

# Taxonomic status and origin of the Egyptian weasel (*Mustela subpalmata*) inferred from mitochondrial DNA

Mónica Rodrigues<sup>1,2</sup> · Arthur R. Bos<sup>3,4</sup> · Richard Hoath<sup>3</sup> · Patrick J. Schembri<sup>5</sup> · Petros Lymberakis<sup>6</sup> · Michele Cento<sup>7</sup> · Wissem Ghawar<sup>8</sup> · Sakir O. Ozkurt<sup>9</sup> · Margarida Santos-Reis<sup>1</sup> · Juha Merilä<sup>2</sup> · Carlos Fernandes<sup>1</sup>

Received: 24 June 2015 / Accepted: 22 February 2016 / Published online: 9 March 2016  
© Springer International Publishing Switzerland 2016

**Abstract** The Egyptian weasel (*Mustela subpalmata*) is a small mustelid with a distribution restricted to the lower Nile Valley and the Nile Delta. Traditionally considered a subspecies of the least weasel (*M. nivalis*), it is currently recognized as a separate species based on morphology. Here we present the first genetic assessment of the taxonomic status of the Egyptian weasel by comparing mitochondrial DNA (Cytochrome *b* gene and control region) sequences to those of least weasels from the western

Palaearctic, with a focus on the Mediterranean region. Our results provide no evidence to support the view that the Egyptian weasel is genetically distinct from the least weasel, as we found that, for both Cytochrome *b* and control region, haplotypes were shared between the two taxa. Specifically, the Cytochrome *b* and control region haplotypes detected in the Egyptian weasel were also present in *M. nivalis* from Turkey and Malta, two populations genetically analysed here for the first time. Our results suggest that the Egyptian weasel is distinct from the least weasel populations currently living in the Maghreb, which were inferred to be the result of an earlier colonization of North Africa, but the genetic data alone do not allow us to determine whether the Egyptian weasel is native or introduced. Nevertheless, the observed genetic patterns, together with the weasel fossil record in Israel and the unique commensal lifestyle of the Egyptian weasel, are consistent with the hypothesis that the Egyptian population is a relict of past range expansion from the Levant into Egypt. We suggest that the large size and characteristic sexual dimorphism of the Egyptian weasel are likely to represent ecotypic variation, but genomic studies are required to clarify the extent of its functional genetic divergence.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10709-016-9889-y) contains supplementary material, which is available to authorized users.

✉ Mónica Rodrigues  
marodrigues@fc.ul.pt

- <sup>1</sup> CE3C – Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisbon, Portugal
- <sup>2</sup> Ecological Genetics Research Unit, Department of Biosciences, University of Helsinki, PO Box 65, 00014 Helsinki, Finland
- <sup>3</sup> The American University in Cairo, PO Box 74, New Cairo 11835, Egypt
- <sup>4</sup> Naturalis Biodiversity Centre, PO Box 9517, 2300 RA Leiden, The Netherlands
- <sup>5</sup> Department of Biology, University of Malta, Msida MSD 2080, Malta
- <sup>6</sup> Natural History Museum of Crete, University of Crete, 71409 Iráklion, Crete, Greece
- <sup>7</sup> SROPU Bird Observation and Protection Station of Rome, 00165 Rome, Italy
- <sup>8</sup> Service of Medical Epidemiology, Institut Pasteur de Tunis, Tunis-Belvédère, Tunisia
- <sup>9</sup> Faculty of Education, Ahi Evran University, Kırşehir, Turkey

**Keywords** *Mustela subpalmata* · Species status · Molecular systematics · Phylogeography · Mitochondrial DNA · Weasels

## Introduction

The least weasel (*Mustela nivalis* Linnaeus, 1766), the smallest mammalian carnivore in the world, has a wide Holarctic distribution stretching from northern Africa and

southern Europe, including most of the larger Mediterranean islands, across Asia–North America (Sheffield and King 1994). Over this vast range, the species displays extensive and complex geographic variation in body size, coat colour and skull measurements, and this has led to several studies concerning its intraspecific taxonomy and evolutionary history (e.g. van Zyll de Jong 1992; Abramov and Baryshnikov 2000; Lebarbenchon et al. 2010), yet many issues remain unresolved.

The little known Egyptian weasel (*Mustela subpalmata* Hemprich and Ehrenberg, 1833), with a distribution confined to the lower Nile Valley and Nile Delta of Egypt, was traditionally considered a subspecies of *M. nivalis* (Osborn and Helmy 1980; Sheffield and King 1994; Kingdon 2001). Given its restricted and isolated distribution, with the nearest populations overland in Lebanon and Tunisia, and being largely a human commensal (Flower 1932; Setzer 1952; Handwerk 1993; Hoath 2009), it has been hypothesized to derive from historical introduction (Frank 1985), possibly by the Romans (Cretzschmar 1826). On the other hand, Dayan and Tchernov (1988) suggested that the Egyptian population is a glacial relict. The Egyptian weasel tends to be larger than least weasels, except possibly those from Malta (Thomas 1895; Barrett-Hamilton 1900; Miller 1912; but see Abramov and Baryshnikov 2000). However, it is similar in size to *M. nivalis* fossils from Israel—from where weasels are currently absent—dated to the Natufian (ca. 11,000 years BP), Chalcolithic (ca. 6000–5300 years BP) and Early Bronze Age (ca. 5000 years BP) (Dayan and Tchernov 1988). The pelage of the Egyptian weasel shows an irregular demarcation line between the brown dorsal region and the pale underside, as well as variable brown patches in the venter (“vulgaris” type colour pattern, Frank 1985; see also Niethammer 1973). Similar coat patterns are found in least weasels from Malta, Sardinia, the Balearic Islands, Turkey, and across the European mainland from the Iberian Peninsula to Poland and Bulgaria (Barrett-Hamilton 1900; Abramov and Baryshnikov 2000).

More recently, the Egyptian weasel has been proposed as a separate species based on cranial morphometrics, differences in the degree of sexual size dimorphism, and body length (van Zyll de Jong 1992; Reig 1997; Abramov and Baryshnikov 2000; McDonald and Hoffmann 2008). Both van Zyll de Jong (1992) and Reig (1997) stressed the importance of assessing the taxonomic status of the Egyptian weasel using genetic data. However, despite several recent molecular studies on the phylogeny of the genus *Mustela* (e.g. Kurose et al. 2008; Harding and Smith 2009) and on the phylogeography of the weasel in the Western Palearctic (Lebarbenchon et al. 2010; McDevitt et al. 2012), samples of the Egyptian weasel have never been genetically analysed.

The aim of this study was to investigate the phylogenetic position and taxonomic status of the Egyptian weasel using mitochondrial DNA (mtDNA). To this end, we compared nucleotide sequences of mitochondrial Cytochrome *b* (Cyt *b*) gene and control region (CR) of Egyptian weasels with those of least weasels from across the western Palearctic, with a particular focus on the Mediterranean region. Because of its relatively fast evolutionary rate, mtDNA has been widely used to infer phylogenetic relationships and to clarify taxonomic issues within species and among closely related species (e.g. Poulakakis et al. 2005; Whittaker et al. 2006; Tamar et al. 2014). The rationale for including CR sequences was that in mammals the nucleotide substitution rate in the CR is higher than in the Cyt *b* gene (Pesole et al. 1999), and thus it might provide improved phylogenetic resolution when divergence is recent (Garcia-Rodriguez et al. 1998). This study has practical implications because although the Egyptian weasel is common and currently not threatened (McDonald and Hoffmann 2008; Hoath 2009), its limited geographic range makes it important to assess its taxonomic status, origin and whether it is a restricted endemic. The results also contribute to a better understanding of the evolutionary and biogeographic history of weasels in North Africa.

