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To be or not to be *tchernovi*: a taxonomic revision of the snake genus *Micrelaps* (Squamata: Serpentes), in Israel

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Abstract

The enigmatic snake genus *Micrelaps* has uncertain phylogenetic affinities. The type species of the genus, *Micrelaps muelleri*, inhabits the Southern Levant. Snakes inhabiting the Jordan River Valley just south of the Sea of Galilee have been described as a new species, *Micrelaps tchernovi,* based on their distinct colour patterns, despite *M. muelleri* being well known to be variable in colour-pattern traits. Here we use morphological and molecular data to examine the taxonomic status and phylogenetic affinity of Levantine *Micrelaps*. We show that all scalation, colour, and pattern-related traits are extremely variable across the range of these snakes. Some morphological features show clinal variation related to temperature and precipitation, and snakes with a '*tchernovi*' morph are merely at one end of a continuum of morphological variation. Both 'classical *muelleri*' and '*tchernovi*' morphs occur in syntopy in the Jordan Valley and elsewhere in Israel. Against this background of high morphological variation, neutral genetic markers show almost no differentiation between snakes, no genetic structure is evident across populations, and no differences are to be found between the two putative species. We conclude that Levantine *Micrelaps* belongs to a single, morphologically variable, and genetically uniform species, *Micrelaps muelleri,* of which *M. tchernovi* is a junior synonym.

Key words: clines, Colour patterns, Jordan Valley, *Micrelaps muelleri*, *Micrelaps tchernovi* molecular phylogenetics, morphology

Hebrew abstract

תקציר

נחשים מהסוג *Micrelaps* (מחרוזן) מצויים בדרום הלבנט ובמזרח אפריקה. המין *Micrelaps muelleri* מצוי בדרום לבנון ודרום-מזרח סוריה, בצפון-מערב ירדן ואזורי הים התיכון של ישראל ובערבות הפלסטינית. נחשים מסוג זה מדרום בקעת הירדן הדרומית הוגדרו כמין נפרד, *Micrelaps tchernovi*, על בסיס דגמי הצבע שלהם, למרות השונות הרבה בדגמים של *M. muelleri*. בחנו את הסטטוס הטקסונומי של הסוג מחרוזן בישראל על בסיס נתונים מורפולוגיים ומולקולריים. מצאנו כי מחרוזונים בישראל מאופיינים בשונות גבוהה של דגמי הצבע. לפרטים רבים דגמי ביניים בין שני הטיפוסים ששימשו לבדל את *M. tchernovi* מ-*M. muelleri*, וחלקם אף מצויים מחוץ לרצף זה. חלק מהתכונות המורפולוגיות ששימשו להפרדת המינים קשורות לטמפרטורה ולמשקעים. נחשים המתאימים לתיאור של *M. tchernovi* מצויים באזור שחון והם במיוחד ולכן ייתכן שמאפייניהם הם אדפטציה לתנאי האקלים בדרום בקעת הירדן. פרטים עם מאפיינים של שני ה'מינים' ופרטים המציגים דגמי ביניים חופפים גיאוגרפית בחלק נרחב של תחום התפוצה של הסוג בישראל. על רקע זה של שונות מורפולוגית גבוהה, לא מצאנו הבדלים בסמנים הגנטיים הניטרליים שבחנו בין פרטים שסווגו מורפולוגית ל-*M. tchernovi* לבין פרטים שזוהו כ-*M. muelleri*, לפרטים להם מופעי ביניים ולפרטים מפוספסים. לא מצאנו מבנה גנטי בין מחרוזונים בישראל ולא הבדלים בין מופעים ובין שני המינים המשוערים. אנו מסיקים לכן כי מחרוזונים מדרום הלבנט שייכים למין יחיד, מגוון מורפולוגית ואחיד גנטית, *Micrelaps muelleri*. *Micrelaps tchernovi* אינו אלא Junior synonym.

Introduction

The genus *Micrelaps* Boettger, 1880 (Squamata: Serpentes) comprises four species of snakes, two distributed in the Levant and two in East Africa (Bouskila & Amitai 2001; Rasmussen 2002; Uetz *et al.* 2020). The gap between the Levantine and African species is some 2400 km at its narrowest point (Roll *et al.* 2017). *Micrelaps muelleri* Boettger, 1880, the type species of the genus, was described from Jerusalem, Israel, and is distributed in the Southern Levant (Fig. 1): in Israel and the Palestinian Authority/West Bank, Jordan, Lebanon, and Syria. The two East African species are *M. vaillanti* (Mocquard, 1888) ranging from Kenya and Tanzania in the south, through Uganda and South Sudan, to Ethiopia and Somalia, and *M. bicoloratus* Sternfeld, 1908, from Kenya and Tanzania. The fourth species, *M. tchernovi* Werner, 2006, was described almost 100 years after the first three, and is endemic to the northern Jordan Valley, south of the Sea of Galilee in Israel and Jordan (Fig. 1). *Micrelaps* is generally recovered within the superfamily Elapoidea, though its phylogenetic position within it is ambiguous: Portillo *et al.* (2018, 2019) recovered the genus as monophyletic, yet its phylogenetic placement shifted between studies and datasets, preventing clear assignation to a family (see also Zaher *et al.* 2019).

The phylogenetics of the two Levantine species, *M. muelleri* and *M. tchernovi*, have never been thoroughly studied. *Micrelaps muelleri* was described based on two specimens, an adult, and a juvenile, from the surroundings of Jerusalem ("stamen aus der Umgebung von Jerusalem in Palästina"; Boettger 1880). *Micrelaps tchernovi* was described by Werner (Werner *et al.* 2006) based on a holotype from Ubeidiya, just south of the Sea of Galilee, in Israel (32.69N, 35.56E), some 105 km north-north-east of Jerusalem. Three *M. tchernovi* paratypes from Israel were collected from Ashdot Ya'akov and Deganya, in the vicinity of the type locality (less than 10 km away; Meiri *et al.* 2018), and another specimen from "Massad" in Israel, presumably Masada (32.68N, 35.60E) some 3.5 km east of the type locality. Two additional paratypes are from localities further south (i.e., closer to Jerusalem) in the Jordanian (Eastern) side of the Jordan Valley ("Kurayyimah" and "Wadi Yabis", see map in Werner *et al.* 2006).

Micrelaps muelleri is better known than *M. tchernovi*. It is small (up to 630 mm total length and a weight of 27 g; Feldman *et al.* 2016; Jamison 2019; Boaz Shacham, pers. comm. to SJ), with a relatively flat head, not distinct from the neck, and very small eyes (Disi *et al.* 2001; Werner *et al.* 2006). It typically has alternating black and white/ yellowish bands across its body. *Micrelaps muelleri* mostly feeds on smaller snakes (ophiophagous) and skinks. It is nocturnal, terrestrial to fossorial, and is endemic to the Mediterranean and semi-arid biomes of the Southern Levant (Amr *et al.* 1997; Disi *et al.* 2001; Werner 2016; Roll *et al.* 2017; Bar & Haimovitch 2018; Jamison 2019). Data on its reproduction is scant, though Goldberg & Feldman (2014) reported two eggs in the oviduct of one female from Israel. *Micrelaps muelleri* is restricted to a ca. 20,000 km^2 area in southwestern Syria, western Lebanon, northwestern Jordan, the West Bank, and northern and central Israel, at altitudes from ~220 below to 1800 m above sea level (Roll *et al.* 2017).

