

RESEARCH ARTICLE

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# A new species of brush-tailed mice of the genus *Calomyscus* from southern Iran (Calomyscidae: Rodentia)

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## Abstract

Calomyscidae is a monotypic family of muroid rodents with nine valid allopatric species distributed in southwestern Asia of which seven species have been so far recognized from Iran. The western and southern Zagros Mountains were thought to be home to a single species, *Calomyscus bailwardi*, but new researches revealed that the region is also home to four highly divergent molecular lineages. One of them was recently described as a new species (*C. behzadi*) but the taxonomic position of the other lineages remained unclear. Here we did an extensive sampling in southern Iran (2017-2018), during which 99 *Calomyscus* specimens were collected. Based on an integrated approach including karyotypic, mitochondrial as well as morphological data, we describe *Calomyscus kermanensis* sp. nov. as a new endemic species from the southern Zagros Mts (including Kohgiluyeh and Boyer-Ahmad, Fars, Kerman, Yazd and Hormozgan provinces), in the region that was previously thought to be occupied by *C. bailwardi*. The new species emerged as a new lineage with high intraspecific mtDNA and chromosome variations. The multivariate and univariate statistical analyses of craniodental measurements also separated *C. kermanensis* sp. nov. from other examined *Calomyscus* species with the highest maximum cranial height being the most distinctive of its craniodental features.

**Key words:** *Calomyscus*, karyotype, mitochondrial genes, morphometry, taxonomy, phylogeny, Zagros Mountains, Iran.

## INTRODUCTION

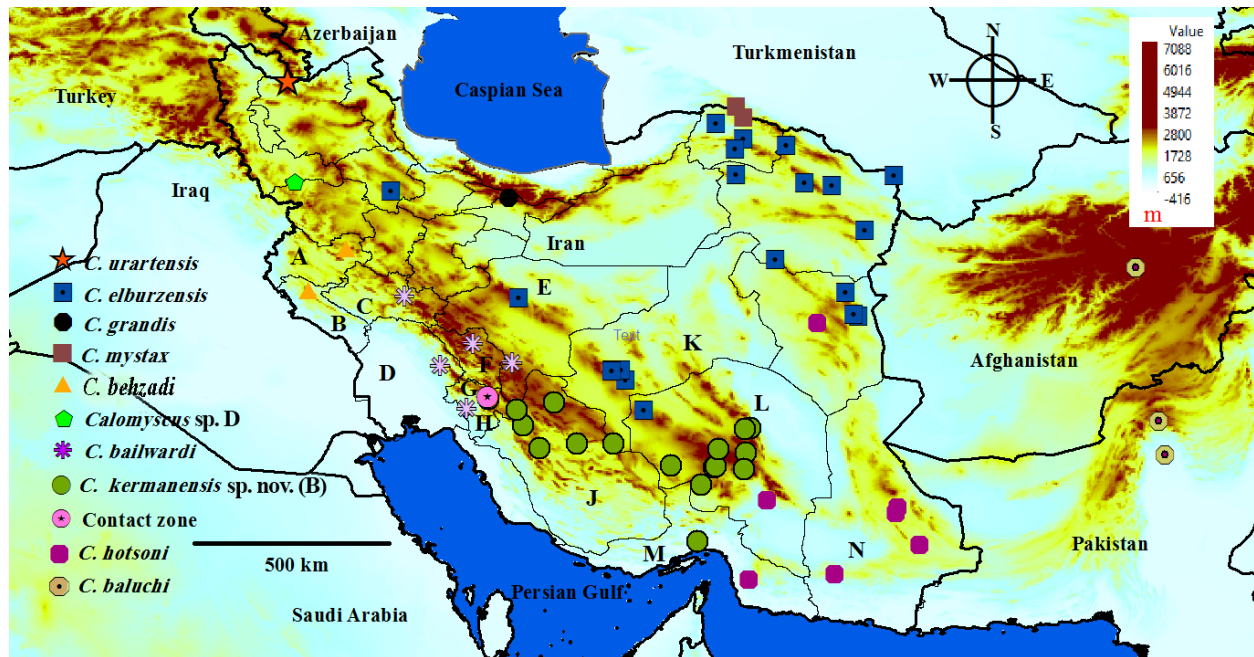
Calomyscidae is one of the oldest monotypic families of the Eumuroida clade, which is the sister group of Nesomyidae, Cricetidae, and Muridae families (Steppan et al., 2004; Steppan & Schenk, 2017). The taxonomic position of the genus *Calomyscus* Thomas, 1905 is still not fully resolved and the exact number of species remained controversial and underwent many changes since its first description. *C. bailwardi* Thomas, 1905 is the type species of the genus which was described from Mala-Imir (Izeh), Khuzestan Province, the South-West of Iran. Subsequently, *C. hotsoni* Thomas, 1920 and *C. baluchi*



Thomas, 1920 were described both from Pakistan based on small differences in skull morphometric and external features. Later, *C. mystax* Kaschkarov, 1925 from Balkhan Mountain, Turkmenistan, *C. elburzensis* Goodwin, 1939 from the Kurkhud Mts, Bojnurd (Iran), *C. grandis* Schlitter and Setzer, 1973 from Fasham, the southern of Elburz, Iran, *C. urartensis* Vorontsov and Kartavseva, 1979 from Nakhichevanskaya, Azerbaijan, and *C. tsolovi* Peshev, 1991 from the southwest of Syria were described, respectively. Some researchers also considered *Calomyscus* as a monotypic genus including *C. bailwardi* and all its nominal forms were classified as subspecies (Corbet & Hill, 1980; Ellerman, 1948; Ellerman & Morrison-Scott, 1951; Lay, 1967; Roberts, 1997). Specific status of some of these forms has been subsequently tested using karyotype analyses (Graphodatsky et al., 2000; Malikov et al., 1999; Akbarirad et al., 2016a, b, c; Meyer and Malikov, 1995, 2000; Shahabi et al., 2010; Rezazadeh et al., 2020; Romanenko et al., 2021), hybridization experiments (Meyer & Malikov, 2000; Graphodatsky et al., 2000), molecular phylogenies (Morshed & Patton, 2002; Norris et al., 2008; Shahabi et al., 2013, Akbarirad et al., 2016a, b; Rezazadeh et al., 2020), multivariate analyses of craniodental measurements (Lebedev et al., 1998; Shahabi et al., 2011; Akbarirad et al., 2016a, Rezazadeh et al., 2020), geometric morphometric analysis (Zarei et al., 2013; Akbarirad et al., 2016), and ecological survey (Hamidi et al., 2017) and niche modeling (Hamidi et al., 2019). The main problems in the taxonomy of this genus are related to high morphologic resemblance between species (e.g., *C. elburzensis* and *C. bailwardi*), intraspecific chromosomal variations (e.g., *C. elburzensis* and *C. hotsoni*), presence of natural hybrids between two different cytotypes of one species both in nature and in captivity (*C. elburzensis*), having the same karyotype in two distinct species (e.g., *C. grandis* and *C. mystax*) (Graphodatsky et al., 2000; Shahabi et al., 2011; Akbarirad et al., 2016a, c). Nevertheless, in the last published mammal checklists of the World (Musser and Carleton, 2005; Kilpatrick, 2017) eight allopatric species have been listed for this genus including: *C. bailwardi*, *C. hotsoni*, *C. baluchi*, *C. elburzensis*, *C. mystax*, *C. urartensis*, *C. grandis*, and *C. tsolovi*. The genus spread throughout the west of Asia in Turkmenistan, Iran, Pakistan, Afghanistan, and Syria (Musser and Carleton, 2005; Kilpatrick, 2017).

According to Akbarirad et al. (2015), six species of the genus *Calomyscus* occur in different mountainous areas in Iran including: *C. elburzensis*, *C. bailwardi*, *C. grandis*, *C. hotsoni*, *C. mystax* and *C. urartensis*. Recent studies have shown that molecular data have more information in determining species boundaries and phylogenetic relationships among the *Calomyscus* species (Norris et al., 2008; Shahabi et al., 2013; Akbarirad et al., 2016a; Rezazadeh et al., 2020).

According to Musser & Carleton (2005), *C. bailwardi* occupies a wide range in western Iran including Kurdistan, Ilam, Western Isfahan, Eastern Khuzistan, Lorestan, Fars to West of Kerman provinces, while the molecular data shown that its range is restricted only to Khuzestan province in Izeh (the type locality) and Behbahan (Akbarirad et al., 2016a). Previously, different cytotypes of *Calomyscus* from different localities along the Zagros Mountains ( $2N = 37 - 52$ ) (Graphodatsky et al., 2000), led to the assumption that the Zagros mountains were inhabited by possible undescribed species of this genus. Cytogenetic analyses can play an important role in the identifying of morphologically similar species but karyotypes in *Calomyscus* genus serve as an ambiguous indicator of their species rank (Romanenko et al., 2021). More recent molecular phylogenies revealed that four additional distinct lineages of *C. bailwardi* exists in the Zagros Mountains that may consider as new species (i) *C. bailwardi* from east of Khuzestan province; (ii) *Calomyscus* sp. group B (*C. cf. bailwardi*) from the southeastern part of the Zagros; (iii) *Calomyscus* sp. group C, the unnamed from Songhor in Kermanshah Province; (iv) *Calomyscus* sp. group D from Saghez in Kurdistan province and (v) *Calomyscus* sp. group G from west of Isfahan province (Akbarirad et al., 2016a; Rezazadeh et al., 2020; Kilpatrick, 2017). The latest study based on integrative methods classified group C from Kermanshah and Ilam provinces (western Iran) as a new species named *C. behzadi* Akbarirad et al, 2021 (Dezhman et al., 2021). However, taxonomic rank, diversity, and distribution of the other unnamed lineages remained obscure due to the lack of diagnostic morphological features as well as inadequate sampling for proper comparisons. In the present study, we describe a new species of brush-tailed mice from the southern part of Iran based on an integrative approach including molecular, morphometric and karyological studies with a considerable geographical sampling.



**FIGURE 1.** Map of *Calomyscus* specimens and localities in the present study was created using ArcGIS 10.7.1. A) Kurdistan, B) Ilam, C) Lorestan, D) Khuzistan, E) Isfahan, F) Chaharmahal and Bakhtiari, G) Contact zone H) Kohgiluyeh and Boyer-Ahmad, J) Fars, K) Yazd, L) Kerman and M) Hormozgan provinces.

**MATERIAL AND METHODS**

In total, 99 the brush-tailed mice were captured from 15 mountainous sites in western and southern Iran (2017-2018), 93 of which were included into the analyses and stored in ZMFUM (Zoological Museum of the Ferdowsi University of Mashhad) (Fig. 1, supplementary Table. 1). The collected specimens of this study are marked in bold. Because there is no useful morphological identification key for *Calomyscus* species, CYTB sequencing and karyotype analyses were used to identify the collected specimens (most of the specimens have CYTB sequences but here our molecular analyses were conducted on specimens that have sequences of both mitochondrial genes, CYTB and CO1. Complementary CYTB and CO1 sequences were downloaded from GenBank and used for phylogenetic analyses. Additional informations about examined specimens is presented in the supplementary Table. 1.

