



With the discovery of a new species of *Oedipina* from the foothills along the Caribbean versant of Costa Rica (see the following article), the number of species of salamanders in the country has risen to 51. When compared to other countries, this diversity of salamanders places Costa Rica 5th among all countries on the planet, behind the United States (1st), Mexico (2nd), China (3rd), and Guatemala (4th). When considering countries with an area greater than 5,000 km², the highest diversity density of salamanders is found in the small country of Costa Rica, with one species/1,000 km². Data calculated by Brian Kubicki from information on AmphibiaWeb (www.amphibiaweb.org) and Wikipedia (www.wikipedia.org).

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A new species of salamander (Caudata: Plethodontidae: *Oedipina*) from the central Caribbean foothills of Costa Rica

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ABSTRACT: I describe a new salamander of the genus *Oedipina*, subgenus *Oedopinola*, from two sites in Premontane Rainforest along the foothills of the central Caribbean region of Costa Rica, at elevations from 540 to 850 m. The type locality lies within the Guayacán Rainforest Reserve, a private reserve owned and operated by the Costa Rican Amphibian Research Center, located approximately 2 km north of Guayacán de Siquirres, in the province of Limón. The new taxon is distinguished from its congeners based on phenotypic and molecular (16S and *cyt b*) characteristics. Additionally, I describe and illustrate a standardized method for taking morphological measurements on bolitoglossine salamanders.

Key Words: Amphibia, Central America, Guayacán, morphometrics, *Oedopinola*

RESUMEN: Describo una nueva salamandra perteneciente al género *Oedipina*, subgénero *Oedopinola*, de dos sitios de Bosque Premontano Lluvioso en las zonas montañosas del Caribe central de Costa Rica, entre los 540 a 850 m de altura. La localidad tipo se encuentra dentro de la Reserva del Bosque Lluvioso de Guayacán (Guayacán Rainforest Reserve), una reserva privada que pertenece y es operada por el Centro de Investigación de Anfibios de Costa Rica (Costa Rican Amphibian Research Center), ubicada aproximadamente a 2 km al norte de Guayacán de Siquirres, en la provincia de Limón. Este nuevo taxón se distingue de sus congéneres basándose en características fenotípicas y moleculares (16S y *cyt b*). Además, describo e ilustro un método estandarizado para tomar medidas morfológicas en las salamandras bolitoglossinas.

Palabras Claves: Amphibia, Centroamérica, Guayacán, morfometría, *Oedopinola*

Citation: Kubicki, B. 2016. A new species of salamander (Caudata: Plethodontidae: *Oedipina*) from the central Caribbean foothills of Costa Rica. *Mesoamerican Herpetology* 3: 819–840.

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Received: 22 August 2016; **Accepted:** 23 October 2016; **Published:** 31 December 2016.

INTRODUCTION

The flora and fauna of the central Caribbean region of Costa Rica remains relatively understudied, and likely contains one of the highest concentrations of biological richness on the planet. The abundance of forest coverage, diverse but stable microclimates, and heterogeneous topography in this region create the conditions necessary to contain an extraordinary amount of biodiversity. Three distinct bioregions come together in this area of Costa Rica—the Cordillera Volcánica Central, the Cordillera de Talamanca, and the Santa Clara lowlands—and their convergence results in a mixture of floral and faunal assemblages. Elevations within this region extend from sea level along the Caribbean coast, to over 3,300 m at the summit of Volcán Turrialba, to above 3,800 m on the highest peak of the Cordillera de Talamanca. The region receives high levels of precipitation, principally due to orographics, with some areas receiving more than 6,000 mm of annual rainfall.

The varying topography, richness of stable high-humidity microclimates, and geographic position between North- and South America has resulted in the high diversity of amphibians that are known to inhabit the central Caribbean region of Costa Rica. According to historical collections and those made by the author during the last two decades, more than 130 species of amphibians inhabit, or at least inhabited, an area of just under 5,000 km² in this part of the country (BK, unpublished). Guayacán de Siquirres is a site in this region known for its amphibian richness, currently with 66 documented species (Kubicki, 2008). This number represents the highest amphibian diversity known from any region in Costa Rica, and additional species likely will be discovered.

MATERIALS AND METHODS

During routine fieldwork in the Costa Rican Amphibian Research Center's Guayacán Rainforest Reserve, located in the upper catchment basin of the Río Siquirres and ca. 2 km N north of Guayacán de Siquirres, in the company of others (see below) I encountered two salamanders of the genus *Oedipina* that could not be assigned to any known species. The Guayacán Rainforest Reserve (49 ha) is privately owned and maintained by the Costa Rican Amphibian Research Center (C.R.A.R.C.); its elevational range is from ca. 450 to 620 m, and its location is in a protected watershed known as the “Zona Protectora Cuenca Río Siquirres” (Fig. 1). Most of the reserve lies within Premontane Rainforest (Holdridge, 1967; Savage, 2002), and receives 5,000–6,000 mm of annual precipitation (data from a precision rain gauge at C.R.A.R.C.).


Two additional specimens later were secured. All of the specimens were fixed in a 10% formalin solution, and later transferred into 70% ethanol for preservation; tissue samples for genetic analyses also were taken, and placed in 96% ethanol. All of the phenotypic characteristics reported herein are from adult specimens ($n = 4$), which are deposited at the Museo de Zoología, Universidad de Costa Rica (UCR), San José, Costa Rica (UCR 22843–45) and the C.R.A.R.C. (paratopotype CRARC 0241). The GPS coordinates provided herein are in datum WGS 84. The following are abbreviations for the collections or museums mentioned in the text: Costa Rican Amphibian Research Center, Guayacán, Limón, Costa Rica (CRARC); University of Kansas, Museum of Natural History, Lawrence, Kansas, United States (KU); Natural History Museum of Los Angeles County, Los Angeles, California, United States (LACM); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States (MCZ); Forschungsinstitut und Natur-Museum Senckenberg, Senckenberg-Anlage, Frankfurt-am-Main, Germany (SMF); Universidad de Costa Rica, Museo de Zoología, San Pedro, San Jose, Costa Rica (UCR); National Museum of Natural History, Washington, D.C., United States (USNM) (Frost, 2016).

Morphometrics

I took measurements with a dissecting scope fitted with an ocular micrometer, and for measurements exceeding 8 mm with a ROHS NORM 2002/95/EC digital caliper, rounded to the nearest 0.1 mm. The morphological measurements and their corresponding abbreviations are as follows (Plates 1–6): standard length (SL) = internarial tip of snout to posterior margin of cloacal opening; tail length (Tal) = posterior tip of tail to posterior margin of cloacal opening; total length (TL) = internarial tip of snout to posterior tip of tail; shoulder width (ShW) = width of shoulders at center axis of upper arms; head width (HeW) = greatest width of head at jaw articulation; neck width (NeW) = width of neck at gular fold crease; eye width (EW) = horizontal distance between anterior/inner and posterior/outer corners of right eye opening; snout length (SnL) = distance between anterior/inner corner of right eye

opening and tip of snout; jaw to snout length (JSL) = distance between posterior angle of buccal opening on right side of head to tip of snout; lateral gular fold to tip of snout (LGFS) = distance between most posterior margin of gular fold on right side of body to tip of snout; nostril height (LNH) = greatest vertically oriented distance of left narial opening; nostril width (RNW) = greatest width of right narial opening; internarial distance (IND) = distance between inner margins of narial openings; naris to lip distance (NLP) = distance between inferior margin of left narial opening and margin of upper lip; intercanthal distance (ICD) = distance between external margins of canthal ridges at anterior/inner corners of eyes; hind limb length (HLL) = distance from right hind limb's juncture with body to tip of Toe III; front limb length (FLL) = distance from right front limb's juncture with body to tip of Finger III; trunk width (TW) = width of trunk at midway point between groin and axilla; midventral gular fold to snout length (VGS) = distance between midventral posterior edge of gular fold to tip of snout; front limb to snout distance (FSL) = distance between anterior margin of left front limb's juncture with body and tip of snout; ulna and hand length (UHL) = distance from external lateral margin of ventral elbow crease to tip of Finger III on left arm; axilla to groin length (AGL) = distance between posterior margin of front limb's juncture with trunk and anterior margin of hind limb's juncture with trunk on left side of body; vent length (VL) = distance between anterior and posterior margins of cloacal opening; hand width (HaW) = distance between exterior lateral margin of Finger I and exterior lateral margin of Finger IV on right hand; hand length (HaL) = distance from center proximal margin of palmar surface to tip of Finger III on right hand; length of Finger III (LF3) = distance from baseline along most proximal



Fig. 1. Aerial image of the Costa Rican Amphibian Research Center's Guayacán Rainforest Reserve, the type locality of a new species of *Oedipina*.  © Brian Kubicki

interdigital margin between fingers II and III and fingers III and IV to tip of Finger III on right hand; foot width (FoW) = distance between exterior margin of Toe I and exterior margin of Toe V on right foot; foot length (FoL) = distance from center proximal margin of plantar surface to tip of Toe III on right foot; and length of Toe III (LT3) = distance from baseline along most proximal interdigital margin between toes II and III and toes III and IV to tip of Toe III on right foot. The following also are expressed as a percentage of standard length (SL): midventral gular fold to snout length (VGS); head width = (HeW); axilla to groin length (AGL); left nostril height (LNH); right nostril width (RNW); right hind limb length (HLL); and right front limb length (FLL). The following are expressed as a percentage of midventral gular fold to snout length (VGS): right hand length (HaL); and right foot length (FoL). The following are expressed as a percentage of the head width (HeW): internarial distance (IND); snout length (SnL); left nostril height (LNH); right nostril width (RNW); right hand width (HaW); right foot width (FoW); and length of Toe III on the right foot (LT3). The following is expressed as a percentage of axilla to groin length (AGL): head width (HeW). The following is expressed as a percentage of right foot width (FoW): length of Toe III on the right foot (LT3). The tooth counts are based on the number of teeth clearly visible in magnified digital photographs, including the premaxillary teeth (PMT), maxillary teeth (MT), and vomerine teeth (VT). The number of maxillary and vomerine teeth also is indicated according to the count on the corresponding right and left sides of the mouth in the following manner (R/L). The limb interval is equal to the number of costal folds between the tips of the longest digits of the addressed front and hind limbs, expressed in 0.5 increments (e.g., 4, 4.5). The capitalized colors and their corresponding color codes (code in parentheses) used in the color in life and color in ethanol descriptions of the holotype follow Köhler (2012).