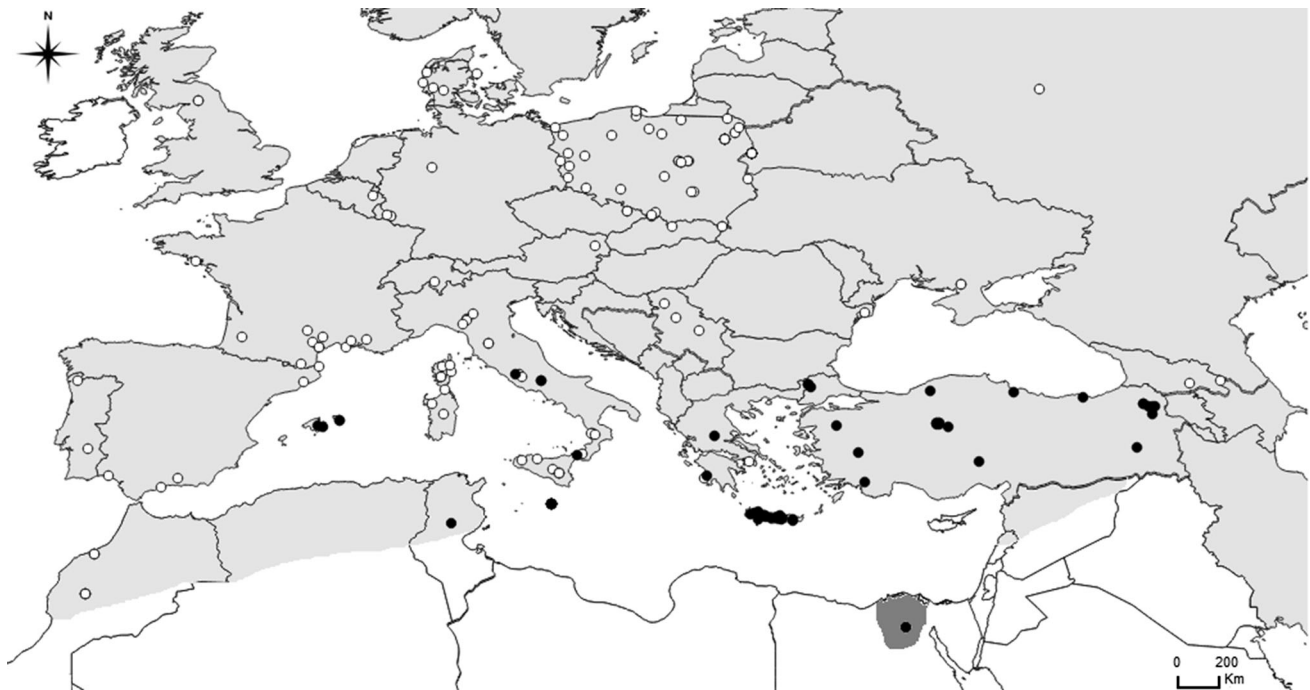
## Materials and methods

### Samples, sequences and laboratory procedures

We gathered samples of the Egyptian weasel ( $n = 3$ ) and of least weasels from Turkey ( $n = 21$ ), Greece (mainland and Crete,  $n = 23$ ), Italy (mainland and Sicily,  $n = 4$ ), Tunisia ( $n = 1$ ), Malta ( $n = 8$ ) and the Balearic Islands ( $n = 3$ ). We also included a previously published comprehensive set of Cyt *b* and CR sequences of least weasels from the western Palearctic (Lebarbenchon et al. 2006, 2010) and additional Cyt *b* sequences from Poland (McDevitt et al. 2012) and CR sequences from central Eurasia (Kurose et al. 2005). Locations and other details of the analysed samples and sequences are given in Fig. 1 and Table A1 of Electronic Supplementary Material.

Tissue samples were obtained from road-kills, animals found dead of unknown causes, live-trapped individuals, and specimens in institutional collections. Samples were preserved in a salt-saturated solution of 20 % DMSO in water or in absolute ethanol and stored at  $-20$  °C. Genomic DNA was extracted from tissue samples using the DNeasy Blood and Tissue Kit (Qiagen) following the standard protocol for animal tissue.

We amplified and sequenced the complete Cyt *b* gene (1140 bp) with the following two primer pairs which generated overlapping fragments: L14979 (5'-



**Fig. 1** Map showing the location of the samples collected in this study (*black dots*) and of previously published sequences included in the analyses (*white dots*). Also shown are the distributions of the

Egyptian weasel (*dark grey*) and least weasel (*light grey*) in the Western Palearctic (McDonald and Hoffmann 2008; Tikhonov et al. 2008)

CCACTATTCCYACATGGA-3') and H15791 (5'-AATGTAGTTGTCTGGGTC-3'); L15533 (5'-CGGTAGAATGRATCTGAG-3') and H16204 (5'-CCCTTTGGYTTACAAGAC-3') (Fernandes et al. 2008). We also sequenced the left domain of the CR using the primers CAN CR F (5'-AAACCCACCRTCAGCAC-3') and MUS CR R (5'-CCGTGACCATTGACTGAA-3') (Costa et al. 2013). Polymerase chain reactions (PCRs) were carried out in 15  $\mu$ l volumes containing 0.6 U of Surf Hot *Taq* DNA polymerase (Stabvida), 1X PCR buffer, 2 mM  $MgCl_2$ , 0.2 mM of each dNTP (Bioline), 0.5  $\mu$ M of each primer and approximately 50 ng of DNA. The PCRs were performed with an initial denaturation at 95  $^{\circ}C$  for 15 min, followed by ten cycles of 94  $^{\circ}C$  for 30 s, 55  $^{\circ}C$  for 30 s, and 72  $^{\circ}C$  for 30 s, 25 cycles of 94  $^{\circ}C$  for 30 s, 50  $^{\circ}C$  for 30 s, and 72  $^{\circ}C$  for 30 s, and a final extension at 72  $^{\circ}C$  for 10 min. The results of the PCR amplifications were visualized on 2 % agarose gels, and the PCR products were purified using ExoSAP (Hanke and Wink 1994) and sequenced in both directions at Macrogen Inc. The *Cyt b* sequences were assembled, aligned, and edited using SEQUENCHER 4.7 (Gene Codes Corporation). Since insertion/deletions (indels) led to uncertainty in the CR alignment, we used M-COFFEE (Wallace et al. 2006), a meta-aligner that combines the solutions of alternative alignment methods, to estimate a consensus alignment. We combined the three top-performing methods (PROBCONS, T-COFFEE and

MAFFT) in a recent benchmark study of sequence alignment algorithms (Thompson et al. 2011), with MAFFT being previously shown to be highly accurate when dealing with indel-rich sequences (Golubchik et al. 2007).

### Statistical analysis

Sequence alignments of the *Cyt b* gene and CR were analysed with FABOX 1.41 (Villesen 2007) to collapse identical individual sequences into representative haplotypes for phylogenetic analysis. Substitution saturation in both data sets was checked using the index of substitution saturation ( $I_{ss}$ ) of Xia et al. (2003) in DAMBE 5.3.74 (Xia 2013); the null hypothesis of this test is that there is saturation. Selective neutrality of the *Cyt b* data was tested with a codon-based likelihood approach for comparing the number of synonymous (dS) and non-synonymous (dN) substitutions per site (Muse and Gaut 1994; Pond and Frost 2005); computations of dN and dS were conducted using HYPHY (Pond et al. 2005) within MEGA 6.0 (Tamura et al. 2013).

Phylogenetic analyses were performed using Bayesian inference (BI) and maximum likelihood (ML) as implemented in MRBAYES 3.2.5 (Ronquist et al. 2012) and GARLI 2.01 (Zwickl 2006), respectively. GARLI has been shown to be one of the most effective ML algorithms in exploring tree islands and in finding good trees on those islands (Morrison 2007). As outgroups, we used sequences

of mountain weasel *Mustela altaica* (Pallas 1811), Siberian weasel *Mustela sibirica* (Pallas 1773), stoat *Mustela erminea* (Linnaeus 1758) and American mink *Neovison vison* (Schreber 1777) downloaded from GenBank (accession numbers respectively for Cyt *b* and CR as follows: KC815122, KC815122; HM106317, HM106317; EF689078, AB049787; EF689073, HM106322). These outgroups were chosen based on previously published phylogenetic hypotheses for the genus *Mustela* (Koepfli et al. 2008; Kurose et al. 2008; Harding and Smith 2009; Sato et al. 2012). The Cyt *b* alignment was partitioned by codon position. For each data set, analyses in MRBAYES were conducted with two parallel runs, each with four Markov chains (one cold and three heated), default heating parameter ( $t = 0.1$ ), and 20,000,000 generations. The first 5,000,000 generations were discarded as burn-in phase, and chains were sampled every 500 generations thereafter. The entire general time-reversible (GTR) substitution model space was sampled within the analyses (Huelsenbeck et al. 2004). Convergence was indicated by an average standard deviation of split frequencies between parallel runs of  $<0.01$ . Support for tree nodes was determined according to the values of Bayesian posterior probability obtained in a majority-rule consensus tree (Holder et al. 2008).

