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Notes sur la distribution et la phylogéographie de deux rares petites gerbilles (Rongeurs, Muridae) au Maroc : Gerbillus simoni *et* Gerbillus henleyi

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ABSTRACT

Even though Gerbillinae rodents represent an important part of the mammalian fauna in North Africa, many gaps remain in our understanding of the distribution, ecology, evolution, and systematics of some lesser known species in this family. We present in this study the most recent findings on two of these species. The first species, *Gerbillus simoni* Lataste, 1881, is a short-tailed, small gerbil, endemic to North Africa. In Morocco, it is present only in a small area in the northeast, where it has not been caught since 1970. In 2014, we captured a small gerbil in this region that was identified as *G. simoni* based on morphology and molecular data (cytochrome *b* gene sequencing). This study represents the first genetic characterization of *G. simoni* in Morocco and the first one outside Tunisia. Populations from Morocco and Tunisia (mainland and Kerkennah Islands) show very little genetic differentiation. The second species, *Gerbillus henleyi* de Winton, 1903, is a long-tailed small gerbil that lives in the Sahel and North Africa with an extension to the Middle East. In Morocco, this species was only known in the southwest. Between 2014 and 2015, we have captured four gerbils in the northeast of the country, which were confirmed genetically and morphologically as belonging to this species. This represents an extension of its known distribution of about 370 km to the northeast of the country. These new Moroccan specimens form a distinct lineage. High genetic diversity is observed throughout the geographic range of *G. henleyi*, suggesting the existence of several cryptic species.

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RÉSUMÉ

Bien que les rongeurs Gerbillinae représentent une part importante de la faune mammalienne d'Afrique du Nord, il subsiste des lacunes dans notre connaissance de leur distribution, écologie, évolution et systématique, notamment en ce qui concerne les espèces les plus petites et les plus rares. Cette étude présente les dernières connaissances sur deux de ces espèces. Ainsi, *Gerbillus simoni* Lataste, 1881 est une petite gerbille à queue courte endémique d'Afrique du Nord. Au Maroc, elle est présente uniquement dans le Nord-Est du pays, où elle n'avait pas été capturée depuis 1970. Un nouveau spécimen collecté en 2014 a été attribué à *G. simoni* sur la base de sa morphologie et des données moléculaires (séquençage du cytochrome *b*). C'est la première caractérisation génétique de l'espèce au Maroc et la première à l'extérieur de la Tunisie. Les populations du Maroc et de la Tunisie (continent et îles de Kerkennah) montrent une différenciation génétique très faible. Une seconde espèce, *Gerbillus henleyi* de Winton, 1903, est une petite gerbille à longue queue qui vit au Sahel, en Afrique du Nord jusqu'au Moyen-Orient. Au Maroc, cette espèce était connue uniquement du Sud-Ouest. Entre 2014 et 2015, nous avons capturé quatre spécimens dans le Nord-Est du pays, et leur identification est confirmée morphologiquement et génétiquement dans ce travail. Cela représente une extension de l'aire de répartition de cette espèce d'environ 370 km vers le Nord-Est du pays. Ces nouveaux spécimens constituent une lignée distincte. Une forte diversité génétique est observée le long de la distribution géographique de *G. henleyi*, ce qui suggère l'existence de plusieurs espèces cryptiques.

1. Introduction

Situated at the western side of North Africa and receiving both Mediterranean and Atlantic influences, Morocco is today considered as a zone of high endemicity and biodiversity [1], and it represents one of the Global 200 priority ecoregions for global conservation [2]. For mammals, the last synthesis by Aulagnier et al. [4] confirmed this richness, and some recent molecular works have highlighted important intra- and interspecific rodent diversity in that region (Ndiaye et al. [5,6] for *Gerbillus*, Nicolas et al. [7] for *Gerbillus campestris*, Lalis et al. [8] for *Meriones shawii*).

The order Rodentia is the most diverse group of mammals, as it contains nearly half of the mammalian species. In this group, the Gerbillinae subfamily, among which the genus *Gerbillus*, represents an important component of the fauna of the arid and semi-arid regions in Africa and Asia [9]. However, the systematics of this subfamily and genus are still a subject of debate [6]. Some of the smallest species of the genus are considered rare or at least difficult to trap and their relationships are far from known. Furthermore, many gaps remain in our understanding of the distribution, ecology, evolution of some lesser known species in this subfamily, especially in Morocco. In this study, we present the most recent findings on two rare dwarf Gerbillinae species: *Gerbillus simoni* and *Gerbillus henleyi*.

The lesser short-tailed gerbil or Simon's gerbil (*Gerbillus simoni*) was first reported and described by Lataste [10], and its type locality is Oued Magra in Algeria. It was often placed into the genus *Dipodillus*, whom which it is the type species [11–14]. Recent molecular analyses have demonstrated that the genus is no longer valid and it is now included into *Gerbillus* [6,15–17]. *Gerbillus kaiseri*, described by Setzer [18] in Egypt and present in the East of Libya and in Egypt, is now considered as synonymous with *G. simoni* [14]. Another species, *Gerbillus zakariai*, was described by Cockrum et al. [19] as being endemic to the island of Kerkennah (Tunisia). It was later included within *G. simoni* by some authors [15,16,20,21], and considered as a separate insular species by others [14,19,22]. Ndiaye et al. [6] sequenced a specimen from mainland Tunisia (Kairouan) and showed that it clusters unambiguously with specimens from Kerkennah Islands. We follow Ndiaye et al. [6] and Happold [16], and consider *G. zakariai* as a synonym of *G. simoni*.

Simon's gerbil is endemic to North Africa and has a discontinuous range. The first part of its range goes from the Northeast of Morocco to the Northwest of Libya, through the North of Algeria and central Tunisia. In Algeria, it is found in the northern edge of the High Plateaus, but not in the coastal regions. The second part of the range goes from the northeastern coast of Libya to the west of the Nile Delta in Egypt [3,16]. In Morocco, this species was previously only captured by Schlitter & Setzer [23] in Oriental Morocco near Ain Beni Mathar, which represents the most western limit of this species. Simon's gerbil occurs in many habitats, especially with clay or loam soils. It is not found in sandy habitats, like many other gerbils. It inhabits lowlands and sporadically vegetated littoral desert, Chotts and salt marshes, steppe grassland vegetation (Alfa and Artemisia), steppes replaced by cropland and fallow fields, vegetated slopes and grassy valleys. It also inhabits relatively humid environments [3,4,16,24].

