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Molecular phylogeny of the *Eremias persica* complex of the Iranian plateau (Reptilia: Lacertidae), based on mtDNA sequences

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The Persian racerunner *Eremias persica* Blanford, 1875 is confined to the Iranian plateau, and forms one of the most widespread but rarely studied species of the family Lacertidae. With many local populations inhabiting a variety of habitats, and exhibiting considerable morphological, genetic, and ecological variations, it represents a species complex. We analysed sequences of mitochondrial cytochrome *b* and *12S* ribosomal RNA (rRNA) genes derived from 13 geographically distant populations belonging to the *E. persica* complex. Using our knowledge of palaeogeographical events, a molecular clock was calibrated to assess the major events in fragmentation, radiation, and intraspecific variation. The sequence data strongly support a basal separation of the highland populations of western Iran from those of the open steppes and deserts, occurring in the east. The subsequent radiation, fragmentation, and evolution of these major assemblages have led to several discernable geographical lineages across the wide area of the Iranian plateau. The results indicate a middle-Miocene origin for the clade as a whole. The first split, isolating the western and eastern clades, appears to have occurred 11–10 Mya. Further fragmentations and divergence within the major clades began about 8 Mya, with an evolutionary rate of 1.6% sequence divergence per million years among the lineages in the genes studied (combined data set). Molecular and morphological data strongly support a taxonomic revision of this species complex. At least four of the discovered clades should be raised to species, and two to subspecies, rank.

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ADDITIONAL KEYWORDS: *12S* – cytochrome *b* – lacertid lizards – molecular clock – rRNA – systematics.

INTRODUCTION

Iran consists of a complex of mountain chains enclosing a series of interior basins that lie at altitudes of 300–1700 m a.s.l. These mountain ranges rise sharply from sea level in the north and south, and from the flat, low-lying plain of Mesopotamia in the west. Eastwards, and in the north-west, the highlands extend, continually and uninterruptedly, beyond Iran. In the east they are prolonged at the massifs of Afghanistan and Baluchestan, and in the north-west as the plateau uplands of Azerbaijan and eastern Asia Minor. This entire upland area has been termed the Iranian plateau by some authors, despite the fact that it is not confined politically within the Iranian borders (Fisher, 1968).

The Eurasian lacertid genus *Eremias s.s.* Fitzinger, 1834 has a wide distribution range from northern China, Mongolia, Korea, and Central Asia, to southern Europe, and then southwards through the

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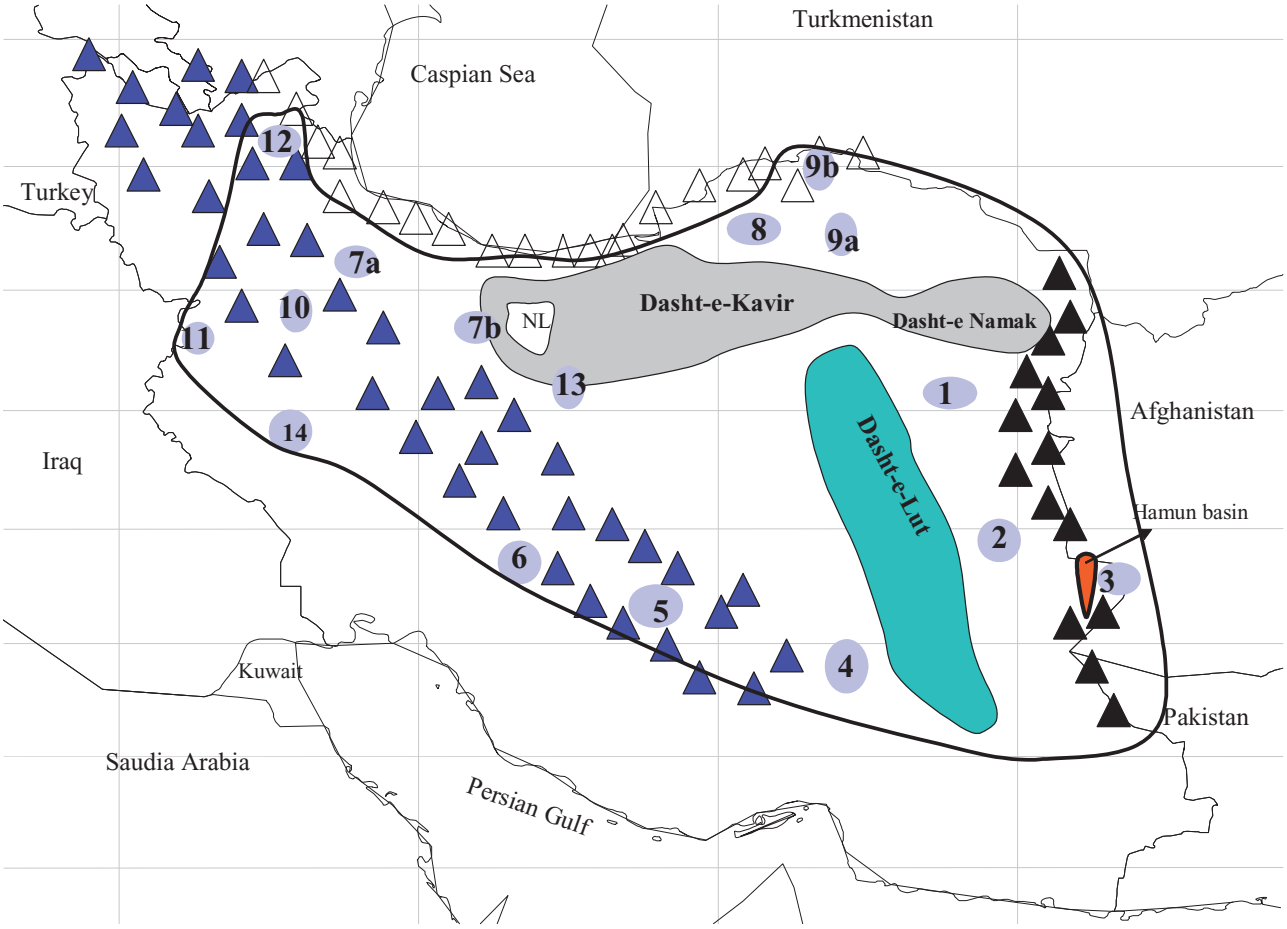

Fig. 1. Map of Iran and neighboring areas, showing the entire distribution range of the *Eremias persica* complex (bold line), and the localities from which the examined materials in this study were collected (circled numbers). The numbers refer to the samples indicated in the Appendix. Key: ▲, Zagros Mountains; △, Elburz Mountains; ▲, eastern mountain system; NL, Namak Lake (Salt Lake).

Iranian plateau (Szczerbak, 1974, 2003; Anderson, 1999). It is hypothesized that the genus is Central Asian in its relationships and affinities (Szczerbak, 1974). It currently comprises five subgenera and some 33 recognized species of mostly sand-, steppe-, and desert-dwelling lizards. A total of 16 species occur on the Iranian plateau, mostly in northern, central, and eastern regions (Rastegar-Pouyani & Nilson, 1997; Anderson, 1999). Over the last three decades several attempts for the taxonomic modification of this genus, based mostly on morphology, hemipenial traits, and ecological considerations, have been made (Szczerbak, 1974, 2003; Arnold, 1986; Anderson, 1999). However, the knowledge of *Eremias* of the Iranian plateau is, to a great extent, anecdotal, and there are still large gaps in the available material from various parts of the plateau.

The Persian racerunner *Eremias persica* Blanford, 1875 is a widespread and mainly Iranian species of the typical subgenus *Eremias*, and is distributed on a large territory stretching from southern Turkmenistan to the entire central and eastern portion of the Iranian plateau, at elevations of 400–2800 m a.s.l. (Fig. 1). In Iran, it extends westwards to the highlands and foothills of the western Zagros Mountains in the Hamadan, Azerbaijan, and Kermanshah provinces. It also extends east and south, through southern Afghanistan and Baluchistan, to Wazirestan, Pakistan (Leviton *et al.*, 1992; Anderson, 1999; Szczerbak, 2003).

In the number and general morphology of scales, *E. persica* is closely related to *Eremias velox* (Pallas, 1771) and *Eremias strauchi* Kessler, 1878; however, they are identifiable by differences in ontogenetic traits and colour patterns (Peters, 1964; Anderson, 1999). As with many other lacertids, the juveniles are easily distinguishable from the adults by obvious differences in the general colour patterns.

Herpetologists have often remarked that the populations of *E. persica* found in various localities of the Iranian plateau have experienced long-term isolation, describing a variety of discernible morphological features that are often distinguishable from one other (Terentjev & Chernove, 1965; Szczerbak, 1974, 2003; Leviton *et al.*, 1992; Anderson, 1999). Within the past ten years some of the morphotypes have been described as distinct species, including *Eremias nigrolateralis* Rastegar-Pouyani & Nilson, 1997, *Eremias montanus* Rastegar-Pouyani & Rastegar-Pouyani, 2001. Thus, this taxon can be considered as a potential species complex. In spite of this, to date, no phylogenetic study has been carried out on the various populations of the complex in its vast range of distribution, and no subspecies have been reported. Genera such as *Eremias*, which are especially speciose and widespread, should be most informative in future biogeographic and phylogeographic analyses of the Iranian plateau herpetofauna.

Whereas herpetologists have traditionally relied upon morphological data for making phylogenetic decisions, contemporary techniques facilitate the discovery of distinct genetic lineages. Indeed, once genetically similar populations are identified, and their geographic distributions determined, analyses focused on morphological differentiation can be initiated. Molecular markers are of great value in the study of intraspecific variation and geographic association, and for inferring the evolutionary history of a species, especially in cases of little or mostly clinal phenotypic variation (Moritz & Hillis, 1996; Cruzan & Templeton, 2000). Indeed, intraspecific phylogenies are less subject to reconstruction artifacts (e.g. long-branch attraction) than high-level phylogenies (Sanderson *et al.*, 2000). Furthermore, in high-level phylogenies the problem of missing (extinct) intermediate clades can be misleading in polarizing evolutionary transitions (Surget–Groba *et al.*, 2001). The intraspecific differentiation of a species is a complex result of geographic, demographic, and ecological factors that have operated throughout the evolutionary history of a species (Walker & Avise, 1998). It should be particularly apparent in taxa that show only limited mobility, such as reptiles. Most studies of intraspecific variability in these vertebrates provide evidence for the existence of distinct lineages or morphotypes that can be strongly correlated with geographic regions (Lenk *et al.*, 1999; Lenk, Joger & Wink, 2001; Guicking, Joger & Wink, 2002; Fritz *et al.*, 2005a, b) These merits notwithstanding, there are also some problems with such low-level phylogenies: the major one is there may be incomplete lineage sorting at such a low level, and the terminal relationships of the genes have a high probability of not matching the relationships of the individuals (Funk & Omland, 2003).