Micrelaps tchernovi is very similar to *Micrelaps muelleri* in gross morphology and colour pattern, but allegedly differs in the shape, width, and number of the light and dark bands (see below). It is also a small snake (maximum 461 mm in total length and weight to 10.5 g; Steinhardt Museum of Natural History TAU.R19142, measured in life, but this maximum is based on a much smaller number of specimens than for *M. muelleri*). Ecologically *M. tchernovi* is assumed to be very similar to *M. muelleri*, although suspected to have an affinity for more arid environments (Werner *et al.* 2006). Its geographic range is small (~360 km^2) and is entirely nested within the range of *M. muelleri* (Fig. 1).

Micrelaps muelleri is known to exhibit great inter- and intra-population morphological variation (Werner *et al.* 2006; Werner 2016; Jamison 2019). This variation is expressed in colour patterns, the size and shape of head scales, the number of transverse black/brown dorsal bands, whether the bands contact the venter laterally and whether the venter is uniformly dark or shows alternating dark and bright bands (i.e., whether there are 'rings' or "saddles'), and the ratio between the width of the light and dark transverse dorsal bands (Werner *et al.* 2006; Werner 2016; Jamison 2019). In some cases, there are even individuals with longitudinal stripes, or with both transverse bands and longitudinal stripes (Werner *et al.* 2006, Bar & Haimovitch 2018; authors' pers. obs.; Fig. 2 and see below). In Israel, *Micrelaps muelleri* also exhibits significant variation in the number of ventral and sub-caudal scales, and in tail length, between males and females (Werner *et al.* 2006; and see below).

The sole molecular phylogenetic studies comprising specimens of *Micrelaps,* by Portillo *et al.* (2018, 2019), included two of the four recognized species of the genus: a single specimen of *M. bicoloratus* and five specimens of *M. muelleri* from Israel. No samples classified as *M. tchernovi,* or of *M. vaillanti,* were included, thus their phylogenetic position and relationships remain unclear.

While conducting natural history research on the species *M. muelleri* during the years 2016–2019, the first author observed a number of specimens which apparently fit the description of *M. tchernovi*, despite being found in regions from where only *M. muelleri* was reported (Jamison 2019). Furthermore, some specimens seemed to display morphologies intermediate between those of *M. muelleri* and *M. tchernovi*, and some apparently agreed with neither form. We have also encountered specimens with both *M. tchernovi* and *M. muelleri* morphologies at the same time of night, during the same periods of the year, on the ground, in similar habitats. Werner *et al.* (2006) report that the two taxa are parapatric, with "no intergradation", except for possible "limited sympatry" in Wadi Yabis in Jordan. However, we observed seemingly intermediate patterns and potentially geographically clinal variation in colouration suggesting neither claim was clear-cut.

FIGURE 1. The known distribution of *M. muelleri* (black) and *M. tchernovi* (yellow). The Northern part of *M. muelleri's* range is not shown. It is poorly understood, resting only on a single vague 1880's verbal report from Latakia, in western Syria (Lortet 1883), a 1952 specimen From "Syria… Tripolis" (presumably Tripoli, NW Lebanon; Battersby 1953), and a 1995 specimen from "10 km W of Qal'at al Hosn – Crac des Chevaliers; 300 m a.s.l." in SW Syria near the Lebanese border (Bischoff & Schmidtler 1997). The map is drawn based on our own observations, the scientific literature, and specimens in the collections of the Hebrew University of Jerusalem and the Steinhardt Museum of Natural History, Tel Aviv University.

The similar morphology and ecology, and the sympatric and syntopic distribution of the two species, together with the significant morphological polymorphism of *M. muelleri*, suggest that a re-evaluation of the taxonomy of Levantine *Micrelaps* is in order. We therefore re-examine the taxonomy of Israeli *Micrelaps* using an integrative approach, combining morphological and molecular data, to establish the number and identity of species found in the Southern Levant. We further examine geographic clines in diagnostic characters across the climatic gradient in Israel.

FIGURE 2. Examples of variability in morphology between *Micrelaps* specimens in the Steinhart Museum of Natural History. Colour pattern terminology after Werner *et al.* (2006): (A) specimen TAU.R19002, Ringed-Dark; (B) TAU.R18862, Other (semi-striped); (C) TAU.R16733, Ringed-Medium; (D) TAU.R1865, Saddled; (E) TAU.R9636, Saddled; Paratype of *M. tchernovi* ; (F) TAU.R14647, Ringed-Medium; (G) TAU.R9544, Striped; (H) TAU.R15700, Ringed-Dark; (I) TAU.R16426, Striped. Not to scale: (J) HUJ.R16864, holotype of *Micrelaps tchernovi*; (K) NMBA 2129 paralectotype of *M. muelleri*.

Methods

Morphological dataset

We examined alcohol-preserved specimens identified as *Micrelaps muelleri* and *Micrelaps tchernovi* from across their range in Israel (Table S1). These specimens are deposited in the herpetological collections of the Steinhardt Museum of Natural History, Tel Aviv (TAU.R, including a *M. tchernovi* paratype) and the Natural History Collections of the Hebrew University, Jerusalem (HUJ.R; including the holotype and other paratypes of *M. tchernovi*), as well as the paralectotype of *M. muelleri* from the Naturhistorisches Museum Basel (specimen NMBA 2129). The Lectotype, Senckenberg Museum für Naturkunde (SMF), SMF 20349 (Mertens 1967), could not be located at the SMF in August 2020 (Linda Mogk, pers. comm. to SM). We examined 27 additional specimens captured in the field during 2016–2019 by SJ (under permits 2016 / 41256 and 2017 / 41617 from the Israeli Nature and Parks authority). Specimens were released after capture and measurement. Individuals were sexed when possible, by internal examination of museum specimens and by examining tail lengths of specimens caught in the field (specimens with tails ~5% of body length are females, male tail/body length ratios are considerably higher; Werner 2016; Jamison, unpublished). Lastly, we analysed 63 photographs of Israeli and two Lebanese *Micrelaps* individuals. Of these photographs, 12 were sent to the first author by Israeli reptile experts (see acknowledgements) and 53 were observed on the social media. We only used verifiable photographic observations, possessing a picture of high enough quality to infer colour pattern with associated reported locality. These photographs were only used in analyses of dorsal (and when possible, ventral) patterns.

Morphological characters

We used the four colouration characters which Werner *et al.* (2006) used to differentiate *M. tchernovi* from *M. muelleri*. All are visible on both live and preserved specimens (Fig. 3): 1. The dark transverse bands contact the ventrals (forming 'rings'; in *M. muelleri*) or are restricted to the dorsal part, not touching the ventrals (forming 'saddles'; in *M. tchernovi*). 2. The ratio between the mean width of the dark bands and the mean width of the light bands (calculated as the mean count of scales on median line across each of three separate successive dark bands, and light intervals, at mid-body). According to Werner *et al.* (2006) in *M. tchernovi* ratios range from 0.28 to 1.43, as opposed to 0.67–5.67 in *M. muelleri* (i.e., *M. tchernovi* specimens are lighter, *M. muelleri* darker overall). 3. *M. tchernovi* has more transverse bands (average of 58, range: 52–66, compared to average of 45 and range of 29–60 in *M. muelleri*). We further note whether there are rings around one part of the body (e.g., the anterior) and saddles elsewhere (classified as 'mixed') – or whether the snake displays longitudinal stripes rather than transverse bands (classified as 'striped'). 4. *M. tchernovi* has uniformly black ventral scales whereas in *M. muelleri* the venter shows alternating dark and light rings, as does the dorsal side (forming 'rings') – but some specimens show a combination of both (mixed).

