



Resolving the identity of PALLARY'S Skink: a new taxon of the genus *Chalcides* (Squamata: Scincidae) from Morocco and Algeria

PHILIPPE GENIEZ¹, DAVE LUTGEN^{2,3}, YVES HINGRAT⁴, VINCENT RIVIÈRE⁵, MENAD BEDDEK^{2,6},
OLIVIER PEYRE^{6,7} & PIERRE-ANDRÉ CROCHET²

¹ CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Biogéographie et Ecologie des Vertébrés, Montpellier, France

² CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France

³ Department of Population Ecology, Friedrich-Schiller University Jena, Jena, Germany

⁴ Research Manager, RENECO International Wildlife Consultants LLC. Po Box 61 741 Abu Dhabi, UAE

⁵ AGIR écologique SARL, 147 ancienne route d'Esparron, 83470 Saint-Maximin-la-Sainte Baume, France

⁶ Naturalia Environnement, Site Agroparc, Avignon, France

⁷ PANDORA, 418 rue du Mas de Verchant 34000 Montpellier, France

Corresponding author: PIERRE-ANDRÉ CROCHET, e-mail: pierre-andre.crochet@cefe.cnrs.fr

Manuscript received: 31 January 2023

Accepted: 13 November 2023 by PHILIPP WAGNER

Abstract. North Africa is the most important centre of diversification for the skinks of the genus *Chalcides*. Morocco alone is inhabited by 16 species of which nine are endemic, while eight species are known from Algeria, none of them endemic. We add here to this diversity a taxon that was first collected by PAUL PALLARY in 1925, discussed by PELLEGRIN in 1926, and whose status has been debated by several authors since without reaching a satisfactory consensus. In 2003 and 2008, two specimens with the same habitus as PALLARY'S specimen were found near Missouri (Morocco) and near Djelfa (Algeria), respectively. A molecular analysis based on mitochondrial and nuclear genes shows that these two recent individuals belong to an undefined lineage that is sister to *Chalcides montanus*, and that we describe here as a new subspecies. It shares many morphological features with the nominate subspecies, but differs most prominently in its colour pattern of five black stripes in the first third of the dorsum, ocelli on the dorsum and on the flanks that disappear roughly in the first third or half of the body, and two broad light dorsolateral bands that disappear around midbody; its genetic divergence is estimated at 4.2% in cytochrome *b* sequence and 0.8% in a concatenated alignment of several nuclear loci. This new taxon is presently known from three specimens and two localities in the Hauts Plateaux of eastern Morocco and Algeria.

Key words. New subspecies, taxonomy.

Introduction

The Maghreb is the most important centre of diversification for the skinks of the genus *Chalcides* LAURENTI, 1768. Morocco alone is inhabited by 16 species while eight species are known from Algeria. Nine of these species are endemic to Morocco: *Chalcides polylepis* BOULENGER, 1890, *C. colosii* LANZA, 1957, *C. manueli* HEDIGER, 1935, *C. montanus* WERNER, 1931, *C. lanzai* PASTEUR, 1967, *C. ebneri* WERNER, 1931, *C. mionecton* (BOETTGER, 1874), *C. trifasciatus* CHABANAUD, 1917, and *C. pseudostriatatus* CAPUTO, 1993. Three other species are northwestern Maghreb endemics shared between Morocco and Algeria: *C. mauritanicus* (DUMÉRIL & BIBRON, 1839), *C. parallelus* DOUMERGUE, 1901, and *C. minutus* CAPUTO, 1993. *Chalcides sphenopsiformis* (DUMÉRIL, 1856) is a western Maghreb endemic that reach-

es Mauritania while *C. delislei* (LATASTE, 1876) and *C. boulengeri* ANDERSON, 1892 have a wider distribution range in the southern and northern Sahara, respectively, including Morocco and Algeria. Lastly, *C. ocellatus* (FORSKÅL, 1775) is a widely distributed circum-Mediterranean species (MATEO et al. 1995, BONIS & GENIEZ 1996, CARRANZA et al. 2008, SINDACO & JEREMČENKO 2008, BROWN et al. 2012, MONTERO-MENDIETA et al. 2017, MARTÍNEZ DEL MÁRMOL et al. 2019). The only molecular phylogeny available for the genus *Chalcides* (CARRANZA et al. 2008) suggests a grouping of these species into a “grass-swimming clade” that includes species with an elongated body, reduced limb size, and reduced numbers of digits (in Morocco, represented by *C. pseudostriatatus*, *C. minutus* and *C. mauritanicus*), and three clades of species with the typical *C. ocellatus* morphology (the “five-fingered” species of MATEO & GENIEZ

1995 with stocky body and long limbs) or which exhibit an elongated body and reduced limbs and digit numbers. This phylogeny was based on relatively short fragments of the mitochondrial DNA (mtDNA) and requires corroboration with additional data. Within each of these clades, several taxonomic questions have remained unanswered (CARRANZA et al. 2008, GIOVANNOTTI et al. 2013, MONTERO-MENDIETA et al. 2017). Among these species, *C. ebneri* is known from only three specimens found in 1930 (1) and 1970 (2), only two of which were collected, and the species has never been seen since then in spite of several search initiatives (MARTÍNEZ DEL MÁRMOL et al. 2019, own data) and has never been investigated genetically.

In addition to these 16 species, one specimen of the skink genus *Chalcides* has so far been defying identification (LANZA 1957, MATEO et al. 1995). This specimen was collected by PAUL PALLARY on 30 December 1925 at Missouri, northeastern Morocco (PELLEGRIN 1926), and is currently preserved in relatively bad shape in the Muséum national d'Histoire naturelle in Paris (MNHN) under catalogue number MNHN-RA-1925.215 (Fig. 1; a photo of the specimen was also published by LANZA [1957]). It clearly belongs to the “five-fingered species group”, which is not a monophyletic clade according to CARRANZA et al. (2008) but whose species have similar phenotypes (see below). PELLEGRIN (1926) labelled it as “*Chalcides ocellatus* var. *parallelus* DOUMERGUE”, but it was later re-identified as *C. ocellatus* by LANZA (1957) and MATEO et al. (1995) and it is still catalogued as such in the Paris collection. However, on the basis of its coloration as well as its rather small size for a presumed adult, GEORGES PASTEUR suggested (pers. comm. to

PG) that this specimen might belong to a low-altitude population of *C. montanus*, a species normally restricted to areas above 1500 m in the High Atlas (BONS & GENIEZ 1996, CARRANZA et al. 2008). Two specimens exhibiting a similar colour pattern have recently been discovered in Morocco (Missour) and Algeria (Djelfa), allowing to gather new data on their morphology and to collect genetic samples.

To clarify the taxonomic status of these unidentified skinks, we first conducted a thorough morphological examination of these three specimens in comparison with 397 other specimens from the eight five-fingered species of the genus *Chalcides* found in North Africa (see Supplementary Table S3). We also gathered mitochondrial and nuclear gene sequences from the two modern specimens and, for the purpose of comparisons, from specimens of other species from Morocco. These data were complemented with sequences from Genbank, facilitating a comprehensive phylogenetic analysis comprising 16 taxa.

Material and methods

Morphological examination

A large majority of the specimens examined come from the Biogéographie et Ecologie des Vertébrés (BEV) collection housed at the Centre d'Ecologie Fonctionnelle et Evolutive (CEFE, EPHE & CNRS) in Montpellier, France (94 specimens) and the collection of the Estación Biológica de Doñana in Sevilla, Spain (EBD, 44 specimens). We also examined PALLARY's *Chalcides* specimen MNHN-RA-1925.215 in the Muséum national d'Histoire naturelle in Paris. In addition,

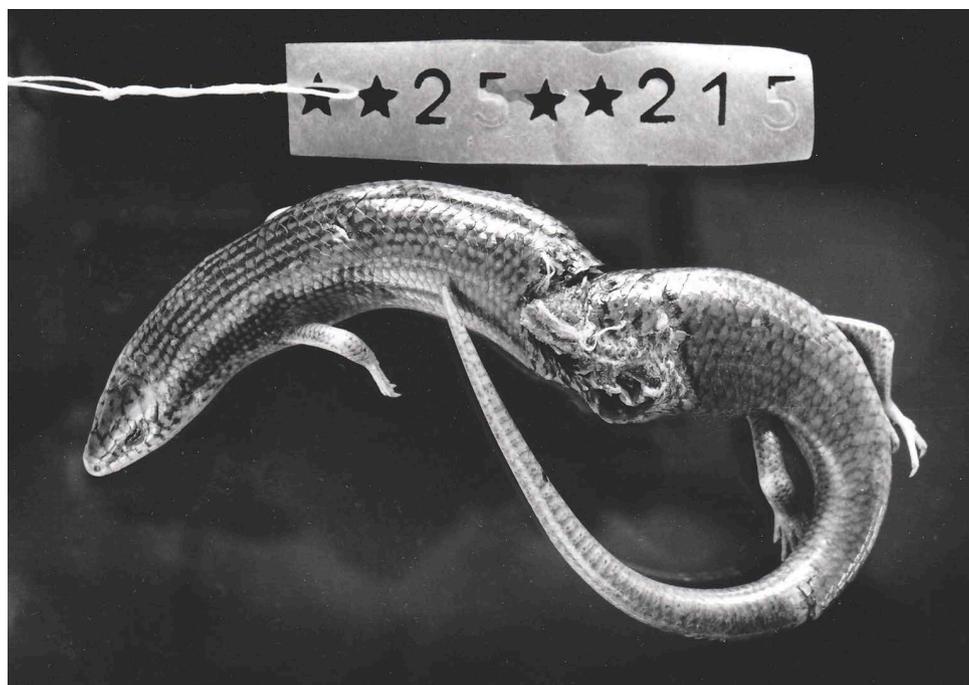


Figure 1. Dorsolateral view of MNHN-RA-1925.215, preserved holotype of *Chalcides montanus pallaryi* ssp. n., adult female collected by PAUL PALLARY at Missouri (Morocco). Photograph by P. GENIEZ.

data on colour pattern were obtained from photos of an additional 227 live specimens in PHILIPPE GENIEZ's iconographic collection (PGe.xxxx numbers, contributed by many photographers, see Acknowledgements and Supplementary Table S3) of which no tissue samples have been preserved, and 34 specimens of which both tissue samples and photos (but not vouchers) were available (BEV.Txxxx numbers).

