



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

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Abstract

We describe five new species of lungless salamanders (Plethodontidae) from high mountain habitats along the border between Costa Rica and Panama: *Bolitoglossa splendida*, *Bolitoglossa aureogularis*, *Bolitoglossa kamuk*, *Nototriton matama*, and *Oedipina nimaso*. We also present phylogenetic hypotheses for the new taxa (with the exception of the *Oedipina*) and their relatives based on mitochondrial DNA sequence data. The new species were discovered on a series of expeditions to remote areas (primarily over 1000 m elevation) of the Cordillera de Talamanca, Costa Rica.

Key words: *Bolitoglossa aureogularis* sp. nov., *B. kamuk* sp. nov., *B. splendida* sp. nov., *Nototriton matama* sp. nov., *Oedipina nimaso* sp. nov., biogeography, Central America, Cordillera de Talamanca, taxonomy

Resumen

Se describen cinco nuevas especies de salamandras sin pulmones (Plethodontidae) de hábitats montanos altos de la región fronteriza entre Costa Rica y Panamá: *Bolitoglossa splendida*, *B. aureogularis*, *B. kamuk*, *Nototriton matama*, y *Oedipina nimaso*. Además, se presentan hipótesis filogenéticas basadas en secuencias de ADN mitocondrial para los nuevos taxones con excepción de *Oedipina*. Las nuevas especies fueron descubiertas durante una serie de expediciones a regiones remotas (principalmente sobre los 1000 m de elevación) de la Cordillera de Talamanca, Costa Rica.

Introduction

Despite its relatively small land area, Costa Rica has a highly diverse amphibian fauna, of which 44 species are salamanders of the family Plethodontidae (www.AmphibiaWeb.org). Among tropical countries only Mexico and Guatemala, both considerably larger, have more known species of plethodontid salamanders, and Costa Rica has more described salamander species for its size than any other country (Bolaños & Wake 2009). While the amphibian fauna of much of the country is well known compared with other countries in Central America, particularly at long-term research sites such as Monteverde and La Selva, other areas of the country have been much less thoroughly explored biologically. The rugged Cordillera de Talamanca of southeastern Costa Rica (southeast of the Chirripó Massif) and western Panama is one of the most poorly explored montane areas of Central America; the portion within the transnational Parque La Amistad is roadless and access is difficult, which has hindered biological exploration in the past. The Cordillera de Talamanca consists of uplifted Neogene-Quaternary rock and reaches elevations up to 3 820 m (Marshall 2007). Collections from other areas of the border region

between Costa Rica and Panama have yielded several new species of salamanders in recent years (Bolaños & Wake 2009; Wake *et al.* 2007), and this border region is one of most species rich sites for salamanders in the Neotropics (Hanken *et al.* 2005; Wake 2005; Bolaños & Wake 2009). We here present the results of a series of herpetological expeditions to explore the region between Cerro Chirripó and the Panamanian border, a gap in existing collections of salamander specimens, which resulted in the discovery of five new salamander species.

Itinerary of expeditions

The first of all our expeditions was on April 17-20, 1984 and was carried out by Douglas C. Robinson, Gilbert Barrantes and F. Bolaños. The trip was part of a larger trip to the Caribbean of Costa Rica and the Talamancan part of the trip started in Suretka (Talamanca, Limón, 9.5785° N, 82.9445° W, 50 m elevation; all GPS coordinates in WGS84 datum), where the team arrived on April 17 (Fig. 1). The next day they hiked past Amubri to Río Lari, arriving at the northeast slope of Cerro Nimaso (9.4833° N, 82.0278° W, 700 m elevation), where they spent two nights. On April 20, they went back to Suretka and moved to another site out of the Talamancan mountain range. A two-day effort was made at the second site and many new records for the country were collected there. The two salamanders collected, both on the NE slope of Cerro Nimaso, were *Oedipina nimaso* **sp. nov.** and the first Costa Rican report of *Bolitoglossa schizodactyla*. All areas sampled were within a reserve for indigenous people, which, while forested, showed clear signs of use.

The Trans-Talamancan expedition took place between February 18 and March 10, 2007. The trip was organized by botanists of the Instituto Nacional de Biodiversidad (INBio), with the participation of E. Boza-Oviedo, whose role was to evaluate amphibians and reptiles. The trip began in the town of Ujarrás (Buenos Aires, Puntarenas, 9.2331° N, 83.3066° W, 500 m elevation) in the Pacific versant of the Talamanca mountain range (Fig. 1). After two days of 6 hr hikes, the team reached the first camp, located near the headwaters of Río Lori (9.3580° N, 83.2295° W, 1817 m elevation), a tributary of Río Coén near the continental divide on the Caribbean versant. The team sampled for nine days in an area of cloud forest vegetation. In the vicinity of the camp, a lone specimen of *Bolitoglossa splendida* **sp. nov.** was found. In a cloud forest at 2100 m elevation (9.3416° N, 83.2320° W), 2 hr from camp on foot, the first three specimens of *B. aureogularis* **sp. nov.** were found. A one-day hike led the team to the second camp (9.3925° N, 83.2119° W), located at 1700 m on the bank of the upper stretches of the Río Coén, where they remained for 6 days; this area is also cloud forest and near the continental divide. Here two additional specimens of *B. aureogularis* **sp. nov.** were found in the vicinity of the camp. The team then began the return trip, spending two days in a third camp and another day in a fourth camp; at the fourth camp (9.4437° N, 83.2040° W), *B. robusta* was captured while trapping beetles at 1000 m elevation. They then walked to the Río Coén and on to Sepeque (9.5611° N, 83.9909° W, 100 m elevation), where they traveled by boat to Suretka. Areas searched on the trip were between 400 m and 2300 m elevation.

The third expedition, to Laguna Dabagri (9.6183° N, 83.2833° W, 1000 m elevation), lasted from July 17–30, 2007. The trip started in Alto Blei (9.6175° N, 83.2489° W, 800 m elevation), an indigenous community near La Amistad International Park in the Caribbean part of the Talamanca Mountain Range (Fig. 1), where the group arrived by helicopter. The trip covered an altitudinal range of 800-1500 m. The lake is located at 1000 m (9.6183° N, 83.2833° W) in Fila Matama (near Fila Lleskila) where most sampling effort was made. Little description of this trip is given because no salamanders were found.

The fourth expedition, to Fila Matama, lasted from October 21 to November 3, 2007. The trip started at the town of Aguas Zarcas (Limón, Limón), also organized by botanists but with the participation of E. Boza-Oviedo and Ruth Delgado to evaluate amphibians and reptiles. From the village, they traveled on the Río Aguas Zarcas, a tributary of Río Banano (Fig. 1). The first camp was established en route to Fila Matama on a hill north of the ridge at 750 m elevation (9.8242° N, 83.1617° W), where only one night of sampling took place. The next day, the group moved to the second camp at 1300 m elevation near the top of the ridge (Fila Matama, 9.8132° N, 83.1681° W), where they sampled for nine days in wet forest. Specimens of *Nototriton matama* **sp. nov.** were found near the camp in moss mats. The team spent two more days in camp 1 on the return trip to Aguas Zarcas. The only other salamander found on this trip was *Bolitoglossa colonnea*, one specimen from ca 750 m (9.8242° N, 83.1617° W) m and another at 1200 m elevation (9.8174° N, 83.1667° W). Areas searched on this trip were between 200 m and 1400 m elevation.

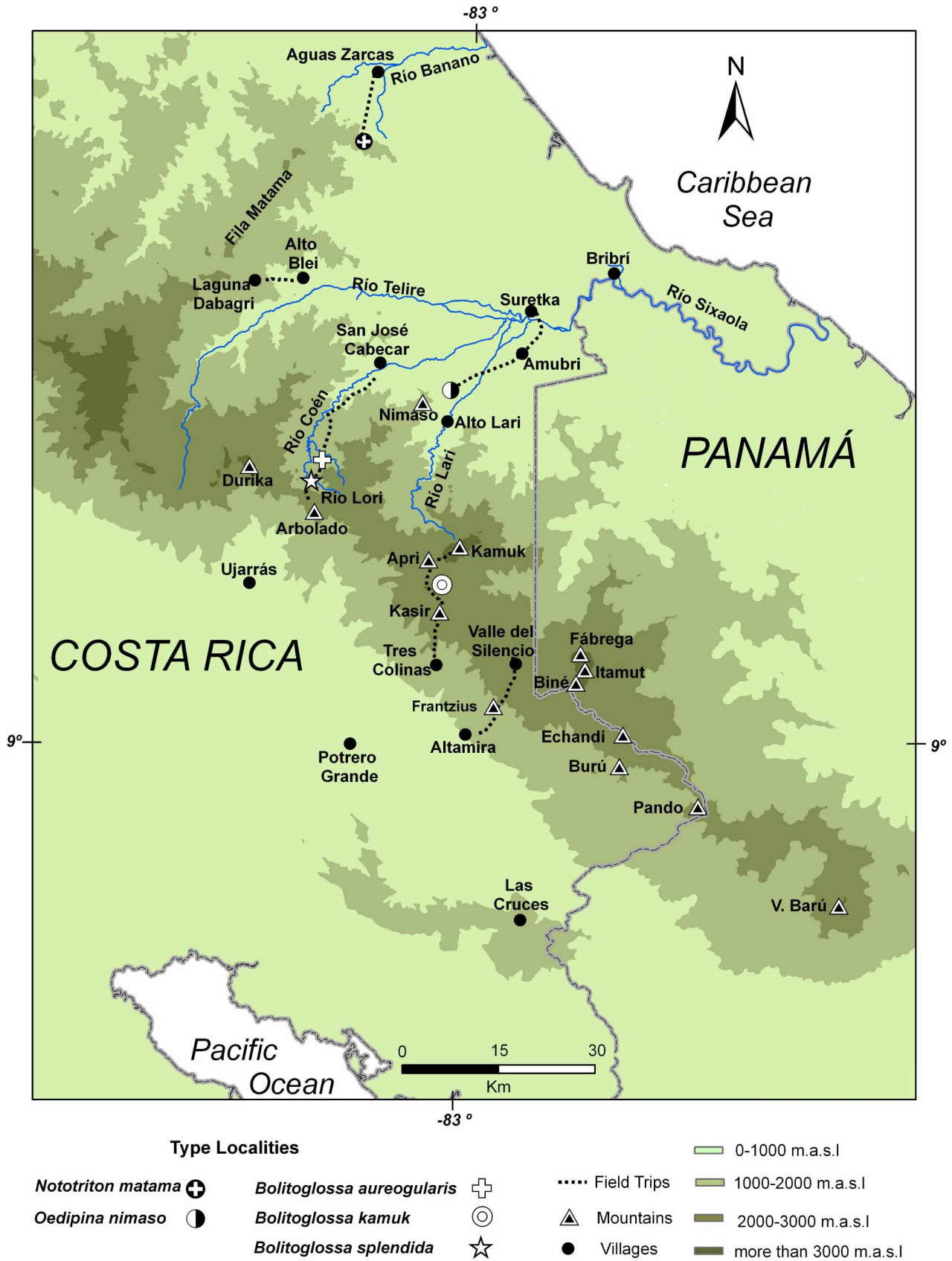


FIGURE 1. Map of the border region between Costa Rica and Panama, showing expedition routes and type localities for new salamander species.

The fifth expedition, to Cerro Kamuk, the highest peak in the eastern Talamancan range, began on December 16, 2007 and involved five participants (L.G. Artavia, G. Chaves, Guido Saborío, S. Rovito and Hugo Solano). Beginning in the small town of Tres Colinas (9.1579° N, 83.0651° W, 1800 m elevation), Puntarenas Province (Fig. 1), a northward route was followed on foot, passing through cloud forest with large oak trees and abundant bamboo (*Chusquea* spp) to Cerro Kasir (9.1966° N, 83.0558° W, 2959 m elevation), where a mixture of lower cloud forest and mossy sub-páramo occurs. Specimens of *Bolitoglossa gomezi* were found in both epiphytic and ground bromeliads in oak forest, as well as under carpets of moss in sub-páramo. No salamanders were taken under rocks or logs or in leaf litter, despite searching. The route descended into oak cloud forest and ascended Cerro Dudu (9.2403° N, 83.0661° W, 3056 m elevation), on the continental divide where a single *B. bramei* was collected under moss. From Cerro Dudu, the route turned northeast from the continental divide and followed a ridge through sub-páramo habitat to Cerro Apri (9.2546° N, 83.0590° W at 3109 m elevation), where three *B. kamuk* **sp. nov.** were collected under carpets of moss and in arboreal bromeliads from small, isolated trees. The expedition reached its final destination atop Cerro Kamuk (9.2727° N, 83.0336° W, 3549 m elevation). Vegetation on Cerro Kamuk consisted of wind-swept páramo with grass and small clumps of shrubs, but no salamanders were found despite extensive searching. The same route was followed on the return journey to Tres Colinas, arriving on December 22. Sampling of bromeliads and moss continued on the return to Tres Colinas, and additional *B. gomezi* were found, particularly in bromeliads in mid-elevation forest (ca. 2100 m) above Tres Colinas.