The Pigmy gerbil or Henley's gerbil was first reported and described by de Winton [25], and its type locality is

Wadi el Natroun in Egypt. Synonyms of *G. henleyi* include *G. mariae* Bonhote, 1909, *G. jordani* Thomas, 1918, *G. makrami* Setzer, 1958 and *G. syrticus* Misonne, 1974, described respectively from Egypt, Algeria, Egypt and Libya [3,16,20,22,26–30].

The Pigmy gerbil lives in the Sahel, from northern Senegal to northern Sudan, and in the southern and northern edges of the Sahara. It is widespread in desert to semi-desert regions in North Africa, from Morocco to Egypt, with an extension in the Middle East and Arabia, from the East of the Sinai desert to Jordan in the North, with dispersed records in western Saudi Arabia, north-eastern Qatar, northern Yemen, and Oman [3,4,21,31–33], and possibly Iran [34]. In Morocco, only few capture points have been reported until now: one in the South of Guelmim [35], several in the surroundings of Tantan and Foum el Hassan, in the Southwest [36], and one in the extreme South in Dakhla Peninsula [37]. Aulagnier et al. [4] mentioned its presence in pellets south of Tafilalt and Oued Ad Deheb close to Aousserd. The habitats of Henley's gerbil include coastal sand dunes covered with halophytes, salt marshes, gravel plains, crop fields, Wadi beds with Anabasis and Retama, stony plains and hamadas [3,33].

The most recent phylogenetic studies that were conducted on these two species are those of Abiadh et al. [15] and Ndiaye et al. [6,38]. These authors did not include Moroccan material in their study, and the overall number of specimens was low compared to the relatively large extension of their distributions.

Thanks to our new captures in Morocco, we improve the knowledge of the morphologic and genetic diversity of these poorly known dwarf gerbil species. Finally, we provide additional data on the distribution range of one of these species.

2. Material and methods

2.1. Sampling

Two field sessions in semi-arid and arid regions of the east of Morocco in October/November 2014 and May 2015 allowed us to catch five individuals of small gerbils.

In late October 2014, we have captured a small gerbil (BMT3) in the North of the Ain Beni Mathar village (North-East of Morocco: 34°07'N, 2°03'W), 23 km north of the capture site of Schlitter & Setzer [23] (33°55'N, 2°02'W), in a steppe with low vegetation in an arid region, replaced by irrigated wheat croplands, with a sandy-clay saline soil. This gerbil was initially identified as *Gerbillus simoni* using its external body features.

In late October and early November 2014, we also have captured three other small gerbils (BMT1, BMT2, BMT4) in the same locality. These gerbils were initially identified as *Gerbillus henleyi* using its body and skull features. During another field session in mid-May 2015, we have captured another small gerbil (BMT18) 29 km south of the first locality (33°52'N, 2°01'W), in a steppe environment of sandy-clay soil and with low vegetation, in an arid region. This gerbil was also initially identified as *G. henleyi* based upon its body and skull features. The animals were captured alive using Sherman traps with an effort of 173 trap-nights in 2014 and 266 trap-nights in 2015. The trapping success of *G. simoni* was 0.23% ($1/439 \times 100 = 0.23$) and for *G. henleyi* was 0.91% ($4/439 \times 100 = 0.91$). The animals were euthanized by cervical dislocation. This protocol was approved by the Cuvier ('Muséum national d'histoire naturelle', Paris) ethics committee. Standard external measurements like weight (WT in g), body length (HB in mm), tail length (T in mm), hind foot length (HF in mm) and ear length (E in mm) were taken. Autopsies allowed us to extract a piece of the liver for the genetic study, and the carcasses were preserved in formaldehyde. The skulls were extracted and prepared for morphometric analysis. Voucher specimens of *G. simoni* and *G. henleyi* have been deposited in the collections of the Laboratory 'Biodiversity, Ecology and Genome' of the Faculty of Sciences of Rabat. Voucher numbers for the individuals BMT3, BMT1, BMT2, BMT4 and BMT18 are respectively FSR-MAR14-BMT3, FSR-MAR14-BMT1, FSR-MAR14-BMT2, FSR-MAR14-BMT4, and FSR-MAR15-BMT18.

2.2. Morphometric study

For the morphometric identification of our specimens, we used the standard external measurements values, head-body length (HB), tail length (T), hind feet length (HF), ear length (E) and weight (WT), plus the ratio of the tail length to head-body length (%T). Skull measurements (mm) were taken with a Mitutoyo caliper on both dorsal and ventral view of the skull. Abbreviations of these values are as follows: greatest length of skull (GLS), breadth of braincase (BB), least interorbital constriction (IO), length of nasals (LN), length of anterior palatine foramina (LAF), length of upper molar series (M1M3), and diagonal length of tympanic bulla (LTB). Following different authors, we also calculated the proportions of the tympanic bulla length to skull length in form of a ratio (%TB).

2.3. Genetic study

The DNA of the five new specimens was extracted and purified using the QIAGEN Kit (DNeasy Blood & Tissue Kit) following the manufacturer's recommendations. Then the cytochrome *b* gene (1040 bp) was amplified via polymerase chain reaction (PCR) using the primers L7 (ACC AAT GAC ATG AAA AAT CAT CGT T) and H15915 (TCT CCA TTT CTG GTT TAC AAG AC) [39]. The PCR comprised an initial denaturation step of 3 min at 94 °C, followed by 38 cycles of 30 sec at 94 °C, 40 s at 52 °C, and 90 s at 72 °C, with a final extension step of 5 min at 72 °C. Double-stranded PCR products were purified and sequenced by Eurofins. Chromatograms were checked and sequences were corrected and aligned both manually and using BioEdit [40]. The sequences were then entered into the Basic Local Alignment Search Tool (BLAST, https://blast.ncbi.nlm.nih.gov/Blast.cgi) to obtain the genetic identification.