The 400 specimens studied represent the following geographic distribution: 71 *Chalcides ocellatus ocellatus* from Algeria (9 specimens), Tunisia (8), Egypt (4), Israel (15), Jordan (4), Syria (1), United Arab Emirates (1), Turkey (7), Cyprus (6), and Greece (16); 80 *Chalcides ocellatus subtypicus* WERNER, 1931 from Morocco (65), Spanish territories, Chafarinas islands (7), and Algeria (8); 92 *Chalcides ocellatus tiligugu* (GMELIN, 1789) from Morocco (1), Algeria (45), Tunisia (9), Malta (9), Sicily (8), and Sardinia (20); 1 *Chalcides humilis* BOULENGER, 1896 from Egypt; 22 *Chalcides colosii* from Morocco; 10 *Chalcides manueli* from Morocco; 13 *Chalcides lanzai* from Morocco; 28 *Chalcides parallelus* from Morocco (9), Spanish territories, Chafarinas islands (5), and Algeria (14); 45 *Chalcides montanus* from Morocco; 35 *Chalcides polylepis* from Morocco; and 3 *Chalcides* sp. (PALLARY's skink) from Morocco (2) and Algeria (1).

Our morphological examination focused on the colour patterns of the various taxa of *Chalcides* in North Africa. We noted the presence and distribution of ocelli (a pale spot on a dorsal or flank scale, paler than the ground colour of the body, sometimes bordered with a darker coloration) on the body and the number of scales separating scales with ocelli, the presence or absence of 5 black lines on the anterior part of the back, the pileus punctuation (uniform, barely spotted, or strongly spotted with dark, with or without white dots), the presence or absence of two light wide dorsolateral stripes, the proportion of uniform pattern (all over the body, on the back of the body, or none at all), the colour of the snout and the tail (orange or not), the colour of the belly (whitish, yellowish or pure yellow). Data on size (snout-vent length) and on scalation (number of scale rows around the body, position of the loreal scale in relation to the supralabials [above the 2nd supralabial or overlapping the 2nd and 3rd]) were largely obtained from BONS & GENIEZ (1995) and supplemented by the examination of additional specimens. A list of all specimens examined morphologically is given in Supplementary Table S3.

In order to check that coloration allows unambiguous separation of the new taxon from its closest relatives *C. montanus*, *C. manueli* and *C. polylepis* (see below), we performed a Principal Component Analysis (PCA) with the software Statistica (Statsoft, Hamburg, Germany). A selection of seven colour variables was coded as follow: 'DOcel' = extent of ocelli on the dorsum (0 = no ocelli; 1 = in the first third; 2 = up to the halfway limit; 3 = up to two thirds; 4 = up to the base of the tail); 'FOcel' = extent of ocelli on the flanks (same codes); 'SPDL' = length of the light supra-dorsolateral stripes along the back (0 = no light dorsolaterals; 1 = in the first third; 2 = up to the halfway limit; 3 = up to two thirds; 4 = up to the hind legs); 'Flanks' = extent of the dark wide stripe along the flanks (0 = no dark stripe

along the flanks; 1 = in the first third; 2 = up to the halfway limit; 3 = up to two thirds; 4 = up to the hind legs); 'Pileus' = extent of dark punctuation on the pileus (1 = no black spots; 2 = weakly spotted; 3 = strongly spotted); 'NDStrL' = number of dark stripes on the nape; 'NDStr' = length of the dark stripes on the nape (as number of dorsal scales covered). These variables were retained from the full list of morphological characters examined because they could be retrieved from voucher specimens as well as from good-quality photographs of non-collected live specimens, allowing us to increase the number of specimens available for several species that have been collected only rarely.

Genetic analyses

For the complete nuclear data set of five nuclear loci, in addition to the two newly found specimens of the unidentified skink, we selected samples from the three species that have previously been linked to PALLARY's specimen (see Introduction): *Chalcides ocellatus* (10), *C. parallelus* (7), and *C. montanus* (2). As for *C. ocellatus*, we selected representatives of the various lineages identified by previous studies (KORNILIOS et al. 2010, LAVIN & PAPENFUSS 2012): 2 *C. o. ocellatus* from Israel, 6 *C. o. tiligugu* (2 from Tunisia and 4 from Algeria), and 2 *C. o. subtypicus* from Morocco. We also added samples of two other species from Morocco, *C. lanzai* (1, Middle Atlas) and *C. colosii* (1, Rif). We thus sequenced samples from all "five-fingered" species reported from northern Morocco and western Algeria except for *C. polylepis*, *C. mionecton*, and *C. trifasciatus*, because these species are easily distinguished by several diagnostic morphological features. The tree was rooted with a selection of five skink species (one individual per species) belonging to the "grass-swimming clade" of CARRANZA et al. (2008): *Chalcides minutus* from Morocco, *C. mertensi* KLAUSEWITZ, 1954 from Algeria, *C. pseudostriatus* from Morocco, *C. striatus* CUVIER, 1829 from France, and *C. guentheri* BOULENGER, 1887 from Lebanon. We chose to root the tree on the branch leading to the node regrouping the five species from the "grass-swimming clade", because this clade constitutes the most basal split within the *Chalcides* phylogeny according to CARRANZA et al. (2008). A total of 25 samples of the genus *Chalcides* were selected from the BEV collection where they are stored as whole specimens (BEV numbers) in ethanol at room temperature or as tissue samples in ethanol at -20°C (BEV.T numbers for tissue samples with no associated vouchers).

Genomic DNA was extracted from ethanol-preserved muscle tissue following the manufacturer's protocol of the DNeasy blood & tissue extraction kit (Qiagen®, Valencia, California, USA). Amplifications were performed through standard Polymerase Chain Reaction (PCR) in final volumes of 20 µL, containing 10 µL TAQ SIGMA reaction buffer, 1 µL of primers (mix of reverse and forward primers at 10 µM), 7 µL H₂O and 2 µL DNA extract. Both strands were sequenced with the primers used for amplification by Eurofins-genomics (Germany).

Table 1. Sequence, annealing temperatures, and references for the primers used in this study. The amplification protocol was as follows: 94°C/3 min; 94°C/30 s; 35–40 cycles of annealing temperature/40 s; 72°C/1 min; 72°C/10 min. Temp. – Annealing temperatures.

Gene	Primer	Primer Sequence	Temp.	References
CYTB	GLUDGE	5'-TGACTTGAARAACCAACCGTTG-3'	46°C	SMITH & PATTON (1993); McGUIRE et al. (2007)
	CYTB2	5'-TCAGAATGATATTTGTCCTCA-3'		
MC1r	MC1r-F	5'-GGCNGCCATYGTCAAGAACCGGAACC-3'	60°C	PINHO et al. (2010)
	MC1r-R	5'-CTCCGRAAGGCRATAATGATGGGGTCCAC-3'		
ODC	ODC-F	5'-GCTACACTAAAAACCAGCAG-3'	60°C	YAO et al. (1995)
	ODC-R	5'-CCACCAATATCAAGCAGGTAC-3'		
PRLR	PRLR-F	5'-GACARYGARGACCAGCAACTRATGCC-3'	54°/60°C	TOWNSEND et al. (2008)
	PRLR-R	5'-GACYTTGTGRACCTCYACRTAATCCAT-3'		
R35	R35-F	5'-GACTGTGGAYGAYCTGATCAGTGTGGTGCC-3'	60°C	BRANDLEY et al. (2011)
	R35-R	5'-GCCAAAATGAGSGAGAARCGCTTCTGAGC-3'		
TROP	TROP-F	5'-CGGTCAGCCTCCTCCGCAATGTGCTT-3'	60°C	FRIESEN et al. (1999)
	TROP-R	5'-GAGTTGGATCGCGCTCAGGAGCG-3'		

We initially tested nine nuclear primer pairs, but only five loci were retained for sequencing as they allowed DNA amplification and showed polymorphism at the corresponding loci: three exons from the RNA fingerprint protein 35 (R35), the melanocortin receptor 1 (MC1r) and the prolactin receptor (PRLR), and two loci with partially coding and non-coding DNA from the tropomyosin gene (TROP) and the ornithine decarboxylase gene (ODC). The ODC sequencing failed in several specimens including many *C. ocellatus* and in all *C. montanus* and *C. lanzai*.

To ensure that our unidentified skink does not belong to any of the described *Chalcides* taxa from Northern Africa (all of which have been sequenced by CARRANZA et al. 2008), even if they are all morphologically distinct, we also compared a short fragment of its mitochondrial cytochrome *b* gene (*cytb*) to published and unpublished *cytb* sequences. Mitochondrial cytochrome *b* sequences were retrieved from GenBank, from BEDDEK et al. (2018) where available, or else a short fragment of the *cytb* gene was amplified and sequenced for the present study. For *C. montanus*, one sample from one of the localities used here had been sequenced by CARRANZA et al. (2008) and we used this *cytb* GenBank sequence. Further *cytb* GenBank sequences were added for *C. polylepis* (3), *C. mionecton* (2), and *C. trifasciatus* (2). As for the nuclear dataset, all five species (one individual per species) belonging to the *Chalcides chalcides* group were also used to root the mitochondrial tree. All sequences produced for this study were deposited in Genbank. Primers and PCR conditions used for the amplification of the molecular markers are detailed in Table 1. The list of all samples with their origin, the genes sequenced for each of them and their GenBank accession numbers are given in Table 2.

Chromatograms obtained from sequencing were visualised and cleansed using Codon code aligner version 4.2.7 (CodonCode Corporation, MA, USA). All sequences were verified by eye, paying particular attention to heterozygous sites that are poorly resolved by the analysis software. The presence of heterozygous indels was furthermore consid-

ered by carefully checking forward and reverse sequences. Alignments were performed manually and verified with Clustal omega (McWILLIAM et al. 2013). The mean between-group genetic distances (p-uncorrected distance, option pairwise deletion) were calculated in Mega v7 (KUMAR et al. 2015). Phylogenetic trees were generated separately for mitochondrial (*cytb*) and concatenated nuclear loci (R35, PRLR, MC1r, TROP, ODC) using Mega v7 or IQ-Tree (NGUYEN et al. 2014) for Neighbor Joining (NJ) and Maximum Likelihood (ML) trees respectively. NJ trees were computed with the K2 + G model chosen by Mega's modelfinder approach as the best model for distance computation, all substitutions included a pairwise option for handling missing data. ML trees were inferred based on the best model of sequence evolution as determined by ModelFinder incorporated in IQ-Tree, for the mitochondrial dataset (JC), or by running partitionfinder v1.1.2 (LANFEAR et al. 2012), which identified five partitions for the concatenated nuclear dataset (R35 (HKY+I), PRLR (GTR+I), MC1r (TrN+I+G), TROP (HKY+I+G), ODC (HKY+I)). The best model of sequence evolution was chosen using the Bayesian Information Criterion (BIC) obtained from IQ-TREE or partitionfinder v1.1.2. Branch support was assessed using 1000 bootstrap replicates for NJ trees and 100 bootstrap replicates for ML trees. For comparative purposes, Bayesian trees were also generated with MrBayes v.3.2.6 (RONQUIST et al., 2012) using 4 chains, 10,000,000 generations, a burn-in of 25%, and the same models and partitions as for the ML analyses or the closest model when a best model was not available in MrBayes (Supplementary Figs S1, S2). Nuclear sequences from the ingroup taxa (i.e., excluding the “grass-swimming clade” members) were phased with DNASP v6 (ROZAS et al. 2017) using the PHASE algorithm and the default options except for the number of iterations (1000) and burn-in iterations (1000). Median-joining networks (BANDELT et al. 1999) were then built using PopART (available from www.popart.otago.ac.nz) using default options and an epsilon value of zero.

New *Chalcides* from North Africa

Table 2. Identity, sampling localities with latitude, longitude (WGS84, decimal degrees), and altitude, voucher code (BEV codes) or sample code (BEV.T codes, no associated vouchers), and Genbank accession numbers for all specimens used in our genetic analyses. * – sequences obtained from Genbank.

Taxon	Locality	Lat., Long.	Elev. (m)	Code	CYTB / MCIr/ ODC / PRLR / R35 / TROP
<i>Chalcides colosii</i>	Morocco, 16 km past Ketama towards Bab Berrret (Rif)	34.9647, -4.7056	1585	BEV.11916	MN604770 MN604796 MN611499 MN604821 MN604745 MN611474
<i>Chalcides colosii</i> *	Morocco, 12 km SE of Tetouan	35.47, -5.29	-	-	EU278161 - - -
<i>Chalcides guentheri</i>	Lebanon, Jebel Niha	33.5771, 35.6118	1217	BEV.T6280	MN604771 MN604797 MN611500 - MN604746 MN611475
<i>Chalcides humilis</i>	Egypt, 10 km S of Assouan	23.98487, 32.89975	184	BEV.9003	MN604772 MN604798 - MN604822 MN604747 MN611476
<i>Chalcides humilis</i>	Egypt, 18 km S of Edfu, Nagaa Az Zanzaqah	24.8061, 32.9059	90	BEV.T6844	MN604773 MN604799 - MN604823 MN604748 MN611477
<i>Chalcides lanzai</i>	Morocco, Midelt, oued Oum Er Rbia	33.4142, -5.1951	1750	BEV.7761	MN604774 MN604800 - MN604824 MN604749 MN611478
<i>Chalcides manueli</i> *	Morocco, Sidi Ifni	29.38, -10.17	-	-	EU278087 - - -
<i>Chalcides manueli</i> *	Morocco, Sidi Ifni	29.38, -10.17	-	-	EU278088 - - -
<i>Chalcides mertensi</i>	Algeria, Tifrit N'ath El Hadj plain	36.78560, 4.41478	655	BEV.15144	MN604775 MN604801 MN611501 MN604825 MN604750 MN611479
<i>Chalcides minutus</i>	Morocco, 1 km past Gaada de Debdou towards Debdou	33.9613, -3.0436	1539	BEV.11922	MN604776 MN604802 MN611502 MN604826 MN604751 MN611480
<i>Chalcides mionecton</i> *	Morocco, south of Safi	-	-	-	EU278097 - - -
<i>Chalcides mionecton</i> *	Morocco, Cap Rhir (= Cap Ghir)	30.63, -9.88	-	-	EU278099 - - -
<i>Chalcides montanus montanus</i>	Morocco, 1 km above Oukaimeden	31.18513, -7.84968	2830	BEV.T465	- MN604803 - MN604827 MN604752 MN611481
<i>Chalcides montanus montanus</i>	Morocco, 5 km past Oukaimeden towards Marrakech	31.23560, -7.81995	2328	BEV.T488	- MN604804 - MN604828 MN604753 MN611482
<i>Chalcides montanus montanus</i> *	Morocco, 5 km past Oukaimeden towards Marrakech	31.23560, -7.81995	2328	BEV.6025	EU278090 - - -
<i>Chalcides ocellatus ocellatus</i>	Israel, Ein Gedi, Wadi Arugot	31.4597, 35.3931	-380	BEV.10202	MN604777 MN604805 MN611503 MN604829 MN604754 MN611483
<i>Chalcides ocellatus ocellatus</i>	Israel, ca 18 km past Dimona towards Beer Sheva	31.1745, 34.965	420	BEV.8479	MN604778 MN604806 MN611504 MN604830 MN604755 MN611484
<i>Chalcides ocellatus subtypicus</i>	Morocco, road N16, 3.9 km W of Aazanen	35.2203, -3.2096	75	BEV.11288	MN604791 MN604815 MN611513 MN604839 MN604764 MN611493
<i>Chalcides ocellatus subtypicus</i>	Morocco, road N6, 6 km past Taourirt towards Guercif	34.4066, -2.9795	165	BEV.11340	MN604790 MN604816 MN611514 MN604840 MN604765 MN611494
<i>Chalcides ocellatus tiligugu</i>	Algeria, Tighilt Boukas	36.74400, 4.49174	747	BEV.15139	- MN604817 MN611515 MN604841 MN604766 MN611495
<i>Chalcides ocellatus tiligugu</i>	Algeria, Chellata Pass	36.52795, 4.46273	1495	BEV.15140	- MN604818 MN611516 MN604842 MN604767 MN611496
<i>Chalcides ocellatus tiligugu</i>	Algeria, Ijmel, Grand Phare beach	36.8152, 5.6952	1	BEV.T8025	MN604792 - - -
<i>Chalcides ocellatus tiligugu</i>	Algeria, Bejaia, Amacine, Amizour	36.6007, 4.8772	210	BEV.T9610	MN604793 - - -
<i>Chalcides ocellatus tiligugu</i>	Tunisia, Chebba, Ilot Jebel (island)	35.20796, 11.16695	0	BEV.T6674	MN604794 MN604819 - MN604843 MN604768 MN611497
<i>Chalcides ocellatus tiligugu</i>	Tunisia, Monastir, Petite Kuriat island	35.76781, 11.01008	1	BEV.T6684	MN604795 MN604820 - MN604844 MN604769 MN611498
<i>Chalcides parallelus</i>	Algeria, road RN 13b, 6.25 km past Ras El Ma towards El Aricha	34.4833, -0.8755	1	BEV.13616	MN604782 MN604809 MN611507 MN604833 MN604758 MN611487
<i>Chalcides parallelus</i>	Algeria, Oran, Bousfer, Île Plane (island)	35.7708, -0.9023	4	BEV.14839	MN604784 MN604810 MN611508 MN604834 MN604759 MN611488
<i>Chalcides parallelus</i>	Algeria, Oran, Bousfer, Île Plane (island)	35.77076, -0.90168	6	BEV.12805	MN604781 - - -
<i>Chalcides parallelus</i>	Algeria, Oran, Canastel dunes	35.7479, -0.5754	54	BEV.13617	MN604783 - - -

Table 1 continued

Taxon	Locality	Lat., Long.	Elev. (m)	Code	CYTB / MC1r / ODC / PRLR / R35 / TROP
<i>Chalcides parallelus</i>	Morocco, 2 km ESE of Ras El Ma	35.1321, -2.3970	16	BEV11917	MN604786 MN604811 MN611509 MN604835 MN604760 MN611489
<i>Chalcides parallelus</i>	Morocco, beach between Saïdia and the Oued Mou-louya mouth	35.1159, -2.3211	1	BEV14730	MN604787 MN604812 MN611510 MN604836 MN604761 MN611490
<i>Chalcides parallelus</i>	Morocco, road N16, 2.8 km ESE of Ras El Ma port	35.1308, -2.3976	30	BEV11306	MN604785
<i>Chalcides polylepis</i> *	Morocco, Azemmour	33.28, -8.35	50	BEV6052	EU278092
<i>Chalcides polylepis</i> *	Morocco, Oulmès	33.43, -6.02	1257	BEV6051	EU278094
<i>Chalcides polylepis</i> *	Morocco, Aguelmam Azigza	32.98, -5.43	1556	BEV9230	EU278093
<i>Chalcides pseudostriatus</i>	Morocco, Cabo Negro	35.663, -5.295	30	BEV8374	MN604788 MN604813 MN611511 MN604837 MN604762 MN611491
<i>Chalcides montanus pallaryi</i> ssp. n.	Algeria, Djelfa, Khanguet-el-Melah near Ain Maadeb	34.83006, 3.08471	918	BEV14238	MN604779 MN604807 MN611505 MN604831 MN604756 MN611485
<i>Chalcides montanus pallaryi</i> ssp. n.	Morocco, Missour, foothill of Jbel Missour	33.00, -4.15	1060	BEV14249	MN604780 MN604808 MN611506 MN604832 MN604757 MN611486
<i>Chalcides striatus</i>	France, Gonfaron	43.3215, 6.2911	165	BEV11410	MN604789 MN604814 MN611512 MN604838 MN604763 MN611492
<i>Chalcides trifasciatus</i> *	Morocco, 21 km N of Tiznit	29.88, -9.72	-	EU278101	-
<i>Chalcides trifasciatus</i> *	Morocco, Sidi Ifni	29.38, -10.17	-	EU278102	-

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:95DB3D86-D9A9-4CC0-A2C7-A4EE516EFE86. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: www.salamandra-journal.com, zenodo.org.

Results

Morphology of PALLARY's specimen

The MNHN specimen collected by P. PALLARY measures 96 mm in snout-vent length and has 30 longitudinal scale rows at midbody. It presents a distinct colour pattern (see Fig. 1): on the nape, five dark stripes run on a pale background and disappear progressively beyond the insertion level of the forelegs, so as to be absent in the posterior portion of the back and on the tail. A wide dark stripe runs along the anterior part of each flank. Some indistinct ocelli are barely visible in the middle section of the back. The pilus is largely concolorous with the back, with some small black markings. The loreal is in contact with the 2nd supralabial only (as is often the case in *C. parallelus*; in *C. ocellatus*, the loreal is in contact with the 2nd and 3rd supralabials). Colour pattern and pholidosis of this specimen are thus unlike in *C. ocellatus*, which occurs in the same area (see Fig. 2). Clearly, this specimen does not fit within the variation of any of the currently described taxa from North Africa.

Morphology of the recent specimens from Missour and Djelfa

On 9 September 2003, one of us (YH) captured a specimen of *Chalcides* in the foothills of the Djebel Missour, near Missour (33.00° N, 4.15° W, 1060 m a.s.l.). This animal (Fig. 3) bears a strong resemblance to PALLARY's specimen: its upper parts are pale brownish with five black continuous stripes in the anterior portion of the dorsum, which turn into indistinct ocelli in the middle section of the back, and then disappear to leave a uniform pale brown coloration on the lower back, legs and tail. The anterior parts of the flanks are blackish with pale spots (ocelli), but this pattern disappears shortly beyond the insertion level of the forelegs and the body sides become the same uniform colour as the back. In the anterior portion of the body the five dorsal stripes and the dark area on the anterior flank delimit two broad pale dorsolateral stripes that fade progressively near the rear end of the first third of the body. The snout

and subcaudal area are pale orange, the throat is white, the belly and the lower side of the tail base are lemon-yellow, and the pileus is uniform except for three very small dark spots on the parietals (Fig. 3). The forelimbs and hindlimbs are well developed with five fingers and toes, respectively. The specimen was not collected, but measured before being released, some scale counts were done, and a blood sam-



Figure 2. *Chalcides ocellatus subtypicus* in life, adult female, Nador, dunes between the sea and the Mar Chica (Morocco). Photograph by V. RIVIÈRE.

ple was taken (BEV.T4249). Its body scales were relatively numerous (30 longitudinal rows at midbody) and the loreal was in contact with the 2nd supralabial. Its snout-vent length was 100 mm and its non-regenerated tail length was 140 mm. The habitat where it was found is an arid steppe at the foothills of a low mountain (Fig. 4). The other squamate species known from Missouri are *Uromastix nigri-ventris* ROTHSCHILD & HARTERT, 1912, *Tarentola mauritanica* (LINNAEUS, 1758), *Acanthodactylus boskianus* (DAUDIN, 1802), *Psammmodromus algirus* (LINNAEUS, 1758), *Chalcides ocellatus subtypicus*, *Spalerosophis dolichospilus* (WERNER, 1923), and *Natrix maura* (LINNAEUS, 1758) (BONS & GENIEZ 1996), but this list is probably incomplete.

On 5 May 2008, a third specimen of PALLARY's Skink was found and photographed in Algeria by VR and Julien Viglione at Khanguet-el-Melah near Aïn Maadeb (province of Djelfa, 34.83006° N, 3.08471°E, 918 m a.s.l.); a tail sample was preserved (BEV.T4238), but the specimen was not collected. This individual (Fig. 5) is very similar to the two previous specimens with the anterior part of the body exhibiting the same colour pattern of five black stripes, poorly marked ocelli except on the wide dark flank stripe from the ear opening to a short distance behind the forelegs, pale broad dorsolateral stripes and black flanks, giving way to a completely uniform light brown coloration in the posterior parts of the body, the hindlimbs and the tail. The pileus has a black pattern (unlike YH's specimen from Missouri but like PALLARY's specimen), and the loreal is situated above the 2nd supralabial. This third locality is situated 680 km east of Missouri, but forms part of the same region of the Algero-Moroccan Hauts Plateaux. The habitat was similar (an arid plateau around 1000 m a.s.l., Fig. 6). Other reptiles and amphibians observed at this place (within a radius of 1 km) were (VR & OP obs.) *Testudo graeca* LINNAEUS, 1758, *Mauremys leprosa* (SCHWEIGGER, 1812), *Agama bibronii* DUMÉRIEL in DUMÉRIEL



Figure 3. *Chalcides montanus pallaryi* ssp. n. in life, BEV.T4249, adult, Jbel Missouri (Morocco). Photograph by Y. HINGRAT.

& DUMÉRIL, 1851, *Chamaeleo chamaeleon* (LINNAEUS, 1758), *Tarentola mauritanica*, *Ptyodactylus oudrii* LATASTE, 1880, *Acanthodactylus boskianus*, *Psammodromus algerus*, *Chalcides ocellatus*, *Trogonophis wiegmanni* KAUP, 1830, *Hemorrhois hippocrepis* (LINNAEUS, 1758), *Psammophis schokari* (FORSKÅL, 1875), and Bufonidae sp. (tadpoles).

Comparison with other *Chalcides* spp.

The unidentified specimens are easily distinguished from most congeneric species by morphological features. *Chalcides ocellatus* and *C. humilis* are larger with adults usually exceeding 110 mm in snout–vent length, lack continuous black stripes in the anterior portion of the dorsum, but exhibit sharply defined ocelli on the body and tail

that are arranged in transverse series and separated from each other by 2 or 3 uniformly coloured scales (no ocelli on the dorsum in the new taxon or, if they exist, ocelli are not clearly defined and are separated from each other by 0 or 1 uniformly coloured scale), and by the loreal scale being contiguous with both the 2nd and 3rd supralabials (with the 2nd supralabial only in the new taxon, suggesting a shorter nose). *Chalcides manuelyi* is either entirely uniform brown (northern population from the Essaouira region) or with 5 black stripes on the dorsum (southern population), which are shorter than in the new taxon, and without ocelli. *Chalcides colosii* has no dark stripes on the dorsum, a broad dark stripe on each flank and a broad light stripe running along each edge of the dorsum up to the level of the hind limbs; the loreal is frequently (but not always) situated above the 2nd and 3rd supralabials. *Chalcides ebneri*



Figure 4. Habitat of *Chalcides montanus pallaryi* ssp. n., Jbel Missouri (Morocco). Photograph by Y. HINGRAT.



Figure 5. *Chalcides montanus pallaryi* ssp. n. in life, BEV.T4238, adult, Khanguet-el-Melah, province of Djelfa (Algeria). Photographs by V. RIVIÈRE.

has a complete black and yellowish striped pattern without any ocelli except on the tail. *Chalcides parallelus* and *C. lanzai* may look similar at a first glance, but bear many ocelli on the whole dorsal body and tail, and the two light wide dorsolateral stripes are frequently (*parallelus*) or always (*lanzai*) missing. *Chalcides polylepis* is frequently larger (up to 153 mm in snout–vent length), has always more scales around the body (33–40 longitudinal scale rows vs. 30), and the loreal scale touches the 2nd and 3rd supralabials, like in *C. ocellatus*. Lastly, *C. mionecton*, *C. trifasciatus*, *C. bouleengeri*, *C. sphenopsiformis*, *C. delislei*, and the species of the “grass-swimming” clade all differ obviously in body (much

elongated) and limb (much shorter) proportions and numbers of digits (less than five except in *C. trifasciatus*).

PALLARY’S Skink is most similar to the Mountain Skink, *Chalcides montanus* (Fig. 7), a taxon endemic to the high altitudes of the High Atlas in Morocco. *Chalcides montanus* shares with PALLARY’S Skink the following features: moderate size (around 100 mm SVL), five black dorsal stripes continuous in the anterior portion of the back, dark anterior part of the flanks delimiting two broad light dorso-lateral stripes, snout with some orange, belly yellow, loreal usually in contact only with the 2nd supralabial, but sometimes reaching both 2nd and 3rd supralabials. It differs from



Figure 6. Habitat of *Chalcides montanus pallaryi* ssp. n., Khanguet-el-Melah, province of Djelfa (Algeria). Photograph by V. RIVIÈRE.



Figure 7. *Chalcides montanus montanus* in life, adult, 5 km below Oukaimeden, 2328 m a.s.l. (Morocco, High Atlas). Photograph by P. GENIEZ.

PALLARY'S Skink by the existence of white and black ocelli all over the body including the flanks at least in adults (but neither on the hindlimbs nor on the tail), a dark wide stripe along the flank, and by having two broad light dorso-lateral stripes reaching the base of the tail. As can be seen from the PCA results (Fig. 8), the colour pattern allows to distinguish all specimens of *C. polylepis*, *C. manueli*, and especially the similar *C. montanus* from the three known specimens of PALLARY'S skink.

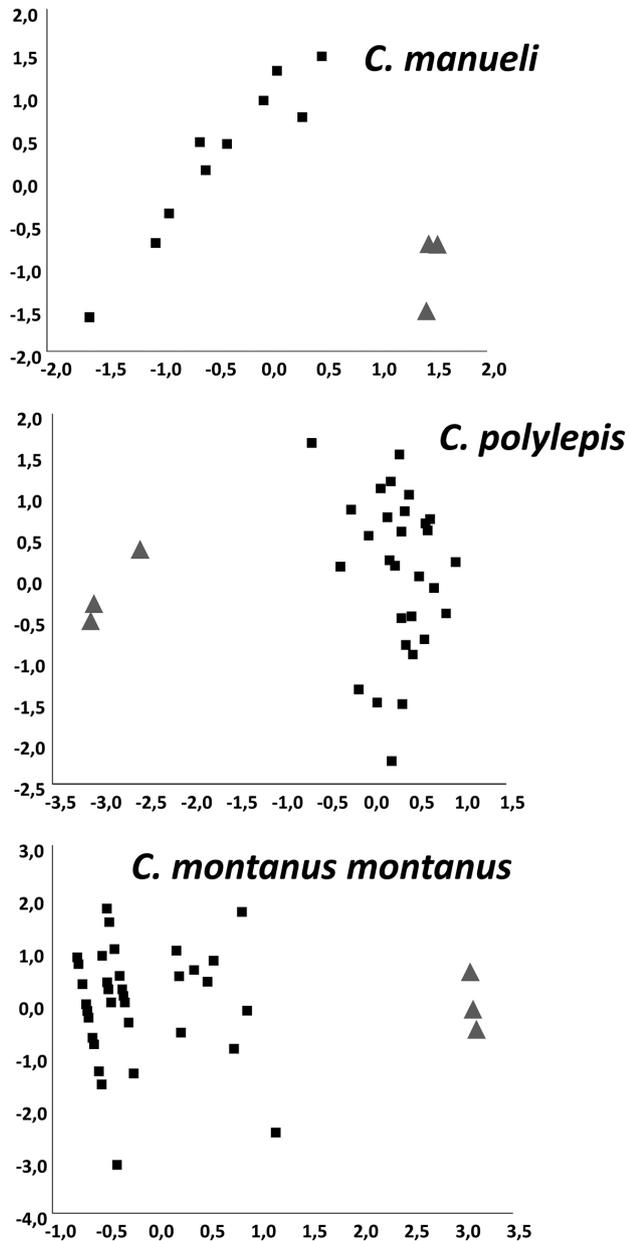


Figure 8. PC1 (horizontal axis) X PC2 (vertical axis) scatterplots of three independent PCAs comparing all three known individuals of PALLARY'S Skink (grey triangles) with specimens of *Chalcides manueli*, *C. polylepis* and *C. montanus montanus*, respectively (black squares).

Genetic results

A 425-base pair (bp) alignment of the *cytb* gene was available for our final analyses, with individual sequence lengths varying from 396 to 425 bp (no indels). For the nuclear loci, the concatenated alignment was made up of approximately 470 bp for TROP, 665 for MC1r, 650 bp for R35, 520 for PRLR, and 540 for OD (including indels for all genes). The loci available for every individual are listed in Table 2, together with the Genbank accession number of each sequence.

Both mitochondrial and nuclear data sets confirm that the two specimens of *Chalcides* from Missouri and Djelfa are so closely related as to be conspecific and that they do not belong to *Chalcides ocellatus* sensu lato (Figs 9–10) or to *C. parallelus*. The individual nuclear gene networks reveal a complete lack of allele-sharing for four loci between the sympatric *Chalcides ocellatus* and the new skink, suggesting strong reproductive isolation (Fig. 11). Both data sets firmly place the new skink as sister to *C. montanus*, and the mitochondrial data suggests they belong to a clade that also includes *C. manueli*, *C. polylepis*, and *C. mionecton*. Both nuclear and mitochondrial data sets also highlight the genetic distinctiveness of the new skink as they do not share nuclear or mitochondrial alleles with their closest relative, *C. montanus*, or with any other *Chalcides* spp. inhabiting Morocco. Genetic distances to the nearest species, *C. montanus*, are 4.2% in *cytb* and 0.8% for the concatenated nuclear loci (Tables 3, 4)

Systematic section

The unidentified taxon represented here by the Missouri and Djelfa specimens is morphologically and genetically distinct from all other described *Chalcides* spp. Even if we could not obtain sequences from PALLARY'S specimen, it is morphologically similar to these two specimens and originates from the same area as the Missouri specimen. We have therefore no doubt that it belongs to the same taxon. These three specimens thus represent a new taxon that is genetically closely related and morphologically similar to *C. montanus*, but is distinct from this taxon in morphology, mitochondrial DNA and nuclear DNA.

These two taxa inhabit distinct ecozones, with *C. montanus* being restricted to the upper forest belt and high-altitude steppe vegetation of the High Atlas above 1782 m and up to 3172 m a.s.l. (CAPUTO et al. 1995, MARTÍNEZ DEL MÁRMOL et al. 2019, present study) while the as yet unnamed specimens have been found in the semi-arid steppe of the Hauts Plateaux (between 900 and 1100 m a.s.l., but only two precise localities are known). It might be worthy of note that we were unable to verify the identification of a specimen of "*Chalcides ocellatus montanus*" from the eastern High Atlas, 20 km NW Talsint, 1750 m a.s.l. (BONS 1960); its locality (question mark in Fig. 12) is situated far from the other known populations of *C. montanus* and the altitude is lower than what is typical for *C. montanus*. Other

species recorded at the same locality include *Psammophis schokari* and *Ptyodactylus oudrii*, amongst others (BONS 1960). We are not convinced that this specimen indeed represents *C. montanus*, and it could be another specimen of PALLARY's skink. This adds to the uncertainty surrounding the relative range limits of *C. montanus* and PALLARY's skink. Their known ranges do not currently overlap, and while a contact zone between *C. montanus* and the new taxon along the northern foothills of the eastern High Atlas is entirely possible, we need to treat the two lineages as allopatric for the time being. The assessment of their status (conspecific or different species) must rest on indirect evidence such as their extent of divergence compared with other closely related species pairs in the same group.

Leaving aside *C. lanzai* and *C. colosii*, whose status relative to *C. parallelus* will clearly require further work, the amount of nuclear genetic divergence (concatenated alignment, see Tables 3a, 3b) between *C. montanus* and the as yet unnamed taxon is similar to the divergence between other widely-recognised species pairs included in our dataset (0.8% versus 0.4% for *pseudostriatus* – *striatus*, 0.6% for *mertensi* – *minutus*, 1.2% for *ocellatus* – *humilis*) while their amounts of mitochondrial divergence are slightly lower (4.2% versus 5.8% for *pseudostriatus* – *striatus*, 15.6% for *mertensi* – *minutus*, 14.8% for *ocellatus* – *humilis*, 10% for *mionecton* – *trifasciatus*, 7.8% for *manueli* – *polylepis*). The divergence between *Chalcides montanus* and the new taxon lies in the grey area between subspecies and closely

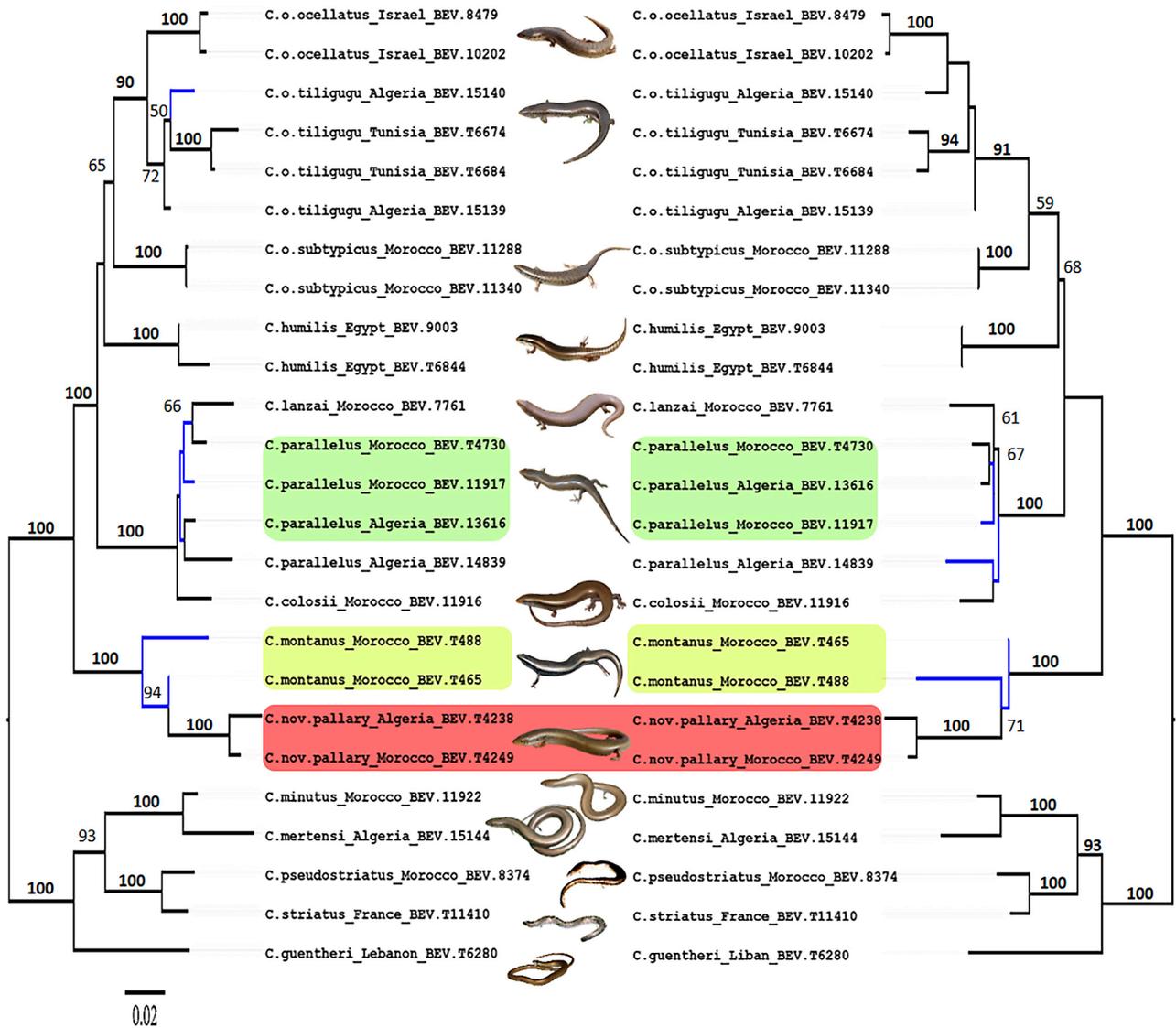


Figure 9. Neighbour-joining (NJ, left) and Maximum likelihood (ML, right) trees of the concatenated nuclear dataset containing 7 of the 16 *Chalcides* species occurring in Morocco. The new subspecies of *C. montanus* is highlighted in red. The values along branches are node bootstrap supports (for support > 50%, values > 90% in bold). Discordances in the tree topology (blue) and branching order of individuals are highlighted in different colours.

related species. Their amount of nuclear genetic divergence is more typical of interspecific comparisons using the same markers in our dataset, they exhibit marked ecological divergence, and a level of phenotypic divergence similar to the divergence between accepted species in the genus *Chalcides* in Morocco. However, they are not unambiguously recovered as reciprocally monophyletic in our trees, and we acknowledge the need for further sampling in the eastern High Atlas and western Hauts Plateaux to better understand if they come in contact or not and assess their amount of reproductive isolation. We thus err on the side of caution here and describe this new taxon as a subspecies of *Chalcides montanus* pending further analyses.

***Chalcides montanus pallaryi* ssp. n.**

ZooBank LSID: urn:lsid:zoobank.org:act:DFBCE8C6-D7D9-4C16-85E5-84AE9D12A618

Holotype. MNHN-RA-1925.215, adult female from Missouri (eastern Morocco) collected by PAUL PALLARY on 30 December 1925 and deposited in the Muséum national d’Histoire naturelle in Paris (Fig. 1).

Etymology. Dedicated to PAUL PALLARY (1869–1942) who collected the holotype. PAUL PALLARY was a teacher working in Algeria and a knowledgeable zoologist (particularly

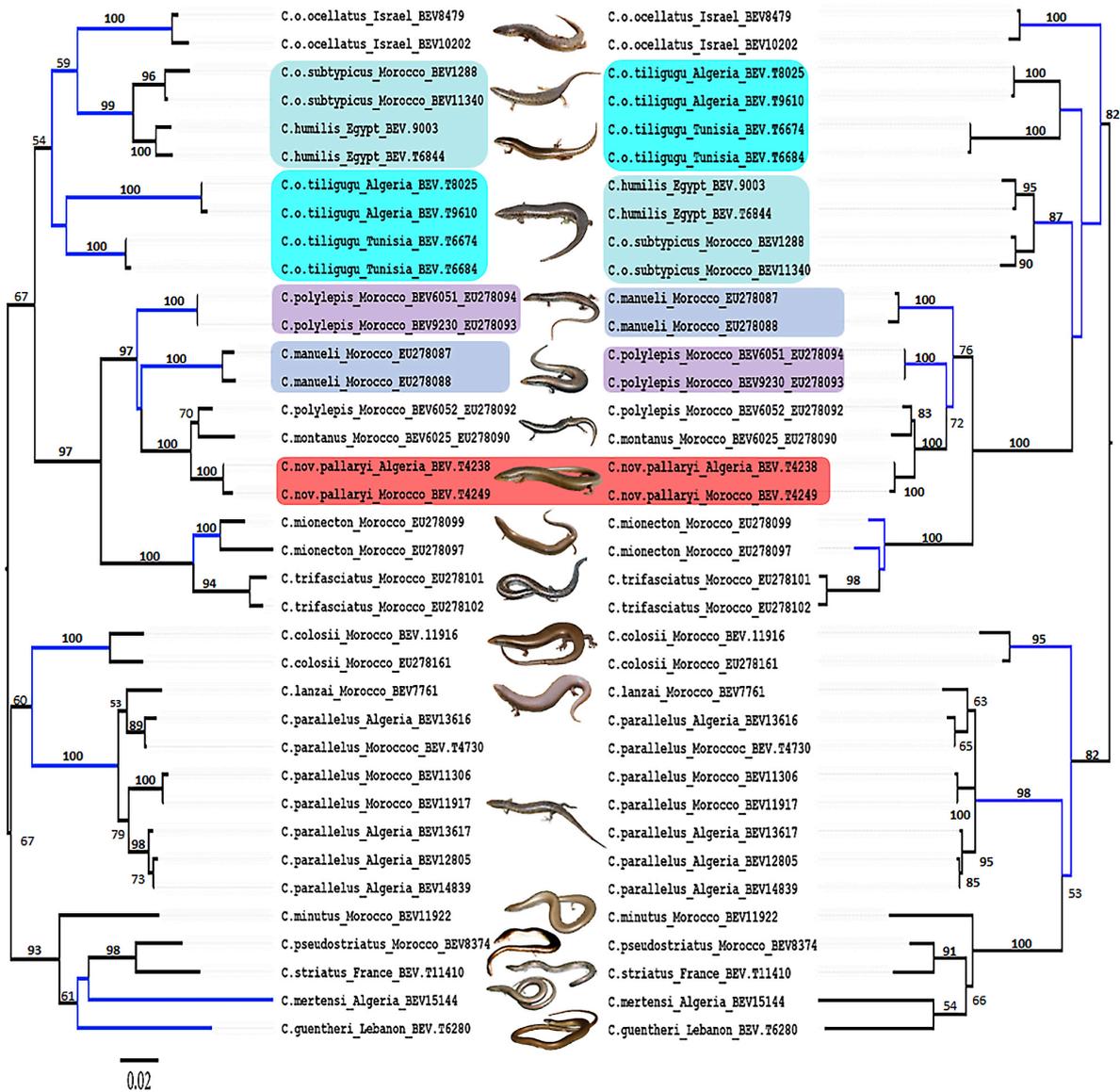


Figure 10. Neighbour-joining (NJ, left) and Maximum likelihood (ML, right) trees of the mtDNA dataset containing 11 of the 16 *Chalcides* species occurring in Morocco. The new subspecies of *C. montanus* is highlighted in red. The values along branches are node bootstrap supports (for support > 50%, values > 90% in bold). Discorances in the tree topology (blue) and branching order of individuals are highlighted in different colours.

New *Chalcides* from North Africa

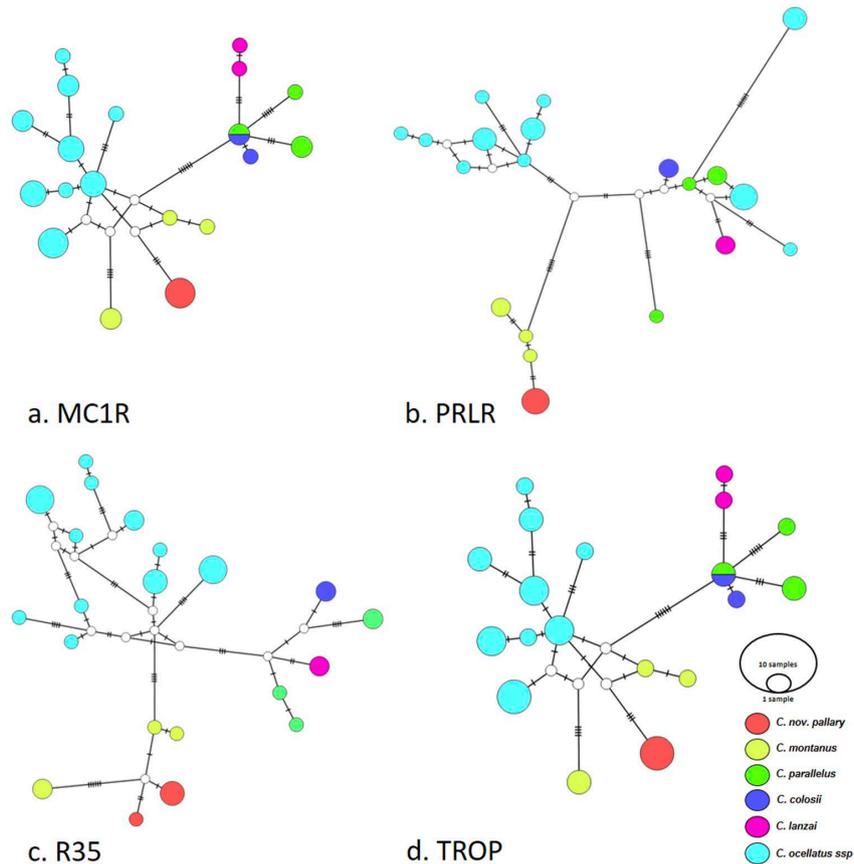


Figure 11. Median-joining networks depicting the relationships between haplotypes of the nuclear genes MC1r (665 bp), PRLR (533bp), R35 (649 bp), and TROP (470 bp). The various haplotypes are depicted in pie charts, with the slices representing a given haplotype relative frequency (the haplotype size/frequency ratio is shown in the bottom right insert). The colours correspond to the mitochondrial lineage assignment as defined by the phylogenetic trees (NJ vs. ML) shown above.

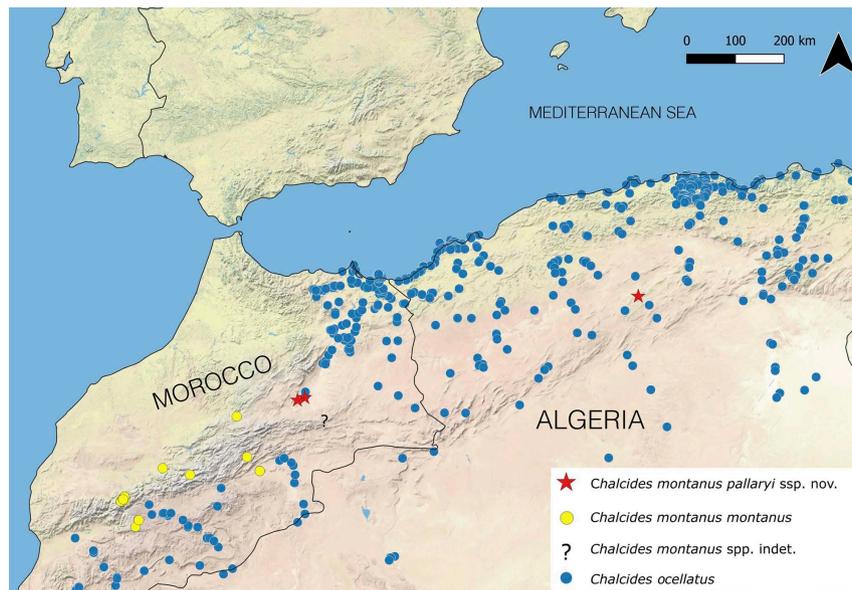


Figure 12. Schematic map of northwestern Africa showing the known distribution ranges of *Chalcides montanus pallaryi* ssp. n. and *C. montanus montanus*, and the distribution of *C. ocellatus* in Morocco and northern Algeria. The question mark points to a locality (20 km NW Talsint) where *C. m. montanus* was recorded by BONIS (1960, see text), but which might in fact refer to *C. m. pallaryi*.

Table 3a. Matrix of pairwise distances between groups for the mitochondrial dataset. Analyses were conducted using the Kimura 2-parameter model, and rate variation was modelled under a gamma distribution (shape parameter = 1).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>C. colosii</i>																		
<i>C. guentheri</i>	0.196																	
<i>C. humilis</i>	0.152	0.216																
<i>C. lanzai</i>	0.128	0.191	0.191															
<i>C. manueli</i>	0.169	0.217	0.180	0.170														
<i>C. mertensi</i>	0.215	0.162	0.206	0.213	0.204													
<i>C. minutus</i>	0.157	0.134	0.211	0.146	0.183	0.156												
<i>C. mionecton</i>	0.189	0.225	0.189	0.217	0.134	0.244	0.223											
<i>C. montanus montanus</i>	0.181	0.234	0.195	0.190	0.079	0.234	0.199	0.151										
<i>C. ocellatus ocellatus</i> (Israel)	0.147	0.197	0.148	0.163	0.169	0.204	0.159	0.216	0.189									
<i>C. montanus pallaryi</i> ssp. n.	0.175	0.235	0.189	0.180	0.078	0.200	0.206	0.145	0.042	0.179								
<i>C. parallelus</i>	0.123	0.171	0.183	0.040	0.172	0.232	0.150	0.212	0.196	0.170	0.194							
<i>C. polylepis</i>	0.177	0.228	0.186	0.193	0.078	0.212	0.184	0.145	0.073	0.178	0.074	0.198						
<i>C. pseudostriatus</i>	0.167	0.139	0.203	0.174	0.157	0.140	0.116	0.221	0.184	0.150	0.192	0.172	0.182					
<i>C. striatus</i>	0.180	0.139	0.194	0.170	0.190	0.160	0.130	0.233	0.189	0.177	0.196	0.172	0.201	0.058				
<i>C. ocellatus subtypicus</i> (Morocco)	0.108	0.207	0.103	0.146	0.152	0.188	0.155	0.156	0.189	0.129	0.175	0.139	0.175	0.182	0.178			
<i>C. ocellatus tiligugu</i> (Algeria)	0.154	0.196	0.125	0.154	0.147	0.213	0.159	0.179	0.169	0.101	0.173	0.178	0.157	0.154	0.178	0.115		
<i>C. ocellatus tiligugu</i> (Tunisia)	0.144	0.201	0.115	0.164	0.160	0.220	0.158	0.186	0.165	0.111	0.164	0.167	0.155	0.167	0.194	0.097	0.044	

Table 3b. Matrix of pairwise distances between groups for the concatenated nuclear dataset. Analyses were conducted using the Kimura 2-parameter model, and rate variation was modelled under a gamma distribution (shape parameter = 1).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>C. colosii</i>															
<i>C. guentheri</i>	0.028														
<i>C. humilis</i>	0.015	0.024													
<i>C. lanzai</i>	0.007	0.030	0.015												
<i>C. mertensi</i>	0.033	0.020	0.030	0.033											
<i>C. minutus</i>	0.029	0.016	0.024	0.029	0.006										
<i>C. montanus montanus</i>	0.017	0.025	0.016	0.019	0.030	0.026									
<i>C. ocellatus ocellatus</i> (Israel)	0.015	0.025	0.012	0.019	0.032	0.027	0.016								
<i>C. montanus pallaryi</i> ssp. n.	0.022	0.032	0.018	0.022	0.037	0.034	0.008	0.023							
<i>C. parallelus</i>	0.005	0.028	0.014	0.005	0.032	0.028	0.017	0.016	0.023						
<i>C. pseudostriatus</i>	0.028	0.019	0.025	0.029	0.017	0.014	0.024	0.028	0.033	0.028					
<i>C. striatus</i>	0.028	0.017	0.025	0.029	0.016	0.013	0.025	0.027	0.032	0.027	0.004				
<i>C. ocellatus subtypicus</i> (Morocco)	0.015	0.026	0.011	0.016	0.030	0.028	0.018	0.013	0.024	0.014	0.027	0.026			
<i>C. ocellatus tiligugu</i> (Algeria)	0.014	0.024	0.012	0.017	0.031	0.026	0.016	0.007	0.022	0.014	0.027	0.026	0.009		
<i>C. ocellatus tiligugu</i> (Tunisia)	0.019	0.030	0.014	0.020	0.032	0.027	0.018	0.009	0.020	0.018	0.027	0.027	0.012	0.005	

in continental malacology and arachnology) exploring Algeria and Morocco; he was also interested in geology, pre-history and archaeology (Anonymous 2023).

Diagnosis. A medium-sized skink (around 100 mm in snout-vent length), with 30 longitudinal scale rows around mid-body, 5 digits on well-developed forelimbs and hindlimbs, five continuous black dorsal stripes in the anterior part on the back giving way to a near-uniform coloration in the rear portion of the body in the shape of brown scales with slightly paler centres, dark anterior part of the flanks delimiting two broad light dorsolateral stripes that disap-

pear at about midbody, pileus uniform or with black markings, and loreal positioned directly above the 2nd supralabial. The combination of five longitudinal black stripes in the first third of the dorsum, ocelli on the dorsum and on the flanks disappearing roughly in the first third or half of the body, and two broad light dorsolateral stripes that disappear at about midbody seems to be diagnostic for *Chalcides montanus pallaryi* ssp. n. See the Results section above for comparison with other species.

Description of the holotype. An adult female in a relatively bad state of preservation measuring 96 mm in snout-vent

length and having 30 longitudinal scale rows at midbody, five dark continuous longitudinal stripes in the anterior portion of the dorsum that are separated from the dark flank by one broad light dorsolateral stripe on each side, this pattern progressively fades to a uniform coloration on the more posterior back, the flanks, the legs and the tail. Loreal above the 2nd supralabial.

Range. Moroccan and Algerian Hauts Plateaux, known only from two areas: Missouri and Jbel Missouri in Morocco, and Khanguet-el-Melah, near Aïn Maadeb, province of Djelfa, in Algeria, (Fig. 12).

Conclusions

The discovery of a new reptile taxon in the Western Palearctic in the 21st century illustrates the challenge of assessing biodiversity erosion while we are still in the process of describing biodiversity. Squamates of arid climates are threatened by human activities and are highly susceptible to climate change (MARTÍNEZ DEL MÁRMOL et al. 2019). Paradoxically, the statuses of many of these taxa remain indeterminate due to a lack of data. The remoteness of their habitats and their particular habits render the study of their biology and demography particularly challenging. The specimen found at Missouri, Morocco, by YH was maintained in captivity for two years before being released where it had been collected. During this period, and although fed ad libitum (live crickets), this individual was active only from March to October, and was active above the surface mainly when feeding. Outside of feeding time and during autumn and winter, the animal remained buried and immobile. This could partly explain the apparent rarity of this species. Indeed, species with such habits are difficult to find and because of this, difficult to survey.

Our results have also identified numerous cases of conflicts between phylogenetic data and currently accepted taxonomy (see for example the *C. parallelus* – *lanzai* – *colosii* clade). While we refrain from proposing taxonomic decisions at this stage, our data (together with the previously published studies by CARRANZA et al. [2008] and BARATA [2013]) highlight the need for the proper systematic revision of several species in Morocco, incorporating genetic, ecological and morphological data on a larger number of specimens.

