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Integrative taxonomy of *Gerbillinae rodents* in Morocco

State of art in karyology, morphometric and phylogeny

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Abstract

An integrative taxonomy synthesis of the previous works on rodents of the *Gerbillinae* family in Morocco could serve as a reference for further research on this group whose systematics is not yet fully resolved. The systematic studies and distribution of certain species in this family started in the mid-sixties, and since then, they have conducted several studies on different species. Advanced techniques for studying them, such as systematics, karyology, morphometry, and molecular biology, have clarified their taxonomic status and precise phylogenetic relationships. Here, we review the relevant literature on this subject and highlight the remaining issues. Such a review has implications for the knowledge of biodiversity, biogeography, and the conservation of rodents in Morocco.

Keywords: Synthesis, work, Gerbillinae, Rodents, Biodiversity, Morocco.

Résumé

Une synthèse des travaux effectués sur les rongeurs de la famille des *Gerbillina*e du Maroc pourrait servir de référence pour des recherches ultérieures sur ce groupe. L'étude de la systématique et de la répartition de certaines espèces de cette famille a débuté au milieu des années soixante, depuis, plusieurs travaux ont été menés sur différentes espèces. Avec l'avancement des techniques d'étude aussi bien celles de la systématique, de la caryologie que de la biologie moléculaire leur statut taxinomique a été précisé et les arbres phylogénétiques ont été établis. Nous proposons ici une révision de la littérature appropriée sur ce sujet et mettons en évidence les problèmes restants. Une telle révision a des implications pour la connaissance de la biodiversité, de la biogéographie et de la conservation des rongeurs du Maroc.

Mots clés : Synthèse, travaux, *Gerbillinae*, Rongeurs, biodiversité, Maroc.

Introduction

With four genera and about 17 species, Morocco's gerbils are part of the country's rodent diversity. Their phylogenetic position has been controversial recently with the era of molecular systematics. Today, they are classified as members of the *Muridae* family (mice and rats) and form the *Gerbillinae* subfamily (Steppan et al., 2017; Denys et al., 2017).

The gerbil family constitutes a distinctive entity for zoologists due to its unique combination of morphological and anatomical characteristics. It originated from the *Cricetidae* directly or through an extinct group of rodents, the *Myocricetodontinae*. The *Cricetidae* family, being very ancient, has gradually been supplanted in many regions by the families it has given rise to, such as the *Microtidae*, *Gerbillinae*, *Muridae*, etc. (Chaline, Mein, and Petter, 1977).

Rodents of the *Cricetidae* and *Muridae* families arrived from Europe during the Messinian Crisis (late Miocene) in North Africa. However, nearly all of these European species went extinct at the beginning of the Pliocene, which allowed for the diversification of local species (*Gerbillus* and *Meriones*) during the Early and Middle Pleistocene. These local species gradually replaced the ancestral group (*Myocricetodontinae* and *Cricetidae*) (Stoetzel, 2013).

General Characteristics of *Gerbillinae*

In Morocco, the *Gerbillinae* family comprises four genera: the genus *Gerbillus*, which has three subgenera (*Gerbillus*, *Dipodillus*, and *Hendecapleura*); the genus *Meriones*; the genus *Psammomys*, and the genus *Pachyuromys*.

Gerbils are almost universally characterized externally by large eyes, soft fur, most often a color adapted to the soil on which they live, and a non-scaly tail, often long, usually equal to or longer than the body, hairy, and ending in a tuft, except in *Pachyuromys*.

The skull of all current *Gerbillinae* is characteristic of the family; it always shows a long muzzle, a triangular shape, an extended zygomatic plate forward and relatively large tympanic bullae, which are sometimes hypertrophied (Fig. 1).

Modern Gerbillinae inhabit all arid and semi-arid regions of Africa and Asia, reaching as far as Mongolia. The family is adapted to live in dry environments.

Several species have sympatric ranges, while others compete and mutually exclude each other. These ranges can extend over large regions and cover several countries or, conversely, be reduced. Their diet depends on the variation of natural resources in the environment in which they live and generally consists of seeds, green plants, and sometimes animal food, such as insects.

Figure 1: Skull of *Meriones Shawii/grandis* dorsal face and ventral face (Aulagnier et al., 2008)

Gerbils typically live in burrows dug in loose, sandy soils, with several entrances or orifices (usually 4 to 5). Most of these burrows have two or even three levels of superimposed galleries with a chamber always furnished with a nest (Petter, 1956). The temperature and humidity conditions inside the burrows allow them to avoid the extreme conditions of their habitat. They are mostly nocturnal, with burrowing, nest building, and food storage activities occurring at night.

In Morocco and North Africa, the first studies on rodents in general and Gerbillinae in particular began in the 1950s (Petter 1952, 1956, Matthey 1953, 1957) by Petter and St Girons (1965) on Moroccan rodents, focusing on their systematics, geographical distribution, and chromosomal formulas but also their ecology.

Subsequent studies in Morocco have furthered the understanding of Gerbillinae systematics, distribution, and the description of new species, some of which have minimal ranges or are endemic to Morocco. Notable contributions include the works of Diane and Schitzer (1972), Lay (1975), Benazzou and Genest Villard (1980), and Zyadi (1988). For other species, taxonomic status has been confirmed (Granjon et al., 1999).

A comprehensive synthesis of rodents, including their description and distribution, has been the focus of several studies by Thevenot and Aulagnier (1986), Benazzou (1997), and more recently, Denys and Bouarakia (2022). Chromosomal preparations of Gerbillinae species and karyotype analyses have also been conducted using chromosomal banding techniques for cytological characterization and phylogenetic reconstruction (Benazzou et al., 1982a, 1982b, 1983, 1984; Benazzou, 1984; Gerbault-Seureau et al., 2015). Their evolutionary history has been further explored by Benazzou (1988) and, more recently, by Stoetzel et al. (2019).

Other studies have focused on the population dynamics of two gerbil species considered pests, *Gerbillus campestris* and *Meriones shawii* (Zyadi 1989; Zyadi & Benazzou 1992), as well as on four additional gerbil species, including *G. campestris* and *M. shawii* (Zaim 1990). Research has also investigated morphological variability and genetic diversity in *G. campestris* using enzymatic polymorphism (Benazzou 1984; Benazzou & Zyadi 1990; Baala, 1995).

Currently, research integrating biometry, cytogenetics, and molecular biology has provided a more refined characterization of this group, elucidating phylogenetic relationships and the geographic structuring of its various species in North Africa (N'diaye et al., 2012, 2014, 2016; Violaine et al., 2014; Lalis et al., 2015; Bouarakia et al., 2018, 2019a, 2019b; Bouarakia, 2020).

Based on these studies, we can establish a summary presenting the taxonomic inventory of Gerbillinae species in Morocco, which we will discuss further (Table 1).

Morocco is distinguished by its remarkable diversity of gerbil species and a wealth of endemic taxa, including *Gerbillus hesperinus*, *Gerbillus hoogstrali*, *Gerbillus occidius*, and a sibling species of *Gerbillus occidius*. These species are primarily found along the coastal regions, ranging from Essaouira to the southernmost parts of the country.

Table 1: Summary of the taxonomic inventory of *Gerbillinae* species in Morocco
(* endemic species of Morocco)

Genus	Subgenus	Species	Species common name
Gerbillus	*Dipodillus*	*Gerbillus campestris*	North African gerbil
		* *Gerbillus maghrebi*	Large -tailed gerbil
		Gerbillus simoni	Short-tailed gerbil
	Hendecapleura	*Gerbillus amoenus*	Pleasant gerbil
		Gerbillus henleyi	Pygmy gerbil
	Gerbillus	*Gerbillus gerbillus*	Lesser Egyptian gerbil
		* *Gerbillus hesperinus*	Moroccan gerbil
		* *Gerbillus hoogstrali* * *Gerbillus sp.*	Hoogstral gerbil Sand Gerbil
		* *Gerbillus occiduus*	Occidental gerbil
		Gerbillus tarabuli	tarabul gerbil
		Gerbillus pyramidum	Large Sand gerbil
Meriones		*Meriones shawii/grandis*	Shaw's Jird
		Meriones libycus	Libyan Jird
		Meriones crassus	Sandewall's Jird
Psammomys		*Psammomys obesus*	Fat sand Rat
Pachyuromys		*Pachyuromys duprasi*	Fat-tailed Jird

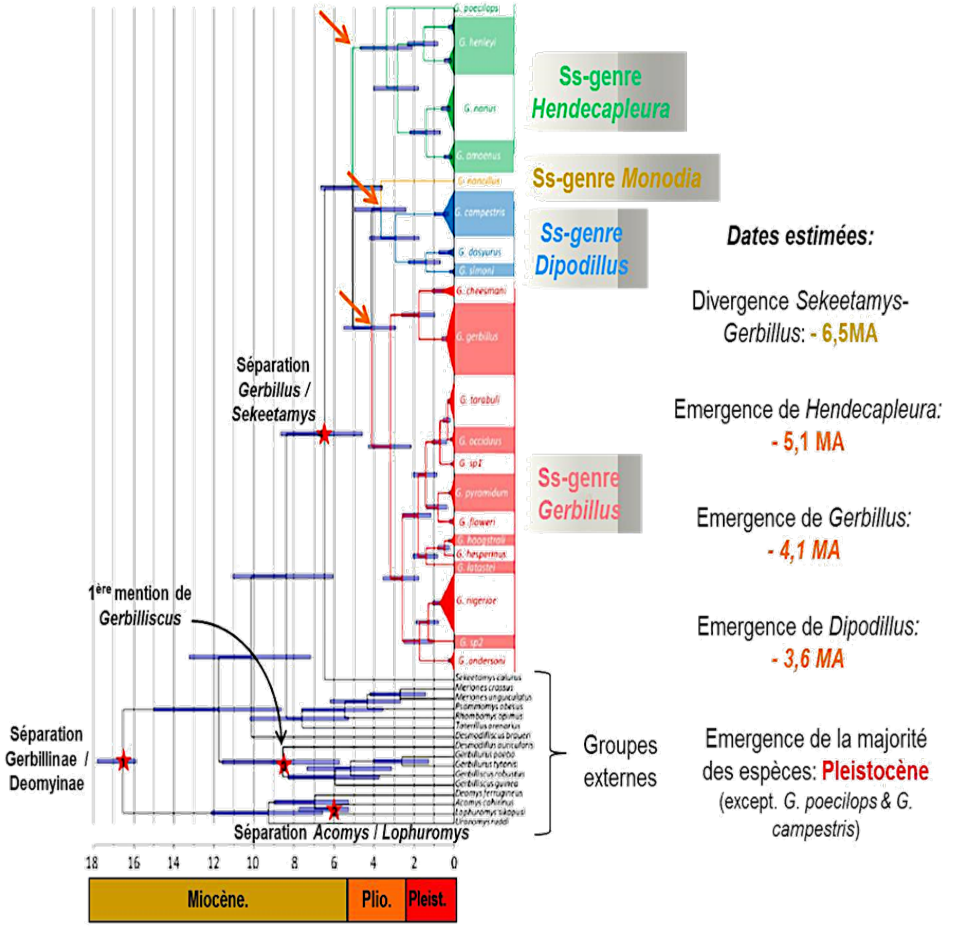
Review of the Systematics, Karyology, and Phylogeny of Moroccan Gerbillinae Species

This study synthesizes existing research on species within this family. It does not describe study techniques and introduces species descriptions and distributions briefly since they have already been extensively documented. It also provides the most recent karyotypes and phylogenetic trees.

Recent molecular data have reinforced the evolutionary systematics of this clade. Findings generally support the conclusion that the generic distinction between *Gerbillus* and *Dipodillus* lacks validity. Additionally, these data have shed light on the group's biogeographical history by estimating emergence events and lineage differentiation and reconstructing the ancestral distribution areas of taxa (Chevret & Dobigny, 2005; Abiadh et al., 2010; Ndiaye et al., 2012; Alhajeri et al., 2015; Ndiaye et al., 2016).