Additionally, Werner *et al.* (2006) found differences in the number of ventral scales (henceforth: ventrals) between males (248–262, mean 256 in *M. tchernovi* vs. 245–267, mean 251.5 in *M. muelleri*, p = 0.049). They did not stress this difference and under "validity" of the new form they discuss only the abovementioned colour differences writing that "Numerous snake species are recognized as distinct solely upon colouration". In our clustering algorithm (see below) we coded band number and width ratios as 0 for snakes with longitudinal dorsal stripes, as they had no dorsal bands.

Testing for geographic clines

To find if *Micrelaps* morphology is discrete, bimodal (supporting the existence of two species), or clinal (supporting the existence of a single species that responds to climatic conditions; Dowling 1950; Sinaiko *et al.* 2018; Hillis 2019, 2020) we tested for correlations between climatic variables at the localities where specimens were collected and the number and relative width of the dorsal bands (characters 2–3, above). All statistical analyses were performed in R v.4.0.2 (R Core Team 2020).
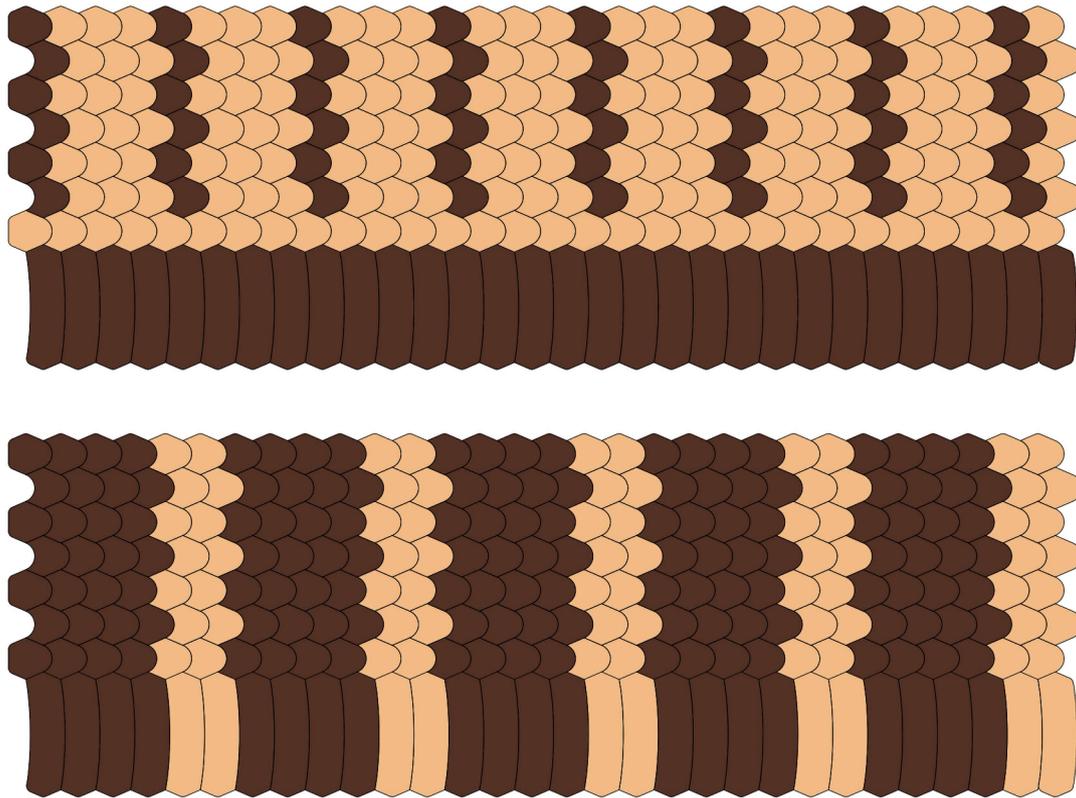
FIGURE 3. Cartoon representations of the putative variation in colour patterns between Micrelaps tchernovi (top) and M. muelleri (bottom). In both, the upper side (narrow dorsal scales) shows the dorsal pattern and the lower side (wide ventral shields) shows the ventral pattern. *Micrelaps muelleri* has fewer bands, which form 'rings' on the venter and the dark bands are wider and less numerous—whereas in *M. tchernovi* the venter is dark, the dorsal bands do not reach it (forming 'saddles'), the dark bands are relatively thinner and more numerous.

We ran ANCOVAs of the mean number of dark bands, and the mean ratio between width of dark bands to light bands (as response variables), against: altitude above sea level (a.s.l.), temperature (mean annual temperature, temperature seasonality, maximum temperature of the warmest month, and mean temperature of the warmest quarter), and precipitation (mean annual precipitation and precipitation seasonality, measured as coefficient of variation) (Bioclim variables BIO 1, BIO4, BIO5, BIO10, BIO12, and BIO15, respectively, downloaded from WORLDCLIM v.2; see Fick & Hijmans 2017). We designated sex as a categorical variable. After omitting specimens with missing data, we analysed 77 specimens for variation in mean number of bands, and 73 specimens for variation in mean ratio of width (Table S1). We first fitted a full model for each response variable, containing all predictor variables. We then performed backwards stepwise selection using the *caret* package (Kuhn 2020), where predictor variables are dropped sequentially based on lack of contribution to model fit, until we arrived at a final model where removal of additional predictors significantly reduced model fit. Model fit was assessed via reductions in root-mean-square error.

Clustering analyses

We used hierarchical clustering to find the optimal number of clusters in our *Micrelaps* dataset, based on morphological similarity using R v.4.0.2. Based on 106 specimens, we used the four aforementioned colour-pattern characters to perform morphological clustering, omitting specimens with missing data in any of the characters (Table S1). We constructed a dissimilarity matrix for all specimens based on the Gower similarity coefficient (Gower 1971) using the 'daisy' function in the *cluster* package (Maechler *et al.* 2019). We then converted the data to ordinated space using Principal Coordinates Analysis (PCoA) implemented in the 'cmdscale' function, so that morphologically similar observations are closely located in ordinated space.

We used specimens' locations in PCoA space to perform agglomerative complete linkage hierarchical clustering using the 'hclust' function, where specimens were grouped together based on similarity in PCoA coordinates, eventually generating a dendrogram representing their similarities. We then used the 'fviz_nbclust' function in the *factoextra* package (Kassambra & Mundt 2020) to calculate the optimal number of unique clusters using the elbow method: we plotted the total within-cluster sum-of-squares for different values of k number of clusters (from 1 to 10), and searched for the value of k at which there is a bend in the curve, i.e., higher values of k do not lead to a large decrease in within-cluster sum-of-squares.

Taxon sampling, DNA extraction and sequence analysis

In order to evaluate the genetic variability of *Micrelaps* in Israel and assess the validity of *M. tchernovi*, we conducted phylogenetic analyses using 16 *Micrelaps* specimens from across its distribution range in Israel: 11 specimens were sequenced in this study and sequences of additional five specimens, all from Israel, from the collections of the Steinhardt Museum of Natural History, were retrieved from GenBank (from Portillo *et al.* 2018). One specimen of *M. bicoloratus* was used as an outgroup (from Kelly *et al.* 2009). The sequences include a specimen, TAU.R19142, that fits the diagnostic characters of *M. tchernovi* (Y. Werner; pers. comm.), collected by SJ and AS from the type locality of *M. tchernovi* at Ubeidiya Site, Israel. Due to the method of specimen preservation, type specimens could not be sequenced. The 16 Israeli snakes sampled for molecular data represent most of the *Micrelaps* morphologies known to date in Israel, including 'classic' *M. muelleri* ('ringed', six specimens) and 'classic' *tchernovi* ('saddled', two specimens), intermediate forms ('mixed', six specimens), and forms that deviated from both descriptions ('striped', two specimens). Information of the specimens, their classified morphology and their GenBank accession numbers is presented in Table S2.

