Zootaxa 5428 (1): 058–074
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5428.1.2
http://zoobank.org/urn:lsid:zoobank.org:pub:BA7A2464-D1D1-458E-B18C-1F0579D5699B

A new species of lava lizard (Iguanidae: Tropidurinae: *Microlophus*) from the Galápagos

OMAR TORRES-CARVAJAL
Museo de Zoología, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador
lotorres@puce.edu.ec; *https://orcid.org/0000-0003-0041-9250*

Abstract

Following Darwin's visit to the Galápagos in 1835, the species of lava lizards inhabiting the archipelago were scientifically described in the remaining decades of the 19th century. Notably, only a single species was found on each of the surveyed islands, with different species on most islands. Many species have also expanded their distributions onto surrounding islets. Based on morphological and genetic evidence, I describe herein a new species of lava lizard from the 0.8 km^2 Gardner islet located 8 km east of the southern island of Floreana. The new species is most similar in morphology and coloration to its sister taxon *M. grayii* from Floreana and nearby Champion, Caldwell, and Enderby islets. Genetic distances, haplotype networks, reciprocal monophyly and differences in scale counts support recognition of specimens from Gardner as a new species. Finally, I discuss a potential biogeographic scenario leading to the evolution of the new species described in this paper.

Key words: Evolution, Iguania, Islands, Systematics, Taxonomy

Resumen

Después de la visita de Darwin en 1835 a las Galápagos, las especies de lagartijas de lava de este archipiélago se describieron científicamente en la siguientes décadas del siglo XIX. Notablemente, se encontró solo una especie en cada una de las islas estudiadas, con especies distintas en la mayoría de islas. Algunas especies también han expandido sus rangos de distribución a los islotes aledaños. En base a evidencia morfológica y genética, describo aquí una nueva especie de lagartija de lava del islote Gardner, que tiene 0.8 km^2 y está ubicado a 8 km al este de la isla sureña de Floreana. La nueva especie es muy similar en morfología y coloración a su especie hermana *M. grayii* de Floreana, y los islotes cercanos Champion, Caldwell y Enderby. Distancias genéticas, redes de haplotipos, monofilia recíproca y diferencias en conteos de escamas respaldan el reconocimiento de los especímenes de Gardner como una especie nueva. Por último, discuto un escenario biogeográfico que pudo haber facilitado la evolución de la nueva especie descrita en este artículo.

Palabras clave: Evolución, Iguania, Islas, Sistemática, Taxonomía

Introduction

The biodiversity of terrestrial reptiles in oceanic archipelagos is shaped mostly by immigration, as opposed to cladogenesis within islands (Ali & Meiri 2019). This phenomenon is clearly illustrated by terrestrial lizards from the Galápagos Archipelago. Of the 11 endemic species of leaf-toed geckos (*Phyllodactylus*), only two cases of sympatry have been reported: *P. andysabini* Arteaga *et al*., 2019 and *P. simpsoni* Arteaga *et al*., 2019 from Isabela Island, and *P. leei* Cope, 1889 and *P. darwini* Taylor, 1942 from San Cristobal Island. However, only the former pair contains sister species that presumably originated through intra-island cladogenesis (Arteaga *et al*. 2019). Conversely, the two species in San Cristobal originated from two separate colonizations from mainland South America (Wright 1983; Torres-Carvajal *et al*. 2014, 2016). By contrast, known species of lava lizards—*Microlophus* Duméril and Bibron, 1837—in the Galápagos do not occur in sympatry (Baur 1891), which further supports the idea that within-island diversification of Galápagos terrestrial lizards is rare.

Accepted by L. Avila: 20 Feb. 2024; published: 20 Mar. 2024

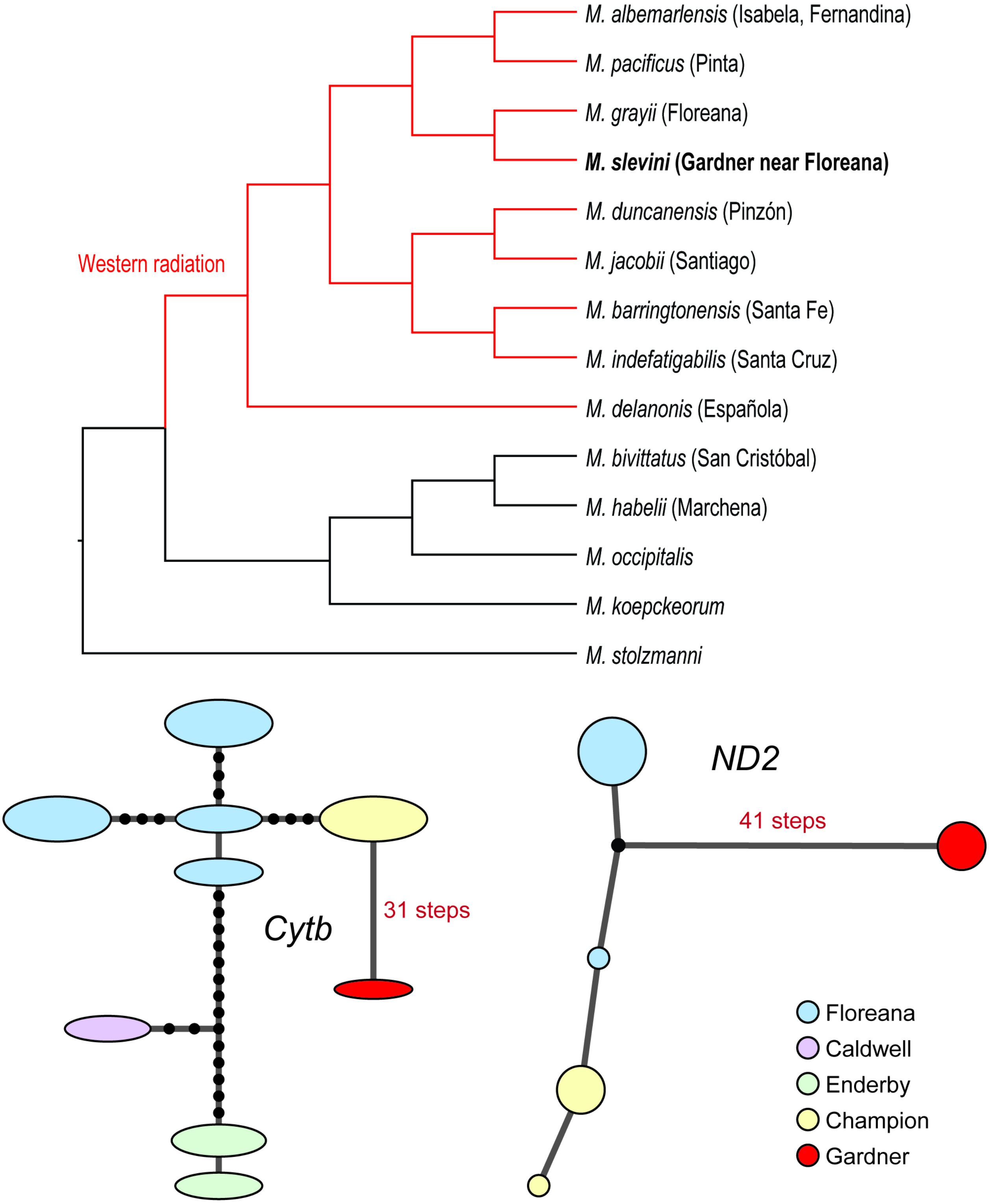

FIGURE 1. Phylogeny and haplotype networks of Galápagos lava lizards. Top: Phylogenetic tree (redrawn from Benavides *et al*. 2009) of species of *Microlophus* from the Galápagos and related continental species. Island of occurrence (islets excluded) is indicated in parentheses for Galápagos species; the western radiation is shown in red, and the new species described in this paper is in bold. The original tree was inferred through maximum-likelihood analyses of 56 terminals, including two from Floreana and one each from Gardner and Enderby islets, as well as 10 nuclear and four mitochondrial gene regions (Benavides *et al*. 2009). Bottom: Cytochrome b (*Cytb*) and NADH dehydrogenase subunit 2 (*ND2*) haplotype networks (redrawn from Benavides *et al*. 2009 and Torres-Carvajal *et al*. 2021, respectively) describing genealogical relationships among populations of lava lizards from Floreana and surrounding islets of Champion, Caldwell, Enderby, and Gardner. Black circles represent inferred haplotypes.