The present study is the first comprehensive attempt to infer the phylogenetic relationships and intraspecific differentiation of the *E. persica* group in its entire range. A taxonomic revision of the group, based on molecular and some outstanding morphological features of the local populations, is outlined and recommended.

MATERIAL AND METHODS

Selection of specimens

Fieldwork was conducted during 2002–2005 on the Iranian plateau. A total of 125 individuals from 13 geographically distinct populations belonging to the *E. persica* complex (including *E. persica*, *E. montanus*, and *E. nigrolateralis*), covering almost all of the range, were collected and examined (Fig. 1, Appendix). Many of the *Eremias* species are superficially similar, and are difficult to discriminate phenotypically; therefore, to avoid the problem of species misidentification, which can confuse the phylogeny, all the specimens included in this study were carefully checked against the most reliable morphological keys available for the genus (Terentjev & Chernove, 1965; Leviton *et al.*, 1992; Anderson, 1999).

Based on the current understanding of the phylogenetic relationships among lacertid lizards (Arnold, 1973, 1986, 1989; Mayer & Benyr, 1994; Fu, 1998, 2000; Harris, Arnold & Thomas, 1998; Arnold, Arribas & Carranza, 2007; Mayer & Pavlicev, 2007), *Ophisops elegans* Ménétries, 1832, *Mesalina brevirostris* Blanford, 1874, and *E. velox*, collected from the same general area, were selected as the out-group taxa. Original tissue and DNA materials were deposited in the Department of Biology, Institute of Pharmacy and Molecular Biotechnology, University of Heidelberg, and voucher specimens were deposited in the State Natural History Museum, Braunschweig, Germany.

Laboratory procedures

As a source for DNA, muscle or liver tissues were collected and preserved in 80% ethanol or EDTA buffer. Total DNA was extracted using a standard phenol/chloroform protocol (Sambrook & Russell, 2001). Standard polymerase chain reaction (PCR) was employed to amplify the marker genes of interest. The complete sequence of the mitochondrial cytochrome *b* gene (cyt *b*) and a partial sequence of ribosomal *12S* rRNA were amplified using the specific primers Lgluk, 5′-AACCG CTGTTGTCTTCAACTA-3′, and NtheH, 5′-GGTTTACAAGACCAGTTGCTTT-3′, located at the flanking region of cyt *b* (W. Mayer, pers. comm.), and *12s*A, 5′-AAACTGGGATTAGATA

CCCCACTAT-3′, and *12s*B, 5′-GAGGGTGACGGGC GGTGTGT-3′ (Kocher *et al.*, 1989), for the*12S* rRNA gene. Additionally, for cyt *b*, two internal primers Mt–E600f, 5′-CCATAATTCACCTTCTTTTCC-3′, and Ei700r, 5′-GGGGTGAAAGGGGATTTT(AG)TC-3′, were designed and used in the sequencing process. The specific conditions and protocols of PCR and cycle sequencing reaction are available from the authors. The amplified fragments were sequenced on an automated sequencer MegaBACE™ 1000 (Amersham Biosciences, now part of GE Healthcare).

Data analysis

The obtained sequences were aligned using ClustalW (Thompson, Higgins & Gibson, 1994), as implemented in the Bioedit program sequence alignment editor (Hall, 1999). The problematic sites were then corrected manually. No ambiguous alignment was scored. To check for sequence errors the sequences were compared with closely related species (the same fragments from other *Eremias* species deposited in GenBank). Furthermore, in the case of cyt *b*, all sequences were checked for unexpected stop codons using the program MEGA 3.1 (Kumar & Nei, 2004).

To test the expediency of combining the data from both genes, the incongruence length difference (ILD) test, also known as the partition homogeneity test (Farris, Kluge & Bult, 1994; Swofford, 2003), was applied to the data set after all invariant characters had been removed (Cunningham, 1997). As saturation might influence the reliability of the results obtained from molecular phylogenetic analyses, the saturation of sequences was tested by a graphical display, in which the pairwise transition and transversion proportions were plotted against the corresponding divergence indices, as implemented in DAMBE v.4.2.7 (Xia & Xie, 2001).

Basic sequence statistics were obtained with the program MEGA. Given that the various phylogenetic methods available often involved different assumptions about models of evolutionary change, the similarity of topologies produced by different methods increases the confidence that the phylogenies involved are representative of the evolutionary history. Therefore, to infer phylogenies, Bayesian inference (BI; Yang & Rannala, 1997), maximum parsimony (MP), and maximum likelihood (ML) were used. We used MODELTEST v.3.06 (Posada & Crandall, 1998) to estimate the optimal evolutionary models to be used for the combined data set. The preferred model was (GTR + I + G), as suggested by the Akaike information criterion. The proportion of invariable sites, $I = 0.2686$, for among-site rate variation followed a gamma distribution, with the shape parameter $\alpha = 0.5762$.

For BI, the program MRBAYES v. 3.0b4 (Huelsenbeck & Ronquist, 2001) was used. The analyses were run with four incrementally heated Markov chains, using the default heating values. They were started with randomly generated trees, and ran for 2×10^6 generations, with sampling at intervals of 100 generations, which produced 20 000 sampled trees. To ensure that the analyses were not trapped on local optima, all data sets were run three times, independently, and with each run beginning with a different starting tree. The log-likelihood values of the 20 000 trees in each analysis were plotted against the generation time. After verifying that stationary had been reached, both in terms of likelihood scores and parameter estimation, the first 1500 trees were discarded in all three runs as burn-in, and a majority-rule consensus tree was generated from the remaining 18 500 trees. The frequency of any particular clade among the individual trees contributing to the consensus tree represents the posterior probability of that clade (Huelsenbeck & Ronquist, 2001).

Bothe the MP and ML analyses were conducted with the program PAUP 4.0b10 (Swofford, 2003), using a heuristic search and the closest step-wise sequence addition algorithm. Most-parsimonious trees were generated with 100 random-addition sequences and the tree-bisection-reconnection (TBR) algorithm, for branch swapping. For the MP analysis, equal weighting of all three codon positions was used, because saturation was generally low. The resulting clades were assessed using bootstrapping with 1000 replicates under the MP criterion (Felsenstein, 1985). A heuristic ML search (Felsenstein, 1981) with ten random-addition sequence replicates and TBR branch swapping was performed with the (GTR + I + G) model.

Even a crude molecular clock may give some idea of the absolute date of colonization, and this can be used to discriminate different kinds of natural colonization (Carranza & Arnold, 2006). In order to assess the dates of speciation events and divergence times among the clades, molecular-clock assumptions were incorporated within our ML trees. Tests for clock-like behavior in the data set were performed with a molecular-clock likelihood ratio test from clock-enforced and clock-unenforced ML analyses. As the taxon rate homogeneity is assumed, the level of variation inherent in the data was estimated by performing relative rate tests using the program PHYLTEST 2.0 (Kumar, 1996).

Regrettably, there is as yet no lacertid fossil record known in Iran, or adjacent areas, to calibrate the molecular clock. However, some well-dated geological events can help to do that with some certainty. The first uplifting of the Zagros Mountains, which mainly led to the fragmentation of the western and eastern

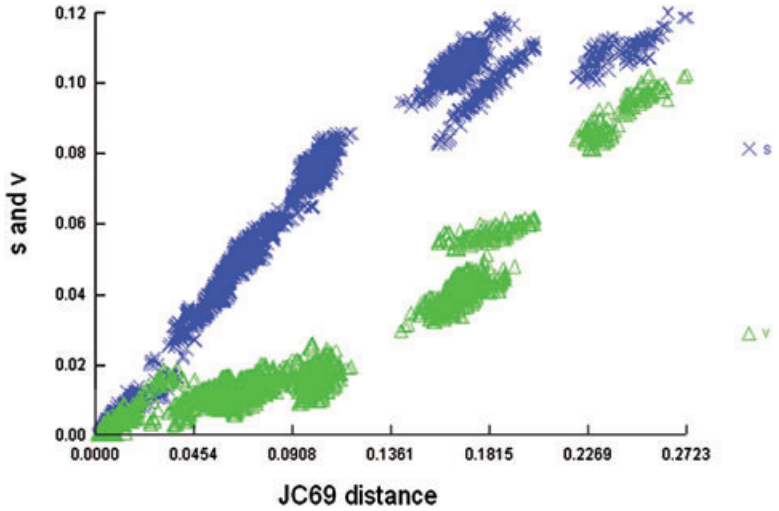

Fig. 2. Patterns of nucleotide substitution. Pairwise proportions of transitions (s) and transversion (v) versus JC69 distance, derived from the combined data set. The graph indicates there is low saturation in the data set.

Iranian plateau herpetofauna, is known to have occurred during the late Miocene (8–11 Mya), and was caused by the Arabian plate impinging on Eurasia (Abdrakhmatove *et al.*, 1996; Macey *et al.*, 1998, 2000a, b). It is likely that this phenomenon caused the western clade of *Eremias* to split from the eastern populations. Based on this calibration point, we calibrated the molecular clock within our ML phylogeny.

RESULTS

A total of 1533 base pairs (1143 bp cyt *b* and 390 bp *12S*) were recovered and aligned for all specimens, including the out-groups. Of these, 684 (45.6%) were variable and 539 (35.3%) were parsimony informative. No gaps were found and no ambiguity remained. The largest pairwise difference between outgroup and ingroup species, in cyt *b*, was 23.4% (*O. elegans* and *Eremias* sp. ERP 361), and the smallest was 15.2% (*E. velox* and *E. persica*, smp 291). As in many other lacertids, the number of nucleotides encoding cyt *b* appears to be constant: 1143, including the stop codon. The ILD test indicated no significant incongruence between the two genes, with a *P* value of 0.654. In addition, separate MP analyses of both fragments produced trees with generally similar topologies (not shown).

As is typical for the mitochondrial genome (e.g. Desjardins & Morais, 1990; Doadrio, Carmona & Machordom, 2002; de Queiroz, Lawson & Lemos–Espinal, 2002; Nagy *et al.*, 2004; Guicking *et al.*, 2006), strong biases against guanidine on the light strand were observed. The average abundances observed on the light strand were: T, 28.1%; C, 29.9%; A, 27.7%; G, 14.3%. Therefore it may be inferred that the sequences represent the functional gene rather than nuclear pseudogenes (Zhang & Hewitt, 1996; Bensasson *et al.*, 2001; Guicking, 2004). The results of graphical saturation tests indicated no saturation effect for the combined data, either for all changes taken together, or for the first and second codon positions separately. Statistical tests based on the measurement introduced by Xia *et al.* (2003) resulted in a significantly smaller substitution saturation index (I_{ss}) than the critical value of I_{ss} ($I_{ss.c}$), at which the sequences will begin to fail to recover the true tree, for all three codon positions, thereby justifying the inclusion of all positions in the analyses. The slopes of Figure 2 also point to the strength of the sequence data.

