NEW SALAMANDERS (CAUDATA: PLETHODONTIDAE) FROM GUATEMALA, WITH MISCELLANEOUS NOTES ON KNOWN SPECIES

JONATHAN A. CAMPBELL, ERIC N. SMITH, JEFFREY STREICHER, MANUEL E. ACEVEDO, and EDMUND D. BRODIE, JR.

MISCELLANEOUS PUBLICATIONS

MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 200

Ann Arbor, October 13, 2010
ISSN 0076-8405

PUBLICATIONS OF THE
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 200

J. B. BURCH, *Editor*
J. L. PAPPAS, *Assistant Editor*

The publications of the Museum of Zoology, The University of Michigan, consist primarily of two series—the *Miscellaneous Publications* and the *Occasional Papers*. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb. Occasionally the Museum publishes contributions outside of these series; beginning in 1990 these are titled Special Publications and are numbered. All submitted manuscripts to any of the Museum's publications receive external review.

The *Occasional Papers*, begun in 1913, serve as a medium for original studies based principally upon the collections in the Museum. They are issued separately. When a sufficient number of pages has been printed to make a volume, a title page, table of contents, and an index are supplied to libraries and individuals on the mailing list for the series.

The *Miscellaneous Publications*, initiated in 1916, include monographic studies, papers on field and museum techniques, and other contributions not within the scope of the *Occasional Papers*, and are published separately. It is not intended that they be grouped into volumes. Each number has a title page and, when necessary, a table of contents.

A complete list of publications on Mammals, Birds, Reptiles and Amphibians, Fishes, Insects, Mollusks, and other topics is available. Address inquiries to Publications, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109–1079.

RECENT *MISCELLANEOUS PUBLICATIONS*

Klimov, P.B. & B.M. OConner. 2008. Morphology, evolution, and host associations of bee-associated mites of the family Chaetodactylidae (Acari: Astigmata) with a monographic revision of North American taxa. *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 199, pp. *i*-*vi*, 1-243, 95 figs., 27 tables, 9 appendices.

Chakrabarty, P. 2007. A morphological phylogenetic analysis of Middle American cichlids with special emphasis on the section '*Nandopsis*' *sensu* Regan. *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 198, pp. *i*-*iii*, 1-31, 37 figs., 1 table, 2 appendices.

Gonçlaves, P.R., P. Myers, J.F. Vilela & J.A. de Oliveira. 2007. Systematics of species of the genus *Akodon* (Rodentia: Sigmodoninae) in southeastern Brazil and implications for the biogeography of the *Campus de Altitude*. *Misc. Publ. Mus. Zool., Univ. Michigan,* No. 197, pp. *i*, 1-24, 9 figs., 4 tables, 2 appendices.

Bochkov, A.V. & B.M. OConner. 2006. Fur-mites of the family Atopomelidae (Acari: Astignata) parasitic on Philippine mammals: systematics, phylogeny, and host-parasite relationships. *Misc. Publ. Mus. Zool., Univ. Michigan,* No. 196, pp. *i*-*iii*, 1-62, 39 figs., 4 tables.

Binford, L.C. 2006. Birds of the Keweenaw Peninsula, Michigan. *Misc. Publ. Mus. Zool., Univ. Michigan,* No. 195, pp. *i*-*iv*, 1-307, 15 figs., 7 tables.

RECENT *OCCASIONAL PAPERS*

Burch, J.B. 2007. A new species of land snail (Stylommatophora: Partulidae) from Raiatea, French Polynesia, Oceania. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 740, pp. 1-8, 3 figs.

Raselimanana, A.P., R.A. Nussbaum & C.J. Raxworthy. 2006. Observations and re-description of *Zonosaaurus boettgeri* Steindachner 1891 and description of a second new species of long-tailed *Zonosaurus* from western Madagascar. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 739, pp. 1-16, 3 figs., 2 tables.

Ng, H.H. & R.M. Bailey. 2006. *Chiloglanis productus*, a new species of suckermouth catfish (Siluriformes: Mochokidae) from Zambia. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 738, pp. 1-13, 5 figs., 1 table.

Chakrabarty, P. 2006. Taxonomic status of the Hispaniolan Cichlidae. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 737, pp. 1-17, 13 figs., 1 table.

Garrison, R.W., N. von Ellenrieder & M.F. O'Brien. 2003. An annotated list of the name-bearing types of species-group names in Odonata preserved in the University of Michigan Museum of Zoology. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 736, 73 pp.

Ann Arbor, Michigan 48109-1079, U.S.A.

COVER ILLUSTRATION—A new species of *Bolitoglossa* (*B. daryorum*) from Guatemala

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 200

NEW SALAMANDERS (CAUDATA: PLETHODONTIDAE) FROM GUATEMALA, WITH MISCELLANEOUS NOTES ON KNOWN SPECIES

JONATHAN A. CAMPBELL, ERIC N. SMITH, JEFFREY STREICHER, MANUEL E. ACEVEDO, and EDMUND D. BRODIE, JR.

Department of Biology
University of Texas at Arlington
Arlington, TX 76019, USA

Escuela de Biología
Universidad de San Carlos de Guatemala
Ciudad Universitaria
Zona 12, Guatemala,
Guatemala

Department of Biology
Utah State University
Logan, UT 84322, USA

Ann Arbor, October 13, 2010
ISSN 0076-8405

NEW SALAMANDERS (CAUDATA: PLETHODONTIDAE) FROM GUATEMALA, WITH MISCELLANEOUS NOTES ON KNOWN SPECIES

Jonathan A. Campbell[1], Eric N. Smith[1], Jeffrey Streicher[1],
Manuel E. Acevedo[2], and Edmund D. Brodie, Jr.[3]

CONTENTS

Abstract....iv
Resumen....iv
Introduction....1
Materials and methods....1
Designation of neotype for *Bolitoglossa morio*....2
Bolitoglossa omniumsanctorum Stuart, 1952....4
Descriptions of new species....5
Discussion....49
Acknowledgments....54
Dedication....54
Literature Cited....54
Appendices....57

[1]Department of Biology, University of Texas at Arlington, Arlington, TX 76019, U.S.A.
[2]Escuela de Biología, Universidad de San Carlos de Guatemala, Ciudad Universitaria, Zona 12, Guatemala, Guatemala.
[3]Department of Biology, Utah State University, Logan, UT 84322, U.S.A.

NEW SALAMANDERS (CAUDATA: PLETHODONTIDAE) FROM GUATEMALA, WITH MISCELLANEOUS NOTES ON KNOWN SPECIES

ABSTRACT

Sixteen new species of salamanders are described from the highlands of Guatemala: *Bolitoglossa centenorum* **sp. n.**; *B. daryorum* **sp. n.**; *B. eremia* **sp. n.**; *B. huehuetenanguensis* **sp. n.**; *B. kaqchikelorum* **sp. n.**; *B. la* **sp. n.**; *B. ninadormida* **sp. n.**; *B. nussbaumi* **sp. n.**; *B. nympha* **sp. n.**; *B. pacaya* **sp. n.**; *B. psephena* **sp. n.**; *B. suchitanensis* **sp. n.**; *B. tzultacaj* **sp. n.**; *B. xibalba* **sp. n.**; *Dendrotriton chujorum* **sp. n.**; and *D. kekchiorum* **sp. n.** A neotype for *B. morio* (Cope, 1869) is designated and *B. omniumsanctorum* Stuart (1952) is resurrected from the synonymy of *B. morio*. Examination of material in the University of Texas at Arlington collections reveals previously unknown species occurring from near the Mexican border in the west across the Guatemalan Plateau and southeastern highlands to the Honduras and El Salvador borders in the east. These new salamanders are members of the genera *Dendrotriton* and *Bolitoglossa*. We describe species from at least three subgenera of *Bolitoglossa*, with emphasis on the *B. morio* group within Magnadigita. These new species are distinguished from their congeners by morphology, including elements of color pattern. We provide a phylogeny for many of the Middle American species based on molecular differences. We collected the material discussed herein during the last 40 years. Unfortunately, the type-localities for many of these salamanders are now badly degraded.

RESUMEN

Dieciséis nuevas especies de salamandras son descritas de las tierras altas de Guatemala: *Bolitoglossa centenorum* **sp. n.**; *B. daryorum* **sp. n.**; *B. eremia* **sp. n.**; *B. huehuetenanguensis* **sp. n.**; *B. kaqchikelorum* **sp. n.**; *B. la* **sp. n.**; *B. ninadormida* **sp. n.**; *B. nussbaumi* **sp. n.**; *B. nympha* **sp. n.**; *B. pacaya* **sp. n.**; *B. psephena* **sp. n.**; *B. suchitanensis* **sp. n.**; *B. tzultacaj* **sp. n.**; *B. xibalba* **sp. n.**; *Dendrotriton chujorum* **sp. n.**; y *D. kekchiorum* **sp. n.** Un neotipo para *B. morio* (Cope, 1869) es designado y *B. omniumsanctorum* Stuart (1952) es resucitado desde la sinonomía de *B. morio*. Estudio de material en la colección de la Universidad de Texas en Arlington revela especies previamente desconocidas, desde la frontera con México hasta las fronteras con El Salvador y Honduras, a todo lo largo de la Meseta de Guatemala y las tierras altas del sureste. Estas nuevas salamandras son miembros de los géneros *Bolitoglossa* y *Dendrotriton*. Nosotros describimos especies de tres subgéneros de *Bolitoglossa*, con énfasis en el grupo de *B. morio* dentro de Magnadigita. Estas nuevas especies se distinguen de sus congéneres por su morfología, incluyendo elementos de su patrón de color. Nosotros proveemos una filogenia molecular para muchas de las especies de Centro América y Sur de México. El material utilizado aquí fue colectado durante los pasados 40 años. Desafortunadamente, las localidades tipo de muchas de estas salamandras se encuentran ahora muy deterioradas.

Key words: Amphibia, Caudata, Plethodontidae, *Bolitoglossa*, *Dendrotriton*, Guatemala, new species.

NEW SALAMANDERS (CAUDATA: PLETHODONTIDAE) FROM GUATEMALA, WITH MISCELLANEOUS NOTES ON KNOWN SPECIES

INTRODUCTION

The Neotropics harbor an impressive diversity of plethodontid salamanders and the known number of species continues to grow. In particular, Nuclear Central America, with Guatemala at its core, is a particularly diverse region where most of the species are endemic (Wake & Lynch, 1976). Despite considerable effort devoted to the salamanders of Guatemala, including Schmidt (1936), Stuart (1943), and a succession of students from University of California Berkeley, our knowledge remains in a surprisingly rudimentary state. Schmidt (1936) reported 15 species of salamanders from Guatemala, and Stuart (1943) added three species to this list.

The reclusive habits of tropical salamanders and the somewhat different collecting techniques required to find them have resulted in often meager museum representation. Many species have only been discovered in recent decades and others doubtlessly remain unnamed. An additional challenge facing salamander taxonomists is that many species are small and possess morphologies conservative with respect to congeners. For some years, we have been aware of new species of salamanders from Guatemala represented in some cases by a single specimen or small series collected years previously, but have refrained from providing descriptions in hopes that additional specimens would become available.

Some of the new salamander taxa discovered in Guatemala during the past 30 years include *Bolitoglossa meliana* (Wake & Lynch, 1982), *Bradytriton silus* (Wake & Elias, 1983), *Nyctanolis pernix* (Elias & Wake, 1983), *Cryptotriton monzoni* (Campbell & Smith, 1998), *C. sierraminensis* (Vásquez-Almazán *et al.*, 2009), *C. wakei* (Campbell & Smith, 1998), *Nototriton brodiei* (Campbell & Smith, 1998), *N. stuarti* (Wake & Campbell, 2000), and *Oedipina stenopodia* Brodie & Campbell, 1993). Many of these remain known only from the type-locality, but we have discovered *Nyctanolis pernix* in the cloud forests of Alta Verapaz; it was previously known only from Baja Verapaz, Huehuetenango, and the adjacent Mexican state of Chiapas. Although our herpetological efforts in Guatemala span over three decades we have not focused on salamanders. Nonetheless, our collections have resulted in the accumulation of a considerable number of salamanders, which, until now, have languished on museum shelves. We herein make use of this material, describing 16 new species of salamanders from Guatemala and designating a neotype for another.

Identification of many species of highland Nuclear Middle American salamanders is obfuscated by extreme intraspecific variation in color patterns and often relatively subtle interspecific morphological variation. Decisions on how to allocate certain populations are best guided by using modern molecular techniques. We are fortunate in having material allowing these analyses for many populations, but have been unable to secure tissue samples for several populations that appear to be representative of new species and are described herein. Despite the paucity of material for several of these new species, we have come to the conclusion that we should proceed with their descriptions. Otherwise, we may not live long enough to collect additional material, or these new species might already be extinct or may become extinct before they are described. Their recognition will perhaps afford them some degree of protection.

MATERIALS AND METHODS

Fieldwork was conducted in the highlands of Guatemala each year from 1993 to 2001 and sporadically since then. Prior to that time, we have made collections in Guatemala almost every year going back into the 1960s. We have examined representatives of all species of *Dendrotriton* occurring in Guatemala and Mexico, and have seen all Guatemalan species of *Bolitoglossa* with which the new taxa might be confused (Appendix 1). Specimens of the species described herein were fixed in formalin (diluted to 10% of stock solution) and transferred within 1–3 mo into 70% ethanol for permanent storage. Certain measurements of the head and feet were made to the nearest 0.01 mm using an ocular micrometer calibrated with a stage micrometer and measurements of the body and tail were taken to the nearest 0.01 mm with a Vernier caliper. Standard length is abbreviated as SL throughtout the paper. A morphological trait that apparently has gone unnoticed in the salamander literature is that in most species of *Bolitoglossa* males possess relatively longer legs than females. This characteristic may relate to mating or ecological differences. Descriptions of color in life were taken from field notes, color transparencies, and digital images housed in the University of Texas at Arlington (UTA) collection.

In assessing the biogeography of Guatemalan salamanders we make use of the faunal provinces first proposed by Stuart (1943) based on salamander distributions. The faunal areas were modified by Campbell & Vannini (1989) on the basis of a comprehensive analysis of the Guatemalan herpetofauna. Their faunal areas maintain the essence of Stuart's recognition of biogeographic discontinuities for faunal assemblages in general and also possess obvious geographic boundaries. The map and vegetation associations provided by Holdridge (1959) have sometimes been useful in assessing the distribution of salamanders.

For generic allocations we are semi-conservative, following most recent reviews in recognizing *Bolitoglossa* for the largest genus of salamanders, which is diagnosed by unique hand and foot and tongue morphology (Parra-Olea *et al.*, 2004). Taylor (1944) perceived several distinct lineages of Neotropical salamanders that he placed into *Magnadigita* and *Bolitoglossa*. Subsequently, Wake & Brame (1963) argued that these genera represented only a single natural group and that only the older name, *Bolitoglossa*, should be recognized. Parra-Olea *et al.* (2004) recognized as subgenera *Bolitoglossa*, *Magnadigita*, and five other taxa within the genus *Bolitoglossa*. Bolitoglossine salamanders have sometimes been partitioned into various species groups (Wake & Lynch, 1976, 1982; Elias, 1984) or subgenera (Parra-Olea, 2004),

and we have found it convenient to follow these groupings.

For some of the species we describe herein, we have molecular evidence available. However, for several species these data are lacking and we have relied on the more traditional approach of basing our decisions on morphology. Montane tropical salamanders tend to have small ranges and we provide diagnoses for new species we describe primarily from other salamanders occurring in the general region. As in previous *Bolitoglossa* phylogenies (*e.g.*, Wiens *et al.*, 2007), our molecular analyses are based solely on mitochondrial DNA (mtDNA) and as such we interpret them with caution. This is because several patterns of genetic inheritance and maintenance unique to mtDNA (i.e., incomplete lineage sorting, introgression, etc.) often do not clearly indicate recent gene flow (*e.g.*, Shaffer & Thomson, 2007). However, high levels of mtDNA divergence typically reflect historical differentiation in sexually reproducing species (Avise & Walker, 1999) and, in instances where divergence levels between species are low, we provide morphological characters or evidence of geographic isolation to distinguish between closely related taxa.

Molecular Sampling.—We analyzed mtDNA gene fragments originating from 66 Guatemalan salamanders in the genus *Bolitoglossa*. These samples included representatives from the subgenera *Bolitoglossa*, *Nanotriton*, *Mayamandra* and *Magnadigita* of Parra-Olea *et al.* (2004). For comparative purposes we included two species from Mexico; *B. hartwegi* from the state of Chiapas and *B. mexicana* from the state of Oaxaca. Outgroup taxa included three species of the genus *Pseudoeurycea* (*P. brunnata*, *P. rex* and *P. werleri*) and *Cryptotriton veraepacis*. We amplified gene fragments from the mitochondrial 12S ribosomal subunit (12S) and cytochrome-*b* (cyt-*b*) genes. Our 12S dataset included all tissues analyzed for the present study and the cyt-*b* dataset contained a subsample of 31 *Bolitoglossa* and 4 *Pseudoeurycea* samples. Using the publically accessible database GenBank, we downloaded additional *Bolitoglossa* cyt-*b* sequences used in Parra-Olea *et al.* (2004). Voucher specimen and GenBank accession information are available in Appendices 2 and 3.

Molecular Methods.—Genomic DNA was isolated from liver or muscle tissue using a DNeasy kit (Qiagen ®, Valencia, California). PCR reactions were performed using the following primer pairs: forward primer 12SF (5' AAA CTG GGA TTA GAT ACC CCA CTA T 3'), reverse primer 12SR (5' GTR CGC TTA CCW TGT TAC GAC TT 3') for 12S (Bossuyt and Milinkovitch, 2000) and forward primer MVZ15 (5' GAA CTA ATG GCC CAC ACW WTA CGN AA 3'), reverse primer MVZ16 (5' AAA TAG GAA ATA TCA TTC TGG TTT AAT 3') for cyt-*b* (Moritz *et al.*, 1992). Thermal cycling profiles followed Streicher *et al.* (2009) for 12S and Moritz *et al.* (1992) for cyt-*b*. These protocols resulted in the amplification of *ca.* 490 base pairs (bp) of 12S and *ca.* 660 bp of cyt-*b*. PCR products were cleaned using Ampure magnetic beads (Agencourt®, Bioscience, Beverly, Massachusetts, USA). Sequencing reactions and sequencing of both primer directions were performed by SeqWright (Houston, Texas, USA; www.seqwright.com) or by the UTA genomics core facility (Arlington, Texas, USA; http://gcf.uta.edu). Automated sequence data were cleaned and aligned using the program Sequencher (GeneCodes, Ann Arbor, Michigan, USA). Codon positions for the cyt-*b* fragment were inferred using the program MacClade 4 (Maddison & Maddison, 2002). The 12S and cyt-*b* fragments corresponded to bases 459 to 910 and 14,012 to 14,670 of the *Bolitoglossa* mitochondrial genome (NC 006346; Mueller *et al.*, 2004), respectively. Two segments of our 12S alignment contained gap motifs that made homology assessment difficult, so in an effort to be conservative we removed these sites, resulting in an indel free alignment. The final indel-free 12S alignment contained 419 bp. Our final alignments and topologies are publicly available via TreeBase (www.treebase.org). We performed a variety of phylogenetic analyses (Minimum evolution [ME], Maximum Parsimony [MP], and Bayesian Markov chain Monte Carlo [BAYES]) on the final alignments using default settings in the programs MEGA 4 (Tamura *et al.*, 2007) for ME, PAUP* v 4.10b (Swofford, 2002) for MP, and MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) for BAYES. We derived support measures for ME and MP analyses via 2000 pseudoreplicates of non-parametric bootstrapping (Hedges, 1992). In MP analyses, the indel-free 12S alignment contained 101 parsimony informative characters and the cyt-*b* dataset contained 341 parsimony informative characters. For BAYES analyses we used the program Modeltest 3.7 (Posada & Crandall, 1998) to select an appropriate model of evolution by gene fragment and codon position (Table 1). Our paired BAYES searches were run over 10 million generations with sampling occurring every 1000 generations. Posterior probabilities associated with these analyses were obtained after discarding the first 6000 tree samples from each run.

To comply with regulations of the International Code of Zoological Nomenclature we have deposited copies of this article at the following publicly accessible libraries: American Museum of Natural History, New York, USA (AMNH); Natural History Museum, London, UK (BMNH); Museum National d'Histoire Naturelle, Paris, France (MNHN); Instituto do Butantan, São Paulo, Brazil (IB); The University of Kansas, Lawrence, Kansas, USA (KU); National Museum of Natural History, Washington, DC, USA (NMNH); University of Michigan, Ann Arbor, Michigan, USA (UMMZ); The University of Texas at Arlington, Arlington, Texas, USA (UTA); and Utah State University, Logan, Utah, USA (UTS).

DESIGNATION OF NEOTYPE FOR *BOLITOGLOSSA MORIO*

Oedipus [*Bolitoglossa*] *morio* was described as "black above; leaden black below; the under surfaces and lower parts of sides, with outer faces of limbs, speckled with indistinct whitish dots." The holotype had the inner toes webbed and the other toes free of webbing (Cope, 1869).

Schmidt (1936) observed, "The proper allocation of the name *morio* has been one of the principal difficulties in reaching a satisfactory conclusion as to the number and distribution of the Guatemalan species of the genus." This situation still exists 140 years after the original description by Cope (1869). The type is lost (*fide* Schmidt, 1936) and our inquiries reconfirm that it has not been relocated. The type-locality is "Mountains of Guatemala". Measurements provided for the type of *B. morio* by Cope (1869) are given in Table 2.

To move forward with taxonomic work on Guatemalan salamanders we here designate a neotype for the species. Our selection of the population represented by the neotype is based on coloration and size, as provided by Cope (1869), as well as this species having a fairly extensive distribution on the Guatemalan Plateau.

Neotype.—UTA A-34090, from 3.7 km S Santa María Visitación, Sololá, Guatemala at 2000–2200 (14.723073° N, 91.330252° W), collected 1 January 1991 by M. B. Harvey, D. P. Lawson, W. W. Lamar, E. N. Smith, and J. A. Campbell.

Description of neotype.—An adult female measuring 55.0 mm SL, 38.2 mm TL, 12.9 mm HL, 8.9 mm HW. There is one intercostal fold between adpressed limbs. Hand width is 4.8 mm and foot width is 6.0 mm; the subdigital pads are well developed. The axilla–groin length is 29.5 mm. The toes have moderate webbing extending to the base of the distal phalange, except for the first digit. The tips of the toes are broad and blunt. Eye–nostril length is 2.00 mm, eye length is 2.40 mm, interocular distance is 4.70 mm, and internarial distance is 2.75 mm. There are 55 combined maxillary and premaxillary teeth. There are 21 vomerine teeth (11/10) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening. The vent is folded and lightly pigmented.

Dorsal coloration is black, grading to a paler color on

Table 1. Evolutionary models selected using Akaike information criterion (AIC) for Bayesian phylogenetic analyses.

Locus	*n*	Model	-lnL	AIC
$12S_{noindels}$	417	GTR+I+G	2246.2417	4512.4834
Cyt-b_{total}	630	TVM+I+G	13867.6230	27753.2461
Cyt-$b_{position\ 1}$	210	TrN+I+G	3008.4214	6190.8428
Cyt-$b_{position\ 2}$	210	TVM+I+G	1466.7296	2951.4592
Cyt-$b_{position\ 3}$	210	GTR+I+G	8626.0713	17272.1426

the venter. The lateral surfaces from the angle of the jaw to the end of the body are covered with orange blotches. The ventral surface of the body and chin is pale with a sprinkling of melanophores and scattered pale orange blotches. The tail venter is black with orange flecking. The legs are heavily flecked with orange (Fig. 1). Toes, except the first one, are free of webbing at the tip; the webbing extends to the base of the terminal phalange. The skin secretion turned orange in formalin.

Diagnosis.—A moderate-sized (adults 40–60 mm SL) salamander of the genus *Bolitoglossa* in the subgenus *Magnadigita*. The dorsal ground color is dark gray to almost black. Scant to moderate white stippling is distributed over the body including the head and limbs. Individuals may be essentially uniformly dark or the flanks may be marked with a few irregular salmon or rust-colored streaks or blotches. The upper surface of the tail is often marked with pale gray or ash-colored blotches. The upper forelimbs and hind limbs of some individuals may have a small amount of salmon, orange, or rust spotting. Juveniles and small individuals are patterned with a pale to medium brown broad dorsal band, with the side of the head, flanks, and limbs conspicuously dark brown. The hands and feet are moderately webbed and the distal phalange is free of webbing; the toes are broad and blunt.

Bolitoglossa morio can be distinguished from members of the *B. mexicana* and *B. dofleini* species groups (subgenera *Bolitoglossa* and *Pachymandra*) by its generally smaller size (*B. dofleini* reaches at least 125 mm SL), more robust body, shorter tail, and its smaller hands and feet that are not fully webbed; from the *B. rufescens* species group (subgenus *Nanotriton*) by its larger size and feet that are not fully webbed or pad-like; and from the *B. veracrucis* group (subgenus *Mayamandra*) by its larger body size and hands and feet that are not fully webbed (*vs*. broad hands and feet that are fully webbed with a distinctive triangular third toe extending from the center of the webbed foot).

Members of the *Bolitoglossa franklini* species group have distinctly longer toes, more webbing on the hands and feet, and a less robust body and tail than *B. morio*; *B. meliana* is uniformly black, including the flanks and venter, whereas *B. lincolni* and *B franklini* have distinct dorsal patterns of red, yellow, or green; *B. lincolni* and *B. meliana* attain a much larger size than *B. morio*. *Bolitoglossa engelhardti* has more webbing on the hands and feet, longer legs, and a brown dorsal ground color, usually with a combination of small pale and dark streaking or flecks. Members of the *B. rostrata* group are smaller and have shorter toes, more webbing, digits that are rounded (*vs*. truncate) at the tips, a less robust body and tail, and a dorsum usually with a pattern or broad band that is distinctly set off from the flank coloration, and *B. flavimembris* has shorter toes, more webbing, digits that are distally rounded, and usually limbs that are distinctly paler than the body.

Bolitoglossa morio is clearly a member of the group of diverse salamanders practically ubiquitous across much of the Guatemalan highlands, previously all allocated to *B. morio*. These species are diagnosed from *B. morio* in following species descriptions.

Variation.—Members of the series from which the neotype is designated are black dorsally with small orange blotches sparsely sprinkled along the flanks and dorsal surfaces of

Table 2. Measurements of type of *Bolitoglossa morio* given by Cope (1869).

Measurement	Inches	Conversion in mm
length (axial) from end muzzle to orbit	0.105	2.67
length (axial) from end muzzle to canthus oris	0.22	5.59
length (axil) from end muzzle to axilla	0.63	16.26
length (axil) from end muzzle to groin	1.66	43.18
length (axil) from end muzzle to end vent	1.94	49.27
length (axil) from end muzzle to end tail	3.29	83.57
Length fore limb	0.45	11.43
Length fore foot	0.145	3.68
Length hind limb	0.45	11.43
Length hind foot	0.17	4.32
Width hind foot (sole)	0.17	4.32
Width head	0.28	7.11
Width body	0.28	7.11
Width sacrum	0.22	5.59

Fig. 1. *Bolitoglossa morio*, UTA A-38614, adult male, 43.2 mm mm SL, from 3.7 km S Santa María Visitación, 2200 m, Sololá, Guatemala. This is the type-locality of designated neotype.

the limbs. Orange blotches are more common on the ventral surfaces of the body and very sparse on the tail venter. A few individuals have pale colored flecking on the dorsal base of the tail. Skin secretion, most abundant from the tail, turns bright orange in formalin. Seven adult males are 40.9 to 44.4 mm standard length; four adult females are 52.6 to 55.0 mm SL. Tails are 0.69–0.81 of SL, head length is 0.23–0.26 of SL, and head width is 0.15–0.17 of SL. Vomerine teeth are 16 to 28 with a mean of 21.36 (1.53 SE); maxillary plus premaxillary teeth are 28 to 33 in males and 50 to 54 in females. There are 0 to 1.5 intercostal folds between adpressed limbs. The mental glands of three adult males average 2.50 mm wide by 2.33 mm long and are reniform in shape.

Distribution, habits, and habitat.—This species occurs over much of the Guatemalan Plateau, recognized as the Chimaltenagan subarea by Campbell and Vannini (1989). It occurs in pine-oak forest and humid broadleaf forest bordering on cloud forest at elevations of about 1400 to above 2500 m.

Comment.—Brocchi (1882) described *Oedipus bocourti* from "Totonicapam" [= Totonicapan, Department of Totonicapan]. This locality on the Guatemalan Plateau is about 25 km (airline) from Santa María Visitación, the type-locality for the neotype of *B. morio*. *Oedipus bocourti* appears to represent a synonym of *B. morio*, a conclusion also reached by Schmidt (1936).

Bolitoglossa omniumsanctorum Stuart, 1952

We take this opportunity to resurrect *Bolitoglossa omniumsanctorum* Stuart (1952) from synonomy of *B. morio*. This taxon was placed in synonymy by Wake & Elias (1983) based on size, form, and coloration. We have examined the type-series consisting of two individuals and examined a series of this species from La Pajonada to the Cumbre del Papal, Cuilco, Huehuetenango, and the western portion of the Sierra de Chuacús, Quiché, Guatemala.

Bolitoglossa omniumsanctorum was distinguished from *B. morio* by having relatively shorter legs, darker coloration, and possibly more vomerine teeth (Stuart, 1952). Stuart's powers of discrimination must have been great, because our measurements reveal that there is a difference in limb length, but this is subtle to the naked eye. A difference also appears to be present in relative head width, with *B. morio* having a slightly wider head. The dorsal ground coloration of *B. morio* (*sensu stricto*) in life is too variable (gray to blackish) to be of diagnostic value. However, the extensive pinkish coloration on the flanks in *B. omniumsanctorum* usually is sufficient to distinguish it from *B. morio* in which this coloration is reduced or absent. In addition, *B. omniumsanctorum* has more maxillary-premaxillary teeth (Table 3).

We investigated size relationships of limb length and head width between the species *Bolitoglossa morio* (N = 18) and *B. omniumsanctorum* (N = 25). To examine these characters we used two separate analyses of covariance (ANCOVA) using the character of interest (limb length/head width) as a dependent variable, species designation as the factor variable, and standard length as the covariate. Data were $\log_{10}$ transformed prior to analyses. After finding no significant interaction between the independent variables, we found that variation in limb length ($F_{1, 40} = 10.71$, $P = 0.002$) and head width ($F_{1, 40} = 7.90$, $P=0.008$) differs significantly between the species (Fig. 2). All statistical analyses were conducted using SYSTAT 11 (Systat Software, Inc., Chicago, Illinois, USA). Comparison of the number of intercostal folds separating adpressed limbs and numbers of vomerine and maxillary plus premaxillary teeth revealed significant differences between adult *B. morio* and *B. omniumsanctorum* (Figs. 3 and 4).

Three adult males are 41.1 to 46.2 mm SL; 12 adult females are 59.5 to 76.6 mm SL. Tails are 0.57–0.87 of SL, head length is 0.20–0.25 of SL, and head width is 0.14–0.15 of SL. Vomerine teeth are 13 to 16 in males and 22 to 31 in females; maxillary plus premaxillary teeth are 35 to 42 in males and 49 to 62 in females. There are 1.5 to 4 intercostal folds between adpressed limbs. All toes are free of webbing at the tip. Males have small roundish mental glands; two males have mental glands that averaged 2.45 mm wide by 2.25 mm long.

Individuals we examined are black dorsally with a paler gray venter. Large pinkish to orange blotches start along the sides as far farward as the head and increase in extent posteriorly on the body, extending on to the tail as irregular spots or blotches; blotches are usually present on the tail dorsum and venter (Fig. 5). A few individuals have sparse, small blotches on the rear half of the dorsum.

