

<https://doi.org/10.11646/zootaxa.4471.1.6>
<http://zoobank.org/urn:lsid:zoobank.org:pub:C7BF13B6-F212-4D89-8D75-6908101C83E2>

A new subspecies of *Zamenis hohenackeri* (Strauch, 1873) (Serpentes: Colubridae) based on morphological and molecular data

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Abstract

Based on morphological characteristics, two subspecies of the Transcaucasian rat snake (*Zamenis hohenackeri*) are currently recognized, namely *Z. h. tauricus* and *Z. h. hohenackeri*. Both subspecies are repeatedly considered to be conspecific colour morphs, or have even been confused with *Z. situla*. Although, few studies involved the Transcaucasian rat snake in a phylogenetic approach, none has so far led to any taxonomic changes. We assessed the intraspecific morphological variation and phylogeographic relationships among specimens from different locations across its updated distribution. Our molecular (1191 bp mtDNA, 565 bp nuDNA) and morphological data provide sufficient evidence to support three distinct lineages within the *Z. hohenackeri* complex with a different arrangement compared to a previous study. These represent the subspecies *Z. h. hohenackeri*, *Z. h. tauricus*, and a lineage from southwestern Turkey which is described as a new subspecies. Aspects of historical biogeography and conservation status are briefly discussed.

Key words: Anatolia, colour pattern, Colubridae, phylogeography, Transcaucasian rat snake, Leopard snake

Introduction

The Transcaucasian rat snake, *Zamenis hohenackeri* (Strauch, 1873), is a small colubrid snake that occurs across the Caucasus, Asia Minor and the northwestern Levant. This taxon was previously considered as a member of the genus *Elaphe* Fitzinger, 1833 (Nikolskij, 1916). Based on morphological and biochemical analyses, Utiger and colleagues (Utiger *et al.*, 2002) assigned this species, together with *Elaphe lineata*, *E. longissima*, *E. persica*, and *E. situla* to the genus *Zamenis* Wagler, 1830. At present, *Z. hohenackeri* contains two subspecies with the nominotypic form distributed in the Caucasus region (type locality: Chanlar, Azerbaijan [Bischoff, 1993], and Tbilisi, Republic of Georgia [Strauch, 1873]; though the former is preferred, see Bischoff, 1993), including Armenia, Azerbaijan, Georgia, and Russia, and from northern and eastern Turkey southward into Iraq and Iran (Afrasiab & Mohamad, 2011; Schulz, 1996). The second subspecies, *Z. h. tauricus* (Werner, 1898) was described from the Taurus Mountains in southern Turkey (type locality: Gülek, Adana), and further records originate from across southwestern Turkey, Israel, Lebanon, and Syria (Schulz, 1996). Based on literature records, both subspecies seem to be geographically separated by mostly unexplored mountain ranges (Fig. 1).

Despite their potentially distinct distribution ranges, *Z. h. hohenackeri* and *Z. h. tauricus* have been frequently debated in terms of their taxonomic status and repeatedly considered to be conspecific colour morphs (Bischoff,

1993; Nilson & Andrén, 1984; Schulz, 1996). While the former is characterized by two rows of dorsal blotches, which are typically separated by a light vertebral area or line, the latter shows predominantly only one row of larger blotches with more or less distinct, dark edges (Schulz, 1996; www.turkherptil.org/). However, substantial intraspecific variability in these traits has been observed (Schulz, 1996, 2013; www.turkherptil.org/). Consequently, many potential cases of misidentification of *Zamenis* subspecies or even more serious confusions concerning their classification are often present in the specialized literature (e.g., the closely related *Z. situla* has been frequently confused with *Z. hohenackeri*; Baran, 1978; Kumlutaş *et al.*, 2004).

Combining molecular and morphological characters can overcome potential subjective interpretation originating from morphological data alone and may provide significant evidence to identify genealogical lineages and assess their evolutionary independence within *Z. hohenackeri*. In fact, a recent study (Jandzik, Avci, & Gvoždík, 2013) indicates substantial incongruence between current taxonomy and molecular data of *Z. hohenackeri* and reported further substructure within the species, which has not been recognized by external morphology so far. According to these authors, *Z. hohenackeri* forms three divergent lineages: one corresponds to the nominotypic subspecies in the north, another comprises individuals from the region of the type locality of *Z. h. tauricus* in southern Anatolia and the third, the “Southern lineage”, occurs in the Amanos (Nur) Mountains, the next larger mountain range across the Adana Basin, and reaches farther south into the Levant. Yet, the single locus approach, the limited number of samples and the lack of morphological data prevented taxonomic changes in this group.

Here we use detailed morphological information, nuclear and extended mitochondrial sequence data sets, as well as samples from additional regions compared to previous analyses to investigate the divergence and taxonomic relationship within the *Z. hohenackeri* complex. Our results reveal three allopatric lineages within *Z. hohenackeri* with high levels of genetic divergence. Of these, one lineage from southwestern Turkey is described as a new subspecies.

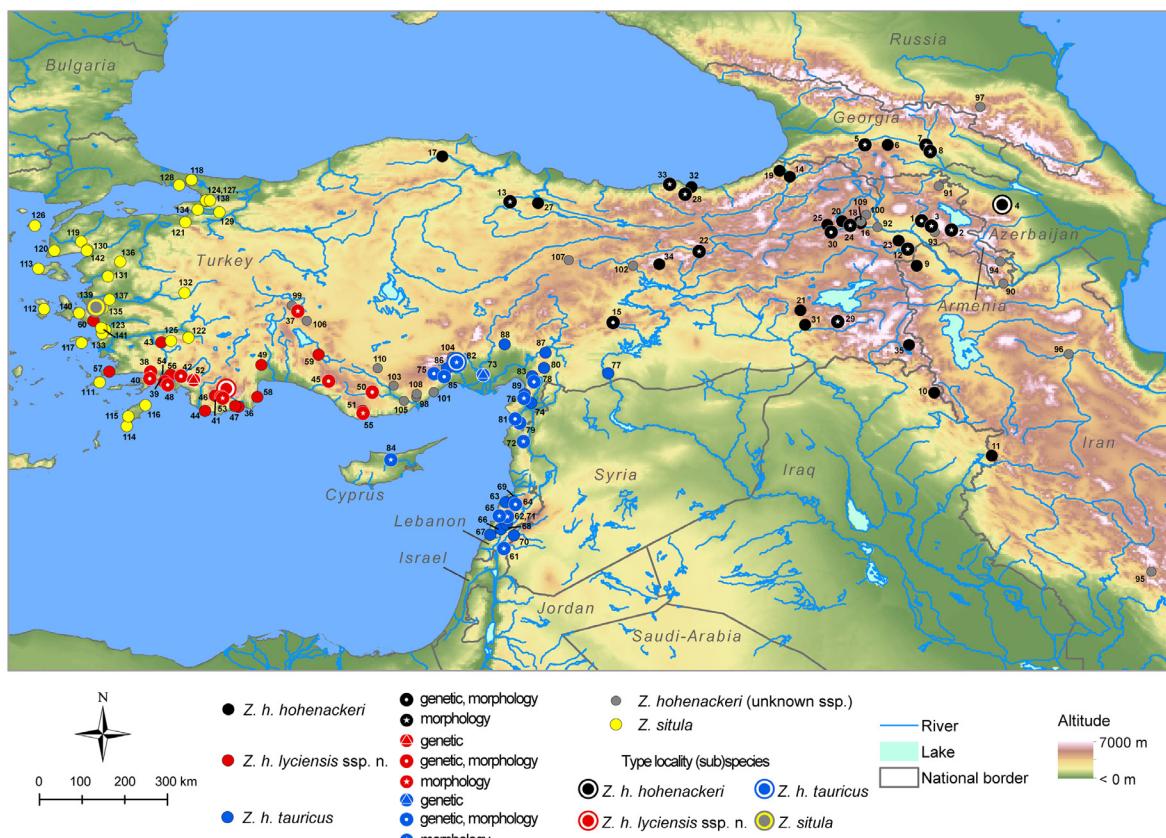


FIGURE 1. Distribution map of *Zamenis hohenackeri* subspecies and locations where *Z. situla* is found with numbers as used in Supplementary Table 1. Sampling localities of specimens used for genetic and/or morphological analysis and holotype localities are indicated with different symbols (see legend). More detailed maps for Iran, and records within the eastern Caucasus (Greater and Lesser), including Russia, Georgia, Armenia, and Azerbaijan can be found in Bischoff (1993), Schulz (1996), and Arakeylan *et al.* (2011).

Material and methods

Sampling, DNA extraction and sequencing. For the molecular analysis we included samples of ethanol-preserved museum vouchers from Turkey ($n = 19$), Lebanon ($n = 2$), and from Armenia ($n = 1$); for details on specimens see Supplementary Table 2 and for morphological investigations of these and further vouchers see the respective section below; localities of the specimens are presented in Fig. 1.

Total genomic DNA was extracted from tissue samples using the Qiagen DNeasy kit (Qiagen Inc.) following the manufacturer's protocol. We amplified partial sequences of the following four loci via the polymerase chain reaction (PCR): two mitochondrial loci, namely *cytochrome oxidase subunit 1* (*co1*, 345 bp) and *cytochrome b* (*cytb*, 846 bp), as well as two nuclear loci, namely *vimentin gene* (*vim*, 291 bp) and *beta-spectrin nonerythrocytic 1 gene, intron 1* (*SPTBN1*, 274 bp). Primers were designed using Primer3 v.4.0.0 (Koressaar & Remm, 2007; Untergasser *et al.*, 2012); see Supplementary Table 3 for a list of primers used and annealing temperature for PCR amplification. Amplicons were purified using a QIAquick PCR Purification Kit (Qiagen, Germany) and sequenced in both directions with the same primers. We identified heterozygotes in electropherograms of the nuclear loci based on secondary peak calling, using Geneious 9.0.5 (Kearse *et al.*, 2012) and the Heterozygote plugin. No evidence, such as premature stop codons, of pseudogenes, was detected in the mtDNA data. All newly found haplotypes were deposited in GenBank (accession numbers: Supplementary Table 2).

Phylogenetic reconstruction. We aligned new sequences of each gene partition along with those available for *Z. hohenackeri* and appropriate outgroup sequences retrieved from GenBank (see Supplementary Table 2) using Muscle 3.8.31 (Edgar, 2004) as implemented in Mega 6.06 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013). All gene fragments were translated into amino acids; no frameshift mutations or premature stop codons were observed. Gaps were treated as missing data in all subsequent analyses. All polymorphic sites were encoded with the appropriate IUPAC ambiguity code. Due to low variation in the nuclear data, we focused our analysis predominantly on the mtDNA data and used the nuclear data as supporting DNA-based diagnostic features and to generate haplotype networks only. For the latter analysis, heterozygous sequences were resolved with PHASE 2.1 (Stephens & Scheet, 2005; Stephens, Smith, & Donnelly, 2001) using the input file generated by SeqPHASE (Flot, 2010) and applying 100 iterations. We choose the allele(s) with the highest posterior probability of the phased nuclear gene copies to represent each individual in subsequent analyses. TCS haplotype networks were inferred with PopART 1.7 (Clement *et al.*, 2002; Leigh & Bryant, 2015).

Prior to phylogenetic reconstruction, substitution saturation of mtDNA was evaluated with Xia's test, as implemented in the program DAMBE (Xia & Lemey, 2009; Xia, Xie, Salemi, Chen, & Wang, 2003). Codon positions 1 and 2 were analysed together while codon position 3 was treated separately. None of the data showed substantial sequence saturation, as indicated by Xia's test (all $\text{Iss} < \text{Iss.c}$, $p < 0.001$ assuming a symmetrical topology). The two mitochondrial sequences were concatenated and data blocks were pre-defined by genes and codon positions for subsequent phylogenetic analyses.

In order to assess the evolutionary distance between the *Zamenis* specimens, we calculated uncorrected *p*-distances among unique haplotypes of the two partial mt genes using Mega 6.06 with the pairwise deletion option and by considering both transitions and transversions.

Phylogenetic relationships were calculated based on Maximum Likelihood (ML) and Bayesian Inference (BI) methods, using RAxML v.8.2.9 (Stamatakis, 2014) as well as BEAST 1.8.4 (Drummond & Rambaut, 2007; Drummond, Suchard, Xie, & Rambaut, 2012). Optimal partitioning schemes and substitution models for each partition were selected using the Bayesian Information Criterion (BIC) in a greedy search algorithm and linked branch lengths in PartitionFinder 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012; Lanfear, Calcott, Kainer, Mayer, & Stamatakis, 2014). BI analyses were then run using models and partitions as selected by PartitionFinder, while all nucleotide substitution model parameters were unlinked across partitions. We used a Yule process as model of speciation, a random tree as starting tree, an uncorrelated log-normal relaxed clock and a diffuse gamma distribution (scale = 1000, shape = 0.001) as prior for the evolutionary rate. Two runs were performed with 20 million generations each, sampling every 2,000 generations and with a burn-in set to 25% of the samples. Convergence and stationary levels were verified with Tracer v.1.7.2. We annotated the tree information with TreeAnnotator v.2.3.1 and visualized it with FigTree v.1.4.3 (Drummond & Rambaut, 2007).

ML tree construction was performed under the GTRGAMMA model using RAxML on the CIPRES Science Gateway (San Diego Supercomputer Center). Nodal support of the tree was assessed by rapid bootstrapping algorithm with 1000 bootstrap replicates.

Divergence time estimation. Divergence dates were estimated using BEAST 1.8.4. In order to place fossil calibration references, we supplemented our data with sequence information of outgroup taxa obtained from GenBank, including sequences of *Pantherophis*, *Lampropeltis*, *Coluber* and *Salvadora* species.

We specified a lognormal prior distribution with a 95% CI for the most recent common ancestor (MRCA) with an offset equal to the minimum age of the oldest fossil and imposed the following five calibrations to the molecular clock (see also Burbrink & Lawson, 2007): (1) A minimum age of 6 Mya of the MRCA of *Zamenis lineatus*, *Z. longissimus* and *Z. situla*, based on fossils considered directly ancestral to *Z. situla* and *Z. lineatus* (*Elaphe longissima*) (Ivanov, 1997). The upper 95 % CI value was set to ~20 Mya, as the first rat snake (genus *Elaphe*) appeared in Europe 20 Mya (Ivanov, 2002); (Mean = 1.00; SD = 0.83; offset = 6.00; 95 % CI: 6.53-19.83). (2) A minimum age of 11 Mya with an upper 95 % CI value of 15 Mya for the *Coluber constrictor* and *Coluber flagellum* split as previously justified (Burbrink & Lawson, 2007); (Mean = 0.60; SD = 0.45; offset = 11.00; 95 % CI: 11.75-15.40). (3) A minimum age of 16 Mya for the MRCA of the earliest *Pantherophis* fossil (Holman, 2000). The upper 95 % CI value was set to 20 Mya as *Pantherophis* is unknown in the fossil record prior to 20 Mya; (Mean = 0.40; SD = 0.54; offset = 16.00; 95 % CI: 16.52-20.30). (4) A minimum age of 15 Mya of the MRCA of *Lampropeltis*, based on the earliest known fossil record of Lampropeltinae from the mid-Miocene (Holman, 2000), and an upper 95 % CI value of 19 Mya; (Mean = 0.40; SD = 0.55; offset = 15.00; 95 % CI: 15.50-19.38). (5) A minimum age of 20 Mya for the MRCA of *Coluber* and *Salvadora* with an upper 95 % CI value of 24 Mya, according to the earliest *Salvadora* fossil; (Mean = 0.40; SD = 0.50; offset = 20; 95 % CI: 20.56-23.97). For run specification in BEAST see previous section.