PHYLOGENETIC RECONSTRUCTIONS

The phylogenetic reconstructions with MP, ML, and BI resulted in very similar branching patterns and topologies. Particularly, all of the major relationships were the same on the ML and BI trees. However, in the MP tree there was one difference concerning locality 13, in which the sister relationship between this clade and specimens of locality 5 were not recovered in the BI and ML trees (Fig. 3). Equally weighted parsimony analysis produced 200 most-parsimonious trees (not shown) with a length of 1773 steps (consistency index $CI = 0.5338$ and retention index $RI = 0.9270$). The trees obtained with three independent runs by BI were almost identical: one of these trees is shown in Figure 3. In addition, the ML analysis using the (GTR +I + G) model was topologically very similar to the Bayesian tree (Figs 3, 4), with very slight differences in the resolution of the terminal clades.

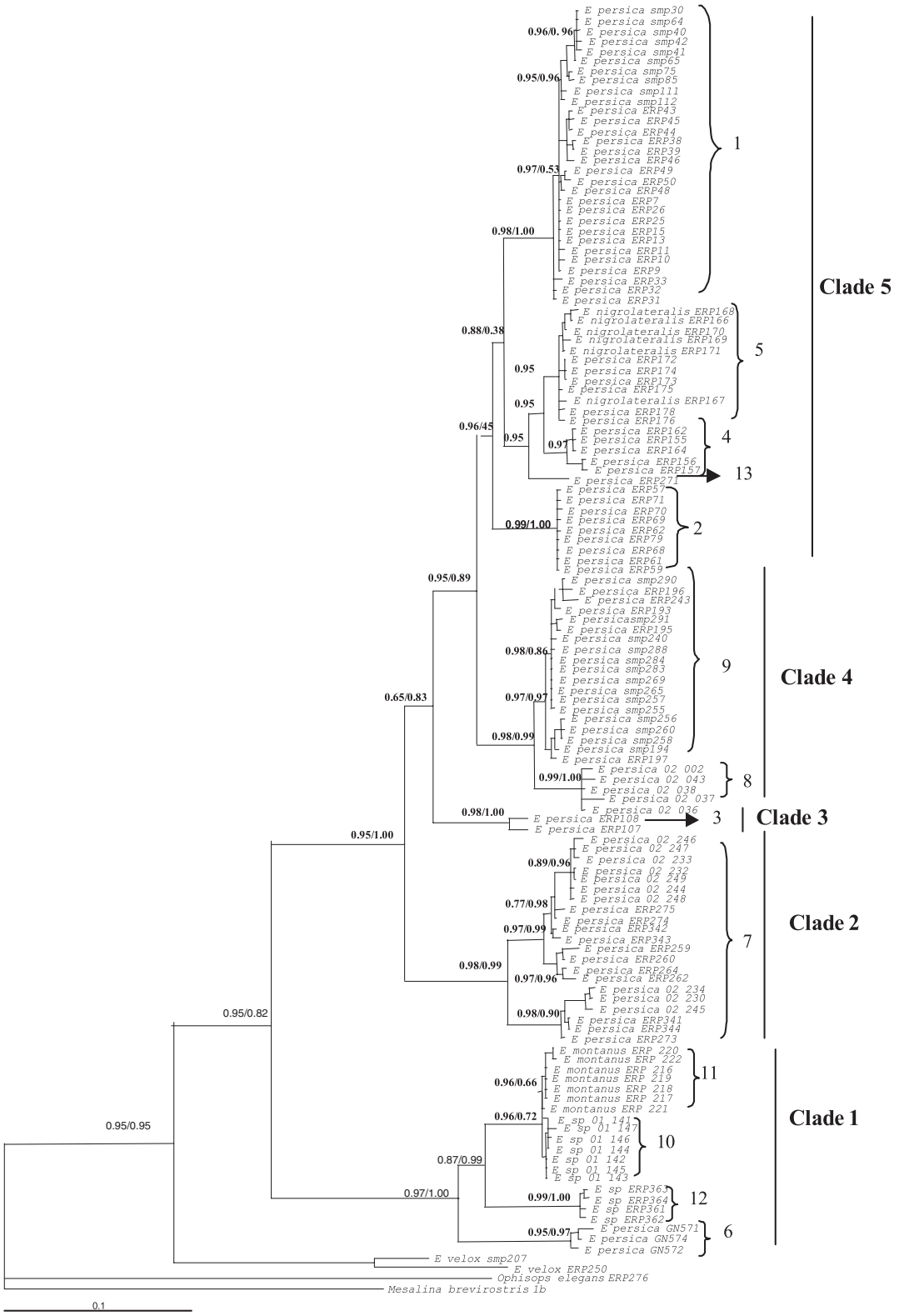

Fig. 3. Bayesian inference phylogram (GTR + I + G model) based on 1533 base pairs of the cytochrome *b* and *12S* sequence data set. The numbers next to the nodes are clade credibility values, from the Bayesian analysis, followed by maximum-parsimony bootstrap values (1000 replicates), and those next to the curved brackets indicate the localities in Figure 1.

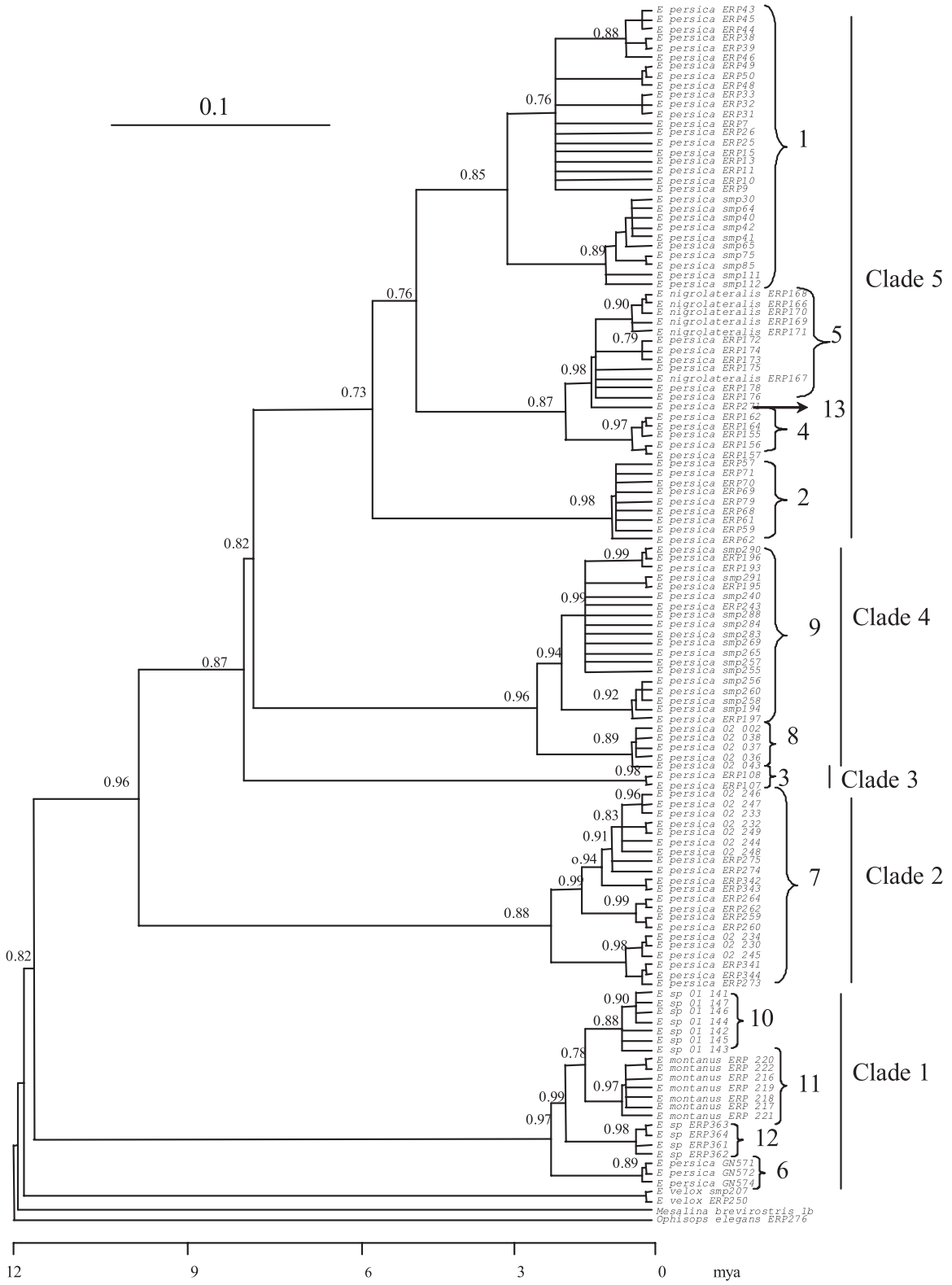

Fig. 4. The maximum-likelihood (ML) chronogram for the evolution of the *Eremias persica* complex of the Iranian plateau. The time scale was calibrated based on palaeogeographical evidence (see the text for details). The time bar represents the approximate time of past branching events in millions of years before the present. The numbers indicate the ML bootstrap values (200 replicates).

The likelihood ratio test did not reject the null hypothesis of a homogeneous clock-like rate of the data set. Comparison of the chronogram and phylogram by this test did not yield significant differences in the likelihood of these trees, suggesting that the error introduced by rate heterogeneity is not great. The log-likelihood value of the ML tree ($ln = 4961.78397$) was compared with that of the same tree constructed under the molecular-clock assumption ($ln = 4973.78653$); therefore, the likelihood ratio test statistic is $LR = 24$, $P < 0.05$. This suggests that we can probably use the genetic distance between populations inhabiting different geographical regions, in conjunction with the geological information about the age of the events that are responsible for the separation of the regions, in order to estimate a local rate of evolution for *Eremias* species. Additionally, the relative rate test performed with PHYLTEST 2.0 (Kumar, 1996) resulted in a relative rate Z statistic of $Z = 0.3916$, indicating that the consistency of the mutation rate at the 5% level is not rejected for our data.

Calculation of a molecular clock-enforced tree based on the sequence data gave two equally good trees, differing only slightly in a few terminal branch lengths (one of the trees is shown in Fig. 4). The calibration of this tree assumed the split between the western clade of *Eremias* inhabiting the highlands of the Zagros Mountains and all eastern clades to have occurred about 10 Mya. Using these calibrations, the divergence rate for the combined data was estimated at 1.6% per million years among the lineages. This value agrees with the reported rates for lacertids in the mitochondrial genome (Maca–Meyer *et al.*, 2003; Carranza, Arnold & Amat, 2004).