For the ML analysis, the best-fit model of nucleotide substitution was determined using the Bayesian information criterion (BIC; Schwarz 1978) in jMODELTEST 2.1.7 (Darriba et al. 2012). The high accuracy and precision of BIC in evolutionary model selection has been recently demonstrated (Luo et al. 2010). The selected models were HKY + I + G for the CR and TrNef + I, HKY and TIM1 for the first, second and third codon positions of Cyt *b*, respectively. The ML analyses in GARLI consisted of ten independent runs, which were terminated automatically after 5000 generations with no significant ( $P < 0.01$ ) improvements in topology scoring. To assess confidence in tree topologies, 1000 bootstrap replicates were executed and majority-rule consensus trees were constructed (Berry and Gascuel 1996). Consensus trees were computed with SUMTREES 3.3.1 of the DendroPy library (Sukumaran and Holder 2010) and visualized and edited with TREEGRAPH 2.4.0 (Stöver and Müller 2010).

Genealogical relationships among haplotypes were also inferred using a median-joining network (Bandelt et al. 1999) created in POPART 1.7 (<http://popart.otago.ac.nz>).

To further investigate the affinities of the Egyptian weasel with least weasels in neighbouring areas of the Mediterranean Basin, we computed the net average distance between populations ( $D_a$ , Nei 1987) and pairwise  $\Phi_{ST}$  (Excoffier et al. 1992) under the Tamura–Nei model (Tamura and Nei 1993) in ARLEQUIN 3.5.2.1 (Excoffier and Lischer 2010). Statistical significance was tested using 20,000 permutations.

## Results

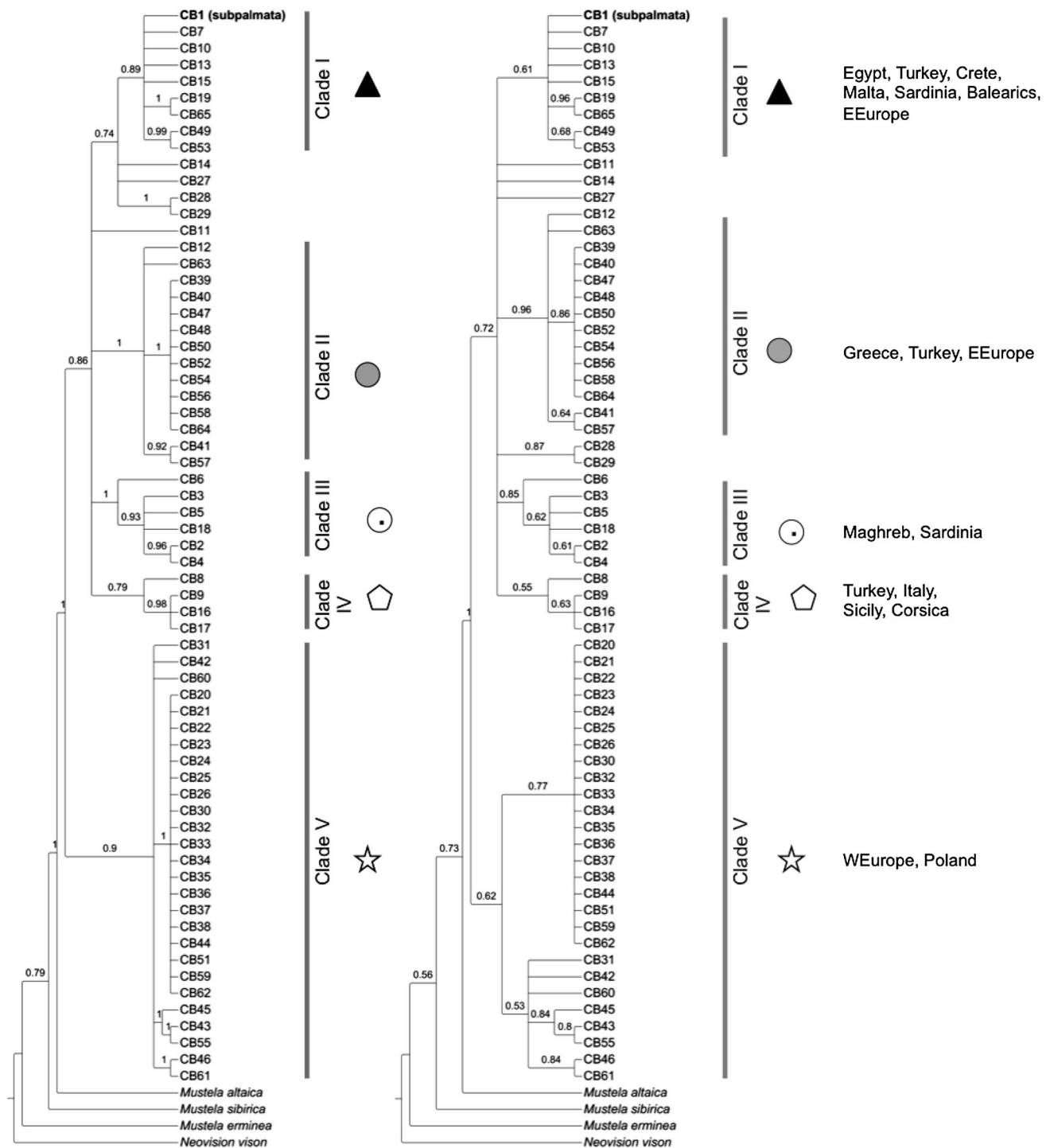
The ingroup Cyt *b* alignment consisting of 171 sequences of 1117 bp contained 100 (9 %) polymorphic sites, of which 56 (5 %) were parsimony informative, and yielded 65 haplotypes. The corresponding CR alignment, with a length of 509 bp, was composed of 138 sequences that contained 11 (2 %) sites with alignment gaps, 30 (6 %) segregating sites and 21 (4 %) informative sites, resulting in 57 haplotypes. New haplotypes were deposited in GenBank (accession numbers KP455993–KP456013; Table A1).

Several observations indicate that the sequences produced were mitochondrial and not nuclear-integrated copies of mtDNA. First, they were unambiguous and highly similar to published homologous sequences of *M. nivalis* (average number of nucleotide differences in Cyt *b* and CR: 12.1 and 3.8, respectively). Second, the two primer combinations for Cyt *b* gave the same sequence in each individual. Lastly, the Cyt *b* alignment did not include indels and stop codons and showed a bias against guanine at third codon positions (4.6 % of guanines compared with 22.3 and 13.4 % at first and second codon positions, respectively) and against second codon position substitutions (average ML pairwise distance of 0.2 % compared with 0.9 and 8.2 % at first and third codon positions, respectively).

No substitution saturation was evident for either Cyt *b* or CR alignments, as in both cases the  $I_{SS}$  was significantly less than the critical value ( $P = 0.000$ ), but DAMBE estimated a greater amount of phylogenetic information in the former data set. The null hypothesis of neutral evolution could not be rejected ( $P > 0.05$ ) for any of the Cyt *b* codons.

The Bayesian and ML inferences of the phylogenetic relationships of the Cyt *b* and CR haplotypes are given in Figs. 2 and A1 of Electronic Supplementary Material, respectively. The Cyt *b* topologies were highly congruent with the exception of a few nodes that had lower support in each tree. Their overall similarity was 96.3 % as determined by Compare2Trees (Nye et al. 2006). The CR trees were less congruent with each other, and the ML tree was less resolved with nodes with lower support (bootstrap proportions  $<0.7$ ). A lower phylogenetic resolution in CR than in Cyt *b* of least weasels was also observed by Lebarbenchon et al. (2010) and this could be due to homoplasy caused by the high mutation rate of the CR.

