Zootaxa 5194 (4): 451–496
https://www.mapress.com/zt/

Article

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

https://doi.org/10.11646/zootaxa.5194.4.1
http://zoobank.org/urn:lsid:zoobank.org:pub:EB6859A0-935C-44BF-9B2C-7FDF6FE76793

Revised taxonomy and distributions of Costa Rican moss salamanders (Caudata: Plethodontidae: *Nototriton*), with descriptions of new taxa

BRIAN KUBICKI[1*], AURA REYES[1,4] & ERICK ARIAS[2,3]
[1] *Costa Rican Amphibian Research Center, Guayacán, Provincia de Limón, Costa Rica.*
[2] *Departamento de Zoología, Instituto de Biología, UNAM, AP 70-153 Ciudad Universitaria, CP 04510, México, D.F., México.*
eapiedra@gmail.com; https://orcid.org/0000-0002-4449-1070
[3] *Escuela de Biología, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica.*
[4] *auralr22@gmail.com; https://orcid.org/0000-0002-5845-0528*
[*] *Corresponding author. crarc@yahoo.com; https://orcid.org/0000-0002-7674-7202*

Abstract

The tiny moss salamanders of the genus *Nototriton* within Costa Rica have long been poorly known and understood. Due to their diminutive size and specialized ecology, this taxon is very rarely studied or even represented in collections, thus resulting in much confusion surrounding the actual taxonomic and distributional status of the species within the country. As a result of hundreds of hours of fieldwork, lab work, and morphological analysis and measurement, herein we provide an updated taxonomic revision of the Costa Rican members of the genus *Nototriton*, with the proposal of a new subgenus and four new species.

Key words: Amphibia, caudate, Central America, morphology, taxonomic revision

Resumen

Las diminutas salamandras de musgo del género *Nototriton* en Costa Rica han sido poco estudiadas. Debido a su pequeño tamaño y ecología muy especializada este taxón ha sido poco investigado, inclusive poco representado en colecciones, lo que ha resultado en mucha confusión sobre el estado actual de la taxonomía y la distribución de las especies dentro del país. Como resultado de cientos de horas de trabajo en el campo, trabajo de laboratorio, análisis y medidas morfológicas, aquí entregamos una revisión taxonómica actualizada de los miembros del género *Nototriton* de Costa Rica, con la propuesta de un subgénero nuevo y cuatro nuevas especies.

Palabras clave: América Central, Amphibia, caudado, morfología, revisión taxonómica

Introduction

One of the most enigmatic groups of amphibians inhabiting the forests of Central America are the miniaturized caudates commonly known as moss salamanders. Moss salamanders belong to the genus *Nototriton*, which is endemic to Central America. Members of the genus *Nototriton* have been documented to inhabit extreme eastern Guatemala, the northern half of Honduras, a couple of highland sites in north-central Nicaragua, and nearly the entire length of the Caribbean slopes of Costa Rica (Fig. 1a) (Arias & Kubicki 2018; AmphibiaWeb 2022; Frost 2022). Of the 20 species of moss salamanders currently known to exist, nine have been described only since the year 2000 (Frost 2022). Given this situation, it goes without saying that there is simply so much that remains to be learned regarding moss salamanders.

Of the 20 known species of *Nototriton*, nine are currently recognized to be endemic to the Caribbean slopes of Costa Rica (Frost 2022). Due to their small size, secretive existence, and cryptic morphology, Costa Rican moss salamanders have been referred to as being one of the most poorly understood elements of the herpetofauna in the

Accepted by M. Vences: 20 Sept. 2022; published: 7 Oct. 2022

country (Savage 2002). Relatively few Costa Rican individuals have been collected and represented as voucher specimens in museums throughout the planet and, furthermore, there are very few genetic sequences available (Fig. 1b). Arias & Kubicki (2018) reported that only seven of the nine Costa Rican species of moss salamanders have been sequenced and in total there are sequences avalaible for only 15 specimens among these taxa. The phylogenetic relationships within the genus *Nototriton*, and more specifically the Costa Rican members, are poorly known and the taxonomic status of two species in particular, *N. major* and *N. matama* is uncertain (Arias & Kubicki 2018). Herein we attempt to clarify the taxonomy of Costa Rican *Nototriton* and add to the current knowledge of this poorly known, yet spectactular genus of secretive and tiny salamanders.

Material and methods

Taxon sampling. All of the specimens collected for this study were humanly euthanized through the use of a topical anesthetic. Following the euthanization process, populational representative individuals had a small sample of tissue, consisting of the tip of the tail, taken and stored in 96% ethanol. The specimens were fixed in a 10% formalin solution. After fixation had occurred, the specimens were washed later and eventually transferred into 70% ethanol for long-term preservation. All of the phenotypic characteristics reported herein are from subadult to adult specimens (*n* = 59) that were collected by Brian Kubicki (BK) especially for this study. Of the 59 individuals of Costa Rican *Nototriton* that were preserved for this study, 42 were used for the genetic analysis. As a result of this study, the number of Costa Rican *Nototriton* individuals with known sequences increased from 15 to 57, a 380% increase (Table 1). The majority of the preserved specimens used for this study are stored within the taxonomic reference collection of the Costa Rican Amphibian Research Center (C.R.A.R.C.), or if designated as type material, at the Museo de Zoología, Universidad de Costa Rica (UCR), San José, Costa Rica. To avoid any potential risk to the populations of moss salamanders discovered as a result of this study, we have decided not to publish any corresponding GPS coordinates herein. The following are abbreviations for the collections or museums mentioned in the text: (FMNH) Field Museum, Division of Amphibians and Reptiles, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, USA; (SMF) Forschungsinstitut und Natur-Museum Senckenberg, Senckenberg-Anlage, Frankfurt-am-Main, Germany; (UCR) Universidad de Costa Rica, Museo de Zoologia, San Pedro, San José, Costa Rica (UCR); (USNM) National Museum of Natural History, Division of Amphibians and Reptiles, Washington, D.C. 20560, USA (Frost, 2022), and (MVZ) Museum of Veterbrate Zoology, University of California Berkeley, California, USA; Costa Rican Amphibian Research Center, Guayacán, Limón, Costa Rica (CRARC).

Fieldwork. During a period of five years, from July 2012 to July 2017, BK conducted hundreds of hours of intensive fieldwork at numerous cloud forest sites throughout the Caribbean slopes of Costa Rica searching for moss salamanders. Many of the sites that were explored by BK represent localities that had not been known to be sampled previously for any amphibian taxa (Fig. 1b). BK was often accompanied in the field by his wife Aura Reyes (AR). During the fieldwork, BK managed to observe more than 200 individuals of Costa Rican moss salamanders in their natural environment and collect 59 specimens that were used to produce the genetic (Fig. 1b) and phenotypic data presented in this study, including additional topotypic specimens of *Nototriton major* and *N. tapanti*, each of which were known previously only from a single specimen, respectively, their holotypes.

Amplification and sequencing. We extracted total genomic DNA from the ethanol preserved tissues (tail tip muscle) of 41 *Nototriton* specimens using the phenol-chloroform standard protocol (Sambrook & Russell 2006). We amplified the large subunit ribosomal RNA (16S), cytochrome *b* (cyt *b*), and cytochrome oxidase subunit I (COI) mitochondrial genes. The primers 16Sar y 16Sbr (Palumbi *et al.* 1991) were used for 16S, primers MVZ15 and MVZ16 (Moritz *et al.* 1992) for cyt *b*, and primers dgLCO y dgHCO (Meyer 2003) for COI. PCR amplifications were performed using a total volume of 15 µL, which contained 1 µL DNA template (*c.* 50 ng μL^{-1}), 0.75 U Taq polymerase (Amplificasa®, Biotecnologias Moleculares), 1X PCR buffer with 1.5 mM $MgCl_2$, 0.2 mM deoxynucleotide triphosphates (dNTPs), and 0.3 µM forward and reverse primers. The PCR conditions were as follow: 16S, an initial cycle of 5 min at 94ºC, followed by 35 cycles of 45 s at 94ºC, 30 s at 55ºC, 45 s at 72ºC, plus a final cycle of 3 min at 72ºC; cyt *b*, an initial cycle of 2 min at 94ºC, followed by 38 cycles of 30 s at 94ºC, 1 min at 48ºC, 1 min at 72ºC, plus a final cycle of 8 min at 72ºC; COI, an initial cycle of 2 min at 94ºC, followed by 35 cycles of 30 s at 94ºC, 30 s at 50ºC, 45 s at 72ºC, plus a final cycle of 5 min at 72ºC. 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). The cycle-sequencing products were column-purified with Sephadex G-50 (GE Healthcare) and run on an ABI 3500xL Genetic Analyzer (Applied Biosystems). Consensus sequences for each individual were constructed using SEQUENCHER 5.3 (Genes Codes Corp.). The resulting sequences were deposited in GenBank (Table 1).

TABLE 1. Institutional voucher numbers, and GenBank accession numbers for the specimens used in the molecular phylogenetic analyses.

Species	Voucher	GenBank 16S	GenBank cyt *b*	GenBank COI
***Nototriton* (*Bryotriton*)**				
N. barbouri	UF: 156538	GU971733	GU971734	JN377401
N. brodie	MVZ: 258035	KP886882	KP735285	KP886938
N. brodie	UTA-A51490	AF199202	AF199139	JN377402
N. lignicola	UF: 156543	GU971735	GU971736	JN377408
N. lignicola	USNM: 497540	AF199204	AF199141	-
N. lignicola	USNM: 497550	-	AF199142	-
N. limnospectator	IRL: 035	JN377385	JN377395	JN377400
N. limnospectator	MVZ: 225866	-	AF199143	-
N. limnospectator	MVZ: 263852	KP735257	JQ899197	KP886937
N. limnospectator	UF: 156539	GU971737	GU971738	JN377397
N. limnospectator	UF: 156540	GU971739	GU971740	JN377398
N. limnospectator	UF: 156541	JN377386	JN377396	JN377399
N. mime	MVZ: 269306	KC905089	KC905092	KX819201
N. mime	USNM: 579870	KC905090	KC905094	KX819200
N. mime	USNM: 579871	KC905091	KC905095	KX819202
N. mime	USNM: 579872	KC905088	KC905093	KX819199
N. nelsoni	USNM: 509333	-	AF199138	-
N. nelsoni	USNM: 578300	JN377387	JN377391	JN377403
N. oreadorum	USNM: 339712	AF199201	AF199136	-
N. oreadorum	USNM: 497552	-	AF199137	-
N. picucha	USNM: 578298	JN377388	JN377392	JN377404
N. picucha	USNM: 578299	JN377389	JN377393	JN377405
N. stuarti	USAC: 3357	JQ899167	JQ899196	-
N. tomamorum	UF: 155377	GU971731	GU971732	JN377407
***Nototriton* (*Nototriton*)**				
N. abscondens	CRARC: 0057	OP325513	OP352095	-
N. abscondens	CRARC: 0082	OP325514	OP352096	OP312092
N. abscondens	CRARC: 0085	OP325515	-	-
N. abscondens	CRARC: 0087	OP325516	OP352097	-
N. abscondens	CRARC: 0198	OP325517	OP352098	OP312093
N. abscondens	CRARC: 0277	OP325518	-	-
N. abscondens	CRARC: 0278	OP325519	-	OP312094
N. abscondens	MVZ: 181351	-	AF199132	-
N. abscondens	MVZ: 194867	-	AF199134	-
N. abscondens	MVZ: 198884	-	AF199133	-
N. abscondens	MVZ: 203743	-	AF199131	-
N. abscondens	UCR: 12071	AF199199	AF199130	-

......continued on the next page

TABLE 1. (Continued)

Species	Voucher	GenBank 16S	GenBank cyt *b*	GenBank COI
N. costaricense	UCR: 22900	MG457736	MG457740	MG457738
N. gamezi	CRARC: 0251	OP325520	-	OP312095
N. gamezi	CRARC: 0252	OP325521	-	OP312096
N. gamezi	MVZ: 207122	AF199200	AF199135	-
N. guanacaste	CRARC: 0202	OP325522	OP352099	OP312097
N. guanacaste	MVZ: 207106	AF199203	AF199140	-
N. kenorum **sp. nov.**	UCR: 23686	OP325523	OP352100	OP312098
N. kenorum **sp. nov.**	UCR: 23687	OP325524	-	OP312099
N. kenorum **sp. nov.**	UCR: 23688	OP325525	-	OP312100
N. lateomuscus **sp. nov.**	UCR: 23694	OP325526	-	OP312101
N. lateomuscus **sp. nov.**	UCR: 23695	OP325527	OP352101	OP312102
N. lateomuscus **sp. nov.**	UCR: 23696	OP325528	OP352101	OP312103
N. maximo **sp. nov.**	CRARC: 0090	OP325529	OP352103	OP312104
N. maximo **sp. nov.**	UCR: 23689	OP325530	OP352104	OP312105
N. maximo **sp. nov.**	UCR: 23691	OP325531	OP352105	OP312106
N. maximo **sp. nov.**	UCR: 23692	OP325532	-	OP312107
N. maximo **sp. nov.**	UCR: 23693	OP325533	OP352106	OP312108
N. picadoi	CRARC: 0061	OP325534	OP352107	-
N. picadoi	CRARC: 0065	OP325535	OP352108	OP312109
N. picadoi	CRARC: 0088	OP325536	OP352109	OP312110
N. picadoi	CRARC: 0096	OP325537	OP352110	-
N. picadoi	CRARC: 0105	OP325538	OP352111	-
N. picadoi	CRARC: 0108	OP325539	OP352112	-
N. picadoi	CRARC: 0205	OP325540	OP352113	OP312111
N. picadoi	CRARC: 0214	OP325541	OP352114	OP312112
N. picadoi	CRARC: 0221	OP325542	OP352115	OP312113
N. picadoi	CRARC: 0222	OP325543	OP352116	-
N. picadoi	CRARC: 0264	OP325544	-	OP312114
N. picadoi	MVZ: 203745	-	AF199145	-
N. picadoi	MVZ: 225899	AF199205	AF199144	-
N. picadoi	UCR: 20215	JQ899166	JQ899195	-
N. saslaya	MVZ: 230241	GU981761	-	-
N. saslaya	N: 650	JN377390	JN377394	JN377406
***Nototriton* (*Taylorotriton*)**				
N. richardi	CRARC: 0053	OP325545	-	OP312115
N. richardi	CRARC: 0069	OP325546	OP352117	OP312116
N. richardi	CRARC: 0083	OP325547	-	-
N. richardi	MVZ: 194885	-	AF199147	-
N. richardi	MVZ: 194887	-	AF199148	-
N. richardi	UCR: 12057	AF199206	AF199146	-
N. tapanti	CRARC: 0051	OP325548	-	OP312117
N. tapanti	CRARC: 0070	OP325550	OP352118	OP312119
N. tapanti	CRARC: 0242	OP325549	-	OP312118

......*continued on the next page*

TABLE 1. (Continued)

Species	Voucher	GenBank 16S	GenBank cyt *b*	GenBank COI
N. vereh **sp. nov.**	UCR: 23681	OP325551	-	OP312120
N. vereh **sp. nov.**	UCR: 23682	OP325552	OP352119	OP312121
N. vereh **sp. nov.**	UCR: 23683	OP325553	OP352120	OP312122

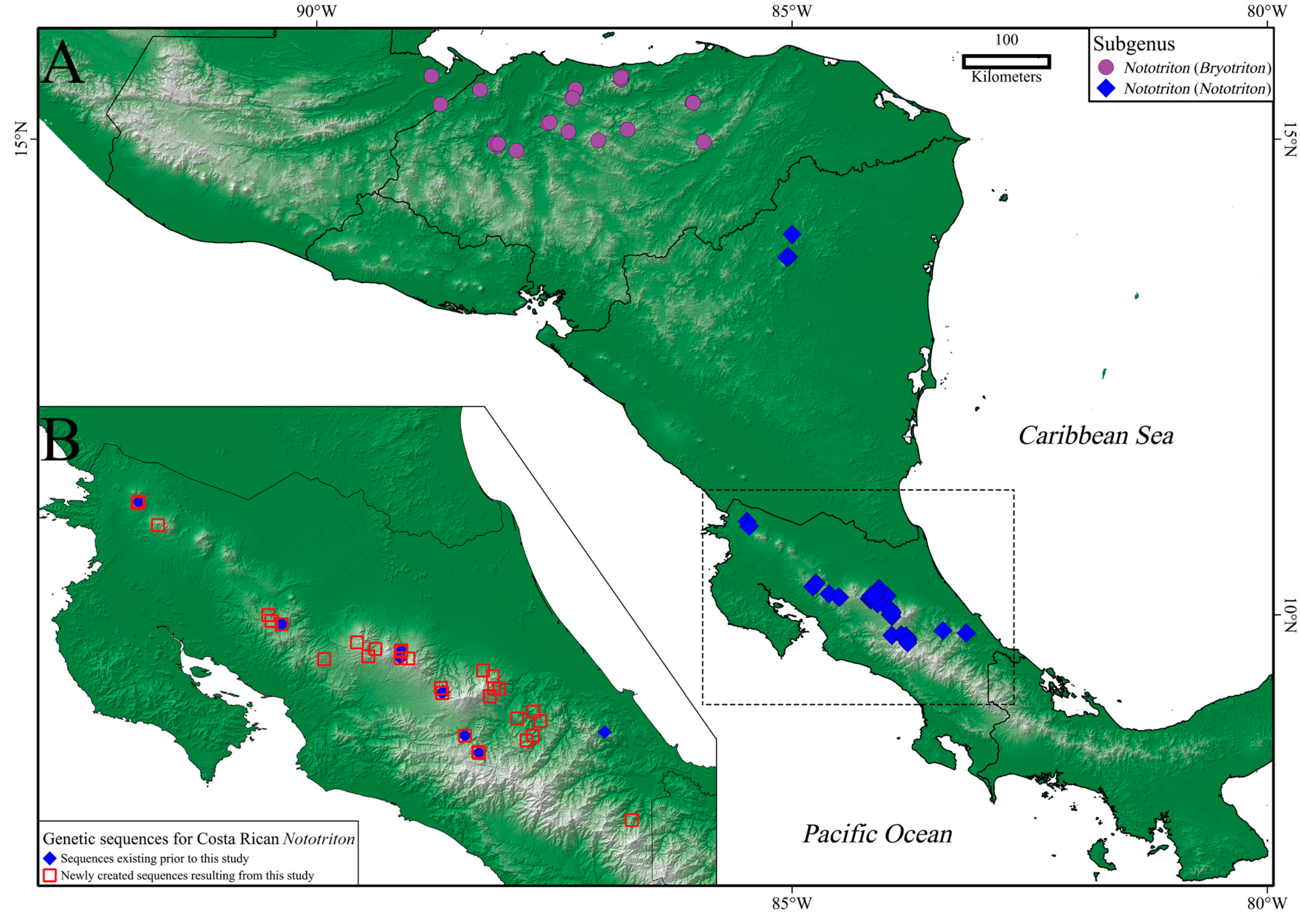


FIGURE 1. A) Map showing the historical distribution of the genus *Nototriton* in Central America, the colors indicate the two know subgenera. **B**) The insert map shows the localities for the genetic sequences from Costa Rica. The solid diamonds indicate the historical sequences, the open squares indicate the newly created sequences resulting from this study.

Phylogenetic analyses. We compared the sequences here obtained with sequences of the large subunit ribosomal RNA (16S), cytochrome *b* (cyt *b*), and cytochrome oxidase subunit I (COI) mitochondrial genes, for 40 specimens of the genus *Nototriton* that were available in GenBank. We used seqeces of *Oedipina nica* as an outgroup and *Bolitoglossa alberchi* to root all trees based on the results of Rovito *et al.* (2015). The list of vouchers and GenBank accession numbers used in this study sare provided in Table 1. Sequence alignments were performed using the MUSCLE 3.7 software (Edgar 2004) with default parameters and trimmed to the point where a majority of the taxa had sequence data. We used PartitionFinder v1.1.1 software (Lanfear *et al.* 2012) and the Bayesian Information Criterion (BIC) to select the best partition scheme and the best model of sequence evolution for each partition. We used a single set of branchlengths across all partitions (*branchlengths=linked*), the search of the best partition scheme was using a heuristic search (*scheme=greedy*). We defined, *a priori,* seven subsets: one for 16S, three for COI, and three for cyt *b* (COI and cyt *b* were partitioned by codon position).

Phylogenetic analyses were performed using both maximun likelihood (ML) and Bayesian inference (BI) methods. We performed the maximum likelihood analysis using Garli 2.01 (Zwickl 2006). To find the best tree, 10 search replicates were ran with the following default setting values: *streefname=random, attachmentspertaxon=24, genthreshfortopoterm=100000, significanttopochange=0.00001*. For bootstrapping, we ran 1000 pseudoreplicates with the previous settings and with the following changes: *genthreshfortopoterm=10000, significanttopochange=0.01,* *treerejectionthreshold=20,* as suggested in the Garli manual to speed up bootstrapping. From these bootstraps, we obtained a majority rule consensus tree using Sumtrees (Sukumaran & Holder 2010a) from DendroPy packages version 4.4.0 (Sukumaran & Holder 2010b). Bayesian phylogenetic analysis was performed using MrBayes 3.2.6 (Ronquist *et al.* 2012) with the partition scheme and the model of sequence evolution for each partition as selected previously. Two separate analyses were run, each consisted of 20 million generations, sampled every 1000 generations, and four chains with default heating parameters. We examined a time-series plot of the likelihood scores of the cold chain to check stationarity using Tracer 1.6 software (Rambaut *et al*. 2014). We discarded the first 25% of trees as burn-in and used the remaining trees to estimate the allcompat consensus tree along with the posterior probabilities for each node and each parameter.

Finally, we also used BEAST v1.8.3 (Drummond *et al*. 2012) to estimate a concatenated ultrametric phylogenetic tree using an uncorrelated lognormal relaxed clock, a Birth-Death process tree prior, and with the partition scheme and the model of sequence evolution for each partition as selected previously. We ran the BEAST analysis for 50 million generations, sampled every 1000 generations, and discarded the first 5000 samples as burn-in when estimating a consensus tree. No fossils of tropical plethodontid salamanders are available for the time calibration of our phylogeny. We used a secondary calibration of 9 Mya for the crown age of *Nototriton* (Rovito *et al.* 2015) using a normal prior distribution with a mean of 9 Mya and SD of 2 in order to place 95% of the prior distribution on 5.7–12.3 Mya. In addition, we calibrated the divergence between *Nototriton* and *Oedipina* in 30 Mya using a normal prior distribution with a mean of 30 Mya and SD of 2 in order to place 95% of the prior distribution on 26.7–33.3 Mya. The Garli, MrBayes, and BEAST analysis were run on the CIPRES portal (Miller *et al.* 2010). Genetic distances (uncorrected *p*-distances, Table 2) were computed using MEGA6 (Tamura *et al.* 2013).