Bolitoglossa omniumsanctorum occurs at the intersection of several of the most ancient highlands of Guatemala including the extreme western portion of the Sierra de Chuacús, as well as the Sierra de los Cuchumatanes and Montañas del Cuilco. These regions were delimited as the Chuacús, Cuchumatan, and Cuilcan Subareas by Campbell and Vannini (1989).

DESCRIPTIONS OF NEW SPECIES

We describe distinctive new species of the genus *Bolitoglossa* from various highland regions of Guatemala, including dry pine-oak forests of the Guatemalan Plateau; high mixed conifer-broadleaf forests of the Sierra de los Cuchumatanes, mesic seasonal broadleaf forest of the southeastern highlands, cloud forest of the Sierra de las Minas, and rainforest of the foothills of eastern Guatemala. A new species of *Dendrotriton* is described from the mixed conifer-broadleaf forest of the northern Sierra de los Cuchumatanes and another from the cloud forest of the eastern extension of the Cuchumatanes. These populations of *Dendrotriton* have previously been referred to *D. rabbi* (Elias, 1984; García-París & Wake, 2000), a species we consider to be restricted to the Montañas de Cuilco.

An unusual salamander was taken in the vicinity of San Juan Sacatepéquez, Guatemala. Based on its generalized morphology and the amount of interdigital webbing, this species undoubtedly is a member of the genus *Bolitoglossa*. It appears to fall within the subgenus *Magnadigita* Taylor, 1944, as recognized by Parra-Olea *et al.* (2004) based on its broad tipped digits and lack of full webbing on hands and feet and is in the *B. morio* group. The relatively dark coloration with a broad pale dorsal stripe is characteristic of many species in several groups of *Bolitoglossa*. This species will be known as:

Bolitoglossa kaqchikelorum new species

Holotype.—UTA A-44132 (original field no. ENS 4558) an adult female from the vicinity of San Juan Sacatepéquez, Guatemala, Guatemala (14.717798° N, 90.650107° W), 1850 m, collected in April of 1993 by H. Gil.

Paratypes.—UTA A-52623, El Encinal, Mixco, Depto. Guatemala, Guatemala, collected by R. García Anleu in April 1996; UTA A-58568, vicinity of San Pedro Sacatepéquez, 3 km from the Sajyuvilla lava crossing, Depto. Guatemala, Guatemala, collected by M. E. Acevedo on 11 August 2003; UTA A-48361–62, UTA A-48379–81, San Lucas, Cerro Alux, Depto. Sacatepéquez, Guatemala, collected by M. E. Acevedo on 28 December 1994; UTA A-58685, vicinity of Antigua, Depto. Sacatepéquez, Guatemala, collected by R. Anzueto circa 1994.

Referred specimens.—UTA A-48360 and 48586, bearing collecting data similar to the holotype, are juvenile, formalin-blackened, brittle specimens that are devoid of any conspicuous pattern. Based on the foot structure of these specimens, which unfortunately is distorted owing to desiccation, we tentatively refer them to *B. kaqchikelorum*. They bear collecting data similar to the holotype of this taxon. A juvenile (UTA A-33638) from Finca Rosario Vista Hermosa, S slope Volcán de Agua, Depto. Escuintla, 1690 m, is also referred to this species.

Diagnosis.—A moderate sized member of the genus *Bolitoglossa* in the subgenus *Magnadigita* that may have a broad orange dorsal stripe extending onto the sides or pale dorsolateral stripes on a brown to gray background. The dorsal stripe is darkly edged laterally, and blotches of the stripe color and/or tiny white flecks may be present on the lateral surfaces, throat and venter. The hands and feet are moderately webbed, with broad, blunt toes.

Bolitoglossa kaqchikelorum can be distinguished from members of the *B. mexicana* species group (subgenus *Bolitoglossa*) by its smaller size, hands and feet that are not fully webbed, and a relatively shorter tail; from the *B. dofleini* group (subgenus *Pachymandra*) by having distinctively less webbing and in being smaller (*B. dofleini* reaches 125+ mm SL); from the *B. rufescens* and *B. hartwegi* species groups (subgenera *Nanotriton* and *Mayamandra*) by its larger size and

Table 3. Measurements and tooth numbers for select salamander species examined for the present study. Mean (SE) are given for measures and counts and ranges are provided for ratios.

Species	No. Adults	SL	TL	TL/SL	HL	HL/SL	HW	HW/SL	VOM	Max-Pre	Adp Limb	Hand Width	Foot Width
B. centenorum	4	49.03 (2.69)	42.78 (1.39)	0.73-0.94	12.40 (0.07)	0.22-0.26	7.10 (0.07)	0.13-0.15	25.0 (2.04)	69.8 (5.07)	1.63 (0.24)	4.10 (0.21)	5.00 (0.14)
B. daryorum	9	46.37 (2.31)	32.26 (2.69)	0.46-0.80	11.03 (0.42)	0.23-0.27	7.58 (0.37)	0.15-0.18	21.3 (1.20)	44.4 (2.10)	1.38 (0.25)	3.94 (0.27)	4.91 (0.26)
B. eremia	14	47.60 (2.04)	34.90 (1.92)	0.62-0.79	11.70 (0.42)	0.22-0.29	7.80 (0.30)	0.14-0.21	28.6 (1.89)	49.4 (2.67)	1.50 (0.20)	4.20 (0.20)	5.10 (0.23)
B. huehuetenanguensis	14	46.75 (1.32)	39.36 (1.40)	0.69-0.94	11.93 (0.29)	0.23-0.27	7.42 (0.22)	0.15-0.17	27.9 (1.09)	63.9 (2.89)	1.46 (0.24)	4.01 (0.14)	5.23 (0.19)
B. kaqchikelorum	4	44.88 (4.42)	34.50 (2.30)	0.70-0.93	11.23 (1.16)	0.22-0.30	7.03 (0.43)	0.14-0.20	25.0 (2.42)	39.2 (3.12)	1.00 (0.25)	3.57 (0.25)	4.47 (0.33)
B. la	20	45.21 (1.20)	32.81 (0.89)	0.63-0.80	11.51 (0.22)	0.24-0.28	7.39 (0.15)	0.15-0.17	26.7 (1.08)	56.2 (1.85)	0.68 (0.12)	3.81 (0.10)	4.72 (0.13)
B. morio	11	46.26 (1.76)	34.74 (1.23)	0.69-0.81	11.33 (0.37)	0.23-0.26	7.30 (0.34)	0.15-0.17	21.4 (1.53)	38.9 (3.09)	0.86 (0.14)	4.02 (0.15)	4.97 (0.21)
B. ninadormida	5	47.12 (3.10)	39.85 (4.15)	0.66-0.89	11.78 (0.51)	0.23-0.27	7.38 (0.33)	0.15-0.17	25.2 (1.50)	59.0 (4.36)	1.10 (0.10)	3.80 (0.21)	4.95 (0.32)
B. nussbaumi	2	51.95 (1.45)	40.00 (5.00)	0.66-0.89	12.25 (0.35)	0.24-0.24	7.95 (0.05)	0.15-0.16	25.0 (3.00)	60.0 (7.00)	2.25 (0.25)	4.45 (0.05)	5.60 (0.30)
B. nympha	22	39.17 (0.40)	31.11 (0.59)	0.70-0.95	9.74 (0.14)	0.21-0.28	6.28 (0.07)	0.15-0.17	11.2 (0.50)	*	3.78 (0.07)	2.67 (0.03)	3.61 (0.04)
B. omniumsanctorum	26	57.17 (2.51)	39.48 (1.65)	0.56-0.87	13.38 (0.47)	0.20-0.27	8.67 (0.30)	0.14-0.17	25.5 (1.03)	49.3 (1.46)	2.16 (0.20)	4.44 (0.16)	5.52 (0.22)
B. pacaya	23	38.51 (.89)	26.91 (.78)	0.60-0.83	9.32 (0.19)	0.23-0.26	6.47 (0.13)	0.16-0.18	19.4 (0.80)	58.3 (3.00)	1.52 (0.16)	3.33 (0.09)	4.14 (0.09)
B. psephena	1	71.5	52.3	0.73	15.8	0.22	11.0	0.15	31	51	3.5	6.1	7.6
B. suchitanensis	5	51.92 (2.40)	38.28 (2.35)	0.72-0.76	12.48 (0.57)	0.23-0.26	8.46 (0.41)	0.16-0.17	24.6 (1.03)	57.2 (1.77)	1.88 (0.11)	4.16 (0.21)	4.86 (0.18)
B. tzultacaj	1	37.0	23.6	0.64	9.4	0.25	6.9	0.19	14	36	4	2.9	3.7
B. xibalba	12	42.96 (1.83)	30.47 (2.02)	0.53-0.86	11.48 (0.41)	0.26-0.30	7.34 (0.26)	0.16-0.20	25.3 (2.29)	51.8 (4.43)	0.38 (0.20)	3.78 (0.21)	4.93 (0.27)
D. chujorum	16	24.52 0(.62)	22.95 (0.73)	0.986-1.10	6.00 (0.15)	0.23-0.27	4.07 (0.12)	0.15-0.21	17.0 (0.50)	37.7 (1.61)	0.54 (0.12)	2.08 (0.16)	2.61 (0.18)
D. kekchiorum	5	31.23 (3.22)	38.90 (0.92)	1.01-1.20	7.56 (0.65)	0.22-0.26	4.97 (0.41)	0.15-0.18	25.0 (2.42)	39.2 (3.12)	1.00 (0.22)	2.55 (0.34)	3.25 (0.46)

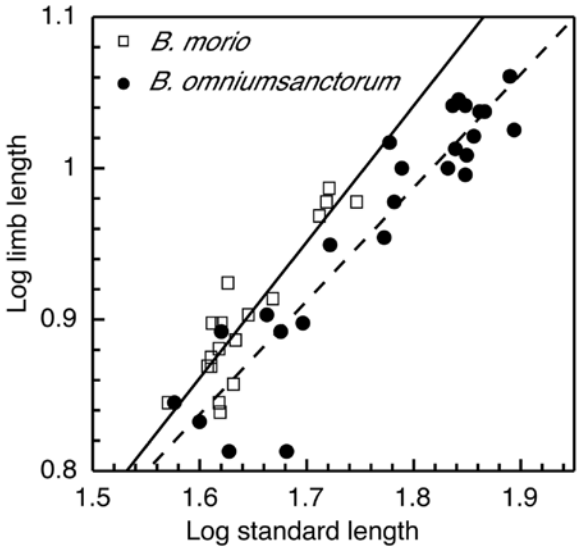

Fig. 2. Comparison of limb length (antebranchium and manus) and standard length between *Bolitoglossa morio* (N = 18) and *B. omniumsanctorum* (N = 25). Both datasets have been fit with a linear smoother.

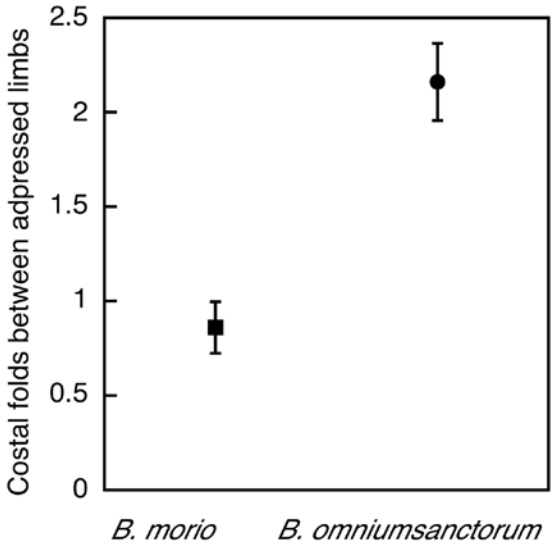

Fig. 3. Comparison of number of costal folds separating adpressed limbs in adult *Bolitoglossa morio* (square, N = 11; Santa María Visitación) and *B. omniumsanctorum* (dot, N = 26; Cuilcos and Chuacús). Mean ± standard error.

feet that are not fully webbed. *Bolitoglossa kaqchikelorum* may be distinguished from most other members of the subgenus *Magnadigita* occurring on the Guatemalan Plateau in having relatively little webbing, larger size, and usually a broad dorsal band with darker flanks. *Bolitoglossa engelhardti* attains a smaller body size and has more webbing on the hands and feet, a brownish ground color with or without paler streaks and flecking; *B. flavimembris* has more webbing on the hands and feet, digits that are rounded (vs. truncate) distally, and limbs that are usually distinctly paler than the dorsal coloration; *B. morio* is more robust and is gray to blackish, usually with white flecking or small irregular markings on the flanks and venter. *Bolitoglossa lincolni* inhabits the Sierra de los Cuchumatanes and differs in having a broad reddish dorsal stripe or blotches and less webbing on the hands and feet. *Bolitoglossa meliana* is widespread across the mountains fringing the northern edge of the Guatemalan Plateau, but is easily distinguished from *B. kaqchikelorum* by having a uniformly blackish coloration and more webbing on the hands and feet.

Description of holotype.—An adult female having a standard length of 53.3 mm, a tail length of 41.0 mm, a head width of 8.0 mm, and a head length of 13.9 mm. The legs are moderately long with 1.5 intercostal folds between adpressed limbs. Hand width is 4.1 and foot width is 5.2 mm (Fig. 6); subdigital pads well developed. Axilla–groin length is 31.0 mm. The toes have webbing extending to the base of the terminal segments (Fig. 6). The tips of the toes are broad and blunt. Eye–nostril length is 2.1 mm, eye length is 2.2 mm, interocular distance is 3.2 mm, and internarial distance is 2.0 mm. There are 45 combined maxillary and premaxillary teeth with the premaxillary teeth somewhat enlarged and reduced in number. There are 24 vomerine teeth (11/13) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening. The vent is folded and lightly pigmented.

Color pattern.—Coloration of the recently preserved holotype was distinctly orange on the dorsal surface with brownish lateral and ventral surfaces. The dorsal stripe starts at the rear of the eyes, joining at the rear of the head, and extends to about one-half way down the tail (the tail may be regenerated). The stripe is broad, covering the entire dorsal surface and onto the lateral surfaces; it is bordered by thin dark lines that extend into the costal grooves. Blotches of stripe color are present on the lower sides, chin and venter. The venter is darkest midventrally with increasing pale pigment laterally. Only a few dark spots (all less than 1 mm) are present within the dorsal stripe.

In preservative, most other specimens have traces of a broad dorsal band that is paler than the flanks. For example, UTA A-48379 is a subadult with a band on the dorsum marked with irregular dark streaks, the flanks and venter are darker, and the base of the tail bears pale blotches dorsally. Several specimens are essentially uniformly colored, but whether this reflects the coloration in life or is an artifact of presevation is unknown. UTA A-58685 is dark brown with small dark markings at the upper end of each costal groove; pale blotches are present on the proximal portion of the tail. In life, some individuals have irregular dorsolateral orangish tan stripes extending from behind the level of the forelimb insertion onto the tail, the dorsum between the stripes is dark brown, the flanks and lateral surfaces of the tail are medium brown with abundant white flecking, and the dorsal surface of the tail is dark brown

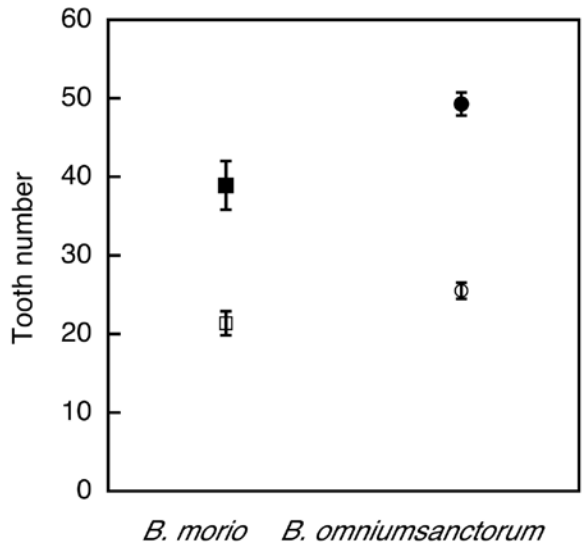

Fig. 4. Comparison of numbers of vomerine (unfilled symbols) and maxillary plus premaxillary (solid symbols) teeth in adult *Bolitoglossa morio* (squares, N = 11, Santa María Visitación) and *B. omniumsanctorum* (circles, N = 26, Cuilcos and Chuacús).

with irregular pale tan blotches (Fig. 7). An individual from Volcán Acatenango, tentatively assigned to *B. kaqchikelorum*, had a dark brown dorsum on the head and shoulders grading to gray posteriorly and the flanks were dark gray.

Etymology.—The specific epithet is taken from the Kaqchikel, an ethnic and linguistic group of Mayans inhabiting the region around the type-locality, and the Latin suffix *orum*, meaning "belonging to."

Distribution, habits, and habitat.—Known from the extreme eastern portion of the Guatemalan Plateau, including the highlands bordering the western side of Guatemala City and near Antigua. The range falls within the Chimaltenangan Subarea of the Huehuetenangan Area as defined by Campbell and Vannini (1989).

Nothing is known about the specific capture data for the holotype of *B. kaqchikelorum*. The specimen came from the vicinity of San Juan Sacatepéquez, which is surrounded by pine-oak forest. Other species obtained by the same collector in this area at approximately the same date are *Plectrohyla guatemalensis* and *Sceloporus acanthinus*. These are typical Guatemalan Plateau species that were known previously from near San Juan Sacatepéquez. Most of the paratypes from Cerro Alux (UTA A-48361–62, A-48379–81) were collected in bromeliads during the dry season in December, but one was taken in July from beneath a rock. One individual (UTA A-58685) was found among orchids that were collected in the environs of Antigua.

Volcán de Pacaya lies about 50 km almost due south of Guatemala City. Its northern slopes are continuous with parts of the southeastern Guatemalan highlands, sometimes referred to as the Las Nubes Highland Block; its southern slopes fall off into the Pacific coastal plain. This volcano reaches about 2550 m and is isolated from Volcán de Agua to the west by about 15 km and the deep entrenchment of the Río Michatoya. Volcán de Pacaya is one of Central America's most active volcanos, having erupted numerous times since the Spanish Conquest (Conway *et al.*, 1992). It has been particularly active in recent decades, and on 27–28 May 2010 experienced a series of eruptions resulting in the death of several persons, the evacuation of over 1700 people, and the closing of the international airport in Guatemala City. The southern and western slopes are covered with extensive lava fields of recent origin, but small patches of forest remain on the southern slopes and higher ridges. The forest consists mostly of humid broadleaf forest, with conifers interspersed in some areas. Much of the upper elevations were incorporated into a National Park in 2001. Beginning about 20 years ago, we made a number of forays onto Volcán de Pacaya and collected several series of salamanders that appear to be the same species that we have collected in the vicinity of San José Pinula on the Las Nubes Highland Block (*sensu* Stuart, 1954*a*). We proposed this species be subsequently known as:

Bolitoglossa pacaya new species

Holotype.—UTA A-33641 (original field no. JAC 16625), an adult male from 4 km (airline) SSE San Vicente Pacaya on W slope Volcán de Pacaya, between 2000 and 2050 m, Depto. Escuintla, Guatemala (14.585821˚ N, 90.609385˚ W), collected by E. D. Brodie, Jr. and J. A. Campbell on 5 July 1990 (Fig. 8, lower).

Paratypes.—UTA A-21448–53, UTA A-21561–67, near San Vicente Pacaya, Volcán de Pacaya, ca. 1700 m, Depto. Escuintla, collected by H. Gil on 14–16 February 1987; UTA A-21454–57, upper elevation of Volcán de Pacaya, Depto. Escuintla, collected by H. Gil in March 1987; UTA A-24919–28, near Aldea El Cedro (also known as Pacoc, 14.407800° N, 90.614713° W), W sope Volcán Pacaya, 1746 m, Depto. Escuintla, collected by E. N. Smith on 14 February 1987; UTA A-33639–40, 33642–57, data same as holotype; UTA A-5495–96, UTA A-26515–16, San Jorge Muxbal, 1981 m, Depto. Guatemala, collected by J. A. Campbell on 23 December 1977 and 5 March 1988, respectively; UTA A-31429–30, near San José Pinula, Km Post 33 on Carretera Nacional to Las Nubes, 1890 m, Depto. Guatemala, collected by E. N. Smith on 19 August 1990; UTA A-33658–59, UTA A-33663–64, near San José Pinula, Km Post 34 on Carretera Nacional to Las Nubes, 1960 m, Depto. Guatemala, collected by E. N. Smith on 31 March and 9 December 1990, respectively; UTA A-40340, Km post 34 between San José Pinula and Mataquescuintla, Depto. Guatemala, collected by R. F. Savage on 14 March 1992; UTA A-33662, near San José Pinula, Km post 37 on Carretera Nacional to Las Nubes, 2000 m, Depto. Guatemala, collected by E. N. Smith on 9 December 1990; UTA A-33660–61, San José Pinula, Las Nubes, 2300 m, Depto. Guatemala, collected

Fig. 5. *Bolitoglossa omniumsanctorum*. (Upper) UTA A-48710, adult female, 69.5 mm SL; Montañas del Cuilco: a Pajonada a Cumbre del Papal, 2650–2870 m, Huehuetenenago, Guatemala. (Lower) UTA A-38632, adult female, 60.5 mm SL; Sierra de los Cuchumatanes: 9.6 km NE (by road) from junction CN-2 and road to Santa Rosa, on road to Santa Rosa, 2430 m, Quiché, Guatemala.

by E. N. Smith on 31 March 1990.

Diagnosis.—A small to moderate sized (adults 36–49 mm SL) member of the genus *Bolitoglossa* in the subgenus *Magnadigita,* highly variable in color pattern. In general, three basic color patterns may be recognized: dorsum of body completely covered with a broad tan to orange-brown stripe, flanks with dark brown to black markings (Fig. 8, upper); dorsum of body with narrow tan to yellowish dorsolateral stripes, middorsum and flanks dark gray to black (Fig. 8, middle); dorsum and flanks of body dark gray to black with numerous scattered pale gray to pale blue stipples (Fig. 8, lower). The venter of the body is dark gray to black with heavy pale gray or blue stippling that is sometimes clumped. The digits on the hands and feet have webbing extending to the base of the terminal phalanges for most of their length, and are broad and blunt.

Bolitoglossa pacaya can be distinguished from members of the *B. mexicana* and *B. dofleini* species groups (subgenera *Bolitoglossa* and *Pachymandra*) by its smaller size and hands and feet that are not fully webbed; from the *B. rufescens* species group (subgenus *Nanotriton*) by its larger size and feet that are not fully webbed. *Bolitoglossa pacaya* has distinctly more webbing on the hands and feet than do members of the *B. franklini* species group, *B. dunni*, *B. morio*, and *B. rostrata*. *Bolitoglossa pacaya* has distinctly less webbing on the hands and feet than *B. cuchumatana*, *B. flavimembris*, *B. hartwegi*, *B. helmrichi*, and *B. stuarti*. *Bolitoglossa pacaya* has less webbing, longer legs, and larger hands and feet than *B. cuchumatana*. *Bolitoglossa pacaya* can be distinguished from *B. engelhardti* by its larger size and patterned venter. *Bolitoglossa lincolni* inhabits the Sierra de los Cuchumatanes and differs in having a broad reddish dorsal stripe and less webbing on the hands and feet. *Bolitoglossa meliana* is widespread across the mountains fringing the northern edge of the Guatemalan Plateau, but is easily distinguished from *B. pacaya* by having a uniformly blackish coloration and more

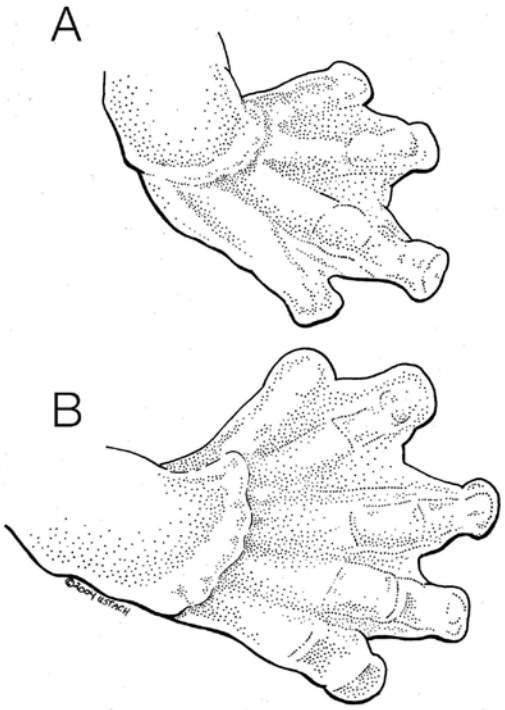

Fig. 6. *Bolitoglossa kaqchikelorum*, UTA A-44132, holotype, (A) hands and (B) feet.

webbing on the hands and feet.

Bolitoglossa pacaya clearly is a member of small but diverse group of salamanders, practically ubiquitous across much of the Guatemalan highlands, previously all allocated to *B. morio*. *Bolitoglossa morio (sensu stricto)* differs in being a much larger species (up to about 60 mm SL), and having longer limbs and fewer maxillary-premaxillary teeth (Table 3). *Bolitoglossa pacaya* has more vomerine and maxillary plus premaxillary teeth and shorter legs than *B. kaqchikelorum*. For diagnosis of *B. pacaya* from other species in the *B. morio* group see subsequent descriptions herein.

Description of holotype.—An adult male having a standard length of 45.3 mm, a tail length of 32.6 mm, a head width of 7.4 mm, and a head length of 10.8 mm (Fig. 8, upper). The legs are moderately long with 0.5 intercostal folds between adpressed limbs. Hand width is 4.0 mm and foot width is 5.0 mm; subdigital pads well developed. Axilla–groin length is 23.9 mm. The toes have webbing extending to the base of the terminal segments. The tips of the toes are broad and blunt. Eye–nostril length is 2.75 mm, eye length is 2.00 mm, interocular distance is 4.70 mm, and internarial distance is 2.60 mm. There are 81 combined maxillary and premaxillary teeth with the premaxillary teeth somewhat enlarged. There are 16 vomerine teeth (8/8) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the nares. The vent is folded and lightly pigmented posteriorly with an unpigmented patch of papillae anteriorly. The testes are two-lobed and unpigmented; the vas deferentia are unpigmented. The mental gland is oval, measuring 4.1 mm wide by 2.8 mm long. The dorsal stripe extends from the head to about one-half way down the tail. In life the stripe color was brownish orange and slightly irregular along the edge; the sides were black and heavily marked with brownish orange. The dorsal surfaces of legs were brownish orange, slightly paler than the dorsum and marked with several large pale blotches. After preservation the dorsal coloration is medium brown, and the lateral stripe is blackish brown. The pale ventral coloration grades into the flank coloration; the ventral surfaces are pale with a dark suffusion darkest at midline. The venter is heavily flecked with pale brown. The toes are distinct with only the first toe fully webbed; well-developed subterminal pads are present.

Variation and color pattern.—Females may attain a larger size than males, but apparently not appreciably so. The largest specimen in our sample is a female, 48.6 mm in SL, whereas the largest male is 45.8 mm SL, and a number of males are > 40 mm SL. The tail length/standard length ratio is 0.66–0.83, the head length/standard length ratio is 0.23–0.26, and the head width/standard length ratio is 0.16–0.18. The number of vomerine teeth vary from 14 to 28 (mean = 19.3), the number of premaxillary plus maxillary teeth are 27–81 (mean = 58.3), and adpressed limbs are separated by 0.5–2.5 (mean = 1.52) intercostal folds.

Dorsal pattern is highly variable and may be one of several distinct color morphs, or be somewhat intermediate between these color patterns (Fig. 8). Some individuals may have a broad tan to yellowish brown dorsal stripe covering the entire back and extending to the dorsolateral region. The dorsal stripe may be slightly to conspicuously darker mid-dorsally. The dorsal stripe starts just posterior to the eyes and extends to about one-half to two-thirds the length of the tail. Pale marking on some individuals include irregularly edged dorsolateral tan to brown stripes, often infused with black, extending from above the insertion of the forelimb to the base of the tail and the dorsum of the tail, which is mostly tan or pale brown with irregular black streaks or mottling (Fig. 8, middle). Other individuals are almost uniformly dark gray or black with pale gray or pale blue stippling on the sides of the head, body, limbs, and tail, heavier on the venter (Fig. 8, lower). The top of the head is mostly dark gray to black from the snout to the parietal region. The tip of the tail is usually yellow. The flanks are dark gray to black as are the limbs, which are stippled with pale gray or pale blue stippling. The gular region is medium gray, sometimes with a slight brownish tinge, with pale stippling. The venter of the body, tail, and limbs is dark gray to purplish black, liberally stippled with pale gray to pale blue (Fig. 9).

The mid-dorsal coloration of preserved specimens may be either distinctly paler or darker than the flanks. The width of the dorsolateral stripes varies from thin lines to broad bands. Some individuals have small, irregular rust-colored markings on the flanks, limbs, or venter. The stripe color in preservative is variable from dark brown to tan to orange. Stripes typically

Fig. 7. *Bolitoglossa kaqchikelorum*. UTA A-60365, ca. 40 mm SL; Cerro Alux, 2107 m, Guatemala, Guatemala.

extend from the eyes to half-way down the tail, but the stripe of some individuals is evident onto the snout. Stripes usually have a thin black border. The lateral surfaces are paler than the dorsum. The venters are pale with variable degrees of dark suffusion; typically the chin and tail are paler than the body. Some individuals have black tail tips as in the holotype but most have yellow tail tips.

Etymology.—The specific epithet is taken from Volcán de Pacaya, the type-locality. The name *pacaya* is used for several species of palms, which are common understory plants in humid tropical and subtropical forests.

Distribution, habits, and habitat.—This species occurs within the western portion of the Jalapan Area as delimited by Campbell & Vannini (1989). It occurs in the highlands that extend unbroken below the 1500 m contour from Volcán de Pacaya northeast around the western edge of Lago Amatitlán to western Depto. Guatemala. The elevational range is 1700–2300 m in humid hardwood or pine-oak forests.

The majority of *Bolitoglossa pacaya* have been found in bromeliads growing on hardwood trees. One series was collected by searching 46 bromeliads, 14 of which contained 20 salamanders. A few individuals have been encountered in bromeliads on pines, on the ground beneath rotting logs, or deep in crevices along dirt banks. Individuals were taken in bromeliads 2–10 m above the ground in both the rainy and dry seasons.

A dark *Bolitoglossa morio*-like salamander was collected at on the Soledad Grande Highland Block (*sensu* Stuart, 1954*a*). This species will be known as:

Bolitoglossa eremia new species

Holotype.—UTA A-38620 (original field no. JAC 17657), an adult female from near La Soledad, on road to Torre de Guatel, 2650 m, Depto. Jalapa, Guatemala (14.530146° N, 90.142417° W), collected by J.A. Campbell on 10 August 1991 (Fig. 10, lower; Fig. 11).

Paratypes.—All from Guatemala: Jalapa. UTA A-33670, 4.7 km SW Miramundo, 2360 m, collected by J. A. Campbell on 3 July 1990; UTA A-38617–19, near Miramundo at Torre de Guatel, 2650 m, collected by C. L. Guirola on 28 September 1991; UTA A-38621, data same as holotype; UTA A-38629–31, near Miramundo, 2550 m, collected by J.A. Campbell on 8 August 1992; UTA A-58387, Cocesna, near Mataquesquintla, Cerro Miramundo, 2660 m, collected by M.E. Acevedo on 17 June 1999; UTA A-58388–89, Miramundo highlands, near Torre de Guatel, 2660 m, collected by M.E. Acevedo on 17 June 1999; UTA A-58552–53, Cerro Miramundo (14.531666° N, 90.147777° W), ca. 2650 m, collected by E. N. Smith on 23 November 1998.