Evolutionary relationships among sequences were estimated by constructing a phylogenetic tree using the Maximum-Likelihood method (ML) in the software MEGA 7.0.26 [41]. The General time reversible (GTR) + I + G model

Table 1
Specimens of *Gerbillus simoni*, *Gerbillus henleyi* and other Gerbillinae used in our cyt *b* phylogenetic analyses.

Species	Field or collection number	Country (locality)	Geographical coordinates	GenBank number	Reference
Gerbillus simoni	BMT3	Morocco (Ain Beni Mathar)	34°07'N, 2°03'W	MH660910	This work
Gerbillus simoni	1989024	Tunisia (Kairouan)	ca. 35°40'N, 10°05'E	LN606694	[6]
Gerbillus simoni	1987003	Tunisia (mainland)	–	LN606695	[6]
Gerbillus simoni	73 K	Tunisia (Kerkennah Islands)	34°42'N, 11°11'E	GU356577	[15]
Gerbillus simoni	74 K	Tunisia (Kerkennah Islands)	34°42'N, 11°11'E	GU356578	[15]
Gerbillus simoni	75 K	Tunisia (Kerkennah Islands)	34°42'N, 11°11'E	GU356579	[15]
Gerbillus henleyi	BMT1	Morocco (Ain Beni Mathar)	34°07'N, 2°03'W	MH660911	This work
Gerbillus henleyi	BMT2	Morocco (Ain Beni Mathar)	34°07'N, 2°03'W	MH660912	This work
Gerbillus henleyi	BMT4	Morocco (Ain Beni Mathar)	34°07'N, 2°03'W	MH660913	This work
Gerbillus henleyi	BMT18	Morocco (Ain Beni Mathar)	33°52'N, 2°01'W	MH660914	This work
Gerbillus henleyi	AD355H	Mali	–	JF704121	[46]
Gerbillus henleyi	N4292 (2)	Niger (Gangara)	ca. 14°37'N, 8°30'E	JQ753050	[47]
Gerbillus henleyi	M5597	Burkina Faso (Markoye)	14°37'N, 0°02'E	KF496220	[38]
Gerbillus henleyi	M4058	Mali (Makana)	15°09'N, 9°29'W	KF496221	[38]
Gerbillus henleyi	MAD355	Mali (Dianbé)	14°36'N, 5°55'W	KF496222	[38]
Gerbillus henleyi	M4947	Mali (Tedouft)	15°55'N, 2°27'E	KF496223	[38]
Gerbillus henleyi	N4291	Niger (Gangara)	14°37'N, 8°31'E	KF496224	[38]
Gerbillus henleyi	N4292	Niger (Gangara)	14°37'N, 8°31'E	KF496225	[38]
Gerbillus henleyi	N4293	Niger (Gangara)	14°37'N, 8°30'E	KF496226	[38]
Gerbillus henleyi	KOR8	Niger (Gangara)	14°22'N, 8°18'E	KF496227	[38]
Gerbillus henleyi	KOR10	Niger (Gangara)	14°22'N, 8°18'E	KF496228	[38]
Gerbillus henleyi	N3272	Niger (Tanout)	14°57'N, 8°53'E	KF496229	[38]
Gerbillus henleyi	AD1066	Senegal (Dodel)	16°28'N, 14°27'W	KF496230	[38]
Gerbillus henleyi	AD2030	Senegal (Dodel)	16°30'N, 14°27'W	KF496231	[38]
Gerbillus henleyi	KB8153	Senegal (Dodel)	16°30'N, 14°26'W	KF496232	[38]
Gerbillus henleyi	AD1054	Senegal (Dodel)	16°28'N, 14°27'W	KF496233	[38]
Gerbillus henleyi	AD1064	Senegal (Dodel)	16°28'N, 14°27'W	KF496234	[38]
Gerbillus henleyi	AD1078	Senegal (Dodel)	16°30'N, 14°27'W	KF496235	[38]
Gerbillus henleyi	AD1079	Senegal (Dodel)	16°30'N, 14°27'W	KF496236	[38]
Gerbillus henleyi	H1	Israel (Makhtesh Ramon)	30°36'N, 34°50'E	KM236126	[6]
Gerbillus henleyi	H2	Israel (Makhtesh Ramon)	30°36'N, 34°50'E	KM236127	[6]
Gerbillus henleyi	H3	Israel (Makhtesh Ramon)	30°36'N, 34°50'E	KM236128	[6]
Gerbillus henleyi	H4	Israel (Makhtesh Ramon)	30°36'N, 34°50'E	KM236129	[6]
Gerbillus henleyi	2002487	Niger (Tanout)	14°57'N, 8°53'E	LN606682	[6]
Other Gerbillinae					
Gerbillus amoenus				KM236112	
Gerbillus andersoni				LN606673	
Gerbillus campestris				LN606674	
Gerbillus cheesmani				KM236117	
Gerbillus dasyurus				LN606677	
Gerbillus floweri				KM236119	
Gerbillus gerbillus				AJ851269	
Gerbillus hesperinus				JN652803	
Gerbillus hoogstrali				JN021414	
Gerbillus latastei				GU356550	
Gerbillus nancillus				LN606684	
Gerbillus nanus				AJ851270	
Gerbillus ni Geriae				AJ430555	
Gerbillus occiduus				JN652805	
Gerbillus perpallidus				JN652806	
Gerbillus poecilops				JQ753064	
Gerbillus pyramidum				JN652812	
Gerbillus rupicola				LN606693	
Gerbillus tarabuli				JN652825	
Taterillus gracilis				AM409394	

[42] was determined by the software jModeltest 2.1.10 [43], as the best-fit model of nucleotide substitution, according to the Akaike information criterion [44]. The robustness of the obtained topologies was tested in all the treatments using 1000 bootstrap replicates. All the sequenced specimens of *G. simoni* and *G. henleyi* present in the GenBank database were included in the molecular analyses (5 *G. simoni* and 24 *G. henleyi*). Representatives of the other species of the genus *Gerbillus* genus were also included in the phylogenetic tree, as well as the outgroup *Taterillus gracilis* (Table 1).