Galápagos lava lizards evolved from two colonization events (Wright 1983; Kizirian *et al*. 2004; Benavides *et al*. 2009), one of which resulted in a large radiation of eight species across western islands and surrounding islets (Fig. 1). Additionally, two species—*M. bivittatus* Peters, 1871 and *M. habeli* Steindachner, 1876—evolved from a second colonization and are currently distributed in the eastern islands of San Cristobal and Marchena, respectively. These two species comprise the sister group to the continental species *M. occipitalis* Peters, 1871, which occurs along the Pacific coast of Ecuador and Peru. All species of lava lizards occur on major islands ranging from the 18-km^2 Pinzon Island (*M. duncanensis* Baur, 1890) to the 4,588-km^2 Isabela Island (*M. albemarlensis* Baur, 1890), with only one species (*M. albemarlensis*) occurring on two major, neighboring islands (i.e., Isabela and Fernandina). Nonetheless, most species also occur on islets surrounding major islands, which can be as small as the 600 m^2 Onan islet near Pinzon Island, where *M. duncanensis* is known to occur (Benavides *et al*. 2009). Based on a large sample size (614 lizards from 78 localities in nine islands), Benavides *et al*. (2009) inferred cytochrome-b haplotype networks showing that islet populations of lava lizards were genetically similar to those from the neighboring major islands, with three notable exceptions. One of them led to the recognition of lava lizards from Santa Cruz and Santa Fe, separated by 21 mutational steps, as two distinct species—*M. indefatigabilis* Baur, 1890 and *M. barringtonensis* Baur, 1892, respectively—, which was further supported by phylogenetic evidence (Benavides *et al*. 2009). Similarly, haplotypes of *M. albemarlensis* from eastern Isabela were separated from those of Cuatro Hermanos islets by 21 mutational steps. However, the largest difference (31 mutational steps) was found between haplotypes of *M. grayii* Bell, 1843 from Floreana Island and Gardner islet (Fig. 1), which lies approximately 8 km east of Floreana. Benavides *et al*. (2009) also showed that a sample from Gardner was reciprocally monophyletic with respect to three samples from Floreana and Enderby based on a phylogenetic analysis of four mitochondrial and 10 nuclear genes. The logical assumption that the population from Gardner represents a distinct lineage was further supported by a recent study of 29 samples from Floreana, Champion and Gardner using the mitochondrial gene NADH dehydrogenase subunit 2, which revealed (1) a large difference (up to 41 mutational steps) between haplotypes from Floreana and Champion islet combined (hereafter Flo-Ch) and haplotypes from Gardner (Fig. 1); (2) a relatively large genetic distance (0.068 on average) between individuals from Gardner and Flo-Ch (interspecific genetic distances within the western radiation vary between 0.038 and 0.149, mean = 0.094); and (3) reciprocal monophyly between samples from Gardner and Flo-Ch (Torres-Carvajal *et al*. 2021). By contrast, morphological differences between *M. grayii* from Floreana and surrounding islets has not been reported. In their monumental taxonomic work on Galápagos lava lizards, van Denburgh & Slevin (1913) described the morphology and color patterns of seven species of lava lizards (N > 2,000 from 24 islands) including *M. grayii* from Floreana (N = 15) and the nearby islets Champion (N = 16), Enderby (N = 31), and Gardner (N = 27). Without performing any statistical analyses, they concluded that "the lizards of Enderby, Champion, and Gardner-near-Charles [Floreana] do not differ from those of the larger island". In this paper, I re-examined the specimens of *M. grayii* of van Denburgh & Slevin (1913), examined other specimens, and recorded additional morphological characters. My results are in agreement with recent molecular studies in that they support the recognition of populations of lava lizards from Gardner-near-Floreana as a separate evolutionary lineage, which I describe as a new species.

Material and Methods

Specimen and character sampling. Morphological data were obtained from the literature (van Denburgh & Slevin 1913) and by examination of 110 specimens collected in the island of Floreana (N = 27) and surrounding islets of Champion (N = 25), Enderby (N = 31), and Gardner (N = 27). Floreana is the second southernmost island in the Galápagos archipelago and has an area of 173 km^2. Surrounding islets included in this study are much smaller—Champion = 0.09 km^2, Enderby = 0.2 km^2, and Gardner = 0.8 km^2—and lie 700 m NE, 2.5 km NE, and 8 km E of Floreana, respectively. Examined specimens (Appendix I and type material below) are deposited in the herpetological collections of the California Academy of Sciences, San Francisco (CAS) and Museum of Vertebrate Zoology, University of California, Berkeley (MVZ).

Snout-vent length (SVL) and tail length (TL) were taken with a ruler and recorded to the nearest 1 mm. All other measurements were made with digital calipers, recorded to the nearest 0.1 mm, and include (1) head length (HL) from anterior margin of tympanum to snout; (2) head maximum width (HW); (3) head height (HH) behind orbits; (4) axilla-groin distance (AGD); (5) right hind limb length (LL) from insertion of hind limb to tip of Toe IV; (6) interparietal maximum length (IL); and (7) interparietal maximum width (IW). Meristic scutellational data included two characters (1, 2) recorded by van Denburgh & Slevin (1913), as well as nine characters (3–11) commonly used in taxonomic studies of tropidurine lizards (Dixon & Wright 1975; Carvalho *et al*. 2018): (1) scales around midbody (SAM), corresponding to the number of longitudinal rows of scales around the body counted about midway between the fore and hind limbs; (2) vertebrals (VER), the number of scales forming the vertebral crest from the point where the crest begins posterior to the head to a point at the level of the anterior surfaces of the thighs, holding the thighs at right angles to the longitudinal axis; (3) postrostrals (PRO), the scales immediately behind and in contact with the rostral; (4) internasals (INA), the scales between the nasals and immediately behind the postrostrals; (5) supralabials (SUL), counted to a point below center of eye; (6) infralabials (INL), counted to a point below center of eye; (7) loreals (LOR), the scales on the side of the head between nasal and preocular, and below canthals; (8) lorilabials (LLA), the scales forming a longitudinal row between supralabials and both loreals (anteriorly) and subocular (posteriorly); (9) gulars (GUL), corresponding to the number of gular scales along an imaginary transverse line between tympana; (10) lamellae on Finger IV, the ventral scales from point of convergence of manual digits III and IV to terminus of digit IV; and (11) lamellae on Toe IV, the ventral scales from point of convergence of pedal digits III and IV to terminus of digit IV. Scale counts 5–8, 10 and 11 were recorded from the right side of the specimen unless this side was damaged. I followed the terminology of Fritts (1974) and Frost (1992) for other characters included in the descriptions. Sex was determined upon examination of external features (e.g., a more pronounced vertebral crest in adult males), as well as inspection of gonads in specimens that had been previously dissected (N = 35).

Statistical analyses of morphological data

Linear Discriminant Analysis (LDA) was performed to test for differences in measurements and scale counts among individuals from the four sampled islands by using island of origin (i.e., Floreana, Champion, Enderby, or Gardner) as the response variable. Tail length was not included in these analyses as many specimens had broken or regenerated tails. Morphometric variables IL and IW were combined into an IL/IW ratio. Most meristic variables lacked both normal distribution (Shapiro-Wilk test) and variance homoscedasticity (Bartlett test). Before LDA analyses, all variables were scaled such that each had a mean of 0 and a standard deviation of 1.