Diagnosis.—A small to moderate sized (adults 38–60 mm SL) member of the genus *Bolitoglossa* in the subgenus *Magnadigita* with a dark gray to black ground color. The dorsum, tail, and limbs are marked with white stippling and the flanks are smudged or mottled with pale pink. The venter is gray, heavily marked with white stippling; these sometimes coalesce forming irregular small streaks. Some individuals have pinkish blotches along their flanks, whereas others are essentially dark with only faint pale blotches. The underside of the head and throat may be mostly pinkish or dark gray with pale speckling. The digits on the hands and feet have webbing extending to the base of the terminal phalanges, with broad and blunt toes.

Bolitoglossa eremia can be distinguished from members of the *B. mexicana* and *B. dofleini* species groups (subgenera *Bolitoglossa* and *Pachymandra*) by its smaller size, hands and

Fig. 8. *Bolitoglossa pacaya*. (Upper) UTA A-33639, male paratype, 36.7 mm SL. (Middle) UTA A-33640, male paratype, 33.3 mm SL. (Lower) UTA A-33641, male holotype, 45.3 mm SL. All from 4 km (airline) SSE San Vicente Pacaya, W slope Volcán de Pacaya, 2000–2050 m, Escuintla, Guatemala.

feet that are not fully webbed, and a relatively shorter tail; from the *B. rufescens* and *B. hartwegi* species groups (subgenera *Nanotriton* and *Mayamandra*) by its larger size and feet that are not fully webbed. *Bolitoglossa eremia* has distinctly more webbing on the hands and feet than members of the *B. franklini* species group. *Bolitoglossa eremia* is distinguished from *B. engelhardti* by its broader, longer, and square-tipped toes with less webbing, and shorter limbs. *Bolitoglossa morio* differs in having fewer vomerine and maxillary-premaxillary teeth (mean = 21.4 and 38.8 vs. 27.2 and 46.6, respectively) and in having relatively longer limbs (mean = 1.5 intercostal folds between adpressed limbs vs. 0.9). *Bolitoglossa pacaya* is a smaller species with fewer vomerine and more maxillary-premaxillary teeth (mean = 19.4 and 58.3 vs 28.6 and 49.4, respectively).

Description of holotype.—An adult female 55.3 mm SL mm, a tail length of 41.0 mm, a head width of 9.1 mm, and a head length of 13.1 mm. The legs are moderately long with 2 intercostal folds between adpressed limbs. Hand width is 5.2 mm and foot width is 6.4 mm; subdigital pads well

Fig. 9. *Bolitoglossa pacaya*. From top to bottom UTA A-33639–41. All from 4 km (airline) SSE San Vicente Pacaya, W slope Volcán de Pacaya, 2000–2050 m, Escuintla, Guatemala.

developed. Axilla–groin length is 28.3 mm. The toes have webbing extending to the base of the terminal segments. The tips of the toes are broad and blunt. Eye–nostril length is 2.10 mm, eye length is 2.40 mm, interocular distance is 5.00 mm, and internarial distance is 2.40 mm. There are 52 combined maxillary and premaxillary teeth. There are 28 vomerine teeth (15/13) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening; the vomerine teeth are arrayed in several rows forming a patch of teeth. The vent is folded and lightly pigmented. In life the dorsal ground color of the head, body, and tail was dark gray; the flanks were colored with an irregular suffusion of pink from axilla to groin; the limbs were dark gray with scant white stippling except for the dorsal surfaces of hands and feet, which were heavily stippled (Fig. 10, lower). The side of the head below the canthus and eye was also heavily stippled with white.

Variation and color pattern.—Females apparently attain a larger size than males. The largest specimen in our sample is a female, 62.1 mm in SL and three females > 50 mm SL, whereas the largest male is 42.3 mm SL. The tail length/SL ratio is 0.62–0.83 (mean = 0.73, the head length/SL ratio is 0.21–0.29 (mean = 0.25), and the head width/SL ratio is 0.14–0.21 (mean = 0.17). The number of vomerine teeth varies from 16 to 44 (mean = 28.6); as with the holotype, vomerine teeth are arrayed in several rows forming a patch. The number of premaxillary plus maxillary teeth are 35–66 (mean = 49.4), and adpressed limbs are separated by 0.5–2.0 (mean = 1.5) intercostal folds.

The top of the head, dorsum of body and tail, and limbs are mostly dark gray with white stippling. The amount of stippling varies from scant to moderate, with the side of the head and upper surfaces of digits often the most heavily stippled areas. The flanks are heavily suffused with pink, sometimes forming large blotches. The pink coloration in some individuals extends well onto the neck and side of the head (Fig. 10). The venter is gray, somewhat paler than the dorsum, with varying amounts of white flecking or stipples; some individuals have mostly pink throats and irregular pink blotches on the venter of the body (Fig. 11). Paratype males have unpigmented testes and pigmented vasa defferential and the premaxillary teeth are enlarged and reduced in number. Mental glands vary from ovoid to reniform. Cloacal linings were unpigmented with patches of papillae. Cirri are well developed.

Etymology.—The specific epithet is taken from the Greek *eremia*, meaning solitude, in reference to the village of La Soledad in the Miramundo highlands, near which the type-series was collected, as well as in reference to the isolated distribution of this species from other members of the *B. morio* group.

Distribution, habits, and habitat.—This salamander is apparently restricted to the isolated Miramundo Highlands, which fall within the Jalapan Area as defined by Campbell & Vannini (1989). This species inhabits montane hardwood forest at elevations of 2360–2660 m. When irritated or injured, this species exudes a yellow tail secretion. The forest occurring above 2000 m on the Soledad Grande Highland Block was described as "temperate-cold upland forest" by

Fig. 10. *Bolitoglossa eremia*. (Upper) UTA A-38631, adult male paratype, 42.3 mm SL; near Miramundo, 2550 m, Jalapa, Guatemala. (Middle) UTA A-38629, adult female paratype, 59.8 mm SL; near Miramundo, 2550 m, Jalapa, Guatemala. (Lower) UTA A-38620, adult female holotype, 55.3 mm SL; La Soledad, on road to Guatel Tower, 2650 m, Jalapa, Guatemala.

Steyermark (1950).

Bolitoglossa eremia was most frequently found on the ground under large rotting logs. However, during wet periods individuals were found under smaller fallen limbs and even large chips of wood. Several salamanders were encountered in September in rotting tree trunks 10–25 cm above the ground and another individual found in July was excavated from a deep crevice along a dirt bank.

Stuart (1954*a*) reported two species of salamanders from the Soledad Grande Highland Block. One he had described previously (Stuart, 1954*b*) as *Pseudoeurycea expectata*. Judging from his collections, this species was relatively

Fig. 11. *Bolitoglossa eremia*. (Upper) UTA A-33670, adult female, 62.1 mm SL; 4.7 km SW Miramundo, 2360 m, Jalapa, Guatemala. (Lower) UTA A-38620, adult female holotype, 55.3 mm SL; UTA A-38620, 55.3 mm SL; La Soledad, on road to Guatel Tower, 2650 m, Jalapa, Guatemala.

abundant. The other species was based on a single juvenile and he reported only as *Magnadigita* sp. He thought this specimen belonged to the *Bolitoglossa dunni* group and possibly was undescribed. It is apparent that this species is the same as we describe here as *B. eremia*. We did not encounter *P. expectata* in the region, but *B. eremia* was not uncommon.

Volcán Suchitán is in the department of Jutiapa. The volcano reaches 2042 m and is covered mostly with secondary growth particularly at lower elevations. We collected a small to moderate sized, dark salamander on the slopes of this volcano that appears to be closely related to *B. eremia*. These two species exhibit relatively slight morphological and molecular differences. However, in view of the fact that they may be distinguished from each other and the extremely

isolated nature of Volcán Suchitán, we suggest the Jutiapan salamander be known as:

Bolitoglossa suchitanensis new species

Holotype.—UTA A-58421 (original field no. MEA 1929), an adult female from Volcán Suchitán, above Aldea Suchitán, Municipio Santa Catarina Mita, 1960 m, Jutiapa, Guatemala (14.403209° N, 89.779753° W), collected by M. E. Acevedo on 13 May 1999.

Paratypes.—UTA A-58149–152, 58419–20, 58422–24 from Volcán Suchitán, above Aldea Suchitán, Municipio Santa Catarina Mita, 1850–1990 m, Jutiapa, Guatemala, collected by M. E. Acevedo on 1–14 May 1999.

Diagnosis.—A small to moderate sized (adults 46–56 mm SL) member of the genus *Bolitoglossa* in the subgenus *Magnadigita* with a dark brownish gray ground color with the lower flanks and venter paler than the dorsum (Fig. 12). Usually there are white markings on the flanks that vary from small spots to abundant mottling. Juveniles may have inconspicuous pale spotting or streaking on the dorsum of the tail, but in adults the tail is uniformly dark. One juvenile (UTA A-58150) has a faint dorsal stripe on the dorsum set off from the slightly darker flanks. The digits on the hands and feet have webbing extending to the base of the terminal phalanges, with broad and blunt toes.

Bolitoglossa suchitanensis can be distinguished from members of the *B. mexicana* and *B. dofleini* species groups (subgenera *Bolitoglossa* and *Pachymandra*) by smaller size, hands and feet that are not fully webbed, and a relatively shorter tail; from the *B. rufescens* and *B. hartwegi* species groups (subgenera *Nanotriton* and *Mayamandra*) by larger size and feet that are not fully webbed. *Bolitoglossa suchitanensis* has more webbing on the hands and feet and is smaller than members of the *B. franklini* species group. *Bolitoglossa suchitanensis* has distinctly less webbing on the hands and feet than do *B. cuchumatana*, *B. helmrichi*, and *B. flavimembris*, and slightly less so than in *B. rostrata*. *Bolitoglossa suchitanensis* can be distinguished from *B. engelhardti* by larger size and larger hands and feet with less webbing. *Bolitoglossa suchitanensis* is a member of the *B. morio* group. It may be distinguished from *B. eremia* and *B. morio* (sensu stricto) by having slightly longer digits with less webbing, a paler ground color, more maxillary-premaxillary teeth, and having somewhat shorter limbs, as reflected in number of intercostal folds between adpressed limbs. *Bolitoglossa suchitanensis* may be distinguished from *B. pacaya* by its larger size, more vomerine teeth, fewer maxillary-premaxillary teeth and somewhat shorter limbs.

Description of holotype.—An adult female having a standard length of 54.3 mm, a tail length of 40.5 mm, a head width of 8.8 mm, and a head length of 12.7 mm (Fig. 12). There are 2.0 intercostal folds between adpressed limbs. Hand width is 4.0 mm and foot width is 5.0 mm; subdigital pads well developed. Axilla–groin length is 27.5 mm. The toes have webbing extending to the base of the terminal segments. The tips of the toes are broad and blunt. Eye–nostril length is 2.75 mm, eye length is 1.65 mm, interocular distance is 5.25 mm, and internarial distance is 2.70 mm. There are 63 combined maxillary and premaxillary teeth. There are 23 vomerine teeth (12/11), extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening. The vent is folded and lightly pigmented. In preservative (alcohol after formalin) the dorsum of entire body (head, trunk, limbs, tail) uniformly dark gray-brown; venter paler, medium brown.

Color pattern.—Most individuals in the paratypic series are similar in coloration to the holotype. Several of the largest individuals (UTA A-58422–24) have pale streaks or spots on the flanks; this pattern is present, but less conspicuous, on a smaller specimen (UTA A-58152). One subadult has a brown dorsum set off by dark gray flanks.

Etymology.—The specific epithet is derived from Suchitán, the volcano that is the type-locality for this species, and the Latin suffix *–ensis*, denoting place.

Distribution, habits, and habitat.—This species is one of the most geographically restricted species of *Bolitoglossa*, known only from 1850 to 1990 m on Volcán Suchitán, but probably occurring to the summit at 2042 m. The upper slopes of the volcano where *B. suchitanensis* was collected support a relatively humid broad-leaf forest with abundant mosses and epiphytes. Other than several well used hiking paths, the vegetation is dense near the crest where slopes can be very steep. This volcano is surrounded by warm, subtropical dry forest and is isolated from the nearest known locality for *B. eremia* by about 40 km. The type-locality falls within the Jalapan Area as delimited by Campbell and Vannini (1989).

The type-specimen was collected buried in moss on a log at about 1615 h near a rest stop on a hiking trail known locally as "La Bandera." Other specimens were collected by day (840–1530 h) beneath rotting logs or in damp leaf litter or at night (1900–2300 h) actively climbing on branches, ferns, or leaves in secondary vegetation 0.6–1.6 m above the ground.

The biota of the Sierra de las Minas and adjacent mountains to the west in Baja Verapaz has remained relatively poorly known until recent decades. We have surveyed the herpetofauna of this range from the Purulhá region in Baja Verapaz eastward through the length of the Sierra de las Minas on slopes drained by both the Río Polochic and Río Motagua. A number of endemic amphibians and reptiles occur in the region (*e.g.*, *Plectrohyla*: Duellman & Campbell, 1984), and the only Guatemalan endemic genus of snake is found at the high elevations of the Sierra de las Minas (*Chapinophis*: Campbell & Smith, 1998). Among our many discoveries was a uniquely patterned salamander, apparently of the *Bolitoglossa morio* group, that will bear the name:

Bolitoglossa daryorum new species

Holotype.—UTA A-59729 (original field no. GAR 197),

Fig. 12. *Bolitoglossa suchitanensis*, UTA A-58421, adult female holotype, 54.3 mm SL; Volcán Suchitán, above Aldea Suchitán, Municipio Santa Catarina Mita, 1960 m, Jutiapa, Guatemala.

an adult female from Biotopo del Quetzal, Plan de Geomaya, 2235 m, Baja Verapaz, Guatemala (15.204732° N, 90.233556° W), collected by R. García Anleu on 3 July 1997.

Paratypes.—UTA A-59730–31, Biotopo del Quetzal, Plan de Geomaya, 2235 m, Baja Verapaz, Guatemala, collected by R. García Anleu on 3 July 1997; UTA A-48580–82, above Albores, Cerro Pinalon, Sierra de las Minas, 2400 m, Depto. El Progreso, Guatemala, collected by a local resident on 24 February 1993; UTA A-34045, above San Agustín Acasaguastlán, S slope of Cerro Pinalon, Sierra de las Minas, ca. 2760 m, Depto. El Progreso, collected by E.N. Smith on 25 February 1990; UTA A-34046–47, above San Agustín Acasaguatlán, on road between La Trinidad and Cerro Pinalon, Sierra de las Minas, 2500 m, collected by E.N. Smith on 17 March 1990; UTA A-58520, S slope Cerro Pinalon, Sierra de las Minas, 2256 m (15.065889° N, 89.985611° W), Depto. El Progreso, collected by E.N. Smith on 1 March 2006.

Diagnosis.—A moderate sized (adults 43–61 mm SL) member of the genus *Bolitoglossa* (subgenus *Magnadigita*) in the *B. morio* group. The gray ground color is very heavily flecked and stippled with white. It has a pattern of large bold white spots on the flanks and most of lateral and ventral surfaces of the tail. The pale markings on flanks are irregular in shape but may extend in length between 1–2 intercostal groves. Pale spots are present on the venter of the head and body, especially laterally. The hands and feet have only moderate webbing, with broad and blunt toes.

Bolitoglossa daryorum can be distinguished from members of the *B. mexicana* and *B. dofleini* species groups (*sensu* Wake & Lynch, 1976; Elias, 1984) by smaller size and hands and feet that are not fully webbed; from the *B. rufescens* and *B. hartwegi* species groups by larger size and feet that are not fully webbed. *Bolitoglossa daryorum* has distinctly more webbing on the hands and feet than do members of the *B. franklini* species group. *Bolitoglossa daryorum* has distinctly less webbing on the hands and feet than do *B. cuchumatana*, *B. flavimembris*, and *B. helmrichi*. *Bolitoglossa daryorum* can be distinguished from *B. engelhardti* by larger size, heavy pale stippling, and striking pattern of bold white spots. *Bolitoglossa lincolni* inhabits the Sierra de los Cuchumatanes and differs in having a broad reddish dorsal stripe and less webbing on the hands and feet. *Bolitoglossa meliana* is widespread across the mountains fringing the northern edge of the Guatemalan Plateau, but is distinguished from *B. daryorum* by having a uniformly blackish coloration and more webbing on the hands and feet. *Bolitoglossa daryorum* may be distinguished from *B. pacaya*, *B. eremia*, and *B. morio* (*sensu stricto*) by its unique color pattern.

Description of holotype.—An adult female having a standard length of 52.0 mm, a tail length of 35.3 mm, a head width of 8.0 mm, and a head length of 11.8 mm (Fig. 13). The legs are moderately long with 1.5 intercostal folds between adpressed limbs. Hand width is 4.7 mm and foot width is 5.7 mm; subdigital pads well developed. Axilla–groin length is 26.0 mm. The toes have moderate webbing extending to the base of the terminal phalange, except for the first digit. The

tips of the toes are broad and blunt. Eye–nostril length is 2.05 mm, eye length is 1.65 mm, interocular distance is 2.50 mm, and internarial distance is 2.25 mm. There are 44 combined maxillary and premaxillary teeth. There are 26 vomerine teeth (13/13) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening of the nares. The vent is folded and pigmented.

Variation and color pattern.—Females apparently attain a larger size than males. The two largest specimens in our sample are females, 52.0 and 60.9 mm SL, whereas the largest male is 46.9 mm SL. The tail length/standard length ratio is 0.64–0.80 (mean = 0.67) in adults, the head length/standard length ratio is 0.22–0.25, and the head width/standard length ratio is 0.15–0.16. The number of vomerine teeth vary from 18 to 26 (mean = 22.8; 10–13 per side), the number of premaxillary plus maxillary teeth are 40–56 (mean = 46.3), and adpressed limbs are separated by 0–2 (mean = 1.38) intercostal folds.

The dorsum of the head, body, tail, and limbs is medium to dark gray, with flanks somewhat paler, and bold white stippling on all surfaces. Large, bold, irregular white blotches, outlined with black, are present on the dorsum (mostly in dorsolateral area) and lateral regions of the body), the dorsum of the proximal portion of the tail, much of the ventral surface of the tail, and sometimes above the insertion of the forelimb and temporal region (Figs. 13 and 14, upper). The venter of the head anterior to the gular fold is pale yellowish gray and heavily stippled with white. The venter of the body is dark purplish gray and heavily suffused with pale stippling, especially laterally (Fig. 14, lower). The palmar and plantar surfaces are dark maroon.

The development of the bold white spotting so characteristic of this species may become more conspicuous with age. In our sample, the largest individuals have the most prominent pale blotches. One small specimen (< 30 mm SL) is mostly devoid of pale blotches except for a few small spots on flanks and the dorsum of the tail (Fig. 14, upper).

Etymology.—The specific epithet is a patronym for the exceptional Dary family of Guatemala, who have done so much to further conservation in that country. Mario Dary Rivera (1928–1981), founded the School of Biology at the Universidad de San Carlos of Guatemala as well as the Biotopo Universitario para la Conservación del Quetzal, which is inhabited by this new species of salamander. He later became Rector of the Universidad de San Carlos of Guatemala. Juan Mario Dary Fuentes, his son, has followed strongly in his father's path, rising to become the Guatemalan Minister of Environment and Natural Resources. The Latin suffix *-orum* means "belonging to."

Distribution, habits, and habitat.—*Bolitoglossa daryorum* is found in rotting logs. Most were on the ground, but 2 individuals were found in rotting vertical trunks about 2 m above the ground. The elevational range is 2400–2760 m in cloud forest. The range of *B. daryorum* falls within the Minan Subarea as recognized by Campbell and Vannini (1989), although the type-locality is near the boundary with the Chuacús Subarea.

In our collections is a single specimen of uniformly dark salamander that cannot be allocated with any known species. It was discovered in the eastern portion of the Sierra de las Minas. In many respects it possesses morphology typical of the *Bolitoglossa morio* group. We propose that it be known as:

Bolitoglossa tzultacaj new species

Holotype.—UTA A-38590, 17.7 km above Jones on road to Finca Alejandria, Sierra de las Minas, 1800 m, Zacapa, Guatemala (15.116067° N, 89.614982° W), collected by R.F. Savage on 16 April 1992.

Diagnosis.—Probably a moderate sized (the only known specimen is a a subadult female 37 mm SL) member of the genus *Bolitoglossa* (subgenus *Magnadigita*) in the *B. morio* group. In alcohol (after formalin) the ground color is uniformly gray, with the venter slightly paler than the dorsum. The hands and feet have moderate webbing extending almost to the distal phalanges of digits exclusive of the pollex and hallux and have broad, blunt toes.

Bolitoglossa tzultacaj can be distinguished from members of the *B. mexicana* and *B. dofleini* species groups (*sensu* Wake & Lynch, 1976; Elias, 1984) by smaller size and hands and feet that are not fully webbed; from the *B. rufescens* and *B. hartwegi* species groups by larger size and feet that are not fully webbed. *Bolitoglossa daryorum* can be distinguished by its distinctive color pattern and longer limbs. *Bolitoglossa tzultacaj* has distinctly less webbing on the hands and feet than do *B. cuchumatana*, *B. flavimembris*, and *B. helmrichi*. *Bolitoglossa tzultacaj* can be distinguished from *B. engelhardti* by a more robust body, shorter tail, and uniform coloration. *Bolitoglossa lincolni* has a broad reddish dorsal stripe and less webbing on the hands and feet. *Bolitoglossa meliana* is widespread across the mountains of Guatemala, including the western portion of the Sierra de las Minas, but is distinguished from *B. tzultacaj* by lacking webbing on the hands and feet, in being a large species (adult females 65–80 mm SL), with a relatively long, slender tail. *Bolitoglossa tzultacaj* may be distinguished from *B. pacaya*, *B. eremia*, *B. suchitanensis* and *B. morio* (*sensu stricto*, see preceeding section) by its uniformly dark color pattern and much shorter limbs.

Description of holotype.—An subadult female having a standard length of 37.0 mm, a tail length of 23.6 mm, a head width of 6.9 mm, and a head length of 9.4 mm (Fig. 15). The legs are short with 4.0 intercostal folds between adpressed limbs. Hand width is 2.9 mm and foot width is 3.7 mm; subdigital pads well developed. Axilla–groin length is 20.4 mm. The toes have webbing extending almost to the distal-most phange. The tips of the toes are broad and blunt. Eye–nostril length is 1.65 mm, eye length is 2.05 mm, interocular distance is 3.50 mm, and internarial distance is 2.10 mm. There are 36 combined maxillary and premaxillary teeth with

Fig. 13. *Bolitoglossa daryorum*, UTA A-59729, adult female holotype, 52.0 mm SL; Biotopo del Quetzal, Plan de Geomaya, 2235 m, Baja Verapaz, Guatemala.

the premaxillary teeth somewhat enlarged and reduced in number. There are 14 vomerine teeth (7/7) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening of the nares. The vent is folded and pigmented.

We did not see the specimen in life, but in preservative it is uniformly dark, devoid of any pale blotching. In life this species may be brown (Fig. 15).

Etymology.—We offer this new species to Tzultacaj, Mayan God of the mountains and valleys, upon whose terrain we have repeatedly trespassed.

Distribution, habits, and habitat.—This species is known only from the southern slopes of the Sierra de las Minas near the junction of the departments of Zacapa, Izabal, and Alta Verapaz. The forest at 1800 m is an admixture of pine-oak forest and cloud forest vegetation, which prevails at higher elevations.

As outlined here, we recognize a series of species in the *Bolitoglossa morio* group distributed across the Guatemalan highlands. From west to east these species are *B. omniumsanctorum* in the west in the Cuchumatanes, Cuilcos, and extreme eastern portion of the Sierra de Chuacús; *B. morio* on the central portion of the Guatemalan Plateau; *B. kaqchikelorum* on the eastern portion of the Guatemalan Plateau; *B. pacaya* in the southeastern highlands on Volcán Pacaya and the the Las Nubes highland block; *B. eremia* on the Soledad Granded highland block; *B. suchitanensis* on the Volcán Suchitán; *B. daryorum* in the western and central portions of the Sierra de las Minas; and *B. tzultacaj* in the extreme eastern Sierra de las Minas (Fig. 16).

A group of small, superficially similar, salamanders occurring across much of the highlands of Guatemala has led to some confusion. These salamanders usually do not exceed 50 mm SL, have relatively long limbs, have a considerable amount of webbing on the hands and feet, extending to the digital pads, a relatively short tail with a variable amount of pigmentation on its venter, ranging from dark to almost immaculate. At least some, and sometimes most, individuals in every population we have examined have pale dorsolateral stripes extending from behind the eye to the base of the tail. In some instances the dorsum is also pale, forming a broad dorsal band distinctly set off by the darker flanks. The venter of the tail is usually mostly pale in *Bolitoglossa helmrichi*, and is variable in *B. cuchumatana, B. rostrata,* and in several undescribed species, that usually have some dark pigment, sometimes in the form of widely scattered melanophores. Elias (1984: table 1) noted that subcaudal coloration is orange and there is relatively extensive webbing in *B. helmrichi*, whereas in *B. cuchumatana* subcaudal coloration is tan and there is relatively less webbing. However, he noted that subcaudal coloration was tan in a few specimens from the eastern portion of the Sierra de las Minas. We have not confirmed the identity of his material of *B. cuchumatana*, which was from various localities in the Sierra de los Cuchumatanes. However, we take this opportunity to point out that all of the specimens he examined of *B. cuchumatana* reportedly from the Montañas de Cuilco, along with many other species, are from nowhere near that range and actually came from localities in the Sierra de los Cuchumatanes. Differences in foot structure among some of these species are slight, but relative digit length, in order from shortest to longest, is *B. cuchumatana, B. helmrichi,* and *B. la*. The relative amount of webbing from least to greatest is *B. la,*

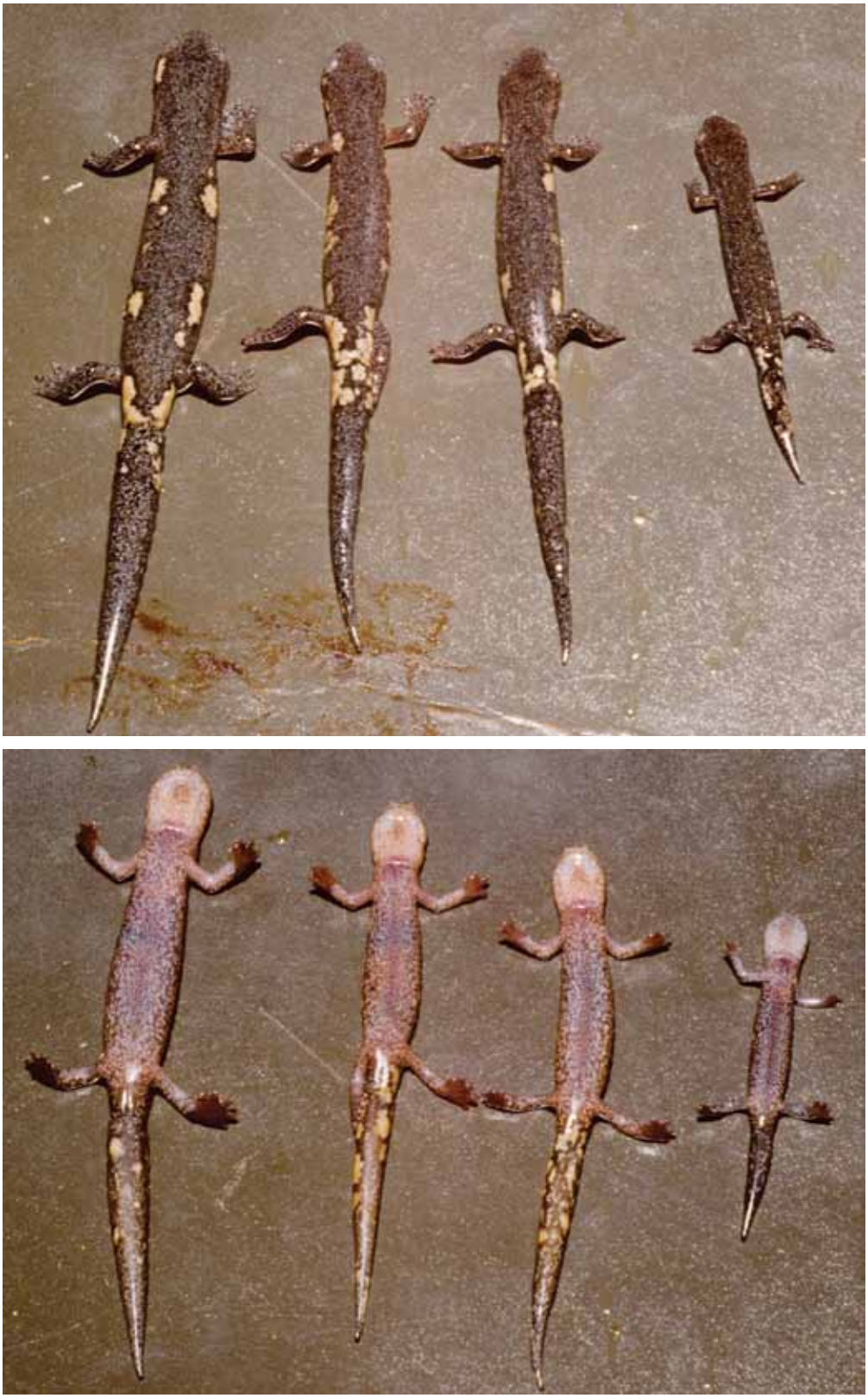

Fig. 14. *Bolitoglossa daryorum*, dorsal (upper) and ventral (lower) aspect, from left to right, UTA A-59729–32; 52.0, 42.7, 43.6, and 31.6 mm SL; female, male, male, juvenile, respectively. Biotopo del Quetzal, Plan de Geomaya, 2235 m, Baja Verapaz, Guatemala.

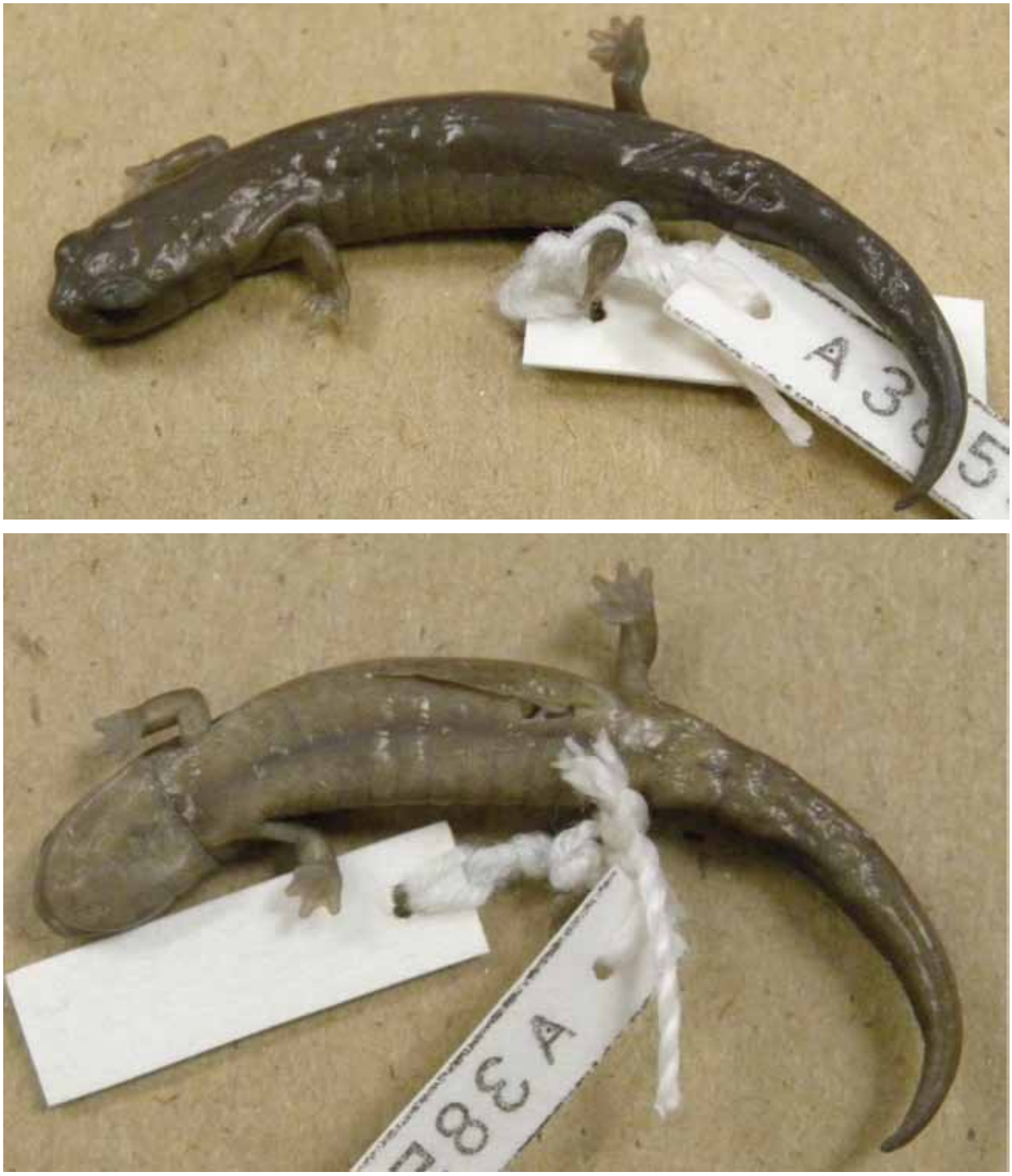

Fig. 15. *Bolitoglossa tzultacaj*, UTA A-38590, dorsal (upper) and ventral (lower) aspect, subadult female holotype, 37.0 mm SL; 17.7 km above Jones on road to Finca Alejandria, Sierra de las Minas, 1800 m, Zacapa, Guatemala.

B. helmrichi, and *B. cuchumatanus*.

Stuart (1943) considered *Bolitoglossa helmrichi*, *B. cuchumatana*, and *B. engelhardti* to be closely related and represent an east-to-west distribution of the group. In their consideration of the *B. helmrichi* group, Wake & Brame (1969) included *B. hartwegi*, *B. stuarti*, and *B. flavimembris*, which do not appear to be closely related to *B. helmrichi*. They also omitted *B. rostrata*, which appears to be properly placed within the group including *B. helmrichi*, *B. cuchumatana*, *B. rostrata*, and additional species described herein. Wake &

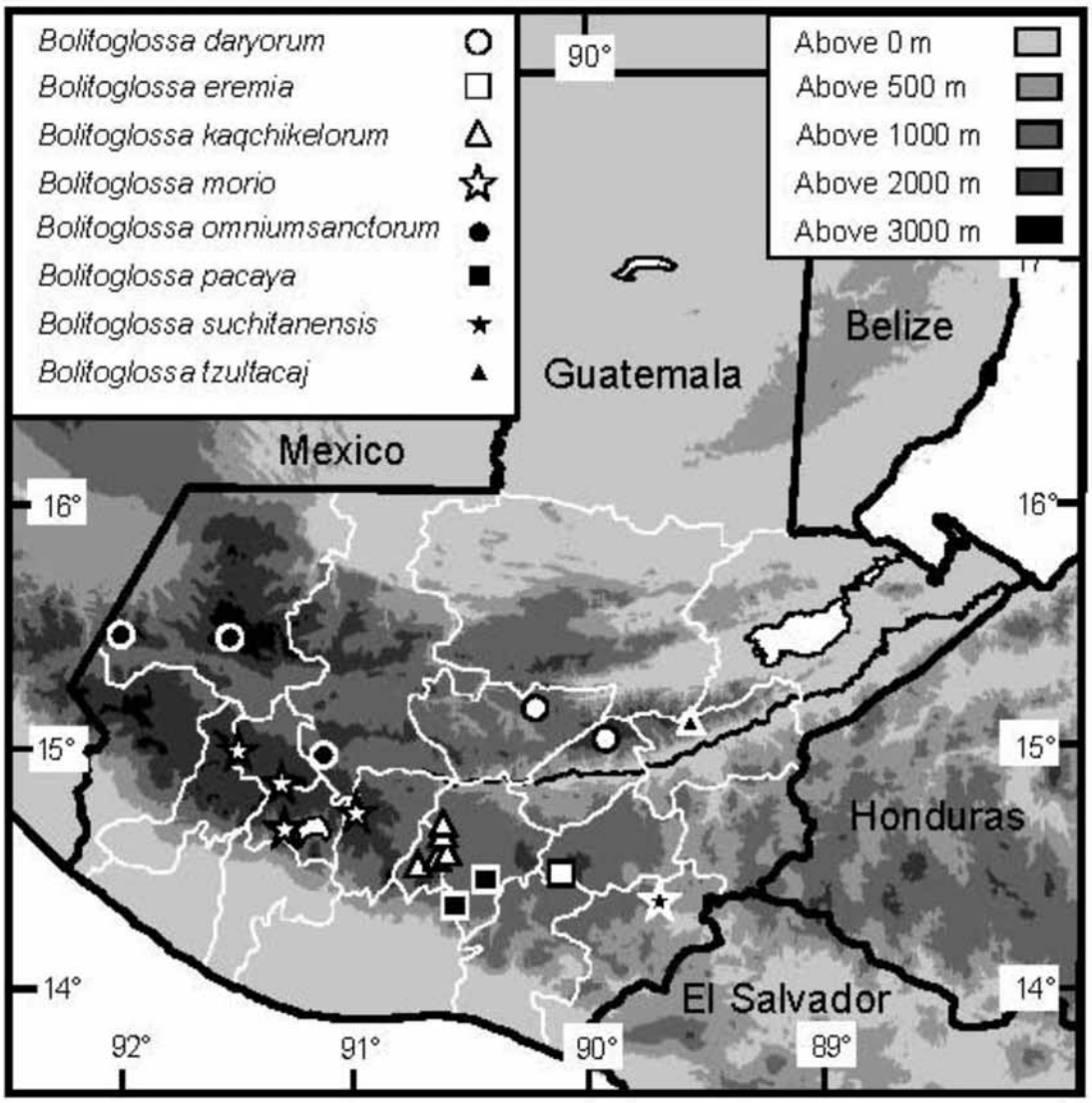

Fig. 16. Distribution of selected species of the *Bolitoglossa morio* group in the Guatemalan highlands. Localities based on material examined.

Lynch (1976) added *B. morio* to the *B. helmrichi* group, but our analyses suggest that *B. morio* is more closely related to the *B. franklini* group.

Part of the key to unraveling the systematic identities of these salamanders is to clarify the situation for *Bolitoglossa cuchumatana*. There is apparent confusion about the degree of foot webbing of this species (Elias, 1984). *Bolitoglossa cuchumatana* (Stuart, 1943) was described on the basis of four specimens, from 2 km north of Nebaj, Depto. El Quiche. Wake & Brame (1963) reported on the three paratypes, and Elias (1984) provided a figure of maxillary tooth number of specimens he considered to be *B. cuchumatana*. Workers in the field have used the name to apply to specimens from many regions of Guatemala. We have examined the type-series and other specimens of *B.* cf. *cuchumatana* in order to evaluate the specific status of salamanders from two regions.

The three series we examined (Appendix 1) correspond closely with the Stuart's (1943) description and the type series. Thirteen adult males were 33.4 to 43.6 mm SL; 17 adult females were 34.0 to 57.5 mm SL. Tails were 0.74 (SE = 0.009) of SL, head length was 0.26 (0.002) SL, and head width was 0.17 (0.001) SL. Vomerine teeth were 17 to 41 in males (mean = 24.7) and 23 to 34 in females (mean = 27.9); maxillary plus premaxillary teeth were 25 to 70 (mean = 47.8) in males and 46 to 67 (mean = 59.7) in females. There were 0 to 1 intercostal folds between adpressed limbs in males and 0.5 to 1.5 in females. The toes were almost fully webbed with indentations between toes and small subterminal pads were present. Mental glands are reniform and for six males averaged 3.4 mm wide and 2.5 mm long.

The dorsal stripe in the type-series has little melanophore encroachment along the margins giving the appearance of

brighter dorsolateral stripes. This is also true of animals from our series. The stripe in life is orange and extends from the snout to the tip of the tail with a highly variable degree of melanophores especially mid-dorsally. At one extreme the stripe becomes series of dorsolateral blotches. Some specimens are very dark and the stripe is visible only with the aid of a microscope (Fig. 17). The sides of the body and tail are flecked with stripe color, more heavily on the tail. Ventral coloration is pale with scattered melanophores; small blotches of stripe color are sprinkled on the ventral surfaces becoming more concentrated on the tail.

We have made a number of trips to one of the deep valleys near the town of Chichicastenango. This rugged ravine contains a relatively pristine patch of montane forest characterized by abundant pines and oaks heavily laden with epiphytes. One of the few viable populations of *Abronia vasconcelosii* persists in the area (Campbell & Frost, 1993) and it is the type-locality of a large species of fossorial colubrid, *Adelphicos ibarrorum* (Campbell & Brodie, 1988). Additionally, we secured a series of a small species of salamander, which we describe here as:

Bolitoglossa la new species

Holotype.—UTA A-38661 (original field no. JAC 17751), an adult female from 3.0 km SSE Chichicastenango, valley between Paxot and Caminibal, 2100 m, El Quiché, Guatemala (14.921181° N, 91.103626° W), collected by local orchid collector in March 1992.

Paratypes.—All from Guatemala: El Quiché. UTA A-21550–54, locality as for holotype, collected by local residents in January 1987; UTA A-24469–79, locality as for holotype, collected by J. A. Campbell on 14 August 1987; UTA A-33635–37, locality as for holotype, collected by a local resident on 16 June 1990; UTA A-38656–60, UTA A-38662–75, data as for holotype; UTA A-21555–60, 2 km S Chichicastenango, collected by a local resident in April 1987; UTA A-51431–37, locality as for holotype, collected by J. A. Campbell on 21 June 1996; UTA A-58390–401, 58403–17, locality as for holotype, collected by J. A. Campbell in August 1992; UTA A-38556, 9.0 km NE (by road) from junction of Carretera Nacional #2 and road to Santa Rosa Chucuyub, on road to Santa Rosa Chucuyub, 2390 m, collected by J. A. Campbell and E. D. Brodie, Jr. on 2 August 1992; UTA A-38557, 7.8 km NE (by road) from junction of Carretera Nacional #2 and road to Santa Rosa Chucuyub, on road to Santa Rosa Chucuyub, 2100 m, collected by J. A. Campbell and E. D. Brodie, Jr on 2 August 1992; UTA A-33635–36, 9.6 km NE (by road) from junction of Carretera Nacional #2 and road to Santa Rosa Chucuyub, on road to Santa Rosa Chucuyub, 2430 m, collected by J. A. Campbell and E. D. Brodie, Jr on 2 August 1992.

Diagnosis.—A moderate sized (adults 40–54 mm SL) member of the genus *Bolitoglossa* (subgenus *Magnadigita*) in the *B. helmrichi* group. The venter of the body is dark with a fine reticulation of small pale spots in *B. la*, it is uniformly pigmented or with small pale spots in *B. cuchumatana*, and it has large spots devoid of melanophores in *B. helmrichi*. The hands and feet with moderate webbing, with narrow, triangular toes. There is less webbing on the hands and feet than in *B. cuchumatana* or *B. helmrichi*.

Bolitoglossa la can be distinguished from members of the *B. mexicana* and *B. dofleini* species groups (subgenera *Bolitoglossa* and *Pachymandra*) by its smaller size and hands and feet that are not fully webbed; from the *B. rufescens* and *B. hartwegi* species groups (subgenera *Nanotriton* and *Mayamandra*) by its larger size and feet that are not fully webbed. *Bolitoglossa la* has distinctly more webbing on the hands and feet than do members of the *B. franklini* species group. It may be distinguished from *B. omniumsanctorum* by its smaller size and longer limbs and from *B. morio* (*sensu stricto,* see preceeding section) by having more maxillary-premaxillary teeth. *Bolitoglossa flavimembris* is larger with a darker ground color and usually pale limbs that contrast with the body coloration, the digits are slightly longer, especially the third finger which noticeably projects. *Bolitoglossa rostrata* is smaller and has longer digits with less webbing. *Bolitoglossa cuchumatana* attains a smaller size and has darker ventral surfaces, including the palmar and plantar surfaces. In *B helmrichi* the venter of the tail is mostly pale (vs. pigmented with or without small pale spots) and the digits are longer and with less webbing.

Description of holotype.—An adult female having a standard length of 57.5 mm, a tail length of 42.9 mm, a head width of 8.5 mm, and a head length of 13.6 mm. The legs are moderately long with 1.0 intercostal folds between adpressed limbs. Hand width is 3.7 mm and foot width is 4.8 mm. Axilla–groin length is 30.0 mm. Digits on the hands and feet bear considerable webbing except for the longest digit. The tips of the toes are narrow and rounded to almost triangular. Eye–nostril length is 2.50 mm, eye length is 2.75 mm, interocular distance is 5.20 mm, and internarial distance is 2.80 mm. There are 46 combined maxillary and premaxillary teeth. There are 23 vomerine teeth (11/12) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening; the vomerine teeth are arrayed in several rows forming a patch. The vent is folded and well pigmented.

Variation and color pattern.—Females attain a larger size than males. Several females exceed 50 mm SL, with the largest being the holotype at 57.5, whereas the largest male is 43.6 mm SL. The tail length/SL ratio is 0.69–0.80, the head length/SL ratio is 0.24–0.28, and the head width/SL ratio is 0.15–0.17. The number of vomerine teeth varies from 19 to 41 (mean = 26.7; 9–20 per side); in many individuals the vomerine teeth are arrayed in a patch or in several rows. The number of premaxillary plus maxillary teeth are 40–70 (mean = 56.2), and adpressed limbs are separated by 0–1.5 (mean = 0.68) intercostal folds. Males have longer limbs than do

Fig. 17. *Bolitoglossa cuchumatana*. (Upper) UTA A-51439, adult male, 33.4 mm SL; Uspantán, just N Aldea Caracol, 2140 m, El Quiché, Guatemala. (Lower) UTA A-51440, adult female, 39.9 mm SL; Uspantán, El Chimel, 2050 m, El Quiché, Guatemala.

females; intercostal folds between adpressed limbs average 0.3 for males and 1.0 for females.

In the holotype (UTA A-38661) the dorsum of the head and body are dark brown; irregular tan mottling extends along the dorsolateral region, with smaller flecks and mottling on the dorsum (Fig. 18, middle); the flanks are dark brown with whitish stipples that are sometimes clumped; the dorsal surfaces of the limbs are dark brown with fine tan mottling, especially on proximal segments of limbs, the distal long segments with less tan mottling, but with numerous pale stipples; the venter of body and tail is paler than the dorsum; the lateral surface of the tail is blackish brown, but the dorsum of the tail is heavily mottled with tan, forming almost continuous but irregular pale marking.

In UTA A-24470 the dorsum of the head and body, as well as the flanks, are mostly grayish black except for a rust-colored spot in the scapular region and a few tiny rust-colored specks on the back; the dorsum of the tail is marked with abundant rust mottling, especially just behind the level of the vent.

Many individuals are dark brown to almost black and have dorsolateral markings varying from discontinuous spotting or mottling to continuous stripes (Fig. 18). The dorsal surface

Fig. 18. *Bolitoglossa la.* (Upper) UTA A-33636, adult female paratype, 49.9 mm SL. (Middle) UTA A-38661, adult female holotype, 57.5 mm SL. (Lower) UTA A-38663, adult female paratype, 47.1 mm SL. All from 3.0 km SSE Chichicastenango, valley between Paxot and Camanibal, 2100 m, El Quiché, Guatemala.

between the dorsolateral stripes varies from dark brown, setting off the dorsolateral stripes, or may be the same color as the stripes, forming a broad dorsal band that is set off from the dark coloration of the flanks. The pale dorsum may be rather uniformly colored, have irregular dark markings, or be marked by irregular paravertebral stripes; a dark blotch may be present extending from the top of the head onto the neck.

Etymology.—The specific epithet is taken the name of a

highland town in Guatemala, Chichicastenango, historically famous for being a major trade center long before the Spanish conquest. The name of this town is derived from *chichicaste*, a type of large leaved nettle with purple flowers (possibly of the genus *Urera*), and tenango, meaning "place of" presumably from an indigenous Nahuatl dialect brought to Guatemala by early Spanish explorers. The term *la* is the K'iche' translation for *chichicaste* (Christenson, 2010).

Distribution, habits, and habitat.—This species is known from the northern edge of the Guatemalan Plateau and the extreme western portion of the Sierra de Chuacús. The two localities are both drained by the upper tributaries of the Río Chixoy and are separated from each other by less than 20 km airline. The elevational range is 2100–2390 m in pine-oak forest. The species is known from near the boundaries of two adjacent faunal regions, the Chimaltenangan and the Chuacús Subareas, as delimited by Campbell & Vannini (1989). *Bolitoglossa rostrata* from the Guatemalan Plateau and an undescribed closely related species from the Sierra de los Cuchumatanes are superficially similar but occur at elevations >2700 m, significantly higher than *B. la*.

In the vicinity of Chichicastenango, *Bolitoglossa la* has been found most frequently in bromeliads up to heights of 6–7 m above the ground. A small series of specimens taken near Santa Rosa Chucuyub were encountered in or beneath rotting logs following rainy periods.

A widespread series of populations of salamanders, occurring across much of the upper reaches of the Guatemalan Plateau, the Pacific Versant (which is continuous with the Guatemalan Plateau), and the Sierra de los Cuchumatantes previously have been allocated to *Bolitoglossa rostrata* (Wake & Lynch, 1976), who also recorded the species from Cerro Zontehuitz on the Meseta Central Of Chiapas. These salamanders appear to represent several species. Brocchi (1883) provided as the type-locality of *B. rostrata* "les hauteurs de Tonicapam [= Totonicapán, Department of Totonicapán] (Guatemala occidental)". Specimens at hand of *B. rostrata* from this region indicate that they are distinct from material from the Sierra de los Cuchumatanes in having a different color pattern of dorsolateral stripes, paler venters in which the melanophores are reduced to minute dark specks, and in having much larger hands and feet. We have identified several populations of salamanders in the Sierra de los Cuchumatanes allied to *B. rostrata* that are differentiated from each other and do provide sufficient evidence to warrant specific recognition. They are differentiated from *B. rostrata* of the Guatemalan Plateau and suggest a succession of vicariance events having progressed from south to north within the Sierra de los Cuchumatanes (see Discussion).

The Guatemalan Plateau is recognized as being distinct faunistically from the Sierra de los Cuchumatanes (Campbell & Vannini, 1989), although they share some amphibian species, especially those occurring at moderate elevations. These two highland regions are separated by the entrenchments of the Río Grijalva and Río Motagua drainages. The highest elevation at the divide between these rivers systems is about 1900 m. The terrain is relatively flat and dry but includes scattered pines. Our collections include a number of individuals from various geographically and ecologically distinct localities of moderate-sized species of *Bolitoglossa*, often with copper or brassy colored dorsal stripes or broad dorsal bands. These appear distinct from both *B. rostrata* from the Guatemalan Plateau and *B. cuchumatana* from the Sierra de los Cuchumatanes. The first of these may be known as:

Bolitoglossa nussbaumi new species

Holotype.—UTA A-59197 (original field number JAC 19792) an adult female from 7.2 km SE Todos Santos, Huehuetenango, Guatemala, 3259 m (15.484167° N, 90.552222° W), collected by J. R. Mendelson III, E. N. Smith, J. A. Campbell on7 June 1998.

Paratypes.—UTA A-60004–06 (JAC 19793–95), data same as for holotype.

Diagnosis.—A moderately sized (about 50 mm SL) species of *Bolitoglossa* often with a dark brown dorsum, with or without darker brown paravertebral stripes, and having distinct toes, free of webbing for most of their length. Members of the *B. mexicana* group (subgenus *Bolitoglossa*) are larger, and have relatively longer tails and usually more extensive interdigital webbing. Members of the *B. rufescens* group (subgenus *Nanotriton*) are smaller, short-tailed species with hands that are pad-like. Species in the *B. veracrucis* group (subgenus *Mayamandra*) have distinctive, broad hands and feet that are fully webbed and a prominent triangular third toe extending from the center of the webbed foot.

Bolitoglossa nussbaumi is distinguished from *B. cuchumatana* by having feet that are not as fully webbed, relatively shorter legs in females (2.0–2.5 intercostal folds between adpressed limbs vs. 1.0) and larger hands and feet; and from *B. la* by having more intercostal folds between adpressed limbs (2.0–2.5 vs. 0.0–0.5). It is distinguished from *B. engelhardti* by a shorter tail and less webbing on the feet. All members of the *B. helmrichi* group have more webbed feet. *Bolitoglossa morio* is a larger species with a dark gray to blackish ground color, paler markings on the flanks, and pale stippling over much of the body. *Bolitoglossa pacaya* is a smaller species and has fewer intercostal folds between adpressed limbs (mean = 1.5 vs. 2.25) and smaller hands and feet than *B. nussbaumi*. *Bolitoglossa rostrata* is a larger, more robust species, with shorter limbs.

Description of holotype.—An adult female measuring 53.4 mm SL, 35.0 mm TL (regenerated), 12.6 mm HL, 8.0 mm HW, 4.5 mm hand width, and 5.3 mm foot width; axilla–groin length 26.8 mm. The toes have webbing extending to the base of the terminal segments. The tips of the toes are broad and blunt. Eye–nostril length is 2.10 mm, eye length

Fig. 19. *Bolitoglossa nussbaumi*. UTA A-59197, dorsal and ventral aspects of adult female holotype, 53.4 mm SL; 7.2 km SE Todos Santos, 3259 m, Huehuetenango, Guatemala.

is 2.50 mm, interocular distance is 4.60 mm, and internarial distance is 3.00 mm. There are 28 vomerine teeth and 53 maxillary-premaxillary teeth. There are 2.5 intercostal folds between adpressed limbs. A broad bronze dorsal band extends from posterior of the eyes onto the base of the tail (Fig. 19). To either side of the dorsal midline is a conspicuous narrow dark brown stripe, extending from a dark brown head cap that terminates in a triangular point posteriorly onto the proximal third of the tail. The broad dorsal band is nearly straight edged along the dorsolateral surface of the body; clearly demarcating the dark brown sides of the body. The dark flanks grade ventrolaterally into the immaculate yellow ventral coloration. The dorsal surfaces of the limbs are also bronze, with a slight suffusion of black. The chin and venter of the tail are also yellow, slightly darker than the belly. The toes are distinct with only the first toe fully webbed; well-developed subterminal pads are present. The skin secretion turned yellow in formalin.

Variation.—An adult female paratype (UTA A-60004) is 50.5 mm SL; the tail is 45.0 mm (0.89 of SL), the head length is 0.24 SL, the head width is 0.16 SL, hand width is 4.4 mm, and foot width is 5.9 mm. There are 22 vomerine teeth and 67 maxillary-premaxillary teeth. There are 2.0 intercostal folds between adpressed limbs. This specimen has a broad dorsal band that in preservative is orange-tan and is paler than in the holotype. The dorsal coloration of the body extends to the tip of the tail. There are no paravertebral dark stripes as in the holotype. The dorsum of the head is dark brown from the snout to the occipital region. The dorsal surfaces of the limbs are orange with some dark suffusion on the distal long segments. The flanks are dark brown and this coloration extends to behind the eye and loreal region, as well through the length of the tail. The throat, body, and tail are immaculate pale yellow. Two of the paratypes are juveniles (UTA A-60005–06). Coloration of these individuals is similar to that of the paratype, however the broad dorsal band is bronze and bordered laterally by narrow pale stripes, conspicuous in the smaller specimen (25 mm SL), less so in a slightly larger individual (33 mm SL).

Etymology.—The specific epithet is a patronym for Ronald A. Nussbaum, the leading authority on caecilians, who joined us on several trips to Guatemala and was tireless in his pursuit of salamanders.

Distribution, habits, and habitat.—*Bolitoglossa nussbaumi* is almost certainly restricted to the Cuchumatan Subarea (Campbell & Vannini, 1989). It is known only from the

type-locality. Individuals of the type-series were collected from within and beneath rotted wood in a wooded ravine of a relatively dry forest containing pines, scattered oaks, laurels, and abundant brushy vegetation along open edges. Other species encountered at this locality were *Sceloporus smaragdinus*, *Mesaspis moreletii* and *Thamnophis fulvus*.

Bolitoglossa centenorum new species

Holotype.—UTA A-58538, an adult female from Cerro Bobic, SSE San Mateo Ixtatán, Huehuetenango, Guatemala, 3250 m (15.815000° N, 91.478000° W), collected by M.E. Acevedo on 20 August 1998.

Paratype.—UTA A-58539, an adult male from near San Mateo Ixtatán, Cerro Bobic, Huehuetenango, Guatemala, 3250 m, collected by M.E. Acevedo on 20 August 1998; UTA A-58541–49, data as for paratypes, but without precise elevational data.

Diagnosis.—A moderately sized, high elevation, member of the genus with a dark brown dorsum bordered on either side by a distinctive, conspicuous narrow yellow dorsolateral stripe extending from behind the eye to a point just posterior to the insertion of the hind limb. The toes are distinct, free of webbing for most of their length. Members of the *Bolitoglossa mexicana* group (subgenus *Bolitoglossa*) are larger, and have relatively longer tails and usually more extensive interdigital webbing. Members of the *B. rufescens* group (subgenus *Nanotriton*) are smaller, short-tailed species with hands that are pad-like. Species in the *B. veracrucis* group (subgenus *Mayamandra*) have distinctive, broad hands and feet that are fully webbed and a prominent triangular third toe extending from the center of the webbed foot.

Bolitoglossa centenorum is distinguished from *B. cuchumatana* by being larger, having feet that are not as fully webbed, relatively shorter legs (1.5–2.0 intercostal folds between adpressed limbs vs. 0.5–1.0), more maxillary-premaxillary teeth, and larger hands and feet; and from *B. la* by its slightly longer tail, more maxillary plus premaxillary teeth, and relatively more intercostal folds between adpressed limbs in females (mean = 1.75 vs. 1.0). It is distinguished from *B. engelhardti* by a shorter tail and less webbing on the feet. All members of the *B. helmrichi* group have more webbed feet. *Bolitoglossa morio* is a larger species with a dark gray to blackish ground color and paler markings on the flanks and pale stippling over much of the body. *Bolitoglossa pacaya* is a smaller species and has a shorter tail, and more intercostal folds between adpressed limbs in females (mean = 3.0 vs. 1.75). *Bolitoglossa nussbaumi* has fewer maxillary-premaxillary teeth and lacks the dark brown dorsum bordered by conspicuous narrow yellow stripes. *Bolitoglossa rostrata* is a larger, more robust species with shorter limbs.

Description of holotype.—An adult female measuring 56.4 mm SL, 41.2 mm TL , 12.5 mm HL, 7.2 mm HW, 4.4 mm hand width, and 5.2 mm foot width; axilla–groin length 25.0 mm. The toes have webbing extending to the base of the terminal segments. The tips of the toes are broad and blunt. Eye–nostril length is 2.60 mm, eye length is 2.15 mm, interocular distance is 4.60 mm, and internarial distance is 3.10 mm. There are 31 vomerine teeth and 74 maxillary-premaxillary teeth. There are 2.0 intercostal folds between adpressed limbs. The dorsum from the top of the head to the tail is dark brown; the vertebral area is slightly paler but not as to form a conspicuous stripe (Fig. 20). The dorsum is bordered on each side by a narrow, conspicuous, yellow stripe that extends from behind the eye to a level just posterior to and above the insertion of the hind limb. The flanks below the dorsolateral stripe are dark brown and this color grades into the venter, which is moderately darkly pigmented. The dorsal surfaces of the limbs are also dark brown.

Variation.—One paratype (UTAA-58539) is an adult female having 48.8 mm SL, 45.6 mm tail length, 24 vomerine teeth (12/12), 82 maxillary-premaxillary teeth, and 1.5 intercostal folds between adpressed limbs. This individual closely resembles the holotype in color pattern. Other paratypes are similar, but somewhat formalin darkened. The average number of vomerine teeth is 25, maxillary-premaxillary teeth 69.8, and intercostal grooves between adpressed limbs 1.0–1.5 in males and 2.0 in females.

Etymology.—The specific epithet is a patronym in honor of the Centeno family of Guatemala. Members of this family have done much to further education and appreciation of nature. Ing. Héctor A. Centeno, Rector *emeritus* (1992–2001) of the Universidad del Valle de Guatemala, has served in many positions, including Vice-presidential Advisor for Science and Technology and founder of the environmental and conservation organization Fundación Defensores de la Naturaleza. His son, Lic. Marco Vinicio Centeno, is founder of the Sociedad Guatemalteca de Ornitología, is a member of the Mesa Nacional de Aviturismo, and teaches biology at the Universidad del Valle de Guatemala. The Latin suffix *-orum* means "belonging to."

Distribution, habits, and habitat.—*Bolitoglossa centenorum* is another species of salamander that may be added to the growing list for the Cuchumatan Subarea (Campbell & Vannini, 1989). It is known only from the type-locality. Individuals of the type-series were collected from beneath rotting logs.

Bolitoglossa ninadormida new species

Holotype.—UTA A-58562 (original field number MEA 1175), an adult female from near Todos Santos Cuchumatán, Carretera between Chiabal and El Rancho, Huehuetenango, Guatemala, ca. 3200 m (15.469815° N, 91.543401° W), collected by M. E. Acevedo on 5 August 1997.

Paratype.—UTA A-58564, adult male, data same as for holotype.

Referred Specimens.—UTA A-29657–63, 22.8 km (by road) SW San Juan Ixcoy, 3180 m, collected by J.A. Campbell *et al.* on 24 Jule 1989; UTA A-30159, 15.9 km (by road) SW

Fig. 20. *Bolitoglossa centenorum*. UTA A-58538, dorsal and ventral aspects of adult female holotype, 56.4 mm SL; from near San Mateo Ixtatán, Cerro Bobic, 3250 m, Huehuetenango, Guatemala.

San Juan Ixcoy, 3220 m, collected by J.A. Campbell *et al.* on 29 July 1989; UTA A-32890, 41.5 km (by road) SSW San Juan Ixcoy, 3020 m, collected by J. A. Campbell *et al.* on 24 July 1989.

Diagnosis.—A moderately sized, high elevation, member of the genus that may have a reddish dorsum mottled with dark brown, a brown dorsum slightly paler in the dorsolateral region, or (small specimens) a brown dorsum with conspicuous relatively broad dorsolateral stripes. The toes are distinct, free of webbing for most of their length. Members of the *Bolitoglossa mexicana* group (subgenus *Bolitoglossa*) are larger, and have relatively longer tails and usually more extensive interdigital webbing. Members of the *B. rufescens* group (subgenus *Nanotriton* are smaller, short-tailed species with hands that are pad-like. Species in the *B. veracrucis* group (subgenus *Mayamandra*) have distinctive, broad hands and feet that are fully webbed and a prominent triangular third toe extending from the center of the webbed foot.

Bolitoglossa ninadormida is distinguished from *B. cuchumatana* by being a larger species and in having feet that are not as fully webbed; and from *B. la* by having less webbing and its color pattern. It is distinguished from *Bolitoglossa engelhardti* by its distinctive dorsal coloration. All members of the *B. helmrichi* group have more webbed feet. *Bolitoglossa morio* is a larger species with a dark gray to blackish ground color and paler markings on the flanks and pale stippling over much of the body. *Bolitoglossa pacaya* is a smaller species with a relatively shorter tail and females have more intercostal folds between adpressed limbs (1.5–3.0 vs. 1.0–1.5) and smaller hands and feet than does *B. ninadormida*. *Bolitoglossa nussbaumi* and *B. centenorum* have longer limbs and are more robust salamanders. *Bolitoglossa rostrata* is a larger, more robust species with shorter limbs.