Amplification and Sequencing

The total genomic DNA was extracted from the preserved tissues using the phenol-chloroform standard protocol (Sambrook and Russell, 2006). The holotype (UCR 22845) was sequenced for the 16S rRNA (16S) and cytochrome *b* (cyt *b*) mitochondrial genes. The primers 16Sar y 16Sbr (Palumbi et al., 1991) were used for 16S and primers MVZ15 and MVZ16 (Moritz et al., 1992) for cyt *b*. The PCR conditions consisted of an initial cycle of 5 min (16S) or 2 min (cyt *b*) at 94°C, followed by 35 (16S) or 38 (cyt *b*) cycles of 45 s (16S) or 30 s (cyt *b*) at 94°C, 30 s at 55°C for 16S or 1 min at 48°C, 45 s (16S) or 1 min at 72°C, plus a final cycle of 3 min (16S) or 8 min (cyt *b*) at 72°C. The PCR products were cleaned with ExoSap-IT (USB Corporation) and sequenced in both directions using the original amplification primers and BigDye termination reaction chemistry (Applied Biosystems). After cycle sequencing, the products were column-purified using a Sephadex G-50 (GE Healthcare) and were run on an ABI PRISM 3100 DNA Analyzer (Applied Biosystems). The consensus sequences for each individual were constructed using SEQUENCHER 5.3 (Genes Codes Corp.). The resulting sequences were deposited in GenBank (Table 1).

Phylogenetic Analyses

The sequences obtained from UCR 22845 were compared with 20 sequences available on GenBank for *Oedipina* (subgenus *Oedopinola*), in addition to using *Nototriton abscondens* as an outgroup (Appendix 1). The individual alignments were performed using the MUSCLE 3.7 software (Edgar 2004). PartitionFinder v1.1.1 (Lanfear et al., 2012) and the Bayesian Information Criterion (BIC) were used to select an appropriate model of the DNA sequence evolution. The following substitution models were selected: GTR+G for 16S and for cyt *b* codon position 2, GTR for cyt *b* codon position 1, and HKY+I for cyt *b* codon position 3. The analyses were performed using both the maximum likelihood (ML) and Bayesian analyses (BA). The ML analyses were performed using RAxML 8.1.11 (Stamatakis, 2014) and run on the CIPRES portal (Miller et al., 2010), including 1,000 bootstrap replicates to evaluate nodal support. The Bayesian phylogenetic analyses were performed using MrBayes 3.2.2 (Huelsenbeck and Ronquist, 2001) and four heated MCMC samples of every 1,000 generations for 50 million generations. A time-series plot of the likelihood scores of the cold chain was examined to check stationarity using Tracer 1.6 software (Rambaut et al., 2014). The first 25% of trees were discarded as burn-in and the remaining trees were used to estimate the consensus tree along with the posterior probabilities for each node and each parameter. The estimates of pairwise evolutionary genetic divergences between species were computed using MEGA7 (Kumar et al., 2016), assuming corrected distances based on the Tamura-Nei (Tamura and Nei, 1993), with uniform rate.

RESULTS

Molecular Genetics

The resulting data matrix had a total sequence length of 905 bp, including gaps; 520 bp for 16S and 385 for *cyt b*. The phylogenies inferred using ML and BA were very similar in supporting the tree shown in Fig. 2, differing only in the placement of *O. maritima*; in ML *O. maritima* was the sister clade to *O. complex* and UCR 22845. The phylogeny shows that UCR 22845 is divergent from the other members of the subgenus *Oedopinola* that were analyzed. According to the results, UCR 22845 is separated by a mean-corrected genetic distance of: *Oedipina alleni* 7.4% (16S) and 14.3% (*cyt b*); *O. carablanca* 7.9% (16S) and 24.4% (*cyt b*); *O. complex* 6.5% (16S) and 12.2% (*cyt b*); *O. elongata* 7.5% (16S) and 20.2% (*cyt b*); *O. gephyra* 7.3% (16S) and 18.4% (*cyt b*); *O. maritima* 6.0% (16S) and 14.5% (*cyt b*); *O. parvipes* 4.9% (16S) and 11.7% (*cyt b*); *O. petiola* 7.2% (16S) and 20.1% (*cyt b*); *O. savagei* 8.7% (16S) and 17.1% (*cyt b*); and *O. tomasi* 8.5% (16S) and 17.7% (*cyt b*). Sequences of 16S rRNA (16S) and cytochrome *b* (*cyt b*) mtDNA were not available for *O. fortunensis* and *O. nimaso*. Based on the molecular analyses and the phenotypic distinctness (comparisons presented below) UCR 22843, UCR 22844, UCR 22845, and CRARC 0241 are recognized as a separate evolutionary unit and described as the following new species:

***Oedipina berlini* sp. nov.** Berlin's Flat-headed Salamander (Fig. 3)

Holotype (Fig. 4): An adult male, UCR 22845, from Costa Rica: Provincia de Limón: Cantón de Siquirres, Distrito de Siquirres, Guayacán de Siquirres, Costa Rican Amphibian Research Center's Guayacán Rainforest Reserve, elevation 540 m asl (10.05750°N, 83.54862°W), collected by Brian Kubicki, in the company of Aura Reyes, on 29 June 2016.

Paratopotype: CRARC 0241 (Fig. 4), an adult male, same data as the holotype, but collected by Brian Kubicki, in the company of Andrew Gray, on 2 July 2016.

Paratypes: UCR 22843 (Fig. 4), an adult male from Costa Rica: Provincia de Limón: Cantón de Siquirres, Distrito de Florida, ca. 4 km SW of Alegria de Siquirres, elevation ca. 850 m asl, obtained by Donald Jiménez and donated by Erick Berlin on 18 September 2014. UCR 22844 (Fig. 4), an adult female, same data as UCR 22843, but obtained by Carlos Fallas and donated by Erick Berlin on 25 November 2015.

Generic Placement: Assigned to the genus *Oedipina* based on the presence of more than 13 costal grooves, and to the subgenus *Oedopinola* based on the presence of fewer than 20 costal grooves and the molecular evidence presented herein.

Diagnosis: The combination of the following characteristics can be used to distinguish *Oedipina berlini* from other species of the subgenus *Oedopinola*: (1) fully webbed hands and feet with the longest digit terminating in a fleshy point (Figs. 5, 6); (2) the webbing margin of the hand lacks any evident indentation at the interdigital spaces; (3) a flat head, more than twice as wide as high, with relatively large protruding eyes (Fig. 7); (4) a relatively long prehensile tail (135–152% of SL); (5) males with few or completely lacking premaxillary teeth; (6) numerous maxillary teeth (19–31); (7) a pale gular patch (Fig. 8); and (8) the dorsum is colored with a mixture of pale earthy tones ranging from tan to dark reddish brown, with finer white and dark brown to black spots and irregular markings scattered throughout.

Comparisons: Because *Oedipina berlini* only is known to occur in the central Caribbean region of Costa Rica and phenotypic and molecular evidence supports its inclusion in the subgenus *Oedopinola*, I narrowed the comparisons in the discussion below to members of this subgenus native to Costa Rica and western Panama, i.e., *O. alleni* Taylor, 1954; *O. carablanca* Brame, 1968; *O. complex* (Dunn, 1924); *O. fortunensis* Köhler et al., 2007; *O. maritima* García-París and Wake, 2000; *O. nimaso* Boza-Oviedo et al., 2012; and *O. savagei* García-París and Wake, 2000. Additionally, because many species of the subgenus *Oedopinola* are known from relatively few specimens, often fewer than 10, our understanding of the potential intra- and interspecific phenotypic variation is limited. Often, subtle differences in phenotypic characteristics, combined with the low number of total specimens known for most species in collections, potentially can result in unrecognized cryptic species; for this reason, to avoid the possibility of extending false characteristics stemming from unrecognized species, I restricted my phenotypic comparisons to *sensu stricto* individuals, based on the information in the original descriptions of the corresponding taxa (i.e., holotypes, and when detailed morphometric or other phenotypic data were provided, paratopotypes).