Referring to the distribution range (Fig. 1) and considering the trees obtained by MP and BI, five major assemblages could be easily distinguished within the phylogeny of the *E. persica* complex.

Clade 1: the Western clade

A basal dichotomy in the tree separates a clade including all of the investigated populations found along the Zagros Mountains in the western part of the Iranian plateau, including *E. montanus*, *Eremias* sp. of the south-west Caspian Sea area, *Eremias* sp. of the South Hamadan, and *E. persica* from the foothills of the central Zagros Mountains in Isfehan province (localities 6, 10, 11, and 12). The clade is well resolved, with high bootstrap and posterior probability support (100 and 97%, respectively). Relationships within the clade are also resolved. Four monophyletic subclades with relatively high genetic distances among any pairs, except for *E. montanus* and *Eremias* sp. of locality 10, are discernable (see Table 1).

Clade 2: the Tehran clade

This association contains populations of south-eastern and south-western Tehran (localities 7a and b). They form a strictly monophyletic group with high statistical support (bootstrap and Bayesian support of 99 and 98%, respectively). The 2.4% uncorrected genetic divergence indicates a high degree of intrapopulation variations within this assemblage (Table 1). It is also noteworthy that six of the 16 examined individuals showed a C → T substitution in 36 particular sites in the amplified fragments. This was the fixed difference that we observed in our data set, and which can have particular biological meanings (see the Discussion). The dichotomy separating this assemblage into two subunits is highly resolved (see Figs 3, 4). In fact, it is one of the most heterogeneous clades among all populations of the *E. persica* complex.

Clade 3: the Zabol clade (extreme eastern clade)

The furthest east population of *E. persica* in this study (locality 3) represents an easily discernable clade, with high support values (89% bootstrap and 95% posterior probability), and significant genetic divergence from any other clade (Table 2). It is separated from clades 4 and 5 by a short internode.

Clade 4: the north-eastern clade

This clade includes specimens from the north-east of the Iranian plateau up to southern Turkmenistan, along with those sampled from the rain-shadow deserts of the south-eastern Elburz Mountains (localities 8, 9a, and b). The clade contains three subunits, corresponding to a latitude gradient from the margin of the Dasht-e-Kavir (locality 8) up to southern Turkmenistan (locality 9b). An uncorrected p-distance of 3.8% between the furthest subunits indicates a high degree of genetic variation within the clade.

Clade 5: the eastern clade

This is the most numerous, heterogeneous, and widespread clade in this phylogeny. Although the posterior probability of 96% indicates good support for the major clade as a monophyletic unit, the bootstrap value, however, is relatively poor (45%). It consists of several monophyletic subunits that are geographically distributed across the eastern portion of the Iranian plateau. The relationships among the subunits are resolved, but this is not strictly true of the clade as a whole, because of the low support from the parsimony bootstrap value (Fig. 3). Although two monophyletic groups within the central Khorasan subunit are observed, the genetic distance separating them is very low (0.09%). The Central Kerman clade (locality 4) forms the sister taxon for *E. nigrolateralis,* and its sympatric *E. persica*, occurring in the wide

Table. 1. Uncorrected genetic divergence (p-distance) within populations (A) and between populations (B), derived from the combined data set

A

Population number	p-distance
1	0.009
2	0.001
3	0.014
4	0.010
5	0.002
6	0.019
7	0.024
8	0.005
9	0.020
10	0.001
12	0.001
13	0.000
Eremias nigrolateralis	0.003
Eremias montanus	0.001

B

	Oe	Mb	Ev	Ep1	Ep2	Ep3	Ep4	Ep5	En5	Ep6	Ep7	Ep8	Ep9	Esp10	Em11	Esp12	Ep13
Oe																	
Mb	0.203																
EV	0.221	0.201															
Ep1	0.209	0.198	0.155														
Ep2	0.214	0.197	0.165	0.053													
Ep3	0.210	0.204	0.161	0.071	0.078												
Ep4	0.211	0.195	0.165	0.050	0.053	0.077											
Ep5	0.214	0.200	0.170	0.053	0.055	0.076	0.030										
En5	0.215	0.201	0.171	0.054	0.056	0.077	0.031	0.003									
Ep6	0.219	0.197	0.168	0.146	0.152	0.153	0.151	0.155	0.156								
Ep7	0.214	0.198	0.160	0.095	0.094	0.095	0.092	0.095	0.096	0.159							
Ep8	0.215	0.199	0.154	0.066	0.071	0.089	0.071	0.077	0.078	0.146	0.099						
Ep9	0.214	0.197	0.152	0.059	0.066	0.084	0.064	0.069	0.071	0.149	0.095	0.038					
Esp10	0.217	0.201	0.164	0.142	0.154	0.151	0.151	0.153	0.153	0.081	0.149	0.145	0.141				
Em11	0.221	0.202	0.166	0.147	0.157	0.157	0.155	0.157	0.158	0.084	0.152	0.148	0.146	0.010			
Esp12	0.228	0.204	0.175	0.144	0.149	0.150	0.147	0.151	0.151	0.088	0.152	0.149	0.148	0.061	0.064		
Ep13	0.210	0.199	0.165	0.055	0.058	0.077	0.041	0.025	0.026	0.148	0.091	0.077	0.067	0.144	0.148	0.146	

Abbreviations: Oe, *Ophisops elegans*; Mb, *Mesalina brevirostris*; Ev, *Eremias velox*; En, *Eremias nigrolateralis*; Em, *Eremias montanus*; Esp, *Eremias* sp.; Ep, *Eremias persica*. Numbers (1–13) correspond to the localities in Figure 1.

Table 2. Within-clade (A) and interclade (B) k2p distances (±SE) for interclade comparisons, derived from the combined data set

A

Clade 1	0.064
Clade 2	0.025
Clade 3	0.014
Clade 4	0.052
Clade 5	0.040

B

	1	2	3	4	5
1					
2	0.168 (0.010)				
3	0.169 (0.010)	0.104 (0.008)			
4	0.158 (0.009)	0.103 (0.007)	0.099 (0.007)		
5	0.161 (0.009)	0.103 (0.007)	0.080 (0.006)	0.078 (0.005)	

valleys of north Fars and south-east Isfehan, in south-central Iran (locality 5). No significant genetic divergence was observed between them. The monophyly of *E. nigrolateralis* at the specific level is not supported by this study. In all analyses *E. nigrolateralis* is paraphyletic with respect to *E. persica* from the same general area. Interestingly, an isolated population found in the hot and dry deserts of the extreme north of Isfehan province (locality 13), on the margin of the Salt Lake (Namak Lake), forms the sister taxon for *E. nigrolateralis*, and its associated *E. persica*, with strong statistical support (95% posterior probability and 95% bootstrap values). The most homogeneous subunit of clade 5 is that of south Khorasan and north Sistan (locality 2).

Genetic diversity

The sequence divergences (uncorrected p-distance) within and among populations are recorded in Table 1. The within-populations sequence divergence ranged from 0.001% in the *Eremias* sp. of the south-west Caspian Sea area to 2.4% in *E. persica* of the Tehran clade. The among-populations divergence ranged from 15.9% (between the South Isfehan and Tehran clades) to 0.010% (between *E. montanus* and the south Hamadan clade). Table 2 presents the genetic distances (Kimura-2 corrected distances) within and among the major clades. The lowest intraclade diversity was scored in clade 2 (1.4%), and the highest intraclade diversity was scored in clade 1 (6.4%). High values of genetic divergence were also obtained between clade 1 and the other clades (with a genetic divergence at least 15.8% with clade 4). A genetic distance of 7.8% between clades 4 and 5 was the lowest interclade divergence (Table 2).

DISCUSSION

The relationships among the populations of the *E. persica* complex are well resolved, with generally high statistical support, indicating the robustness of the recovered phylogeny, and the efficiency of the marker genes in recovering lower level phylogenies, and support the findings of a number of recent studies (Maca–Meyer *et al.*, 2003; Carranza *et al.*, 2004; Carranza & Arnold, 2006; but see Corneli & Ward, 2000; de Queiroz *et al.*, 2002).

According to our results, especially given the observed level of divergence and considering the morphological features of the populations studied, five major assemblages within the *E. persica* complex are easily discernible. All of the individuals examined are unambiguously attributed to one of these major clades. The DNA sequences have recovered the phylogenetic relationships on most of the branches with remarkable levels of support (Fig. 3). These clades relate well to the geographic regions of the Iranian plateau.

The western clade (clade 1) is genetically, morphologically, and ecologically well separated from all of the other clades. A high degree of genetic divergence and an apparent difference in morphological characteristics (unpubl. data) on the one hand, and the unique habitats as highland- and mountain-inhabiting lizards on the other, provide robust evidence to separate this clade from the others. Relationships within this clade are established and correspond well with the geographic isolation. The subunits of the clade are differentiated, and are both genetically and morphologically recognizable. *Eremias montanus* (locality 11) constitutes a highly substantiated monophyletic clade; however, the

genetic divergence between this unit and *Eremias* sp. of south-west Hamadan (locality 10) is very low (0.01%). A recent comparative study of both populations (N. Rastegar-Pouyani, pers. comm., December 2005) showed no significant morphological differences between these two units. Therefore, the *Eremias* sp. of south-west Hamadan can be considered as conspecific with *E. montanus*. They merely present a newly discovered population of this taxon approximately 200 km eastwards from the type locality. The *Eremias* sp. of the south-west Caspian Sea area and those of south-west Isfehan (localities 12 and 6, respectively) are easily discernible genetically and morphologically. The Tehran clade (clade 2) is a complicated group, which is genetically highly differentiated with a unique colour pattern and high degree of intrapopulation heterogeneity. The 36 C → T substitutions in six individuals (out of the 16 specimens examined) of this population, at fixed positions along the fragments analysed, may indicate that this population come from two distinct evolutionary lineages. Thus, this clade may have resulted from an introgression event. Both geographically and morphologically, particularly in colour pattern, they clearly show an intermediate form between the highland-inhabiting population of south-west Hamadan (the *Eremias* sp. of locality 10 that, according to this study, are conspecific with *E. montanus*; see below) and the typical *E. persica* of Isfehan province (localities 5 and 13). It can also be assumed that this pattern indicates the degree of gene flow between the above populations, with a clinal variation. However, we failed to find the taxa in this hypothetical intermediate or possibly 'hybrid' zone. Further investigation is necessary to test whether they are a hybrid or a mixed species (which would be indicative of gene flow between the western and eastern clades). [Such a study is in progress: screening the genome, using intersequence-specific repeat (ISSR)-PCR, with microsatellite primers.] However, regardless the outcome of such investigations, the unit is a resolved and strictly monophyletic clade. The relatively great genetic divergence (9.1% with the closest relatives) and outstanding morphological peculiarities provide robust evidence for the clade being a distinguished cluster from all other assemblages, and make it possible to revise the taxonomic status of the group.