**TABLE 1.** Kimura-2-parameters genetic distance matrix on CYTB sequences (*Italics* are intraspecific distances).

	1	2	3	4	5	6	7	8	9	10
1. <i>C. bailwardi</i>	<i>0.018</i>									
2. <i>C. kermanensis sp. nov. (B)</i>	0.105	<i>0.035</i>								
3. <i>C. hotsoni</i>	0.102	0.094	<i>0.012</i>							
4. <i>C. behzadi</i>	0.160	0.158	0.148	<i>0.016</i>						
5. <i>C. elburzensis</i>	0.155	0.143	0.146	0.105	<i>0.018</i>					
6. <i>C. baluchi</i>	0.105	0.090	0.085	0.158	0.144	<i>0.018</i>				
7. <i>C. grandis</i>	0.149	0.154	0.144	0.092	0.086	0.155	<i>0.000</i>			
8. <i>C. urartensis</i>	0.172	0.148	0.154	0.096	0.091	0.142	0.096	<i>0.000</i>		
9. <i>Calomyscus sp. Group D</i>	0.158	0.139	0.140	0.106	0.095	0.135	0.092	0.069	<i>0.000</i>	
10. <i>C. mystax</i>	0.156	0.148	0.133	0.104	0.098	0.137	0.098	0.086	0.086	<i>0.022</i>

### DNA extraction and phylogenetic analyses

Genomic DNA was extracted from 99% of ethanol-preserved tissues using DENAzist Asia's Animal DNA isolation kit (S-1033-1). Polymerase chain reaction (PCR) amplification was conducted for two mitochondrial genes: CYTB using primers L7: 5'-ACT AAT GAC ATG AAA AAT CAT CGT/T3' and H6: 5'-TCT TCATTT TTG GTT TAC AAG AC-3' (Montgelard et al., 2002) and CO1 using BatL5310 (5' CCTACTCRGCCATTTTACCTATG 3') and R6036R (5' ACTTCTGGGTGTCCAAAGAATCA 3') (Herbeteau et al., 2011; Robins et al., 2007). Amplified DNA fragments were sequenced by MacroGen Inc, South Korea. Ambiguous sequence sites were checked using the Chromas (2.6.6) program and aligned using the CLUSTAL W algorithm in BioEdit software (Hall, 1999). Phylogenetic analyses were performed on a single combined matrix of CYTB and CO1 sequences. Best-fit models of nucleotide substitution were found with Bayesian inference information criterion using jModelTest2 (Darriba et al., 2012). Bayesian inference was (BI) performed using MrBayes 3.2.7a (Ronquist and Huelsenbeck, 2003) on the CIPRES Science Gateway3.3 (available online: [www.phylo.org](http://www.phylo.org)). We used the GTR+G+I model, two simultaneous runs with four Markov Chain Monte Carlo (MCMC), 80 million generations, sampling after every 10000 generations and discarding of the first 25% trees as 'burn-in'. The Maximum Likelihood (ML) trees based on GTR+ G+ I model and the bootstrap method with 1000 replications was constructed using software PhyML (Guindon et al., 2010). The average Kimura 2-parameters genetic distances for within and between species were calculated by MEGA 6 (Tamura et al., 2013) and ExcaliBAR (Aliabadian et al., 2014). *Spalax* from Spalacidae and *Rhizomys* from Rhizomyidae were chosen as outgroups following Akbarirad et al. (2016a).

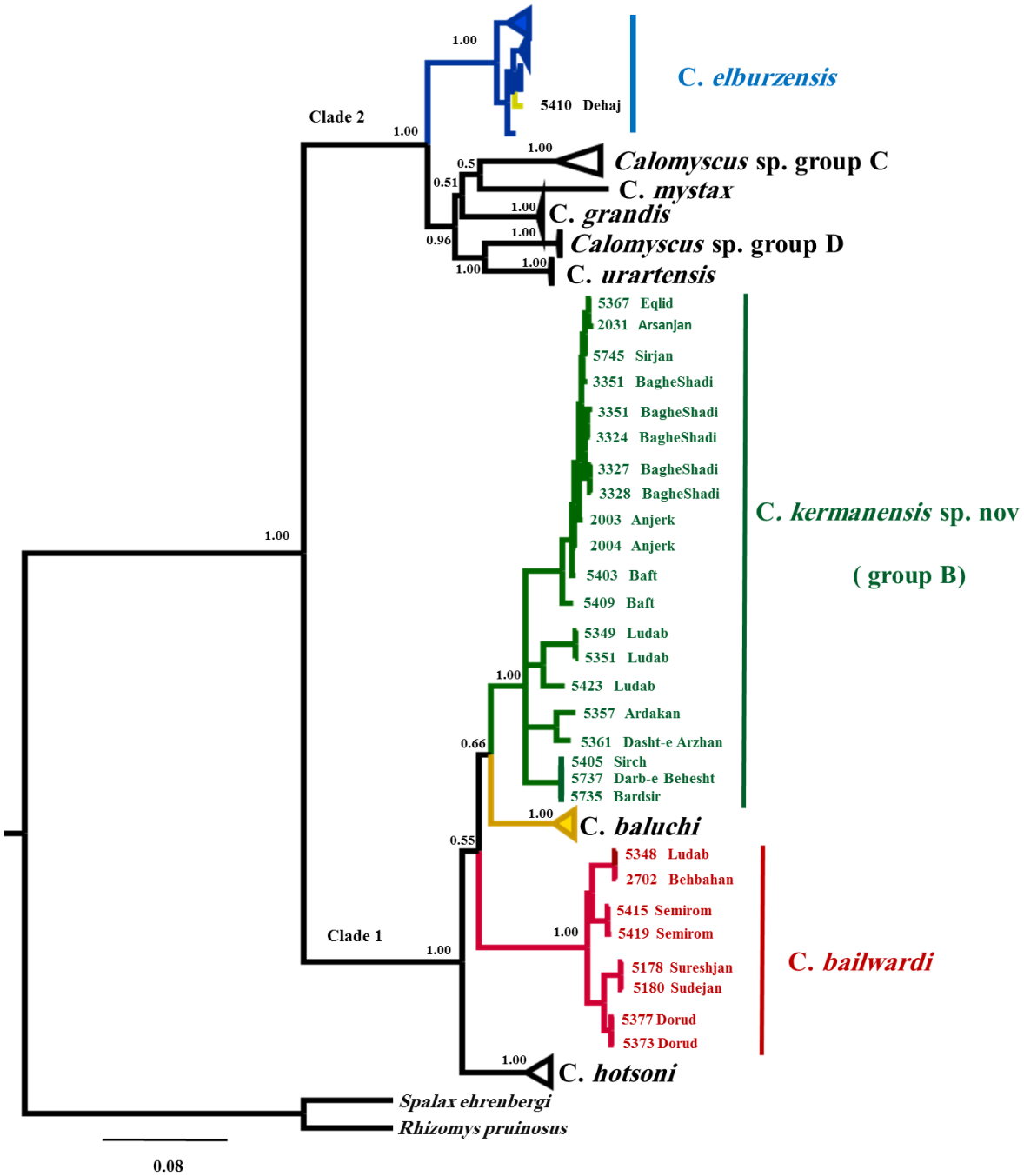
### Karyology analyses

For karyological study, 21 specimens (indicated by asterisked in the S Table 1) from different localities were transported alive to the laboratory. The conventional cytogenetic study was conducted according to Yosida (1973) and Dutrillaux et al. (1982) methods. The brush-tailed mice were exposed for 45 min at a dose of 10% vinblastine solution (1 ml/100 g of body weight) by intraperitoneal injection. Metaphase chromosome spreads were obtained from bone marrow cells. For each specimen, 15 slides were prepared and stained with Giemsa. Spreads of each specimen were subsequently photographed using a 100× magnification digital CCD camera attached to the Olympus BX53 microscope. The Ideogram of each specimen was prepared with the best metaphase spread photo by the Chromosome Image Processing software (CIP) Programmed in the Rodentology Research Department of the Ferdowsi University of Mashhad to determine the diploid chromosome number (2n), the fundamental number of autosomal arms (FN<sub>a</sub>), and the number of all chromosomal arms (FN).

### Morphometric analyses

In the present study, 181 specimens including 88 recently collected and 93 specimens deposited at ZMFUM Zoological Museum were studied (Fig. 1, S Table 1). We only used adults with fully erupted molars in morphometric analyses. Four external and thirty-one craniodental features were measured. We used a dissecting microscope equipped with an eyepiece graticule for dental measurements and a digital dial caliper (0.1 mm) for other measurements. The measurements were defined according to Peshev (1991) and Shahabi et al. (2011). For variables definition see S Fig. 1. Statistical analyses were performed on both uncorrected data (size + shape) and size-out data (shape) according to Navarro et al. (2004). In this size normalization, size is defined as the geometric mean between variables for every individual and shape is the log ratios of original variables divided by size. Data were checked for distribution normality and homogeneity of variance by Shapiro-Wilk (Shapiro and Wilk, 1965) and Levene's tests (Levene, 1960), respectively. Kruskal-Wallis ANOVA and Median test used for non-normal external measurement in univariate analyses. We used Welch's t-test and Student's t-test for normally distributed measurement with un-equal and equal variances, respectively. For pairwise comparison, one-way analysis of variance (ANOVA) and the Fisher LSD posthoc test were carried out to check for the statistically significant differences between groups. A Two-way multivariate analysis of variance (MANOVA) was performed to

evaluate sexual dimorphism and differences between species. A discriminant analysis (DA) was performed on the classified craniodental measurements to confirm between-group separation in multivariate space. All morphometric statistical analyses were conducted with the STATISTICA 12 software (Statsoft, 2015). We obtained a distance matrix derived from squared Mahalanobis distances of craniodental measurements among *Calomyscus* groups, as obtained in discriminant analysis and an unweighted UPGMA phenetic tree was constructed using MEGA 6 (Tamura et al., 2013).



**FIGURE 2.** Combined tree resulted from a Bayesian analysis on CYTB and CO1 genes. The posterior probability is indicated with numbers on each node.