Morphological analysis. A total of 34 alcohol-preserved voucher specimens of *Zamenis hohenackeri* were available to us (Armenia, n = 3; Georgia, n = 4; Lebanon, n = 3; Turkey, n = 24). Specimens originated from the Natural History Museum of Geneva (MHNG) and the Natural History Museum Basel (NHMB), Switzerland, the Natural History Museum in Vienna (NHMW), Austria, as well as the Zoological Research Museum Alexander Koenig in Bonn (ZFMK), the Bavarian State Collection of Zoology in Munich (ZSM), Germany, and the Ege University in Izmir (EU), Turkey. Further morphological data and photographs of *Z. hohenackeri* and *Z. situla* records were obtained from literature and online resources. Localities of vouchers and literature data are shown in Fig. 1, and listed as well as partly illustrated in the corresponding Supplementary Table 1 and Supplementary Figs. 1-4.

Specimens were examined for the following characters: Snout-vent length [SVL], measured from the tip of the snout to the posterior edge of the anal plate, and tail length [TL], from posterior margin of anal plate to tip of tail (both measured to the nearest 5 mm using a piece of string and a measuring tape); number of dorsal scale rows [DOR 1/2/3], counted at position of the 10th ventral plate, at midbody (i.e., at position of the ventral plate corresponding to half the total number of ventrals), and at one head length before the anal plate; number of all ventral scales [VEN]; number of subcaudals [SC], without the terminal scute; presence/absence of uni-coloured yellowish-reddish dorsal blotches surrounded by a black border due to dorsals with dark edges primarily on their outer margins [deDOR]; occurrence of dark edges on dorsals inside of blotches [deiDOR]; number of dorsal blotches counted on left side, between head and tail tip [noDBleft]; width of the anterior dorsal blotches, including dark borders, counted along the body axis by the number of dorsal scales, either of the single mid-dorsal blotch, or of the left-sided blotch if the dorsal blotches are separated into two paravertebral blotches ([wDB], we used the minimum number in our statistical analyses), two semi-covered dorsal scales were counted as one scale, whereas the presence of only one semi-covered dorsal scale in a single blotch was not counted. In addition, we compared the shape and arrangement of the dorsal colour patterns, e.g. whether they consisted of single mid-dorsal blotches or were separated into two paravertebral rows of blotches.

Sex of specimens was determined by the presence or absence of hemipenes, inspected through a subcaudal incision at the tail base. Some vouchers were badly damaged road-killed specimens, making it impossible to record measurements or precisely count scales. Even so, the size and shape of blotches were recorded in those parts of the body where they could be easily distinguished.

A principal component analysis (PCA) was conducted with the metric and meristic variables using the 'stats' package for R v3.4.1 (RDevelopmentCoreTeam, 2017). Prior to analyses, missing values were imputed using the R-package 'mice' (van Buuren & Groothuis-Oudshoorn, 2011) with 500 imputations, a Bayesian linear regression imputation approach for numeric and a logistic regression for 2-level categorical variables. Due to a higher number of missing values in the morphological data, we performed all analyses on (i) a reduced dataset which included

only individuals that had less than 50 % missing values in total and no missing values for the categorical variables ($n = 28$), and ii) on the complete dataset ($n = 50$). Overall, the reduced and full dataset contained 13 % and 31 % missing values, respectively. To avoid size dependent intercorrelation effects in TL we calculated regression residuals using SVL as a covariate.

Subspecies comparisons of variables were analysed based on the original (non-imputed) data through one-way ANCOVA with sex as covariate followed by Tukey HSD post hoc (SC, VEN, noDBleft), or by the Kruskal–Wallis H test and Dunn's post hoc test (DORs, relative tail length, wDB). Binomial variables were analysed using a Fisher's exact test (deDOR, deiDOR).

To increase the resolution of the identification key (see Results), the taxon-specific distribution and all available photos of wild *Zamenis hohenackeri* which show the dorsal pattern of the anterior body available from literature and online resources were investigated for consistent variation in colour pattern. These traits (namely: shape of anterior dorsal blotches [large and rounded or translaterally elongated, from oblong to bar-shaped], number of single translateral blotches with the anterior 20 blotches, instead of shaped as unilateral or twin spots) were not statistically tested, but integrated in the identification key and discussed where appropriate.

Results

Phylogenetic reconstruction, divergence time and species delimitation. The aligned concatenated sequences used for phylogenetic inference and divergence time estimations comprised 38 *Zamenis* and 13 outgroup sequences with a maximal length of 1191 bp for the mitochondrial genes. Data on nuclear gene fragments consisted of 21 and 22 *Zamenis* sequences (all but one from *Z. hohenackeri*) for *sptbn1* and *vim*, respectively, with a total length of 565 bp. The mtDNA dataset contained 390 variable and 292 parsimony informative characters (151 and 120 without outgroups), while the nuDNA contained four variable and one parsimony informative site.

The BI and ML phylogenetic reconstructions were well-resolved and yielded highly concordant tree topologies, in particular with respect to the major clades recovered within the genus *Zamenis* (Fig. 2, Supplementary Fig. 5). Phylogenetic relationships of nominal *Zamenis* species were in line with recent studies (Salvi, Mendes, Carranza, & Harris, 2018; Zheng & Wiens, 2016). Both analyses identified three distinct lineages within the highly supported monophyletic *hohenackeri* complex which are consistent with morphological data (see further below): one consists of specimens from north-eastern Anatolia and the Caucasus, representing the nominotypic subspecies *Z. h. hohenackeri*; a second corresponds to *Z. h. tauricus* from the Lebanon Mountains and provinces around the bay of Iskenderun into Province Mersin in southern Turkey; a third, so far unknown southwestern lineage (hereinafter 'SW Anatolian clade') comprises haplotypes from regions south of the Büyük Menderes River, Provinces Aydin and Denizli, to west of the Göksu River, Province Mersin (Fig. 2), although the relative position of this lineage within the *Z. hohenackeri* clade was poorly supported. Within *Z. h. tauricus*, we recovered additional subclades (Fig. 2, Supplementary Fig. 5).

Genetic distances between specimens of these different subspecies and the SW Anatolian clade ranged between 4.9 % and 7.4 % in the *co1*, and between 4.9 % and 5.4 % in the *cytb*; while distances within subspecies or within the SW Anatolian clade were considerably lower (up to 2.9 % *co1*, 2.3 % *cytb*). Among nominal *Zamenis* species *p*-distances ranged between 8.7 % and 14.8 % in the *co1*, and between 8.5 % and 14.9 % in the *cytb*. For nuclear data, genetic distances between specimens of *Z. h. hohenackeri*, *Z. h. tauricus*, and the SW Anatolian clade were marginal. However, in most cases the lineages (subspecies) might be differentiated from each other by a certain combination of character states of the nuDNA sequence code (Supplementary Table 4, Supplementary Fig. 6). Accordingly, a single deletion was detected in all but one sequences of *sptbn1* of the SW Anatolian clade, while a further substitution was recovered in *vim* (*Z. h. hohenackeri* + *Z. h. tauricus* vs. SW Anatolian clade).

Molecular dating yielded estimates for basal nodes that roughly agreed with other recent studies of rat snake divergence times (Burbrink & Lawson, 2007; Kyriazi *et al.*, 2013; but see Salvi *et al.* 2018, in which divergence times were in part significantly younger); Supplementary Table 5. Our chronogram places the early diversification of the *Zamenis* to the lower Miocene (MRCA of *Zamenis* taxa *ca.* 22.2 Mya; Fig. 2, Supplementary Table 5). Accordingly, the divergence between the nominotypic subspecies *Z. h. hohenackeri* and the remaining *Z. hohenackeri* subspecies was inferred to have happened during the late Miocene to early Pliocene (*ca.* 6.0 Mya). However, given the uncertain position of the new subspecies within the *Z. hohenackeri* clade, its divergence time remains unknown.

Morphological analysis. More than 60 % of the total variation in the complete and 70 % in the reduced morphological dataset was explained by the first three PCs (Supplementary Table 6 and Supplementary Fig. 7 for variable contributions). The first principal component (PC1) accounted for 31 % and 38 % of the total variance in the complete and reduced datasets. For both datasets, PC1 had high contributing factor loadings from variables deiDOR, deDOR, noDBleft and the wDB, whereas PC2 was loaded most strongly by the number of dorsal scale rows (DOR1, DOR3; both datasets) and the number of ventral scales (both datasets), and accounted for ~20 % of the total variance. PC3 was loaded primarily by dorsal scale row number (DOR1) for the complete data or by the number of subcaudals for the reduced dataset, explaining 14 % and 13 % of the variance, respectively. The SW Anatolian clade was separated from *Z. h. hohenackeri* and *Z. h. tauricus* particularly due to wider dorsal blotches, the continuous black border of the reddish dorsal blotches, and a higher number of ventral scales. In contrast, *Z. h. tauricus* and *hohenackeri* showed higher morphological similarity, indicated by a substantial overlap in morphological variance (Supplementary Table 6 and Supplementary Fig. 7).

The three taxa differ significantly from one another in the width of dorsal blotches (wDB; Kruskal–Wallis $H_2 = 27.69$, $p < 0.001$, Dunn's post hoc test $p < 0.05$ for all pairings). Moreover, the SW Anatolian clade differ significantly from *Z. h. hohenackeri* and *Z. h. tauricus* subspecies in the number of ventral scales and dorsal blotches (ANCOVA VEN: $F_{2,42} = 8.63$; $p < 0.001$; noDBleft: $F_{2,24} = 16.42$; $p < 0.001$), as well as (from *Z. h. tauricus*) by the presence of dark edged dorsals outside blotches, and the absence of dark edged dorsals inside blotches (Fisher's exact test deDOR: $p_{[SW\ Anatolian\ clade /tauricus]} < 0.001$; $p_{[hohenackeri / SW\ Anatolian\ clade]} = 0.083$; deiDOR: $p_{[SW\ Anatolian\ clade /tauricus]} < 0.001$; $p_{[hohenackeri / SW\ Anatolian\ clade]} < 0.001$; Supplementary Table 7 and Supplementary Fig. 8). No significant differences between the subspecies were observed for the remaining traits.

Colour pattern in *Zamenis hohenackeri*. The dorso-lateral ground colour of *Z. hohenackeri* specimens varies from tan to greyish with a dorsal pattern consisting of brown to reddish-brown dorsal blotches of different shape which are more or less distinctly dark-bordered. In all specimens investigated, the lateral surfaces have small dark brown spots which are alternately arranged between two dorsal blotches. The first blotch of the dorsal pattern is a horseshoe-shaped mark on the neck pointed posteriorly. The ventral colour anteriorly is greyish and speckled with dark blotches, as are the posterior edge of (typically, every second) ventral plate. The speckled ventral pattern intensifies toward mid-body and turns completely dark grey to black afterwards. In some specimens of *Z. h. tauricus*, especially from the eastern Mediterranean region, the ventral side is completely black. On the upper side of the head numerous irregular dark speckles are present. The supralabials are marked by a black line, which sometimes continues across the infralabials. A dark and broad postocular line extends from behind each eye diagonally to the angle of the mouth. The pattern on the head's lower side varies independently of the subspecies/lineages; in some specimens there are no markings, whereas others have numerous irregular dark speckles or the surface is completely black.

The most obvious distinguishing characters among the previously established subspecies and the SW Anatolian clade are related to the dorsal pattern, which can be divided into two main types: one with small twin spotted blotches, occasionally fused into two longitudinal dorsal lines, separated by a light or ground coloured mid-dorsal line (*Z. h. hohenackeri*), and the other with predominantly one row of dorsal blotches formed as translateral bars, saddles or dumb-bells across the mid-dorsum (*Z. h. tauricus* and SW Anatolian clade). Between the latter two lineages, rounded dorsal blotches, occasionally fused longitudinally to form a wavy dorsal band, differentiate the SW Anatolian clade from *Z. h. tauricus* with comparatively smaller blotches (see above and identification key below). Whereas in *Z. h. tauricus* blotches are 1-2 dorsals in width (along the body axis) with scales exhibiting variable amounts of black tips or edges throughout a blotch, specimens of the SW Anatolian clade have larger blotches that are 2-3 dorsals in width, continuously and distinctly black bordered without black edges/tips on scales within a blotch.

Systematics. Based on the combined results of the molecular and morphological analyses of *Z. hohenackeri*, we describe another, previously unrecognized subspecies. The erection of this new taxon is justified by the morphological distinctiveness and the substantial genetic divergence as described above, as well as by the geographical restriction of this new taxonomic entity (for details see Discussion).

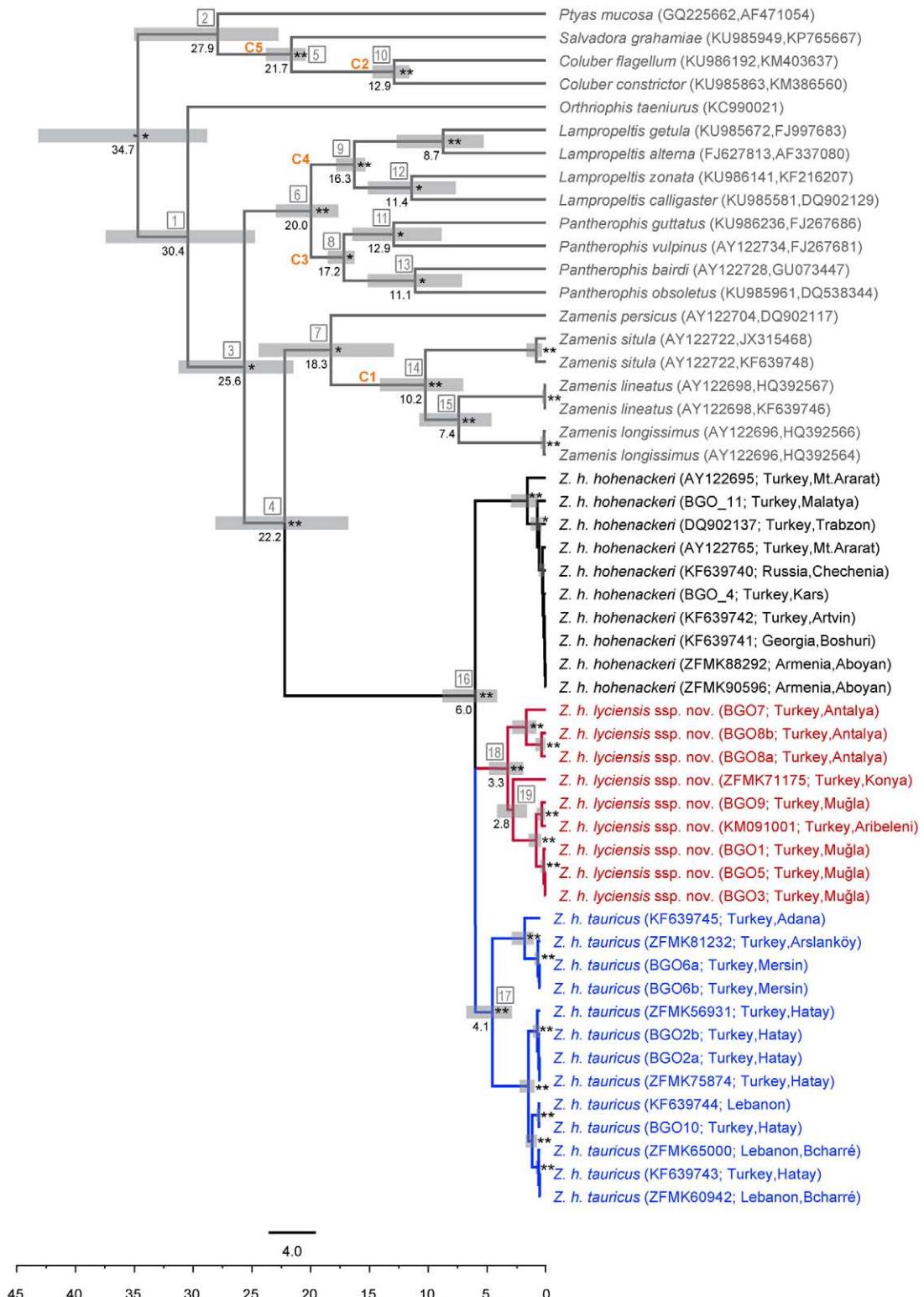


FIGURE 2. Time-calibrated BI phylogeny based on the combined *coI* + *cytb* mtDNA data analysis. The divergence times (in Mya) were estimated using calibration points (C1-C5) available from literature (text for details). Grey bars indicate 95 % highest posterior density (HPD) intervals of estimated node ages; an asterisk at nodes denotes Bayesian posterior (pp) support values ≥ 0.9 , two asterisks indicate pp ≥ 0.9 and bootstrap values $\geq 80\%$; node numbers correspond to Supplementary Table 5 that specifies the individual values and 95% credible intervals. Tip labels consist of the taxon name, original sample ID followed by the origin of sample (in brackets). Colour code is as follows: black—*Zamenis hohenackeri hohenackeri*; blue—*Z. h. tauricus*; red—*Z. h. lyciensis* ssp. nov..