Genomic DNA was extracted from alcohol-preserved tissue samples using the Qiagen DNeasy tissue kit (Qiagen Inc., Valencia, CA, USA). Fragment of 1,077 bp of the mitochondrial gene Cytochrome b (*cytb*) and of 411 bp of the nuclear gene oocyte maturation factor MOS (*c-mos*) were amplified by a Polymerase Chain Reaction (PCR) using the L14910 and H16064 primers by Burbrink *et al.* (2000) and the FU-F and FU-R primers by Gamble *et al.* (2008), respectively. The PCR for the *cytb*/*c-mos* gene fragments, respectively, was performed in a volume of 25 μl with an initial denaturation step of 94°C for 5 minutes (min), followed by 40/35 cycles of denaturation at 94°C for 40/30 seconds (s), annealing at 46°C for 30s/53°C for 45s, and extension at 72°C for 1 min/1 min 30s; final extension step was set for 72°C for 5 min. Amplicons were visualized on a 1% agarose gel stained with SYBR Safe DNA gel stain (Invitrogen Corp., Carlsbad, CA, USA). Purifying and bi-directional sequencing was carried out by Macrogen (Macrogen Inc., Spain). Chromatographs were checked and the forward and reverse sequence contigs for each specimen were assembled and edited using Geneious R7 (v.7.1.9; Kearse *et al.* 2012). Sequences of each marker were aligned independently using MAFFT v.7.3 (Katoh & Standley 2013) with default parameters. The final alignments were translated to amino acids and no stop codons were detected.

Phylogenetic analyses and genetic diversity estimation

Phylogenetic analyses were performed for each marker independently under maximum likelihood (ML) and Bayesian inference (BI) frameworks. The ML analysis was conducted in RAxML v.8.1.2 as implemented in raxmlGUI v.1.5 (Silvestro & Michalak 2012). The analysis was performed with the GTRGAMMA model of sequence evolution and 100 random addition replicates. Nodal support was assessed with 1,000 bootstrap replicates. We conducted the BI analysis with MrBayes v.3.2.6 (Ronquist *et al.* 2012). We used jModelTest v.2.1.7 (Guindon & Gascuel 2003; Darriba *et al.* 2012) to select the best model of nucleotide substitution under the Bayesian information criterion (BIC), which resulted in the TrN+I model for *cytb* (nst=6, rate=equal) and F81 for *c-mos* (nst=1, rates=equal). The data were allowed to evolve at different rates. Two simultaneous parallel runs were performed with four chains per run (three heated, one cold) for two million generations with sampling frequency of every 200 generations. After examining the standard deviation of the split frequencies between the two runs and the Potential Scale Reduction Factor (PSRF) diagnostic, we discarded the first 25% of trees of each run and as burn-in. The remaining trees were combined in a majority rule consensus tree. Phylogenetic trees were visualized with FigTree v.1.4.3 (Rambaut 2016).

We used DnaSP v.5.10.01 (Librado & Rozas 2009) to estimate the genetic diversity for the mitochondrial marker *cytb*: Number of polymorphic (segregating) sites [S], number of mutations [Eta], Number of Haplotypes [h], Haplotype diversity [Hd], Nucleotide diversity [Π], Average number of nucleotide differences [k]. Inter-specific uncorrected *p*-distances with pairwise deletion and the number of conservative (C), variable (V), and parsimony informative (Pi) sites were calculated in MEGA v.7.0.14 (Kumar *et al.* 2016). Because the nuclear marker showed no variation (see Results) we did not repeat this procedure for it.

Results

Morphology

The morphological dataset comprised 112 museum specimens (99 identified in the collection as *M. muelleri*, six as *M. tchernovi* and seven intermediate or agree with neither description), 27 additional specimens were captured in the field (20 identified as *M. muelleri*, one as *M. tchernovi*, and six undetermined/intermediate; four of these 27 were released after a genetic sample was taken, hence they are counted as museum specimens as well). Finally, we used photographs of 66 specimens of Israeli and Lebanese *Micrelaps* snakes (53 *M. muelleri*, three *M. tchernovi*, 10 undetermined/intermediate; Table S1). The combinations of the colour patterns are presented in Table 1.

TABLE 1 – variation in the four morphological measures across the sample.

dorsal colour-pattern	ventral pattern	n	dark/light band width ratio			number of bands		
			minimum	maximum	mean	minimum	maximum	mean
Mixed	mixed	6	1.5	4.0	2.6	45.0	56.5	49.4
Mixed	NA	3	0.9	2.0	1.3	45.0	49.0	47.3
NA	NA	2	1.5	2.0	1.8	50.0	53.5	51.8
Rings	mixed	16	1	2.8	1.7	42.5	63.0	50.6
Rings	NA	64	1.0	3.8	2.0	32.0	59.0	45.6
Rings	rings*	77	1.1	3.3	2.1	30.5	55.0	45.1
Saddles	dark**	16	0.4	1.7	0.9	45.0	66.5	56.3
Saddles	mixed	1	1.3	1.3	1.3	54.5	54.5	54.5
Saddles	NA	6	0.5	1.5	1.2	46.0	54.5	49.2
Striped	dark	3	NA	NA	NA	NA	NA	NA
Striped	mixed	1	NA	NA	NA	NA	NA	NA
Striped	NA	5	1.6	1.6	1.6	60.5	60.5	60.5

N – number of snakes conforming to each pattern
NA –a character not available
*: 'classical' *M. muelleri* pattern: rings around the whole body
** 'classical' *M. tchernovi* pattern: dorsal 'saddles' and dark venter

The number of dark bands varied between 30.5 and 66.5 (Mean 46.6; Fig. 4A). The three specimens with the largest number of bands (65.5–66.5, n = 3, the next highest number is 63; Fig. 4A) are all from near the type locality of *M. tchernovi* (Fig. S1A). However, much variation is present, both between and within populations, and among specimens belonging to the same populations and areas. Specimens fitting the colour pattern of *M. muelleri* (dark bands reaching the venter forming rings around the body, wide black bands, and narrow yellow bands) can have as many as 63 bands (specimen a89: Table S1). Furthermore, 76% of the specimens identified as *M. tchernovi* based on having wide yellow bands, and dark bands forming saddles and not reaching the venter, have saddle counts within the range of overlap (52–63) between the species as defined by Werner *et al.* (2006).