## RESULTS

### Phylogenetic analysis

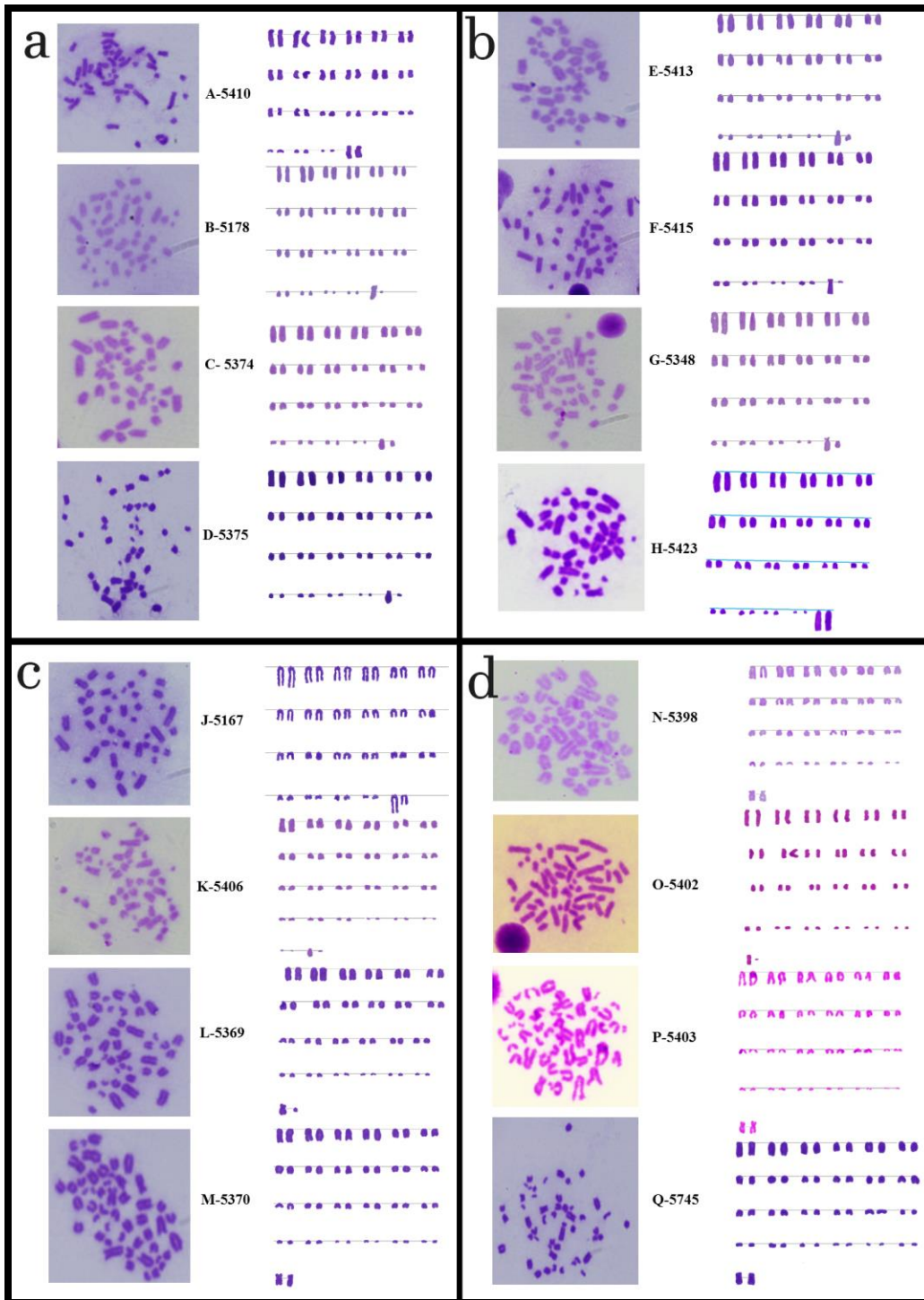
We sequenced 1,534 bp of two concatenated mitochondrial genes (988 bp of CYTB and 546 bp of CO1), which was found to have 441 variable sites (28 % of total sequence) and 523 mutations of which 403 (26%) were parsimony informative. The phylogenetic tree resulting from a combined matrix of CYTB and CO1 sequences by Bayesian inference is presented in Fig. 2. Two major clades with high supporting posterior values (BPP=1) found in the BI analyses. Clade 1 is comprised of *C. elburzensis*, *C. mystax*, *C. urartensis*, *C. grandis*, *C. behzadi* and *Calomyscus* sp. group D and clade 2 consisted of *C. bailwardi*, group B as new lineage, *C. hotsoni* and *C. baluchi*. *Calomyscus* sp. group B was placed as a sister taxon to *C. baluchi* and groups B + *C. baluchi* which in turn are the closest relatives of *C. bailwardi*. Interspecies relationships among *Calomyscus* sp. group B, *C. baluchi* and *C. bailwardi* are not resolved rather showing a polytomic branching. The Maximum likelihood tree also showed a similar topology to the Bayesian tree, except in the ML tree four subclades of Group B retrieved with moderate to low statistical support (S Fig. 2). Phylogenetic analyses showed that specimens from Dorud (Lorestan Province), Semirom (Isfahan Province), Sudejan, Sureshjan (Chaharmahal and Bakhtiari Province) and Ludab (Kohgiluyeh and Boyer-Ahmad Province) belonged to *C. bailwardi* (Fig. 1(C, E, H, F), 2) and specimens of northwest of Kerman province were placed into *C. elburzensis* (Fig. 1L, 2). Group B contains the specimens from the southern part of the Zagros and the Jebal-Barez mountains chain, including brush-tailed mice from Ludab, Kakan (Kohgiluyeh and Boyer-Ahmad Province), Ardakan, Dashte Arzhan, Eqlid, Arsanjan (Fars Provinces), Sirch, Baft, Khabr, Darbe Behesht, Sirjan (Kerman Province), BagheShadi (Yazd Province) and Genu mountains (Hormozgan Province) (Fig. 1; points H, J, K, L, M and Fig. 2).

### Genetic divergence

We found large genetic differences (Kimura 2-parameter) in the CYTB gene between all *Calomyscus* species groups ranging from 6.9% (between *C. urartensis* and *Calomyscus* sp. group D) to 17.2% (between *C. urartensis* and *C. bailwardi*) (Table 1). Group B was separated from other *Calomyscus* lineages by deep genetic K2P-distances (with *C. elburzensis* (14.3%), *C. mystax* (14.8%), *C. urartensis* (14.8%), *C. grandis* (15.4%), *C. behzadi* (15.8%), *Calomyscus* sp. group D (13.9%), *C. bailwardi* (10.5%), *C. hotsoni* (9.4%), and *C. baluchi* (9%). Among all examined brush-tailed mice, group B showed the highest mean (3.5%) of within lineage K2P-distance value (Table 1).

### Karyological results

A female specimen from Dehaj (northwest of Kerman province) had a karyotype of  $2n = 44$  and  $FNa = 70$  (Fig. 3A). Cytogenetic analysis of specimens from Dorud (Lorestan Province) ( $n=2$ ), Semirom (Isfahan Province) ( $n=2$ ), Sureshjan (Chaharmahal and Bakhtiari Province) ( $n=1$ ) and Ludab (Kohgiluyeh and Boyer-Ahmad Province) ( $n=1$ ) showed  $2n = 46$ ,  $FNa = 44$ ,  $FN = 48$  (Fig. 3B, C, D, E, F, G). This complement was composed of 22 pairs of acrocentric chromosomes and X and Y chromosomes were medium subtelocentric and short acrocentric, respectively. We found three different karyotypes for the populations belonging to the *Calomyscus* group B molecular clade: a specimen from Sirch (Kerman Province) presented a complement of  $2n = 52$ ,  $FNa = 56$  (Fig. 3K), specimens from Baft ( $n=3$ ), Sirjan (Kerman Province) ( $n=1$ ), and Eqlid ( $n=2$ ) showed  $2n = 50$ ,  $FNa = 48$  (Fig. 3L, M, N, O, P, Q) and one male and one female from Ludab (Kohgiluyeh and Boyer-Ahmad Province) indicated  $2n = 46$ ,  $FNa = 44$ ,  $FN = 46$  (Fig. 3H, J), the latest complement comprised 22 pairs of acrocentric autosomal chromosomes and X chromosomes were large acrocentric while the Y chromosome was short acrocentric. The karyotype of specimens from Ardakan and Dasht-e Arzhan (Fars Province) did not result in good chromosome spreads.



**FIGURE 3.** The karyotypes of *Calomyscus* specimens from different localities of southern Iran: A a female from Dehaj,  $2n = 44$  and  $FN_a = 70$  (*C. elburzensis isatissus*); B: a male from Sureshjan, C: a male from Dorud, D: a male from Dorud, E: a male from Semirom, F: a male from Semirom, G: a male from Ludab,  $2n = 46$ ,  $FN_a = 44$ ,  $FN = 48$  (*C. bailwardi*); H: a female from Ludab, J: a male from Ludab,  $2n = 46$ ,  $FN_a = 44$ ,  $FN = 46$ , K: a male from Sirch,  $2n = 52$ ,  $FN_a = 56$ , L: a male from Eqlid, M: a female from Eqlid, N: a female from Baft, O: a male from Baft, P: a female from Baft, Q: a female from Sirjan,  $2n = 50$ ,  $FN_a = 48$  (*Calomyscus* sp. group B). In each ideogram, sex chromosomes are placed at the end (XX or XY).

### Morphometric results

Based on MANOVA results, interaction between “sex” and “species” was not significant in both uncorrected data (Wilk’s = 0.48,  $F = 1.23$ , d.f. = 78,  $p = 0.09$ ) and shape data (Wilk’s = 0.41,  $F = 9$ , d.f. = 120,  $p = 0.6$ ). Multivariate analysis of variance showed that *Calomyscus* group B presented a significant difference with all other groups ( $p$ -values < 0.000007). Discriminant analysis (DA) based on craniodental variables correctly identified 91.71% and 90% of examined specimens according to uncorrected data and shape data, respectively. This analysis demonstrated that the first and second canonical functions explained 59% and 58% of the whole variance, respectively. The cross-validation test indicated that 94.59% and 94% of specimens in group B were classified to the actual group in size and size-free data, respectively. The plot of *Calomyscus* specimens based on the first two functions showed that the samples belonging to group B were distinct from the other groups (Fig 4, 5). Univariate analysis on skull size (geometric mean between variables) showed that group B had a significantly different value in comparison with all other groups ( $P < 0.05$ ) (except with *C. behzadi*). The skull size is larger than *C. elburzensis* and *C. hotsoni* and smaller than *C. bailwardi*, *C. baluchi*, *C. grandis* and *Calomyscus* sp. group D. This group had significantly smaller dental size compared to *Calomyscus* sp. group D, *C. behzadi* and *C. baluchi* (S Table 2). The UPGMA tree based on Squared Mahalanobis Distances of both uncorrected data and shape data revealed that group B and *C. bailwardi* are morphologically more similar (Fig 6). The result of Welch’s t-test and Student’s t-test was similar to the result of a One-way analysis of variance (ANOVA) with the Fisher’s LSD post-hoc test. The result of Welch’s t-test and Student’s t-test are presented in (S Table 2). These results show that group B is significantly different from other species in several craniodental measurements.

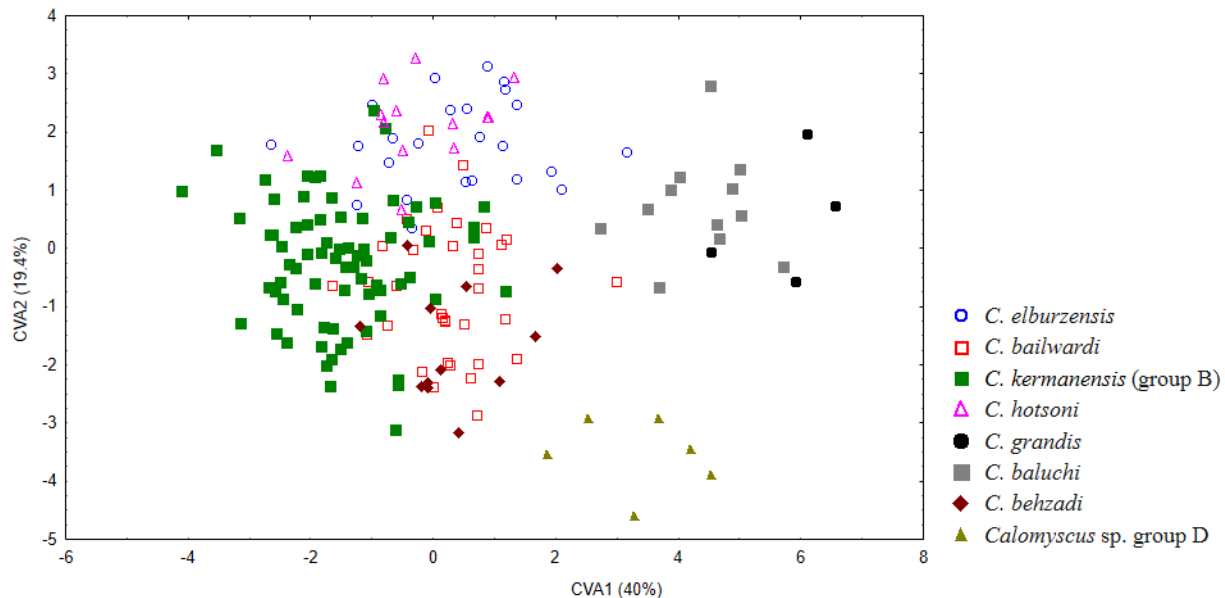


FIGURE 4. Scatter plot of the first two canonical functions for craniodental measurements (Size + shape)

### DISCUSSION

#### Taxonomy

#### *Calomyscus kermanensis* sp. nov.

#### Holotype

ZMFUM-5406, ♂, Sirch region of Kerman province (Fig. 8J), Iran (30°11'60"N, 57°32'60"E), Elevation of 1862 m, collected on 30 August 2017 by M. Dezhman. The holotype consists of skin skull (Fig. 7), karyotype slides and tissues preserved in 99% ethanol (all parts in good condition).

