

Research article

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(Mammalia: Talpidae)****Haluk Kefelioğlu¹, Boris Kryštufek², Ahmet Yesari Selçuk³, Rainer Hutterer^{4,*} & Jonas J. Astrin⁵**^{1,3}Department of Biology, Faculty of Science, Ondokuz Mayıs University, Samsun, Turkey²Slovenian Museum of Natural History, Prešernova 20, SI-1000 Ljubljana, Slovenia^{4,5}Zoologisches Forschungsmuseum Alexander Koenig, Leibniz-Institut für Biodiversität der Tiere, Adenauerallee 160, D-53113 Bonn, Germany*Corresponding author: Email: R.Hutterer@leibniz-zfmk.de¹[urn:lsid:zoobank.org:author:592452AF-02D3-4DC3-A350-0DFCE829A3F5](https://zoobank.org/urn:lsid:zoobank.org:author:592452AF-02D3-4DC3-A350-0DFCE829A3F5)²[urn:lsid:zoobank.org:author:FB4835B1-618E-4A0E-8917-078A90328D97](https://zoobank.org/urn:lsid:zoobank.org:author:FB4835B1-618E-4A0E-8917-078A90328D97)³[urn:lsid:zoobank.org:author:2F906968-32C8-4359-AC96-76049F6E229B](https://zoobank.org/urn:lsid:zoobank.org:author:2F906968-32C8-4359-AC96-76049F6E229B)⁴[urn:lsid:zoobank.org:author:16023337-0832-4490-89A9-846AC3925DD8](https://zoobank.org/urn:lsid:zoobank.org:author:16023337-0832-4490-89A9-846AC3925DD8)⁵[urn:lsid:zoobank.org:author:50661540-FD30-4ABA-8415-6B3069105E93](https://zoobank.org/urn:lsid:zoobank.org:author:50661540-FD30-4ABA-8415-6B3069105E93)

Abstract. This paper examines the distribution and the morphological and genetic variation of *Talpa levantis*. Previous records from Thrace were re-identified as *Talpa martinorum*, restricting the range of *Talpa levantis* to northern Asia Minor and the Caucasus in Georgia, Armenia and Russia. Within *Talpa levantis*, we found three moderately distinct populations in western, central, and eastern Turkey. While the central one is *T. l. levantis* and the eastern one *T. l. transcaucasica*, the western subspecies had not been recognized before and is therefore named as a new subspecies.

Key words. Cytochrome *b*, molecular taxonomy, morphology, phylogeography, subspecies, *Talpa levantis*, *Talpa martinorum*.

INTRODUCTION

Mammalian systematics is dynamic and new species are continuously being recognized. The number of mammal species, estimated at 5,416 in 2005 (Wilson & Reeder 2005) increased to 6,495 just 13 years later (Burgin et al. 2018), an astonishing 20% increase. This progress was at least partly generated by a wide application of new research tools, above all the highly effective DNA-based methods which are capable of delimiting morphologically cryptic species (Baker & Bradley 2006).

Our focus in this study is the evolutionary divergence, taxonomy and species richness of the Eurasian mole genus *Talpa* Linnaeus, 1758 in Turkey. The genus is endemic to the western Palaearctic region and is well known to the lay public for its distinctive external appearance and the characteristic heaps of soil, mole-hills, which are abundant in temperate zone meadows. Less known to the public is the fact that species delimitation in *Talpa* has been progressing very slowly and continuing disagreements among experts over the number of species exist (Kryštufek & Motokawa 2018). Strong selective pressures for a semifossorial life blur the phylogenetic signal in morphological structures and convergences/

parallelisms are overwhelming. Traditional taxonomy therefore heavily underestimated the species richness of moles. The state of knowledge progressed only when the information in nucleotide sequences was combined with a wide taxonomic sampling (Bannikova et al. 2015). Between 2005 and 2020, the number of recognized species in the genus *Talpa* increased from nine (Hutterer 2005) to fourteen (Kryštufek & Motokawa 2018, Kryštufek et al. 2018a, Demirtaş et al. 2020), an increase of 56%.

Bannikova et al. (2015) pointed out several unresolved taxonomic problems, which required further attention. One of these problems concerns the Levant mole *Talpa levantis* Thomas, 1906, which displays a very high intra-specific genetic divergence. Earlier on, the Levant mole was thought to range from the south-eastern Balkans across northern Turkey into the Caucasus and the Caspian coast of Iran. It was subsequently shown that the western-most populations represent a species new to science (*Talpa martinorum* Kryštufek et al. 2018), that those from the Caspian coast are identical with *T. talyschensis* Vereschagin, 1945, and that the rest can be split into the western *T. levantis* proper, and the eastern *T. transcaucasica* Dahl, 1945 (Demirtaş et al. 2020). In this paper we are re-addressing the geographical variability of Levant

moles occupying Turkey by combining, for the first time, molecular evidence with morphological data. Our aim was to gain a more holistic view on the taxonomic structure of the Levant mole.

MATERIAL & METHODS

Specimens. We studied small blind moles from throughout Turkey (Fig. 1, Appendix I) which were earlier classified as *T. levantis*. The European material was taken into consideration because it had so far not been screened genetically and because Demirtaş et al. (2020) suggested these populations to be conspecific to those occupying Anatolia.

Tissue samples for DNA analysis were placed in non-denaturated 96% ethanol and subsequently refrigerated. The cytochrome *b* (*Cyt b*) gene was sequenced for 20 Levant moles and these new sequences were analyzed together with 17 additional Levant mole sequences from Turkey and the Caucasus region. Furthermore, we downloaded from the GenBank database 23 sequences of 10 *Talpa* species, and an outgroup Talpinae sequence (*Urotrichus talpoides*). Collecting data associated with the new sequences and all GenBank numbers for Levant moles are given in Table 1 [sequences submitted to GenBank]; for the remaining GenBank numbers see Table 1.

Specimen vouchers (skins and skulls) are deposited in the following collections (acronyms in parentheses): National Museum of Natural History, Washington D. C.