I also used Two Sample t-tests to compare individuals from Gardner against all other islands grouped together (i.e, Floreana + Champion + Enderby). I tested again for variance homogeneity using the Levene Test as it is less sensitive to departures from normality than the Bartlett test (Wang *et al*. 2017). For those variables with unequal variances (i.e., $p < 0.05$ in Levene test), Welch's t-tests were used instead. All statistical analyses were performed in R version 4.2.1 (R Core Team 2022).

Genetic variation. I analyzed genetic variation in a 764-nucleotide long fragment of the mitochondrial gene NADH dehydrogenase subunit 2 (*ND2*) across all species of *Microlophus* from the western radiation except *M. barringtonensis* from Santa Fe Island, for which DNA samples or *ND2* sequences were not available. My analysis is based on 50 DNA sequences obtained from GenBank (Table 1), which were generated in previous studies (Kizirian *et al*. 2004; Torres-Carvajal *et al*. 2021). Sequences were aligned in GENEIOUS Prime 2020.2.2 (https://www.geneious.com) under default settings for MUSCLE 3.8.425 (Edgar 2004). Intra- and interspecific uncorrected *p* genetic distances among species of *Microlophus* were calculated in DIVEIN (Deng *et al*. 2010).

Species delimitation. The taxonomic conclusions of this study are based on the integrative study of external morphological features, pairwise genetic distances, haplotype networks, and inferred phylogenetic divergences (Benavides *et al*. 2009; Torres-Carvajal *et al*. 2021). I consider phenetic distinguishability, genetic differentiation and reciprocal monophyly as species delimitation criteria following a general lineage or unified species concept (de Queiroz 1998, 2007).

TABLE 1. Vouchers, locality data, and *ND2* GenBank accession numbers of taxa analyzed in this study. All specimens are from the Galápagos Archipelago in Ecuador. LACM = Natural History Museum of Los Angeles County, Los Angeles, U.S.A.; QCAZ = Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Taxon	Voucher	Island	GenBank accession number
M. albemarlensis	LACM106244	Fernandina: Punta Espinosa	AY625177
M. albemarlensis	LACM106254	Fernandina: Punta Espinosa	AY625176

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TABLE 1. (Continued).

Taxon	Voucher	Island	GenBank accession number
M. albemarlensis	LACM106185	Isabela: Black Cove	AY625175
M. albemarlensis	LACM106193	Isabela: Black Cove	AY625174
M. albemarlensis	LACM106205	Isabela: Cartago Bay	AY625173
M. delanonis	LACM106327	Espanola: Gardner Bay	AY625167
M. delanonis	LACM106314	Gardner near Española	AY625168
M. delanonis	LACM106315	Gardner near Española	AY625169
M. duncanensis	LACM106340	Pinzon: east side	AY625184
M. grayii	QCAZ16748	Champion	MW714196
M. grayii	QCAZ16755	Champion	MW714197
M. grayii	QCAZ16756	Champion	MW714198
M. grayii	QCAZ16757	Champion	MW714199
M. grayii	QCAZ16759	Champion	MW714200
M. grayii	QCAZ16762	Champion	MW714202
M. grayii	QCAZ16764	Champion	MW714203
M. grayii	QCAZ16765	Champion	MW714204
M. grayii	QCAZ16738	Floreana: Bahía del Correo	MW714186
M. grayii	QCAZ16739	Floreana: Bahía del Correo	MW714187
M. grayii	QCAZ16740	Floreana: Bahía del Correo	MW714188
M. grayii	QCAZ16741	Floreana: Bahía del Correo	MW714189
M. grayii	QCAZ16742	Floreana: Bahía del Correo	MW714190
M. grayii	QCAZ16743	Floreana: Bahía del Correo	MW714191
M. grayii	QCAZ16744	Floreana: Bahía del Correo	MW714192
M. grayii	QCAZ16745	Floreana: Bahía del Correo	MW714193
M. grayii	QCAZ16746	Floreana: Bahía del Correo	MW714194
M. grayii	QCAZ16747	Floreana: Bahía del Correo	MW714195
M. grayii	LACM106363	Floreana: Black Beach	AY625170
M. indefatigabilis	LACM106273	Baltra	AY625181
M. indefatigabilis	LACM106282	Daphne	AY625183
M. indefatigabilis	LACM106288	Daphne	AY625182
M. indefatigabilis	LACM106162	Santa Cruz: Academy Bay	AY625179
M. indefatigabilis	LACM106168	Santa Cruz: Academy Bay	AY625174
M. indefatigabilis	LACM106181	Santa Cruz: Conway Bay	AY625178
M. jacobi	LACM106267	Bartolome	AY625189
M. jacobi	LACM106268	Bartolome	AY625188
M. jacobi	LACM106217	Santiago: James Bay	AY625185
M. jacobi	LACM106206	Santiago: Sullivan Bay	AY625187

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TABLE 1. (Continued).

Taxon	Voucher	Island	GenBank accession number
M. jacobi	LACM106207	Santiago: Sullivan Bay	AY625186
M. pacificus	LACM106398	Pinta: southwest side	AY625171
M. pacificus	LACM106399	Pinta: southwest side	AY625172
M. slevini **sp. nov.**	QCAZ16768	Gardner near Floreana	MW714205
M. slevini **sp. nov.**	QCAZ16769	Gardner near Floreana	MW714206
M. slevini **sp. nov.**	QCAZ16770	Gardner near Floreana	MW714207
M. slevini **sp. nov.**	QCAZ16772	Gardner near Floreana	MW714208
M. slevini **sp. nov.**	QCAZ16774	Gardner near Floreana	MW714210
M. slevini **sp. nov.**	QCAZ16776	Gardner near Floreana	MW714211
M. slevini **sp. nov.**	QCAZ16779	Gardner near Floreana	MW714212
M. slevini **sp. nov.**	QCAZ16781	Gardner near Floreana	MW714213
M. slevini **sp. nov.**	QCAZ16782	Gardner near Floreana	MW714214

Results

Multivariate analyses

The linear discriminant model with meristic variables correctly predicted the island (i.e., Floreana, Champion, Enderby, Gardner) for 79% of the observations; conversely, the model with morphometric variables correctly predicted the island for only 39% of the observations (Fig. 2). The former model yielded trace proportions of 0.69 for LD1 and 0.24 for LD2, whereas the latter model yielded trace proportions of 0.65 for LD1 and 0.26 for LD2.

Systematic account

Microlophus slevini **sp. nov.**

https://zoobank.org/NomenclaturalActs/F7C84D25-0BA5-46B3-A455-E3BF5B6C4A91

Tropidurus grayii (part)—van Denburgh & Slevin (1913):164.
Microlophus grayii (part)—Benavides *et al*. (2009):1608.
Proposed standard English name: Slevin's lava lizards
Proposed standard Spanish name: lagartijas de lava de Slevin

Holotype. CAS 9428, adult male from Gardner-near-Floreana islet, 1°19.9'S, 90°17.75'W, Galápagos Archipelago, collected by Joseph R. Slevin on 3 October 1905.

Paratypes (27). 10 females: CAS 9421, 9424, 9426, 9429, 9431, 9432, 9437, 9439, 9443, 9446; 13 males: CAS 9422, 9423, 9425, 9427, 9428, 9430, 9433–9436, 9438, 9444, 9445; and four juveniles: CAS 9440–9442, 9447. Same collection data as holotype; CAS 9443–9447 were collected by E. S. King.