Zamenis hohenackeri lyciensis ssp. nov.

For a list of synonyms and chresonyms see Supplementary Table 1.

Proposed English name: Lycian Ratsnake.

Holotype: An adult male (MHNG 2403.007) from Kohu Dağ, Elmali, Antalya, Turkey (N36.502690, E29.819595; 1700 m a.s.l.), collected in 1987 by W. Zinniker (Fig. 3).



FIGURE 3. Holotype of *Zamenis hohenackeri lyciensis* ssp. nov. MHNG2403.007 from Kohu Dağ, Elmali, Antalya, Turkey; dorsal view.

Paratype: An juvenile female (NHMW15173) from Akşehir, Konya, Turkey (N38.341464, E31.408311), collected in 1911 by Bodo v. Bodemeyer (Fig. 4).

Diagnosis: *Zamenis hohenackeri lyciensis* ssp. nov. is a relatively slender snake with a maximum SVL of 760 mm (Müller, 1939; female from Sultan Mountains). This subspecies can be distinguished from *Z. h. hohenackeri* and *Z. h. tauricus* by its distinctly blotched dorsal pattern which is twice as large as in the other two subspecies, and in having a higher mean of ventral count (224 vs. 211 or 210, Supplementary Table 7).

Description of the holotype (Fig. 3): Total length 602 mm (SVL 502 mm, TL 100 mm); head distinct from the rest of the body (head length from tip of snout to the ends of parietals: 15 mm, head width from eye to eye: 7 mm); eyes medium large; parietals longer than wide; nostril present more anteriorly to the snout than to the eye (eye to nostril: 4 mm, tip of the snout to eye: 7 mm); nasal divided; supralabials (left/right) 8/8, the 4th to 5th supralabial in contact with the eye (on both sides); 10 infralabials on both sides; 1 praecocular on both sides; 2 postoculars on both sides; temporals (left/right) 5(2+3)/5(2+3); dorsals 25–23–19: 25 on neck (counted at position of the 10th ventral plate), 23 mid-body (counted at position of the 111th ventral plate), 18 before anal plate (counted at position of the 212th ventral plate); 219 ventrals; 66 subcaudals; anal plate divided. Hemipenes everted.

Colouration of holotype in life: Life photos of the specimen in Schärtti & Baran (1988), p. 306, and Schulz (1996), Plate 14C. Dorsal and lateral ground colour tan; 55 dorsal saddle blotches on trunk, 19 blotches on tail; with few consecutive trunk blotches connected with each other, were counted as one blotch; blotches light

brown and distinctly black-bordered, changing at ca. 10 blotches anterior the anal plate into a pattern of twin-spots posteriorly, 3–5 dorsals in width (along body axis), space between the blotches 1–2 dorsals; small, alternating lateral blotches, extending to the outer edges of the ventrals; a horseshoe-shaped light brown, black-bordered dorsal blotch in the neck, its anterior peak reaching the parietals, the posterior open sides connected with the first dorsal blotch; upper side of head tan and mottled with black dots; a black postocular line beginning behind each eye and extending to the angle of the mouth; a further black mark below each eye between the 4th and 5th supralabial shield, extending over the infralabials; tip of the snout and anterior lower part of head black (including inframaxillars); anterior part of ventrals spotted with white and black patches; black colour increasing toward mid-body; becoming almost entirely black from 65th ventral plate on; subcaudals mottled black and white.

Colouration of holotype in ethanol (Fig. 3): Dorsal ground colour light grey, with dark grey (anthracite) blotches.

Distribution and natural history: *Zamenis hohenackeri lyciensis ssp. nov.* has a wide distribution across all southwestern Turkey (Fig. 1); the Mediterranean poses the south and southwestern distribution limits, whereas the northern and inland limits begin in the west in the mountains south of Izmir, reaching east to the Sultan Mountains of Konya province, and from there continue south along or near the Göksu River to the Mediterranean coast (e.g. localities 45, 50, 51, 55 and 59; Fig. 1). It inhabits moderately humid valleys to sparsely vegetated rocky slopes from or near sea level (Franzen, Bussmann, Kordges, & Thiesmeier, 2008) to at least 1,800 m asl. (our obs. at locality 41, Fig. 1, and Supplementary Fig. 1), but can also be found at forest edges and open patches. It is a particular secretive snake, rarely seen, being crepuscular and probably spending most of its diurnal thermoregulation under stony cover (thigmothermy). In warmer parts of its range, it was observed on the surface during cooler (<20°C) weather situations, such as early or late in the season or day, and before or during rainfall (see Schulz, 1996; pers. obs.). Presumably, the colourful dorsal pattern may have an aposematic or mimetic function (resembling the Ottoman Viper *Montivipera xanthina*), startling a potential predator, when the snake is active on the surface or is being uncovered. There is no specific information on the diet and egg clutches for the Lycian Ratsnake, but the Transcaucasian Ratsnake, in general, is known to feed on mice and lizards, partly also insects, and lays up to seven eggs (Franzen *et al.*, 2008 and refs. therein).

Etymology: The subspecies name is derived from the Latin word 'Lycia'. Lycia was an ancient geopolitical region in Anatolia along the southwestern coasts of Turkey what is now in the Turkish provinces of Antalya and Muğla. It represents the centre of *Zamenis hohenackeri lyciensis ssp. nov.* and most specimens were recorded in that region.

Description of the paratype (Fig. 4): Total length 310 mm (SVL 270 mm, TL 40 mm); head distinct from the rest of the body (head length from tip of snout to ends of parietals: 10 mm, head width eye to eye: 7 mm); eyes medium large; parietals longer than wide; nostril present more anterior to snout than to eye (eye to nostril: 3 mm, tip of snout to eye: 4.2 mm); nasal divided; 9 supralabials (left/right) 9/8, 4th to 5th in contact with eye (on both sides); 10 infralabials on both sides; 1 praecocular on each side with a distinct central groove; 2 postoculars on both sides; temporals (left/right) 1+3+2/1+3+4; dorsals 21–23–17; 222 ventrals, first plate on head reduced in size; 58 subcaudals; anal plate divided.

Colouration of paratype in ethanol (Fig. 4): Overall colour strongly faded, no blackish shades visible; dorsal and lateral ground colour tan; 57 dorsal saddle blotches on trunk, 16 blotches on tail; some trunk blotches at mid-body connected with each other (two connected blotches counted as one blotch); blotches 3–5 dorsals in width, space between blotches 2–3 dorsals; small, alternating lateral blotches, extending to outer edges of ventrals; a horseshoe-shaped light brown, black-bordered dorsal blotch in the neck, its anterior peak reaching the parietals; upper side of head tan, mottled with brown dots; a dark brown postocular line behind each eye, extending to the angle of the mouth; a further dark brown mark below each eye reaching in between the 4th and 5th supralabial shield, and extending over the infralabials; lower part of head fawn speckled with some brown on the inframaxillars; anterior part of ventrals spotted with beige and brown; increasing brown colour toward mid-body, from 59th ventral plate on changing to almost brown; subcaudals fawn and indistinctly mottled with brown.



FIGURE 4. Paratype of *Zamenis hohenackeri lyciensis* ssp. nov. NMW 15173 from Akşehir, Konya, Turkey; (a) dorsal and (b) ventral view.

Key to snake taxa of *Zamenis hohenackeri* and *Z. situla*

For examples of principal colour morphs and taxa see Fig. 5.

- 1a Upper side of head with three groups of distinct markings (Fig. 6): 1) the anterior end of the dorsal band or equivalent horse-shoe-shaped nuchal blotch reaching as a thick line along the parietal suture up/into to the frontal plate, 2) upper ends of the bilateral postocular line beginning above each eye on the supraoculars/parietals/frontal, 3) a thick line reaching across the suture of the frontal/prefrontals, connecting the eyes, but in some specimens being dissolved into broad blotches; 25–27 dorsals at mid-body; dorsal blotches usually rusty, reddish or orangish in juveniles and adults, 3–5 dorsal in width along the body axis; dorsal blotches can form two paravertebral lines; 220–255 ventrals *Zamenis situla*
- 1b Upper side of head usually without distinct black markings (Fig. 6); 1) the nuchal blotch barely reaching the parietals or continuing along the suture only as a thin line, sometimes with a blotch on each parietal, 2) upper end of the thick postocular line beginning at mid-level (postocular) of the eye, not above, 3) no line across the snout anterior the eyes; 23, rarely 25 dorsals at mid-body 2
- 2a Dorsal blotches 1–3 dorsals in width (along body axis, Fig. 7), usually >70 blotches that are indistinctly black bordered with scales often exhibiting black edges or tips throughout the blotch 3
- 2b Dorsal blotches light brown or reddish brown in adults (similar to *Z. situla*, Fig. 7), 3–5 dorsals in width (along body axis), rounded, usually <70 blotches that are distinctly black bordered and no or few scales within the blotch with black edges or tips, brown blotches in juveniles; 214–244 ventrals *Zamenis hohenackeri lyciensis* spp. nov.
- 3a Dorsal blotches 1–2 dorsals in width (along body axis, Fig. 7), commonly dorsal blotches arranged in 2 rows (twin-spotted) and separated by a light coloured vertebral line, whereas some of the first 20 dorsal blotches posterior the nuchal band might be formed as translateral bars, but never all 20; colour of blotches brown in juveniles and adults; 200–225 ventrals *Zamenis hohenackeri hohenackeri*
- 3b Dorsal blotches 2–3 dorsals in width (along body axis, Fig. 7), usually all of the first 20 blotches posterior the nuchal blotch formed as elongated (oblong to oval) translateral bars (and >50% over the entire trunk), with some dorsal blotches separated into twin spots more posteriorly; colour of blotches brown to olive in juveniles and adults; 196–224 ventrals *Zamenis hohenackeri tauricus*



FIGURE 5. Principal body colour pattern of *Zamenis situla* and *Z. hohenackeri* taxa: A) *Z. situla* blotched, Agora, Izmir (locality 139, Fig. 1); B) *Z. situla* striped, Izmir (locality 139, Fig. 1); C) *Z. h. lyciensis* spp. nov. Kirkpinar Karanfill, Aribeleni Yaylası, Muğla (locality 52, Fig. 1); D) *Z. h. tauricus* Aladağ, Mersin (locality 85, Fig. 1); E) *Z. h. hohenackeri* Günindi, Kars (locality 18, Fig. 1). See more examples in Supplementary Figs. 1–3.

Discussion

So far, the taxonomic classification of the *Z. hohenackeri* complex has not been consistently defined, recognizing either two subspecies (Schulz, 1996), or considering these groups as conspecific colour forms (Nilson & Andrén, 1984). Our study confirms the validity of the taxonomic status of *Z. h. hohenackeri* and *Z. h. tauricus* and provides a revision of their distribution ranges (Fig. 1). Furthermore, we found robust evidence for the existence of another unique evolutionary lineage from the Lycian coast and the interior of southwestern Turkey which is genetically distinct, morphologically distinguishable and geographically (largely consistent with colour pattern differences) separated from its conspecifics, justifying the description of a new subspecies. Our results extend and complement those by Jandzik *et al.* (2013), which were based solely on *cytb* sequence data and did not include morphology nor samples of the *Z. h. lyciensis* ssp. nov. lineage.

To briefly summarize the different lines of evidences for the delimitation of three subspecies of the *Z. hohenackeri* complex: i) all three lineages (taxa) are clearly differentiated by mtDNA markers and show high levels of genetic distances between each other (~ 5 %; intraspecific distances <3 %); however, these divergences are still considerably smaller than the distances between nominal *Zamenis* species (between 9 %-15 %); ii) the *Z. h. lyciensis* ssp. nov. is supported by a specific combination of nuDNA sequences, although the divergence is limited to a single deletion and/or substitution per marker; iii) all three lineages are distinguished by differences in colour pattern, easiest perceived by distinctive traits in the dorsal blotches, and *Z. h. lyciensis* ssp. nov. is further distinguished from the two nominal subspecies by the higher number of ventral scales; and iv) all three lineages are largely allopatric, but might meet along potential contact zones. The probability that any of these lineages are sympatric (without intergradation) seems to be unlikely, as we could not find any indication of such discrete taxa in the same general area, despite extensive searches in the field, literature and of museum material. Yet, in particular the vastly unexplored regions of the Central Anatolian Plateau in eastern and the mountain ranges in western Turkey require further investigations to find the most proximate populations between subspecies or even contact zones. According to the current status quo of knowledge, the nominotypic *Z. h. hohenackeri* is distributed from the Caucasus region into northern Turkey as far west as the province Kastamonu (locality 17, Fig. 1, and Supplementary Fig. 2), and south into, at least, Malatya province (locality 15, and Supplementary Fig. 2), whereas in its eastern range it extends along mountains far south into Iraq and Iran. The second subspecies *Z. h. tauricus* occurs in south-central Turkey, and extends along mountain ranges from northwestern Syria to Lebanon and Israel (Fig. 1). Aside from potential contact zones (see below), both taxa seem to be geographically separated within the Tauride orogenic belt, which creates significant barriers to precipitation due to elevation of more than 3 km in places (Schemmel, Mikes, Rojay, & Mulch, 2013). As we show, *Z. h. hohenackeri* and the two southern lineages (*Z. h. tauricus/ Z. h. lyciensis* ssp. nov.) diverged in the late Miocene/lower Pliocene (ca. 6 Mya), coinciding roughly with the massive 2 km surface uplift of the southern margin of the Central Anatolian Plateau that started during the Late Miocene between 8 and 5 Mya (Çine *et al.*, 2015; Cosentino *et al.*, 2012 and refs. therein). A recent study points to a similar time frame (late Miocene/Pliocene) for several cladogenetic events in *Zamenis* (Salvi *et al.* 2018). In the course of the dramatic regional uplift during that period the entire Mut basin became isolated from the eastern Mediterranean (Şafak, Kelling, Gökcen, & Gürbüz, 2005), apparently leading to the separation of *Z. h. lyciensis* ssp. nov. and *Z. h. tauricus*. Consequently, the modern distribution range of the new subspecies seems to be restricted (presumably as the result of postglacial re-expansion) northwest as far as Tahtali Dam in the Karaca Mountains (Karacadağ) between Izmir and the Büyük Menderes River (locality 60, Fig. 1). Here it meets its close relative, the Leopard Snake *Z. situla*, an ecological and morphological equivalent, which potentially impedes a continued expansion of *Z. h. lyciensis* ssp. nov. to the north. The *Z. h. lyciensis* from the Tahtali Dam (locality 60, Fig. 1, and Supplementary Fig. 3) is surrounded by records of *Z. situla*, e.g. ca. 30 km to the north at Urla and Izmir (localities 140 and 135, Fig. 1, and Supplementary Fig. 3) and ca. 22 km to the south at Yoncaköy, Selçuk, Izmir, (locality 141, Fig. 1, and Supplementary Fig. 3). The two species were also found <20 km straight distance apart across suitable habitat (localities 43 of *Z. h. lyciensis* ssp. nov., and 125 of *Z. situla*, Fig. 1 and Supplementary Fig. 3); yet, a northern boundary farther inland can't be specified due to the lack of data. At its eastern distribution the Göksu River and the Mut basin may act as phylogeographic barrier, as it is suggested from other montane biota, such as between the mountain vipers *Montivipera xanthina* and *M. bulgardaghica* (Stümpel, Rajabizadeh, Avcı, Wüster, & Joger, 2016), or possibly as an eastern range limit for *Vipera anatolica* (Göçmen, Mebert, Karış, Oğuz, & Ursenbacher, 2017).