The genus *Gerbillus* consists of four primary lineages, which we may classify as subgenera: **Hendecapleura** (*G. poecilops, G. henleyi, G. nanus,*and *G. amoenus*);

Monodia (*G. nancillus*); **Dipodillus** (*G. campestris, G. dasyurus,* and *G. simoni*); **Gerbillus** (*G. cheesmani, G. gerbillus, G. tarabuli, G. occiduus, G. pyramidum, G. floweri, G. hoogstrali, G. hesperinus, G. latastei, G. nigeriae, G. andersoni*, and two yet-to-be-identified or described species).



According to Granjon et al. (2018), this figure shows the organization of the genus *Gerbillus* and its spatio-temporal evolution since its emergence. The chronogram produced using BEAST software shows the phylogenetic relationships of the *Gerbillus* genus in a temporal framework. Red stars: calibration points (using fossil data mentioned in Ndiaye et al. (2016), orange arrows: events of emergence of lineages (subgenera, see the corresponding dates on the right of the figure)

Genus: ***Gerbillus*, Desmarest, 1804**

Subgenus: *Gerbillus*

Gerbillus occiduus Lay, 1975 Occidental Gerbil
Endemic of Morocco, *Gerbillus occiduus* is of medium size, with light dorsal fur and white ventral fur extending to the base of the hairs. The feet are covered with white fur on both sides, and the nails are also white. The tail is covered with fur and ends in a tuft (Fig. 2).

Figure 2: *Gerbillus occiduus* (@ L. Granjon, via IRD)

Geographical distribution

Gerbillus occiduus is endemic to southern Morocco, inhabiting sandy environments in the Draa-Tarfaya region. It is known by a few individuals collected and studied by a few authors, and some of the last records date from 2013 (Moores & Brown, 2013).

The chromosomal formula is 2n = 40 (NF = 80), with all chromosomes being metacentric or submetacentric. The X and Y chromosomes are submetacentric (Fig.3). Ndiaye et al. (2012), sequenced the type specimen and some others and found the species valid; its closest relative would be *G.tarabuli*.

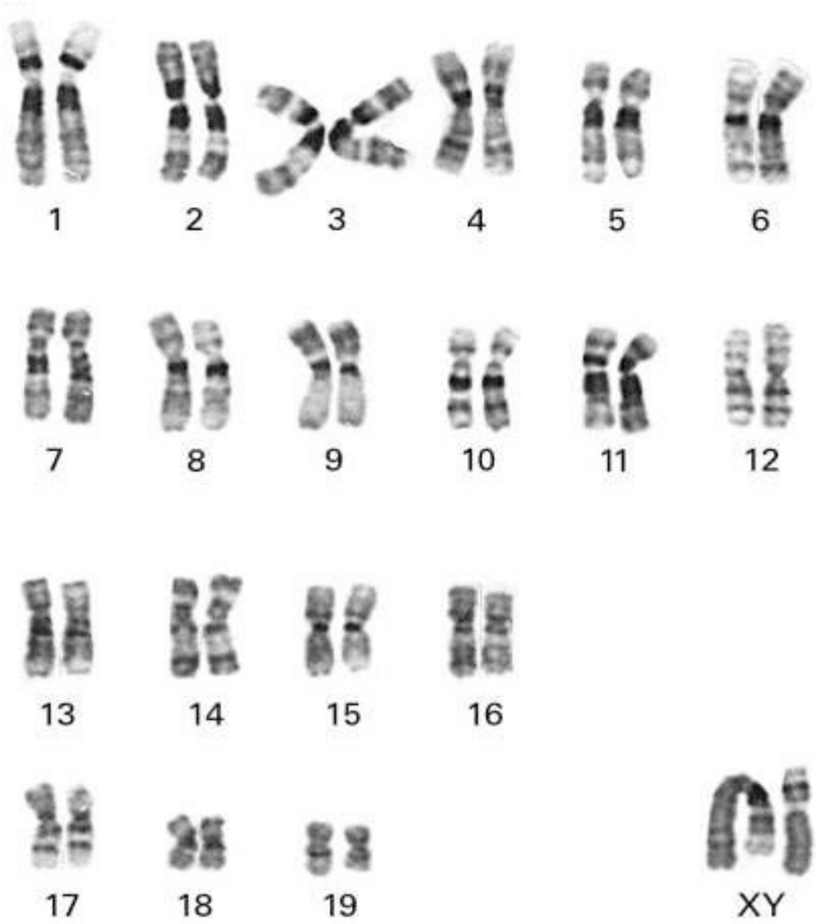


Figure 3: GBG bands karyotype of *Gerbillus occiduus* (Aniskin et al., 2006)

Gerbillus hoogstrali **Lay, 1975 - Hoogstral gerbil**

Endemic of Morocco, *Gerbillus hoogstrali* has dorsal fur ranging from cinnamon to chamois brown, with white ventral fur. The foot soles are covered with fur. The tail is covered with fur and ends in a tuft (Fig. 4).

Geographical Distribution

Gerbillus hoogstrali is an endemic species of Morocco. It inhabits sandy habitats in the low valleys of the Souss River. Its range extends north of Agadir and east of Taroudant to the south, towards the mouth of the Massa River. The last collected individuals were found in 2012. IUCN classifies this gerbil as Vulnerable.

Figure 4. *Gerbillus hoogstrali* (@ L. Granjon via IRD)

Ndiaye et al. (2012) found this species as a sister taxon of *G.hesperinus* and in the same clade as *G.lastastei* from Algeria.

The chromosomal formula is 2n = 72 (NF = 86). Apart from pair 1, all other chromosomes are acrocentric, and the X chromosomes are submetacentric (Fig. 5).

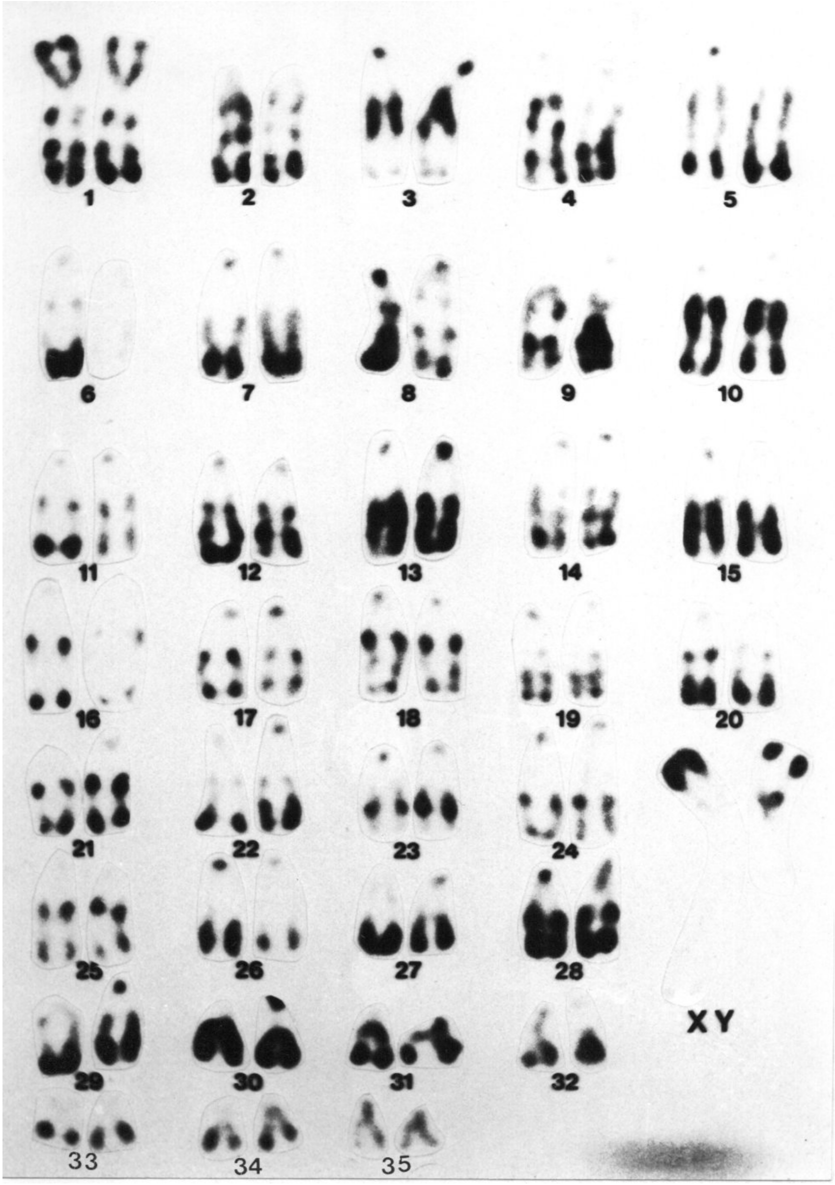


Figure 5: RBG bands karyotype of *Gerbillus hoogstrali* (Benazzou 1984)

Gerbillus hesperinus Cabrera, 1906 - Moroccan gerbil

Endemic of Morocco, *Gerbillus hesperinus* has a dark fawn and speckled dorsal fur, with ochre fawn flanks and pure white ventral fur. The upper part of the feet is covered with white fur, while the fur on the toes is washed with fawn on both sides, similar to the fur on the foot soles. The tail is longer than the body, covered with fur, and ends in a relatively inconspicuous tuft. *Gerbillus hespirinus* is an endemic species of Morocco, with its distribution limited to the sand dune area south of Essaouira and classified as Endangered by IUCN. Ndiaye et al. (2012) confirmed the species' validity and found it close to *G. hoogstrali*.

The chromosomal formula is 2n = 58 (NF = 74), with 9 pairs of metacentric or submetacentric chromosomes and 19 pairs of acrocentric chromosomes. The X chromosomes are submetacentric (Fig.6).

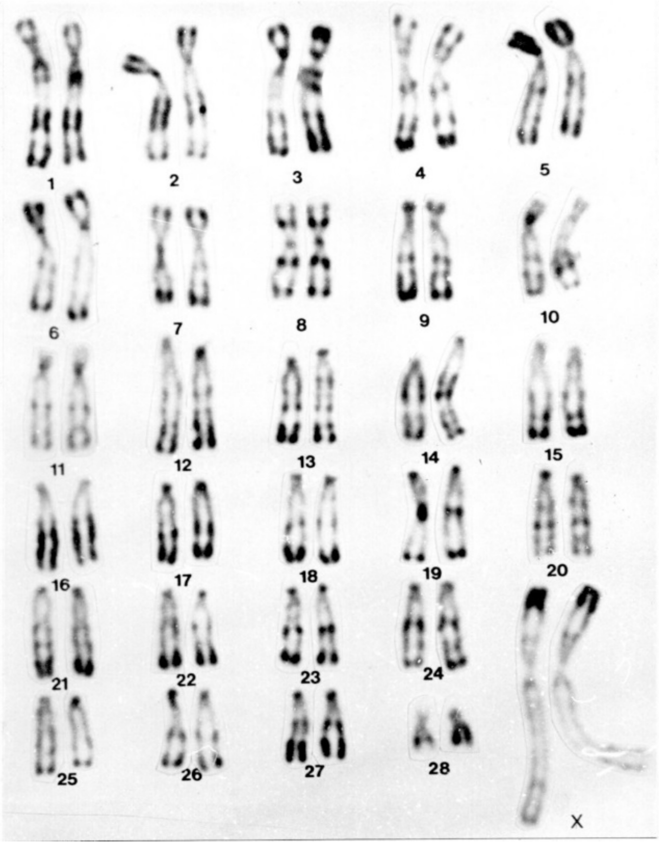


Figure 6: RBG bands karyotype of *Gerbillus hesperinus* (Benazzou, 1984)

Gerbillus tarabuli Thomas, 1902 - Tarabul gerbil or Libyan gerbil

Gerbillus tarabuli is medium in size, with light dorsal fur and white ventral fur extending to the base of the hairs. The feet are covered with white fur on both sides (Fig. 7).

Figure 7: *Gerbillus tarabuli* (L.Granjon, via IRD bottom @J.J Lemasson)

Geographical distribution

G. tarabuli is known from the south and southeast of Morocco to the region of Bouarfa. It is widely distributed in desert and semi-desert areas.

Ndiaye et al. (2014) and Nicolas et al. (2014) found *G. tarabuli* valid and close to *G. occiduus*. Both are distant from *G. pyramidum* in which this taxon was initially described as a sub-species.