The sixth expedition, also organized by botanists, was from February 19 to March 2, 2008, and included the participation of four herpetologists (Carlos Solano, E. Boza-Oviedo, José Hernández, and G. Chaves). The first day, they traveled by car to the first camp at 1050 m in an area of old secondary forest (9.0975° N, 83.1133° W). The only salamander species found near the camp was *Bolitoglossa lignicolor*. On February 23, walking to the top of Cerro Amuo (9.1226° N, 83.0993° W), they found a single *B. gomezi* on a tree trunk under moss at 1575 m elevation. The next day, they moved to a second camp (9.1209° N, 83.0885° W, 1800 elevation) where no salamanders were found. On February 26, the first two herpetologists moved to a second locality at Tres Colinas where 7 specimens of *B. gomezi* were also found at elevations between 2100 and 2150 m (9.1381° N, 83.0700° W). Areas sampled on this trip were between 975 m and 2300 m elevation.

The last expeditions were on July 8–12 and September 14–15, 2008 to survey Valle del Silencio — a highland valley located on the east side of the Cordillera de Talamanca close to the Costa Rica and Panama border (Fig. 1). The first trip was conducted by a team of eight participants including G. Chaves, A. García-Rodríguez and L.G. Artavia; the second involved four people including G.C. and A.G. The trips began in Altamira (9.0125° N, 83.0095° W, 1391 m elevation) on the Pacific slope of Cordillera de Talamanca. On the first trip, a 14 km trail was surveyed for 4 days for amphibians and reptiles; the second trip was only 2 days long. The route runs through Cerro Frantzius (9.0624° N, 82.9837° W, 2134 m elevation), Cerro Quemado (9.0693° N, 82.9796° W, 2250 m elevation) and up to the continental divide (9.0963° N, 82.9790° W, 2550 m elevation), before reaching Valle del Silencio (9.1093° N, 82.9625° W, 2500 m elevation) on the Caribbean versant of the Cordillera de Talamanca. With the exception of the first three kilometers (secondary growth), the trail went through a damp mature oak forest with an understory dominated by *Chusquea* spp and with giant terrestrial bromeliads (*Greigia sylvicola*). Arboreal bromeliads, moss, and leaf litter were searched for salamanders. None of the species here described were found during these trips, but salamanders found were used in phylogenetic analyses and contributed to our understanding of Talamancan biogeography. On the first, one specimen of *Bolitoglossa bramei* was collected on top of Cerro Frantzius and another in Valle del Silencio, where a *B. robinsoni* was also found. On the second trip a *B. compacta* was collected in Valle del Silencio.

Materials and methods

Fieldwork and sampling methods: Salamanders were sought by day in moss mats, under logs, by raking through leaf litter, and by opening bromeliads both in trees and on the ground. By night, salamanders were sought using lights. Identification of plant species as part of habitat descriptions was with the help of botanists, who studied fresh material collected during these surveys. Temperature measurements were taken using a standard laboratory alcohol thermometer. All salamanders were fixed in 10% formalin and transferred to ethanol for long-term storage. Tissue samples (liver or tail tip) were taken from salamanders from all but the 1984 trip to Cerro Nimaso, and tissues were preserved in DMSO buffer or in 95% ethanol.

Morphology: The following measurements were used for morphological comparison: snout to posterior angle of vent (standard length, SL), head width (HW), snout to gular fold (SG), head depth at posterior angle of jaw (HD), eyelid length (EL), eyelid width (EW), anterior rim of orbit to tip of snout (ES), horizontal eye diameter (ED), interorbital distance between angle of eyes (intercanthal distance, IC), interorbital distance between eyelids (IO), snout to forelimb (SF), distance separating external nares (internarial distance, IN), snout projection beyond mandible (SP), shoulder width (SW), snout to anterior angle of vent (SAV), axilla-groin distance (AX), number of costal interspaces between adpressed limbs (limb interval, LI), forelimb length (FLL), hind limb length (HLL), hand width (HAW), foot width (FW), length of third (longest) toe (T3), length of fifth toe (T5). Measurements were made using digital or dial calipers or a dissecting microscope fitted with an ocular micrometer; standard length (SL) was measured from the anterior tip of the snout to the posterior angle of the vent. Limb interval equals the number of costal interspaces between the tips of adpressed fore- and hind limbs, measured in one-half increments (e.g., 3, 3.5). Radiographs were prepared for the holotype of the newly described *Oedipina*. Counts of presacral (trunk) vertebrae do not include the first, or atlas, vertebra. Tooth counts are based on direct counts of clearly ankylosed teeth. Numbers of maxillary (MT) and vomerine (VT) teeth in each holotype are provided for right and left sides, along with number of premaxillary teeth (PMT); these counts are summed for other individuals. Institutional abbreviations are as listed in Leviton *et al.* (1985). Color information was derived from photographs of living specimens.

Phylogenetic analysis: DNA was extracted from liver tissue or tail tips using a Qiagen DNEasy tissue kit (Qiagen, Valencia, California). We sequenced DNA from field-collected samples of *Bolitoglossa* and *Nototriton* for the 16S rRNA (16S) and cytochrome *b* (*cyt b*) mitochondrial genes. Primers MVZ117 and MVZ98 (Palumbi *et al.* 1991) were used for 16S and primers MVZ15 and MVZ16 (Moritz *et al.* 1992) for *cyt b*. Reactions were run at 94 °C for 2 min, 38 cycles of 94 °C for 30 s, 48 °C for 30 s (16S) or 1 min (*cyt b*), 72 °C for 1 min, with a final cycle at 72 °C for 8 min. A list of samples used for DNA sequencing and phylogenetic analysis, along with GenBank numbers, is given in Table 1. We aligned these sequences with available sequences for Talamancan salamanders (*Bolitoglossa*) or other members of the genus (*Nototriton*) from GenBank using the program MUSCLE 3.6 (Edgar 2004) and concatenated alignments for 16S and *cyt b*. Sequences of *cyt b* for *Nototriton* were trimmed to match the shorter fragment length of available sequences from GenBank. The aligned 16S sequences had a length of 529 bp (*Bolitoglossa*) and 517 bp (*Nototriton*), while the *cyt b* alignment had a length of 809 bp (*Bolitoglossa*) and 385 bp (*Nototriton*). We used the program RAxML (Stamatakis 2006) to estimate a phylogeny with maximum likelihood under the General Time Reversible substitution model (Tavaré 1986) with invariable sites and among-site rate variation (GTR+I+G) substitution model with 4 data partitions (corresponding to 16S and codon positions 1, 2 and 3 of *cyt b*) for both *Bolitoglossa* and *Nototriton*, and 1000 bootstrap replicates were performed to assess nodal support. We also estimated the phylogeny using a partitioned Bayesian phylogenetic analysis implemented in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). As for the ML analysis, the data were partitioned by gene (16S and *cyt b*), and the cytochrome *b* gene was partitioned by codon position. We used MrModeltest 2.2 (Nylander 2004) to select a substitution model for each partition. The following substitution models were used for each partition: GTR+I+G for *Bolitoglossa* 16S, *Bolitoglossa cyt b* codon position 3, and *Nototriton* 16S, Kimura (1980) model with a rate heterogeneity parameter (K80+G) for *Bolitoglossa cyt b* codon position 1, K80+I+G for *Nototriton cyt b* codon position 1, Hasegawa-Kishino-Yano (Hasegawa *et al.* 1985) model with a rate heterogeneity parameter (HKY+G) for *Bolitoglossa cyt b* codon position 2, HKY for *Nototriton cyt b* codon position 2, and GTR+G for *Nototriton cyt b* codon position 3. The analysis was run for 20,000,000 generations, and 5,000,000 generations were discarded as burn-in. *Bolitoglossa mexicana* was used as an outgroup for all phylogenetic analyses for *Bolitoglossa*, and *Oedipina alleni* was used as an outgroup for all phylogenetic analysis for *Nototriton*. Convergence of split frequencies was assessed using the compare and sliding window plots in program AWTY (Nylander *et al.* 2008). Average pairwise Tamura-Nei (TN) (Tamura & Nei 1993) distances between taxa for both 16S and *cytb* were calculated using Arlequin v3.5 (Excoffier *et al.* 2005).

TABLE 1. Voucher numbers and GenBank accession numbers for all samples used in phylogenetic analyses.

Voucher Number	Species	GenBank 16S	GenBank cyt <i>b</i>
UCR 19858	<i>Bolitoglossa aureogularis</i>	JQ899151	JQ899182
UCR 19859	<i>Bolitoglossa aureogularis</i>	JQ899152	—
UCR 19892	<i>Bolitoglossa aureogularis</i>	JQ899153	—
UCR 19893	<i>Bolitoglossa aureogularis</i>	JQ899154	JQ899183
UCR 20483	<i>Bolitoglossa bramei</i>	JQ899159	JQ899189
UCR 20484	<i>Bolitoglossa bramei</i>	JQ899160	JQ899190
UCR 20851	<i>Bolitoglossa bramei</i>	JQ899142	JQ899172
MVZ 225893	<i>Bolitoglossa bramei</i>	—	AF212066
MVZ 233516	<i>Bolitoglossa cerroensis</i>	AF199233	AF199195
UCR 20532	<i>Bolitoglossa compacta</i>	JQ899163	JQ899193
MVZ 181260	<i>Bolitoglossa epimela</i>	AY526120	AF212097
UCR 20399	<i>Bolitoglossa gomezi</i>	JQ899155	JQ899184
UCR 20413	<i>Bolitoglossa gomezi</i>	—	JQ899185
UCR 20414	<i>Bolitoglossa gomezi</i>	JQ899156	JQ899186
UCR 20415	<i>Bolitoglossa gomezi</i>	JQ899157	JQ899187
UCR 20417	<i>Bolitoglossa gomezi</i>	JQ899158	JQ899188
UCR 20843	<i>Bolitoglossa gomezi</i>	JQ899140	JQ899170
UCR 20844	<i>Bolitoglossa gomezi</i>	JQ899147	JQ899177
UCR 20845	<i>Bolitoglossa gomezi</i>	JQ899148	JQ899178
UCR 20846	<i>Bolitoglossa gomezi</i>	JQ899149	JQ899179
UCR 20847	<i>Bolitoglossa gomezi</i>	—	JQ899180
UCR 20848	<i>Bolitoglossa gomezi</i>	JQ899139	JQ899169
UCR 20849	<i>Bolitoglossa gomezi</i>	JQ899141	JQ899171
UCR 20850	<i>Bolitoglossa gomezi</i>	JQ899146	JQ899176
MVZ 229171	<i>Bolitoglossa gracilis</i>	AY526122	AF212068
UCR 20852	<i>Bolitoglossa kamuk</i>	JQ899143	JQ899173
UCR 20853	<i>Bolitoglossa kamuk</i>	JQ899144	JQ899174
UCR 20854	<i>Bolitoglossa kamuk</i>	JQ899145	JQ899175
MVZ 210286	<i>Bolitoglossa marmorea</i>	AF218493	U89627
MVZ 176838	<i>Bolitoglossa mexicana</i>	GU725457	GU725470
MVZ 225870	<i>Bolitoglossa minutula</i>	AY526124	AF212098
UCR 20539	<i>Bolitoglossa nigrescens</i>	JQ899164	JQ899194
UCR 12068	<i>Bolitoglossa pesrubra</i>	AY526132	AF212069
MVZ 210360	<i>Bolitoglossa pesrubra</i>	EU448105	—
MVZ 225879	<i>Bolitoglossa pesrubra</i>	—	AF212071
MVZ 190923	<i>Bolitoglossa pesrubra</i>	EU448104	AF212074
MVZ 190928	<i>Bolitoglossa pesrubra</i>	—	AF212072
MVZ 195598	<i>Bolitoglossa pesrubra</i>	—	AF212076
MVZ 225881	<i>Bolitoglossa pesrubra</i>	—	AF212075