Diagnosis. *Microlophus slevini* differs from all other species of *Microlophus* in the Galápagos, except *M. grayii*, in having conspicuous neck folds (rictal, longitudinal, gular, antegular, postauricular, oblique, and antehumeral); granular scales within folds; small, imbricate, and keeled scales on sides of neck (>4X smaller than dorsal neck scales), distinctive black spots on flanks, fore limbs, and hind limbs in males, less than 80 scales around midbody, and no more than 50 vertebral scales. The new species (N = 23) can be distinguished from *M. grayii* (N = 64, character states in parentheses) by having more gulars, 27–39, mean 31.86 ± 3.54 SD (23–30, mean 25.98 ± 1.74 SD; t-value = -7.316, p = 0.000); fewer loreals, 3–5, mean 4.18 ± 0.66 SD (2–10, mean 5.67 ± 1.56 SD, t-value = 6.172, p = 0.000); more lamellae on Finger IV, 19–21, mean 19.91 ± 0.51 SD (16–21, mean 17.86 ± 1.10 SD; t-value

= -11.799, p = 0.000); more lamellae on Toe IV, 25–30, mean 27.74 ± 1.29 SD (22–27, mean 24.47 ± 0.99 SD; t-value = -12.504, p = 0.000); among other scutellational characters (Table 2).

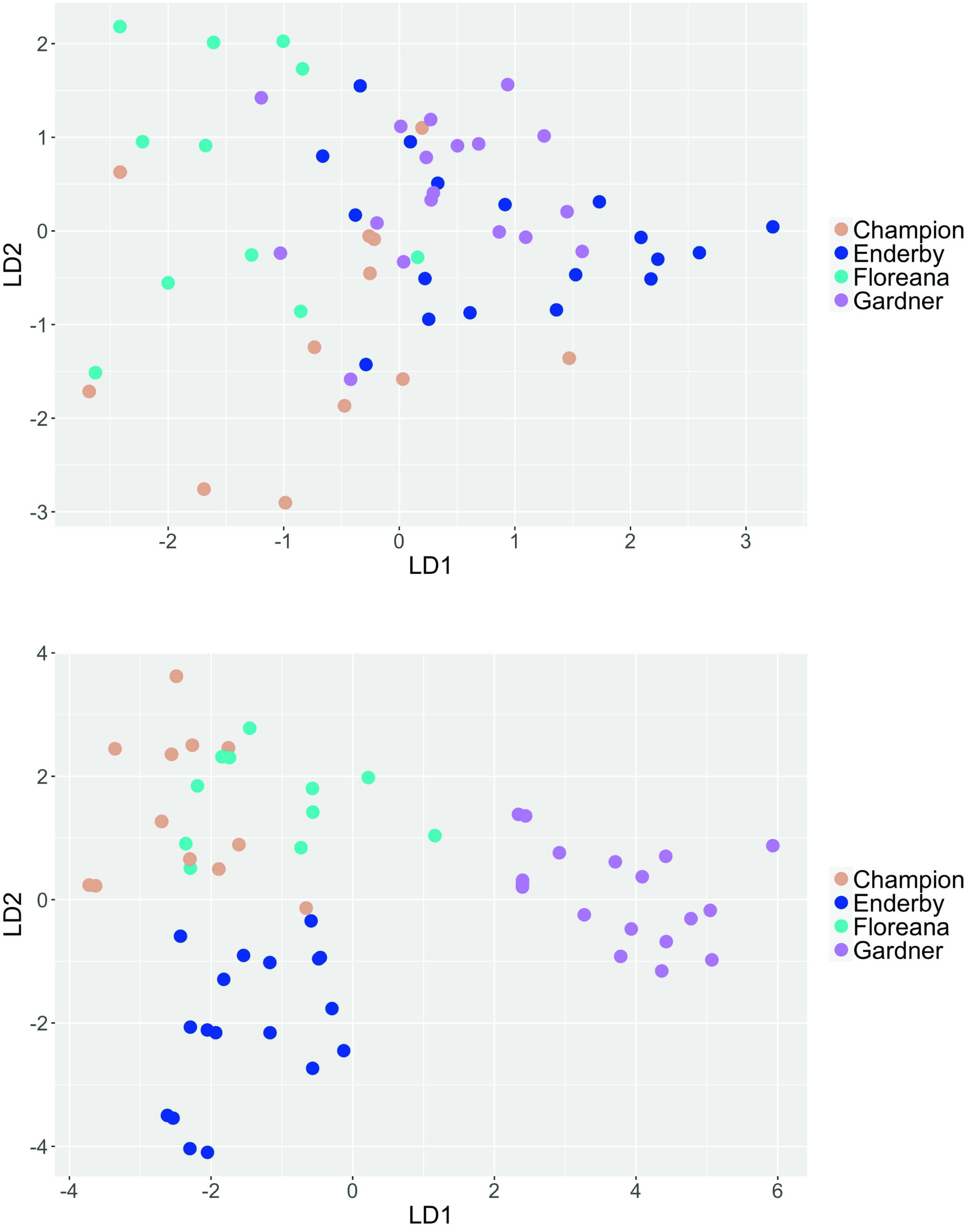

FIGURE 2. Scatterplots of LD1 and LD2 generated by discriminant analyses performed on the morphometric (top) and meristic (bottom) variables recorded in this study for *Microlophus* lava lizards from Floreana and surrounding islets of Champion, Enderby and Gardner.

TABLE 2. Summary of lepidosis and measurements (mm) of *Microlophus slevini* and *M. grayii*. Range followed by mean ± standard deviation are presented. For each character, except maximum SVL, the t-value and corresponding p-value ($p < 0.05$ with asterisks) calculated with Two sample t-tests are given. Italics indicate that a t-test assuming unequal variances (i.e., $p < 0.05$, Levene test) was performed.

Character	*Microlophus slevini* (N = 23)	*M. grayii* (N = 64)	t-value	p-value
scales around midbody	63–72 68.39 ± 2.04	58–77 66.28 ± 4.81	*-2.823*	*0.006**
vertebrals	38–45 41.61 ± 2.44	36–50 43.21 ± 2.84	2.396	0.019*
postrostrals	2–4 3.14 ± 0.56	2–5 3.79 ± 0.60	4.497	0.000*
internasals	3–5 4.05 ± 0.38	3–5 3.95 ± 0.28	-1.225	0.224
supralabials	3–5 4 ± 0.30	3–5 4 ± 0.25	0.000	1.000
infralabials	5–6 5.52 ± 0.51	4–6 5.08 ± 0.37	*-3.821*	*0.001**
loreals	3–5 4.18 ± 0.66	2–10 5.67 ± 1.56	*6.172*	*0.000**
lorilabials	6–10 8.70 ± 1.02	4–11 8.22 ± 1.43	-1.468	0.146
gulars	27–39 31.86 ± 3.54	23–30 25.98 ± 1.74	*-7.316*	*0.000**
lamellae Finger IV	19–21 19.91 ± 0.51	16–21 17.86 ± 1.10	*-11.799*	*0.000**
lamellae Toe IV	25–30 27.74 ± 1.29	22–27 24.47 ± 0.99	-12.504	0.000*
head length	14.1–19.57 16.79 ± 1.74	10.9–22.15 16.59 ± 2.74	*-0.324*	*0.746*
head width	10.8–15.49 13.24 ± 1.40	8.81–17.32 13.08 ± 2.11	*-0.337*	*0.737*
head height	8.43–14.14 10.89 ± 1.53	6.21–14.28 10.25 ± 1.96	-1.384	0.170
interparietal width/length	0.91–1.23 1.12 ± 0.09	0.95–1.49 1.15 ± 0.10	1.495	0.139
distance between limbs	24.3–39.24 30.25 ± 3.46	18.79–43.89 30.02 ± 6.42	*-0.164*	*0.870*
hind limb length	47.01–67.83 58.42 ± 6.55	35.33–73.37 56.80 ± 9.46	*-0.756*	*0.452*
maximum SVL in males	86 (N = 13)	98 (N = 33)	—	—
maximum SVL in females	77 (N = 10)	71 (N = 31)	—	—