The two genetic samples we analysed from near the putative eastern end of the Lycian Ratsnake (locality 45 from Gündoğmuş, eastern Antalya [Supplementary Fig. 2] and locality 50 from Kayaönü, southern Karaman provinces, Fig. 1) are, indeed, assigned to *Z. h. lyciensis* ssp. nov. and the next genetic sample 140 km to the east (locality 75 at Arslanköy, Mersin, Fig. 1) across the Göksu River is *Z. h. tauricus*. However, notably, some samples in the region between localities 50 to 75 show somewhat intermediate colour patterns between *Z. h. lyciensis* ssp. nov. and *Z. h. tauricus*, e.g. large, clean, round blotches with thick black border anteriorly as in *Z. h. lyciensis* ssp. nov., but changing to more bar-shaped blotches with blackish edged dorsals inside the blotches posteriorly as in *tauricus*. Such intermediate characters can be seen also in more northern populations from the Sultan Mountains in northwestern Konya province (e.g. localities 99, 106; Fig. 1), with some individuals exhibiting even a double row of small squarish blotches posteriorly as in the nominotypical taxon *Z. h. hohenackeri*. However, whether these fuzzy trait compositions can be attributed to gene flow between subspecies demands in-depth molecular analysis based on a highly extended sampling across populations at the subspecies' distribution margins.

To the east, *Z. h. tauricus* ranges around the Gulf of İskenderum along Amanos Mountains farther south, confirmed by its mtDNA sequence data and predominantly a single row of mid-dorsal bar-like blotches. The typical *Z. h. tauricus*-pattern also dominates in morphologically assessed samples from Adana and Kahramanmaraş provinces (e.g. localities 82, 87, 88, Fig. 1; *Z. h. tauricus*-haplotype from Adana, locality 73, Fig. 1) showing a separation of two dorsal blotches into twin spots within the anterior first 20 dorsal blotches. The next (nearest) northern sample to a *Z. h. tauricus*-like morph (locality 87 in Kaharamamaraş, Fig. 1; no genetic sample) originates from Malatya province (locality 15 in Fig. 1; Supplementary Fig. 2) and shows less than 20 bar-shaped dorsal blotches and a clear nominotypical *Z. h. hohenackeri*-haplotype. The region between these two localities stretches over 140 km and might be a potential transition zone between these two subspecies. However, without a comprehensive sampling, any conclusions in this regard remain speculative.

In summary, we present here a substantially increased sample size of *Z. hohenackeri* compared to a previous study (Jandzik *et al.*, 2013), which allows us to identify a distinct geographic structure reflecting three subspecies based on molecular and morphological data, including the occurrence of the new subspecies *Z. h. lyciensis* ssp. nov. in southwestern Turkey, from where it was barely known one decade ago (Franzen *et al.*, 2008). The species' remarkable distributional extension of 160 km into Kastamonu province northwestern Turkey indicate that *Z. hohenackeri* may occur even farther west in dry valleys in the north. Given the results of our morphological investigation and individual findings, potential contact areas of the subspecies may exist. Yet, the current lack of samples from central regions in Turkey and in particular from southeastern Turkey hampers a reliable conclusion on that.



FIGURE 6. Comparison of head colour pattern differences between (a) *Zamenis hohenackeri lyciensis* ssp. nov. Kirkpinar Karanfill, Muğla, and (b) *Z. situla*, Lake Yliki, Greece.

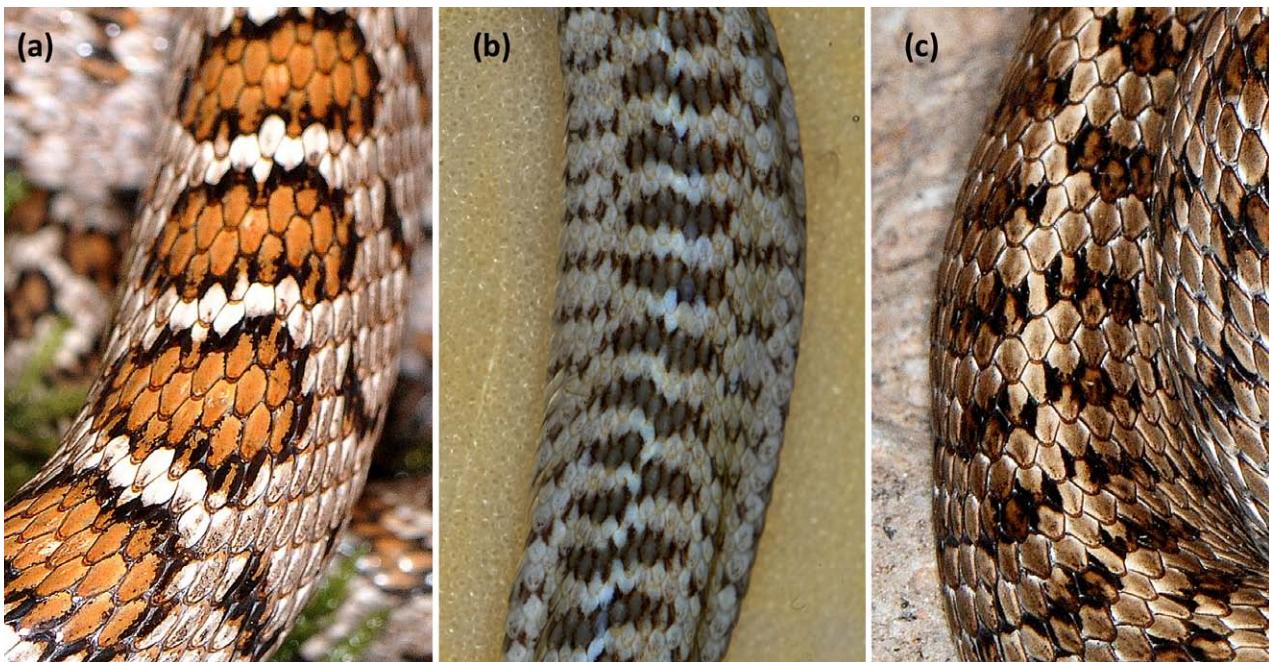


FIGURE 7. Comparison of dorsal colour pattern differences among the three subspecies of *Zamenis hohenackeri*: (a) *Z. h. lyciensis* ssp. nov.; (b) *Z. h. tauricus*; (c) *Z. h. hohenackeri*.

Conservation status. Despite being currently assigned to the “Least Concern” category by the IUCN (Hraouï-Bloquet *et al.*, 2009), the long-term viability of populations of *Z. hohenackeri* subspecies, in particular those of the proposed new subspecies, might be rather unclear.

The species is locally threatened by intensive habitat loss, e.g. in parts of Lebanon and Turkey. Forests along coastal areas of south-west Turkey, where *Z. hohenackeri* also occurs (although it is not restricted exclusively to forests), are substantially affected by human-caused fires that are linked to increased standards of living among the local population (Brauch, Liotta, Marquina, Rogers, & Selim, 2003). Further anthropogenic habitat degradation of the mountainous steppes includes dam construction, overgrazing, and intensive agriculture (Mebert, Göçmen, Karış, İğci, & Ursenbacher, 2016). Moreover, intensive anthropogenic destruction of the mountainous-arid regions in the eastern part of the Caucasian Isthmus has led to significant declines of the rat snake populations (Hraouï-Bloquet *et al.*, 2009).

We recommend continued monitoring of populations of *Z. h. hohenackeri* and *Z. h. tauricus* and a preliminary assessment of the conservation status of *Z. h. lyciensis* ssp. nov. that considers the potential impact of further habitat loss/alteration. The new subspecies should then be incorporated into the implementation of regional management schemes.

Acknowledgements

We are grateful to Nasit İgci, Mert Karis, Anil Oguz, Sylvain Ursenbacher, Thomas Ott, Mücahit Cakmak, Adem Adakul, Cagatay Altin, and Mehmet Zülfü Yıldız for substantial help in the field. We thank Michael Franzen for morphological data and information on specimens from the ZSM. Klaus Henle (UFZ, Germany) is gratefully acknowledged for providing facilities at the UFZ to carry out the analyses. Many persons provided photographic material, for which we would like to express our sincere thanks. These persons are named or credited in the respective Appendix.

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SUPPLEMENTARY FILE

Zootaxa

SUPPORTING INFORMATION

A new subspecies of *Zamenis hohenackeri* (Strauch, 1873) (Serpentes: Colubridae) based on morphological and molecular data

Sylvia Hofmann, Konrad Mebert, Klaus-Dieter Schulz, Notker Helfenberger, Bayram Göçmen & Wolfgang Böhme

Electronic Supplementary Table 1 – Information on sequence data used in the molecular analyses: Taxa, sample/isolate ID or voucher numbers, sample localities and GenBank accession numbers. *Z.* = *Zamenis*. MHNG = Natural History Museum Geneva; NHMW = Natural History Museum, Vienna; ZFMK = Zoological Research Museum Alexander Koenig.

Taxon	Locality	ID / No	Reference	mtDNA (<i>coI/cytb</i>)	nDNA (<i>vim/sptbn1</i>)
<i>Z. h. hohenackeri</i>	Armenia, Aboyan	ZFMK90596		AY122765 / KF639741	MH036677 /
<i>Z. h. hohenackeri</i>	Armenia, Aboyan	ZFMK88292	this study	AY122765 / KF639741	MH036676 / MH036696
<i>Z. h. hohenackeri</i>	Turkey, Artvin	hapH3	[1], NCBI	– / KF639742	– / –
<i>Z. h. taureicus</i>	Lebanon, Bcharra	ZFMK65000	this study	– / MH036670	MH036692 / MH036711
<i>Z. h. taureicus</i>	Lebanon, Bcharra	ZFMK60942	this study	MH036650 / MH036669	MH036691 / MH036710
<i>Z. hohenackeri</i>	Turkey, Aribeleni	KM091001	this study	MH036646 / MH036658	MH036684 / MH036703
<i>Z. hohenackeri</i>	Turkey, Konya	ZFMK71175	this study	MH036642 / MH036653	MH036685 / MH036704
<i>Z. h. taureicus</i>	Turkey, Hatay	ZFMK75874	this study	MH036649 / MH036666	– / MH036712
<i>Z. h. taureicus</i>	Turkey, Arslanköy	ZFMK81232	this study	– / MH036664	MH036693 / MH036713
<i>Z. hohenackeri</i>	Turkey, Muğla	BGO_1	this study	– / MH036661	MH036678 / MH036697
<i>Z. h. taureicus</i>	Turkey, Hatay	ZFMK56931	this study	– / MH036665	MH036690 / MH036709
<i>Z. h. taureicus</i>	Turkey, Hatay	BGO_2a	this study	– / MH036667	MH036686 / MH036705
<i>Z. h. taureicus</i>	Turkey, Hatay	BGO_2b	this study	– / MH036668	MH036687 / MH036706
<i>Z. hohenackeri</i>	Turkey, Muğla	BGO_3	this study	– / MH036654	– / –
<i>Z. hohenackeri</i>	Turkey, Kars	BGO_4	this study	MH036651 / MH036671	– / –
<i>Z. hohenackeri</i>	Turkey, Muğla	BGO_5	this study	MH036648 / MH036660	MH036679 / MH036698
<i>Z. h. taureicus</i>	Turkey, Mersin	BGO_6a	this study	– / MH036662	MH036688 / MH036707
<i>Z. h. taureicus</i>	Turkey, Mersin	BGO_6b	this study	– / MH036663	MH036689 / MH036708
<i>Z. hohenackeri</i>	Turkey, Antalya	BGO_7	this study	MH036643 / MH036655	MH36680 / MH036699
<i>Z. hohenackeri</i>	Turkey, Antalya	BGO_8a	this study	MH036644 / MH036656	MH036681 / MH036700
<i>Z. hohenackeri</i>	Turkey, Antalya	BGO_8b	this study	MH036645 / MH036657	MH036682 / MH036701
<i>Z. hohenackeri</i>	Turkey, Muğla	BGO_9	this study	MH036647 / MH36659	MH036683 / MH036702
<i>Z. hohenackeri</i>	Turkey, Hatay	BGO_10	this study	– / MH036672	MH036674 / MH036694
<i>Z. h. hohenackeri</i>	Turkey, Malatya	BGO_11	this study	MH036652 / MH036673	MH036675 / MH036695
<i>Z. h. hohenackeri</i>	Turkey, Mt. Ararat	SH1061	[2], NCBI	AY122765 / –	– / –
<i>Z. h. hohenackeri</i>	Turkey, Mt. Ararat	SH555	[2], NCBI	AY122695 / –	– / –

<i>Z. h. hohenackeri</i>	Turkey, Trabzon	hapGB	[3], NCBI	- / DQ902137	- / -
<i>Z. h. hohenackeri</i>	Russia, Chechenia	hapH1	[1], NCBI	- / KF639740	- / -
<i>Z. h. tauricus</i>	Turkey, Hatey	hapS1	[1], NCBI	- / KF639743	- / -
<i>Z. h. tauricus</i>	Lebanon, Les Cédres	hapS2	[1], NCBI	- / KF639744	- / -
<i>Z. h. tauricus</i>	Turkey, Adana	hapT1	[1], NCBI	- / KF639745	- / -
<i>Z. lineatus</i>			[2, 4], NCBI	AY122698 / HQ392567	- / -
<i>Z. lineatus</i>			[1, 2], NCBI	AY122698 / KF639746	- / -
<i>Z. longissimus</i>			[2, 4], NCBI	AY122696 / HQ392564	- / -
<i>Z. longissimus</i>			[2, 4], NCBI	AY122696 / HQ392566	- / -
<i>Z. persicus</i>			[2, 5], NCBI	AY122704 / DQ902117	KM870863 / KM870821
<i>Z. situla</i>			[2, 6], NCBI	AY122722 / JX315468	- / -
<i>Z. situla</i>			[1, 2], NCBI	AY122722 / KF639748	- / -
<i>Orthriophis taeniurus</i>			NCBI	KC990021 / KC990021	- / -
<i>Ptyas mucosa</i>			NCBI	GQ225662 / AF471054	- / -
<i>Pantherophis bairdi</i>			NCBI	AY122728 / GU073447	- / -
<i>Pantherophis guttatus</i>			NCBI	KU986236 / FJ267686	- / -
<i>Pantherophis obsoletus</i>			NCBI	KU985961 / DQ538344	- / -
<i>Pantherophis vulpinus</i>			NCBI	AY122734 / FJ267681	- / -
<i>Lampropeltis zonata</i>			NCBI	KU986141 / KF216207	- / -
<i>Lampropeltis alterna</i>			NCBI	FJ627813 / AF337080	- / -
<i>Lampropeltis calligaster</i>			NCBI	KU985581 / DQ902129	- / -
<i>Lampropeltis getula</i>			NCBI	KU985672 / FJ997683	- / -
<i>Coluber flagellum</i>			NCBI	KU986192 / KM403637	- / -
<i>Coluber constrictor</i>			NCBI	KU985863 / KM386560	- / -
<i>Salvadora grahamiae</i>			NCBI	KU985949 / KP765667	- / -

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Electronic Supplementary Table 2. Primer and annealing temperature used for DNA amplification (amp) and sequencing (seq).