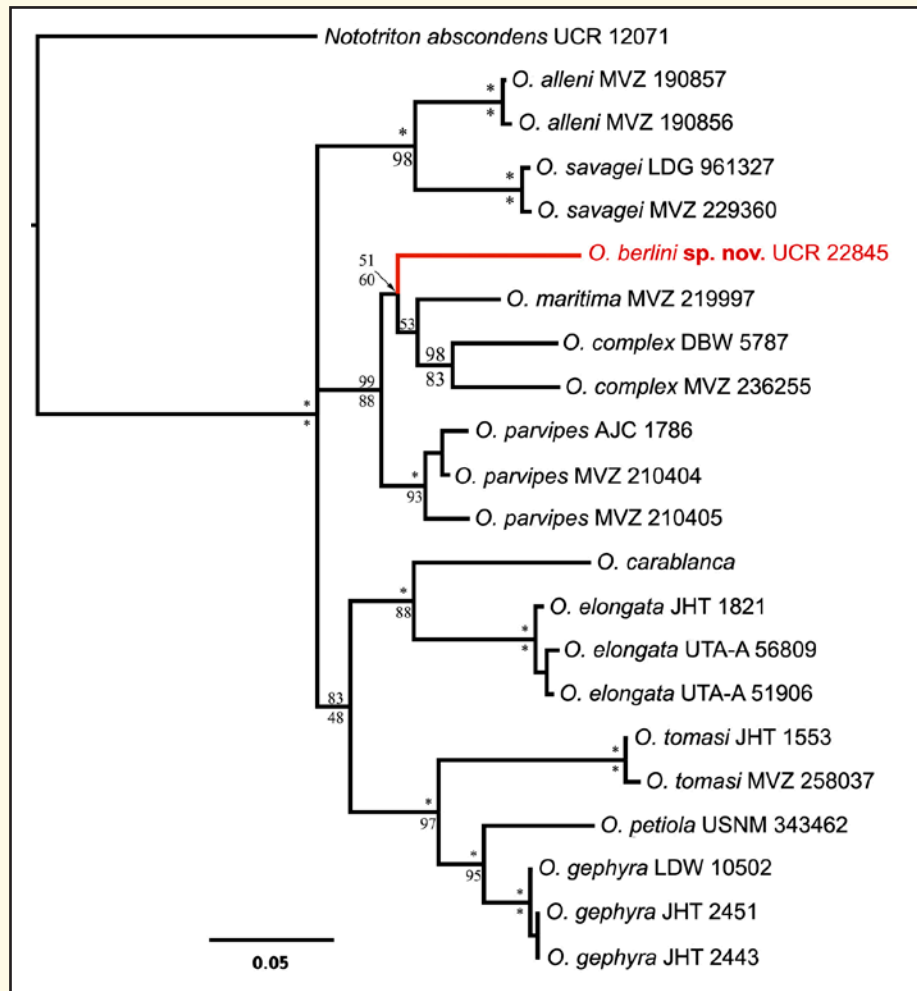


Fig. 2. Bayesian phylogenetic inference of the relationships of *Oedipina berlini* sp. nov. within the subgenus *Oedipina* based on the 16S and *cyt b* mitochondrial DNA genes. Bayesian posterior probabilities (multiplied by 100) are shown above the branch; maximum likelihood bootstrap values from the RAxML analysis are shown below the branches. The scale bar refers to the estimated substitutions per site. The support values of any node within the species are not shown. The asterisks represent support of 100. Figure courtesy of Erick Arias

I present the contrasting characteristics between each of the above-mentioned species and those of *O. berlini* in parentheses at the end of each character. *Oedipina allenii* (adult female holotype, KU 34926, Palmar, Costa Rica) has fewer maxillary teeth (4) that do not extend posterior of the choanae (vs. numerous maxillary teeth [19–31] that extend posterior of the choanae to about the anterior margin of the orbits); and fewer vomerine teeth (12) (vs. 16–19). *Oedipina carablanca* (adult male holotype, LACM 1727, and adult male paratopotype, LACM 1728, Guápiles, Costa Rica) are larger in size (SL = 47.1–53.7 mm) (vs. 30.1–38.7 mm); the dorsal coloration is dark brown to black, with contrasting white pigmentation ranging in size from large spots or patches on the head, limbs, and tail to small spots on the neck and body (vs. dorsum consisting of pale earthy tones); and lacks maxillary teeth (vs. 19–31 maxillary teeth). *Oedipina complex* (young male holotype, MCZ 9408, Canal Zone, Panamá) has a shorter tail (Tal = 35 mm, Tal/SL = 109 %) (vs. Tal 40.9–56.1 mm, Tal/SL = 135–153 %); 9 costal folds between the adpressed limbs (vs. 6 to 7 costal folds between the adpressed limbs); and a brownish black dorsum with brown flecks (vs. dorsum consisting of pale earthy tones). *Oedipina fortunensis* (adult male holotype, SMF 85064, Chiriquí, Panamá) has shorter hind limbs (HLL = 4.3 mm, HLL/SL = 12.8 %) (vs. longer hind limbs [HLL = 6.3–8.4 mm, HLL/SL = 20.9–21.7 %]); Finger III and Toe III do not terminate in pointed fleshy tips (vs. Finger III and Toe III terminate in pointed fleshy tips); and toes I and II contain clearly defined rounded tips, and are bordered by evident interdigital indentations (Köhler et al., 2007: fig. 2) (vs. tips of toes I and II covered with webbing, and lack evident interdigital



Fig. 3. *Oedipina berlina* sp. nov. UCR 22845, adult male holotype.

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Fig. 4. In life images of the type series of *Oedipina berlina* sp. nov.

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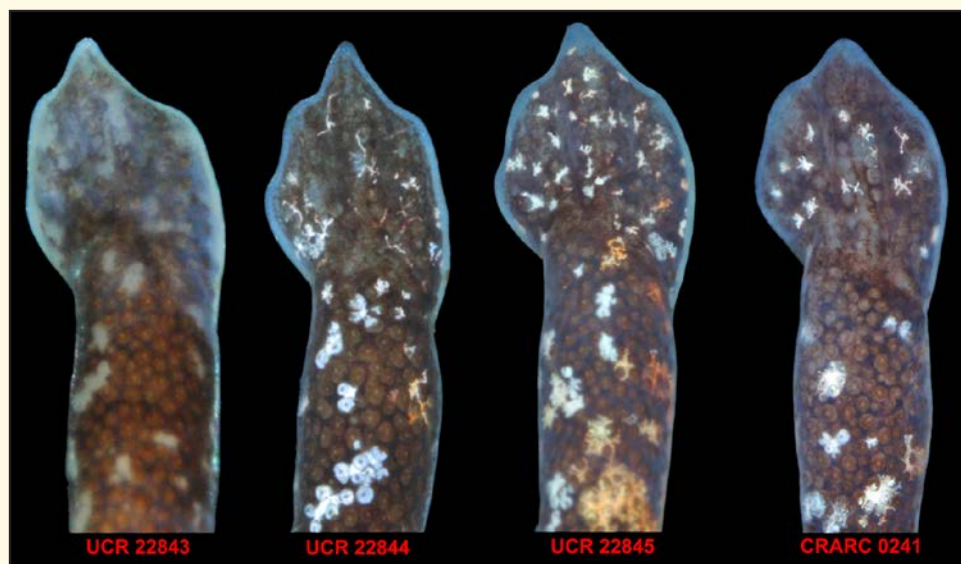


Fig. 5. Dorsal view of the right hand of each specimen in the type series of *Oedipina berlina* sp. nov.

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indentations). *Oedipina maritima* (adult female holotype, USNM 529981, Bocas del Toro, Panamá) has a darker dorsal coloration (vs. dorsum consisting of pale earthy tones); smaller inconspicuous eyes (EW = 0.9 mm) that mostly are directed laterally (vs. larger protuberant eyes [EW = 1.5–1.6 mm] that are directed frontally); and a narrow, cylindrical head (vs. a flat head, more than twice as wide as high). *Oedipina nimaso* (subadult male holotype, UCR 8391, Talamanca, Costa Rica) has a uniform dark brown dorsal coloration (Fig. 9) (vs. dorsum consisting of pale earthy tones); a narrower head (HeW = 3.6 mm) (vs. a wider head [HeW = 4.1–5.1 mm]); smaller eyes (EW = 0.7 mm) (vs. larger protuberant eyes [EW = 1.5–1.6 mm]); a narrower intercanthal distance (ICD = 1 mm) (vs. a wider intercanthal distance [ICD = 2.0–2.8 mm]); and a shorter head (VGS = 4.8 mm, FSL = 7.3 mm) (vs. a longer head [VGS = 5.2–6.8 mm, FSL = 8.1–10.3 mm]). *Oedipina savagei* (adult female holotype, LACM 109558, San Vito, Costa Rica) has fewer maxillary teeth (MT = 7) (vs. more maxillary teeth [MT = 19–31]).

Furthermore, *Oedipina berlini* is distinguished from *O. alleni*, *O. carablanca*, *O. complex*, *O. maritima*, and *O. savagei* by large differences in the sequences of the mitochondrial genes 16S rDNA and cytochrome *b*; mitochondrial gene sequences for *O. fortunensis* and *O. nimaso* were not available for comparison.