The karyotype of *Gerbillus tarabuli* is 2n = 40 (NF = 74), with 17 pairs of metacentric or submetacentric chromosomes and two pairs of acrocentric chromosomes. The X chromosome is submetacentric, and the Y is acrocentric (Fig. 8).

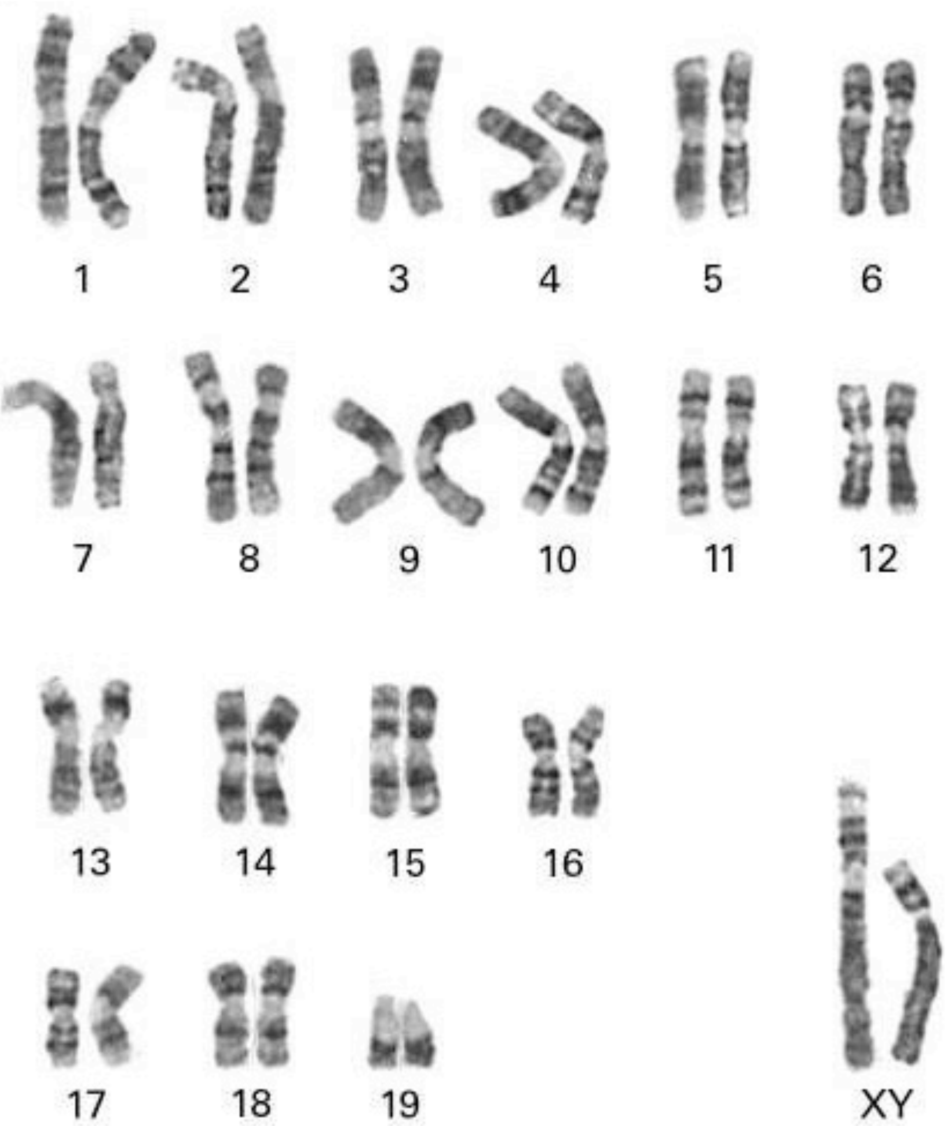


Figure 8: GBG bands karyotype of *Gerbillus tarabuli* (Aniskin and al., 2006)

Gerbillus gerbillus Olivier, 1800 - Lesser Egyptian gerbil

Gerbillus gerbillus has a uniformly ochre dorsal coloration and white ventral fur. Its hind feet have proportionally longer toes, and the foot soles are covered with long fur. The tail, longer than the body, is covered with fur (Fig. 9).

Figure 9 : *Gerbillus gerbillus* (L. Granjon via IRD)

Geographical distribution

Gerbillus gerbillus has an extensive distribution in the south and southeast of Morocco, inhabiting sandy habitats.

The chromosomal formula is 2n = 43 (NF = 65) in males and 2n = 42 (NF = 64) in females. The karyotype includes 15 pairs of metacentric or submetacentric chromosomes, and 5 pairs, as well as the unpaired element, have a more or less developed short arm. The X and Y chromosomes are submetacentric (Fig. 10).

Figure 10: RBG bands karyotype of *G. gerbillus* (Benazzou 1984)

Gerbillus pyramidum Geoffroy, 1803 - Large Sand Gerbil

Gerbillus pyramidum is large in size, with dorsal fur of ochre fawn and pure white ventral fur, a long tail covered with fur ending in a grayish tuft and relatively large feet with hairy foot soles. This species has significant biometric variability (Figs. 11-a and 11-b).

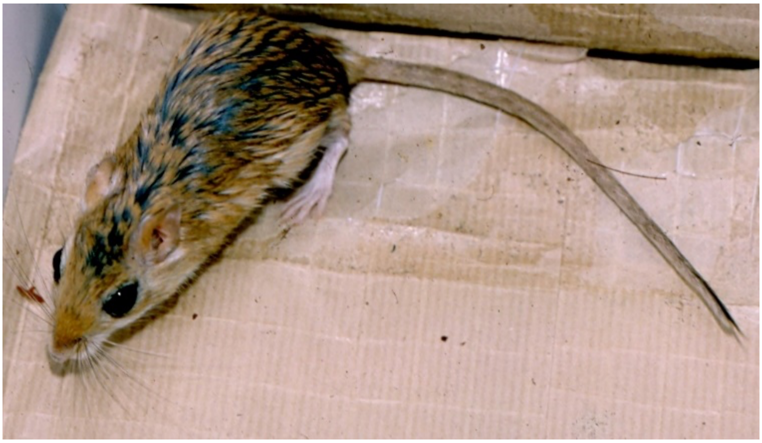


Figure 11-a: *Gerbillus pyramidum* (Benazzou 1984)

Figure 11-b: *Gerbillus pyramidum* (L.Granjon via IRD)

Geographical distribution

Gerbillus pyramidum shares the same distribution range as *G. gerbillus,* inhabiting all arid and desert areas in the extreme south of Morocco.

The chromosomal formula is 2n = 38 (NF = 76), with all pairs being metacentric or submetacentric. The X and Y chromosomes are submetacentric (Fig. 12).

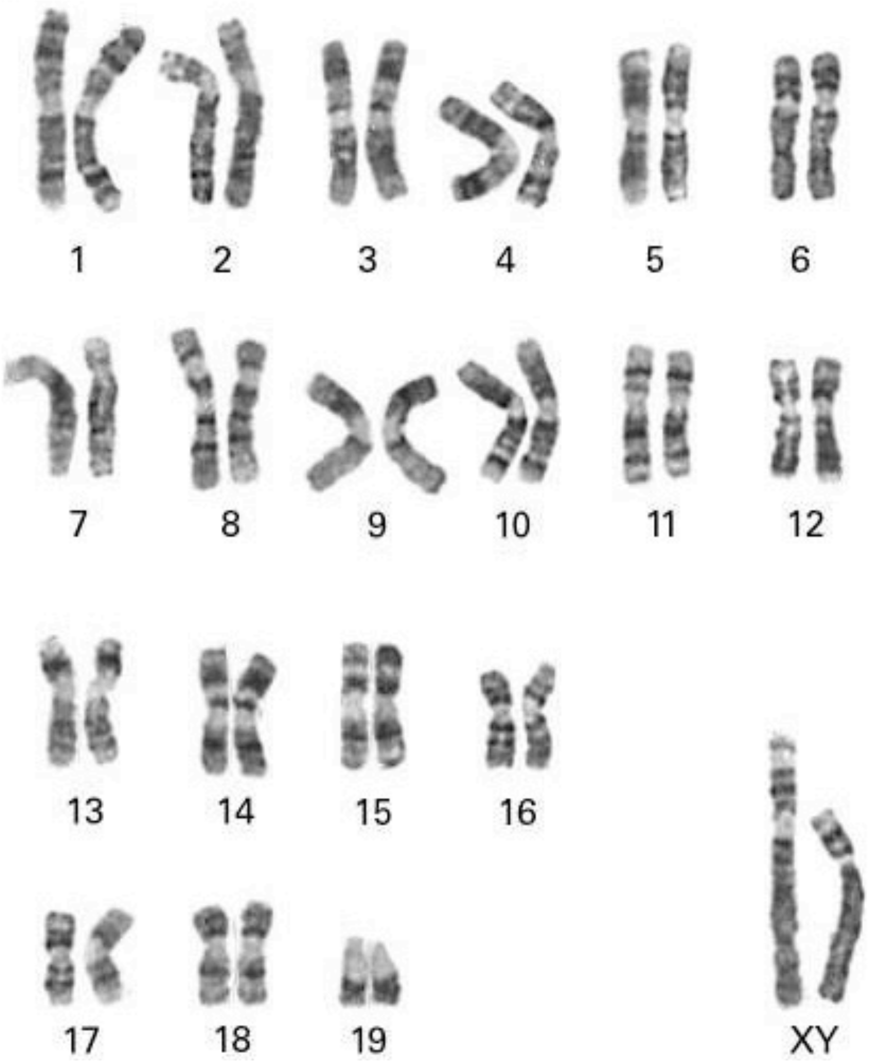


Figure 12: GBG bands karyotype of *G. pyramidum* (Aniskin and al. 2006)

Gerbillus sp.

Endemic of Morocco, *Gerbillus* sp. is a sabling species with hairy foot soles.

The studies of skull morphology and their analysis based on phenetic distances confirmed that *Gerbillus* sp. and *Gerbillus occiduus* plus *G. tarabuli* belong to the same clade (N'Diaye et al., 2012).

Geographical distribution

Restricted to the coastal sandy plains between the Sous and Massa Rivers (N'Diaye et al., 2012).

The karyotype is unknown.

Figure 13: Sand gerbils burrow (T. Benazzou)

Genus: *Gerbillus* Desmarest, 1804

Sub-genus: *Dipodillus*

Gerbillus Dipodillus campestris, Loche, 1867 -North African gerbil.

Gerbillus campestris is a medium-sized species with dorsal fur ranging from dark brown to light brown. It has naked foot soles and a long tail ending in a tuft (Fig. 14).

Figure 14 : *Gerbillus campestris* (L. Granjon)

Geographical distribution

Gerbillus campestris has an extensive distribution in Morocco, ranging from subhumid to desert areas. It inhabits various habitats, from forests to sandy soils.

According to Granjon et al. (2018) *G.campestris* would be the sister taxon of *G.dasyurus* + *G.simoni.*

The chromosomal formula is 2n = 56 (NF = 68), with seven pairs of metacentric or submetacentric chromosomes; the remaining pairs are acrocentric. The X chromosomes are metacentric. There is chromosomal polymorphism within this species (Fig. 15).

Morphological and molecular studies have shown the existence of strong morphological and molecular structuration inside the North African populations of this species and the existence of at least seven distinct geographical lineages for

Morrocco (Bouarakia, 2020; Bouarakia et al., 2018). According to Granjon et al. (2018), G.campestris would be the sister taxon of G.dasyurus + G.simoni.

