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Biogeographic history of *Gerbillus campestris* (Rodentia, Muridae) in Morocco as revealed by morphometric and genetic data

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Abstract. *Gerbillus campestris* is a widely distributed small rodent that lives in various habitats in North Africa and can be a potential agricultural pest. We conducted a biogeographic study of this species with an integrative approach using morphometric data from body and craniomandibular distances and molecular genetic data from the cytochrome b gene of the mitochondrial DNA. We collected 96 individuals in six localities from central, northern and eastern Morocco. Data from 18 morphological characters were used in multivariate statistical analyses and molecular data were analysed using maximum likelihood and median-joining networks. Our analyses confirmed the high morphological variability in this species and allowed to discriminate four groups containing the studied populations. We found that a few craniomandibular measurements had the highest contribution in the differences between populations, and that this variability reflected a spatial and environmental differentiation. In the genetic analyses, we placed our six populations and six individuals from four other countries in nine previously identified phylogenetic lineages in this species, and we also added a tenth lineage. Limited gene flow, isolation by distance and biogeographic barriers were further explored to explain this genetic structuration. We also jointly examined morphometric and genetic variability and found that the morphological groups were congruent with the genetic lineages and the geographic distribution. A better knowledge of the phenotypic plasticity and genetic diversity of this gerbil can be used to comprehend the micro-evolutionary processes in other small mammals in North Africa.

Key words. North Africa, cytochrome b gene, craniometry, populations, Gerbillinae, agriculture.

INTRODUCTION

The Gerbillinae subfamily and the genus *Gerbillus* are the most diverse group of rodents in North Africa. Like other small rodents, the species of this genus represent suitable models for the construction of biogeographic history thanks to their brief generation time and prolific reproduction rates; their rather limited dispersion capacities and strong affiliation to arid and/or open habitats (Avise 2000; Nicolas et al. 2009). A few recent molecular studies have attempted to review the systematics of the various species of *Gerbillus* inhabiting North Africa and Morocco, or to better understand their biogeography (Abiadh et al. 2010; Ndiaye et al. 2012, 2013a, 2016; Nicolas et al. 2014; Bouarakia et al. 2018). Among this genus, the most widespread species in Morocco is the North African Gerbil, *Gerbillus campestris* Loche, 1867, which is also considered as an agricultural pest (Giban & Haltebourg 1965; Ouzaouit 1980; Zyadi & Benazzou 1992). It is a long tailed, middle sized gerbil, with naked hind feet, that lives throughout the Mediterranean part of North Africa from Egypt, west of the Nile River and Delta, to Morocco in the West. It is also present but less widely distributed in the Sahara Desert and Sahel region, in Sudan, Niger and Mali (Happold 2013; Granjon et al. 2016; Denys et al. 2017). The species dwells in different habitats, from subhumid to arid and desertic regions, except high mountains, forests and sandy desert areas. It occupies steppes, arable lands, rocky habitats and oases; and digs its burrow in sandy or clay soils (Petter & Saint Girons 1965; Happold 1967; Aulagnier & Thevenot 1986; Kowalski & Rzebik-Kowalska 1991; Dobigny et al. 2002; Musser & Carleton 2005; Aulagnier et al. 2017).

Previous studies have investigated the intraspecific variability of *Gerbillus campestris*. Petter & Saint-Girons (1965) suggested the subdivision of the species in

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Morocco into to two subspecies based on coloration criteria. In Tunisia, due to geographic variation in size, the existence of two subspecies was suggested (Ranck 1968; Jordan et al. 1974). By combining the variation of skull size and characters, external size and pelage colour, two to five subspecies were identified in Egypt, Libya and Sudan (Setzer 1958; Ranck 1968; Osborn & Helmy 1980). Benazzou & Zyadi (1990) and Baala (1995) displayed the presence of a geographic biometric variation between five populations in Morocco, while Baala (1995) showed the absence of biochemical polymorphism between these five populations. On a chromosomal level, the most common diploid number of chromosomes for *G. campestris* is 2n = 56. This karyotype is present in Algeria, Tunisia, Egypt, Mali and Niger (Matthey 1952; Wassif et al. 1969; Jordan et al. 1974; Dobigny et al. 2001, 2002). However, chromosomal polymorphism was documented in Morocco with 2n = 56 in Taroudant locality and 2n = 57, 58 in Goulimine locality (Lay et al. 1975). More recently, Nicolas et al. (2014) presented a complex phylogeographic pattern in Morocco and North Africa using cytochrome b sequences. The wide distribution of *G. campestris*, the multiplicity of habitats it occupies, the rich geographic diversity of the region and the extreme environmental changes that occurred in North Africa during the Pleistocene, parallel this important intraspecific diversity.

To complete the phylogeographic structuration uncovered by Nicolas et al. (2014), we increased sample size in three localities and added three new ones in Morocco, to perform a study of genetic variability based on the cytochrome b gene of the mitochondrial DNA. The additional sampling from north-western Morocco helped us to explore the existence of barriers to gene flow in this part of Morocco, namely the Sebou River. In addition, the new sampling from north-eastern Morocco on both the eastern and western sides of the Moulouya River was useful to investigate the role of the Moulouya River and/or its arid valley as a major geographic barrier and to verify the suggested east-west genetic differentiation around this river (Nicolas et al. 2014; Lalis et al. 2016; Beddek et al. 2018). We also included samples from GenBank from four new localities (Mali, Tunisia, Libya and Egypt) to better identify past gene flow in other parts of the distribution range of the species.

Furthermore, we used body and craniomandibular distance-based measurements of genetically typed individuals from six localities from central, northern and eastern Morocco in a comparative study of morphometric variability, to explore the influence of spatial, geographic and environmental factors on phenotypic diversity. Finally, we jointly examined the morphological and genetic interpopulation variability to verify their congruence in defining the biogeographic history of the species in Morocco.

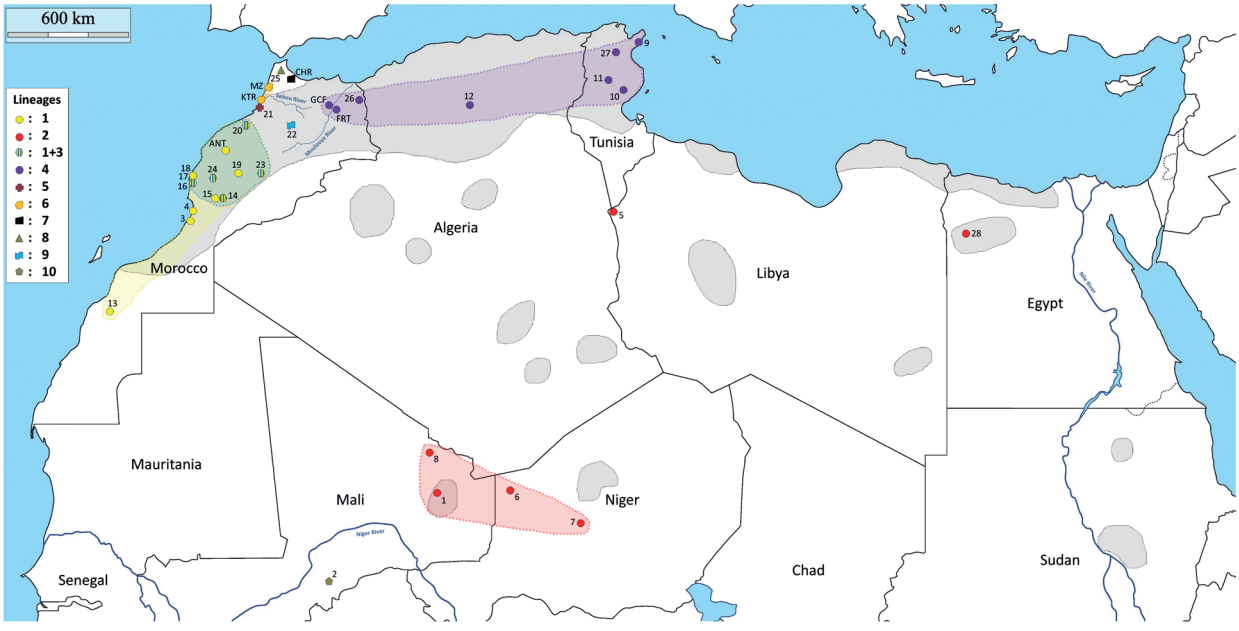

Fig. 1. Map displaying the geographic range (grey area, as mentioned by Granjon et al. 2016) of *Gerbillus campestris* and the distribution of the ten mitochondrial lineages. Dotted lines surround the geographic groupings of five lineages (1, 2, 3, 4 and 6). Based on Nicolas et al. (2014), only the localities of Mali and Niger were included in the geographic grouping of lineage 2. Localities from the present work (CHR, ANT, KTR, MZ, GCF, FRT) and from bibliography (numbered from 1 to 28) are indicated (see Appendix I). Localities 14, 16, 20, 23 and 24 shelter haplotypes from both lineages 1 and 3. Moulouya, Sebou, Niger and Nile Rivers are also shown in the map.

MATERIAL AND METHODS

Sampling. We collected 96 specimens of *Gerbillus campestris* between 2011 and 2015 in six localities in Morocco from various regions: 10 specimens in the Tingitane peninsula in Chrouda locality (named hereafter CHR); 13 in central Morocco in Aounate locality (ANT); 24 in Kenitra (KTR) and 25 in Merja Zerga (MZ) in the Gharb region north of the Sebou River; five in Guercif (GCF) on the west side of the Moulouya River and 19 in Fritissa (FRT) on the east side of the river in the Oriental region (Fig. 1, see Appendix I). We captured the animals alive using Sherman traps then we euthanized them by cervical dislocation. This protocol was approved by the Cuvier (Museum National d'Histoire Naturelle, Paris) ethics committee. We extracted a piece of the liver for the genetic study and preserved the carcasses in formaldehyde. Later, we extracted and prepared the skulls for the morphometric study. Then, we deposited voucher specimens in the collections of the Laboratory 'Biodiversity, Ecology and Genome' of the Faculty of Sciences of Rabat, except those from the Chrouda locality, that are preserved in the collections of the Museum National d'Histoire Naturelle of Paris (see Appendix I).

Morphometric study. We used the standard body measurements, head-body length (HB), tail length (T), hind feet length (HF), ear length (E), weight (WT) and the ratio of tail length to head-body length (%T). Using a Mitutoyo caliper accurate to 0.01 mm, we took 10 skull measurements (mm) on dorsal, ventral and lateral view of the skull. We also took three mandibular measurements (mm). Abbreviations of these craniomandibular values are as follows: greatest length of skull (GLS), width of the zygomatic arch (WZYG), breadth of braincase (BB), length of nasals (LN), least interorbital constriction (IO), occipital height from the tympanic bulla to the parietal-interparietal suture (HOCC), length of anterior palatine foramina (LAF), length of upper molar series (M1M3), width of the palate between the first two molars M1 at the anterocone (WP), diagonal length of tympanic bulla (LTB), length of the mandible from the tip of the lower incisor to the angular process (LMDB), height of the mandible taken above the mandibular condyle (HMDB), length of lower molar series (LM1M3).

The body and skull variability in each population was first calculated using descriptive statistics (minimum, maximum, mean, standard deviation). Multivariate analyses were conducted on log transformed body and craniomandibular measurements to make them more homogenous. To represent the body and skull variability we performed a principal component analysis (PCA). The results of the PCA were analysed to identify the factors influencing the structure of the data point clouds as visualized in the bi-plot graphs of the analyses.

A multivariate analysis of variance (MANOVA) was made to test the sexual dimorphism for the body and skull variables. We made another MANOVA to test the effect of the "locality" variable on the measurements. The standard significance threshold for the MANOVA was set at 5%. To visualize the morphological variability without the influence of sex, we performed a PCA separately within each sex. We also conducted a discriminant function analysis (DFA) within each sex to quantify the rate of discrimination based on the "locality" variable. In this DFA, we did not include the two individuals of CHR locality. An additional DFA was conducted on the data of the combined sexes to quantify the rate of discrimination based on the "locality" variable, and to identify the measurements that best categorise morphological variability. Finally, we tested the influence of altitude, latitude, longitude and annual precipitations using MANOVA

Table 1. Geographic data for the six localities studied in Morocco.