Our data suggest a different origin for the populations of the southern and western margins of the Namak Lake (localities 7 and 13). Whereas the affinity of the population of locality 13 with the southern clades is not in doubt, this is not the case for the population of locality 7. This pattern is possibly a result of the Salt Lake (Namak Lake), and its vast, hot, and arid surrounding area acting as a geographical barrier. This barrier seemingly prevented the further distribution of the western populations towards the east, and vice versa. Studying other groups of reptiles or small mammals inhabiting both sides of the hypothetical barrier can test this hypothesis. However, in spite of a short geographical distance (approximately 70 km), the present study strongly suggests different affinities and a long term of isolation for these populations. Apparently, this is also the case for the Zabol clade (clade 3). Geographically this area is relatively close to south Khorasan, but the substantial genetic distance between this clade and the rest indicates a long time of isolation. Although the extraordinary homogeneity among the species of clade 3 can be attributed to the small size of the samples examined, severe isolation of the clade within a small area can also be partially responsible. In fact, the area representing the eastern boundary of the distribution range of *E. persica* is almost isolated from all other habitats of the mainland of Iran by the vast, muddy, and sandy basin of Hamun, which is impossible to cross for reptiles (Fig. 1). According to Szczerbak (1974) and Anderson (1999), this clade would have expanded into south-western Afghanistan and north-west Pakistan, in the form of some isolated populations. Although the affinity of Afghan/Pakistani populations with the Zabol clade has been asserted (Szczerbak, 1974; Leviton *et al.*, 1992; Anderson, 1999), it remains putative and uncertain in our study because of a lack of material. To resolve the relationships among these clades, further sampling within the mainland of Afghanistan and Balutchistan, Pakistan, is desirable, including all Afghan and Pakistani populations, as well as *Eremias afghanistanica* Böhme & Scerbak, 1991, which, based on morphological and ecological features (Böhme & Szczerbak, 1991), intuitively should belong to this clade. Such a study will most likely result in a clear-cut picture of the relationships and taxonomic status of the extreme eastern populations of the *E. persica* complex.

The north-eastern clade (clade 4) ranges across an enormous area. Three resolved groups are discernible within the clade, corresponding to the geographic latitudinal gradient from the northern margin of the Central Desert (Dasht-e-Kavir) up to southern Turkmenistan. The subunits are geographically distant (approximately 200 km apart), but no outstanding barrier can be defined as isolating them. The assemblage as a whole is, to a great extent, isolated from all other populations. Further dispersal of the clade towards the south seems to have been prevented by the gravel desert of Dasht-e-Kavir, which is followed eastwards by the Dasht-e-Namak desert. This association forms a continuum of enormous, salty, and gravel desert, beginning from south-east Tehran and stretching to eastern parts of Khorasan province, close to the Iran–Afghan border. It forms a vast,

west–east barrier, which limits the north–south dispersal of terrestrial animals in the eastern portion of the Iranian plateau (Fig. 1). The Elburz Mountains form the other barrier, preventing the further dispersal of the clade westwards.

The molecular similarity among the subunits of the fifth clade possibly reflects a very recent divergence. The southern Khorasan population is limited westwards to the eastern margin of the other geographic barrier in south-east Iran, the Dasht-e-Lut desert, with a south–north orientation. The desert extends for approximately 450 km (Fig. 1), and is impossible to cross for any terrestrial animal. In spite of this, the materials from Kerman province (locality 4), nearly 400 km further south, are closely related to the south Khorasan clade. The southern part of the Sistan basin seems to be the only bridge connecting these clades, but as yet no *Eremias* has been reported from this area. The relationships of the north Fars and sout-heast Isfehan provinces (locality 5) are highly resolved (Figs 3, 4). The former area is reported as the terra typica for *E. nigrolateralis* (Rastegar-Pouyani & Nilson, 1997). Whereas it has been asserted that morphologically this species is distinguished from *E. persica* of the same general area (Rastegar-Pouyani & Nilson, 1997), no molecular evidence corroborating this separation was observed in our study. *Eremias nigrolateralis* forms a monophyletic clade, along with *E. persica* of the area, and the interpopulation sequence divergence observed is very low (Table 1). Furthermore, seven specimens of *E. nigrolateralis* collected from the type locality were morphologically compared with all other populations of *E. persica* belonging to the eastern clades (clades 4, 5). No considerable morphological evidence was found to support the separation of *E. nigrolateralis* from *E. persica*. We emphasize that the most important morphological peculiarity of *E. nigrolateralis* was the colour pattern frequently seen among the examined specimens of clades 4 and 5. However, it should not be an indication of a further expansion of *E. nigrolateralis* east and northwards, because in all investigated populations no molecular evidence was observed to support this assumption. In contrast, in many cases sequences derived from both of the colour morphs, within the same population, were identical, or nearly so. Thus, our data strongly suggest that *E. nigrolateralis* is conspecific with *E. persica* of the same general area. Possibly, misidentification has occurred because of the lack of available material from eastern clades of the *E. persica* group.

The south and central Khorasan clades are from the most homogeneous units (localities 1 and 2). Their distribution area is confined between the mountain systems of the Iran–Afghan border eastwards, and the Dasht-e-Kavir and Dasht-e-Lut deserts west and northwards (Fig. 1). No considerable barrier isolating these clades from each other can be defined. They are also morphologically the most similar clades. However, the considerable genetic divergence between them (5.3%) is possibly just an indication of the presence of clinal variations. The contiguous populations show some level of variation in genetic and general morphology.

EVOLUTIONARY HISTORY AND BIOGEOGRAPHICAL IMPLICATIONS

There are many ambiguities in the application of any molecular clock (Avise *et al.*, 1992; Easteal, Collet & Betty, 1995; Arbogast *et al.*, 2002), and most phylogeographical scenarios can provide only approximations of divergence times. By taking into account the evolutionary rate estimate for the mitochondrial DNA in lacertids (Guillaume, 1989; Böhme & Corti, 1993; Carranza *et al.*, 2000, 2004; Maca–Meyer *et al.*, 2003), or among other reptiles (Mindell & Honeycutt, 1990; Hillis & Dixon, 1991; Carranza *et al.*, 2000, 2001, 2002; Carranza & Arnold, 2003; Nagy *et al.*, 2004; Guicking *et al.*, 2006), and considering the palaeogeographic evidence with which the molecular clock was calibrated, we assume that the genetic distance between the highland-inhabiting populations of central and western Zagros and the desert-dwelling populations of the eastern clades reflects independent evolution since the middle Miocene (some 11–12 Mya), with an evolutionary rate of 1.6% per million years among the lineages, which generally agrees with the other estimations for the same genes within the family Lacertidae (Brehm *et al.*, 2002; Min–Lin, Chen & Lue, 2002; Maca–Meyer *et al.*, 2003; Carranza *et al.*, 2004; Harris, Batista & Carretero, 2004).

The phylogeny proposed here exhibits broad geographical regularity that corresponds with the geological events leading to the present topographic pattern of the Iranian plateau. The mountain systems of the Iranian plateau have inevitably greatly influenced radiation, isolation, and differentiation, and the subsequent evolution of the herpetofauna occurring on the Iranian plateau. The uplifting of these mountain systems was caused by a collision of the Indian and Arabian plates with Eurasia during the middle Miocene to middle Pliocene, 12–3 Mya (Sborshchikov, Savostin & Zonenshan, 1981; Girdler, 1984; Abdrakhmatove *et al.*, 1996; Macey *et al.*, 1998, 2000a, b). Subsequently, the Miocene and Pliocene mountain uplifts caused the central and eastern portion of the Iranian plateau to sink. This area later gradually became arid, and formed the flat gravel and sandy desert of the Dasht-e-Kavir and Dasht-e-Lut. In the

north-eastern portion of the Iranian plateau, the Dasht-e-Kavir connects with the Sistan and Helmand basins of the extreme eastern Iran, and provides a low elevation barrier of flat gravel and sandy desert (Macey *et al.*, 1998).

Based on the assumed molecular clock, the ancestor of the *E. persica* complex underwent the first fragmentation some 9–11 Mya (Fig. 4), when the Zagros Mountain system began to uplift as a result of the Arabian plate impinging on Eurasia. The western Zagros is the frontal collision point. This fragmentation produced two lineages, which are indicated in the trees as clade 1 and clades 2–5. The former lineage has subsequently been adapted and distributed along the rugged areas of the western Iranian plateau. Further splitting events in the late Pliocene (2–3 Mya) fragmented this lineage into three distinct assemblages along the foothills and highlands of the Zagros Mountain chain. This phenomenon would have been caused by the intensive uplifting of the Zagros and Caucasus mountains in the Pliocene (Girdler, 1984; Macey *et al.*, 1998). Today, this lineage is represented in our phylogeny by the subunits of clade 1 found along the Zagros Mountains from southern Isfehan up to the south-west Caspian Sea area. Further investigations along the poorly studied mountainous area of north-western Iran, up to Turkey and Azerbaijan, will record more populations of this lineage. The break between clade 2 and clades 3–5 reflects another split that might have taken place around 6–8 Mya, when folding on the margins of the Iranian plates occurred. This tectonic period seems to have been a pause in the north–south movement, and was overtaken by east–west compression (Macey *et al.*, 2000a). The sunken internal basins of the Iranian plateau began to emerge and gradually became arid in the middle Pliocene. Subsequently, the eastern clade began to disperse and fragment into the emerged areas. The drying out of the basins roughly coincided with the beginning of the Pleistocene. The genetic divergence among the eastern clades (clades 3–5) indicates the recent isolation and diversification of these units. The earliest split separated the extreme eastern clade of Zabol (clade 3) in the late Miocene, some 6–7 Mya. Further divergence isolated clades 4 and 5. These isolations would have occurred through the progressive drying out of the Sistan and Helmand basins, which led to the flat gravel and sandy desert region of Dasht-e-Lut, and ultimately provided a barrier preventing gene flow between western and eastern populations of the Sistan basin. The eastern populations subsequently dispersed across the lowlands and basins of Afghanistan and Pakistan. Clade 5 was separated in the late Pliocene, and spread across the wide valleys, open plains, and steppes of the south-east, east, and north-east of the Iranian plateau. The flat gravel and sandy deserts of Dasht-e-Lut and Dasht-e-Namak have largely contributed to the isolation of this clade. It is notable that geographically they are not separated as completely isolated populations. In particular, no significant geographical barrier can be defined between the southern and central Khorasan clades. This is also the case for the other subclades (localities 4, 5, and 2). The sister-group relationship between populations of south central Iran (localities 4 and 5) with those in extreme north Isfehan (locality 13), on the southern margin of the Salt Lake, indicates the rigorous role of the Salt Lake and central desert of Iran (Dasht-e-Kavir) as a geographical barrier to the distribution of reptiles. If a clade has two or more lineages in a restricted area, it is most parsimonious to assume that it has been in the region concerned since at least the time the lineages first diverged. This case increases in strength with the number of lineages involved (Carranza *et al.*, 2004). On this basis, clades 3, 4, and 5 may have been in the south-central and eastern portion of the Iranian plateau at least since these units diverged at 6–4 Mya.