<i>gene</i>	<i>Primer</i>		<i>Direction</i>	<i>Sequence 5' → 3'</i>	<i>annealingTm</i>	<i>Reference</i>
<i>cytochrome oxidase subunit 1 (co1)</i>	co1_F	amp + seq	forward	CATCCTGGGAGCAATTAAATTTCATC	59.7°C	this study
	co1_R	amp + seq	reverse	CCCGTATAGAATGTAATGATACTC	57.6°C	this study
<i>cytochrome b (cyt b)</i>	cytv60_1F	amp + seq	forward	TCTCAACCTGATGAAACTTC	53.2°C	this study
	cytv60_1R	amp + seq	reverse	GATGATAGTGAATGGAAGGATG	56.5°C	this study
<i>vimentin gene, intron (vim)</i>	cytv60_2F	amp + seq	forward	TCCATTCACTATCATCTCAATA	52.8°C	this study
	cytv60_2R	amp + seq	reverse	GACGAAAAGTTATGGGTG	54.5°C	this study
<i>beta-spectrin nonerythrocytic 1 gene, intron 1 (SPTBN1)</i>	vim_F	amp + seq	forward	TTAATGTACAATGCTAACATTTGCATG	58.2°C	this study
	vim_R	amp + seq	reverse	ACAGTGCAGAAGGAAACCTATTTC	59.3°C	this study
	SPTBN1_F	amp + seq	forward	GCCTATTCCATCATACACCTGTG	58.9°C	this study
	SPTBN1_R	amp + seq	reverse	GAAGAAACCCCAGGTAGAGTAC	60.3°C	this study

Electronic Supplementary Table 3. Details on *Zamenis hohenackeri* and *Z. situla* records shown in Figure 1. Coordinates were partly derived from Google maps. Chresonyms correspond to the references given with the localities (each separated by a semicolon). Specimens and references used for morphological evaluation are indicated in the “comment” column, as are those that refer to the respective type locality. Samples for molecular analyses are indicated in bold. BGO: Bayram Göcmen, private collection; BMNH: British Museum of Natural History; FMNH: Field Museum of Natural History, Chicago; MHNG: Natural History Museum of Geneva, Switzerland; NHMW: Natural History Museum in Vienna, Austria; NHMB: Natural History Museum Basel, Switzerland; ZDEU: Zoology Department, Ege University, Turkey; ZFMK: Zoological Research Museum Alexander Koenig, Germany; ZSM: Bavarian State Collection of Zoology in Munich, Germany. Reference numbers are given in brackets.

(Sub)species	Chresonym	Details on source and locality	No	Lat N_y	Long E_x	comment
	? <i>Zamenis hohenackeri</i>	Turkey, Abanoz, Anamur, Mersin: p. 148 [1]				<i>Haemorrhois ravergieri</i>
<i>Z. h. hohenackeri</i>		Armenia, Aboyan [Abovian]: vouchers ZFMK88292 , ZFMK90596	1	40.248385	44.609685	morphology
<i>Z. h. hohenackeri</i>	<i>Elaphe hohenackeri</i>	Armenia, Achmangan Dag: [2] reprinted in plate X [3], probably referring to Armaghan Mt., with high altitudes as low as 2250 m asl, yet suitable lower altitudes exist 15 km south in the Vardenis Mts.	2	40.051201	45.241284	morphology
<i>Z. h. hohenackeri</i>		Armenia, Gegard: voucher ZFMK24754	3	40.133333	44.816667	morphology
<i>Z. h. hohenackeri</i>		Armenia: voucher ZFMK17841, ZFMK17843		unknown	unknown	morphology (n=2)
<i>Z. h. hohenackeri</i>	<i>Coluber hohenackeri</i>	Azerbaijan, Chanlar (Göygöl): type locality acc. to [4]; p. 69, plate 2 [5]	4	40.583333	46.316667	type locality
<i>Z. h. hohenackeri</i>		Georgia, Borzhomi: voucher MHNG2008.6, ZFMK38232	5	41.854167	43.412500	morphology
<i>Z. h. hohenackeri</i>		Georgia, Boshuri: p. 580, Fig. 1 [6]	6	41.854549	43.894903	
<i>Z. h. hohenackeri</i>		Georgia, Mzcheta: p. 317[4]; voucher ZFMK24753	7	41.846888	44.703544	morphology
<i>Z. h. hohenackeri</i>		Georgia, Tbilissi: voucher ZFMK46912	8	41.710000	44.790000	morphology
<i>Z. h. hohenackeri</i>	<i>Elaphe hohenackeri taurica</i>	Iran, Maku, West-Azerbaijan: p. 158, 164, Fig. 3 [6] voucher FMNH171139	9	39.296124	44.508570	
<i>Z. h. hohenackeri</i>	<i>Zamenis hohenackeri</i>	Iraq, Choman, Erbil (Arbil): p. 19-21, Fig. 1b [7]	10	36.618278	44.878811	
<i>Z. h. hohenackeri</i>	<i>Zamenis hohenackeri</i>	Iraq, Hanai Dn (Hanay Den), Khormal, Halabdscha: p. 19-21, Fig. 1a [7]	11	35.283756	46.093386	
<i>Z. h. hohenackeri</i>		Turkey (NE): voucher NHMB21004		unknown	unknown	morphology
<i>Z. h. hohenackeri</i>	<i>Elaphe (hohenackeri) hohenackeri</i> ; <i>Elaphe hohenackeri</i> [partim]; <i>Elaphe hohenackeri</i> ; <i>Elaphe hohenackeri</i> [partim]; <i>Zamenis hohenackeri</i> ; <i>Zamenis hohenackeri</i> hohenackeri	Turkey, Agri Dagi (Mt. Ararat), İğdir: p. 14 [8]; p. 164 Fig. 2 [9]; p. 4 [10]; p. 124 [11]; voucher MHNG2403.8	12	39.652805	44.319217	morphology (voucher)
<i>Z. h. hohenackeri</i>	<i>Coluber hohenackeri</i> ; <i>Elaphe taurica</i> [partim]; <i>Elaphe hohenackeri</i> hohenackeri; <i>Elaphe hohenackeri</i> hohenackeri [partim]; <i>Elaphe hohenackeri</i> [partim]	Turkey, Amasya: p. 42 [12]; p. 1099 [13]; p. 274 [14]; p. 88 [15] vouchers BMNH 89.11.8.6-7, NHMW 15174.1, 2 and 15175; p. 123, Fig. 66 [16]; p. 158 [9]	13	40.651661	35.903797	morphology [12]
<i>Z. h. hohenackeri</i>	<i>Elaphe hohenackeri</i> ; <i>Zamenis hohenackeri</i>	Turkey, Artvin: p. 580 [6]	14	41.178983	41.824844	
<i>Z. h. hohenackeri</i>		Turkey, Asipinar-Doğanşehir, Malatya: voucher BGO_11/BGO_1606_11 , Supplementary Fig. 2C	15	38.101339	38.083703	morphology
<i>Z. h. hohenackeri</i>	<i>Elaphe hohenackeri</i>	Turkey, Aydinkavak, Kagizman, Aras valley, Kars: p. 332 [17] and pers. obs.	16	40.193455	43.320350	

		Konrad Mebert 2013				
Z. h. hohenackeri		Turkey, Badere, Hanönü, Kastamonu (pers. comm.); photo voucher with lower resolution available	17	41.610550	34.463964	
Z. h. hohenackeri		Turkey, between Günindi and Kuruyayla, Kars: 3 specimens in 2014 and 2015 by Mebert, Igci, Oguz, Kars, incl. photo vouchers	18	40.220600	43.294220	
Z. h. hohenackeri	<i>Elaphe hohenackeri</i>	Turkey, Cubula, Erenköy, between Borçka and Murgul, Artvin: p. 1163 [18]	19	41.305950	41.607439	
Z. h. hohenackeri		Turkey, Cukuraya, Kagizman, Kars: photo voucher by K. Mebert 2013	20	40.235658	42.928258	
Z. h. hohenackeri	<i>Zamenis hohenackeri hohenackeri</i>	Turkey, Deliktaş, Bitlis: p. 200, plate 89B [19], and photos by Sergé Bogaerts 02.05.2006 on turkherptil.org	21	38.356778	42.047314	
Z. h. hohenackeri		Turkey, Erzincan, 40 km from the city Erzincan: voucher ZSM 83/1996	22	39.602747	39.903288	morphology
Z. h. hohenackeri	<i>Zamenis hohenackeri</i>	Turkey, İğdır: p. 63 [20]; same as in p. 93 [21]	23	39.829466	44.120390	
Z. h. hohenackeri		Turkey, Kagizman, Kars: voucher MHNG1379.27	24	40.150000	43.100000	morphology
Z. h. hohenackeri	<i>Elaphe hohenackeri; Zamenis hohenackeri hohenackeri</i>	Turkey, Karakurt, Kars: p. 63[20]; p. 200, plate 89E [19]	25	40.162439	42.617660	
Z. h. hohenackeri		Turkey, Kaunos, Dalyan, Muğla: photo voucher on herpsafari.nl [22] by Bobby Bok	26	36.832777	28.632046	
Z. h. hohenackeri		Turkey, Kozlu Bucagi, Tokat: photo voucher on turkherptil.org, by M. Cakmak and A. Adakül, 27.04.2012	27	40.620511	36.495506	
Z. h. hohenackeri	<i>Elaphe hohenackeri hohenackeri</i>	Turkey, Macka, 25 km south of Trabzon, 1250 ft (381 m asl); p. 6, 54 [23]	28	40.809560	39.603153	morphology [23]
Z. h. hohenackeri		Turkey, Mokyc (Moxoene), Bahçesaray, Van: voucher ZSM 86/1918, probably Monastery of the Holy Savior of Moks ("Beyaz Kilise")	29	38.116203	42.835337	morphology
Z. h. hohenackeri		Turkey, Sarıkamış-Kazıkkaya, Kars: voucher BGO_4/2012_156 , Supplementary Fig. 2D	30	40.009900	42.696225	morphology
Z. h. hohenackeri	<i>Elaphe hohenackeri hohenackeri; Elaphe hohenackeri hohenackeri [partim]</i>	Turkey, Soganlı, Müküs, Siirt: p. 88 [15]; p. 123, Fig. 66[16]	31	38.051617	42.141343	
Z. h. hohenackeri	<i>Coluber leopardinus; Elaphe situla [partim]; Elaphe hohenackeri; Elaphe hohenackeri hohenackeri [partim]; Elaphe hohenackeri hohenackeri; Zamenis hohenackeri</i>	Turkey, Trabzon: p. 1098 [13]; p. 274 [14]; p. 67 [24]; p. 123, Fig. 66 [16]; p. 88 [15] with voucher NMSF 45309; p. 580 [6] citing p. 177 [25]	32	40.959125	39.737223	
Z. h. hohenackeri	<i>Elaphe hohenackeri hohenackeri; Elaphe hohenackeri hohenackeri [partim]</i>	Turkey, Vakfıkebir, Trabzon: p. 54 [23]; p.123, Fig. 66 [16]	33	41.023090	39.277305	morphology [23]
Z. h. hohenackeri		Turkey, Yeşilyazı-Ovacık, Tunceli: photo voucher on turkherptil.org, by Seyhan Yürek, 17.06.2014	34	39.331436	39.058742	
Z. h. hohenackeri	<i>Elaphe hohenackeri</i>	Turkey, Yüksekova, Hakkari: p. 63 [20]	35	37.630712	44.346867	
Z. h. lyciensis ssp. nov.		Turkey, 15 km ESE of Kumluca, Antalya: voucher ZFMK81224	36	36.320266	30.153063	
Z. h. lyciensis ssp. nov.	<i>Coluber tauricus; Elaphe taurica [partim]; Elaphe hohenackeri taurica [partim]</i>	Turkey, Akşehir, Konya: p. 499 [26]; p. 274 [14]; p. 176 [27]; voucher NHMW15173, p. 89 [15] and p. 123, Fig. 66 [16] and p. 45 [28]	37	38.341464	31.408311	morphology (voucher)
Z. h. lyciensis ssp. nov.		Turkey, Akyaka, Muğla: voucher BGO_1/2015_113 , Supplementary Fig. 1A	38	37.050811	28.297186	morphology
Z. h. lyciensis ssp. nov.	<i>Zamenis situla</i>	Turkey, Candır, S. Lake Köyceğiz, Muğla: p. 208-209 Fig 7 [29]	39	36.844739	28.588154	morphology
Z. h. lyciensis ssp. nov.		Turkey, Çetibeli-Marmaris, Muğla: voucher BGO_5/2012_55 , Supplementary	40	36.915759	28.277618	morphology

		Fig. 1B				
Z. h. lyciensis ssp. nov.		Turkey, Çığlıkara-Elmalı, Antalya: voucher BGO_7/Zh_1 , Supplementary Fig. 1F	41	36.522300	29.790236	morphology
Z. h. lyciensis ssp. nov.		Turkey, Demirli-Köyceğiz, Muğla: voucher BGO_9/BG_1504_9 , Supplementary Fig. 1D, and another specimen on turkerptil.org	42	36.966172	28.937344	morphology
Z. h. lyciensis ssp. nov.	<i>Elaphe hohenackeri taurica</i>	Turkey, Dutagacköy (Dutagaç fide [29]) Aydin: p. 149 and plate 14 Fig. B [30], and Supplementary Fig. 3F	43	37.675433	28.525776	
Z. h. lyciensis ssp. nov.	<i>Zamenis hohenackeri tauricus</i>	Turkey, east of Kalkan, Antalya: p. 270-273 incl. figs and map [29]	44	36.229110	29.448558	
Z. h. lyciensis ssp. nov.		Turkey, Gelesandra-Gündoğmuş, Antalya: voucher BGO_8/BG_160605 , two specimens, Supplementary Fig. 3A	45	36.862117	32.060803	morphology (n=2)
Z. h. lyciensis ssp. nov.	<i>Zamenis hohenackeri tauricus</i>	Turkey, Gömbe, Antalya: p. 204 and Plate 91B [19]	46	36.551877	29.657975	
Z. h. lyciensis ssp. nov.	<i>Elaphe situla</i>	Turkey, Gülmez Mountains (Gülmez Dağ), Antalya: p. 28 [31]	47	36.333300	30.083300	
Z. h. lyciensis ssp. nov.		Turkey, İztuzu-Gökbel, Muğla: voucher BGO_3/2012_177 , Supplementary Fig. 1C	48	36.777722	28.658589	morphology
Z. h. lyciensis ssp. nov.	<i>Elaphe situla</i>	Turkey, Karaveliler, Antalya: p. 26 [32]	49	37.203587	30.636391	
Z. h. lyciensis ssp. nov.		Turkey, Kayaönü, Karaman: voucher ZFMK 71175	50	36.627361	32.986025	morphology
Z. h. lyciensis ssp. nov.		Turkey, Kılıç, Anamur: photo voucher by Hikmet Meydan on turkiyeyabanhayati.org, 15.3.2018	51	36.232706	32.786479	
Z. h. lyciensis ssp. nov.		Turkey, Kirkpinar Karanfill, Aribeleni Yaylası, Muğla; tissue voucher KM091001 , p. 203 and Plate 90 F [19], Supplementary Fig. 1E	52	36.881224	29.202902	
Z. h. lyciensis ssp. nov.	<i>Elaphe hohenackeri</i> [partim]; <i>Elaphe hohenackeri taurica</i> ; <i>Zamenis hohenackeri</i>	Turkey, Kohu Dag, Elmalı, Antalya: p. 306, Fig. 1, [33], voucher MHNG2403.007; p. 149, plate 14 Fig. C [30];	53	36.502690	29.819595	type locality; morphology [33]
Z. h. lyciensis ssp. nov.	<i>Zamenis hohenackeri tauricus</i>	Turkey, Köyceğiz Lake, sw Hamitköy, Dalyan, Muğla: p. 270-273 incl. several Figs. [29]; p. 204 and Plate 91A, C [19]	54	36.896723	28.597647	
Z. h. lyciensis ssp. nov.	<i>Elaphe hohenackeri taurica</i> [partim]; <i>Elaphe hohenackeri</i> [partim]	Turkey, Küktür Köyü, Anamur, Mersin: p. 264 [34]; p. 306, Fig. 1 [33], voucher SZE 232/1976	55	36.183926	32.790931	morphology [33, 34]
Z. h. lyciensis ssp. nov.	<i>Zamenis situla</i>	Turkey, N Köyceğiz Lake, Dalyan, Yesilköy, Muğla: p. 208-209 Fig 7 [29]	56	36.992088	28.715952	
Z. h. lyciensis ssp. nov.		Turkey, Pedasa Antik Kenti, Merkez, Konacık, Bodrum, Mugla: photo voucher Supplementary Fig. 3H by Peter Graveson 6.3.2018, also provided by Orhan Taştekin on turkiyeyabanhayati.org,	57	37.062895	27.419382	
Z. h. lyciensis ssp. nov.	<i>Zamenis situla</i>	Turkey, Phaselis, Kemer, Antalya: p. 147 [35]	58	36.525266	30.552327	
Z. h. lyciensis ssp. nov.	<i>Elaphe situla</i> [partim]	Turkey, Sedişehir, Konya: p. 123, Fig. 66 [16]	59	37.419463	31.848279	
Z. h. lyciensis ssp. nov.		Turkey, Tahtali Dam, district Menderes, Izmir: photo voucher Supplementary Fig. 3D by Raşit Acar, also on turkiyeyabanhayati.org, 5.3.2018	60	38.136170	27.081826	
Z. h. tauricus	<i>Elaphe hohenackeri</i> ; <i>Elaphe hohenackeri taurica</i> ; <i>Zamenis hohenackeri tauricus</i> ; <i>Zamenis hohenackeri</i> cf. <i>hohenackeri</i>	Israel, Mt. Hermon: p. 67-70, Fig. 1-3 [36] voucher UHD; p. 263, Fig. 2 [37]; p. 193 [38]; p. 45, Fig. 6 [39]; p. 202 [40]; pp. 168-169, incl. Figs. [41]; p. 202 plate 90A [19]	61	33.323134	35.768526	morphology [36]
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Lebanon, 7 road-km east of Feraya, probably near Aayoun al Simane: p. 68-69, Fig. -4 [36], voucher HUJ8469	62	33.993825	35.845272	morphology