**Holotype measurements:** BL: 78; TL: 92; FL: 21; EL: 21; CBL: 22.67; SH: 8.23; Mndl: 13.37



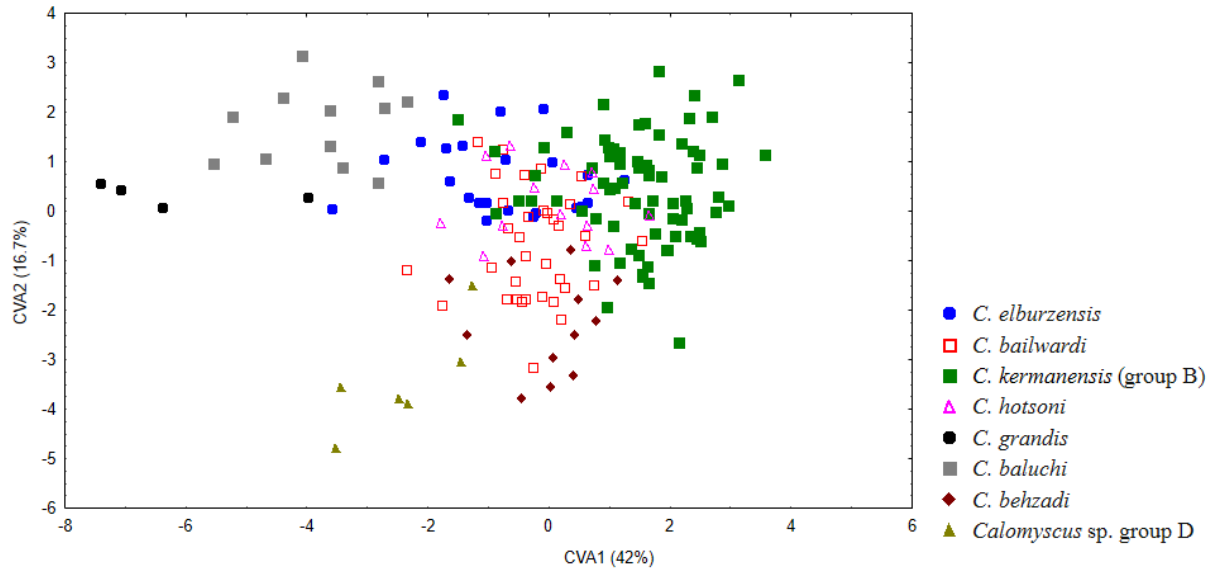


FIGURE 5. Scatter plot of the first two canonical functions for craniodental measurements (Shape).

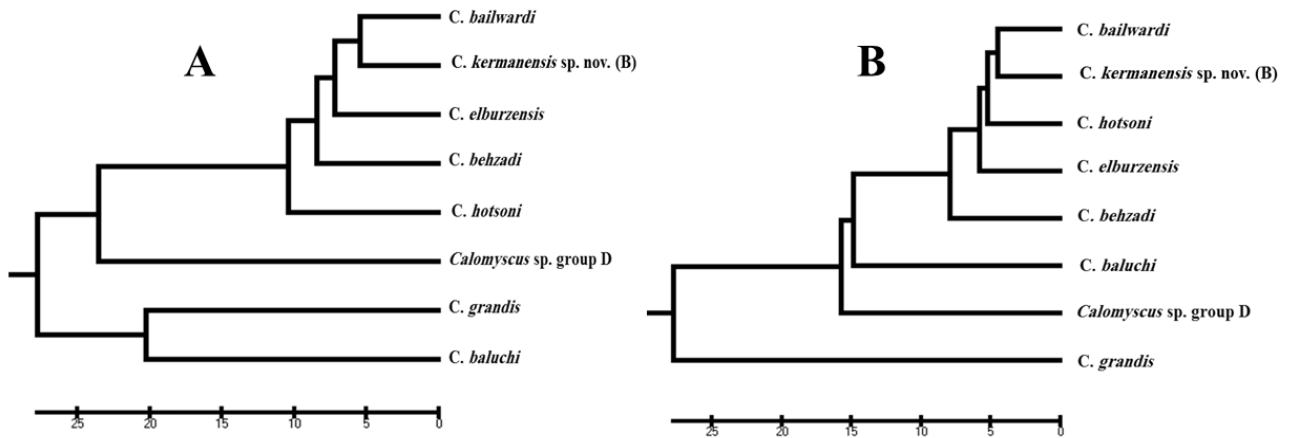


FIGURE 6. UPGMA tree derived from Mahalanobis distances of craniodental measurements between *Calomyscus* groups A: size+shape and B: shape.

**Paratypes**

ZMFUM-5407, ♀; ZMFUM-5389, ♂; ZMFUM-5391, ♀; ZMFUM-5392, ♂ and ZMFUM-5394, an ♀ from Sirch in Kerman province, Iran (30° 11' 60"N, 57° 32' 60"E), other data same as holotype.

**Paratype measurements**

ZMFUM-5407: BL: 78; TL: 94; FL: 21; EL: 20; CBL: 22.60; SH: 8.36; Mndl: 13.53; ZMFUM-5389: BL: 78; TL: 87; FL: 21; EL: 19; CBL: 22.56 SH: 8.1; Mndl: 13.03; ZMFUM-5391: BL: 78; TL: 88; FL: 21; EL: 20; CBL: 23.25; SH: 8.08; Mndl: 13.06; ZMFUM-5392: BL: 78; TL: 89; FL: 21; EL: 20; CBL: 23.13; SH: 8.39; Mndl: 13.49; ZMFUM-5394: BL: 74; TL: 93; FL: 21; EL: 20; CBL: 22.45; SH: 8.2; Mndl: 13.1



**FIGURE 7.** lateral (a), dorsal (b) and ventral (c) views of body, dorsal (d) and ventral (e) side of the cranium and external view of mandible (f) in holotype of *C. kermanensis* sp. nov. (Sirch region of Kerman province, Iran).

**Etymology:** The new species name refers to Kerman province where holotype and paratypes were collected.

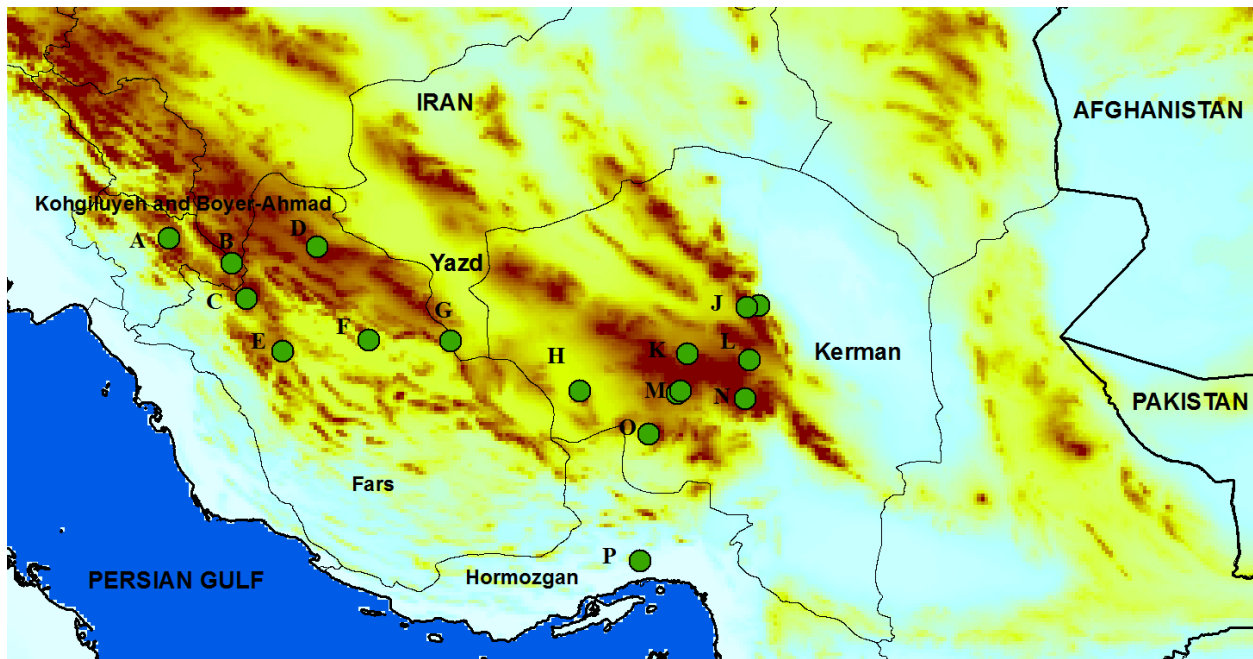
**Description:** The medium-size brush-tailed mice with body length 65–91 mm, tail length 74–102 mm, ear length 17–21 mm, hindfoot length 18–23 mm. The coloration of the specimens is similar to *C. bailwardi*. Adult specimens have light brown color on their back. Hairs of the middle part of dorsal side are grey in the base and tip and were light brown in the middle. Ventral side is pure white. The ears are long and nearly naked. The tail is longer than the head and body length and is bicolored, greyish buff above and darkening terminally to blackish and covered by sparse hairs throughout the length with a slight brush at the tip. The skull is small and narrow. The rostrum is long and narrow and the braincase is rounded. The incisors are smooth and compressed. The first molar is the longest and the third molar is the shortest. The molars are brachyodont, with an asymmetrical bi-serial arrangement of five cusps on the first two molars and the third molar only with three cusps.

**Diagnosis:** Although the external morphology of *Calomyscus* species is so similar, several craniodental measurements can distinguish *C. kermanensis* sp. nov. from the majority of others (S Table. 2). *C. kermanensis* sp. nov. has the highest cranial height in uncorrected data, but it does not differ significantly from *C. bailwardi*. The new species has a longer condylobasal than *C. hotsoni* and *C. elburzensis*, but it is shorter than *C. baluchi*, *C. behzadi*, *Calomyscus* sp. group D., and *C. bailwardi*. *C. kermanensis* sp. nov. has a longer mandible than *C. hotsoni* and *C. elburzensis*, but it is shorter than *C. baluchi*, *C. behzadi*, *Calomyscus* sp. group D., and *C. bailwardi*. The new species has longer ears than *C. grandis*, *C. behzadi*, *C. hotsoni* and *C. elburzensis*. *C. kermanensis* sp. nov. has shorter nasal than *C. hotsoni*, *C. behzadi*, *Calomyscus* sp. group D, *C. grandis* and *C. elburzensis* and narrower than *C. behzadi*, *Calomyscus* sp. group D, *C. bailwardi* and *C. baluchi* and *C. grandis*. This new species has shorter palatal than *Calomyscus* sp. group D, *C. behzadi*, *C. baluchi* and *C. grandis* and longer than *C. hotsoni*. *C.*

*kermanensis* sp. nov. has narrower interorbital than *C. behzadi*, *Calomyscus* sp. group D, *C. bailwardi* and longer interorbital than *C. elburzensis* and *C. baluchi*. Also, M2 is shorter than *C. baluchi*, *C. behzadi*, *Calomyscus* sp. group D and *C. elburzensis* and narrower than *C. baluchi*, *C. behzadi*, *Calomyscus* sp. group D, *C. grandis* and *C. hotsoni*. In addition to, zygomatic is wider than *C. hotsoni* and narrower than *C. behzadi*, *Calomyscus* sp. group D, *C. bailwardi* and *C. baluchi*.

According to size-free data, the new species has the highest cranium height of all the studied species, and nasal is wider than *C. grandis* but narrower than *C. elburzensis*, *C. bailwardi*, *C. baluchi*, *C. behzadi* and *Calomyscus* sp. group D., and nasal is shorter than *C. elburzensis*, *C. bailwardi*, *C. grandis* and *C. hotsoni*. Palatal is shorter than *C. elburzensis*, *C. baluchi* and *C. behzadi*. In this new species, occipitonasal is longer than *C. elburzensis*, *C. baluchi* and *C. grandis*. Bull is larger than *C. bailwardi*, *C. baluchi* and *C. behzadi*. *C. kermanensis* sp. nov. has longer M1 than *C. grandis*, *C. behzadi* and *Calomyscus* sp. group D and M1 is wider than *C. behzadi* and *Calomyscus* sp. group D and narrower than *C. hotsoni* and *C. baluchi*. M2 is shorter than *C. grandis*, *C. elburzensis* and *C. baluchi* and narrower than *C. grandis*, *C. hotsoni* and *C. baluchi*.