The present pattern of isolation and distribution of the eastern clades may be indicative of clinal variation. This kind of variation is paramount in studying wide-ranging taxa such as the *E. persica* complex. A large part of the range of the species, especially the central parts, is occupied by a series of essentially contiguous populations. Variation in such a population continuum is essentially clinal, and this could be the case, with one of the eastern clades as the central core for all other clades. The clinal hypothesis is supported by smooth changes in scale count and general morphology among the eastern clades. Thus, we can explain the present patterns of morphological, genetic, and geographical variation among the eastern assemblages in the light of clinal variation.

The estimated divergence times for the *E. persica* complex generally agree with our present knowledge on the origin and fragmentation of the genus *Eremias* (Arnold, 1989; Fu, 1998, 2000; Arnold *et al.*, 2007; Mayer & Pavlicev, 2007). According to Arnold (1989), and which is generally accepted in Arnold *et al.* (2007), the ancestor of Ethiopian lacertids entered Africa via Arabia during the Miocene, when the African–Arabian plate made more or less permanent contact with western Eurasia, some 15–18 Mya. Considerably later, the advanced xeric forms of lacertids (*Acanthodactylus*, *Ophisops*, *Mesalina*, and *Eremias*) were derived from an Afrotropical ancestor, and spread north into the arid region of Eurasia. The divergence of the ancestor of *Eremias*, *Mesalina*, and *Ophisops*, as presented here, is estimated to have occurred around 13–11 Mya. This is highly concordant with the time estimated by Mayer & Pavlicev

(2007). The short, deep internodes in the tree (Figs 3, 4) indicate that the ancestor of *Eremias* has undergone a rapid cladogenesis soon after the first fragmentation from the common ancestor of *Mesalina* and *Ophisops*.

TAXONOMIC IMPLICATIONS

Although sequence divergence does not give a direct indication of the taxonomic status of a population, it can be a source of useful information in cases when the taxonomy based on morphology and ecological criteria appears doubtful. On this basis, the phylogeny information presented here and the mitochondrial sequences make it clear that a revision of the taxonomic status of the *E. persica* complex is essential. Eight of the geographic units recovered in this study show a substantial divergence from each other (see Table 1). We emphasize here that the level of divergence scored between the populations currently attributed to the same species are, in some cases, of the same or even larger order of magnitude as those scored between different species. Compared with other taxa of lower vertebrates, the *E. persica* complex shows a high level of divergence. Moritz *et al.* (1989) reported that the greatest intraspecific mtDNA divergence among *Cnemidophorus* was 6.7%. However, lizards from populations in close geographic proximity often show less than 1% divergence of mtDNA, which is in the range for terrestrial vertebrates (Guicking, 2004; Carranza & Arnold, 2006).

Except for *E. montanus* and the *Eremias* sp. of locality 10, the genetic distances among subunits of clade 1 are high (at least 6.1% in the combined data set, and 7.5% in cyt *b* sequences; not shown). In addition, these forms are morphologically discernible; therefore, three species within this major clade are well established. The second clade from locality 7 is morphologically and genetically identifiable with all other clades (p-distances from the closest relatives are 9.1% in the combined data set and 9.9% in cyt *b* sequences; not shown). We therefore suggest that the recognition of this clade as *E. persica* be discontinued. A distinct species rank for this clade is needed.

Within the eastern clades (clades 3–5), the extreme eastern population of Zabol (locality 3) is distinguishable from the others either morphologically or genetically (with a p-distance of 7.1% with the closest relatives). We thus suggest a species rank for this group too. The situation within clade 4, and particularly clade 5 and its three subclades, is more complicated. The fact that several genetic units are discernable within these clades should not be used as grounds for partitioning them into several separate species. Morphologically, the group is well defined. The populations of localities 1, 2, 4, 5, 8, and 9 are easily recognized as belonging to the same morphospecies, but this is not strictly true of its subunits, which are difficult to define morphologically, and therefore we suggest a single species name for all these units. However, The Semnan population (locality 8) shows a few peculiarities in general morphology and pattern. Bearing this in mind, and considering the level of genetic divergence between this population and the south Isfehan clade, locality 5 (the type population, see below), the classification of this lineage as a distinct subspecies of the typical *E. persica* is recommended.

The type locality for *E. persica* is reported to be near Isfehan. Although the exact locality is not clear, long-established descriptions of this taxon (Terentjev & Chernove, 1965; Szczerbak, 1974; Anderson, 1999) correspond well with the populations of the south-east Isfehan and north Fars provinces (locality 5): we therefore consider this unit as the type population for *E. persica*. As noted, our phylogeny provided no evidence corroborating species or subspecies rank for the recently described species *E. nigrolateralis*. Its phylogenetic affinity as belonging to the type population of *E. persica* is well resolved. Moreover, the morphological features that have been used to distinguish *E. nigrolateralis* as a distinct species from *E. persica* are now questioned. We thus suggest that the recognition of *E. nigrolateralis* as a distinct species from *E. persica* be discontinued. It should instead be regarded as belonging to the nominal subspecies of *E. persica*.

In short, raising four clades of the *E. persica* complex to species rank (localities 3, 6, 7, and 12), two to subspecies rank (localities 8 and 5), and recognizing *E. nigrolateralis* as conspecific from the typical *E. persica*, are recommended by the present study.

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REFERENCES

Abdrakhmatove K, Aldazhanove Y, Hager SA, Hamburger BH, Herring MW, Kalabaev TA, Makarov KB, Molnar VI, Panasyuk P, Prilepin SV, Reilinger MT, Sadybakasove RE, Souter IS, Trapeznikov BJ, Tsurkov YA, Zubovich AV. 1996. Relatively recent construction of the Tien Shan inferred from GPS measurements of present day crustal deformation rates. *Nature* **384:** 450–453.

Anderson SC. 1999. *The lizards of Iran*, Vol. 15. Contributions to Herpetology. Ithaca, NY: Society for the Study of Amphibians and Reptiles.

Arbogast BS, Edwards SV, Wakeley J, Beerli P, Slowinski JB. 2002. Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annual Review of Ecology and Systematics* **33:** 707–740.

Arnold EN. 1973. Relationships of the Palaearctic lizards assigned to the genera Lacerta, Algyroides and Psammodromus (Reptilia, Lacertidae). *Bulletin of the British Museum (Natural History) Zoology* **25:** 291–366.

Arnold EN. 1986. The hemipenis of lacertid lizards (Reptilia: Lacertidae): structure, variation and systematic implications. *Journal of Natural History* **20:** 1221–1257.

Arnold EN. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old–World family of lizards derived from morphology. *Bulletin of the British Museum (Natural History) Zoology* **55:** 209–257.

Arnold EN, Arribas O, Carranza S. 2007. Systematics of the palaearctic and oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with description of eight new genera. *Zootaxa* **1430:** 1–86.

Avise JC, Bowen BW, Lamb T, Meylan AB, Bermingham E. 1992. Mitochondrial DNA evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in the Testudines. *Molecular Biology and Evolution* **9:** 457–473.

Bensasson D, Zhang DX, Hart DL, Hewitt GM. 2001. Mitochondrial pseudogenes: evolution's misplaced witnesses. *Trends in Ecology and Evolution* **16:** 314–321.

Brehm A, Jesus J, Spinola H, Alvez C, Vicente L, Harris DJ. 2002. Phylogeography of the Maderian endemic lizard Lacerta dugesii inferred from Mitochondrial DNA sequences. *Molecular phylogenetics and Evolution* **26:** 222–230.

Böhme W, Corti C. 1993. Zoogeography of the lacertid lizards of the western Mediterranean basin. In: Valakos ED, Böhme W, Perez–Mellado V, Maragou P, eds. *Lacertas of the Mediterranean*. Athens: Helenic Zoological Society, 17–33.

Böhme W, Szczerbak NN. 1991. Ein neuer Wüstenrenner aus dem Hochland Afghanistans, *Eremias (Eremias) afghanistanica* sp.n. (Reptilia: Sauria: Lacertidae). *Die Eidechse, Bonn/Bremen* **4:** 26–28.

Carranza S, Arnold EN. 2003. Investigating the origin of transoceanic distributions: mtDNA shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. *Systematics and Biodiversity* **1:** 275–282.

Carranza S, Arnold EN. 2006. Systematics, biogeography and evolution of Hemidactylus geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **38:** 531–545.

Carranza S, Arnold EN, Mateo JA, L'opez–Jurado LF. 2000. Long–distance colonization and radiation in gekkonid lizards, Tarentola (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society of London Series B Biological Sciences* **267:** 637–649.

Carranza S, Arnold EN, Mateo JA, L'opez–Jurado LF. 2001. Parallel gigantism and complex colonization patterns in Cape Verde scincid lizards Mabuya and Macroscincus (Reptilia: Scincidae) revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society of London Series B Biological Sciences* **268:** 1595–1603.

Carranza S, Arnold EN, Mateo JA, Geniez P. 2002. Relationships and evolution of the North African geckos, Geckonia and Tarentola (Reptilia: Gekkonidae), based on mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* **23:** 244–256.

Carranza S, Arnold EN, Amat F. 2004. DNA phylogeny of Lacerta (Iberolacerta) and other lacertinae lizards (Reptilia: Lacertidae): did competition cause long–term mountain restriction? *Systematic Biodiversity* **2:** 57–77.

Corneli PS, Ward IH. 2000. Mitochondrial genes and Mammalian phylogenies: increasing the reliability of branch length estimation. *Molecular Phylogenetics and Evolution* **17:** 224–234.

Cruzan MB, Templeton AR. 2000. Paleoecology and coalescence: phylogeographic analysis of hypotheses from the fossil record. *Trends in Ecology and Evolution* **15:** 491–496.

Cunningham CW. 1997. Can three incongruence tests predict when data should be combined? *Molecular Biology and Evolution* **14:** 733–740.

Desjardins P, Morais R. 1990. Sequence and gene organization of the chicken mitochondrial genome. *Journal of Molecular Biology* **212:** 599–634.

Doadrio I, Carmona JA, Machordom A. 2002. Haplotype diversity and phylogenetic relationships among the Iberian barbels (*Barbus*, Cyprinidae) reveal two evolutionary lineages. *Journal of Heredity* **93:** 140–147.