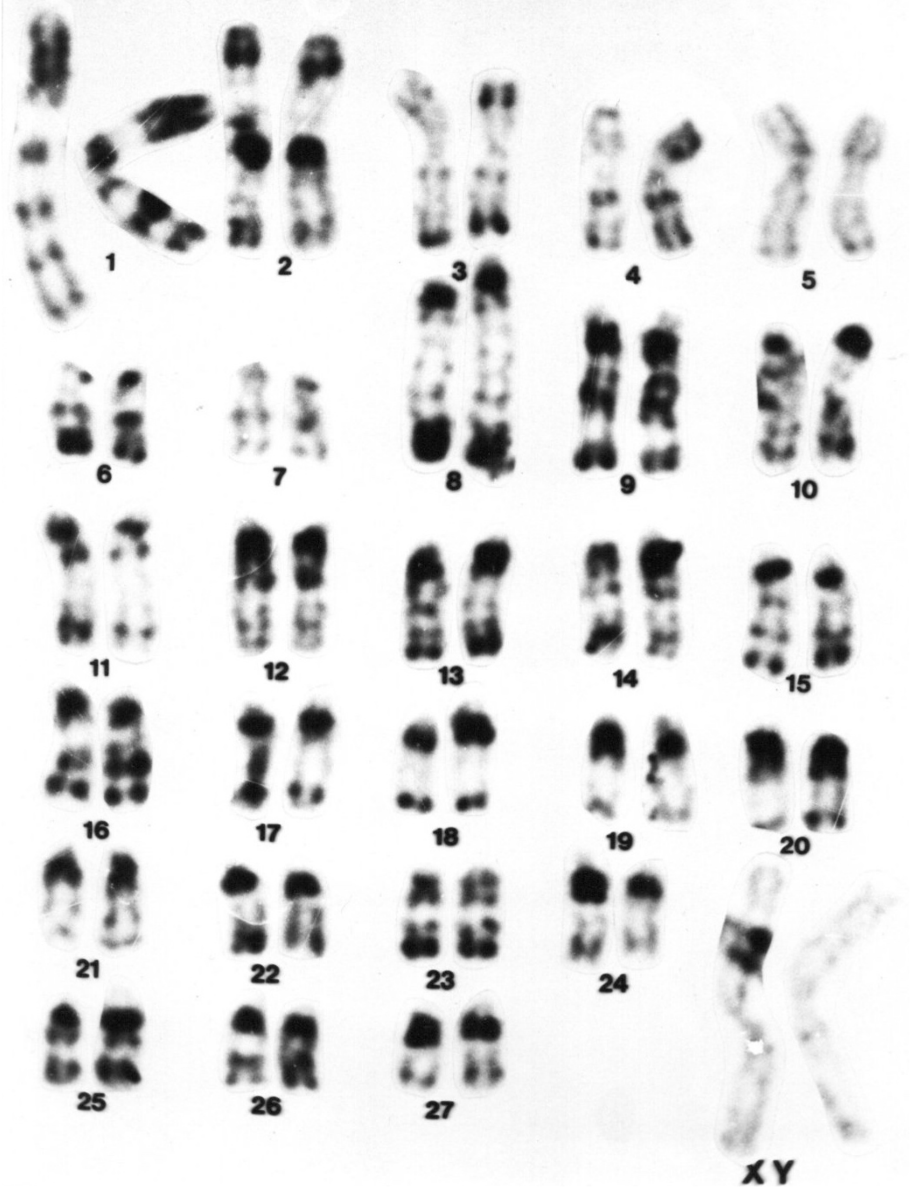


Figure 15: RBG bands karyotype of *G. campestris* (Benazzou 1984)

Gerbillus simoni Lataste, 1881 - Lesser short-tailed gerbil

Gerbillus simoni has a small size, with soft and dense brownish fur, white on the ventral side. The tail is very short (approximately equal to the head plus body length) and does not end in a brush; the plantar soles of the hind feet are bare (Fig.16).

Figure 16 : *Gerbillus simoni* (Aulagnier et al., 2008)

Geographical distribution

G. simoni has a very limited distribution in Morocco's eastern region, which is very rare.

Its karyotype has never been established for Morocco.

The first genetic data about *G. simoni* were obtained recently and validate the presence of this species in Morocco (Bouarakia et al., 2018). *G. simoni* is the sister taxon of G.dasyurus (Granjon et al., 2018).

Lay (1975) listed a chromosomal formula for *G.simoni*: 2N=60 Number acrocentrics 50/52. Lay et al. (1975), and Osborn & Helmy (1980) provide a 2N=60, FN=68-69 for Egyptian and Tunisian specimens attributed to this species.

Gerbillus maghrebi Schlitter & Setzer, 1972 - the large short-tailed gerbil

An endemic species of Morocco, *Gerbillus maghrebi* has short grayish-fawn dorsal fur and light reddish ventral fur, with naked foot soles. The tail is relatively short and lacks a terminal tuft.

Geographical distribution

The distribution of *G. maghrebi* is very limited to the west around Taounate and the southern slopes of the Rif, with its range slightly extending southwards (region of Sidi Chiker). Some specimens were recently described in Morocco (Rihane, 2006).

Unfortunately, there are no photos of this species nor anyany data on its karyotype.

Gerbillus Hendecapleura henleyi de Winton, 1903 - Pygmy gerbil

Sub-genus: *Hendecapleura*

Gerbillus henleyi has a small size, with ash-grayish dorsal and white ventral fur. The foot soles of the hind feet are naked, and the tail is long and ends in a tuft (Fig. 17).

Figure 17 : *Gerbillus henleyi* (Aulagnier et al, 2008)

Geographical distribution

Its distribution range extends from the south (region of Tantan, Guelmime, and Tafilalt, etc.) to northeast Morocco (Ain Beni Mathar).

G. henleyi is the sister taxon of *G. nanus*+ *G. amoenus* in the most recent molecular tree (Granjon et al., 2018; Ndiaye et al., 2016).

Its chromosomal formula is 2n = 52 (NF = 66), with six pairs being submetacentric, all the others acrocentric, and the X chromosome being submetacentric (Fig. 18). Its karyotype is similar to that of *G. amoenus*.

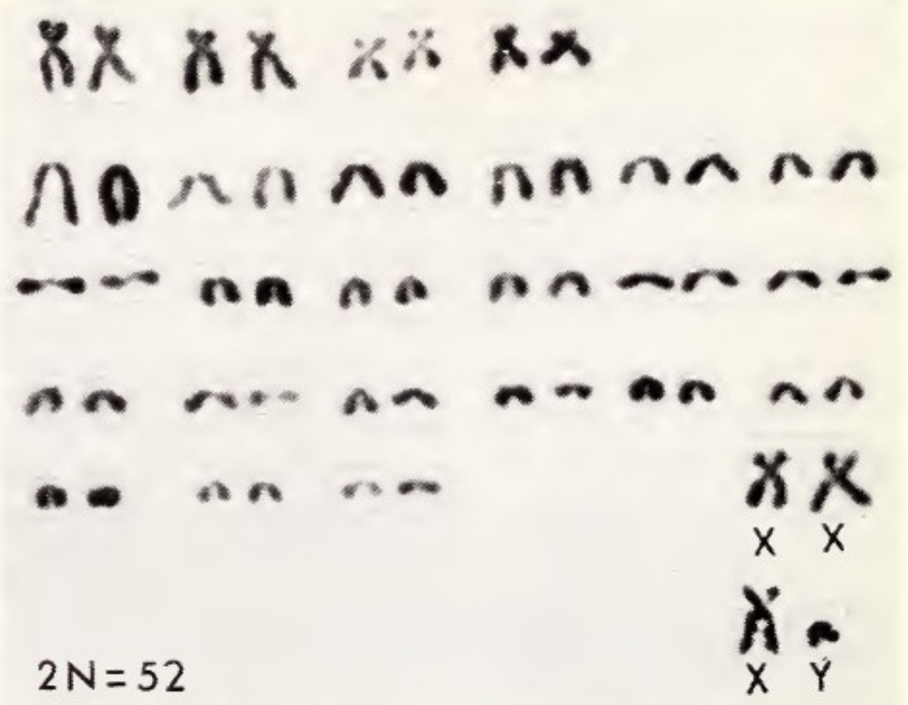


Figure 18: Standard Karyotype of *G. henleyi* from Morocco (Lay et al., 1976)

Gerbillus amoenus de Winton 1902 - Pleasant Gerbil

Gerbillus amoenus has greyish-fawn dorsal fur and white ventral fur, a long tail ending in a brownish tuft, and naked foot soles (Fig. 19).

It was initially called *G. nanus* in Morocco, but a molecular study has shown that the two species are geographically distinct. *G. amoenus* is found only in North Africa, while *G. nanus* would be more of a Middle Eastern and Asiatic species.

Figure 19 : *Gerbillus amoenus* (Benazzou)

Geographical distribution

The *G. amoenus*' distribution covers all desert regions of southern Morocco up to the northeast.

Its chromosomal formula is 2n = 52 (NF = 60), with the first pairs being metacentric or submetacentric, while all other chromosomes are acrocentric. The X chromosomes are submetacentric (Fig. 20).

Figure 20: RBG bands karyotype of *G. amoenus* (Benazzou, 1984)

Genus *Meriones*, Illiger, 1811

Meriones shawii/*grandis* Duvernoy, 1942; Cabrera, 1907 – Shaw's Jird, Moroccan Jird. *M. shawii/grandis* has a dorsal fur color ranging from ochre to fawn, with white ventral fur. The legs are white, and the foot soles of the hind legs are covered with fur. The tail is long, with a black terminal tuft (Fig. 21).

Figure 21: *M. shaw*ii/*grandis* (T.Benazzou)

Geographical distribution

Shaw's Jird is found in all territories north of the Draa River valley and is widespread in plains and mountains. It is a very common species and is considered a pest for cultures.

The chromosomal formula is 2n = 44 (NF = 78), with 16 pairs of metacentric or submetacentric chromosomes and five pairs of acrocentric chromosomes. The X chromosomes are submetacentric (Fig. 22).

We retain the *Meriones shawii/grandis* designation since both *M. shawii* and *M. grandis* are present in Morocco. *M. grandis* occupies most of the territory, while *M. shawii* is found in the far eastern part of the country.

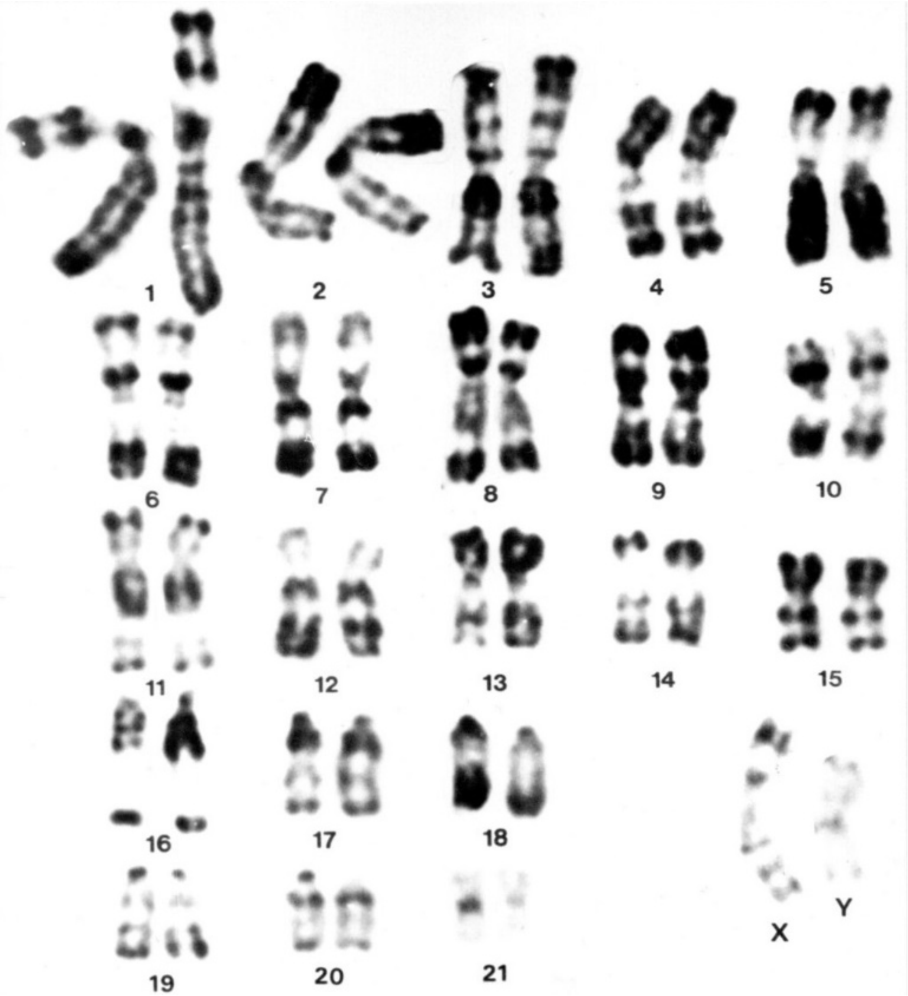


Figure 22: RBG bands karyotype of *M. shawii* (Benazzou, 1984)

The distinction between *Meriones shawii* and *Meriones grandis* is only based on subtle size differences (Djellaila et al., 2018), but there is no consensus about the existence of a second species in the Eastern part of Morocco (Aulagnier & Thevenot, 2009; Pavlinov, 2000). New molecular studies have shown the existence of two molecular clades in Morocco that could validate both species (Lalis et al., 2016). In none of these studies has it been possible to incorporate the type specimen of *M. shawii*, which is supposedly lost, so we prefer to keep both species as synonyms for the moment.