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TABLE 1. (Continued)

Voucher Number	Species	GenBank 16S	GenBank <i>cyt b</i>
MVZ 231322	<i>Bolitoglossa pesrubra</i>	—	AF212074
DBW 5117	<i>Bolitoglossa pesrubra</i>	—	AF212081
DBW 5118	<i>Bolitoglossa pesrubra</i>	—	AF212082
Cerro Asunción	<i>Bolitoglossa pesrubra</i>	—	AF212080
Cerro Sakira	<i>Bolitoglossa pesrubra</i>	—	AF212079
23.5 km SE El Empalme	<i>Bolitoglossa pesrubra</i>	—	AF212078
La Georgina	<i>Bolitoglossa pesrubra</i>	—	AF212083
Ojo de Agua	<i>Bolitoglossa pesrubra</i>	—	AF212077
Salsipuedes	<i>Bolitoglossa pesrubra</i>	—	AF212070
Villa Mills	<i>Bolitoglossa pesrubra</i>	—	AF212084
UCR 20489	<i>Bolitoglossa robinsoni</i>	JQ899161	JQ899191
UCR 19835	<i>Bolitoglossa splendida</i>	JQ899150	JQ899181
CH 7478	<i>Bolitoglossa sombra</i>	JQ899165	JQ899168
UCR 225871	<i>Bolitoglossa sombra</i>	AY526136	AY526174
MVZ 194828	<i>Bolitoglossa subpalmata</i>	AF212091	EU448107
UCR 12065	<i>Bolitoglossa tica</i>	AY526137	AF212089
UCR 20514	<i>Bolitoglossa tica</i>	JQ899162	JQ899192
UCR 12071	<i>Nototriton abscondens</i>	AF199130	AF199130
JHT 2420	<i>Nototriton barbouri</i>	GU971734	GU971734
UTA A-51490	<i>Nototriton brodiei</i>	AF199139	AF199139
MVZ 207122	<i>Nototriton gamezi</i>	AF199135	AF199135
MVZ 207106	<i>Nototriton guanacaste</i>	AF199140	AF199140
USNM 497540	<i>Nototriton lignicola</i>	AF199141	AF199141
MVZ 263852	<i>Nototriton limnospectator</i>	JN377383	JQ899197
UCR 20215	<i>Nototriton matama</i>	JQ899166	JQ899195
MVZ 225899	<i>Nototriton picadoi</i>	AF199144	AF199144
UCR 12057	<i>Nototriton richardi</i>	AF199146	AF199146
MVZ 230241	<i>Nototriton saslaya</i>	GU981761	—
USNM 339712	<i>Nototriton sp.</i>	AF199136	AF199136
USAC 3357	<i>Nototriton stuarti</i>	JQ899167	JQ899196
UF 155377	<i>Nototriton tomamorum</i>	GU971731	GU971732
MVZ 190857	<i>Oedipina alleni</i>	AF199207	AF199149

Descriptions of the new species

Bolitoglossa splendida sp. nov.

Splendid Web-footed Salamander

Figure 2

Holotype. UCR 19835, an adult female from the headwaters region of the Lori branch of the Río Coén near Cerro Arbolado (coordinates 9.3567° N, 83.229° W) at 1826 m elevation, Provincia de Limón, Costa Rica, collected 19 February, 2007 by Marco Moraga and Eduardo Boza-Oviedo.

Diagnosis. Assigned to *Bolitoglossa* because it lacks a sublingual fold (Wake & Elias 1983), and to subgenus *Eladinea* based on mtDNA sequence data. A moderate-sized species of *Bolitoglossa* (subgenus *Eladinea*) with only slightly webbed digits of the hands and feet that differs from all other species in the genus in its brilliant coloration (Fig. 2) of jet black ground color with a bright reddish-orange broad dorsal band extending from the back of the head at least to the base of the tail, and with bright enamel-yellow spots scattered along lateral and ventrolateral surfaces; it differs further from close relatives *B. pesrubra*, *B. subpalmata*, *B. tica*, *B. gomezi*, *B. gracilis*, and *B. bramei* in having a relatively broader head.

Description. A moderately robust species of moderate size compared to other members of genus. SL of unique specimen (47.8 mm) close to mean value of related species such as *Bolitoglossa pesrubra*, *B. subpalmata* (García-París *et al.* 2008), and *B. gomezi* (Wake *et al.* 2007). Tail missing. Head relatively broad (Wake & Brame 1972); SL/HW = 5.9. Somewhat bluntly pointed snout broadly rounded and of moderate length. Species has small nostrils, which are typical for this genus, although nasolabial protuberances are prominent as small, knob-like structures that are pale and stand out from black background. Eyes relatively small; do not protrude beyond lateral margins of head and are not visible in ventral view. Teeth moderate in size and numerous (57 MT, 6 PMT, 28 VT) in comparison with related taxa. Limbs relatively short (SL/HLL= 3.9) with LI of 3.5. Hands and feet moderate in size; FW = 5.1. Digits well differentiated but short and knob-like with distinct subdigital pads on longer digits. Tip of fourth digit of right hind limb damaged or malformed. Webbing relatively great although incomplete, extending to between first and second phalangeal articulations of longest digits; webbing more extensive in foot than in hand. Fingers, in order of decreasing length, are 3-4-2-1; toes are 3-4-2-5-1. Postiliac glands pale and inconspicuous.

Measurements (in mm), limb interval and tooth counts of the female holotype (Table 2). HW 8.1, SG 11.5, HD 4.1, EW 1.5, EL 2.7, ES 2.5, ED 1.9, IC 3.8, IO 2.3, SF 14.1, IN 1.9, SP 0.6, SW 5.6, SL 47.8, SAV 43.1, AX 24.5, LI 3.5, FLL 11.0, HLL 11.1, HAW 3.7, FW 5.1, T5 0.6, T3 1.1. Number of teeth: PMT 6, MT 27/30, VT 13/15.

TABLE 2. Measurements for specimens used in description of new species, as well as other specimens collected on Talamanca expeditions used for comparison to new taxa.

Species	Number	Sex	SVL	TL	AX	FLL	HLL	SG	HW	FW	T3	PMT	MT	VT	LI
<i>Bolitoglossa aureogularis</i>	UCR19893	female	48.8	36.2, cut	26	9.3	10.2	10	6.1	4.3	1	6	57	27	7
<i>Bolitoglossa aureogularis</i>	UCR19857	male	34.8	22.3, cut	18	7.3	7.6	8.1	4.8	2.3	1	4	49	17	5
<i>Bolitoglossa kamuk</i>	UCR20852	male	34.8	35.2	19	9	9.3	8.5	5.8	3.7	1	2	34	16	2
<i>Bolitoglossa kamuk</i>	UCR20853	male	33	32.4	19	8	8.2	7.9	5.3	3.6	1		13	2	
<i>Bolitoglossa splendida</i>	UCR19835	female	47.8		25	11.1	11.1	12	8.1	5.1	1	6	57	18	4
<i>Bolitoglossa compacta</i>	UCR20532	female	75.8	ca. 68	42	17.6	20.4	16	12	8.4	3				4
<i>Bolitoglossa robinsoni</i>	UCR20489	male	51.5	63.8	28	15.4	16.5	14	9	7.1	3	4	62	19	0
<i>Oedipina nimaso</i>	UCR8391	male	30.8	42.0, broken	20	6.2	6.9	4.8	3.6	1.2	1	1	20	12	10
<i>Nototriton matama</i>	UCR20215	female	23.6	11.0, broken	13	3.7	4.2	4.2	3.2	1.2	1	4	31	11	5

Coloration of the holotype in life (Fig. 2). Specimen is glossy dark black, somewhat paler ventrally than dorsally and laterally. A broad bright red to orange-red band arises on back of head and extends to posterior end of body. Band is bifurcated anteriorly into two stripes that arise from posterior margin of eyelids. Medial borders of

these stripes converge, meeting at about level of nuchal fold, behind angle of the jaw and about 3 mm anterior to level of gular fold. Band bright and uninterrupted although there is some fine speckling of melanin in area anterior to shoulders. Lateral border of band irregular, encroaching onto the dorsal surface immediately in front of shoulders and then descending onto upper flanks immediately behind shoulders. Black pigment present between band and insertion of both forelimbs and hind limbs. Bright yellow spots with glossy enamel-like finish present laterally and ventrolaterally. On right side there is one spot in front of limbs, six spots on side of trunk, and one behind limbs; on left side there are five spots on side of trunk and one on posterior insertion of hind limb. Venter immaculate.



FIGURE 2. A) Dorsal and B) ventral views of the holotype (UCR 19835) of *Bolitoglossa splendida* in life. C) Dorsal view of left hand and D) left foot of holotype of *B. splendida*. Photos A and B by Alex Monro and E. Boza-Oviedo, C and D by A. García-Rodríguez. The bar in hand and feet are 1 mm length.

Habitat and range. The species is known only from the type locality, which lies a short distance north of the continental divide along a well-known trail that crosses from the Pacific side to the Caribbean side of the main Cordillera de Talamanca in eastern Costa Rica. The type locality lies along the Río Lori, a highland tributary of the Río Coén, which flows north and east toward the Caribbean. The crest of the Cordillera de Talamanca is relatively low in this area, and the type locality is below Cerro Arbolado (2500 m elevation). The specimen was active on the upper side of a *Heliconia* sp. leaf at 19:50 h, 1.1 m above ground. It was about 100 m from the river and 30 m from a smaller stream. Air temperature was 13 °C on a day that had a heavy rain at 11:00-14:00, and the vegetation and soil were moist. The vegetation at this locality is mature cloud forest, consisting primarily of members of the Araceae (e.g. *Philodendron*, *Anthurium*, *Monstera*), Heliconiaceae (*Heliconia*), Marantaceae, Begoniaceae, Acanthaceae, Arecaceae (*Geonoma*), Commelinaceae, Rubiaceae, Urticaceae, Melastomataceae, Bromeliaceae, Ericaceae, Piperaceae, bryophytes and ferns.

Etymology. This species name is derived from *splendidus* (L.), a word that denotes the exceptionally brilliant coloration of this species.

***Bolitoglossa aureogularis* sp. nov.**

Yellow-throated Web-footed Salamander

Figure 3

Holotype. UCR 19893, an adult female from along the Río Coén on the Trans-Talamancan trail near Cerro Arbolado (9.3925° N, 83.2119° W) at an elevation of 1680 m approximately 8 km N of the continental divide, Provincia de Limón, Costa Rica, collected by Eduardo Boza-Oviedo on 1 March 2007.

Paratypes. UCR 19892, same data as holotype; UCR 19857–59 (3 specimens), 9.3416° N, 83.232° W, 2102 m, in headwaters area of Río Coén, about 2 km N continental divide, Provincia de Limón, Costa Rica, collected by Eduardo Boza-Oviedo on 22 February 2007.

Diagnosis. Assigned to *Bolitoglossa* because it lacks a sublingual fold (Wake & Elias 1983), and to subgenus *Eladinea* based on mtDNA sequence data. A medium-sized member of the genus *Bolitoglossa* (subgenus *Eladinea*) with moderate webbing of the digits of the hands and feet that differs from all other species in the genus by its unique coloration (Fig. 3) of reddish tan to yellow dorsal coloration with black flanks and a venter marked by bright yellow gular and yellow-brown chest regions, with a pair of dirty white patches on the ventrolateral surfaces of the posterior venter. In comparison to members of the *B. robinsoni* complex, this species is much smaller and more slender, in addition to the coloration differences.



FIGURE 3. A) Dorsal and B) ventral views of holotype (UCR19893) of *Bolitoglossa aureogularis* in life. C) Paratype (UCR19857) of *B. aureogularis* in life. D) Dorsal view of right hand and E) right foot of holotype. Photos A, B and C by E. Boza-Oviedo and Roney Samaniego, D and E by Adrián García-Rodríguez. The bar in hand and feet are 1 mm length.