Easteal S, Collet CC, Betty D. 1995. *The mammalian molecular clock*. Heidelberg: Springer-Verlag.

Farris JS, Kluge AG, Bult C. 1994. Testing significance of incongruence. *Cladistics* **10:** 315–319.

Felsenstein J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* **17:** 368–376.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39:** 783–791.

Fisher WB. 1968. *The land of Iran*, Vol. 1. The Cambridge history of Iran. Cambridge, England: Cambridge University Press.

Fritz U, Siroky P, Kami H, Wink M. 2005a. Environmentally caused dwarfism or a valid species—Is Testudo weissingeri Bour, 1996 a distinct evolutionary lineage? New evidence from mitochondrial and nuclear genomic markers. *Molecular Phylogenetics and Evolution* **37:** 389–401.

Fritz U, Fattizzo T, Guicking D, Tripepi S, Grazia Pennisi M, Lenk P, Joger U, Wink M. 2005b. A new cryptic species of pond turtle from southern Italy, the hottest spot in the range of the genus Emys (Reptilia, Testudines, Emydidae). *Zoologica Scripta* **34:** 351–371.

Fu J. 1998. Toward the phylogeny of the family Lacertidae: implications from mitochondrial DNA *12S* and 16S gene sequences (Reptilia: Squamata). *Molecular Phylogenetics and Evolution* **9:** 118–130.

Fu J. 2000. Towards the phylogeny of the family Lacertidae –

why 4708 base pairs of mtDNA sequences cannot draw the picture. *Biological Journal of the Linnean Society* **71:** 203–217.

Funk DJ, Omland KE. 2003. Species–Level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology and Systematics* **34:** 397–423.

Girdler RW. 1984. The evolution of the Gulf of Aden and Red Sea in space and time. *Dee Sea Research, Part A* **31:** 747–762.

Guicking D. 2004. Molecular phylogeography and evolution of western palearctic water snakes (genus Natrix, Reptilia). PhD thesis, Faculty of Life Science, University of Heidelberg, Germany.

Guicking D, Joger U, Wink M. 2002. Molecular phylogeography of the viperine snake (Natrix maura) and the Dice snake (Natrix tessellata): first results. *Biota* **3:** 49–59.

Guicking D, Lawson R, Joger U, Wink M. 2006. Evolution and phylogeny of the genus *Natrix* (Serpentes: Colubridae). *Biological Journal of the Linnean Society* **87:** 127–143.

Guillaume CP. 1989. Utilization de quelques techniques recentes non morphologiques en systematique et phylogenie des amphibians et des reptiles: quelques examples (2ieme partie). *Bulletin of Society of Herpetology, France* **50:** 19–42.

Hall TA. 1999. BioEdit: a user–friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41:** 95–98.

Harris DJ, Arnold EN, Thomas RH. 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proceedings of the Royal Society of London Series B Biological Sciences* **265:** 1939–1948.

Harris DJ, Batista V, Carretero MA. 2004. Assessment of genetic diversity within Acanthodactylus erythrurus (Reptilia: Lacertidae in Morocco and the Iberian Peninsula using mitochondrial DNA sequence data. *Amphibia–Reptilia* **25:** 227–232.

Hillis DM, Dixon RT. 1991. Ribosomal DNA: Molecular evolution and phylogenetic inference. *Quarterly Review of Biology* **66:** 411–453.

Huelsenbeck JP, Ronquist F. 2001. Mr Bayes: Bayesian inference of phylogenetic trees. *Bioinformatics Applications Note* **17:** 754–755.

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pabo S, Villablanca FX, Wilson AC. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the United States of America* **86:** 6196–6200.

Kumar S. 1996. *Phyltest: a program for phylogenetic hypothesis testing*. University Park, PA, USA: Institute of Molecular Evolutionary Genetics and Department of Biology. Pennsylvania State University.

Kumar SK, Nei M. 2004. MEGA3.1: integrated software for molecular evolutionary genetics analysis and sequence alignment. *Briefings in Bioinformatics* **5:** 150–163.

Lenk P, Fritz U, Joger U, Wink M. 1999. Mitochondrial phylogeography of the European pond turtle Emys orbicularis (Linnaeus 1758). *Molecular Ecology* **8:** 1911–1922.

Lenk P, Joger U, Wink M. 2001. Phylogenetic relationshi among European ratsnakes of the genus *Elaphe* Fitzinger based on mitochondrial DNA sequence comparsions. *Amphibia–Reptilia* **22:** 329–339.

Leviton AE, Anderson SC, Adler KK, Minton SA. 1992. *Handbook to middle east amphibian and reptiles*. Contribution to Herpetology. Oxford, OH: Society for study of Amphibians and Reptiles.

Maca–Meyer N, Carranza S, Rando JC, Arnold EN, Cabrera V. 2003. Status and relationships of the extinct giant Canary Island lizard Gallotia goliath (Reptilia: Lacertidae), assessed using ancient mitochondrial DNA from its mummified remain. *Biological Journal of the Linnean Society* **80:** 659–670.

Macey JR, Shulte JA, Ananjeva NB, Larson A, Rastegar-Pouyani N, Shamakove SM, Papenfuss TJ. 1998. Phylogenetic relationshi among agamid lizards of the *Laudakia caucasia* species group: testing the hypotheses of biogeographic fragmentation and an area caldogram for the Iranian Plateau. *Molecular Phylogenetics and Evolution* **10:** 118–131.

Macey JR, Shulte JA, Larson A, Ananjeva NB, Wang Y, Petiyagoda R, Rastegar-Pouyani N, Papenfuss TJ. 2000a. Evaluating trans tethys migration: an example using acrodont lizards phylogenetics. *Systematic Biology* **49:** 233–256.

Macey JR, Shulte JA, Kami HG, Ananjeva NB, Larson A, Papenfuss TJ. 2000b. Testing Hypothesis of vicariance in the agamid lizard Laudakia caucasia from the mountain rages on the northern Iranian Plateau. *Molecular Phylogenetic and Evolution* **14:** 479–483.

Mayer W, Benyr G. 1994. Albumin–Evolution und Phylogenese in der Familie Lacertidae (Reptilia: Sauria). *Annalen des Naturhistorischen Museums in Wien (Serie B)* **96:** 621–648.

Mayer W, Pavlicev M. 2007. Phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: convergent adaptation to arid habitats within the subfamily Eremiainae. *Molecular Phylogenetics and Evolution* **44:** 1155–1163.

Mindell D, Honeycutt RL. 1990. Ribosomal RNA: evolution and phylogenetic applications. *Annual Review of Ecology and Systematics* **21:** 541–566.

Min–Lin S, Chen CA, Lue KY. 2002. Molecular phylogeny and biogeography of the grass lizards genus Takydromus (Reptilia: Lacertidae) of East Asia. *Molecular Phylogenetics and Evolution* **22:** 276–288.

Moritz C, Hillis DM. 1996. Molecular systematics: context and controversies. In: Hillis DM, Moritz C, Mable BK, eds. *Molecular systematics*. Sunderland, MA, USA: Sinauer Associates, 1–113.

Moritz C, Brown WM, Densmore LD, Wright JW, Vyas D, Donnellan S, Adams M, Baverstock P. 1989. Genetic diversity and the dynamics of hybrid parthenogenesis in *Cnemidophorus* (Teiidae) and *Heteronotia* (Geckonidae). In: Dawley RM, Bogart JP, eds. *Evolution and ecology of unisexual vertebrates*. New York: New York State Museum, Bulletin 446, 87–112.

Nagy ZT, Lowson R, Joger U, Wink M. 2004. Molecular

phylogeny and systematics of racers, whipsnakes and relatives (Reptilia: Colubridae) using mitochondrial and nuclear markers. *Journal of Zoological Systematics and Evolutionary Research* **42:** 223–233.

Peters G. 1964. Sekundäre Geschlechtmerkmale, Wachstum und Fortpflanzung bei einigen transkaukasischen Eremias Formen. *Senkenbergiana Biologie* **45:** 445–476.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14:** 817–818.

de Queiroz A, Lawson R, Lemos–Espinal JA. 2002. Phylogenetic relationships of North American garter snakes (Thamnophis) based on four mitochondrial genes: how much DNA sequence is enough? *Molecular Phylogenetics and Evolution* **22:** 315–329.

Rastegar-Pouyani N, Nilson G. 1997. A new species of Eremias (Sauria, Lacertidae) from Fars province, South–Central Iran. *Russian Journal of Herpetology* **4:** 94–101.

Rastegar-Pouyani N, Rastegar-Pouyani E. 2001. A new species of Eremias (Sauria: Lacertidae) from highlands of Kermanshah Province, western Iran. *Asiatic Herpetological Research* **9:** 1–6.

Sambrook J, Russell DW. 2001. *Molecular cloning: a laboratory manual*. New York: Cold Spring Harbor Laboratory Press.

Sanderson MJ, Wojciechowski MF, Hu JM, Sher KT, Brady SG. 2000. Error, bias, and long branch attraction in data for two chloroplast photosystem genes in seed plants. *Molecular Biology and Evolution* **17:** 782–797.

Sborshchikov IM, Savostin LA, Zonenshan LP. 1981. Present plate tectonics between Turkey and Tibet. *Tectonophysics* **79:** 5–73.

Surget–Groba Y, Heulin B, Guillaume CP, Thrope RS, Kupryanova L, Vogrin N, Maslak R, Mazzotti S, Venczel M, Ghira L, Odierna G, Leontyeva O, Monney JC, Smith N. 2001. Intraspecific phylogeography of *Lacerta vivipara* and the evolution of viviparity. *Molecular Phylogenetics and Evolution* **18:** 449–459.

Swofford DL. 2003. *PAUP*. Phylogenetic analysis using parsimony (* and other methods)*, Version 4.0b10. Sunderland: Sinauer Associates.

Szczerbak NN. 1974. *The palearctic deserts lizards*. Akadeimya Nauk Ukrienskoi SSR Institut Zoologii. Kiev: Naokova Dumka. (in Russian).

Szczerbak NN. 2003. *Guides to the reptiles of the Eastern Palaearctic*. Malabar, FL: Krieger Publishing Company.

Terentjev PV, Chernove SA. 1965. *Key to amphibian and reptiles* (English Translation of 1949 edition). Kochva L, Trans. Washington, D.C.: Israel Program for Scientific translation, Smithsonian Institution.

Thompson JD, Higgins DG, Gibson TJ. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific ga penalties and weight matrix choice. *Nucleic Acids Research* **24:** 4876–4882.

Walker D, Avise JC. 1998. Principles of phylogeography as illustrated by freshwater and terrestrial turtles in southeastern United States. *Annual Review of Ecology and Systematics* **29:** 23–58.

Xia X, Xie Z. 2001. DAMBE: Software package for data analysis in molecular biology and evolution. *Journal of Heredity* **92:** 371–373.