Locality	Altitude (m)	Latitude	Longitude	Precipitations (mm)
Chrouda (CHR)	209	35.360	-5.170	795
Aounate (ANT)	185	32.746	-8.244	317
Kenitra (KTR)	43	34.445	-6.520	579
Merja Zerga (MZ)	25	34.817	-6.310	622
Guercif (GCF)	410	34.206	-3.424	222
Fritissa (FRT)	510	34.161	-3.231	218

(Tab. 1). All statistical analyses were performed using the software XLSTAT version 2016 (Addinsoft 2012).

To minimize age-related bias, two individuals were excluded from the statistical analyses because they were identified as juveniles. This age estimation was done using the dental wear scheme of the upper molar series established by Zyadi (1989) and the age classes based on weight made by Zyadi & Benazzou (1992). Also, in all the multivariate analyses, we did not include 11 individuals due to missing data in the measurements.

Molecular study. We extracted and purified the DNA of the 96 individuals using the QIAGEN Kit (DNeasy Blood & Tissue Kit) following the manufacturer recom-

Table 2. Body measurements of *Gerbillus campestris* in six populations in Morocco. Abbreviations: head-body length (HB); tail length (T); hind feet length (HF); ear length (E); weight (WT); ratio of tail length to head-body length (%T); sample size (N); minimum (Min); maximum (Max); standard deviation (S.d.).

		Chrouda (CHR)	Aounate (ANT)	Kenitra (KTR)	Merja Zerga (MZ)	Guercif (GCF)	Fritissa (FRT)	All populations
HB (mm)	N	2	12	24	24	5	19	86
	Min	95	83	83	78	81	89	78
	Max	105	103	103	98	116	108	116
	Mean	100.00	92.33	94.42	90.87	102.40	98.37	94.60
	S.d.	7.07	7.02	5.72	4.75	14.54	6.49	7.27
T (mm)	N	2	12	22	24	5	18	83
	Min	109	99	94	93	106	111	93
	Max	119	117	112	117	149	134	149
	Mean	114.00	110.64	106.27	107.54	126.80	121.33	112.29
	S.d.	7.07	5.16	5.07	5.59	18.40	7.07	10.09
HF (mm)	N	2	12	24	24	5	19	86
	Min	26	23	23	23	24	25	23
	Max	28	26	25	26	29	28	29
	Mean	27.00	24.67	24.52	24.44	25.60	26.55	25.09
	S.d.	1.41	0.78	0.60	0.71	2.07	0.88	1.23
E (mm)	N	2	12	24	24	5	19	86
	Min	12	13	14	13	11	15	11
	Max	15	16	16	16	16	18	18
	Mean	13.50	14.92	15.10	14.56	14.00	16.18	15.06
	S.d.	2.12	1.16	0.77	0.68	1.87	0.80	1.14
WT (g)	N	2	12	24	24	5	19	86
	Min	34	16.8	17.8	16	18	22.5	16
	Max	40	32	35	25	37.5	36.5	40
	Mean	37.00	23.77	24.85	20.57	29.00	28.13	24.75
	S.d.	4.24	5.37	4.52	2.55	8.31	4.66	5.60
%T	N	2	12	22	25	5	18	83
	Min	104	111	97	99	117	104	97
	Max	125	131.5	131	144	131	138	144
	Mean	114.54	121.36	113.02	118.72	123.96	123.72	119.08
	S.d.	15.17	6.98	9.17	8.77	5.96	10.03	9.97

mendations. Then we amplified the cytochrome b gene (1040 bp) 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) (Ducroz et al. 2001). The PCR included an initial denaturation step of 3 min at 94°C, followed by 38 cycles of 30 sec at 94°C, 40 sec at 52°C, and 90 sec at 72°C, with a final extension step of 5 min at 72°C. Double-stranded PCR products were purified and sequenced by Eurofins. We checked the chromatograms then we corrected and aligned the sequences both manually and using ClustalW in the software BioEdit (Hall 1999). To attain the genetic identification, we entered the sequences into the Basic Local Alignment Search Tool (BLAST, https://blast.ncbi.nlm.nih.gov/Blast.cgi). All the sequences were submitted to GenBank (see Appendix I).

To choose the model of nucleotide substitution for our phylogenetic analysis, we used the software jModeltest 2.1.10 (Darriba et al. 2012). The General time reversible (GTR)+I+G model (Gu et al. 1995) was determined as the best-fit model of nucleotide substitution, according to the Akaike information criterion (Akaike 1973). We constructed a phylogenetic tree using the Maximum Likelihood method (ML) in the software MEGA 7.0.26 (Tamura et al. 2013). The robustness of the obtained topologies was estimated in all the treatments using a bootstrap analysis (1000 replicates). We included in the molecular analysis all the *cytb* sequences of *G. campestris* present in the GenBank database (108 sequences). We removed the beginning and the end of all the sequences used in the analysis because these parts of the sequences were missing in many specimens from GenBank, and we maintained a fragment of 1033 pb. We rooted the phylogenetic tree with one representative from each of the three subgenera of *Gerbillus*: *G. simoni* for the subgenus *Dipodillus*, *G. hesperinus* for the subgenus *Gerbillus* and *G. henleyi* for the subgenus *Hendecapleura* (see Appendix I). We also used the Median Joining algorithm through the software NETWORK version 4.500 (Bandelt et al. 1999) to estimate evolutionary relationships among the haplotypes. Finally, the Pairwise Kimura two-parameter (K2P) genetic distances (Kimura 1980) between the lineages were computed using MEGA 7.0.26 (Tamura et al. 2013).

RESULTS

Morphometric study. In the descriptive statistics of the body and craniomandibular measurements, we observe the existence of a variability between the six populations (Tabs 2–3). In general terms concerning body and craniomandibular size, the highest mean values belong to the populations of CHR, GCF and FRT; while the lowest mean values belong to the populations of ANT, KTR and MZ.

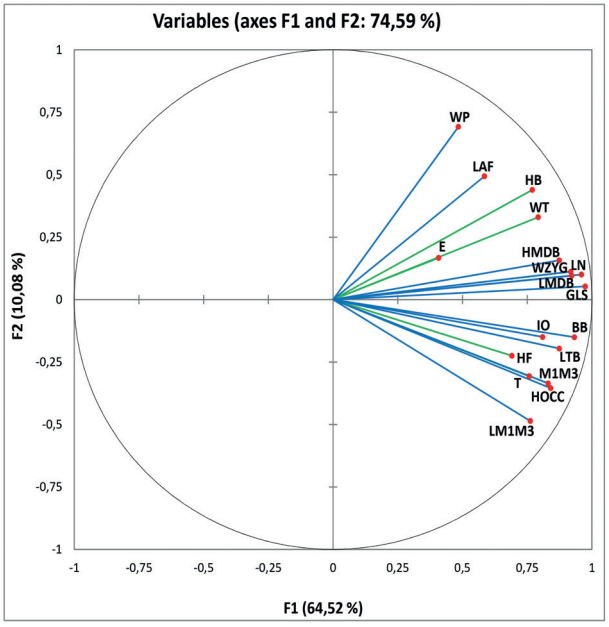

Fig. 2. Correlation circle obtained by the principal component analysis (PCA) of the body and craniomandibular variables in the factor space of (F1 and F2).

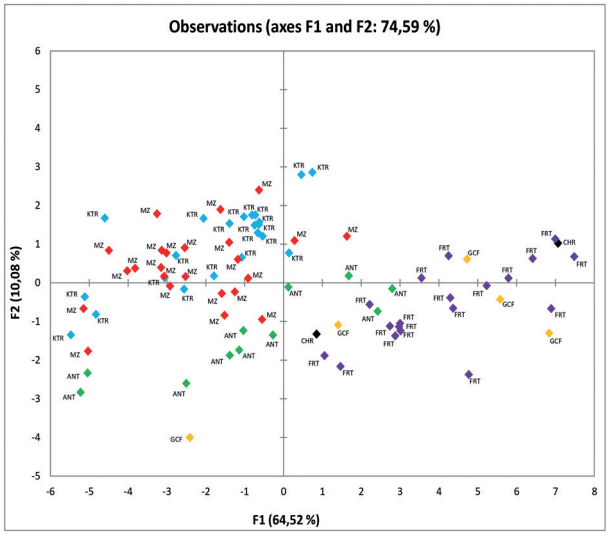

Fig. 3. Projection of individuals on the first two axes (F1 and F2) of the principal component analysis (PCA). Different colours represent different localities (Chrouda: black; Aounate: green; Kenitra: blue; Merja Zerga: red; Guercif: orange; Fritissa: purple).

For the PCA, we visualize in the correlation circle, the first two axes F1 and F2 that represent respectively 64.52% and 10.08% of the total variance (Fig. 2). The projection of the 18 body and craniomandibular variables on the F1xF2 plane shows that the F1 axis is positively

Table 3. Craniomandibular measurements of *Gerbillus campestris* in six populations in Morocco. Abbreviations: greatest length of skull (GLS), width of the zygomatic arch (WZYG), breadth of braincase (BB), length of nasals (LN), least interorbital constriction (IO), occipital height from the tympanic bulla to the parietal-interparietal suture (HOCC), length of anterior palatine foramina (LAF), length of upper molar series (M1M3), width of the palate between the first two molars M1 at the anterocone (WP), diagonal length of tympanic bulla (LTB), length of the mandible from the tip of the lower incisor to the angular process (LMDB), height of the mandible taken above the mandibular condyle (HMDB), length of lower molar series (LM1M3); sample size (N); minimum (Min); maximum (Max). standard deviation (S.d.).

		Chrouda (CHR)	Aounate (ANT)	Kenitra (KTR)	Merja Zerga (MZ)	Guercif (GCF)	Fritissa (FRT)	All populations
	N	2	12	24	24	5	19	86
	Min	28.77	25.42	25.66	25.36	26.98	28.09	25.36
GLS	**Max**	32.66	29.77	28.63	28.98	31.07	31.74	32.66
	Mean	30.71	27.90	27.43	27.21	29.68	30.12	28.23
	S.d.	2.75	1.36	0.83	0.80	1.79	1.02	1.62
	N	2	12	24	24	5	19	86
	Min	12.5	10.77	10.81	10.01	10.97	12	10.01
WZYG	**Max**	13.8	12.64	12.4	12.25	13.26	13.77	13.8
	Mean	13.15	11.81	11.62	11.29	12.32	12.83	11.90
	S.d.	0.92	0.61	0.47	0.49	0.97	0.53	0.81
	N	2	12	24	24	5	19	86
	Min	13.82	12.83	12.57	12.59	13.34	13.69	12.57
BB	**Max**	14.53	14.18	13.55	13.65	15.59	15.27	15.59
	Mean	14.17	13.52	13.13	13.17	14.57	14.24	13.55
	S.d.	0.50	0.42	0.26	0.33	0.85	0.41	0.64
	N	2	12	24	24	5	19	86
	Min	11.26	10.09	10.09	9.84	10.43	11.08	9.84
LN	**Max**	13.51	12.12	12.17	11.73	12.87	13.08	13.51
	Mean	12.38	11.27	11.13	11.00	11.89	12.32	11.45
	S.d.	1.59	0.67	0.49	0.48	1.10	0.49	0.79
	N	2	12	24	24	5	19	86
	Min	5.24	4.52	4.62	4.55	4.88	5.01	4.52
IO	**Max**	5.8	5.43	5.2	5.46	5.63	5.94	5.94
	Mean	5.52	5.00	4.91	4.99	5.29	5.43	5.10
	S.d.	0.40	0.27	0.14	0.20	0.27	0.25	0.30
	N	2	12	24	24	5	19	86
	Min	11.2	10.42	9.94	10.05	10.71	11.11	9.94
HOCC	**Max**	11.44	11.06	10.87	10.89	11.91	11.94	11.94
	Mean	11.32	10.82	10.44	10.44	11.24	11.43	10.78
	S.d.	0.17	0.21	0.26	0.26	0.47	0.23	0.49
	N	2	12	24	24	5	19	86
	Min	5.2	4.44	4.2	4.42	4.38	4.9	4.2
LAF	**Max**	5.64	5.29	5.69	5.65	5.52	6.08	6.08
	Mean	5.42	4.97	5.23	5.13	5.16	5.46	5.22
	S.d.	0.31	0.29	0.35	0.31	0.48	0.32	0.36

