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Are cryptic species of the Lesser Egyptian Jerboa, *Jaculus jaculus* (Rodentia, Dipodidae), really cryptic? Re-evaluation of their taxonomic status with new data from Israel and Sinai

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Abstract

Two clades of the lesser Egyptian jerboa *Jaculus jaculus* sensu lato were recently described in North Africa and considered as cryptic species. Members of both clades are also found in Israel, where they can be easily identified according to fur and tail colouration and morphology of the male external genitalia, but cannot be separated confidently using skull characters. Examination of type specimens demonstrated that the correct names for the two species are *Jaculus jaculus* (Linnaeus 1758) and *Jaculus hirtipes* (Lichtenstein, 1823). Comparisons of geographic and habitat differences of the two species revealed a high niche divergence between them, slightly higher in the sympatric North African populations than in the parapatric populations of Israel and Sinai. A low niche divergence was detected between North African and Middle Eastern populations of *J. jaculus*, and a low niche convergence between North African and Middle Eastern populations of *J. hirtipes*. The levels of niche differentiation coincide with those of genetic differences.

Key words: Geographic distribution – ecological differentiation – genetic differentiation – taxonomy – nomenclature

Introduction

The lesser Egyptian jerboa, *Jaculus jaculus* (Linnaeus, 1758), inhabits North Africa, the Horn of Africa, the Arabian Peninsula and south-western Asia, from Morocco, Western Sahara, Mauritania and Senegal in the west, to Syria, Iraq, south-western Iran, Arabia, Sudan, Eritrea and Somalia in the east, and Mali, Niger, Nigeria, Chad and Sudan in the south. This extremely wide geographic distribution, together with the morphological and ecological polymorphism observed within and among localities, has resulted in attempts to divide the species into two independent sympatric species, the psammophilous *J. jaculus* and the sclerophyllous *J. deserti* (Ranck, 1968). However, these attempts were criticized by Harrison (1978) and Corbet (1978), who considered these two forms as eco-morphs rather than true species. Corbet and Harrison suggested that all key characters proposed for discrimination of the two forms by Ranck (1968) were extremely variable among individuals of the same populations. Nevertheless, the existence of these two forms in Egypt was supported and discussed by Osborn and Helmy (1980), who considered them to be 'colour phases' of the same species. The same two colour phases in Israel and Sinai were considered as different subspecies of *J. jaculus* by Mendelssohn and Yom-Tov (1999), who nonetheless reported that the two subspecies 'occur side by side in an area south-west of Be'er Sheva, and no intergrades have been found. In captivity 'mixed' pairs did not breed whereas 'pure' pairs of both subspecies reproduced' (Mendelssohn and Yom-Tov 1999, p386).

Recently, specimens from North Africa and the Middle East were intensively studied for morphometric, chromosomal, allozyme and DNA variability (Shahin 2003; Ben Faleh et al. 2009, 2010a,b,c; Ben Faleh et al. 2012, 2013; Boratyński et al. 2012, 2014). These studies provide evidence for the existence of three distinct clades which are well differentiated based on nuclear and mitochondrial DNA markers. Two of these three clades are widely sympatric across North Africa, and the genetic distance

between them is above the average recorded between sister rodent species (Ben Faleh et al. 2012; Boratyński et al. 2012, 2014). Hypotheses, such as a 'pronounced phylogeographic signature within the taxon *J. jaculus*' resulting from the ancient climate changes or the existence of pseudogenes, were considered and rejected (Ben Faleh et al. 2010a). The third clade seems to be allopatric, occurring in the Arabian Peninsula and the Middle East (Ben Faleh et al. 2012; Boratyński et al. 2014; B. Kryštufek, personal communication). The taxonomic status of this third (eastern) clade remains unclear because of its non-overlapping distribution with the first two clades and intermediate level of genetic divergence (between typical intraspecific and typical interspecific) from the second clade. Allozyme variation among Tunisian samples supports the existence of two African clades (Ben Faleh et al. 2010c), whereas results for Egypt (Shahin 2003) are not so clear. Analysis of skull morphometric characters (Ben Faleh et al. 2010a,c, 2013) demonstrated a significant morphological differentiation among the two North African species. The level of this separation, however, was insufficient to allow the allocation of each individual into its appropriate clade. No karyological differentiation was found between the two North African species (Ben Faleh et al. (2010a,b) – perhaps unsurprisingly, given the extremely stable karyotype of jerboas (Vorontzov and Malygina 1973). The above findings led Ben Faleh et al. (2010a,b,c) to categorize these two forms as 'cryptic' species.

The discovery of at least two separate species, within what was formerly considered as one polymorphic species, *J. jaculus*, raised some nomenclature problems. Ben Faleh et al. (2010c) and Boratyński et al. (2012) used the names *J. jaculus* and *J. deserti* for the North African species, following Ranck (1968). Aware of the nomenclature problems, however, Ben Faleh et al. (2010a,b,c) and Boratyński et al. (2014) cautiously used neutral terms (clades A and B or clades 1 and 2) for these forms. Ranck (1968) considered the first species as the nominate form (*Mus jaculus* Linnaeus, 1758) based on a comparison with topotypes but not with the holotype. This is problematic, because the two species are largely sympatric. It is difficult to understand why

Ranck (1968) chose the name *Dipus deserti* Loche, 1867 for the second species without taking potential senior synonyms into consideration.

Here, we sought to identify the species of the *Jaculus jaculus* complex occurring in Israel and its neighbouring countries, to solve arising nomenclature problems, to estimate the level of ecological divergence within and among species and to analyse how their genetic divergence is related to ecological divergence.

Materials and methods

Sampling

Thirty-five jerboas were caught at night in a hand-thrown net in different locations of the Negev Desert of Israel, after searching by foot with a flashlight. A small piece was cut from the ear lobe of each individual and fixed in 90% alcohol for subsequent DNA sequencing. Each individual was weighed, sexed, photographed and then released (under Israel Nature and Natural Parks Protection Authority permit no. 2013/39984). Geographic positions of capture sites were recorded by GPS.

DNA extraction, amplification, sequencing and phylogeny reconstruction

DNA was extracted using AccuPrep[®] Genomic DNA Extraction Kit (BioNEER K-3032), Bioneer Inc., Alameda, California, USA following the manufacturer's instructions from 14 of 35 available samples. The mitochondrial Cytochrome *b* (*cyt b*) gene was amplified with the modified forward primer L14723 (5'-ACCAATGACATGAAAAATCATNGT-3') and the reverse H15915 (Lecompte et al. 2002). Accession numbers of sequences sequenced in the present study are provided in Table 1, while sequences from GenBank are listed in Table S1. Sequences were aligned with the ClustalW algorithm (Thompson et al. 1994) implemented in MEGA 6 (Tamura et al. 2013) with default parameters. The best model of nucleotide substitution based on maximum-likelihood estimation using both the Bayesian Information Criterion and the corrected Akaike Information Criterion was the Hasegawa-Kishino-Yano (HKY+G+I) model, with the gamma distribution parameter equal to 1.11146 and the fraction of evolutionarily invariable sites equal to

Table 1. New *Jaculus* samples from Israel investigated in the present study. Voucher numbers starting with M are from Steinhardt Museum of Natural History, Tel-Aviv University, and starting with S – from Zoological Museum of Moscow University.

Locality	Latitude	Longitude	Voucher number	GenBank accession code
<i>Jaculus jaculus</i> (clade I)				
Agur Sands, 5 km S	31.1641	34.4549	M-14330	KM257927
Gvulot			M-14331	KM257928
Agur Sands, 7 km W Ashalim	30.9670	34.6294	M-13739	KM257926
Revivim, 9 km NW	31.1050	34.6588	M-14332	KM257929
Revivim, 1 km ENE	31.0486	34.7330	M-13740	KM257925
<i>Jaculus hirtipes</i> (clade II)				
Revivim, 6.5 km E	31.0383	34.7906	M-13741	KM244578
Makhtesh Ramon	30.6355	34.9199	M-14328	KM244576
			M-14329	KM244577
			S-191324	KP059288
			S-191325	KP059289
			S-191326	KP059290
			S-191327	KP059291
Samar	29.7912	35.0368	M-12570	KM244575
Uvda	30.0156	34.9769	M-13742	KM244579

0.4941. The selected model was applied for phylogenetic reconstruction using maximum-likelihood tree estimation in PhyML (Guindon and Gascuel 2003) and Bayesian phylogenetic analysis using MRBAYES (Ronquist and Huelsenbeck 2003) algorithms with TOPALi 2.5 software (Milne et al. 2004). As support for the nodes we used bootstrap values in maximum-likelihood and posterior probabilities in Bayesian phylogenetic analyses. Genetic divergence among and within clades was calculated with MEGA 6 using the Kimura's two-parameter model (K2P).