Description of the holotype (Figs 3, 4). SVL 86 mm; remaining tail length 101 mm, regenerated tail length 33 mm; head length 19.36 mm; head width 15.49 mm; head height 12.55 mm; interparietal width 4.84 mm, interparietal length 5.03 mm; distance between fore and hind limbs 39.24 mm; hind limb length 64.58 mm. Scales on frontonasal region juxtaposed, not imbricating posteriorly; conspicuous lenticulate organs on frontonasal and supraocular regions; rostral wider than high, 4.9 mm x 1.67 mm, highest medially, in contact with first supralabial, first lorilabial and three postrostrals; nasal single, slightly protruding, longitudinally elongated, in contact with postrostral anteriorly, first lorilabial and first loreal laterally, three tiny scales posteriorly and posteromedially, lateralmost internasal anteromedially, and postrostral anteriorly; nostril posteriorly located, about one half the size of nasal, posterolaterally oriented; five elongated supralabials followed posteriorly by four smaller scales up to rictus oris; supralabials not in contact with subocular; canthals two; four laminate supraciliaries anteriorly, in contact with a single supraciliary posteriorly; preocular single, keeled, in contact with canthal, three loreals and subocular; subocular single, elongate, with longitudinal keel dorsally, separated from supralabials by 5–6 lorilabials; palpebrals granular; medial row of supraoculars enlarged, the largest being more than half the width of the supraocular disk, in contact laterally with smaller scales more or less disposed in 2–3 longitudinal rows; three (two on left side) circumorbitals in contact with posteromedial margin of supraocular disk; interparietal enlarged, slightly longer than wide (5.03 mm x 4.84 mm), with concave lateral margins and convex anterior and posterior margins; parietal eye located slightly anterior to center of interparietal; temporals slightly keeled or multicarinate, smaller than lateral neck scales above folds; tympanum recessed; ear opening oval in shape, partially covered anteriorly by six (four on left side) projected smooth, lanceolate scales; mental slightly wider than high (2.81 mm x 2.22 mm), highest medially, in contact with first infralabials laterally and one pair of postmentals posteriorly; six (five on left side) elongate infralabials followed posteriorly by four (five on left side) smaller scales up to rictus oris; three pairs of postmentals, with only the anterior pair in contact medially; seven (eight on right side) elongate sublabials; gulars 32, smooth, imbricate, usually bearing one apical pit, decreasing in size laterally.

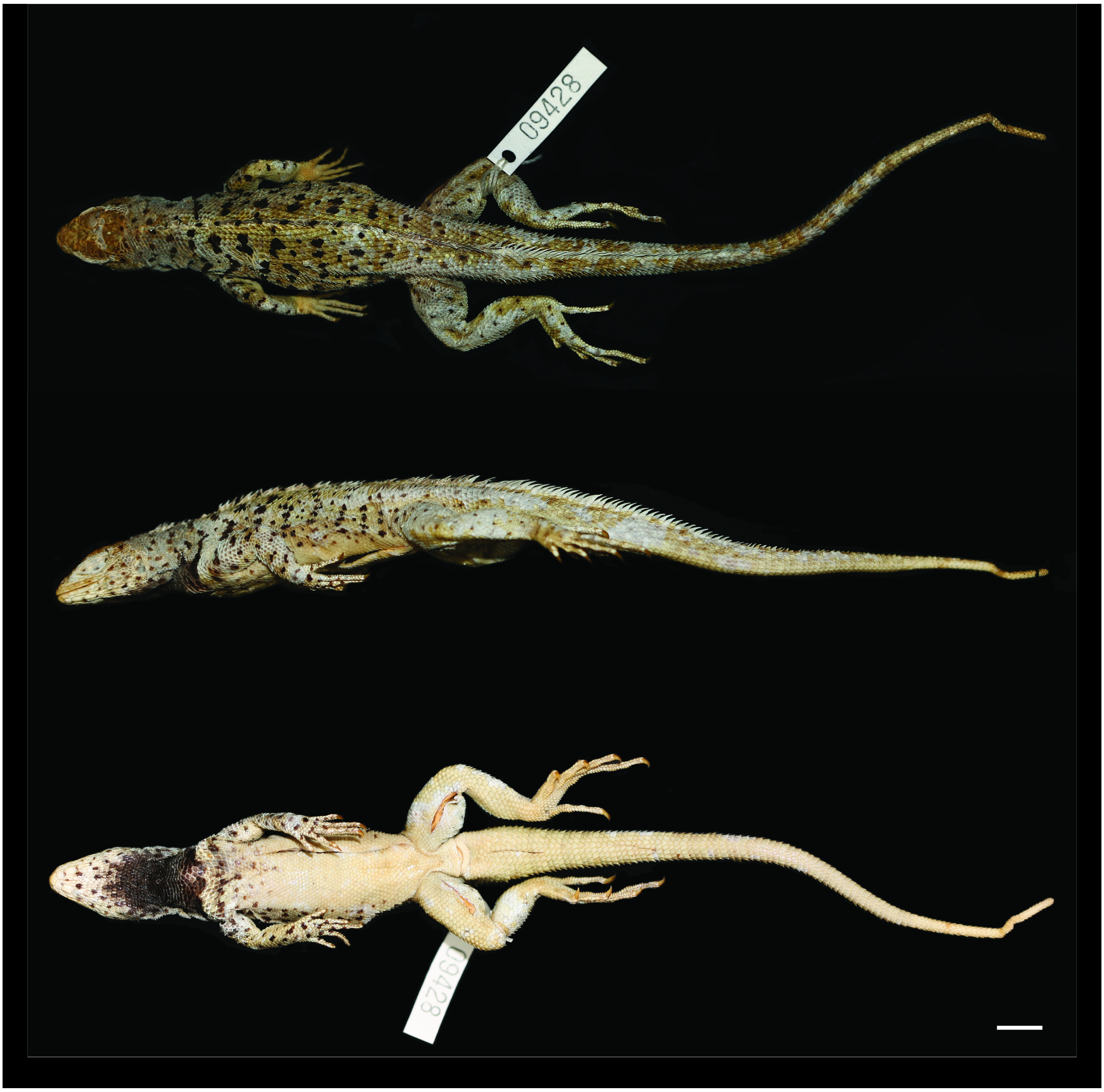

FIGURE 3. Male holotype (CAS 9428; SVL = 86 mm) of *Microlophus slevini* **sp. nov.** in dorsal (top), lateral (middle) and ventral (bottom) views. Photographs by Erica Ely. Scale bar: 10 mm.

FIGURE 4. Head of the holotype (CAS 9428) of *Microlophus slevini* **sp. nov.** in dorsal (top), lateral (middle), and ventral (bottom) views. Photographs by Erica Ely. Scale bar: 5 mm.

Vertebral crest prominent, with vertebrals on posterior half of body and anterior quarter of tail nearly twice as high as anterior vertebrals; dorsals strongly keeled and mucronate, gradually decreasing in size on flanks as they approach venter; dorsals on neck smaller than dorsals at midbody; lateral neck scales less than half the size of dorsals; ventral neck scales similar in size to dorsals, but smooth; rictal, longitudinal, gular, antegular, postauricular, oblique, and antehumeral neck folds present; scales within folds granular; keels on dorsal and caudal scales aligned to form anteroventrally oriented longitudinal ridges; posthumeral region with granular or small, flat, and smooth scales; ventrals smooth or slightly keeled, imbricate, non-mucronate, nearly half the size of dorsals; hands with smooth and imbricate scales dorsally, of which many bear an apical notch; palm scales and subdigital lamellae with 3–4 mucrons each; arm and forearm with keeled and imbricate scales dorsally (mucronate in arm), and smaller, smooth and imbricate scales ventrally; thighs with large, keeled, imbricate and mucronate scales dorsally, and smaller (less than half the size), smooth scales on posterior surface; scales on anterior and ventral aspects of thighs similar in size to dorsals, smooth and imbricate; shanks with keeled, imbricate and mucronate scales dorsally, and smooth and imbricate scales ventrally; most plantars and subdigital lamellae with three mucrons each, of which the medial one is more projected; dorsal foot scales and supradigitals imbricate, smooth or slightly keeled, most with apical notch; tail incomplete, slightly compressed, with conspicuous vertebral crest (verterbrals more than twice the size of adjacent dorsals) on anterior half; three scale whorls per autotomic segment; caudals keeled, mucronate, and imbricate; subcaudals smooth and imbricate.