The Egyptian weasel showed a single haplotype both for Cyt *b* (CB1) and CR (CR1). Haplotype CB1 was also found in Turkey, Crete, Malta and Minorca, while haplotype CR1 was shared with Turkey, Malta, Minorca, Mallorca, Sardinia and Romania (Table A1). In both BI and ML analyses, haplotype CB1 clustered with haplotypes from

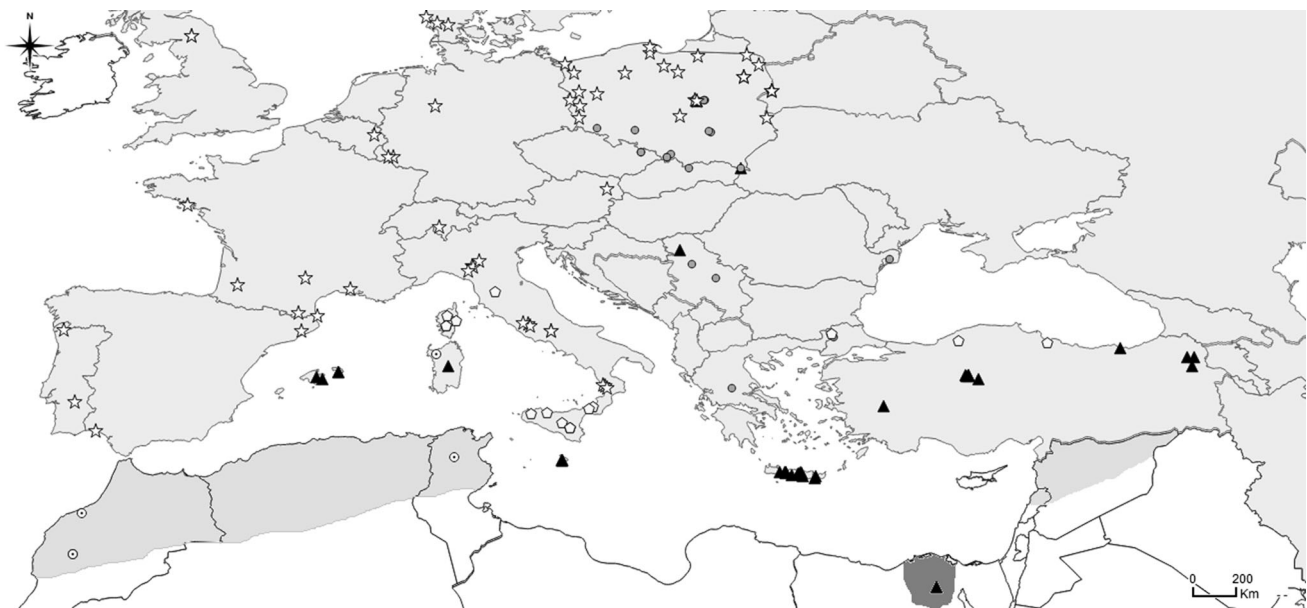


**Fig. 2** Majority-rule consensus trees of the Bayesian (*left*) and maximum likelihood (*right*) analyses of Cytochrome *b* haplotypes. Numbers above branches are, respectively, Bayesian posterior probabilities and bootstrap values. Haplotype codes are as in

Table A1. The haplotype found in the Egyptian weasel (CB1) is indicated in *bold*. Symbols next to clade names correspond to those used in Fig. 3. Geographic distribution of clades is given on the *right*

Turkey, Crete, Mallorca, Sardinia, Serbia and Poland (Clade I; Fig. 2). In the Bayesian tree, Clade I further grouped with haplotypes from mainland Greece (CB27–29) and the remaining haplotype from Crete (CB14). Other

clades consistent between the two phylogenetic methods included haplotypes from Eastern Europe (Clade II), the Maghreb (Clade III), Turkey–Italy–Sicily–Corsica (Clade IV) and from across mainland Europe (Clade V; Figs. 2, 3).



**Fig. 3** Geographic distribution of the clades identified in the phylogenetic analyses of Cytochrome *b*. *Black triangles* Clade I, *grey circles* Clade II, *white circles with black dot* Clade III, *white pentagons* Clade IV, *white stars* Clade V. *Dark and light grey*

represent respectively the distributions of the Egyptian weasel and least weasel in the Western Palearctic (McDonald and Hoffmann 2008; Tikhonov et al. 2008)

The Cyt *b* median-joining network (Fig. 4) revealed a haplotype genealogy concordant with the phylogenetic trees, whereas the CR network (not shown) contained several loops, i.e. equally parsimonious alternative connections among haplotypes, which are indicative of homoplasies. The Cyt *b* network displayed more information on the relationship between clades and between haplotypes within each clade than the phylogenetic trees.

Pairwise Cyt *b*  $D_a$  distances between the Egyptian weasel and least weasels from neighbouring areas of the Mediterranean Basin varied from 0 to 1.34 % (Table 1), well within the range of Cyt *b* variation observed in least weasels (Lebarbenchon et al. 2010) and in mammals in general (Bradley and Baker 2001). Differentiation measured by  $\Phi_{ST}$  ranged from zero between Egypt and Turkey or Malta to 0.89 between Egypt and Sicily (Table 1).

## Discussion

This is the first molecular study to assess the phylogenetic position and taxonomic status of the Egyptian weasel. Our results provide no evidence to support the view that the Egyptian weasel, currently classified as *M. subpalmata*, is genetically distinct from the least weasel *M. nivalis*. In the following, we discuss the implications of the findings of this study for our understanding of the origin and taxonomy of the Egyptian weasel.

## Origin and history of the Egyptian weasel

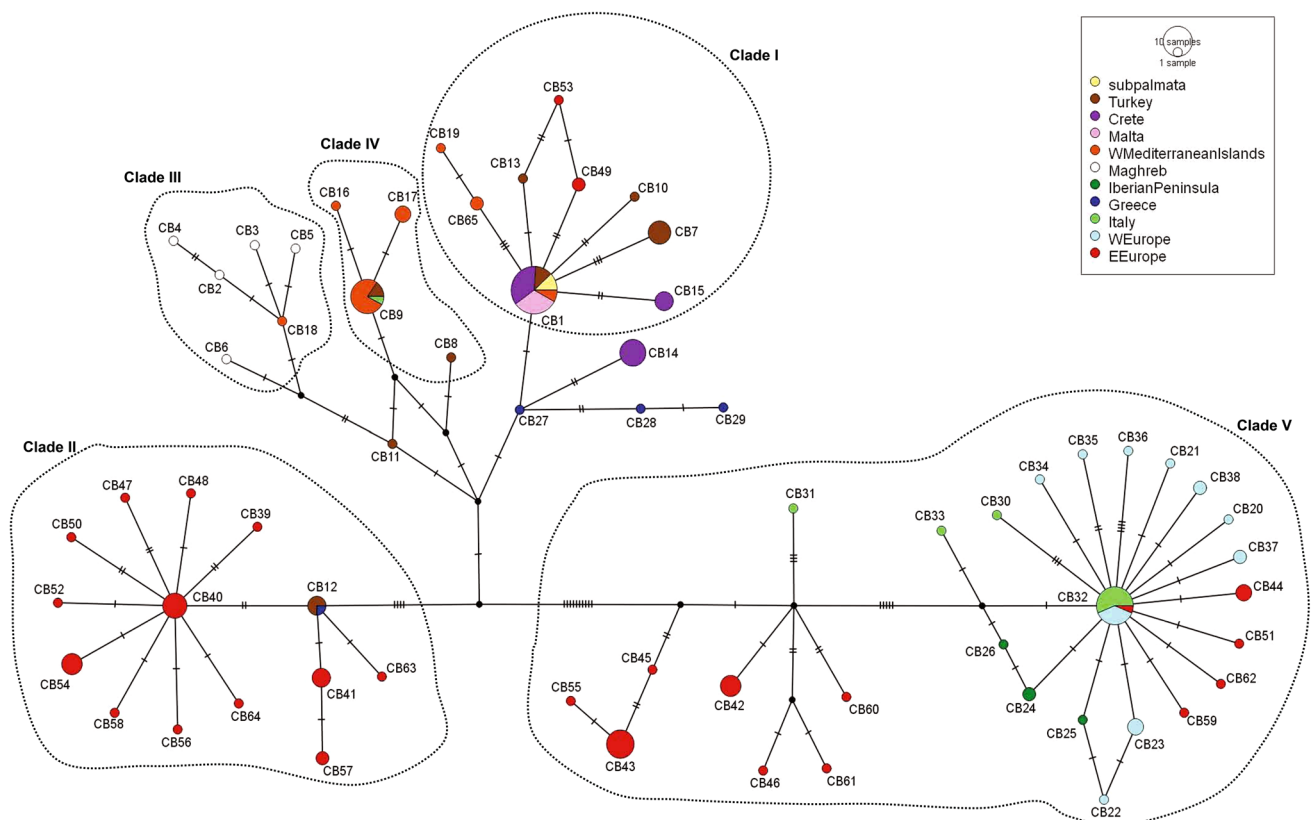
Texts from Classical Antiquity show evidence that weasels were used for rodent control (Frank 1985; Masseti 1995). In the Near East, rodents such as the house mouse *Mus musculus* and the black rat *Rattus rattus* have been commensal since at least the Neolithic and the Chalcolithic (Cucchi and Vigne 2006; Ruffino and Vidal 2010). It is likely that weasels would have been attracted to cultivated fields and grain storages, as they are today in rural areas across their range (Sheffield and King 1994). Moreover, the fact that the only known *M. nivalis* fossils from Cyprus are dated to the Late Bronze Age or Early Iron Age (1600–1050 years BC; Lehmann and Nobis 1979), a period in which Canaanite-Phoenician trade and presence in Cyprus intensified (Negbi 1992), may indicate ancient anthropogenic transport in the eastern Mediterranean. Therefore, a hypothesis for the origin of the Egyptian weasel is through introduction from the Levant in the Late Bronze Age when the region was under Egyptian control (Weinstein 1981) or later, in the Early Iron Age, as Egypt remained an important destination for Phoenician trade (Ballard et al. 2002; Evian 2011), including wildlife (Goudsmit and Brandon-Jones 2000). Introduction from Crete, which is relatively close geographically to Egypt and where the least weasel population shares haplotype CB1 with the Egyptian weasel, is contradicted by the absence of haplotype CR1 in the Cretan weasel and by the