Morphological and morphometric analyses

Skulls, skins and alcohol-fixed specimens were studied in the Steinhardt Museum of Natural History, Tel-Aviv University (TAU), and the National Natural History Collections at the Hebrew University, Jerusalem (HUJ). Detailed descriptions and/or colour photographs of some additional specimens (including relevant type specimens) were obtained from the Zoological Museum of Uppsala University (ZMUU), Museum für Naturkunde Berlin (MfNB), the Field Museum of Natural History (Chicago) (FMNH) and Florence Museum of Zoology and Natural History 'La Specola' (FMZNH).

Skulls were measured with dial calipers to the nearest 0.1 mm according to Shenbrot (1990). Fourteen cranial measurements were analysed: condylo-basal length (Lcb), rostrum length (Lr), zygomatic length (Lz), mastoid breadth (Bm), zygomatic breadth (Bz), braincase breadth (Bb), interorbital breadth (Bi), rostrum breadth (Br), rostrum height (Hr), height of infra-orbital foramen (Hif), tympanic bulla length (Lb), tympanic bulla width (Wb), upper tooth row length (Lmr) and incisor width (Wi). Only adult specimens (reproductively mature individuals after at least one winter, more than 9 months old) were included in the analyses. Age was assessed based on molar wear patterns, and criteria were the same as provided by Shenbrot et al. (2008) for *Jaculus blanfordi* (Murray, 1884) and Shenbrot (2013) for *Jaculus orientalis* Erxleben, 1777 (Fig. S1).

Data were analysed using principal components and canonical discriminant function analyses. Analyses were performed on non-transformed data. Principal component analysis was done with a correlation matrix, a standard approach in rodent skull morphometric studies which allows identification of both size and shape variation. To characterize among-group differences, standard statistics (including mean, standard error and pairwise *t*-tests) were applied. In spite of the large number of *t*-tests made, we do not use the Bonferroni correction because of this correction, and even the more liberal sequential Bonferroni analyses came under much scrutiny for being overly conservative and restrictive (Perneger 1998; Moran 2003; Garcia 2004; Nakagawa 2004).

Glans penis morphology of alcohol-fixed specimens was examined under a dissection microscope. We recorded the size and shape of the glans penis and the morphology of the scales covering it. The number of scallops was counted on the 30 largest scales in the central part of the dorsal surface of the glans penis of each individual.

Estimation of niche differentiation

Estimation of niche divergence/conservatism is usually made through comparison of species distribution models (SDM) using ENM tools developed by Warren et al. (2008). However, environmental data are usually spatially auto-correlated, potentially confounding niche divergence with geographic distance (McCormack et al. 2009). The tests revealed significant niche differentiation in cases in which background conditions were non-overlapping and cannot be used as a true evidence of niche differentiation (Peterson 2011). To avoid this confounding effect, it is necessary to compare the observed niche differences with differences in background environments. We used the procedure described in detail by Shenbrot (2013) which is not based on SDM comparisons. To estimate the level of niche differentiation relative to differences in background environments, we performed canonical discriminant analysis based on values of 15 environmental variables drawn from four samples: two sets of occurrence points in two regions and two sets of random points in these regions; the number of random points was equal to the number of occurrence points in each region. As the metric for pairwise comparisons, Shenbrot (2013) used the ratio of Mahalanobis distance (DM) between occurrence points to Mahalanobis distance between random points ($R_M = DM_{A-B}/DM_{a-b}$). Mahalanobis distance is the normalized distance

between-group centroids in the canonical space. A ratio >1 indicates true niche divergence, whereas a ratio of <1 indicates true niche convergence. In allopatry, when environmental differences are high enough, this metric works well. However, in the case of sympatric populations, the environment of the two populations is the same (the difference is close to zero), and the index value becomes extremely high, even if the absolute values of niche differences (DM_{A-B}) are very low. To avoid this problem, we modified the index of relative niche differentiation to $\bar{R}_M = (\log_2(DM_{A-B} + 2)) / (\log_2(DM_{a-b} + 2))$. As with the original index, a value >1 indicates niche divergence and a value <1 indicates niche convergence, while in the case of identical niches and identical environments, the value is equal to one. Statistical significance of the metric was assessed with 100 bootstrap replicates of occurrence and background samplings points (in all cases, stable values of mean and SE were attained after the first 50 replicates).

Records of occurrences of North African genetic clades of *J. jaculus* s. lato were taken from the studies by Ben Faleh et al. (2010a, 2012) and Boratyński et al. (2012, 2014). For Israel and Sinai, we used our field data and museum records. Most of the published data and our field localities had GPS coordinates. Geo-referencing of the museum specimens (including specimens from the National Museum of Natural History, Smithsonian Institution, USA, reported by Boratyński et al. 2014) was made based on data provided by the collectors.

Environmental data for the niche divergence analysis were used as 30-arc-second grids (approximately 1-km resolution) and were represented by climate, relief, sand cover and variables. The climate variables (annual mean temperature, mean monthly temperature range, mean temperatures of coldest and warmest quarters, maximal temperature of warmest month, minimal temperature of coldest month, temperature annual range, annual precipitation and precipitation of wettest quarter) were obtained from WORLDCLIM Version 1.4 (Hijmans et al. 2005) available at <http://www.worldclim.org>. Slope data were derived from altitude (extracted from GTOPO30 data set distributed with ArcGIS) using the Spatial Analyst module of ARCMAP. Data on the percentage area covered by sand were obtained using ARCGIS Desktop 10.1 from the Land-Use layer of the Digital Chart of the World corrected with satellite images (available at <http://landsatlook.usgs.gov>). The obtained polygons of sand dune areas were converted to raster with resolution three arc-seconds, and this raster

was resampled to 30-arc-seconds resolution. This operation resulted in values of the percentage area covered by sand for each grid cell. For subsequent analyses, these data were log-transformed. Data on normalized difference vegetation index (NDVI) were obtained from VEGETATION Programme (<http://www.spot-vegetation.com>; now <http://www.vito-eodata.be>; data for 1998–2007, each a 10-day estimate) and averaged by seasons (winter, spring, summer and autumn) across all available years. The NDVI is an index of greenness that is directly correlated with productivity and green vegetation biomass and is widely used in ecological studies (Pettorelli et al. 2005).

All operations with maps were performed with ARCMAP 10.1 including Hawth's Tools application. Statistical analyses were carried out in STATISTICA (StatSoft Inc., Tulsa, Oklahoma, USA, for Windows Release 7.0 package).

Results

Phylogenetic position of Israeli specimens

All 14 individuals of *J. jaculus* s. lato studied for cyt b belonged to clades I (five individuals) and II (nine individuals) of the study by Ben Faleh et al. (2012). Israeli specimens belonging to clade I formed a separate, poorly supported, subclade (posterior probability: 0.56, bootstrap support: 59%); specimens of clade II from Israel likewise formed a separate subclade but without a significant support, together with two specimens (JX855187 and JX855194) from northern Egypt (two of three specimens from Burg El Arab) (Fig. 1, S1, S2).