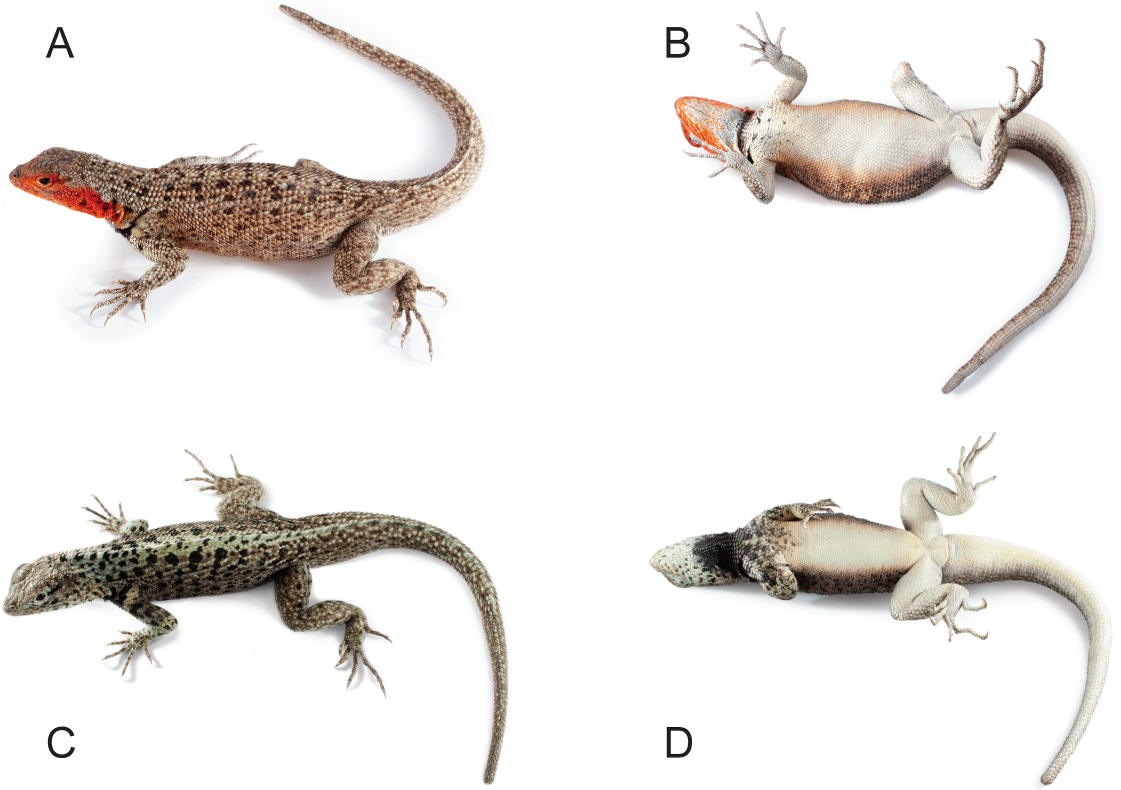

FIGURE 5. Live adult female (A, B) and male (C, D) specimens of *M. grayii* from Floreana. Color in life between *M. grayii* and *M. slevini* **sp. nov.** is very similar. Photographs from Bioweb.bio.

Color in preservative of holotype. Dorsal aspect of head, body, limbs and tail light brown, or light gray on those scales that have lost their outer surface; dorsum, flanks and neck with a series of black dots (1–3 scales large) approximately arranged in transverse rows that meet medially along vertebral crest; dorsal surface of limbs, anterior end of tail (dorsally), chin, sides of head and pectoral region covered by smaller black or dark brown dots; conspicuous black gular patch extending laterally as far as longitudinal neck fold; chin and ventral surfaces of body, limbs and tail yellowish cream (Figs 3, 4).

Color in life. I was not able to examine live specimens of *M. slevini*. However, because there seem to be no differences in coloration between *M. grayii* from Floreana and *M. slevini* (van Denburgh & Slevin 1913; Arteaga *et al*. 2019), I describe here the color in life of two specimens of *M. grayii* from Floreana that I photographed and examined in situ in 2010.

Adult female (Fig. 5): Dorsal background of body, limbs and tail light brown with scattered dark brown spots, which are approximately arranged in transverse rows along body; thin, short, dark gray bar extending posterodorsally from anterior insertion of fore limb across scapular region; dorsal surface of head light brown with tiny, interspersed orange dots; bright orange face mark covering lateral aspect of both head and neck, as well as mental, postmentals, sublabials and a few adjacent gulars; gular region grayish cream, with irregular orange marks on most scales; ventral background of body, limbs and tail with grayish-cream tones; sides of venter between fore- and hind limbs with orange hue; pectoral region with a few faint, gray dots.

Adult male (Fig. 5): Dorsal background of head, body, limbs and tail light brown with scattered dark brown to black spots (except on head), larger towards dorsal midline; sage dots scattered on hind limbs, posterior body and tail; vertebral crest with alternate smoky black and greyish green segments; ventral background of body, limbs and tail with yellowish-cream tones; sides of venter between fore- and hind limbs with brown hue; pectoral region with faint, black irregular marks; conspicuous black gular patch extending posterodorsally underneath antehumeral and oblique neck folds; ventral aspect of head anterior to gular patch cream with a few scattered black or dark brown spots.

Morphological variation. Measurements and scutellation of *Microlophus slevini* are presented in Table 2. The vertebral crest is more pronounced in adult males. This is more evident on the anterior half of the tail and posterior part of the body, where vertebrals are at least more than twice the size of adjacent dorsals in males, but similar in size to adjacent dorsals in females. This species attains a maximum SVL of 86 mm in males and 77 mm in females. Although sample size of specimens with complete tails was small (N = 4 in females; N = 5 in males), tail length / SVL ratio was similar in both sexes (1.72–1.94, mean = 1.79 ± 0.10 SD in females; 1.73–1.90, mean = 1.80 ± 0.06 SD in males). Similarly, no sexual differences were found in head width (HW/HL 0.74–0.84, mean = 0.79 ± 0.03 SD in females; 0.76–0.81, mean = 0.79 ± 0.02 in males) or hind limb length (LL/SVL 0.70–0.90, mean = 0.80 ± 0.06 in females; 0.73–0.85, mean = 0.80 ± 0.04 in males). Sexual variation for additional mensural characters in *M. slevini* is presented in Table 3.

Genetic variation. Uncorrected *p* genetic distances (Table 4) between *M. slevini* and its sister species *M. grayii* range between 0.055 and 0.065 (mean 0.061 ± 0.000 SE) for the *ND2* gene. Other species pairs (species name followed by island of occurrence; approximate shortest distance between island pairs in brackets) of lava lizards belonging to the western radiation with similar or lower mean distance values are *M. pacificus* Pinta / *M. albemarlensis* Isabela (0.024–0.031, mean 0.027 ± 0.001 SE, [75.4 km]), *M. duncanensis* Pinzón / *M. jacobii* Santiago (0.056–0.059, mean 0.058 ± 0.001 SE, [24.5 km]), and *M. indefatigabilis* Santa Cruz / *M. jacobii* (0.062–0.071, mean 0.065 ± 0.000 SE, [19.5 km]). The largest genetic distance in the western radiation is between *M. slevini* and *M. delanonis* Española (0.162–0.173, mean 0.167 ± 0.001 SE, [60.7 km]).