Description of holotype.—An adult female measuring 57.1 mm SL, 48.8 mm TL, 13.6 mm HL, 8.5 mm HW, 4.3 mm hand width, and 5.6 mm foot width; axilla–groin length 27.9 mm. The toes have relatively scant webbing not extending, or just barely so, to the base of the terminal phalnges. The tips of the toes are broad and blunt. Eye–nostril length is 2.85 mm, eye length is 2.25 mm, interocular distance is 4.80 mm, and internarial distance is 2.90 mm. There are 29 vomerine teeth (16/13) and 74 maxillary-premaxillary teeth. There are 1.5 intercostal folds between adpressed limbs. In life the dorsum of the body and tail are orange-brown with darker brown to black mottling; the top of the head was slightly darker than then the body (Fig. 21). The dorsal surfaces of the limbs are orange-brown with sparse fine brown mottling. The flanks were darker than the dorsum with some black pigment restricted to the upper lateral region; the lower flanks in the ventrolateral region are mostly purple. A dark brown line extended through

Fig. 21. *Bolitoglossa ninadormida*. (Upper) UTA A-58562, adult female holotype, 57.1 mm SL; near Todos Santos Cuchumatán, Carretera entre Chiabal and El Rancho, ca. 3200 m, Huehuetenango, Guatemala. (Lower) UTA A-58564, adult male paratype, data same as for holotype.

the loreal and lower temporal regions. The dorsum of the tail was paler than the dorsum of the body, heavily marked with irregular dark brown. The throat and venter are relatively pale purple, softly suffused with brown pigment and slightly darker on the posterior of the body.

Variation.—The male paratype (UTA A-58564) is an adult with the following measurements: 41.8 mm SL, 37.4 mm TL, 10.9 mm HL, 6.5 mm HW, 3.5 hand width, and 4.5 foot width. There are 21 (9/12) vomerine, 50 maxillary-premaxillary teeth, and 1.0 intercostal fold between adpressed limbs. The mental gland is wider (2.6 mm) than long (1.8 mm).

In life, the dorsum of the male paratype was dark brownish purple with a few irregular yellowish streaks or spots on the back, these becoming more numerous on the tail. The flanks were slightly darker than the dorsum but not conspicuously so as in the female holotype. The dorsal surfaces of the limbs were brownish purple, but somewhat paler than the dorsum. The venter was pale purple. Most of the referred specimens are juveniles or subadults and have a brown middorsum and well defined pale dorsolateral stripes extending from the back of the eye onto the tail.

Etymology.—The specific epithet is the feminine gender for the Spanish *niño dormido*, meaning sleeping child, the widespread name applied to salamanders in Guatemala.

Distribution, habits, and habitat.—The holotype and paratype were collected in rotting trunks in a fir (*Abies*) and cypress (*Cupressus*) forest at 1600–1800 hr.

Bolitoglossa huehuetenanguensis new species

Holotype.—UTA A-51320 (original field number JAC 19170) an adult female from 14.0 km NW junction of San Mateo

Ixtatán–Barillas road to Nentón, Huehuetenango, Guatemala, at 2780 m elevation (15.891944° N, 91.564166° W), collected by J.A. Campbell and E.N. Smith on 10 November 1996.

Paratypes.— UTA A-51297–319, on road to Patalcal, 6.0 km (by road) NW intersection of Guatemala Hwy 9N near San Mateo Ixtatán, 2835 m, collected by by M. Sasa-Marin, E. N. Smith, J.R. Mendelson III and J. A. Campbell on 18 June 1996; UTA A-51321–23, 14.0 km NW junction of San Mateo Ixtatán–Barillas road to Nentón, Huehuetenango, Guatemala, at 2780 m elevation (15.891944° N, 91.564166° W), collected by E.N. Smith and J.A. Campbell on 10 November 1996; UTA A-51324–32, 5.6 km NW junction of San Mateo Ixtatán–Barillas road and road to Nentón, Huehuetenango, Guatemala, 2800 m (15.858611° N, 91.517222° W), collected by E.N. Smith and J.A. Campbell on 10 November 1996; UTA A-51333–54, 4.5 km NW junction of San Mateo Ixtatán–Barillas road and road to Nentón, Huehuetenango, Guatemala, 2713 m, collected by E.N. Smith and J.A. Campbell on 11 November 1996; UTA A-51355–60, 4.5 km NW junction of San Mateo Ixtatán–Barillas road and road to Nentón, 2450 m, collected by E.N. Smith and J.A. Campbell on 11 November 1996.

Diagnosis.—A moderate sized (38–56 mm SL), moderately high elevation (2450–2800 m), member of the genus often with copper or brassy colored dorsal stripes and distinct toes, free of webbing for most of their length. Members of the *B. mexicana* group (subgenus *Bolitoglossa*) are larger, and have relatively longer tails and usually more extensive interdigital webbing. Members of the *B. rufescens* group (subgenus *Nanotriton*) are smaller, short-tailed species with hands that are pad-like. Species in the *B. veracrucis* group (subgenus *Mayamandra*) have distinctive, broad hands and feet that are fully webbed and a prminent triangular third toe extending from the center of the webbed foot.

Bolitoglossa huehuetenanguensis is distinguished from *B. cuchumatana* by having feet that are not as fully webbed, relatively shorter legs in females (2.0–2.5 intercostal folds between adpressed limbs vs. 0.5–1.0) and larger hands and feet; and from *B. la* by a longer tail, more maxillary plus premaxillary teeth (mean = 63.9 vs. 55.8), and more intercostal folds between adpressed limbs in females (mean = 2.0–2.5 vs. 0.5–1.5). It is distinguished from *B. engelhardti*, which has a longer tail and color pattern of dorsolateral stripes. All members of the *B. helmrichi* group have more webbed feet. *Bolitoglossa morio* is a larger species with a dark gray to blackish ground color and paler markings on the flanks and pale stippling over much of the body. *Bolitoglossa pacaya* is a smaller species and has a shorter tail, fewer vomerine teeth, and smaller hands and feet than *B. huehuetenanguensis*. *Bolitoglossa rostrata* is a larger, more robust species with shorter limbs. *Bolitoglossa nussbaumi* has less sharply defined dorsolateral stripes, is larger, has a paler venter, and has about 2.25 costal folds (vs 1.5) between adpressed limbs. *Bolitoglossa centenorum* has wider dorsolateral stripes and is slightly larger. *Bolitoglossa ninadormida* often lacks well defined dorsolateral stripes and has proportionally larger hands and feet; stripes may be present in juveniles and subadults and are wider than in *B. huehuetenanguensis*.

Description of holotype.—An adult female measuring 56.0 mm SL, 43.6 mm TL, 13.6 mm HL, 9.4 mm HW, 4.8 mm hand width, and 6.2 mm foot width; axilla–groin length is 29.4 mm. The toes have webbing extending to the base of the terminal segments. The tips of the toes are broad and blunt. Eye–nostril length is 2.25 mm, eye length is 2.50 mm, interocular distance is 5.00 mm, and internarial distance is 2.90 mm. There are 30 vomerine teeth and 87 maxillary plus premaxillary teeth. There are 2.0 intercostal folds between adpressed limbs. The broad dorsal band extends from posterior of the eyes onto the tail (Fig. 22, upper). In life the stripe color was copper colored and nearly straight edged; the sides were black with only a slight infusion of paler color. The legs were copper but more heavily flecked with black. The ventral surfaces were pale with scattered melanophores; small light flecks were sparsely distributed becoming more common on the tail. The chin was pigmented like the body venter. The toes are distinct with only the first toe fully webbed; well-developed subterminal pads are present. The skin secretion turned yellow in formalin, a trait shared by *Bolitoglossa nussbaumi*, *B. centenorum*, *B. ninadormida*, *B rostrata*, and *B. helmrichi*.

Variation.—Seven adult males are 38.5 to 50.5 mm SL; seven adult females (including the holotype) are 43.9 to 56.0 mm SL. In adults, the tail is 0.67–0.94 of the standard length, the head length is 0.23–0.27 SL, the head width is 0.15–0.17 SL, average hand width is 4.01 mm, and average foot width is 5.23. There are 21–33 vomerine teeth in males and 27–31 in females; there are 49–74 maxillary-premaxillary teeth in males and 57–87 in females. There are 0 to 1.5 intercostal folds between adpressed limbs in males and 2.0 to 2.5 in females. Some individuals in the type series had straight-edged copper or brassy colored dorsal stripes in life (in preservative the metalic brassy color is lost), extending from in front of the eyes to, or very nearly to, the tip of the tail. Small pale blotches were abundant on the dorsum and coalesced with the dorsolateral coloration (Fig. 22). Lateral surfaces are dark and most lack pale blotches; a few individuals had a moderate amount of tiny metalic flecking. The limbs are sometimes paler than the sides with sparse pale flecks. The ventral surfaces are as in the type. Many released skin secretion when preserved and in each individual it turned yellow. In males the testis and vas deferens are pigmented or not; the mental gland is roundish, measuring slightly wider than long, the largest is 3.5 mm wide and 3.1 mm long.

Etymology.—The specific epithet is derived from Huehuetenango, the Guatemalan department encompassing the majority of the Sierra de los Cuchumatanes and the provenance of the type-series of this salamander and the Latin suffix *–ensis*, meaning place.

Distribution, habits, and habitat.—*Bolitoglossa huehue-*

Fig. 22. *Bolitoglossa huehuetenanguensis*. (Upper) UTA A-51320, adult female holotype, 56.8 mm SL. (Lower) UTA A-51321, adult male paratype, 42.2 mm SL. Both from 14.0 km NW junction of San Mateo Ixtatán–Barrillas road and road to Nentón, 2780 m, Huehuetenango, Guatemala.

tenanguensis probably is restricted to the Cuchumatan Subarea (Campbell & Vannini, 1989). Additional work is necessary to clarify the status of populations inhabiting the higher elevations of the Meseta Central of Chiapas, the higher Guatemalan volcanos, and certain areas with in the Sierra de los Cuchumatanes previously allocated to *B. rostrata*, but we suspect at least some of these populations may prove to be specifically distinct.

Individuals of the type-series of *Bolitoglossa huehuetenanguensis* were collected mostly from within and beneath rotted wood and a few were taken under rocks. Most of the trees had been felled in the area and salamanders were also encountered under the loose bark at the base of stumps. Other species collected nearby were *Abronia frosti*, *Incilius bocourti*, *Mesaspis moreletii*, and *Sceloporous taeniocnemis*.

Bolitoglossa huehuetenanguensis and *B. rostrata* appear to be closely related, with the former occurring in the Sierra de los Cuchumatanes and the latter restricted to the Guatemalan Plateau from the Tecpán Ridge westward across the Cumbre María Tecún to the Volcán Tajumulco region in San Marcos. *Bolitoglossa huehuetenanguensis* inhabits montane forests containing oaks, pines, and firs; on the Guatemalan Plateau, *B. rostrata* occurs in pine-cypress forest and pine-bunchgrass habitats.

In our collections from Guatemala we have a single specimen of a large dark salamander (black in preservative) that might be mistaken for *Bolitoglossa meliana*. The affinities of this salamander are unknown and may lie within the *B. franklini* group (*B. meliana*, *B. franklini*, *B. lincolni*; *B resplendens* was synonymized with *B. lincolni* by Wake & Lynch, 1988) or within the *B. morio* group. Morphologically it most closely resembles *B. lincolni* or *B. morio*. We propose it be known as:

Bolitoglossa psephena new species

Holotype.—UTA A-48204 (original number RFS 636), Finca Santa Elena, 5.2 km W of Health Center at Agua Escondida, Chimaltenango, Guatemala, 2500 m, (14.791487° N, 91.051613° W), collected by R.F. Savage on 11 August 1992.

Diagnosis.—A large (females to at least 70 mm SL), medium brown salamander resembling members of the *Bolitoglossa franklini* group in body proportions, overall size, and in having stout digits with slight webbing on the hands and feet. It is distinguished from *B. franklini* in having a snout that is rounded (rather than squared) in dorsal profile, in having a uniformly dark dorsum (rather than a pattern of silvery gray, greenish, or orange spots and blotches on a black background), in having more webbing on the hands and feet. *Bolitoglossa lincolni* is a large species that is most easily distinguished by its dramatic pattern of red and black. *Bolitoglossa meliana* is most similar to *B. psephena* in being mostly dark, but differs is having a distinctly squared snout in dorsal profile, having a more slender body, longer toes with less webbing, and truncate toe tips. In *B. psephena* the digits and toe pads are not nearly as broad as in *B. meliana* and the antebranchium and lower leg are considerably more robust than in either *B. meliana* or *B. franklini*. *Bolitoglossa meliana* is similar to *B. psephena* is having a uniformly dark dorsum, but attains a larger size (ca. 80 mm SL in females *fide* Wake & Lynch, 1982); it lacks webbing on the feet, has truncate toe tips, and longer limbs. *Bolitoglossa meliana* occurs in highland forest ranging from relatively dry pine-oak forest to cloud forest at elevations of 1550–2730 m.

Bolitoglossa morio is similar to *B. psephena* in many respects. Although large female *B. morio* may occasionally rival and even exceed *B. psephena* in SL, they are usually smaller, slightly more robust, and have a proportionately shorter tail. *Bolitoglossa psephena* is almost uniformly darkly pigmented on the dorsum, flanks, and venter, whereas in *B. morio* irregular white or pinkish spots or mottling are present on the flanks and venter. *Bolitoglossa morio* has slightly longer digits free of webbing, perhaps most easily seen in the length of the second toe.

Description of holotype.—An adult female measuring 71.5 mm SL, 52.3 mm TL, 15.8 mm HL, 11.0 mm HW, 3.5 intercostal folds between adpressed limbs, 6.1 mm hand width, and 7.6 mm foot width. The tips of toes broad and blunt with terminal phalanges free of webbing; the toes have webbing extending to the base of the terminal segments. There are 31 (14/17 vomerine teeth and 51 maxillary plus premaxillary teeth. Axilla–groin length is 38.5 mm. The toes have webbing extending to the base of the terminal segments. The tips of the toes are broad and blunt. Eye–nostril length is 2.25 mm, eye length is 2.50 mm, interocular distance is 5.00 mm, and internarial distance is 3.50 mm.

In preservative the type is uniformly dark gray; in life, based on the sole image we have available, the species appears to be mostly medium brown with a faint trace of paler brown mottling on the flanks (Fig. 23).

Etymology.—The specific epithet is derived from the Greek *psephena*, meaning dark or obscure, in allusion to the uniformly dark coloration of this species.

Distribution, habits, and habitat.—This species is known only from the highlands often referred to as the María Tecúm or the Tecún Umán Ridge, which occurs in the western half of the Chimaltenangan Subregion (Campbell & Vannini, 1898). The species occurs in montane wet forest that has abundant pines, cypress, firs, oaks, alders, and laurels. The type was taken at about 2500 m but the highest elevation attained in the area is the crest of the Tecún Umán Ridge at 3400 m. Relatively good patches of forest are still present and until recently the area was inhabited by the rare, highland Horned Guan (Anderle, 1967).

In Guatemalan and Chiapan transects *Bolitoglossa franklini* was restricted almost exclusively to cloud forest, just barely entering the upper montane rainforest zone on the Pacific versant (Wake *et al.*, 1980). *Bolitoglossa lincolni* inhabits drier oak-pine-cypress forest, but enters cloud forest at several localities. Both of these species occur at high elevations: *B. franklini* occurring at 1500 to 3000 m and *B. lincolni* ranging from about 2000 to 3000 m (Campbell & Vannini, 1989; Wake & Lynch, 1982; Wake *et al.*, 1980). Whereas *B. franklini* is restricted to Pacific slopes, *B. lincolni* has a much broader distribution, occurring on the Meseta Central of Chiapas, the Pacific slopes in western Guatemala, the Sierra de Cuilco, the western portion of the Guatemalan Plateau, and the Cuchumatanes. *Bolitoglossa franklini* and *B. lincolni* are largely allopatric except for one small region in extreme western Guatemala (Wake *et al.*, 1980)

Many Neotropical salamanders have remained rare in collections despite having been described decades ago. One such species is *Bolitoglossa stuarti* described over 40 years ago (Wake & Brame, 1969). We have accumulated a small series of this species, the details of which we present here.

Bolitoglossa stuarti Wake & Brame, 1969

Specimens Examined.—UTA A-58144, along road between La Trinidad and Finca San Francisco (Lago Bravo), 1660 m, Depto. Huehuetenango, Guatemala (15.861388° N,

Fig. 23. *Bolitoglossa psephena*. UTA A-48204, adult female holotype, 71.5 mm SL; Finca Santa Elena, 5.2 km W of Health Center at Agua Escondida, 2500 m, Chimaltenango, Guatemala.

19.610000° W), collected by J. A. Campbell on 3 June 1997; UTA A-58145–47, 1.6 km W Yalambojoch, 1580 m, Depto. Huehuetenango Guatemala (15.989722° N, 19.592500° W), collected by J. A. Campbell on 10 June 1997; UTA A-58566, 1.4 km W Yalambojoch at Río Salchilá, 1505 m, Depto. Huehuetenango, Guatemala (15.985277° N, 91.566944° W), collected by J. A. Campbell on 10 June 1997; UTA A-58684, 59736–37, Finca San Francisco, Aldea Yalambojoch, Nentón, 1270–1275 m (15.065833° N, 89.985555° W), Depto. Huehuetenango, Guatemala, collected by M. E. Acevedo on 25 May 1998.

Diagnosis.—This species may be distinguished from almost all other Guatemalan salamanders by having distinctively webbed hands and feet that are notably broad and have a triangular third toe projecting from the foot. *Bolitoglossa hartwegi* of the Meseta Central of Chiapas shares the character of a projecting third toe, but differs from *B. stuarti* in being smaller, having less extensive webbing on the hands and feet, and having a color pattern of dark brown mottled with reddish brown. A third species of salamander having a projecting third toe is described and diagnosed in a subsequent section herein. Members of the *B. mexicana* group (subgenus *Bolitoglossa*) also have extensive webbing on hands and feet, but are usually larger (> 60 mm SL), have relatively longer tails, and often have brightly colored conspicuous patterns of yellow or orange on a dark dorsal background. *Bolitoglossa rufescens* and *B. occidentalis* also have extensive webbing on small hands and feet that are pad-like, and are small salamanders (SL usually < 40 mm vs > 40 in *B. stuarti*). The hands and feet are fully webbed in *B. dofleini* but this robust, giant species (SL to at least 125 mm) has a gray to gray-brown dorsal coloration usually with irregular dark gray to black spots, especially in the dorsolateral region, and is unlikely to be confused on the basis of size alone. Members of the *Magnadigita* subgroup of *Bolitoglossa* are morphologically heterogeneous but none have hands and feet that are fully webbed and the digits are usually well defined with broad tips.

Variation and color pattern.—Females apparently attain a larger size than males. The two largest specimens in our sample are females, 56.8 and 57.0 mm in SL; the holotype is slightly larger at 60.0 mm SL (Wake & Brame, 1969). The largest male in our sample is 51.1 mm SL. The tail length/standard length ratio is 0.72–0.80 (0.59 in one specimen that may have a regenerated tail), the head length/standard length ratio is 0.17–0.18, and the head width/standard length ratio is 0.14–0.16. The number of vomerine teeth vary from 34 to 43 (mean = 38.5; 16–23 per side), the number of premaxillary-maxillary teeth are 72–84 (mean = 76.7), and adpressed limbs are separated by 2–2.5 intercostal folds. The axilla–groin length in the largest female is 30.6 mm. The toes have extensive webbing extending to the distal portion of the distal phalange. Eye–nostril length is 3.00 mm, eye length is 2.20 mm, interocular distance is 4.50 mm, and internarial distance is 2.50 mm.

Fig. 24. *Bolitoglossa stuarti*. (Upper) UTA A-58144, adult female, 57.0 mm SL; along road between La Trinidad and Finca San Francisco (Lago Bravo), 1660 m, Huehuetenango, Guatemala. (Lower) UTA A-58145, adult female, 56.8 mm SL; 1.6 km W Yalambojoch, 1580 m, Huehuetenango, Guatemala.

In life the dorsum of the body is mottled with ochreous and dark brown (Fig. 24). Elias (1984) reported the dorsal coloration to be unicolor. The top of the head, including the eyelids, and the dorsum may be uniformly dark brown or distinctly mottled. The tip of the snout from the level anterior to the eyes, and the subocular region to the jaw are dark brown in all specimens. The dorsum of the tail is paler than the body and from about half to the entire length of the tail is mostly pale ochreous brown with small irregular dark markings. The flanks and limbs are brownish mauve with white or pale pink stippling.

Distribution, habits, and habitat.—One individual was taken at night on vegetation along a dirt road. One individual was taken from a bromeliad about 2 m above the ground and another was found during the early afternoon in a bromeliad that had fallen to the forest floor. One salamander was collected at 20:30 hrs crawling on the surface of a leaf (Araceae) about 1 m above the surface of the ground near the edge of a small

stream. The holotype was reported from 950 m, however our series comes from somewhat higher with the elevational range of 1270–1660 m in cloud forest.

This species previously has been reported from only two localities, both along the Pan American Highway. In Chiapas it is known from 2.2 km S of La Trinitaria, and in Guatemala from 12.5 km SE of Ciudad Cuauhtémoc (Chiapas) in southern Huehuetenango. Our specimens were collected about 55–65 km from either locality in the northern portion of the Depto. of Huehuetenango. The region is covered by pine-oak and hardwood forests. The range of this species as presently known is moderate elevations of slopes drained by the upper tributaries of the Río Grijalva.

During the course of extensive surveys in the western Guatemalan highlands, we encountered salamanders at several widely scattered localities that appear related to *B. hartwegi* of Chiapas, but are distinctive and warrant separate recognition. For this species we propose:

Bolitoglossa xibalba new species

Holotype.—UTA A-34546 (original field number JAC 16397) an adult female from 7.0 km by road SW San Juan Ixcoy, Huehuetenango, Guatemala, at 2750 m elevation (15.570678° N, 91.441228° W), collected by J. A. Campbell, E. D. Brodie, Jr., and R. A Nussbaum on 29 July 1989.

Paratypes.—Guatemala, Huehuetenango, Sierra de los Cuchumatanes: UTA A-30164–65, 4.4 km by road SSE Santa Eulalia, 2460 m, collected by J. A. Campbell, E.D. Brodie, Jr., and R.A. Nussbaum on 24 July 1989; UTA A-30166, 15.9 km by road SW San Juan Ixcoy, 3220 m, collected by J. A. Campbell, E. D. Brodie, Jr., and R. A. Nussbaum on 28 July 1989; UTA A-34545, 34547, data same as holotype; UTA A-51428, near San Mateo Ixtatán, 2450 m, collected by E. N. Smith and J. A. Campbell on 11 November 1996. Guatemala, Huehuetenango, Montañas del Cuilco: UTA A-51424, near La Democracia, east side of crest between Ojo de Agua and Hoja Blanca, collected by M. E. Acevedo on 25 July 1996; UTA A-58688, crest between Ojo de Agua and Hoja Blanca, 2120–2150 m, collected by M. E. Acevedo on 11 September 1996. Guatemala, El Quiché, Sierra de los Cuchumatanes: UTA A-51451–55, near Uspantán, on road between El Chimel and San Pablo El Baldio (15.512000˚ N, 90.792000˚ W), 1980–2125 m, collected by E. N. Smith on 12–13 August 1996; UTA A-51456, 19.3 km N Uspantán, N of Aldea El Caracol, 2140 m (15431667° N, 90.806667° W), collected by J. A. Campbell on 17 November 1996.

Diagnosis.—This species may be distinguished from almost all other Guatemalan salamanders by having distinctively webbed hands and feet that are notably broad and have a triangular third toe projecting from the hand and foot; this projecting toe is particularly conspicuous on the hand, sometimes less so on the foot. There is slightly less webbing on the hands and feet of *B. xibalba* (as evinced by slightly deeper scalloping between digits) than in *B. hartwegi*. *Bolitoglossa stuarti* shares the character of a projecting third toe, but differs from *B. xibalba* in being larger (maximum SL ca. 60 mm vs. 51 mm). *Bolitoglossa stuarti* also has many more vomerine teeth and maxillary-premaxillary teeth and shorter limbs than *B. xibalba*. Based on meager available material, *Bolitoglossa hartwegi* may also achieve a slightly larger size than *B. xibalba* (SL ca. 54 mm vs. 51) and shorter limbs. The venter of *B. xibalba* is boldly patterned with dark brown mottling on a pale background, whereas in *B. hartwegi* and *B. stuarti* the venter is dark, either uniformly or sometimes with small white spots that may be visible only under magnification. Extensive webbing on the hands and feet is present in members of the *B. mexicana* group (subgenus *Bolitoglossa*), but these salamanders are usually larger (> 60 mm SL), have relatively longer tails, and usually have brightly colored conspicuous patters of yellow or orange on a dark dorsal background. Although *Bolitoglossa rufescens* and *B. occidentalis* have extensive webbing, the hands and feet are unusual in being pad-like, they generally lack maxillary teeth, and they reach only a small size (SL < 42 mm). *Bolitoglossa dofleini* is a robust, giant species (SL > 0.125 mm SL) with fully webbed hands and feet and an overall gray to brownish gray coloration. Members of the *Magnadigita* subgroup of *Bolitoglossa* are morphologically heterogeneous but none have hands and feet that are fully webbed and the digits are usually well defined with broad tips.

Description of holotype.—An adult female having a standard length of 46.3 mm, a tail length of 31.0 mm, a head width of 7.6 mm, and a head length of 12.2 mm. The legs are moderately long with 1 intercostal fold between adpressed limbs. Hand width is 4.2 mm and foot width is 5.0 mm; subdigital pads well developed. Axilla–groin length is 23.1 mm. The toes have extensive webbing extending to digit tips. The tips of the toes are rounded except for the longest toe which is pointed. Eye–nostril length is 2.00 mm, eye length is 1.80 mm, interocular distance is 4.65 mm, and internarial distance is 2.25 mm. There are 58 combined maxillary and premaxillary teeth. There are 29 vomerine teeth (15/14) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening of the nares. The vent is folded and lightly pigmented.

Variation and color pattern.—The largest specimen in our sample is a male, 50.9 mm in SL, and the next largest male is 43.1 mm SL, whereas six adult females have SLs of 44.1 to 49.7 mm SL. The tail length/standard length ratio is 0.65–0.86 (mean = 0.72), the head length/standard length ratio is 0.26–0.27 (mean = 0.27), and the head width/standard length ratio is 0.16–0.18 (mean = 0.17). The number of vomerine teeth varies from 18 to 42 (mean = 26.2; 9–21 per side), the number of premaxillary-maxillary teeth are 40–71 (mean = 56.8), and adpressed limbs are separated by 1–1.5 (mean = 0.4) intercostal folds. A small female, presumably a subadult (UTA A-30165, 32.4 mm SL), has 16 vomerine and 32 premaxillary

Fig. 25. *Bolitoglossa xibalba*. UTA A-51456, dorsal and ventral aspects of adult female paratype, 44.1 mm SL, 19.3 km N Uspantán, N of Aldea El Caracol, 2140 m, Quiché, Guatemala.

plus maxillary teeth.

This is a highly variable species with regard to color and pattern (Figs. 25–27). The type (Fig. 26), an adult female from near San Juan Ixcoy, has a brown dorsum of the head, body, and limbs with pale lavender stippling and a few irregular black spots that are more numerous on the dorsum of the tail. The pale stippling is somewhat heavier on the flanks and dorsal surfaces of the limbs. A black canthal line extends from the anterior of the snout to the anterior edge of the eye, continuing from behind the eye through the lower temporal region onto

Fig. 26. *Bolitoglossa xibalba*. UTA A-34546, adult female holotype, 46.3 mm SL, 7.0 km by road SW San Juan Ixcoy, 2750 m, Huehuetenango, Guatemala.

the neck and as a series of irregular spots above the insertion of the forelimb.

Another large female (UTA A-30166) from near San Mateo Ixtatán has a pale purplish gray dorsum (head, body, and limbs), with a darker tail. There is a blackish Y-shaped marking with branches extending from behind the eyes converging on the posterior of the head. There are a number of very small, irregular black markings on the dorsum of the body and larger black markings on the tail, especially the proximal portion. The flanks are distinctly paler than the dorsum, being pinkish white with series of tiny black spots along some of the costal grooves. A male (UTA A-34545), also from near San Juan Ixcoy, is similar in coloration to the previous specimen, but is somewhat darker with the proximal portion of the tail mostly orangish brown on top and heavy black pigment outlining the costal grooves.

The dorsum of the head, body, tail, and limbs of a large female from near San Mateo Ixtatán (UTA A-51424) is mostly dark reddish brown with tiny pale stipples. There is a large, irregular orange blotch on the top of the tail at the level of the caudal basal constriction. The flanks are paler than the dorsum. The throat and venter of the body are pale with heavy dark brown mottling and smudging. The venter of the tail is mostly white and the palmar and plantar surfaces are dark purplish brown.

Individuals from the eastern portion of the Sierra de los Cuchumatanes also show considerable variation, some of which is encompassed by specimens described above. One salamander (UTA A-51453) exhibits a clear demarcation between the coloration on the dorsum that is brown and the flanks that are black with fine pale stipples. The throat is mottled with dark brown on a pale background, the venter of the body and tail are mottled with black on a pale background, and the palmar and plantar surfaces are dark gray.

Etymology.—We name this species after Xibalba, the Underworld of Mayan mythology ruled by the Maya Death Gods. This is in homage to the many tens of thousands of Guatemalans who perished in the highland regions inhabited by this salamander during Guatemala's long and brutal civil war (predominantly fought 1960–1996), the longest war in Latin American history. For insights into a few details of this horrific war see Falla (1992).

Distribution, habits, and habitat.—Most specimens of *B. xibalba* were found under bark or moss at the base of rotting tree trunks. Individuals from the Montañas de Cuilco were taken between 19:30–21:00 hrs 50–120 cm above the surface of the ground on leaves along the side of a trail. The elevational range is 1980–2760 m in wet montane forest. The holotype is a female containing eggs.