Clade-specific morphological features

In external morphology, all specimens classified as clade I represented the 'orange colour phase' described by Osborn and Helmy (1980). They had yellow–orange dorsal hair, an incomplete black band on the ventral side of the tail banner, dissected by the white stripe along the tail rod (Fig. 2, left), white hair on the soles and

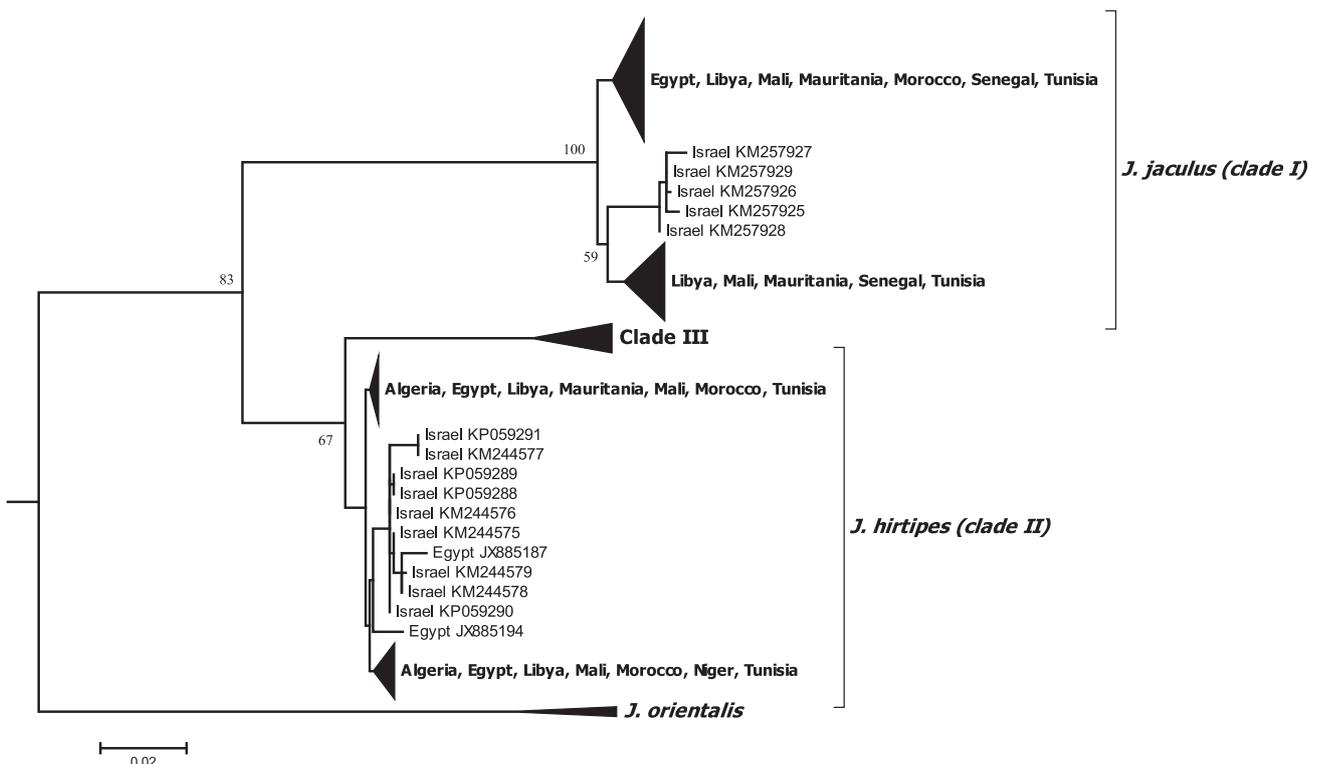


Fig. 1. Simplified maximum-likelihood tree of *cyt b* sequences of *Jaculus* jerboas. Values above branches indicate bootstrap values.



Fig. 2. Colouration of the tail banner of *Jaculus* jerboas, view from the ventral side; left – *Jaculus jaculus* (no. TAU M-14332), right – *Jaculus hirtipes* (no. TAU M-14328)

white colouration of the basal part of the vibrissae. All specimens of clade II were in the ‘brownish colour phase’. They had brownish-grey dorsal hair colour, a complete ventral black band on the tail banner, with no white stripe along the tail rod (Fig. 2, right), black or brownish hair of the soles and dark grey colouration of the basal part of the vibrissae. These characters did not demonstrate intraspecific variability: in the area where only clade I animals were recorded (the northern part of Agur Sands), all 20 individuals (12 observed in the field and eight from TAU collections, three of which were sequenced) belonged to the ‘orange colour phase’, whereas in the area where only clade II specimens were recorded (Makhtesh Ramon and the vicinity of Mitzpe Ramon), all 38 individuals (34 observed in the field and four from TAU and HUI collections, three of which were sequenced) belonged to the ‘brownish colour phase’.

Examination of the glans penis of specimens in the TAU collection (seven specimens identified by external characters as clade I and six specimens identified as clade II) demonstrated that the two clades had identical ranges of size variation (8–9 mm in length and 3–4 mm in diameter). In both clades, the glans penis also has a similar shape: cylindrical, subdivided by deep longitudinal folds into five lobes, one dorsal, two lateral and two ventral. The surface of the lobes is covered by comb-like scales, with scallops at their proximal edges. The size of the scales is maximal in the middle part of the dorsal lobe and gradually decreases towards the distal, proximal and ventral areas (Fig. 3a,b). The two clades significantly differ in the shape of these scales. In clade I, the scales are all of fairly similar length and ended with a few long scallops (Fig. 3c,e). In clade II, the scales are wider than long, and their proximal edge has many short scallops (Fig. 3d,f). The number of scallops varies within and between individuals and is 2–6 (usually 3–4, 3.73 on average) in clade I and 7–16 (usually 10–12, mean = 10.95) in clade II (Fig. 4).

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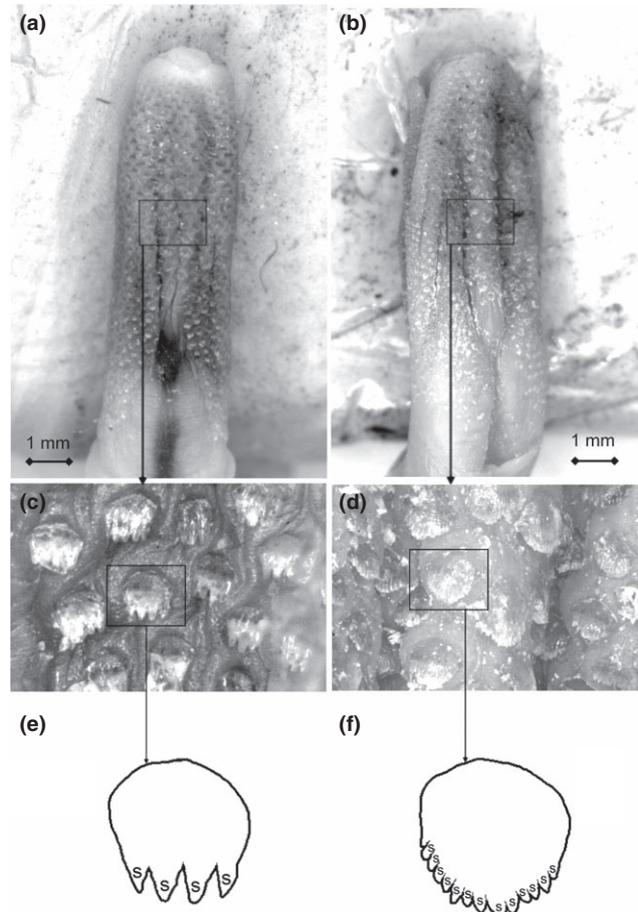


Fig. 3. Glans penis of *Jaculus* jerboas, view from the dorsal side; a, c, e – *Jaculus jaculus* (no. TAU M-14332), b, d, f – *Jaculus hirtipes* (no. TAU M-14328). (a, b) general view; (c, d) enlarged view of the scales in the central part of dorsal side; (e, f) schematic draw of scales (‘s’ letters marked separate scallops)

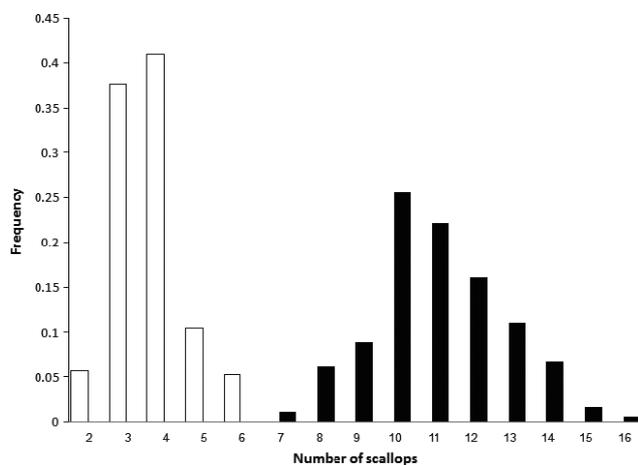


Fig. 4. Frequency distribution of the number of scallops per one scale in the central part of dorsal surface of glans penis in *Jaculus jaculus* (white bars) and *Jaculus hirtipes* (black bars)