Morphometrics. Measurements used herein follow those proposed by Kubicki & Arias (2016), Kubicki (2016), and Arias & Kubicki (2018). At total of 31 different morphological measurements were made on each of the 59 specimens of Costa Rican *Nototriton* that were examined in this study, resulting in the realization of more than 1800 independent measurements being taken (Table 3). The measurements were made with a dissecting microscope fitted with an ocular micrometer, or with measurements exceeding 8 mm a ROHS NORM 2002/95/EC digital caliper, and rounded to the nearest 0.1 mm, with the exception of LNH, RNW, WF3, LF2, LF3, WT3, LT2, and LT3, which are rounded to the nearest 0.01 mm due to their very fine scale sizes and were measured with a dissecting microscope at 30x power fitted with an ocular micrometer. Morphological measurements taken and the abbreviations used herein are as follows: standard length (SL) = internarial tip of snout to posterior margin of cloacal opening; 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 interdigital margin between fingers II and III and fingers III and IV to tip of Finger III on right hand; width of Finger III (WF3) = distance between the widest external margins of the terminal pad on Finger III on right hand; length of Finger II (LF2) = distance from the baseline along the most proximal interdigital margin between fingers

I and II and the tip of Finger II 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; width of Toe III (WT3) = distance between the widest external margins of the terminal pad on Toe III on right foot; length of Toe II (LT2) = distance from the baseline along the most proximal interdigital margin between toes I and II and the tip of Toe II 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) (appendices I, II, III, IV, V, VI). Due to the fact that there is very significant overlap in the quantity of teeth found in the different *Nototriton* species known to exist within Costa Rica (Taylor 1948, 1949; Good & Wake 1993; García-París & Wake 2000; Boza-Oviedo *et al*. 2012; Arias and Kubicki 2018), we decided not to attempt to count the number of teeth in the specimens examined in this study. We feel that attempting to accurately count the number of teeth in such small specimens (SL range of the 59 specimens examined in this study, 18.3–34.4 mm), most of which were fixed with their mouths in a closed position, requires a high-level of invasive manipulation that would most likely result in causing significant and unnecessary damage to the mouth cavity. The limb interval is equal to the number of costal folds between the tips of the longest digits of the adpressed front and hind limbs, expressed in 0.5 increments (e.g., 4, 4.5).

Morphometric statistics. To avoid allometric effects relative to the differences in the size and shape between species and between individuals we transformed the data using the method of Lleonart *et al.* (2000). In this method a logarithmic transformation to the continuous variables is performed to reduce the extreme values. All transformed variables are used in the allometric transformation by means of equation $Y_i^* = Y_i \left[\frac{X_0}{X_i}\right]^b$, Y* corresponds to the value of each of the dependent variable corrected for size and shape, Y_i corresponds to the value of each of the dependent morphometric variable, X_0 is the average of the SL variable for all populations, X_i is the SL value for each individual and *b* is the regression line intercept with the Y-axis resulting from the regression of each dependent variable with X_0. The intercept is used as an allometric transformation factor and is unique for each variable. The morphometric transformation was performed separately for each species group, *N. picadoi* and *N. richardi,* because that the average of the SL general (X_0) is strongly affected, due that the specimens of the species group *N. richardi* are significant smaller that those in the species group *N. picadoi.* The additional proportions reported here include: IND/HeW, HeW/AGL, SnL/HeW, RNW/HeW, LNH/HeW, HaL/VGS, FoL/VGS, HaW/HeW, FoW/HeW, LT2/FoL, LF2/HaL, WT3/FoW, WF3/HaW, HaL/HaW, and FoL/FoW.

We calculated the mean, standard deviation, and range for each morphometric variable without correction. We performed a discriminant analysis by subgenus to determining whether the morphometric variables were effective to predict the species. The following variables were used in the discriminant analysis for *N. picadoi*: ShW, HeW, EW, LNH, IND, RNW, VGS, HaW, HaL, WF3, LF3, FoW, LT3, IND/HeW, RNW/HeW, LNH/HeW, HaW/HeW, FoW/HeW, WF3/HaW, and FoL/FoW. The following variables were used in the discriminant analysis for *N. richardi*: LNH, TW, UHL, WF3, WT3, FoL, LNH/HeW, RNW/HeW, FoL/VGS, HaW/HeW, HaL/HaW, and FoL/FoW. All the analyses were performed using R v3.3.3 (R Development Core Team 2013).

Results

Molecular phylogenetic. The mitochondrial dataset include samples of all described species for the genus *Nototriton*. The resulting data matrix had a total sequence length of 1923 bp, including gaps; 518 bp for 16S, 658 bp for COI, and 747 for cyt *b*. Four partitions were identified with the following substitution models: HKY+I+G for 16S + cyt *b* codon position 2, GTR+G for codon position 1 of COI and cyt b, HKY+I for codon position 3 of COI and cyt *b*, and SYM+G for COI codon position 2. The phylogenies from Garli, MrBayes, and BEAST were similar in topology to one another (Figures 2 & 3). The phylogentic analyses found *Nototriton* to be composed of three major clades, the *Nototriton barbouri* species group (subgenus *Bryotriton*), the *Nototriton picadoi* species group, and the *Nototriton richardi* species group (both of the latter currently recognized as comprising a single subgenus, *Nototriton*). The first major clade, (*Bryotriton* subgenus) contains 10 species, all of which are distribuited in Nuclear Central America. The main change between phylogenetic analyses within of the *Bryotriton* clade was the position of *N. lignicola* that was the sister taxon to the clade that contains *N. nelsoni, N. oreadorum, N. stuarti,* and *N. brodiei* in the MrBayes tree. The second major clade that branches off the tree (*N. richardi* clade) was composed of an undescribed species as a sister taxon to *N. richardi* and *N. tapanti,* and is distribuited in the Central Volcanic and Talamanca mountain ranges of Costa Rica. No major inconsistencies were found within the *N. richardi* clade among the phylogenetic analyses.

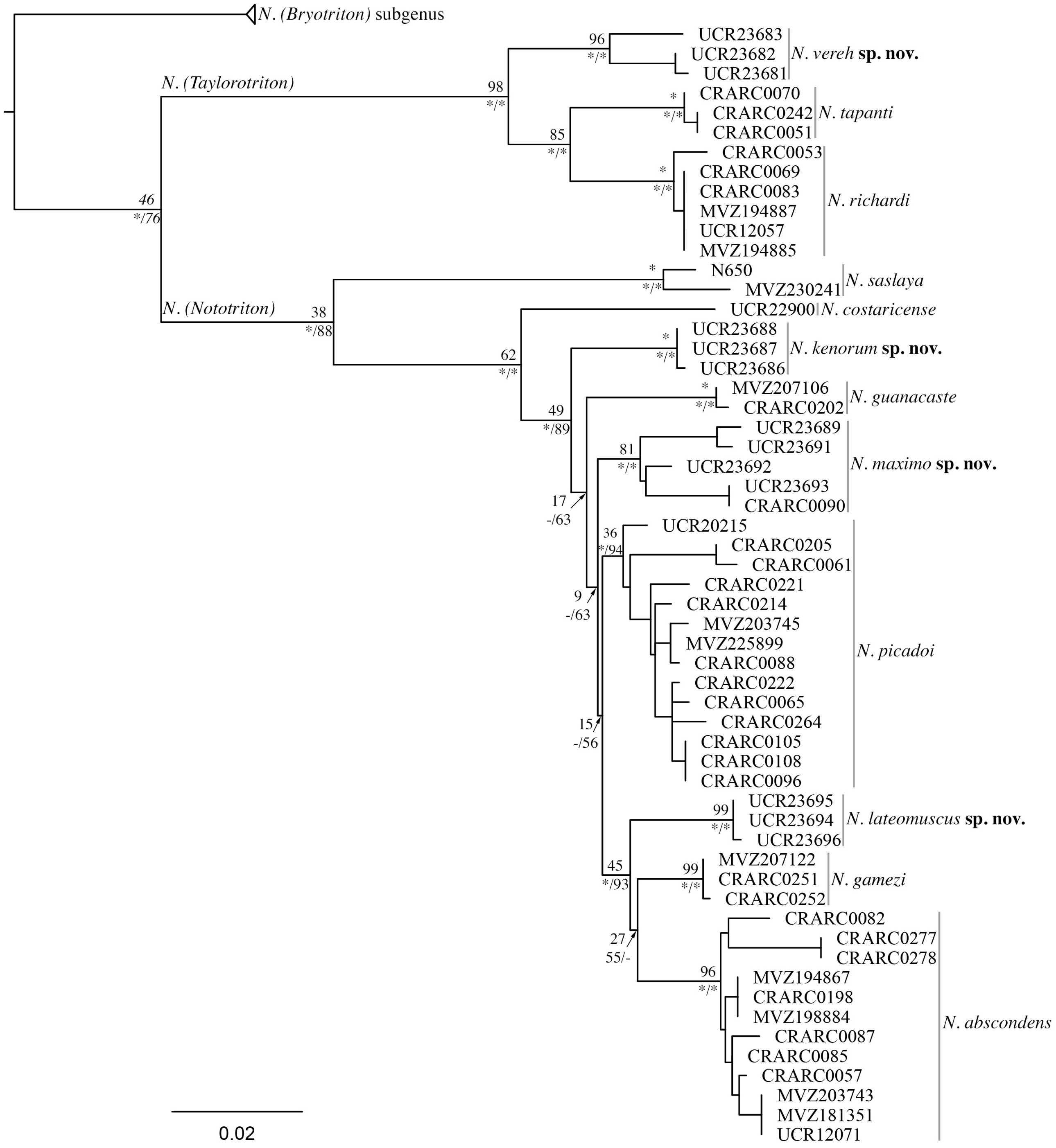


FIGURE 2. Maximum likelihood phylogeny (log likelihood = -10741.341147) showing the relationships of the subgenera *Nototriton* and *Taylorotriton* based on the 16S, cyt *b,* and COI mitochondrial DNA genes fragment. Bootstraps proportions are shown above branches, below the branches are shown posterior probabilities (multiplied by 100) from BEAST analysis (left) and posterior probabilities (multiplied by 100) from MrBayes analysis (right). The scale bar refers to the estimated substitutions per site. The support values of any node within species are not shown. The asterisks represent support of 100.

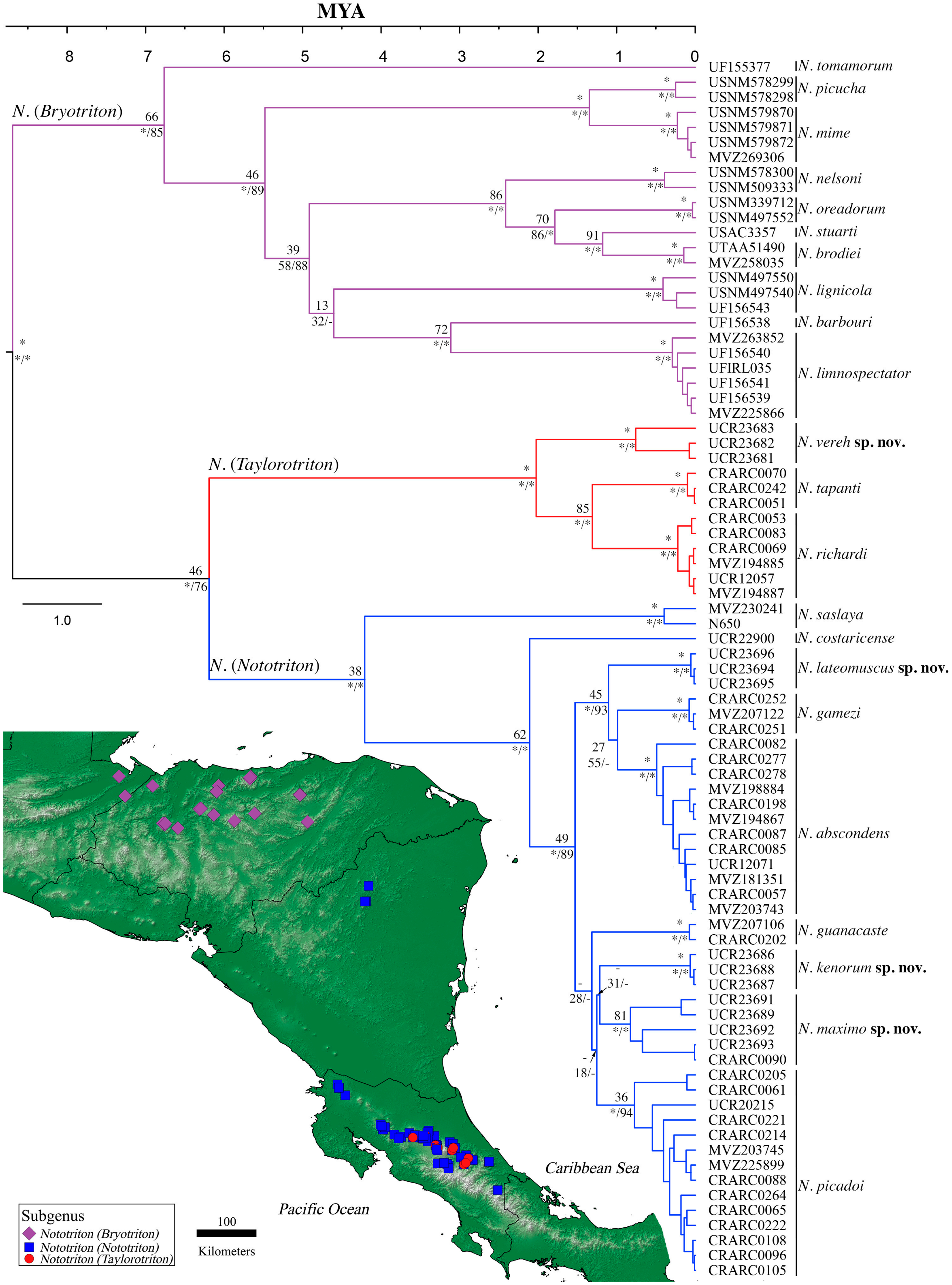


FIGURE 3. Time-calibrated phylogeny from BEAST analysis of concatenated data set including all species of the genus *Nototriton* with sequence data available. The map insert shows the distribution range of the three subgenera within the genus *Nototriton*.

TABLE 2. Mean uncorrected genetic distances among species of the subgenera *Nototriton* and *Taylorotriton* using the 16S (right), COI (above/left), and cyt *b* (below/left) mitochondrial genes.

	N. abscondens	*N. costaricense*	*N. gamezi*	*N. guanacaste*	*N. kenorum* **sp. nov.**	*N. lateomuscus* **sp. nov.**
N. abscondens		1.36–1.94	1.75–1.95	1.36–1.75	1.55–1.95	0.97–1.36
N. costaricense	4.26–5.94 3.81–4.79		2.33	1.94–2.14	1.55–1.75	1.36
N. gamezi	1.98–3.8 1.81–2.34	4.41–4.57 4.36		1.94–2.14	1.94–2.14	1.75
N. guanacaste	3.34–5.09 3.66–4.16	4.62 4.9–5.79	3.34–3.5 2.74–3.9		1.17–1.55	1.75–1.94
N. kenorum **sp. nov.**	2.74–4.65 4.06–5.13	3.96–4.17 6.18	2.28–2.56 3.7	3.82–3.85 4.31–4.84		2.14–2.33
N. lateomuscus **sp. nov.**	2.89–4.91 2.62–3.83	3.93–3.96 4.98–5.16	2.43–2.95 1.75–2.17	3.76–3.97 3.52–3.89	2.74–3.11 3.23–3.27	
N. maximo **sp. nov.**	2.89–5.72 2.71–4.3	4.11–5.25 4.98–6.12	2.58-3.62 2.71–3.0	3.02–4.29 3.25–4.52	2.58–4.33 3.85–4.27	3.34–4.13 2.98–3.82
N. picadoi	2.62–4.81 2.32–3.42	4.57–5.02 4.09–5.47	2.24–3.53 1.16–1.98	3.28–4.33 2.44–3.77	3.34–4.01 1.85–3.05	2.78–4.17 1.63–2.71
N. saslaya	8.21–9.27 6.19–7.43	9.44 8.22	8.81–8.91 5.75	9.38 6.85–7.69	9.12–9.29 6.78	8.81–8.84 7.51–7.87
N. richardi	11.7–13.07 7.98–10.42	12.02–12.18 7.9–9.66	12.31–12.77 7.76–8.57	12.08 8.23–9.74	11.4–11.86 10.44–10.54	11.85–12.27 8.67–9.79
N. tapanti	10.94–12.54 8.72–10.56	11.42–11.71 10.53	11.25–11.86 8.1	10.81–10.85 7.48–9.84	10.79–11.22 10.48	10.49–11.02 10.16
N. vereh **sp. nov.**	11.55–13.33 8.32–9.57	11.87–12.3 9.76–10.09	12.01–12.81 8.46–8.48	11.45–11.76 8.16–9.19	11.09–11.75 8.32–9.05	11.25–12.28 8.92–9.27

......*continued on the next page*

TABLE 2. (Continued)

	N. maximo **sp. nov.**	*N. picadoi*	*N. saslaya*	*N. richardi*	*N. tapanti*	*N. vereh* **sp. nov.**
N. abscondens	0.78–2.14	0.58–2.33	2.86–3.25	3.50–4.09	3.50–4.09	3.11–3.7
N. costaricense	1.75–2.14	1.17–2.14	3.07–3.24	3.50	3.31–3.50	3.11
N. gamezi	1.75–1.94	1.36–1.94	2.66–2.83	3.5	4.09–4.28	3.89
N. guanacaste	0.58–1.75	0.78–1.36	2.25–2.63	3.5–3.7	4.09–4.47	3.89–4.09
N. kenorum **sp. nov.**	0.97–1.94	1.17–2.14	2.66–3.04	2.92–3.11	3.31–3.7	2.92–3.31
N. lateomuscus **sp. nov.**	1.55–1.75	0.97–1.55	3.27–3.44	4.47	4.28–4.47	4.09
N. maximo **sp. nov.**		0.78–1.75	2.45–3.24	3.31–4.09	3.5–4.47	3.31–4.09
N. picadoi	3.03–4.97 1.63–3.88		2.66–3.64	3.89.447	3.7–4.67	3.5–4.47
N. saslaya	9.42–10.17 6.66–7.42	7.9–8.81 5.21–7.76		3.85–4.1	4.46–4.92	4.10–4.67
N. richardi	11.4–12.56 7.86–9.49	11.25–12.5 7.81–10.16	12.46 9.59–9.64		1.75–1.95	2.72–3.11
N. tapanti	10.33–11.76 9.34–9.52	10.18–11.7 8.72–10.56	11.55–12.2 9.77	3.34–4.07 3.43–3.51		2.14–2.72
N. vereh **sp. nov.**	10.79–12.28 7.71–9.33	11.22–11.97 7.68–9.53	11.7–12.63 8.92–9.28	4.04–5.17 4.23–7.14	3.86–5.17 4.52–6.49	

The third major clade was the *N.* (*Nototriton*) subgenus, which consisted of ten taxa that occur collectively in northern Nicaragua and the Caribbean slopes of Costa Rica (*i.e.* Guanacaste, Tilarán, Central Volcanic, and Talamanca mountain ranges). The three inferences were consistent in the positions of *N. saslaya* and *N. costaricense.* Also, the clade formed by *N. abscondens, N. gamezi,* and an unnamed taxon described herein below was supported by all three phylogenetic analyses, although the MrBayes tree supported *N. gamezi* as sister taxon of *N. abscondens* + the unnamed taxon. The Garli and MrBayes trees were identical in topology within this third major clade, except in the position of *N. gamezi* as mentioned above.

Morphometric analyses. The morphometric variation among the species of *Nototriton* that inhabit Costa Rica are shown in Table 3. The discriminant analysis within the *Nototriton richardi* clade, which we are proposing as a new subgenus herein below, correctly classified 100% of the specimens to the species (Fig. 4), showing a clear separation between the specimens of a new species that we are also describing herein below and the specimens of *N. richardi* and *N. tapanti.* The ratio of Hand Length (HaL) to Hand Width (HaW) was different among *N. tapanti* and the newly proposed species and between *N. tapanti* and *N. richardi*. Additionally, the ratio of Foot Length (FoL) to Foot Width (FoW) was different between *N. richardi* and the newly proposed species and between *N. tapanti* and the newly proposed species. Also, the ratio of Left Naris Height (LNH) to Head Width (HeW) was different between *N. tapanti* and the newly proposed species.

The discriminant analysis within the *Nototriton picadoi* clade (following the changes proposed herein, having its members recognized as making up the subgenus *Nototriton*) correctly classified 99% of the specimens to species, with the exception of a single individual of *N. abscondens,* which grouped with *N. picadoi* (Fig. 5). Nevertheless, the diagnosis is not possible using morphometric variables due the overlapping values among the different species for all the measurements. Only another taxon that we describe as a new species herein below from the northern slopes of the Turrialba Volcano can be recognized due its extremely small LNH and RNW.

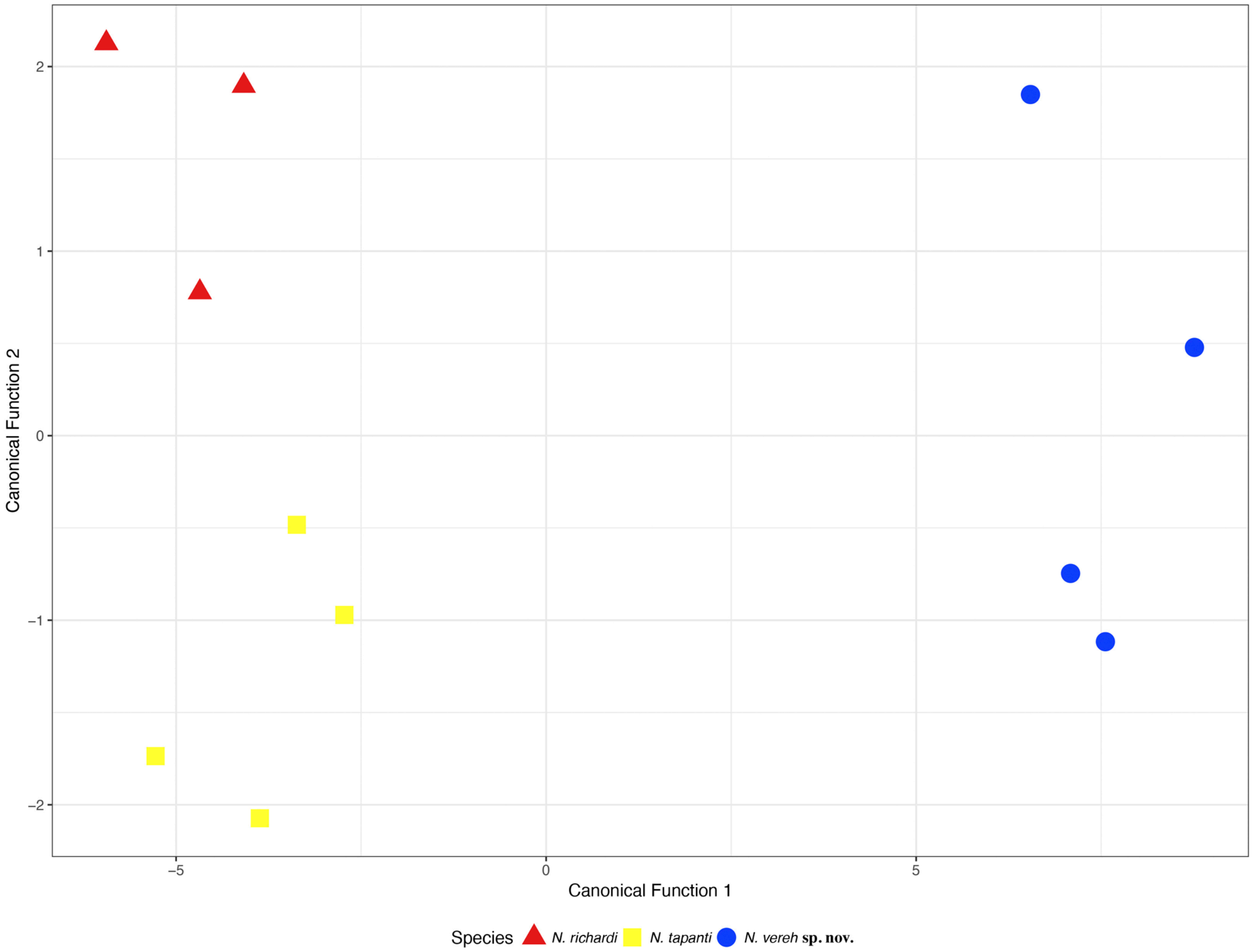


FIGURE 4. Linear discriminant analysis showing the morphological separation among the three species within the subgenus *Taylorotriton*.