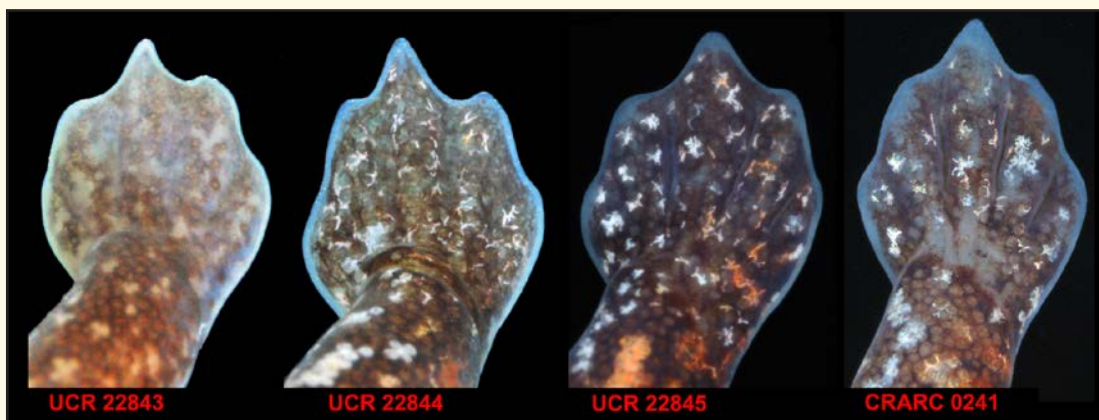



Fig. 6. Dorsal view of the right foot of each specimen in the type series of *Oedipina berlini* sp. nov.

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Description of holotype: Adult male with SL of 38.7 mm. Head flat, more than twice as wide as high (Figs. 7, 10), slightly wider than neck and shoulders (HeW = 4.9 mm, NeW = 4.1 mm, ShW = 4.6 mm), with greatest width at jaw articulations; snout raised anterodorsally, bluntly rounded in dorsal outline and rounded in profile (Figs. 10, 11), relatively long (SnL = 1.4 mm, 20.6 % of VGS); nostrils tiny, nearly terminal, non-protruding, directed anterolaterally (LNH = 0.06 mm, RNW = 0.09 mm); and internarial area rounded convexly in dorsal and lateral views. Eyes relatively large, directed forward, strongly protruding in life (EW = 1.6 mm, 114 % of SnL), with distinct suborbital groove; and preserved specimen with eyes barely protruding beyond dorsal and ventral outline of head, result of eyes partially receding into skull during euthanization. Top of head flat and smooth, tapering slightly toward anterior terminus, lacking contrasting interorbital or other dermal structures. Canthus rostralis distinct and rounded; intercanthal area slightly convex; and loreal region slightly concave. Obvious cirri (nasolabial protuberances) and nasolabial grooves present on tip of snout; nasolabial grooves start at lateral margins of nares and extend ventrally, with a slight outward orientation, and terminate prior to reaching tips of cirri; and cirri protrude slightly (0.4 mm) beyond margin of upper lip, terminating in bluntly rounded tips. Gular fold well-defined, starting on dorsolateral portion of neck, and wrapping around lateral section of head and crossing venter as a smooth anterior-oriented curve. Tip of snout markedly protruding beyond edge of lower lip in ventral view; and no mental gland visible under skin of anterior intermandibular region. Nuchal groove well defined, starting posterior to jaw articulation, about level with lower margin of eye, and extending vertically on side of head and crossing venter as a poorly visible transverse line, lacking a distinct forward curve at posteromedial margin of mandibular bones. A weakly discernible groove starts at posterodorsal margin of orbit and extends dorsolaterally to anterior margin of gular fold.



Fig. 7. Views showing the flat head of the paratopotype (CRARC 0241) of *Oedipina berlina* **sp. nov.** (A) Head profile in life, showing the large protruding eyes and flat head; and (B, C) dorsal and profile views of the head after preservation.  © Brian Kubicki

Vomerine teeth (9/10) present in two arching rows, starting just posterior to choanae and curving postero-medially toward center of roof of mouth; rows of vomerine teeth not in contact medially; maxillary teeth (13/13) situated in long arching rows on opposite/outer margins of upper mouth, extending from maxillary bones; and prevomerine teeth absent. Choanae moderately large, elongated, and teardrop-shaped, with weak, narrow groove emerging laterally from each opening and curving posteriorly beneath eyes. A patch of numerous paravomerine teeth present on medial roof of mouth, lying posterior to vomerine tooth rows. Sublingual fold indiscernible; and distal surface of tongue flat and rounded, but slightly damaged.

Arms relatively long and slender (FLL = 6.8 mm, 17.9% of SL), without noticeable hypertrophied forearm compared to upper arm. Hands small (HaL = 1.9 mm, 26.5% of VGS; HaW = 1.4 mm, 28.6 % of HeW); fingers fully covered in webbing, lacking distinct indentation at interdigital spaces; Finger III terminates in sharply-rounded fleshy tip, protruding 0.41 mm beyond terminus of fingers II and IV; and tips of fingers lack visible terminal pads. Palmar surface smooth. Dorsal surface of hand contains discernible interdigital grooves, extending from webbing margins to metacarpal region. Relative lengths of fingers on right hand I < II < IV < III (Fig. 5).

Legs relatively long and slender (HLL = 8.4 mm, 21.7 % of SL), with little perceivable difference between thickness of upper and lower leg. Feet small (FoL = 2.2 mm, 32.4 % of VGS; FoW = 1.8 mm, 36.7 % of HeW); toes fully covered in webbing, lacking distinct indentation at interdigital spaces; Toe III terminating in a sharply-rounded fleshy tip, protruding 0.45 mm beyond terminus of toes II and IV; and tips of toes lack visible terminal pads. Plantar surface smooth. Dorsal surface of foot with discernible interdigital grooves, extending from webbing margins to metatarsal region. Relative lengths of toes on right foot $I < V < II < IV < III$ (Fig. 6).

Body subcylindrical (wider than high) in cross section, and relatively slender (TW = 4.5 mm). Between axilla and groin, 15 weak but discernible costal grooves visible, 17 if counting axillary and inguinal grooves; costal grooves most visible on ventral and lateral portions of body. Adpressed limbs separated by 6.5 costal folds; 16 costal folds between axilla and groin. Slight middorsal depression extends longitudinally along length of body, starting at base of head and becoming indiscernible on anterior portion of tail. Tail long, cylindrical in cross section, lacking discernible caudal grooves or constriction at base, and tapering evenly to a pointed terminus. Skin on surfaces of head, body, limbs, and tail smooth.

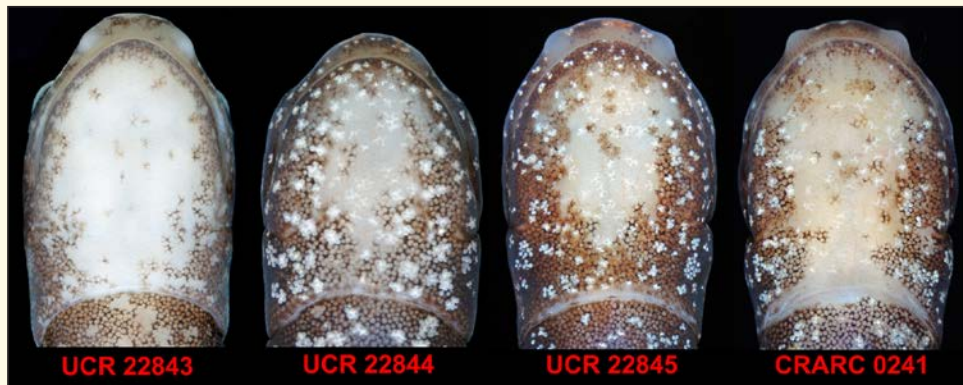


Fig. 8. Ventral views of the head of each specimen in the type series of *Oedipina berlina* sp. nov.

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Coloration in life (Fig. 12): The coloration of the dorsal surfaces of the head, body, and tail of the holotype consisted of a mottled mixture of medium to pale earthy tones. The dominant ground colors of the dorsum were Flame Scarlet (73), Light Pratt's Rufous (71), and Pratt's Rufous (72). The dorsum also was accented with smaller, irregular, pale or dark blotches or spots that consisted primarily of Pale Pinkish Buff (3) or Jet Black (300). Additionally, fine gray to white speckles were scattered sparsely throughout dorsal surfaces of head and body, and less so on the tail. A pale diamond-shaped patch of skin was present on the dorsal surface of the head, which consisted of a mixture of pigments ranging from Light Buff (2) to Salmon Color (58), from the tip of the snout and extending posteriorly between the canthal ridges, widening onto the upper eyelids, and tapering back to a rough point on the anterior base of the head. A patch of pigment on the shoulders and dorsolateral margin of trunk was similar in coloration and tone to that of the dorsal surface of the head. A weak Salmon Color (58) caudal ring was present on the dorsal surface of the base of the tail. The dorsal surfaces of the upper arms and legs consisted primarily of a mixture of pale tones, Light Buff (2) to Salmon Color (58), whereas the tone of the lower arms and legs changed to Flame Scarlet (73), Light Pratt's Rufous (71), and Pratt's Rufous (72). Irregular Jet Black (300) blotches also were present along the entire dorsal surface of the arms and legs. The dorsal surfaces of the hands and feet were dominantly Jet Black (300), but accented with finer spots or speckles ranging in color from Light Pratt's Rufous (71) and Pratt's Rufous (72) to white.