Z. h. tauricus	<i>Elaphe hohenackeri taurica</i> [partim]	Lebanon, Amnioum (Amioun): p. 158 [9], voucher 1957.13.1.89a	63	34.299016	35.808875	
Z. h. tauricus	<i>Elaphe hohenackeri taurica; Zamenis hohenackeri; Zamenis hohenackeri cf. hohenackeri</i>	Lebanon, Bcharré (Bischarri): p. 28-30, 30, Fig. 11 [42]; p. 580 [6]; p. 199 Fig. 37 and p. 202 plate 90B [19]; vouchers ZFMK60942 , CS97Eh1, ZFMK65000 , ZSM 2719/2005	64	34.259131	36.018009	morphology (vouchers, n=3)
Z. h. tauricus	<i>Elaphe hohenackeri</i> [partim]	Lebanon, Ghazir (former Syria): p. 23 [10], voucher NHMB8969	65	34.010515	35.675349	morphology
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Lebanon, Mazboud, Ain Zhalta: p. 41 [43]; voucher at AUB (Am. Univ. of Beirut)	66	33.733333	35.700000	
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Lebanon, Mazboud, Chim (Shhim, Chehime): p. 41 [43]; voucher at AUB (American Univ. of Beirut)	67	33.616667	35.483333	
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Lebanon, Mazboud, Dahr es (el) Souane (at Chtaura): p. 41 [43]; voucher at Lebanese University	68	33.828862	35.831852	
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Lebanon, Mazboud, Horj Ehden (Horsh Ehden): p. 41 [43]; voucher at American University of Beirut	69	34.316667	35.975483	
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Lebanon, Mazboud, NE of Saida: p. 41 [43]; voucher at American University of Beirut	70	33.600000	35.983333	
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Lebanon, Mazboud, Sannine (Mt. Sannin): p. 41 [43], voucher at Lebanese University	71	33.937270	35.844653	
Z. h. tauricus	<i>Zamenis hohenackeri tauricus</i>	Syria, Slenfe (Slinfah): p. 36, Fig. 3 [44]	72	35.582437	36.185002	morphology
Z. h. tauricus	<i>Zamenis hohenackeri</i>	Turkey, Adana: p. 580, Fig. 1 [6] genetic (NCBI)	73	36.991419	35.330829	
Z. h. tauricus	<i>Zamenis hohenackeri</i>	Turkey, Antakya, Hatay: p. 182 [45], 2 specimens; adjusted to the nearest rocky habitat 10 km west at 36.411355, 36.238441 since original coordinates point to unsuitable agriculture fields	74	36.401829	36.349788	
Z. h. tauricus		Turkey, Arslanköy, Mersin: voucher ZFMK81232	75	37.018567	34.289681	morphology
Z. h. tauricus	<i>Elaphe hohenackeri taurica</i> [partim]; <i>Elaphe hohenackeri</i> [partim]	Turkey, Bélen, Hatay: p. 264 [34]; p. 306 [33], voucher SZE111/1972	76	36.494651	36.193966	morphology
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Turkey, Birecik, Sanliurfa: p. 394 [46]	77	37.024993	37.977476	
Z. h. tauricus		Turkey, Çardak, Dörtçol-Hassa, Hatay;: voucher BGO_10/BGO_1604_10 , Supplementary Fig. 2E	78	36.843383	36.405572	morphology
Z. h. tauricus	<i>Elaphe hohenackeri</i>	Turkey, east of Saksak, ca. 20 km south of Harbiye, Antakya, Hatay, ca. 1000 m asl: p. 119 [47]; vouchers ZFMK56931 and ZFMK75874	79	35.973739	36.108890	morphology (vouchers, n=2)
Z. h. tauricus		Turkey, Gökcedağ-Hasanbeyli, Osmaniye: photo voucher on turkherptil.org, by Ali Bali, 19.05.2013	80	37.136211	36.617961	
Z. h. tauricus	<i>Zamenis hohenackeri cf. hohenackeri</i>	Turkey, Gözene, Yayladagh (Yayladağı) Mountains, Hatay: p. 202-203, plate 90C, E; BGO_2/2007_57 , 2 specimens, Supplementary Fig. 2F	81	36.063686	36.011753	morphology (vouchers, n=2)
Z. h. tauricus	<i>Coluber tauricus</i> Werner, 1898; <i>Elaphe hohenackeri taurica</i> [partim]	Turkey, Gülek, near Adana, Taurus Mountains, Mersin: <i>tauricus</i> type locality: p. 217 [48]; p. 123, Fig. 66 [16]; p. 45 [28]	82	37.257247	34.768648	type locality; morphology (n=2) [48]
Z. h. tauricus		Turkey, Keldaz, Osmaniye: photo voucher on turkherptil.org 21.7.2012 by Mehmet Celik and Süleyman Salkutlu	83	36.963821	36.369151	
Z. h. tauricus	<i>Zamenis situla</i>	Turkey, Küçük Kaymaklı-Nicosia, Northern Cyprus: p. 17 [49]; voucher ZDEU28/1962 and Supplementary Fig. 4	84	35.200000	33.38000	morphology
Z. h. tauricus		Turkey, Mersin, Aladağ: voucher BGO_6/2012_79 , two specimens,	85	36.952389	34.506933	morphology (vouchers, n=2)

		Supplementary Fig. 2B				
Z. h. tauricus	<i>Elaphe hohenackeri taurica</i> [partim]	Turkey, Sebil Köyü Tarsus, Mersin: p. 89-90 [15]; p. 123, Fig. 66 [16]; p. 45 [28]	86	37.129180	34.562318	
Z. h. tauricus		Turkey, Uludaz-Büyüksır, Kaharamamaras: photo voucher on turkherptil.org, by Tolga Demir, 09.06.2014	87	37.461522	36.651122	
Z. h. tauricus		Turkey, Yanalerki, Kozan, Adana: photo voucher on turkherptil.org, by Mehment Yıldız, 10.04.2014	88	37.636829	35.785948	
Z. h. tauricus		Turkey, Yarikkaya, İskenderun, Hatay: photo voucher on turkherptil.org, by Umit Kaplan and Savas Yıldır, 30.10.2011	89	36.582167	36.213394	
Z. hohenackeri	<i>Zamenis hohenackeri</i>	Armenia, Alvank: Plate 14, map point in Fig. 56b [50]	90	38.923968	46.342249	
Z. hohenackeri	<i>Zamenis hohenackeri</i>	Armenia, east of Atan: Plate 14, map point in Fig. 56b [50]	91	40.980864	44.973838	
Z. hohenackeri	<i>Zamenis hohenackeri</i>	Armenia, Jerwandaschat: Plate 14, map point in Fig. 56b [50]	92	40.110472	43.677939	
Z. hohenackeri	<i>Elaphe h. hohenackeri</i>	Armenia, Khosrov Forest State Reserve: p. 200, Plate 89D [19]	93	40.009585	44.890665	
Z. hohenackeri	<i>Zamenis hohenackeri</i>	Armenia, Tatev: Plate 14, map point in Fig. 56b [50]	94	39.388061	46.276608	
Z. hohenackeri	<i>Elaphe h. hohenackeri</i>	Iran, Kuh-e Rangrazi (Kuh Rang), Chuzestan-Isfahan: p. 158 [6] with voucher FMNH 171140	95	32.831848	49.471469	
Z. hohenackeri	<i>Elaphe hohenackeri taurica</i>	Iran, Miyaneh (Mianeh), East-Azerbaijan: p. 158 [6]	96	37.431122	47.721660	
Z. hohenackeri		Russia, Chechenia: p. 580, Fig. 1 [6]; point set into the Caucasus, however, there is no further locality information than Chechenia	97	42.659085	45.851653	
Z. hohenackeri		Turkey, Çaltıbozkır Mahallesi, Silifke, Mersin: pers. comm.; photo voucher with lower resolution available	98	36.524733	33.918897	
Z. hohenackeri	Zamenis hohenackeri taurica; Zamenis hohenackeri	Turkey, Dereçine, Afyonkarahisar: p. 493 [51]; p.236 [52]	99	38.462709	31.284179	
Z. hohenackeri		Turkey, Digor, Kars: pers. comm. by Mario Schweiger; no voucher	100	40.371486	43.436556	
Z. hohenackeri		Turkey, Erdemli, Mersin: pers. comm.; photo voucher with lower resolution available	101	36.628350	34.288675	
Z. hohenackeri		Turkey, Esertepé-Kemaliye, Erzincan: photo vouchers, several specimens, turkherptil.org, by Şevket Gültekin, 2011-2015	102	39.299600	38.504339	
Z. hohenackeri		Turkey, Güney Toroslar, Mersin: p.89-90 [15]; p. 123, Fig. 66 [16]; coordinates just represent the approx. overlay of the locality point on the map in Fig. 66	103	36.765331	33.436919	
Z. hohenackeri	<i>Elaphe hohenackeri</i>	Turkey, Kar Bogaz, Adana: p. 22-23 [53]	104	37.375330	34.678178	
Z. hohenackeri	<i>Elaphe hohenackeri taurica</i> [partim]	Turkey, Kargıcak (Kargıcak) Köyü Silifke, Mersin: p.89-90 [15], voucher SZE100.1965; p. 123, Fig. 66 [16]; p. 45 [28]	105	36.444655	33.655570	
Z. hohenackeri	<i>Elaphe hohenackeri taurica</i> ; <i>Elaphe hohenackeri taurica</i> [partim]	Turkey, Sultan Dagh, Akşehir, Konya: voucher ZSM-coll. Müller Nr. 2315 on p. 91, 94, Fig. 3 [2]; p. 66, plate X Fig. c [3]; p. 89-90 with voucher SZE79.1970 (=ZSM [SLM] 2315, considered lost) [15], p. 123, Fig. 66 [16]; p. 45 [28]	106	38.134465	31.598613	
Z. hohenackeri	<i>Elaphe hohenackeri</i>	Turkey, Tecer Mts., Ulaş, Sivas: p. 25 [53]	107	39.419306	37.143019	
Z. hohenackeri		Turkey, Uzungaburç, Silifke, Mersin: pers. comm.; photo voucher with lower resolution available	108	36.587593	33.925658	
Z. hohenackeri		Turkey, Yaglıca, Kars, 2000 m: pers. comm. (Mario Schweiger), no voucher	109	40.233055	43.328234	

<i>Z. hohenackeri</i>		Turkey, Yazılı, Karaman: photo voucher on turkherptil.org, by Ali Yağcı, 23.10.2014	110	37.134606	33.100169	
<i>Z. situla</i>		Greece, Asfendiou, Kos Island: photo voucher in Supplementary Fig. 3G by Bert Van de Bosch on 11.05.2015	111	36.834902	27.217867	
<i>Z. situla</i>		Greece, Chios Island: map 36, p. 244 [30]	112	38.386182	26.041619	
<i>Z. situla</i>		Greece, Lesvos Island: map 36, p. 244 [30]	113	39.234883	25.918777	
<i>Z. situla</i>		Greece, Rhodes Island: map 36, p. 244 [30]	114	35.912282	27.789273	
<i>Z. situla</i>		Greece, Rhodes Island: map 36, p. 244 [30]	115	36.118461	27.822178	
<i>Z. situla</i>		Greece, Rhodes Island: map 36, p. 244 [30]	116	36.347978	28.186335	
<i>Z. situla</i>		Greece, Samos Island: map 36, p. 244 [30]	117	37.666218	26.833817	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]	Turkey, Beykoz Istanbul: p. 123, Fig. 66 [16]; p. 67 [24]	118	41.112935	29.160311	
<i>Z. situla</i>	<i>Elaphe situla</i>	Turkey, Biga Peninsula, se Bayramic district, Çanakkale: p. 67, 71 with Fig. 1 [54]	119	39.806197	26.824654	
<i>Z. situla</i>	<i>Zamenis situla</i>	Turkey, Biga Peninsula, western Ayvacık district, Çanakkale: p. 67, 71 with Fig. 1 [54]	120	39.617764	26.256967	
<i>Z. situla</i>	<i>Zamenis situla</i>	Turkey, Bursa: photo voucher on turkherptil.org, by Semih Özen, 1.6.2017	121	40.217871	29.030373	
<i>Z. situla</i>	<i>Elaphe situla</i>	Turkey, Denizli: p. 63 [3]	122	37.783016	29.096333	
<i>Z. situla</i>	<i>Elaphe situla</i> ; <i>Zamenis situla</i>	Turkey, Efesus, Selçuk, Izmir: a specimen each by p. 579 [55]; p. 123, Fig. 66 [16]; Fig. on p. 274, and p. 277 [29]	123	37.942850	27.338154	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]	Turkey, Geyikdere Köyü, Altinova, Yalova: p. 123, Fig. 66 [16]	124	40.662921	29.473777	
<i>Z. situla</i>	<i>Zamenis situla</i>	Turkey, Geyre, Aydin: p. 234-235, Plate 106E [19]; photo voucher in Supplementary Fig. 3E by Bayram Göçmen and on turkherptil.org	125	37.708587	28.724887	
<i>Z. situla</i>	<i>Zamenis situla</i>	Turkey, Gökçeada Island, se. Gökçeada- or Zeytinli-Reservoir, Çanakkale: p. 77 [56]; p. 71, Fig. 1 [54]	126	40.143536	25.845743	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]	Turkey, Havuzdere Köyü, Altinova, Yalova: p. 123, Fig. 66 [16]	127	40.675647	29.464040	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]; <i>Elaphe situla</i>	Turkey, İstanbul: p. 1098 [13]; p. 274 [14]; p. 123, Fig. 66 [16]; p. 67 [24]; p. 18 [57]; p. 63, Plate IXd [3]	128	41.000000	28.900000	
<i>Z. situla</i>		Turkey, Iznik, Bursa: p. 28 [58]	129	40.428767	29.753708	
<i>Z. situla</i>	<i>Zamenis situla</i>	Turkey, Kaz Dag, Mehmetalani, Balıkesir: photo voucher on turkherptil.org, by Sükrü Cam, 8.5.2016	130	39.641993	26.957290	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]	Turkey, Kınık (Kınık), Izmir: p. 123, Fig. 66 [16]	131	39.076166	27.390502	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]	Turkey, Kürkü, border Usak-Manisa provinces: p. 63 [3]; p. 123, Fig. 66 [16]	132	38.727213	29.013034	
<i>Z. situla</i>	<i>Z. situla</i>	Turkey, Kuşadası, Izmir: p. 21 [59]	133	37.866667	27.266667	
<i>Z. situla</i>	<i>Zamenis situla</i>	Turkey, Orhangazi, Bursa: photo voucher on turkherptil.org, by Yüksel Calikoglu, 18.5.2015	134	40.484464	29.288645	
<i>Z. situla</i>		Turkey, Rasathane, Nif Mt., Izmir: photo voucher in Supplementary Fig. 3B by Bayram Göçmen on 25.03.2008	135	38.399664	27.277203	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]	Turkey, Savaştepe Balıkesir: p. 123, Fig. 66 [16]	136	39.382366	27.653896	