Pairwise Kimura two-parameter (K2P) genetic distances [45] were computed using MEGA 7.0.26 [41]. The K2P model was chosen for sake of comparison with other studies made on this group. The closest species to *G. simoni* and *G. henleyi* in the known phylogeny were used for

Table 2
Body measurements of the newly collected specimen and comparison with measurements of *Gerbillus simoni* according to literature data.

Reference	Country	Specimen	HB	T	% T	HF	E	WT
This work	**Morocco**	**BMT3**	83	73	88	21	13	19
[10]	**Algeria (specimens of the type locality)**	**A1**	78	70	90	–	–	–
		A2	75	73	97	–	–	–
[48]	**Egypt**	**E1**	76	64	84	–	–	–
		E2	86	81	94	–	–	–
		E3	86	83	97	–	–	–
		E4	79	82	104	–	–	–
		E5	87	85	98	–	–	–
		E6	89	91	102	–	–	–
		E7	82	85	104	–	–	–
		E8	93	76	82	–	–	–
[49]	**Algeria**	***Min***	70	57	81	20	11	–
		Max	95	84	88	22	14	–
[50]	**Tunisia (mainland)**	**T1**	75.3	71	94	–	–	–
		T2	69	71	103	–	–	–
		T3	71	69	97	–	–	–
		T4	85.8	73.8	86	–	–	–
[29]	**Libya**	**L1**	81	83	102	21	12	–
		L2	88	81	92	21	12	–
		L3	81	77	94	20	12	–
[23]	**Morocco**	**M1**	81	71	88	19	13	18
		M2	83	71	86	20	13	16
	Egypt	**E9**	85	92	108	22	13	–
		E10	85	87	102	22	12.5	–
	Libya	***Min***	81	71	88	21	12	–
		Max	85	84	99	21	13	–
[19]	**Tunisia (Kerkennah Islands)**	**K1**	97	78	80	21	13	26
		K2	89	83	93	21	14	20
		K3	85.5	85.5	100	–	–	–
		K4	97	78	80	–	–	–
		K5	86	79	92	–	–	–
	Tunisia (mainland)	**T5**	84	72	86	–	–	–
		T6	77.5	73	94	–	–	–
		T7	78	73	94	–	–	–
		T8	81.8	72.8	89	–	–	–
		T9	87.3	73	84	–	–	–
		T10	82	72	88	–	–	–
		T11	83	70.6	85	–	–	–
[13]	**Egypt**	***Min***	72	72	100	19	12	12
		Max	89	96	108	22	14	22
[51]	**Algeria**	**A3**	73.7	74	100	22	12.9	16.81

Abbreviations: head-body length (HB); tail length (T); ratio of tail length to head-body length (%T); hind feet length (HF); ear length (E); weight (WT); Minimum (*Min*); Maximum (*Max*). Measurements in mm.

comparison of the genetic distances. For *G. simoni*, the species *G. dasyurus*, *G. rupicola* and *G. campestris* of the subgenus *Dipodillus* were used. For *G. henleyi*, the species *G. amoenus*, *G. nanus* and *G. poecilops* of the subgenus *Hendecapleura* were used.

3. Results

3.1. Morphological identification

The specimen BMT3 (an adult male) was initially identified as *Gerbillus simoni* using the external body features. *G. simoni* is different from all the other gerbils due to a combination of distinctive characters – the hind feet are naked, the length of the tail is similar to the length of the head and body and the tail does not have a pencil [11,20,23].

The body and cranial measurements of this single specimen, along with the measurements found in literature, are presented in Tables 2 and 3. We can observe that the body measurements of our newly collected specimen fit within the variability of other specimens of *G. simoni*. Our specimen has a short tail (73 cm with a ratio of tail length to head-body length of 88%), which is a characteristic of the species *G. simoni*. According to literature data (Table 2), the ratio of tail length to head-body length in *G. simoni* is between 80 and 108% (and generally below 100%, with an average of 94%). The tail length seems to be higher towards the east (in Kerkennah Islands, Libya, and Egypt), compared to the west (Morocco, Algeria, and mainland Tunisia).

In a similar way to external body variation, we show an important variability in cranial measurements in *G. simoni* across its distribution in North Africa (Table 3). We can observe that the cranial measurements of our specimen fit within the variability of the other specimens of *G. simoni*.

The four specimens BMT1 (adult male), BMT2 (adult female), BMT4 (adult male), and BMT18 (adult female) were initially identified as *Gerbillus henleyi* using the body and skull features. *G. henleyi* is a very small gerbil

Table 3
Cranial measurements of the newly collected specimen and comparison with measurements of *Gerbillus simoni* according to literature data.

Reference	Country	Specimen	GLS	BB	IO	LN	LAF	M1M3	LTB	%TB
This work	**Morocco**	**BMT3**	25.49	12.84	4.55	9.94	4.91	3.7	7.48	29.3
[49]	**Algeria**	***Min***	23.5	–	–	–	–	3.5	–	–
		Max	26	–	–	–	–	4	–	–
[50]	**Tunisia**	***Min***	–	11.5	–	–	–	–	7.3	–
		Max	–	11.7	–	–	–	–	8.1	–
[29]	**Libya**	**L1**	25.8	–	5.1	9.6	–	3.5	8.4	32.6
		L2	26.3	–	4.7	9.7	–	3.8	8.6	32.7
		L3	24.4	–	4.6	9.4	–	3.5	8.1	33.2
[23]	**Morocco**	**M1**	24.4	–	–	9.6	4.8	3.4	6.6	27
		M2	24.4	–	–	9.4	4.7	3.4	6.5	26.6
	Egypt	**E1**	25.8	–	–	9.5	4.8	3.5	7.2	27.9
		E2	26	–	–	9.6	4.9	3.4	7.1	27.3
	Libya	***Min***	24.6	–	–	9.1	4.5	3.2	6.9	28
		Max	26.5	–	–	10.3	5.2	3.4	7.5	28.3
[19]	**Tunisia (Kerkennah Islands)**	**K1**	27.2	13.4	4.7	10.5	4.9	4	8.2	30.1
		K2	25.8	13	4.5	9.8	4.8	4	7.6	29.5
	Tunisia (Kerkennah Islands)	***Min***	25.3	12.7	4.5	9.6	4.7	4	7.6	30
		Max	26.7	13	4.8	10.3	4.9	4	8.3	31.1
	Tunisia	***Min***	24.5	12.7	4.4	8.9	4.6	3.3	7.5	30.6
		Max	24.7	12.9	4.6	9.7	5.3	3.6	8	32.4
[13]	**Egypt**	***Min***	23.2	11.5	–	8.4	4.4	3.2	6.7	28.9
		Max	26.7	12.6	–	10	5.6	4	7.4	27.7