**Comparison:** Based on uncorrected data, in comparison with *C. bailwardi*, the new species has a smaller hind foot, narrower cranium, shorter upper diastema, narrower zygomatic, shorter occipitonasal, narrower interorbital, shorter condylobasal, shorter nasal, shorter lower diastema, lower height of lower diastema, lower mandibular height, longer mandible, narrower m2 and in shape data higher cranium, longer tympanic bulla, wider distance between two meatus, shorter and narrower nasal, shorter lower diastema and narrower m2. Comparison with the other groups is shown in S Table 2. The new species, *C. kermanensis* sp. nov. has three different cytotypes (or karyotypes) including: (1)  $2n = 52$ , FNa = 56, FN = 60; (2)  $2n = 50$ , FNa = 48, FN = 52 (this karyotype is similar to one of the karyotypes belonging to *C. hotsoni*) and (3)  $2n = 46$ , FNa = 44, FN = 46 (this karyotype is similar to the karyotype has already in *C. bailwardi* but they differ in X chromosome which is medium subtelocentric in *C. bailwardi* and large acrocentric in *C. kermanensis* sp. nov.



**FIGURE 8.** Sampling localities of *C. kermanensis* sp. nov. from the Zagros Mountains, south of Iran. A: Ludab; B: Kakan; C: Ardakan; E: Dasht-e Arzhan, D: Eqlid, F: Arsanjan; G: BagheShadi; J: Sirch, K: Bardsir L: Rayen, M: Baft, O: Khabr, N: Darb-e Behesht, H: Sirjan, and P: Genu Mountains.

**Distribution:** *C. kermanensis* sp. nov. is an endemic species in Iran and known from Ludab, Kakan (Kohgiluyeh and Boyer-Ahmad Province), Ardakan, Dasht-e Arzhan, Eqlid, Arsanjan (Fars Province),

Sirch, Baft, Khabr, Darb-e Behesht, Sirjan (Kerman Province), BagheShadi (Yazd Province) and Genu Mountains (Hormozgan province) in the northeast of Persian Gulf (Fig.8).

**Habitat:** *C. kermanensis* sp. nov. inhabits barren rocky and scarcely vegetated mountainsides with an altitude between 1773 to 2878 m (our own data) but reported only from 500 meters above sea level in Genu Mountains by Morshed & Patton (2002). One female gave birth to three offspring in captivity (June 2017). It seems that this new species has many fragmented populations and there are no major threats for its conservation.

The phylogenetic tree obtained from combined CYTB and COI sequences indicated two major clades within the genus *Calomyscus* which are consistent with recent studies based on nuclear and mitochondrial genes (Akbarirad et al., 2016a; Rezazadeh et al., 2020). Clade 1 includes *C. hotsoni*, *C. bailwardi*, *C. baluchi* and *C. kermanensis* sp. nov., and clade 2 includes *C. elburzensis*, *C. mystax*, *C. urartensis*, *C. grandis*, *C. behzadi* and *Calomyscus* sp. group D. In clade 2, *C. hotsoni* is a basal clade and *C. bailwardi* is the sister taxon of *C. kermanensis* sp. nov. + *C. baluchi* clade, but there is a polyphyletic pattern within this major clade. Also, in previous molecular studies based on mitochondrial genes, the relationships of this major clade were not fully resolved (Akbarirad et al., 2016a; Rezazadeh et al., 2020) but the only Bayesian tree obtained from the nuclear gene Rbp3 for a few specimens of brush-tailed mice showed that relationships of species in clade 1 were fully resolved. *C. baluchi* was basal clade and *C. bailwardi* and group B (*C. kermanensis* sp. nov.) were sister taxa and then *C. hotsoni* joined them (Rezazadeh, 2020). Furthermore, the Rbp3 gene network and genomic analyses separated specimens belong to group B (*C. kermanensis* sp. nov.) from *C. hotsoni* and *C. baluchi* and suggested that it could be a new species (Weller, 2019; Rawson, 2019).

Based on our molecular results, the range of *C. elburzensis isatissus* expanded to the northwest of Kerman Province. This subspecies occurs in Shirkuh Mountains in Yazd, Karkas Mt. in Isfahan and Qeydar Mts. in Zanjan Province (Akbarirad et al., 2016b). Also, one karyotype of our specimens ( $2n=44$  and  $Fna=70$ ) is the same with the complement reported for this subspecies (Graphodatsky et al., 2000; Shahabi et al., 2010; Akbarirad et al., 2016b). In previous studies, it was believed that *C. bailwardi* (with its type locality of Mala-i-Mir (or Izeh), Khuzistan Province) distributed in the Zagros Mountains from western and southwestern to east Iran, as far as Kerman and Hormozgan provinces (Thomas, 1905; Morshed and Patton, 2002; Musser and Carleton, 2005; Shahabi et al., 2013) with an unconfirmed report from Turkey only based on morphological features (Krystufek & Vohralik, 2009). While based on the molecular data, it has been confirmed so far from Izeh (type locality) and Behbahan (Khuzistan Province) (Akbarirad et al., 2016a). For the first time, our phylogenetic results and karyotypes data approve that *C. bailwardi* in addition to Izeh and Behbahan locality occurs in Dorud (Lorestan Province), Semrom (south of Isfahan), Sureshjan, Sudejan (Chaharmahal and Bakhtiari Province), and Ludab (Kohgiluyeh and Boyer-Ahmad Province) (Fig. 1, 2). The mean genetic distance based on CYTB sequences between *C. kermanensis* sp. nov. and all other examined *Calomyscus* groups is greater than 9% (9-15.8%), this range of distance values are commonly used to consider as interspecific divergences level in *Calomyscus* species (>6.9%) and other rodents (Bradley and Baker, 2001; Shahabi et al., 2013; Rosa et al., 2012). *C. kermanensis* sp. nov. has the highest interspecific K2P-distance value (3.5%), which is bigger than *C. elburzensis* (1.8%) with three known subspecies (Akbarirad et al., 2016b). This suggests that we need further analyses for a better understanding of intraspecific divergence in *C. kermanensis* sp. nov.

Our cytogenetic analysis, as well as Akbarirad et al. (2016a) and Romanenko et al. (2021) demonstrated that Zagros Mountains *Calomyscus* has only one karyotype,  $2n = 46$ ,  $FNa = 44$ ,  $FN = 46$ . Our phylogenetic analyses showed that specimens from Ludab, Kakan (Kohgiluyeh and Boyer-Ahmad Province), Ardakan, Dasht-e Arzhan, Eqlid, Arsanjan (Fars Province), Sirch, Baft, Khabr, Darb-e Behesht, Sirjan (Kerman Province), BagheShadi (Yazd Province) and Genu Mountains (Hormozgan province) are forming a new species (*C. kermanensis* sp. nov.). This result is consistent with Akbarirad et al. (2016a). For this new species, three different karyotypes were observed: (A)  $2n = 52$ ,  $FNa = 56$  for specimens from Sirch and Bardsir (Kerman Province), this karyotype has also been reported from Sirch

(Kerman Province) (Graphodatsky et al., 2000; Romanenko et al., 2021); (B)  $2n = 50$ ,  $FN_a = 48$  from Baft, Eqlid and Sirjan localities (Kerman Province). So far, two karyomorphs  $2n = 50$ ,  $FN_a = 48$  and  $2n = 50$ ,  $FN_a = 50$  have been reported from the same region (probably the same specimen) in Sivand (Fars Province) by Malikov et al. (1999) and Graphodatsky et al. (2000), respectively that according to the present study one of them is correct and a mistake has happened in sex chromosome recognition, so complement  $2n = 50$ ,  $FN_a = 48$  is correct. This karyotype of *C. kermanensis* sp. nov. is similar to one karyotype of *C. hotsoni* ( $2n = 50$ ,  $FN_a = 48$ ) from Saravan (Shahabi et al., 2010). Another similar karyotype was found for *C. mystax* and *C. grandis* ( $2n = 44$ ,  $FN_a = 46$ ) which can be explained by the existence of a shared ancestral cytotype in different region of the range or as an effect of convergent evolution (Graphodatsky et al., 2000); (C)  $2n = 46$ ,  $FN_a = 44$ ,  $FN = 46$  for specimens from Ludab (Kohgiluyeh and Boyer-Ahmad Province), although this karyotype in  $2n$  and  $FN_a$  are similar to the karyotype reported for *C. bailwardi* from the same locality and all of *C. bailwardi*'s distribution range, they differ in  $FN$  (48 vs. 46). In *C. bailwardi*, the X chromosome was submetacentric but specimens of the new lineage have a large acrocentric X chromosome. Cytogenetics analyses play an important role in identifying species with similar morphology (Romanenko et al., 2021). In the previous works, there was an unanswered question whether the extensive karyotypic diversity in *Calomyscus* indicates recent speciation incidents or an appearance of intraspecific polymorphism (Shahabi et al., 2010; Graphodatsky et al., 2000, Romanenko et al., 2021). Our result shows that each different karyotype usually has a distinct geographical distribution. The brush-tailed mice have patchily distributed populations which some of them being geographically isolated and increase random genetic drift effect and it may be a substantial factor in the rapid evolution of karyotypes (Graphodatsky et al., 2000). However, karyotype of *Calomyscus* individuals is an ambiguous indicator of their species status (Romanenko et al., 2021).

Based on both karyological and molecular data from Ludab (Kohgiluyeh and Boyer-Ahmad Province), *C. bailwardi* and *C. kermanensis* sp. nov. are sympatric so this locality was identified as a new contact zone (Fig. 1G), but gene flow among these two divergent lineages is unknown and will require further nuclear gene sequencing. This contact zone probably resulted from population expansion events by one or both species during the warmer interglacial periods. Other contact zones and hybridization have been reported in this genus between two divergent clades of *C. elburzensis* in the central Iranian Plateau (Shirkooch, Yazd province) (Haddadian and Darvish, 2018) and another one in central Kopet Dag Mountains (Meyer & Malikov, 2000). There is a report of male sterility in hybrids between two subspecies of *C. elburzensis* with two different cytotypes (Meyer & Malikov, 2000; Graphodatsky et al., 2000; Norris et al., 2008).

Forms (color, size, cranial and dental measurements) in the *Calomyscus* genus are so similar that they were often considered conspecific prior to investigations of karyotype, hybridization, and molecular analyses (Kilpatrick, 2017). Although *Calomyscus* species are similar in external morphology but univariate and multivariate analysis on craniodental measurements allowed us to separate *C. kermanensis* sp. nov. from the other *Calomyscus* groups in both uncorrected and shape data. Previous studies also showed that craniodental measurements can discriminate *Calomyscus* species while external features were not useful for species delimitation (Lebedev et al., 1998; Shahabi et al., 2011; Akbarirad et al., 2016a, Rezazadeh et al., 2020). This recommended new species share most of the morphometric characters with *C. bailwardi*.

In conclusion, we used an integrative taxonomic approach that included karyotypic, mitochondrial DNA and morphometric data and we found that *C. kermanensis* sp. nov. is an endemic species in southern Iran with significant craniodental and molecular variations. So, this result emphasizes the importance of integrative taxonomy in resolving the systematics of this genus. Intraspecific relationships in *C. kermanensis* sp. nov. were not resolved in our phylogenetic tree with high genetic and karyotype diversity; therefore, further studies should include more specimens, nuclear and mitochondrial markers as well as population genetic methods to clarify diversity, evolutionary history and phylogeography of the newly described species. We must also underline that the taxonomic structure of the other new lineages in this genus is still unclear.