Description. A slender species of moderate size compared to other members of its genus. SL of holotype, the only adult specimen available (48.8 mm), nearly identical to that of its close geographic neighbor *Bolitoglossa splendida* and close to mean value of such Talamancan species as *B. pesrubra*, *B. subpalmata* (García-París *et al.* 2008), and *B. gomezi* (Wake *et al.* 2007). Tail slender but relatively short (tip broken). Head narrow (Wake & Brame 1972); SL/HW = 8.0. Relatively short snout broadly rounded. Small nostrils are typical for this genus. Nasolabial protuberances not pronounced; paler than surroundings and appear to be pigmented with white. Eyes small, do not protrude beyond lateral margins of head, not visible in ventral view. Teeth moderate in size and numerous (57 MT, 6 PMT, 27 VT). Limbs relatively short with LI of 3.5. Hands and feet moderate in size; FW = 5.1 mm. Digits well-differentiated but short and knob-like with distinct subdigital pads on longer digits. Webbing, reaching between first and second phalangeal articulations of longest digits; webbing more extensive in foot than in hand. Fingers, in order of decreasing length, are 3-4-2-1; toes are 3-4-2-5-1. Postiliac glands pale and inconspicuous.

Measurements (in mm), limb interval and tooth counts of the female holotype (Table 2). HW 6.1, SG 10.1, HD 2.3, EW 1.3, EL 2.7, ES 1.7, ED 2.2, IC 3.5, IO 2.4, SF 12.5, IN 1.5, SP 0.4, SW 4.8, SL 48.8, SAV 45.0, AX 26.2, LI 6.5, FLL 9.3, HLL 10.2, HAW 3.3, FW 4.3, T5 0.9, T3 1.4. Numbers of teeth: PMT 6, MT 29/28, VT 13/14.

Coloration of the holotype in life (Fig. 3). Dorsal coloration golden-tan with some bright highlights on dorso-lateral regions and with some narrow streaks of dark brown. Golden-tan coloration in form of broad band extending from snout onto tail. Tail becomes increasingly reddish brown posteriorly. Lateral surfaces dark brown with numerous white speckles. Dark coloration forms lateral margin of dorsal band and continues onto tail and forward all the way to eye and is present almost to tip of snout. Dark coloration extends to area above limb insertions so light band does not contact limbs. Dorsal surfaces of limbs similar to dorsal band in color. White pigment present ventrolaterally along trunk and becomes prominent on venter, where pair of lightly colored patches is separated by region of dark pigmentation. Gular area bright yellow, which becomes golden on chest before fading into darker color in midtrunk region. Venter of tail speckled with white and tan spots. Iris golden.

Habitat and range. The species is known from two nearby localities on the Caribbean slope of the Cordillera de Talamanca, both with mature cloud forest similar to the habitat at the type locality of *Bolitoglossa splendida*. The first locality is at ca. 2100 m elevation, 700 m from the nearest stream; the second, the type locality, is located at 1680 m elevation near the river edge.

Variation. There are four paratypes but only one approaches maturity in size. All specimens show coloration typical of the holotype, but some are more reddish gold dorsally and they are covered with tiny white speckles. Even the smallest individual (UCR 19858, 9.2 mm SL) displays the characteristic ventral coloration. This is a slender species with a small, narrow head and slender trunk and tail.

Etymology. The species name is derived from *aurea* (L.), golden, and *gula* (L.), throat, in recognition of the unusual bright yellow coloration of the gular and chest regions of this species.

Natural history and behavioral observations. The specimens from the first site were inactive in bromeliads (2.8–6.2 m above ground) during daytime, one in a cavity formed by the bromeliad roots in the trunk of the tree and the other two inside the leaves. All were in different plants in two trees, with two found in separate branches of the same tree; the temperature of the retreats was 12 °C with an air temperature of 15 °C. The juvenile and holotype from the second locality were found active at night on low vegetation or in the leaf litter (0–1.45 m), 1.8–3.7 m from the river with an air temperature of 15–18 °C during the observation period. Behavioral observations were made from 20:00–00:03 before collecting both specimens. The juvenile moved within the Araceae leaf where it was found but never went away. The adult female (holotype) climbed to the top of two shrubs and one palm seedling and moved through the leaf litter between plants. On two occasions, it held up a third of its body off surface of the leaf, and sometimes used its tail as a prehensile organ when moving along stems.

***Bolitoglossa kamuk* sp. nov.**

Kamuk Web-footed Salamander

Figure 4

Holotype. UCR 20852, a young adult male from the sub-páramo region atop Cerro Apri in the Kamuk Massif (coordinates 9.2546° N, 83.059° W) at an elevation of 3126 m, on the continental divide, Provincia de Limón, Costa Rica, collected 18 December, 2007, by Guillermo Artavia, Gerardo Chaves, Sean Rovito, Guido Saborío and Hugo Solano.

Paratypes. UCR 20853, 20854; same data as holotype.

Diagnosis. Assigned to *Bolitoglossa* because it lacks a sublingual fold (Wake & Elias 1983), and to subgenus *Eladinea* based on mtDNA sequence data. A slender member of the *subpalmata* group of *Bolitoglossa* (*Eladinea*) distinguished from all other members of the group by mitochondrial DNA sequences; further distinguished from *B. pesrubra* by absence of reddish proximal limb segments and absence of dorsal spots and blotches; from *B. gracilis* by more robust habitus and absence of yellowish coloration; from *B. tica* by smaller hands and feet.

Description. Known only from juveniles and small adults. Appears to be relatively small, slender compared to other members of genus. SL in two small adult males is 34.8 mm and 33.0 mm. Tails slender, about same length as SL; SL/TL in two males is 0.99 and 0.98. Head narrow; SL/HW is 6.0 and 6.2. Head well demarcated from neck.

Snout broadly rounded to truncated, not prominent. Nostrils small and nasolabial protuberances poorly developed but lightly pigmented. Eyes moderately prominent, protrude slightly beyond lateral margins of head and are relatively frontal in orientation. Holotype has 2 PMT, but large paratype (UCR 20853) has a damaged snout and teeth cannot be counted. MT 34 in holotype, and 15 on one side of large paratype. VT number 16 (holotype) and 13. Limbs slender, moderate in length; LI 1.5 (holotype) and 2. Hands and feet narrow (3.7 and 3.6 mm in holotype) with little webbing; fewer than two distal-most phalanges of longest digits are free of webbing. Digital tips truncate to slightly pointed and bear small but distinct subterminal pads. Fingers, in order of decreasing length, are 3-4-2-1; toes are 3-4-2-5-1. Postiliac glands not evident. Gonads of the holotype compact and rounded with some spotting of black pigmentation, and they appear to be sexually mature.

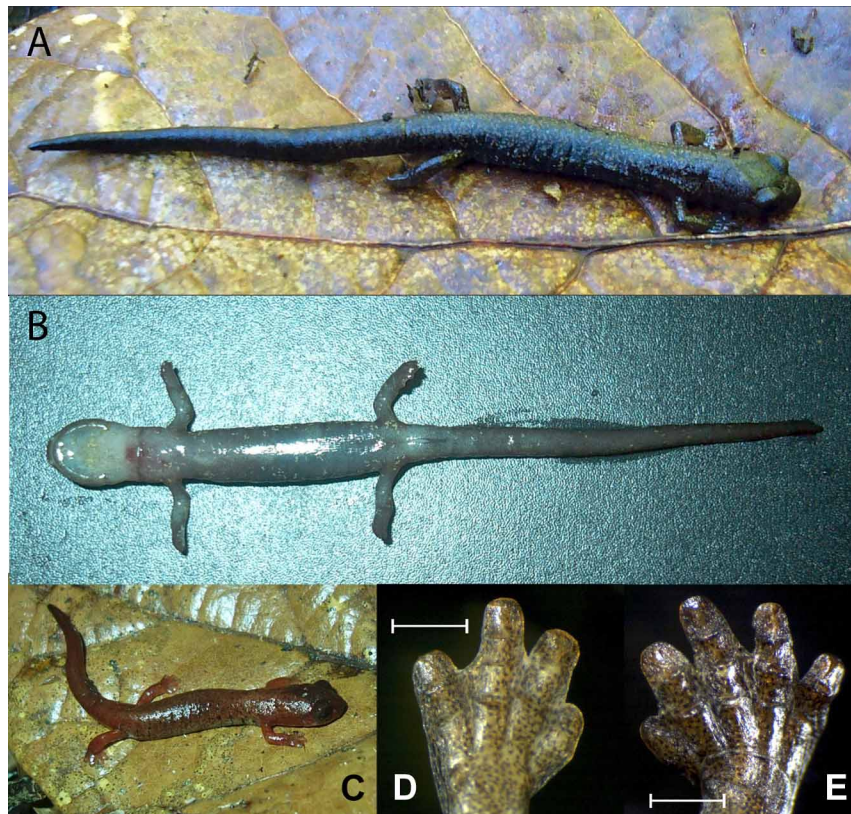


FIGURE 4. A) Dorsal and B) ventral photos of holotype (UCR 20852) of *Bolitoglossa kamuk* in life. C) Juvenile paratype (UCR 20854) of *B. kamuk* in life, showing variation in coloration. D) Dorsal view left hand and E) right foot of preserved holotype. Photos A, B and C by S. Rovito, D and E by Adrián García-Rodríguez. The bar in hand and feet are 1 mm length.

Measurements (in mm), limb interval and tooth counts of the male holotype (Table 2). HW 5.8, SG 8.5, HD 3.1, EW 1.0, EL 2.5, ES 1.7, ED 1.6, IC 2.6, IO 2.6, length of groove extending posteriorly from eye 2.3, distance between nuchal groove and gular fold 2.6, SF 10.8, IN 1.1, SP 0.4, SL 34.8, SAV 32.0, AX 19.2, LI 1.5, TL 35.2, tail width at base 2.4, tail depth at base 3.0, FLL 9.0, HLL 9.3, HAW 2.5, FW 3.7, T5 0.7, T3 1.1, mental gland width 1.3, mental gland length 1.2. Numbers of teeth: PMT 2, MT 17/17, VT 8/8, arranged in a single row.

Coloration of the holotype in life (Fig. 4). Dorsum and dorsal surface of tail and hind limbs black with numerous, uniformly distributed gold flecks. This coloration extends to lateral midline, where gold flecks become much less numerous. Background of fore limbs somewhat lighter. Gold flecks less numerous on top of head. Venter is dark grey, with a few gold specks, particularly towards sides of body. Gular region, underside of limbs, and anterior portion of tail pale grey with a few golden specks, while posterior half of the tail darker grey.

Coloration of the holotype in alcohol. Region of head between snout and eyes brown but darkened due to presence of skin glands that are heavily pigmented peripherally; frontal and parietal areas brown with skin glands with lighter edges; orbits completely black, canthus rostralis strongly marked numerous black spots on dark brown background; ventral area cream with numerous black spots that are even more concentrated in anterior region, making gular region lighter. Dorsum of trunk dark brown that darkens posteriorly; flanks marked with numerous

black spots on background passing from brown to clear cream from dorsum to venter; venter cream with numerous dots but still noticeably lighter than dorsum. Tail dark; dorsal part of first three post-sacral segments vertebrae and underside of first 11 caudal segments maintains color of trunk, while progressively darkening posteriorly, and becoming completely black. Both hind limbs and forelimbs appear black due to presence of numerous black spots on dark brown background; dorsal part of hands and ventral part of hands and feet lighter than rest of limb.

Variation. The juvenile paratype (UCR 20854) is orange in dorsal coloration with both dark grey and lighter colored specks. A darker grey patch is present on the top of the head posterior to the eyes and on the orbits. The dorsal surface of the limbs and tail are bright orange, changing to a darker orange-grey at the tip of the tail. The gular region is a pale yellow-orange color, while the venter is a pale golden color with numerous black specks. The underside of the tail is a uniform orange.

Habitat and range. This species is known only from the type locality on Cerro Apri, southwest of Cerro Kamuk just off the continental divide. Habitat consists of sub-páramo vegetation with extensive, deep moss mats, spongy soil, ferns, and small, isolated trees with arboreal bromeliads. The species was found both within these bromeliads and under moss.

Etymology. The species is from the Kamuk Massif, named for one of the dominant peaks in the region, Cerro Kamuk. The scientific name is a noun in apposition.

Nototriton matama sp. nov.

Matama Moss Salamander

Figure 5

Holotype. UCR 20215, an apparently mature female from the southeastern end of the Fila Matama (coordinates: 9.8071° N, 83.1683° W) at an elevation of 1300 m, collected on 30 October 2007, by Eduardo Boza-Oviedo and Ruth Delgado.

Paratypes. UCR20168, 20169, 20171, same data as holotype.