The lateral surface of the head, body, and tail were dominated by the coloration of the dorsum on the upper half of the body, whereas the base coloration on the lower half was Jet Black (300) accented with white speckles or irregular blotches and extremely fine Kingfisher Rufous (28) spots.



Fig. 9. Comparison of dorsal pigmentation among four species of *Oedipina* native to Costa Rica after at least 22 months in ethanol (70%).
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Fig. 10. Dorsal, lateral, and ventral views of the head of the holotype (UCR 22845) of *Oedipina berlina* sp. nov.

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The ventral coloration was dominantly Kingfisher Rufous (28) and Pinkish White (216), but accented with an extremely fine Jet Black (300) reticulation and irregular white spots or small blotches. A contrasting, ovoid, fleshy white gular patch was present. The ventral surface of the tail also had small to medium-sized, irregular, Light Buff (2) to Salmon Color (58) spots and blotches. The gular fold was Pinkish White (216) to Light Pinkish Rose (217).

The ground color of the iris was Jet Black (300), with a fine reticulation consisting of a mixture of gold and copper pigments.

In life, no metachrosis was observed in the holotype or any member of the type series.

Coloration in ethanol: When writing this, the holotype only had been stored in ethanol (70%) for a relatively short period of time, so its ultimate appearance remains unknown. The paratype (UCR 22843), however, has been in ethanol for nearly two years, and shows significant color and tonal shifts (Fig. 13).



Fig. 11. Anterodorsal and anteroventral views of the snout of the holotype (UCR 22845) of *Oedipina berlini* sp. nov. © Brian Kubicki

Measurements (in mm), tooth counts, limb interval, and percentages of the holotype: SL = 38.7; Tal = 56.1; TL = 94.8; ShW = 4.6; HeW = 4.9; NeW = 4.1; EW = 1.6; SnL = 1.4; JSL = 4.3; LGFS = 8.0; LNH = 0.06; RNW = 0.09; IND = 1.7; NLP = 0.6; ICD = 2.8; HLL = 8.4; FLL = 6.8; TW = 4.5; VGS = 6.8; FSL = 10.2; UHL = 4.6; AGL = 22.3; VL = 2.6; HaW = 1.4; HaL = 1.8; LF3 = 0.41; FoW = 1.8; FoL = 2.2; and LT3 = 0.45. Limb interval = 6.5. Number of teeth: PMT = 0; MT = 13/13; and VT = 9/10. Measurements in related percentages: VGS/SL = 17.6%; IND/HeW = 34.7%; AGL/SL = 58.0%; HeW/SL = 12.7%; Hew/AGL = 22.0%; SnL/HeW = 29.0%; LNH/HeW = 1.2%; LNH/SL = 0.15%; RNW/HeW = 1.84%; RNW/SL = 0.23%; HLL/SL = 21.7%; FLL/SL = 17.6%; HaL/VGS = 26.5%; FoL/VGS = 32.4%; Haw/HeW = 28.6%; FoW/HeW = 36.7%; LT3/HeW = 9.2%; and LT3/FoW 23.7%.

Variation: The snout in the female paratype (UCR 22844) was shorter (SnL = 0.9 mm vs. 1.3–1.5 mm in the three males of the type series) and the internarial distance was narrower (IND = 1.0 mm vs. 1.4–1.7 mm in the three males of the type series). A weak to distinctive Salmon Color (58) was present in the caudal ring at the base of the tail of all the males.



Fig. 12. Dorsal, lateral, and ventral views of the coloration in life of the holotype (UCR 22845) of *Oedipina berlina* sp. nov.

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Measurements (in mm), tooth counts, limb intervals, and percentages of the paratopotype and paratypes:

SL = 30.1–38.0; Tal = 40.9–45.9; TL = 71.1–76.0; ShW = 3.5–4.3; HeW = 4.1–5.1; NeW = 3.8–4.1; EW = 1.5–1.6; SnL = 0.9–1.5; JSL = 3.3–4.4; LGFS = 6.0–8.0; LNH = 0.0–0.9; RNW = 0.0–0.16; IND = 1.0–1.5; NLP = 0.5–0.9; ICD = 2.0–2.4; HLL = 6.3–8.3; FLL = 5.5–6.8; TW = 3.8–4.2; VGS = 5.2–6.6; FSL = 8.1–10.3; UHL = 3.6–4.3; AGL = 17.5–21.7; VL = 2.2–2.5; HaW = 1.0–1.4; HaL = 1.5–1.9; LF3 = 0.25–0.33; FoW = 1.5–1.9; FoL = 2.0–2.5; and LT3 = 0.33–0.45. Limb interval = 6–7. Number of teeth = PMT 0–4, MT = 11–16/8–15, and VT = 8–9/8–8. Measurements in related percentages: VGS/SL = 17.2–19.3%; IND/HeW = 24.4–32.6%; AGL/SL = 57.0–59.8%; HeW/SL = 13.4–14.3%; Hew/AGL = 23.4–23.9%; SnL/HeW = 22.0–30.2%; LNH/HeW = 0.0–2.2%; LNH/SL = 0.0–0.3%; RNW/HeW = 0.0–3.9%; RNW/SL = 0.0–0.53%; HLL/SL = 20.9–21.8%; FLL/SL = 17.9–18.9%; HaL/VGS = 25.9–28.8%; FoL/VGS = 34.5–40.4%; Haw/HeW = 25.6–27.5%; FoW/HeW = 37.2–39.0%; LT3/HeW = 7.7–10.0%; and LT3/FoW = 20.6–25.6%.

Molecular genetics: The molecular data demonstrate that *Oedipina berlina* is highly divergent from other members of the subgenus *Oedopinola*, based on the available 16S and *cyt b* sequences in GenBank (Fig. 2). The congener with the closest distance to *O. berlina* is *O. parvipes* 4.9% (16S) and 11.7% (*cyt b*)

Etymology: The specific epithet is a patronym honoring Mr. Erick Berlin, a naturalist native to the United States but living in Costa Rica since 1972, and who has a deep passion for the conservation of nature in the central Caribbean region of Costa Rica, especially along the northeastern slopes of Volcán Turrialba. Erick has been a close friend for many years, and during this time has supported and encouraged my research and conservation efforts with Costa Rican amphibians. I am extremely grateful for his friendship and encouragement.

Habitat and natural history observations: *Oedipina berlina* has been found within leaf litter in young secondary to old-growth forest with varying topography. This species is known from five individuals, so a detailed accounting of its natural history cannot be presented here.

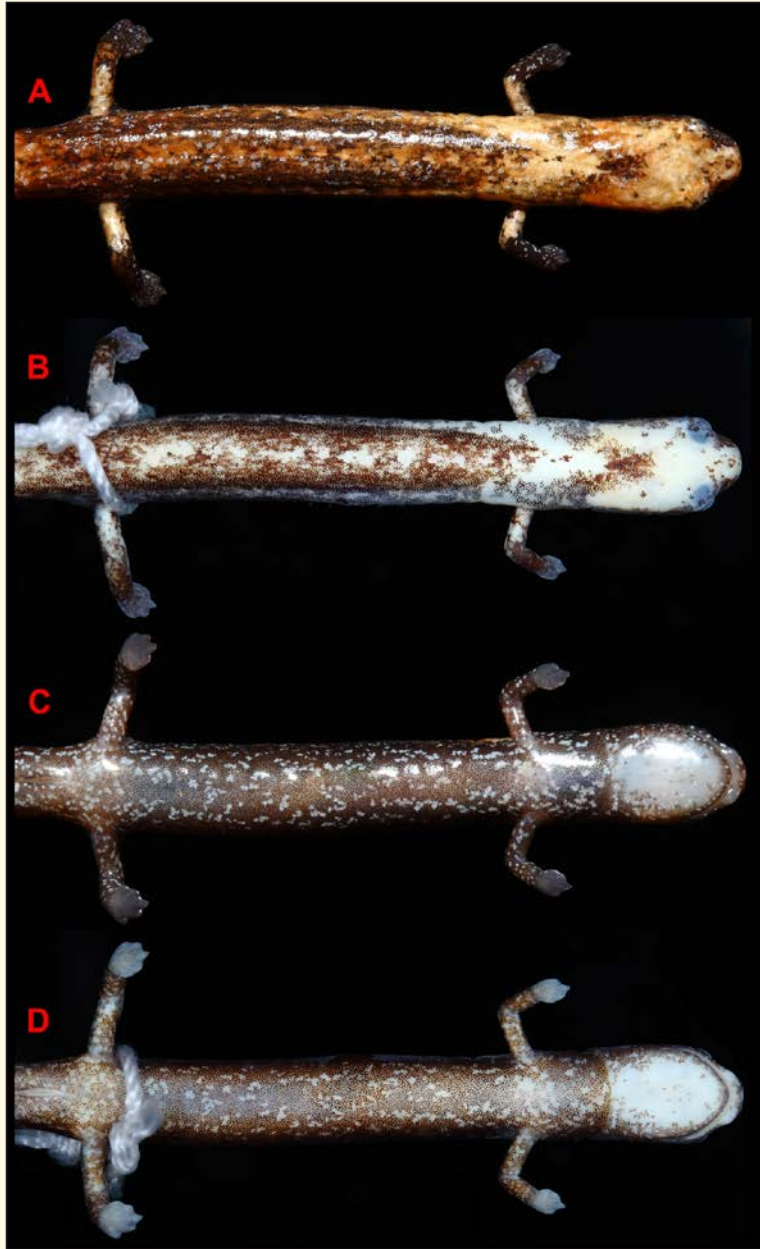


Fig. 13. Differences in the coloration of UCR 22843 in life and after 22 months in 70% ethanol. (A) Dorsal coloration in life; (B) dorsal coloration after 22 months in 70% ethanol; (C) ventral coloration in life; and (D) ventral coloration after 22 months in 70% ethanol.