<i>Z. situla</i>	<i>Elaphe situla</i>	Turkey, Spil Mountain National Park, Spil Dağı, south of Manisa: p. 65 [60], and photo voucher 15.4.2011 on turkherptil.org. by Bayram Göçmen	137	38.582898	27.426725	
<i>Z. situla</i>	<i>Elaphe situla</i> [partim]	Turkey, Tokmak Köyü Altınova, Yalova: p. 123, Fig. 66 [16]	138	40.677548	29.548851	
<i>Z. situla</i>	<i>Coluber situla</i> Linnaeus, 1758; <i>Coluber leopardinus</i> ; <i>Elaphe situla</i> [partim]; <i>Zamenis situla</i> ; <i>Elaphe situla</i>	Turkey, type locality re-designated to Izmir: p. 63 [3]; p. 1098 [13]; p. 274 [14]; p. 123, Fig. 66 [16]; p. 234, Plate 106 D [19]	139	38.423694	27.142890	type locality
<i>Z. situla</i>		Turkey, Urla, Izmir: photo voucher in Supplementary Fig. 3A by Ozgur Can Sonmez, also on turkiyeyabanhayati.org, 27.3.2017	140	38.295704	26.783432	
<i>Z. situla</i>		Turkey, Yoncaköy, Selcuk, Izmir: photo voucher in Supplementary Fig. 3C by Tanju Yavuz, provided by Yusuf Kumlutas	141	37.986402	27.251123	
<i>Z. situla</i>	<i>Zamenis situla</i>	Turkey, Zeytinli, Balıkesir: p. 3 [61]	142	39.616839	26.947118	

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Electronic Supplementary Fig. 1. Selected life *Zamenis hohenackeri lyciensis* sp. nov. illustrating some geographic variation from west to east. **A)** Akyaka, district Ula, Muğla (locality 38, Fig. 1); **B)** Çetibeli, district Marmaris, Muğla (locality 40, Fig. 1); **C)** İztuzu-Gökbel, district Ortaca, Muğla (locality 48, Fig. 1); **D)** Demirli, district Köyceğiz, Muğla (locality 42, Fig. 1); **E)** Kirkpinar Karanfilli, Aribeleni Yaylasi, district Dalaman, Muğla (locality 52, Fig. 1); **F)** Çığlıkara, district Elmalı, Antalya (locality 41, Fig. 1). All photos taken by Bayram Göçmen, except E) by Konrad Mebert.



Electronic Supplementary Fig. 2. Selected life *Zamenis hohenackeri* ssp. illustrating some geographic variation. Alphabetic sequence of capital letters in figures reflects records from west to east (A to D) followed by more southern records (E and F). **A**) dimorphic gender in *Z. lyciensis* ssp. nov.: orange-, light-border blotched female and yellow-, thick-bordered blotched male from Gelesandra, district Gündoğmuş, Antalya (locality 45, Fig. 1); **B**) two subadults *tauricus* from Aladağ, district Toroslar, Mersin (locality 85, Fig. 1); **C**) *hohenackeri* from Asipaşar, district Doğanşehir, Malatya (locality 15, Fig. 1); **D**) *hohenackeri* from Kazıkkaya, district Sarıkamış, Kars (locality 30); **E**) *tauricus* from Çardak, district border between Dörtyol and Hassa, Hatay; **F**) *tauricus* from Gözene, Samandag, Hatay (locality 81, Fig. 1). All photos taken by Bayram Göçmen.

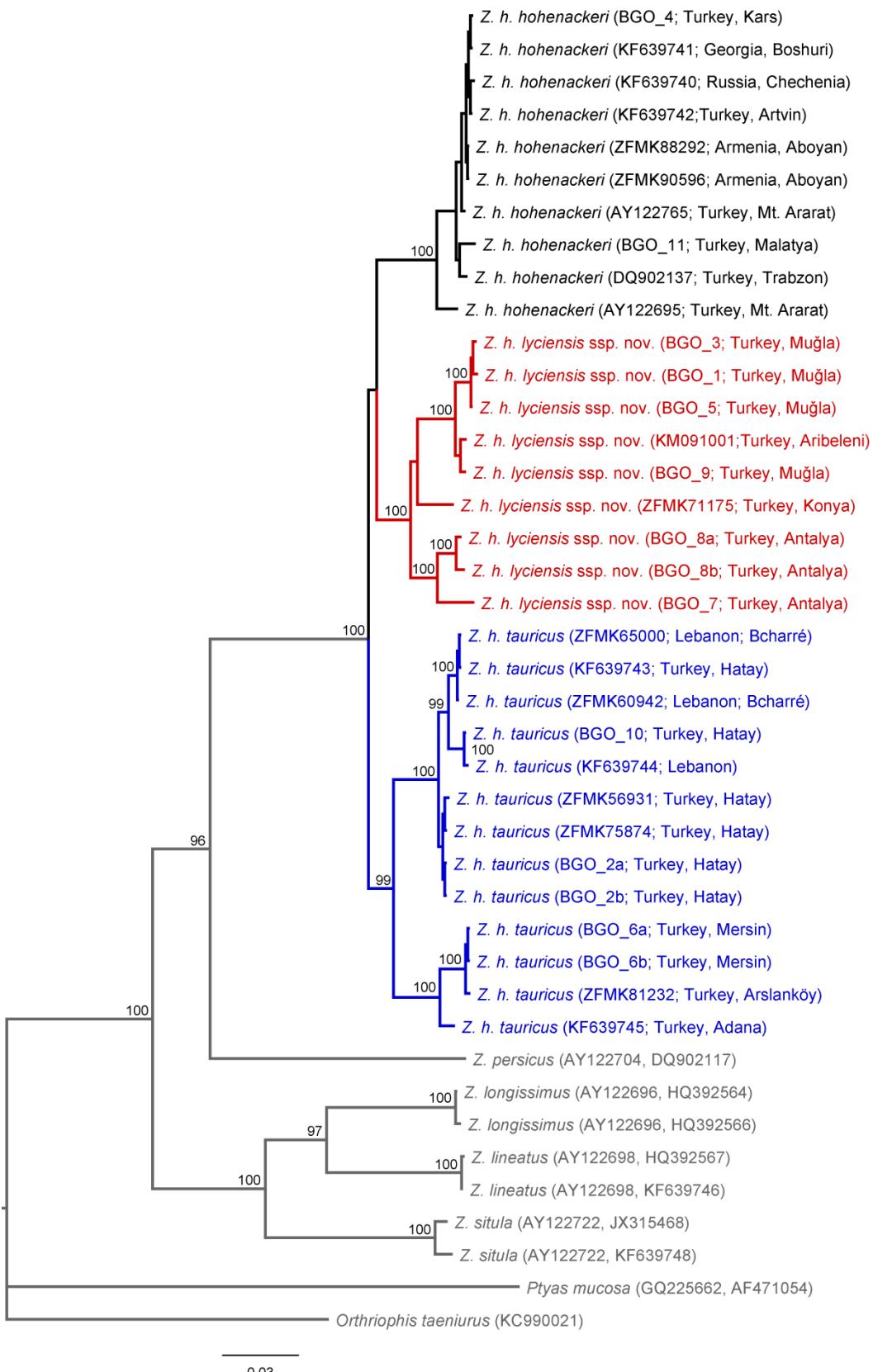


Electronic Supplementary Fig. 3. Proximate records and potential contact zone (sympatry) of *Zamenis situla* and *Z. hohenackeri* in western Turkey with specimens displayed from north to

south. Associated locality numbers in Fig. 1 are given in parenthesis: **A)** *Z. situla* from Urla, Izmir (locality 140), photo via Ozgur Can Sonmez; **B)** *Z. situla* from Rasathane, Nif Mountain, Izmir (locality 135), photo by Bayram Göçmen; **C)** *Z. situla* from Yoncaköy, Selcuk, Izmir (locality 141), photo by Tanju Yavuz via Yusuf Kumlutus; **D)** *Z. h. lyciensis* ssp. nov. from Tahtalı Dam, district Menderes, Izmir (locality 60), photo by Rasit Acar; the photo is only available in lower resolution. The red lines in the inset image (**D**) point to traits typical for *Z. hohenackeri*. This Lycian Ratsnake record is surrounded by records of herein depicted *Z. situla* at ca. 30 km northwest (specimen **A**), and northeast (specimen **B**), and 22 km south (specimen **C**). Most proximate records between *Z. situla* and *Z. hohenackeri* in southeastern Aydin province: **E)** *Z. situla* from Geyre, Aydin (locality 125), photo by Bayram Göçmen; **F)** *Z. h. lyciensis* ssp. nov. from Dutagacköy, Aydin (locality 43), photo by L. Trutnau. These two specimens were found <20 km straight distance apart from each other across suitable habitat. Proximate records 30 km straight line between **G)** *Z. situla* from Kos Island, Greece (locality 111), photo by Bert Van de Bosch, and **H)** *Z. h. lyciensis* ssp. nov. from Pedasa Antik Kenti, Merkez, Konacik, district Bodrum, Mugla province (locality 57), photo by Peter Graveson, provided by Orhan Taştekin. The minimum distance across sea surface, Kos strait, between island and mainland is 5 km. Photos and use, coordinates or other locality information from external sources were provided with permission by the respective authors.



Electronic Supplementary Fig. 4. *Zamenis hohenackeri tauricus* from Northern Cyprus: Dorsal view and head close up of the male (ZDEU28/1962) from Küçük Kaymaklı-Nicosia, leg. Hürmüz A. Cemal, 01.09.1962. Image contrast enhanced to increase resolution of the colour pattern. This specimen is the only record from Cyprus; it might represent a translocated specimen from the mainland to east (Levant) or northeast (Bay of Iskenderun), or part of a native Cypriot population. Suitable habitat exists at Lapithos (Kyrenian Mt. Range, western parts).



Electronic Supplementary Fig. 5. Maximum-likelihood tree based on 1191 bp sequenced from *co1* and *cytb* genes. The tree was reconstructed by RAxML v.8.2.9 using the GTRGAMMA model. Bootstrap values $\geq 95\%$ are shown above the nodes. Sample/voucher number and locality are shown in parenthesis. Z. = *Zamenis*; Z. h. = *Zamenis hohenackeri*.

Electronic Supplementary Table 4. Potential diagnostic nucleotide sites among *Zamenis hohenackeri* sequences of the *sptbn1* (274 bp) and the *vim* (291 bp) gene fragment. ‘Altstate’ is the site present in the remaining taxa and indicated in light blue in the aligned sequences under the table. Further variable sites are denoted in yellow. Taxa abbreviated as follows: Ho = *Z. h. hohenackeri*, Ly = *Z. h. lyciensis* ssp. nov., Ta = *Z. h. tauricus*.

Site	Subspecies	State	Altstate
<i>sptbn1</i> : 260 bp Pos.	HoTa	C	deletion (all <i>lyciensis</i> sequences except one [BGO1])
<i>vim</i> : 72 bp Pos.	HoTa	G	A or R

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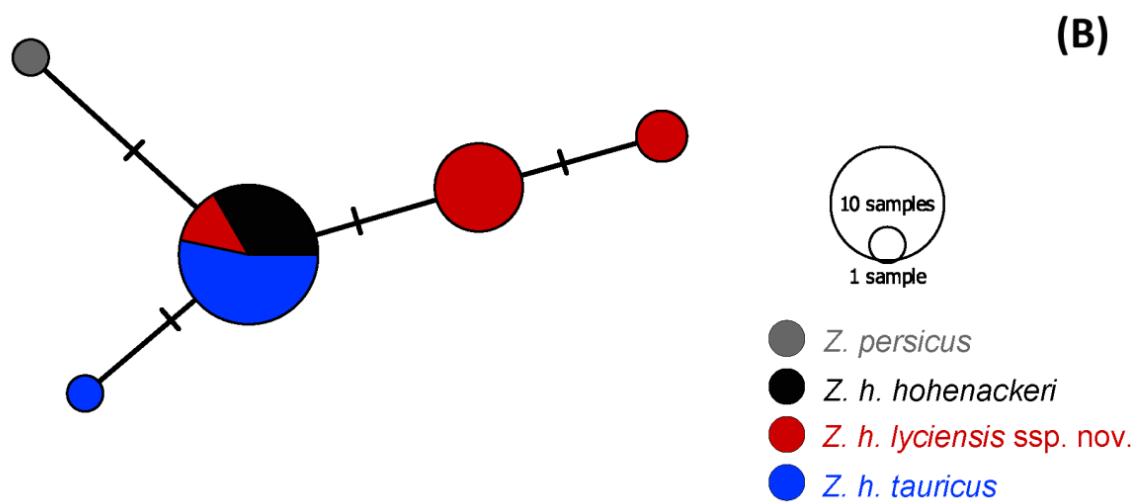
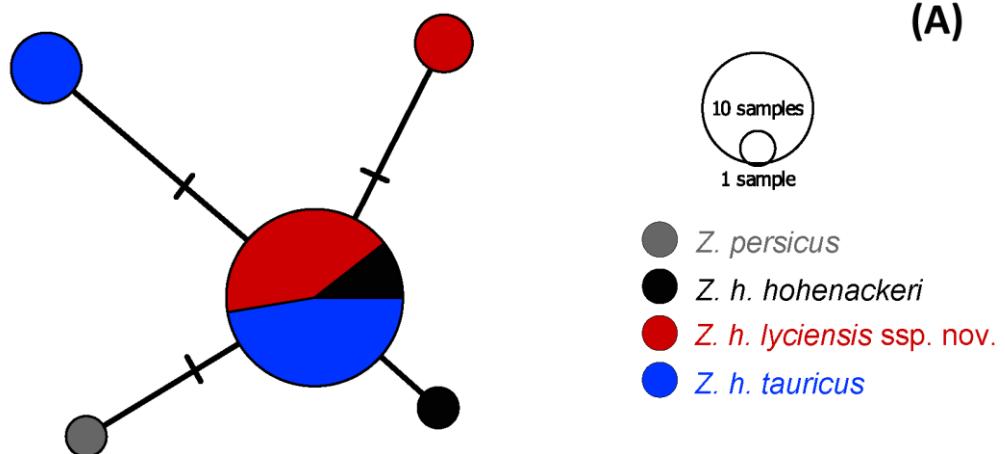
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>lyciensis_BGO5_vim
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ACTCATCAAAGCTAGTCAGAATATTTCATATAATTCAAGGTCAATTGTTGGCTATCACTAATCTAAATGATTCCCTGTGTTATCCTGAAGCTGCAAGACAGAAATAGGTTCTTCTGCAGTGT



Electronic Supplementary Fig. 6. TCS haplotype networks obtained by PopART v.1.7 for subspecies of *Zamenis hohenackeri* and *Z. persicus* inferred from individual nuclear loci (*sptbn1* and *vim*). Note that PopART masks any gaps during analysis (e.g. in *Z. h. lyciensis* ssp. nov., see Supplementary Table 4).