Diagnosis. Assigned to *Nototriton* because it has a well-developed sublingual fold and has fewer than 17 vertebrae in the trunk, and to the *picadoi* group based on mtDNA sequence data and on the basis of having rounded digital tips rather than pointed ones (as in the *richardi* group). A small member of the *Nototriton picadoi* group distinguished from all other members of the group by relatively enlarged and elongated nostrils and small, very narrow hands and feet and narrow heads; distinguished from *N. picadoi* by smaller size (holotype 23.6 mm SL, *N. picadoi* reaches 32 mm SL), relatively larger nostril (0.02 times SL, vs. 0.010–0.016 in *N. picadoi*), and very narrow feet (0.05 times SL, vs. 0.06–0.07 in *N. picadoi*) with pointed outer toe tips (vs. rounded toe tips); distinguished from members of the *N. richardi* group by discrete columnar digits not fused together and by rounded rather than pointed tips of the longest digits.

Description. A diminutive, slender species compared to other members of its genus. Sole adult specimen (based on size and proportions), the holotype, has a SL of 23.6 mm. Because the holotype is a female, typically the larger sex, maximum size of this species is expected to be not much larger than this specimen. Head small and narrow (SG/SL= 0.17; HW/SL= 0.14) with broadly truncated snout. Nostrils enlarged and elongated, with maximal dimension of 0.5 mm. One can see into nostrils from a dorsal view; nostrils oriented mainly frontally. Eyes relatively large and protuberant, visible protruding from side of head when viewed ventrally. Head only moderately differentiated from trunk, mainly by somewhat enlarged parotoid glands located in temporal region of head. Parotoid glands clearly evident as swollen, lightly pigmented oval structures. Teeth moderately abundant; PMT 4, MT 31, VT 11 in holotype. Trunk slender, limbs relatively short (0.18 SL, LI 5). Slender tail only slightly tapered before a break. Hands and feet bear well-formed, columnar digits that are only slightly webbed basally. Longer digits terminate in rounded tips, but shorter digits have bluntly pointed tips. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-4-2-5-1.

Measurements (in mm), limb interval and tooth counts of the female holotype (Table 2). HW 3.2, SG 4.2, HD 1.8, EW 0.6, EL 1.3, ES 0.8, ED 1.0, IC 1.8, IO 0.9, length of groove extending posteriorly from eye 1.0, distance between nuchal groove and gular fold 0.9, SF 6.8, IN 0.4, SP 0.2, SL 23.6, SAV 21.8, AX 13.4, LI 5, tail broken at 11.0, tail width at base 1.6, tail depth at base 1.8, FLL 3.7, HLL 4.2, HAW 1.0, FW 1.2, T5 0.2, T3 0.6, parotoid width 0.5, parotoid length 1.3, nostril diameter 0.5. Number of teeth: PMT 4, MT 15/16, VT 5/6.

Coloration of the holotype in life. A colorful individual with a generally light golden brown dorsal coloration. Light dorsal band bordered by short streaks of white and tan that constitute an irregular border, especially in pelvic area. Tail more uniformly golden in coloration and a little lighter than trunk. Parotoid region at back of head pale golden. Along generally darker flanks are some dark brown speckles. Broad band of light coloration under dark flanks.

Coloration of the holotype in alcohol. Colorful specimen more sharply differentiated into light and dark areas than in life. Specimen grey-brown to tan. Two pale temporal/paratoid patches. Distinct pale stripe extends from shoulder to tail, which is bright yellow and brown. Some suffusion of melanin present on trunk. Ventrolateral parts of trunk cream-colored. Dark interrupted dorsolateral line of pigment extends from shoulder to pelvis. Venter dark with whitish streaks in two ragged rows. Yellow patch in temporal areas descends to gular area in front of gular fold but not on midgular area. Gular area blackish but lighter than midventer region. Small speckles of white on ventral surfaces. Hint of herringbone pattern of dark chevrons present in dorsal stripe.



FIGURE 5. A) Dorsal view of holotype (UCR 20215) and B) ventral photo of the paratype (UCR 20169) of *Nototriton matama* in life. C) Dorsal view of right hand and D) right foot of holotype. Photo A by E. Boza-Oviedo, B by Alex Monro and E. Boza-Oviedo, C and D by A. García-Rodríguez. The bar in hand and feet are 1 mm length.

Habitat and range. The species is known only from the type locality along the Matama ridge of the Caribbean slope of the Chirripó Massif. The locality has mature cloud forest that includes members of: Araceae (e.g. *Philodendron*, *Anthurium*, *Monstera*), *Begonia* (Begoniaceae), palms (Arecaceae), Ericaceae, Melastomataceae, Marantaceae, Urticaceae (e.g. *Pilea*), Acanthaceae, Cyclanthaceae (e.g. *Cyclanthus*, *Carludovica*), Rubiaceae, *Heliconia* (Heliconiaceae), Piperaceae (e.g. *Piper*), bromeliads, ferns (e.g. Cyatheaceae and no tree ferns), and bryophytes. Humidity was at or near 100% during the time spent at the site. The specimens were found during daytime in moss mats at 0.95–2.1 m above ground and 400–600 m from the nearest stream. One specimen was found between a plant stem and the moss, while the others were within the moss (35–90 mm wide), some in moss in vertical parts of the trunk and others in moss hanging off the branches. *Plagiochila* spp was the most frequent bryophyte in the moss mats. The temperature ranged from 16–17 °C within moss mats and 17–18 °C in the air. Three specimens were found in the same tree.

Etymology. The species was discovered near the terminus of the Fila de Matama, a large mountain ridge that arises as a part of Cerro Chirripó, the highest mountain in Costa Rica. The scientific name is a noun in apposition.

Oedipina nimaso sp. nov.

Nimaso Worm Salamander

Figure 6

Holotype. UCR 8391, a subadult male from Cerro Nimaso, Prov. Limón, Costa Rica, 1093 m, collected by D. Robinson, Federico Bolaños, and Gilbert Barrantes on April 14, 1984.

Diagnosis. A small, extremely slender member of *Oedipina* (*Oedopinola*), based on having greater than 14 but fewer than 20 trunk vertebrae (García-París & Wake 2000; McCranie *et al.* 2008), distinguished from other members of that clade by the combination of its small size, slender habitus, its long pointed snout and very narrow hands and feet with pointed digital tips. Distinguished from Costa Rican and Panamanian members of the clade as follows: from *O. carablanca* by smaller size, very narrow pes (vs. very broad and webbed in *O. carablanca*) and manus relative to SVL with reduced numbers of phalanges (0-1-2-1 manus vs. 1-2-3-2 in *O. carablanca*; 0-1-2-1-1 pes vs. 1-2-3-(2,3)-2 in *O. carablanca*) and little white dorsal pigment vs. extensive white pigment on head and body in *O. carablanca*; from *O. parvipes* and *O. maritima* by narrower and more syndactylous hands and feet, rounded snout and relatively large and numerous maxillary teeth (max 8 in *O. maritima*, fewer than 5 in Panamanian *O. parvipes*); from *O. alleni* in being much smaller and less robust with much narrower pes and shorter digits, and in having more maxillary teeth (20 vs. 5 or fewer in *O. alleni*); from *O. savagei* by being less robust and in having shorter limbs (limb interval 9.5 vs. less than 7 in *O. savagei*) and narrower pes (1.2 vs. 1.9 in *O. savagei*), and in lacking white pigment on the back of the head and a dorsal stripe on the trunk; from *O. fortunensis* by having shorter limbs (limb interval 9.5 vs. 8 in *O. fortunensis*), narrower pes (1.2 mm vs. 1.7 in *O. fortunensis*), and a shorter, more pointed head (SL/SG = 6.4 vs. 5.2 in *O. fortunensis*); and from *O. complex* by having a longer tail (SVL/TL less than 0.73 vs. 0.89 in *O. complex*), broader head (SVL/HW 8.6 vs. 10.2 in *O. complex*) and narrower pes with a long, pointed third toe (vs. short rounded toe in *O. complex*).

Description. A diminutive, slender species compared to other *Oedopinola*. Sole specimen, the holotype, has a SL of 30.8 mm. Holotype very slender (Fig. 6) with narrow head (SL/HW 8.6) and rather long snout (SL/SG = 6.4) that is more rounded than pointed. Eyes small and only slightly protuberant. Limbs long and slender (SL/HLL = 4.5) and the right hindlimb is missing. Manus and pes flat and very narrow (SL/FW = 25.7), with digits poorly defined and fused together. Longest digit with long, sharply pointed tip that is slightly bent in a preaxial direction. Relatively numerous maxillary teeth relatively large and single premaxillary tooth is long and hooked, suggesting that individual is near or at sexual maturity.



FIGURE 6. A) Dorsal and B) ventral views of preserved holotype (UCR 8391) of *Oedipina nimaso*. C) Dorsal view of left hand and D) left foot of holotype. Photos A and B by Humberto Lezama, C and D by A. García-Rodríguez. The bar in hand and feet are 1 mm length.

Measurements (in mm), limb interval and tooth counts of the male holotype (Table 2). HW 3.6, SG 4.8, HD 1.6, EW 0.4, EL 1.1, ES 1.3, ED 0.7, IC 1.0, IO 1.2, length of groove extending posteriorly from eye 0.8, distance between nuchal groove and gular fold 1.4, SF 7.3, IN 1.0, external naris to snout 0.4, SP 0.3, SL 30.8, SAV 26.6, AX 19.8, LI 9.5, TL 42.0 (tail broken at tip, only slightly longer in life), tail width at base 2.1, tail depth at base 1.8, FLL 6.2, HLL 6.9, HAW 1.0, FW 1.2, T5 0.8, T3 1.1, parotoid width 1.4, parotoid length 2.9, nostril diameter 0.6. Number of teeth: PMT 1, MT 9/11, VT 6/6.

Coloration of the holotype in alcohol. Brown to reddish-brown generally, with small amount of whitish pigment on head, mainly concentrated between eyes. Venter lighter than other surfaces and covered with tiny whitish patches or speckles.

Habitat and range. Known only from the type locality. The locality is essentially mature forest within a sparsely inhabited indigenous reserve. The forest is very humid tropical forest in a transition zone to premontane forest.

Etymology. The scientific name is a noun in apposition and refers to the type locality at Cerro Nimaso.

Remarks. This specimen is badly desiccated. Osteological information has been derived from radiographs. There are 18 trunk vertebrae, one sacral, two caudosacral and 31 caudal vertebrae, with the very tip of the tail missing. The phalangeal formula for the manus is 0-1-2-1 and for the pes is 0-1-2-1-1. The basic formula for *Oedipina* is 1-2-3-2, and 1-2-3-3-2 (Wake 1966, Brame 1968, García-París & Wake 2000) so there has been a considerable reduction in this species. Some other members of *Oedopinola* from Costa Rica and Panama also have relatively few phalanges. The last trunk vertebra that bears ribs is number 16. Mesopodial elements are unmineralized cartilage. A preorbital process is present on the vomers. Nasals are moderately protuberant and are the anterior-most skeletal bones. The skull bones are fully articulated and well-developed, suggesting a near adult state of development, so this is likely a miniaturized species compared to other members of its genus.