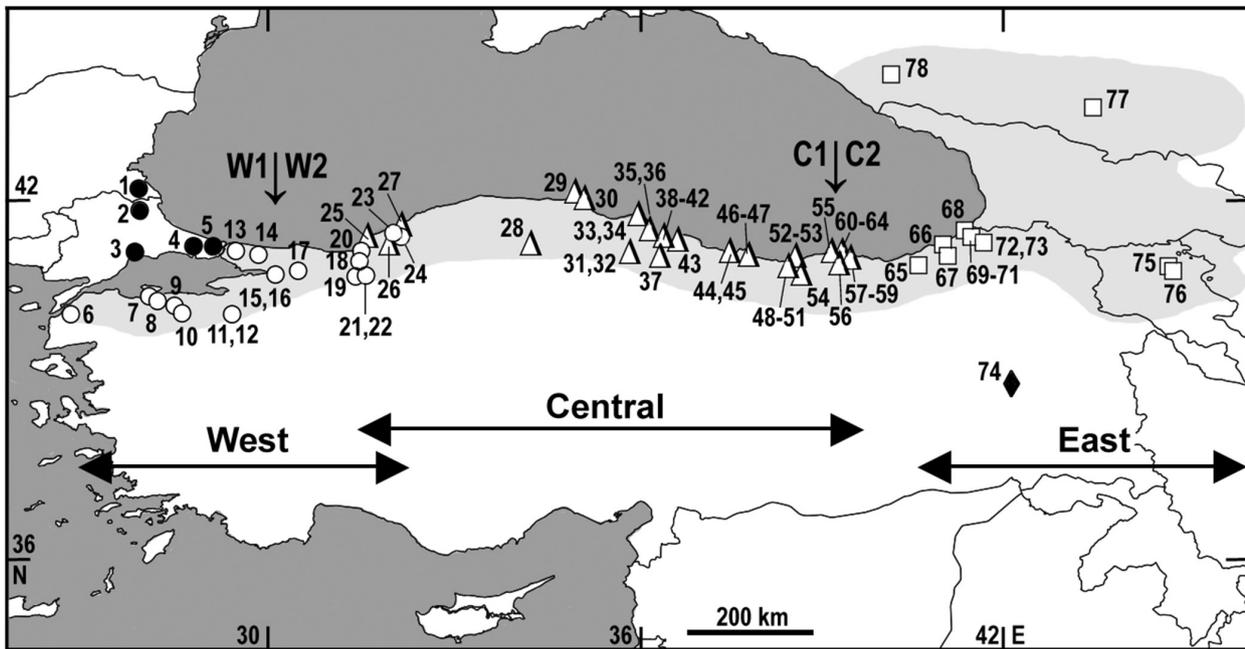


Fig. 1. Sample locations of *Talpa levantis* and *T. martinorum*. Symbols: ○ *Talpa levantis dogramacii* ssp. nov.; △ *T. levantis levantis*; □ *T. l. transcaucasica*; ◆ *T. levantis* ssp.; ● *T. martinorum*. Symbols correspond to those in Fig. 1 and Table 1. Tentative range of *Talpa levantis* is shaded grey and tentative longitudinal ranges of lineages are shown by left-right arrows. Downwards arrows show contact points between the sublineages of Western (W1, W2) and Central (C1, C2) lineages. Population near Lake Van (pt. 74) is presumably an isolate of unknown genetic identity, known from a single locality. Bulgaria: 1–Kondolovo. Turkey: 2–Kırklareli, Dupnisa; 3–Tekirdağ, Çorlu; 4–İstanbul, Çatalca; 5–İstanbul, Bahçeköy, Belgrad Ormanı; 6–Çanakkale; 7–Kapıdağ, Balıkesir; 8–Balıkesir, Manyas; 9–Balıkesir, Bandırma; 10–Bursa, Karacabey; 11–Bursa, Uludağ; 12–Bursa, Kirazlıyayla, Uludağ; 13–İstanbul, Mahmutşevketpaşa; 14–İstanbul, Şile; 15–İzmit; 16–İzmit, Kandıra; 17–Adapazarı, Kazımpaşa, Alandüzi köyü; 18–Düzce; 19–Bolu, Abant; 20–Kocaman forestry, half was between Akçakoca and Alaplı; 21–Bolu, Seben; 22–Bolu, Karadere; 23–Zonguldak, Uzungüney Köyü; 24–Zonguldak, Çaycuma; 25–Zonguldak, Alaplı; 26–between Zonguldak and Bolu; 27–Zonguldak, between Sefercik and Filyos; 28–Tosya, Kastamonu; 29–Sinop, Abalı Köyü; 30–Sinop, Gerze; 31–Amasya; 32–Amasya, Tatlıcak köyü; 33–Samsun, Bafra; 34–Samsun, Kızılırmak delta, Bafra; 35–Samsun, Erikli Köyü; 36–Samsun, Ondokuzmayıs, Derneköy; 37–Taşova District, Borabay Lake; 38–Samsun, Karakavuk; 39–Samsun, İncesu Köyü; 40–Samsun; 41–Samsun, Kurupelit; 42–Samsun, Tekkeköy; 43–Samsun, 3 km south Çarşamba; 44–Ordu, Fatsa; 45–Ordu, Fatsa, Geyikçeli Köyü; 46–Ordu, Ulubey; 47–Ordu; 48–Giresun, Yavuzkema; 49–Giresun, Batlama Deresi; 50–Giresun, Kümbet; 51–Giresun, Dereli; 52–Giresun; 53–Giresun, Ülper; 54–Trabzon, Meryem Ana; 55–Giresun, Görele; 56–Ordu, Torul, Gümüşhane; 57–Trabzon, Maçka; 58–Trabzon, Maçka, Altındere; 59–Trabzon, Maçka, Sümela Manastırı; 60–Trabzon; 61–Trabzon, Khotz; 62–Trabzon, Özdil; 63–Trabzon, Oymaltepe; 64–Trabzon, Yomra; 65–Rize, Ovit, Ovit Yaylası; 66–Rize, Ardeşen; 67–Ayder, İlicasi; 68–Artvin, Hopa, Sugörenköyü; 69–Artvin, Hopa 8 km east; 70–Artvin; 71–Artvin, Ardanuç; 72–Artvin, Yalnızcamgeçidi; 73–Ardahan, Çam Geçidi; 74–Bitlis, Tatvan, Lake Van. Armenia: 75–Margahovit; 76–Fioletovo. Russia: 77–Kabardino-Balkaria, Nalchik; 78–Adygea.

Table 1. Details of sample localities (mapped in Figure 1) for Levant moles s. lat. and cytochrome *b* haplotypes found within them.

Location No.	Country	Locality	Haplo-type	Voucher No.	GenBank Acc. No. (bold = new)	References
● <i>T. martinorum</i>						
1	Turkey	Kırklareli, Dupnisa	TR13		MT738563	This study
2	Bulgaria	Mt. Strandzha, Kondolovo		ZFMK-MAM-2017.1151	MH093595	Kryštufek et al. 2018a
4	Turkey	İstanbul, Çatalca	TR15		MT738565	This study
○ <i>T. levantis</i> West						
7	Turkey	Kapıdağ, Balıkeşir	TR18	OMU 1346	MT738568	This study
11		Bursa, Uludağ	TR6	OMU 1350	MT738556	This study
			TR7	OMU 1352	MT738557	This study
			TR8	OMU 1353	MT738558	This study
				PMS 10650	FN640571	Colangelo et al. 2010
23		Zonguldak, Uzungüney Köyü			KP717336	Bannikova et al. 2015
25		Düzce	TR16	OMU 1344	MT738566	This study
			TR17	OMU 1345	MT738567	This study
29		Zonguldak, Çaycuma			KP717338	Bannikova et al. 2015
△ <i>T. levantis</i> Central						
20		Zonguldak, Alaplı			KP717340	Bannikova et al. 2015
26		Bolu-Zonguldak	TR19	OMU 1343	MT738569	This study
28		Zonguldak, Sefercik – Filyos			KP717339	Bannikova et al. 2015
					KP717343	Bannikova et al. 2015
33		Amasya	TR14		MT738564	This study
42		Samsun	TR11		MT738561	This study
				PMS 10299	FN640572	Colangelo et al. 2010
46		Ordu, Fatsa	TR9		MT738559	This study
49		Ordu	TR20		MT738570	This study
			TR12		MT738562	This study
51		Giresun	TR10	OMU 1349	MT738560	This study
52		Giresun, Ülper	TR20	OMU 1340	MT738552	This study
53		Giresun, Kümbet	TR5		MT738555	This study
59		Trabzon, Maçka	TR1	OMU 1354	MT738551	This study
64		Trabzon, Özdil	TR4	OMU 1351	MT738554	This study
65		Trabzon, Oymaltepe	TR3	OMU 1347	MT738553	This study
□ <i>T. levantis</i> East						
76	Turkey	Ardahan, Cam Geçidi		PMS 21658	FN640570	Colangelo et al. 2010
77	Armenia	Margahovit			KP717335	Bannikova et al. 2015
78		Fioletovo			KP717337	Bannikova et al. 2015
					KP717342	Bannikova et al. 2015
79	Russia	Kabardino-Balkaria, Nalchik			KP717334	Bannikova et al. 2015
					KP717341	Bannikova et al. 2015
		Kabardino-Balkaria			FN640573	Colangelo et al. 2010
					FN640574	Colangelo et al. 2010
80	Russia	Adygea			KP717344	Bannikova et al. 2015
					KP717345	Bannikova et al. 2015
					KP717346	Bannikova et al. 2015

(NMNH), Natural History Museum London (BMNH), Naturhistorisches Museum Wien, Vienna (NMW), Zoologische Staatssammlung München, Munich (ZSM), Mammal Collection in the Ondokuz Mayıs University, Samsun (OMU), and Slovenian Museum of Natural History, Ljubljana (PMS). Vouchers in OMU, PMS and ZSM were examined by us in December 2019 and February 2020. Material from the remaining collections was examined by BK prior to this study and records were compiled to contain measurement data, drawings and photographs.

All field procedures involving handling of animals in this study were in compliance with guidelines approved

by the American Society of Mammalogists (Sikes et al. 2011). Recent collecting was carried out under permit B.30.2.ODM.0.20.09.00-050.04-09 issued on February 14, 2014, by the Ethic Committee at the Ondokuz Mayıs University.

Molecular protocols. Total genomic DNA was extracted from ethanol-preserved muscle tissue using silica membrane columns of the Blood and Tissue kit by Qiagen (Hilden, Germany). DNA extracts are available from the ZFMK Biobank, Bonn (DNA voucher IDs are listed in Table 1). For PCR amplifications of the mitochon-