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I found the holotype (UCR 22845) at night on 29 June 2016, crawling in leaf litter in secondary forest along the Ilex Trail at the C.R.A.R.C. Guayacán Rainforest Reserve; if not for a short length of its tail exposed from under a leaf, the individual likely would have gone unnoticed. I also found the paratopotype (CRARC 0241) at night on 2 July 2016, as it was crawling on leaf litter in old-growth forest. The paratopotype was encountered on the Palm Trail, about 100 m (straight line distance) from where the holotype was found. A third individual of *O. berlina*, which only was photographed, was observed at night by the author and a group of visitors within the Guayacán Rainforest Reserve on 3 August 2016. The third individual was found ca. 500 m SE of the type locality, crawling on the surface of a thick layer of Pílon (*Hieronyma alchorneiodes*) leaves along the margin of an abandoned pasture

and a large patch of mature secondary forest. Thus, the three individuals of *O. berlini* found within the Guayacán Rainforest Reserve were observed at night crawling within or on top of leaf litter; additionally, all were seen following moderate to heavy rains in the late afternoon. The paratypes (UCR 22843, 22844) also were discovered in leaf litter, but during the day (E. Berlin, pers. comm.). Despite *O. berlini* being known from only a limited number of individuals and observations in the field, this species likely is a leaf litter specialist that lives on the forest floor, where courtship and oviposition probably take place.

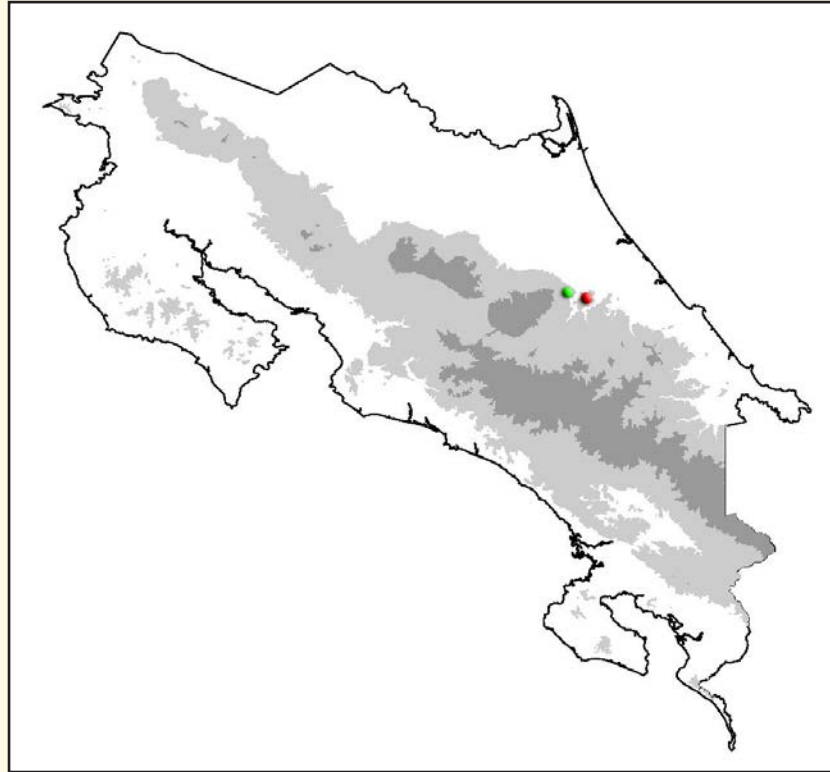


Fig. 14. Map showing the type locality (red circle) and paratype locality (green circle) for *Oedipina berlini*. Pale gray area represents elevations from 500 to 1,500 m, and darker gray area elevations above 1,500 m.

Distribution: *Oedipina berlini* is known only from two sites along the central Caribbean slopes of Costa Rica (Fig. 14), the type locality on the northeastern slopes of the Cordillera de Talamanca, within the Guayacán Rainforest Reserve, about 2 km N of Guayacán de Siquirres at an elevation of 540–560 m, and the paratype locality in the Cordillera Volcanica Central, along the lower northeastern slopes of Volcán Turrialba, ca. 4 km SW of Alegria de Siquirres at an elevation ca. 850 m. Both sites are in the Cantón de Siquirres, in the province of Limón, and within the Area de Conservacion La Amistad Caribe (ACLAC) under the Sistema Nacional de Areas de Conservacion (SINAC). Presently, *O. berlini* only is known to occur in Premontane Rainforest (Holdridge, 1967; Savage, 2002).

Remarks: With the description of *Oedipina berlini*, the number of salamanders known from Costa Rica now is 51, of which 27 are assigned to the genus *Bolitoglossa*, eight to the genus *Nototriton*, and 16 to the genus *Oedipina* (AmphibiaWeb, 2016; Kubicki and Arias, 2016). Five members of the subgenus *Oedopinola* now are known from Costa Rica (Fig. 15), of which three species are endemic to the Caribbean versant of the country (*O. berlini*, *O. carablanca*, and *O. nimaso*). Collectively, the Caribbean members of the subgenus *Oedopinola* are known from fewer than 10 specimens in museum collections: *O. berlini* is known from the four specimens presented here; *O. nimaso* is known only from the holotype, collected in 1984 on Cerro Nimaso at an elevation of 1,093 m (Boza-Oviedo et al., 2012); and *O. carablanca*, which until recently was known only from two male specimens (the holotype and

paratopotype), collected near Guápiles in 1959 at an elevation of ca. 300 m (Brame, 1968). *Oedipina carablanca* was rediscovered at three sites in the central Caribbean foothills: the first was near Guayacán de Siquirres at an elevation of ca. 700 m; the second was near Pocora at an elevation of ca. 225 m; and the third was near Alegria de Siquirres at an elevation of ca. 850 m. Despite the rediscovery of *O. carablanca* at three new sites, only two specimens were collected and deposited in a museum, both at the Museo de Zoología, Universidad de Costa Rica (UCR 17376, 17377); both specimens are from Guayacán de Siquirres at an elevation of ca. 700 m. The rediscovery of *O. carablanca* at the three new sites has occurred within the last 15 years. At the site near Pocora, a few individuals were found inside rotten branches infested with termites, in a section of early-stage secondary forest (E. Berlin, pers. comm.). Brame (1968) noted that both the holotype and paratopotype of *O. carablanca* were found under the bark of a single log, and that various beetle grubs, earwigs, earthworms, centipedes, ants, and termites were sharing the same microhabitat.

At times I have encountered ambiguity with exactly how morphological measurements in species descriptions of bolitoglossine salamanders were taken. Thus, I consider it important to highlight the need for a clearly illustrated, standardized method for taking morphological measurements in this group of salamanders. Because ambiguous measurements can result in confusion with morphometric analyses and intra- and interspecific comparisons, herein I included an illustrated guide with standardized methodology that clearly demonstrates how the morphological measurements presented in this study were collected, and suggest that these defined measurements be considered in future endeavors with bolitoglossine morphometric analyses and descriptions (Plates 1–6). Additionally, I believe that the descriptions of newly proposed species should present detailed depictions of as many phenotypic characteristics as possible. Subtle morphological differences often are present in bolitoglossine salamanders, and thus the descriptions of new species should provide adequate comparisons to assist others working with alpha-level taxonomy or simply those interested in making accurate identifications.