Molecular phylogenetics

Two of the new species, *Bolitoglossa splendida* and *B. kamuk*, are part of the *B. subpalmata* clade (BS=100, PP=1.0), comprising *B. subpalmata*, *B. pesrubra*, *B. bramei*, *B. gomezi*, *B. gracilis*, and *B. tica* (Fig. 7). This clade corresponds to the *B. subpalmata* species group of Parra-Olea *et al.* (2004) and includes additional species not described at the time. *Bolitoglossa kamuk* is strongly supported as the sister taxon of *B. pesrubra* (BS=92, PP=0.99). *Bolitoglossa tica* and *B. subpalmata* are supported as sister species (BS=96, PP=0.97), while relationships between other members of the clade, including *B. splendida*, are not resolved. The recently described *B. gomezi* (Wake *et al.* 2007), which previously lacked molecular data, is a member of this group based on the mtDNA phylogeny. A group of several species (*B. epimela*, *B. cerroensis*, *B. marmorea*, and *B. minutula*) is resolved as the sister clade of the *B. subpalmata* clade with strong support (BS=100, PP=0.90). *Bolitoglossa aureogularis* is the sister species of the recently described *B. robinsoni* (Bolaños & Wake 2009) with strong support (BS=100, PP=1.0), based on a single specimen identified as *B. robinsoni* from Valle del Silencio (Fig. 7). *Bolitoglossa compacta*, *B. nigrescens*, and *B. sombra* form a clade that is strongly supported in the Bayesian results (PP=0.95), but not in the likelihood results (BS=42). *Bolitoglossa compacta* was included in the *B. adspersa* species group of Parra-Olea *et al.* (2004), while *B. nigrescens* was included in the *schizodactyla* species group. These species have few members of their species groups represented in our phylogeny, which focuses primarily on montane Talamancan taxa. The sample of *B. sombra* is nearly identical in sequence to both a newly sequenced sample of *B. nigrescens* from Tarbaca, Prov. San José, Costa Rica (UCR 20539) (GTR distance of 0.002 for 16S and 0.003 for *cyt b*) and a sample of *B. sombra* from western Panama (CH 7478) (GTR distance of 0 for 16S and 0.001 for *cyt b*). The Bayesian and ML results conflict in the placement of the *B. compacta*-*B. nigrescens* and *B. aureogularis* clades. In the Bayesian results, the *B. compacta*-*B. nigrescens* clade is the sister group of *B. aureogularis* and *B. robinsoni* (PP=0.95). In the ML results, the *B. aureogularis*-*B. robinsoni* clade is sister to the *B. subpalmata* and *B. epimela* clades (BS=96), while the *B. compacta*-*B. nigrescens* clade is sister to all other Costa Rican salamanders included in the analysis. Additional sequence data, as well as an expanded taxon set that includes more members of the *adspersa* and *schizodactyla* species groups, may be needed to resolve the relationships between these clades. Genetic distances between species included in our phylogenetic analysis are given in Table 3.

The sequenced sample of *Nototriton matama* is part of a clade containing other members of the *N. picadoi* group (Papenfuss & Wake 1987; García-París & Wake 2000), including *N. saslaya* (Köhler 2002), with strong support (BS=97, PP=97), and is closely related to *N. picadoi*, *N. gamezi* and *N. abscondens* (Fig. 8). The relationships between *N. matama*, *N. picadoi*, *N. abscondens* and *N. gamezi* are not resolved in the mtDNA phylogeny. The genetic distances between members of the *N. picadoi* group are rather small. The largest genetic distances within the group are between *N. saslaya* and *N. picadoi* for 16S (GTR distance=0.034) and between *N. abscondens* and *N. guanacaste* for *cyt b* (0.043); a *cyt b* sequence was not available for *N. saslaya*. The smallest divergence within the clade is between *N. matama* and *N. picadoi* (GTR distance=0.006 for 16S and 0.011 for *cyt b*). Genetic distances between species of *Nototriton* included in our phylogenetic analyses are given in Table 4.

TABLE 3. Tamura-Nei (TN) distances between *Bolitoglossa* species used in phylogenetic analysis. Numbers above diagonal are for 16S and numbers below diagonal are for cytb.

Species	Bgom	Bbra	Bkam	Bpes	Bspl	Btic	Bsub	Bgra	Baur	Brob	Bcom	Bnig	Bsom	Bmin	Bepi	Bcer	Bmar
<i>B. gomezi</i>	—	0.028	0.020	0.029	0.028	0.034	0.022	0.041	0.041	0.045	0.060	0.051	0.052	0.037	0.050	0.047	0.035
<i>B. bramei</i>	0.063	—	0.017	0.026	0.033	0.030	0.019	0.029	0.044	0.048	0.057	0.049	0.048	0.040	0.050	0.051	0.040
<i>B. kamuk</i>	0.072	0.070	—	0.009	0.020	0.025	0.010	0.033	0.035	0.039	0.052	0.040	0.039	0.024	0.050	0.043	0.026
<i>B. pesrubra</i>	0.071	0.069	0.077	—	0.022	0.032	0.019	0.042	0.041	0.045	0.060	0.048	0.047	0.033	0.055	0.053	0.035
<i>B. splendida</i>	0.112	0.112	0.115	0.099	—	0.036	0.022	0.043	0.043	0.048	0.067	0.055	0.054	0.041	0.054	0.052	0.043
<i>B. tica</i>	0.072	0.072	0.081	0.079	0.104	—	0.015	0.036	0.045	0.050	0.065	0.061	0.060	0.046	0.059	0.057	0.044
<i>B. subpalmata</i>	0.077	0.085	0.093	0.087	0.107	0.068	—	0.024	0.037	0.041	0.054	0.051	0.050	0.031	0.052	0.050	0.033
<i>B. gracilis</i>	0.076	0.082	0.082	0.078	0.102	0.077	0.089	—	0.054	0.061	0.063	0.059	0.058	0.052	0.065	0.061	0.048
<i>B. aureogularis</i>	0.192	0.201	0.186	0.184	0.225	0.210	0.206	0.180	—	0.008	0.045	0.048	0.047	0.041	0.056	0.047	0.045
<i>B. robinsoni</i>	0.204	0.212	0.202	0.194	0.219	0.213	0.198	0.188	0.050	—	0.045	0.048	0.047	0.046	0.061	0.052	0.050
<i>B. compacta</i>	0.186	0.198	0.193	0.193	0.225	0.209	0.181	0.206	0.142	0.150	—	0.032	0.030	0.063	0.081	0.074	0.062
<i>B. nigrescens</i>	0.192	0.193	0.192	0.195	0.212	0.186	0.182	0.194	0.167	0.187	0.138	—	0.001	0.053	0.071	0.060	0.053
<i>B. sombra</i>	0.182	0.177	0.174	0.185	0.181	0.169	0.182	0.184	0.161	0.184	0.138	0.002	—	0.052	0.070	0.059	0.052
<i>B. minutula</i>	0.186	0.188	0.181	0.205	0.188	0.196	0.192	0.192	0.202	0.198	0.189	0.187	0.189	—	0.046	0.029	0.016
<i>B. epimela</i>	0.177	0.188	0.178	0.191	0.197	0.197	0.197	0.183	0.207	0.207	0.195	0.201	0.200	0.137	—	0.041	0.046
<i>B. cerroensis</i>	0.152	0.142	0.166	0.163	0.152	0.161	0.157	0.168	0.164	0.189	0.175	0.192	0.180	0.118	0.112	—	0.031
<i>B. marmorea</i>	0.154	0.154	0.150	0.170	0.140	0.166	0.168	0.166	0.155	0.178	0.185	0.183	0.185	0.100	0.123	0.093	—

TABLE 4. Tamura-Nei (TN) distances between *Nototriton* species used in phylogenetic analysis. Numbers above diagonal are for 16S and numbers below diagonal are for cyt**b**.

Species	Nmat	Nabs	Ngam	Nbar	NspA	NspB	Nbro	Ngua	Nlig	Nlim	Npica	Nric	Ntam	Nsas	Npicu	Nstu
<i>N. matama</i>	—	0.016	0.014	0.063	0.064	0.066	0.068	0.010	0.068	0.060	0.006	0.043	0.058	0.032	0.055	0.075
<i>N. abscondens</i>	0.030	—	0.018	0.059	0.060	0.062	0.059	0.014	0.059	0.056	0.018	0.039	0.054	0.032	0.051	0.066
<i>N. gamezi</i>	0.016	0.024	—	0.061	0.062	0.064	0.066	0.020	0.066	0.058	0.016	0.036	0.056	0.030	0.053	0.073
<i>N. barbouri</i>	0.119	0.122	0.126	—	0.036	0.034	0.041	0.061	0.036	0.015	0.066	0.042	0.047	0.060	0.021	0.039
<i>N. sp. A</i>	0.133	0.126	0.137	0.116	—	0.022	0.014	0.062	0.045	0.036	0.066	0.053	0.052	0.062	0.036	0.016
<i>N. sp. B</i>	0.167	0.144	0.170	0.119	0.058	—	0.018	0.064	0.046	0.030	0.068	0.055	0.056	0.057	0.026	0.020
<i>N. brodiei</i>	0.122	0.136	0.139	0.111	0.061	0.064	—	0.066	0.044	0.036	0.070	0.057	0.053	0.063	0.036	0.010
<i>N. guanacaste</i>	0.030	0.043	0.041	0.134	0.139	0.166	0.127	—	0.066	0.058	0.012	0.037	0.056	0.026	0.053	0.073
<i>N. lignicola</i>	0.120	0.127	0.134	0.091	0.120	0.126	0.108	0.130	—	0.032	0.066	0.049	0.045	0.066	0.024	0.036
<i>N. limnospectator</i>	0.139	0.142	0.146	0.081	0.135	0.135	0.126	0.142	0.113	—	0.062	0.045	0.036	0.057	0.016	0.034
<i>N. picadoi</i>	0.011	0.030	0.016	0.119	0.137	0.163	0.125	0.035	0.127	0.146	—	0.045	0.061	0.034	0.058	0.078
<i>N. richardi</i>	0.094	0.097	0.094	0.139	0.123	0.123	0.095	0.097	0.148	0.139	0.094	—	0.052	0.045	0.045	0.060
<i>N. tomamorurum</i>	0.123	0.113	0.116	0.126	0.143	0.139	0.138	0.123	0.124	0.125	0.123	0.134	—	0.056	0.038	0.051
<i>N. saslaya</i>	0.057	0.072	0.063	0.147	0.150	0.176	0.148	0.072	0.132	0.160	0.057	0.107	0.143	—	0.049	0.070
<i>N. picucha</i>	0.126	0.116	0.133	0.106	0.126	0.123	0.131	0.125	0.116	0.115	0.119	0.117	0.107	0.132	—	0.030
<i>N. stuarti</i>	0.137	0.130	0.147	0.125	0.072	0.078	0.058	0.129	0.110	0.128	0.137	0.116	0.144	0.145	0.133	—

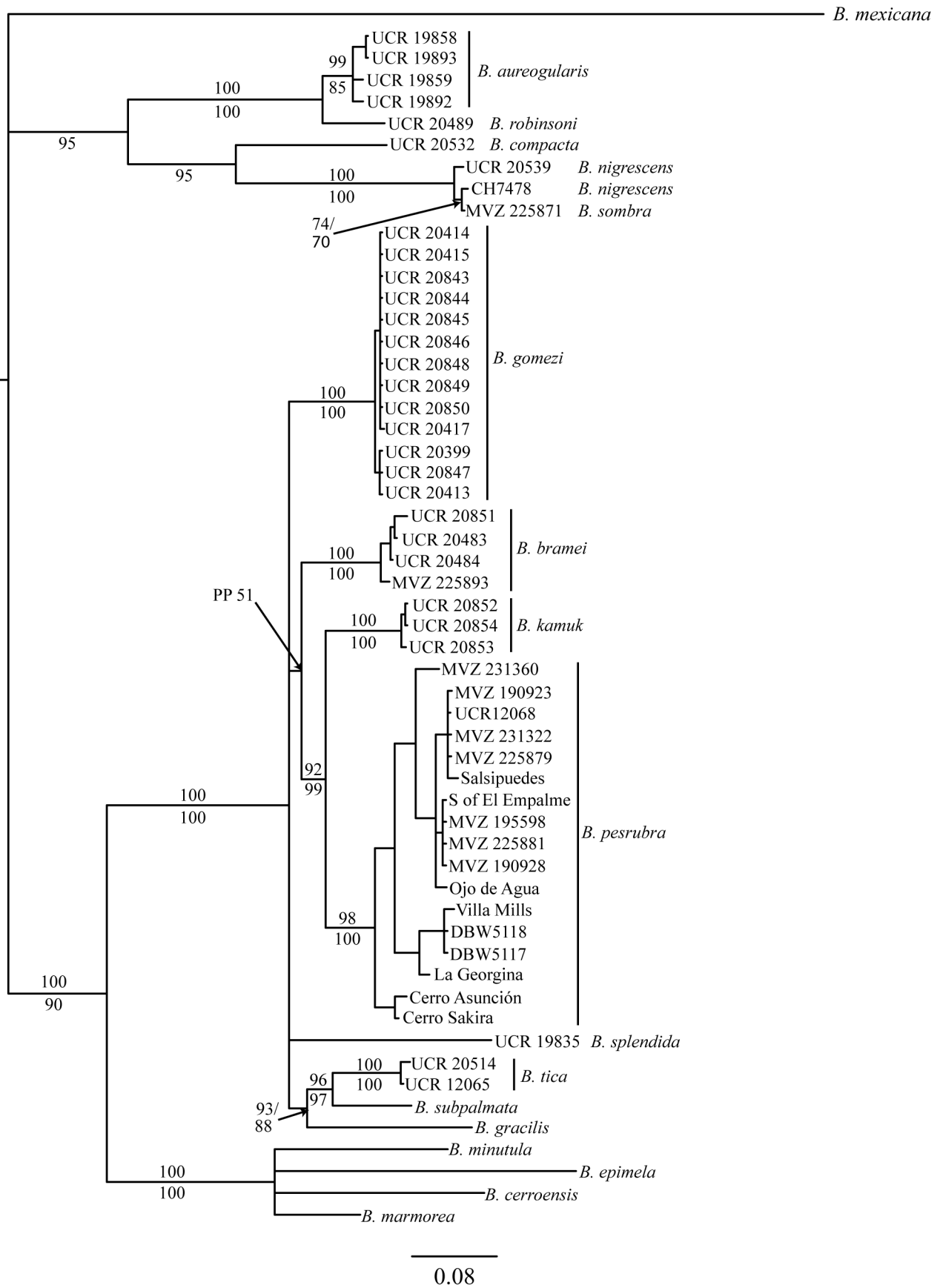


FIGURE 7. Phylogeny of mtDNA data for *Bolitoglossa* constructed using Bayesian analysis. Maximum likelihood bootstrap values from RAXML analysis shown above branches, Bayesian posterior probabilities (multiplied by 100) shown below branches. Support values below 50 not shown.