Abbreviations: greatest length of skull (GLS); breadth of braincase (BB); least interorbital constriction (IO); length of nasals (LN); length of anterior palatine foramina (LAF); length of upper molar series (M1M3); diagonal length of tympanic bulla (LTB); proportions of the tympanic bulla length to skull length in form of a ratio (%TB); Minimum (*Min*); Maximum (*Max*). Measurements in mm.

with naked and unpigmented plantar soles. The tail is long, thin, and has a thin, dark and inconspicuous, about one-fourth or less of the length, terminal brush. The back coat is dark grey-brown with more or less distinct white areas behind the ear and on the rump. The ventral pelage is white and the ears are unpigmented. The skull has large tympanic bullae, compared to the size of the skull, that slightly exceed the occipital condyle [13,27]. The molars are particularly small (upper molar row ≤ 3 mm) [3,4].

The body and cranial measurements of these four specimens, along with the measurements found in the literature, are presented in Tables 4 and 5. We can observe that the body measurements of our four specimens fit within the variability of the other specimens of *Gerbillus henleyi*, from North Africa, the Sahel, and the Middle East, even if the %T values tend to be small in our specimens.

Similarly, the skull measurements of the four newly collected specimens correspond well with the other published values for *Gerbillus henleyi*, except for the breadth of the braincase (BB), which appears to be larger in our specimens. This difference may be due to the different way of measuring this part of the skull by each author. Individuals from Algeria have the longest skulls and those from the Middle East (Jordan) and the Sahel (Senegal and Niger) have the longest tympanic bullas and especially the biggest ratio of tympanic bulla length to skull length.

3.2. Genetic analysis

According to the phylogenetic tree (Fig. 1), our specimen BMT3 clusters unambiguously (bootstrap value of 100%) with Tunisian specimens of *Gerbillus simoni* (mainland Tunisia and Kerkennah Islands). The K2P genetic distance between all the *G. simoni* specimens varies from 0.4 to 2.2%. The genetic distance between *G. simoni* and the three closest relative species (*G. dasyurus*, *G. campestris* and *G. rupicola*) varies from 7.7 to 14.2%.

According to the phylogenetic tree (Fig. 2), our four specimens (BMT1, BMT2, BMT4, BMT18) cluster with *Gerbillus henleyi*. Our analysis allowed us to identify three lineages within this species:

- lineage 1 groups specimens from Mali, Niger, Burkina Faso, Senegal, and Israel;
- lineage 2 groups specimens from Mali and Niger;
- lineage 3 contains all our specimens from Morocco.

Lineages 2 and 3 form a strongly-supported monophyletic group (Group 2).

The K2P genetic distance between these three lineages varies from 3.8% (between lineages 2 and 3) to 10.7% (between lineages 1 and 3). The genetic distance between *G. henleyi* and the three closest relative species (*G. amoenus*, *G. nanus* and *G. poecilops*) varies from 12.5 to 15.8%.

4. Discussion

Gerbillus simoni

Our specimen has a short tail with no pencil, which is a characteristic of the species *Gerbillus simoni*. Other species of gerbils from Morocco generally have a longer tail and the ratio of tail length to head-body length is generally comprised between 115% and 145%, in *G. amoenus*,

Table 4
Body measurements of the four new specimens and comparison with measurements of *Gerbillus henleyi* according to literature data.

Reference	Country	Specimen	HB	T	% T	HF	E	WT
This work	**Morocco**	**BMT1**	60	73	122	20	9	8
		BMT2	70	83	119	19	11	12.5
		BMT4	62	73	118	20	10	8.7
		BMT18	71	85	120	18	9	14
[27]	**Egypt**	**E1**	74	98	132	21	9	10
[49]	**Algeria**	***Min***	60	70	117	18	8	–
		Max	70	90	129	19	10	–
[20]	**Egypt (western desert)**	***Min***	–	–	102	–	–	–
		Max	–	–	148	–	–	–
		***Mean* (*N* = 15)**	–	–	129	–	–	–
	Egypt (eastern desert)	***Min***	–	–	129	–	–	–
		Max	–	–	159	–	–	–
		***Mean* (*N* = 8)**	–	–	140	–	–	–
	Saudi Arabia	***Min***	–	–	113	–	–	–
		Max	–	–	170	–	–	–
		***Mean* (*N* = 12)**	–	–	148	–	–	–
Duplantier 1989 (unpublished)	**Senegal**	**S1**	64	76	119	17	8.5	9
		S2	67	103	154	17	9	10
[28]	**Arabia, Jordan, Israel**	***Min***	52	73	140	15.8	7.8	–
		Max	75	107	143	20	10	–
		***Mean* (*N* = 11)**	65.8	85.6	–	19	9	–
[31]	**Israel**	***Min***	60	93.1	155	18.2	8.4	8.01
		Max	65.6	103.5	158	19.4	9.6	10.99
		***Mean* (*N* = 24)**	62.8	98.3	–	18.8	9	9.5
Garba 2000 (unpublished)	**Niger**	**N1**	68	92	135	18	10	13.99
[52]	**Niger**	***Min***	64	85	133	18	9.5	–
		Max	69	100	145	20	10	–
		***Mean* (*N* = 4)**	66.3	91.3	–	19.3	9.9	–
[32]	**Jordan**	***Min***	60	74	123	19	7	6
		Max	68	96	141	20	9	11
Papillon 2003 (unpublished)	**Mali**	**M1**	68	83	122	18	9	11
[34]	**Iran**	**I1**	62	78	126	20	10	10
[53]	**Algeria**	**A1**	71	101	142	20.48	10.87	10.41
		A2	69	105	152	20.44	10.25	11.67
		A3	78	104	133	19.27	–	10.2
		A4	68	115	169	21.15	9.7	16.66
		A5	79	108	137	20.3	10.98	22
[54]	**Israel (Agur south)**	***Min***	–	85	–	16.8	–	7.5
		Max	–	94.5	–	19	–	9
	Israel (Agur north)	***Min***	–	75	–	17	–	6.5
		Max	–	102	–	20	–	12.5
	Israel (Mifrasit)	***Min***	–	83	–	16.1	–	7.6
		Max	–	99	–	19	–	14
	Israel (Mashabim)	***Min***	–	82	–	17	–	7
		Max	–	97	–	19	–	10
	Israel (Mamshit)	***Min***	–	84	–	17	–	7.2
		Max	–	94.5	–	19.5	–	8.7
[55]	**Algeria**	**A6**	75	67	89	17.6	10	11.7
		A7	88	103	117	21.13	10	14.6
		A8	81	71	88	14.1	11	17.2
		A9	71	98	138	17.26	10	11.6
		A10	75	67	89	17.6	10	11.7
[33]	**Algeria, Tunisia, Senegal, Mali, Burkina Faso, Niger, Chad**	***Min***	55	75	136	17	8	8
		Max	73	103	141	20	11	13.9
		***Mean* (*N* = 16)**	64.9	86.7	–	17.8	9.3	10.6
[38]	**Burkina Faso, Mali, Mauritania, Niger, Senegal**	***Min***	51	64	125	16	7.5	6.5
		Max	72	95	132	19	10	13.9
		***Mean* (*N* = 15)**	65.47	84.67	–	17.87	9.21	10.16