For example, at the foot hills north east of the Gilboa mountain range, we found specimens with *M. muelleri* colour-pattern (few wide dark bands with narrow yellow bands between them, light-coloured venter), *M. tchernovi* colour-pattern (many narrow dark bands with wide yellow bands between them, dark-coloured venter), and intermediate colour-pattern (few, but wide dark bands, and a uniformly dark venter), all within a 500 meter radius.
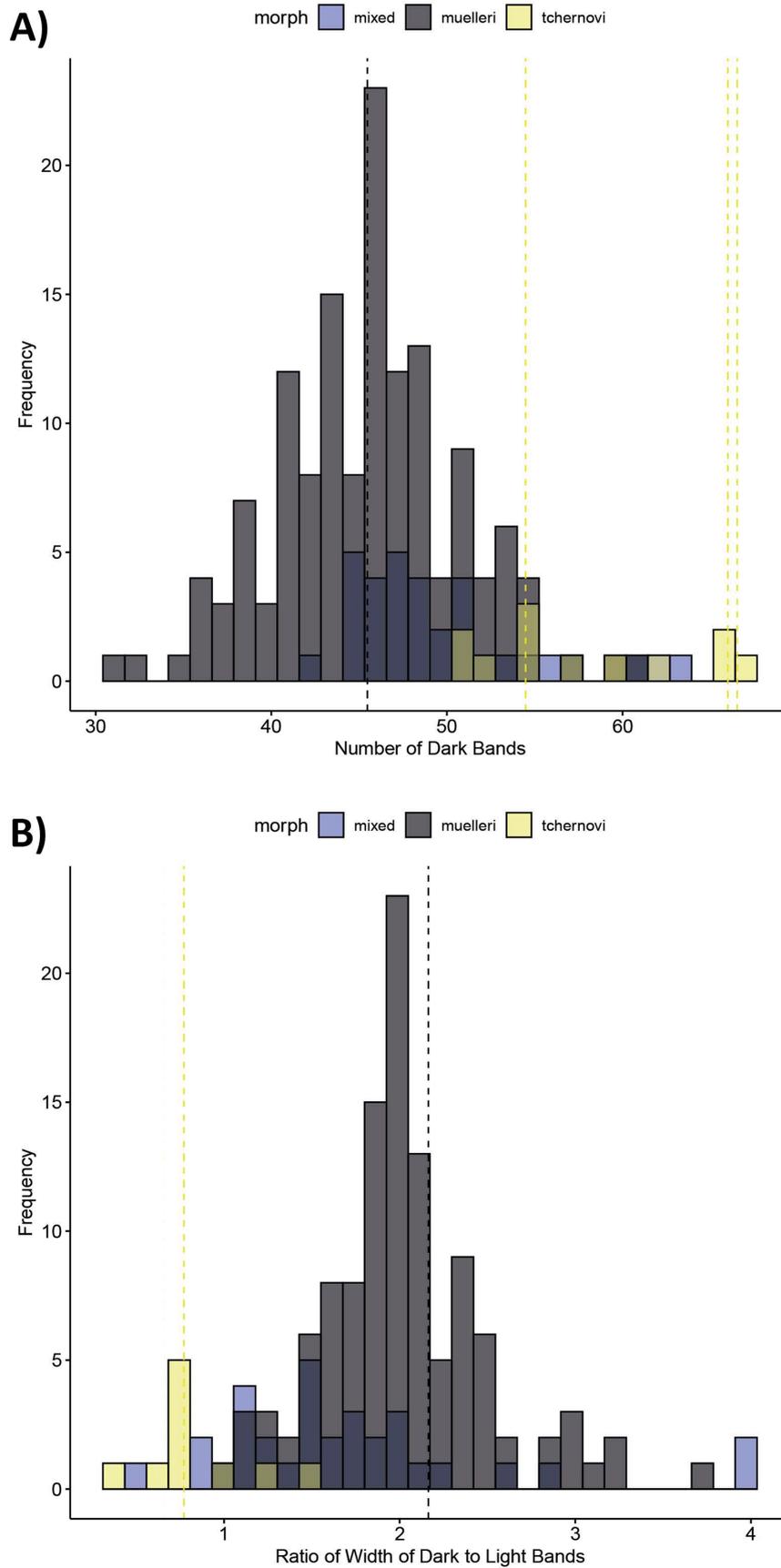
FIGURE 4. Histograms of A. the number of dark bands and B. the mean ratio of width of dark to light bands for Israeli *Micrelaps*. Histograms are coloured based on classified morphologies: *M. muelleri* in black, *M. tchernovi* in yellow, and mixed pattern in blue. Horizontal dashed lines represent the positions of type specimens.

Between Malkishua on the Gilboa and Bet Alpha 8.5 km to the north our dataset contains 25 specimens, including 18 ringed, four saddled and two mixed-morph individuals. Ventral colouration data are available for 16 of these: nine are ringed, three have a dark venter, and four a mix of rings and dark venter. They have 39–62 bands and dark/light band width ratios of 1–2.66 (Table S1).

The ratio of the widths of the dark bands to light bands varied from 0.4 to 5.0 (mean 1.9; Fig. 4B). Ten of 158 specimens had ratios lower than 1 (low ratios are supposedly a *M. tchernovi* characteristic). The lowest ratio (0.4) is from a specimen from the Jordan Valley (32.53N, 35.54E), 18 km south of the type locality of *M. tchernovi*, whereas the second lowest (0.5) is from near Meitar some 140 km to the south–south east (31.94N, 34.98E). The highest ratio (4.0) belongs to a specimen from Alummot (32.91N, 35.55E, HUJ.R20835), in the Jordan Valley, just 2.5 km north of the type locality of *M. tchernovi*.
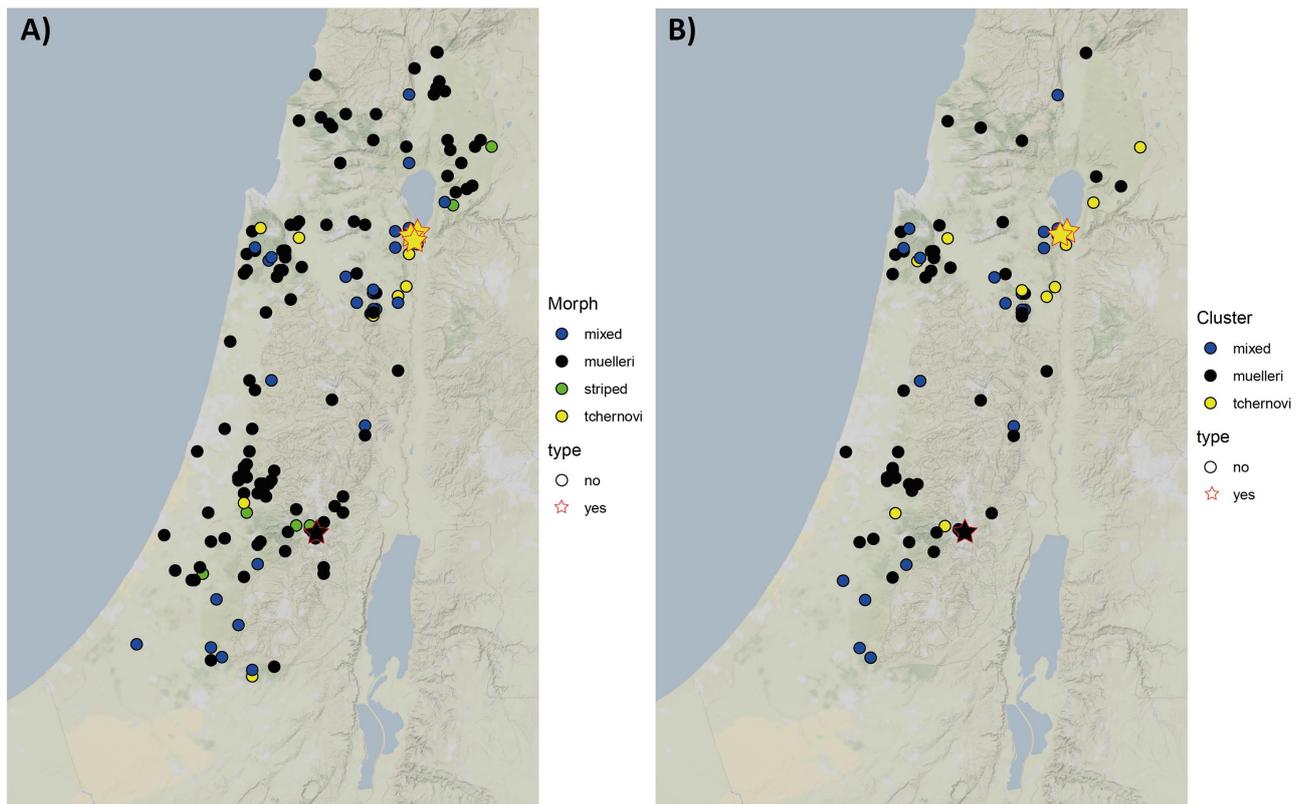

FIGURE 5. *Micrelaps* colour patterns in Israel and the West Bank according to A. classification based on the descriptions in Werner *et al.* (2006) and our observations, and B. hierarchical clustering with *k*=3 clusters. Colours are based on classified colour pattern: *M. muelleri* in black, *M. tchernovi* in yellow, mixed pattern in blue, and in green striped or partially striped conforming to neither morphology (note this category only exists in panel A). Type specimens are marked as stars with a red outline.