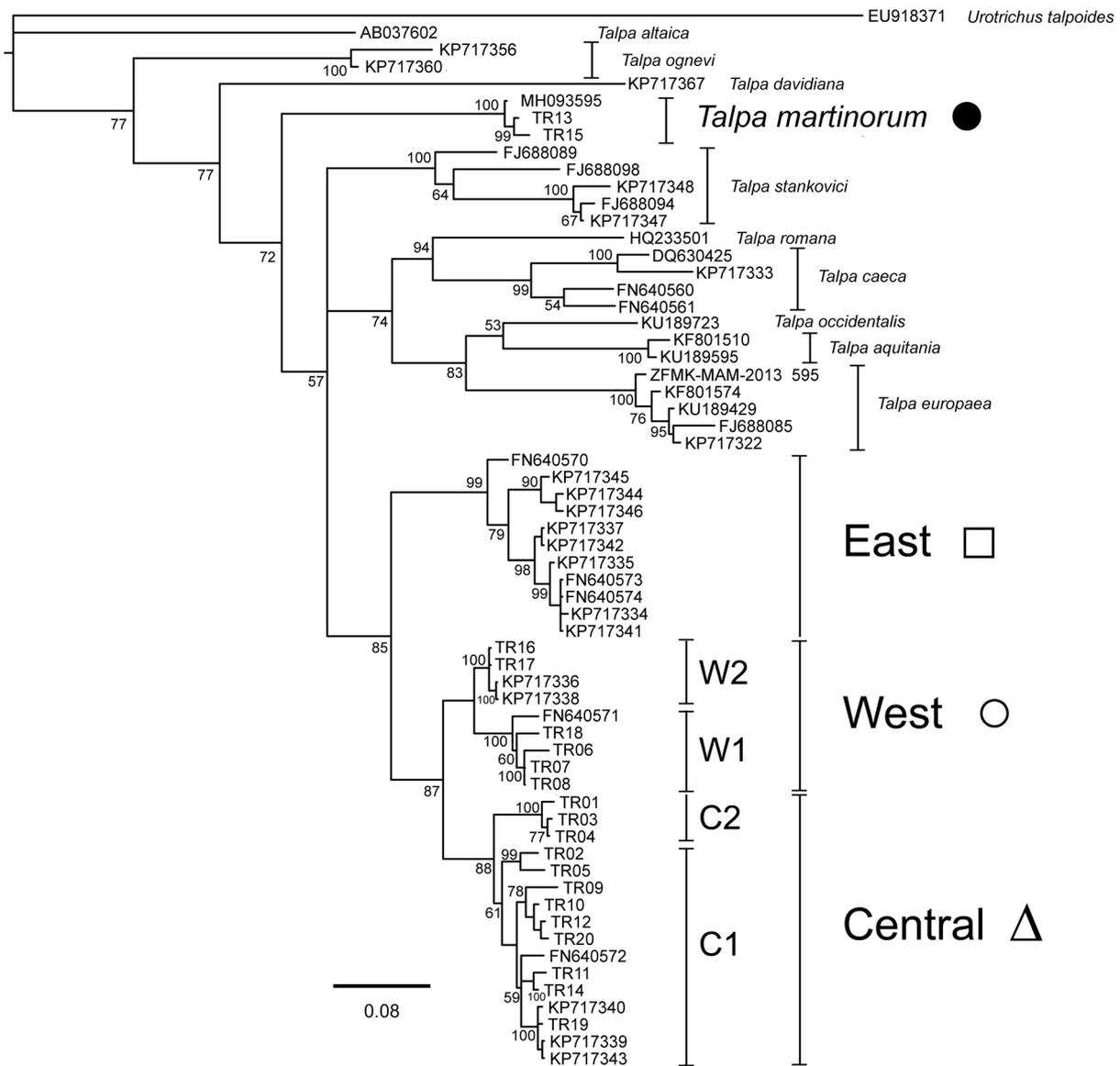


Fig 2. 50% Majority Rule Bayesian tree inferred from 1043 bp of the mitochondrial cytochrome *b* gene for 11 species of the genus *Talpa*. Posterior probability values are shown on the nodes. The tree is rooted with *Urotrichus talpoides*. Symbols correspond to those in Fig. 1 and Table 1.

drial Cytochrome *b* (Cyt *b*) gene, we used the Qiagen Multiplex PCR kit, following the manufacturer's specifications and based on 2 µl undiluted DNA template in 20 µl total reaction volumes. DNA fragments of 1043 bp were amplified with an Applied Biosystems GeneAmp PCR System 2700 (Life Technologies), applying the primers L14724ag (5'-ATGATATGAAAAACCATC-GTTG-3') and H15915ag (5'-TTTCCNTTCTG-GTTTACAAGAC-3'; Guillén-Servent & Francis 2006). PCR routine followed a 'touch-down' protocol: Taq activation: 15 min at 95°C; first cycle set (15 repeats): 35 s denaturation at 94°C, 90 s annealing at 60°C (-1°C per cycle) and 90 s extension at 72°C. Second cycle set (25 repeats): 35 s denaturation at 94°C, 90 s annealing at 50°C, and 90 s extension at 72°C.

After enzymatic clean-up, all PCR products were Sanger-sequenced at Macrogen, Europe's commercial Sanger sequencing service (Amsterdam, NL). Sequences were assembled, inspected and aligned using Geneious vers. R7 (Biomatters, Auckland, New Zealand).

Bayesian analyses were conducted using MrBayes vers. 3.2 (Ronquist & Huelsenbeck 2003). Specific parameters for a GTR+G model were equated by the program. GTR+G is a typical substitution model that includes sufficient degrees of freedom and factors in heterogeneity of substitution rates among sites, but avoids overparameterization as potentially induced by modelling invariable sites (Jia et al. 2014 showed the irrelevance of including invariable site assumptions in datasets below species level). Parameters were unlinked between the 3rd versus 1st plus 2nd codon positions, based on the fact that third codon 'wobble' positions are less influenced by selective pressure and much less conserved than 1st and 2nd positions, hence requiring separate parameter calculation. MrBayes was run for 20 million generations and using the default number of chains. Every 1000th tree was sampled. Negative log-likelihood score stabilization was determined in a separate visualization. Accordingly, we retained 39,960 trees, which were used for building a 50%-majority rule consensus tree with posterior probabilities (Fig. 2).

Morphological analyses. Our study was based on visual examination of museum specimens, both macroscopically and under a stereomicroscope at different magnifications. Skull morphology was quantified by means of five cranial variables, which were scored using a Vernier calliper with accuracy to the nearest 0.1 mm (acronyms in parentheses): condylobasal length of skull (CbL), length of maxillary tooth-row (MxT; canine to 3rd molar), breadth of braincase (BcB), breadth of rostrum over canines (RoC), and breadth of rostrum over molars (RoM). The length of the posterior part of braincase was measured on printed skull photographs. External measurements were obtained from specimen tags: body mass (BWt), length of head and body (H&B), length of tail (TL), and length

of hind foot (HfL). Body mass is given in grams and the remaining measurements in millimetres.

Based on molecular results, the specimens were grouped into three operational taxonomic groups (OTUs), which were essentially identical to phylogenetic lineages. Because molecular characters were not known for all museum specimens, we presumed that the lineages are allopatric and classified skulls on this basis. Specimens from the zone of overlap between the Western and the Central lineages were excluded, while specimens from the little-known contact zone between the Central and the Eastern lineages were assigned to the group using classification criteria derived from a discriminant function analysis based on securely identified vouchers. We used the same labels for denomination of phylogenetic lineages and morphological OTUs (Western, Central and Eastern). Moles from Lake Van (pt. 74 in Fig. 1) are traditionally classified as *T. levantis* although they are an isolate with unknown molecular identity. We used morphometric analysis to compare this sample with the three OTUs of *T. levantis*.

Heterogeneity between OTUs was evaluated in one-way or two-way analyses of variance (Anova). To characterize the craniometric variation among samples and to find patterns in our high-dimensional data, we performed a principal components analysis (PCA) and a discriminant function analysis (DFA) on log₁₀-transformed cranial variables. Rates of correct classification of *a priori* defined species were evaluated in a discriminant analysis. To evaluate the performance of the DFA and avoid the risk of overfitting the data, all analyses were cross-validated using the jack-knife procedure, in which each specimen is classified into a group using the discriminant function derived from all specimens except the specimen being classified. Relative length of maxillary tooth row (MxT%) and relative breadth of rostrum over molars (RoM%) were expressed as quotients with the condylobasal length of skull and multiplied by 100. Because of undesirable statistical properties of ratios, we did not use them in multivariate analyses. Statistical tests were run in Statistica 7.0 (StatSoft Inc., OK, USA) and SPSS Statistics 2012 (IBM Analytics, NY).

RESULTS

Molecular results. Sequencing of the new Turkish samples resulted in 19 haplotypes of the length 1043 bp (one sequence missing one base, another three). A further sequence that showed a clear (and accordingly trimmed) read for only 403 bp was integrated in the dataset (sample TR09 from Fatsa Ordu). Overall, the dataset included 6 ambiguous positions in individual sequences (see attached alignment in Appendix II).

In the Bayesian tree (Fig. 2), haplotypes clustered according to the earlier results of Bannikova et al. (2015),

although tree topologies differed in some minor respects. Moderate nodal supports prevent us from discussing the deeper branching topology (outside *T. levantis*) in detail. Turkish samples grouped into four clusters. The only two haplotypes from European Turkey (TR13, TR15) aligned with the reference sequence of *T. martinorum* from Bulgaria. Levant mole haplotypes grouped into three lineages, which showed strong geographic associations and were designated as the Western, Central and Eastern lineage. The Eastern lineage holds a moderately supported basal position with regard to the Western and Central lineages. The collecting sites of specimens associated genetically with the Central and Eastern lineages were separated by a distance of about 225 km, without any genetically screened samples in-between. On the other hand, the ranges of the Western and Central lineages overlapped to the east of the city of Zonguldak for a distance of at least 30 km in west-to-east direction. Besides this, the Western and Central lineages were further sub-structured, each into two allopatric sub-lineages. In

the Western lineage, the sublineages W1 and W2 were tentatively delimited by Sakarya, while the sub-lineages C1 and C2 of the Central lineage had a contact between Rize and Trabzon. The C2 sublineage occupies the majority of the range of Levant moles in Turkey by stretching along the Black Sea coast in west-to-east direction for ca. 650 km.

Within the Levant moles of Anatolia, the *Cyt b* divergence was highest between the Eastern and the Central lineages (highest pairwise *p*-distance at 8.0%), and amounted to 5.9% between the Central and the Western lineages. Genetic variation within the lineages was highest in the Central lineage (mean *p*-distance of 2.0%, highest pair-wise *p*-distance 3.4%), closely followed by the Western lineage (mean 1.7%, highest 2.9%), and was lowest in the Western lineage (mean 1.0%, highest 2.6%). In our dataset, the lowest *p*-distance among lineages was between the Central and Western lineages, with 3.5%.