Table 3. (continued)

		Chrouda (CHR)	Aounate (ANT)	Kenitra (KTR)	Merja Zerga (MZ)	Guercif (GCF)	Fritissa (FRT)	All populations
	N	2	12	24	24	5	19	86
	Min	4.21	3.71	3.38	3.41	3.97	3.76	3.38
M1M3	**Max**	4.22	4.2	3.89	3.86	4.27	4.36	4.36
	Mean	4.21	3.89	3.64	3.65	4.13	4.07	3.81
	S.d.	0.01	0.14	0.12	0.11	0.11	0.15	0.24
	N	2	12	24	24	5	19	86
	Min	3.02	2.66	2.88	2.73	2.85	2.95	2.66
WP	**Max**	3.53	3.2	3.54	3.54	3.41	3.58	3.58
	Mean	3.27	2.99	3.19	3.19	3.18	3.23	3.17
	S.d.	0.36	0.17	0.16	0.17	0.22	0.18	0.19
	N	2	12	24	24	5	19	86
	Min	8.11	8.14	8.14	7.89	8.55	8.85	7.89
LTB	**Max**	9.1	8.95	8.91	8.87	9.87	9.75	9.87
	Mean	8.60	8.71	8.44	8.44	9.25	9.36	8.73
	S.d.	0.70	0.25	0.18	0.24	0.49	0.27	0.46
	N	2	12	24	24	5	19	86
	Min	16.37	14.42	14.77	14.71	15.32	16.26	14.42
LMDB	**Max**	18.56	17.18	16.51	16.8	18.35	18.35	18.56
	Mean	17.46	16.05	15.81	15.71	17.17	17.13	16.22
	S.d.	1.55	0.89	0.50	0.52	1.38	0.63	0.92
	N	2	12	24	24	5	19	86
	Min	6.67	6.31	6.23	6.42	6.58	7.04	6.23
HMDB	**Max**	7.81	7.49	7.44	7.61	7.74	8.26	8.26
	Mean	7.24	6.92	6.85	6.94	7.28	7.51	7.07
	S.d.	0.81	0.37	0.28	0.30	0.50	0.36	0.42
	N	2	12	24	24	5	19	86
	Min	3.75	3.59	3.27	3.3	3.8	3.74	3.27
LM1M3	**Max**	4.05	4.03	3.66	3.64	4.15	4.13	4.15
	Mean	3.90	3.81	3.53	3.50	3.97	3.92	3.68
	S.d.	0.21	0.13	0.10	0.11	0.12	0.10	0.22

correlated with all the variables, which indicates a size axis. On the other hand, several variables are positively correlated with the F2 axis, while several others are negatively correlated with this axis. The most strongly positively correlated variable with the F2 axis is the variable WP, with a correlation value of 0.69. The scatter plot of the PCA (Fig. 3) does not allow to visualize different distinct groups, but all the specimens from FRT and CHR and virtually all those from GCF are located on the positive side of the F1 axis. Contrarily, the specimens from MZ and KTR are located mainly on the negative side of F1. Specimens from ANT show high size variation.

Among the 83 individuals (55% males, 45% females), the average size of females seems somewhat larger than the one of males, and the Wilks' test in the MANOVA showed the existence of sexual dimorphism (Wilks' λ = 0.598, *F statistics* = 2.386, $DF_1 = 18$, $DF_2 = 64$, $p < 0.05$), which means that sex has a slightly significant influence on the dispersal of the observations on the PCA. For the PCA of the male individuals, we visualize the scatter plot of the two first axes F1 and F2 that represent respective-

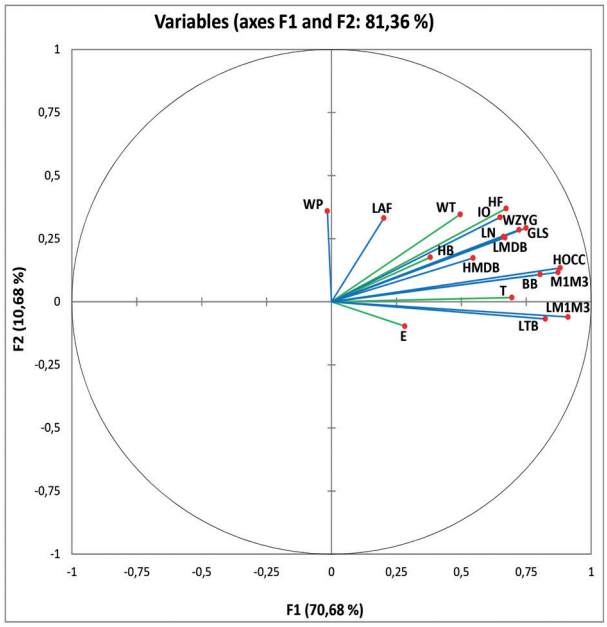

Fig. 4. Correlation circle obtained by the discriminant function analysis (DFA) of the body and craniomandibular variables in the factor space of (F1 and F2).

ly 66.45% and 10.17% of the total variance (see Appendix II). For the PCA of the female individuals, we visualize the scatter plot of the two first axes F1 and F2 that represent respectively 62.55% and 13.46% of the total variance (see Appendix III). In both the PCA of males and females, the F1 axis is positively correlated with all the variables indicating a size axis; with the craniomandibular measurements HOCC, LTB, WZYG, BB, LN, HMDB, LMDB and GLS being the most strongly correlated variables with F1 (values ranging from 0.83 to 0.98). In both scatter plots (males and females), individuals from MZ and KTR are the smallest, while those from FRT are the largest. Male individuals from GCF are almost as large as the individuals from FRT, while the female individuals from GCF have a high size variation. Male individuals from ANT show a medium size and the females show high size variation. The male individual from CHR is one of the largest individuals and the female from CHR has a medium size. In the DFA, we were able to quantify the discrimination between five populations within each sex: in the males, 100% of the individuals of ANT were correctly classified, 86.67% for KTR, 81.25% for MZ, 100% for GCF and 100% for FRT; while in the females, 100% of the individuals were correctly classified in each one of the five populations.

The Wilks' test in the MANOVA revealed the presence of a highly significant morphological difference between the various localities (Wilks' $\lambda = 0.01$, *F statistics* = 5.146, $DF_1 = 90$, $DF_2 = 296$, $p < 0.0001$). According to this result, we performed a discriminant function analysis (DFA) to quantify the morphological variability based on a locality effect. In the correlation circle (Fig. 4), the first two axes F1 and F2 of the DFA represent respectively 70.68% and 10.68% of the total variance. The projection of the 18 body and craniomandibular variables on the F1xF2 plane shows that the F1 axis is positively correlated with all the variables except WP (-0.02). In the F1 axis, the most discriminating variables are LM1M3 (0.91), HOCC (0.88), M1M3 (0.87), LTB (0.82), BB (0.80) and GLS (0.75).

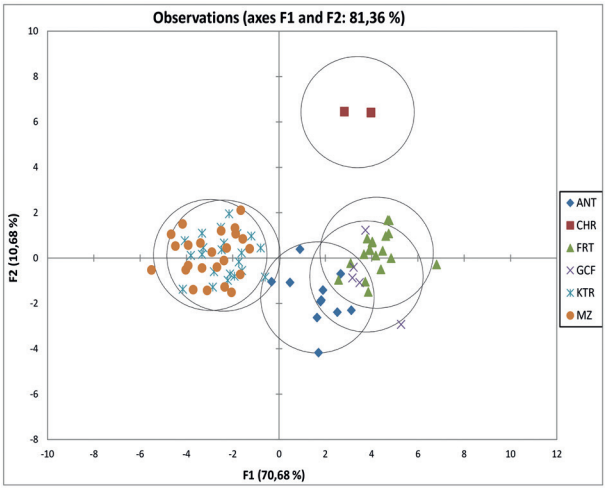

Fig. 5. Projection of individuals on the first two axes (F1 and F2) of the discriminant function analysis (DFA). Different symbols represent different localities. Also shown are confidence circles for each locality using covariance hypothesis.

On the scatter plot of the two first axes of the DFA (Fig. 5), although some overlap can be observed, we can distinguish four major groups:

– Group I composed of the individuals of Merja Zerga (MZ) and Kenitra (KTR);
– Group II composed of the individuals of Aounate (ANT);
– Group III composed of the individuals of Guercif (GCF) and Fritissa (FRT);
– Group IV composed of the individuals of Chrouda (CHR).

This structuration is integrated by the F1 axis that isolates Group I on the negative side of the axis and Groups III and IV on the positive side, while Group II is located in an intermediate position along this axis. The F2 axis allows a complete separation between Group IV and Group III. The DFA has also allowed to quantify the discrimination between the six populations: 100% of the

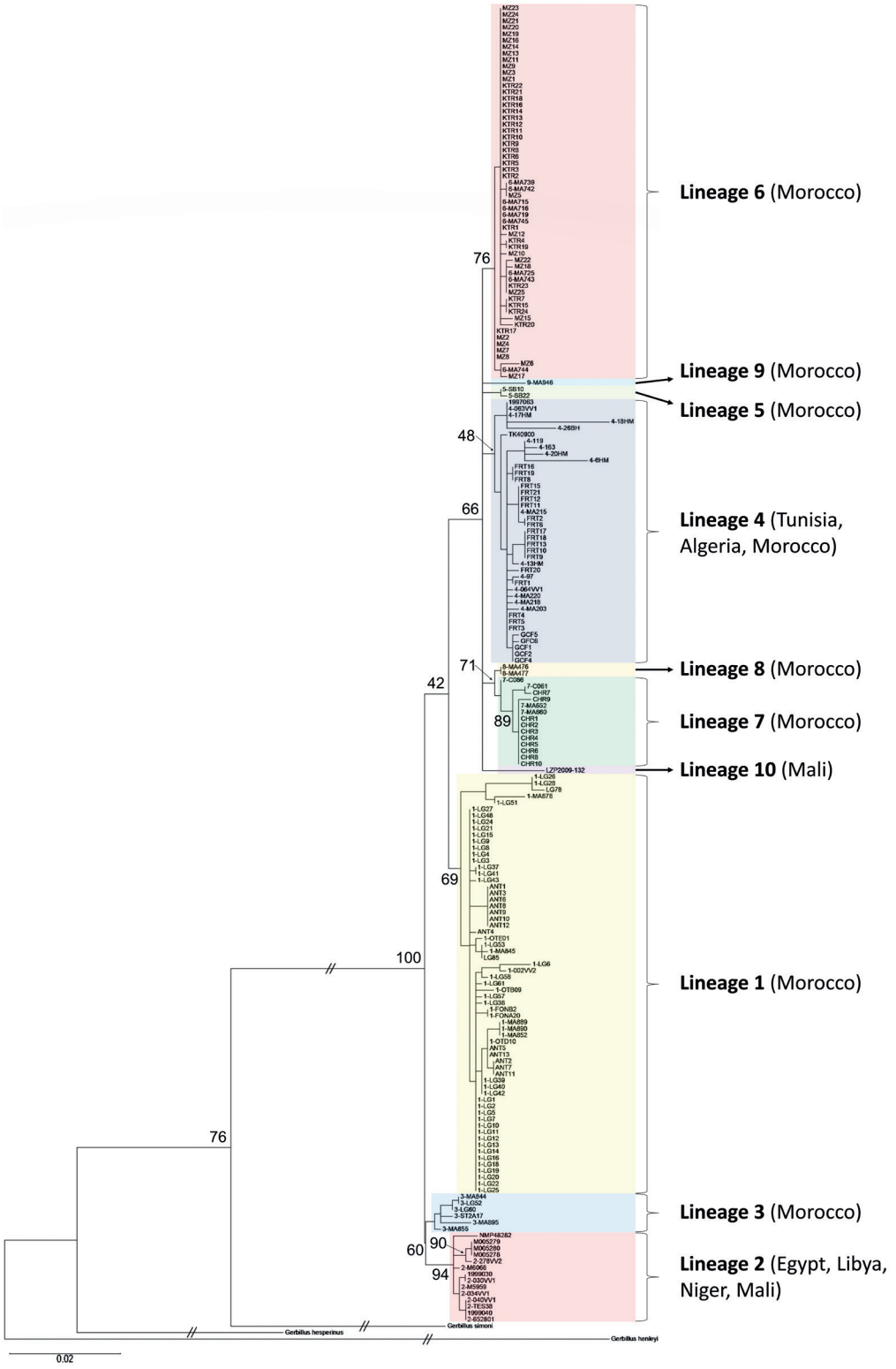

Fig. 6. Phylogenetic tree of *Gerbillus campestris* for the cytochrome b gene resulting from the Maximum-Likelihood analysis (GTR + I + G substitution model). Numbers at nodes represent ML bootstrap support. To improve clarity, values of the most apical nodes are not shown. The scale bar represents the branch length measured in the number of substitutions per site. The ten mitochondrial lineages are presented on the right border along with their geographic origin.

individuals of ANT were correctly classified, 86.4% for KTR, 87.5% for MZ, 80% for GCF, 100% for FRT and 100% for CHR.