fact that this population has a pelage coloration of the “nivalis” type, in which the demarcation line between the upper-brown and the lower-white colours is straight (Bate 1905).

The sharing of both CB1 and CR1 haplotypes between the Egyptian weasel and the least weasel population in Turkey is also compatible with the hypothesis that the Egyptian weasel is a relict of past range expansion from the Levant into Egypt (Dayan and Tchernov 1988), possibly during a mesic period of the Holocene (Dobson 1998). Accordingly, the Egyptian weasel is similar in size to *M. nivalis* fossils from the Pleistocene–Holocene transition up to the Early Bronze Age of Israel (Dayan and Tchernov 1988). In contrast, signs of body size reduction in weasels in the Levant, compared with fossils from the mid-Holocene (Dayan and Tchernov 1988), may be inferred from fossils from the Iron Age (1200–475 years BC; Dayan 1997) and Hellenistic period of Israel (250–150 years BC; Bar-Oz and Dayan 2001). This size reduction could be due to the climatic cooling after the Holocene climatic optimum (Staubwasser and Weiss 2006; Finné et al. 2011), as size in weasels is positively correlated with temperature

(Marciszak and Socha 2014). Thus, the hypothesis that the Egyptian weasel originates from an earlier natural colonization is more consistent with the known weasel fossils in Israel.

The weasel is currently not found in the Levant south of Lebanon but was present in Israel and Jordan at least until the first millennium BC (Bar-Oz and Dayan 2001). Increased aridity in the region during the last two millennia BC (Kaniewski et al. 2008; Finné et al. 2011) may have caused the extinction of the weasel in the southern Levant. Meanwhile, the Egyptian population may have found a mesic refuge in the Nile Delta and, by establishing a commensal relationship, would have been able to survive in an increasingly humanized habitat (Dayan and Tchernov 1988; Dayan 1997). An early onset of commensalism, when human settlements were still not significantly challenging habitats, would have facilitated coping with the subsequent increased urbanization (Bateman and Fleming 2012). To our knowledge, the least weasel is nowhere commensal in the sense of depending on a human-derived food supply, and tends to avoid urban environments (e.g. Baker and Harris 2007). At most, in agricultural



**Fig. 4** Median-joining network based on Cytochrome *b* haplotypes. Circles represent haplotypes and their size is proportional to the frequency observed. Coloured pie charts indicate the frequency of haplotypes in the Egyptian weasel (*subpalmata*) and in local or regional populations of *M. nivalis*. Small black circles represent

hypothetical haplotypes. Dashes on lines connecting haplotypes represent the number of nucleotide substitutions separating them. Haplotype codes are given in Table A1. The clades identified in the phylogenetic analyses are also indicated

**Table 1** Pairwise Cyt *b*  $D_a$  distances in percentage (below diagonal) and  $\Phi_{ST}$  values (above diagonal) between the Egyptian weasel and least weasels from neighbouring areas in the Mediterranean Basin

	Egypt	Turkey	Crete	Greece (mainland)	Italy (mainland)	Sicily	Malta	Maghreb
Egypt		<i>0.00</i>	<i>0.07</i>	<i>0.27</i>	0.77	0.89	<i>0.00</i>	0.73
Turkey	<i>0.06</i>		0.20	<i>0.11</i>	0.72	0.45	0.13	0.48
Crete	<i>0.04</i>	0.08		0.35	0.81	0.73	0.19	0.71
Greece (mainland)	0.12	<i>0.06</i>	0.09		0.73	0.68	0.53	0.55
Italy (mainland)	1.34	1.18	1.25	1.19		0.82	0.83	0.79
Sicily	0.46	0.30	0.43	0.36	1.39		0.93	0.76
Malta	<i>0.00</i>	0.06	0.04	0.12	1.34	0.46		0.84
Maghreb	0.51	0.41	0.49	0.41	1.49	0.43	0.51	

Non-significant values ( $P > 0.05$ ) are in italics

landscapes, preferred habitat includes hedgerows, hedges with ditches, stone walls, and fences (Moors 1975; Sheffield and King 1994), that is, movement corridors that provide protection from predators and access to prey in fields, meadows and haylofts. Commensalism, as the colonization of a new ecological niche, may imply significant changes in behaviour, ecology and physiology. These include tolerance to human presence, ability to use anthropogenic structures for denning, a different foraging behaviour and diet, smaller home ranges, higher population densities and hence increased territorial interactions. The changes in social behaviour associated with a commensal lifestyle are also likely to require physiological adjustments to reduce agonistic response (Frynta et al. 2005). Given that commensalism involves a complex set of adaptations and has not been reported in least weasels, it seems more likely that the commensal Egyptian weasel is the result of gradual evolution of a local population pre-adapted to disturbance (Dayan 1997; Lomolino and Channell 1995) rather than descent from introduced weasels.

Fossils could help clarify the origin of the Egyptian weasel through radiocarbon dating and genetic analyses, or the age of its commensalism using stable isotopes (Hu et al. 2014). Unfortunately, weasel remains from Egypt are lacking. Nevertheless, the debate about introduction versus natural colonization for the origin of the Egyptian weasel should be further addressed in future genetic studies. Ideally, these should include more samples from Egypt, of the extant populations in Lebanon and Syria, and of the available fossils from Israel, Jordan and Cyprus.

### Least weasels in the Maghreb

Our results show that the Egyptian weasel is genealogically distinct from weasels currently living in the Maghreb, a finding consistent with the fact that the latter have a

“nivalis” type coat pattern (Abramov and Baryshnikov 2000). Weasels in the Maghreb formed a separate clade (Clade III) that also contained a haplotype found in Sardinia (CB18) (Fig. 2). This haplotype in Sardinia is best interpreted as the result of introduction from the Maghreb, where it was not sampled or became extinct, since the haplotype was not found elsewhere other than in Sardinia. In the median-joining network, the closest haplotype to the likely ancestral node of Clade III was found in Anatolia (haplotype CB11), pointing to a Near Eastern origin of the weasels in Northwest Africa (Fig. 4). The genealogical relationships of the Maghreb sequences and their relatively low nucleotide diversity (0.3 %) are more suggestive of a single colonization. The high number of haplotypes in the Maghreb, when compared with that on each Mediterranean island, and the fact that they were not found in the Eastern Mediterranean seem to support a natural invasion from the Near East, a possibility already considered by Lebarbenchon et al. (2010). Moreover, the hypothesis of a recent demographic expansion for the Maghreb population was rejected by Tajima’s  $D$  (Tajima 1989) and Fu’s  $F_S$  (Fu 1997) tests ( $\alpha = 0.05$ ). Thus, overall, our results suggest that the colonization of the Maghreb is older and unrelated to the origin of the extant Egyptian weasel. The weasel fossil record in Northwest Africa is limited and unclear but the presence of the species in this region in the Late Pleistocene is accepted by several authors (Romer 1928; Savage and Russell 1983; Dayan and Tchernov 1988; Kowalski and Rzebik-Kowalska 1991; Sheffield and King 1994).