Etymology. The specific epithet is a noun in the genitive singular case based on the unlatinized surname Slevin and is a patronym for American herpetologist Joseph R. Slevin (1881–1957), who during “a couple of hours” on October 3rd 1905 collected most specimens of the new species reported in this paper as part of the famous 1905-1906 Galápagos expedition by the California Academy of Sciences (Fritts & Fritts 1982); the remaining type series was collected by his field assistant E. S. King. Remarkably, Slevin examined and recorded scale counts of 1,500 specimens included in van Denburgh & Slevin’s (1913) seminal work on lava lizards from the Galápagos.

Distribution. *Microlophus slevini* occurs in 0.8 km^2 Gardner islet, 8 km east of Floreana Island, southern Galápagos, Ecuador (Fig. 6). Type specimens were collected from the coast to the top of the island at 227 m (field notes, October 3rd, 1905, J. R. Slevin).

Natural History. The type specimens of *Microlophus slevini* were found active in the day (after 9:45 am) along a steep slope covered with lava fragments and cactus shrubs, from the NW coast to the top of Gardner (field notes, October 3, 1905, J. R. Slevin). The smallest female of *Microlophus slevini* with enlarged vitellogenic follicles had a SVL of 60 mm (CAS 9432). The smallest females of *M. grayii* with enlarged vitellogenic follicles from Floreana, Champion and Enderby had SVLs of 49 mm (CAS 11058), 47 mm (CAS 11056), and 52 mm (CAS 11628), respectively. Although no adult females of *M. slevini* with eggs were found, I examined females of *M. grayii* with two eggs from Floreana (CAS 104710, 58 mm SVL; MVZ 57557, 61 mm SVL), Champion (CAS 104702, 69 mm SVL), and Enderby (CAS 11624, 69 mm SVL). Juveniles of *M. slevini*, for which sex could not be determined, ranged between 38 mm (CAS 9442) and 41 mm (CAS 9441). Six of the 10 examined females and eight of 13 males had broken or regenerated tails, the latter representing 1–53% and 16–73% of the total tail length, respectively. This species is known to be one of the main prey items of the snake *Pseudalsophis biserialis* and the Floreana mockingbird *Mimus trifasciatus* (Ortiz-Catedral *et al*. 2019; Wittmer-Naranjo *et al*. 2021).

TABLE 3. Sexual variation in scutellation and measurements of *Microlophus slevini*. Range followed by mean ± standard deviation are presented.

Character	Females (N = 10)	Males (N = 13)
scales around midbody	63–70 67.80 ± 2.10	66–72 68.85 ± 1.95
vertebrals	38–45 42.50 ± 2.42	38–44 40.92 ± 2.33
postrostrals	2–4 3.11 ± 0.60	2–4 3.15 ± 0.55
internasals	4–5 4.11 ± 0.33	3–5 4.00 ± 0.41
supralabials	3–4 3.90 ± 0.32	4–5 4.08 ± 0.28
infralabials	5–6 5.70 ± 0.48	5–6 5.38 ± 0.51
loreals	4–5 4.56 ± 0.53	3–5 3.92 ± 0.64
lorilabials	8–10 9.20 ± 0.92	6–10 8.31 ± 0.95
gulars	27–32 29.90 ± 1.73	27–39 33.64 ± 3.88
lamellae Finger IV	19–20 19.60 ± 0.52	20–21 20.15 ± 0.38
lamellae Toe IV	25–29 27.20 ± 1.23	26–30 28.15 ± 1.21
head length	14.10–17.26 15.33 ± 1.20	16.21–19.57 17.80 ± 1.27
head width	10.80–13.42 12.03 ± 0.86	12.70–15.49 14.08 ± 1.03
head height	8.43–11.89 9.59 ± 1.09	10.23–14.14 11.79 ± 1.08
interparietal width/length	1.07–1.23 1.17 ± 0.06	0.91–1.19 1.07 ± 0.09
distance between limbs	24.30–30.69 28.28 ± 1.96	27.69–39.24 31.77 ± 3.65
hind limb length	47.01–65.27 53.26 ± 6.04	56.67–67.83 62.39 ± 3.46
maximum SVL	77	86

Discussion

Soon after Charles Darwin's acclaimed visit to the Galápagos in 1835 aboard the HMS Beagle, European herpetologists became highly interested in discovering and describing the biota of the archipelago. The first species of lava lizard to be scientifically described was *Microlophus grayii* based upon specimens collected by Darwin in the islands of Santiago and Floreana (Bell 1843). Thanks to subsequent expeditions to the Galápagos and exemplary museum-based research, the last two—*M. barringtonensis* and *M. jacobii* Baur, 1892—of all currently recognized species of lava lizards from the Galápagos were described by the end of the 19th century

(Baur 1892). Remarkably, the taxonomic arrangement proposed by Baur in 1892 based on morphology, which has been repeatedly modified mostly by synonymizing species (Boulenger 1891; Heller 1903; van Denburgh & Slevin 1913), is fully supported by recent molecular systematic studies based on large geographical and genetic samples (Benavides *et al*. 2007, 2009). Thus, all ten species of Galápagos lava lizards proposed by Baur (1892) are currently recognized (Torres-Carvajal *et al*. 2019). Reciprocal monophyly based on mitochondrial and nuclear markers, haplotype networks, genetic distances (Table 4) and morphological characters (Table 2) support recognition of populations of lava lizards from the 0.8-km^2 islet of Gardner-near-Floreana as a new species (Benavides *et al*. 2009; Torres-Carvajal *et al*. 2021), which I have described in this paper. Not surprisingly, the new species is most similar to its sister taxon *M. grayii* (Fig. 1) from nearby Floreana Island and Champion, Caldwell, and Enderby islets (Fig. 6).

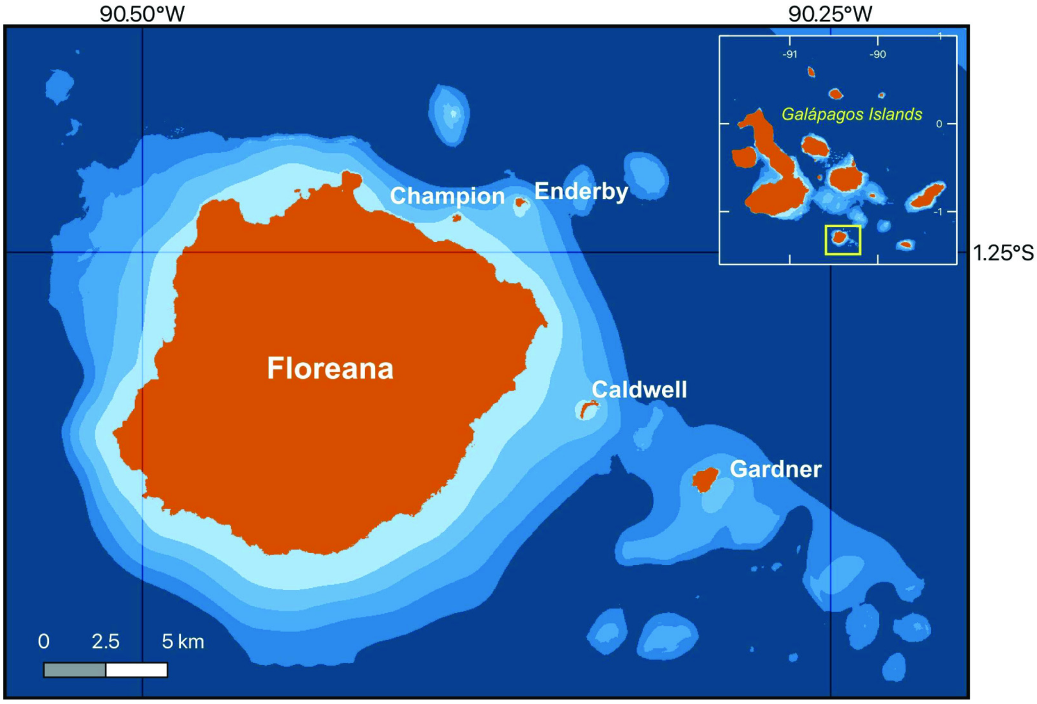

FIGURE 6. Map of the Galápagos Archipelago with a close-up of Floreana Island and surrounding islets. Bathymetric contour lines delimit depths of 50 m (lighter blue), 100 m, 150 m, 200 m and >200m (darker blue). *Microlophus slevini* **sp. nov.** occurs on Gardner, whereas *M. grayii* is known from Floreana, Champion, Caldwell, and Enderby.