Based on the results of the MANOVA, all the geographic parameters (altitude, latitude, longitude, annual precipitations; Tab. 1) have a highly significant effect: Wilks' $\lambda = 0.01$, *F statistics* = 5.146, $DF_1 = 90$, $DF_2 = 296$, $p < 0.0001$). A supplementary observation concerning the body variation between our suggested morphometric groups is the difference of dorsal coat colour, being dark brown for Group I, II and IV; and yellowish brown for Group III.

Molecular study. Based on the results of the phylogenetic tree (Fig. 6) and the haplotypes network (Fig. 7), the individuals from the six localities belong to four of the nine phylogenetic lineages previously identified by Nicolas et al. (2014):

– All the ten individuals from Chrouda (CHR) are found in lineage 7, which was previously composed of four specimens from this same locality.
– All the 13 individuals from Aounate (ANT) are found in lineage 1, which is widely distributed in Morocco and contains specimens from many localities south of the Bou Regreg River.
– All the 24 individuals from Kenitra (KTR) and the 25 individuals from Merja Zerga (MZ) are found in lineage 6, that was previously composed of only nine specimens from Merja Zerga.
– All the five individuals from Guercif (GCF), west of Moulouya River, and the 19 individuals from Fritissa (FRT), east of Moulouya River, are found in lineage 4 that previously contained only specimens from the east of this river (Morocco, Algeria and Tunisia).

Moreover, we have added three individuals from Egypt (Khalifa et al. 2018) and one from Libya (Chevret et al. 2014) to lineage 2, that was previously composed only of specimens from Niger and Mali (Tessalit and Adrar des Iforas localities). We also added one individual from Tunisia (Alhajeri et al. 2015) to lineage 4. Furthermore, we have attributed one individual from Mali (Sinkerma locality) (Schwan et al. 2012) to a new suggested lineage 10. The K2P genetic distance between lineage 10 and the other lineages goes from 1.4% with lineage 8, to 2.6% with lineage 2.

DISCUSSION

Morphological adaptation. The results of the morphometric study revealed a significant morphological variability among *Gerbillus campestris* in Morocco. The significant difference in the MANOVA testing the effect of "locality" variable; and the relatively high rate of discrimination of the DFA indicates a spatial structuration between populations. This structuration was represented by Group I (Merja Zerga and Kenitra populations), Group II (Aounate population), Group III (Guercif and Fritissa populations) and Group IV (Chrouda population). The parameters that contribute the most to this clustering are the lower and upper molar series length, the skull height, the tympanic bulla length and the braincase breadth. The variation of these parameters shows a gradual increase in size, from Group I being the smallest, to Group IV and Group III being the largest; while Group II has a medium size. In Morocco, a few previous studies were made on the geographic variation in biometrics for *G. campestris* (Benazzou & Zyadi 1990; Baala 1995). Apart from the Kenitra locality, they showed for different localities than ours an interpopulational variation in size, with Kenitra being the smallest. Another type of body variation reported in Morocco was related to the dorsal coat colour, being fawn grey in the northern regions and gradually brightening towards the south, until becoming light fawn in desertic habitats (Petter 1961).

In our study, the morphological variability was slightly influenced by sex, as we showed in the MANOVA the existence of a weak sexual dimorphism when males and females were analysed together. The PCA of the variability within each sex shows almost similar results between males and females; and roughly a similar distribution of individuals in the F1xF2 plane. Also, there is a strong rate of discrimination between the populations within each sex. All these reasons support a weak influence of sex on the clustering of our populations in distinct groups. In the precedent study of *G. campestris* in Morocco, Baala (1995) found no significant sexual dimorphism in five populations. In Tunisia, Jordan et al. (1974) found sexual difference in only one character. Additionally, sexual dimorphism has seldom been confirmed in Muridae rodents using classical morphometric analysis (Csanády & Mošanský 2018). Thus, larger samples from each population are needed to verify if the minor sexual dimorphism that we uncovered is not due to sampling bias.

The morphometric structuration that we showcased in *G. campestris* is explained by the wide distribution of this species in Morocco and the vast environmental diversity of this country. The significant differences found in the MANOVA for the geographical factors (altitude, latitude, longitude, precipitations) give more explanation to support this spatial and environmental differentiation. A similar result was found for *Rattus rattus* in Tunisia, where latitude, longitude, altitude and precipitation variables exhibited a significant control on size parameters (Ben Faleh et al. 2012a).

Our different populations are located in diverse bioclimates: subhumid for Group I (Kenitra and Merja Zerga) and Group IV (Chrouda), semi-arid for Group II (Aounate) and arid for Group III (Guercif and Fritissa) (Mokhtari et al. 2013). The influence of varying biocli-

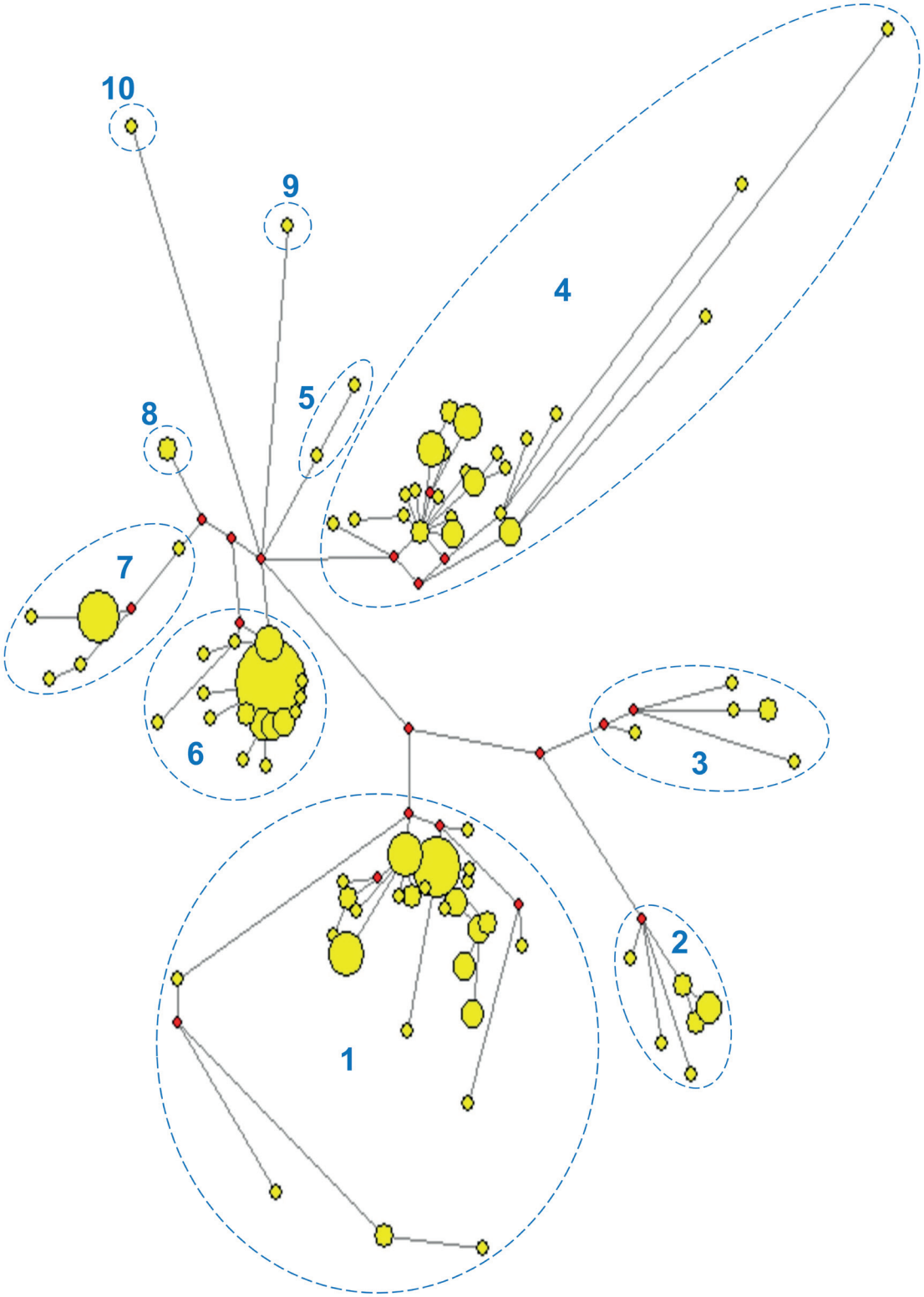

Fig. 7. Minimum spanning network of *Gerbillus campestris* for the cytochrome b gene haplotypes. Circle sizes are proportional to the number of similar haplotypes observed in the data set. Branch lengths are proportional to the number of mutations between haplotypes. The dashed ellipses (added for clarity) represent the ten mitochondrial lineages.

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mates and rainfall patterns on the populations acts indirectly through the availability and type of food resources (Yom-Tov & Geffen 2011; Breno et al. 2011). Previous studies showed an influence of climate on the skull of rodents, through variations in the type and availability of food (Renaud et al. 2005; Samuels 2009). The quality and quantity of food were shown to influence growth rates and skull morphology in the multimammate rat, *Mastomys natalensis* (Lalis et al. 2009; Breno et al. 2011). In the muskrat, *Ondatra zibethicus*, the high availability of food to each individual accelerated its growth, but if food was less abundant, there was an extension of the growth phase and an increase in growth variability (Pankakoski et al. 1987). Pocket gophers inhabiting alfalfa crops had larger body and skull size compared to those living in natural dry environments (Patton & Brylski 1987). In another example, a high difference in protein content in the diet of captive rats, *Rattus norvegicus*, caused a clear modification in adult skull shape but much less modification in the adult body and skull size (Miller & German 1999; Reichling & German 2000). However, squirrel monkeys, *Saimiri sciureus* that were fed a diet varying in protein content had different skull sizes but similar shape (Ramirez Rozzi et al. 2005). Surprisingly in our study, the individuals of Kenitra and Merja Zerga are the smallest even if they occupy the fertile agricultural fields of the Gharb region, characterized by high food availability and the abundance of peanut crops known to be rich in protein; as opposed to the individuals of Guercif and Fritissa, that are the largest even if they occupy habitats with low food availability in the Oriental region.