### Taxonomy and conservation of the Egyptian weasel

Our results suggest that the Egyptian weasel *M. subpalmata* is not specifically distinct from the least weasel *M. nivalis*. Indeed, following explicit subspecies definition



criteria (Awise and Ball 1990; O'Brien and Mayr 1991), *M. subpalmata* does not even qualify as a subspecies. The Egyptian weasel has been proposed as a separate species from *M. nivalis* based on cranial morphometrics, differences in the degree of sexual size dimorphism, and body length (van Zyll de Jong 1992; Reig 1997; Abramov and Baryshnikov 2000). However, least weasels show considerable geographic variation in size throughout their range (King 1989), hence the large size of the Egyptian weasel needs to be put in perspective. For example, the condylobasal skull length—a measure highly correlated with body length in weasels (Ralls and Harvey 1985)—is as different between male weasels from Egypt and southern Europe as between the latter and male weasels in north-eastern Europe (King 1989; Abramov and Baryshnikov 2000). Similarly, in both discriminant function and principal component analyses of cranial measurements (van Zyll de Jong 1992; Abramov and Baryshnikov 2000), male least weasels from southern Europe fell closer to male Egyptian weasels than to male least weasels from north-eastern Europe. In contrast, the skull of female Egyptian weasel falls much further from the range of size variation in the skull of female least weasel observed throughout its Holarctic distribution (van Zyll de Jong 1992). Therefore, the main morphological distinction between Egyptian and least weasels seems to be a difference in the degree of sexual dimorphism of size (van Zyll de Jong 1992; Abramov and Baryshnikov 2000). However, there are possible ecological explanations for the large size of the Egyptian weasel and the greater size difference between female Egyptian weasels and female least weasels, compared to that in the males. Least weasels in the Mediterranean region tend to be larger than elsewhere (Abramov and Baryshnikov 2000). This may be due to the absence of a larger congeneric competitor (the stoat) (Dayan and Tchernov 1988), to energy savings that can be allocated to growth in temperate climates (King 1989), and/or to allow exploitation of various large prey (Erlinge 1987; King 1989). In the Egyptian weasel, where the size of both sexes reaches that of the respective sexes of the stoat of Western Europe (Miller 1912; Flower 1932), this trend may have been reinforced by commensalism and access to anthropogenic food sources (Handwerk 1993; Yom-Tov 2003). Moreover, weasels are polygynous and large size in males is likely to be an advantage in inter-male competition for mates (Erlinge 1979; Moors 1980). Thus, abundant food may allow males to reach their full potential size (Ralls and Harvey 1985), particularly when other constraints such as interspecific competition and predation are reduced, and this could explain the large male size in the commensal Egyptian weasel. Female weasels attain smaller maximum sizes than males, which may be determined by their energy requirements for reproduction: females raise their young

alone and may use the extra energy available to produce larger litters and offspring in better condition (Erlinge 1979; Moors 1980). Nevertheless, in weasels the sexes covary in size (Ralls and Harvey 1985) and increased female size may be a correlated response to selection for increased male size (Lande 1980; King 1989). This, together with food abundance and a wide range of available prey sizes (Erlinge 1987; King 1989) may be behind the remarkably large size of female Egyptian weasels in comparison with females of least weasel across its range, and the lower sexual dimorphism in the Egyptian weasel compared with least weasels in the Mediterranean region (van Zyll de Jong 1992).

Thus, the large size of the commensal Egyptian weasel, as well as indirectly its characteristic sexual dimorphism, may be due to the synergy of improved nutrition (Yom-Tov 2003) and reduced competition and predation (Grant 1972; Angerbjörn 1986; Dayan and Tchernov 1988; Lomolino 2005). The morphological differences of the Egyptian weasel may therefore simply reflect phenotypic plasticity rather than genetically based differentiation (West-Eberhard 1989; Stearns 1989). However, given the observations of East and Lockie (1964), the differences in skull shape (Reig 1997), and studies of morphological differentiation among geographic populations of other species (e.g. Alatalo and Gustafsson 1988; Niewiarowski and Roosenburg 1993), genetic contributions to morphological differentiation cannot be ruled out. Genetic divergence could be expected due to selection associated with adaptation to living in and around increasingly urbanized human settlements, as this is likely to involve changes in physiological, behavioral and social traits (Frynta et al. 2005). Future genomic studies are needed to clarify the extent of functional genetic divergence and the genetic basis of phenotypic differences between Egyptian and least weasels.

Therefore, although our study does not support the taxonomic distinctiveness of *M. subpalmata*, evaluation of adaptive divergence is needed before a definite conclusion can be made. Genetically isolated populations may share mtDNA haplotypes due to incomplete lineage sorting, but ecologically driven adaptive differences may have accumulated (Fraser and Bernatchez 2001). Similarly, due to their relatively recent origins, commensal and domestic animals often possess identical or closely related mtDNA haplotypes to those of their wild ancestors (e.g. Driscoll et al. 2007; Thalmann et al. 2013), but important differences in biology may justify their recognition as distinct species.

While further research is needed to ascertain the taxonomic status of the Egyptian weasel, this study underlines that it may be a naturally occurring relict as proposed by Dayan and Tchernov (1988). Being geographically isolated and occupying a commensal niche, this population became

behaviourally, ecologically and morphologically distinct among weasels (Handwerk 1993). Given the lack of gene flow with other populations, its unusual habitat and the circumscribed range, the conservation of the Egyptian weasel is warranted. Peripheral populations are often important in the evolutionary process and may be sites of future speciation (Lesica and Allendorf 1995). Further study with a larger sample size and using fast-evolving molecular markers, such as microsatellites, is needed to assess the genetic diversity of the Egyptian weasel. Fortunately, the population is currently faring well and there are no known major threats (McDonald and Hoffmann 2008). Even if future research were to demonstrate that the Egyptian weasel is anthropochorous, its biological uniqueness would still justify its protection as long this does not negatively affect local native species (Gippoliti and Amori 2002).

**Acknowledgments** We thank Lluís Parpal (COFIB, Spain), Afif Ben Salah (Institut Pasteur de Tunis); Maurizio Gattabria (Museo Civico di Zoologia de Roma), Federico Striglioni and Gino Damiani (Parco Nazionale del Gran Sasso e Monti della Laga), and Parco Nazionale d’Abruzzo, Lazio e Molise for providing samples. We also thank Jacquelin DeFaveri (University of Helsinki) for reviewing the manuscript and two anonymous reviewers for their helpful comments and suggestions. MR and CF acknowledge financial support from Fundação para a Ciência e Tecnologia (FCT, MCTES, Portugal) through, respectively, the PhD Fellowship SFRH/BD/60595/2009 and the Ciência 2007 Contract C2007-UL-342-CBA1. JM acknowledges support from the Academy of Finland (Grants 200940, 108601 and 118673). ARB acknowledges financial support from the American University in Cairo through a faculty research grant. PJS thanks the Malta Environment and Planning Authority for granting permits to work on the protected Maltese weasel. SOO acknowledges support from the Turkish National Science Foundation (TUBITAK) through the project 110T930.

#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This article does not contain any studies with animals performed by any of the authors.