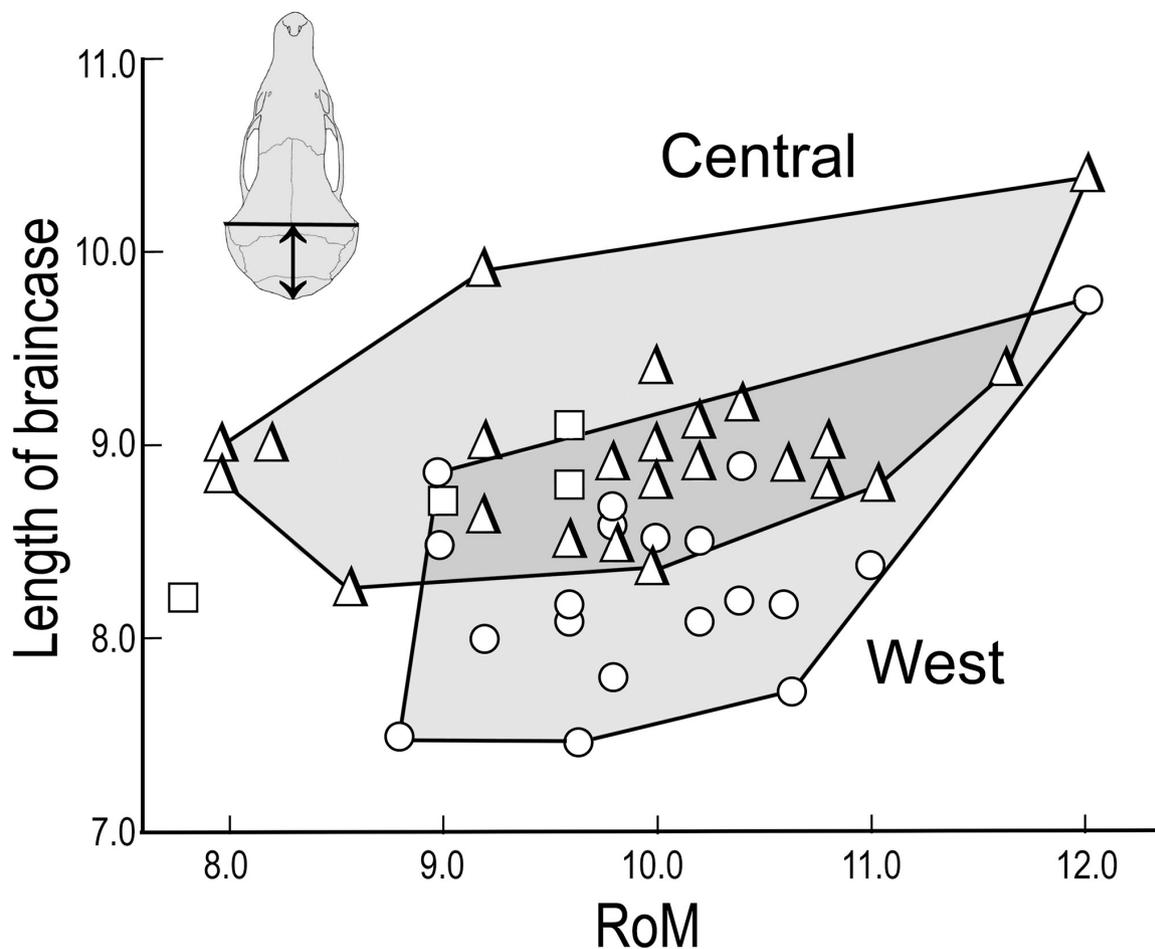


Fig. 3. Bivariate plot of length of neurocranium (see the left upper inset) against breadth of rostrum across molars (RoM) for three operational taxonomic units of *Talpa levantis*. Symbols are same as in Fig. 1.

Morphology. Moles from Turkish Thrace lack the parastyle on the anterior upper molars and were therefore classified as *T. martinorum* (cf. Kryštufek et al. 2018a). The parastyle is present in the majority of Anatolian individuals, as long as their molars are still comparatively unworn. Visual examination of skulls retrieved no quantitative cranial or dental traits among the *T. levantis* OTUs.

In the results of a two-way Anova, the major source of morphometric variation was the OTU and not the sexual category (Table 2). Therefore, five variables (H&B, HfL, CbL, MxT, RoM) showed significant heterogeneity among the OTUs and only three traits (BWt, H&B, BcB) were also sexually dimorphic. With the exception of the length of tail, there was no interaction between these two factors. Out of 27 pairwise comparisons, only ten showed significant differences in the Fisher LSD test. Six of them fell between the Central and Eastern OTUs, while two comparisons were significant between the Western and Central OTUs, and further two between the Western and Eastern OTUs, respectively. Males were more prone to the heterogeneity among OTUs (7 significant pairwise comparisons) than females (3 significant comparisons). The two quotients (MxT% and RoM%) showed a similar pattern as the linear measurements (Table 2).

When inspecting skulls macroscopically, we spotted slight differences in their shape and proportion. Therefore, in the Western OTU, the posterior outline of the braincase was less bowed than in the Central OTU, the overlap however was considerable (Fig. 3). Furthermore, the relative length of the maxillary tooth-row (MxT%) and the width of rostrum across molars (RoM%) showed a steady increase from the Eastern OTU to the Western OTU; the Central OTU was intermediate in both cases. Again, the overlap among the OTUs was sizeable (Fig. 4). We therefore tested our data set for possible longitudinal trends. Two external traits (BWt, TL), three craniodental variables (MxT, RoC, RoM) and both quotients (MxT% and RoM%) showed significant trends of a west-to-east decline (Table S1). The remaining traits (H&B, HfL, CbL, BcB) showed extremely low F-values ($F < 0.30$, $p > 0.59$). Moles in the west were therefore the heaviest, with longer tails, absolutely and relatively longer maxillary tooth-rows, relatively and absolutely broader rostra and less bowed posterior braincases. The eastern moles showed the lowest values for all these indices, while geographically intermediate moles were also transitional in these traits.

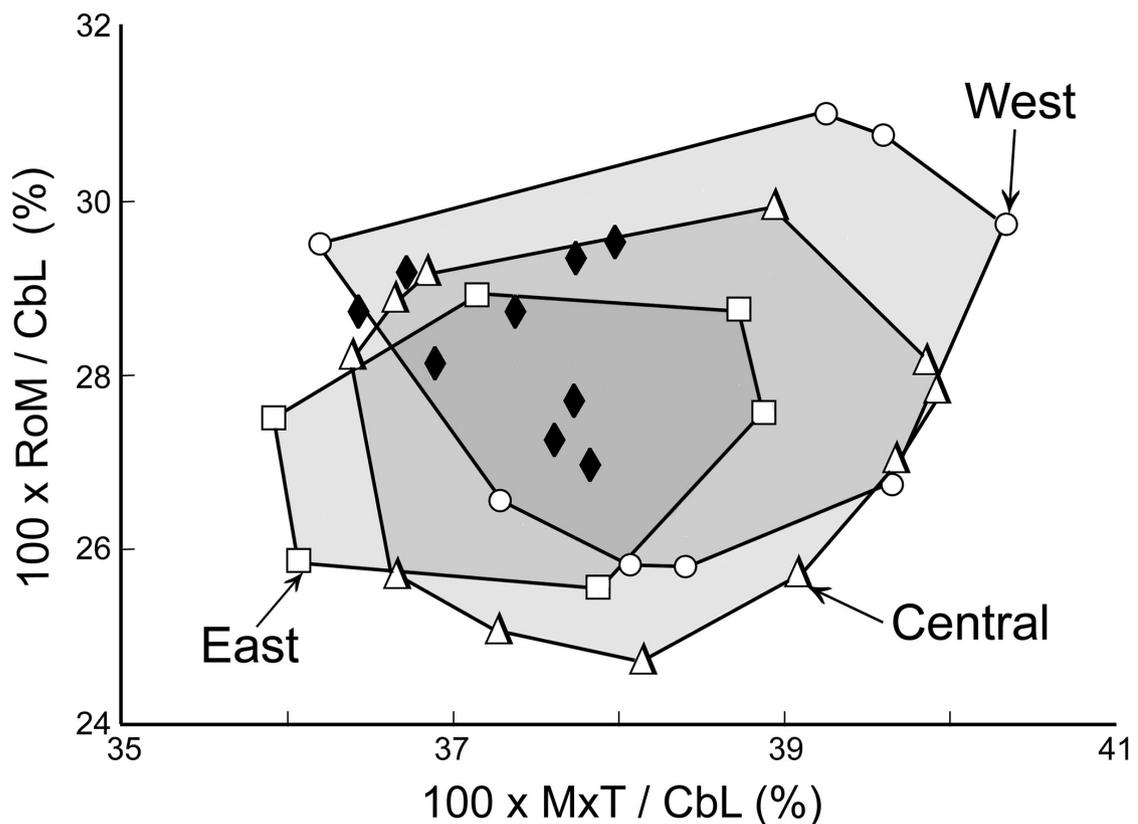


Fig. 4. Bivariate plot of breadth of rostrum across molars (RoM) against length of maxillary tooth-row (MxT), both expressed as quotients of the condylobasal length of skull and multiplied by 100, for three operational taxonomic units of *Talpa levantis* and the sample from Lake Van. Symbols are same as in Fig. 1.

Table 2. Descriptive statistics (mean and standard error) for three operational taxonomic units (OTUs) of *Talpa levantis*. Results of two-way Anova (sex and OTU as factors) and Fisher LSD test between the OTUs (W–Western; C–Central; E–Eastern) are shown in four columns on the right-hand side.