Meriones lybicus Lichtenstein, 1823 - Libyan Jird

The Libyan Jird has pale greyish-fawn dorsal fur and white ventral fur. The foot soles of the hind legs are hairy, and the tail is long and ends in a black tuft (Fig. 23).

Geographical distribution

This Jird is found in arid and semi-arid regions. It typically digs its burrows around the base of the jujube tree. Its burrow is excavated in moist sand, with relatively wide galleries and at least three exits spanning two to three levels (Fig. 24).

Figure 23: *Meriones lybicus* (Benazzou)

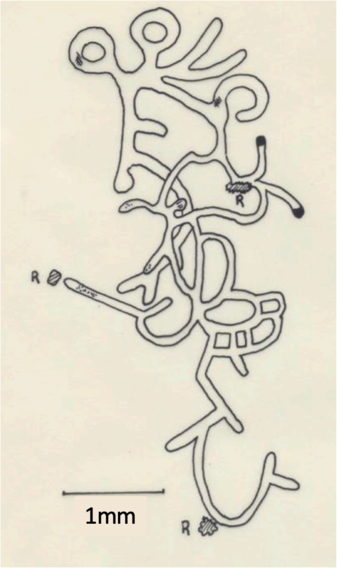


Figure 24: Burrow of *M. libycus* (Petter, 1961)

The chromosomal formula is 2n = 44 (NF = 73), with 15 pairs of metacentric or submetacentric chromosomes and 6 pairs of acrocentric chromosomes. The X chromosome is acrocentric, and the Y is submetacentric (Fig. 25).

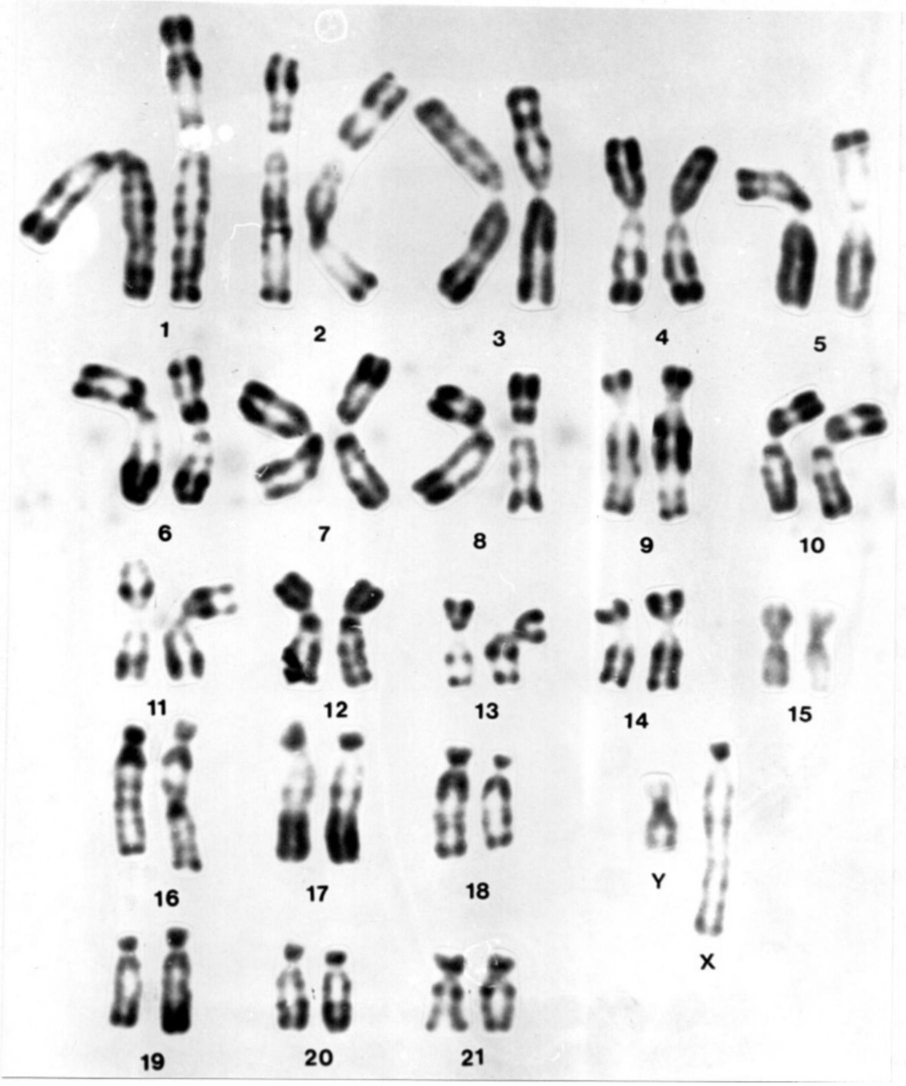


Figure 25: RBG bands karyotype of *M. lybicus* (Benazzou, 1984)

The molecular analysis of *Meriones lybicus* was conducted, allowing its placement in the phylogenetic tree of Gerbillinae, positioned closer to *Meriones crassus* (Fig. 42).

Meriones crassus Sundevall, 1842 – Sundevall's Jird

The Sundevall's Jird is extensive, with soft, light fawn fur on its back and white fur on its belly. The tail is as long as the body and ends in a tuft. The fur covers the soles of the foot and hind legs (Fig. 26).

Figure 26: *Meriones crassus* (Benazzou)

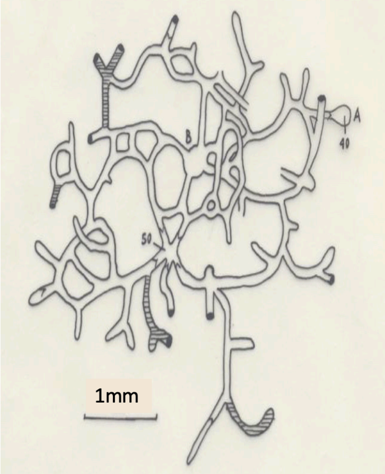


Figure 27: Burrow of *M. crassus* (Petter 1961)

Geographical distribution

The Desert Meriones inhabits desert and arid regions of the country. Its burrow is dug in hard soil, with at least five exits, and the galleries are pretty deep (Figs. 27, 28 and 29).

Figure 28: Biotope of *M.crassus*

Figure 29: Burrow of *M.crassus* (Benazzou)

Its karyotype is 2n = 60 (NF = 68), with six pairs of metacentric or submetacentric chromosomes and 22 pairs of acrocentric chromosomes. The sex chromosomes are submetacentric (Fig. 30).

In a general phylogeny of the genus, Ito et al. (2010) found *M. crassus* in a same clade as *M. rex* and *M. libycus*. The sequence of Moroccan specimens of this species put them in the same clade as *M. crassus* from Egypt, Saudi Arabia and Iran and the sister taxon of *M. tristrami* (Bouarakia et al., 2021).

Figure 30: RBG bands karyotype of *M. crassus* (Benazzou, 1984)

Genre *Psammomys*, Cretzschmar, 1828

Psammomys obesus Cretzschmar, 1828 - Fat Sand Rat

Psammomys obesus is the only diurnal species of the family in Morocco. It has a large head, brown fur, and a long tail shorter than the body, ending in a black tuft. The ventral fur is yellowish, and the hind legs are hairy (Fig. 31).

Figure 31: *Psammomys obesus* (© MinoZig, via Wikimedia Commons)

Geographical distribution

P. obesus lives in the steppes of the pre-Saharan regions, the arid and semi-arid areas from the southern Anti-Atlas to the northeastern High Atlas. It digs its burrows in wadi beds or chenopod-rich salt flats, which constitute most of its diet.

In winter, it comes out during the warm hours of the day and in summer, from sunrise to sunset. It is recognizable by its standing position next to its burrow (Fig. 32).

Figure 32: Biotope and burrow of *P.obesus* (T.Benazzou)

Its chromosomal formula is 2N = 48 (NF = 54), with 13 metacentric or submetacentric chromosomes, while the others are acrocentric. The X chromosome is a large submetacentric, and the Y is a small metacentric (Fig. 33).

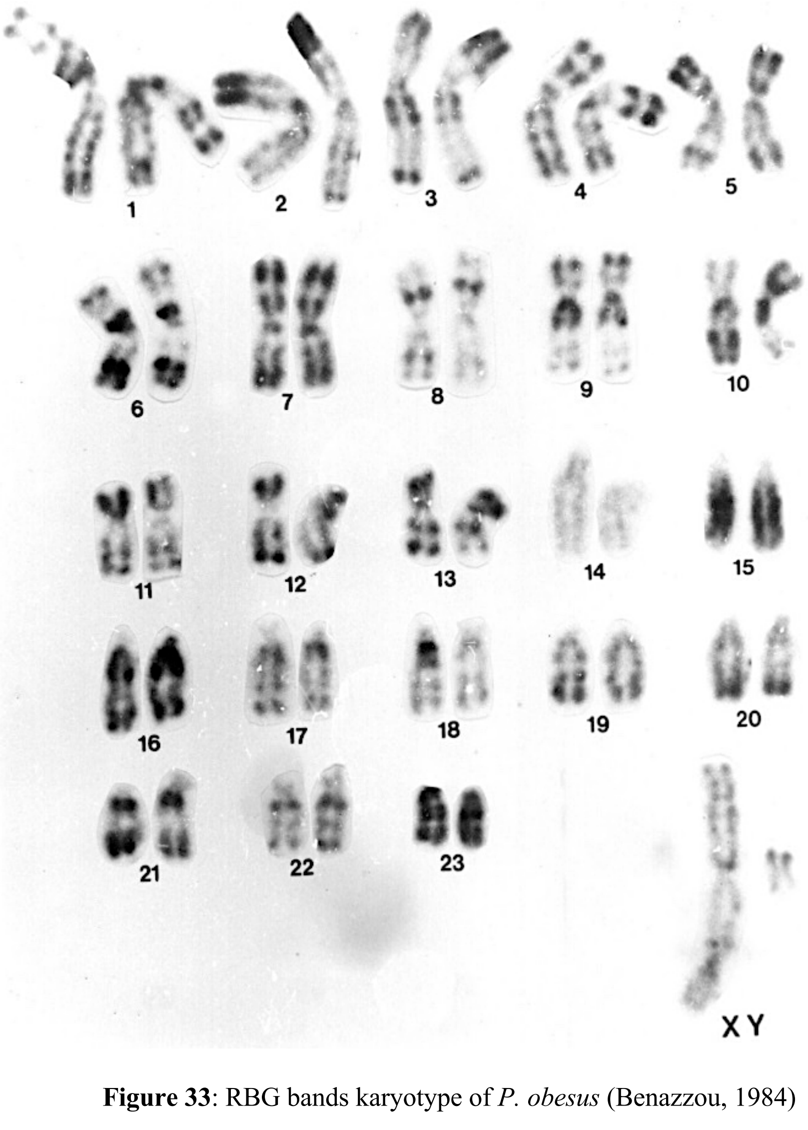


Figure 33: RBG bands karyotype of *P. obesus* (Benazzou, 1984)

Genre *Pachyuromys,* Lataste, 1880

Pachyuromys duprasi Lataste, 1880 - Fat-tailed Jird

Psammomys duprasi has a small size, with greyish-yellow fur and white ventral fur. The tail is small, pale pink, sparsely hairy, and ends in a thickened club-like structure. The hind legs are hairy (Fig. 34).

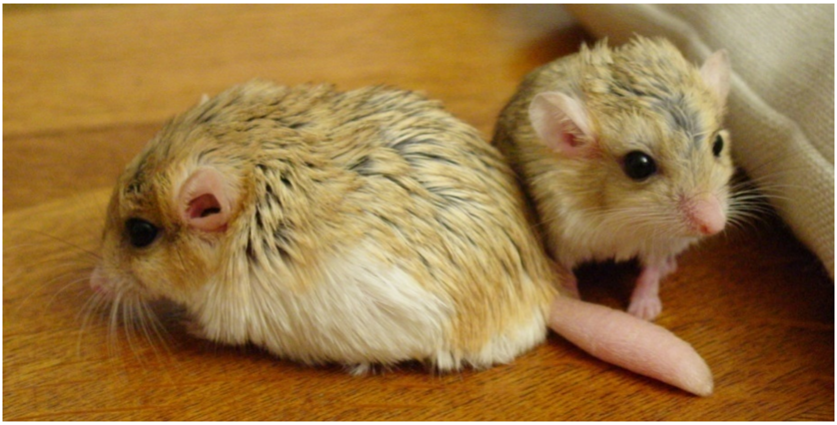


Figure 34: *P. duprasi* (Maas P.H.I., via Wikimedia commons)

Geographical distribution

P. duprasi inhabits the Sahara Desert south of the Anti-Atlas and east of the High Atlas, extending eastwards towards the Mediterranean (Fig. 35).

Figure 35: Biotope and burrow of *P. duprasi* in steppe environment (Benazzou)

Its chromosomal formula is 2n = 54 (NF = 66), with only five pairs of metacentric or submetacentric chromosomes, and the sex chromosomes are submetacentric (Fig. 36).

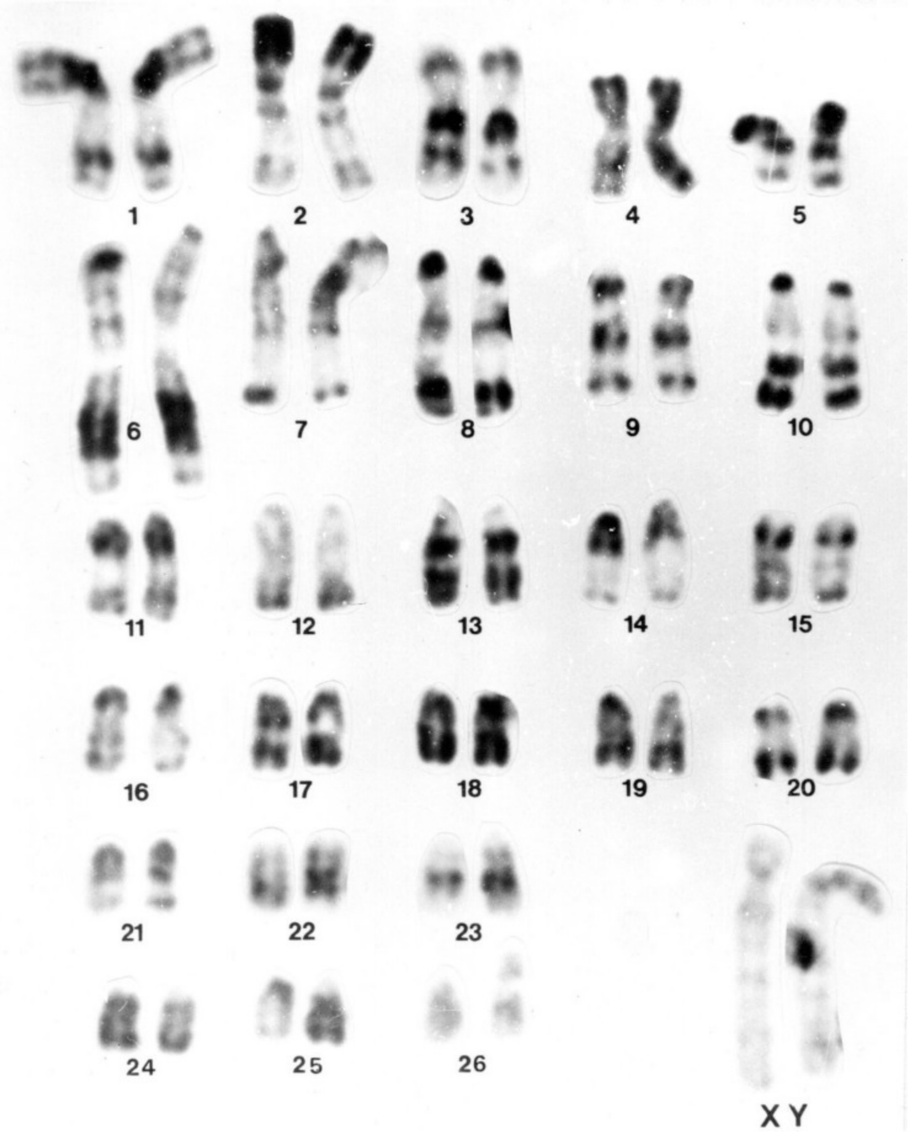


Figure 36. RBG bands karyotype of *P. duprasi* (Benazzou, 1984)

Phylogeny

Evolutionary schemas of the gerbil family have been proposed since the early twentieth century based on either molar cusp patterns (Petter 1956, 1959, 1973) (Fig. 37), dental alveoli (Herold & Niethammer, 1963) (Fig. 38), or systematic and paleontological data (Pavlinov 1980, 2000 Tong, 1989 et Chevet et Bobigny, 2005) (Fig. 39 a, b, c). Overall, these phylogenetic trees reveal some significant evolutionary differences within this family. However, it is consistently noted that *Psammomys* and *Pachyuromys* are closely related to *Meriones* species found in North Africa.

Establishing an evolutionary systematic hierarchy among gerbils based solely on morphological criteria remained a subject of debate, necessitating the use of other criteria for studying phylogenetic relationships in this group.

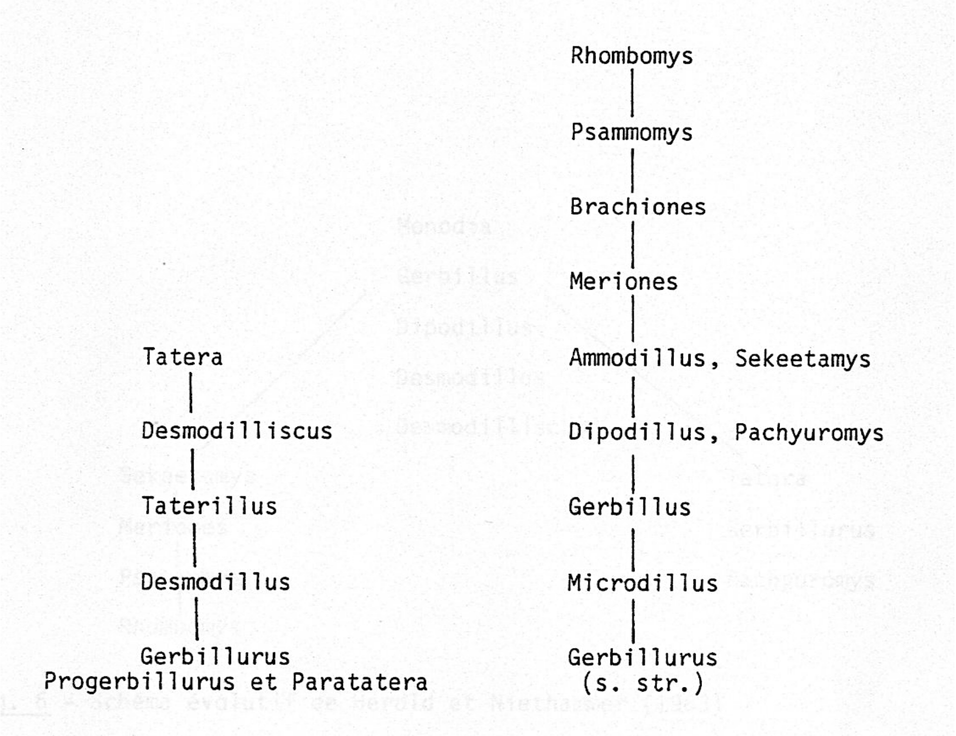


Figure 37: Evolutionary schema (Petter 1956, 1959, 1973)

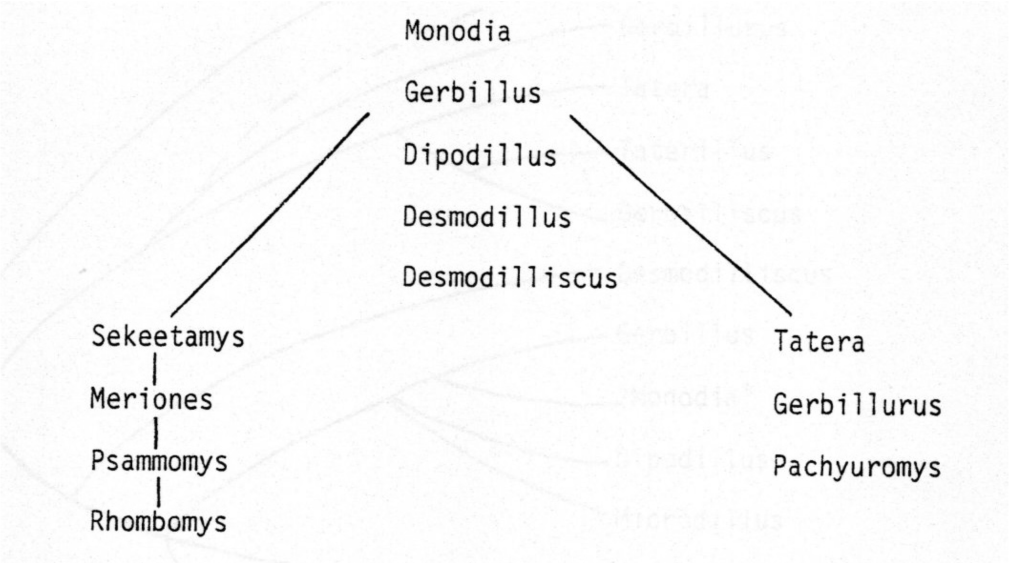


Figure 38: Evolutionary schema (Herold & Niethammer, 1963)

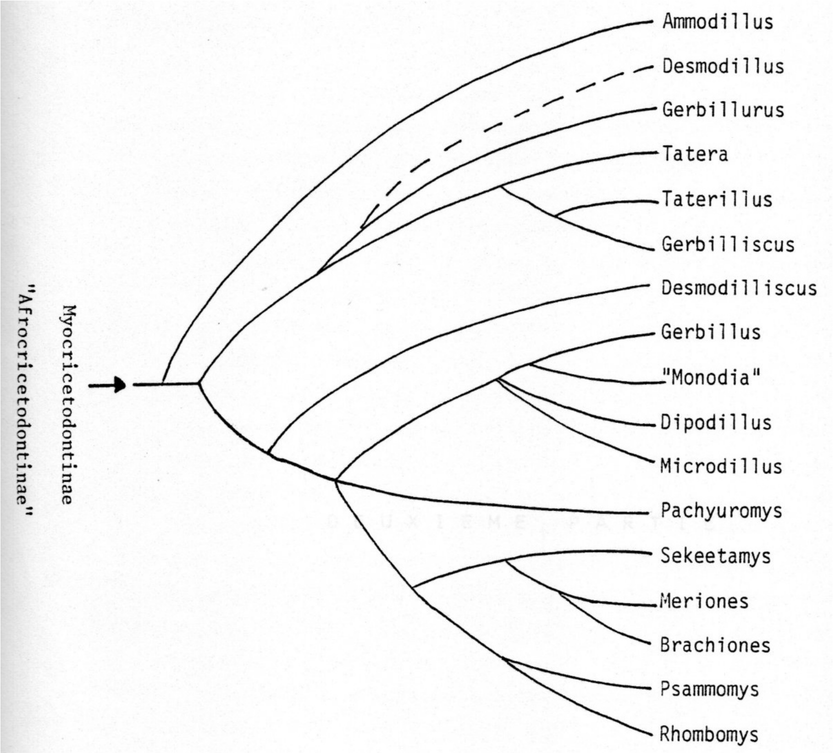


Figure 39-a: Evolutionary schema (Pavlinov, 1980)