## References

Abramov AV, Baryshnikov GF (2000) Geographic variation and intraspecific taxonomy of weasel *Mustela nivalis* (Carnivora, Mustelidae). *Zoosyste Ross* 8:365–402

Alatalo RV, Gustafsson L (1988) Genetic component of morphological differentiation in coal tits under competitive release. *Evolution* 42:200–203

Angerbjörn A (1986) Gigantism in island populations of wood mice (*Apodemus*) in Europe. *Oikos* 47:47–56

Avise JC, Ball RM (1990) Principles of genealogical concordance in species concepts and biological taxonomy. *Oxf Surv Evol Biol* 7:45–67

Baker PJ, Harris S (2007) Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mamm Rev* 37:297–315

Ballard RD, Stager LE, Master D, Yoerger D, Mindell D, Whitcomb LL, Singh H, Piechota D (2002) Iron age shipwrecks in deep water off Ashkelon, Israel. *Am J Archaeol* 106:151–168

Bandelt H, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Mol Biol Evol* 16:37–48

Bar-Oz G, Dayan T (2001) Weasels from the Hellenistic period of Israel. *Isr J Zool* 47:271–274

Barrett-Hamilton GEH (1900) Note on the weasel, *Putorius (Ictis) nivalis*, Linn., and some of its subspecies. *J Nat Hist* 5:41–50

Bate DMA (1905) On the mammals of Crete. *Proc Zool Soc Lond* 75:315–323

Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. *J Zool* 287:1–23

Berry V, Gascuel O (1996) Interpretation of bootstrap trees: threshold of clade selection and induced gain. *Mol Biol Evol* 13:999–1011

Bradley RD, Baker RJ (2001) A test of the genetic species concept: cytochrome-*b* sequences and mammals. *J Mammal* 82:960–973

Costa M, Fernandes C, Birk JDS, Kitchener AC, Santos-Reis M, Bruford W (2013) The genetic legacy of the 19th-century decline of the British polecat: evidence for extensive introgression from feral ferrets. *Mol Ecol* 22:5130–5147

Cretzschmar PJ (1826) Atlas zu der Reise im nördlichen Afrika von Eduard Rüppell. Erste Abteilung Zoologie. Senckenbergischen naturforschenden Gesellschaft, Frankfurt am Main

Cucchi T, Vigne JD (2006) Origin and diffusion of the house mouse in the Mediterranean. *Hum Evol* 21:95–106

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nat Methods* 9:772

Dayan T (1997) Weasels from the Iron Age of Israel: a biogeographic note. *Isr J Zool* 43:295–298

Dayan T, Tchernov E (1988) On the first occurrence of the common weasel (*Mustela nivalis*) in the fossil record of Israel. *Mammalia* 52:165–168

Dobson M (1998) Mammal distributions in the western Mediterranean: the role of human intervention. *Mamm Rev* 28:77–88

Driscoll CA, Menotti-Raymond M, Roca AL, Hupe K, Johnson WE, Geffen E, Harley EH, Delibes M, Dominique P, Kitchener AC, Yamaguchi N, O’Brien J, Macdonald DW (2007) The Near Eastern origin of cat domestication. *Science* 317:519–523

East K, Lockie JD (1964) Observations on a family of weasels (*Mustela nivalis*) bred in captivity. *Proc Zool Soc Lond* 143:359–363

Erlinge S (1979) Adaptive significance of sexual dimorphism in weasels. *Oikos* 33:233–245

Erlinge S (1987) Why do European stoats *Mustela erminea* not follow Bergmann’s rule? *Ecography* 10:33–39

Evian SBD (2011) Egypt and the levant in the Iron Age I–IIA: the ceramic evidence. *Tel Aviv* 38:94–119

Excoffier L, Lischer HE (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol Ecol Resour* 10:564–567

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 131:479–491

Fernandes CA, Ginja C, Pereira I, Tenreiro R, Bruford MW, Santos-Reis M (2008) Species-specific mitochondrial DNA markers for identification of non-invasive samples from sympatric carnivores in the Iberian Peninsula. *Conserv Genet* 9:681–690

Finné M, Holmgren K, Sundqvist HS, Weiberg E, Lindblom M (2011) Climate in the eastern Mediterranean, and adjacent regions, during the past 6000 years—a review. *J Archaeol Sci* 38:3153–3173

- Flower SS (1932) 22. Notes on the recent mammals of Egypt, with a list of the species recorded from that kingdom. Proc Zool Soc Lond 102:369–450
- Frank F (1985) Zur Evolution und Systematik der kleinen Wiesel (*Mustela nivalis* Linnaeus, 1766). Z Saugetierkd 50:208–225
- Fraser DJ, Bernatchez L (2001) Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Mol Ecol 10:2741–2752
- Frynta D, Slabova M, Vachova H, Volfova R, Munclinger P (2005) Aggression and commensalism in house mouse: a comparative study across Europe and the near east. Aggress Behav 31:283–293
- Fu YX (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925
- Garcia-Rodriguez AI, Bowen BW, Domning D, Mignucci-Giannoni AA, Marmontel M, Montoya-Ospina RA, Morales-Vela B, Rudin M, Bonde RK, McGuire PM (1998) Phylogeography of the West Indian manatee (*Trichechus manatus*): how many populations and how many taxa? Mol Ecol 7:1137–1149
- Gippoliti S, Amori G (2002) Anthropochorous wild mammal taxa and conservation lists. Conserv Biol 6:1162–1164
- Golubchik T, Wise MJ, Eastale S, Jermiin LS (2007) Mind the gaps: evidence of bias in estimates of multiple sequence alignments. Mol Biol Evol 24:2433–2442
- Goudsmit J, Brandon-Jones D (2000) Evidence from the baboon catacomb in North Saqqara for a west Mediterranean monkey trade route to Ptolemaic Alexandria. J Egypt Archaeol 86:111–119
- Grant PR (1972) Convergent and divergent character displacement. Biol J Linn Soc 4:39–68
- Handwerk VJ (1993) Zur Biologie und Ökologie ägyptischer Wiesel, *Mustela subpalmata* Hemprich und Ehrenberg, 1833. Zool Middle East 9:5–30
- Hanke M, Wink M (1994) Direct DNA sequencing of PCR-amplified vector inserts following enzymatic degradation of primer and dNTPs. Biotechniques 17:858–860
- Harding LE, Smith FA (2009) *Mustela* or *Vison*? Evidence for the taxonomic status of the American mink and a distinct biogeographic radiation of American weasels. Mol Phylogenet Evol 52:632–642
- Hoath R (2009) A field guide to the mammals of Egypt. The American University in Cairo Press, Cairo
- Holder MT, Sukumaran J, Lewis PO (2008) A justification for reporting the majority-rule consensus tree in Bayesian phylogenetics. Syst Biol 57:814–821
- Hu Y, Hu S, Wang W, Wu X, Marshall FB, Chen X, Hou L, Wang C (2014) Earliest evidence for commensal processes of cat domestication. Proc Natl Acad Sci 111:116–120
- Huelsenbeck JP, Larget B, Alfaro ME (2004) Bayesian phylogenetic model selection using reversible jump Markov chain Monte Carlo. Mol Biol Evol 21:1123–1133
- Kaniewski D, Paulissen E, Van Campo E, Al-Maqdissi M, Bretschneider J, Van Lerberghe K (2008) Middle East coastal ecosystem response to middle-to-late Holocene abrupt climate changes. Proc Natl Acad Sci 105:13941–13946
- King CM (1989) The advantages and disadvantages of small size to weasels, *Mustela* species. In: Gittleman JL (ed) Carnivore behavior, ecology, and evolution. Chapman and Hall, London, pp 302–334
- Kingdon J (2001) The Kingdom field guide to African mammals. Academic Press, London
- Koepfli KP, Deere KA, Slater GJ, Begg C, Begg K, Grassman L, Lucherini M, Veron G, Wayne RK (2008) Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biol 6:10
- Kowalski K, Rzebik-Kowalska B (1991) Mammals of Algeria. Ossolineum, Wrocław
- Kurose N, Abramov AV, Masuda R (2005) Comparative phylogeography between the ermine *Mustela erminea* and the least weasel *M. nivalis* of Palaearctic and Nearctic regions, based on analysis of mitochondrial DNA control region sequences. Zool Sci 22:1069–1078
- Kurose N, Abramov AV, Masuda R (2008) Molecular phylogeny and taxonomy of the genus *Mustela* (Mustelidae, Carnivora), inferred from mitochondrial DNA sequences: new perspectives on phylogenetic status of the back-striped weasel and American mink. Mamm Study 33:25–33
- Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305
- Lebarbenchon C, Poitevin F, Montgelard C (2006) Genetic variation of the weasel (*Mustela nivalis*) in Corsica based on mitochondrial control region sequences. Mamm Biol 71:164–171
- Lebarbenchon C, Poitevin F, Arnal V, Montgelard C (2010) Phylogeography of the weasel (*Mustela nivalis*) in the western-Palaearctic region: combined effects of glacial events and human movements. Heredity 105:449–462
- Lehmann EV, Nobis G (1979) Subfossile Mauswiesel, *Mustela nivalis* Linne, 1766 aus Enkomi-Alasia auf Zypern. Bonn Zool Beitr 30:32–38
- Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? Conserv Biol 9:753–760
- Lomolino MV (2005) Body size evolution in insular vertebrates: generality of the island rule. J Biogeogr 32:1683–1699
- Lomolino MV, Channell R (1995) Splendid isolation: patterns of geographic range collapse in endangered mammals. J Mamm 76:335–347
- Luo A, Qiao H, Zhang Y, Shi W, Ho SY, Xu W, Zhang A, Zhu C (2010) Performance of criteria for selecting evolutionary models in phylogenetics: a comprehensive study based on simulated datasets. BMC Evol Biol 10:242
- Marciszak A, Socha P (2014) Stoat *Mustela erminea* Linnaeus, 1758 and weasel *Mustela nivalis* Linnaeus, 1766 in palaeoecological analysis: a case study of Biśnik Cave. Quat Int 339–340:258–265
- Masseti M (1995) Quaternary biogeography of the Mustelidae family on the Mediterranean islands. Hystrix 7:17–34
- McDevitt AD, Zub K, Kawałko A, Oliver MK, Herman JS, Wójcik JM (2012) Climate and refugial origin influence the mitochondrial lineage distribution of weasels (*Mustela nivalis*) in a phylogeographic suture zone. Biol J Linn Soc 106:57–69
- McDonald R, Hoffmann M (2008) *Mustela subpalmata*. The IUCN red list of threatened species. doi:10.2305/IUCN.UK.2008.RLTS.T41660A10504103.en
- Miller GS (1912) Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. Trustees of the British Museum, London
- Moors PJ (1975) The food of weasels (*Mustela nivalis*) on farmland in north-east Scotland. J Zool 177:455–461
- Moors PJ (1980) Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. Oikos 34:147–158
- Morrison DA (2007) Increasing the efficiency of searches for the maximum likelihood tree in a phylogenetic analysis of up to 150 nucleotide sequences. Syst Biol 56:988–1010
- Muse SV, Gaut BS (1994) A likelihood approach for comparing synonymous and nonsynonymous nucleotide substitution rates, with application to the chloroplast genome. Mol Biol Evol 11:715–724
- Negbi O (1992) Early Phoenician presence in the Mediterranean islands: a reappraisal. Am J Archaeol 96:599–615