Trait		West			Central			East			Two-Way Anova		Scheffé test	
		N	Mean	SE	N	Mean	SE	N	Mean	SE	F-value	p		
BWt	males	26	54.88	1.448	25	55.32	1.477	6	51.25	3.014	OTU	1.18	0.311	
	females	13	52.00	2.048	29	47.63	1.371	7	49.14	2.791	Sex	5.90	0.017	
											Interaction	1.47	0.236	
H&B	males	29	122.41	1.244	34	126.09	1.149	14	121.57	1.791	OTU	4.27	0.015	W-C, C-E
	females	13	119.54	1.859	29	122.10	1.244	10	118.50	2.119	Sex	6.33	0.013	
											Interaction	0.09	0.912	
TL	males	29	27.90	0.469	34	27.32	0.433	14	28.00	0.675	OTU	2.37	0.098	
	females	13	28.62	0.700	29	28.31	0.469	9	25.56	0.842	Sex	0.24	0.626	
											Interaction	3.94	0.022	
HfL	males	29	18.76	0.245	34	19.12	0.227	14	17.94	0.354	OTU	3.93	0.022	C-E
	females	13	18.54	0.366	29	19.00	0.246	10	18.42	0.418	Sex	0.03	0.861	
											Interaction	0.58	0.563	
CbL	males	29	31.15	0.229	32	31.76	0.218	14	30.63	0.330	OTU	11.68	0.00002	C-E
	females	13	30.44	0.343	27	31.35	0.238	9	29.64	0.412	Sex	7.96	0.006	W-C, C-E
											Interaction	0.49	0.62	
MxT	males	30	11.95	0.095	35	12.09	0.084	14	11.51	0.133	OTU	12.60	0.00001	W-E, C-E
	females	14	11.75	0.133	28	12.01	0.094	9	11.36	0.166	Sex	1.99	0.161	C-E
											Interaction	0.19	0.824	
BcB	males	29	15.25	0.089	33	15.46	0.083	14	15.29	0.128	OTU	2.40	0.091	
	females	13	14.96	0.133	29	15.17	0.089	9	15.02	0.160	Sex	8.70	0.004	
											Interaction	0.00	0.996	
RoC	males	30	4.61	0.181	35	4.23	0.168	14	3.96	0.265	OTU	1.03	0.361	
	females	14	4.14	0.265	28	4.23	0.188	9	4.04	0.331	Sex	0.45	0.504	
											Interaction	0.83	0.439	
RoM	males	30	8.83	0.097	35	8.60	0.089	14	8.31	0.141	OTU	4.31	0.016	W-E
	females	14	8.70	0.141	29	8.72	0.098	9	8.40	0.176	Sex	0.09	0.770	
											Interaction	0.74	0.481	
Quo- tiens	males	28	38.42	0.159	32	38.19	0.148	14	37.55	0.225	OTU	7.50	0.0007	W-E, C-E
	females	13	38.62	0.234	27	38.27	0.162	8	37.67	0.298	Sex	0.90	0.345	W-E
											Interaction	0.00	0.984	
RoM%	males	29	28.34	0.222	32	27.04	0.211	14	27.11	0.319	OTU	9.08	0.0002	W-C, W-E
	females	13	28.53	0.331	27	27.74	0.230	8	27.83	0.422	Sex	4.82	0.030	
											Interaction	0.59	0.556	

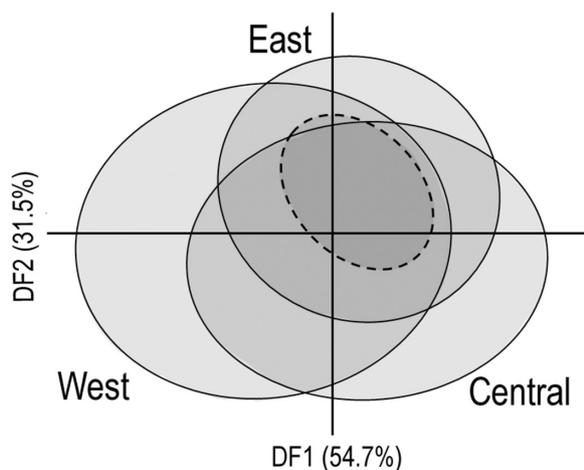


Fig. 5. The 95% confidence ellipses for dispersion of scores of four operational taxonomic units of *Talpa levantis* onto the first two discriminant axes derived from discriminant factor analyses of \log_{10} -transformed cranial variables. The proportion of variance explained by an axis is in parentheses. The ellipse for the Lake Van sample is shown by a dashed line.

The principal components analysis was run on a correlation matrix of all five cranial traits. One-way Anova retrieved significant heterogeneity among OTUs in four principal components (pc) out of a total of five. Quite remarkably, the highest F-values were by pc3 and pc5, i.e. two components which explained only a small proportion of variance (=10.4%) in the original data set (Table S2). Projection of specimen scores onto these components revealed a high overlap among OTUs and moles from Lake Van overlapped with all three OTUs (not shown).

Forward stepwise discriminant analysis on five cranial variables and with four groups (three OTUs and sample from Lake Van) as classification factor resulted in a moderately high Wilk's lambda ($=0.587$, $p<0.001$). All variables were included into the analysis, except for the braincase width ($F\text{-to-enter}=2.255$, $p=0.85$). Condylbasal length of the skull and maxillary tooth-row length had the highest $F\text{-to-remove}$ values (10.656 and 8.175, respectively; $p<0.00005$) and therefore contributed most to a discrimination between groups. Putting aside the Lake Van sample, the Mahalanobis squared distance (D^2) was high between the Western and the Eastern OTUs ($D^2=2.125$), moderate between the Western and the Central OTUs ($D^2=1.667$) and low between the Central and the Eastern OTU ($D^2=1.355$; all significant at $p<0.002$; $F>4.5$). The Lake Van sample was most similar to the Eastern sample ($D^2=1.690$, $p=0.046$), followed by the Central OTU ($D^2=2.006$, $p=0.006$) and the Western OTU ($D^2=2.759$, $p=0.001$). Predictability of classification was rather low and only 54.7% of cases were allocated into the actual group; this ranged from 80.0% of correct classifications for the Van sample, across 56.8% for the West-

ern OTU and 52.9% for the Eastern OTU, to 45.8% in the Eastern OTU. Cross-validation of classification with leave-one-out yielded very similar results with 52.0% of individuals being allocated to the actual group. The overlap between groups was therefore considerable and was evident also from the projection of specimen scores onto the first two discriminant axes, explaining 86.2% of variance in the original data set (Fig. 5). On the other hand, the cross-validation of classification results showed that we avoided the risk of overfitting data in our DFA. We therefore conclude that differences between the groups are slight but genuine.

DISCUSSION

Survival in Pleistocene refugia. There is a deep genealogical divergence among the three main *Cyt b* lineages of the Levant mole and such a pattern is a clear indication that these lineages originated from an allopatric fragmentation event (Avice 2000). The most ancient divergence in the Levant mole, which is between the Western + Central and the Eastern lineages, is estimated to have occurred at ca. 1.91 Mya (Demirtaş et al. 2020). The current phylogeographic pattern of the Levant mole is therefore clearly the legacy of climatic changes during the glacial-interglacial cycles of the Pleistocene when the newly emerged biogeographic barriers created by novel climatic conditions fragmented populations, prevented gene flow and triggered divergence in isolation.

Contrary to Europe where periodic expansion of ice sheets and the consequent cooling of temperatures profoundly impacted the survival of temperate biota throughout the Pleistocene (Hewitt 2000), the Quaternary environments in Anatolia were different in many respects. Glaciers persisted only at elevations above 2200 m (Eriņç 1978) while the lowlands were affected by aridification (Webb & Bartlein 1992). In a highly diverse landscape of Anatolia, the endurance of temperate taxa was facilitated along the altitudinal gradient in a network of mountain refugia which provided moist conditions at intermediate elevations (Ansell et al. 2011). Fossorial moles are highly sensitive to soil humidity, which supports prey consisting primarily of earthworms (Kryštufek & Motokawa 2018). It is therefore feasible to presume that during the Pleistocene the progressing aridification pushed the Levant moles to higher elevations where they endured in humid enclaves. This fragmented the mole's range, just as an expansion of glaciers and tundra habitats repeatedly fragmented continuous distributions of numerous temperate taxa in Europe (Hewitt 2000). A combination of Anatolian topography and climatic history may have promoted a long-term local survival of the Levant mole in the Black-Sea (Pontic) Mountains, and simultaneously facilitated the independent evolutionary divergence of vicariant populations. At least five refugia can be deduced from

the topology of Cyt *b* trees (Demirtaş et al. 2020, and this study), which matches a spatially explicit picture of a wider pattern of endemism in Anatolia (e.g., Roces-Díaz et al. 2018). The Marmara region, which emerged in our study as an important refugial area for the Western lineage, has been identified by mammalogists as part of a permeable corridor for faunal exchanges between Europe and south-western Asia (Hosey 1982) but was never considered as being of particular importance for mammalian endemism.

The phylogeographic structuring of the Levant mole cannot be attributed to the external barriers. Demirtaş et al. (2020) stressed this for the Eastern part of the Pontic Mts. where no obvious obstacles separate the Central and the Eastern lineages. The situation is even more puzzling on the western end of the range where the Central haplotypes are parapatric with the Western ones.