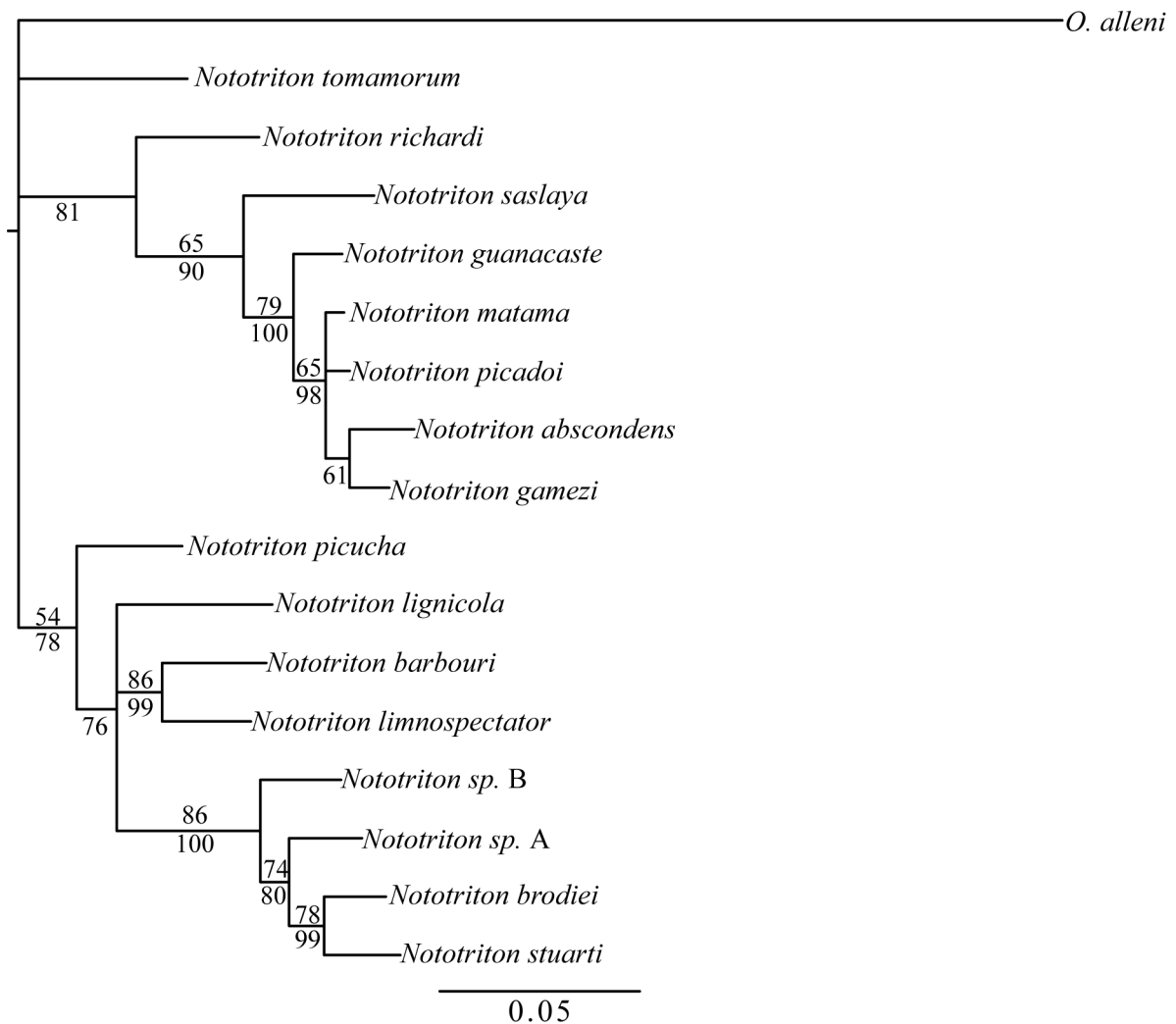


FIGURE 8. Phylogeny of mtDNA data for *Nototriton* constructed using Bayesian analysis. Maximum likelihood bootstrap values from RAXML analysis shown above branches, Bayesian posterior probabilities (multiplied by 100) shown below branches. Support values below 50 not shown.

Discussion

Taxonomic comments and comparisons. *Bolitoglossa* is the largest and most widespread plethodontid genus, with about 120 described species. Its known geographic distribution occupies nearly all of the tropical range of salamanders in Central and South America. With the three new species, the genus is represented by 26 species in Costa Rica. The eastern Talamancan region is especially rich in species of *Bolitoglossa*, which range nearly to the tops of the highest mountains; for example, *B. bramei*, *B. kamuk*, *B. pygmaea*, and *B. robinsoni* have been found above 3000 m elevation. Until now, these Talamancan species have generally been represented by few specimens. Further complicating matters is the fact that certain taxa have lacked tissue samples. In this study we present a phylogenetic hypothesis based on mitochondrial DNA sequences, and there are some surprises. As anticipated, the *B. subpalmata* group is widely distributed in eastern Costa Rica, and here we add two new species, *B. splendida* and *B. kamuk*. The former is represented by a single individual, but it has a distinctive, unique color pattern and we also have tissue that shows how genetically distinctive the species is within the group. The latter species, *B. kamuk*, is less distinctive; the three individuals sampled for mtDNA are nearly identical and together they form a clade that is sister to the remaining samples of *B. pesrubra*. In the phylogeny presented, *B. pesrubra*-*B. kamuk*, *B. bramei*, *B. gomezi*, *B. splendida* and a clade comprising ((*B. tica*-*B. subpalmata*)(*B. gracilis*)) form essentially a polytomy. These taxa are mainly allopatric, as far as current knowledge is concerned. While the known distributions of *B.*

bramei and *B. gomezi* closely approach each other near the Costa Rica-Panama border, *B. gomezi* has generally been found at lower elevations (1170–2120 m) than *B. bramei* (1900–3200 m). To the northwest, along the cordilleran spine, *B. gomezi* and *B. kamuk* are sympatric at Potrero Grande. Although the distribution of *B. kamuk* is poorly known, it is replaced further to the northwest by *B. pesrubra*, which occurs as far to the southeast as Cerro Chirripó Grande. *Bolitoglossa pesrubra* then persists to the northwest in the region known as Cerro de la Muerte and neighborhood until being replaced at lower elevation (about 2500 m) by *B. tica*. We suspect *B. tica* and *B. gracilis*, which occurs at even lower elevation (to 1200 m) to the east of the main cordilleran spine, may occur in sympatry between the Río Reventazón valley in the vicinity of Tapantí and El Empalme. Finally, *B. subpalmata* occurs in the Cordillera Volcánica Central and mountains to the northwest as far as Volcán Cacao. Thus, members of the *B. subpalmata* group occupy much of the suitable terrain above about 1200 m from northwestern Costa Rica to western Panama.

Our phylogeny of *Bolitoglossa* includes several species for which no published sequence data exists. We assign UCR 20532 to *B. compacta* based on its red-orange blotched dorsal color pattern; this specimen is from Valle del Silencio, an area where *B. compacta* is known to occur (Hanken *et al.* 2005). *Bolitoglossa robinsoni* is known from the type locality at Cerro Echandi on the Costa Rica-Panama border, with several other morphologically divergent populations along the continental divide near the border tentatively assigned to this species. These divergent populations, including Valle del Silencio, the farthest locality from Cerro Echandi, may belong to a separate species from *B. robinsoni* (Bolaños & Wake 2009); the Valle del Silencio specimen is here assigned to *B. robinsoni* based on overall morphology, pending the acquisition of topotypic material. We assigned UCR 20539, from Tarbaca, Aserrí, San José to *B. nigrescens* because *B. nigrescens* is the only large, black *Bolitoglossa* that is known from the area (Hanken *et al.* 2005; García-París *et al.* 2008). We assigned another specimen (CH 7478) used in our phylogenetic analysis to *B. sombra*, based on both geographic distribution and its similarity in mtDNA sequence to *B. sombra*, although we lack morphological data for this specimen. Finally, we tentatively assign several samples collected on the trips to Cerro Kamuk, Cerro Amuo and Tres Colinas to *B. gomezi*, based on external morphological similarity to other specimens of *B. gomezi* and because these specimens cannot be assigned to *B. bramei* or *B. robinsoni*. As with *B. robinsoni*, definitive identification of these specimens will require additional material from the type locality of *B. gomezi*.

A surprise from our molecular analysis was the discovery of a previously unknown clade including, at present, two taxa, *B. aureogularis* and *B. robinsoni*. This well supported clade (BS=100, PP=0.85) is either the sister group (in the ML results) to the two clades (*B. subpalmata* and *B. epimela*) previously considered to constitute the Central American subclade of *Bolitoglossa (Eladinea)* (Parra-Olea *et al.* 2004), or the sister clade (in the Bayesian results) to the largely South American subclade of *Bolitoglossa (Eladinea)* here represented by *B. compacta*, *B. nigrescens*, and *B. sombra*, (Parra-Olea *et al.* 2004; Hanken *et al.* 2005). The known geographic distributions of the two species in this new clade are separated, *B. aureogularis* to the north and west in eastern Costa Rica, and *B. robinsoni* to the south and east in the border region and into western Panama. The larger and more robust *B. robinsoni* is easily distinguished from the smaller and more slender *B. aureogularis* by coloration and body form.

While our phylogeny supports higher species diversity in the Talamanca region than was previously known, it also calls into question the distinctiveness of *B. sombra*. Although *B. sombra* was originally distinguished from *B. nigrescens* based on morphological differences (more slender trunk, shorter limbs, and fewer teeth compared to *B. nigrescens*), these differences were very slight (shown in Fig. 3–4 of Hanken *et al.* 2005). In our mtDNA phylogeny, a sample of *B. sombra* (MVZ 225875) from the type locality near Las Tablas, Costa Rica and another from Panama are nearly identical in sequence to the available sample of *B. nigrescens*. The lack of sequence divergence between the two taxa, coupled with the lack of substantial morphological differences, does not support the status of *B. sombra* as a distinct species. The type specimen of *B. nigrescens* is a subadult, and no additional topotypic specimens are available for the species. Furthermore, we have not had the opportunity to examine the Panamanian specimen of *B. sombra* whose sequence we used in our phylogenetic analysis. We refrain from declaring *B. sombra* to be a synonym of *B. nigrescens* at present, pending discovery and study of topotypic material for *B. nigrescens*.

Nototriton includes fifteen described species presently arranged in three species groups: *barbouri* (*N. barbouri*, *N. brodiei*, *N. lignicola*, *N. limnospectator*, *N. picucha*, *N. stuarti*), *picadoi* (*N. abscondens*, *N. gamezi*, *N. guanacaste*, *N. major*, *N. saslaya* and *N. matama*) and *richardi* (*N. richardi*, *N. tapanti*) (García-París & Wake 2000; Köhler 2002). Townsend *et al.* (2010) described *N. tomamorum* but refrained from assigning it to an existing species group. The known distribution of the *barbouri* group is restricted to eastern Guatemala and Honduras

(Wake & Campbell 2000). All remaining species are known only from Costa Rica, except the Nicaraguan *N. saslaya* (Köhler 2002). Assignment of *N. matama* to the *picadoi* group is based on the molecular evidence, but morphology also supports this arrangement. Its columnar digits are rounded rather than pointed (as in the *richardi* group) at the terminus of the longest toes.