If we define *M. tchernovi* as snakes with saddled dorsum, a dark venter, a ratio of dark to light band width <1.45 and more than 51 bands, and *M. muelleri* as snakes with a ringed dorsum and venter, a ratio of 0.67 or higher, no more than 60 bands, according to the ranges in the description of *M. tchernovi* (Werner *et al.* 2006), 143 specimens adhere to the *M. muelleri* morph (including the paralectotype), and 15 to *M. tchernovi* (including all *M. tchernovi* types; we assign specimens with missing data as if they conform to type, e.g., saddled with high light/dark ratio are assigned to *M. tchernovi* if we have no band count). However, 33 specimens present a mixed suite of characters and nine are, at least partially, striped, hence conforming to neither. Geographically, both *M. tchernovi*–like and the mixed morphs are more widespread than previously thought (Fig. 5).

Our hierarchical clustering analysis recovered an optimal number of three clusters (Figs. 6 & S2). The first cluster included 15 specimens with saddled or striped dorsal colouration, uniformly dark dorsal colouration, 40–66 dark bands, and 0.4–1.72 width ratio. This cluster included the *M. tchernovi* type specimens. The second cluster included 68 specimens with ringed dorsal colouration, banded or uniformly dark ventral colouration, 37–55 dark bands, and 1.11–3.25 width ratio. This cluster included the paralectotype of *M. muelleri*. The third cluster included 23 specimens with ringed, saddled, or mixed dorsal colouration, mixed ventral colouration, 42.5–63 dark bands, and

1 to 4 width ratios. In general, the hierarchical clustering was mostly concordant with our own classification, with the main difference being our 'striped' morph falling within the *M. tchernovi* cluster (based on ventral colouration), one specimen we classified as *M. tchernovi* within the 'mixed' cluster (TAU.R19816), and four specimens we classified as 'mixed' within the *M. tchernovi* cluster (a9, a67, TAU.R18904, and TAUR.18905).
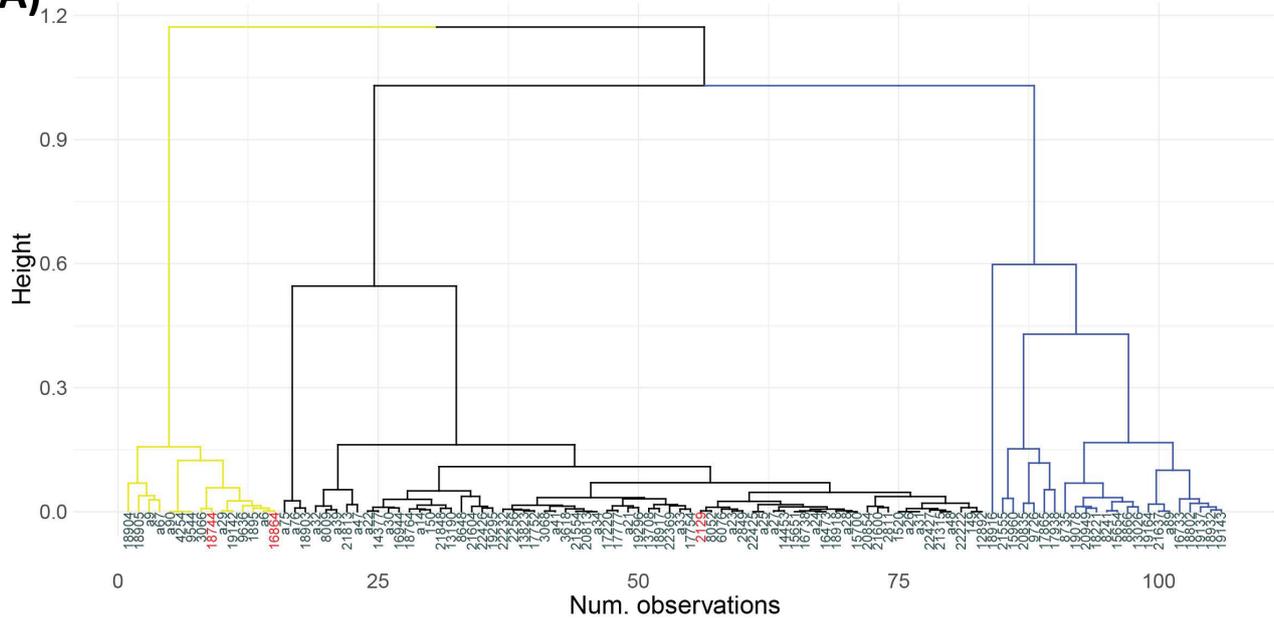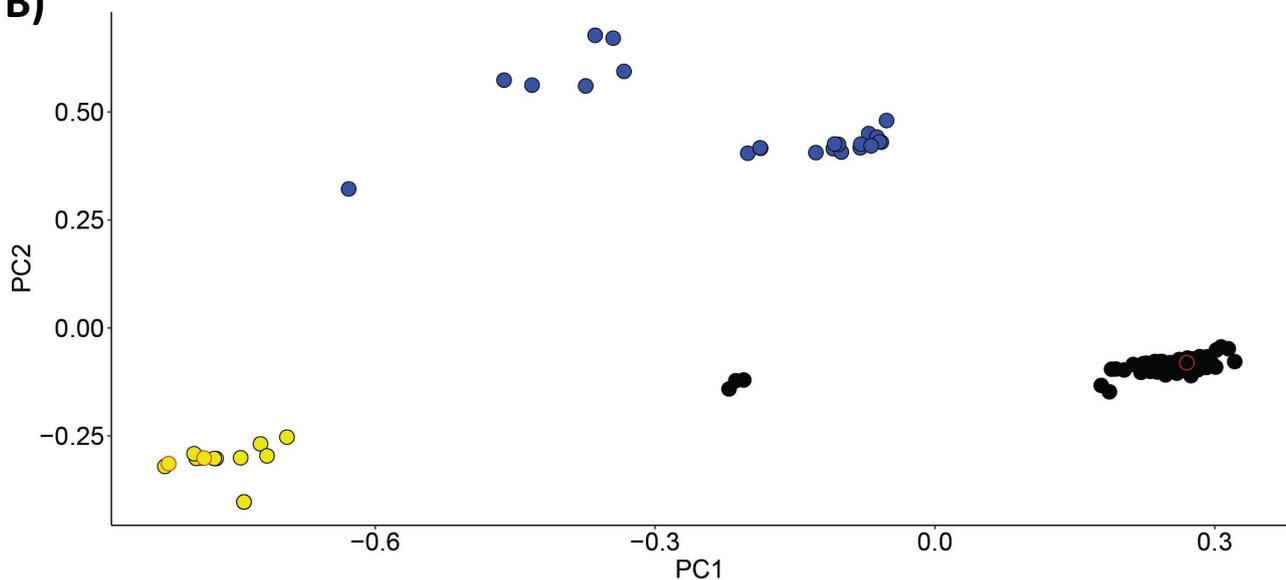
FIGURE 6. A. Hierarchical clustering of Israeli *Micrelaps*, based on morphological similarity. B. Positions of Israeli *Micrelaps* in PCoA space. Colours correspond to three colour pattern clusters: black for *M. muelleri*, yellow for *M. tchernovi*, and blue for mixed. Type specimens are marked by red text (in panel A) or red outline (in panel B).

