowledge the tissue samples provided by pet shop owners in Gauteng Province. This study was supported by the South African DSI/NRF Centre of Excellence for Invasion Biology (CIB).

### ORCID

Ndivhuwo Maligana: <https://orcid.org/0000-0002-9336-9813>

Rolanda S Julius: <https://orcid.org/0000-0002-1208-5641>

Tinyiko C Shivambu: <https://orcid.org/0000-0003-3157-4712>

Christian T Chimimba: <https://orcid.org/0000-0002-8366-9994>

## References

- Abhyankar A, Park H B, Tonolo G, Luthman H. 2009. Comparative sequence analysis of the non-protein-coding mitochondrial DNA of inbred rat strains. *PLoS ONE* 4: e8148. doi: 10.1371/journal.pone.0008148
- Aplin K P, Brown P R, Jacob J, Krebs C J, Singleton G R. 2003. *Field methods for rodent studies in Asia and the Indo-Pacific*. Canberra, Australia : ACIAR Monograph.
- Bastos A D, Nair D, Taylor P J, Brettschneider H, Kirsten F, Mostert E, Von Maltitz E, Lamb J M, Van Hooft P, Belmain S R, et al. 2011. Genetic monitoring detects an overlooked cryptic species and reveals the diversity and distribution of three invasive *Rattus* congeners in South Africa. *BMC Genetics* 12: 26. doi: 10.1186/1471-2156-12-26
- Baumans V, Coke C, Green J, Moreau E, Morton D, Patterson- Kane E, Reinhardt A, Reinhardt V, Van Loo P. 2007. *Making lives easier for animals in research labs*. Washington, DC, USA : Animal Welfare Institute. pp 27 – 28.
- Bayona-Bafaluy M P, Acín-Pérez Z R, Mullikin J C, Park J S, Moreno- Loshuertos R, Hu P, Pérez-Martos A, Fernández-Silva P, Bai Y, Enríquez J A. 2003. Revisiting the mouse mitochondrial DNA sequence. *Nucleic Acids Research* 31: 5349 – 5355. doi: 10.1093/nar/gkg739
- Carbone L. 2016. Adoption options for laboratory animals. *Lab Animal* 32: 37–41. doi: 10.1038/labani1003-37
- Cooper J E, Williams D L. 2014. The feeding of live food to exotic pets: issues of welfare and ethics. *Journal of Exotic Pet Medicine* 23: 244 – 249. doi: 10.1053/j.jepm.2014.06.003
- Cooper R G. 2008. Care, husbandry and diseases of the African giant rat (*Cricetomys gambianus*). *Journal of the South African Veterinary Association* 79: 62 – 66.
- Cox L, Montrose V T. 2016. Quantity discrimination in domestic rats, *Rattus norvegicus* . *Animals (Basel)* 6: 46. doi: 10.3390/ani6080046
- Driscoll C A, Macdonald D W, Brien S J O. 2009. From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences of the United States of America* 106 (Suppl 1): 9971–9978. doi: 10.1073/pnas.0901586106
- Goios A, Pereira L, Bogue M, Macaulay V, Amorim A. 2007. mtDNA phylogeny and evolution of laboratory mouse strains. *Genome Research* 17: 293 – 298. doi: 10.1101/gr.5941007
- Huelsenbeck J P, Ronquist F. 2001. MRBAYES : Bayesian inference of phylogenetic trees. *Bioinformatics (Oxford, England)* 17: 754–755. doi: 10.1093/bioinformatics/17.8.754
- Irwin D M, Kocher T D, Wilson A C. 1991. Evolution of cytochrome-b in mammals. *Journal of Molecular Evolution* 32: 128–144. doi: 10.1007/BF02515385