Food hardness, too, has an influence on skull development. This is an important factor of differentiation between our suggested morphometric groups, especially that the most discriminating variables in the DFA are the lower and upper molar series length. It was established in various species of rodents that skull morphology can be associated with the structure of food. In the prairie deer mouse, *Peromyscus maniculatus*, a softer diet caused a reduction in size of the masseteric tubercles and a narrowing of the zygomatic plate (Myers 1996). In laboratory rats, individuals feeding on a soft diet suffered a 12% loss of the mass of the skull and mandible, 4% decrease in the length of the angular process and 1% to 2% decrease in the dimensions of the cranial and facial skeleton, compared to the individuals feeding on a normal diet (Moore 1965). Other studies performed on rats demonstrated that maxillary breadth was markedly increased in the hard-diet reared individuals (Beecher & Corruccini 1981); that a modification in food consistency altered the masticatory muscle function and thus had an impact on craniofacial morphology (Kiliaridis 2006); and that a harder diet increased the growth of craniomandibular structures, especially those connected to the masticatory function (Abed et al. 2007). Feeding on a harder diet also relatively augmented the skull width of other mammals (Corruccini & Beecher 1984; Ciochon et al. 1997). In our studied populations, the smallest individuals, representing Group I populations (Kenitra and Merja Zerga) feed on various crops but primarily on peanut crops, in the form of seeds at the seedling stage, or the plant at the vegetative stage, or the pods at maturity (Zyadi & Benazzou 1992). On the opposite, the biggest individuals, representing Group III (Guercif and Fritissa), feed mainly on wheat and other cereals, in the form of plants and their hard grains. Our explanations connecting the morphological differences to the quantity and quality of food resources are hypothetical but reasonable, even if we do not possess quantifiable data on the food resources available to the studied populations or the stomach content of the individuals.

Differentiation between our morphometric groups was also partly due to the increase in size of the occipital part of the skull, represented by an increase in the size of the tympanic bulla, and therefore an increase in skull height and braincase breadth. This hypertrophy is observed in our populations with the increase of aridity, from Group I with the smallest bullae, found in a subhumid bioclimate, to Group III with the largest, found in an arid bioclimate. The size increase of the bullae also seems to go along with the decline of the population's density, from Group I of the Gharb region where *G. campestris* is prolific and can pullulate (Zyadi & Benazzou 1992), to Group III of the Oriental region where this species is much less abundant. Bioclimate variability, through the change of aridity levels, causes variations in vegetation cover and the abundance of food resources. At first, fewer food resources are available in the more arid habitats, and consequently there is a lowering of the rodent population density. Secondly, more arid habitats are characterized by a lower vegetation cover and thus more open habitats. Hypertrophy of the tympanic bullae, and consequently enhanced auditory sensitivity, is considered as an adaptation to these conditions of arid habitats. Gerbillinae rodents were distinguished to be one of the rodent families most predisposed to the hypertrophy of their bullae (Petter 1961). A better hearing acuity facilitates the encounter of the sexes and reproduction in low population densities (Petter 1961) and can help in evading predators in these more open habitats (Lay 1972; Webster & Webster 1975; Alhajeri et al. 2015). Similar to our results, Colangelo et al. (2010) found in *Gerbilliscus* that modifications in the molar row and the tympanic bulla were related to climate.

Other possible factors influencing morphological variability are predation pressure and intra- and interspecific competition (Yom-Tov & Geffen 2011). The different degrees of predation pressure by various predators (birds of prey, reptiles, small carnivores, rats, dogs) as well as competition over resources with the other rodents that we have captured in the studied localities (*Mus musculus*, *Mus spretus*, *Rattus rattus*, *Rattus norvegicus*, *Meriones shawii*), need to be tested by joint ecological studies.

Phylogeographic distribution. Previously, Nicolas et al. (2014) revealed a complex phylogeographic structuration of *Gerbillus campestris* in the form of nine mitochondrial lineages in Morocco, North Africa (Algeria and Tunisia) and the western Sahel region (Mali and Niger). According to these authors, different factors contributed to this structuration: isolation by distance; the climatic fluctuations of the Pleistocene marked by warming and cooling conditions, and the period of aridification at the end of the Pleistocene; and the role of the Moulouya River and Bou Regreg River as biogeographical barriers to genetic flow. The new sampled specimens and populations in our study give additional details concerning the distribution of the various lineages (Fig. 1).

The supplementary individuals from Chrouda locality reinforce the presence of lineage 7 in this locality as an allopatric lineage, in spite of the small geographic distance between this locality and the Esperada locality where exists the allopatric lineage 8, that forms a recent monophyletic group with lineage 7 beyond the Rif mountains in the extreme north of Morocco.

The added individuals from Aounate locality show that lineage 1 is still the only lineage present in this locality, even though this lineage is sympatric with lineage 3 in almost all the localities surrounding Aounate locality, in the north, east and south; between the Bou Regreg River and Souss River.

In the allopatric lineage 6, the Merja Zerga locality and the new locality of Kenitra are both located between the northern side of the Sebou River, the largest river in Morocco, and the southern side of the Loukkos River. However, on the southern side of the Sebou River, in the Sidi Boughaba locality just nearly 30 km from the Kenitra locality, we find the allopatric lineage 5. This suggests that the Sebou River is a significant barrier to gene flow for this species. Studies on different plant species have found that the Sebou River was a major geographical limit to gene flow (*Hypochaeris salzmanniana* DC. by Ortiz et al. 2007; *Chamaerops humilis* L. by García-Castaño et al. 2014; *Onopordum dissectum* Murb. by Balao et al. 2017). The north-west of Morocco is surrounded by the Rif and Middle Atlas Mountains and comprises several long rivers (Bou Regreg, Sebou and Loukkos Rivers) originating in these mountains and extending to the Atlantic coast at different latitudes, creating large estuaries and floodplains (Chichagov 2008), that probably acted as barriers separating the populations of *G. campestris* and promoting genetic isolation.

Lineage 4 was thought to be restricted to the eastern bank of the Moulouya River in Morocco and extending to the north of Algeria and to the north of Tunisia (Nicolas et al. 2014). However, thanks to our sampling in the new localities of Guercif and Fritissa, we showed that lineage 4 originating on the eastern bank of the Moulouya has later spread towards the western bank of the river. For another North African Gerbillinae rodent, *Meriones shawii*, Lalis et al. (2016), using both mtDNA and nDNA, suggested to split it into two species with an east-west structuration roughly around the Moulouya, though samples were missing from the western side of the Moulouya and from Northern Morocco. On the contrary, in the Greater Egyptian Jerboa, *Jaculus orientalis*, one of the three identified *cytb* lineages is found both in northern Morocco west of the Moulouya and in northern Algeria (Ben Faleh et al. 2012b). Based on Beddek et al. (2018), the structuration of mitochondrial diversity of reptiles and amphibians species around the Moulouya, between northern Morocco and north-western Algeria, can be assembled into three groups: i) the same lineage exists in north-western Algeria and northern Morocco, on both sides of the Moulouya (*Timon tangitanus*, *Trogonophis wiegmanni*, *Podarcis vaucheri*, *Acanthodactylus erythrurus*); ii) north-western Algeria is inhabited by the same lineage that is found in northern Morocco but only on the eastern side the Moulouya (*Natrix maura*); iii) a continuity between Moroccan populations from the two sides of the Moulouya, but with a separation from the populations of north-western Algerian (*Pelophylax saharicus*, *Natrix maura*). For these reptiles and amphibians, the origin of the east-west phylogeographic break around the Moulouya was attributed to the former marine Rifian corridor that joined the Atlantic Ocean with the Mediterranean Sea, east of the Rif mountains, between 8.0 Mya and 5.6 Mya (Barhoun & Bachiri 2008; Beddek et al. 2018). Although part of this marine corridor was located on the present Moulouya valley, this paleogeographic barrier cannot be applied, at least not directly, to the case of *G. campestris* since the history of this species has occurred starting from the middle Pleistocene (0.4-0.5 Mya) (Tong 1989). Our results may lessen the role of the Moulouya River and the valley encompassing it, in preventing the spread of *G. campestris* towards western Morocco at some point in the past, but the real geographic differentiation in this region is complex and should be further explored. An alternative possible explanation for the occurrence of lineage 4 on the western bank of the Moulouya River is a human-mediated transport of individuals, which can represent a counterbalancing factor to the genetic differentiation caused by geographic barriers.

Surprisingly, and although they originate from very distant localities, the specimens from Libya and Egypt belong to the Saharan lineage 2 along with the individuals of Niger and Mali (Tessalit and Adrar des Iforas localities), which makes lineage 2 the most widespread lineage, being present in Mali and Niger in the south and west; and Libya and Egypt in the north and east. *Gerbillus campestris* has a large distribution and occupies a wide variety of habitats, except in the Sahara Desert where it has a sporadic distribution and is restricted to rocky massifs. The Sahara Desert acts as a barrier to genetic flow between north and south of the desert, for species that are not adapted to extremely arid and san-

dy habitats, like *G. campestris*. However, the presence of lineage 2 from Mali and Niger in the south, to Egypt and Libya in the north of the Desert can represent a relic of a larger distribution during more favourable periods of the Pleistocene. Paleoenvironmental data and climatic reconstructions show that North Africa regularly shifted from wetter to drier climatic conditions throughout the Quaternary (deMenocal 2004; Schuster et al. 2006; Tabel et al. 2016), leading to periodic contraction/expansion of the Sahara Desert. Similarly, Nicolas et al. (2018) showed through ecological niche modelling and genetic data that presently unsuitable arid areas of the Saharan Desert were suitable for the amphibian *Bufotes boulengeri* throughout most of the Quaternary.

Another unexpected result concerns the specimen from south central Mali (Sinkerma locality) representing the added lineage 10. Even if it is geographically close to the specimens from north-east Mali (Tessalit and Adrar des Iforas localities), the Sinkerma individual is genetically very distant from lineage 2 (2.6%) and seems to be genetically closer to lineages from the north of Morocco. In this case, the high genetic differentiation between the adjacent populations eliminates the role of isolation-by-distance as a cause of genetic variability. The Sinkerma locality is found south of the Niger River, the third longest river in Africa, compared to the two other localities that are situated north of the river. Therefore, the Niger River may have played a role as a barrier to gene flow between lineages, similarly to what was suggested for other rodents (Nicolas et al. 2008, 2009; Brouat et al. 2009; Dobigny et al. 2010; Hima et al. 2011; Colangelo et al. 2013). Also, phylogeographic studies for different rodents showed the existence of distinct phylogroups in this region of West Sahel (*Mastomys erythroleucus* by Brouat et al. 2009; *Acomys chudeaui* by Nicolas et al. 2009; *Gerbillus henleyi* by Bouarakia et al. 2018). To explain the phylogeographic discontinuity for *G. campestris* in Mali, more samples from this region are needed to evaluate the combined actions of barriers and allopatric differentiation or the effects of lineage sorting from a highly polymorphic ancestral gene pool (Avise 2000).

Relationship between morphometric and molecular variability. A crucial goal of this work is the confrontation of the results of the morphometric study to those of the molecular study. Previously, Baala (1995) showed in five populations in Morocco, that the biometric variability was not accompanied by allozymic variability based on biochemical differentiation of proteins. However, in our study, the morphometric results are congruent with the genetic results and the geographic distribution. The geographic structuring of the six populations of *G. campestris* in Morocco has produced sufficient phenotypic differentiation and high levels of sequence divergence that allows their discrimination into four groups:

– Group I of the morphometric study, composed of the populations of Merja Zerga and Kenitra, corresponds to the genetic lineage 6 and is present in north-western Morocco.
– Group II, representing the population of Aounate, corresponds to the genetic lineage 1 and is present in central Morocco;
– Group III, composed of the populations of Guercif and Fritissa, corresponds to genetic lineage 4 and is present in north-eastern Morocco;
– Group IV representing the population of Chrouda, corresponds to the genetic lineage 7 and is present in the extreme north of Morocco.

A notable point is the clarification of the phylogeographic status of the populations of Guercif and Fritissa in relation to the populations present either on the eastern bank or the western bank of Moulouya River. This river was considered to be a major barrier reducing dispersal rates and thus hindering gene flow between the eastern populations (Tunisia, Algeria and east of Morocco) and the western ones (west of Morocco). Yet, both the morphological and genetic analyses showed that the populations of Guercif (west of Moulouya) and Fritissa (east of Moulouya) belong to the same group.