Demirtaş et al. (2020) suggested for the Levant mole to occupy both sides of the Marmara and Bosphorus (also called the Turkish) straits. The idea of the intermittent continental bridge at the Turkish strait dates back to times of classical zoogeography (Kosswig 1955, Hosey 1982). As confirmed by recent phylogeographic studies, mammals crossed the Turkish straits moving from Europe to Anatolia (e.g., *Glis glis*; Helvacı et al. 2012), from Anatolia to Europe (e.g., *Microtus hartingi*; Kryštufek et al. 2018b) or in both directions (e.g., *Crocidura leucodon*; Dubey et al. 2007). The Levant mole, however, was obviously not such a transcontinental migrant. As already suggested by Kryštufek et al. (2018a) and confirmed in this study, the small blind moles from European Turkey are conspecific with *T. martinorum* from Bulgarian Thrace. *Talpa levantis* is therefore a species endemic to the Caucasus and the Pontic Mts. of south-western Asia.

Species delimitation in Levant moles. One of the central aims of our study was a translation of phylogenetic results into taxonomy. In the interpretation of Demirtaş et al. (2020) the Cyt *b* K2P divergence by 7.28% (8.0% maximum uncorrected distance in our results, 6.4% as a median) between their eastern and western sublineages (identical to Eastern and Western + Central lineages in this study) justify their ranking as distinct species, namely *Talpa levantis* s. str. and *T. transcaucasica*. Given that the K2P value of 7.28% is the lowest interspecific distance in the genus *Talpa*, Demirtaş et al. (2020) justified their taxonomic split by pointing on a “robust and geographically coherent” topology of their phylogenetic tree. Furthermore, they stressed that subterranean mammals are “morphologically constrained” which makes traditional delineation between species “intrinsically difficult”. Indeed, at least one newly recognized species of *Talpa*, i.e. *T. ognevi*, was elevated to the rank of species in its own right (Kryštufek & Motokawa 2018) entirely on the basis of genetic distances provided by Bannikova et al. (2015). On the other hand, two recent studies established new

species of *Talpa* (*T. aquitania* and *T. martinorum*) on the basis of both, genetic distances and unique craniodental traits (Nicolas et al. 2017, Kryštufek et al. 2018a) and the independent species status for *T. talyschensis* was proposed on morphological evidence (Zaytsev et al. 2014) before this was revealed by nucleotide sequences (Bannikova et al. 2015).

While ranking the three Cyt *b* lineages of Levant moles, we had the following in mind:

1. Genetic distances between the lineages of the Levant mole are below the lowest inter-specific pairwise distance in the genus *Talpa*.
2. Craniometric distances calculated in our study do not match the genetic distances. Genetically the most distinct were the Central and the Eastern lineages, while the greatest Mahalanobis squared D2 distance was retrieved between the Western and Central OTUs.
3. Univariate and multivariate analyses of morphometric variables displayed a pattern of a gradual longitudinal cline with no evidence of discontinuity on the contact zones of the three lineages. Such a smooth transition may not be due to a putative gene flow but can equally well indicate morphological response to the environment, which frequently changes gradually and was not tested in our study.
4. Our study retrieved a wide zone of overlap between the Western and Eastern lineages, which is most likely due to a secondary admixture of allopatrically evolved populations (Avice 2000). The Cyt *b* evidence on its own unfortunately does not allow a conclusion regarding gene flow, or lack of it, between the two lineages. Consulting more and nuclear markers would help future investigations on the topic.

We suggest a polytypic species concept as the appropriate taxonomic solution for the observed pattern of variation in the Levant mole. Subsequently we classify the three lineages as distinct subspecies. Subspecies are usually defined as allopatric groups of populations with independent histories, which are definable by geographically structured attributes, be they either, or both, morphological and molecular characteristics (Patton & Conroy 2017). As long as they are part of one and the same species, subspecies are by definition inter-fertile. Our hypothesis of three reproductively compatible, rather than reproductively isolated groups of populations of Levant moles can be falsified and is therefore testable. This hypothesis can be tested on the contacts of divergent phylogeographic lineages. We urge for further field sampling and molecular screening of moles in the zone of overlap between the Western and the Central lineages around the city of Zonguldak and to the west of it, and between Trabzon and Rize, where one can expect the Central and the Eastern lineages to meet.

Taxonomy of *Talpa levantis*

Talpa levantis Thomas, 1906

Diagnosis. Distinguishable from all other species of the genus *Talpa* by nuclear and mitochondrial DNA sequences (Bannikova et al. 2015, Demirtaş et al. 2020).

Description. *T. levantis* is a smaller mole (H&B=103–149 mm, CbL=28.6–33.5 mm) with eyelids sealed and the eyes covered by a transparent skin. External morphology shows no peculiarities. Skull is of average shape (Kryštufek et al. 2018a): relative width (as a percentage of CbL) of rostrum over canines is 11.8–14.9% and width of rostrum over molars is 24.7–31.0%. The maxillary tooth-row is comparatively short (MxT%=35.6–38.9%). However, the 1st upper molar has a parastyle, which shows heavy tooth-wear. The pelvis is of the caecoidal type, i.e., with the 4th sacral foramen opened posteriorly (Doğramacı 1989b). Diploid number of chromosomes is $2n = 34$ and the fundamental number of autosomal arms is $NFa = 64$. All subspecies were karyotyped and no variation was reported (Sokolov & Tembotov 1989,

Kefelioğlu & Gençoğlu 1996; Sevindik 2013, Selçuk & Kefelioğlu 2017).

Comparisons. *T. levantis* can be separated by morphological and karyological characteristics from other moles occupying Turkey (Kefelioğlu & Gençoğlu 1996, Kryštufek & Vohralík 2001, Kryštufek et al. 2018a). *T. ognevi* is larger (CbL= 33.6–35.9 mm) and has a higher diploid number ($2n = 38$; Selçuk & Kefelioğlu 2017). *T. davidiana* has a more robust skull with a comparatively wider rostrum; the breadth across canines accounts for 12.1–14.5% of the condylobasal length in *T. levantis* as opposed to 14.9–17.3% in *T. davidiana*. *T. levantis* is smaller than *T. europaea* from European Turkey (CbL=32.4–37.0 mm) and has eyelids grown together, while they are free in *T. europaea*. *T. levantis* has a parastyle on the 1st upper molar while *T. martinorum* lacks it. Overall comparison of cranial shape in Turkish species of *Talpa* is summarised in Selçuk et al. (2017).

Distribution. Range embraces the coast and mountains in northern Turkey along the Sea of Marmara and the

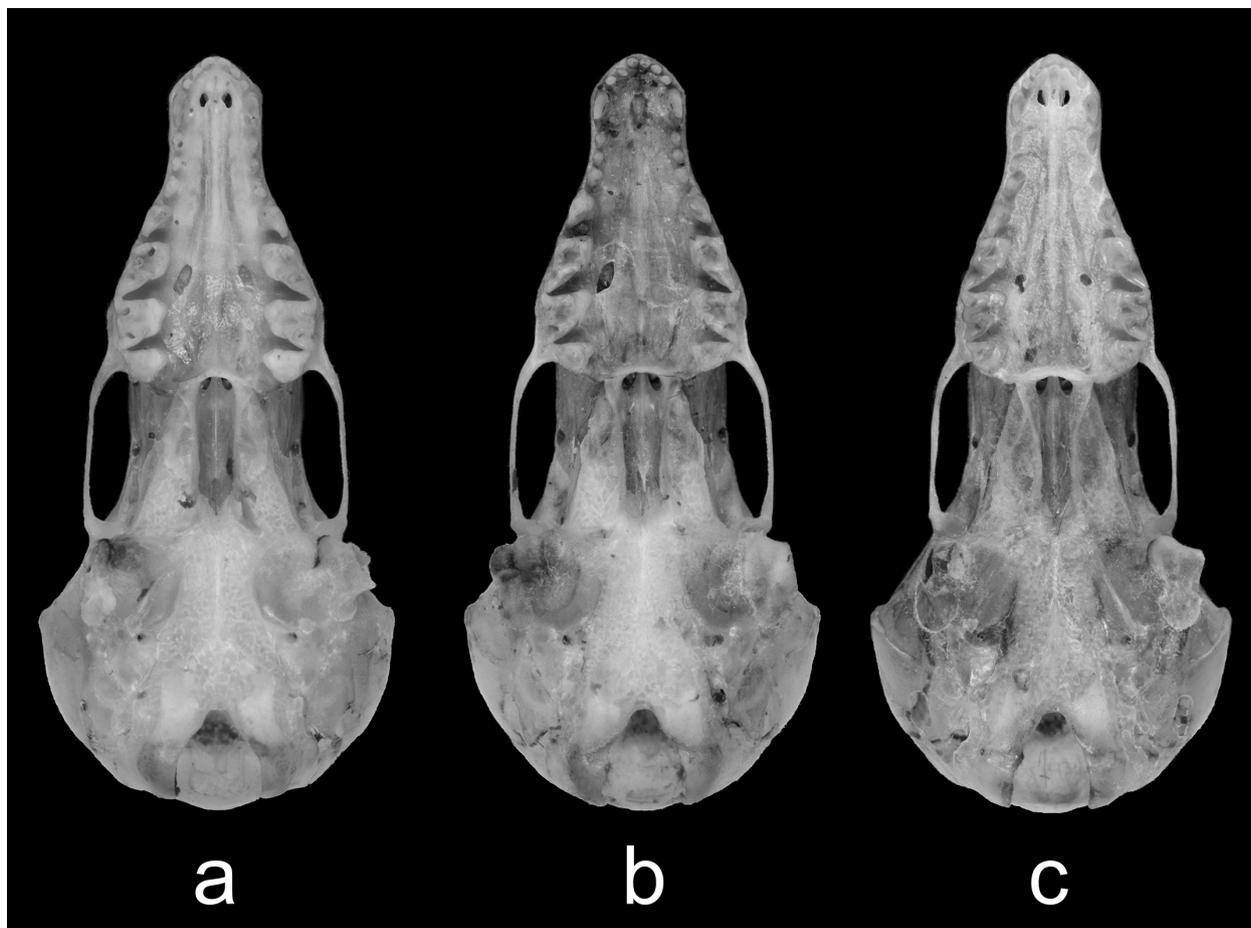


Fig. 6. Ventral cranium of subspecies of *Talpa levantis*. **a.** *T. l. dogramacii* ssp. nov. PMS 10650 (paratype; condylobasal length of skull = 30.2 mm). **b.** *T. l. levantis* PMS 10299 (31.3 mm). **c.** *T. l. transcaucasica* PMS 21658 (30.3 mm).