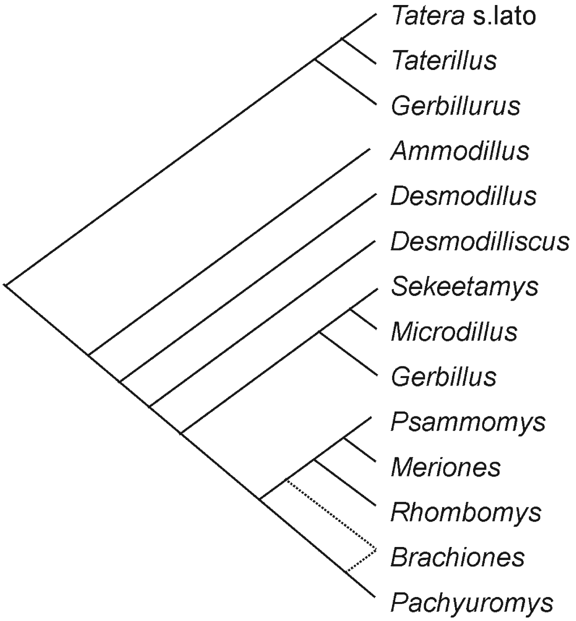


Figure 39-b: Evolutionary schema (Tong, 1989)

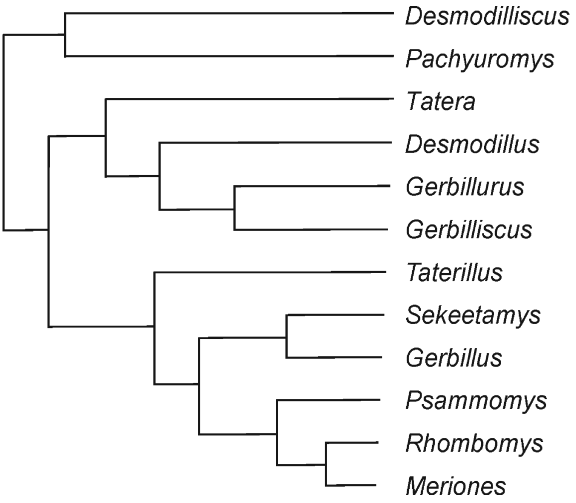


Figure 39-c: Evolutionary schema (Chevet & Bobigny, 2005)

Chromosomal phylogeny

The development of cytogenetic with chromosome marking in the 1970s was also a means to establish phylogenies in zoological groups. This method was applied to the Gerbillinae as well (Benazzou, 1984) (Fig. 40).

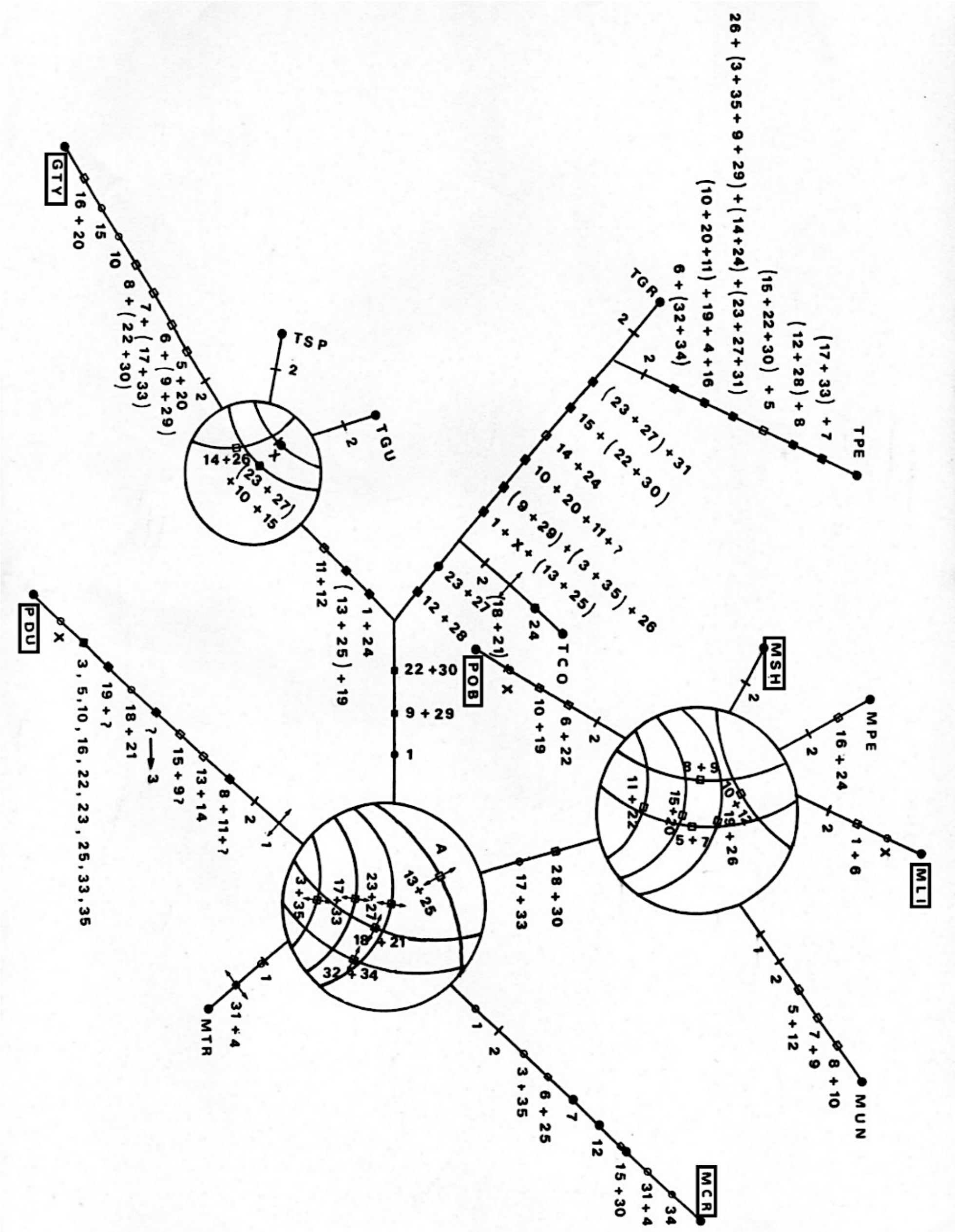


Figure 40: Chromosomal phylogeny (Benazzou, 1984). PDU: *Pachyuromys duprasi*, MCR: *Meriones crassus*, MLI: *Meriones lybicus,* MSH*: Meriones shawii,* POB: *Psammomys obesus*, GTY: *Gerbillus tytonis* (Genus *Gerbillus*). The circles, squares, and lines indicate different chromosomal rearrangements.

This chromosomal phylogeny is based on the comparison of chromosomes treated and colored in R-bands. It shows a population-level evolution of the different genera within this family. It is noted that *Pachyuromys* and *Meriones crassus* are derived from the same population, reflecting their life in a desert environment, while *Meriones lybicus*, *M. shawii*, and *Psammomys* originate from a group living in less arid environments. Other gerbils that are not found in Morocco live in different environments and come from another branch. This chromosomal evolution provides us with some more details on the phylogenetic evolution among the Gerbillinae.

Indeed, it appears that the genus *Meriones* is ancestral and that it split into two populations, from which the current species of this genus and a few related genera, such as *Psammomys* and *Pachyuromys*, likely originated (Fig. 40).

A comparison between chromosomal phylogeny and phylogeny based on morphological traits reveals that the genus *Psammomys* is quite closely related to the genus *Meriones*, whereas the genus *Gerbillus* forms a distinctly separate group.

Molecular Phylogeny

Molecular phylogenetic has made significant advances thanks to the analysis of mitochondrial DNA. This DNA has the advantage of being abundant in cells, having maternal transmission without recombination, and evolving rapidly. Here, the cytochrome b (or cytb) is studied.

Most Moroccan species have undergone this molecular analysis. We present here two phylogenetic trees created by Bouarakia O., to which these species are attached. Figure 41 groups the gerbil species, including those from Morocco (colored in red), while Figure 42 groups the three species of Meriones present in Morocco as well as Psammomys and Pachyuromys.

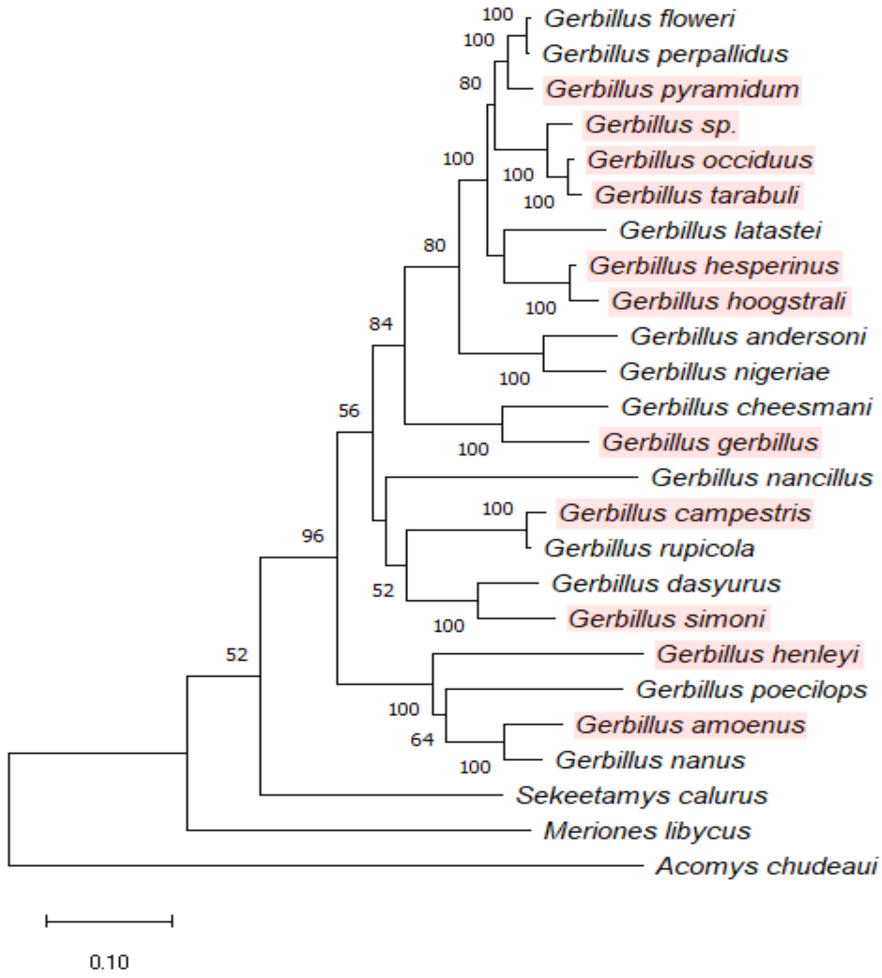


Figure 41: Phylogenetic tree of the genus *Gerbillus* for the gene Cytb (Cytochrome b) resulting from maximum likelihood analysis (GTR+I+G substitution model). The numbers at the nodes represent Bootstrap values (values below 50 are not shown). The scale bar represents branch length measured in a number of substitutions per site. Gerbillus species present in Morocco are highlighted in red. Two representatives of the subfamily Gerbillinae (Sekeetamys calurus, *Meriones libycus*) and one representative of the subfamily Deomyinae (*Acomys chudeaui*) are included as outgroups.