TABLE 3. Morphometric data for all known species of *Nototriton* that inhabit Costa Rica. These data were obtained previous to morphometric correction.

Variable/Species	*N. abscondens*	*N. costaricense*	*N. gamezi*	*N. guanacaste*	*N. kenorum* **sp. nov.**	*N. maximo* **sp. nov.**
SL	26.833.69	21.90	26.602.26	27.401.08	26.224.16	30.282.67
	21.50–34.40		25.00–28.20	26.20–28.30	22.00–31.90	27.50–33.50
ShW	3.050.36	2.90	3.200.28	3.400.26	3.060.49	3.700.42
	2.40–3.70		3.00–3.40	3.20–3.70	2.60–3.70	3.20–4.10
HeW	3.540.49	3.30	3.850.21	3.570.25	3.560.43	4.330.38
	2.90–4.30		3.70–4.00	3.30–3.80	3.10–4.00	3.90–4.80
NeW	3.130.39	3.00	3.150.21	3.300.30	3.220.36	3.850.37
	2.40–3.80		3.00–3.30	3.00–3.60	2.90–3.70	3.40–4.20
EW	1.300.15	1.10	1.150.07	1.400.17	1.280.20	1.450.13
	1.10–1.50		1.10–1.20	1.30–1.60	1.10–1.60	1.30–1.60
SnL	0.980.14	0.70	0.850.07	0.970.06	1.000.16	1.030.15
	0.80–1.20		0.80–0.90	0.90–1.00	0.80–1.20	0.90–1.20
JSL	3.280.29	2.50	3.150.07	3.400.17	3.200.37	3.750.34
	2.80–3.70		3.10–3.20	3.20–3.50	2.70–3.70	3.30–4.10
LGFS	5.610.57	4.60	5.550.49	5.900.26	5.500.61	6.580.51
	4.80–6.40		5.20–5.90	5.70–6.20	4.80–6.40	6.00–7.00
LNH	0.160.05	0.34	0.290.01	0.210.02	0.180.05	0.070.04
	0.09–0.25		0.28–0.29	0.19–0.22	0.12–0.25	0.00–0.09
IND	0.880.13	0.70	0.750.07	0.830.06	0.840.15	1.030.10
	0.70–1.10		0.70–0.80	0.80–0.90	0.70–1.00	0.90–1.10
NLP	0.460.09	0.40	0.500.00	0.430.06	0.460.11	0.530.13
	0.30–0.60		0.50–0.50	0.40–0.50	0.30–0.60	0.40–0.70
ICD	1.680.15	1.60	1.650.07	1.700.10	1.700.10	1.880.21
	1.40–1.90		1.60–1.70	1.60–1.80	1.60–1.80	1.70–2.10
RNW	0.160.04	0.31	0.240.02	0.150.02	0.140.04	0.060.04
	0.09–0.22		0.22–0.25	0.12–0.16	0.09–0.19	0.00–0.09
HLL	4.940.70	4.80	5.000.28	5.000.35	4.640.52	5.330.50
	3.80–6.50		4.80–5.20	4.80–5.40	4.10–5.20	4.80–6.00
TW	3.420.51	3.20	3.350.21	3.530.40	3.520.65	3.900.58
	2.60–4.30		3.20–3.50	3.10–3.90	2.80–4.40	3.30–4.40
FLL	4.590.48	4.40	4.400.14	4.670.15	4.320.34	4.650.31
	4.10–5.70		4.30–4.50	4.50–4.80	4.00–4.80	4.30–5.00

......continued on the next page

TABLE 3. (Continued)

Variable/Species	*N. abscondens*	*N. costaricense*	*N. gamezi*	*N. guanacaste*	*N. kenorum* **sp. nov.**	*N. maximo* **sp. nov.**
VGS	4.960.54	4.10	5.200.42	5.070.12	4.720.56	5.680.59
	4.10–5.80		4.90–5.50	5.00–5.20	4.00–5.30	5.10–6.40
FSL	7.230.70	6.40	7.400.85	7.670.23	7.040.75	8.030.48
	6.00–8.20		6.80–8.00	7.40–7.80	6.20–8.00	7.50–8.60
UHL	3.110.36	2.70	3.050.21	3.270.15	3.020.51	3.430.33
	2.70–3.70		2.90–3.20	3.10–3.40	2.50–3.60	3.10–3.80
AGL	15.562.36	12.00	15.351.34	15.800.69	15.322.84	17.401.48
	12.50–0.40		14.40–16.30	15.00–16.20	12.50–19.30	16.00–19.30
VL	1.670.31	1.40	1.800.00	1.770.15	1.500.45	1.800.14
	1.20–2.10		1.80–1.80	1.60–1.90	0.90–2.00	1.60–1.90
HaW	1.280.21	1.00	1.200.14	1.330.15	1.260.24	1.330.21
	1.10–1.70		1.10–1.30	1.20–1.50	1.00–1.60	1.10–1.50
HaL	1.530.26	1.20	1.400.00	1.670.12	1.380.26	1.580.22
	1.20–1.90		1.40–1.40	1.60–1.80	1.00–1.70	1.30–1.80
WF3	0.290.04	0.22	0.270.01	0.280.00	0.290.05	0.350.08
	0.22–0.34		0.26–0.28	0.28–0.28	0.22–0.34	0.28–0.43
LF2	0.590.09	0.47	0.530.04	0.670.09	0.610.09	0.690.07
	0.50–0.78		0.50–0.56	0.62–0.78	0.47–0.71	0.62–0.78
LF3	0.510.10	0.47	0.470.05	0.630.07	0.570.12	0.590.10
	0.34–0.71		0.43–0.50	0.58–0.71	0.43–0.71	0.47–0.68
FoW	1.550.31	1.40	1.400.14	1.730.31	1.560.30	1.700.24
	1.00–2.10		1.30–1.50	1.40–2.00	1.30–2.00	1.40–1.90
FoL	1.690.36	1.60	1.750.21	1.870.31	1.780.31	2.100.24
	1.00–2.10		1.60–1.90	1.60–2.20	1.40–2.10	1.80–2.30
WT3	0.290.03	0.26	0.260.04	0.300.02	0.310.05	0.360.08
	0.25–0.31		0.23–0.28	0.28–0.31	0.25–0.37	0.28–0.43
LT2	0.670.09	0.71	0.580.11	0.820.09	0.690.11	0.690.17
	0.57–0.81		0.50–0.65	0.74–0.91	0.53–0.79	0.50–0.87
LT3	0.650.09	0.54	0.520.07	0.710.07	0.580.14	0.750.09
	0.53–0.78		0.47–0.57	0.65–0.78	0.40–0.71	0.65–0.87

......*continued on the next page*

TABLE 3. (Continued)

Variable/Species	*N. abscondens*	*N. costaricense*	*N. gamezi*	*N. guanacaste*	*N. kenorum* **sp. nov.**	*N. maximo* **sp. nov.**
IND/HeW	0.250.03	0.21	0.190.01	0.230.01	0.240.02	0.240.02
	0.19–0.29		0.19–0.20	0.22–0.24	0.20–0.25	0.21–0.26
HeW/AGL	0.230.02	0.28	0.250.01	0.230.01	0.230.02	0.250.02
	0.21–0.27		0.25–0.26	0.22–0.23	0.21–0.25	0.23–0.27
SnL/HeW	0.280.04	0.21	0.220.03	0.270.03	0.280.02	0.240.02
	0.21–0.34		0.20–0.24	0.24–0.30	0.26–0.30	0.21–0.25
LNH/HeW	0.050.02	0.10	0.070.01	0.060.01	0.050.02	0.020.01
	0.02–0.08		0.07–0.08	0.05–0.07	0.03–0.08	0.00–0.02
RNW/HeW	0.050.02	0.09	0.060.00	0.040.00	0.040.01	0.010.01
	0.02–0.07		0.06–0.06	0.04–0.04	0.03–0.05	0.00–0.02
HaL/VGS	0.310.04	0.29	0.270.02	0.330.02	0.290.03	0.280.02
	0.26–0.40		0.25–0.29	0.32–0.35	0.25–0.32	0.25–0.31
FoL/VGS	0.350.05	0.39	0.340.01	0.370.05	0.380.02	0.370.02
	0.23–0.38		0.33–0.35	0.32–0.42	0.35–0.40	0.35–0.39
HaW/HeW	0.360.03	0.30	0.310.02	0.370.02	0.350.03	0.310.03
	0.31–0.43		0.30–0.33	0.36–0.39	0.31–0.40	0.28–0.34
FoW/HeW	0.460.06	0.42	0.360.02	0.490.09	0.440.04	0.390.03
	0.33–0.53		0.35–0.38	0.39–0.55	0.41–0.50	0.36–0.43
LT2/FoL	0.410.09	0.44	0.330.02	0.440.03	0.390.02	0.330.09
	0.31–0.62		0.31–0.34	0.41–0.46	0.38–0.43	0.22–0.44
LF2/HaL	0.410.04	0.39	0.380.03	0.400.03	0.450.03	0.440.06
	0.34–0.44		0.36–0.40	0.39–0.43	0.41–0.49	0.36–0.50
WT3/FoW	0.190.03	0.19	0.180.01	0.180.04	0.200.01	0.210.02
	0.15–0.25		0.18–0.19	0.16–0.22	0.19–0.22	0.18–0.23
WF3/HaW	0.220.02	0.22	0.230.04	0.210.02	0.230.03	0.260.02
	0.20–0.26		0.20–0.25	0.19–0.23	0.20–0.28	0.23–0.29
HaL/HaW	1.190.15	1.20	1.170.14	1.250.07	1.100.14	1.190.05
	1.06–1.50		1.08–1.27	1.20–1.33	0.91–1.30	1.13–1.25
FoL/FoW	1.090.09	1.14	1.250.03	1.080.07	1.140.09	1.240.04
	1.00–1.25		1.23–1.27	1.00–1.14	1.05–1.27	1.21–1.29

......continued on the next page

TABLE 3. (Continued)

Variable/Species	*N. picadoi*	*N. lateomuscus* **sp. nov.**	*N. richardi*	*N. tapanti*	*N. vereh* **sp. nov.**
SL	29.163.00	25.045.24	20.872.23	23.532.67	20.951.77
	23.60–34.30	19.20–29.32	18.30–22.30	20.20–26.10	18.60–22.80
ShW	3.430.38	2.970.45	2.400.26	2.850.39	2.480.05
	2.60–4.10	2.50–3.40	2.10–2.60	2.30–3.20	2.40–2.50
HeW	3.760.31	3.430.51	2.930.38	3.350.37	2.830.17
	3.10–4.40	3.00–4.00	2.50–3.20	2.90–3.70	2.60–3.00
NeW	3.410.38	2.970.42	2.500.26	2.850.37	2.450.10
	2.70–4.10	2.50–3.30	2.20–2.70	2.50–3.30	2.30–2.50
EW	1.430.13	1.270.06	1.130.06	1.200.12	1.130.05
	1.20–1.60	1.20–1.30	1.10–1.20	1.10–1.30	1.10–1.20
SnL	1.030.16	0.870.23	0.800.10	0.900.18	0.780.13
	0.70–1.20	0.60–1.00	0.70–0.90	0.70–1.10	0.60–0.90
JSL	3.460.31	3.030.55	2.730.29	2.930.46	2.650.13
	2.90–4.00	2.40–3.40	2.40–2.90	2.50–3.50	2.50–2.80
LGFS	6.130.50	5.400.79	4.530.46	4.900.61	4.500.34
	5.00–6.90	4.50–6.00	4.00–4.80	4.30–5.70	4.10–4.90
LNH	0.170.07	0.210.08	0.260.02	0.270.03	0.270.02
	0.06–0.29	0.12–0.25	0.25–0.28	0.25–0.31	0.25–0.28
IND	0.920.11	0.730.06	0.730.06	0.880.17	0.730.10
	0.70–1.10	0.70–0.80	0.70–0.80	0.70–1.10	0.60–0.80
NLP	0.460.06	0.400.10	0.370.06	0.450.13	0.400.08
	0.30–0.50	0.30–0.50	0.30–0.40	0.30–0.60	0.30–0.50
ICD	1.780.14	1.570.15	1.470.06	1.650.17	1.430.10
	1.50–2.00	1.40–1.70	1.40–1.50	1.50–1.90	1.30–1.50
RNW	0.170.06	0.200.06	0.210.02	0.210.04	0.240.03
	0.09–0.28	0.14–0.25	0.19–0.22	0.16–0.25	0.22–0.28
HLL	5.380.46	5.100.72	3.670.57	4.300.36	4.050.10
	4.40–6.20	4.50–5.90	3.20–4.30	3.90–4.60	3.90–4.10
TW	3.770.48	3.070.49	2.430.31	3.380.88	2.550.13
	3.00–5.10	2.50–3.40	2.10–2.70	2.50–4.60	2.40–2.70

......continued on the next page

TABLE 3. (Continued)

Variable/Species	*N. picadoi*	*N. lateomuscus* **sp. nov.**	*N. richardi*	*N. tapanti*	*N. vereh* **sp. nov.**
FLL	4.880.34	4.470.51	3.670.42	4.100.47	3.700.37
	4.30–5.40	3.90–4.90	3.20–4.00	3.80–4.80	3.30–4.10
VGS	5.360.43	4.770.81	3.930.38	4.230.57	3.980.21
	4.40–6.00	3.90–5.50	3.50–4.20	3.70–5.00	3.70–4.20
FSL	7.870.62	7.071.21	5.900.61	6.700.47	5.950.48
	6.50–8.90	5.70–8.00	5.20–6.30	6.20–7.30	5.40–6.40
UHL	3.420.32	2.970.49	2.300.20	2.700.26	2.350.13
	2.80–4.00	2.40–3.30	2.10–2.50	2.40–3.00	2.20–2.50
AGL	17.001.96	14.402.72	11.671.36	13.381.68	11.781.26
	13.30–20.20	11.40–16.70	10.10–12.50	11.50–15.20	10.20–13.10
VL	1.810.18	1.700.17	1.470.12	1.680.15	1.480.21
	1.50–2.20	1.60–1.90	1.40–1.60	1.50–1.80	1.20–1.70
HaW	1.510.14	1.130.25	0.730.12	0.930.17	0.730.05
	1.20–1.70	0.90–1.40	0.60–0.80	0.70–1.10	0.70–0.80
HaL	1.630.15	1.300.26	1.000.17	1.150.17	0.980.05
	1.40–2.00	1.10–1.60	0.80–1.10	0.90–1.30	0.90–1.00
WF3	0.310.04	0.250.05	0.250.04	0.300.05	0.220.00
	0.25–0.39	0.22–0.31	0.22–0.29	0.22–0.34	0.22–0.22
LF2	0.670.07	0.560.19	0.320.04	0.360.07	0.330.05
	0.51–0.78	0.37–0.74	0.29–0.37	0.31–0.47	0.28–0.40
LF3	0.670.10	0.430.11	0.220.05	0.240.03	0.210.03
	0.50–0.87	0.34–0.56	0.16–0.25	0.19–0.26	0.19–0.25
FoW	1.920.23	1.400.26	0.970.15	1.130.17	0.850.06
	1.50–2.30	1.10–1.60	0.80–1.10	0.90–1.30	0.80–0.90
FoL	2.070.22	1.700.36	1.170.15	1.380.13	1.200.00
	1.70–2.50	1.40–2.10	1.00–1.30	1.20–1.50	1.20–1.20
WT3	0.330.04	0.270.03	0.270.02	0.300.03	0.220.01
	0.25–0.40	0.25–0.31	0.25–0.29	0.26–0.33	0.22–0.23
LT2	0.760.12	0.690.19	0.380.04	0.420.07	0.380.04
	0.56–1.00	0.53–0.90	0.34–0.42	0.34–0.50	0.31–0.40

......continued on the next page

TABLE 3. (Continued)

Variable/Species	*N. picadoi*	*N. lateomuscus* **sp. nov.**	*N. richardi*	*N. tapanti*	*N. vereh* **sp. nov.**
LT3	0.780.11	0.540.16	0.240.07	0.280.04	0.240.03
	0.57–0.96	0.37–0.68	0.17–0.31	0.22–0.31	0.22–0.28
IND/HeW	0.250.02	0.220.02	0.250.03	0.260.03	0.260.02
	0.20–0.28	0.20–0.23	0.22–0.28	0.22–0.30	0.23–0.29
HeW/AGL	0.220.02	0.240.02	0.250.01	0.250.03	0.240.03
	0.19–0.25	0.22–0.26	0.25–0.26	0.21–0.29	0.21–0.28
SnL/HeW	0.280.04	0.250.05	0.280.05	0.270.05	0.280.05
	0.18–0.33	0.20–0.30	0.22–0.32	0.19–0.31	0.21–0.32
LNH/HeW	0.050.02	0.060.02	0.090.01	0.080.01	0.100.00
	0.01–0.09	0.04–0.08	0.08–0.10	0.07–0.09	0.09–0.10
RNW/HeW	0.050.02	0.060.02	0.070.01	0.060.01	0.080.01
	0.02–0.08	0.04–0.07	0.06–0.09	0.05–0.08	0.08–0.10
HaL/VGS	0.300.02	0.270.02	0.250.02	0.270.03	0.250.02
	0.27–0.34	0.24–0.29	0.23–0.27	0.24–0.31	0.23–0.27
FoL/VGS	0.390.02	0.360.03	0.300.01	0.330.02	0.300.02
	0.34–0.44	0.33–0.38	0.29–0.31	0.30–0.36	0.29–0.32
HaW/HeW	0.400.02	0.330.03	0.250.01	0.270.02	0.260.02
	0.36–0.44	0.30–0.35	0.24–0.26	0.24–0.30	0.23–0.28
FoW/HeW	0.510.04	0.410.04	0.330.02	0.330.02	0.300.02
	0.45–0.56	0.37–0.45	0.31–0.35	0.31–0.35	0.27–0.32
LT2/FoL	0.370.04	0.400.03	0.320.02	0.300.02	0.310.04
	0.28–0.43	0.38–0.43	0.31–0.34	0.28–0.33	0.26–0.33
LF2/HaL	0.410.03	0.420.08	0.330.04	0.320.04	0.330.05
	0.36–0.46	0.34–0.48	0.28–0.36	0.28–0.36	0.28–0.40
WT3/FoW	0.170.01	0.200.03	0.290.02	0.260.02	0.260.02
	0.15–0.21	0.17–0.23	0.26–0.31	0.25–0.29	0.24–0.29
WF3/HaW	0.210.02	0.230.03	0.350.03	0.320.02	0.300.02
	0.18–0.24	0.20–0.26	0.31–0.37	0.31–0.34	0.28–0.31
HaL/HaW	1.080.07	1.150.07	1.360.02	1.250.07	1.350.15
	0.94–1.18	1.09–1.22	1.33–1.38	1.18–1.33	1.13–1.43
FoL/FoW	1.080.07	1.220.13	1.210.04	1.230.09	1.420.10
	1.00–1.20	1.07–1.31	1.18–1.25	1.15–1.33	1.33–1.50

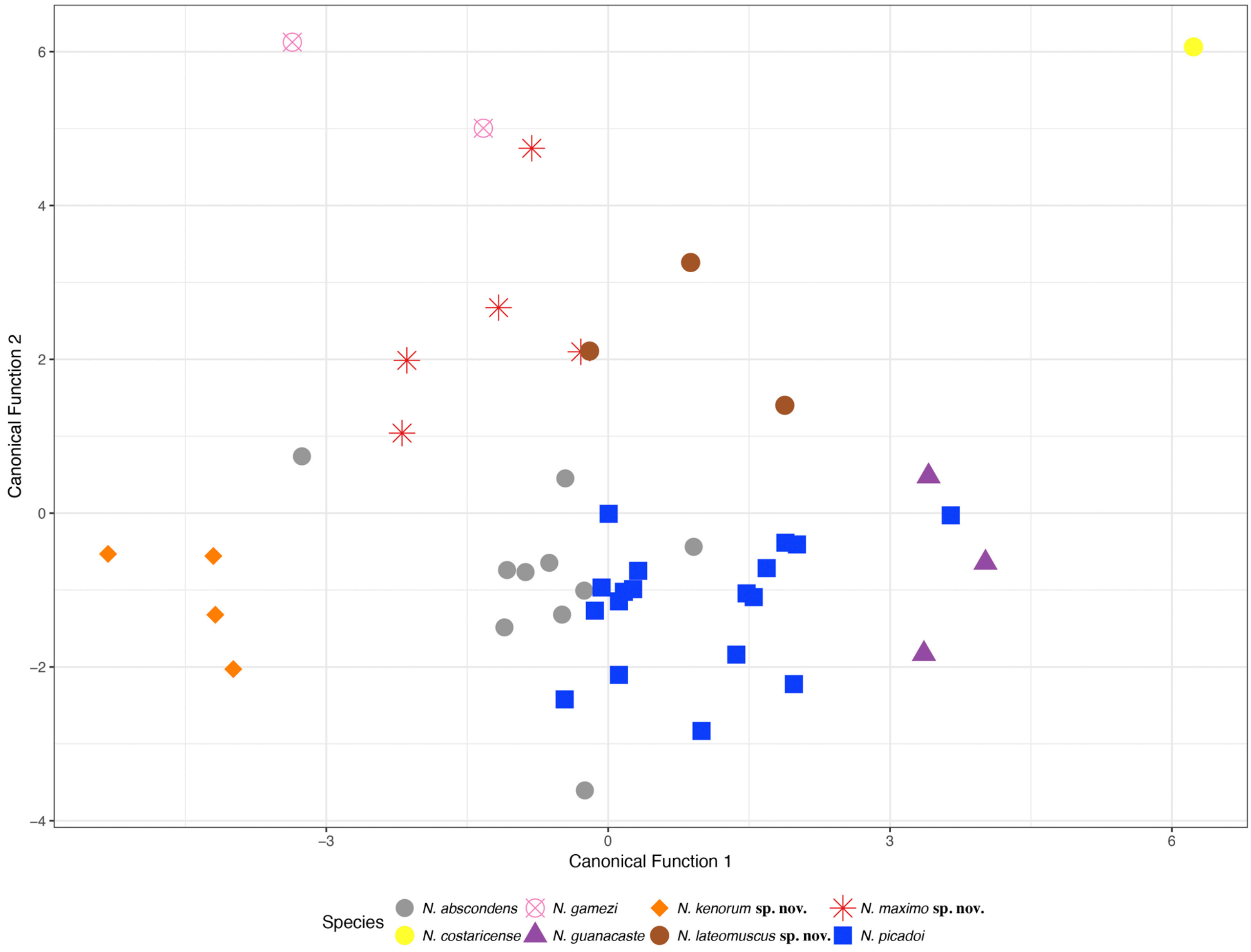


FIGURE 5. Linear discriminant analysis showing the morphological separation among the eight species within the subgenus *Nototriton*.

Sytematics

Taylorotriton **subgen. nov.**

Type species. *Parvimolge richardi* Taylor, 1949.

Diagnosis. Diminutive salamanders with a standard length not known to exceed 27 mm. Possessing tiny hands and feet that are pad-like in appearance, with at the most the distal phalanx on each digit protruding in a bluntly pointed tip beyond the fleshy palmar and plantar tissue. Hand width not known to exceed 30% of head width. Relatively large nostril openings; width of nostril typically exceeding 5% of head width. The members of this subgenus are also diagnosed by evident divergence in their mtDNA sequences.

Etymology. *Taylorotriton*, is formed from Taylor (a surname) and the Greek word *Triton* (a Greek god of the sea, son of Poseidon and Amphitrite) (Day 2007). Triton is a commonly used word for salamanders, and is a root in several genera and subgenera of bolitoglossine salamanders. We propose this subgeneric name in honor of Edward Harrison Taylor (1889–1978), the legendary alpha-taxonomist who greatly expanded the knowledge and understanding of Costa Rica's amphibians, including salamanders, during his work in the country especially during middle decades (40s and 50s) of the 20th century.

Composition. Only three species are recognized to comprise this subgenus, The two former members of the *Nototriton richardi* species group (*N. richardi* and *N. tapanti*) and a newly proposed species described herein below.

Distribution. All three members of the subgenus *Taylorotriton* are known to be endemic to Costa Rica and restricted to the Caribbean slopes of the Central Volcanic Range and northeastern Talamanca, at elevations from roughly 1300–2250 masl (Fig. 6).

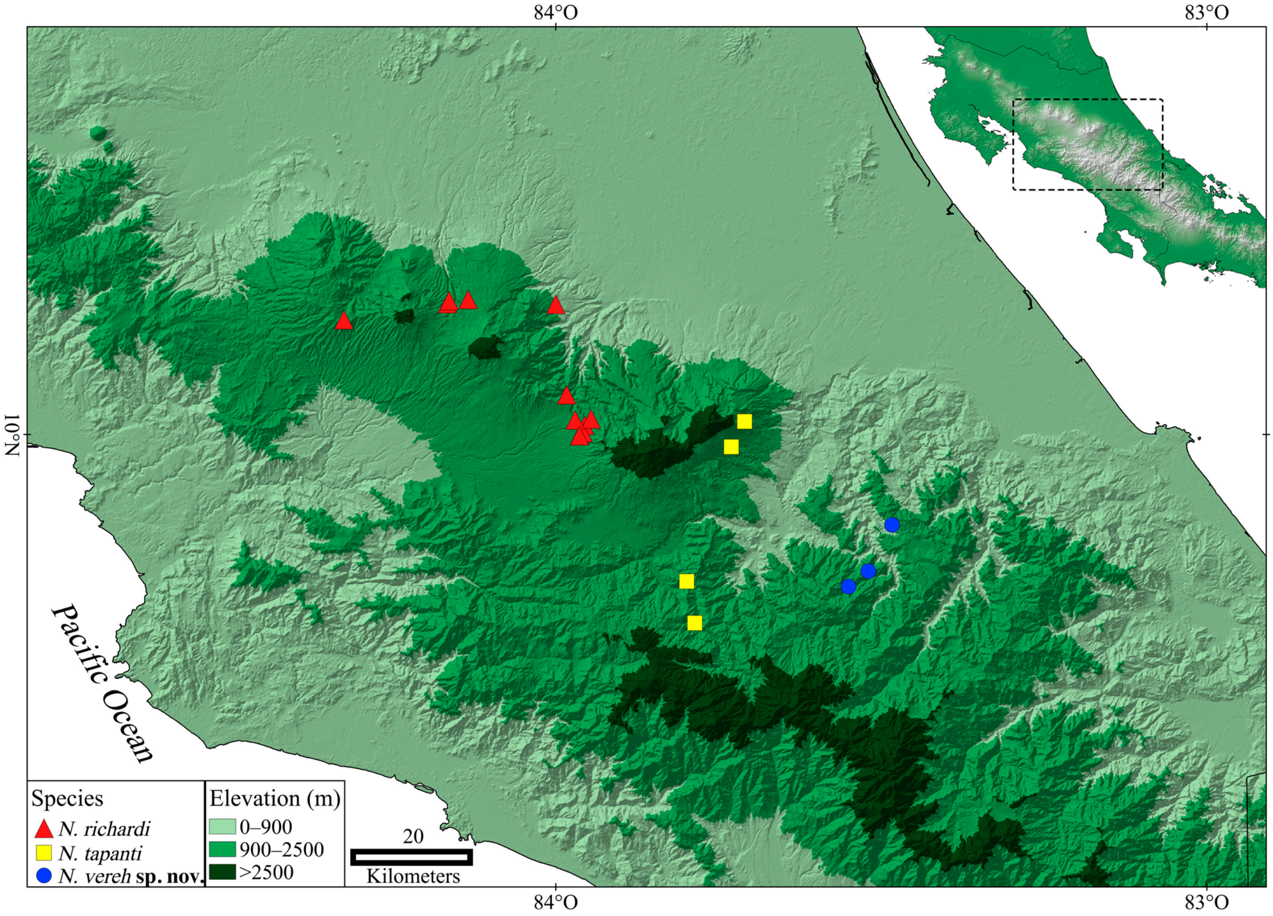


FIGURE 6. Map of Costa Rica showing the distribution range of the three species within the subgenus *Taylorotriton.*

Nototriton vereh **sp. nov.**
Vereh moss salamander

Holotype. UCR 23681 (Figs. 7–9), an adult female from Costa Rica: Provincia de Cartago: Cantón de Turrialba: Distrito de Chirripó: a private property owned by Brian Kubicki and referred to as the Río Vereh Cloud Forest Reserve, 1400 m a.s.l., collected by Brian Kubicki on 15 October 2016.

Paratypes. UCR 23682, an adult female from Costa Rica: Provincia de Limón: Cantón de Turrialba: Distrito de Chirripó: moss on bank of road between Jicotea and Río Vereh, ca. 1250 m a.s.l., collected by Brian Kubicki in the company of Aura Reyes on 2 November 2013. UCR 23683, an adult male from Costa Rica: Provincia de Cartago: Cantón de Turrialba: Distrito de Chirripó: edge of road between Bajo Pacuare and Grano de Oro, ca. 1250 m a.s.l., collected by Brian Kubicki, in the company of Aura Reyes, on 13 April 2013; UCR 23684, an adult male: same locality data as UCR 23683, but collected by Brian Kubicki, in the company of Aura Reyes, on 21 March 2013.

Generic Placement. Assigned to the genus *Nototriton* due to having fewer than 14 costal grooves, reduced *manus* and *pes* that are longer than wide, and the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

Subgeneric Placement. *Nototriton vereh* is further assigned to the subgenus *Taylorotriton* due to the combination of its known geographic distribution (endemic to the central Caribbean region of Costa Rica), its tiny hands and feet that are pad-like in appearance, with at the most the distal phalanx on each digit protruding in a bluntly pointed tip beyond the fleshy palmar and plantar tissue, and again the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

FIGURE 7. Holotype of *Nototriton vereh* **sp. nov.** in life on white background. Photograph by BK.

Diagnosis. The combination of the following characteristics can be used to distinguish *Nototriton vereh* from the other described species of the genus *Nototriton*: (1) having tiny hands and feet, with at the most only the distal phalanges on the fingers and toes free of palmar and plantar tissue; (2) large nostril openings, greater than 0.25 mm in height (Fig. X); (3) 16S, COI, and cyt *b* mtDNA distances.

Comparisons. Since *Nototriton vereh* is only known to occur within Costa Rica and the phenotypic and molecular evidence presented herein strongly supports it forming part of the newly proposed *Taylorotriton* subgenus, the phenotypic comparisons presented are only with respect to other members of that subgeneric taxon (i.e. *N. richardi,* and *N. tapanti*).

Contrasting characteristics for *Nototriton vereh* are presented in parentheses. *Nototriton richardi* (Taylor, 1949) can be distinguished from *N. vereh* by having relatively narrower feet, average FoW = 0.97 mm (average FoW = 0.85 mm); shorter hind limbs, average HLL = 3.7 mm and HLL = 15.7–19.5 % of SL (longer hind limbs, average HLL = 4.1 mm and HLL = 18.0–21.0 % of SL). *Nototriton tapanti* Good & Wake, 1993 has wider hands and feet, average HaW = 0.9 mm, HaW = 24.1–29.7 % of HeW, average FoW 1.1 = mm, FoW = 31.0–35.1 % of HeW (narrower hands and feet, average HaW = 0.7 mm, HaW = 23.3–27.6 % of HeW, average FoW 0.9 = mm, FoW = 26.7–32.1 % of HeW).

Description of holotype. Subadult to adult female having a SL of 18.6 mm. Head slightly wider than neck and shoulders (HeW 2.9 mm, NeW 2.5 mm, ShW 2.5 mm), with greatest width of head just posterior to the articulation of the jaws; snout raised anterodorsally, spadate to rounded in dorsal outline, and rounded in profile; snout relatively short (SnL 0.6 mm, 3.2 % of SL), with nearly terminal non-protruding large nostrils (LNH 0.28 mm, RNW 0.22 mm) directed anterolaterally; internarial area convex in dorsal outline. Eyes relatively large (EW = 183 % of SnL), weakly protruding beyond dorsal and ventral outline of head, directed anterolaterally, with a distinct suborbital groove. Top of head flat and smooth, tapering slightly toward anterior terminus, lacking contrasting interorbital or other dermal structures. Canthus rostralis weakly rounded; intercanthal area flat to slightly convex; and loreal region slightly concave. No obvious cirri (nasolabial protuberances), but nasolabial grooves weakly discernible on tip of snout; nasolabial grooves start at ventrolateral margins of nares and extend ventrally, with a slight outward orientation, and terminate prior to reaching upper lip margin. Gular fold well-defined, starting on dorsolateral portion of neck, below postorbital groove, wrapping around posteriolateral section of head at a slightly anterior angle and crossing venter as a smooth anterior-oriented curve. Nuchal grooves very weakly evident, starting above postorbital groove and converging medially at occiput. Postorbital grooves weakly evident, starting at the posterior corner of eyes and traveling horizontally along the inferior margin of parotoid glands, terminating at gular fold on the lateral portion of neck. Horizontal mandibular groove moderately defined, starting at corner of mouth and extending horizontally to vertical portion of mandibular groove. Mandibular groove not a single continuous structure, but rather two independent structures on each side of head. Vertical portion of mandibular grooves starting along the inferior margins of postorbital grooves and traveling vertically to gular region, terminating at or just medially of intersections with inner mandibular grooves. Inner mandibular groove not a single continuous structure, but rather two independent and laterally postioned structures. Inner mandibular grooves moderately evident, starting at anterior termini or margin of mandibular grooves, running medially parallel to mandibular bones, becoming indiscernible near anterior tip of lower jaw. Pair of weak, but discernibly raised parotoid glands present on dorsolateral margin of head between orbits, postorbital grooves, and occiput. Snout protruding beyond anterior margin of lower lip in lateral view. No mental gland visible under skin of anterior intermandibular region.

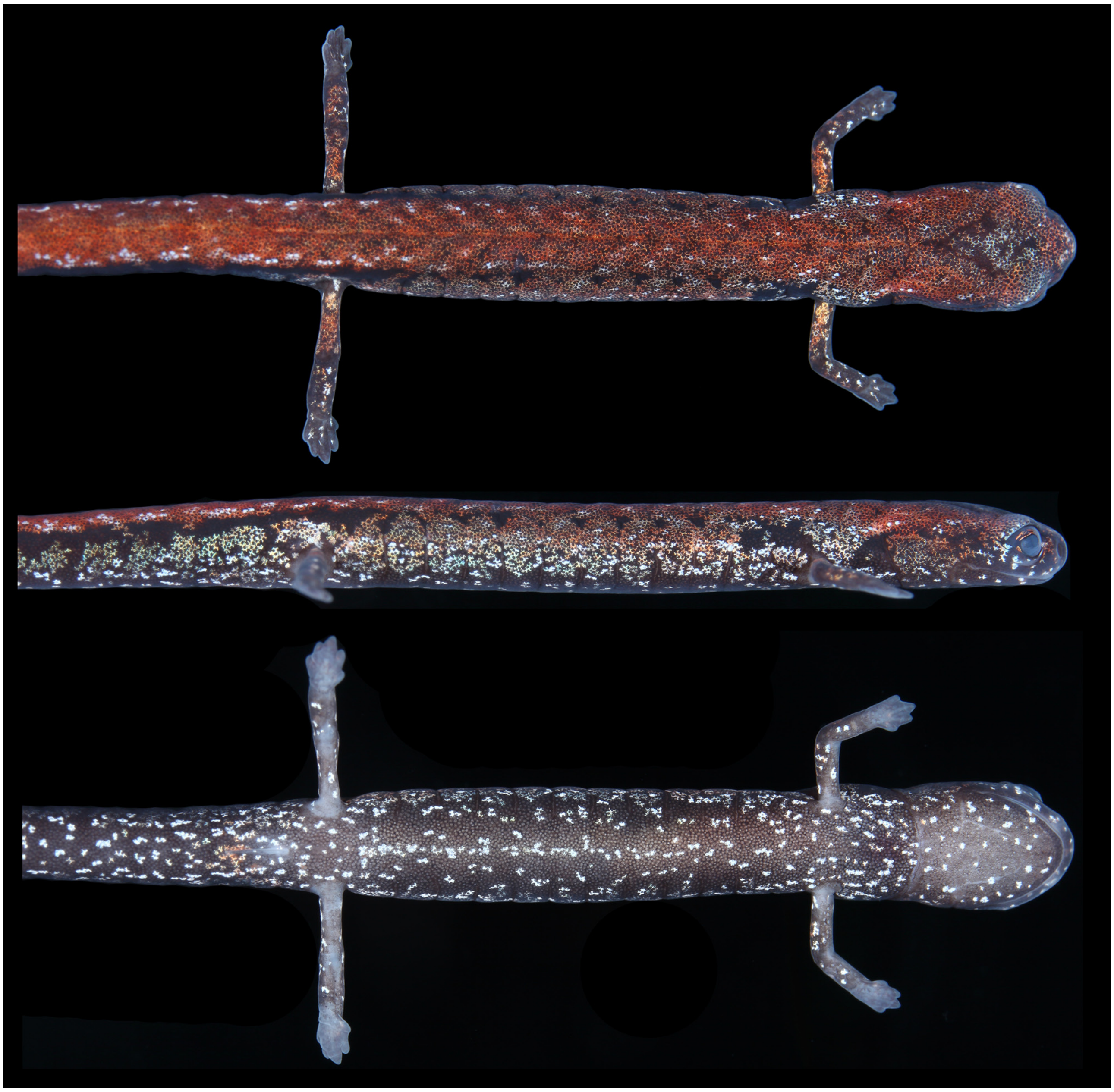


FIGURE 8. Dorsal, lateral, and ventral views of the body of the holotype of *Nototriton vereh* **sp. nov.** in preservation. Photograph by BK.

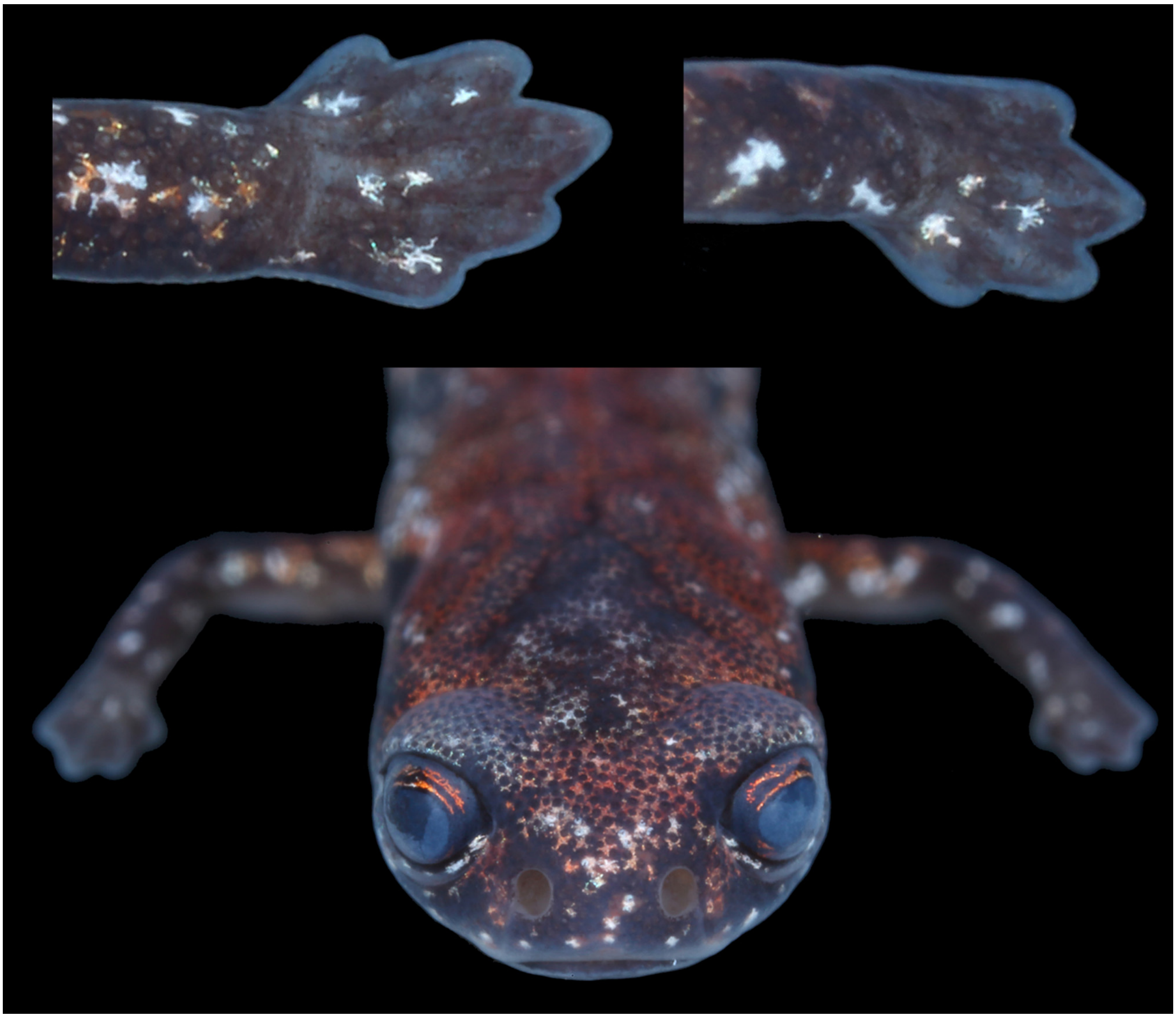


FIGURE 9. Dorsal views of the hand and foot and detail of the face of the holotype of *Nototriton vereh* **sp. nov.** in preservation. Photograph by BK.

Arms relatively short and slender (FLL = 3.3 mm, 17.7 % of SL), without noticeable hypertrophied forearm compared to upper arm. Hands very small and slender (HaL = 0.9 mm, 22.5 % of VGS; HaW = 0.8 mm, 27.6 % of HeW). Fingers II and III protruding slightly beyond interdigital tissue margin (LF2 0.31 mm, LF3 0.19 mm), fingers I and IV with minimal indentation at interdgitial spaces, barely receding proximally beyond tips of latter mentioned digits. Finger III most free of interdigital tissue, with about entire distal phalanx protruding. Tips of fingers rounded (fingers I, II, IV) to acutely rounded (Finger III). Terminal pads weakly discernible on ventral surface of fingers. Palmar surfaces appearing to be smooth overall, but with an evident dermal crease extending transversally along proximal margin of tip of Finger III. Dorsal surfaces of hands with discernible interdigital grooves that start at interdigital tissue margins and cross metacarpal region. Relative lengths of fingers on right hand I < IV < II < III.

Legs relatively short and slender (HLL 3.9 mm, 21.0 % of SL), with lower leg being slightly thicker than upper leg. Feet small and slender (FoL 1.2 mm, 30.0 % of VGS; FoW 0.9 mm, 31.0 % of HeW). Toes II and III protruding slightly beyond interdigital tissue margin (LT2 0.40 mm, LT3 0.22 mm), toes I, IV, and V with minimal indentation at interdgitial spaces, barely receding proximally beyond tips of latter mentioned digits. Toe III most free of interdigital tissue, with about entire distal phalanx protruding. Tips of toes rounded (toes I, II, IV, V) to accutely rounded (Toe III). Terminal pads weakly discernible on ventral distal surface of toes, especially on toes II, III, and IV. Plantar surfaces appearing to be smooth overall, but with some evident dermal creases. Dorsal surfaces of feet with discernible interdigital grooves that start at interdigital tissue margins and cross metatarsal region. Relative lengths of toes on right foot I < V < II < IV < III.

Body subcylindrical (slightly wider than high) in cross section, and relatively robust (TW = 2.4 mm; TW = 23.5 % of AGL). Between axilla and groin, 11 costal grooves visible, 13 if counting axillary and inguinal grooves; costal grooves most visible on ventral and lateral portions of body. Adpressed limbs separated by 4 costal folds; 12 costal folds total between axilla and groin. Slight middorsal depression extends longitudinally along length of body, starting at base of head (occiput) and becoming indiscernible on anterior portion of tail. Tail long, cylindrical in cross section, lacking an evident constriction at base, and evenly tapering to pointed terminus; in life, some caudal grooves discernible on anterior portion of tail. Skin on surfaces of head, body, limbs, and tail smooth.

Coloration in life. The ground color of the dorsal and dorsolateral surfaces of the head and trunk consisted of a mixture of reddish-brown earthy tones. Secondary coloration on the dorsal and dorsolateral surfaces of the head and trunk consisted of larger irregular black markings (especially concentrated along the dorsolateral region of the trunk and dorsal surface of the head), numerous closely spaced darker chevron marks visible along upper dorsum of the trunk, and numerous fine to very fine pale orange to white patches of chromatophores scattered randomly throughout the dorsal surface. The iris was bright orange with a dark brownish-black reticulation.

The upper surfaces of the arms and legs were a mixture of chromatophore patches of irregular shapes and sizes, ranging in color from pale orange, pinkish-orange, dark brown, and black. Additionally, there were some fine to very fine patches of white chromatophores scattered randomly throughout the dorsal surface of the limbs.

The dorsal and dorsolateral surfaces of the tail were nearly uniform reddish-orange, with some fine to very fine patches of white chromatophores scattered randomly throughout.

The ventrolateral surfaces of the body and tail were contrasted from the superior surfaces by consisting of a concentration of fine white or pale markings on a dark gray background.

The ventral surfaces of the head, body, limbs, and tail were pale brown to gray with numerous fine to very fine white spots and irregular markings scattered throughout. Just posterior to the cloaca, there was a concentration of contrasting pale orangish spots and irregular markings. The ventral surfaces of the limbs and gular patch were slightly paler in comparison to the ventral surfaces of the body and tail. The palmar and plantar surfaces were pale grayish-white.

Coloration in ethanol. After more than 5 years in ethanol (70%), the overall coloration of the holotype has darkened throughout and contains a principal dark brown tone.

Measurements (in mm), limb interval, and percentages of the holotype. SL 18.6; ShW 2.5; HeW 2.9; NeW 2.5; EW 1.1; SnL 0.6; JSL 2.5; LGFS 4.1; LNH 0.28; RNW 0.22; IND 0.7; NLP 0.4; ICD 1.4; HLL 3.9; FLL 3.3; TW 2.4; VGS 4.0; FSL 5.4; UHL 2.2; AGL 10.2; VL 1.2; HaW 0.8; HaL 0.9; LF2 0.31; LF3 0.19; WF3 0.22; FoW 0.9; FoL 1.2; LT2 0.4; LT3 0.22; WT3 0.22. Limb interval 4. Measurements in related percentages: VGS/SL 21.5 %; IND/HeW 24.1 %; AGL/SL 54.8 %; HeW/SL 15.6 %; Hew/AGL 28.4 %; SnL/ HeW 20.7 %; LNH/HeW 9.7 %; LNH/SL 1.5 %; RNW/HeW 7.6 %; RNW/SL 1.2 %; HLL/SL 21.0 %; FLL/SL 17.7 %; HaL/VGS 22.5 %; FoL/VGS 30.0 %; Haw/HeW 27.6 %; FoW/HeW 31.0 %; LT2/FoL 33.3 %; LF2/HaL 34.4 %; WT3/FoW 24.4 %; WF3/HaW 27.5%.

Noteworthy variation. The male paratypes (UCR 23683 and UCR 23684) had more truncate snouts, and much more defined and protruding cirri or nasalabial protruberances, sexually dimorphic features that are often observed among plethodontids, including bolitoglossines.

Measurements (in mm), limb intervals, and percentages of the paratypes. SL 20.8–22.8; ShW 2.4–2.5; HeW 2.6–3.0; NeW 2.3–2.5; EW 1.1–1.2; SnL 0.8–0.9; JSL 2.6–2.8; LGFS 4.4–4.9; LNH 0.25–0.28; RNW 0.22–0.28; IND 0.6–0.8; NLP 0.3–0.5; ICD 1.3–1.5; HLL 4.1; FLL 3.5–4.1; TW 2.5–2.7; VGS 3.7–4.2; FSL 5.7–6.4; UHL 2.3–2.5; AGL 11.4–13.1; VL 1.5–1.7; HaW 0.7; HaL 1.0; LF2 0.28–0.40; LF3 0.19–0.25; WF3 0.22; FoW 0.8–0.9; FoL 1.2; LT2 0.31–0.40; LT3 0.22–0.28; WT3 0.22–0.23. Limb intervals 5–6 . Measurements in related percentages: VGS/SL 17.1–19.2 %; IND/HeW 23.1–28.6 %; AGL/SL 54.8–57.5 %; HeW/SL 12.0–13.5 %; Hew/AGL 21.0–24.6 %; SnL/HeW 26.7–32.1 %; LNH/HeW 9.3–10.0 %; LNH/SL 1.2–1.4 %; RNW/HeW 7.7–10.0 %; RNW/SL 1.0–1.3 %; HLL/SL 18.0–19.7 %; FLL/SL 16.2–18.8 %; HaL/VGS 23.8–27.0 %; FoL/VGS 28.6–32.4 %; Haw/HeW 23.3–26.9 %; FoW/HeW 26.7–32.1 %; LT2/HeW 7.7–10.0 %; LT3/FoW 20.6–25.6 %; LT2/FoL 25.8–33.3 %; LF2/HaL 28.0–40.0 %; WT3/FoW 24.4–28.8 %; WF3/HaW 31.4%**.**

Etymology. The specific epithet is a noun in apposition, and refers to the region where the holotype was collected, the upper catchment basin of the Vereh River.

Habitat and natural history observations. *Nototriton vereh* has been found to inhabit moss growing on the ground and on the lower sections of tree trunks (within a meter above the ground). One specimen (UCR 23684) was found within a clump of moss that had fallen from a tree above; this moss had been on the ground for a while judging by its appearance, so it is highly unlikely that this individual had been living within the moss high up in the canopy. We feel that it is most likely that UCR 23684 was living within the terrestrial leaf litter and was taking diurnal refuge within the fallen moss clump when BK and AR discovered it. Two individuals (UCR 23682 and UCR 23683) were found by BK and AR during the day within moss growing on the ground in highly disturbed roadside habitats. The holotype (UCR 23681) was discovered by BK within a section of abandonded pasture in his private property referred to as the Rio Vereh Cloud Forest Reserve. The holotype was discovered during the day within a thick patch of moss (approximately 5 cm in thickness) growing on the lower trunk of a small tree, approximately 50 cm above the ground.

Distribution. *Nototriton vereh* is endemic to Costa Rica, and currently only known to inhabit a very small section of cloud forest within the Tropical Premontane Rainforest life zone (Holdridge 1967) along the northern Caribbean foothills of the Cordillera de Talamanca. The known altitudinal range for *N. vereh* is from ca. 1250–1400 m a.s.l.

Other members of the subgenus *Taylorotriton*

Nototriton (*Taylorotriton*) *richardi* (Taylor, 1949)
Richard's moss salamander

Parvimolge richardi Taylor (1949: 284)
Chiropterotriton richardi Wake & Lynch (1976: 60)
Nototriton richardi Wake & Elias (1983: 11)
Nototrtion (*Nototriton*) *richardi* Dubois & Raffaëlli (2012: 141)

Holotype. RCT 1436 (Richard C. Taylor field number), by original designation, but currently housed at the Chicago Field Museum of Natural History, FMNH 178295, an adult female from Costa Rica: Provincia de Alajuela: Cantón de Alajuela: Distrito de Sarapiquí: Isla Bonita: American Cinchona Plantation, ca. 6500 feet (ca. 1980 m a.s.l.), collected by Richard Clark Taylor on 1 August 1947.

Etymology. The specific epithet is a patronym, used as a noun in the masculine genitive case, in dedication to Richard Clark Taylor (1926–2002), the son of Edward Harrison Taylor (1889–1978). Richard Taylor joined his father while searching for reptiles and amphibians during an expedition to Costa Rica in 1947, and collected the hototype of this taxon.

Distribution. *Nototriton richardi* is endemic to Costa Rica and is only known to inhabit the Caribbean slopes of the Cordillera Volcanica Central at elvations from roughly 1300–1800 m a.s.l. (Savage 2002). Specimens have been collected from within a swath ranging from the northwestern slopes of the Irazu Volcano to the eastern flanks of Juan Castro Blanco National Park.

Nototriton (*Taylorotriton*) *tapanti* Good & Wake, 1993
Tapanti moss salamander

Nototriton tapanti Good & Wake (1993: 134).
Nototriton (*Nototriton*) *tapanti*: Dubois & Raffaëlli (2012: 141).

Holotype. MVZ 203746, by original designation, an adult female from Costa Rica: Provincia de Cartago: Cantón de Paraíso: Distrito de Orosi: Río Quirí, near Tapanti National Park, ca. 1300 m a.s.l., collected by A. Collazo and D. A. Good on 25 May 1986.

Etymology. The specific epithet is a noun in apposition and was given in recognition of the site where the holotype of this taxon was collected, a small settlement near what is presently known as Tapantí National Park.

Distribution. *Nototriton tapanti* is endemic to Costa Rica and was only known from a single specimen, the holotype, collected near Río Quirí on the northern section of the Cordillera de Talamanca, but during this study BK discovered and collected additional specimens that resulted in extending the known range approximately four kilometers to the south of the type locality within Tapanti National Park (ca. 1400 m a.s.l.) and 30 kilometers to the

NNE along the eastern flank of the Turrialba Volcano (ca. 2250 m a.s.l.), which is part of the Cordillera Volcanica Central. With the additional individuals of this poorly known taxon discovered during this study, *Nototriton tapanti* is now known to inhabit sites within the northern Cordillera de Talamanca and extreme eastern Cordillera Volcanica Central at elevations from roughly 1300–2250 m a.s.l.

Noteworthy observations or remarks. *Nototriton tapanti* was only known from a single specimen, the holotype, until additional specimens were discovered and collected during this study.

Subgenus *Nototriton* Dubois & Raffaëlli, 2012

Type species. *Spelerpes picadoi* Stejneger, 1911.

Diagnosis. Diminutive to small salamanders with a standard length not known to exceed 38 mm, but with adult sizes typically exceeding 25 mm. Possessing small hands and feet that are longer than wide, with the hand width not known to exceed 2.0 mm and foot width not known to exceed 2.5 mm. Digits of hands and feet, excluding Finger I and Toe I, free of the palmar and plantar tissue for the majority of their lengths, with most digits having the ultimate and parts of the penultimate phalanges free of interdigital tissue. The members of this subgenus are also diagnosed by evident divergence in their mtDNA sequences.

Etymology. *Nototriton*, is formed from the Greek words *notos* (meaning south) and *Triton*, the name of a Greek sea-god. The term "triton" is commonly used word for salamanders, and is a root in several genera and subgenera of bolitoglossine salamanders (Wake & Elias 1983).

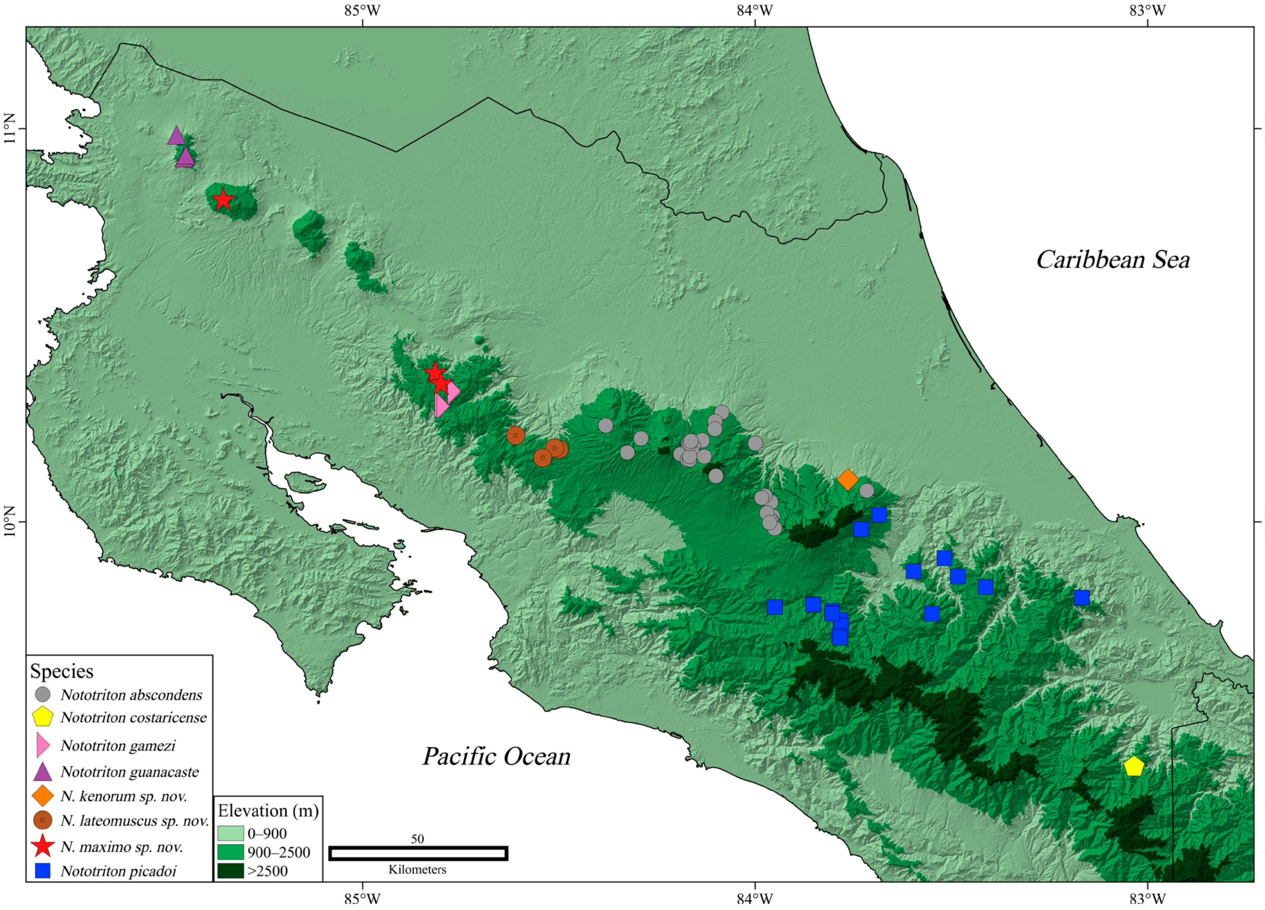


FIGURE 10. Map of Costa Rica showing the distribution range of the eight species within the subgenus *Nototriton.*

Composition. We recognize nine species to comprise this subgenus; the following six formerly recognized members of the *Nototriton picadoi* species group (*N. abscondens, N. costaricense, N. gamezi, N. guanacaste, N. picadoi,* and *N. saslaya*) and three newly proposed taxa described herein below. With the addition of fresh material collected by BK from near the type locality of *Nototriton major* that strongly agreed morphologically with the diagnositic characteristics of that taxon (Good and Wake 1993) we were able make a detailed taxonomic review of this species. *Nototriton major* was previously known from just a single specimen ever collected, the holotype, and no genetic material was available until now for analysis. Following our comparison of the morphological characteristics, genetics, and geographic proximity of known sites, we concluded that *N. major* can best be recognized as a junior synonym of *Nototriton picadoi*. Additionally, following our detailed review of the situation regarding *Nototriton matama*, in similar manner, we propose that this taxon also be recognized as a junior synonym of *N. picadoi*, due to its very low genetic distance and weakly supported morphological diagnostics that are more of a result of poorly preserved specimens than actual characteristics present on living or well preserved individuals.

Distribution. The nine members of the subgenus *Nototriton* are known to have a disjunct distribution, with *N. saslaya* only being known from two high-elevation sites in northern Nicaragua, whereas the remaining eight species are known to be restricted to the Caribbean slopes of Costa Rica. The members of this subgenus are known from elevations ranging between roughly 750–2500 masl (Fig. 10).

***Nototriton kenorum* sp. nov.**

Kens' moss salamander

Holotype. UCR 23685 (Figs. 11–13), an adult female from Costa Rica: Provincia de Limón: Cantón de Guácimo: Distrito de Guácimo: along edge of small road on the northern slopes of the Turrialba Volcano, approximately 9 kilometers south of Jiménez, ca. 750 m a.s.l., collected by Brian Kubicki on 10 May 2014.

FIGURE 11. Holotype of *Nototriton kenorum* **sp. nov.** in life on white background. Photograph by BK.

Paratopotypes. UCR 23686 and UCR 23687, same collection data as the holotype. UCR 23688, same locality data as the holotype, but collected by Brian Kubicki on 23 July 2016.

Generic Placement. Assigned to the genus *Nototriton* due to having fewer than 14 costal grooves, reduced *manus* and *pes* that are longer than wide, and the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

Subgeneric Placement. *Nototriton kenorum* is assigned to the subgenus *Nototriton* due to its known geographic distribution (endemic to Costa Rica), its small hands and feet with the majority of the lengths of fingers II, III, and IV and toes II, III, IV, and V being free of extended palmar or plantar tissue, and by the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

Diagnosis. The combination of the following characteristics can be used to distinguish *Nototriton kenorum* from the other described species of the subgenus *Nototriton*: (1) having small hands and feet, with at least the distal phalanges on the fingers II, III, and IV and toes II, III, IV, and V being free of the margin of the palmar and plantar tissue; (2) tiny nostril openings, both RNW and LNH not known to exceed 0.09 mm; (3) a wide head, with HeW known to exceed 4.5 mm; (4) very narrow hands and feet, narrowest among the known members of the subgenus *Nototriton* within Costa Rica, HaW not known to exceed 34.1 % of HeW and FoW not known to exceed 43.2% of HeW; (5) 16S, COI, and cyt *b* mtDNA distances.

FIGURE 12. Dorsal, lateral, and ventral views of the body of the holotype of *Nototriton kenorum* **sp. nov.** in preservation. Photograph by BK.

FIGURE 13. Dorsal views of the hand and foot and detail of the face of the holotype of *Nototriton kenorum* **sp. nov.** in preservation. Photograph by BK.

Description of holotype. Adult female having a total length of 73.5 mm and SL of 33.5 mm. Head slightly wider than neck and shoulders (HeW 4.4 mm, NeW 4.1 mm, ShW 4.0 mm), with greatest width of head just posterior to the articulation of the jaws; snout raised anterodorsally, spadate to rounded in dorsal outline, and rounded in profile; snout relatively short (SnL 1.1 mm, 3.3 % of SL), with nearly terminal non-protruding tiny nostrils (LNH 0.09 mm, RNW 0.09 mm) directed anterolaterally; internarial area convex in dorsal outline. Eyes relatively large (EW = 145 % of SnL), protruding beyond dorsal and ventral outline of head, directed anterolaterally, with a distinct suborbital groove. Top of head flat and smooth, tapering slightly toward anterior terminus, lacking contrasting interorbital or other dermal structures. Canthus rostralis weak to rounded along posterior half, indiscernible along anterior half; intercanthal area flat to slightly convex; and loreal region flat to slightly concave. No obvious cirri (nasolabial protuberances) present, but nasolabial grooves very weakly discernible on tip of snout; nasolabial grooves start at lateral margins of nares and extend ventrally at first, but take a drastic backwards curve about halfway to lip; nasolabial grooves terminate just prior to reaching margin of upper lip. Gular fold well-defined, starting on dorsolateral portion of neck, below postorbital groove, wrapping around posterolateral section of head at a slightly anterior angle and crossing venter as a smooth and weak anterior-oriented curve. Nuchal grooves weakly evident, starting above postorbital groove and converging medially at occiput. Postorbital grooves weakly defined, starting at the posterior corner of eyes and traveling horizontally along the inferior margin of parotoid glands, terminating at gular fold on the lateral portion of neck. Horizontal mandibular grooves weakly discernible, but vertical mandibular groove well-defined. Horizontal mandibular groove starting at corner of mouth and extending horizontally to vertical portion of mandibular groove. Mandibular groove existing as a single solid structure, starting along inferior margins of postorbital grooves and traveling vertically to and crossing gular region, just posterior of inner mandibular grooves. Inner mandibular grooves weakly evident, principally discernible for a small section, running medially parallel to posterior portion of mandibular bones, becoming indiscernible near anterior tip of lower jaw. Pair of very weakly, but discernible, raised parotoid glands present on dorsolateral margin of head between orbits, postorbital grooves, and occiput. Snout not evidently protruding beyond anterior margin of lower lip in lateral view. No mental gland visible under skin of anterior intermandibular region.

Arms relatively long and slender overall (FLL = 4.8 mm, 14.3 % of SL), without noticeable hypertrophied forearm compared to upper arm. Hands very small and slender (HaL = 1.7 mm, 26.6 % of VGS; HaW = 1.5 mm, 34.1 % of HeW). Fingers II, III, and IV short and thick, protruding freely, with at least ultimate and all to part of penultimate phalanges being free beyond interdigital tissue margin (LF2 0.62 mm, LF3 0.53 mm); no discernible indentation at interdgital space between fingers I and II. Tips of fingers rounded, with terminal pads discernible on ventral surface. Palmar surfaces appearing to be smooth overall. Dorsal surfaces of hands with discernible interdigital grooves, especially between fingers II-III and III-IV, that start at interdigital tissue margins and cross onto metacarpal region. Relative lengths of fingers on right hand I < IV < II < III.

Legs relatively long and slender overall (HLL 5.3 mm, 15.8 % of SL), with lower leg being very slightly thicker than upper leg. Feet very small and slender (FoL 2.3 mm, 35.9 % of VGS; FoW 1.9 mm, 43.2 % of HeW). Toes II, III, IV and V protruding freely, with at least ultimate (toes II, IV, and V) and penultimate (Toe III) phalanges being free beyond interdigital tissue margin (LT2 0.78 mm, LT3 0.65 mm), Toe I with very minimal indentation at interdgitial space. Tips of toes rounded, with terminal pads discernible on ventral surfaces. Plantar surfaces appearing to be smooth overall, without any evident dermal creases. Dorsal surfaces of feet with discernible interdigital grooves, especially between toes II-III, III-IV, and IV-V, which start at interdigital tissue margins and cross onto metatarsal region. Relative lengths of toes on right foot I < V < II < IV < III.

Body subcylindrical (slightly wider than high) in cross section, and relatively robust (TW = 4.4 mm; TW = 22.8 % of AGL). Between axilla and groin, 11 costal grooves visible, 13 if counting axillary and inguinal grooves; costal grooves most visible on ventral and lateral portions of body. Adpressed limbs separated by six costal folds; 12 costal folds total between axilla and groin. Slight middorsal depression extends longitudinally along length of body, starting at base of head (occiput) and becoming indiscernible on anterior portion of tail. Tail long, 40.0 mm in length, cylindrical in cross section, having a weakly discernible constriction at base, and evenly tapering to pointed terminus; in life, approximately 20 caudal grooves discernible on anterior 4/5$^{\text{ths}}$ of tail. Skin on surfaces of head, body, limbs, and tail smooth.

Coloration in life. The ground color of the dorsal and lateral surfaces of the head and trunk consisted of a nearly uniform fleshy-orange coloration. There were not many secondary markings on the dorsal and lateral surfaces of the head and trunk, but a small concentration of larger irregular dark brown markings were visible on the snout, nuchal region, and hips. Additionally, there were numerous very fine white chromatophores scattered thourghout the dorsal dorsal and lateral surfaces of the head and body. The iris was bright orangish-red with a dark brownish-maroon reticulation.

The upper surfaces of the arms and legs were very similar in coloration and pattern to that of the above-mentioned chromatic characteristics of the dorsal and lateral surfaces of the head and body, but there appeared to be a slightly brighter orange hue on the dorsal surfaces of the limbs.

The dorsal and dorsolateral surfaces of the tail were nearly uniform fleshy-orange, but were similar to that of the limbs in having a slightly more brighter orange hue. Additionally, there were some irregular dark brown patches, one very evident patch was found about one third down (anterior towards posterior orientation) the length of the tail. As on the rest of the dorsal and lateral surfaces of the holotype, numerous very fine white chromatophores were visible scattered randomly throughout the tail.

The ventrolateral surfaces of the head, limbs, body, and tail were contrasted from the superior surfaces by consisting of a concentration of fine white or pale fleshy-orange markings on a darker brownish-gray background. The gular patch was slightly more pale in comparison to the other ventral surfaces. The palmar and plantar surfaces were pale gray, lacking discernible chromatophores, however a red reticulated pattern was discernible under the skin, formed by a network of blood-filled capillaries.

Coloration in ethanol. After more than five years in ethanol (70%), the overall coloration of the holotype has darkened throughout and contains a principal dark brown tone on the dorsal surfaces of the head and body. Two pale tannish-yellow patches are visible on the posterior dorsolateral surfaces of the head, where the parotoid glands are located. The dorsal surface of the entire tail is also a pale tannish-yellow coloration, with the exception of a darker brownish gray transversal band, located about one third down (anterior towards posterior orientation) the length of the tail. The ventral surfaces of the body and tail are darker brownish-gray. The ventral surface of the head has an evident paler tone compared to that of the rest of the body and tail.

Measurements (in mm), limb interval, and percentages of the holotype. SL 33.5; total length 73.5; tail length 40.0; ShW 4.0; HeW 4.4; NeW 4.1; EW 1.6; SnL 1.1; JSL 3.9; LGFS 7.0; LNH 0.09; RNW 0.09; IND 1.1; NLP 0.5; ICD 2.0; HLL 5.3; FLL 4.8; TW 4.4; VGS 6.4; FSL 8.6; UHL 3.6; AGL 19.3; VL 1.9; HaW 1.5; HaL 1.7; LF2 0.62; LF3 0.53; WF3 0.40; FoW 1.9; FoL 2.3; LT2 0.78; LT3 0.65; WT3 0.43. Limb interval six. Measurements in related percentages: VGS/SL 19.1 %; IND/HeW 25.0 %; AGL/SL 57.6 %; HeW/SL 13.1 %; Hew/AGL 22.8 %; SnL/ HeW 25.0 %; LNH/HeW 2.0 %; LNH/SL 0.27 %; RNW/HeW 2.0 %; RNW/SL 0.27 %; HLL/SL 15.8 %; FLL/SL 14.3 %; HaL/VGS 26.6 %; FoL/VGS 35.9 %; Haw/HeW 34.1 %; FoW/HeW 43.2 %; LT2/FoL 33.9 %; LF2/HaL 36.5 %; WT3/FoW 22.6 %; WF3/HaW 26.7 %.

Noteworthy variation. The paratopoype UCR 23688 had discernible nasolabial protruberences that extended slightly beyond the upper lip margin, where as the holotype and other two paratopotypes did not have evident nasolabial protruberences. Additionally, UCR 23688 completely lacked any discernible nostril openings, even when viewed under a disecting scope at 30x magnification. Although we did not perform any internal examination to determine the sexes of the type series specimens, we feel that it is very likely that UCR 23688 is a male and the holotype UCR 23685 and the other two paratopotypes (UCR 23686 and UCR 23687) are females**.**

Measurements (in mm), limb intervals, and percentages of the paratopotypes. SL 27.5–31.3; ShW 3.2–4.1; HeW 3.9–4.8; NeW 3.4–4.2; EW 1.3–1.5; SnL 0.9–1.2; JSL 3.3–4.1; LGFS 6.0–7.0; LNH 0.00–0.09; RNW 0.00–0.09; IND 0.9–1.1; NLP 0.4–0.7; ICD 1.7–2.1; HLL 4.8–6.0; FLL 4.3–5.0; TW 3.3–4.4; VGS 5.1–5.9; FSL 7.5–8.2; UHL 3.1–3.8; AGL 16.5–17.8; VL 1.6–1.9; HaW 1.1–1.5; HaL 1.3–1.8; LF2 0.65–0.78; LF3 0.47–0.68; WF3 0.28–0.43; FoW 1.4–1.9; FoL 1.8–2.3; LT2 0.50–0.87; LT3 0.71–0.87; WT3 0.28–0.43. Limb intervals six . Measurements in related percentages: VGS/SL 18.4–18.8 %; IND/HeW 21.4–25.6 %; AGL/SL 56.9–58.2 %; HeW/SL 14.2–15.3 %; Hew/AGL 22.5–27.0 %; SnL/HeW 21.4–25.0 %; LNH/HeW 0.0–2.1 %; LNH/SL 0.0–0.31 %; RNW/HeW 0.0–1.9 %; RNW/SL 0.0–0.28 %; HLL/SL 17.5–19.2 %; FLL/SL 15.6–16.0 %; HaL/VGS 25.5–30.5 %; FoL/VGS 35.3–39.0 %; Haw/HeW 28.2–31.3 %; FoW/HeW 35.9–39.6 %; LT2/FoL 21.7–43.5 %; LF2/HaL 43.3–50.0 %; WT3/FoW 17.5–22.6 %; WF3/HaW 23.3–28.6 %.

Etymology. The specific epithet "*kenorum*" is a patronym, used as a noun in the plural masculine genitive case. This taxon is named in honor of Kenneth Marc Kubicki (1946–2008), the father of the senior author who was always very supportive of BK's interests, including a life-long passion with nature (especially fishes and amphibians) and natural history. Additionally, this taxon is named for Kenneth Marc Kubicki-Reyes (2009–), the son of BK and AR; to symbolize our hope and optimism with the continued study, protection, and appreciation of our world's natural resources, which are soon going to fall into the hands of our children and their future generations.

Habitat and natural history observations. *Nototriton kenorum* has been found exclusively within moss growing on the trunks and branches of trees. More than twenty different individuals of *N. kenorum* have been observed by the senior author in the wild, and all were found within moss in arboreal situations. Likely *N. kenorum* can also inhabit moss and other microhabitats that offer similar physical parameters, growing on rocks and terrestrial surfaces, but until now none have been discovered to inhabit such sites.

Distribution. *Nototriton kenorum* is endemic to Costa Rica, and currently only known to inhabit a very small section of unusually low elevation cloud forest habitat within the lower portion of the Tropical Premontane Rainforest life zone (Holdridge 1967) along the northern slopes of the Turrialba Volcano. The known altitudinal range for *N. kenorum* is from ca. 775–900 masl. This is the only species of Costa Rican moss salamander that is thus far known to exclusively inhabit elevations below 1000 masl.

***Nototriton lateomuscus* sp. nov.**

San Ramon moss salamander

Holotype. UCR 23694 (Figs. 14–16), an adult female from Costa Rica: Provincia de Alajuela: Cantón de San Ramón: Distrito de Angeles: Edge of road, approximately 3 kilometers west of Balsa, ca. 1200 m a.s.l., collected by Brian Kubicki in the company of Aura Reyes on 21 October 2016.

FIGURE 14. Holotype of *Nototriton lateomuscus* **sp. nov.** in life on white background. Photograph by BK.

Paratopotypes. UCR 23695, same collection data as the holotype. UCR 23696, same locality data as the holotype, but collected by Brian Kubicki in the company of Aura Reyes on 12 October 2013.

Generic Placement. Assigned to the genus *Nototriton* due to having fewer than 14 costal grooves, reduced *manus* and *pes* that are longer than wide, and the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

Subgeneric Placement. *Nototriton lateomuscus* is assigned to the subgenus *Nototriton* due to its known geographic distribution (endemic to Costa Rica), its small hands and feet with the majority of the lengths of fingers II, III, and IV and toes II, III, IV, and V being free of extended palmar or plantar tissue, and by the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

Diagnosis. *Nototriton lateomuscus* is distinguished from the other described species of the subgenus *Nototriton* by its16S, COI, and cyt *b* mtDNA distances.

Comparisons. Since the molecular evidence presented herein strongly supports *N. lateomuscus* forming part of clade with *N. abscondens* and *N. gamezi*, and due to the fact that all three of these species have adjoining distributions, morphological comparisons are only going to be focused on distinguishing *N. abscondens* and *N. gamezi* from *N. lateomuscus*.

Contrasting characteristics for *Nototriton lateomuscus* are presented in parentheses. *Nototriton abscondens* (Taylor, 1948) can be distinguished from *N. lateomuscus* by having relatively smaller nostril openings, average LNH = 0.16 mm and RNW = 0.16 (average LNH = 0.21 mm and RNH = 0.2 mm); wider internarial distance, average IND = 0.9 mm (average IND = 0.7 mm). *Nototriton gamezi* (García-París & Wake, 2000) has larger nostril openings, average LNH = 0.29 mm and RNH = 0.24 mm (average LNH = 0.21 mm and RNH = 0.2 mm).

FIGURE 15. Dorsal, lateral, and ventral views of the body of the holotype of *Nototriton lateomuscus* **sp. nov.** in preservation. Photograph by BK.

Description of holotype. Adult female having a total length of 66.2 mm and SL of 29.3 mm. Head slightly wider than neck and shoulders (HeW 4.0 mm, NeW 3.3 mm, ShW 3.4 mm), with greatest width of head just posterior to the articulation of the jaws; snout raised anterodorsally, spadate to rounded in dorsal outline, and rounded in profile; snout relatively short (SnL 1.0 mm, 3.4 % of SL), with nearly terminal non-protruding large nostrils (LNH 0.25 mm, RNW 0.25 mm) directed anterolaterally; internarial area convex in dorsal outline. Eyes relatively large (EW = 130 % of SnL), protruding beyond dorsal outline of head, directed anterolaterally, with a distinct suborbital groove. Top of head flat and smooth, tapering slightly toward anterior terminus, lacking contrasting interorbital or other dermal structures. Canthus rostralis rounded; intercanthal area flat to slightly convex; and loreal region flat to slightly concave. No obvious cirri (nasolabial protuberances) present, but nasolabial grooves weakly discernible on tip of snout; nasolabial grooves start at lateral margins of nares and extend ventrally with a slight outward orientation; nasolabial grooves start at lateral margins of nares and extend ventrally at first, but take a drastic backwards curve about halfway to lip; nasolabial grooves terminate just prior to reaching margin of upper lip. Gular fold well-defined, starting on lateral portion of neck, below postorbital groove, wrapping around posterolateral section of head at a slightly anterior angle and crossing venter as a smooth and anterior-oriented curve. Nuchal grooves very weak to indiscernible. Postorbital grooves discernible, starting at posterior corner of eyes and traveling horizontally along the inferior margin of parotoid glands, terminating at gular fold on the lateral portion of neck. Horizontal mandibular grooves indiscernible, but vertical mandibular groove well-defined. Vertical mandibular grooves starting at inferior margins of postorbital grooves and extending vertically to and crossing onto gular region, but becoming indiscernible just medially of inner mandibular grooves. Inner mandibular grooves evident, nearly forming a single curving structure, but become indiscernible at anterior portion of gular patch. Pair of very weakly but discernibly raised parotoid glands present on dorsolateral margin of head between orbits, postorbital grooves, and occiput. Upper lip protruding slightly beyond edge of lower lip in ventral and lateral views; no mental gland discernible under skin of anterior intermandibular region.

FIGURE 16. Dorsal views of the hand and foot and detail of the face of the holotype of *Nototriton lateomuscus* **sp. nov.** in preservation. Photograph by BK.

Arms relatively long and slender overall (FLL = 4.9 mm, 16.7 % of SL), without noticeable hypertrophied forearm compared to upper arm. Hands small and slender (HaL = 1.6 mm, 29.1 % of VGS; HaW = 1.4 mm, 25 % of HeW). Fingers II, III, and IV protruding freely, with at least ultimate and all to part of penultimate phalanges being free beyond interdigital tissue margin (LF2 0.74 mm, LF3 0.56 mm). Finger I with minimal indentation at interdgitial space. Tips of fingers rounded, with terminal pads discernible on ventral surfaces. Palmar surfaces appearing to be smooth overall, but with weakly discernible depressions radiating out from palmar section to interdigital margins between fingers. Dorsal surfaces of hands with discernible interdigital depressions or grooves, especially between fingers II-III and III-IV, that start at interdigital tissue margins and cross onto metacarpal region. Relative lengths of fingers on right hand I < IV < II < III.

Legs relatively long and slender overall (HLL 5.9 mm, 20.1 % of SL), without discernible differences between thickness of lower and upper legs. Feet small and slender (FoL 2.1 mm, 38.2 % of VGS; FoW 1.6 mm, 40.0 % of HeW). Toes II, III, IV and V protruding freely, with at least ultimate (toes II and V) and penultimate (toes III and IV) phalanges being free beyond interdigital tissue margin (LT2 0.9 mm, LT3 0.68 mm). Toe I with very minimal indentation at interdgitial space. Tips of toes rounded, with terminal pads discernible on ventral surfaces. Plantar surfaces appearing to be smooth overall, but with very weakly discernible depressions or groove along interdigital spaces. Dorsal surfaces of feet with discernible interdigital grooves, especially between toes II-III, III-IV, and IV-V, that start at interdigital tissue margins and cross onto metatarsal region. Relative lengths of toes on right foot I < V < II < IV < III.

Body subcylindrical (slightly wider than high) in cross section, and relatively slender (TW = 3.3 mm; TW = 19.7 % of AGL). Between axilla and groin, 11 costal grooves visible, 13 if counting axillary and inguinal grooves; costal grooves most visible on ventral and lateral portions of body. Adpressed limbs separated by 4.5 costal folds; 12 costal folds total between axilla and groin. Slight middorsal depression extends longitudinally along length of body, starting at base of head (occiput) and becoming indiscernible on anterior portion of tail. Tail long, 36.9 mm in length, cylindrical in cross section, lacking a discernible constriction at base, evenly tapering from cloaca to pointed terminus. Skin on surfaces of head, body, limbs, and tail smooth.

Coloration in life. The ground color of the dorsal and lateral surfaces of the head and trunk consisted of a brownish-orange coloration. Scattered throughout the dorsal and lateral surfaces of the head and trunk there were numerous dark brownish-black markings of irregular size and shape, in addition to numerous very fine white chromatophores. The parotoid glands where a contrasted paler tone compared to the surrounding dorsal surfaces. The iris was bright copper-orange with a black reticulation.

The upper surfaces of the arms and legs are very similar in coloration and pattern to that of the above-mentioned chromatic characteristics of the dorsal and lateral surfaces of the head and body.

The dorsal and dorsolateral surfaces of the anterior third of the tail were a paler shade of reddish-orange, but the posterior two-thirds of the tail was similar to dorsal surfaces of the trunk. There were also some very fine white chromatophores scattered randomly throughout the tail, but at a much lesser concentration compared to the body and head.

The ventral and ventrolateral surfaces of the head, limbs, and body were contrasted from the superior surfaces by consisting of a concentration of fine white chromatophores on a darker brownish-gray background. The gular patch was slightly more pale in comparison to the ventral surfaces of the trunk. The palmar and plantar surfaces were pale grayish-brown, lacking evident chromatophores. Directly surrounding the cloaca there was a concentration of bright orange chromatophores. The anterior third of the vental surface of the tail had an overall similar pattern and coloration to that of the ventral surface of the trunk. The ventral surface along the posterior two-thirds of the tail had a dark reddish orange ground color with numerous dark brown markings of irregular size and shape in addition to a relatively large concentration of very fine white chromatophores.

Coloration in ethanol. After more than a year and a half in ethanol (70%), the overall coloration of the holotype has changed to principally consisting of a mixture of tan and brown mottling. Two pale tannish-yellow patches are visible on the posterior dorsolateral surfaces of the head, where the parotoid glands are located. The dorsal surface of the anterior third of the tail is also pale tannish-yellow. The ventral surfaces of the body and tail are dark brownish-gray. The ventral surface of the head has an evident paler tone compared to that of the rest of the body and tail.

Measurements (in mm), limb interval, and percentages of the holotype. SL 29.3; total length 66.2; tail length 36.9; ShW 3.4; HeW 4.0; NeW 3.3; EW 1.3; SnL 1.0; JSL 3.4; LGFS 6.0; LNH 0.25; RNW 0.25; IND 0.8; NLP 0.5; ICD 1.6; HLL 5.9; FLL 4.9; TW 3.3; VGS 5.5; FSL 8.0; UHL 3.3; AGL 16.7; VL 1.9; HaW 1.4; HaL 1.6; LF2 0.74; LF3 0.56; WF3 0.31; FoW 1.6; FoL 2.1; LT2 0.9; LT3 0.68; WT3 0.31. Limb interval 4.5. Measurements in related percentages: VGS/SL 18.8 %; IND/HeW 20.0 %; AGL/SL 57.0 %; HeW/SL 13.7 %; Hew/AGL 24.0 %; SnL/ HeW 25.0 %; LNH/HeW 6.3 %; LNH/SL 0.85 %; RNW/HeW 6.3 %; RNW/SL 0.85 %; HLL/SL 20.1 %; FLL/SL 16.7 %; HaL/VGS 29.1 %; FoL/VGS 38.2 %; Haw/HeW 35.0 %; FoW/HeW 40.0 %; LT2/FoL 42.9 %; LF2/HaL 46.3 %; WT3/FoW 19.4 %; WF3/HaW 22.1 %.

Measurements (in mm), limb intervals, and percentages of the paratopotypes. SL 19.2–26.6; ShW 2.5–3.0; HeW 3.0–3.3; NeW 2.5–3.1; EW 1.2–1.3; SnL 0.6–1.0; JSL 2.4–3.3; LGFS 4.5–5.7; LNH 0.12–0.25; RNW 0.14–

0.22; IND 0.7; NLP 0.3–0.4; ICD 1.4–1.7; HLL 4.5–4.9; FLL 3.9–4.6; TW 2.5–3.4; VGS 3.9–4.9; FSL 5.7–7.5; UHL 2.4–3.2; AGL 11.4–15.1; VL 1.6; HaW 0.9–1.1; HaL 1.1–1.2; LF2 0.37–0.57; LF3 0.34–0.4; WF3 0.22–0.23; FoW 1.1–1.5; FoL 1.4–1.6; LT2 0.53–0.65; LT3 0.37–0.56; WT3 0.25. Limb interval 4–6 . Measurements in related percentages: VGS/SL 18.4–20.3 %; IND/HeW 21.2–23.3 %; AGL/SL 56.8–59.4 %; HeW/SL 12.4–15.6 %; Hew/AGL 21.9–26.3 %; SnL/HeW 20.0–30.3 %; LNH/HeW 3.6–8.3 %; LNH/SL 0.45–1.3 %; RNW/HeW 4.2–7.3 %; RNW/SL 0.53–1.1 %; HLL/SL 18.4–23.4 %; FLL/SL 17.3–25.5 %; HaL/VGS 24.5–28.2 %; FoL/VGS 32.7–35.9 %; Haw/HeW 30.0–33.3 %; FoW/HeW 36.7–45.5 %; LT2/FoL 37.9–40.6 %; LF2/HaL 33.6–47.5 %; WT3/FoW 16.7–22.7 %; WF3/HaW 18.2–25.6 %.

Etymology. The specific epithet is formed from the Latin words *lateo*, which means to lie hidden, and *muscus*, which means moss. This taxon is named due to the fact that it often "lies hidden" within moss.

Habitat and natural history observations. *Nototriton lateomuscus* is known only from three specimens that have been found exclusively within moss growing on the trunks and branches of trees.

Distribution. *Nototriton lateomuscus* is endemic to Costa Rica, and currently only known to inhabit a single site on the extreme eastern margin of the Tilaran mountains (ca. 1200 masl), north of the city of San Ramon.

Nototriton maximo sp. nov.

Maximo's moss salamander

Holotype. UCR 23689 (Fig. 17), an adult female from Costa Rica: Provincia de Guanacaste: Cantón de Tiláran: Distrito de Tronadora: edge of road approximately 3 kilometers NNW of the entrance to the Santa Elena Reserve, Monteverde, ca. 1425 m a.s.l., collected by Brian Kubicki in the company of Aura Reyes on 22 February 2013.

FIGURE 17. Holotype of *Nototriton maximo* **sp. nov.** in life on white background. Photograph by BK.

Paratopotype. UCR 23690, same collection data as the holotype.

Paratypes. UCR 23691 Provincia de Guanacaste: Cantón de Tiláran: Distrito de Tronadora: edge of road approximately 200 meters NNE of the entrance of the Santa Elena Reserve, Monteverde, ca. 1600 m a.s.l., collected by Brian Kubicki in the company of Aura Reyes on 26 April 2013. UCR 23692 same locality data as UCR 23691, but collected by Brian Kubicki in the company of Aura Reyes on 5 July 2016. UCR 23693, a subadult from Costa Rica: Provincia de Alajuela: Cantón de Upala: Distrito de Aguas Claras: moss on tree trunk about 3 meters above the ground, northeastern slope of the Rincon de la Vieja Volcano, Rincon de la Vieja National Park, ca. 1450 m a.s.l., collected by Brian Kubicki in the company of Aura Reyes on 17 December 2013.

Generic Placement. Assigned to the genus *Nototriton* due to having fewer than 14 costal grooves, reduced *manus* and *pes* that are longer than wide, and the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

Subgeneric Placement. *Nototriton maximo* is assigned to the subgenus *Nototriton* due to its known geographic distribution (endemic to Costa Rica), its small hands and feet with the majority of the lengths of fingers II, III, and IV and toes II, III, IV, and V being free of extended palmar or plantar tissue, and by the molecular evidence (16S, COI, and cyt *b* mtDNA distances) presented herein.

Diagnosis. The combination of the following characteristics can be used to distinguish *Nototriton maximo* from the other described species of the subgenus *Nototriton*: (1) having small hands and feet, with at least the distal phalanges on the fingers II, III, and IV and toes toes II, III, IV, and V being free of the margin of the palmar and plantar tissue; (2) typically shorter front and hind limbs, HLL known to range from 4.1–5.2 mm and FLL known to range from 4.0–4.8 mm; (3) 16S, COI, and cyt *b* mtDNA distances.

Description of holotype. Adult female having a total length of 71.8 mm and SL of 31.9 mm. Head slightly wider than neck and shoulders (HeW 4.0 mm, NeW 3.7 mm, ShW 3.7 mm), with greatest width of head just posterior to the articulation of the jaws; snout raised anterodorsally, spadate to rounded in dorsal outline, and rounded to truncate in profile; snout relatively short (SnL 1.2 mm, 3.8 % of SL), with nearly terminal non-protruding small nostrils (LNH 0.12 mm, RNW 0.12 mm) directed anterolaterally; internarial area convex in dorsal outline. Eyes relatively large (EW = 133 % of SnL), protruding well beyond dorsal and ventral outline of head, directed anterolaterally, with a distinct suborbital groove. Top of head flat and smooth, tapering toward anterior terminus, lacking contrasting interorbital or other dermal structures. Canthus rostralis distinct; intercanthal area flat to slightly convex; and loreal region flat to slightly concave. No obvious cirri (nasolabial protuberances) present. Nasolabial grooves discernible on tip of snout, starting at lateral margins of nares and extending nearly vertically (with a slight outward angle) to a point just above upper lip margin. Gular fold well-defined, starting on dorsolateral portion of neck, below weakly discernible postorbital groove, wrapping around posteriolateral section of head at a slightly anterior angle and crossing venter as a smooth and weak anterior-oriented curve. Nuchal grooves very weak to indiscernible. Postorbital grooves very weak, nearly indiscernible, starting at the posterior corner of eyes and traveling horizontally along the inferior margin of parotoid glands, terminating at gular fold on the lateral portion of neck. Horizontal mandibular grooves nearly indiscernible, starting at corners of mouth and extending horizontally to vertical mandibular groove. Vertical mandibular grooves discernible, but weak starting along inferior margins of postorbital grooves and extending vertically to gular region, terminating at junction with inner mandibular grooves. Inner mandibular grooves evident, running medially parallel to mandibular bones, becoming indiscernible near anterior tip of lower jaw. Pair of nearly indiscernible and weakly raised parotoid glands present on dorsolateral margin of head among orbits, postorbital grooves, and occiput. Snout not evidently protruding beyond anterior margin of lower lip in lateral view. No mental gland visible under skin of anterior intermandibular region.

Arms relatively long and slender overall (FLL = 4.8 mm, 15.0 % of SL), without noticeable hypertrophied forearm compared to upper arm. Hands very small and slender (HaL = 1.7 mm, 32.1 % of VGS; HaW = 1.6 mm, 40.0 % of HeW). Fingers II, III, and IV long and slender, protruding freely, with at least ultimate and penultimate phalanges being free beyond interdigital tissue margin (LF2 0.71 mm, LF3 0.71 mm); a weak, but evident indentation at interdgitial space between fingers I and II. Tips of fingers rounded, with terminal pads discernible on ventral surfaces, especially fingers II and III. Palmar surfaces appearing to be smooth overall. Dorsal surfaces of hands with discernible interdigital grooves that start at interdigital tissue margins and cross onto metacarpal region. Relative lengths of fingers on right hand I < IV < II < III.

Legs relatively long and slender overall (HLL 5.2 mm, 16.3 % of SL), with lower leg being very slightly thicker than upper leg. Feet very small and slender (FoL 2.1 mm, 39.6 % of VGS; FoW 2.0 mm, 52.5 % of HeW). Toes II, III, IV and V protruding freely, with at least ultimate (Toe V) and penultimate (toes II, III, and IV) phalanges being free beyond interdigital tissue margin (LT2 0.79 mm, LT3 0.68 mm); very minimal to indiscernible indentation at interdgitial space between toes I and II. Tips of toes rounded, with terminal pads discernible on ventral surfaces. Plantar surfaces appearing to be smooth overall, without any evident dermal creases. Dorsal surfaces of feet with discernible interdigital grooves, especially between toes II-III, III-IV, and IV-V that start at interdigital tissue margins and cross onto metatarsal region. Relative lengths of toes on right foot I < V < II < IV < III.

Body subcylindrical (slightly wider than high) in cross section, and relatively robust (TW = 4.4 mm; TW = 22.8 % of AGL). Between axilla and groin, 11 costal grooves visible, 13 if counting axillary and inguinal grooves; costal grooves most visible on ventral and lateral portions of body. Adpressed limbs separated by six costal folds; 12 costal folds total between axilla and groin. Slight middorsal depression extends longitudinally along length of body, starting at base of head (occiput) and becoming indiscernible on anterior portion of tail. Tail long, 39.9 mm in length, cylindrical in cross section, having a very slight constriction at base, and evenly tapering to pointed terminus; in life, no caudal grooves were discernible. Skin on surfaces of head, body, limbs, and tail smooth.

Coloration in life. The ground color of the dorsal and lateral surfaces of the head and trunk reddish-orange. There were several pale fleshy colored dash-like markings on the lateral and dorsolateral surface of the body. Additionally, there were some scattered dark brown to black small irregular markings and tiny white spots on the dorsal and lateral surfaces of the head and body. The iris was dark reddish-orange with dark brownish-black reticulation.

The upper surfaces of the arms and legs were very similar in overall coloration and pattern to that of the above-mentioned chromatic characteristics of the dorsal and lateral surfaces of the head and body.

The dorsal and dorsolateral surfaces of the tail were uniform bright reddish-orange.

The ventrolateral surfaces of the head, limbs, body, and tail were contrasted from the superior surfaces by consisting of a concentration of fine white or pale fleshy-orange markings on a brown to brownish-orange background. The area directly surrounding the cloaca had a concentration of bright orange chromatophores.

Coloration in ethanol. After more than eight years in ethanol (70%), the overall ground coloration of the holotype has shifted to a pale fleshy tan dorsally. Throughtout the dorsal and dorsolateral surfaces of the head and body there are also numerous fine to medium-sized darker markings and spots; on the dorsolateral section of each side of the trunk, there are a series of darker dash-like markings. The ventral surfaces of the head, body, limbs, and tail are darker brownish-gray with very small pale patches scattered throughout.

Measurements (in mm), limb interval, and percentages of the holotype. SL 31.9; total length 71.8; tail length 39.9; ShW 3.7; HeW 4.0; NeW 3.7; EW 1.6; SnL 1.2; JSL 3.7; LGFS 6.4; LNH 0.12; RNW 0.12; IND 1.0; NLP 0.5; ICD 1.8; HLL 5.2; FLL 4.8; TW 4.4; VGS 5.3; FSL 8.0; UHL 3.6; AGL 19.3; VL 1.9; HaW 1.6; HaL 1.7; LF2 0.71; LF3 0.71; WF3 0.34; FoW 2.0; FoL 2.1; LT2 0.79; LT3 0.68; WT3 0.37. Limb interval six. Measurements in related percentages: VGS/SL 16.6 %; IND/HeW 25.0 %; AGL/SL 60.5 %; HeW/SL 12.5 %; Hew/AGL 20.7 %; SnL/ HeW 30.0 %; LNH/HeW 3.0 %; LNH/SL 0.38 %; RNW/HeW 3.0 %; RNW/SL 0.38 %; HLL/SL 16.3 %; FLL/SL 15.0 %; HaL/VGS 32.1 %; FoL/VGS 39.6 %; Haw/HeW 40.0 %; FoW/HeW 52.5 %; LT2/FoL 37.6 %; LF2/HaL 41.8 %; WT3/FoW 18.5 %; WF3/HaW 21.3 %.

Noteworthy variation. The paratype (UCR 23693) has discernible differences in the overall structure of the hands and feet, which are especially evident while comparing the digits to those of other members of the type series. The digits on the hands and feet of UCR 23693 are shorter and more tapered distally than on the other type series specimens; this could be related to ontogenesis, given the smaller size (22.0 mm) of UCR 23693, but UCR 23690, with a SL of 22.5 mm, has clearly visible differences in the structure of the digits from UCR 23693. The overall digit structure of UCR 23690 is similar to that of UCR 23689, UCR 23691, and UCR 23692.

Measurements (in mm), limb intervals, and percentages of the paratopotypes. SL 22.0–28.5; ShW 2.6–3.4; HeW 3.1–4.0; NeW 2.9–3.5; EW 1.1–1.3; SnL 0.8–1.1; JSL 2.7–3.4; LGFS 4.8–5.7; LNH 0.15–0.25; RNW 0.09–0.19; IND 0.7–1.0; NLP 0.3–0.6; ICD 1.6–1.8; HLL 4.1–5.2; FLL 4.0–4.5; TW 2.8–3.9; VGS 4.0–5.2; FSL 6.2–7.5; UHL 2.5–3.4; AGL 12.5–16.9; VL 0.9–1.4; HaW 1.0–1.4; HaL 1.0–1.5; LF2 0.47–0.68; LF3 0.43–0.68; WF3 0.22–0.31; FoW 1.3–1.7; FoL 1.4–2.0; LT2 0.53–0.76; LT3 0.4–0.71; WT3 0.25–0.34. Limb interval five–six . Measurements in related percentages: VGS/SL 18.2–19.1 %; IND/HeW 20.0–25.0 %; AGL/SL 56.8–59.3 %; HeW/SL 13.4–14.2 %; Hew/AGL 23.3–24.8 %; SnL/HeW 25.8–28.6 %; LNH/HeW 4.0–7.8 %; LNH/SL 0.56–1.11 %; RNW/HeW 2.6–5.0 %; RNW/SL 0.34–.0.71 %; HLL/SL 16.8–19.5 %; FLL/SL 15.8–18.2 %; HaL/VGS 25.0–30.2 %; FoL/VGS 34.9–39.6 %; Haw/HeW 31.3–35.5 %; FoW/HeW 40.6–42.9 %; LT2/FoL 37.9–42.7 %; LF2/HaL 41.3–47.0 %; WT3/FoW 19.2–21.5 %; WF3/HaW 20.0–28.0 %**.**

Etymology. The specific epithet "*maximo*" is a patronym, used as a noun apposition. This taxon is named in honor of Maximiliano "Maximo" Flores (1964–2016), who was a good friend and neighbor of BK and AR. Maximo's friendship and help with the efforts of the Costa Rican Amphibian Research Center and at the Guayacán Rainforest Reserve, another private property owned by BK, will always be very much appreciated. Maximo was always very willing to join BK during both diurnal and nocturnal field outings, and he accompanied BK and AR on numerous trips throughout the cloud forest regions of Costa Rica searching for moss salamanders.

Habitat and natural history observations. *Nototriton maximo* has been found within moss growing on the ground, fallen and standing tree trunks and accessable branches of trees.

Distribution. *Nototriton maximo* is endemic to Costa Rica, and currently only known to inhabit two very small distinct cloud forest regions in northwestern Costa Rica. The first region is along the continental divide just north and northwest of the Monteverde Cloud Forest Reserve. The second region is along the northern slopes of the Rincón de la Vieja Volcano. The known altitudinal range for *N. maximo* is from ca. 1425–1600 masl.

Other members of the subgenus *Nototriton*

***Nototriton* (*Nototriton*) *abscondens* (Taylor, 1948)**

Concealed moss salamander

Chiropterotriton abscondens Taylor (1948: 177).
Nototriton abscondens: Good & Wake (1993: 139).
Nototriton (*Nototriton*) *abscondens*: Dubois & Raffaëlli (2012: 141).

Holotype. RCT 1414 (Richard C. Taylor field number), by original designation, but currently housed at the Chicago Field Museum, FMNH 178285. An adult female from Costa Rica: Provincia de Alajuela: Cantón de Alajuela: Distrito de Sarapiquí: Isla Bonita: American Cinchona Plantation, ca. 5500 feet (ca. 1675 m a.s.l.), collected by Richard Clark Taylor on 1 August, 1947.

Etymology. The specific epithet comes from the Latin prefix *ab*- (meaning from or away) and *condo* (meaning hidden).

Distribution. *Nototriton abscondens* is endemic to Costa Rica and is only known to inhabit the Caribbean slopes of the Cordillera Volcánica Central at elvations from roughly 1000–2500 masl (Savage 2002). Specimens have been collected from within a swath ranging from the northern slopes of the Turrialba Volcano to the western flanks of Juan Castro Blanco National Park.

***Nototriton* (*Nototriton*) *costaricense* Arias & Kubicki, 2018**

Southern moss salamander

Holotype. UCR 22900, by original designation, a subadult from Costa Rica: Provincia de Limón: Cantón de Talamanca: Distrito de Telire: Cerro Pat, Parque Internacional La Amistad, ca. 1500 m a.s.l., obtained by Erick Arias on 11 March 2015.

Etymology. The specific epithet refers to the Spanish word meaning Costa Rican, "costaricense". The name represents the fact that the holotype and species was discovered in Costa Rica. Given the close proximity of the type locality to the Costa Rica-Panama border, we speculate that one day it may indeed be discovered within Panama as well (Arias & Kubicki 2018).

Distribution. *Nototriton costaricense* is known from a single site within the Lower Montane Rain Forest life zone (Holdridge 1967) along the mid-elevation slopes of the extreme southeastern Cordillera de Talamanca, within Parque Internacional La Amistad, in the vicinity of Cerro Pat, ca.1500 m (Arias & Kubicki 2018).

***Nototriton* (*Nototriton*) *gamezi* García-París & Wake, 2000**

Monteverde moss salamander

Nototriton gamezi García-París & Wake (2000: 55).
Nototriton (*Nototriton*) *gamezi*: Dubois & Raffaëlli (2012: 141).

Holotype. MVZ 207122, by original designation, an adult female from Costa Rica: Provincia de Alajuela: Cantón de San Ramón: Distrito de Peñas Blancas: Monteverde Cloud Forest Reserve: Carril Bosque Eterno at junction with Pantanosa Trail, 1600 m a.s.l. (N 10°19', W 84°47.5'), collected by D. C. Cannatella, D. A. Good, W. Guindon, and D. B. Wake on 14 August 1987.

Etymology. The specific epithet is a patronym, used as a noun in the masculine genitive case, in dedication to Mr. Rodrigo Gámez, the first director of the Instituto Nacional de Biodiversidad (García-París & Wake 2000).

Distribution. *Nototriton gamezi* is currently only known to inhabit the Monteverde Cloud Forest Reserve between roughly 1500–1600 masl, but following further exploration in the surrounding mountains its range will likely extend beyond the reserve.

***Nototriton* (*Nototriton*) *guanacaste* Good & Wake, 1993**

Guanacaste moss salamander

Nototriton guanacaste Good & Wake (1993: 138).
Nototriton (*Nototriton*) *guanacaste*: Dubois & Raffaëlli (2012: 141).

Holotype. MVZ 207111, by original designation, an adult male from Costa Rica: Provincia de Guanacaste: Cantón de Liberia: Distrito de Mayorga: Guanacaste National Park: upper slopes of the Cacao Volcano, 1580 m a.s.l., collected by D. C. Cannattela and D. A. Good on 24 August 1987 (Good & Wake 1993).

Etymology. The specific epithet is a noun in apposition and was chosen in celebration of establishment of Guanacaste National Park, where this species is known to be restricted (Good & Wake 1993).

Distribution. *Nototriton guanacaste* is currently only known to inhabit two small patches of cloud forest within Guanacaste National Park, both located on the upper slopes of the Orosi and Cacao volcanoes between roughly 1400–1650 masl (Savage 2002).

***Nototriton* (*Nototriton*) *picadoi* (Stejneger, 1911)**

Picado's moss salamander

Spelerpes picadoi Stejneger (1911: 285).
Oedipus picadoi: Dunn (1924: 99).
? *Pseudoeurycea picadoi*: Taylor (1949: 279).
Chiropterotriton picadoi: Wake & Lynch (1976: 59).
Nototriton picadoi: Wake & Elias (1983: 11).
Nototriton major Good & Wake (1993: 137).
Nototriton matama Boza-Oviedo *et al*. (2012: 48).
Nototriton (*Nototriton*) *picadoi*: Dubois and Raffaëlli (2012: 141).

Holotype. USNM 48280, by original designation, gender not provided in the description: Provincia de Cartago: Cantón de El Guarco: Distrito de San Isidro: La Estrella, ca. 2000 m a.s.l. (Picado 1913), Collected by Clodomido Picado (Stejneger 1911).

Etymology. The specific epithet is a patronym, used as a noun in the masculine genitive case, in dedication to Dr. Clodomiro Picado Twight (1887–1944), who was a very distinguished Costa Rican scientist and the person that collected the holotype of this taxon.

Distribution. *Nototriton picadoi* is endemic to Costa Rica and is only known to inhabit the Caribbean slopes of extreme eastern portion of the Cordillera Volcánica Central, specifically along the eastern flank of the Turrialba Volcano into the northern and eastern sections of the Cordillera de Talamanca. The reported altitudinal range for this taxon is from 1200–2200 masl (Savage 2002), but during this study the lower limit was discovered to extend down to 900 masl (BK personal observation).

Noteworthy observations or remarks. Due to the very low genetic distances, adjoining distributional ranges, and weakly supported morphological diagnostics, we herein recognized *N. major* (Good & Wake, 1993) and *N. matama* (Boza-Oviedo *et al*., 2012) as junior synonyms under *N. picadoi*.

***Nototriton* (*Nototriton*) *saslaya* Köhler, 2002**

Saslaya moss salamander

Nototriton saslaya Köhler, 2002: 205).
Nototriton (*Nototriton*) *saslaya*: Dubois & Raffaëlli (2012: 141).

Holotype. SMF 79408, by original designation, an adult female from Nicaraugua: Región Autónoma Atlático Norte: southern slope of the Cerro Saslaya, 1371 m a.s.l., collected by Gunther Köhler on 12 July 1999 (Köhler 2002).

Etymology. The specific epithet is a noun in apposition and was chosen in reference to the type locality and mountain where the type series of the species was collected and where it is probably restricted (Köhler 2002).

Distribution. *Nototriton saslaya* is currently only known to inhabit two small patches of cloud forest within Saslaya National Park in north-central Nicaragua, Cerro Saslaya and Cerro El Torro, 1280 to 1370 m.a.s.l. (Köhler 2011).

Discussion

Defining the alpha-level taxonomy among the Costa Rican members of the genus *Nototriton* is not an easy matter. These tiny salamanders are very conservative in regards to the presence of morphological characters, especially those that can be detected and measured. The miniaturized stature of Costa Rican moss salamanders complicates this due to the fact that if any such morphological characters might exist, in our experience, even through detailed examination under magnification, they are simply too small for us to perceive. Not only did we run into the above-mentioned difficulty in being able to perceive clearly repeated phenotypic traits to consistently delineate the separation of species, but even our analysis of the genetic differences gave us confusing results due to the lack of deep divergences among the samples taken from different sites or populations throughout Costa Rica. Prior to our study, eight species of salamanders belonging to the genus *Nototriton* were known to exist in Costa Rica (*Nototriton abscondens, N. gamezi, N. major*, *N. matama*, *N. picadoi*, *N. richardi*, and *N. tapanti*). These species had been proposed during previous works byStejneger 1911; Taylor 1948; Taylor 1949; Good & Wake 1993; Garcia-Paris & Wake 2002; Boza *et al.* 2012.

Our studies of the phenotypic and genetic evidence we had collected showed what would likely be perceived by many as very limited differences among our samples and those that were available to us on Genbank. However, despite the generally lower genetic divergences and limited phenotypic differences, we did see some very interesting results that we thought were especially significant when viewed according to the very small geographic scale of Costa Rica. Two such examples we would like to highlight here are the genetic divergences of two of the newly proposed taxa described herein and their comparison to nearby samples of other previously recognized *Nototriton* species. The first case is with the genetic divergence of two paratopotypic individuals of *Nototriton kenorum* **sp**. **nov**. (UCR 23686 and UCR 23687) and two specimens of *Nototriton abscondens* (CRARC 0277 and CRARC 0278). The 16S mitochondrial genes between UCR 23686 and CRARC 0277 and CRARC 0278 both had a divergence of 1.94%. UCR 23687 had a difference of 1.75% from both CRARC 0277 and CRARC 0278. The COI distances between UCR 23686 and CRARC 0278 was 4.65% and between UCR 23687 and CRARC 0278 4.40%. This might be viewed by many as a generally low genetic distance between two distinct species, but it is important note that the geographic distance between the sites where the above-mentioned samples of *N. kenorum* and *N. abscondens* were collected was only 4.9 kilometers. Furthermore, this 4.9 kilometers of space between these samples of *N. kenorum* and *N. abscondens* simply consisted of homogenous forest along a smooth topographic gradient, lacking any type of significant features that could be viewed as a barrier that would not allow for the potential mixture of individuals or genes. The second case is with the genetic divergence of two paratype individuals of *Nototriton maximo* **sp**. **nov**. (UCR 23691 and UCR 23692) and *N. gamezi* (CRARC 0251 and CRARC 0252). The 16S mitochondrial gene differences between UCR 23691 and CRARC 0251 and CRARC 0252 were both 1.94%. The 16S mitochondrial gene differences between UCR 23692 and CRARC 0251 and CRARC 0252 were both 1.75%. The COI gene differences between UCR 23691 and CRARC 0251 and CRARC 0252 were 2.86% and 3.02%. The COI gene differences between UCR 23692 and CRARC 0251 and CRARC 0252 were 2.58% and 2.74%. Once again, these differences might not seem like much, but when you consider that a distance of just 2.9 kilometers lies between the sites where the two specimens of *N. maximo* and the two specimens of *N. gamezi* were collected, it needs to be recognized that something very significant is definitely going on here. As in the case for the above-mentioned samples of *N. kenorum* and *N. abscondens*, the 2.9 kilometer space between the samples of *N. maximo* and *N. gamezi* consisted of only homogenous forest at a similar altitude along a ridgeline.

After trying to mentally digest all the results according to our phenotypic and genetic analysis, we were faced with the conclusion that two basic options existed for us to approach the taxonomic status of the moss salamanders of Costa Rica, especially so with the members of our redefined herein subgenus *Nototriton*. The first option consists of synonymizing all the Costa Rican members of the subgenus *Nototriton* under the senior taxon *Nototriton picadoi*. The second option consists of clearly acknowledging the limited, but very significant differences among the different populations of this subgenus throughout the country by recognizing numerous closely related but distinct species.

We decided that rather than recognize just *N. picadoi*, and in doing so undervalue the evolutionary importance of the differences we found among our samples, we would rather take the approach of trying to recognize to the fullest the importance of the differences among the different sites and populations of the subgenus *Nototriton* through the recognition of numerous closely related, but distinct taxa. With that said, we do acknowledge the potential limitations of our conclusions being that our genetic anaylses were based solely off the results of mitochondrial genes. Recent studies have shown discordance in genetic structures when comparing mitochondrial and nuclear genes (Pabijan *et. al*. 2016; Bisconti *et. al*. 2018), emphasizing the importance of including detailed nuclear genetic studies among samples. With a detailed review of the genetic structure of Costa Rican moss salamanders, one including a well-balanced sampling of nuclear genes as well, the results might support a different layout of the inter and/or intraspecific structure. Unfortuantely in the case with Costa Rican moss salamanders at the time of our study, mitochondrial genes were all that we had available to compare our samlples to so we concentrated on them for our analysis. It is with the highest hopes that in the future someone will be able to invest all the required time, money and last but not least, physical effort in the field to gather a broad sampling of Costa Rican moss salamander samples to conduct a more indepth study looking at the nuclear genetics to test our hypothesis presented herein.

Acknowledgements

We would like to acknowledge the Costa Rican Ministerio de Ambiente y Energía (MINAE) for providing BK with the following scientific collecting permits used during this study (089-2012-SINAC, 212-2012-SINAC, and SINAC-SE-CUS-PI-R-058-2016) and the Comisión Nacional para la Gestión de la Biodiversidad (CONAGEBIO) for providing the following permit to BK to conduct the molecular studies (R-028-2016-OT-CONAGEBIO). We are also grateful to Larry David Wilson and Miguel Vences for their comments and suggestions during the review process, which greatly improved the quality of the manuscript. EA would like to show a special acknowledgement to the Posgrado en Ciencias Biológicas (UNAM), and the CONACyT for the students grant (CVU/Becario) 626946/330343 for their support, which made the molecular data produced for this study possible.

References

AmphibiaWeb (2022) AmphibiaWeb: Information on Amphibian Biology and Conservation. Web application. Berkeley, California. Available from: http://amphibiaweb.org (accessed 13 March 2022)

Arias, E. & Kubicki, B. (2018) A new moss salamander, genus *Nototriton* (Caudata: Plethodontidae), from the Cordillera de Talamanca, in the Costa Rica-Panama border región. *Zootaxa*, 4369 (4), 487–500.
https://doi.org/10.11646/zootaxa.4369.4.2

Bisconti, R., Porretta, D., Arduino, P., Nascetti, G. & Canestrelli, D. (2018) Hybridization and extensive mitochondrial introgression among fire salamanders in peninsular Italy. *Scientific Reports*, 8, 13187.
https://doi.org/10.1038/s41598-018-31535-x

Boza-Oviedo, E., Rovito, S.M., Chaves, G., García-Rodríguez, A., Artavia, L.G., Bolaños, F. & Wake, D.B. (2012) Salamanders from the eastern Cordillera de Talamanca, Costa Rica, with descriptions of five new species (Plethodontidae: *Bolitoglossa*, *Nototriton*, and *Oedipina*) and natural history notes from recent expeditions. *Zootaxa*, 3309 (1), 36–61.
https://doi.org/10.11646/zootaxa.3309.1.2

Day, M. (2007) *100 Characters from Classical Mythology*. Quarto Inc., London, 160 pp.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29, 1969–1973.
https://doi.org/10.1093/molbev/mss075

Dubois, A. & Raffaëlli, J. (2012) A new ergotaxonomy of the order Urodela Duméril, 1805 (Amphibia, Batrachia). *Alytes*, 28, 77–161.

Dunn, E.R. (1924) New salamanders of the genus Oedipus with a synoptical key. *Field Museum Natural History*, Zoological Series, 12 (7), 95–100.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
https://doi.org/10.1093/nar/gkh340

Frost, D.R. (2022) Amphibian Species of the World: an Online Reference. Version 6.0. American Museum of Natural History, New York. Available from: http://research.amnh.org/herpetology/amphibia/index.html (accessed 13 March 2022)

García-París, M. & Wake, D.B. (2000) Molecular phylogenetic analysis of relationships of the tropical salamander genera

Oedipina and *Nototriton*, with descriptions of a new genus and three new species. *Copeia*, 2000, 42–70. https://doi.org/10.1643/0045-8511(2000)2000[0042:MPAORO]2.0.CO;2

Good, D.A. & Wake, D.B. (1993) Systematic studies of the Costa Rican moss salamanders, genus *Nototriton*, with descriptions of three new species. *Herpetological Monographs*, 7, 131–159. https://doi.org/10.2307/1466956

Holdridge, L.R. (1967) *Life Zone Ecology*. Revised edition. Tropical Science Center, San Jos, 206 pp.

Köhler, G. (2002) A new species of salamander of the genus Nototriton from Nicaragua (Amphibia: Caudata: Plethodontidae). *Herpetologica*, 58, 205–210. https://doi.org/10.1655/0018-0831(2002)058[0205:ANSOSO]2.0.CO;2

Köhler, G. (2011) *Amphibians of Central America*. Herpeton, Offenbach, 378 pp.

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

Kubicki, B. & Arias, E. (2016) A beautiful new yellow salamander, genus *Bolitoglossa* (Caudata: Plethodontidae), from the northeastern slopes of the Cordillera de Talamanca, Costa Rica. *Zootaxa*, 4184 (2), 329–346. https://doi.org/10.11646/zootaxa.4184.2.5

Lanfear, R., Calcott, B., Ho, S.Y. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701. https://doi.org/10.1093/molbev/mss020

Lleonart, J., Salat, J. & Torres, G.J. (2000) Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology*, 205, 85–93. https://doi.org/10.1006/jtbi.2000.2043

Meyer, C.P. (2003) Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society*, 79, 401–459. https://doi.org/10.1046/j.1095-8312.2003.00197.x

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, 1–8. https://doi.org/10.1109/GCE.2010.5676129

Moritz, C., Schneider, C.J. & Wake, D.B. (1992) Evolutionary relationships within the *Ensatina eschscholtzii* complex confirm the ring species interpretation. *Systematic Biology*, 41, 273–291. https://doi.org/10.1093/sysbio/41.3.273

Pabijan, M. Zielinski, P., Dudek, K., Stuglik, M. & Babik, W. (2017) Isolation and gene flow in a speciation continuum in newts. *Molecular Phylogenetic and Evolution*, 116, 1–12. https://doi.org/10.1016/j.ympev.2017.08.003

Palumbi, S., Martin, A., Romano, S., McMillan, W.O., Stice, L. & Grabowski, G. (1991) *The simple fool's guide to PCR. Version 2.0*. Special Publication, Department of Zoology and Kewalo Marine Laboratory, University of Hawaii, Honolulu, Hawaii, 45 pp.

R Core Team (2013) R: A Language and Environment for Statistical Computing. Available from: https://www.R-project.org/ (accessed 20 September 2022)

Rambaut, A., Suchard, M.A., Xie, W. & Drummond, A.J. (2014) Tracer. Version 1.6.1. Available from: http://beast.bio.ed.ac.uk/Tracer (accessed 20 September 2022)

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. https://doi.org/10.1093/sysbio/sys029

Rovito, S.M., Parra-Olea, G., Recuero, E. & Wake, D.B. (2015) Diversification and biogeographical history of Neotropical plethodontid salamanders. *Zoological Journal of the Linnean Society*, 175, 167–188. https://doi.org/10.1111/zoj.12271

Sambrook, J. & Russell, D.W. (2006) Purification of nucleic acids by extraction with phenol: chloroform. *Cold Spring Harbor Protocols*, 2006, pdb-prot4455. https://doi.org/10.1101/pdb.prot4455

Savage, J.M. (2002) *The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas*. The University of Chicago Press, Chicago, Illinois, 934 pp.

Sukumaran, J.M. & Holder, M.T. (2010a) SumTrees: Phylogenetic Tree Summarization. Version 4.4.0. Available from: https://github.com/jeetsukumaran/DendroPy (accessed 20 September 2022)

Sukumaran, J.M. & Holder, M.T. (2010b) DendroPy: A Python library for phylogenetic computing. *Bioinformatics*, 26, 1569–1571. https://doi.org/10.1093/bioinformatics/btq228

Stejneger, L.H. (1911) Descriptions of three new batrachians from Costa Rica and Panama. *Proceedings of the United States National Museum*, 41, 285–288. https://doi.org/10.5479/si.00963801.1857.285

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis

version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
https://doi.org/10.1093/molbev/mst197

Taylor, E.H. (1948) New Costa Rican salamanders. *Proceedings of Biological Society of Washington*, 61, 177–180.

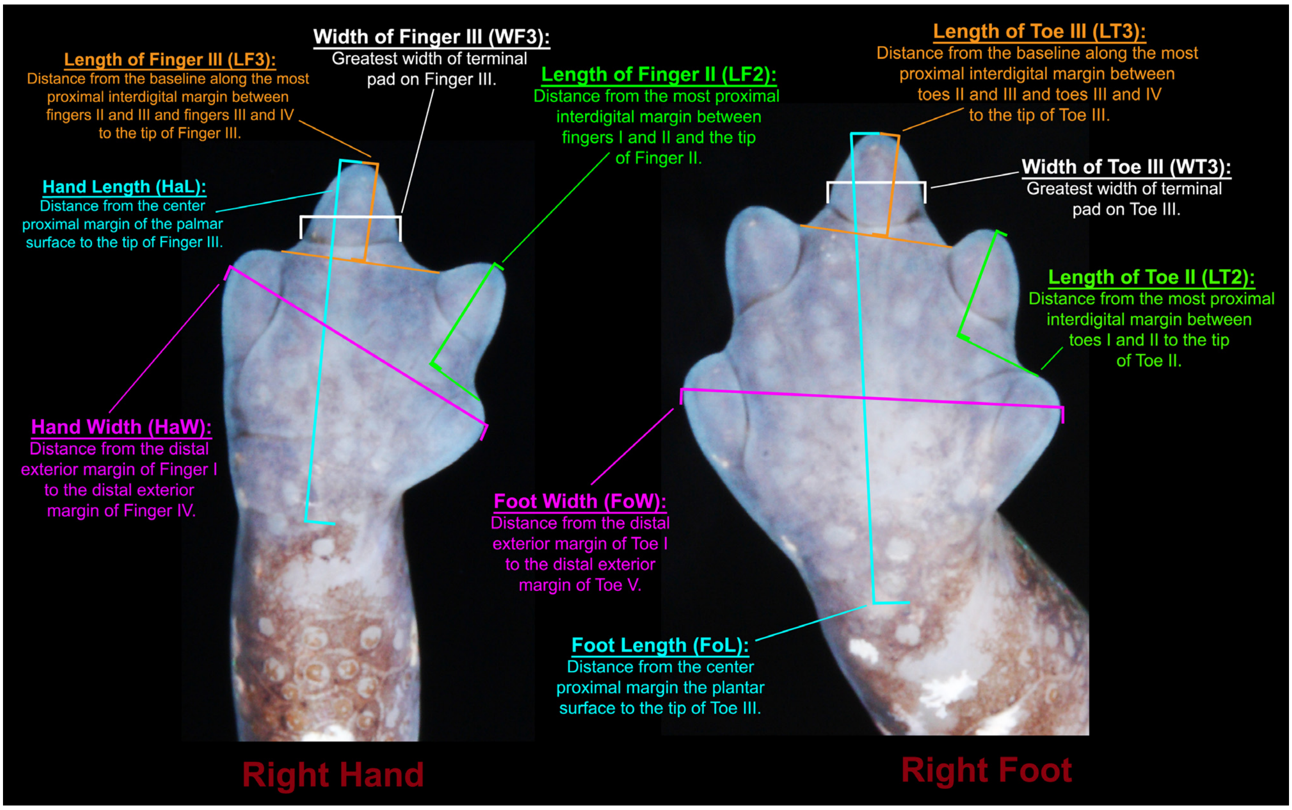
Taylor, E.H. (1949) New salamanders of Costa Rica. *University of Kansas Science Bulletin*, 33, 279–288.
https://doi.org/10.5962/bhl.part.16130

Wake, D.B. & Elias, P. (1983) New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). *Contributions in Science. Natural History Museum of Los Angeles County*, 345, 1–19.
https://doi.org/10.5962/p.208170

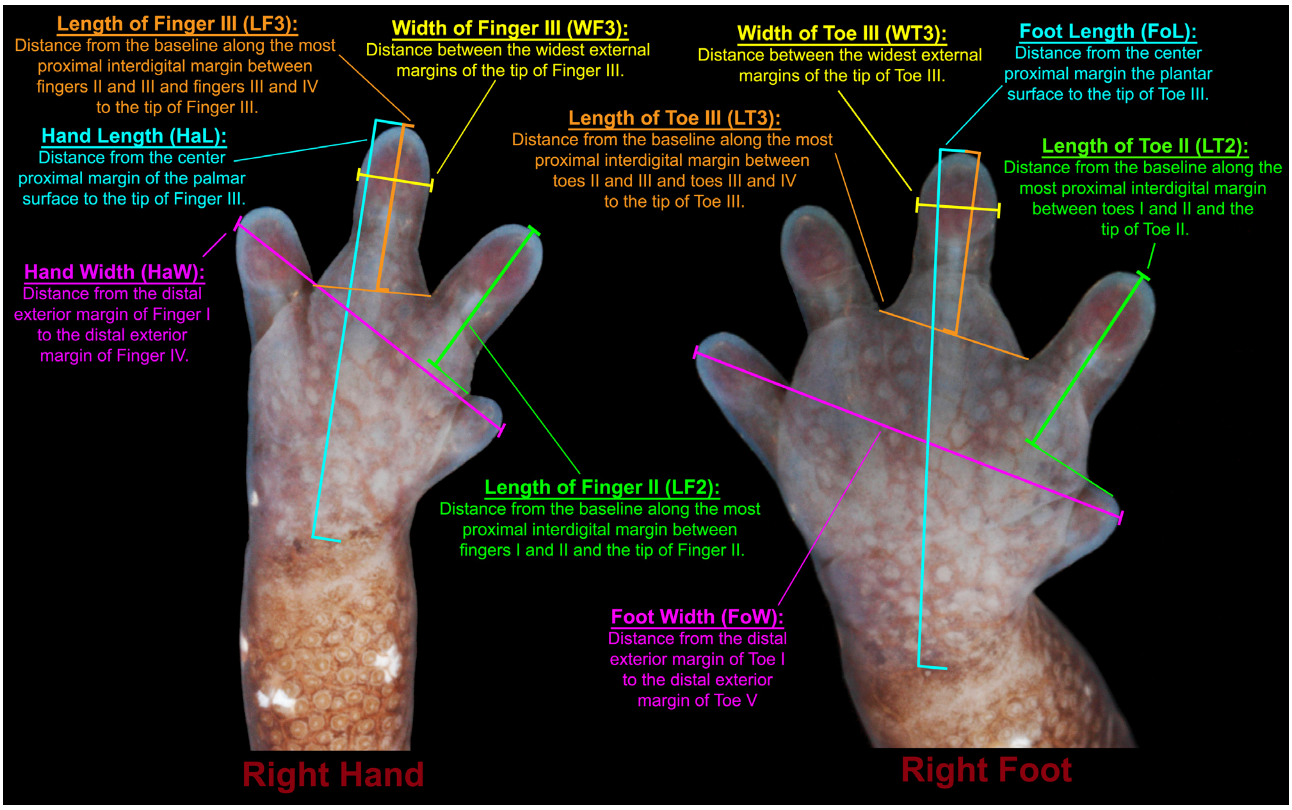
Wake, D.B. & Lynch, J.F. (1976) The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Scientific Bulletin Natural History Museum of Los Angeles Country*, 25, 1–65.

Zwickl, D.J. (2006) *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Ph.D. Dissertation, The University of Texas, Austin, Texas, 125 pp.

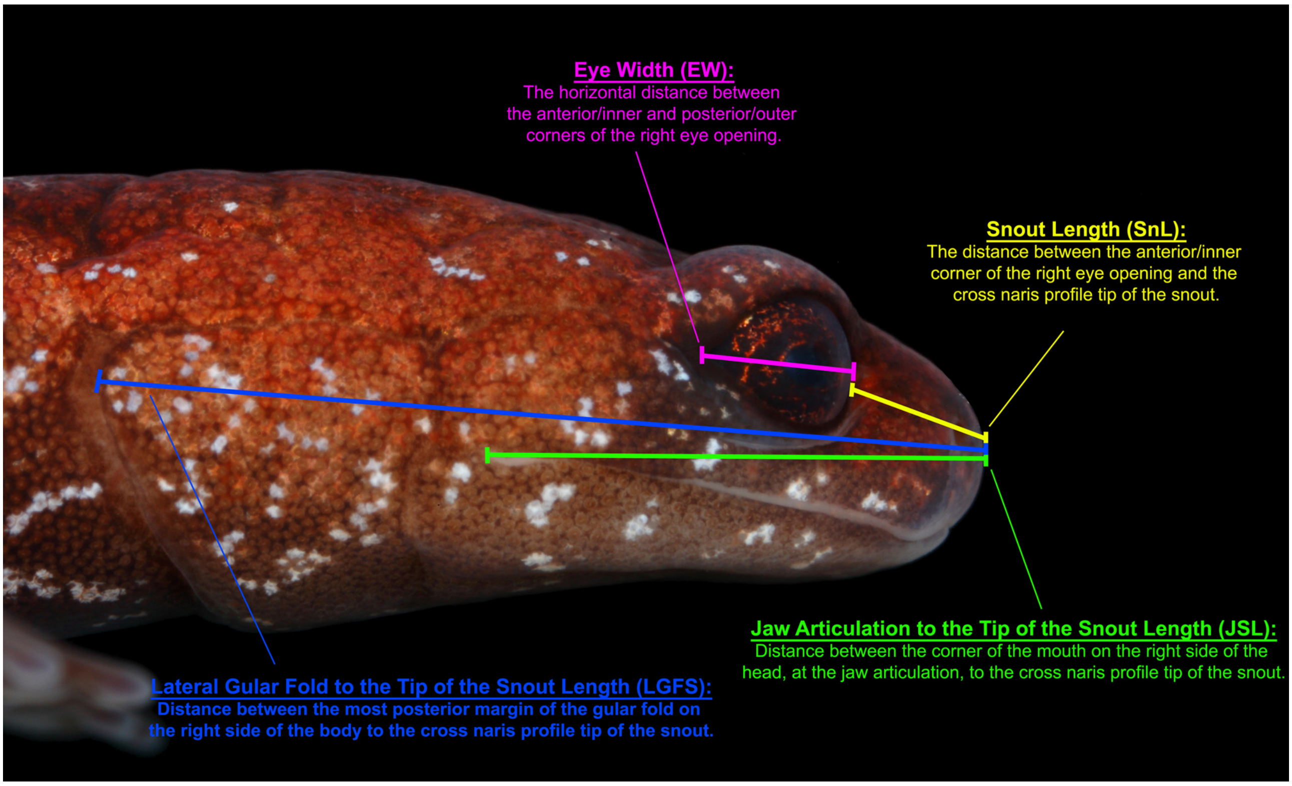
APPENDIX I. Morphological measurements taken for the right hands and right feet of members of the *Taylorotriton* subgenus.



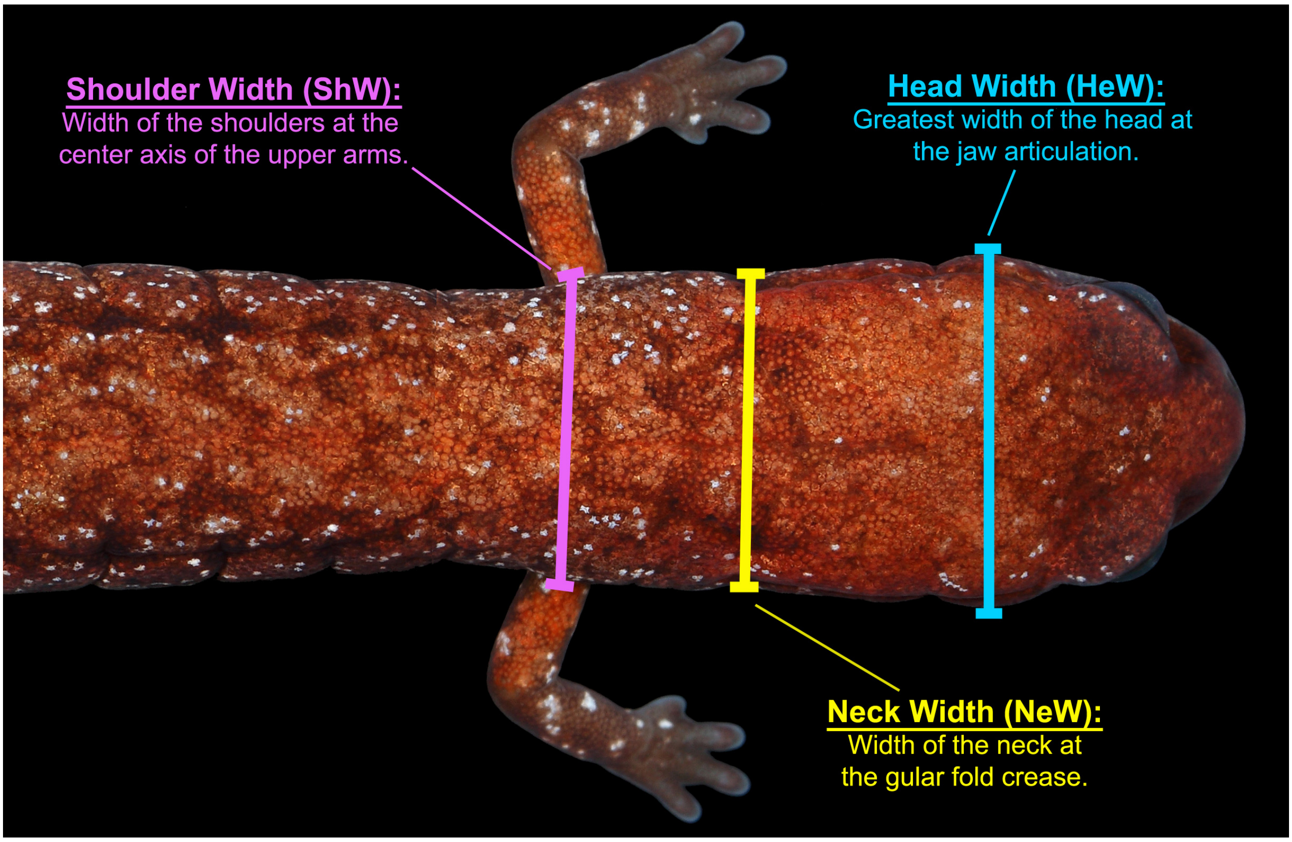
APPENDIX II. Morphological measurements taken for the right hands and right feet of members of the *Nototriton* subgenus.



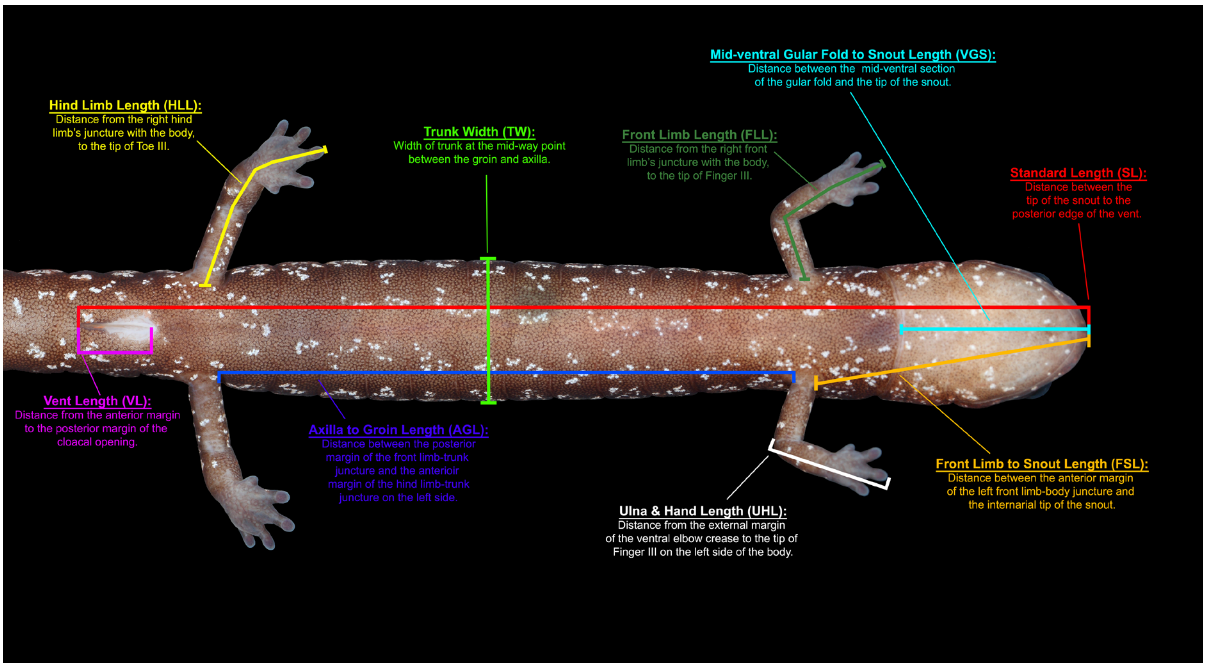
APPENDIX III. Morphological measurements taken for the right side of the head.



APPENDIX IV. Morphological measurements taken for the dorsal region of the head, neck, and shoulders.



APPENDIX V. Morphological measurements taken for the ventral region of the body.



APPENDIX VI. Morphological measurements taken for the face.