A group of diminuitive, short-tailed salamanders is widespread in the lowlands and foothills of Middle America from about central Mexico southward to Honduras. These salamanders have small hands and feet that are pad-like and males have a prominent mental gland. Two species have usually been recognized. *Bolitoglossa rufescens* (Cope, 1869; Fig. 28, upper) occurs on the Atlantic versant from

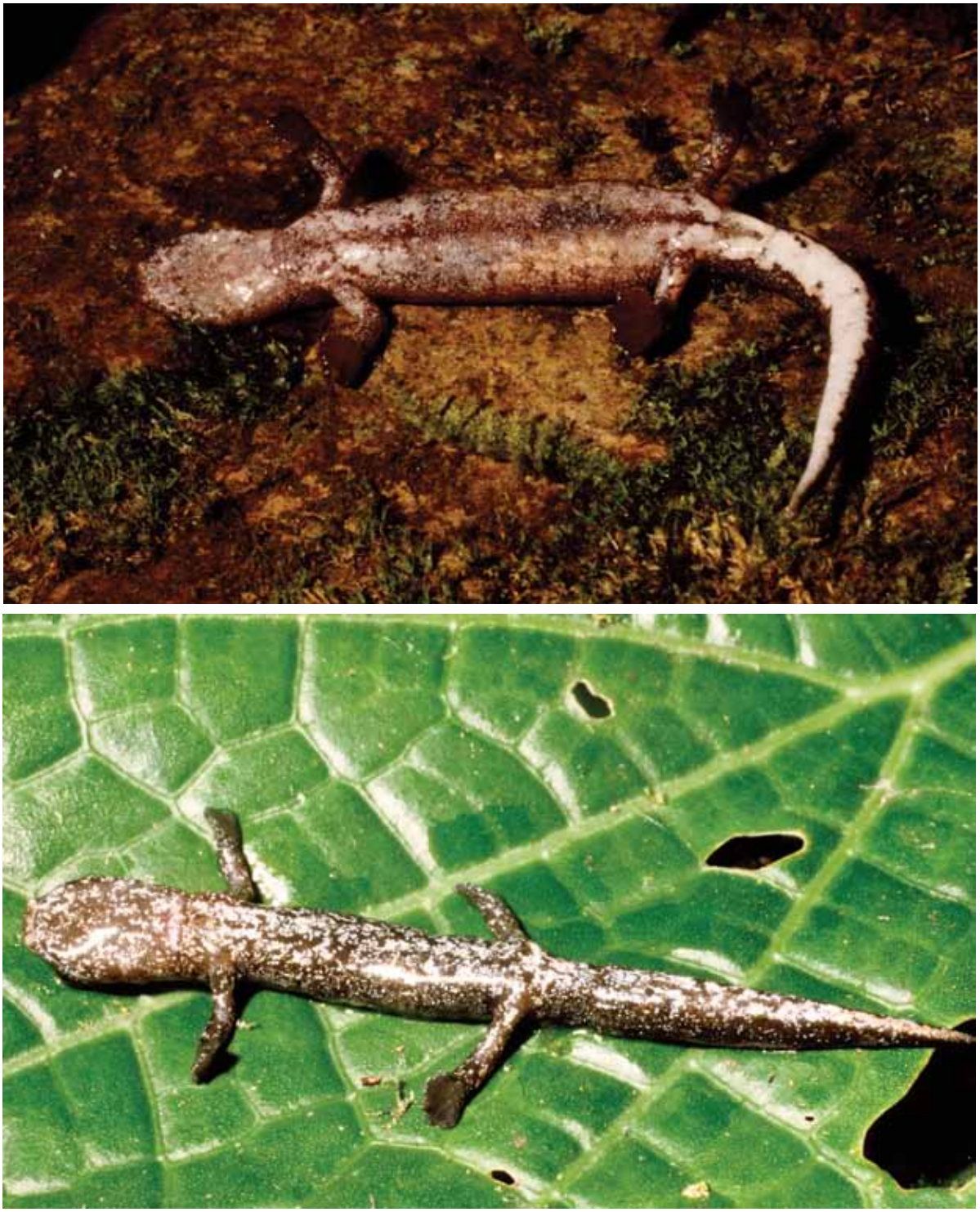

Fig. 27. *Bolitoglossa xibalba*. (Upper) UTA A-51424, adult female paratype, 48.6 mm SL; near La Democracia, east side of crest between Ojo de Agua and Hoja Blanca, Huehuetenango, Guatemala. (Lower) UTA A-51453, adult female paratype, 30.5 mm SL, Camino entre El Chimel y San Pablo El Baldio, Municipio Uspantán, 2085 m, Quiché, Guatemala.

eastern San Luis Potosí, Mexico southward, including some of the Yucatán Peninsula, Belize, and Guatemala to western Honduras. *Bolitoglossa occidentalis* Taylor (1941; Fig. 28, lower) occurs on the Pacific Versant from southeastern Oaxaca, Mexico, through southern Chiapas and Guatemala to west-central Honduras. The type-locality for *B. occidentalis* is La Esperanza [near Escuintla], Chiapas, Mexico. With regard to the *B. rufescens* group, Wake & Lynch (1976) stated that they

Fig. 28. (Upper) *Bolitoglossa rufescens*, MZFC, ca. 30 mm SL, Carretera Coconales–Zacatepec, 1625 m, Oaxaca, Mexico. (Middle) *B. incertae sedis*, UTA A-32922, adult female, 40.0 mm SL; 12.0 km WSW Puerto Santo Tomás, E slope Montañas del Mico, 786 m, Izabal, Guatemala. (Lower) *B. occidentalis*, UTA A-21476, adult male, 35.3 mm SL ; Finca El Faro, ca. 4.0 km N El Palmar, S slope Volcán Santa María, 875 m, Quezaltenango, Guatemala.

doubted whether recognition of even two taxa in the group was justified. Our analyses suggest that *B. rufescens* and *B. occidentalis* are valid species. Our sample of *B. rufescens* is from Guatemala and the type-locality for this species is "Orizava" [= Orizaba, Veracruz, Mexico] (Cope, 1869). A more detailed consideration of this taxon, as presently recognized, may reveal specific differences in Atlantic populations on either side of the Isthmus of Tehuantepec Depression, as well as distinctive populations in the isolated Sierra de Los Tuxtlas (Veracruz, Mexico) and the Montañas del Mico (Izabal, Gautemala; Fig. 28 middle). Additionally, our analyses reveal that the population in Guatemala southeast of the Río Motagua

Depression previously allocated to *B. rufescens* is specifically distinct and the sister-species to the *B. rufescens* group + the *B. hartwegi* group.

During our surveys of the mountains along the eastern border of Guatemala we obtained a series of these salamanders and, given their Atlantic slope provenance, at first presumed them to be *B. rufescens*. However, upon scrutiny they are easily distinguished from this species based on morphology and subsequent molecular analyses further confirmed their distinct identity. We propose they be known as:

Bolitoglossa nympha new species

Holotype.—UTA A-45328 (original field number JAC 18242) an adult female from E of San Miguelito, along tributary of Río Bobos, Sierra de Caral, Municipio de Morales, Izabal, Guatemala, between 510–550 m elevation (15.357485°N, 88.719444°W), collected by P. C. Ustach, D. P. Lawson, E. N. Smith, and J. A. Campbell on 29 July 1993.

Paratypes.—All from Sierra de Caral, Municipio de Morales, Izabal, Guatemala: UTA A-38651 on 21 June 1991, Aldea Mirador, ca. 275 m, E. N. Smith; UTA A-38652–53 on 25 June 1991, UTA A-45330–62 on 31 July 1993, UTA A-48218–23 on 10 June 1994, UTA A-48228–29 on 12–13 June 1994, UTA A-48231–40 on 13 June 1994, UTA A-48245, UTA A-48249–59 on 9 July 1994, UTA A-48655–57 on 2–3 July 1995, Aldea Negro Norte, Cerro Negro Norte, 1100–1150 m, collected by E N. Smith; UTA A-45322–27 on 9–29 July 1993, UTA A-45329 on 29 July 1993, UTA A-48214–15 on 8 June 1994, UTA A-48264 on 10 September 1993, San Miguelito, 445–600 m, collected by E. N. Smith and J. A. Campbell; UTA A-48216–17 on 10 June 1994, UTA A-48224–27 on 11 June 1994, UTA A-48230 on 13 June 1994, UTA A-48241–44 on 8 July 1994, UTA A-48260–63 on 10–12 July 1994, Aldea Negro Norte, Cerro Pozo de Agua, 1040–1165 m, collected by E. N. Smith; UTA A-48246–48 on 9 July 1994, La Firmeza–Cerro Pozo de Agua, 1050–1100 m, collected by E. N. Smith; UTA A-48662–63 on 3 January 1996, Finca La Firmeza, Camino a Aldea Negro Norte, 890–910 m, collected by E. N. Smith; UTA A-51398–402 on 16–18 Jul 1996, Camino Finca Quebradas–Cerro Pozo de Agua, 820–1060 m, on 16 July 1996, collected by E. N. Smith; UTA A-51403 on 24 September 1996, Carretera Quebradas–La Firmeza, 935 m (15.374722° N, 88.695555° W), collected by E. N. Smith; UTA A-58560 on 3 July 1995, Finca La Firmeza, 900 m, collected by E. N. Smith.

Diagnosis.—A small (adults 28–42 mm SL) member of the genus *Bolitoglossa* in the *B. rufescens* group (subgenus *Nanotriton*). In life the dorsum varies from tan to reddish brown, the flanks are pale to dark gray and may be sharply set off from or grade into the dorsal color, the venter varies from cream with scattered tiny melanophores to mostly dark, but not as dark as the flanks. This species is similar to *B. rufescens* and *B. occidentalis* in being diminutive, with a relatively short tail and in having small hands and feet that are fully webbed. *Bolitoglossa nympha* has distinctly shorter limbs (mean = 3.8 intercostal folds between adpressed limbs) than either *B. occidentalis* (mean = 1.6 folds) or *B. rufescens* (mean = 1.7 folds).

Members of the *B. mexicana* group (subgenus *Bolitoglossa*) are much larger and have a relatively long tail; members of the subgenus *Magnadigita* do not have fully webbed hands and feet; *B. dofleini* is a huge species with a relatively longer tail, shorter and more truncate snout, and a dull gray or brownish gray dorsal coloration that does not distinctly contrast with the flanks; species in the *B. veracrucis* group (subgenus *Mayamandra*) usually are larger than *B. nympha* and have broad and fully webbed hands and feet, with a distinctive triangular third toe extending from the center of the webbed foot. The third digit of the hand in *B. rufescens* distinctly protrudes and is sharply pointed. In *B. nympha* this digit protrudes less and is more rounded distally.

Given the large amount of variation in this group, we have found little to distinguish the various species of these diminutive salamanders, and have based our conclusions mostly on molecular evidence (presented below). In contrast to *Bolitoglossa occidentalis*, *B. rufescens* has been reported to lack maxillary teeth, and this character historically has been offered as the main feature distinguishing *B. rufescens* from *B. occidentalis* (Elias, 1984; Poglayen & Smith, 1958; Smith & Taylor, 1948; Stuart, 1963). Individuals we have examined of *B. nympha* almost invariably lack maxillary teeth. However, the presence or absence of maxillary teeth is apparently variable. Specimens of *B. occidentalis* we have examined from the Pacific versant of Guatemala also lack maxillary teeth.

Description of holotype.—An adult female having a standard length of 38.4 mm, a tail length of 28.4 mm, a head width of 6.0 mm, and a head length of 9.9 mm (Fig. 29, lower). The legs are short with 4 intercostal folds between adpressed limbs. Hand width is 2.5mm and foot width is 3.5 mm; subdigital pads well developed. The axilla–groin length is 20.0 mm. The toes have extensive webbing extending to digit tips, forming pad-like hands and feet. The tips of the toes are acutely rounded. Eye–nostril length is 1.75 mm, eye length is 2.00 mm, interocular distance is 3.75 mm, and internarial distance is 2.10 mm. There are no maxillary or premaxillary teeth. There are 12 vomerine teeth (6/6) extending from the midline forward to just posterior to the internal nares and then lateral to beyond the opening. The vent is folded and lightly pigmented.

Variation and color pattern.—Adult males and females are similar in size, averaging 39.2 mm SL. The tail length/standard length ratio is 0.70–0.86 in females and 0.75–0.95 in males. Head length/standard length is 0.21–0.28, and the head width/standard length ratio is 0.15–0.17. The number of vomerine teeth varies from 6 to 14 (mean = 11.2; 2–8 per side), maxillary teeth usually absent (one 39.5 mm SL female, 39.5

Fig. 29. *Bolitoglossa nympha*. (Upper) UTA A-45327, San Miguelito, 445–600 m, adult female, 38.2 mm SL. (Lower) UTA A-45328, adult female holotype, 38.4 SL; E of San Miguelito, along tributary of Río Bobos, between 510–550 m. Both from Sierra de Caral, Municipio de Morales, Izabal, Guatemala.

mm SL, had a single maxillary tooth), premaxillary teeth were present in all males (3–4, mean = 3.3) and one premaxillary tooth was present in 5 of 11 females. Adpressed limbs are separated by 3–4 (mean = 3.8) intercostal folds.

The dorsum varies from yellowish, tan, medium brown, and reddish brown and may be nearly immaculate or spotted or streaked with brown or black (Fig. 29). The flanks are dark brown to almost black, usually distinctly contrasting with the dorsum. The upper border of the flanks may form a straight edge or it may grade into the dorsal color or form a highly irregular edge. Except for the palmar and plantar surfaces, the limbs are colored similarly to the flanks. The venter is most often dark with closely spaced melanophores, but in some individuals the melanophores are relatively sparse and

Fig. 30. *Dendrotriton chujorum*. (Upper) UTA A-51391, adult female holotype, 27.6 mm SL. (Lower) UTA A-51392, adult male paratype, 31.6 mm SL. Both from 14.0 km (by road) on road to Nentón NW of the junction with the San Mateo Ixtatán to Barillas road, 2780 m, Huehuetenango, Guatemala.

scattered, such that the venter is pale. The flank color extends forward above the insertion of the forelimb onto the neck and side of the head below the canthus. Posteriorly, the flanks pattern extends over the insertion of the hind limb and extends for most of the length of the tail.

Etymology.—The specific epithet is taken from the Latin *nympha*, a maiden-spirit supposed to inhabit the woods.

Distribution, habits, and habitat.—Most specimens of *Bolitoglossa nympha* were found after dark sitting on leaves of low vegetation. The majority of individuals were taken less than a meter from the ground, but a few were encountered 1.6–2.0 m high. Nights following afternoon showers were especially productive in finding these salamanders, although they were also active during light night rains or mists. Although they might be found practically anywhere in the forest, they appeared to be more abundant in the humid environments presented by streamside vegetation. Most of our collecting efforts were in primary forest but we did find individuals in secondary vegetation, especially when banana trees were present. They were found in banana leaf axils, on banana leaves after dark, and beneath piles of roting banana plants. A few specimens were taken from within or under decaying logs within the forest.

Salamanders that appear to represent undescribed species have been collected from several localities in the Sierra de los Cuchumatanes in western Guatemala. The overall habitus of these salamanders including the long, slender body and tail, long legs, broad hands and feet, and long broad-tipped digits identify these salamanders as representatives of the genus *Dendrotriton*. These specimens were taken from bromeliads or climbing in vegetation, habits typical of other members of the genus. Both of the species we describe have been confused

Fig. 31. *Dendrotriton chujorum*, type-series including holotype and paratypes, from left to right UTA A-51391–51394.

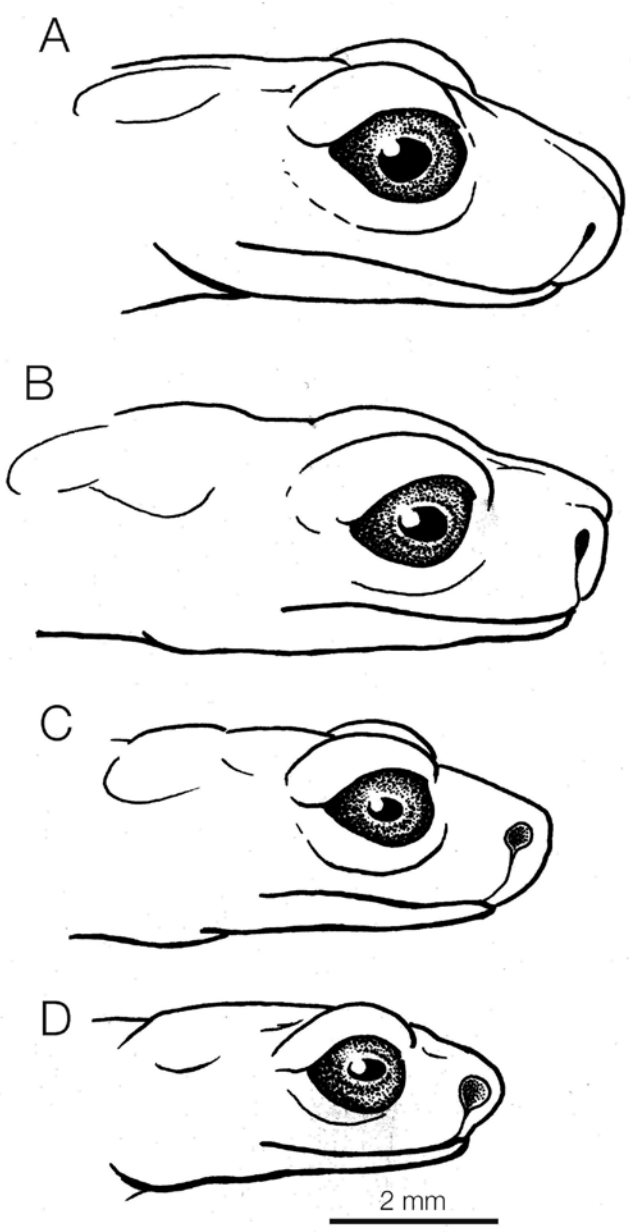

Fig. 32. *Dendrotriton chujorum*, type-series, showing variation in size of nostrils. A. UTA A-51392, standard length 31.6 mm; B. UTA A-51391, standard length 27.6 mm; C. UTA A-51393, standard length 23.8 mm; D. 51394, standard length 17.9 mm.

previously with *D. rabbi*, a species occurring in the Montañas de Cuilco (Elias, 1984).

A small series of salamanders were among the first collections to be made along the new road from Nentón to San Mateo Ixtatán, which amounts to little more than a narrow, muddy ribbon up precipitous slopes. This species will be known as:

Dendrotriton chujorum new species

Holotype.—UTA A-51391 (original field number JAC 19176), an adult female from 14.0 km by road on the road to Nentón NW of the junction with the San Mateo Ixtatán to Barillas road, Huehuetenango, Guatemala, at 2780 m elevation (15.892222° N, 91.564167° W) (Fig. 30). Collected 10 November 1996 by J. A. Campbell and E. N. Smith.

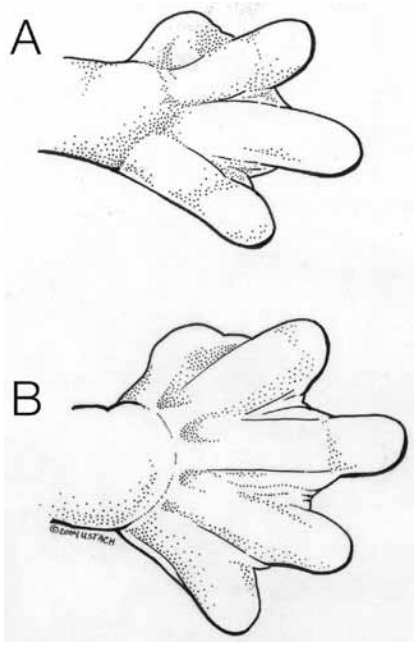

Fig. 33. *Dendrotriton chujorum*, adult female holotype, UTA A-51391, (A) hands and (B) feet.

Paratypes.—UTA A-51392–51393 (males) and 51394 (juvenile female), with same data as holotype (Fig. 31). MVZ 167804 (female) and 167805 (male) from 4 km NW San Mateo Ixtatán, Huehuetenango, 2799 m elevation, collected 1 February 1979 by E.J. Koford. MVZ 149189, 149374 –149380 (4 males, 2 females, 2 juveniles), Montaña Madrón, Huehuetenango-Barillas Rd. Km #314 (2 km S San Juan Ixcoy, Huehuetenango, 2792 m elevation, collected 25 June 1977 by H. B. Shaffer and P. Elias.

Referred Material.—MVZ 160422–160428, 160430–160435 (5 males and 8 juveniles) 3 km NNW San Mateo Ixtatán, Huehuetenango, 2652 m elevation, collected 23 June 1978 by E. J. Koford, and MVZ 160437 (male) from same locality at 2697 m, on 24 June 1978.

Diagnosis.—A small species of *Dendrotriton* (smaller in SL than any other species except *D. cuchumatanus* and *D. sanctibarbarus*) with wide head, short legs for the genus, and large feet. Nostril diameter is large in small individuals and adult females (0.4–0.5 mm) and small in adult males (0.15 mm) (Fig. 32). *Dendrotriton chujorum* is distinguished from *D. sanctibarbarus* by shorter legs, fewer maxillary-premaxillary teeth, and smaller nostrils; from *D. cuchumatanus* by nostrils that decrease in size with greater body size (in males), smaller nostrils in adult males, slightly shorter legs, and larger feet. *Dentrotriton chujorum* is distinguished from *D. rabbi* by smaller size, larger nostrils for adult females, wider head, and

Fig. 34. *Dendrotriton kekchiorum*, UTA A-51086, adult female holotype, dorsum and venter, 34.2 SL; from between El Chimel and San Pablo El Baldío, 2100 m, Quiché, Guatemala.

larger feet; from *D. bromeliacia* by smaller size, wider head, and larger feet; from *D. megarhinus* by smaller size, more vomerine teeth, and smaller nostrils; from *D. xolocalcae* by somewhat smaller size, larger nostrils in adult females, and larger feet; and from a species to follow by smaller size, shorter tail, fewer vomerine teeth, and larger nostrils in adult females.

Description of holotype.—An adult female having a standard length of 27.6 mm, a tail length of 30.3 mm, a head width of 4.8 mm, and a head length of 7.0 mm. The legs are short for the genus with 1.0 intercostal fold between adpressed limbs. Hand width is 3.6 and foot width is 4.4 mm. Axilla–groin length is 15.5 mm. The first digits of the hands and feet are short with webbing extending to the tip; webbing on the other toes is moderate (Fig. 33). The order of decreasing finger length is 3, 4, 2, 1, and 3, 4, 2, 5, 1 for the toes. Eye–nostril length is 1.4 mm, eye length is 2.0 mm, interocular distance is 2.5 mm, and internarial distance is 2.5 mm. The nostril diameter is 0.5 mm. There are 45 combined maxillary and premaxillary teeth. There are 15 vomerine teeth (8/7) curving forward from the midline to the midpoint of the internal nares. The vent is folded and lightly pigmented.

Variation.—The holotype and paratypes from the type-locality (Fig. 31) include an adult male (31.6 mm SL) with a well developed mental gland and with the premaxillary teeth enlarged and reduced in number. The maxillary plus premaxillary tooth number of this specimen is 33. A smaller male (23.8 mm SL) appears to be a male just reaching maturation. The testes are swollen and heavily pigmented, the mental gland is poorly developed, and the premaxillary teeth are somewhat enlarged and reduced in number. The last of

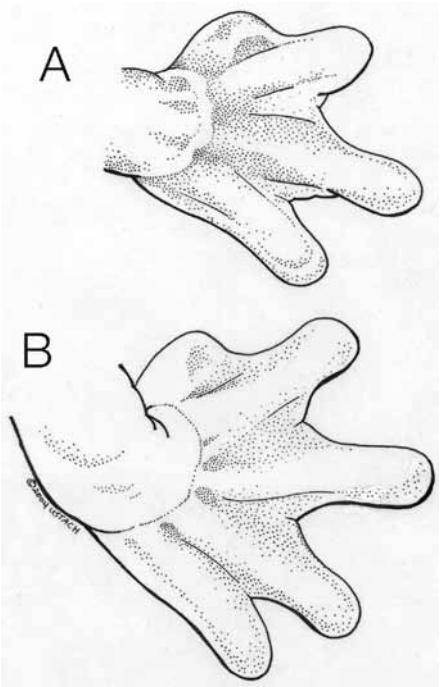

Fig. 35. *Dendrotriton kekchiorum*, adult female holotype, (A) hands and (B) feet.

the UTA paratypes is a small female (17.9 mm SL) in which the ovaries are starting to develop. Five male paratypes from the MVZ ranged from 23.1 to 26.7 mm SL and had nostril diameters of 0.33 to 0.52 mm; three females were 22.4 to 24.9 mm SL with nostril diameters of 0.49 to 0.52 mm, respectively; and two juvenile paratypes were 17.4 and 17.6 mm SL with nostril diameters of 0.49 and 0.46 mm, respectively. This species appears to mature at a smaller size than reported for other *Dendrotriton*. The nostrils tend to be relatively large on the holotype, female paratypes, and juveniles but very small on large adult males. Nostril diameter increases with body size in *D. megarhinus*, *D. bromeliacia*, and *D. cuchumatanus*, but it decreases with body size in *D. rabbi* and *D. xolocalcae* (Lynch and Wake, 1975, 1978). The condition of the nostrils was not indicated for *D. sanctibarbarus* by McCranie and Wilson (1996) or Wake (1998). In *D. chujorum* it appears as if the nostril remains large in adult females and decreases in adult males.

Color pattern.—In life, the holotype (UTA A-51391) had a mostly rusty red dorsum, including the head, body, and tail; a distinctive, narrow pale interorbital bar; some black mottling encroaching in the suprascapular and pelvic regions; dorsum of tail with scattered, irregular dark brown to black mottling; sides of body and tail with a mosaic of rusty and black mottling, heavily suffused with white stippling that becomes heavier ventrolaterally; upper surfaces of limbs mostly rusty red with scant dark brown mottling; upper surfaces of hands and feet mostly brown; undersurfaces of limbs mostly gray, palmar and plantar surfaces darker gray; venter of throat pale

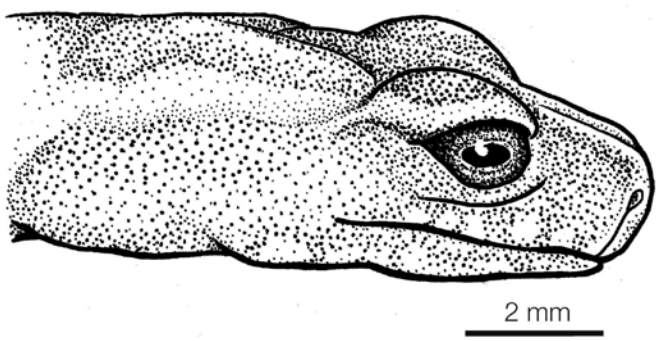

Fig. 36. *Dendrotriton kekchiorum*, adult female holotype, nostril

gray; venter from gular fold onto tail dark gray brown, set off from ventrolateral coloration by an irregular line formed by concentration of white stipples; iris bronze with black reticulations. The dorsum of the head and body of a paratype (UTA A-51392) was tannish with dark brown mottling; the dorsum of the tail was rusty red; the sides of the body were dark brown and set off from the dorsum by a yellow line that extended along a glandular ridge; the upper surfaces of the limbs were mottled with yellow and pale brown; the ventral surfaces of the limbs was pinkish yellow; the distal portion of the digits, but not the palmar and plantar surfaces, are dark brown; the chin was smoky gray, becoming yellow on the throat; the venter of the body and tail was purplish gray; the ventral coloration of the neck and body was outlined on either side by heavy white stippling which extended onto the venter of the tail.

In preservative (alcohol after formalin), in UTA A-51392 the dorsum of head and body with irregular dark brown mottling, laterally body cream with irregular dark brown blotches, and venter of throat, body, and tail mostly pale with tiny black stippling; in UTA A-51394 the dorsum pale cream grading to dark brown on flanks and even darker on venter; in UTA A-51391 the dorsum is medium brown; pale glandular ridge extending from axilla to groin may be yellow (UTA A-51392) or colored similarly to lateral or ventral coloration (UTA A-51391, 51393, 51394); interorbital bar inconspicuous (UTA A-51392) to prominent (UTA A-51391, 51393, 51394).

Etymology.—The specific epithet is derived from the Chuj, an ethnic and linguistic group of Mayans inhabiting the region around the type-locality, and the Latin suffix *-orum*, meaning "belonging to."

Distribution, habits, and habitat.—This species occurs in the northern portion of the Sierra de los Cuchumatanes. The slopes from where it was collected are drained by the upper tributaries of the Río Grijalva and are covered by small remnants of a mostly hardwood forest that is conspicuously drier than the forest at higher elevations or on opposing slopes of this range. All specimens were taken from bromeliads 3–10 m above the ground.

A new species of salamander was taken in the mountains

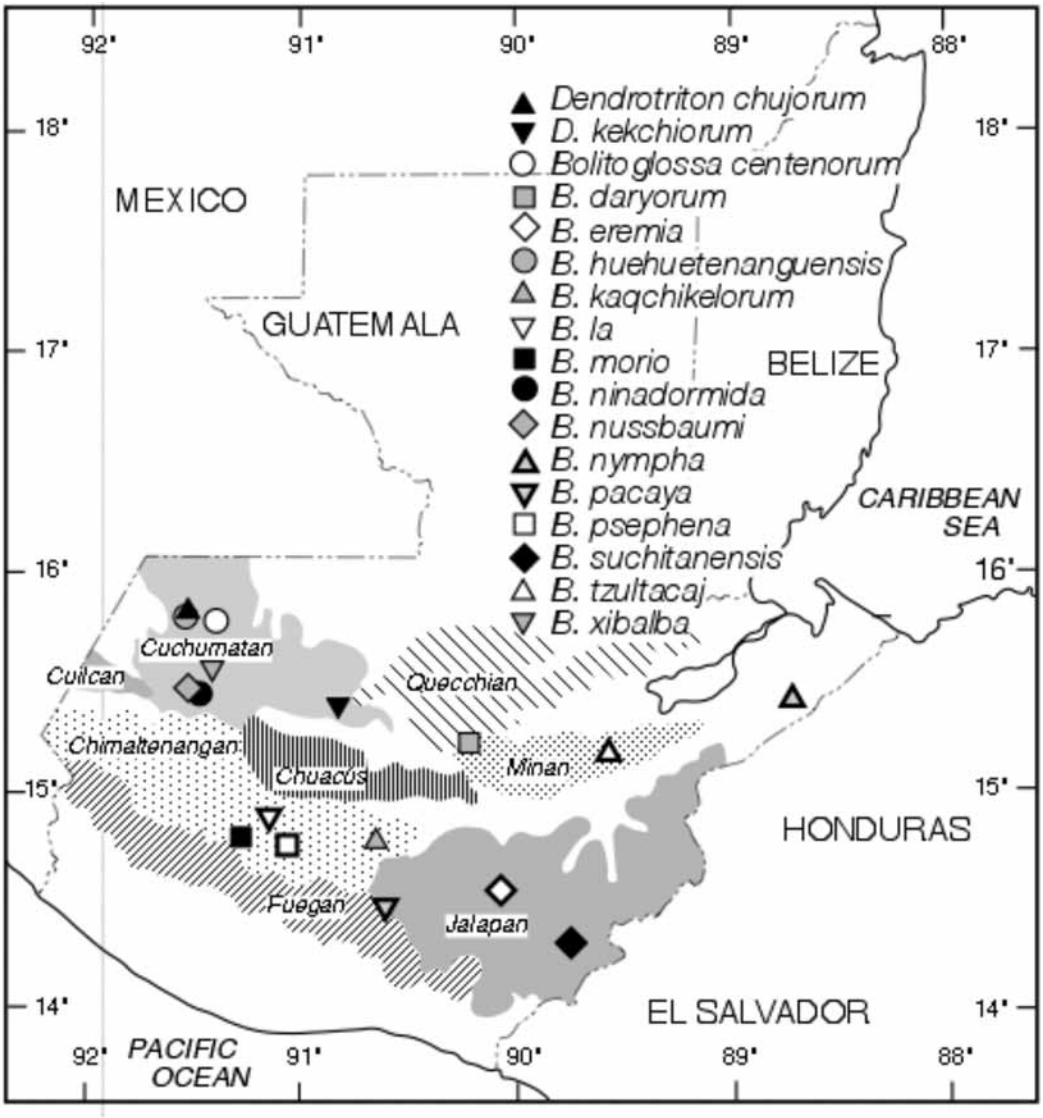

Fig. 37. Selected highland faunal regions of Guatemala (after Campbell & Vannini, 1989), showing type-localities for salamander species described herein and neotype of *Bolitoglossa morio*.

to the north of Uspantán. Unfortunately, daily encounters with guerrillas, who were active in the area at the time, strained our field activities and we were able to secure only a single individual. Four additional individuals are available in the MVZ. This species will be known as:

Dendrotriton kekchiorum new species

Holotype.—UTA A-51086 (original field number ENS 8068), an adult female from road between El Chimel and San Pablo El Baldío, El Quiché, Guatemala, at 2100 m elevation (15.511944° N, 90.791944° W) (Fig. 34). Collected 12 August 1996 by E. N. Smith, M. Sasa-Marin, and F. Castañeda-Moya.

Paratypes.—MVZ 149381 (female), on ridge 2.5 km W and 2 km N Uspantán, Quiché, Cuchumatanes Mountains, 2591 m, collected 31 July 1977 by P. Elias and J. Jackson; MVZ 149382 (female), on ridge 2.5 km W and 2 km N Uspantán, Quiché, Cuchumatanes Mountains, 2560 m, collected 6 August 1977 by P. Elias and J. Jackson.