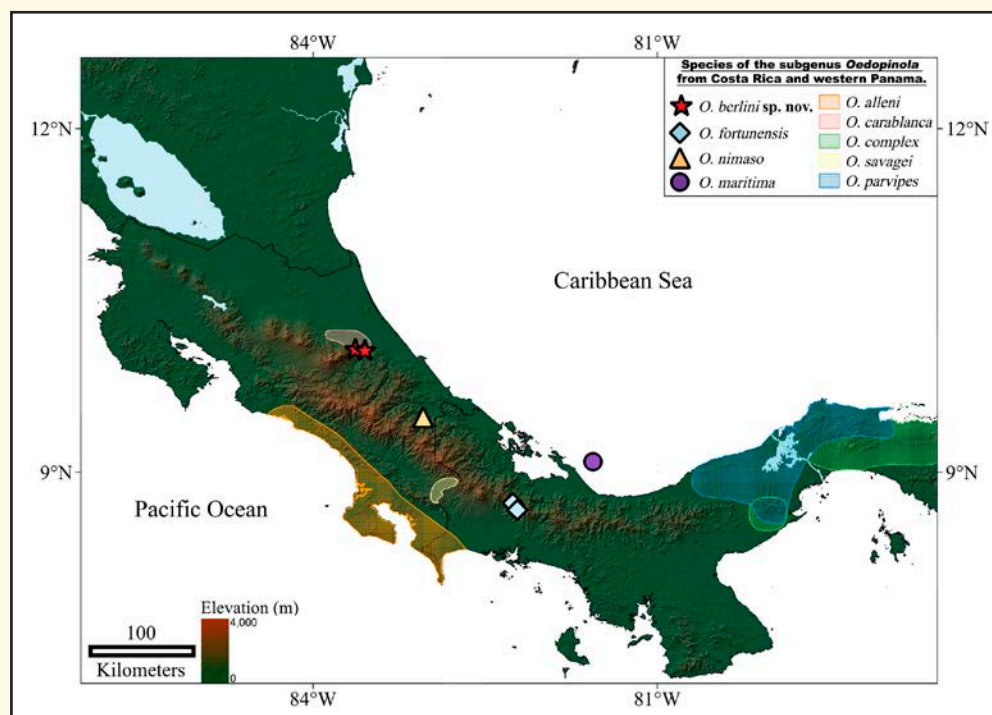


Fig. 15. Map showing the known distributions of members of the subgenus *Oedipinola* in Costa Rica and western Panama. Map courtesy of Erick Arias.

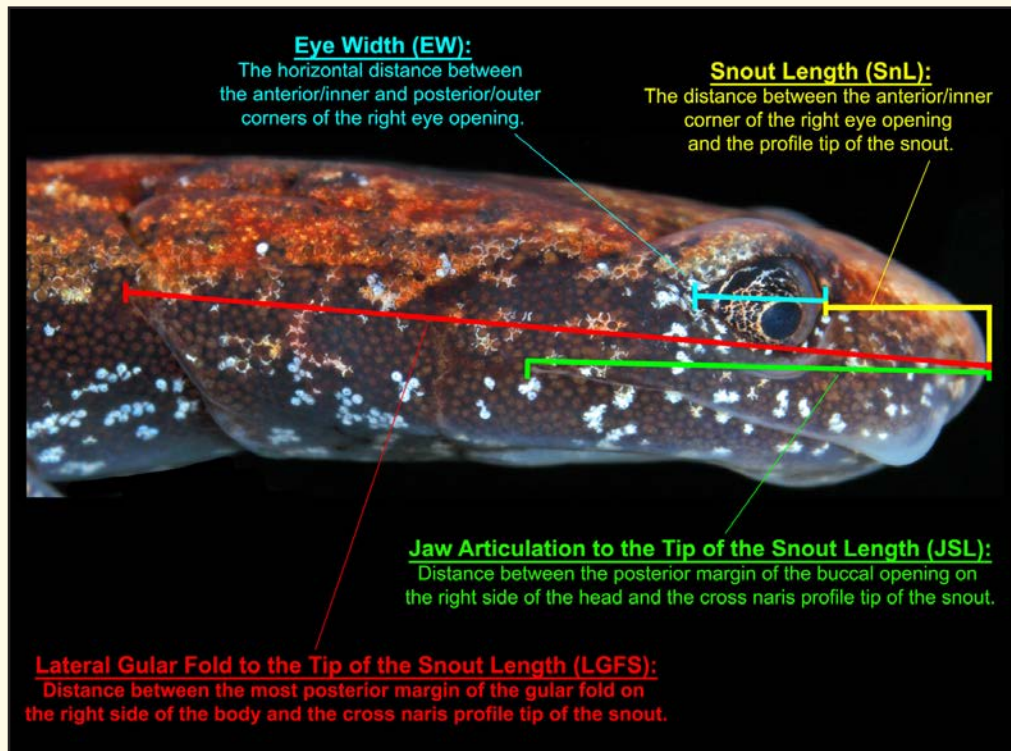


Plate 1. Measurements taken from the right lateral portion of the head.

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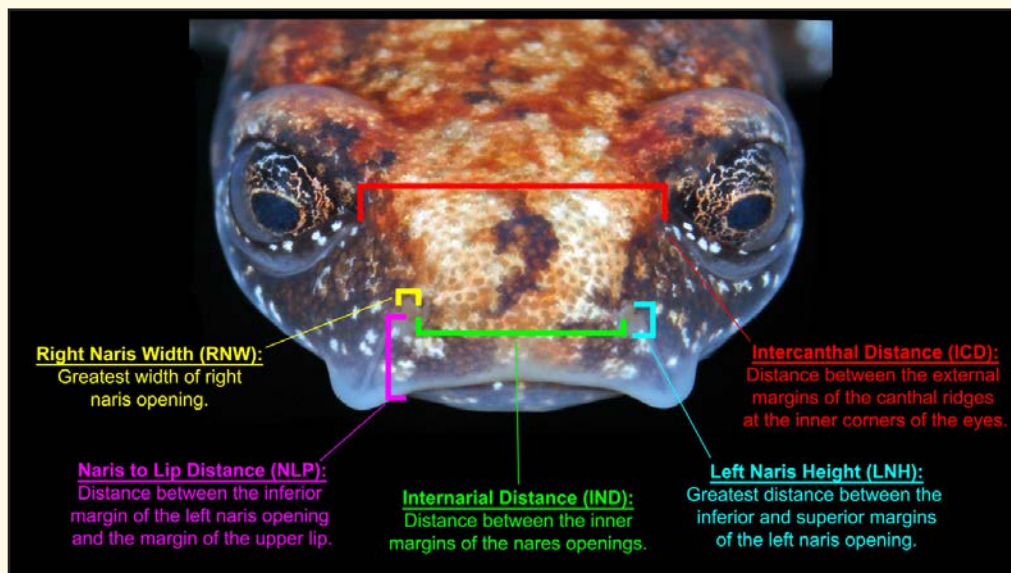


Plate 2. Measurements taken from the snout.

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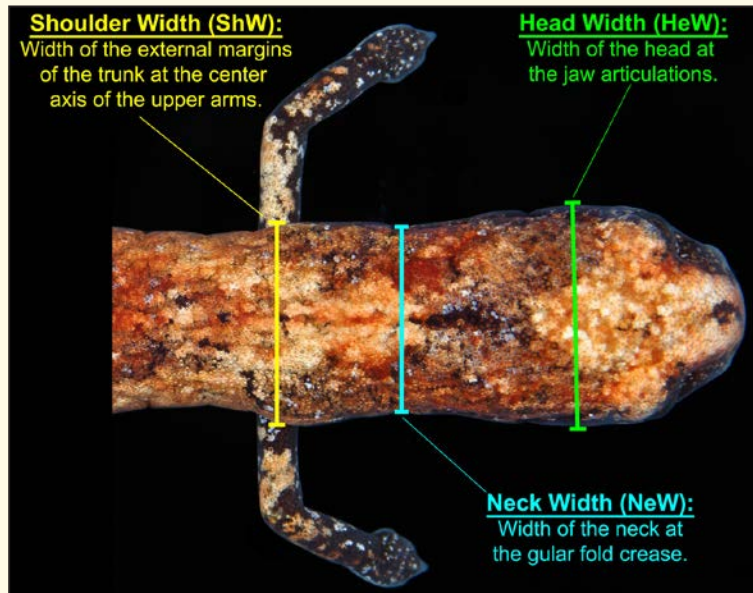


Plate 3. Measurements taken from the antero-dorsal portion of the body.

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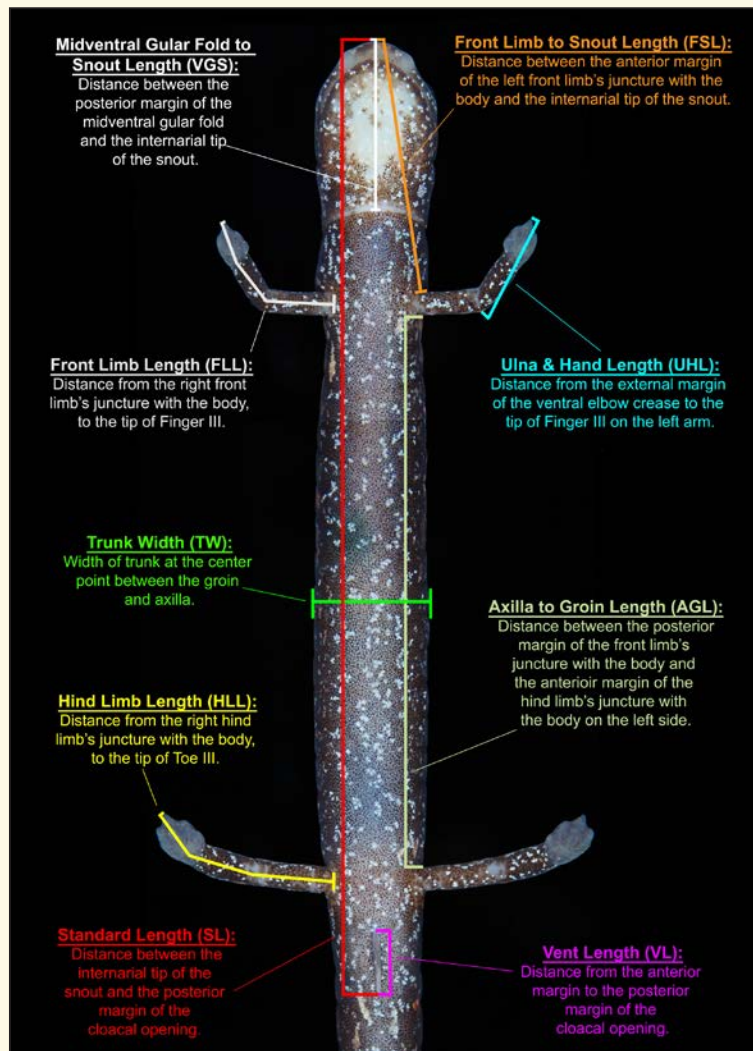


Plate 4. Measurements taken from the ventral portion of the body.