Although we did not determine the specific relationship between morphological and genetic variation, we were able nonetheless to demonstrate for *G. campestris* its high plasticity, its capacity of adaptation and the micro-evolutionary processes at work. In summary, *G. campestris* is a widely distributed species that can be divided in Morocco into different assemblages of populations that experienced variable degrees of geographic isolation and adapted to different local environmental conditions, resulting in a strong morphological differentiation and genetic structuration. But systematically speaking, the question to be asked is whether we should see this variability as a progressive gradient or must divide the species into different diverging subspecies. Several subspecies were previously described based on geographic variations of pelage coloration, external size and/or skull characters (Setzer 1958; Petter & Saint-Girons 1965; Ranck 1968; Jordan et al. 1974; Osborn & Helmy 1980). Based only on their geographic distribution, we may attribute some populations used in the current study to these different subspecies. For example, the individuals from Tunisia and Algeria belonging to lineage 4 may be attributed to the subspecies *G. campestris campestris* Levaillant, 1857. However, in other cases, specimens from the same lineage fall within different subspecies: the individuals from Egypt fit with *G. campestris haymani* Setzer, 1958; while the one from Libya fits with *G. campestris dodsoni* Thomas, 1902. Furthermore, Petter & Saint-Girons (1965) suggested that only two subspecies are found in Morocco and they were identified based merely on coloration criteria (*G. c. campestris* and *G. c. dodsoni*), which

does not correspond to the complex phylogeographic structuration revealed in this country. *Gerbillus hilda* Thomas, 1918, first described as a new species in Morocco on the northern Atlantic coast (122 km south-west of Tangiers), approached the dimensions of *G. campestris* externally and cranially but was characterized by a small band of hairs on the hind feet soles (Thomas 1918). Specimens captured 17 km south-west of Rabat and described as *G. hilda* by Schlitter & Setzer (1972) appear to be closer in body and skull dimensions to the *G. campestris* individuals of Group I. *G. hilda* was later regarded as a subspecies of *G. campestris* (Petter 1975 and Corbet 1978, as cited in Lay 1983), while Lay (1983) viewed it as a subspecies of *G. nanus*. If we want to reconsider the taxonomy of *Gerbillus campestris* on an intraspecific level, genetic variability and morphological characteristics must be further identified across the range of the species.

CONCLUSIONS

Supplementary sampling from the whole distribution area of *Gerbillus campestris* should be carried out, and different markers must be used in the genetic study to better explore the genetic diversity of this species in the Sahara Desert (Mali, Niger) and in Algeria. In addition, the study of morphological variability should be refined in order to include specimens from all the geographic range of the species and all the genetic lineages. Classical morphometry is not sufficient and craniomandibular variation should be further studied using geometric morphometric methods. Further research should focus on how morphological and genetic variations could be related to the adaptation capacity of this rodent to anthropized habitats, increasing its pullulation capacity and the damage it can cause to agricultural crops.

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APPENDIX I.

List of specimens used in the genetic study, with their geographic origin, GenBank number, voucher number and reference.

Species	Spec. code	Country	Locality	Locality code	GenBank N°	Voucher N°	Reference
G. campestris	CHR1	Morocco	Chrouda	CHR	MK452133	C112	This work
G. campestris	CHR2	Morocco	Chrouda	CHR	MK452134	C115	This work
G. campestris	CHR3	Morocco	Chrouda	CHR	MK452135	C116	This work
G. campestris	CHR4	Morocco	Chrouda	CHR	MK452136	C129	This work
G. campestris	CHR5	Morocco	Chrouda	CHR	MK452137	C142	This work
G. campestris	CHR6	Morocco	Chrouda	CHR	MK452138	C145	This work
G. campestris	CHR7	Morocco	Chrouda	CHR	MK452139	C150	This work
G. campestris	CHR8	Morocco	Chrouda	CHR	MK452140	C168	This work
G. campestris	CHR9	Morocco	Chrouda	CHR	MK452141	C180	This work
G. campestris	CHR10	Morocco	Chrouda	CHR	MK452142	C182	This work
G. campestris	ANT1	Morocco	Aounate	ANT	MK452143	FSR-MAR14-ANT1	This work
G. campestris	ANT2	Morocco	Aounate	ANT	MK452144	FSR-MAR14-ANT2	This work
G. campestris	ANT3	Morocco	Aounate	ANT	MK452145	FSR-MAR14-ANT3	This work
G. campestris	ANT4	Morocco	Aounate	ANT	MK452159	FSR-MAR14-ANT4	This work
G. campestris	ANT5	Morocco	Aounate	ANT	MK452146	FSR-MAR14-ANT5	This work
G. campestris	ANT6	Morocco	Aounate	ANT	MK452147	FSR-MAR14-ANT6	This work
G. campestris	ANT7	Morocco	Aounate	ANT	MK452148	FSR-MAR14-ANT7	This work
G. campestris	ANT8	Morocco	Aounate	ANT	MK452160	FSR-MAR14-ANT8	This work
G. campestris	ANT9	Morocco	Aounate	ANT	MK452149	FSR-MAR14-ANT9	This work
G. campestris	ANT10	Morocco	Aounate	ANT	MK452150	FSR-MAR14-ANT10	This work
G. campestris	ANT11	Morocco	Aounate	ANT	MK452151	FSR-MAR14-ANT11	This work
G. campestris	ANT12	Morocco	Aounate	ANT	MK452152	FSR-MAR14-ANT12	This work
G. campestris	ANT13	Morocco	Aounate	ANT	MK452153	FSR-MAR14-ANT13	This work
G. campestris	KTR1	Morocco	Kenitra	KTR	MK452161	FSR-MAR14-KTR1	This work
G. campestris	KTR2	Morocco	Kenitra	KTR	MK452162	FSR-MAR14-KTR2	This work
G. campestris	KTR3	Morocco	Kenitra	KTR	MK452163	FSR-MAR14-KTR3	This work

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APPENDIX I. (continued)

Species	Spec. code	Country	Locality	Locality code	GenBank N°	Voucher N°	Reference
G. campestris	KTR4	Morocco	Kenitra	KTR	MK452164	FSR-MAR14-KTR4	This work
G. campestris	KTR5	Morocco	Kenitra	KTR	MK452165	FSR-MAR14-KTR5	This work
G. campestris	KTR6	Morocco	Kenitra	KTR	MK452166	FSR-MAR14-KTR6	This work
G. campestris	KTR7	Morocco	Kenitra	KTR	MK452167	FSR-MAR14-KTR7	This work
G. campestris	KTR8	Morocco	Kenitra	KTR	MK452168	FSR-MAR14-KTR8	This work
G. campestris	KTR9	Morocco	Kenitra	KTR	MK452169	FSR-MAR14-KTR9	This work
G. campestris	KTR10	Morocco	Kenitra	KTR	MK452170	FSR-MAR14-KTR10	This work
G. campestris	KTR11	Morocco	Kenitra	KTR	MK452171	FSR-MAR14-KTR11	This work
G. campestris	KTR12	Morocco	Kenitra	KTR	MK452172	FSR-MAR14-KTR12	This work
G. campestris	KTR13	Morocco	Kenitra	KTR	MK452173	FSR-MAR14-KTR13	This work
G. campestris	KTR14	Morocco	Kenitra	KTR	MK452174	FSR-MAR14-KTR14	This work
G. campestris	KTR15	Morocco	Kenitra	KTR	MK452175	FSR-MAR14-KTR15	This work
G. campestris	KTR16	Morocco	Kenitra	KTR	MK452176	FSR-MAR14-KTR16	This work
G. campestris	KTR17	Morocco	Kenitra	KTR	MK452177	FSR-MAR14-KTR17	This work
G. campestris	KTR18	Morocco	Kenitra	KTR	MK452178	FSR-MAR15-KTR18	This work
G. campestris	KTR19	Morocco	Kenitra	KTR	MK452179	FSR-MAR15-KTR19	This work
G. campestris	KTR20	Morocco	Kenitra	KTR	MK452180	FSR-MAR15-KTR20	This work
G. campestris	KTR21	Morocco	Kenitra	KTR	MK452181	FSR-MAR15-KTR21	This work
G. campestris	KTR22	Morocco	Kenitra	KTR	MK452182	FSR-MAR15-KTR22	This work
G. campestris	KTR23	Morocco	Kenitra	KTR	MK452183	FSR-MAR15-KTR23	This work
G. campestris	KTR24	Morocco	Kenitra	KTR	MK452184	FSR-MAR15-KTR24	This work
G. campestris	MZ1	Morocco	Merja Zerga	MZ	MK452185	FSR-MAR14-MZ1	This work
G. campestris	MZ2	Morocco	Merja Zerga	MZ	MK452186	FSR-MAR14-MZ2	This work
G. campestris	MZ3	Morocco	Merja Zerga	MZ	MK452187	FSR-MAR14-MZ3	This work
G. campestris	MZ4	Morocco	Merja Zerga	MZ	MK452188	FSR-MAR14-MZ4	This work
G. campestris	MZ5	Morocco	Merja Zerga	MZ	MK452189	FSR-MAR14-MZ5	This work
G. campestris	MZ6	Morocco	Merja Zerga	MZ	MK452190	FSR-MAR14-MZ6	This work
G. campestris	MZ7	Morocco	Merja Zerga	MZ	MK452191	FSR-MAR14-MZ7	This work

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APPENDIX I. (continued)

Species	Spec. code	Country	Locality	Locality code	GenBank N°	Voucher N°	Reference
G. campestris	MZ8	Morocco	Merja Zerga	MZ	MK452192	FSR-MAR14-MZ8	This work
G. campestris	MZ9	Morocco	Merja Zerga	MZ	MK452193	FSR-MAR14-MZ9	This work
G. campestris	MZ10	Morocco	Merja Zerga	MZ	MK452194	FSR-MAR14-MZ10	This work
G. campestris	MZ11	Morocco	Merja Zerga	MZ	MK452195	FSR-MAR14-MZ11	This work
G. campestris	MZ12	Morocco	Merja Zerga	MZ	MK452196	FSR-MAR14-MZ12	This work
G. campestris	MZ13	Morocco	Merja Zerga	MZ	MK452197	FSR-MAR14-MZ13	This work
G. campestris	MZ14	Morocco	Merja Zerga	MZ	MK452198	FSR-MAR14-MZ14	This work
G. campestris	MZ15	Morocco	Merja Zerga	MZ	MK452199	FSR-MAR14-MZ15	This work
G. campestris	MZ16	Morocco	Merja Zerga	MZ	MK452200	FSR-MAR14-MZ16	This work
G. campestris	MZ17	Morocco	Merja Zerga	MZ	MK452201	FSR-MAR14-MZ17	This work
G. campestris	MZ18	Morocco	Merja Zerga	MZ	MK452202	FSR-MAR14-MZ18	This work
G. campestris	MZ19	Morocco	Merja Zerga	MZ	MK452203	FSR-MAR14-MZ19	This work
G. campestris	MZ20	Morocco	Merja Zerga	MZ	MK452204	FSR-MAR14-MZ20	This work
G. campestris	MZ21	Morocco	Merja Zerga	MZ	MK452205	FSR-MAR15-MZ21	This work
G. campestris	MZ22	Morocco	Merja Zerga	MZ	MK452206	FSR-MAR15-MZ22	This work
G. campestris	MZ23	Morocco	Merja Zerga	MZ	MK452207	FSR-MAR15-MZ23	This work
G. campestris	MZ24	Morocco	Merja Zerga	MZ	MK452208	FSR-MAR15-MZ24	This work
G. campestris	MZ25	Morocco	Merja Zerga	MZ	MK452209	FSR-MAR15-MZ25	This work
G. campestris	GCF1	Morocco	Guercif	GCF	MK452154	FSR-MAR14-GCF1	This work
G. campestris	GCF2	Morocco	Guercif	GCF	MK452155	FSR-MAR14-GCF2	This work
G. campestris	GCF4	Morocco	Guercif	GCF	MK452156	FSR-MAR15-GCF4	This work
G. campestris	GCF5	Morocco	Guercif	GCF	MK452157	FSR-MAR15-GCF5	This work
G. campestris	GCF6	Morocco	Guercif	GCF	MK452158	FSR-MAR15-GCF6	This work
G. campestris	FRT1	Morocco	Fritissa	FRT	MK452210	FSR-MAR15-FRT1	This work
G. campestris	FRT2	Morocco	Fritissa	FRT	MK452211	FSR-MAR15-FRT2	This work
G. campestris	FRT3	Morocco	Fritissa	FRT	MK452129	FSR-MAR15-FRT3	This work
G. campestris	FRT4	Morocco	Fritissa	FRT	MK452130	FSR-MAR15-FRT4	This work
G. campestris	FRT5	Morocco	Fritissa	FRT	MK452131	FSR-MAR15-FRT5	This work