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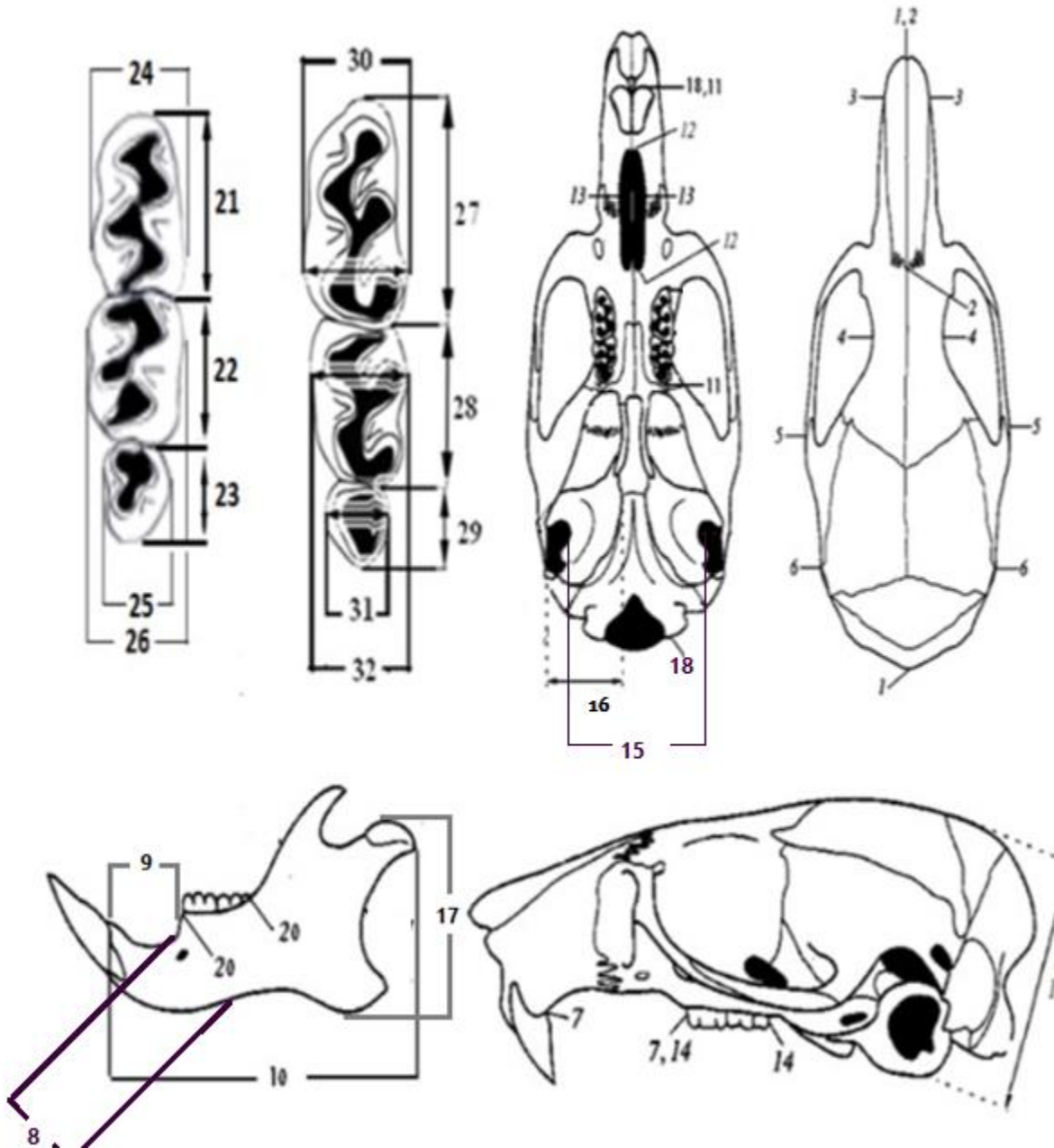
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**SUPPLEMENTARY FIGURE 1.** Thirty two craniodental characters were measured in examined samples of *Calomyscus* (Shahabi et al., 2011): 1- occipitonasal length (Occl); 2- nasal length (NL); 3- nasal width (NW); 4- interorbital width (Intw); 5- zygomatic width (ZW); 6- cranium width (CW); 7- upper diastema length (UDL); 8- height of lower diastema (HLD); 9- length of lower diastema (LLD); 10- mandible length (Mndl); 11- palatal length (Patl); 12- length of anterior palatine foramen (Forl); 13- width of anterior palatine foramen (Forw); 14- maxillary tooth row length (Mxl); 15- distance between two meatus (DB2M); 16- length of tympanic bulla (BULL); 17- maximum mandibular height (MH); 18- condylobasal length (CBL); 19- maximum cranial height (SH); 20- mandibular tooth row length (Mnl); 21- length of m1 (m1L); 22- length of m2 (m2L); 23- length of m3 (m3L); 24- width of m1 (m1W); 25- width of m2 (m2W); 26- width of m3 (m3W); 27- length of M1 (M1L); 28- length of M2 (M2L); 29- length of M3 (M3L); 30- width of M1 (M1W); 31- width of M2 (M2W); 32- width of M3 (M3W).



**Supplemental Table 1:** Details of sampled localities, tissue and voucher numbers and accession numbers of specimens examined in this study (for each sample the first accession number is for CYTB and the second is for CO1 genes). The specimens collected in this study are marked in **bold**. The specimens with successful karyotyping are indicated with an asterisk (Voucher no.).

Species	Locality (city, province)	Voucher no.	Accession no.	
			CYTB	CO1
<i>Calomyscus</i> sp. Group D	Saghez, Kurdistan	ZMFUM3869	KT878596	KT878556
<i>Calomyscus</i> sp. Group D	Saghez, Kurdistan	ZMFUM3870	KT878597	KT878557
<i>Calomyscus</i> sp. Group D	Saghez, Kurdistan	ZMFUM3878	KT878600	KT878560
<i>Calomyscus</i> sp. Group D	Saghez, Kurdistan	ZMFUM3881	KT878598	KT878558
<i>Calomyscus</i> sp. Group D	Saghez, Kurdistan	ZMFUM3882	KT878599	KT878559
<i>Calomyscus</i> sp. Group D	Saghez, Kurdistan	ZMFUM3897	KT878601	KT878561
<i>Calomyscus</i> sp. Group C	Songhor, Kermanshah	ZMFUM3871	KT878603	KT878563
<i>Calomyscus</i> sp. Group C	Songhor, Kermanshah	ZMFUM3880	KT878605	KT878565
<i>Calomyscus</i> sp. Group C	Songhor, Kermanshah	ZMFUM3891	KT878604	KT878564
<i>Calomyscus</i> sp. Group C	Songhor, Kermanshah	ZMFUM3896	KT878602	KT878562
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5380</b>	<b>MW888456</b>	
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5381</b>	<b>MW888461</b>	
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5382</b>	<b>MW888462</b>	<b>MW892625</b>
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5383</b>	<b>MW888457</b>	
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5384</b>	<b>MW888460</b>	<b>MW892623</b>
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5385</b>	<b>MW888459</b>	<b>MW892624</b>
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5386</b>	<b>MW888458</b>	
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5387</b>	<b>MW888463</b>	
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5388</b>		
<i>C. behzadi</i>	<b>Ilam, Ilam</b>	<b>ZMFUM 5379</b>		
<i>C. grandis</i>	Fasham, Tehran	ZMFUM 3992	KT884559	KT884587
<i>C. grandis</i>	Fasham, Tehran	ZMFUM1985	KT878591	KT878551
<i>C. grandis</i>	Fasham, Tehran	ZMFUM3992	KT878592	KT878552
<i>C. grandis</i>	Fasham, Tehran	ZMFUM1948	KT878593	KT878553
<i>C. grandis</i>	Fasham, Tehran	ZMFUM1943		
<i>C. mystax</i>	Taklah Quz, North Khorasan	ZMFUM 2984	KU129019	KU129021
<i>C. mystax</i>	Taklah Quz, North Khorasan	ZMFUM 3084	KU129020	
<i>C. elburzensis</i>	Mashhad, Khorasan-e-Razavi	ZMFUM1542	KT878581	KT878542
<i>C. elburzensis</i>	Mashhad, Khorasan-e-Razavi	ZMFUM2023		
<i>C. elburzensis</i>	Sarakhs, Khorasan-e-Razavi	ZMFUM1874	KT878585	KT878546
<i>C. elburzensis</i>	Sarakhs, Khorasan-e-Razavi	ZMFUM1922	KT878586	KT878547
<i>C. elburzensis</i>	Torbat, Khorasan-e-Razavi	ZMFUM2088	KT878587	KT878548
<i>C. elburzensis</i>	Saluk, North- Khorasan	ZMFUM2978	KT878588	KU043034
<i>C. elburzensis</i>	Shirvan, North- Khorasan	ZMFUM3533	KT878590	KT878550

<i>C. elburzensis</i>	Chenaran, North- Khorasan	ZMFUM3100		
<i>C. elburzensis</i>	Bijand, Gazik, South Khorasan	ZMFUM 4529	KT884557	KT884586
<i>C. elburzensis</i>	KhajeMor, Khorasan-e-Razavi	ZMFUM 1546	KT884547	KT884576
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2148	KT884550	KT884580
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2152	KT884551	KT884581
<i>C. elburzensis</i>	Ghaen, HajiAbad, South Khorasan	ZMFUM 3304	KT884553	KT884583
<i>C. elburzensis</i>	Kurkhud, North Khorasan	ZMFUM 3629	KT884555	KT884584
<i>C. elburzensis</i>	Sabzevar, Khorasan-e-Raza	ZMFUM 4490	KT884556	KT884585
<i>C. elburzensis</i>	Taft, Shirkuh, Godar-Nir, Yazd	ZMFUM 1	KU042999	KU043023
<i>C. elburzensis</i>	Taft, Shirkuh, Godar-Nir, Yazd	ZMFUM4	KU043000	KU043024
<i>C. elburzensis</i>	Taft, Shirkuh, Godar-Nir, Yazd	ZMFUM9	KU043001	KU043025
<i>C. elburzensis</i>	Taft, Shirkuh, Godar-Nir, Yazd	ZMFUM 10	KU043002	KU043026
<i>C. elburzensis</i>	Taft, Shirkuh, Yazd	ZMFUM 2932	KU043004	KU043027
<i>C. elburzensis</i>	Taft, Shirkuh, Cheshme, Yazd	ZMFUM 2948	KU043007	KU043029
<i>C. elburzensis</i>	Taft, Shirkuh, Yazd	ZMFUM 2952	KU043010	KU043030
<i>C. elburzensis</i>	Taft, Shirkuh, Tezerjan, Yazd	ZMFUM 3039	KU043015	KU043036
<i>C. elburzensis</i>	Qeidar, Zanjan	ZMFUM 3925	KU043020	KU043037
<i>C. elburzensis</i>	Qeidar, Zanjan	ZMFUM 3937	KU043021	KU043038
<i>C. elburzensis</i>	Karkas, Isfahan	ZMFUM 3938	KU043022	KU043039
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2144		
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2149		
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2172		
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2156		
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2169		
<i>C. elburzensis</i>	Neyshabur, Khorasan-e-Razavi	ZMFUM 2158		
<i>C. elburzensis</i>	Esfarayen, North Khorasan	ZMFUM 3224		
<i>C. elburzensis</i>	Saluk, Bojnurd,	ZMFUM 3085		
<i>C. elburzensis</i>	Bojnord, North Khorasan	ZMFUM 2616		
<i>C. elburzensis</i>	Esfaraieen, North Khorasan	ZMFUM 3216		
<i>C. elburzensis</i>	Nishapur, Razavi Khorasan	ZMFUM 2176		
<i>C. elburzensis</i>	Shirkuh , Yazd	ZMFUM 2949		
<i>C. elburzensis</i>	Shirkuh , Yazd	ZMFUM 2968		
<i>C. elburzensis</i>	Shirkuh , Yazd	ZMFUM 2945		
<i>C. elburzensis</i>	Mahriz, Kuhe-Bakhtaki, Yazd	ZMFUM 3088		
<i>C. elburzensis</i>	Shirkuh , Yazd	ZMFUM 3057		
<i>C. elburzensis</i>	<b>Dehaj, Kerman</b>	<b>ZMFUM 5410*</b>	<b>OP795973</b>	<b>OP784805</b>
<i>C. elburzensis</i>	<b>Dehaj, Kerman</b>	<b>ZMFUM 5411</b>		
<i>C. elburzensis</i>	<b>Dehaj, Kerman</b>	<b>ZMFUM 5414</b>		