Unlike Werner *et al.* (2006), we found no differences in the number of ventrals between *M. tchernovi* and *M. muelleri* after correcting for the effect of sex (males: 253.9 in *M. muelleri* vs. 255 in *M. tchernovi,* t = 0.70, p = 0.49; females: 278 in the single *M. tchernovi*, 273.3 in *muelleri*).

The band numbers and width ratios are negatively correlated, with darker animals (higher ratios) having fewer bands (slope -0.037±0.008, t = -4.61, p < 0.0001, R^2 = 0.12, n = 154). The relationship is generally linear with no ob-

vious breaks suggesting anything but a smooth cline. Furthermore, both the number of bands and the ratio between dark band and light band widths varied clinally. Ratios tended to be higher (i.e. the animals were darker) in wetter regions (slope = 0.002 ± 0.001, $t = 2.8$, $p = 0.006$, $R^2 = 0.1$), and the number of bands increased with temperature (slope = 2.88 ± 1.03, $t = 2.79$, $p = 0.007$, $R^2 = 0.09$). For both traits, the best model contained only these single predictors.

Molecular analyses

Our genetic dataset includes six specimens conforming to the *M. muelleri* morphology, two conforming to the *M. tchernovi* morph, six snakes with intermediate colour-pattern (some characters more *M. tchernovi*–like, others more *M. muelleri*–like), and two striped specimens. The datasets of the *cytb* and *c-mos* gene fragments used in the phylogenetic analyses included 17 and 15 specimens, respectively (including the outgroup), with a total length of 1,077 bp (C=917, V=160, Pi=28) and 411 bp (C=407, V=4, Pi=0), respectively. The Israeli dataset of *M. muelleri* and *M. tchernovi* included 16 specimens for the mitochondrial *cytb* marker (C=1033, V=44, Pi=21). The 14 sequences of the nuclear marker *c-mos* were all identical. For both markers, the ML and BI phylogenetic trees recovered similar topologies, with all 16 specimens collected from Israel, of all four colour patterns, clustering together as one well-supported group with no internal structure. In the BI tree of *cytb* (Fig. 7) two specimens from the southern Golan Heights (TAU.R16426, a striped specimen and TAU.R18905 – a saddled specimen with only 48 dark bands but wide light-coloured bands that we classify in the 'mixed' morph); both outside the putative geographic range of *M. tchernovi*) are genetically differentiated from the other samples, whereas in the maximum likelihood tree these samples cluster together with all the remaining samples.
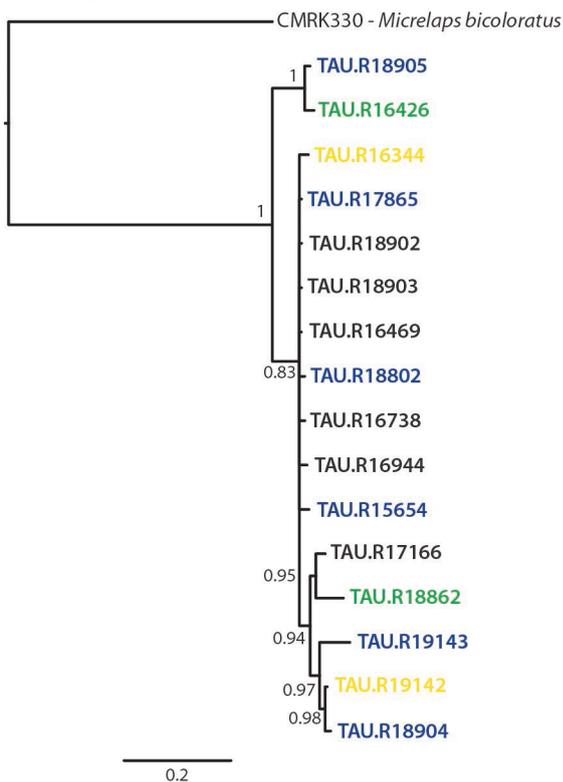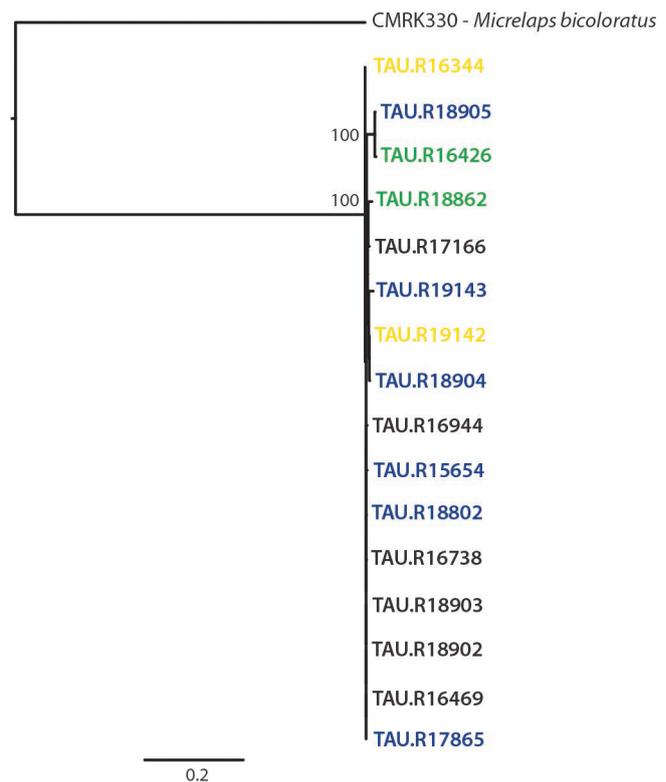

FIGURE 7. Phylogenetic trees of *Micrelaps* based on *cytb* sequences. Support values are indicated near the nodes (Bayesian posterior probabilities and ML bootstrap). Sample codes correlate to specimens in Table S2. Colours correspond to four classified colour patterns: *M. muelleri* in black, *M. tchernovi* in yellow, mixed in blue, and striped in green.

Genetic diversity estimated within the Israeli *Micrelaps* sequences (n=16, S=44, Eta=45, h=13, Hd=0.950, Π=0.00869, k=9.250) showed little variation compared to the dataset including the African species *M. bicoloratus* (n=17, S=155, Eta=161, h=14, Hd=0.956, Π=0.02304, k=23.757). The uncorrelated mitochondrial genetic divergence ranged between 12.8–13.0% between *M. bicoloratus* and the Israeli specimens classified into four colour-

pattern characteristics (*M. tchernovi, M. muelleri,* mixed, or striped). In contrast, the genetic distance between the six specimens presenting the wide-ranging *M. muelleri* and the two individuals with a '*M. tchernovi*' colour-pattern, was extremely low (0.5%). Genetic distances among the four colour-pattern groups ranged from 0.5% (*tchernovi* vs. *muelleri*) to 1.5% (mixed vs. striped).