Black Sea (Fig. 1) and the Caucasus in Georgia, Armenia (as far south as Lake Sevan), and Russia (south of Kuban and Sulok rivers in Krasnodar, Adygea, Karachay-Cherkessia, Ingushetia, Chechnya, and Dagestan; Sokolov & Tembotov 1989). A population in the Lake Van area is obviously an isolate (Kryštufek & Motokawa 2018).

Miscellaneous. Reviewed by Kryštufek & Motokawa (2018); Sokolov & Tembotov (1989) provided a detailed review of the Caucasian populations. We subsequently list three subspecies (Fig. 6). The population from Lake Van was not assigned to any of them and requires a molecular screening.

***Talpa levantis levantis* Thomas, 1906**
(Fig. 5b)

Talpa caeca levantis Thomas, 1906:416. Type locality is “Scalita, S. of Trebizond”, now “Altındere, south of Trabzon, Turkey” (Kryštufek & Vohralik 2001:100). The type is a skin and skull in the Natural History Museum London (No. 6.3.6.5); type was seen.

Talpa levantis: Spitzzenberger, 1973 (in Felten et al. 1973:229). First use of current name combination.

Diagnosis. Identical to the Central lineage of *Talpa levantis* as retrieved in the phylogenetic analysis of the mitochondrial Cyt *b* gene. In our dataset, the subspecies *levantis* has unique mutations in comparison with sequences of both ssp. *transcaucasica* and *T. l. dogramacii* new subspecies at 6 positions of our Cyt *b* alignment (see Appendix II): 150:C, 447:T, 852:G, 933:G, 990:T, 1020:T.

Description and comparison. Similar to the remaining subspecies and the differences are on average. The nominotypical subspecies differs significantly from ssp. *transcaucasica* in four linear variables (H&B, HfL, CbL, MxT) and both quotients (MxT%, RoM%) in males and in two linear variables (CbL, MxT) in females. The nominotypical subspecies attained higher means in all comparisons but had a relatively shorter maxillary tooth-row (MxT%) than ssp. *transcaucasica*. For comparison with *T. l. dogramacii* ssp. nov. see under that subspecies.

Distribution. The Black Sea coast and mountains from vicinity of Zonguldak to Trabzon. Endemic to Turkey.

***Talpa levantis transcaucasica* Dahl, 1945**
(Fig. 5c)

Talpa europaea transcaucasica Dahl, 1945: 48. The year of publication on the cover page is 1944; with 1945 we follow Pavlinov & Rossolimo 1998: 8). Type locality (p. 49): “Окрестности села Воскресеновски (Кироваканский р-н Арм. ССР) ... Высота 1845 м

над уровнем моря [Surroundings of the village of Voskresenovka (Kirovakan district of the Armenian Soviet Socialist Republic) ... Altitude 1845 m above sea level]”. Since names of places changed since 1945, the type locality is now: Lermontovo (formerly Voskresenovka), Lori Province (formerly Kirovakan district), Armenia.

Talpa minima Deparma, 1959:31. Type locality is “Сев.-зап. Кавказ, верховья реки Белой, близ поселка Хамышки, 500 м ур. м.” – [“north-western Caucasus, the upper stream of River Beloy, near the settlement Khamyshki, 500 m a. s. l.”] (from Borissenko et al. 2001: 164), Adygea (Adyghe) Republic, Russia. In Deparma 1960: 97, the type locality is cited as: “Chamischki am Oberlauf des Flusses Belaja; NW-Kaukasus; 500 m ü. M. [Meter über Meereshöhe = metres above sea level]”

T[alpa] o[rientalis] transcaucasica: Vereschagin, 1959:388.

T[alpa] h[ercegoviensis] minima: Kuzyakin, 1965:50.

T[alpa] c[aece] minima: Gromov, Gureev, Novikov, Sokolov, Strelkov & Chapskiy, 1963:79.

T[alpa] l[evantis] minima: Sokolov & Tembotov, 1989:249.

T[alpa] l[evantis] transcaucasica: Sokolov & Tembotov, 1989:249. First use of current name combination.

T[alpa] transcaucasica: Demirtaş, Silsüpür, Searle, Bilton & Gündüz, 2020 (unpaginated early online release).

Diagnosis. Identical to the eastern sublineage of Demirtaş et al. (2020) and to the Eastern lineage of *Talpa levantis* as retrieved in this study through the phylogenetic analysis of the mitochondrial Cyt *b* gene. In our dataset, the subspecies *transcaucasica* has unique mutations in comparison with sequences of both the nominotypical subspecies and *T. l. dogramacii* new subspecies at the following positions of our Cyt *b* alignment (see Appendix 2): 42:T, 54:G, 162:G, 213:C, 219:T, 223:C, 225:A, 231:G, 246:T, 279:C, 396:A, 480:C, 603:T, 640:T, 651:C, 667:C, 675:G, 678:C, 858:G, 867:T, 913:T, 1008:T.

Description and comparison. Similar to the remaining subspecies and the differences are on average. For comparisons see under *T. l. dogramacii* ssp. nov. and the nominate subspecies.

Distribution. The north-eastern and eastern Black Sea coast, the Lesser Caucasus in north-eastern Turkey, Georgia, and Armenia, and the Greater Caucasus in Georgia and Russia.

Miscellaneous. Deparma published the taxonomic description and naming of *Talpa minima* in two papers, in Russian (Deparma 1959) and in German (Deparma 1960). This caused the inconsistency in reporting the year of publishing the name. While Russian authors con-

sistently quoted 1959 (Gureev 1979, Gromov et al. 1963, Kuzyakin 1965, Pavlinov & Rossolimo 1987, Sokolov & Tembotov 1989, Zaytsev et al. 2014), Western authors were aware only of the German version and cited 1960 (Hutterer 2005).

Sokolov & Tembotov (1989) recognized *minima* as subspecifically distinct from *transcaucasica*. The former is smaller (mean CbL is 28.66 mm in males and 28.25 mm in females) and occupies the western Caucasus; the latter is larger (mean CbL is 30.12 mm in males and 30.02 mm in females) and lives in the north-central Piedmont of the Greater Caucasus and the eastern Lesser Caucasus (Sokolov & Tembotov 1989).

***Talpa levantis dogramacii* ssp. nov.** Kefelioğlu, Kryštufek, Selçuk, Hutterer & Astrin
(Figs. 6a, 7)

urn:lsid:zoobank.org:act:E3600CE0-7682-422B-830B-D0A6556FCD7B

Holotype and type locality. Skin, skull, pelvis and tissue sample in ethanol of an adult male (OMU 1352; Fig. 7); tissue also deposited in ZFMK (ZFMK-TIS-35886), collected by Ahmet Yesari Selçuk in March 2019 near Baraklı village, Mt. Uludağ, Bursa, Turkey (39.96056 N,

29.2633 E, 1100 m above sea level). DNA of this specimen has been deposited (ZFMK-DNA- FD02298704) at ZFMK, Bonn, and the cytochrome *b* sequence is available from GenBank (Accession number MT738557) and Appendix II.

Measurements of holotype. Body mass 58 g, head and body 120 mm, tail 28 mm, hind foot 18 mm, condylobasal length of skull 29.8 mm, maxillary tooth-row 11.6 mm, breadth of braincase 14.7 mm, breadth of rostrum over canines 4.0 mm, breadth of rostrum over molars 8.7 mm, greatest length of pelvis 22.1 mm, breadth of pelvis 11.9 mm.

Diagnosis. Identical to the Western lineage of *Talpa levantis* as retrieved in the phylogenetic analysis of the mitochondrial Cyt *b* gene. In our dataset, the new subspecies has unique mutations in comparison with sequences of both the nominotypical subspecies (corresponding to Central lineage) and *T. transcaucasica* (Eastern lineage) at five positions of our Cyt *b* alignment (see Appendix II): 522: T, positions 654, 731, 786, 1005: G. The new subspecies has a proportionally longer maxillary tooth-row, a proportionally broader rostrum over molars and the least bowed posterior margin of the braincase compared to the other two subspecies of *T. levantis*.