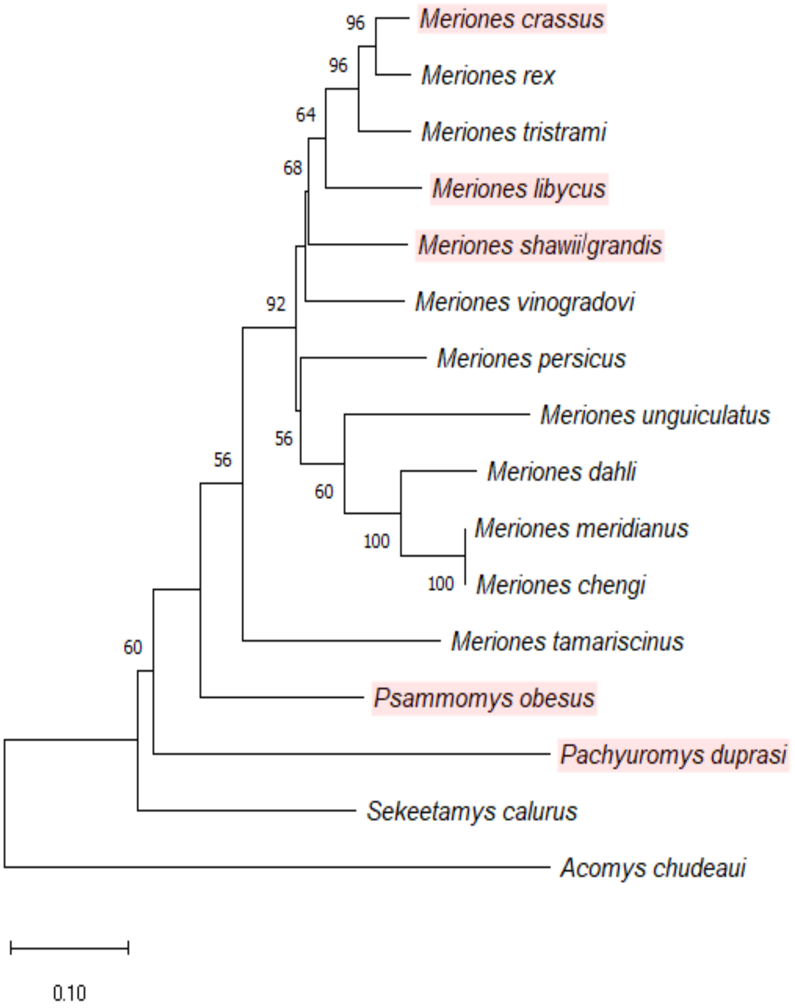


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Figure 42: Phylogenetic tree of the genus *Meriones*, *Psammomys*, and *Pachyuromys* for the gene Cytb (Cytochrome b) resulting from maximum likelihood analysis (GTR+I+G substitution model). The numbers at the nodes represent Bootstrap values (values below 50 are not shown). The scale bar represents branch length measured in number of substitutions per site. Species of *Meriones*, *Psammomys*, and *Pachyuromys* present in Morocco are highlighted in red. One representative of the subfamily Gerbillinae (*Sekeetamys calurus*) and one representative of the subfamily Deomyinae (*Acomys chudeaui*) are included as outgroups.

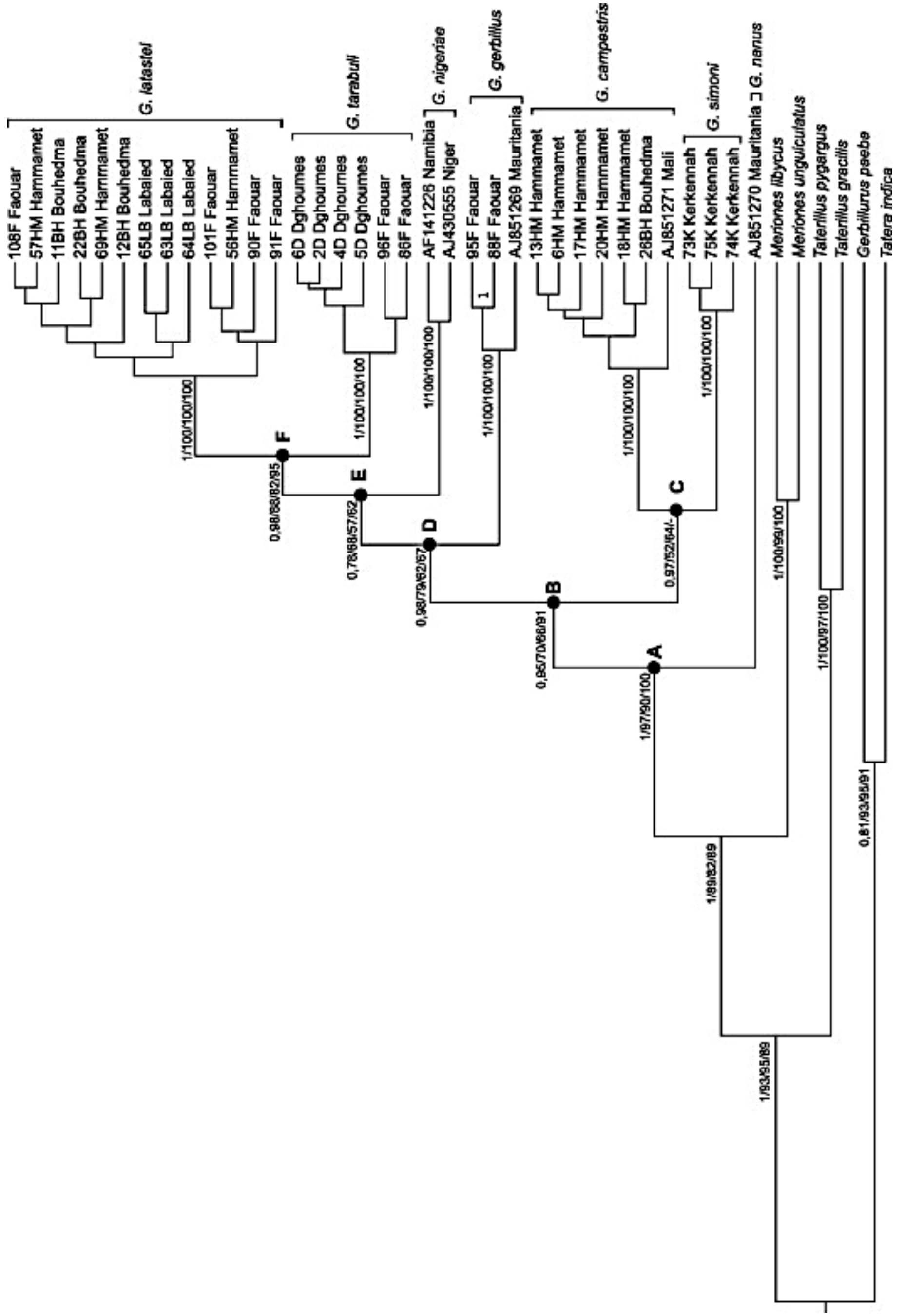

Figure 43: Phylogeny of gerbillus (Abidah et al., 2010)

The chromosomal phylogeny indicates that evolution within this family occurred at the population level, with certain chromosomal rearrangements distinguishing species from one another; for example, in the cases of *Meriones, Psammomys*, and *Pachyuromys*. Additionally, molecular phylogeny reveals that Meriones are closely related to *Psammomys* and *Pachyuromys*, as they share common DNA sequences.

Study of haplotypes

A haplotype is defined as a unique DNA sequence that differs from other haplotypes by at least one mutation. Unlike phylogenetic trees, a haplotype tree features multiple branching points (multifurcations).

A study of haplotypes was carried out on species from Morocco, namely *Gerbillus Campestris* (Nicolas et al., 2014; Bouarakia, 2020) and *Gerbillus henleyi* and *Meriones shawi/grandis* (O. Bouarakia, 2020), to understand their geographical structuring all those species have a geographical structuring whit several haplotypes.

We give here as an example the study of haplotypes conducted on Gerbillus campestris, a species with a wide distribution in Morocco and notable morphological variation across its different populations. The study aimed to determine whether it exhibits genetic structuring. The results of the phylogenetic tree and haplotype network reveal that individuals of G. campestris belong to seven identified phylogenetic lineages, which remain intercommunicating. (Fig. 44).

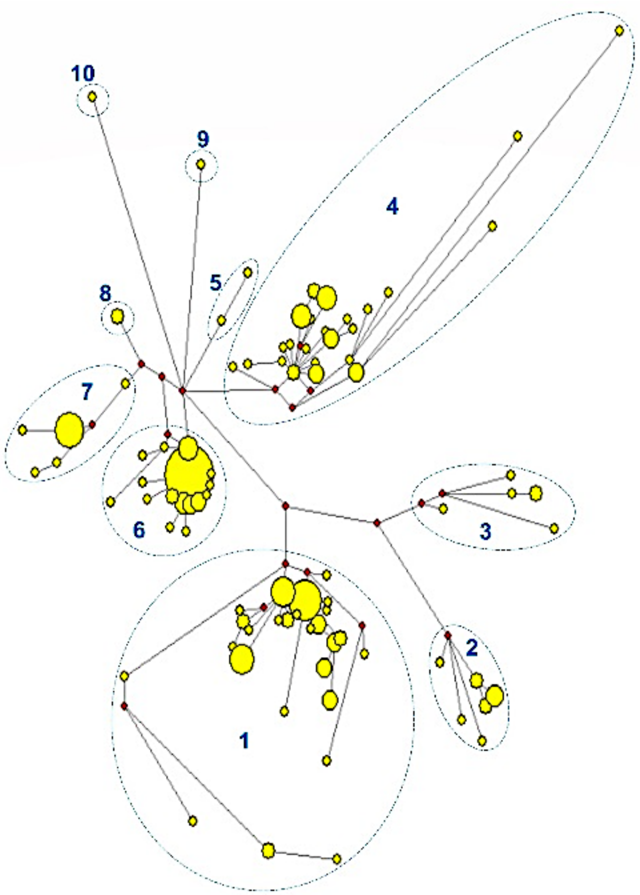

Figure 44. Minimal spanning network of *Gerbillus campestris* for cytb gene haplotypes. The size of the circles is proportional to the number of similar haplotypes observed in the dataset. The length of the branches is proportional to the number of mutations between haplotypes. Dashed ellipses (added for clarity) represent the ten mitochondrial lineages

Conclusion

This comprehensive synthesis of the work conducted on the various species in this group offers an overview of past research while tracing the evolution of study techniques from classical systematics to karyology and, more recently, molecular biology approaches. This analysis highlights the progress in understanding the classification of different species within the group and their phylogeny. These new studies also allow for a discussion of their origins.

Indeed, the distribution ranges of some species have been expanded to other areas experiencing increasingly arid conditions, possibly due to climate change or a lack of exploration in these regions. On the other hand, some species previously classified in one genus or subgenus are now assigned to another subgenus, such as *G. campestris*, which moves from the subgenus *Dipodillus* to the genus *Gerbillus* and back to *Dipodillus*.

Others have changed status: in Morocco, we now have *G. amoenus* from the subgenus *Hendecapleura* instead of *G. nanus*; the same applies to *M. shawii*, which is now *M. shawii/grandis*, occupying almost the entire distribution range of this species in Morocco.

The establishment of a hierarchy of some Gerbillinae species based on morphological and karyological criteria has recently been supplemented by molecular phylogeny, helping to better position the different species from Morocco within the *Gerbillinae* family specis.

However, only two species, *Dipodilus maghrebi* and *Gerbillus* sp., from the Guelmime region are described, but their karyotypes remain to be studied. Further works should refine the phylogeny of these taxa. Further paleontological works in Morocco should also provide new data about the diversification of this taxon during the Plio-Pleistocene times.

Finally, these taxonomic clarifications improve the conservation issues regarding some of Morocco's endemic rare species.

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An integrative taxonomy synthesis of the previous works on rodents of the *Gerbillinae* family in Morocco could serve as a reference for further research on this group whose systematics is not yet fully resolved. The systematic studies and distribution of certain species in this family started in the mid-sixties, and since then, they have conducted several studies on different species. Advanced techniques for studying them, such as systematics, karyology, morphometry, and molecular biology, have clarified their taxonomic status and precise phylogenetic relationships. Here, we review the relevant literature on this subject and highlight the remaining issues. Such a review has implications for the knowledge of biodiversity, biogeography, and the conservation of rodents in Morocco.