Xia X, Xie Z, Salemi M, Chen L, Wang Y. 2003. An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution* **26:** 1–7.

Yang Z, Rannala B. 1997. Bayesian phylogenetic inference using DNA sequence: a Markov chain Monte Carlo method. *Molecular Biology and Evolution* **14:** 717–724.

Zhang DX, Hewitt GM. 1996. Nuclear integration: challenges for mitochondrial DNA markers. *Trends in Ecology and Evolution* **11:** 247–251.

APPENDIX

List of the specimens analysed, their geographical origin, institute (IPMB) and field numbers, and the GenBank accession numbers for both genes. Note that the locality numbers correspond to those marked in Figure 1.

				Accession number	
Sample name	Institute number	Field number	Locality	Cytochrome *b*	*12S*
Eremias persica	40760	ERP7	1	FJ 416260	FJ445330
Eremias persica	40761	ERP9	1	FJ 416261	FJ445331
Eremias persica	40762	ERP10	1	FJ 416262	FJ445332
Eremias persica	40763	ERP11	1	FJ 416263	FJ445333
Eremias persica	40765	ERP 13	1	FJ 416264	FJ445334
Eremias persica	40767	ERP15	1	FJ 416266	FJ445335
Eremias persica	40768	ERP25	1	FJ 416269	FJ445336
Eremias persica	40769	ERP 26	1	FJ 416272	FJ445337
Eremias persica	40770	ERP31	1	FJ 416276	FJ445339
Eremias persica	40771	ERP 32	1	FJ 416277	FJ445340
Eremias persica	40772	ERP33	1	FJ 416274	FJ445338
Eremias persica	40773	ERP38	1	FJ 416278	FJ445341
Eremias persica	40774	ERP39	1	FJ 416279	FJ445342
Eremias persica	40775	ERP43	1	FJ 416248	FJ445343
Eremias persica	40776	ERP44	1	FJ 416249	FJ445344
Eremias persica	40777	ERP 45	1	FJ 416251	FJ445345
Eremias persica	40778	ERP46	1	FJ 416253	FJ445346
Eremias persica	40779	ERP48	1	FJ 416255	FJ445347
Eremias persica	40782	ERP49	1	FJ 416257	FJ445348
Eremias persica	40783	ERP50	1	FJ 416259	FJ445349
Eremias persica	40695	SMP30	1	FJ 375934	FJ445258
Eremias persica	40696	SMP64	1	FJ 416183	FJ445262
Eremias persica	40697	SMP65	1	FJ 416184	FJ445263
Eremias persica	40698	SMP75	1	FJ 416185	FJ445264
Eremias persica	40700	SMP85	1	FJ 416186	FJ445265
Eremias persica	40701	SMP111	1	FJ 416187	FJ445266
Eremias persica	40702	SMP112	1	FJ 416188	FJ445267
Eremias persica	40722	SMP40	1	FJ 416182	FJ445261
Eremias persica	40723	SMP41	1	FJ 416180	FJ445259
Eremias persica	40724	SMP42	1	FJ 416181	FJ445260
Eremias persica	40784	ERP57	2	FJ 416265	FJ445350
Eremias persica	40785	ERP59	2	FJ 416267	FJ445351
Eremias persica	40786	ERP 61	2	FJ 416268	FJ445352
Eremias persica	40787	ERP 62	2	FJ 416273	FJ445355
Eremias persica	40788	ERP 68	2	FJ 416270	FJ445353
Eremias persica	40789	ERP69	2	FJ 416275	FJ445356
Eremias persica	40790	ERP70	2	FJ 416280	FJ445357
Eremias persica	40791	ERP71	2	FJ 416281	FJ445358
Eremias persica	40792	ERP79	2	FJ 416271	Fj445354
Eremias persica	40793	ERP107	3	FJ 416244	FJ445323
Eremias persica	40794	ERP108	3	FJ 416247	FJ445322
Eremias persica	40795	ERP155	4	FJ 416286	FJ445363
Eremias persica	40796	ERP156	4	FJ 416282	FJ445359
Eremias persica	40797	ERP157	4	FJ 416283	FJ445360
Eremias persica	40798	ERP162	4	FJ 416284	FJ445361
Eremias persica	40799	ERP 164	4	FJ 416285	FJ445362
Eremias persica	40800	ERP172	5	FJ 416246	FJ445324
Eremias persica	40801	ERP 173	5	FJ 416250	FJ445325
Eremias persica	40802	ERP 174	5	FJ 416252	FJ445326

APPENDIX *Continued*

Sample name	Institute number	Field number	Locality	Accession number	
				Cytochrome *b*	*12S*
Eremias persica	40803	ERP175	5	FJ 416254	FJ445327
Eremias persica	40804	ERP176	5	FJ 416256	FJ445328
Eremias persica	40806	ERP 178	5	FJ 416258	FJ445329
Eremias nigrolateralis	40827	ERP166	5	FJ 416288	FJ445374
Eremias nigrolateralis	40828	ERP167	5	FJ 416289	FJ445375
Eremias nigrolateralis	40829	ERP168	5	FJ 416287	FJ445373
Eremias nigrolateralis	40830	ERP169	5	FJ 416290	FJ445376
Eremias nigrolateralis	40831	ERP170	5	FJ 416291	FJ445364
Eremias nigrolateralis	40832	ERP171	5	FJ 416292	FJ445365
Eremias persica	40609	GN-571	6	FJ 416203	FJ445280
Eremias persica	40610	GN-572	6	FJ 416204	FJ445281
Eremias persica	40611	GN-574	6	FJ 416205	FJ445282
Eremias persica	41033	ERP273	7a	FJ 416227	FJ445304
Eremias persica	41034	ERP274	7a	FJ 416221	FJ445298
Eremias persica	41035	ERP275	7a	FJ 416220	FJ445297
Eremias persica	41037	ERP341	7a	FJ 416225	FJ445302
Eremias persica	41038	ERP342	7a	FJ 416218	FJ445295
Eremias persica	41039	ERP343	7a	FJ 416219	FJ445296
Eremias persica	41040	ERP344	7a	FJ 416226	FJ445303
Eremias persica	41026	ERP259	7b	FJ 416229	FJ445306
Eremias persica	41027	ERP260	7b	FJ 416230	FJ445307
Eremias persica	41029	ERP262	7b	FJ 416231	FJ445308
Eremias persica	41031	ERP264	7b	FJ 416228	FJ445305
Eremias persica	40494	02-233	7a	FJ 416214	FJ445291
Eremias persica	40495	02-230	7a	FJ 416224	FJ445301
Eremias persica	40496	02-232	7a	FJ 416211	FJ445288
Eremias persica	40497	02-234	7a	FJ 416223	FJ445300
Eremias persica	40555	02-249	7a	FJ 416217	FJ445294
Eremias persica	40556	02-244	7a	FJ 416213	FJ445290
Eremias persica	40607	02-248	7a	FJ 416216	FJ445293
Eremias persica	40603	02-246	7a	FJ 416212	FJ445289
Eremias persica	40604	02-247	7a	FJ 416215	FJ445292
Eremias persica	40602	02-245	7a	FJ 416222	FJ445299
Eremias persica	40519	02-002	8	FJ 416206	FJ445283
Eremias persica	40524	02-043	8	FJ 416210	FJ445287
Eremias persica	40525	02-037	8	FJ 416208	FJ445285
Eremias persica	40527	02-036	8	FJ 416207	FJ445284
Eremias persica	40554	02-038	8	FJ 416209	FJ445286
Eremias persica	40703	SMP194	9a	FJ 416189	FJ445268
Eremias persica	40704	SMP240	9b	FJ 416190	FJ445269
Eremias persica	40705	SMP255	9b	FJ 416191	FJ445270
Eremias persica	40706	SMP256	9a	FJ 416192	FJ445271
Eremias persica	40707	SMP257	9b	FJ 416193	FJ445272
Eremias persica	40708	SMP258	9a	FJ 416194	FJ445273
Eremias persica	40709	SMP260	9a	FJ 416195	FJ445274
Eremias persica	40711	SMP265	9b	FJ 416196	FJ445275
Eremias persica	40712	SMP269	9b	FJ 416197	FJ445276
Eremias persica	40713	SMP283	9b	FJ 416198	FJ445277
Eremias persica	40714	SMP284	9b	FJ 416199	FJ445377
Eremias persica	40715	SMP288	9b	FJ 416200	FJ445278
Eremias persica	40716	SMP290	9b	FJ 416201	FJ445279
Eremias persica	40717	SMP291	9b	FJ 416202	FJ445378

APPENDIX *Continued*

Sample name	Institute number	Field number	Locality	Accession number	
				Cytochrome *b*	*12S*
Eremias persica	40807	ERP193	9b	FJ 416241	FJ445318
Eremias persica	40808	ERP195	9b	FJ 416242	FJ445319
Eremias persica	40809	ERP196	9b	FJ416243	FJ445320
Eremias persica	40810	ERP197	9a	FJ 416245	FJ445321
Eremias persica	41025	ERP243	9b	FJ 416232	FJ445309
Eremias sp.	40544	01-141	10	FJ 416236	FJ445313
Eremias sp.	40545	01-142	10	FJ 416234	FJ445311
Eremias sp.	40546	01-143	10	FJ 416235	FJ445312
Eremias sp.	40547	01-144	10	FJ 416237	FJ445314
Eremias sp.	40548	01-145	10	FJ 416238	FJ445315
Eremias sp.	40549	01-146	10	FJ 416239	FJ445316
Eremias sp.	40550	01-147	10	FJ 416240	FJ445317
Eremias montanus	40833	ERP216	11	FJ 416293	FJ445366
Eremias montanus	40834	ERP217	11	FJ 416294	FJ445367
Eremias montanus	40835	ERP218	11	FJ 416295	FJ445368
Eremias montanus	40836	ERP219	11	FJ 416296	FJ445369
Eremias montanus	40837	ERP220	11	FJ 416297	FJ445370
Eremias montanus	40838	ERP221	11	FJ 416298	FJ445371
Eremias montanus	40839	ERP222	11	FJ 416299	FJ445372
Eremias sp.	41013	ERP361	12	FJ 416176	FJ445254
Eremias sp.	41014	ERP362	12	FJ 416177	FJ445255
Eremias sp.	41015	ERP363	12	FJ 416178	FJ445256
Eremias sp.	41016	ERP364	12	FJ 416179	FJ445257
Eremias persica	41032	ERP 271	13	FJ 416233	FJ445310
Eremias velox	41041	ERP250	9	FJ 416175	FJ445253
Eremias velox	40730	Smp207	9	FJ 416174	FJ445252
Ophisops elegans	41036	ERP276	7	FJ 416172	FJ445250
Mesalina brevirostris	41081	1b	14	FJ416173	FJ445251