Paratypes. Three individuals collected on Mt. Uludağ and preserved as museum vouchers, tissue samples and with cytochrome *b* sequences deposited in the GenBank (see Table 1). OMU 1350, an unsexed individual; preserved as a skull; tissue ZFMK-TIS-35885; DNA sample: ZFMK-DNA- FD02298617; GenBank No. MT738556. OMU 1353: an unsexed individual; preserved as a skull; tissue ZMMU-TIS-35887; DNA sample: ZFMK-DNA- FD02298696; GenBank No. MT738558. All paratypes in OMU were collected in August 2018 by Ahmet Yesari Selçuk. PMS 10,650: a female collected on 30 June 1994 by B. Kryštufek, preserved as a skull, skin and postcranial skeleton; GenBank No. FN640571.

Measurements of paratypes. External measurements of a female PMS 10,650: body mass 55 g, head and body 118 mm, tail 28 mm, hind foot 17 mm. Skull measurements of OMU 1350, OMU 1353, and PMS 10,650: condylobasal length of skull 31.2, 29.8, 30.2 mm, maxillary tooth-row 12.1, 11.4, 11.8 mm, breadth of braincase 14.9, damaged, 14.4 mm, breadth of rostrum over canines 4.1, 4.1, 3.9 mm, breadth of rostrum over molars 8.9, 8.8, 8.9 mm.

Description and comparisons. *Talpa levantis dogramacii* ssp. nov. is of about the same external appearance and body proportions as the remaining subspecies of *T. levantis*. It differs significantly from the nominotypical subspecies by a shorter head and body (males), shorter



Fig. 7. Skull and mandible of the type specimen of *Talpa levantis dogramacii* ssp. nov. OMU 1352. Scale bar = 5 mm.

condylobasal length (females) and broader rostrum over molars (females). *Talpa l. dogramacii* ssp. nov. differs significantly from ssp. *transcaucasica* in having a longer maxillary tooth-row, both absolutely (in males) and relative to length of skull (in both sexes), a narrower breadth across molars, both absolutely and relative to length of skull (both in males; Table 2), and a less bowed posterior outline of the braincase (Fig. 3).

Distribution. The western-most part of the range of *T. levantis*, i.e., along the Anatolian coast of the Sea of Marmara and westward until Zonguldak.

Etymology. *Talpa levantis dogramacii* ssp. nov. is an eponym to Dr. Salih Dođramacı (1 July 1941, Elena, Bulgaria – 30 September 1993, Samsun; Fig. 8), a Professor of zoology at the Ondokuz Mayıs University, Samsun, and an outstanding Turkish mammalogist. Among others, Professor Dođramacı published works of crucial importance for the taxonomy of *Talpa* in Turkey (Dođramacı 1988, 1989a, b) and a revised list of Turkish mammals (Dođramacı 1989c). He published in Turkish and in journals with limited circulation outside of Turkey and is therefore not well known beyond his native country. Salih Dođramacı built an important research collection of Turkish small mammals with well prepared and meticulously labelled museum vouchers. The collection is deposited at the Ondokuz Mayıs University and also provided an invaluable source of information for the present study. *Microtus dogramacii* Kefeliođlu & Kryřtufek, 1999, a species of social vole endemic to south-western Asia, is another eponym to the late Professor Dođramacı.

Miscellaneous. *Talpa levantis dogramacii* ssp. nov. was first recognized as distinct from *T. levantis* in a craniometric study (Kryřtufek 2001) and was separated from *T. levantis* under the tentative name *Talpa caeca* (Kryřtufek & Vohralík 2001).

Species of the genus *Talpa* in Turkey

Demirtaş et al. (2020) stressed that Turkey is “home to six distinct species [of moles], more than any other comparable geographical region” which “[emphasises] the importance of this region as a global centre of mole diversification.” Measuring, quantifying and comparing biodiversity can be tricky when dealing with a complex geopolitical entity like Turkey. First, the country spreads across two continents, which since the last glacial maximum were separated by the sea, but in the past were intermittently connected by a land bridge. As discussed above, the land bridge at the Turkish straits both facilitated and filtered the transcontinental faunal migrations. As poor dispersers (Kryřtufek & Motokawa 2018) moles were obviously filtered by this land corridor. As we have seen, our study falsified the hypothesis of Demirtaş et al.



Fig. 8. Dr. Salih Dođramacı and his wife (Foto Yener, Ankara).

(2020) regarding the transcontinental range of *Talpa levantis*. The two sides of the Turkish straits have no mole species in common and their species evolved in different centres of diversification, the south-eastern European centre and in south-west Asia with further two similar centres.

Moles with restricted distributions are usually endemic to the Quaternary refugia and each of the main southern-European peninsulas has at least two small-range endemics of the genus *Talpa* (cf. Kryřtufek & Motokawa 2018). The number of mole endemics is remarkably similar between centres of endemism being either two or three endemics per centre (Table 3). Turkey does not contain all endemics from any of the three centres it encompasses, but on the other hand, comprises three out of total five such centres, as we know them in the western Palearctic (Table 3). The number of centres encompassed by Turkey is the reason for the sum of partial regional species numbers, which is high enough to rank the country higher than any other in the species richness of the genus *Talpa*. This conclusion does not downgrade the high biodiversity richness of Turkey, but makes it explicable.

Subsequently, we briefly review mole species, other than *T. levantis*, occupying Turkey. The genus has been reviewed by Dođramacı (1989a), Kefeliođlu & Gençođlu (1996), and Kryřtufek & Vohralík (2001). For karyotypes see Sevindik (2013; for *T. europaea*), Kefeliođlu & Gençođlu (1996; *T. ognevi*), and Sözen et al. (2012; *T. davidiana*).

Table 3. Presence of moles in five centers of endemism. Presences in Turkey are shown by dots. *Talpa europaea* is a wide-spread species while the remaining moles are endemic to two centres (*T. caeca*) or a single centre (the rest). Centres of endemism: Ip – Iberian Peninsula; It – Italian Peninsula; Ba – Balkan Peninsula; PC – Pontic Mts. and the Caucasus; AH – Anatolian-Iranian High Plateau and the Hyrcanian coast. Based on Kryštufek & Motokawa (2018).

Species	Centre of endemism				
	Ib	It	Ba	PC	AH
<i>T. europaea</i>		○	●		
<i>T. occidentalis</i>	○				
<i>T. aquitania</i>	○				
<i>T. romana</i>		○			
<i>T. caeca</i>		○	○		
<i>T. stankovici</i>			○		
<i>T. martinorum</i>			●		
<i>T. levantis</i>				●	
<i>T. ognevi</i>				●	
<i>T. caucasica</i>				○	
<i>T. davidiana</i>					●
<i>T. talyschensis</i>					○
Species total	2	3	4	3	2

Talpa europaea Linnaeus, 1758

Talpa europaea Linnaeus, 1758:52. Type locality (originally Europe) subsequently restricted to Sweden, Kristianstad, Engelholm.

Reported for Turkey by Osborn (1964). Occupies European Turkey; range mapped by Dođramacı (1989a).

Talpa martinorum Kryštufek, Nedyalkov, Astrin & Hutterer, 2018

Talpa martinorum Kryštufek, Nedyalkov, Astrin & Hutterer, 2018 (Kryštufek et al. 2018a:45). Type locality: near Zvezdets, Mt. Strandzha, Bulgaria.

Reported for Turkey as *Talpa caeca* Savi, 1822 (Osborn 1964, Dođramacı 1988, 1989b), and afterwards as *T. levantis* (Vohralík 1991, Kryštufek & Vohralík 2001). Presence in eastern Turkish Thrace postulated by Kryštufek et al. (2018a) and for the first time confirmed in this study.

Talpa ognevi Stroganov, 1944

Talpa romana ognevi Stroganov, 1944:131. Type locality: “Бақуриани, Грузия [Bakuriani, Georgia]”.

Reported for Turkey as *Talpa caucasica* Satunin, 1908 (Dođramacı 1989b). The name *ognevi* was elevated to species in Kryštufek & Motokawa (2018), following the evidence provided by Bannikova et al. (2015). Range is in Georgia and NE Turkey (Hopa region).

Talpa davidiana (A. Milne Edwards, 1884)

Scaptochirus davidianus A. Milne Edwards, 1884:1143.

Type locality: “environs d’Akbes, sur les confins de la Syrie et de l’Asie Mineure” (p. 1142), now Meydanekbez, southwest of Gaziantep, Turkey (Kryštufek et al. 2001:140)

Earlier reported for Turkey as *Talpa streeti* Lay, 1965; the name is a junior synonym of *Scaptochirus davidianus*, which is a member of the genus *Talpa* (Kryštufek et al. 2001). Occupies south-eastern Turkey and Lake Van area (Kryštufek et al. 2001, Sözen et al. 2012).

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APPENDICES

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APPENDIX I.

The list of museum vouchers used in this study.

APPENDIX II.

Sequencing of the new Turkish samples.

APPENDIX III.

Table S1. Results of regression analysis of morphometric variables and two quotients against the latitude for *Talpa levantis* in Northern Anatolia. Shown are only variables showing significant correlation coefficient (at $p < 0.05$). Acronyms for traits are explained in text.

Table S2. Summary statistics for the principal components analysis on five cranial measurements transformed to logarithms. One-way Anova was performed with OTU as the categorical value. Acronyms for skull measurements are explained in text.