Discussion

Our study shows that Israeli *Micrelaps* snakes are as morphologically variable as they are genetically conservative. While the specimens examined exhibit great variation in colouration, the genetic data showed little structure, suggesting no differentiation between populations. Furthermore, some of the characteristics allegedly differentiating *M. muelleri* from *M. tchernovi*, based on Werner *et al.* (2006), varied clinally, suggesting they represent local adaptation to temperature and precipitation conditions – or phenotypic plasticity (e.g., in relation to temperature during embryogenesis) rather than implying species boundaries (Hillis 2019; Mason *et al.* 2020). Thus, our results fail to support the existence of more than one, morphologically varied, species of *Micrelaps* in Israel.

The great colour-pattern diversity was found both at the inter-population and intra-population scales. Thus *M. tchernovi*-like specimens were found in different regions throughout Israel (Fig. S3), and some populations include *M. muelleri*-like specimens, *M. tchernovi*-like specimens, and snakes with mixed colour-pattern. Moreover, even in the type locality of *M. tchernovi* (Tel Ubeidiya) we found two specimens in sympatry, one with a clear *M. tchernovi* phenotype (TAU.R19142, saddles, dark venter, 52 bands and a 0.7 dark bands/light bands width ratio, clustering with *M. tchernovi* in the PCoA) and another with a mixed phenotype reminiscent of *M. muelleri* (TAU.R19143, rings and a partially ringed/partially dark venter, 50.5 bands and a 1.66 dark bands/light bands width ratio, clustering with the mixed morph in the PCoA; Fig. S4), both with almost no genetic differentiation.

The proportions of the different colour-pattern characteristics change with climate. Geographic clines (e.g., those related to climate such as Bergmann's and Allen's rules; Bergmann 1847; Symonds & Tattersall 2010; Pincheira-Donoso & Meiri 2013; Slavenko *et al.* 2019) are usually taken as evidence that inter-population differences reflect selection and local adaptation rather than speciation (Huxley 1938; Mayr 1942; Dowling 1950; Kitchener & Yamaguchi 2010; Hillis 2019, 2020). For example, Sinaiko *et al.* (2018) found that the number of ventral scales varied with latitude in Israeli specimens of the colubrid snake *Platyceps saharicus*, and argued that this, along with little genetic differentiation, is evidence for a single species rather than supporting the common notion that high and low scale counts at the range extremes represent different species.

The description of *M. tchernovi* (Werner *et al.* 2006) was based on six specimens, including a single female. In both *M. muelleri* and *M. tchernovi,* statistically significant sexual dimorphism can be observed in certain traits (e.g., the number of ventral scales, see Werner *et al.* 2006; Werner 2016; in our dataset females have, on average, $274.4\pm7.5_{SD}$ ventrals vs. 252.9 ± 6.7 in males). Therefore, it is not surprising that some morphological traits designated as the criteria to describe and differentiate *M. tchernovi* from *M. muelleri* were limited in power. Werner *et al.* (2006) characterized *M. tchernovi* by dark saddle-like transverse bands (black/brown) with wider yellow bands between them, and a uniformly dark venter. However, some specimens of Israeli *Micrelaps* elude diagnosis by these characters. For instance, our sample from the vicinity of the Sea of Galilee and Hula Valley included specimens with light bands not touching the venter, very wide dark bands, and a uniformly dark venter (e.g., TAU.R19002; see Fig. 2 specimen A). Based on the key in Werner *et al.* (2006) it is impossible to classify such specimens as either *M. muelleri* or *M. tchernovi*.

The key provided by Werner *et al.* (2006) points to a substantial overlap in all continuous characters between the two putative species (hence the large number of 'mixed' morphs in our sample). We contend that the ratio between the mean width of dark and light bands is not a reliable diagnostic trait as it varies clinally and varies considerably within sites. Furthermore, the relative width of the bands can vary greatly even along the anterior-posterior axis of the same specimen.

The average number of bands is likewise not informative for differentiating *Micrelaps* species, because there is a high intra- and inter-population variety in this character. According to Werner *et al.* (2006) both species have a wide range of bands (*M. muelleri* 30.5–60 and *M. tchernovi* 52–66), with some overlap (52–60). With a much higher sample size we found that snakes with a ringed colour pattern can have as many as 63 bands (Fig. 4; specimen a89). Only three specimens in our entire sample had more bands (the *M. tchernovi* holotype only has 54.5). Due

to this significant overlap, properly identifying specimens with 52–63 bands is impossible using this criterion. We conclude that designating 52 saddles as a low threshold for delimiting a species is arbitrary and see no evidence for a bimodal distribution of bands around this or any other value (Fig. 4).

Colour is an imprecise and uninformative trait in Israeli *Micrelaps*. Many combinations of colour occur in populations (Fig. 2), and both the dark and light bands are highly variable in number, colour, shape, and width, rather than showing a clear dichotomy. It is unclear why the specific combination of certain morphological characteristics (e.g. the wide yellow bands and black saddle-shaped bands, in addition to uniformly dark ventral scales) was determined to be diagnostically sufficient to elevate certain populations in Israel to a specific level, whereas other colour characteristics (e.g., longitudinal stripes) were not.

Werner *et al.* (2006) wrote they "tentatively regard the remaining morphs" (patterns they defined as "pseudo-saddled", "striped" and "semi-striped"), "found in single specimens within the geographic range of the ringed morph, as mutants of the ringed morph" (*M. muelleri*), due to the scarcity of these morphs throughout *M. muelleri* populations. Our results suggest that these and additional phenotypes are neither as rare as previously assumed, nor do they correspond to differences in other morphological traits or to particular DNA sequences. We suggest this variety represents natural, partially clinal, variability within *Micrelaps muelleri*. We hypothesize that the '*M. tchernovi*' morph reflects phenotypic plasticity, or local adaptations, in response to particular climatic characteristics during time of pregnancy/incubation rather than an evolutionary break between populations (see e.g., Sweet 1985; King & Lawson 1995; Cox & Davis-Rabosky 2013). Other morphs probably represent different climatic combinations. The prevalence of saddled specimens with wide yellow bands in the hot and arid northern Jordan Valley may reflect local adaptation. Dry brown/yellow plants dominate the region for long periods of the year, which may give specimens with more yellow/beige/brown colouration an advantage over darker morphologies (in agreement with Gloger's rule, at least for precipitation; e.g., Yom-Tov 1967; Delhey 2019). In the semi-arid south east edge of the distribution range of this species in the region, which is characterized by lower vegetation levels, *Micrelaps* specimens with wide yellow bands are very common.

Our molecular results suggest of genetic uniformity and low variability within *Micrelaps* snakes in Israel, as no internal genetic structure was found among individuals sampled from across Israel and which represent different colour-pattern phenotypes. This is especially evident in the nuclear marker *c-mos* for which all sequences were 100% identical. Our molecular results thus show a contrasting pattern to the great morphological variability found in Israel and no relationships between DNA sequences in neutral genetic markers and morphology.

In summary, the data obtained in this study suggest that there is insufficient morphological and genetic evidence to justify the recognition of two *Micrelaps* species in Israel. The morphological differences between different individuals and populations do not show clear gaps and are likely to reflect either local adaptation or phenotypic plasticity. This hypothesis is amenable to experimental testing in the lab, including common garden experiments and experimental manipulations. Based on both the morphological and molecular results of this study we conclude that *Micrelaps tchernovi* is but one of many morphological phenotypes exhibited by *M. muelleri* in Israel. We thus suggest treating *Micrelaps tchernovi* Werner, 2006 as a junior synonym of *Micrelaps muelleri* Boettger, 1880. *Micrelaps muelleri* is therefore the only species of *Micrelaps* known from Israel specifically and from Asia in general.

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