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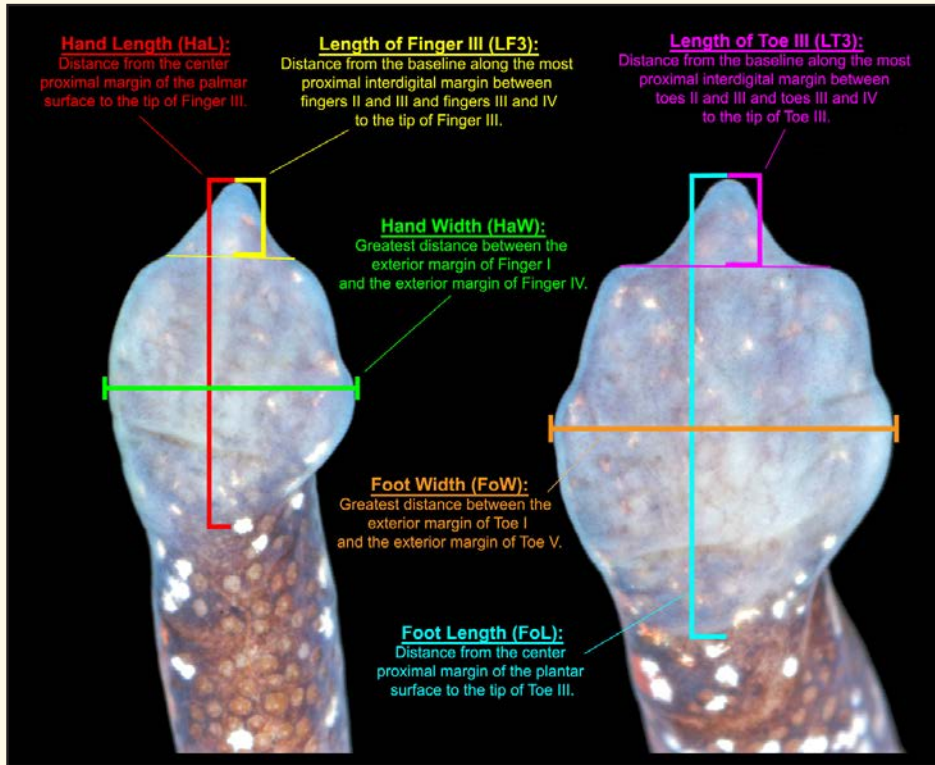


Plate 5. Measurements for species with digits fully encased in webbing; measurements are taken from the ventral side of the right hand and right foot. © Brian Kubicki

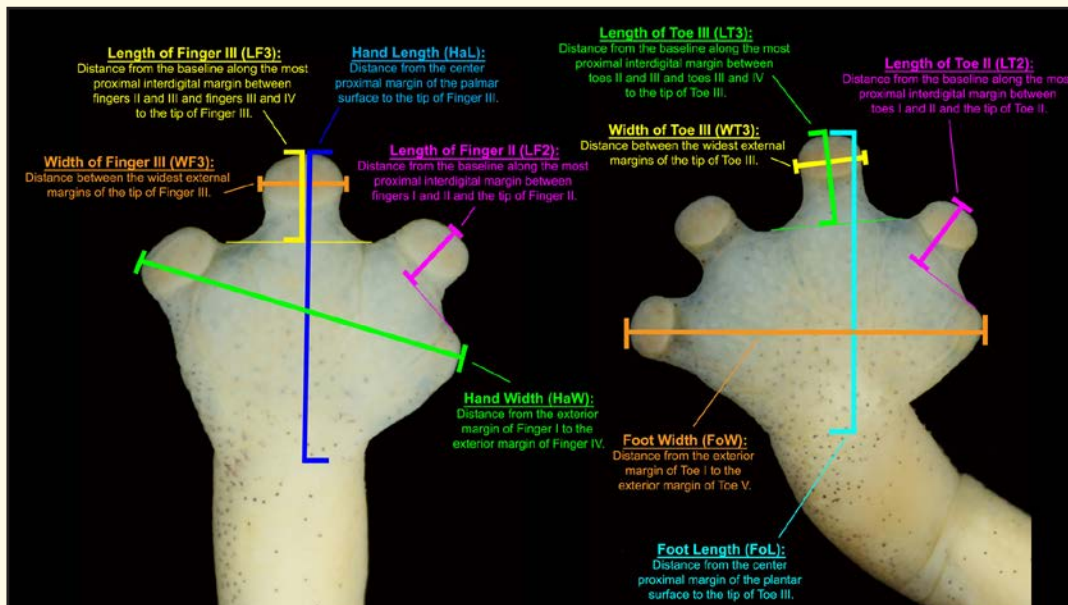


Plate 6. Measurements for species with digits not fully encased in webbing; measurements are taken from the ventral side of the right hand and right foot. © Brian Kubicki

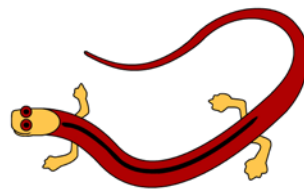
Acknowledgments.—A special thanks to Erick Arias for providing the molecular data, figures 2 and 15, and for his helpful advice with the manuscript and this study. I am especially grateful to Larry David Wilson, Joseph R. Mendelson III, and Louis W. Porras for their numerous comments and suggestions during the review process, which greatly improved the quality of the manuscript. Additionally, I acknowledge the Ministerio de Ambiente y Energía (MINAE) for providing the scientific collecting permits (SINAC-SE-CUS-PI-R-058-2016) and the Comisión Nacional para la Gestión de la Biodiversidad (CONAGEBIO) for the permit to conduct the molecular studies (R-028-2016-OT-CONAGEBIO). Finally, I thank Erick Berlin for donating the paratype specimens found on his property to the Costa Rican Amphibian Research Center, and Federico Bolaños and Gerardo Chaves from the Museo de Zoología, Universidad de Costa Rica, for allowing me to borrow the holotype of *Oedipina nimaso*.

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Appendix 1. DNA sequences and accession codes used in this study.

Species	Voucher	GenBank 16S	GenBank <i>cyt b</i>
<i>Oedipina berlini</i> sp. nov.	UCR: 22845	KX792143	KX792144
<i>Oedipina alleni</i>	MVZ: 190856	—	AF199150
<i>Oedipina alleni</i>	MVZ: 190857	AF199207	AF199149
<i>Oedipina carablanca</i>	—	FJ196862	FJ196869
<i>Oedipina complex</i>	MVZ: 236255	AF199213	AF199157
<i>Oedipina complex</i>	DBW: 5787	AF199212	AF199156
<i>Oedipina elongata</i>	JHT: 1821	—	JN190938
<i>Oedipina elongata</i>	UTA-A: 56809	JN190932	—
<i>Oedipina elongata</i>	UTA-A: 51906	AF199216	AF199160
<i>Oedipina gephyra</i>	LDW: 10502	AF199218	AF199162
<i>Oedipina gephyra</i>	UF-JHT: 2451	JN190931	JN190937
<i>Oedipina gephyra</i>	UF-JHT: 2443	JN190930	JN190936
<i>Oedipina maritima</i>	MVZ: 219997	AF199221	AF199166
<i>Oedipina parvipes</i>	MVZ: 210404	AF199210	AF199154
<i>Oedipina parvipes</i>	MVZ: 210405	AF199211	AF199155
<i>Oedipina parvipes</i>	AJC: 1786	FJ784316	—
<i>Oedipina petiola</i>	USNM: 343462	AF199217	AF199161
<i>Oedipina savagei</i>	MVZ: 229360	—	AF199153
<i>Oedipina savagei</i>	LDG: 961327	AF199209	AF199152
<i>Oedipina tomasi</i>	UF-JHT: 1553	JN190929	JN190935
<i>Oedipina tomasi</i>	MVZ: 258037	HM068305	KP900079
<i>Nototriton abscondens</i>	UCR: 12071	DQ640041	AF199130



Brian Kubicki is a self-taught scientific naturalist who has been living in Costa Rica since 1998. He moved to Costa Rica specifically to dedicate his life to studying the country's amphibians, and during the last 18 years has conducted thousands of hours of fieldwork throughout the country. Brian's principal interests are in the areas of alpha-level taxonomy, natural history, biogeography, and the conservation of Costa Rican amphibians. In 2002 he started the Costa Rican Amphibian Research Center (C.R.A.R.C.; www.cramphibian.com), which was a first of its kind project dedicated specifically to the study and conservation of the country's amphibians.