- Nei M (1987) Molecular evolutionary genetics. Columbia University Press, New York
- Niethammer J (1973) Das Mauswiesel (*Mustela nivalis*) in Afghanistan. Bonn Zool Beitr 24:1–6
- Niewiarowski PH, Roosenburg W (1993) Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. Ecology 74:1992–2002
- Nye TM, Lio P, Gilks WR (2006) A novel algorithm and web-based tool for comparing two alternative phylogenetic trees. Bioinformatics 22:117–119
- O'Brien SJ, Mayr E (1991) Bureaucratic mischief: recognizing endangered species and subspecies. Science 251:1187–1188
- Osborn DJ, Helmy I (1980) The contemporary land mammals of Egypt (including Sinai). Fieldiana Zool 5:1–579
- Pesole G, Gissi C, De Chirico A, Saccone C (1999) Nucleotide substitution rate of mammalian mitochondrial genomes. J Mol Evol 48:427–434
- Pond SLK, Frost SD (2005) Not so different after all: a comparison of methods for detecting amino acid sites under selection. Mol Biol Evol 22:1208–1222
- Pond SLK, Frost SDW, Muse SV (2005) HyPhy: hypothesis testing using phylogenies. Bioinformatics 21:676–679
- Poulakakis N, Lymberakis P, Tsigenopoulos CS, Magoulas A, Mylonas M (2005) Phylogenetic relationships and evolutionary history of snake-eyed skink *Ablepharus kitaibelii* (Sauria: Scincidae). Mol Phylogenet Evol 34:245–256
- Ralls K, Harvey PH (1985) Geographic variation in size and sexual dimorphism of North American weasels. Biol J Linn Soc 25:119–167
- Reig S (1997) Biogeographic and evolutionary implications of size variation in North American least weasels (*Mustela nivalis*). Can J Zool 75:2036–2049
- Romer AS (1928) Pleistocene mammals of Algeria: fauna of the Paleolithic station of Mechta-el-Arbi. Logan Mus Bull 1:80–163
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61:539–542
- Ruffino L, Vidal E (2010) Early colonization of Mediterranean islands by *Rattus rattus*: a review of zooarcheological data. Biol Invasions 12:2389–2394
- Sato JJ, Wolsan M, Prevosti FJ, D'Elía G, Begg C, Begg K, Hosoda T, Campbell KL, Suzuki H (2012) Evolutionary and biogeographic history of weasel-like carnivores (Musteloidea). Mol Phylogenet Evol 63:745–757
- Savage DE, Russell DE (1983) Mammalian paleofaunas of the world. Addison-Wesley, Reading
- Schwarz G (1978) Estimating the dimension of a model. Ann Stat 6:461–464
- Setzer HW (1952) Notes on mammals from the Nile Delta region of Egypt. Proc US Natl Mus 102:343–369
- Sheffield SR, King CM (1994) *Mustela nivalis*. Mamm Species 454:1–10
- Staubwasser M, Weiss H (2006) Holocene climate and cultural evolution in late prehistoric–early historic West Asia. Quat Res 66:372–387
- Stearns SC (1989) The evolutionary significance of phenotypic plasticity. Bioscience 39:436–445
- Stöver BC, Müller KF (2010) TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. BMC Bioinform 11:7
- Sukumaran J, Holder MT (2010) DendroPy: a Python library for phylogenetic computing. Bioinformatics 26:1569–1571
- Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595
- Tamar K, Carranza S, Sindaco R, Moravec J, Meiri S (2014) Systematics and phylogeography of *Acanthodactylus schreiberi* and its relationships with *Acanthodactylus boskianus* (Reptilia: Squamata: Lacertidae). Zool J Linn Soc 172:720–739
- Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol Biol Evol 10:512–526
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. Mol Biol Evol 30:2725–2729
- Thalmann O, Shapiro B, Cui P, Schuenemann VJ, Sawyer SK, Greenfield DL, Germonpré MB, Sablin MV, López-Giráldez F, Domingo-Roura X, Napierala H, Uerpmann H-P, Loponte DM, Acosta AA, Giemsch L, Schmitz RW, Worthington B, Buikstra JE, Druzhkova A, Graphodatsky AS, Ovodov ND, Wahlberg N, Freedman AH, Schweizer RM, Koepfli KP, Leonard JA, Meyer M, Krause J, Pääbo S, Green RE, Wayne RK (2013) Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. Science 342:871–874
- Thomas O (1895) On the long-lost *Putorius africanus*, Desm., and its occurrence in Malta. Proc Zool Soci Lond 63:128–131
- Thompson JD, Linard B, Lecompte O, Poch O (2011) A comprehensive benchmark study of multiple sequence alignment methods: current challenges and future perspectives. PLoS One 6:e18093
- Tikhonov A, Cavallini P, Maran T, Kranz A, Herrero J, Giannatos G, Stubbe M, Conroy J, Kryštufek B, Abramov A, Wozencraft C, Reid F, McDonald R (2008) *Mustela nivalis*. The IUCN red list of threatened species. doi:10.2305/IUCN.UK.2008.RLTS.T14021A4383128.en
- van Zyll de Jong CG (1992) A morphometric analysis of cranial variation in Holarctic weasels (*Mustela nivalis*). Z Saugetierkd 57:77–93
- Villesen P (2007) FaBox: an online toolbox for fasta sequences. Mol Ecol Notes 7:965–968
- Wallace IM, O'Sullivan O, Higgins DG, Notredame C (2006) M-Coffee: combining multiple sequence alignment methods with T-Coffee. Nucleic Acid Res 34:1692–1699
- Weinstein JM (1981) The Egyptian empire in Palestine: a reassessment. Bull Am Schools Orient Res 241:1–28
- West-Eberhard MJ (1989) Phenotypic plasticity and the origins of diversity. Annu Rev Ecol Syst 20:249–278
- Whittaker DJ, Ting N, Melnick DJ (2006) Molecular phylogenetic affinities of the simakobu monkey (*Simias concolor*). Mol Phylogenet Evol 39:887–892
- Xia X (2013) DAMBE5: a comprehensive software package for data analysis in molecular biology and evolution. Mol Biol Evol 30:1720–1728
- Xia X, Xie Z, Salemi M, Chen L, Wang Y (2003) An index of substitution saturation and its application. Mol Phylogenet Evol 26:1–7
- Yom-Tov Y (2003) Body sizes of carnivores commensal with humans have increased over the past 50 years. Funct Ecol 17:323–327
- Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin