Extended description, variation, and biology of *Mediodactylus bartoni* (Reptilia: Squamata: Gekkonidae)

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Abstract. Recent phylogenetic studies of the Mediterranean gecko of the genus *Mediodactylus* revealed that the population inhabiting Crete and adjacent islands represents an endemic species *M. bartoni* (Štěpánek, 1934). However, the taxonomic and nomenclatural position of two "island" subspecies (*Gymnodactylus kotshyi wettsteini* Štěpánek, 1936 and *G. k. stubbei* Wettstein, 1952) to *Mediodactylus bartoni* remained unclear. Here, based on morphological examinations and genetic analyzes of four markers, we synonymize the names *Gymnodactylus kotshyi wettsteini* and *Gymnodactylus kotshyi stubbei* with the name *Mediodactylus bartoni* and provide an extended description of *M. bartoni*.

Key words. Crete, endemic geckos, taxonomy, *Gymnodactylus kotschyi stubbei*, *Gymnodactylus kotschyi wettsteini*.

INTRODUCTION

During his first research trip to central Crete in 1934, the Czech herpetologist Otakar Štěpánek (1903–1995) discovered a new taxon of gecko, which he described as a new species of the genus *Gymnodactylus* (*G. bartoni* Štěpánek, 1934; see Štěpánek 1934). Later, Štěpánek re-evaluated the taxonomic position of his gecko and classified it as a subspecies of *Gymnodactylus kotschyi* Steindachner, 1870 (*G. k. bartoni* Štěpánek, 1934; see Štěpánek 1937a, b). In the following years, four more subspecies of *G. kotschyi* were described from the small coastal islands around Crete – *G. k. wettsteini* Štěpánek 1937 (from the islet of Mikronisi at Agios Nikolaos), *G. k. kalypsae* Štěpánek, 1939 (from the island of Gavdos), *G. k. rarus* Wettstein, 1952 (from the island of Chrysi), and *G. k. stubbei* Wettstein, 1952 (from the island of Koufonisi). Despite the turbulent changes in the generic assignment of Štěpánek's gecko taxon (gradually: *Cyrtodactylus* Gray, 1827; *Tenuidactylus* Šerbak et Golubev, 1984; *Cyrtopodion* Fitzinger, 1843; *Mediodactylus* Šerbak et Golubev, 1977; see e. g. Šerbak & Golubev 1986, Kluge 1993, Szczerbak 2003, Sindaco & Jeremčenko 2008, Bauer et al. 2013) as well as the very weak description of the individual subspecies, the subspecific status of the taxa *bartoni* and *wettsteini* was not questioned until 2005 when the first molecular phylogeny of *Mediodactylus kotschyi* was published (Kasapidis et al. 2005).

The latter authors found out that taxonomic classification at the subspecies level is not in good agreement with the molecular phylogeny. They defined nine major geographically structured clades within their *Cyrtopodion kotschyi*, with Cretan geckos (except of the individuals from Gavdos) forming the first most basal one (Clade I). In this Cretan clade, the subspecies *wettsteini* (represented by samples from the islets of Avgo, Chrysi, Petalida and Pontikonisi) appeared to be

paraphyletic with respect to the subspecies *bartoni* (represented by one sample from Nida plateau). The following thorough phylogenetic study of *Mediodactylus kotschyi* complex (Kotsakoizi et al. 2018) led to the recognition of five highly supported monophyletic units (Clades A–E), which were assigned full species status: *M. bartoni* (Štěpánek, 1934), *M. danilewskii* (Strauch, 1887), *M. kotschyi* (Steindachner, 1870), *M. oertzeni* (Boettger, 1888), and *M. orientalis* (Štěpánek, 1937). According to this new taxonomy, the name *Mediodactylus bartoni* was applied to Clade D comprising samples of *M. bartoni* from its type locality (Nida plateau, Psiloritis Mt., central Crete) and samples of geckos from coastal island/islets of Avgo, Chrysi, Dia, Elasa, Mikronisi, Petalida, and Psira; the geckos from the island of Gavdos were identified as *M. danilewskii kalypsae* (Štěpánek, 1936). Despite that the analyzed material included samples from the type locality of *Gymnodactylus kotschyi rarus* (Chrysi islet), the intraspecific taxonomy of *M. bartoni* could not be resolved sufficiently as the samples from the type localities of *Gymnodactylus kotschyi wettsteini* (Mikronisi islet at Agios Nikolaos, northern coast of eastern Crete) and *G. k. stubbei* (Koufonisi islet) were not available (coordinates of Mikronisi referred to different islet lying at the southern coast of Crete and samples from Koufonisi were missing).

Considering the above facts, the presented study has the following objectives: (1) to extend the description of the species *Mediodactylus bartoni*, (2) to elucidate the intraspecific taxonomy of *M. bartoni* based on an analysis of additional material from the type localities of *Gymnodactylus kotschyi wettsteini* and *G. k. stubbei*, (3) to provide additional data on the type locality, morphological variation, and biology of *Mediodactylus bartoni*.

Fig. 1. Map of Crete and the localities mentioned in this study. Stars represent type localities. Colours correspond to those in Fig. 2.

MATERIAL AND METHODS

Summary of material

We externally examined lectotype (NMP P6V 5279) and two paralectotypes (NMP P6V 5280–5281) of *Gymnodactylus bartoni* Štěpánek, 1934 and five paralectotypes (NMP P6V 5299, 35191–35194) of *G. kotschyi wettsteini* Štěpánek, 1937 deposited in the vertebrate collection of the National Museum, Prague (NMP P6V). In addition, we examined three specimens of *Mediodactylus bartoni* (NMP P6V 5282–5284) collected by O. Štěpánek at the species type locality and in the mountains of western Crete.

Other comparative data were obtained from the material housed in the herpetological collection of the Natural History Museum of Crete (NHMC) and from living individuals examined in the field (Psiloritis Mt., islet of Mikronisi near the town of Agios Nikolaos). For localities of all examined *Mediodactylus* specimens and their tissue samples used for the comparative phylogenetic analyses see Fig. 1.

Morphological data

The following metric characters were taken using a digital caliper and a dissecting microscope: snout-vent length (SVL) – distance from the snout tip to cloaca; head length (HL) – distance from the snout tip to angle of jaw; head width (HW) – reatest width of the head; head depth (HD) – greatest depth of the head; eye-nostril distance (END) – straight line distance between anterior corner of orbit and posterior margin of external nares; horizontal eye diameter (ED); horizontal ear opening diameter (EOP); tail length (TL) – from cloaca to the tail tip, if original. All examined characters were taken to the nearest 0.1 mm.

Meristic pholidotic characters were counted and evaluated as follows: number of supralabials – from the rostral to the mouth corner (left/right), last labial defined by its considerably larger size compared with posteriorly adjacent scales; number of infralabials – from mental to the mouth corner (left/right); numbers of scales between uppermost nasals; number of longitudinal rows of dorsal tubercles; number of tubercles in the paravertebral longitudinal row – from the neck to the level of cloaca; ventrals across belly – defined by their width; number of scales between mental shield and cloacal cleft – in a straight medial line; number of postanal tubercles (left/right); subdigital scales under the first toe (left/right) – the one touching the claw included; number of subdigital scales under the fourth toe (left/right) – the one touching the claw included; length of the largest dorsal tubercle in the paravertebral row.

Qualitative morphological characters were evaluated as follows: contact of the first pair of postmentals (not in contact / punctual contact / in contact); contact of the first pair of postmentals with the second infralabials (not in contact / in contact on one side / in contact on both sides); rugosity of dorsal tubercles (tubercles mostly smooth / slightly keeled / distinctly keeled); dorsal colour patter (interrupted narrow transverse streaks / uninterrupted transverse chevron-like bars). Notes on the colouration in life were taken from the field notes and photographs.

Molecular phylogeny

In order to elucidate the phylogenetic relationships and taxonomy within *Mediodactylus bartoni* (Clade D in Kotsakiozi et al. 2018) and the taxonomic status of *Gymnodactylus kotschyi wettsteini* and *G. kotschyi stubbei*, we analyzed specimens from Crete and its satellite islands and islets, including individuals from the type localities of the two focal latter taxa. Our molecular dataset included sequences of 29 specimens of *Mediodactylus*. We retrieved from GenBank sequences of 20 specimens of *Mediodactylus bartoni* (from the studies of Kasapidis et al. 2005 and Kotsakiozi et al. 2018), and sequenced seven new samples in this study: five samples (JM1–5) from the islet of Mikronisi at Agios Nikolaos, eastern Crete, the type locality of *Gymnodactylus kotschyi wettsteini*, collected by J. Moravec on 12 August 2020; one sample (JM6) from Nida Plateau, Psiloritis Mt., central Crete, the type locality of *G. bartoni*, collected by J. Moravec on 1 June 2022; and one specimen (NHMC 80.3.85.1952) from Koufonisi Island, eastern Crete, the type locality of *G. kotschyi stubbei*, collected by Mr. Vardinoyannis on 3 May 2018. Two specimens of *Mediodactylus oertzeni* (Clade E in Kotsakiozi et al. 2018) from the Southeastern Aegean were used as outgroup (Kotsakiozi et al. 2018). Information of all samples used in the phylogenetic analyses and their GenBank accession numbers is presented in Appendix 1.

We extracted DNA from ethanol-preserved tissue samples using the Geneaid Genomic DNA Mini Kit. The final dataset comprised four gene fragments of a concatenated length of 1,813 bp: two protein-coding mitochondrial markers, cytochrome *c* oxidase subunit I (*COI*; 515 bp) and cytochrome *b* (*cytb*; 290 bp), and two nuclear, melano-cortin 1 receptor (*MC1R*; 640 bp) and recombination activating gene 2 (*RAG2*; 368 bp). Primers and PCR conditions used for the amplification and sequencing of all markers are as detailed in Kotsakiozi et al. (2018). In all amplifications, both strands of the PCR products were sequenced at Macrogen Inc. (Amsterdam, the Netherlands). We checked, assembled and edited chromatographs using Geneious v.7.1.9 (Biomatter Ltd.). We aligned the sequences for each marker using MAFFT v.7.3 (Katoh & Standley 2013). We translated protein-coding genes into amino acids, and we detected no stop codons, suggesting that they were not pseudogenes. For the nuclear markers, we identified heterozygous positions and coded them according to the standard IUPAC ambiguity codes and resolved these sites, for each gene independently, by using the PHASE 2.1.1 algorithm (Stephens et al. 2001, Stephens & Donnelly 2003) implemented in DNASP v.6 (Rozas et al. 2017) with probability threshold=0.9. We tested the occurrence of recombination for the two phased nuclear-gene

alignments using the Pairwise Homoplasy Index (PhiTest; Bruen et al. 2006) implemented in SplitsTree v.4.14.5 (Huson & Bryant 2006), and we detected no evidence of recombination.

For the phylogenetic analyses, we partitioned our dataset by gene and selected substitution models for each marker using JModelTest v.2.1.7 (Guindon & Gascuel 2003, Darriba et al. 2012). The best models were as follows: TrN+G, HKY+G, F81, and JC for *COI*, *cytb*, *MC1R* and *RAG2*, respectively. We analysed the complete concatenated dataset under Maximum Likelihood (ML) and Bayesian Inference (BI) frameworks. We treated alignment gaps as missing data, and the nuclear gene sequences were not phased. We performed the ML analysis using IQ-TREE v. 1.6 (Nguyen et al. 2015) through the web interface (Trifinopoulos et al. 2016). Branch support was assessed with the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010) and the ultrafast bootstrap (UFBoot; Hoang et al. 2018), both with 1,000 replicates, and the standard bootstrap (Felsenstein 1985) with 100 replicates. We conducted BI analyses using MrBayes v.3.2.7 (Ronquist et al. 2012) with nucleotide substitution model parameters unlinked across partitions. The different partitions were allowed to evolve at different rates. Two simultaneous parallel runs were performed with four chains per run for 10^6 generations with sampling every 100 generations. We examined the standard deviation of the split
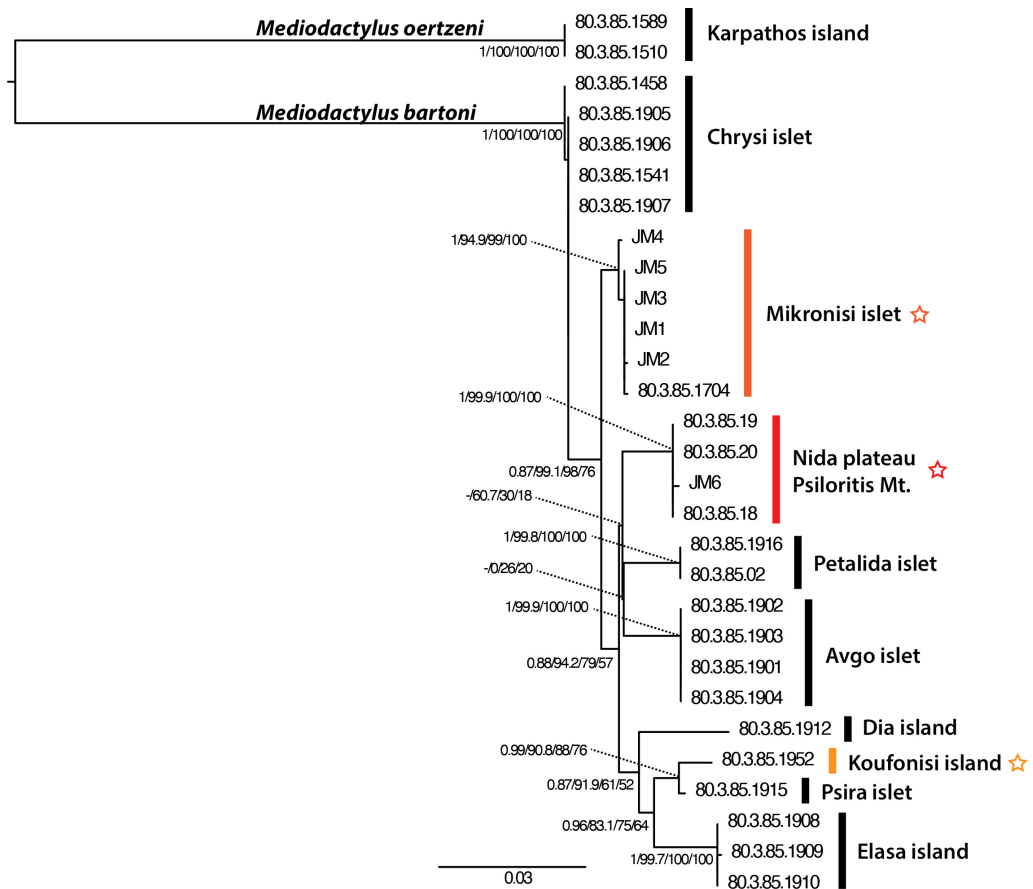

Fig. 2. Maximum Likelihood phylogenetic tree of *Mediodactylus* Ŝerbak et Golubev, 1977 reconstructed from the complete concatenated dataset (*COI, cytb, MC1R, RAG2*). Support values are indicated near the nodes (Bayesian posterior probabilities/SH-aLrT/UFBoot/Standard bootstrap). Colours correspond to those in Fig. 1. Information on the samples is in Appendix 1.

frequencies between the two runs and the potential scale reduction factor (PSRF) diagnostic; convergence was assessed by confirming that all parameters had reached stationarity and had sufficient effective sample sizes (>200) using Tracer v.1.7.2 (Rambaut et al. 2018). We conservatively discarded the first 25% of trees as burn-in.

RESULTS

Phylogenetic relationships

The phylogenetic analyses of *Mediodactylus bartoni* (Clade D in Kotsakiozi et al. 2018) using BI and ML methods of the concatenated dataset resulted in similar topologies and are shown in Fig. 2. The phylogenetic structure within *Mediodactylus bartoni* recovered nine geographic groups correlating with collection localities of island/islets (Avgo islet, Chrysi islet, Dia island, Elasa island, Mikronisi islet, Petalida islet, Psiloritis Mt., Psira islet, Koufonisi island). Although each group is strongly supported, the relationships among them are weakly supported. The BI phylogenetic tree recovered a polytomy of the following three groups: Avgo islet, Petalida islet, and Psiloritis Mt., though the ML analyses resulted in a sister-group relationship of the former two groups with no support. The sample from the type locality of *Gymnodactylus bartoni* (JM6) from Nida plateau in Psiloritis Mt. clustered with geographically proximate samples. The five samples from the type locality of *G. kotschyi wettsteini* (JM1–5) from Mikronisi islet lying at Agios Nikolaos cluster together with a sample designated by Kotsakiozi et al. (2018) as 081_Mikr_1704 (NHMC 80.3.85.1704, Mikronisi islet, 34.9275°N, 24.8061°E). This finding shows that Kotsakiozi et al. (2018) confused the islet of Mikronisi at Agios Nikolaos with another islet of the same name located at the southern coast of Crete. The sample from the type locality of *G. kotschyi stubbei* in Koufonisi Island (NHMC 80.3.85.1952) was recovered in a sister relationship with a sample from Psira islet.

Based on the recovered phylogeny, indicating that intraspecific genetic diversity within *Mediodactylus bartoni* does not exceed subspecific level, we follow the concept adopted by Kotsakiozi et al. (2018) and consider *M. bartoni* a monotypic species. As a result, we include the names *Gymnodactylus kotschyi wettsteini* Štěpánek, 1937 and *Gymnodactylus kotschyi stubbei* Wettstein, 1952 into the synonymy of *Mediodactylus bartoni* (Štěpánek, 1934)

Mediodactylus bartoni (Štěpánek, 1934)

Gymnodactylus bartoni Štěpánek, 1934: 8.
Gymnodactylus kotschyi bartoni Štěpánek, 1937: 273.
Gymnodactylus kotschyi wettsteini Štěpánek, 1937: 272.
Gymnodactylus kotschyi rarus Wettstein, 1952: 251 (synonymy by Kotsakoizi et al. 2018).
Gymnodactylus kotschyi stubbei Wettstein, 1952: 251.

TYPE MATERIAL. **Lectotype**: NMP P6V 5279 (designated by Štěpánek 1939: 343). **Paralectotypes** (n=2): NMP P6V 5280, 5281.

TYPE LOCALITY. "Montes Psilloritis, 1 500 m, Creta centr." (Štěpánek 1934: 9). Specified type locality: "Nida (Psilloriti, Crete centr.), about 1 400 meters above sea level" (corrected by Štěpánek 1939: 434). Exact type locality: Nida plateau, Psiloritis mountain, central Crete, 35.2005°N, 24.8430°E, 1360 m a. s. l. (for further details see Distribution).

LECTOTYPE DESCRIPTION. Adult female (Fig. 3) collected on 26 May 1934 by O. Štěpánek.

Beside of the basic measurements and pholidotic data summarized in the Table 1, the lectotype shows the following morphological characters: Length of the regenerated tail = 42.4 mm; E–N = 4.1 mm; ED = 2.4 mm; EOP = 0.9 mm. Head scales smooth; nostril in contact with rostral, first supralabial and three nasal shields; tubercles in temporal area absent; 3 pairs of submental

shields (submentals of the third pair considerably smaller, not in contact with sublabials); dorsal tubercles round, low, smooth to very slightly keeled; dorsal scales smooth, about half of length of dorsal tubercles; dorsal tubercles separated by 2–3(4) dorsal scales in transversal direction and by (1)2–3 scales in longitudinal direction (towards the body axis); ventral scales smooth, cycloid, subimbricate, some of them slightly denticulated posteriorly; dorsal surfaces of thighs and tibias with scattered subconical tubercles; tail tubercles on anterior tail segments larger than dorsal tubercles, smooth, pointed and upturned caudally; one tail segment bearing 6 tubercles (1 dorsal pair and 2 lateral pairs), tubercles of the dorsal pair smaller and less obvious than tubercles of the lateral pairs; subcaudal scales smooth, enlarged, arranged in 2 longitudinal rows. In alcohol, gray dorsally with irregular narrow dark brown to black interrupted transverse streaks (fusing in chevron-like spots on tail); light gray to whitish ventrally.

Variation. Variation in measurements and basic morphological characters within NMP *Mediodactylus bartoni* series is summarized in Table 1. A more detailed comparison of the museum individuals from the mountain regions of central and western Crete with the individuals from the Mikronisi islet near Agios Nikolaos (Štěpánek's "subspecies" *wettsteini*) shows that obvious differences in the shape and rugosity of the dorsal scales and tubercles as well as in dorsal colour pattern can be found between these two populations. The Mikronisi individuals differ as follows (characters of the Nida population given in parentheses): scales in temporal area clearly hete-

Fig. 3. The lectotype of *Gymnodactylus bartoni* Štěpánek, 1934; NMP P6V 5279 (scale in mm), photo by J. Moravec.

Table 1. Morphological characters of Štěpánek's original series of *Gymnodactylus bartoni* Štěpánek, 1934 and *G. kotschyi wettsteini* Štěpánek, 1937 (measurements in mm; * lectotype, † paralectotype). Distribution of qualitative characters: 1st pair of postmentals in contact (0, not in contact; 0.5, punctual contact; 1, in contact); 1st pair of postmetals in contact with 2nd sublabials (0, not in contact; 0.5, in contact on one side; 1, in contact on both sides); rugosity of dorsal tubercles (0, mostly smooth; 0.5, slightly keeled; 1, distinctly keeled); dorsal colour pattern (0, narrow interrupted transverse streaks; 1 uninterrupted transverse chevron-like bars). Abbreviations: SVL = snout-vent length; TL = tail length; HL = head length; HW = head width; HD = head depth; SBUN = scales between uppermost nasals; 1PPC = 1st pair of postmentals in contact; 1PPC2S = 1st pair of postment. in contact with 2nd sublab.; LRDT = longitudinal rows of dorsal tubercles; DTPR = dorsal tubercles in paravertebral row; SBMSCC = scales between mental shield and cloacal cleft; SS1T = subdigital scales under 1st toe; SS4T = subdigital scales under 4th toe; LLPT = length of the largest paravertebral tubercle; RDT = rugosity of dorsal tubercles

taxon / character	*Gymnodactylus bartoni*						*Gymnodactylus kotschyi wettsteini*				
NMP P6V	5279*	5280†	5281†	5283	5282	5284	5299†	35191†	35192†	35193†	35194†
sex	♀	♀	♀	♀	♂	♂	♂	♂	♂	juv	juv
SVL	46.2	44.3	42.2	41.4	34.7	34.5	36.8	38.8	27.3	24.2	24.2
TL	–	–	–	–	38.1	–	41.1	–	32.2	–	–
HL	12.3	11.8	11.8	11.4	9.7	9.8	11.2	10.7	8.7	7.9	7.7
HW	9.5	9.5	8.8	8.9	7.0	7.7	8.4	8.5	6.3	5.6	5.2
HD	5.5	5.8	5.5	5.0	5.2	4.9	5.4	5.8	4.4	3.8	3.9
supralabials	7/8	7/8	8/9	9/8	7/7	7/8	7/9	7/6	7/8	8/9	8/8
sublabials	6/7	6/7	7/6	7/6	6/6	6/6	5/6	6/6	5/5	6/6	5/6
SBUN	1	1	1	1	1	2	1	1	1	1	1
1PPC	0.5	1	1	1	1	1	1	1	1	1	1
1PPC2S	1	1	1	0	0.5	0.5	0	1	0	0.5	0
LRDT	10	10	10	10	10	12	12	10	10	10	10
DTPR	20	20	18	22	23	22	22	25	24	26	26
ventrals across belly	20	20	20	18	20	18	22	20	20	22	20
SBMSCC	108	105	104	108	98	105	105	101	100	106	99
postanal tubercles	2/2	2/2	1/1	1/1	2/2	2/2	2/2	2/2	2/2	3/2	2/2
SS1T	9/10	10/10	8/8	9/9	8/8	10/10	9/10	10/9	9/9	8/9	9/9
SS4T	17/17	16/16	16/15	16/17	16/16	18/18	16/17	17/18	16/16	18/18	16/16
LLPT	0.7	0.8	0.7	0.8	0.6	0.6	0.7	0.8	0.5	0.5	0.5
RDT	0	0	0	0	0.5	0.5–1	1	1	1	?	?
preanal pores	–	–	–	–	–	–	–	–	–	–	–
colour pattern	0	0	0	0	0	0	1	1	1	?	?

rogenous in size (mostly homogenous); scales on the brachium, thigh and crus keeled (mostly smooth); dorsal tubercles oval and distinctly keeled (round, smooth to slightly keeled; Fig. 7); tail tubercles on anterior tail segments keeled, sharply pointed, distinctly upturned (smooth, pointed, less upturned); tubercles on the brachium, thigh and crus conical, smooth to keeled (subconical, smooth); ventral scales usually denticulated posteriorly (mostly smooth posteriorly); dorsal colour pattern of dark brown uninterrupted transverse chevron-like bars (narrow interrupted transverse streaks; Figs. 4–5).

In addition, measurements of living *M. bartoni* obtained in the field show that SVL of the largest specimens can reach higher values than known from the museum material: the SVL of the largest female of the Nida population was 50 mm and the SVL of the largest female of the Mikronisi population was 40 mm.

DISTRIBUTION. *Mediodactylus bartoni* is an endemic species of the Cretan archipelago, which forms several mutually isolated island populations. Populations that have been genetically confirmed to belong to *M. bartoni* occur in Crete and eight small surrounding islands/islets – Avgo islet,

Fig. 4. Adult female of *Mediodactylus bartoni* (Štěpánek, 1934) (uncollected) from the exact type locality (Nida plateau, Psiloritis Mt., central Crete, 35.2005°N, 24.8430°E, 1360 m a. s. l.), photo by J. Moravec.

Fig. 5. Adult female of *Mediodactylus bartoni* (Štěpánek, 1934) (uncollected) from the type locality of *Gymnodactylus kotschyi wettsteini* Štěpánek, 1937 (Mikronisi islet at Agios Nikolaos, eastern Crete, 35.2031°E, 25.7315°N, 10 m a. s. l.), photo by J. Moravec.

Chrysi islet, Dia island, Elasa island, Mikronisi islet at Agios Nikolaos, Petalida islet, Psira islet, Koufonisi island (see Kasapidis et al. 2005, Kotsakoizi et al. 2018; this study, Fig. 1).

Interestingly, while on the small coastal islands around Crete *M. bartoni* reaches high population densities (e. g. 10 individuals were observed during two hours on Mikronisi islet on 12 August 2020 by J. Moravec), on Crete itself it appears to be very rare and restricted to only a few mountainous localities (see also the map in Valakos et al. 2008). In Psiloritis Mt. (central Crete), *M. bartoni* is known from the area of Nida plateau only. Štěpánek (1934, 1939) designated Nida plateau as the type locality of his *Gymnodactylus bartoni*, nevertheless, he did not provide the exact location of the place where his type specimens were collected and also the altitudes he stated (1,500 m and 1,400 m a. s. l.) are indicative only. Therefore, we focused on finding the exact location of the capture of the type individuals according to the photographs of the type locality taken by Štěpánek and his companion E. Troníček on Nida plateau in 1936 (Fig. 8A). After comparison of the landscape horizon on the photograph with the real horizon of Nida plateau we identified the place of collection of the type specimens as a limestone rock outcrop in the central plateau (35.2005°N, 24.8430°E) at an altitude of 1,360 m a. s. l. (Fig. 8B). During two surveys of Psiloritis Mt. (performed by J. Moravec in June 2015 and May/June 2022; altogether nine research days) *Mediodactylus bartoni* appeared to be extremely rare in this area. In all, 5 specimens were

Fig. 6. Adult specimen of *Mediodactylus bartoni* (Štěpánek, 1934) (uncollected) from the vicinity of the village Anopoli, region of Lefka Ori, western Crete; photo by P. Lymberakis.

Fig. 7. Comparison of the shape and rugosity of dorsal tubercles in *Mediodactylus bartoni* (Štěpánek, 1934): top – an adult female from the type locality (Nida plateau), below – adult female from the islet of Mikronisi at Agios Nikolaos, photo by J. Moravec.

observed directly at the type locality and one clutch of two eggs was found ca. 3 km northeast of it (35.2158°N, 24.8719°E; 1,470 m a. s. l.).

The second known area of occurrence of *M. bartoni* on Crete is the mountain region of Lefka Ori in western part of the island. Our voucher specimen originates from the wider surroundings of the village of Askyfou (NMP P6V 5284, collected by O. Štěpánek in 1938). Another individual is documented by photograph taken by P. Lymberakis in the vicinity of the village Anopoli (Fig. 6). In addition, undocumented but reliable reports for *M. bartoni* from Rouvas forest in southwestern Psiloritis (ca. 35.1740°N, 24.9090°E) and from the vicinity of Vosakou monastery (ca. 35.3850°N, 24.8960°E) have been registered by the NHMC. Nevertheless, the presence of the species in these localities remains to be confirmed.

Habitat and biology. *Mediodactylus bartoni* inhabits two basic types of habitats. Cretan populations occupy rocky montane habitats up to at least 1,470 m a. s. l. (Fig. 9), whereas populations on small island/islets live at low altitudes on stony and scree slopes covered with phrygana (Figs. 10, 11). The finding of eggs at an altitude of 1,470 m shows that the geckos can reproduce successfully at the highest limit of their occurrence (egg size: 9.0×8.3 mm and 9.1×8.4 mm). In both coastal and mountain habitats, geckos hide under stones or in rock crevices. During the morning hours the geckos thermoregulate by conduction beneath the flat sun-heated stones, rarely they bask directly on sun.

DISCUSSION

Crete's biogeography is directly linked to its complex history. During the Miocene Crete was a part of a land mass that included the present-day Greek mainland, the Aegean Sea and Asia Minor. Gradually, during the middle to late Miocene tectonic movements in the Mediterranean region separated Crete from the other landforms (Rögl 1999, Koufos et al. 2005, van Hinsbergen et al. 2020). According to the divergence time estimates in Kotsakiozi et al. (2018) *Mediodactylus bartoni* diverged during that time ca. 11 million years ago. Later, the geological location of Crete along the transition zone between the African and Eurasian plates, and sea level fluctuations have changed the structure of the island. During the Pliocene, when sea level rose, Crete was divided into several smaller islands and attained its present form when sea level fell (Mourtzas et al. 2016 and see references within). The divergence within *M. bartoni*, around 0.72 million years ago in the Pleistocene (Kotsakiozi et al. 2018), is harder to interpret, especially due to the un-supported topology in most studies (e.g., Kotsakiozi et al. 2018), including ours. The history of Crete's satellite islets and islands is diverse in terms of formation, age, and past connections to Crete. In general, geological activity, sea level fluctuations, over sea dispersal, as well as human mediated introductions, facilitated greatly the spread of *Mediodactylus* around the Eastern Mediterranean (Kotsakiozi et al. 2018).

This study presents an intra-specific taxonomic assessment and additional data to the description of *Mediodactylus bartoni* (Štěpánek 1934; Clade D in Kotsakiozi et al. 2018) using both phylogenetic analyses and morphological examinations. The incorporation of additional samples in our molecular dataset, including from the type localities of *Gymnodactylus bartoni*, *G. kotschyi stubbei*, and *G. kotschyi wettsteini*, allowed us to better interpret the taxonomy of these taxa. The inferred phylogenetic relationships within *Mediodactylus bartoni* in our study were mostly congruent across analyses and generally support those of Kasapidis et al. (2005) and Kotsakiozi et al. (2018), and present division into nine geographical groups correlating with islets and islands. Phylogenetic relationships among the groups, including from the type localities of the three taxa, indicate the clustering of *Gymnodactylus kotschyi stubbei* and *G. kotschyi wettsteini* as separate

Fig. 8. Photographs of the exact place of collection of the type specimens of *Mediodactylus bartoni* (Štěpánek, 1934) in Nida plateau: top – situation in 1936 (O. Štěpánek staying on the top of the limestone outcrop), photo by E. Troníček; below – situation in 2022, photo by J. Moravec.

Fig. 9. Habitat of *Mediodactylus bartoni* (Štěpánek, 1934) in Nida plateau, Psiloritis Mt., central Crete: top – general view of the plateau, below – the habitat in detail, photo by J. Moravec.

groups, yet together with *Mediodactylus bartoni* in the same clade. This phylogenetic topology suggests *Mediodactylus bartoni* to be monotypic (as in Kotsakiozi et al. 2018) and name priority implies the synonymization of *Gymnodactylus kotschyi stubbei* and *G. kotschyi wettsteini* under the former taxon.

On the other hand, the phylogenetic structure of *Mediodactylus bartoni* correlating with islands/islets and the existence of morphological differences between the island populations indicate that the isolated populations have undergone different evolutionary and adaptive processes (it was the existence of morphological differences that led to the separation of traditional subspecies in the past). The question therefore is how to treat these evolutionary unique entities for purposes of their conservation. In this respect, it appears appropriate to use the concept of evolutionary significant units (ESUs; sensu Waples 1991, 1995 and Moritz 1994) as proposed by Pérez-Cembranos et al. (2019) for the island populations of the Balearic lizard *Podarcis lilfordi* (Günther, 1874). According to Waples (1991, 1995) an ESU is a population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units, and (2) represents an important component in the evolutionary legacy of the species. It seems that application of ESUs to isolated island populations of *Mediodactylus bartoni* would

Fig. 10. Habitat of *Mediodactylus bartoni* (Štěpánek, 1934) in the islet of Mikronisi at Agios Nikolaos, photo by J. Moravec.

Fig. 11. Coastal habitat of the island of Koufonisi, photo by J. Moravec.

provide a useful tool for the conservation of intraspecific diversity of this endemic gecko. Individual ESUs could bear the names of former subspecies or respective islands/islands and could be individually addressed in conservation practice (e.g. in a detailed assessment for the IUCN Red List of Threatened Species).

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Data on the samples used in the phylogenetic analyses in this study and related GenBank accession numbers. [NHMC] Natural History Museum of Crete. Species names in parentheses show previous taxonomic names. Species names correspond to changes proposed in this study.

species	NHMC ID	sample	locality
Mediodactylus bartoni	80.3.85.1901	035_Avg_1901	Avgo islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1902	036_Avg_1902	Avgo islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1903	037_Avg_1903	Avgo islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1904	038_Avg_1904	Avgo islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1905	043_Chr_1905	Chrysi islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1906	044_Chr_1906	Chrysi islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1907	045_Chr_1907	Chrysi islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1458	046_Chr_1458	Chrysi islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1541	047_Chr_1541	Chrysi islet (Crete), Greece
Mediodactylus bartoni	80.3.85.1912	058_Gla_1912	Dia island (Crete), Greece
Mediodactylus bartoni	80.3.85.1908	048_Ela_1908	Elasa island (Crete), Greece
Mediodactylus bartoni	80.3.85.1909	049_Ela_1909	Elasa island (Crete), Greece
Mediodactylus bartoni	80.3.85.1910	050_Ela_1910	Elasa island (Crete), Greece
Mediodactylus bartoni (*M. kotschyi stubbei*)	80.3.85.1952	NHMC_KUF	Koufonisi island (Crete), Greece
Mediodactylus bartoni	80.3.85.1704	081_Mikr_1704	Mikronisi islet (Crete), Greece
Mediodactylus bartoni (*M. kotschyi wettsteini*)		JM1	Mikronisi islet, Agios Nikolaos (Crete), Greece
Mediodactylus bartoni (*M. kotschyi wettsteini*)		JM2	Mikronisi islet, Agios Nikolaos (Crete), Greece
Mediodactylus bartoni (*M. kotschyi wettsteini*)		JM3	Mikronisi islet, Agios Nikolaos (Crete), Greece
Mediodactylus bartoni (*M. kotschyi wettsteini*)		JM4	Mikronisi islet, Agios Nikolaos (Crete), Greece
Mediodactylus bartoni (*M. kotschyi wettsteini*)		JM5	Mikronisi islet, Agios Nikolaos (Crete), Greece
Mediodactylus bartoni	80.3.85.1916	098_Ptl_1916	Petalida islet (Crete), Greece
Mediodactylus bartoni	80.3.85.02	099_Ptl_02	Petalida islet (Crete), Greece
Mediodactylus bartoni	80.3.85.18	088_Cre_18	Psiloritis Mt. (Crete), Greece
Mediodactylus bartoni	80.3.85.19	089_Cre_19	Psiloritis Mt. (Crete), Greece
Mediodactylus bartoni	80.3.85.20	090_Cre_20	Psiloritis Mt. (Crete), Greece
Mediodactylus bartoni		JM6	Nida Plateau, Psiloritis Mt.(Crete), Greece
Mediodactylus bartoni	80.3.85.1915	108_Psi_1915	Psira islet (Crete), Greece
Mediodactylus oertzeni	80.3.85.1589	040_Kar_1589	Tristomo, Karpathos (Southeastern Aegean), Greece
Mediodactylus oertzeni	80.3.85.1510	064_Kar_1510	Karpathos island (Southeastern Aegean), Greece

latitude °N	longitude °E	reference	COI	CYTB	RAG2	MC1R
35.6028	25.5769	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677682	MH144964		
35.6028	25.5769	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677682	MH144965		
35.6028	25.5769	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677682	MH144966		
35.6028	25.5769	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677682	MH144967		
34.8695	25.7013	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677683	MH144971		
34.8695	25.7013	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677683	MH144972		
34.8695	25.7013	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677683	MH144973	MH145253	MH145210
34.8695	25.7013	Kotsakiozi et al. 2018	MH145097	MH144974		
34.8695	25.7013	Kotsakiozi et al. 2018	MH145098	MH144975		
35.4419	25.2184	Kasapidis et al. 2005, Kotsakiozi et al. 2018	MH145104	MH144984		
35.2731	26.3345	Kotsakiozi et al. 2018	MH145099	MH144976		
35.2731	26.3345	Kotsakiozi et al. 2018	MH145100	MH144977		
35.2731	26.3345	Kotsakiozi et al. 2018	MH145101	MH144978		
34.9397	26.1377	this study	OR352473	OR351988	OR351973	OR351973
35.2031	25.7315	Kotsakiozi et al. 2018	MH145124	MH144998	MH145260	MH145217
35.2031	25.7315	this study	OR352467	OR351983	OR351977	OR351971
35.2031	25.7315	this study	OR352468	OR351984	OR351978	OR351975
35.2031	25.7315	this study	OR352470	OR351987	OR351979	OR351972
35.2031	25.7315	this study	OR352471	OR351986	OR351980	OR351974
35.2031	25.7315	this study	OR352469	OR351985	OR351982	OR351970
35.5053	23.5630	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677684	MH145011		
35.5053	23.5630	Kotsakiozi et al. 2018		MH145012		
35.1964	24.8383	Kotsakiozi et al. 2018		MH145004		
35.1964	24.8383	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677686	MH145005	MH145263	MH145220
35.1964	24.8383	Kasapidis et al. 2005, Kotsakiozi et al. 2018	AY677686	MH145006		
35.2004	24.8429	this study	OR352472	OR351989	OR351976	OR351969
35.1897	25.859	Kotsakiozi et al. 2018	MH145142	MH145017		
35.7997	27.2043	Kotsakiozi et al. 2018	MH145094	MH144969	MH145251	MH145208
35.7787	27.2038	Kotsakiozi et al. 2018	MH145110	MH144988	MH145256	MH145213