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APPENDIX I. (continued)

Species	Spec. code	Country	Locality	Locality code	GenBank N°	Voucher N°	Reference
G. campestris	FRT6	Morocco	Fritissa	FRT	MK452132	FSR-MAR15-FRT6	This work
G. campestris	FRT8	Morocco	Fritissa	FRT	MK452212	FSR-MAR15-FRT8	This work
G. campestris	FRT9	Morocco	Fritissa	FRT	MK452213	FSR-MAR15-FRT9	This work
G. campestris	FRT10	Morocco	Fritissa	FRT	MK452214	FSR-MAR15-FRT10	This work
G. campestris	FRT11	Morocco	Fritissa	FRT	MK452215	FSR-MAR15-FRT11	This work
G. campestris	FRT12	Morocco	Fritissa	FRT	MK452125	FSR-MAR15-FRT12	This work
G. campestris	FRT13	Morocco	Fritissa	FRT	MK452126	FSR-MAR15-FRT13	This work
G. campestris	FRT15	Morocco	Fritissa	FRT	MK452127	FSR-MAR15-FRT15	This work
G. campestris	FRT16	Morocco	Fritissa	FRT	MK452128	FSR-MAR15-FRT16	This work
G. campestris	FRT17	Morocco	Fritissa	FRT	MK457759	FSR-MAR15-FRT17	This work
G. campestris	FRT18	Morocco	Fritissa	FRT	MK457760	FSR-MAR15-FRT18	This work
G. campestris	FRT19	Morocco	Fritissa	FRT	MK457761	FSR-MAR15-FRT19	This work
G. campestris	FRT20	Morocco	Fritissa	FRT	MK457763	FSR-MAR15-FRT20	This work
G. campestris	FRT21	Morocco	Fritissa	FRT	MK457762	FSR-MAR15-FRT21	This work
G. campestris	M005278	Egypt	El Zaiytona (Siwa Oasis)	28	KX786155		Khalifa et al. (2018)
G. campestris	M005279	Egypt	El Zaiytona (Siwa Oasis)	28	KX792478		Khalifa et al. (2018)
G. campestris	M005280	Egypt	El Zaiytona (Siwa Oasis)	28	KX792479		Khalifa et al. (2018)
G. campestris	1997063	Tunisia	Sidi Bouzid	11	LN606674		Ndiaye et al. (2016)
G. campestris	TK40900	Tunisia	Jebel Ain Es Seed	27	KR089016		Alhajeri et al. (2015)
G. campestris	4-MA203	Morocco	Guenfouda	26	KC835828		Nicolas et al. (2014)
G. campestris	4-MA215	Morocco	Guenfouda	26	KC835829		Nicolas et al. (2014)
G. campestris	4-MA218	Morocco	Guenfouda	26	KC835830		Nicolas et al. (2014)
G. campestris	4-MA220	Morocco	Guenfouda	26	KC835831		Nicolas et al. (2014)
G. campestris	8-MA476	Morocco	Esperada	25	KC835832		Nicolas et al. (2014)
G. campestris	8-MA477	Morocco	Esperada	25	KC835833		Nicolas et al. (2014)
G. campestris	7-MA652	Morocco	Chrouda	CHR	KC835834		Nicolas et al. (2014)
G. campestris	7-MA660	Morocco	Chrouda	CHR	KC835835		Nicolas et al. (2014)
G. campestris	7-C086	Morocco	Chrouda	CHR	KC835861		Nicolas et al. (2014)

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APPENDIX I. (continued)

Species	Spec. code	Country	Locality	Locality code	GenBank N°	Voucher N°	Reference
G. campestris	7-C061	Morocco	Chrouda	CHR	KC835917		Nicolas et al. (2014)
G. campestris	6-MA715	Morocco	Merja Zerga	MZ	KC835836		Nicolas et al. (2014)
G. campestris	6-MA716	Morocco	Merja Zerga	MZ	KC835837		Nicolas et al. (2014)
G. campestris	6-MA719	Morocco	Merja Zerga	MZ	KC835838		Nicolas et al. (2014)
G. campestris	6-MA725	Morocco	Merja Zerga	MZ	KC835839		Nicolas et al. (2014)
G. campestris	6-MA739	Morocco	Merja Zerga	MZ	KC835840		Nicolas et al. (2014)
G. campestris	6-MA742	Morocco	Merja Zerga	MZ	KC835841		Nicolas et al. (2014)
G. campestris	6-MA743	Morocco	Merja Zerga	MZ	KC835842		Nicolas et al. (2014)
G. campestris	6-MA744	Morocco	Merja Zerga	MZ	KC835843		Nicolas et al. (2014)
G. campestris	6-MA745	Morocco	Merja Zerga	MZ	KC835844		Nicolas et al. (2014)
G. campestris	3-MA844	Morocco	Sidi L'Moctar	24	KC835845		Nicolas et al. (2014)
G. campestris	1-MA845	Morocco	Sidi L'Moctar	24	KC835846		Nicolas et al. (2014)
G. campestris	1-MA852	Morocco	Sour El'Az	23	KC835847		Nicolas et al. (2014)
G. campestris	3-MA855	Morocco	Sour El'Az	23	KC835848		Nicolas et al. (2014)
G. campestris	1-MA878	Morocco	Sour El'Az	23	KC835849		Nicolas et al. (2014)
G. campestris	1-MA889	Morocco	Sour El'Az	23	KC835850		Nicolas et al. (2014)
G. campestris	1-MA890	Morocco	Sour El'Az	23	KC835851		Nicolas et al. (2014)
G. campestris	3-MA895	Morocco	Sour El'Az	23	KC835852		Nicolas et al. (2014)
G. campestris	9-MA946	Morocco	Boutkhoubaye	22	KC835853		Nicolas et al. (2014)
G. campestris	1-OTB09	Morocco	Aounate	ANT	KC835854		Nicolas et al. (2014)
G. campestris	1-OTD10	Morocco	Aounate	ANT	KC835855		Nicolas et al. (2014)
G. campestris	1-OTE01	Morocco	Aounate	ANT	KC835918		Nicolas et al. (2014)
G. campestris	5-SB10	Morocco	Sidi Boughaba	21	KC835856		Nicolas et al. (2014)
G. campestris	5-SB22	Morocco	Sidi Boughaba	21	KC835857		Nicolas et al. (2014)
G. campestris	1-FONB2	Morocco	Oued Nfifikh	20	KC835858		Nicolas et al. (2014)
G. campestris	1-FONA20	Morocco	Oued Nfifikh	20	KC835859		Nicolas et al. (2014)
G. campestris	3-ST2A17	Morocco	Oued Nfifikh	20	KC835860		Nicolas et al. (2014)
G. campestris	1-LG1	Morocco	20 km N Marrakech	19	KC835867		Nicolas et al. (2014)

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APPENDIX I. (continued)

Species	Spec. code	Country	Locality	Locality code	GenBank N°	Voucher N°	Reference
G. campestris	1-LG2	Morocco	20 km N Marrakech	19	KC835868		Nicolas et al. (2014)
G. campestris	1-LG3	Morocco	20 km N Marrakech	19	KC835869		Nicolas et al. (2014)
G. campestris	1-LG4	Morocco	20 km N Marrakech	19	KC835870		Nicolas et al. (2014)
G. campestris	1-LG5	Morocco	20 km N Marrakech	19	KC835871		Nicolas et al. (2014)
G. campestris	1-LG6	Morocco	20 km N Marrakech	19	KC835872		Nicolas et al. (2014)
G. campestris	1-LG7	Morocco	20 km N Marrakech	19	KC835873		Nicolas et al. (2014)
G. campestris	1-LG8	Morocco	20 km N Marrakech	19	KC835874		Nicolas et al. (2014)
G. campestris	1-LG9	Morocco	20 km N Marrakech	19	KC835875		Nicolas et al. (2014)
G. campestris	1-LG10	Morocco	20 km N Marrakech	19	KC835876		Nicolas et al. (2014)
G. campestris	1-LG11	Morocco	20 km N Marrakech	19	KC835877		Nicolas et al. (2014)
G. campestris	1-LG12	Morocco	20 km N Marrakech	19	KC835878		Nicolas et al. (2014)
G. campestris	1-LG13	Morocco	20 km N Marrakech	19	KC835879		Nicolas et al. (2014)
G. campestris	1-LG14	Morocco	20 km N Marrakech	19	KC835880		Nicolas et al. (2014)
G. campestris	1-LG15	Morocco	20 km N Marrakech	19	KC835881		Nicolas et al. (2014)
G. campestris	1-LG16	Morocco	20 km N Marrakech	19	KC835882		Nicolas et al. (2014)
G. campestris	1-LG18	Morocco	20 km N Marrakech	19	KC835883		Nicolas et al. (2014)
G. campestris	1-LG19	Morocco	20 km N Marrakech	19	KC835884		Nicolas et al. (2014)
G. campestris	1-LG20	Morocco	20 km N Marrakech	19	KC835885		Nicolas et al. (2014)
G. campestris	1-LG21	Morocco	20 km N Marrakech	19	KC835886		Nicolas et al. (2014)
G. campestris	1-LG22	Morocco	20 km N Marrakech	19	KC835887		Nicolas et al. (2014)
G. campestris	1-LG24	Morocco	20 km N Marrakech	19	KC835888		Nicolas et al. (2014)
G. campestris	1-LG25	Morocco	20 km N Marrakech	19	KC835889		Nicolas et al. (2014)
G. campestris	1-LG26	Morocco	3 km S Essaouira	18	KC835890		Nicolas et al. (2014)
G. campestris	1-LG27	Morocco	3 km S Essaouira	18	KC835891		Nicolas et al. (2014)
G. campestris	1-LG28	Morocco	3 km S Essaouira	18	KC835892		Nicolas et al. (2014)
G. campestris	1-LG37	Morocco	5 km S Essaouira	17	KC835893		Nicolas et al. (2014)
G. campestris	1-LG38	Morocco	5 km S Essaouira	17	KC835894		Nicolas et al. (2014)
G. campestris	1-LG39	Morocco	5 km S Essaouira	17	KC835895		Nicolas et al. (2014)

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APPENDIX I. (continued)