- Kiebish M A, Seyfried T N. 2005. Absence of pathogenic mitochondrial DNA mutations in mouse brain tumors. *BMC Cancer* 5: 102. doi: 10.1186/1471-2407-5-102
- Kumar S, Stecher G, Tamura K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874. doi: 10.1093/molbev/msw054
- Kumarasamy S, Gopalakrishnan K, Shafton A, Nixon J, Thangavel J, Farms P, Joe B. 2010. Mitochondrial polymorphisms in rat genetic models of hypertension. *Mammalian Genome* 21: 299 – 306. doi: 10.1007/s00335-010-9259-5
- Lankau E W, Sinclair J R, Schroeder B A, Galland G G, Marano N. 2017. Public health implications of changing rodent importation patterns—United States, 1999–2013. *Transboundary and Emerging Diseases* 64: 528–537. doi: 10.1111/tbed.12396
- Long J L. 2003. *Introduced mammals of the world: Their history, distribution, and influence*. Wallingford, United Kingdom : Csiro Publishing. pp 589.
- Mazlan N, López-Salesansky N, Burn C, Wells D. 2014. Mouse identification methods and potential welfare issues: a survey of current practice in the UK. *Animal Technology and Welfare* 13: 1–10.
- Motokawa M, Lu K, Harada M, Lin L. 2001. New records of the polynesian rat. *Zoological Studies (Taipei, Taiwan)* 40: 299–304.
- NEMBA . 2016. National Environmental Management: Biodiversity Act (NEMBA) (Act No. 10 of 2004). South Africa: Government Gazette (40116).
- Pagès M, Chaval Y, Herbreteau V, Waengsothorn S, Cosson J F, Hugot J P, Morand S, Michaux J. 2010. Revisiting the taxonomy of the Rattini tribe: a phylogeny–based delimitation of species boundaries. *BMC Evolutionary Biology* 10: 184. doi: 10.1186/1471-2148-10-184
- Pak J W, Vang F, Johnson C, Mckenzie D, Aiken J M. 2005. MtDNA point mutations are associated with deletion mutations in aged rat. *Experimental Gerontology* 40: 209 – 218. doi: 10.1016/j.exger.2004.12.005
- Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1253–1256. doi: 10.1093/molbev/msn083
- Puckett E E, Munshi-South J. 2018. Brown rat demography reveals pre-commensal structure in eastern Asia prior to expansion into Southeast Asia during the Song dynasty. *Genome Research* 29: 762–770. doi: 10.1101/gr.235754.118
- Rambaut A. 2016. FigTree v1.4.3. Available at: <http://tree.bio.ed.ac.uk/software/figtree/>. [Accessed 17 April 2017].
- Reeves W K, Cobb K D. 2005. Ectoparasites of house mice (*Mus musculus*) from pet stores in South Carolina, USA. *Comparative Parasitology* 72: 193–195. doi: 10.1654/4178



- Rowe K C, Reno M L, Richmond D M, Adkins R M, Steppan S J. 2008. Pliocene colonization and adaptive radiations in Australia and New Guinea (Sahul): multilocus systematics of the old endemic rodents (Muroidea: Murinae). *Molecular Phylogenetics and Evolution* 47: 84–101. doi: 10.1016/j.ympev.2008.01.001
- Russol R M, Chimimba C T, Bloomer P. 2006. Mitochondrial DNA differentiation between two species of *Aethomys* (Rodentia: Muridae) from southern Africa. *Journal of Mammalogy* 87: 545–553. doi: 10.1644/05-MAMM-A-222R3.1
- Sachadyn P, Zhang X M, Clark L D, Naviaux R K, Heber-Katz E. 2008. Naturally occurring mitochondrial DNA heteroplasmy in the MRL mouse. *Mitochondrion* 8: 358 – 366. doi: 10.1016/j.mito.2008.07.007
- SARBU (South African Rat Breeders Union) . Available at: <http://sarbu.webs.com/sarbu-ratteries>. [Accessed 17 April 2017].
- Schlick N E, Jensen-Seaman M I, Orlebeke K, Kwitek A E, Jacob H J, Lazar J. 2006. Sequence analysis of the complete mitochondrial DNA in 10 commonly used inbred rat strains. *American Journal of Physiology. Cell Physiology* 291: C1183 – C1192. doi: 10.1152/ajpcell.00234.2006
- Shimizu A, Mito T, Hayashi C, Ogasawara E, Koba R, Negishi I, Takenaga K, Nakada K, Hayashi J I. 2014. Transmitochondrial mice as models for primary prevention of diseases caused by mutation in the tRNALys gene. *Proceedings of the National Academy of Sciences of the United States of America* 111: 3104 – 3109. doi: 10.1073/pnas.1318109111
- Sirois M. 2015. *Laboratory animal and exotic pet medicine: principles and procedures* . St. Louis, Missouri, USA : Elsevier Health Sciences. pp 97.
- Stewart J B, Freyer C, Elson J L, Wredenberg A, Cansu Z, Trifunovic A, Larsson N G. 2008. Strong purifying selection in transmission of mammalian mitochondrial DNA. *PLoS Biology* 6: e10. doi: 10.1371/journal.pbio.0060010
- Suzuki H, Nunome M, Kinoshita G, Aplin K P, Vogel P, Kryukov A P, Jin M L, Han S H, Maryanto I, Tsuchiya K, Ikeda H. 2013. Evolutionary and dispersal history of Eurasian house mice *Mus musculus* clarified by more extensive geographic sampling of mitochondrial DNA. *Heredity* 111: 375–390. doi: 10.1038/hdy.2013.60
- Walsh M G. 2014. Rat sightings in New York City are associated with neighborhood sociodemographics, housing characteristics, and proximity to open public space. *PeerJ* 2: p. e533. doi: 10.7717/peerj.533
- Witmer G W, Shiels A B. 2017. Ecology, impacts, and management of invasive rodents in the United States. (pp 193–220) In: PittWC, BeasleyJ, WitmerGW (Eds). *Ecology and management of terrestrial vertebrate invasive species in the United States*. New York, USA : CRC Press.

Yu X, Gimsa U, Wester-Rosenlöf L, Kanitz E, Otten W, Kunz M, Ibrahim S M. 2009. Dissecting the effects of mtDNA variations on complex traits using mouse conplastic strains. *Genome Research* 19: 159–165. doi: 10.1101/gr.078865.108