Referred Material.—MVZ 160895–96 (males), 3.5 km NNW (by air) of Uspantán, Quiche, Cuchumatanes Mountains, 2690 and 2640 m, respectively, collected 17 July 1978 by D. B. Wake.

Diagnosis.—A large species of *Dendrotriton* with a long tail, small nostrils, short legs for the genus, small feet, high numbers of maxillary plus premaxillary teeth, and high numbers of vomerine teeth. *Dendrotriton kekchiorum* is distinguished from *D. bromeliacia*, *D. cuchumatanus*, *D. megarhinus*, and *D. sanctibarbarus* by having dramatically smaller nostrils. *Dendrotriton kekchiorum* is distinguished

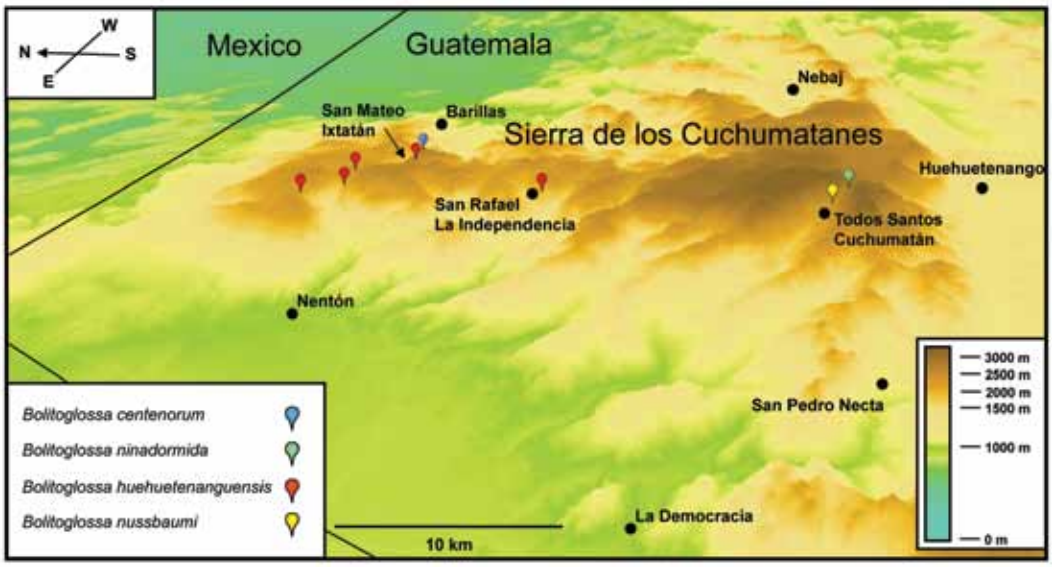

Fig. 38. Distribution of salamanders in the Sierra de los Cuchumatanes.

from *D. rabbi* by having shorter limbs and a larger hands; from *D. xolocalcae* by a long tail, and digits that are expanded at the tip; and from *D. chujorum* by larger size, longer tail, more teeth, and smaller nostrils in adult females.

Description of holotype.—An adult female having a standard length of 34.2 mm, a tail length of 41.2 mm, a head width of 5.5 mm, and a head length of 8.5 mm. The legs are short for the genus with 1.5 intercostal folds between adpressed limbs. Hand width is 2.8 and foot width is 3.8 mm. Axilla–groin length is 18.7 mm. The first digits of the hands and feet are short with webbing extending to the tip; webbing on the other toes is moderate (Fig. 35). The digits, except the first one are expanded at the tip. The order of decreasing finger length is 3, 4, 2, 1, and 3, 4, 2, 5, 1 for the toes. Eye–nostril length is 1.6 mm, eye length is 1.6 mm, interocular distance is 1.8 mm, and internarial distance is 2.0 mm. The nostril diameter is 0.1 mm (Fig. 36). There are 59 combined maxillary and premaxillary teeth. There are 23 vomerine teeth (11/12) curving forward from the midline to beyond the internal nares. The vent is folded and lightly pigmented.

Variation.—The two mature female paratypes in the MVZ are 34.9 and 38.0 mm SL. The nostrils are 0.16 in both individuals. Two other referred specimens (MVZ 160895–96) are not well preserved. These individuals have a SL of 19.6 and 29.4 mm and nostril diameters of 0.39 and 0.23 mm, respectively.

Color pattern of holotype:—Top of head dark brown with yellowish brown interorbital bar; dark brown on head continuing posteriorly as band onto proximal portion of tail where it becomes narrower and breaks up into several dark brown spots; distinctive orange stripes begining posterior to eye and continuing posteriorly on body where they become wider and finally merge on proxomal portion of the tail; most of dorsum of tail uniformly orange; dark brown stripes extending from lower posterior edge of eye posteriorly above insertion of forelimb down flanks, above insertion of hind limb, and the length of the tail; posterior portion of lateral glandular ridge forming distinctive diagonal yellow slash within brown lateral stripe in inguinal region; dorsal surfaces of limbs orange, heavily mottled with dark brown; ventral surface of thighs mostly dark brown with sparse white stippling; ventral surfaces of forelimbs and shanks pale chartreuse; palmar and plantar surfaces heavily suffused with brown. Below the brown lateral stripe there is greenish yellow ventrolateral pigment present, forming an irregular line where it encroaches on the dark pigment of the venter; the juncture of brown ventral pigment and greenish yellow ventrolateral pigment is bounded with concentration of white dots; venter of throat mostly yellow, marked with small white dots, especially anteriorly, and irregular dark brown stippling; midventer of body and tail from just anterior to gular fold onto tail mostly dark brown with scattered white dots that become more numerous on tail; iris copper with dark brown reticulations.

In preservative (alcohol after formalin), top of head and dorsum medium brown; dorsolateral stripes and interorbital bar pale cream; venter of throat cream with dark brown stippling; venter of body and tail dark brown.

Etymology.—The specific epithet is derived from the Kekchi, an ethnic and linguistic group of Mayans inhabiting the region around the type-locality, and the Latin suffix *-orum*, meaning "belonging to."

Distribution, habits, and habitat.—The holotype was collected on a rainy evening at about 1900 h at an air temperature of 12˚C. The specimen was sitting about 1 m above the ground on a fern along a small forest path.

DISCUSSION

Guatemala was divided into eight faunal areas or subareas

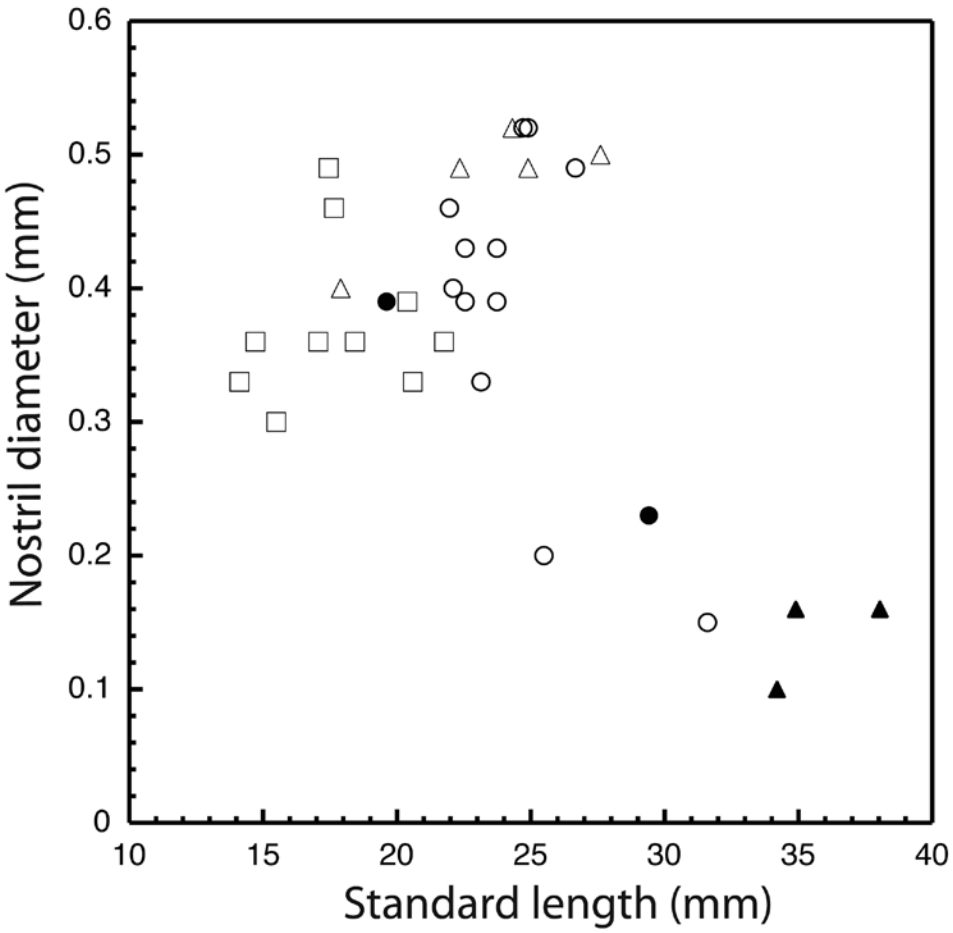

Fig. 39. Nostril diameter of *Dendrotriton*. Males designated by circles, females by triangles, and juveniles by squares. *Dendrotriton chujorum* designated by open symbols; *D. kekchiorum* by closed symbols.

based on herpetofaunal assemblages (Campbell & Vannini, 1989). The topography, climate, and vegetational cover of Guatemala are complex and 11 highland faunal regions were recognized by these authors. The species of salamanders described herein include the Chucumatan and Chimaltenangan areas, which together with the Pacific Versant (Fuegan area) contain the greatest salamander diversity in Guatemala. The Sierra de los Cuchumatanes is the most extensive highland area in Central America and up until recent decades was covered with montane and lower montane humid forest. Although the Cuchumatan and Chimaltenangan areas harbor a moderate number of endemic amphibians, many of the species occurring in these mountains are shared with the Sierran and Fuegan areas (Campbell & Vannini, 1989). Provenances of salamanders described herein practically span the breadth of Guatemalan highlands from the Mexican border in the west to the El Salvador and Honduras borders in the east (Fig. 37). Previously only one endemic species of salamander was known from the Jalapan area of Guatemala; we herein add three other species. We are aware of many additional novel species of Guatemalan salamanders that will be the subject of our future studies.

The Sierra de los Cuchumatanes extend some 65–70 km from north-to-south, unbroken below the 2100 m contour. Despite the apparent relative uniformity of highland forests, few species of salamanders have broad distributions in the region. *Bolitoglossa nussbaumi* and *B. ninadormida* are known only from high elevations in the highlands near Todos Santos in the southern part of the range (Fig. 38). *Bolitoglossa centenorum* is known only from Cerro Bobic in the north. The most wide-ranging species appears to be *B. huehuetenanguensis*, which occurs at slightly lower elevation in about the northern half of the Cuchumatanes.

The seasonally dry highlands of the Guatemalan Plateau are generally not considered to possess great salamander diversity and the region is relatively well collected. Over the Guatemalan Plateau soils are mostly of volcanic origin and therefore porous and subject to rapid drying in the absence of frequent rains. In areas of dense forest there usually is scant undergrowth although an abundance of leaf litter and rotting

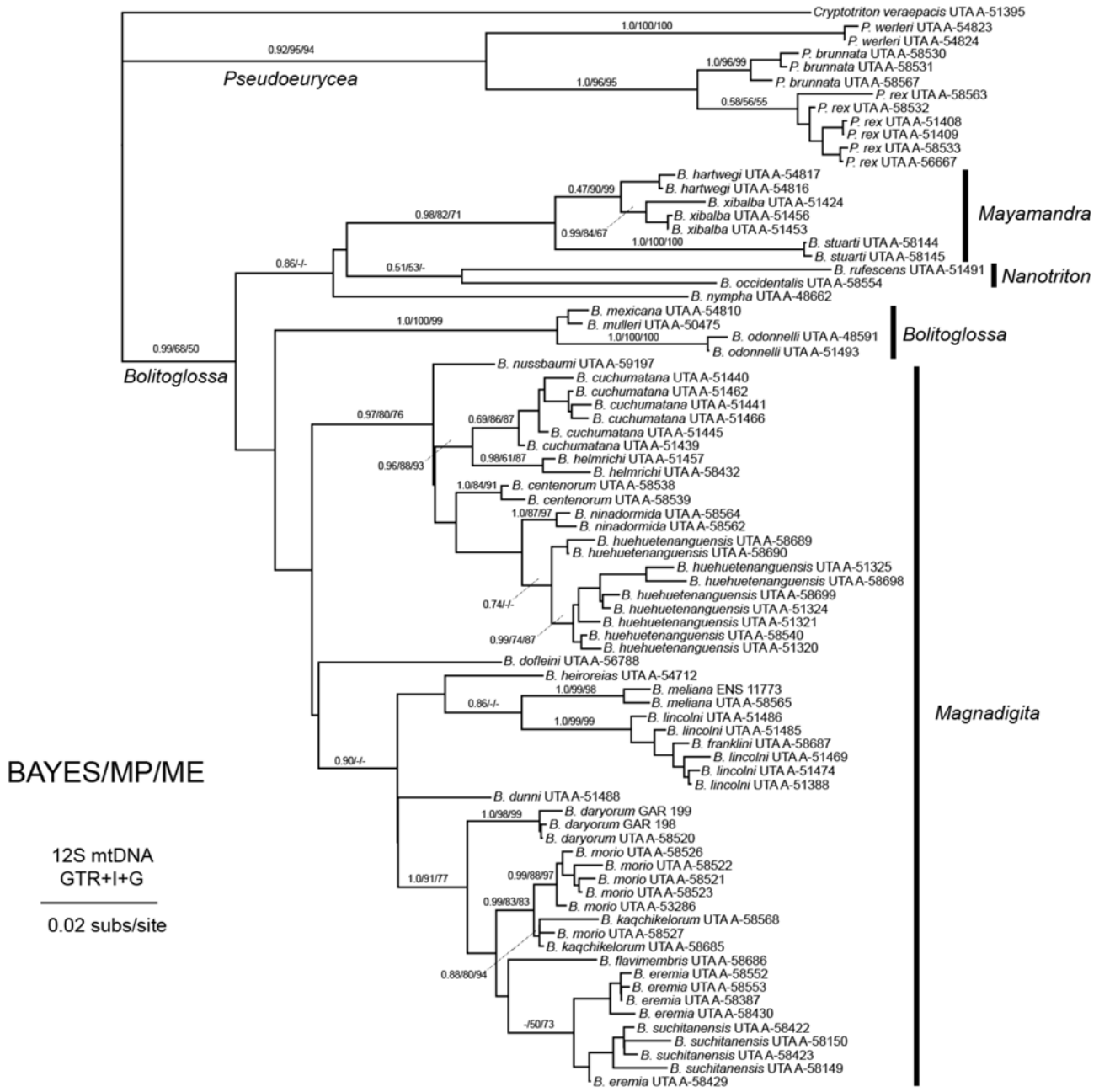

Fig. 40. Bayesian phylogram derived from a fragment of the mitochondrial DNA 12S ribosomal subunit gene. For relevant nodes, support values appearing above branches correspond to posterior probabilities (BAYES), parsimony bootstrap (MP), and minimum evolution bootstrap (ME), respectively. Subgenera from Parra-Olea et al. (2004) are shown adjacent to terminal nodes.

logs may be present. This forest becomes quite dry from about November to May, but during the rainy season a profuse understory of herbaceous plants and ferns may develop in areas of secondary growth or along the edges of clearings and the ground remains generally damp in shady places. Slopes previously cleared and undergoing secondary succession are dominated with pines, whereas those few slopes that retain mostly virgin forest are covered mostly by oaks, laurels, and other hardwoods interspersed with pines.

The Guatemalan Plateau was the focus of several major collecting expeditions of the 19th Century: that of the British Museum of Natural History led by Salvin and Godman and that of the Paris Museum led by Bocourt. These efforts culminated in the publications of the *Biologia Centrali-America* (Günther, 1885–1902) and the *Mission Scientifique* (Brocchi, 1881–1883; Duméril, Bocourt & Mocquard, 1870–1900). Stuart

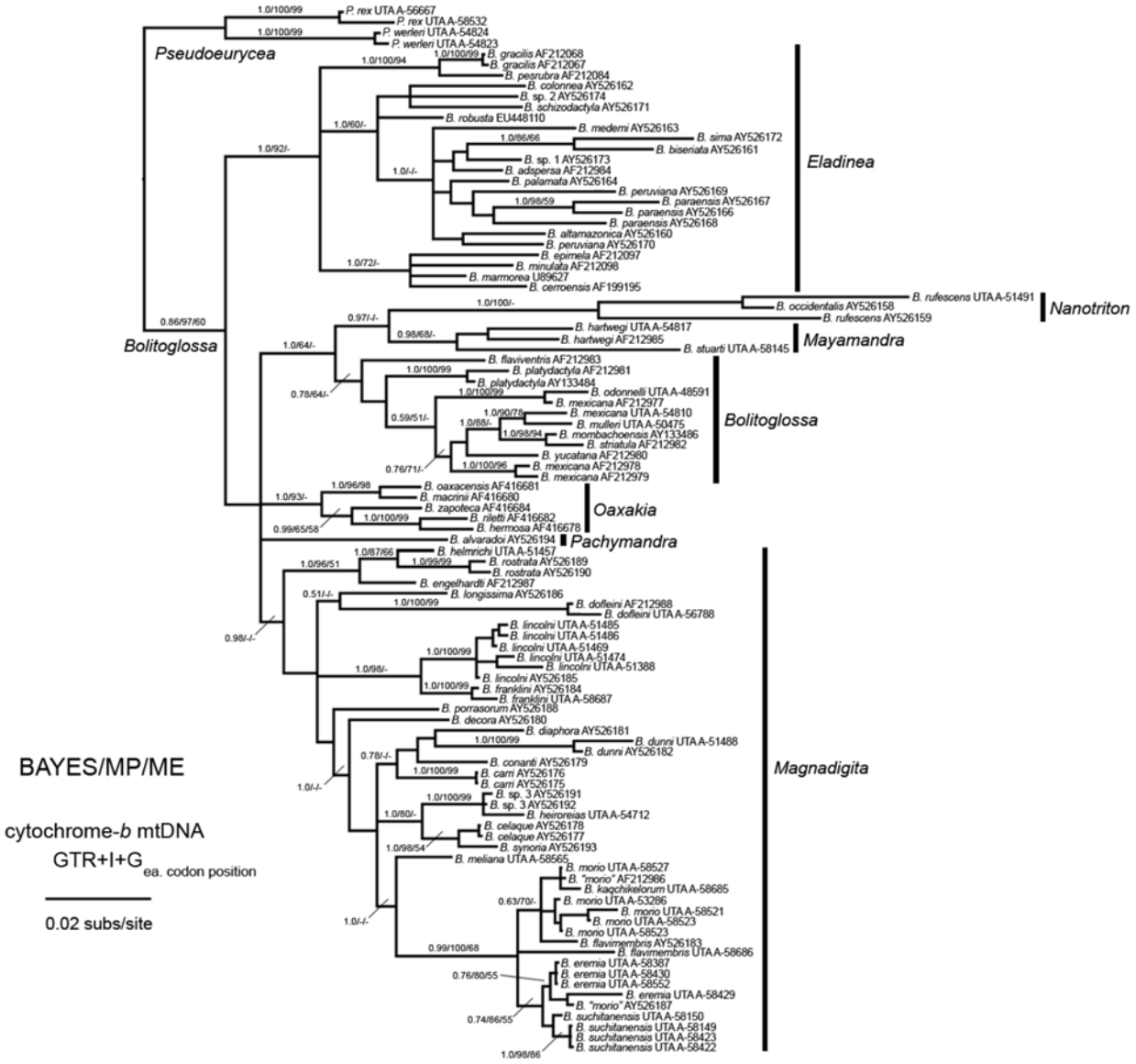

Fig. 41. Mixed-model Bayesian phylogeny derived from a fragment of the mitochondrial DNA cytochrome b gene including select sequence data from Parra-Olea et al. (2004). For relevant nodes, support values appearing above branches correspond to posterior probabilities (BAYES), parsimony bootstrap (MP), and minimum evolution bootstrap (ME) respectively. Subgenera from Parra-Olea et al. (2004) are shown adjacent to terminal nodes.

Table 4. Pairwise genetic distances (uncorrected "p") between select *Bolitoglossa* species examined for the present study

Species Pair	**12S**	**cytochrome-*b***
B. hartwegi (UTA A-54817) and *B. xibalba* (UTA A-51453)	0.76%	N/A
B. hartwegi (UTA A-54817) and *B. stuarti* (UTA A-58145)	6.12%	13.63%
B. nympha (UTA A-48662) and *B. occidentalis* (UTA A-58554)	7.38%	N/A
B. daryorum (UTA A-58520) and *B. morio* (UTA A-58523)	3.22%	N/A
B. nussbaumi (UTA A-59197) and *B. ninadormida* (UTA A-58562)	2.67%	N/A
B. centenorum (UTA A-58538)and *B. huehuetenaguensis* (UTA A-58698)	1.67%	N/A
B. morio (UTA A-58523) and *B. kaqchikelorum* (UTA A-58685)	1.67%	2.45%
B. eremia (UTA A-58552) and *B. suchitanensis* (UTA A-58150)	0.33%	1.96%

(1943) reviewed certain salamanders from Guatemala and noted the paucity of salamanders on the Guatemalan Plateau in comparison with most other highland regions in the country. In his survey of the southwestern Guatemalan highlands, Stuart (1951) listed only three species of salamanders: *Bolitoglossa morio*, *B. rostrata*, and *Pseudoeurycea rex*. To these we now add *B. la*, *B. psephena*, and *B. kaqchikelorum*.

Lynch & Wake (1975) provided several analyses for five species of *Dendrotriton* and concluded that *D. xolocalcae* was the least modified species in the group and *D. bromeliacia* was the most derived species. Collins-Rainboth & Buth (1990) re-analyzed phylogenetic relationships among these five species using morphometric, meristic, and osteological data. In their single most parsimonius Wagner tree these authors found a pattern of increasing nostril size, in agreement with the findings of Lynch & Wake (1975), but produced a different tree topology. Wilkinson (1997) pointed out that neither the results obtained by Lynch & Wake (1975) nor by Collins-Rainboth & Buth (1990) were problem-free with regard to their treatment of data, and that neither analysis was demonstrably better than the other. He suggested that the data available to these researchers provided little phylogenetic signal and little basis for well supported hypotheses of relationships.

Subadults and juveniles of certain species of *Dendrotriton* are characterized by external nares that become smaller in adults (Lynch & Wake, 1975). *Dendrotriton xolocalcae* and *D. rabbi* share this feature, which appears to be derived in *D. chujorum* and *D. kekchiorum* and thus suggests that these form a monophyletic group (Fig. 39).

Members of the genus *Dendrotriton* are distributed in allopatric populations of small geographic extent in mesic forests on both Pacific (*megarhinus, xolocalcae, bromeliacia*) and Atlantic (*chujorum, chuchumatanus, kekchiorum, santibarbarus*) versants. *Dendrotriton rabbi* occurs in the Montañas del Cuilco, a range that is geographically close to the Pacific, but which is drained by the headwaters of the Río Grijalva flowing to the Atlantic. The elevational range for the genus is 2100–2900 m. Most species occur in what can be aptly considered cloud forest, but most species inhabit forests that experience relatively dry periods from about December to April during which time many salamanders take refuge in bromeliads.

Our molecular phylogenetic analyses are concordant with the hypotheses provided by Parra-Olea *et al.* (2004) for several monophyletic groups within *Bolitoglossa* (Figs. 40 and 41). The 12S and cyt-*b* analyses support the monophyly of the subgenera *Bolitoglossa*, *Magnadigita*, *Mayamandra* and *Nanotriton*. Additionally, our topological results for the cyt-*b* dataset agree with Parra-Olea *et al.* (2004) in recovering the subgenera *Eladinea* and *Oaxakia* as monophyletic. While we feel that the mtDNA datasets analyzed herein are insufficient to discuss higher level phylogenetic relationships between subgenera, our expanded molecular sampling of *Bolitoglossa* (most notably within the subgenus *Magnadigita*) does allow us to report on the putative phylogenetic placement of several species, including some of the new species described in the present study. Pairwise uncorrected genetic distances for several focal taxa are presented in Table 4.

Several members of the *Bolitoglossa morio* group were included in our molecular analyses. This group was found to be the most derived *Magnadigita* clade within our sampling. *Bolitoglossa daryorum* occupies a basal placement to a clade of closely related species containing *B. eremia, B. flavimembris, B. kaqchikelorum, B. morio, and B. suchitanensis* in the 12S topology. While we were unable to include cyt-*b* sequence data for *B. daryorum*, the phylogenetic relationships between *B. eremia, B. flavimembris, B. kaqchikelorum, B. morio, and B. suchitanensis* for this locus are quite similar to those in the 12S phylogeny, including their derived placement within *Magnadigita*. Based on mtDNA, there are 2 closely related species pairs in the *B. morio* group: (1) *B. eremia* and *B. suchitanensis* and (2) *B. morio* and *B. kaqchikelorum*. While these groups were found to be geographically and morphologically distinct, our molecular analysis did not differentiate confidently between species pairs. In one specimen of *B. morio* (UTA A-58527) we found a *B. kaqchikelorum* haplotype for both 12S and cyt-*b* loci, which may suggest historical introgression or contemporary gene flow between these species. Further examination and geographic sampling of these species pairs will be necessary to ultimately determine species boundaries for these denizens of the Guatemalan Plateau. The cyt-*b* sequences for *B. morio* used in Parra-Olea *et al.* (2004) appear to be closely related to *B. eremia* (AY526187) and *B. kaqchikolorum* (AF212986) in our topology.

We included several species in the *Bolitoglossa helmrichi* group in our 12S phylogeny including sequences derived from type and examined material for *B. centenorum*, *B. huehuetenanguensis*, *B. ninadormida*, and *B. nussbaumi*. Samples of *B. cuchumatana* and *B. helmrichi* were also included in this analysis. This group of six species was found to monophyletic and nested within the subgenus *Magnadigita*. These data also indicate, as mentioned earlier in this study, that the *B. helmrichi* group is sister to a reciprocally monophyletic clade containing the *B. franklini* and *B. morio* groups. Among the sampled *B. cuchumatana* and *B. huehuetenanguensis* we recovered multiple divergent haplotypes indicating that, much like their lower Central American congeners (García-París *et al.*, 2000), many of the Guatemalan lineages discussed herein may exhibit substantial phylogeogeographic structure. In light of this, these species may serve as ideal candidates for addressing hypotheses related to the tempo and mode of speciation in the terrestrial faunas of montane northern Central America.

The 12S and cyt-*b* datasets both support *Bolitoglossa stuarti* as a distinct lineage belonging to the subgenus *Mayamandra*. The new species *B. xibalba* is a close relative of *B. hartwegi* and as such should be placed in the subgenus *Mayamandra*. In our 12S phylogeny, *B. nympha* was found to be most

closely related to members of the subgenera *Nanotriton* and *Mayamandra*; however, our analysis did not confidently place *B. nympha* within either of these groups. Additionally, the *B. rufescens* cyt-*b* sequence (AY526159) from Parra-Olea *et al.* (2004) may be assignable to *B. nympha* given (1) that it was collected in Belize not far from the Guatemalan type locality of *B. nympha*, and (2) its distant phylogenetic relatedness to the other *B. rufescens* sequence (UTA A-51491) included in our analysis of cyt-*b*. The sequences from *B. lincolni* and *B. franklini* used in our 12S analysis do not form separate clades whereas in the cyt-*b* analysis they appear to do so. Our addition of a new *B. dofleini* sample in the cyt-*b* analysis recovered this taxon as nested within the subgenus *Magnadigita* (with strong nodal support in the BAYES analysis; Fig. 41) suggesting that the subgenus *Pachymandra* may be paraphyletic despite the strong support for this grouping reported in previous studies (*e.g.*, Wiens *et al.*, 2007; Parra-Olea *et al.*, 2004). The unassigned taxon *Bolitoglossa* sp. 3 of Parra-Olea *et al.* (2004) is closely allied to the *B. heiroreias* sample used in our study.

It is an unfortunate fact that it is becoming an almost *pro forma* epilogue in many papers describing new tropical American amphibians to state that the habitat around the type-localities of the salamanders described herein have been dramatically altered to the point where it may be doubtful that these species will long survive. Many of the taxa described in this paper are no exception.

ACKNOWLEDGMENTS

We are grateful to the following museum staff for allowing us to examine material in their care: Darrel Frost (American Museum of Natural History), A. Resetar (Field Museum of Natural History), D. Wake (Museum of Vertebrate Zoology), O.F. Lara, C.R. Vásquez AlmazEan, and F. Castañeda Moya (Universidad de San Carlos de Guatemala), and R.A. Nussbaum and G. Schneider (University of Michigan Museum of Zoology). Ana L. Macvean kindly suggested the name *la* as used for "chichicaste", used in naming one salamander. Paul Ustach prepared drawings for several of the species of new salamanders. We were helped in many ways by the late J.L. Camarillo Rangel during the course of our Mexican fieldwork. Field assistance was kindly provided by M. Sasa-Marin, R. Gutberlet, D. Figueroa, D.P. Lawson, M.B. Harvey, J.R. Mendelson III, W.W. Lamar, D.R. Formanowicz, V. McKenzie**,** I.M. Asmundsson, M.V. Centeno, C.L. Guirola, R. Schiele, C. Paniagua, R.F. Savage, J. Monzón-Sierra, J.C. Schuster, E. Cano, R. García Anleu, S. Lou-Vega, and F. Castañeda-Moya. Permits for conducting research in Guatemala were granted by officials of the Consejo Nacional de Areas Protegidas (CONAP). We thank present and former CONAP officials, Lic. E. Díaz de Gordíllo, K. Duchez, E.G. Flores, Lic., M. García de Solorzano, Lic. F. Herrera, and M. Sc. O. F. Lara. This paper is based on work supported by the National Science Foundation (DEB-9705277, 061382) and the Texas Advanced Research Program (grant 003656-001) to J.A. Campbell. The National Geographic Society supported field work by E.D. Brodie, Jr. Field work by E.N. Smith has been supported by the Wildlife Conservation Society, Instituto Bioclon, the Audubon Society and the National Science Foundation (DEB-0416160). Field support for M.E. Acevedo and M.V. Centeno was provided by the "Fauna Project" by the Consejo Nacional de Ciencia y Tecnologia (CONCYT), the Dirección General de Investigación (DIGI), and the Centro de Estudios Conservacionistas (CECON). Finally, we (EDB and JAC) are grateful to the late Brutus and Oaxaca for their immeasurable contribution to the quality of our lives.

DEDICATION

We dedicate this contribution to Laurence Cooper Stuart (1907–1983), known affectionately throughout many parts of Guatemala as "Pancho Mata Culebra". He served as a faculty member at the University of Michigan from 1934 until his retirement in 1969. His tireless explorations of Guatemala extended from 1933 until his death in 1983 and he was intimately familiar with this country as few others have ever been. His comprehensive herpetological collections are housed in the Museum of Zoology at the University of Michigan. We are indebted to him for helping to lay the foundation in Guatemala for future generations of biologists.

L.C. Stuart at work in Ann Arbor, Michigan, 4 March 1936.

LITERATURE CITED

Anderle, R.F. 1967. The horned guan in Mexico and Guatemala. *The Condor*, 1967: 93-109.

Avise, J.C. & D. Walker. 1999. Species realities and numbers in sexual vertebrates: Perspectives from an asexually transmitted genome. *Proceedings of the National Academy of Sciences, USA*, 96, 992-995.

Bossuyt, F., & M.C. Milinkovitch. 2000. Convergent adaptive radiations in

Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences, USA*, 97, 6585-6590.