Acknowledgements

We thank PATRICIA SOURROUILLE for her help with the genetic analyses, and BENJAMIN ALLEGRINI, JEAN-MARIE BALLOUARD, ABDELKRIM BELHADJ, RAFIK BENMERAD, FRANÇOIS BONHOMME, JACQUES BONS, JACQUES CASSAIN, JULES CHIFFARD, ALEXANDRE CLUCHIER, BOUALEM DELLAOUI, KIM ESCATLLAR, SOUMIA FAHD, MICHEL GENIEZ, CLAUDE P. GUILLAUME, ALBAN GUILLAUMET, MAHMOUD LARIBI, RAPHAËL LEBLOIS, JOSÉ ANTONIO MATEO, JULIEN MAZENAUER, AURÉLIEN MIRALLES, ALEXANDRE TEYNIÉ, ERROL VELA, and JULIEN VIGLIONE for sending us samples or for

helping with collecting samples in the field. THIERRY HOAREAU provided insightful comments on a previous version of this manuscript. Lastly, our thanks are due to the naturalists mentioned in Supplementary Table S3 who kindly made their photographs of live specimens available for the examination of colour pattern features.

References

- Anonymous (2023): Article Paul Pallary de Wikipédia en français. – https://fr.wikipedia.org/wiki/Paul_Pallary, consulted on 13 November 2023.
- BANDELIT, H., P. FORSTER & A. RÖHL (1999): Median-joining networks for inferring intraspecific phylogenies. – *Molecular Biology and Evolution*, **16**: 37–48.
- BARATA, M. (2013): High altitude phylogeography of selected Moroccan herpetofauna. – Unpublished PhD thesis, Faculdade de Ciências da Universidade do Porto, Portugal.
- BEDDEK, M., S. ZENBOUDJI-BEDDEK, P. GENIEZ, R. FATHALLA, P. SOURROUILLE, V. ARNAL, B. DELLAOUI, F. KOUDACHE, S. TELAILIA, O. PEYRE & P.-A. CROCHET (2018): Comparative phylogeography of amphibians and reptiles in Algeria suggests common causes for the east-west phylogeographic breaks in the Maghreb. – *PLoS ONE*, **13**: e0201218.
- BONS, J. & P. GENIEZ (1996): Amphibiens et Reptiles du Maroc, Sahara Occidental compris. Atlas biogéographique. – Asociación Herpetológica Española, Barcelona.
- BRANDLEY, M. C., Y. WANG, X. GUO, A. N. M. DE OCA, M. FERÍA-ORTÍZ, T. HIKIDA & H. OTA (2011): Accommodating heterogeneous rates of evolution in molecular divergence dating methods: an example using intercontinental dispersal of *Plestiodon* (*Eumeces*) lizards. – *Systematic Biology*, **60**: 3–15.
- BROWN, R. P., T. TEJANGKURA, E. H. EL MOUDEN, M. A. AIT BAAMRANE & M. ZNARI (2012): Species delimitation and digit number in a North African skink. – *Ecology and Evolution*, **2**: 2962–2973.
- CAPUTO, V., B. LANZA & R. PALMIERI (1995): Body elongation and limb reduction in the genus *Chalcides* Laurenti 1768 (Squamata Scincidae): a comparative study. – *Tropical Zoology*, **8**: 95–152.
- CARRANZA, S., E. N. ARNOLD., P. GENIEZ, J. L. ROCA & J. A. MATEO (2008): Radiation, multiple dispersal and parallelism in Moroccan skinks, *Chalcides* and *Sphenops* (Squamata: Scincidae), with comments on *Scincus* and *Scincopus* and the age of the Sahara Desert. – *Molecular Phylogenetics and Evolution*, **46**: 1071–1094.
- FRIESEN, V. L., B. C. CONGDON, M. G. KIDD & T. P. BIRT (1999): Polymerase chain reaction (PCR) primers for the amplification of five nuclear introns in vertebrates. – *Molecular Ecology*, **8**: 2141–2152.
- GIOVANNOTTI, M., P. NISI CERIONI, A. SPLENDIANI, M. KALBOUSI, P. RUGGERI & V. CAPUTO BARUCCHI (2013): Mitochondrial DNA reveals high genetic divergence between populations of *Chalcides mertensi* Klausewitz, 1954 (Reptilia: Scincidae) from Tunisia. – *Amphibia-Reptilia*, **34**: 389–399.
- KORNILIOS, P., P. KYRIAZI, N. POULAKALIS, Y. KUMLUTAŞ, Ç. ILGAZ, M. MYLONAS & P. LYMBERAKIS (2010): Phylogeography of the ocellated skink *Chalcides ocellatus* (Squamata, Scincidae), with the use of mtDNA sequences: A hitch-hiker's guide to the Mediterranean. – *Molecular Phylogenetics and Evolution*, **54**: 445–456.

- KUMAR, S., G. STECHER & K. TAMURA (2016): MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. – *Molecular Biology and Evolution*, **33**: 1870–1874.
- LANFEAR, R., B. CALCOTT, S. Y. W. HO & G. GUINDON (2012): PartitionFinder: Combined Selection of Partitioning Schemes and Substitution Models for Phylogenetic Analyses. – *Molecular Biology and Evolution*, **29**: 1695–1701.
- LANZA, B. (1957): Su alcuni “*Chalcides*” del Marocco (Reptilia, Scincidae). – *Monitore zoologico italiano*, **65**: 85–98.
- LAVIN, B. R. & T. J. PAPPENFUSS (2012): The phylogenetic position of *Chalcides ocellatus* (Squamata: Scincidae) from Yemen and Somalia. – *Zootaxa*, **3221**: 26–36.
- MARTÍNEZ DEL MÁRMOL, G., D. J. HARRIS, P. GENIEZ, P. DE POUS & D. SALVI (2019): Amphibians and Reptiles of Morocco. – Edition Chimaira, Frankfurt am Main.
- MATEO, J. A., P. GENIEZ & J. BONS (1995): Saurians of the genus *Chalcides* Laurenti 1768 (Reptilia, Scincidae) in Morocco, I: review and distribution. – *Revista Española de Herpetología*, **9**: 7–36.
- MCGUIRE, J. A., C. C. WITT, D. L. ALTSHULER & J. V. REMSEN JR. (2007): Phylogenetic Systematics and Biogeography of Hummingbirds: Bayesian and Maximum Likelihood Analyses of Partitioned Data and Selection of an Appropriate Partitioning Strategy. – *Systematic Biologists*, **56**: 837–856.
- MCWILLIAM, H., W. LI, M. ULUDAG, S. SQUIZZATO, Y. M. PARK, N. BUSO, A. P. COWLEY & R. LOPEZ (2013): Analysis Tool Web Services from the EMBL-EBI. – *Nucleic Acids Research*, **41** (Web Server Issue).
- MONTERO-MENDIETA, S., J. FERRER, M. AIT HAMMOU, W. DAHMANI, D. SANUY & S. CARAMASA (2017): Another record or a new taxon? A candidate species of *Chalcides* Laurenti, 1768, in North Africa (Squamata: Sauria: Scincidae). – *Herpetozoa*, **29**: 155–161.
- NGUYEN, L.-T., H. A. SCHMIDT, A. VON HAESELER & D. Q. MINH (2014): IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. – *Molecular Biology and Evolution*, **32**: 268–274.
- PELLEGRIN, J. (1926): Reptiles, batraciens et poissons du Maroc oriental recueillis par M. P. Pallary. – *Bulletin du Muséum national d’Histoire naturelle de Paris*, **32**: 159–161.
- PINHO, C., S. ROCHA, B. M. CARVALHO, S. LOPES, S. MOURÃO, M. VALLINOTO, T. O. BRUNES, C. F. B. HADDAD, H. GONÇALVES, F. SEQUEIRA & N. FERRAND N. (2009): New primers for the amplification and sequencing of nuclear loci in a taxonomically wide set of reptiles and amphibians. – *Conservation Genetics Resources*, **2** (Suppl. 1): 181.
- RONQUIST, F., M. TESLENKO, P. VAN DER MARK, D. L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M.A. SUCHARD & J. P. HUELSENBECK (2012): MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. – *Systematic Biology*, **61**: 539–542.
- ROZAS, J., A. FERRER-MATA, J. C. SÁNCHEZ-DELBARRIO, S. GUIRAO-RICO, P. LIBRADO, S.E. RAMOS-ONSINS & A. SÁNCHEZ-GRACIA (2017): DnaSP 6: DNA Sequence Polymorphism Analysis of Large Data Sets. – *Molecular Biology and Evolution*, **34**: 3299–3302.
- SINDACO, R. & V. K. JEREMČENKO (2008): The Reptiles of the Western Palearctic. 1. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. – *Belvedere, Latina*.
- SMITH, M. F. & J. L. PATTON (1993): The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. – *Biological Journal of the Linnean Society*, **50**: 149–177.
- TOWNSEND, T. M., R. E. ALEGRE, S. T. KELLEY, J. J. WIENS & T. W. REEDER (2008): Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: An example from squamate reptiles. – *Molecular Phylogenetics and Evolution*, **47**: 129–142.
- YAO, J., D. ZADWORNÝ, U. KÜHNLEIN & J. F. HAYES (1995): Molecular cloning of a bovine ornithine decarboxylase cDNA and its use in the detection of restriction fragment length polymorphisms in Holsteins. – *Genome*, **38**: 325–331.

Supplementary data

The following data are available online:

- Supplementary Figure S1. Bayesian tree of the concatenated nuclear dataset.
- Supplementary Figure S2. Bayesian tree of the mtDNA datasets.
- Supplementary Table S3. Complete list of the examined specimens.