Species	Spec. code	Country	Locality	Locality code	GenBank N°	Voucher N°	Reference
G. campestris	1-LG40	Morocco	5 km S Essaouira	17	KC835896		Nicolas et al. (2014)
G. campestris	1-LG41	Morocco	5 km S Essaouira	17	KC835897		Nicolas et al. (2014)
G. campestris	1-LG42	Morocco	5 km S Essaouira	17	KC835898		Nicolas et al. (2014)
G. campestris	1-LG43	Morocco	5 km S Essaouira	17	KC835899		Nicolas et al. (2014)
G. campestris	1-LG48	Morocco	20 km S Essaouira	16	KC835900		Nicolas et al. (2014)
G. campestris	1-LG51	Morocco	20 km S Essaouira	16	KC835901		Nicolas et al. (2014)
G. campestris	3-LG52	Morocco	20 km S Essaouira	16	KC835902		Nicolas et al. (2014)
G. campestris	1-LG53	Morocco	20 km S Essaouira	16	KC835903		Nicolas et al. (2014)
G. campestris	1-LG57	Morocco	3 km S Oued Souss	15	KC835904		Nicolas et al. (2014)
G. campestris	1-LG58	Morocco	3 km S Oued Souss	15	KC835905		Nicolas et al. (2014)
G. campestris	3-LG60	Morocco	5 km S Oued Souss	14	KC835906		Nicolas et al. (2014)
G. campestris	1-LG61	Morocco	5 km S Oued Souss	14	KC835907		Nicolas et al. (2014)
G. campestris	1-002VV2	Morocco	Boujdour	13	KC835916		Nicolas et al. (2014)
G. campestris	4-97	Algeria	Hadjeb El Djemel	12	KC835862		Nicolas et al. (2014)
G. campestris	4-119	Algeria	Hadjeb El Djemel	12	KC835863		Nicolas et al. (2014)
G. campestris	4-163	Algeria	Hadjeb El Djemel	12	KC835864		Nicolas et al. (2014)
G. campestris	4-063VV1	Tunisia	Sidi Bouzid	11	KC835910		Nicolas et al. (2014)
G. campestris	4-064VV1	Tunisia	Sidi Bouzid	11	KC835911		Nicolas et al. (2014)
G. campestris	4-26BH	Tunisia	Bouhedma	10	GU356565		Nicolas et al. (2014)
G. campestris	4-18HM	Tunisia	Hammamet	9	GU356566		Nicolas et al. (2014)
G. campestris	4-6HM	Tunisia	Hammamet	9	GU356567		Nicolas et al. (2014)
G. campestris	4-20HM	Tunisia	Hammamet	9	GU356568		Nicolas et al. (2014)
G. campestris	4-13HM	Tunisia	Hammamet	9	GU356569		Nicolas et al. (2014)
G. campestris	4-17HM	Tunisia	Hammamet	9	GU356570		Nicolas et al. (2014)
G. campestris	2-M5959	Mali	Tessalit	8	KC835865		Nicolas et al. (2014)
G. campestris	2-M6066	Mali	Tessalit	8	KC835866		Nicolas et al. (2014)
G. campestris	2-TES38	Mali	Tessalit	8	KC835919		Nicolas et al. (2014)
G. campestris	2-030VV1	Mali	Edjerir (Adrar des Iforas)	1	KC835912		Nicolas et al. (2014)

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APPENDIX I. (continued)

G. campestris	2-034VV1	Mali	Edjerir (Adrar des Iforas)	1	KC835913	Nicolas et al. (2014)
G. campestris	2-652801	Niger	Aïr	7	JN652801	Nicolas et al. (2014)
G. campestris	2-040VV1	Niger	Aïr	7	KC835914	Nicolas et al. (2014)
G. campestris	2-278VV2	Niger	Gougaram	6	KC835915	Nicolas et al. (2014)
G. campestris	NMP48282	Libya	Gadamis	5	KM236116	Chevret et al. (2014)
G. campestris	1999040	Niger	Aïr (Agadez)	7	KF496218	Ndiaye et al. (2013b)
G. campestris	LG78	Morocco	Souss Massa PN	4	JN021400	Ndiaye et al. (2012)
G. campestris	LG85	Morocco	Aglou	3	JN021401	Ndiaye et al. (2012)
G. campestris	LZP2009-132	Mali	Sinkerma	2	JX292894	Schwan et al. (2012)
G. campestris	1999030	Mali	Edjerir (Adrar des Iforas)	1	AJ851271	Chevret & Dobigny (2005)
G. henleyi		Morocco			MH660911	Bouarakia et al. (2018)
G. hesperinus		Morocco			JN652803	Ndiaye et al. (2012)
G. simoni		Morocco			MH660910	Bouarakia et al. (2018)

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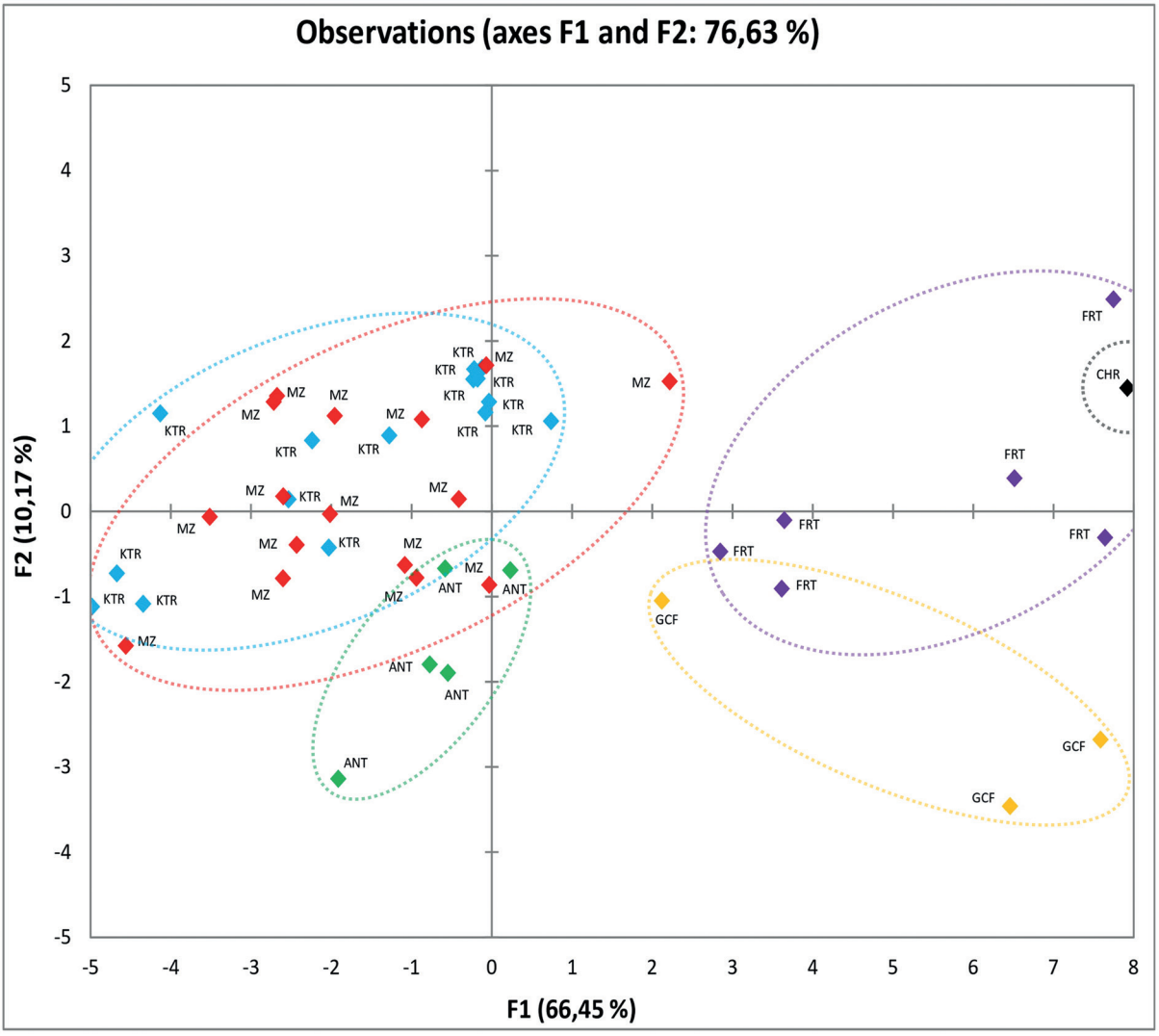
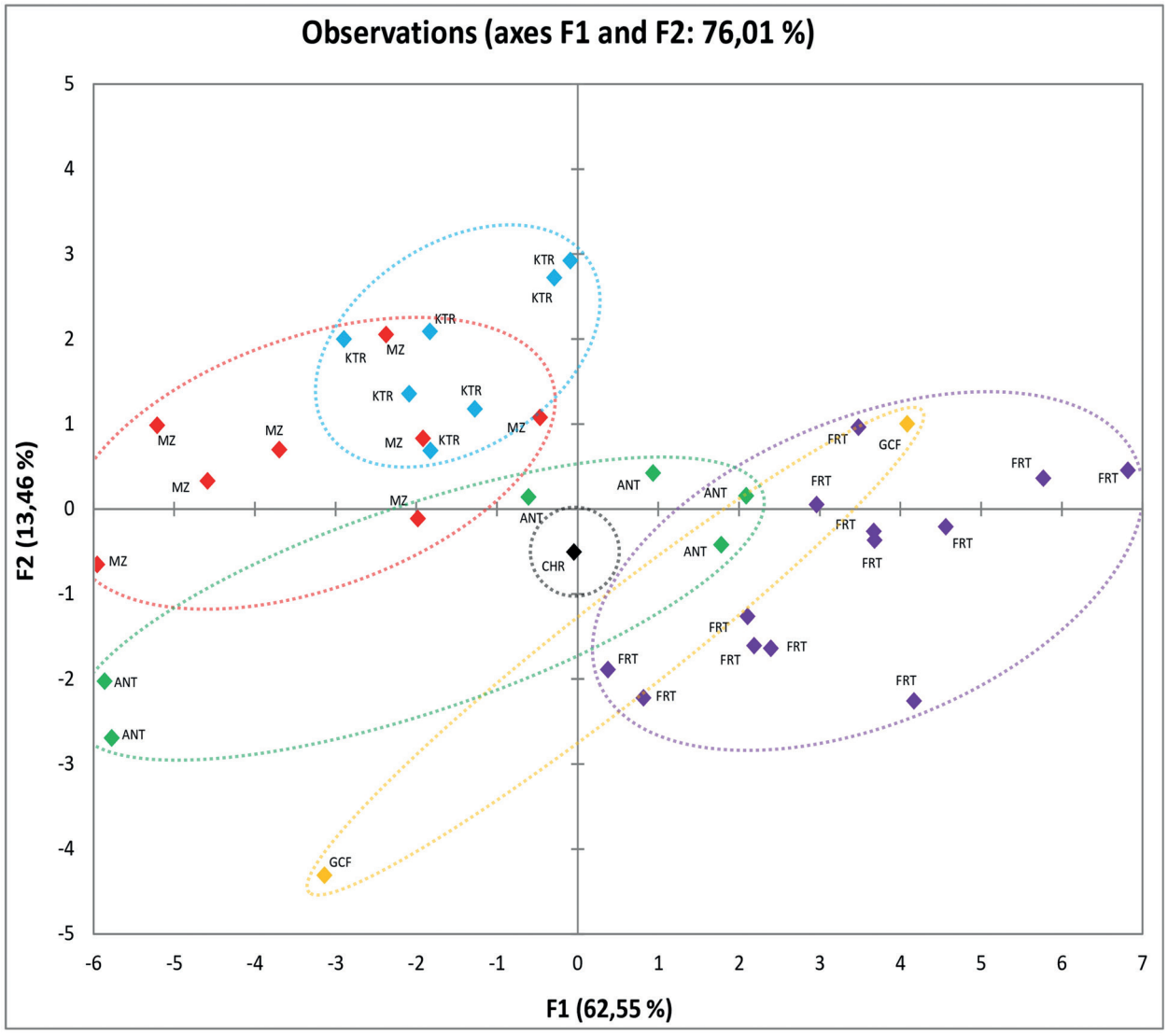
APPENDIX II.

Projection of male individuals on the first two axes (F1 and F2) of the principal component analysis (PCA). Different colours represent different localities (Chrouda: black; Aounate: green; Kenitra: blue; Merja Zerga: red; Guercif: orange; Fritissa: purple). The dashed ellipses (added for clarity) represent the six populations.



APPENDIX III.

Projection of female individuals on the first two axes (F1 and F2) of the principal component analysis (PCA). Different colours represent different localities (Chrouda: black; Aounate: green; Kenitra: blue; Merja Zerga: red; Guercif: orange; Fritissa: purple). The dashed ellipses (added for clarity) represent the six populations.



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Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.

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