Our phylogenetic hypothesis of *Nototriton* includes six species (*N. barbouri*, *N. matama*, *N. picucha*, *N. saslaya*, *N. stuarti*, and *N. tomamorum*) not available to García-París and Wake (2000). The results of their parsimony and neighbor-joining phylogenetic analyses also showed *N. abscondens*, *N. guanacaste*, and *N. picadoi* to form a clade of close relatives, with relationships between these taxa not well resolved. Although genetic divergence is low between *N. matama* and other members of the *N. picadoi* group, the morphological differences between these taxa support the status of *N. matama* as a species. The phylogeny of Townsend *et al.* (2010), which included all species except *N. matama*, *N. picucha*, *N. saslaya*, and *N. stuarti* is concordant with our phylogeny; while our results show *N. abscondens* and *N. gamezi* to be sister species, rather than *N. gamezi* and *N. picadoi*, this relationship has almost no support (BS<50, PP=56). Our phylogeny also differs from the results of Townsend *et al.* (2011) in the placement of *N. saslaya*, *N. tomamorum*, and *N. picucha*, but none of these relationships are well-supported in our phylogeny.

The Costa Rican *Nototriton* with the largest known geographic range is *N. abscondens*, from the middle part of the Cordillera Volcánica Central. It is sympatric over a part of its range with *N. richardi*, a smaller, more slender species that has larger nostrils and diminutive limbs and digits, the latter syndactylous with pointed tips. The known distributions of the other species are more restricted; *N. guanacaste* is known only from Volcán Orosí and Volcán Cacao in the northwestern Cordillera de Guanacaste, *N. gamezi* is known only from near Monteverde in the northwestern Cordillera de Tilarán, and *N. picadoi* is known only from the vicinity of the upper Río Reventazón valley (especially Tapantí reserve) on the northeastern margin of the Cordillera de Talamanca. The remaining species, *N. tapanti*, *N. major*, and *N. matama*, are known only from their type localities, on the northeastern margins of the Cordillera de Talamanca, the first two represented only by single specimens. Each of the species has diagnostic characters and those that have been subjected to molecular analysis (all except *N. major*) have also proven to be phylogenetically distinct (Good & Wake 1993, García-París & Wake 2000). The new species differs strongly from *N. major*, the largest species in the genus and one that has distinct columnar digits with rounded tips and small nostrils.

Oedipina is well represented in Costa Rica, with two of the three major clades and 15 of the 31 currently recognized species known from the country. *Oedipina nimaso* is a member of the subgenus *Oedopinola*, characterized by a short vertebral column [18 in *O. nimaso*, 18–19 trunk vertebrae in the subgenus as a whole, versus at least 20 in *Oedipina* and *Oeditriton* (Brame 1968; McCranie *et al.* 2008)] and typically rather robust habitus. If the holotype is near adult (as seems likely from the well articulated skull and hooked premaxillary tooth), this species may be the smallest and most attenuate of the clade *Oedopinola*. With the addition of *O. nimaso*, *Oedopinola* includes 12 species: *O. alleni* (Pacific coastal lowlands [i.e., below 500 m elevation] Costa Rica, barely entering Panama; known from ca. 15 museum specimens), *O. carablanca* (lowlands of northeastern Costa Rica, known from 3 museum specimens), *O. elongata* (lowlands of eastern Chiapas, Mexico, to northwestern Honduras, known from fewer than 20 museum specimens), *O. complex* (lowlands of central Panama, known from about 20 museum specimens, but some likely misidentified [reported from Isla Gorgona, off the Pacific Coast of western Colombia, and from 800 m elevation in northeastern Colombia, Brame & Wake 1963, but these are almost certainly misidentified]), *O. fortunensis* (from 1270 m in western Panama, known from two specimens), *O. gephyra* (from over 1700 m in northwestern Honduras, known from about 10 specimens), *O. maritima* (from Isla Escudo de Veraguas, in the Caribbean Sea off the north coast of Panama, known from eight museum specimens), *O. nimaso* (from about 1100 m in extreme southeastern Costa Rica, known from the unique holotype), *O. parvipes* (from northwestern Colombia, presumably in the lowlands, and reported, probably erroneously, from Panama; collectively known from a substantial number of museum specimens but in need of taxonomic revision), *O. petiola* (from northern Honduras, known from the unique holotype, collected at nearly 1600 m elevation), *O. savagei* (from a small area along the western border of Costa Rica and Panama at elevations between 1200 and 1400 m, known from fewer than 10 museum specimens), and *O. tomasi* (from 1800 m in northwestern Honduras, known from two museum specimens).

Only *O. elongata* has much of a geographic range, excluding the likely multispecies complexes of *O. complex* and *O. parvipes*. The northern *O. elongata*, *O. gephyra*, *O. petiola*, and *O. tomasi* (the latter three close relatives in

a subclade proposed as the sister taxon of *O. elongata* + *O. carablanca*, McCranie & Townsend 2011) are known only from central/northern Honduras and to the north as far as Chiapas, southern Mexico. Based on their small geographic ranges and distance from Costa Rica, all are unlikely to be conspecific with, or even related closely to *O. nimaso*. The new taxon is readily distinguished by its minute size from species that reach much larger sizes (*O. elongata* to over 66 mm SL, *O. tomasi* to 63 mm SL, *O. gephyra* to over 58 mm SL, *O. alleni* to over 57 mm SL, *O. carablanca* to over 54 mm SL, *O. parvipes* to over 52 mm SL; Brame 1968, McCranie 2006). All of these species have a broader manus and pes than *O. nimaso*. Because sample sizes are so small, statistical comparisons are effectively impossible, but if we use molecular studies of the subgenus (e.g., García-París & Wake 2000, McCranie & Townsend 2011) for comparisons, species ranges are typically very small, and thus any species from west of the cordilleran divide in Costa Rica/Panama are unlikely on distribution alone to be conspecific with *O. nimaso*; in addition, they are all larger and more robust. If we restrict our consideration to species that are known to occur north and east of the cordilleran divide, the candidates are *O. fortunensis*, *O. maritima*, *O. complex*, and *O. parvipes*. Only the latter two are represented by good sample sizes, but both are likely to be species complexes, or agglomerations of morphologically similar forms that may not even be close relatives (based on unpublished morphological studies of DBW). Brame (1968) presents plots of head width against SL, maxillary tooth totals against SL, hind limb length against SL, and foot width against SL for his samples identified as *O. complex* and *O. parvipes*. The single specimen of *O. nimaso* falls approximately on the same regression as *O. complex* with respect to foot width, but the specimen of *O. complex* closest in size to the holotype is much larger, and *O. parvipes* has broader feet. The limb length of the holotype of *O. nimaso* is roughly on the regression line for *O. parvipes* but above (longer) than for *O. complex*. Total numbers of maxillary teeth are much higher than for either *O. complex* of roughly comparable size, or for all sizes of Panamanian representatives of *O. parvipes*. Head widths appear to be comparable in the three species.

McCranie and Townsend (2011) present the most complete molecular phylogeny for *Oedopina*, including 10 of the 12 species. The *gephyra* subclade has been discussed above and on morphological grounds *O. nimaso* is readily excluded from this northern subclade. A second subclade includes *O. alleni* and *O. savagei*, morphologically differentiated taxa from the Pacific coast and nearby slopes, and we think it unlikely that *O. nimaso* is related to them. The final subclade includes *O. complex* (topotypic material), *O. maritima* (topotypic material), and *O. parvipes* (from central Panama, unlikely to be conspecific with topotypic material, which is unavailable for molecular studies). We think it likely, on geographic as well as morphological grounds, that *O. nimaso* will prove to be a member of this subclade. *O. fortunensis* (the only taxon other than *O. nimaso* excluded from the molecular analysis) might be a member either of this subclade or the *alleni* - *savagei* subclade.

Despite having only a single specimen, we decided that the most responsible course of action is to recognize *O. nimaso* as a new taxon. Both specimens of *O. fortunensis* have a unique color pattern (see Köhler *et al.* 2007, AmphibiaWeb) and the holotypes (the only specimens for which measurements are available) differ in important morphological traits, so there is no basis for assigning the single specimen to *O. fortunensis*. To assign it to either *O. complex* or *O. parvipes* seems unwise, given that the unique specimen does not fit into either of these complexes with respect to morphology, and especially in light of the likelihood that both are species complexes (or, most likely, taxa of convenience, given the large geographic ranges of each in a subgenus noted for the narrow, restricted geographic distributions of the included species).

Biogeography. The results of our fieldwork and phylogenetic analyses shed light on the biogeography of the Talamancan region. Based on present knowledge of the geographic distributions of salamanders in southern Central America, *Bolitoglossa (Eladinea)* reaches its northern limit in northwestern Costa Rica, with *B. subpalmata* and *B. robusta* on Volcán Cacao (Savage 2002). The subgenus *Eladinea* thus does not cross the Nicaraguan depression, and is restricted to the Chorotega and Chocó blocks of Central America (Marshall 2007) as well as northern South America. Within the Cordillera de Talamanca, if we restrict our discussion to elevations above 1500 m, the majority of known salamanders are members of the *subpalmata* and *epimela* species groups of *Eladinea* (Parra-Olea *et al.* 2004); both of these species groups are restricted to the Chorotega block. The only salamanders that have been found above 1500 m in the Cordillera de Talamanca from other species groups are *B. compacta* (in the *adpersa* group), *B. aureogularis* and *B. robinsoni*, and the large, black species (such as *B. nigrescens*, *B. robusta*, and *B. sombra*) that are members of the *schizodactyla* group. Parra-Olea *et al.* (2004) placed *B. diminuta* in the *schizodactyla* species group based on partial mtDNA sequences, while Savage (2002) stated that it probably belongs to the *subpalmata* species group. The description of two new species (*B. kamuk* and *B. splendida*) within

the *B. subpalmata* clade from the Cordillera de Talamanca, along with the recent description of *Bolitoglossa tica* (García-París *et al.* 2008), make this clade almost entirely endemic to the Cordillera de Talamanca. Only *B. subpalmata*, which occurs in the Cordillera Volcánica Central, Cordillera de Tilarán, and Cordillera Volcánica de Guana-caste of Costa Rica, is found outside of the Cordillera de Talamanca. The sister clade of the *B. subpalmata* clade in both our analyses and that of Parra-Olea *et al.* (2004), which contains members of the *epimela* species group, is known only from the Cordillera de Talamanca and adjacent areas of western Panama. The presence of nearly all species of these two clades in the Cordillera de Talamanca suggests that they represent an autochthonous element of the fauna of southern Costa Rica and western Panama.

Although the results of our Bayesian phylogenetic analyses support a sister group relationship between (*Bolitoglossa aureogularis* + *B. robinsoni*) and (*B. nigrescens* + *B. sombra*), our maximum likelihood analysis recovers *B. aureogularis* + *B. robinsoni* as the sister clade to the larger clade of primarily Talamancan salamanders (containing the *subpalmata* and *epimela* species groups) discussed above. If the latter relationship is correct, this would suggest that the great majority of all species of *Bolitoglossa* currently found in montane regions of southern Costa Rica and western Panama are descended from a common ancestor from the region. A more inclusive phylogenetic analysis with additional taxon sampling of South American and Panamanian species, particularly from the *adpersa* species group, will be necessary to resolve relationships between the clades found in the Talamanca. Our present results suggest that the Cordillera de Talamanca is not only a site of high salamander species richness within southern Costa Rica, but appears to represent a focal region of diversification.

With the five salamanders described here and including *Bolitoglossa sombra*, the known Costa Rican salamander fauna is now comprised of 49 species, including 26 *Bolitoglossa*, eight *Nototriton* and 15 *Oedipina*. Adding the five species described here results in a value of 9.59 salamander species/10000 km², making Costa Rica the country with the largest known salamander fauna in the world relative to its total area. In decreasing order, the next three countries are Guatemala (5.51, 60 species), Panama (3.71, 28) and Honduras (2.93, 33) (www.AmphibiaWeb.org). Mexico (132 species) and United States of America (187 species) are the most diverse countries in terms of total salamander species richness, but have much lower values of salamander species per area (0.67 and 0.19 respectively) (AmphibiaWeb2011) due to their large land areas. Given the small ranges of most Costa Rican salamanders and high species turnover between sites and along elevational gradients (Wake 1987), we suspect that additional species remain to be discovered within the region.

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