Brocchi, P. 1881–1883. Études des batraciens de l'Amérique Centrale. In: *Mission Scientifique au Mexique et dan l'Amérique Centrale—Recherches zoologiques*, Part 3, Sect. 2, 122 pp.

Brodie, E.D., Jr., & J.A. Campbell. 1993. A new salamander of the genus *Oedipina* (Caudata: Plethodontidae) from the Pacific versant of Guatemala. *Herpetologica*, 49: 259-265.

Campbell, J.A., & E.N. Smith. 1998. A new genus and species of colubrid snake from the Sierra de las Minas of Guatemala. *Herpetologica*, 54(2): 207-220.

Campbell, J.A. & E.D. Brodie, Jr. 1989 [dated 1988]. A new colubrid snake of the genus *Adelphicos* from Guatemala. *Herpetologica*, 44(4): 416-422.

Campbell, J.A. & D.R. Frost. 1993. Anguid lizards of the genus *Abronia*: Revisionary notes on the species of Nuclear Central America and adjacent Mexico, descriptions of four additional species, with a phylogenetic hypothesis for the genus and an identification key. *Bulletin of the American Museum of Natural History*, 216: 1-121.

Campbell, J.A. & E.N. Smith. 1998. New species of *Nototriton* (Caudata: Plethodontidae) from eastern Guatemala. *Scientific Papers, Natural History Museum, The University of Kansas*, 6: 1-8.

Campbell, J.A. & J.P. Vannini. 1989. Distribution of amphibians and reptiles in Guatemala and Belize. *Proceedings of the Western Foundation of Vertebrate Zoology*, 4(1): 1-21.

Christenson, A.J. Accessed 13 May 2010. K'iche'—English Dictionary and Guide to the Pronunciation of the K'iche'–Maya Alphabet http://www.famsi.org/mayawriting/dictionary/christenson/quidic_complete.pdf

Collins-Rainboth, A. & D.G. Buth. 1990. A reevaluation of the systematic relationships among species of the genus *Dendrotriton* (Caudata: Plethodontidae). *Copeia*, 1990(4): 955-960.

Conway, F.M., J.F. Diehl & O. Matías. 1992. Paleomagnetic constraints on eruption patterns at the Pacaya composite volcano. *Guatemala Bulletin of Volcanology*, 55: 25-32.

Cope, E.D. 1869. A review of the species of the Plethodontidae and Desmognathidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 21: 93–118.

Duellman, W.E. & J.A. Campbell. 1984. Two new species of Plectrohyla from Guatemala (Anura: Hylidae) *Copeia*, 1984(2): 390-397.

Duméril, A., M.F. Bocourt & F. Mocquard. 1870–1909. Études sur les reptiles. In: *Mission Scientifique au Mexique et dan l'Amérique Centrale—Recherches zoologiques,* Part 3, Sect. 1 1012 pp.

Elias, P. 1984. Salamanders of the northwestern highlands of Guatemala. *Contributions in Science, Natural History Museum of Los Angeles County*, 348: 1-20.

Elias, P. & D.B. Wake. 1983. *Nyctanolis pernix*, a new genus and species of plethodontid salamander from northwestern Guatemala and Chiapas, Mexico. Pp. 1–12 in A.G.J. Rhodin & K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. The Museum of Comparative Zoology, Cambridge, Mass.

Falla, Ricardo. 1992. Masacres de la Selva, Ixcán, Guatemala (1975-1982). *Editorial Universitaria*, Vol. 1, Colección 500 Años, Guatemala 31 pp.

García-París, M., D.A. Good, G. Parra-Olea & D.B. Wake. 2000. Biodiversity of Costa Rican salamanders: Implications of high levels of genetic differentiation and phylogeographic structure for species formation. *Proceedings of the National Academy of Sciences, USA*, 97, 1640-1647.

García-París, M. & D.B. Wake. 2000. Molecular phylogenetic analysis of relationships of the tropiical salamander genera *Oedipina* and *Nototriton*, with descriptions of a new genus and three new species. *Copeia*, 2000: 42-70.

Günther A.C.L.G. 1885-1902. *Biologia Centrali-Americana*. Reptilia and Batrachia. Taylor and Francis. London. 575 pp.

Hedges, S.B. 1992. The number of replications needed for accurate estimation of the bootstrap *P* value in phylogenetic studies. *Molecular Biology and Evolution*, 9: 366-369.

Holdridge, L.R. 1959. Mapa ecológico de Guatemala, C.A. Instituto Interamericano de Ciencias Agrícolas de la Organización de Estados Americanos, Proyecto 39, Programa de Cooperación Técnica, San José, Costa Rica, in 2 sheets.

Lynch, J.F. & D.B. Wake. 1975. Systematics of the *Chiropterotriton* bromeliacia group (Amphibia: Caudata), with descriptions of two new species from Guatemala. *Contributions in Science, Natural History Museum of Los Angeles County*, 265: 1-45.

Lynch, J.F., & D.B. Wake. 1978. A new species of *Chiropterotriton* (Amphibia: Caudata) from Baja Verapaz, Guatemala, with comments on relationships among Central American members of the genus. *Contributions in Science, Natural History Museum of Los Angeles County*, 294: 1-22.

Maddison, D.R. & W.P. Maddison. 2002. *MacClade: Analysis of phylogeny and character evolution*. Sinauer, Sunderland, Massachusetts. 398 pp.

McCranie, J.R., & L.D. Wilson. 1996. A new species of salamander of the genus *Nototriton* (Caudata: Plethodontidae) from Montaña de Santa Bárbara, Honduras. *The Southwestern Naturalist*, 41: 111-115.

Moritz, C., C.J. Schneider & D.B. Wake. (1992) Evolutionary relationships within the *Ensatina eschscholtzii* complex confirm the ring species interpretation. *Systematic Biology*, 41, 273-291.

Mueller, R.L., J.R. Macey, M. Jaekel, D.B. Wake & J.L. Boore. 2004. Morphological homoplasy, life historyevolution, and historical biogeography of plethodontid salamanders inferred from complete mitochondrial genomes. *Proceedings of the National Academy of Sciences, USA*, 101: 13820-13825.

Parra-Olea, G., M. García-Paris & D. B. Wake. 2004. Molecular diversification of salamanders of the tropical American genus *Bolitoglossa* (Caudata: Plethodontidae) and its evolutionary and biogeograpical implications. *Biological Journal of the Linnean Society*, 813: 325-346.

Poglayen, I. & H.M. Smith. 1958. Noteworth herptiles from Mexico. *Herpetologica*, 14: 11-15.

Posada, D. & K.A. Crandall. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14, 817-818.

Ronquist, F. & J.P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572-1574.

Schmidt, K.P. 1936. Guatemalan salamanders of the genus *Oedipus*. *Zoological Series of Field Museum of Natural History*, 20: 135-166.

Shaffer, H.B. & R.C. Thomson. 2007. Delimiting species in recent radiations. *Systematic Biology*, 56, 896-906.

Smith, H.M. & E.H. Taylor. 1948. An annotated checklist and key to the Amphibia of Mexico. *United States National Museum Bulletin*, 194: 1-118.

Streicher, J.W., A.J. Crawford & C.W. Edwards. 2009. Multilocus molecular phylogenetic analysis of the montane *Craugastor podiciferus* species comples (Anura: Craugastoridae) in Isthmian Central America. *Molecular Phylogenetics and Evolution*, 53: 620-620.

Steyermark, J.A. 1950. Flora of Guatemala. *Ecology*, 31: 368-372.

Stuart, L.C. 1943. Taxonomic and geographic comments on Guatemalan salamanders of the genus *Oedipus*. *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 56: 1-37.

Stuart, L.C. 1951. The herpetofauna of the Guatemala plateau, with special reference to its distributions on the southwestern highlands. *Contributions from the Laboratory of Vertebrate Biology.* University of Michigan Press. 49:1-71.

Stuart, L.C. 1952. Some new amphibians from Guatemala. *Proceedings of the Biological Society of Washington*, 65: 1-12.

Stuart, L.C. 1954*a*. Herpetofauna of the southeastern highlands of Guatemala. *Contributions from the Laboratory of Vertebrate Biology*, 68: 1-73.

Stuart, L.C. 1954*b*. Descriptions of some new amphibians and reptiles from Guatemala. *Proceedings of the Biological Society of Washington*, 67: 159-78.

Stuart, L.C. 1963. A checklist of the herpetofauna of Guatemala. Miscellaneous *Publications of the Museum of Zoology of the University of Michigan*, 122: 1-150.

Swofford, D.L. 2002. *PAUP: Phylogenetic Analysis Using Parsimony* (**and other methods*), Version 4.0b10, Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Tamura K., J. Dudley, M. Nei & S. Kumar. 2007. *MEGA4*: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution,* 24:1596-1599.

Taylor, E.H. 1941. New Amphibia from the Hobart M. Smith Mexican collections. *University of Kansas Science Bulletin*, 27: 141-167.

Taylor, E.H. 1944. The genera of plethodont salamanders in Mexico, Part I. *University of Kansas Science Bulletin*, 30: 189-232.

Vásquez-Almazán, C.R., S. M. Rovito, D.A. Good & D.B. Wake. 2009. A new species of *Cryptotriton* (Caudata: Plethodontidae) from eastern Guatemala. *Copeia*, 2009: 313-319.

Wake, D.B. 1998. On the taxonomic status of *Nototriton sanctibarbarus* McCranie and Wilson (Amphibia: Caudata). *The Southwestern Naturalist*, 43: 88-106.

Wake, D.B. & A.H. Brame, Jr. 1963. The status of the plethodontid salamander genera Bolitoglossa and Magnadigita. *Copeia*, 1963: 382-387.

Wake, D.B. & A.H. Brame, Jr. 1969. Systematics and evolution of Neotropical salamanders of the *Bolitoglossa helmrichi* group. *Contributions in Science, Natural History Museum of Los Angeles County*, 175: 1-40.

Wake, D.B. & J.A. Campbell. 2000. A new species of diminutive salamander (Amphibia: Caudata: Plethodontidae: *Nototriton*) from the Montañas del Mico of Guatemala. *Proceedings of the Biological Society of Washington*, 113: 815-819.

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

Wake, D.B. & J.F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Science Bulletin, Natural History Museum of Los Angeles County*, 25: 1-65.

Wake, D.B. & J.F. Lynch. 1982. Evolutionary relationships among Central American salamanders of the *Bolitoglossa franklini* group, with a description of a new species from Guatemala. *Herpetologica*, 38: 257-272.

Wake, D.B. & J.F. Lynch. 1988. The taxonomic status of *Bolitoglossa resplendens* (Amphibia: Caudata). *Herpetologica*, 44: 105-108.

Wake, D.B., S.Y. Yang & T.J. Papenfuss. 1980. Natural hybridization and its evolutionary implications in Guatemalan plethodontid salamanders of the genus *Bolitoglossa*. *Herpetologica*, 36: 335-345.

Wiens, J.J., G. Parra-Olea, M. García-París & D.B. Wake. 2007. Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society London B*, 274: 919-928.

Wilkinson, M. 1997. On phylogenetic relationships within *Dendrotriton* (Amphibia: Plethodontidae): is there sufficient evidence? *Herpetological Journal,* 7(2): 55-65.

APPENDIX 1. (*BOLITOGLOSSA*)

Specimens Examined

For sake of brevity, only Guatemalan Departments and museum numbers are given.

Bolitoglossa centenorum*.—Huehuetenango**: UTA A-58538 (holotype), 58539, 58541–49. ***Bolitoglossa conanti*.—Izabal**: UTA A-32865, 38582, 45399, 48623; **Zacapa**: UTA A-38576–81, 38585–86, 45511–33, 48384–89, 58141; **Honduras**: UTA A-27441. ***Bolitoglossa cuchumatana*.—Quiché**: ANSP 29387–92, 29882, UMMZ 89110 (holoype), UMMZ 89111–13, UTA A-51440, 51441–46, 51439. ***Bolitoglossa daryorum*.—Baja Verapaz**: 59729 (holotype), 58730–32; **El Progreso**: UTA A-34045–47, 48580–82, 58520. ***Bolitoglossa dofleini*.—Alta Verapaz**: UTA A-29694–96; **Izabal**: UTA A–21409, 29697–98, 32854–55, 32625, 32627, 32855, 33626, 34051–54, 34082, 38558–75, 40336, 43511–12, 45293–317, 48392–414, 53002; **Zacapa**: 45318–20, 45757. ***Bolitoglossa dunni*.—Izabal**: UTA A-51488, 58140; **Honduras**: UTA A-27442. ***Bolitoglossa engelhardti.—**Sololá**: CM 9305; UMMZ 80925(3); **Quezaltenango**: UMMZ 107717, 107718(3); **El Salvador**: UMMZ 118338. ***Bolitoglossa eremia*.—Jalapa**: UTA A-33670, 38617–19, 38620 (holotype), 38621, 38629–31, 58387–89, 58429–30, 58552–53. ***Bolitoglossa flavimembris*.—San Marcos**: UTA A-18230–32, 32872, 48646–54, 48682–86, 51389–90, 58686. ***Bolitoglossa franklini*.—San Marcos**: UTA A-18233–35, 42569–71, 48363, 48520–21, 48669, 58687. ***Bolitoglossa hartwegi***.—**MX: Chiapas**: AMNH 97509, CM 29543–44, UMMZ 121557 (holotype), UTA A-3524, 54816–17. ***Bolitoglossa heiroreias*.—Chiquimula**: UTA A-48364, 54712. ***Bolitoglossa helmrichi*.—Alta Verapaz**: UTA A-38588–89, 48415–16, 48418–20, 48585; **Baja Verapaz**: UTA A-5310–32, 6172–76, 6276–79, 7300–79, 17190–205, 21413–16, 26514, 32873–74, 38587, 51457–58, 58431–36, 58448, 58557–58, 59733; **Progreso**: UTA A-32875–76. ***Bolitoglossa huehuetenanguensis***.—**Huehuetenango**: UTA A-21477–538, 29664–74, 30148–49, 31, 32891–95, 41982–004, 51297–319, 51320 (holotype), 51321–60, 58540, 58555–56, 58561, 58689–99, 58691–97. ***Bolitoglossa kaqchikelorum*.—Chimaltenango**: CM 41984, 41986, 41989, 42008, 42029, 42038, 42041, 42047, 42058, 42060, 42088, 42091, 42106, 42119, 42150–51, 42159, 42161, 42188, 42191, 42197, 42201, 42214, 42229, 42242, 42247, 42251, 42266, 42273, 42282, UMMZ 100489(2), 100490(7), UTA A-59734–35; **Escuintla**: UTA A-33638; **Guatemala**: UTA A-44132 (holotype), 48360, 48586, 52623, 58568; **Quezaltenango**: UTA A-26513; **Sacatepéquez**: UTA A-48361–62, 48379–81, 58685. ***Bolitoglossa la*.—Quiché**: UTA A-21550–54, 24469–79, 21555–60, 33635–37, 38556–57, 38656–60, 38662–75, 38661 (holotype), 51431–37, 53890–401, 58403–17 ***Bolitoglossa lincolni*.—Huehuetenango**: UTA A-51484–86, 51499, 58148. **Quiché**: UMMZ 89107 (holotype), 89108–09, UTA A-51447–50, 51469–83; **San Marcos**: UMMZ 123275–27, 129149–150, 137058–61, 137063, 137100, 137106–07, 137366(7), 137372(3), UTA A-18237–38; **MX: Chiapas**: UMMZ 118823–24. ***Bolitoglossa meliana*.—Alta Verapaz**: UTA A-48587; **Baja Verapaz**: UTA A-58565; **Progreso**: UTA A-32877; **Quiché**: UTA A-38591–613. ***Bolitoglossa mexicana*.—Alta Verapaz**: UTA A-52909–13; **Izabal**: 45495, 45497, 45499, 45502–04, 45507–10, 48193–202, 48588–90, 48593–94; **MX: Oaxaca**: 54810. ***Bolitoglossa morio*.—Chimaltenango**: CAS 69480, 69492, 69494, FMNH 202241; UMMZ 101462, UTA A-48696–99; **Quezaltenango**: UTA A-58521–29; **San Marcos**: UMMZ 137358, 137371(2), 138334, UTA A-18236, 33669, 48668, 48695, 51388; **Sololá**. UTA A-33665–68, 34084-100, 38614, 40338, 48363, 48672–73; **Suchitepéquez**: FMNH 64723; **Totonicapan**: UTA A-34192, 48670, 53286. ***Bolitoglossa mulleri*.—Alta Verapaz**: UTA A-44072, 50475; **Huehuetenango**: UTA A-34193. ***Bolitoglossa ninadormida*.—Huehuetenango**: UTA A-29657–63, 30150, 32890, 58562 (holotype), 58564. ***Bolitoglossa nussbaumi*. Huehuetenango**: UTA A-59197 (holotype), 60004–06. ***Bolitoglossa nympha*.—Izabal**: UTA A-38651–53, 45321–27, 45328 (holotype), 45329–62, 48214–27, 48229–64, 48655–57, 48662–63, 51398–403, 58560; **Zacapa**: 38645–50. 45363–65, 48213. ***Bolitoglossa occidentalis*.—Quezaltenango**: UTA A-21458–76, 24519–39, 25399–411; **MX: Oaxaca**: UTA A-12842. ***Bolitoglossa omniumsanctorum*.—Huehuetenango**: UMMZ 102285 (holotype), 102286, 48700–25; **Quiché**: UTA A-38622–28, 38632–44. ***Bolitoglossa pacaya*.—Escuintla**: UTA A-21448–57, 21561–67, 24919–20, 33639–40, 33641 (holotype), 33642–57; **Guatemala**: UTA A-5495–96, 26515–16, 31429–30, 33658–64, 40340. ***Bolitoglossa psephena*.—Chimaltenango**: UTA A-48204 (holotype). ***Bolitoglossa rostrata*. Chimaltenango**: FMNH 19448, 20234(4), 20240(4), 20286, 20753(5), 217350, 217353, 217362–63, 217367; UTA A-48518–19; **San Marcos**: UTA A-18240–42; **Totonicapan**: UMMZ 98123(4), 100491(9), 100531(3), 106761(6), 126323(6), 126325(3); UTA A-25413. ***Bolitoglossa rufescens*.—Alta Verapaz**: UTA A-29690–93, 51383, 58701–02; **Baja Verapaz**: UTA A-51382; **Huehuetenango**: UTA A-32918, 32929–34, 51491–92, 58703–06; **Izabal**: UTA A-21539–41, 24916–18, 30146–47, 32900–17, 32919–28, 33672–82, 51397, 51404, 58550–51, 58700, 59925; **Petén**: UTA A-45290; **MX: Oaxaca**: UTA A-12843. ***Bolitoglossa stuarti*.—Huehuetenango**: UTA A-58144–47, 58566, 58684, 59736–37. ***Bolitoglossa suchitanensis*.—Jutiapa**: UTA A-58149–52, 58419–20, 58421 (holotype), 58422–24. ***Bolitoglossa tzultacaj*.—Zacapa**: UTA A-38590 (holotype). ***Bolitoglossa xibalba*.—Huehuetenango**: UTA A-30164–66, 34545, 34546 (holotype), 34547, 51424, 51428, 51451–56, 58588.

APPENDIX 2.

Genbank accession numbers and corresponding voucher information.

Taxon	Locality	Museum ID	Field ID	12S	Cyt-b
Cryptotriton veraepacis	Guatemala: Baja Verapaz	UTA A-51395	GAR 063	HQ009906	None
Genus *Pseudoeurycea*					
P. brunnata	Guatemala: Quetzaltenango	UTA A-58530	ENS 10467	HQ009983	None
P. brunnata	Guatemala: Quetzaltenango	UTA A-58531	ENS 10468	HQ009979	None
P. brunnata	Guatemala: Totonicapán	UTA A-58567	ENS 10458	HQ009980	None
P. rex	Guatemala: Huehuetenango	UTA A-58563	MEA 1182	HQ009971	None
P. rex	Guatemala: Huehuetenango	UTA A-58532	MEA 1626	HQ009952	HQ009990
P. rex	Guatemala: Huehuetenango	UTA A-56667	MEA 1628	HQ009956	HQ009995
P. rex	Guatemala: Huehuetenango	UTA A-58533	MEA 1627	HQ009953	None
P. rex	Guatemala: Huehuetenango	UTA A-51408	JAC 19205	HQ009967	None
P. rex	Guatemala: Huehuetenango	UTA A-51409	JAC 19206	HQ009969	None
P. werleri	México: Veracruz	UTA A-54823	ENS 10359	HQ009907	HQ010014
P. werleri	México: Veracruz	UTA A-54824	ENS 10360	HQ009957	HQ010018
Genus *Bolitoglossa*					
B. centenorum	Guatemala: Huehuetenango	UTA A-58538	MEA 1633	HQ009946	None
B. centenorum	Guatemala: Huehuetenango	UTA A-58539	MEA 1634	HQ009933	None
B. cuchumatana	Guatemala: Quiché	UTA A-51439	ENS 7812	HQ009925	None
B. cuchumatana	Guatemala: Quiché	UTA A-51440	ENS 8306	HQ009958	None
B. cuchumatana	Guatemala: Quiché	UTA A-51441	JAC 19348	HQ009978	None
B. cuchumatana	Guatemala: Quiché	UTA A-51445	JAC 19352	HQ009965	None
B. cuchumatana	Guatemala: Quiché	UTA A-51466	ENS 8199	HQ009912	None
B. cuchumatana	Guatemala: Quiché	UTA A- 51462	ENS 8116	HQ009905	None
B. daryorum	Guatemala: El Progreso	UTA A-58520	ENS 11771	HQ009966	None
B. daryorum	Guatemala: Baja Verapaz	UTA A-59730	GAR 198	HQ009960	None
B. daryorum	Guatemala: Baja Verapaz	UTA A-59731	GAR 199	HQ009902	None
B. dofleini	Guatemala: Yoro	UTA A-56788	ENS 10604	HQ009915	HQ010015
B. dunni	Guatemala: Izabal	UTA A-51488	ENS 7825	HQ009955	HQ010011
B. eremia	Guatemala: Jalapa	UTA A-58429	MEA 1975	HQ009939	HQ009992
B. eremia	Guatemala: Jalapa	UTA A-58430	MEA 1999	HQ009963	HQ009998
B. eremia	Guatemala: Jalapa	UTA A-58387	MEA 2019	HQ009920	HQ009988
B. eremia	Guatemala: Jalapa	UTA A-58553	ENS 10114	HQ009910	None
B. eremia	Guatemala: Jalapa	UTA A-58522	ENS 10113	HQ009921	HQ010005
B. flavimembris	Guatemala: San Marcos	UTA A-58686	ENS 9377	HQ009928	HQ010013
B. franklini	Guatemala: San Marcos	UTA A-58687	ENS 9378	HQ009948	HQ010016
B. hartwegi	México: Chiapas	UTA A-54816	ENS 10302	HQ009932	None
B. hartwegi	México: Chiapas	UTA A-54817	ENS 10303	HQ009945	HQ009996
B. helmrichi	Guatemala: Baja Verapaz	UTA A-51457	ENS 7802	HQ009941	AY691755*/HQ010002
B. helmrichi	Guatemala: Alta Verapaz	UTA A-58432	JAC 20487	HQ009942	None
B. heiroreias	Guatemala: Chiquimula	UTA A-54712	ENS 9847	HQ009962	HQ010010
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-58689	MEA 1276	HQ009908	None

Appendix 2. (continued)

B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-58690	MEA 1277	HQ009909	None
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-51325	JAC 19198	HQ009976	None
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-58698	JAC 19219	HQ009940	None
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-58699	JAC 19220	HQ009944	None
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-51324	JAC 19197	HQ009970	None
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-51321	JAC 19171	HQ009968	None
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-58540	MEA 1635	HQ009943	None
B. huehuetenanguensis	Guatemala: Huehuetenango	UTA A-51320	JAC 19170	HQ009975	None
B. kaqchikelorum	Guatemala: Sacatepéquez	UTA A-58685	ENS 10283	HQ009911	HQ010020
B. kaqchikelorum	Guatemala: Guatemala	UTA A-58568	ENS 11770	HQ009972	None
B. lincolni	Guatemala: Huehuetenango	UTA A-51486	MEA 627	HQ009926	HQ010008
B. lincolni	Guatemala: Huehuetenango	UTA A-51485	MEA 626	HQ009947	HQ010003
B. lincolni	Guatemala: Quiché	UTA A-51469	ENS 7811	HQ009927	HQ010007
B. lincolni	Guatemala: Quiché	UTA A-51474	ENS 8055	HQ009913	HQ010006
B. lincolni	Guatemala: San Marcos	UTA A-51388	ENS 8327	HQ009950	HQ010019
B. meliana	Guatemala: Baja Verapaz	UTA A-58565	GAR 145	HQ009954	HQ010004
B. meliana	Guatemala: Zacapa	N/A	ENS 11773	HQ009923	None
B. mexicana	México: Oaxaca	UTA A-54810	ENS 10307	HQ009918	HQ009994
B. mulleri	Guatemala: Alta Verapaz	UTA A-50475	MEA 1018	HQ009916	HQ010012
B. morio	Guatemala: Totonicapan	UTA A-53286	ENS 10459	HQ009961	HQ009989
B. morio	Guatemala: Quetzaltenango	UTA A-58523	ENS 10471	HQ009924	HQ010000
B. morio	Guatemala: Quetzaltenango	UTA A-58521	ENS 10469	HQ009929	HQ009991
B. morio	Guatemala: Quetzaltenango	UTA A-58522	ENS 10470	HQ009931	None
B. morio	Guatemala: Quetzaltenango	UTA A-58526	ENS 10474	HQ009959	None
B. morio	Guatemala: Quetzaltenango	UTA A-58527	ENS 10475	HQ009934	HQ009987
B. ninadormida	Guatemala: Huehuetenango	UTA A-58562	MEA 1175	HQ009974	None
B. ninadormida	Guatemala: Huehuetenango	UTA A-58564	MEA 1183	HQ009981	None
B. nussbaumi	Guatemala: Huehuetenango	UTA A-59197	JAC 19792	HQ009938	None
B. nympha	Guatemala: Izabal	UTA A-48662	ENS 7802	HQ009949	None
B. occidentalis	Guatemala: San Marcos	UTA A-58554	JAC 19896	HQ009919	None
B. odonnelli	Guatemala: Izabal	UTA A-48591	MEA 446	HQ009930	HQ009993
B. odonnelli	Guatemala: Izabal	UTA A-51493	ENS 7862	HQ009904	None
B. rufescens	Guatemala: Huehuetenango	UTA A-51491	JAC 19278	HQ009984	HQ010017
B. stuarti	Guatemala: Huehuetenango	UTA A-58144	JAC 19443	HQ009914	None
B. stuarti	Guatemala: Huehuetenango	UTA A-58145	JAC 19518	HQ009935	HQ010009
B. suchitanensis	Guatemala: Jutiapa	UTA A-58422	MEA 1933	HQ009922	HQ010001
B. suchitanensis	Guatemala: Jutiapa	UTA A-58149	MEA 1911	HQ009985	HQ009986
B. suchitanensis	Guatemala: Jutiapa	UTA A-58423	MEA 1936	HQ009937	HQ009999
B. suchitanensis	Guatemala: Jutiapa	UTA A-58150	MEA 1926	HQ009951	HQ009997
B. xibalba	Guatemala: Huehuetenango	UTA A-51424	MEA 633	HQ009901	None
B. xibalba	Guatemala: Quiché	UTA A-51453	ENS 8069	HQ009903	None
B. xibalba	Guatemala: Quiché	UTA A-51456	JAC 19347	HQ009973	None

*Sequence obtained from Parra-Olea (2004). UTA = University of Texas at Arlington, ENS = Eric N. Smith personal field series, JAC = Jonathan A. Campbell personal field series, MEA = Manuel E. Acevedo personal field series, GAR = Rony García Anleu personal field series.

APPENDIX 3.

GenBank cytochrome-*b* Sequences Examined (Fig. 41)

Bolitoglossa adspersa: Colombia, Cundinamarca:

AF212984. *Bolitoglossa altamazonica*: Perú, Loreto, AY526160. *Bolitoglossa alvaradoi*: Costa Rica, Heredia: AY526194. *Bolitoglossa biseriata*: Panamá, Nusagandi: AY526161. *Bolitoglossa carri*: Honduras, Cerro Cantagallo: AY526175–6. *Bolitoglossa celaque*: Honduras, Lempira: AY526177–8. *Bolitoglossa cerroensis*: Costa Rica, San José: AF199195. *Bolitoglossa colonnea*: Panamá, Chiriquí: AY526162. *Bolitoglossa conanti*: Honduras, Cortés: AY526179. *Bolitoglossa decora*: Honduras, Olancho: AY526180. *Bolitoglossa diaphora*: Honduras, Cortés: AY526181. *Bolitoglossa dofleini*: Guatemala, Alta Verapaz: AF212988. *Bolitoglossa dunni*: Honduras, Cortés: AY526182. *Bolitoglossa engelhardti*: Guatemala, San Marcos: AF212987. *Bolitoglossa epimela*: Costa Rica, Cartago: AF212097. *Bolitoglossa flavimembris*: Guatemala, San Marcos: AY526183. *Bolitoglossa flaviventris*: México, Chiapas: AF212983. *Bolitoglossa franklini*: México, Chiapas: AY526184. *Bolitoglossa gracilis*: Costa Rica Cartago: AF212067–8. *Bolitoglossa hartwegi*: México, Chiapas: AF212985. *Bolitoglossa hermosa*: México, Guerrero: AF416678. *Bolitoglossa lincolni*: Guatemala, San Marcos: AY526185. *Bolitoglossa longissima*: Honduras, Olancho: AY526186. *Bolitoglossa macrinii*: México, Oaxaca: AF416680. *Bolitoglossa marmorea*: Panamá, Chiriquí: U89631. *Bolitoglossa medemi*: Panamá, Nusagandi: AY526163. *Bolitoglossa mexicana*: Belize, Toledo: AF212099; Honduras, Atlántida: AF212975; México, Chiapas: AF212976. *Bolitoglossa minutula*: Costa Rica, Puntarenas: AF212098. *Bolitoglossa mombachoensis*: Nicaragua, Granada: AY133485. *Bolitoglossa morio*: Guatemala, San Marcos: AF212986 & AY526187. *Bolitoglossa oaxacensis*: México, Oaxaca: AF416681. *Bolitoglossa occidentalis*: México, Chiapas: AY526158. *Bolitoglossa palmata*: Ecuador, Napo: AY526164. *Bolitoglossa paraensis*: Brazil, Acre, AY526168; Amazonas: AY526166–7. *Bolitoglossa peruviana*: Ecuador, Napo: AY526170; Sucumbíos: AY526169. *Bolitoglossa pesrubra*: Costa Rica, Cartago: AF212084. *Bolitoglossa platydactyla*: México, Veracruz: AF212981 & AY133484. *Bolitoglossa porrasorum*: Honduras, Atlántida: AY526188. *Bolitoglossa riletti*: México, Oaxaca: AF416682. *Bolitoglossa robusta*: Costa Rica, Alajuela: EU448110. *Bolitoglossa rostrata*: Guatemala, Huehuetenango: AY526188–9. *Bolitoglossa rufescens*: Belize, Toledo: AY526159. *Bolitoglossa schizodactyla*: Panamá, Coclé: AY526171. *Bolitoglossa sima*: Colombia, Valle del Cauca: AY526172. *Bolitoglossa striatula*: Costa Rica, Cartago: AF212982. *Bolitoglossa synoria*: Honduras, Ocotepeque: AY526193. *Bolitoglossa yucatana*: México, Quintana Roo: AF212980. *Bolitoglossa zapoteca*: México, Oaxaca: AF416684. *Bolitoglossa* sp.: Colombia, Cundinamarca: AY526173; Costa Rica, Puntarenas: AY526174; El Salvador, Santa Ana: AY526191–2.