Mus minutoides (Smith, 1834), the odd rodent with three sex chromosomes

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Introduction. *Mus minutoides* is a small rodent species found in Africa, particularly in regions such as Angola, Namibia, Botswana, and South Africa (Chevret et al 2014; Lamb et al 2014; Krásová et al 2021). *M. minutoides*, commonly known as the African pygmy mouse or Angolan pygmy mouse (Figure 1), exhibits a unique and intriguing sex determination system known as XY* that differs from the more common XY-XX system found in many other mammals. Like most mammals, *M. minutoides* has a pair of sex chromosomes that determine the individual's sex, and not two, but three sex chromosomes can be found within the population: X, Y and X*, where X* is the dominant feminizing chromosome (Saunders et al 2022).

Figure 1. The African pygmy mouse, *Mus minutoides* (photo: Alouise Lynch, Wikipedia.org).

Typical Mammalian sex determination. In many mammals, including humans, sex is determined by the combination of sex chromosomes inherited from the parents. Typically, females have two X chromosomes (XX), while males have one X and one Y chromosome (XY). The presence of the Y chromosome triggers male development due to the presence of the Sry gene, which initiates the development of male reproductive organs (Gavriloaie 2023).

The XY* system in *M. minutoides*. In *M. minutoides*, the sex determination system is termed XY*. XY* system involves the typical X and Y chromosomes but with a significant twist: the Y chromosome in this species has a gene (designated *Sry') that is similar to the Sry gene found on the Y chromosome in other mammals, including humans. However, the *Sry' gene in *M. minutoides* is not always functional. It can be either active (expressed) or inactive (non-expressed) in different individuals. The expression of the *Sry' gene on the Y chromosome determines whether an individual develops as a male or a female. Saunders et al (2022) suggests that inactivation of Y is due to the presence of the dominant X* chromosome.

Determining factors in the case of XY* system. In individuals where the *Sry' gene is expressed (active), typical male development occurs, and they develop into males. In individuals where the *Sry' gene is not expressed (inactive), the default developmental pathway leads to female development. In this species, all males have XY genotype, while females have one of the three following genotypes: XX, XX*, or X*Y (Veyrunes et al 2010).

Implications and variability. The presence or absence of the *Sry' gene expression leads to natural variability within *M. minutoides* populations. This variability can result in the production of both males and females within a litter, even if they have the same genetic makeup (XY). It also adds a layer of complexity to the understanding of sex determination and evolution in mammals.

Evolutionarily speaking, X* is a newly emerged chromosome in *M. minutoides*. In this species, Sounders et al (2022) took the opportunity to study the newly appeared X* chromosome. They set out to investigate one of the evolutionary forces hypothesized to cause such transitions, namely sex chromosome drive (i.e., biased transmission of sex chromosomes to the next generation) (Saunders et al 2022). Through extensive molecular sexing of pups at weaning, they revealed the existence of a remarkable male sex chromosome drive system in this species, whereby direction and strength of drive are conditional upon the genotype of males' partners: males transmit their Y at a rate close to 80% when mating with XX or XX* females and only 36% when mating with X*Y females (i.e., non-Mendelian; Saunders et al 2022) (Table 1). Using mathematical modeling, they explored the joint evolution of these unusual sex-determining and drive systems, revealing that different sequences of events could have led to the evolution of this bizarre system and that the ''conditional'' nature of sex chromosome drive plays a crucial role in the spread and maintenance of a newly evolved sex chromosome (Saunders et al 2022).

Table 1

Expected vs observed sex ratio at weaning (expressed as the proportion of males) in the progenies of the three types of females

Female genotype	XX	XX*	X*Y
Expected sex ratio	0.5	0.25[a]	0.33[a]
Observed sex ratio (overall number of offspring)	0.79 ± 0.13 (206)	0.37 ± 0.17 (370)	0.42 ± 0.14 (670)
Departure from expected sex ratio (binomial test)	p % 2.2e-16	p = 1.967e-07	p = 6.701e-05

a - The expected sex ratio in the progenies of XX* and X*Y females is different from 0.5 because they produce viable offspring of respectively four genotypes (XX, XX*, X*Y, and XY) and three genotypes respectively (XX*, X*Y, XY) (Saunders et al 2022).

Conclusions. The XY* sex determination system in *M. minutoides*, characterized by the presence of the *Sry' gene on the Y chromosome, demonstrates a unique mechanism where the expression of this gene determines whether an individual develops as male or female, adding complexity and variability to sex determination in this species. In this rodent three sex chromosomes can be found: X, Y and X*, where X* is the dominant feminizing chromosome. Inactivation of Y is due to the presence of the dominant X* chromosome. Scientists study *M. minutoides* to better understand the mechanisms and evolution of sex determination systems. Research on this species provides insights into the genetic and environmental factors influencing sexual development and reproductive strategies in mammals.

Conflict of interest. The authors declare no conflict of interest.

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