Electronic Supplementary Table 5. Age estimates (in million years) for each node referenced in Figure 2. Estimates (div. time) are given in millions of years, with the 95% highest posterior density interval (HPDI). Divergence time estimation based on node constraints obtained from fossil records (=this study), and estimated ages in previous studies (Burbrink & Lawson 2007; Kyriazi et al. 2012; Salvi et al. 2018).

Node no	This study div. time	95% HPDI	Burbrink & Lawson 2007	Kyriazi et al. 2012	Salvi et al. 2018
1	30.4	24.7-37.4	29.3-30.6		
2	27.9	22.7-35.0			
3	25.3	21.5-31.2	26.5-28.1		9.7-17.5
4	22.2	16.8-28.1	ca. 24.0	ca. 22.0	6.4-11.4
5	21.7	20.4-23.8	27.2-30.5	ca. 21.5	
6	20.0	17.6-23.0	ca. 23.7	ca. 20.0	7.0-12.5
7	18.3	12.9-24.4	22.0	17.0	5.0-8.9
8	17.2	16.3-18.5	16.2-16.9		
9	16.3	15.4-17.8			
10	12.9	11.6-14.7	13.0-24.6	ca. 12.0	
11	12.9	8.9-16.5			
12	11.4	7.7-15.1			
13	11.1	7.1-15.2	ca. 12.0		
14	10.2	7.0-14.1	10.8-12.3		3.8-6.8
15	7.4	4.6-10.8			2.9-5.3
16	6.0	4.2-8.8			
17	4.1	2.4-6.3			
18	3.3	1.9-4.8			
19	2.8	1.6-4.2			
...	<2.0				

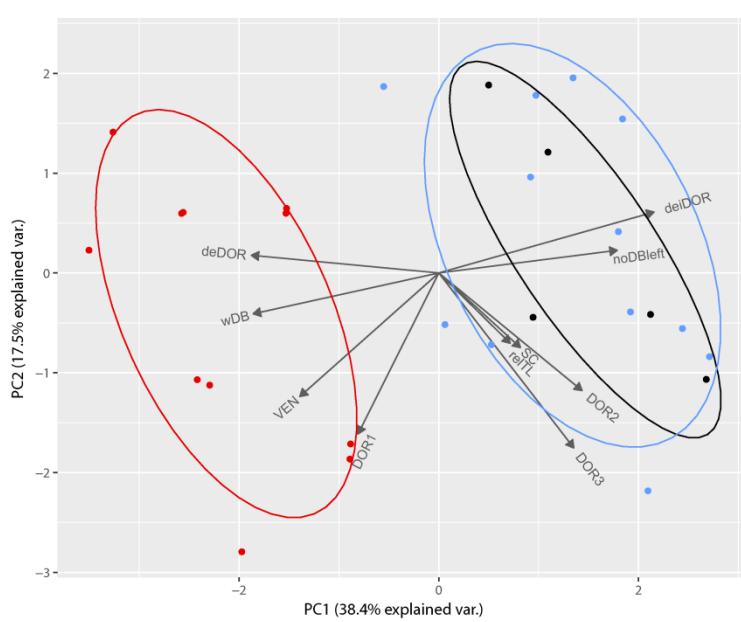
References

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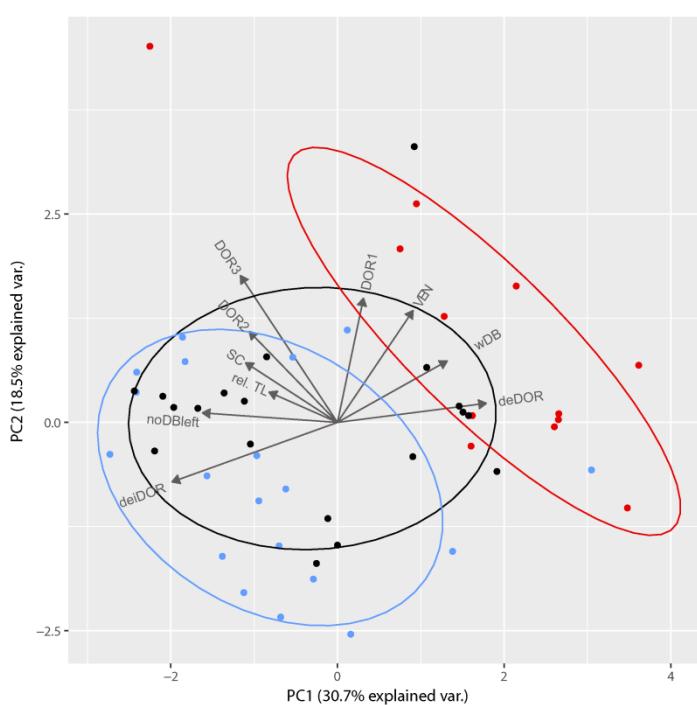
Electronic Supplementary Table 6. Results of principal component analyses on 10 morphological traits of *Zamenis hohenackeri* based in the imputed reduced (n = 28) and complete (n = 50) dataset.
deDOR = dark edges on surrounding dorsals of blotches; deiDOR = dark edges on inner dorsals of blotches; DOR1/2/3 = number of dorsal scale rows at position of the 10th ventral plate, at mid-body, and at one head length before the anal plate; wDB = width of dorsal blotches in dorsal scales; noDBleft = number of dorsal blotches counted on the left side; SC = number of subcaudals; relTL = relative tail lengths (residuals of the regressed on SVL); VEN = number of ventral scales. Main loadings on PC1 are indicated in bold.

REDUCED DATASET	PC1	PC2	PC3
<i>Eigenvalues</i>	3.84	1.75	1.37
Traits	Factor loadings		
<i>deDOR</i>	-0.40	0.06	-0.15
<i>deiDOR</i>	0.46	0.19	-0.11
<i>DOR1</i>	-0.17	-0.50	-0.17
<i>DOR2</i>	0.30	-0.37	0.28
<i>DOR3</i>	0.29	-0.55	-0.11
<i>wDB</i>	-0.39	-0.13	0.30
<i>noDBleft</i>	0.38	0.07	-0.18
<i>relTL</i> (residuals TL~SVL)	0.15	-0.22	-0.51
<i>SC</i>	0.17	-0.23	0.64
<i>VEN</i>	-0.29	-0.39	-0.21
Total variance explained (%)	0.38	0.18	0.14
Cumulative total variance explained (%)	0.38	0.56	0.70
COMPLETE DATASET	PC1	PC2	PC3
<i>Eigenvalues</i>	3.07	1.85	1.28
Traits	Factor loadings		
<i>deDOR</i>	0.44	0.07	-0.21
<i>deiDOR</i>	-0.49	-0.23	0.10
<i>DOR1</i>	0.08	0.47	-0.55
<i>DOR2</i>	-0.26	0.34	0.39
<i>DOR3</i>	-0.28	0.56	-0.14
<i>wDB</i>	0.32	0.23	0.34
<i>noDBleft</i>	-0.40	0.04	0.15
<i>relTL</i> (residuals TL~SVL)	-0.20	0.12	-0.07
<i>SC</i>	-0.27	0.23	-0.26
<i>VEN</i>	0.22	0.42	0.51
Total variance explained (%)	0.31	0.18	0.13
Cumulative total variance explained (%)	0.31	0.49	0.62

(a)



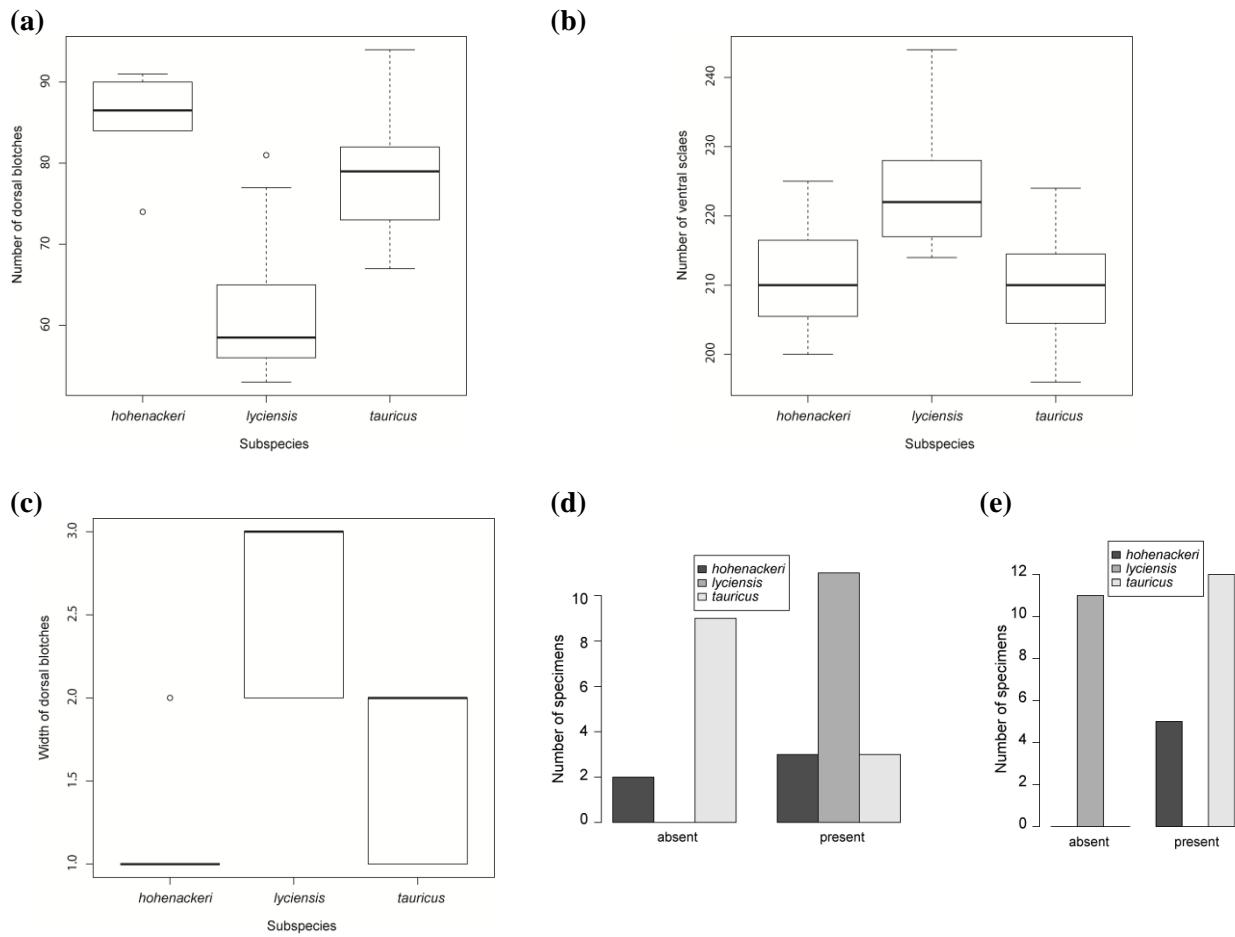
(b)



Electronic Supplementary Fig. 7. Position of *Zamenis hohenackeri* specimens belonging to the different subspecies along PC1 and PC2 based (a) on the imputed reduced (n = 28) and (b) complete (n = 50) dataset. *hohenackeri* = *Z. h. hohenackeri*; *lyciensis* = *Z. h. lyciensis* spp. nov.; *tauricus* = *Z. h. tauricus*; deDOR = dark edges on surrounding dorsals of blotches; deiDOR = dark edges on inner dorsals of blotches; DOR1/2/3 = number of dorsal scale rows at position of the 10th ventral plate, at mid-body, and at one head length before the anal plate; wDB = width of dorsal blotches in dorsal scales; noDBleft = number of dorsal blotches counted on the left side; SC = number of subcaudals; relTL = relative tail lengths (residuals of the regressed on SVL); VEN = number of ventral scales.

Electronic Supplementary Table 7. Variation in morphological traits in the *Zamenis hohenackeri* subspecies (means in parentheses). deDOR = dark edges on surrounding dorsals of blotches (percentage of specimens where trait is present/number of specimens); deiDOR = dark edges on inner dorsals of blotches (percentage of specimens where trait is present/number of specimens); DOR1/2/3 = number of dorsal scale rows at position of the 10th ventral plate, at mid-body, and at one head length before the anal plate; wDB = width of dorsal blotches in dorsal scales; noDBleft = number of dorsal blotches counted on the left side; SC = number of subcaudals; SVL = snout-vent length; TL = tail lengths; VEN = number of ventral scales.

Taxon	deDOR	deiDOR	DOR1	DOR2	DOR3	wDB	noDBleft	SC	SVL	TL	VEN
<i>Z. h. hohenackeri</i> (n=19)	60/5	100/6	23-25 (24)	23	17-19 (18)	1-2	74-91 (85)	52-78 (63)	220-727 (484)	38-200 (97)	200-225 (211)
<i>Z. h. lyciensis</i> ssp. nov. (n=12)	100/11	0/11	23-25 (24)	21-25 (23)	17-19 (18)	2-3	53-81 (62)	50-68 (60)	270-760 (473)	40-190 (96)	214-244 (224)
<i>Z. h. tauricus</i> (n=19)	16/3	100/5	23-25 (23)	23-25 (23)	17-19 (18)	1-2	67-94 (80)	50-73 (61)	220-666 (393)	40-142 (79)	196-224 (210)



Electronic Supplementary Fig. 8. Box- and barplots of the diagnostic variables to separate *Zamenis hohenackeri lyciensis* ssp. nov. from the two known subspecies. **(a)** Number of dorsal blotches (noDBleft): ANCOVA $F_{2,24} = 16.42$, $p < 0.001$; Tukey's post hoc test, t-value $_{lyciensis/tauricus} = 4.75$, p-value < 0.001 ; t-value $_{hohenackeri/lyciensis} = -5.08$, $p < 0.001$. **(b)** Number of ventral scales (VEN): ANCOVA $F_{2,42} = 8.63$, $p < 0.001$; Tukey's post hoc test, t-value $_{[lyciensis/tauricus]} = -3.90$, p-value < 0.001 ; t-value $_{[hohenackeri/lyciensis]} = 3.62$, $p < 0.01$. **(c)** Width of dorsal blotches (wDB): Kruskal–Wallis $H_2 = 27.69$, $p < 0.001$, Dunn's post hoc test $p < 0.05$ for all pairings. **(d)** Presence/absence of dark edged dorsals around blotches (deDOR): Fisher's exact test, $p < 0.001$, $p_{[lyciensis/tauricus]} < 0.001$; $p_{[hohenackeri/lyciensis]} = 0.083$; $p_{[hohenackeri/tauricus]} = 0.280$. **(e)** Presence/absence of dark edged inner dorsals of blotches (deiDOR): Fisher's exact test, $p < 0.001$, $p_{[lyciensis/tauricus]} < 0.001$; $p_{[hohenackeri/lyciensis]} < 0.001$; absent in *Z. h. lyciensis* spp. nov., while present in *Z. h. hohenackeri* and *Z. h. tauricus* specimens.