Abbreviations: head-body length (HB); tail length (T); ratio of tail length to head-body length (%T); hind feet length (HF); ear length (E); weight (WT); Minimum (*Min*); Maximum (*Max*). Measurements in mm.

G. henleyi, *G. hoogstrali*, *G. occiduus*, *G. hesperinus*, and *G. campestris* [16]. Only *G. maghrebi* has a relatively short tail (ratio of 95%), but it is a larger species and it displays a pencil at the tip of its tail [23]. The sequencing of the cytochrome *b* gene allowed us to confirm this species identification. This represents the first genetic characterization of this species in Morocco and the only one outside Tunisia [6,15].

In agreement with Cockrum et al. [19] and Osborn & Helmy [13], we observed an increase in tail length throughout North Africa from west to east. We also show an important variability in cranial measurements in

Table 5
Cranial measurements of the four new specimens and comparison with measurements of *Gerbillus henleyi* according to literature data.

Reference	Country	Specimen	GLS	BB	IO	LN	LAF	M1M3	LTB	%TB
This work	**Morocco**	**BMT1**	21.52	11.98	3.93	8.83	3.55	2.8	6.74	31.3
		BMT2	22.38	12.45	4.02	9.1	3.82	3.03	7.22	32.3
		BMT4	22.35	12.5	4.15	8.81	3.78	3.02	7.14	31.9
		BMT18	22.49	12.39	4.07	8.84	3.55	3.09	6.9	30.7
Alluaud 1906 (unpublished)	**Sudan**	**S1**	22.4	–	–	–	–	2.9	–	–
[27]	**Egypt**	**E1**	21.3	–	3.8	–	3.8	2.7	7.5	35.2
[49]	**Algeria**	***Min***	21.3	–	–	–	–	3	6.18	29
		Max	22.2	–	–	–	–	3	7.1	32
[28]	**Arabia**	***Min***	–	10.5	–	–	–	2.2	–	–
		Max	–	11.6	–	–	–	2.7	–	–
[32]	**Jordan**	***Min***	20.5	10.4	3.7	–	2.8	2.4	8.1	39.5
		Max	22.2	11	4.2	–	3.7	2.7	9.2	41.4
[34]	**Iran**	**I1**	–	11.6	–	–	–	3.3	–	–
[53]	**Algeria (Lagraff)**	**A1**	23.28	10.76	4.39	–	3.74	3.55	7.61	32.7
		A2	24.72	11.71	4.66	–	3.8	3.71	8.64	35
	Algeria (Nacer)	***Min***	24.82	10.09	4.34	–	3.72	3.6	7.85	31.6
		Max	25.59	11	5.74	–	4.05	3.68	8.29	32.4
		***Mean* (*N* = 3)**	25.18	10.61	4.97	–	3.87	3.64	8.14	–
[55]	**Algeria (Ghamra)**	***Min***	22.1	9.5	3.7	6.6	2.5	2.8	6.3	28.5
		Max	24.2	11.2	5.1	9.1	3.9	3.8	8.3	34.3
	Algeria (Hassi Khalifa)	***Min***	23	10.3	4.5	8.3	2.5	2.6	6.9	30
		Max	24.4	11.2	5.4	9.1	3.3	3	7.5	30.7
[33]	**Algeria, Tunisia, Senegal, Mali, Burkina Faso, Niger, Chad**	***Min***	20.5	10.6	–	–	–	2.7	–	–
		Max	22.3	11.6	–	–	–	2.9	–	–
[38]	**Senegal and Niger**	***Min***	18.57	10.82	3.57	–	–	3.07	6.99	37.6
		Max	22.78	11.78	4.58	–	–	3.41	8.98	39.4
		***Mean* (*N* = 11)**	21.35	11.53	4.12	–	–	3.26	8.31	–

Abbreviations: greatest length of skull (GLS); breadth of braincase (BB); least interorbital constriction (IO); length of nasals (LN); length of anterior palatine foramina (LAF); length of upper molar series (M1M3); diagonal length of tympanic bulla (LTB); proportions of the tympanic bulla length to skull length in form of a ratio (%TB); Minimum (*Min*); Maximum (*Max*). Measurements in mm.

G. simoni throughout North Africa. Osborn & Helmy [13] observed, in data from Algeria to Egypt, a geographic variation from west to east: decrease in the greatest width of the skull, reduced inflation of the auditory bullae, and considerable variation in colour. In our study, we could not clearly confirm this west–east variation due to the lack of sufficient data from the different countries.