<i>C. elburzensis</i>	<b>Dehaj, Kerman</b>	<b>ZMFUM 5416</b>		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 4391		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 4392		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 4393		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 4386		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5012		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 4404		
<i>C. kermanensis</i> sp. nov	Arsanjan, Fars	ZMFUM 2045		
<i>C. kermanensis</i> sp. nov	Geno, Hormozgan	ZMFUM 26		
<i>C. kermanensis</i> sp. nov	Geno, Hormozgan	ZMFUM 36		
<i>C. kermanensis</i> sp. nov	Geno, Hormozgan	ZMFUM 309		
<i>C. kermanensis</i> sp. nov	Geno, Hormozgan	191929 MVZ	KT878615	
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5011		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 4391		
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM 3050		
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM 3325		
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM 3340		
<i>C. kermanensis</i> sp. nov	Arsanjan, Fars	ZMFUM2029	-	
<i>C. kermanensis</i> sp. nov	Arsanjan, Fars	ZMFUM2030	KT878606	KT878569
<i>C. kermanensis</i> sp. nov	Arsanjan, Fars	ZMFUM2031	KT878607	KT878570
<i>C. kermanensis</i> sp. nov	Arsanjan, Fars	ZMFUM2044		
<i>C. kermanensis</i> sp. nov	Arsanjan, Fars	ZMFUM2046		
<i>C. kermanensis</i> sp. nov	Arsanjan, Fars	ZMFUM2048		
<i>C. kermanensis</i> sp. nov	<b>Ardakan, Fars</b>	<b>ZMFUM 5356</b>		
<i>C. kermanensis</i> sp. nov	<b>Ardakan, Fars</b>	<b>ZMFUM 5357</b>	<b>OP795976</b>	<b>OP784808</b>
<i>C. kermanensis</i> sp. nov	<b>Ardakan, Fars</b>	<b>ZMFUM 5358</b>		
<i>C. kermanensis</i> sp. nov	<b>Ardakan, Fars</b>	<b>ZMFUM 5359</b>		
<i>C. kermanensis</i> sp. nov	<b>Dasht-e Arzhan, Fars</b>	<b>ZMFUM 5360</b>		
<i>C. kermanensis</i> sp. nov	<b>Dasht-e Arzhan, Fars</b>	<b>ZMFUM 5361</b>	<b>OP795968</b>	<b>OP784800</b>
<i>C. kermanensis</i> sp. nov	<b>Dasht-e Arzhan, Fars</b>	<b>ZMFUM 5362</b>		
<i>C. kermanensis</i> sp. nov	<b>Ludab, Kohgiluyeh and Boyer-Ahmad</b>	<b>ZMFUM 5167*</b>		

<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5346		
<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5347		
<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5349	OP795975	OP784807
<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5351	OP795970	OP784802
<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5352		
<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5353		
<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5355		
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5363		
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5364		
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5365		
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5366	OP795972	OP784804
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5367	OP795977	OP784809
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5368		
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5369*		
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5370		
<i>C. kermanensis</i> sp. nov	Eqlid, Fars	ZMFUM 5371		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5389		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5390		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5391		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5392		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5394		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5398*		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5399		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5400		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5401		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5402*		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5403*	OP795966	OP784798
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5404		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5406*		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM 5407		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5408		
<i>C. kermanensis</i> sp. nov	Baft, Kerman	ZMFUM 5409	OP795965	OP784797



<i>C. kermanensis</i> sp. nov	Ludab, Kohgiluyeh and Boyer-Ahmad	ZMFUM 5423*	OP795979	OP784811
<i>C. kermanensis</i> sp. nov	Bardsir, Kerman	ZMFUM 5731		
<i>C. kermanensis</i> sp. nov	Bardsir, Kerman	ZMFUM 5732		
<i>C. kermanensis</i> sp. nov	Bardsir, Kerman	ZMFUM 5733		
<i>C. kermanensis</i> sp. nov	Bardsir, Kerman	ZMFUM 5734		
<i>C. kermanensis</i> sp. nov	Bardsir, Kerman	ZMFUM 5735		
<i>C. kermanensis</i> sp. nov	Darbehehesht, Kerman	ZMFUM 5736		
<i>C. kermanensis</i> sp. nov	Darbehehesht, Kerman	ZMFUM 5737	OP795980	OP784812
<i>C. kermanensis</i> sp. nov	Darbehehesht, Kerman	ZMFUM 5738		
<i>C. kermanensis</i> sp. nov	Darbehehesht, Kerman	ZMFUM 5739		
<i>C. kermanensis</i> sp. nov	Darbehehesht, Kerman	ZMFUM 5740		
<i>C. kermanensis</i> sp. nov	Sirjan, Kerman	ZMFUM 5741		
<i>C. kermanensis</i> sp. nov	Sirjan, Kerman	ZMFUM 5742		
<i>C. kermanensis</i> sp. nov	Sirjan, Kerman	ZMFUM 5743		
<i>C. kermanensis</i> sp. nov	Sirjan, Kerman	ZMFUM 5746		
<i>C. kermanensis</i> sp. nov	Sirjan, Kerman	ZMFUM 5744*		
<i>C. kermanensis</i> sp. nov	Sirjan, Kerman	ZMFUM 5745*		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM4392		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM4393		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM4386		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM5012		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM4404		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM5011		
<i>C. kermanensis</i> sp. nov	Kakan, Kohgiluyeh and Boyer-Ahmad	ZMFUM 391		
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM3324	KT878608	KT878571
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM3327	KT878609	KT878572
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM3328	KT878610	KT878573
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM3333	KT878611	KT878574
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM3351	KT878612	KT878575
<i>C. kermanensis</i> sp. nov	BagheShadi, Yazd	ZMFUM3353		
<i>C. kermanensis</i> sp. nov	Anjerk, Kerman	ZMFUM2003	KT878613	KT878566
<i>C. kermanensis</i> sp. nov	Anjerk, Kerman	ZMFUM2004	KT878614	KT878567

<i>C. kermanensis</i> sp. nov	Eqlid, Fras	ZMFUM5370*		
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	ZMFUM5405	OP795978	OP784810
<i>C. kermanensis</i> sp. nov	Khabr, Kerman	192039 MVZ	KT878616	
<i>C. kermanensis</i> sp. nov	Sirch, Kerman	191923 MVZ	KT878617	
<i>C. kermanensis</i> sp. nov	Rayen, Kemran	191936 MVZ	KT878618	
<i>C. kermanensis</i> sp. nov	Rayen, Kemran	191938 MVZ	KT878619	
<i>C. baluchi</i>	Pakistan, Sibi Dist	980 (OUT-13)		KT884596
<i>C. baluchi</i>	FATA, North Waziristan, Pakistan		EU135591.1	
<i>C. baluchi</i>	Balochistan, Kalat Dist., Pakistan		EU135586.1	
<i>C. baluchi</i>	Balochistan, Kalat, Pakistan		AY288509.1	
<i>C. baluchi</i>	Ziarat, Pakistan	ZTNH897		KT878579
<i>C. baluchi</i>	Datta Khel, Tore Shore, Pakistan	ZTNH1262		KT878580
<i>C. baluchi</i>	Bamyan, Afghanistan	ZMFUM2798		
<i>C. baluchi</i>	Takhte Waras, Afghanistan	ZMFUM2782		
<i>C. baluchi</i>	Yakawlang, , Afghanistan	ZMFUM2786		
<i>C. baluchi</i>	Bamyan, Afghanistan	ZMFUM2800		
<i>C. baluchi</i>	Yakawlang, , Afghanistan	ZMFUM2787		
<i>C. baluchi</i>	Yakawlang, , Afghanistan	ZMFUM2820		
<i>C. baluchi</i>	Yakawlang, , Afghanistan	ZMFUM2789		
<i>C. baluchi</i>	Surkh Joy, Afghanistan	ZMFUM2813		
<i>C. baluchi</i>	Afghanistan	ZMFUM 2718		
<i>C. baluchi</i>	Afghanistan	ZMFUM 2821		
<i>C. baluchi</i>	Afghanistan	ZMFUM2810		
<i>C. baluchi</i>	Pitab-Joy, Afghanistan	ZMFUM2784		
<i>C. hotsoni</i>	Bashagard, Hormozgan	ZMFUM4739		
<i>C. hotsoni</i>	Khash, Sistan and Baluchestan	ZMFUM 3563		
<i>C. hotsoni</i>	Zahedan, Sistan and Baluchestan	ZMFUM3564		
<i>C. hotsoni</i>	Zahedan, Sistan and Baluchestan	ZMFUM3529	KT884569	
<i>C. hotsoni</i>	Balouchestan, Sistan and Baluchestan	ZMFUM4409		
<i>C. hotsoni</i>	Saravan, Sistan and Baluchestan	ZMFUM3287	KT884565	
<i>C. hotsoni</i>	Bashagard, Sistan and Baluchestan	ZMFUM19		
<i>C. hotsoni</i>	Bashagard, Sistan and Baluchestan	ZMFUM4785		

<i>C. hotsoni</i>	Bashagard, Sistan and Baluchestan	ZMFUM4761		
<i>C. hotsoni</i>	Birjand, South Khorasan	ZMFUM4024		
<i>C. hotsoni</i>	Birjand, South Khorasan	ZMFUM4012		
<i>C. hotsoni</i>	Birjand, South Khorasan	ZMFUM4013		
<i>C. hotsoni</i>	Saravan, Sistan-o-Baluchistan	ZMFUM2068	KT884560	KT878577
<i>C. hotsoni</i>	Saravan, Sistan-o-Baluchistan	ZMFUM2069	KT884561	KT878578
<i>C. hotsoni</i>	Saravan, Sistan-o-Baluchistan	ZMFUM2102	KT884562	KT884588
<i>C. hotsoni</i>	Saravan, Sistan-o-Baluchistan	ZMFUM2103	KT884563	KT884589
<i>C. hotsoni</i>	Saravan, Sistan-o-Baluchistan	ZMFUM3286	KT884564	KT884590
<i>C. hotsoni</i>	Khash, Sistan-o-Baluchistan	ZMFUM3306	KT884567	KT884591
<i>C. hotsoni</i>	Zahedan, Sistan-o-Baluchistan	ZMFUM3962	KT884571	KT884593
<i>C. hotsoni</i>	Bagheran, Bijand, South Khorasan	ZMFUM4013	KT884573	KT884594
<i>C. bailwardi</i>	<b>Ludab, Kohgiluyeh and Boyer-Ahmad</b>	<b>ZMFUM5348*</b>	<b>OP795982</b>	<b>OP784814</b>
<i>C. bailwardi</i>	<b>Ludab, Kohgiluyeh and Boyer-Ahmad</b>	<b>ZMFUM</b>	<b>OP795974</b>	<b>OP784806</b>
<i>C. bailwardi</i>	<b>Sureshjan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5174</b>		
<i>C. bailwardi</i>	<b>Sureshjan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5175</b>		
<i>C. bailwardi</i>	<b>Sureshjan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5176</b>		
<i>C. bailwardi</i>	<b>Sureshjan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5177</b>		
<i>C. bailwardi</i>	<b>Sureshjan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5178*</b>	<b>OP795967</b>	<b>OP784799</b>
<i>C. bailwardi</i>	<b>Sureshjan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5179</b>		
<i>C. bailwardi</i>	<b>Sudejan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5180</b>	<b>OP795981</b>	<b>OP784813</b>
<i>C. bailwardi</i>	<b>Sudejan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5181</b>		
<i>C. bailwardi</i>	<b>Sureshjan, Chaharmahal and Bakhtiari</b>	<b>ZMFUM5158</b>		
<i>C. bailwardi</i>	<b>Dorud, Lorestan</b>	<b>ZMFUM5372</b>		
<i>C. bailwardi</i>	<b>Dorud, Lorestan</b>	<b>ZMFUM5373</b>	<b>OP795983</b>	<b>OP784815</b>
<i>C. bailwardi</i>	<b>Dorud, Lorestan</b>	<b>ZMFUM5374*</b>		
<i>C. bailwardi</i>	<b>Dorud, Lorestan</b>	<b>ZMFUM5375*</b>		
<i>C. bailwardi</i>	<b>Dorud, Lorestan</b>	<b>ZMFUM5376</b>		