Lava lizards have colonized all of the main islands in the Galápagos archipelago. Interestingly, there is only one species per island, which suggests that recolonization events, if any, have failed. This seems unexpected as both lava lizards and geckos from South America have successfully colonized the Galápagos at least five times (Wright 1983; Benavides *et al*. 2009; Torres-Carvajal *et al*. 2016), suggesting that inter-island dispersal should be achievable (Kizirian *et al*. 2004). Benavides *et al*. (2009) proposed that lava lizards have failed to successfully recolonize islands due to ecological factors, such as interspecific competition and sexual selection. Notably, lava lizards have also colonized the smaller islets around the main islands. In all cases, the species on the islets are the same as the species on the main island. For example, *M. indefatigabilis* inhabits Santa Cruz and several surrounding islets, such as Baltra, Plaza Norte, Plaza Sur, Guy Fawkes, among others. In this paper, I report the first case of a speciation event involving an islet (Gardner) and a nearby larger island (Floreana, only 8 km away). Interestingly, other islets around Floreana (Champion, Caldwell, Enderby) are inhabited by *M. grayii*, also known from Floreana. One possible evolutionary scenario to explain the origin of *M. slevini*—sister taxon of *M. grayii*—in Gardner is that the populations of lava lizards on this islet have remained isolated for longer than those in other islets around Floreana. Unlike Champion, Caldwell and Enderby, sea depth contours (Fig. 6) reveal that Gardner remained fully isolated from Floreana throughout Pleistocene sea level fluctuations (Geist *et al*. 2014), which might have facilitated the evolution of Gardner lava lizard populations into a separate species through genetic drift in isolation. This scenario is further supported by the phylogenetic chronogram presented by Benavides *et al*. (2009), in which among the four samples of "*M. grayii*", the one from Gardner (i.e., *M. slevini* **sp. nov.**) diverged first (~250,000 years ago) followed by Enderby, which diverged ~120,000 years ago from the remaining samples from Floreana. A similar scenario has been proposed for the evolutionary split between *M. indefatigabilis* from Santa Cruz and *M. barringtonensis* from Santa Fe, which is located ~18 km SE of Santa Cruz (Benavides *et al*. 2009).

Despite genetic similarity and geographical proximity, populations from Floreana do not share haplotypes with those from the closest islets (Benavides *et al*. 2009; Torres-Carvajal *et al*. 2021). A similar pattern was detected in populations of lava lizards (*M. indefatigabilis*) from Santa Cruz and surrounding islets; although merged during Pleistocene glaciations, microsatellite data revealed strong genetic differentiation among these populations (Jordan & Snell 2008). This further suggests that seawater has acted as a significant barrier to gene flow among islands/islets in recent times (i.e, Pleistocene through present), allowing for genetic differentiation through drift in isolation. This process seems to have facilitated the evolution of a new species of lava lizard in Gardner-near-Floreana, which has been isolated from Floreana longer than other surrounding islets.

TABLE 4. Uncorrected pairwise *ND2* genetic distances between species of the western radiation of Galápagos *Microlophus* lava lizards. For each species pair, distance range followed by mean distance value ± standard error are shown.

	M. albemarlensis	*M. delanonis*	*M. duncanensis*	*M. grayii*	*M. indefatigabilis*	*M. jacobii*	*M. pacificus*
M. delanonis (N = 3)	0.131–0.139 0.134±0.001						
M. duncanensis (N = 1)	0.072–0.076 0.074±0.001	0.157–0.166 0.16±0.003					
M. grayii (N = 19)	0.084–0.094 0.089±0	0.154–0.166 0.159±0	0.104–0.111 0.106±0				
M. indefatigabilis (N = 6)	0.078–0.087 0.082±0	0.126–0.137 0.129±0.001	0.072–0.078 0.074±0.001	0.102–0.111 0.106±0			
M. jacobii (N = 5)	0.069–0.075 0.072±0	0.149–0.156 0.151±0.001	0.056–0.059 0.058±0.001	0.109–0.117 0.113±0	0.062–0.071 0.065±0		
M. pacificus (N = 2)	0.024–0.031 0.027±0.001	0.128–0.142 0.134±0.002	0.069–0.071 0.07±0.001	0.085–0.101 0.092±0.001	0.07–0.078 0.073±0.001	0.068–0.071 0.069±0	
M. slevini **sp. nov.** (N = 9)	0.075–0.09 0.083±0.001	0.162–0.173 0.167±0.001	0.096–0.105 0.1±0.001	0.055–0.065 0.061±0	0.093–0.101 0.097±0	0.1–0.111 0.105±0.001	0.072–0.089 0.08±0.001

Acknowledgments

I thank Rayna Bell and Lauren Scheinberg (CAS), as well as Rebecca Tarvin (MVZ) for providing access to specimens. This manuscript benefited from critical reviews by David A. Kizirian, Oliver Hawlitschek, and two anonymous reviewers. I also thank Erica Ely for taking photographs of CAS specimens and Diego Paucar for editing some photographs. GenBank sequences of QCAZ specimens were originally generated under permit MAE-DNB-CM-2016-0060 issued by the Ecuadorian Ministry of Environment. My visit to the California Academy of Sciences was funded by the Lakeside Foundation (CAS PI: R. Bell).

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APPENDIX 1. Specimens examined. Institutional codes are provided in the methods.

Microlophus grayii (N = 83).—ECUADOR: Galápagos province: CAS 9452, 9455–9457 (females), CAS 9449–9451, 9453, 9454, 9461 (males), CAS 9458–9460 (juveniles), Champion islet, 1º14'22.7"S, 90º23'41.6"W, 3 October 1905, J. R. Slevin; CAS 11054 (male), CAS 11055, 11056 (females), Champion islet, 1º14'22.7"S, 90º23'41.6"W, 26 February 1906, F. T. Nelson; CAS 104698, 104700, 104702, 104704, 104705 (females), CAS 104699, 104701, 104703 (males), Champion islet, 1º14'22.7"S, 90º23'41.6"W, 12 February 1967, I. L. Wiggins; CAS 11616–11626, CAS 11628–11631 (females), CAS 11601–11615, 11627 (males), Enderby islet, 1º13'54"S, 90º21'46"W, 14 May 1906, J. R. Slevin; CAS 104707, 104708, 104710 (females), CAS 104706, 104709, 104711 (males), Floreana island, Post Office Bay, just N of Cormorant Point, 1º13'17"S, 90º25'35"W, 14 February 1967, I.L. Wiggins; CAS 11057–11059 (females), CAS 11060 (male), Floreana island, lava pile near lagoon, NE end of island, 1º13'39"S, 90º25'32"W, 26 February 1906, J. R. Slevin; CAS 9533, 9534 (females), CAS 9535 (male), Floreana island, lava pile near lagoon, NE end of island, 1º13'39"S, 90º25'32"W, 5 October 1905, J. R. Slevin & E. S. King; CAS 9537–9543 (females), CAS 9536 (male), Floreana island, lava pile near lagoon, NE end of island, 1º13'39"S, 90º25'32"W, 6 October 1905, J. R. Slevin & R. H. Beck; MVZ 57557–57559 (females), MVZ 57561 (juvenile), MVZ 57560, 57562 (males), Floreana island, 4.8 km NE Black Beach, 1°15.13'S, 90°28.16'W, 20 July 1951, W. Woodin.