Contrary to morphometric data, genetic data show little genetic variability in North Africa (less than 2.2% of sequence divergence between specimens from Morocco, mainland Tunisia, and Kerkennah Islands). Low genetic divergence between populations from north-eastern Morocco and Tunisia was also observed in other Gerbillinae rodents. For example, Lalis et al. [8] and Nicolas et al. [7], showed that *Meriones shawii* and *Gerbillus campestris* individuals from eastern Morocco belong to the same genetic clade than those present in Algeria and Tunisia.

According to Cockrum et al. [19], the population discovered on Kerkennah Islands was completely unexpected and those individuals were so morphologically distinct from the mainland samples that their relations appear best expressed by describing them as a distinct species (*Gerbillus zakariai*). Our genetic data show an average K2P distance of 1.0% between the specimens from Kerkennah Islands and those of mainland Tunisia. This genetic distance is much lower than the one recorded between *G. simoni* and its closest related species *G. dasyurus* (8.4%) or between clearly characterized but closely related species of the genus *Gerbillus*, like *G. occiduus* and *G. tarabuli* (1.8%) [5].

This low genetic divergence is another proof that these two geographically distant and isolated populations are indeed part of the same species *Gerbillus simoni*. The limited data concerning the karyotypes of this species reinforce this hypothesis, as they show an identical diploid number of $2n = 60$. Wassif et al. [56] reported the karyotype in Egypt as $2n = 60$, 8 to 10 biarms, FN = 68, 69. Karyotypes of individuals from mainland Tunisia obtained by Cockrum et al. [19] are the same ($2n = 60$ with 8 to 10 biarms). The first karyotype described for specimens of *G. simoni* from Kerkennah Islands was $2n = 60$, aFN = 72 [57]. The karyotype ($2n = 60$, aFN = 72) was later described by Abiadh et al. [15] for the three individuals of Kerkennah Islands used in our genetic study.

Even though this species has a discontinuous distribution in North Africa, and despite the fact that it is rarely trapped, it is not considered as endangered by the IUCN. Its conservation status in Morocco should be "Not Applicable", because it is present exclusively in a small area of the Oriental region.

Gerbillus henleyi

Our morphometric study has allowed us to identify our four specimens as *Gerbillus henleyi*, but a genetic confirmation was needed because the measurements of *G. henleyi* can be similar to those of other long-tailed small gerbils with naked hind feet, for example *Gerbillus amoenus*. According to Granjon [33], the latter species is slightly larger (HB = 73–96 mm, T = 99–116 mm, GLS = 24.4–26.3 mm) compared to *G. henleyi* (HB = 55–73 mm, T = 75–103 mm, GLS = 20.5–22.3 mm), but all samples are very small and juveniles may be confusing for identifications.

Fig. 1. Phylogenetic tree of *Gerbillus simoni* based on mitochondrial DNA resulting from the Maximum-Likelihood analysis (GTR + I + G substitution model). Numbers at nodes represent ML bootstrap support. The scale bar represents the branch length measured in the number of substitutions per site. The origin of the specimens of *G. simoni* is written on the right-hand side of the figure.

In this study, we present the first genetic characterization of this species in Morocco and North Africa, a species considered difficult to catch using classical live traps [58]. Furthermore, our study allows the extension of the known distribution of *G. henleyi* in Morocco 370 km to the northeast of the country, compared to the previous northernmost record that was in the south of Tafilalt from pellet remains [4].

This result could be interpreted as a possible northward extension of the geographic range of the species following desertification, as opposed to the possible southward extension of the range, in north Burkina Faso and north Senegal [33,59,60]. This species, along with desert and pre-desert Palaearctic fauna, are advancing northward due to the climatic change that touches North Africa, namely the aridification tendency. This helps in documenting the modifications in plant and animal composition of this region. Consequently, the occurrence of *G. henleyi*, previously unknown at this latitude in Morocco, seems to reflect a wider and perhaps continuous distribution along the northwestern border of the Sahara. It is also possible that this species was already present since a long time in this region of Morocco, characterized by an arid bioclimate, where several "southern" species extend north of the High Atlas Mountains (e.g., *Paraechinus aethiopicus*, *Pipistrellus rueppellii*, *Poecilictis libyca*, *Jaculus*, *Pachyuromys duprasi*, *Meriones libycus*, *Psammomys obesus*, *Ctenodactylus gundi*) and where "Mediterranean" species are absent (e.g., *Crocidura russula*, *Crocidura whitakeri*, *Oryctolagus cuniculus*, *Apodemus sylvaticus*, *Lemniscomys barbarus*). And its presence may have been unnoticed because it is a rare small gerbil, difficult to catch [54], and due to the lack of trapping campaigns and owl pellet identification. More detailed investigations in neighbouring areas can confirm whether the presence of *G. henleyi* in the Northeast of Morocco is exceptional or whether the recent climatic changes in North Africa favour the expansion of this species.

Our phylogeographic analyses highlighted the existence of three cyt *b* lineages within *G. henleyi*. The first is represented by individuals from Mali, Niger, Burkina Faso, Senegal, and Israel. The second contains individuals from