Comparison of skull dimensions of individuals from Israel and Sinai identified by external characters as clade I or clade II demonstrated that these two forms significantly differ in eight of the 14 studied measurements (Table 2). Specimens of clade I

Table 2. Skull measurements (upper row – min-max; lower row – M ± SE) of *Jaculus jaculus* and *J. hirtipes* from Israel and Sinai and its standard statistical comparisons (*t*-test)

Variable	<i>J. jaculus</i>	<i>J. hirtipes</i>	<i>t</i>
<i>N</i>	24	32	
Lcb	29.4–31.8 31.71 ± 0.11	29.4–31.8 30.70 ± 0.12	1.03 ^{NS}
Lr	10.3–11.2 10.74 ± 0.06	10.1–11.3 10.75 ± 0.05	–0.20 ^{NS}
Lz	15.0–17.2 15.92 ± 0.10	13.8–16.3 15.09 ± 0.09	6.03 ^{***}
Bm	22.1–24.7 23.72 ± 0.12	21.4–25.2 23.82 ± 0.14	–0.57 ^{NS}
Bz	21.4–23.8 22.77 ± 0.14	20.6–24.1 22.22 ± 0.15	2.60 [*]
Bb	18.8–20.7 20.01 ± 0.10	19.0–21.5 20.17 ± 0.11	–0.96 ^{NS}
Bi	12.1–13.5 12.75 ± 0.07	11.4–13.1 12.26 ± 0.08	4.28 ^{***}
Br	4.2–5.1 4.71 ± 0.05	4.3–5.3 4.85 ± 0.05	–2.12 [*]
Hr	6.2–6.9 6.54 ± 0.05	6.3–7.3 6.71 ± 0.05	–2.38 [*]
Hif	5.8–7.7 6.94 ± 0.08	5.5–7.5 6.81 ± 0.08	1.51 ^{NS}
Lb	14.4–16.0 15.31 ± 0.08	14.9–16.7 15.52 ± 0.08	–1.79 ^{NS}
Wb	12.2–13.5 12.79 ± 0.08	12.3–13.8 13.01 ± 0.06	–2.22 ^{NS}
Lmr	4.8–5.4 5.14 ± 0.03	4.9–5.5 5.23 ± 0.03	–2.28 ^{NS}
Wi	1.6–2.0 1.86 ± 0.02	1.9–2.2 2.01 ± 0.02	–5.40 ^{***}

NS, differences are not significant; Lcb, condylo-basal length; Lr, rostrum length; Lz, zygomatic length; Bm, mastoid breadth; Bz, zygomatic breadth; Bb, braincase breadth; Bi, interorbital breadth; Br, rostrum breadth; Hr, rostrum height; Hif, height of infra-orbital foramen; Lb, tympanic bulla length; Wb, tympanic bulla width; Lmr, upper tooth row length; Wi, incisor width.
 ****p* < 0.001, **p* > 0.05

Table 3. Results of principal components analysis of skull measurements of *Jaculus jaculus* s. lato from Israel and Sinai

Variable	Factor loadings			
	PC1	PC2	PC3	PC4
Lcb	0.2911	0.3512	0.6979	0.4108
Lr	0.1056	–0.0751	0.9104	0.1490
Lz	0.1175	0.8028	0.4043	–0.1056
Bm	0.7537	0.2859	0.1266	0.3863
Bz	0.4195	0.6987	0.1913	0.0302
Bb	0.7865	0.1154	0.1491	0.0350
Bi	0.0928	0.8046	–0.0934	0.1338
Br	0.7256	–0.0653	0.0060	0.3129
Hr	0.6403	–0.0009	0.3785	0.3651
Hif	0.6065	0.3057	0.4782	–0.1485
Lb	0.2463	0.0486	0.2023	0.7662
Wb	0.5425	–0.0931	–0.0585	0.6477
Lmr	0.0497	–0.0875	0.1185	0.8430
Wi	0.2707	–0.6183	0.1552	0.3020
Eigenvalue	5.3127	2.5672	1.2263	1.0632
Proportion of total explained variance	0.3795	0.1834	0.0876	0.0760

The bold values indicate variables with highest factor loadings. For abbreviation, see Table 2.

have longer and wider zygomatic arches and broader interorbital space, but lower and narrower rostrum, narrower incisors and bullae and shorter upper molar row length than in clade II. Prin-

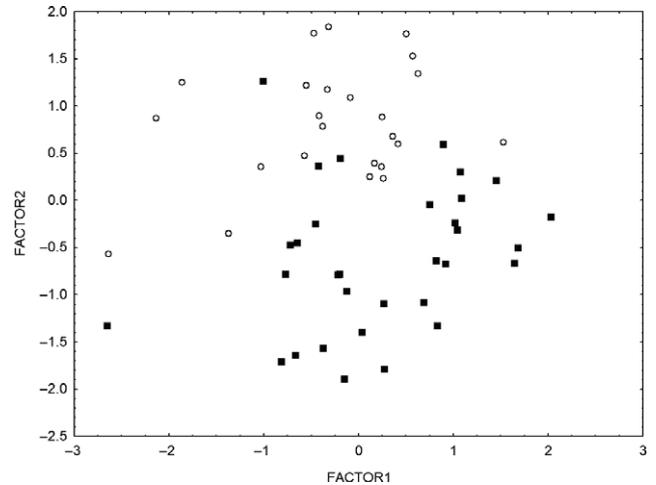


Fig. 5. Distribution of the studied specimens of *Jaculus* in the morphospace of the first two principal components; white circles – *J. jaculus*, black squares – *J. hirtipes*

cipal component analysis (Table 3, Fig. 5) revealed that specimens of the two species occupy different areas along the first two principal components but with some overlaps. Discriminant analysis enabled correct classification of 52 of the 56 individuals (92.9%) with all data and 50–51 of 54 individuals (92.6–94.4%) using jackknife procedure of cross-validation.

Identification of type specimens

Colouration characters that were found to be stable within each of the two North African clades of *Jaculus jaculus* s. lato and different between these clades allow us to identify the type specimens in this group.

Mus jaculus Linnaeus, 1758. Type specimen no. 119, ZMUU. The type locality was noted by Linnaeus (1758) as ‘Arabia and Kalmukia’, but was placed as the Giza Pyramids in Egypt by Allen (1939) without further justification. The type specimen was collected by F. Hasselquist (see Wallin 2001) in 1750 in the area of the Giza Pyramids, Egypt (29°58’N, 31°08’E) (Hasselquist and Linnaeus 1766). The fur colour of this specimen has faded, probably as a result of previous fixation in alcohol (E. Mejlon, personal communication), and the original black colour now appears as a yellowish light brown, while the white colour remains intact. The specimen has a clear white stripe along the tail rod of the tail banner on the ventral side and white colouration of the basal part of the vibrissae, identifying it as the ‘orange colour phase’. Thus, the name *Jaculusjaculus* (Linnaeus 1758) should be applied to Ben Faleh et al.’s clade I.

Dipus hirtipes Lichtenstein, 1823. Six syntypes (five skulls and five skins): nos. 1308, 1311–1313, 1315–1316, MfNB. The specimens were collected by W. F. Hemprich and C. G. Ehrenberg in 1821 (see Baker 1997) in the desert east of Sakharam [Saqqara in the current transliteration], between Cairo and Faiyum (29°52’N, 31°13’E) (not near Aswan, as pointed out by Cockrum and Setzer 1976), Egypt. All five specimens with preserved skins are the ‘brownish colour phase’, with brownish-grey dorsal hair colour, complete black band on the ventral side of the tail banner, brownish hair of the soles and dark grey colouration of the basal part of the vibrissae. Thus, the name *hirtipes* Lichtenstein, 1823 seems to be the senior name available for Ben Faleh et al.’s clade II.

Dipus macrotarsus Wagner, 1840. The type specimen from Sinai (the type locality was restricted to Mount Sinai – 28°34’N

33°57'E – by Allen 1915) was originally held by the Zoological Collection of the Bavarian Academy of Sciences (now Zoologische Staatssammlung München) but is now lost (C. Lang, personal communication). The topotype (no. 89.132, Zoologisches Forschungsmuseum Alexander Koenig, Bonn) has external characters typical of *J. hirtipes* (B. Krystufek, personal communication). Another topotype (no. 317068, National Museum of Natural History, Smithsonian Institution, Washington D.C.) (USNM) reported by Boratyński et al. (2014) genetically belongs to Ben Faleh et al.'s clade II.

Dipus schlueteri Nehring, 1901. Three syntypes (preserved in alcohol, no. 15235, MfNB) from sands south of Jaffa, Israel (31°59'N, 34°44'E), and several topotypes from the collections of TAU and HUJ, all have external characters typical to *J. jaculus*.

In addition, the names *Jaculus jaculus butleri* Thomas, 1922 described from Sudan, Khartoum, *Jaculus jaculus elbanensis* Setzer, 1955 from Sudan, Jebel Elba, Wadi Darawena and *Jaculus jaculus favillus* Setzer, 1955 from Egypt, Salum, Bir Bosslanga, can be clearly identified by their tail colouration as *J. hirtipes*, the former based on its original description (Thomas, 1922), and the latter two based on the description of the type specimens (*elbanensis* – no. 82295 and *favillus* – no. 75708FMNH) provided by B. Patterson (personal communication).

Geographic distribution in Israel and Sinai

Both genetic and morphological identifications indicate that *J. jaculus* is distributed along the coastal plain and sand massifs

of the northern Negev and Sinai; one isolated point of occurrence of this species is in Hatzeva (northern part of the Arava Valley) near the Jordanian border (Fig. 6). *J. hirtipes* is distributed in central and southern parts of Sinai and the Negev, the Arava Valley and southern part of the Jordan Valley. The two species co-occur in the narrow strip along the southern border of sand massifs in northern Sinai and the northern Negev as well as in Hatzeva (Fig. 6).

Habitat preferences and niche differentiation

Geographic locations of the samples used for analysis of habitat preferences and niche differentiation are presented in Fig. 7 and Table S1. Estimates of the values of environmental variables at the points of occurrence of the two species separately for North Africa and for Israel and Sinai are provided in Table 4, and the relative importance of these variables in the niche differentiation is provided in Table 5. In North Africa, *J. jaculus* occurs in more arid environments with a more continental climate (higher temperatures, higher annual and monthly temperature variation, lower precipitation and lower abundance of green vegetation) than does *J. hirtipes*. In Israel and Sinai, the situation is opposite: *J. jaculus* occurs in less arid environments with a less continental climate than does *J. hirtipes* (Tables 4 and 5). *J. jaculus* is more psammophilous than *J. hirtipes*, especially in Israel and Sinai (Table 4). In Israel, all cases in which *J. jaculus* was recorded out of sand massifs were in areas of former sands that have since become agricultural lands, or in wide wadis with sandy beds which are not reflected in maps as sands. In contrast, records of *J. hirtipes* in sand massifs were usually at the edge of

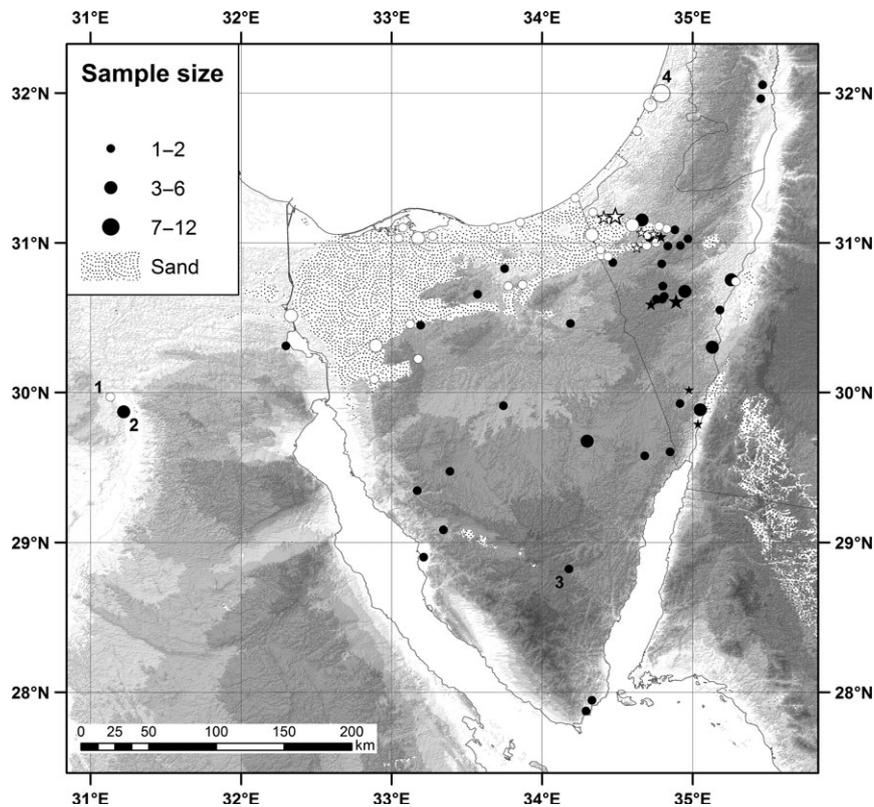


Fig. 6. Geographic distribution of the studied specimens of *Jaculus* in Israel, Sinai and eastern Egypt; stars – genetically studied specimens, circles – morphologically studied specimens; white symbols – *J. jaculus*, black symbols – *J. hirtipes*. Numbers indicate the type localities: 1 – *Mus jaculus*, 2 – *Dipus hirtipes*, 3 – *Dipus macrotarsus*, 4 – *Dipus schlueteri*. A – total area, B – enlarged part of the map demonstrating the sympatry zone of *J. jaculus* and *J. hirtipes*

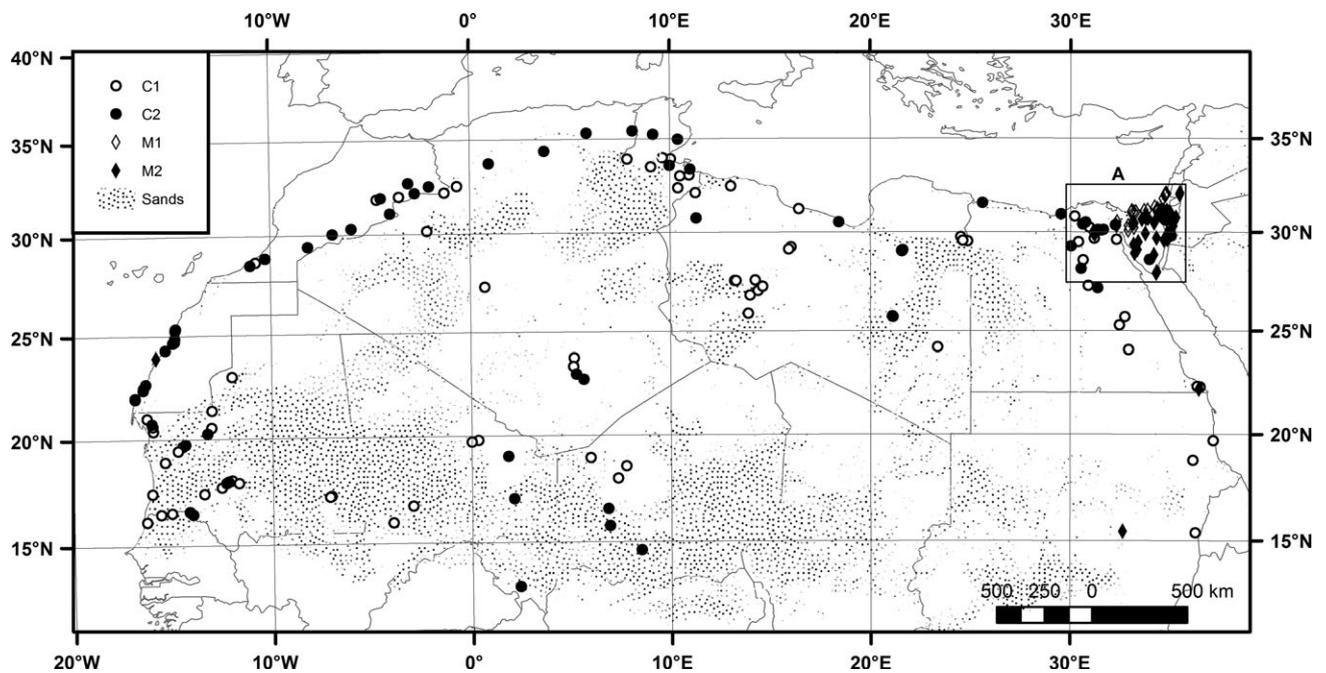


Fig. 7. Geographic distribution of *Jaculus* specimens used for habitat distribution and niche differentiation analysis in North Africa, Israel and Sinai. C – genetically identified specimens of the clade I (C1) and clade II (C2); M – morphologically identified specimens of *J. jaculus* (M1) and *J. hirtipes* (M2). The framed region A indicates the area shown in Fig. 6.

Table 4. Values of environmental variables (M±SE) in the points of occurrences of *Jaculus jaculus* and *J. hirtipes* in North Africa and Israel and Sinai. NDVI – normalized difference vegetation index

Variables	<i>Jaculus jaculus</i>		<i>Jaculus hirtipes</i>	
	North Africa (n = 90)	Israel and Sinai (n = 45)	North Africa (n = 62)	Israel and Sinai (n = 47)
Altitude (m a.s.l.)	245.12 ± 27.15	148.24 ± 19.93	339.23 ± 48.59	378.17 ± 48.84
Autumn NDVI	51.79 ± 1.04	55.51 ± 1.80	53.87 ± 1.51	47.85 ± 0.58
Spring NDVI	50.07 ± 0.76	61.71 ± 2.51	53.18 ± 1.54	49.53 ± 0.84
Summer NDVI	50.13 ± 0.80	57.51 ± 2.02	52.52 ± 1.24	49.06 ± 0.48
Winter NDVI	52.26 ± 0.91	64.40 ± 2.89	54.92 ± 1.38	50.62 ± 1.03
Autumn precipitation (mm)	27.09 ± 2.70	38.16 ± 4.65	33.79 ± 3.56	15.36 ± 1.36
Spring precipitation (mm)	9.47 ± 1.54	34.53 ± 2.73	18.45 ± 3.46	24.04 ± 2.27
Summer precipitation (mm)	32.01 ± 5.44	0.00 ± 0.00	34.89 ± 9.08	0.00 ± 0.00
Winter precipitation (mm)	15.04 ± 2.51	123.71 ± 15.84	27.47 ± 3.67	58.91 ± 6.34
Slope	9.11 ± 1.12	8.87 ± 0.89	11.44 ± 1.32	21.64 ± 3.93
Annual temperature range (°C)	29.27 ± 0.55	24.38 ± 0.22	27.09 ± 0.87	26.50 ± 0.22
Monthly temperature range (°C)	14.03 ± 0.19	10.86 ± 0.14	12.93 ± 0.31	11.81 ± 0.12
Mean temp. of warmest month (°C)	38.39 ± 0.37	31.98 ± 0.18	35.54 ± 0.58	33.15 ± 0.38
Annual mean temperature (°C)	23.98 ± 0.36	19.83 ± 0.11	21.90 ± 0.49	19.75 ± 0.31
Mean temp. of coldest month (°C)	9.11 ± 0.47	7.60 ± 0.13	8.45 ± 0.61	6.66 ± 0.26
Sand cover (%)	26.76 ± 3.86	64.00 ± 5.98	4.85 ± 2.47	7.09 ± 2.49

large massifs occupied by *J. jaculus*. However, the first author found *J. hirtipes* in two small isolated sand islands: Makhmal Dune in Makhtesh Ramon and Nahal Kosuy Dune field in the Uvda Valley, where *J. jaculus* was absent.

Estimates of niche differentiation and genetic distances are provided in Table 6. Absolute niche shift is minimal for North African sympatric populations of *J. jaculus* and *J. hirtipes* and maximal in the case of allopatric North African and Israel-Sinai populations of *J. jaculus*. However, values of niche shifts relative to the environmental differences indicate a high niche divergence between *J. jaculus* and *J. hirtipes* in North Africa and in Israel-Sinai, low but significant niche divergence between Israel-

Sinai and North African populations of *J. jaculus* and low but significant niche convergence between Israel-Sinai and African populations of *J. hirtipes*. Thus, the level of niche differentiation increases with genetic distance.

Discussion

Taxonomic status of the two forms of the Lesser Egyptian Jerboas

The two genetically distinct species that were described in North Africa by Ben Faleh et al. (2010a, 2012) are also found in Israel.

Table 5. Relative importance of environmental variables for ecological segregation of species/populations estimated by the results of discriminant analyses as standardized coefficients of canonical discriminant functions

Variables	jNA versus hNA	jIS versus hIS	jNA versus jIS	hNA versus hIS
Autumn NDVI	-0.22494	-0.84447	0.11742	2.07148
Spring NDVI	-0.76222	-1.96634	-1.24801	0.69633
Summer NDVI	0.27283	0.93807	0.26376	-1.05762
Winter NDVI	0.68445	1.94922	0.84856	-1.44876
Autumn precipitation (mm)	0.08780	4.35382	-1.43580	-2.20928
Spring precipitation (mm)	0.61879	1.49539	0.68428	0.12461
Summer precipitation (mm)	-1.02514	0.00000	0.47786	0.62265
Winter precipitation (mm)	-0.38785	-5.67323	0.91830	1.35158
Slope	-0.14089	-0.04117	0.06103	0.24693
Annual temperature range (°C)	0.63794	-1.16735	0.31818	1.78684
Monthly temperature range (°C)	-0.09813	0.89226	-0.60391	-2.40751
Mean temp. of warmest month (°C)	-0.43236	0.32539	-0.76015	0.79990
Annual mean temperature (°C)	1.39404	-0.06685	0.47470	0.06439
Mean temp. of coldest month (°C)	0.00000	0.00000	0.00000	0.00000
Sand cover [Ln (% +1)]	0.71161	0.65978	0.49598	0.04747

jNA, *Jaculus jaculus* from North Africa; jIS, *J. jaculus* from Israel and Sinai; hNA, *J. hirtipes* from North Africa; hIS, *J. hirtipes* from Israel and Sinai; NDVI, normalized difference vegetation index. The bold values indicate variables with highest importance for ecological segregation.

Table 6. Estimations of niche shifts (above diagonal; M \pm SD, first row – absolute shift DM , second row – relative shift \tilde{R}_M) and genetic distances (below diagonal; values of K2P corrected mean between-group distances, M \pm SE). For abbreviation, see Table 5.

	jNA	jIS	hNA	hIS
jNA		4.530 \pm 0.233	1.498 \pm 0.164	
jIS	0.022 \pm 0.003	1.048 \pm 0.032*	1.888 \pm 0.161***	
hNA	0.123 \pm 0.013			2.428 \pm 0.155
hIS		0.122 \pm 0.013	0.010 \pm 0.002	

*Significantly ($p < 0.05$) higher than 1, *Significantly ($p < 0.01$) lower than 1, ***Significantly ($p < 0.001$) higher than 1

We demonstrate that whereas the two species can be easily identified, even in the field, by external characters (fur and tail colouration), they cannot be identified confidently using skull characters because these partially overlap. A situation, in which two species can be easily identified through external morphology, but not with skull characters, is common in jerboas. For example, a similar situation was described for the two Mongolian species, *Allactaga bullata* Allen, 1925 and *A. balikunica* Hsia and Fang, 1964 (Sokolov et al. 1998). While there are many definitions of the term ‘cryptic’ or ‘hidden’ species (reviewed by Bickford et al. 2006), we accept the general definition that ‘two or more species are ‘cryptic’ if they are, or have been, classified as a single nominal species because they are at least superficially morphologically indistinguishable’ (Bickford et al. 2006). We further accept a more specific definition of cryptic species for mammals: ‘Species of mammals that would likely not be recognized based solely on classical studies of morphology of voucher specimens housed in museums’ (Baker and Bradley 2006). These definitions cannot be applied to our case, however, and the two *Jaculus* species thus should not be considered cryptic.

We have also demonstrated here that the two species differ in the morphology of the glans penis. Differences in glans penis morphology between species, genera and subfamilies are typical for jerboas and are often used as diagnostic characters (Vinogradov 1937; Ognev 1948; Shenbrot et al. 2008). Among three-toed jerboas (Dipodinae), genera and species differ in the number and shape of lobes of the glans penis, in the presence/absence, shape and position of the pair of large distally directed spines, and in the shape of the small scales covering the surface of the glans penis (Shenbrot et al. 2008). In three-toed jerboas, scales similar in shape to those we found in *J. hirtipes* (comb-like,

with numerous short scallops at their proximal edges) were described for the species with plesiomorphic morphological characters of skull and molars [*Dipus sagitta* (Pallas, 1773)], the species with most derived skull and molar characters [*Paradipus ctenodactylus* (Vinogradov, 1929)] and for *Jaculus blanfordi* (Murray, 1884), a species with relatively primitive molars and relatively derived skull characters (Shenbrot et al. 2008). Phylogenetic reconstructions (Lebedev et al. 2013) demonstrated that the first two forms represent basal branching of the tree-toed jerboa’s tree, whereas the last one is the product of the most terminal branching. Consequently, this state of the scales’ shape should be considered as symplesiomorphic for Dipodinae (Lebedev et al. 2013). The most derived morphology of scales, with only two large scallops, was described for *Eremodipus lichtensteini* (Vinogradov, 1927) (Shenbrot et al. 2008). The scales’ morphology of *J. jaculus* (3–4 relatively large scallops) seems to reflect an intermediate stage in the reduction in the number and increase in size of the scallops.

The two forms have a complicated taxonomic history. They were considered as independent sympatric species by Ranck (1968) based mainly on his field observations. However, he was unsuccessful in determining the diagnostic characters, which resulted in strong criticism by Harrison (1978) and Corbet (1978), who considered these two forms as eco-morphs rather than true species. The authoritative nature of the above critiques would seem to have convinced Osborn and Helmy (1980) and Mendelssohn and Yom-Tov (1999) into accepting these forms as ‘colour phases’ of the same species or as different subspecies of *J. jaculus*, in spite of the existing evidence of their co-occurrence provided by Osborn and Helmy (1980) and their reproductive isolation in captivity described by Mendelssohn and Yom-Tov (1999).

Solution to the nomenclature problems

Examination of available type specimens demonstrated that the correct name for the first of the North African species recognized by Ben Faleh et al. (2012) (genetic clade I) is *Jaculus jaculus* (Linnaeus 1758). Twenty-nine names are listed by Holden and Musser (2005) as synonyms of *Jaculus jaculus*. The oldest of these, *Dipus hirtipes* Lichtenstein, 1823, belongs to Ben-Faleh's genetic clade II, and thus, the correct name for this species is *Jaculus hirtipes* (Lichtenstein, 1823). Among the other synonyms of *J. jaculus*, Holden and Musser (2005) included *Dipus aegyptius* Lichtenstein, 1827, following Ellerman and Morrison-Scott (1951). Cockrum and Setzer (1976), however, demonstrated that *Dipus aegyptius* Lichtenstein, 1827 is a synonym of *Jaculus orientalis* Erxleben, 1777. Genetic data on paratypes of *Jaculus jaculus arenaceus* Ranck, 1968 (USNM322809, USNM322811, Libya, Fezzan, Edri), *Jaculus jaculus collinsi* Ranck, 1968 (USNM325789, Libya, Cyrenaica, Tazerbo Oasis), *Jaculus jaculus cufrensis* Ranck, 1968 (USNM319773, Libya, Cyrenaica, Cufra Oasis, El Giof) and *Jaculus jaculus tripolitanicus* Ranck, 1968 (USNM325770, Libya, Tripolitania, 25 km N Gharian) provided by Boratyński et al. (2014) showed that these names should be considered as junior synonyms of *Jaculus jaculus*. A specimen from the type locality of *Dipus macrotarsus* (USNM317068, Sinai Peninsula, Mount Sinai, wadi Raha) genetically belongs to *Jaculus hirtipes* (data of Boratyński et al. 2014). Here, we have provided morphological evidence (see above) that the name *Dipus schlueteri* should be considered as a junior synonym of *J. jaculus*, and the names *Dipus macrotarsus*, *Jaculus jaculus butleri*, *Jaculus jaculus elbanensis* and *Jaculus jaculus favillus* should be considered as junior synonyms of *Jaculus hirtipes*. Type specimens or topotypes of the remaining 13 African synonyms, *Dipus deserti* Loche, 1867 (Algeria, Ouargla), *Dipus darricarrerei* Lataste, 1883 (Algeria, Bou Saada), *Dipus microtis* Reichenow, 1887 (Eritrea, Samar), *Jaculus gordonii* Thomas, 1903 (Sudan, Darfur, Kaga Hills), *Jaculus jaculus fawnicus* Thomas, 1913 (Mauritania, Trarza), *Jaculus jaculus vulturinus* Thomas, 1913 (Somali, Berbera), *Jaculus jaculus airensis* Thomas et Hinton, 1921 (Niger, Aderbissinat), *Jaculus jaculus sefrius* Thomas et Hinton, 1921 (Algeria, Ain Sefra), *Jaculus jaculus centralis* Thomas et Hinton, 1921 (Algeria, In-Salah, N of, Oued el Abiad), *Jaculus jaculus whitchurchi* Ranck, 1968 (Libya, Cyrenaica, 10 km S Agedabia), *Jaculus deserti fuscipes* Ranck, 1968 (Libya, Tripolitania, 7 km W El Gheddahia), *Jaculus deserti rarus* Ranck, 1968 (Libya, Cyrenaica, Gebel Uweinat, Ain Zueia) and *Jaculus deserti vastus* Ranck, 1968 (Libya, Cyrenaica, Wadi er Rueis, Gebel el Harug el Asued, 340 km WNW Tazerbo Oasis) need to be re-examined in order to identify their specific affiliation. This is especially important in the case of *Dipus deserti* Loche, 1867 because this name was proposed as a senior name for Clade II. This name cannot be used for the clade II as a senior name because it is predated by *Dipus hirtipes* Lichtenstein, 1823. Moreover, its type specimen is unavailable, and the specimen noted by Thomas and Hinton (1921) as a topotype (Algeria, 46 km E of Ghardaia) is not really a topotype because of its location 145 km distant from the type locality (Algeria, Ouargla). The lack of diagnostic characters in the original description does not allow an unequivocal decision as to which of the two co-occurring species (*J. hirtipes* or *J. jaculus*) the name *deserti* belongs.

The third genetic clade was found in Kuwait (Ben Faleh et al. 2012), south-western Iran (Boratyński et al. 2014) and Syria (Karyatein, B. Kryštufek, personal communication). Its genetic distance (mean between-group K2P value) from *J. hirtipes* is 6.3% – slightly above the arbitrary minimal value advanced to

distinguish between closely related rodent species (Baker and Bradley 2006). We studied specimens from Syria (Deir ez Zor, two skins and skulls and one glans penis). In skull morphology and colouration, they are similar with *J. hirtipes*, scales covered glans penis are closer to *J. jaculus* and the shape of glans penis differs from both. Thus, this lineage probably represents another cryptic species, but its taxonomic status needs to be clarified with the additional data. There are five synonyms for populations from the Arabian Peninsula and the Middle East: *Dipus loftusi* Blanford, 1875 (Iran, Mohumrah [=Khorramshahr]), *Jaculus loftusi vocator* Thomas, 1921 (Arabia, Muscat, Sohar), *Jaculus jaculus syrius* Thomas, 1922 (Syria, Karyatein), *Jaculus florentiae* Cheesman and Hinton, 1924 (Saudi Arabia, Jabrin, Jebal Aquia) and *Jaculus florentiae oralis* Cheesman and Hinton, 1924 (Kuwait). The correct name for the Asian form (its taxonomic status – species, semispecies or subspecies – needs to be clarified) should therefore be *Jaculus loftusi* (Blanford, 1875), which is the senior synonym. Although the use of this name remains to be validated by molecular data, such validation is anticipated because the type locality of *loftusi* is situated between two genetically studied regions, Kuwait (data of Ben Faleh et al. 2012) and Taj Maleki (Iran, Bushehr, specimen USNM 350757 studied by Boratyński et al. 2014); molecular data are also not yet available for *vocator* and *florentiae*.

Geographic distribution

Jaculus jaculus and *J. hirtipes* are widely sympatric in the northern and south-western Sahara (Ben Faleh et al. 2012; Boratyński et al. 2012). The type localities of these two species are only 15 km apart. There is no genetic evidence for the presence of *J. hirtipes* in Sudan yet. The presence of *J. jaculus* in Sudan, however, was supported by genetic data. Taking into account the wide sympatry of the two species in North Africa, we have little doubt that the *J. hirtipes* (*J. j. butleri* and *J. j. elbanensis* identified as *J. hirtipes* by morphological features) also occur in Sudan. There is no evidence that *J. jaculus* is present in the Horn of Africa. All available specimens from there (the sample from Somalia is deposited in the FMZNH; P. Agneli, personal communication) can be identified by colour characters as *J. hirtipes*. However, this area is geographically remote from specimens that were genetically sampled; taxonomic affinity of Somali specimens should be verified genetically. At the same time, our data demonstrate a parapatric distribution of *J. jaculus* and *J. hirtipes* in Israel and Sinai, although molecular sampling needs to be increased to make this conclusion stronger. An isolated occurrence record of *J. jaculus* in Hatzeva probably indicates the presence of this species in large sand massifs of the Jordanian part of the Arava Valley, about 5 km to the east of our point.

Habitat distribution and niche differentiation

Ranck's (1968) suggestion concerning habitat specialization of *J. jaculus* and *J. 'deserti' = hirtipes* is supported by the recent publications. Boratyński et al. (2012) found that in the western part of the Sahara Desert, both species were associated mainly with rocky desert and bare areas, but *J. jaculus* was recorded in sandy desert more frequently than *J. hirtipes*. Boratyński et al. (2014) demonstrated that throughout North Africa and the Middle East, the ecological separation of the two species was indicated by the substrate colouration; records of *J. jaculus* were more associated with lighter (sandy) areas, while records of *J. hirtipes* were more associated with darker (rocky) areas, although with substantial overlap between the species. Our

results support this conclusion for North Africa and demonstrate significant geographic variation in habitat preferences of *J. jaculus*. In North Africa, it can be considered as a habitat generalist with a relatively well-expressed preference for sandy habitats, whereas in Israel and Sinai, it becomes a true sand-dwelling specialist. *Jaculus hirtipes* mainly occurs in hammada-like habitats, but in a few cases, it was recorded in sandy habitats. Boratyński et al. (2014) hypothesized that *J.hirtipes* is competitively excluded by the more dominant *J. jaculus* from the optimal (sandy) habitat. Our field observations support this hypothesis: *J. hirtipes* was found to occupy small sand massifs in the absence of *J. jaculus*.

Boratyński et al. (2012) found that in the western part of the Sahara desert, *J. jaculus* occurred in hotter and wetter climates than did *J.hirtipes*. For the whole Sahara area, we found that *J. jaculus* inhabited more arid environments with a more continental climate than did *J. hirtipes*. In Israel and Sinai, the situation was opposite: *J. jaculus* occurred in less arid environments with a less continental climate than did *J. hirtipes*. These observed differences might be explained by the geographic differences in the distribution of main sand massifs. In the western part of the Sahara, sand massifs are situated mainly in its southern half, whose climate is influenced by monsoon rains. In the central and eastern parts of the Sahara, most sand massifs are inland, in areas with an arid continental climate. In Israel and Sinai, the main sand massifs are situated along the Mediterranean coast, in an area of Mediterranean and semi-arid climate (Laity 2008). The main environmental factor supporting the ecological segregation and coexistence of the two species must thus be the type of substrate, whereas between-species differences in the values of climatic variables in the areas of their occurrence are simply a reflection of geographic differences in the spatial distribution of sandy and non-sandy areas.

The observed differences in skull morphology between the two species correspond well to the differences in their preferred habitats. *J. hirtipes* has a more massive rostrum than *J. jaculus*. Three-toed jerboas (Dipodinae) use their incisors for burrow excavation, and among the different species, the harder the substrate they inhabit, the more massive their incisors and the rostral part of the skull, as an adaptation for burrowing (Shenbrot et al. 2008).

If the suggestions concerning habitat preferences of the two species and the interspecific competition between them discussed above are correct, their habitat distribution can be described using the distinct preferences model of density-dependent habitat selection for the system of two species and two habitats. This model (Pimm and Rosenzweig 1981; Rosenzweig 1981; Rosenzweig 1991; Shenbrot 2014) assumes that both species can exist in both habitats, but that one species prefers one of the habitats and the other species prefers the other. A parallel increase in densities of species with distinct habitat preferences will not alter the patterns of their habitat use. However, this model takes into account only exploitative competition. In the case of behavioural interference, competition should be density dependent because of the increased probability of between-individual encounters with the density growth (Shenbrot and Krasnov 2002). Thus, with a parallel increase in densities of species with distinct habitat preferences, asymmetric interference competition will lead to exclusion of the subordinate species from its secondary habitat. The sand massifs in Israel and Sinai are situated in more productive areas (Mediterranean and semi-desert) than the North African sands (true and extra-arid desert). As a result, population densities of *Jaculus* in sands and their surrounding areas in Israel and Sinai are likely to be higher than in North Africa. Consequently, differences in distribution patterns (parapatric in Israel and Sinai versus sympatric in the Sahara) of *J. jaculus* and *J. hirtipes* can

be explained by density-dependent intensity of interspecific competition.

We found that absolute values of niche shifts were maximal between Saharan and Middle Eastern populations of *J. jaculus* and minimal between Saharan sympatric populations of *J. jaculus* and *J. hirtipes*. However, the environments were quite different in the first case and almost identical in the second one. Taking into account these background environmental differences, we found high niche divergence between *J. jaculus* and *J.hirtipes*. While the North African and Middle East populations of *J. jaculus* demonstrated low niche divergence, the North African and Middle East populations of *J.hirtipes* demonstrated low niche convergence.

As in the case of another jerboa species, *Jaculus orientalis*, studied by Shenbrot (2013), we found that the level of niche differentiation coincided with the level of genetic differences. Peterson et al. (1999) hypothesized that ecological niches evolve little at or around the time of speciation events, whereas niche differences accumulate later. Many estimates of niche divergence/conservatism, using comparison of SDM, have been published in the recent years. The results of these estimates are quite controversial, and some of them contradict the hypothesis that the level of niche divergence is related to length of the postspeciation period (e.g. Warren et al. 2008; Kalkvik et al. 2012). It should be noted that SDM-based tests demonstrating significant niche similarity/identity can be considered as a true indication of niche conservatism (although without the differentiation of niche equivalence and convergence). However, the tests that have demonstrated significant niche differentiation in cases when background conditions were non-overlapping cannot be presented as a true evidence of niche differentiation (Peterson 2011). Nevertheless, a review of SDM-based tests of niche conservatism/differentiation published between 1999 and 2008 (Peterson 2011) demonstrated that niche conservatism was found in more than 70% of cases of within-species and between sister species comparisons, but in <50% of cases in comparisons among closely related (but not sister) species and across monophyletic lineages of species. We found high niche similarity (low divergence, convergence or equivalence) in our within-species comparison, but high niche divergence between *J. jaculus* and *J. hirtipes*. The genetic distance between these two species is above the average recorded between sister rodent species, and the time of divergence between them was estimated to be 3.1 Mya (Ben Faleh et al. 2012). Thus, our data seem to support the hypothesis that the level of niche divergence is related to the length of the postspeciation period.

We found that niche divergence between *J. jaculus* and *J.hirtipes* was slightly higher in the case of sympatric North African population of the two species than in the case of the parapatric populations of Israel and Sinai. These findings would appear to reflect the existence of strong selection processes (past or present) directed at habitat segregation, allowing the coexistence of closely related species in the case of their sympatric distribution, or maintaining parapatric distribution. These results support the idea that niche divergence is the consequence of ecological segregation of species during their secondary contact following an allopatric speciation event (Diamond 1973; McCormack et al. 2009).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Molar surface wearing patterns in different age groups of *Jaculus jaculus*.

Figure S2. Bayesian (a) and maximum-likelihood (b) trees of *cyt b* sequences of *Jaculus jaculus*.

Table S1. Geographic location of the samples used for phylogeny reconstruction and analyses of habitat preferences and niche differentiation.