<i>C. bailwardi</i>	Dorud, Lorestan	ZMFUM5377	OP795984	OP784816
<i>C. bailwardi</i>	Dorud, Lorestan	ZMFUM5378		
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5412		
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5413*		
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5415*	OP795969	OP784801
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5417		
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5418		
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5419	OP795971	OP784803
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5420		
<i>C. bailwardi</i>	Semirom, Isfahan	ZMFUM5421		
<i>C. bailwardi</i>	Behbahan, Khuzestan	ZMFUM2536		
<i>C. bailwardi</i>	Izeh, Khuzistan	ZMFUM3569	KT878621	
<i>C. bailwardi</i>	Izeh, Khuzistan	ZMFUM3570	KT878622	
<i>C. bailwardi</i>	Izeh, Khuzistan	ZMFUM3571	KT878623	
<i>C. bailwardi</i>	Izeh, Khuzistan	ZMFUM3578	KT878624	
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2514		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2516		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2522		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2524		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2529		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2536		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2700		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2701		
<i>C. bailwardi</i>	Behbahan, Khuzistan	ZMFUM2702	KT878620	
<i>C. urartensis</i>	Kordasht, Eastern Azerbaijan	ZMFUM2253	KT878594	KT878554
<i>C. uratensis</i>	Kordasht, Eastern Azerbaijan	ZMFUM2908	KT878595	KT878555

**Supplemental Table 2.** Means and standard errors of craniodental measurements in *Calomyscus* groups: *C. kermanensis* sp. nov. (Ke), *C. elburzensis* (El), *C. grandis* (Gr), *C. behzadi* (C), *Calomyscus* sp. group D (D), *C. bailwardi* (Bai), *C. hotsoni* (Ho), and *C. baluchi* (BA). Statistically significant differences are marked with a greater or lesser sign (>, <).

Variables	<i>C. elburzensis</i>	<i>C. bailwardi</i>	<i>C. kermanensis</i> sp. nov. (Group B)	<i>C. hotsoni</i>	<i>C. grandis</i>	<i>C. baluchi</i>	<i>C. behzadi</i>	<i>Calomyscus</i> sp. Group D	T test and Welch T test result (size + shape)	Shape data
BL	79.29±0.92	83.17±1.13	80.01±0.60	74.78±1.81	80.25±3.52	77.75±2.61	83.25±0.89	79.5±1.84		
TL	89.87±1.09	90.44±1.02	89.21±0.56	84.42±1.62	91.5±2.60	92.08±2.47	92.25±0.45	89.66±1.54		
El	17.54±0.39	19.64±0.26	19.34±0.10	17.5±0.59	13.75±1.75	17.5±0.66	18.08±0.23	18.5±0.43	Ke>El, Ke>C, Ke>Gr, Ke>Ho	
FL	20.16±0.19	21.92±0.26	20.80±0.12	19.07±0.35	20.75±0.48	20.66±0.33	21±0.28	20.83±0.48	Ke<Bai, Ke>Ho	
LLD	3.81±0.04	4.04±0.06	3.80±0.03	3.61±0.03	4.00±0.03	3.90±0.07	3.91±0.08	3.98±0.06	Ke<Gr, Ke>Ho, Ke<Bai	Ke <Bai, Ke<BA
HLD	2.29±0.02	2.37±0.03	2.27±0.01	2.29±0.02	2.37±0.05	2.4±0.02	2.23±0.04	2.38±0.02	BA>Ke, Ke<D, Ke<Bai	Ke<El, Ke<Ho, Ke>C
MH	5.86±0.04	6.08±0.04	5.91±0.03	6.01±0.07	6.12±0.07	6.07±0.03	6.00±0.06	6.30±0.07	BA>Ke, Ke<D, Ke<Bai	Ke<Ho
UDL	6.68±0.03	6.97±0.08	6.72±0.05	6.34±0.08	7.29±0.10	6.97±0.06	6.92±0.10	7.00±0.15	BA>Ke, Gr>Ke, Ke>Ho, Ke<Bai	Ke>Ho, Ke<Gr
NL	9.54±0.09	10.01±0.09	9.35±0.05	9.43±0.17	10.67±0.10	9.76±0.08	9.56±0.10	9.82±0.11	BA>Ke, Gr>Ke, Ke<D, Ke<El, Ke<Bai	Ke<El, Ke <Bai, Ke<Ho, Ke<Gr
ZW	12.35±0.06	12.69±0.10	12.32±0.05	11.96±0.09	12.67±0.09	12.96±0.09	12.61±0.015	12.91±0.13	BA>Ke, Ke>Ho, Ke<C, Ke<D, Ke<Bai	Ke<El, Ke<BA
Forl	4.81±0.04	4.89±0.06	4.79±0.03	4.64±0.07	5.31±0.04	5.00±0.05	4.71±0.09	4.79±0.09	BA>Ke, Gr>Ke	Ke<Gr, Ke>C
NW	2.92±0.03	3.09±0.03	2.89±0.03	2.87±0.06	3.41±0.06	3.44±0.07	3.12±0.08	3.57±0.07	BA>Ke, Gr>Ke, Ke<C, Ke<D,	Ke<El, Ke <Bai, Ke>Gr, Ke<BA,

									Ke<Bai	Ke<C, Ke<D
Patl	11.58±0.04	11.86±0.12	11.62±0.05	11.26±0.12	12.09±0.12	12.04±0.05	11.93±0.12	12.02±0.14	BA>Ke, Gr>Ke, Ke>Ho, Ke<C, Ke<D	Ke<El, Ke<BA, Ke<C
SH	7.89±0.04	8.07±0.04	8.15±0.02	7.76±0.07	7.76±0.12	7.91±0.05	8.02±0.07	7.95±0.11	BA<Ke, Gr<Ke, Ke>Ho, Ke>C, Ke>D, Ke>El	Ke>El, Ke >Bai, Ke>Ho, Ke>Gr, Ke>BA, Ke>C, Ke>D
Occl	25.05±0.10	26.31±0.22	25.55±0.10	24.80±0.21	26.01±0.23	25.98±0.07	25.98±0.19	26.25±0.29	BA>Ke, Ke>Ho, Ke>El, Ke<Bai	Ke>El, Ke>Gr, Ke>BA
CW	11.59±0.04	11.82±0.07	11.62±0.03	11.24±0.08	11.80±0.09	12.25±0.08	11.60±0.06	12.06±0.08	BA>Ke, Ke>Ho, Ke<D, Ke<Bai	Ke<BA, Ke>C
INTW	4.0±0.01	4.34±0.03	4.20±0.01	4.05±0.01	4.15±0.08	4.25±0.03	4.28±0.02	4.44±0.06	Ke>Ho, Ke<C, Ke<D, Ke>El, Ke<Bai	Ke>El, Ke>Gr
BULL	5.70±0.04	5.88±0.05	5.85±0.03	5.65±0.05	6.00±0.0	5.71±0.07	5.75±0.05	6.04±0.06	Gr>Ke, Ke>Ho, Ke>El	Ke >Bai, Ke>BA, Ke>C
CBL	22.09±0.10	23.09±0.17	22.55±0.09	21.69±0.18	23.24±0.17	23.22±0.08	22.91±0.12	23.45±0.24	BA>Ke, Ke>Ho, Ke<C, Ke<D, Ke>El, Ke<Bai	Ke<El, Ke>Ho
DB2M	8.10±0.06	8.26±0.06	8.20±0.04	7.99±0.08	8.89±0.11	8.81±0.04	8.16±0.06	8.41±0.14	BA>Ke, Gr>Ke	Ke >Bai, Ke<Gr, Ke<BA
Mxl	3.40±0.02	3.42±±0.03	3.40±0.01	3.41±0.03	3.32±0.04	3.51±0.04	3.50±0.04	3.45±0.07	BA>Ke, Ke<C	Ke>Ho, Ke>D
Mnl	3.37±0.02	3.33±0.03	3.34±0.01	3.37±0.04	3.33±0.04	3.47±0.06	3.47±0.02	3.54±0.04	BA>Ke, Ke<C, Ke<D	Ke<C, Ke<D
Mndl	12.92±0.06	13.42±0.09	13.10±0.05	12.61±0.08	13.51±0.14	13.43±0.04	13.50±0.05	13.70±0.08	BA>Ke, Ke>Ho, Ke<C, Ke<D, Ke>El, Ke<Bai	Ke<C
MIL	1.68±0.01	1.67±0.02	1.68±0.01	1.69±0.02	1.61±0.03	1.76±0.01	1.69±0.01	1.62±0.02	BA>Ke, Gr<Ke, Ke>D	Ke>Gr, Ke>C, Ke>D

M1W	1.13±0.01	1.11±0.01	1.11±0.01	1.15±0.01	1.13±0.01	1.19±0.01	1.11±0.01	1.10±0.01	BA>Ke, Ke<Ho	Ke<Ho, Ke<BA, Ke>C, Ke>D
M2L	1.27±0.01	1.23±0.01	1.22±0.01	1.24±0.02	1.27±0.02	1.32±0.02	1.28±0.02	1.27±0.04	BA>Ke, Ke<C, Ke<D, Ke<El	Ke<El, Ke<Gr, Ke<BA
M2W	1.07±0.01	1.07±0.01	1.06±0.01	1.09±0.01	1.12±0.01	1.15±0.01	1.09±0.01	1.12±0.01	BA>Ke, Gr>Ke, Ke<Ho, Ke<C, Ke<D	Ke<Ho, Ke<Gr, Ke<BA
M3L	0.62±0.01	0.64±0.01	0.64±0.01	0.64±0.01	0.61±0.03	0.66±0.01	0.66±0.02	0.71±0.02	Ke<D	
M3W	0.72±0.01	0.72±0.01	0.73±0.01	0.72±0.02	0.74±0.01	0.75±0.01	0.77±0.01	0.79±0.02	Ke<C, Ke<D	
m1l	1.44±0.01	1.46±0.02	1.46±0.01	1.49±0.02	1.47±0.03	1.48±0.01	1.49±0.02	1.50±0.02		Ke>El, Ke>BA,
m1W	0.96±0.01	1.00±0.01	1.00±0.01	1.01±0.01	0.97±0.01	1.01±0.01	0.99±0.01	1.00±0.01	Gr<Ke, Ke>El	Ke<El, Ke>BA, Ke>C
m2l	1.25±0.01	1.25±0.01	1.23±0.01	1.27±0.02	1.24±0.02	1.28±0.01	1.25±0.00	1.30±0.02	BA>Ke, Ke<Ho, Ke<C, Ke<D, Ke<El	Ke<El, Ke<Ho, Ke>C
m2W	1.05±0.01	1.10±0.01	1.06±0.00	1.08±0.01	1.06±0.01	1.11±0.01	1.07±0.01	1.06±0.02	BA>Ke, Ke<Bai	Ke>El, Ke<Bai, Ke>D
m3L	0.79±0.01	0.79±0.01	0.77±0.01	0.79±0.01	0.72±0.02	0.76±0.02	0.82±0.01	0.86±0.01	Gr<Ke, Ke<C, Ke<D	Ke>Gr, Ke>BA, Ke<C, Ke<D
m3w	0.71±0.01	0.72±0.01	0.71±0.00	0.71±0.01	0.70±0.02	0.74±0.01	0.72±0.02	0.75±0.01	BA>Ke, Ke<D	
dental size	6.14±0.029	6.13±0.045	6.11±0.020	6.17±0.059	6.06±0.063	6.35±0.045	6.28±0.048	6.3±0.080	C>Ke, BA>Ke, D>Ke	
Skull size	45.86±0.16	47.72±0.33	46.48±0.16	45.03±0.33	48±0.32	47.83±0.16	47.22±0.28	48.13±0.42	Ke>El, Ke<Bai, Ke>Ho, Ke<Gr, BA>Ke, Ke<D	