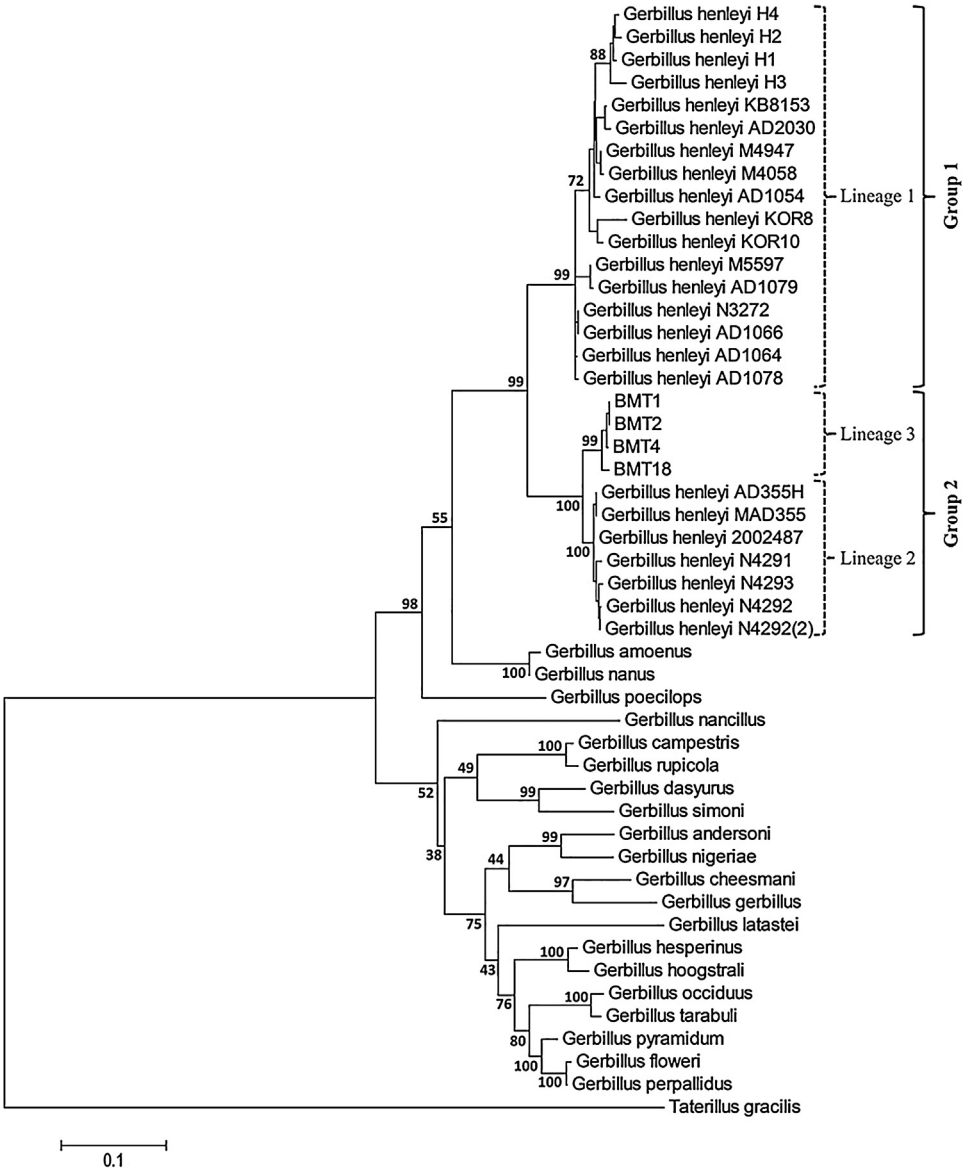

Fig. 2. Phylogenetic tree of *Gerbillus henleyi* based on mitochondrial DNA resulting from the Maximum-Likelihood analysis (GTR + I + G substitution model). Numbers at nodes represent ML bootstrap support. To improve clarity, values of the most apical nodes are not included. The scale bar represents the branch length measured in the number of substitutions per site. The identified lineages of *G. henleyi* are on the right border.

Mali and Niger. Ndiaye et al. [6], showed a divergence as early as 1.5 Mya between these two lineages. The third lineage contains the Moroccan individuals and appears to be closer to the 'Sahelian' lineage 2 (3.8%) than to the 'Sahelian–Middle Eastern' lineage 1 (10.7%). The small genetic distance between lineages 2 and 3 may be due to a relatively recent differentiation, resulting from the last episodes of drying of the Sahara that further separated the Sahelian population from the North African population of this species. Unexpectedly, we found that the genetic distance between some geographically distant populations was low, and that the genetic distance between some neighbouring populations was high. Notably, individuals from the same locality (Gangara and Tanout in the south of Niger) can be found both in lineages 1 and 2.

More importantly, we can observe that the genetic distance between lineage 1 and lineages 2 + 3 is 10.4%. This value is far greater than the one documented between distinct species of the genus *Gerbillus*, like between *G. occiduus* and *G. tarabuli* (1.8%) or between *G. pyramidum* and *G. perpallidus* (3.1%) [5]. This value is also higher to what is commonly observed between sister species of rodents [61], and specifically between the two twin species *G. amoenus* and *G. nanus* (6.5%) of the subgenus *Hendecapleura*, that *G. henleyi* belongs to [47]. These preliminary genetic data (high genetic diver-

gence in parapatric lineages) suggest the existence of two cryptic species within *G. henleyi*.

Cytogenetic data show that *G. henleyi* shares a common diploid number of chromosomes ($2n = 52$) with several other species of the subgenus *Hendecapleura* (*G. poecilops*, *G. amoenus*, and *G. nanus*) [62,63]. Only banding analysis can unambiguously distinguish *G. henleyi* ($2n = 52$; aFN = 58 to 62) from its sister species *G. amoenus* ($2n = 52$; aFN = 58 to 60) [52,62]. Within *G. henleyi*, the chromosome formula varies little despite the wide distribution of the species: aFN = 59 to 61 in Egypt [56], aFN = 58 in Morocco [35], NF = 66 and aFN = 62 in Burkina Faso [59,62], NF = 64 in Senegal [60], aFN = 62 in Tunisia [62], aFN = 59 to 62 in Niger [52,63]. The only apparent changes concern a variation of the acrocentric/metacentric proportion [59], e.g., eight bi-armed autosomes in Morocco [35], 11 to 13 in Egypt [56], 12 in Burkina Faso [59]. Similarly, in the subgenus *Hendecapleura*, the *cytb* divergence that differentiated the twin species *G. amoenus* and *G. nanus* (6.5%) was not complemented by substantial chromosomal modification, as individuals from both species had very similar karyotypes ($2n = 52$, aFN = 58) [47]. This weak chromosomal differentiation between the populations of *G. henleyi* needs to be further investigated with more specimens from the species range. Moreover, it brings us to the necessity of using nuclear DNA for a deeper understanding of the divergence between the two suggested cryptic species of *G. henleyi*.

Finally, the two species presented in this study were caught in the same locality and habitat along with a species of jirds and a species of jerboas. A similar situation was found in Egypt [13], where *Gerbillus simoni* was parapatric in salt marshes with *Gerbillus henleyi*, *G. amoenus*, *G. campestris* and two species of jerboas. Hence, more research must be conducted on the spatial, temporal, and trophic partitioning in these rodent communities.

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