Taxonomy, zoogeography, and conservation of the herpetofauna of Nicaragua

Dissertation

zur Erlangung des Doktorgrades

der Naturwissenschaften

vorgelegt beim Fachbereich Biologie

der Goethe-Universität

in Frankfurt am Main

von

Javier Sunyer Mac Lennan

aus Madrid, Spanien

Frankfurt am Main, 2009

Gedruckt mit Unterstützung des Deutschen Akademischen Austauschdienstes

vom Fachbereich Biowissenschaften der Goethe-Universität als Dissertation angenommen.

Dekan: Prof. Dr. Volker MÜLLER

Gutachter: Prof. Dr. Bruno STREIT (Frankfurt am Main)

Prof. Dr. Wolfgang BÖHME (Bonn)

Datum der Disputation:

ABSTRACT

Central America is one of the world's most herpetological diverse areas in relation to its size. Nicaragua is the largest country in this region and separates Nuclear from Lower Central America. It is one of the least herpetological explored countries in Central America and few studies dealing with the herpetofauna of a potion or the entire country have been published. I here update the checklist of the Nicaraguan herpetofauna, present taxonomic revisions of some difficult species complexes, compare the similarities of the composition of the herpetofaunal communities in the major forest formations present in the country within a zoogeographical context, and identify those species with a greater vulnerability risk in Nicaragua.

Taxonomy

The herpetofauna of Nicaragua currently consists of 244 species representing 134 genera and 42 families with 78 amphibian species representing 35 genera and 15 families, and 166 reptile species representing 99 genera and 27 families, which includes six marine species. Sixteen species (12 amphibians and four reptiles) are endemic to the country. Of the 12 endemic amphibian species, three are here described. In addition, five genera (*Anotheca, Cerrophidion, Duellmanohyla, Isthmohyla,* and *Rhinobothryum*) and two species *(Rhadinea godmani* and *Urotheca decipiens*) are known to occur both north and south of Nicaragua although there are no voucher specimens of these taxa to confirm their presence in country.

I complete a bibliographic research updating the nomenclature changes and provide a brief herpetological history of Nicaragua, a recompilation of all species described upon Nicaraguan material and their current synonymy, the first time each species was recorded from the country, and a list of all recognized subspecies occurring in Nicaragua. I discuss the taxonomic uncertainties among the Nicaraguan populations of amphibians and reptiles and take further detailed taxonomic revisions on selected Nicaraguan species groups from the genera *Anolis, Bolitoglossa*, and *Craugastor* along their known distributional range. I describe five new species of herpetofauna (three of which are based on Nicaraguan material), redescribe five species of *Anolis* (three of which occur in

Nicaragua), and provide voucher specimens of five other species for the first time in Nicaragua. In detail:

- I studied the pholidosis, morphometrics as well as hemipenis and dewlap morphology in *Anolis wermuthi*, an anole endemic to the highlands of northern Nicaragua. I examine patterns of geographic variation using discriminant function analysis and discuss the characters that vary both individually and among populations. The results indicate that *A. wermuthi* is a single species with several disjunct, slightly divergent populations. I provide a standardized description, illustrations of the everted hemipenis of an adult topotype, the male and female dewlap, and a distribution map. I also provide brief descriptions of the localities where this species occurs and some ecological notes.

- I studied the pholidosis, morphometrics as well as hemipenis morphology in the Central American anole species *Anolis humilis, A. quaggulus,* and *A. uniformis*. The three taxa are distinct in hemipenis morphology. However, very little differentiation in pholidotic and morphometric characters is documented. I document interspecific variation in several characters but with overlap of the documented ranges. A discriminant function analysis based on five pholidotic characters yielded a scatter diagram that showed large overlap between the clusters of the three taxa. I provide head scalation illustrations, an identification key, a distribution map, and standardized descriptions of the commonly distributed in Nicaragua *A. quaggulus* as well as of the other two species.

- I describe two new species of anoles (genus *Anolis*) from Panama formerly referred to as *Anolis limifrons*. The two new species, *Anolis apletophallus* and *Anolis cryptolimifrons*, differ from *A. limifrons* by having a large bilobed hemipenis (small and unilobed in *A. limifrons*). The new species differ from each other in male dewlap size and coloration. I provide illustrations of the head scalation, everted hemipenis, and dewlap, an identification key, a distribution map, and standardized descriptions of the commonly distributed in Nicaragua *A. limifrons* and the two new species described herein.

- I describe two new species of salamanders of *Bolitoglossa* from southern Nicaragua. *Bolitoglossa indio* is known from Río Indio in the lowlands of the Río San Juan area and *Bolitoglossa insularis* from the premontane slopes of Volcán

Maderas on Ometepe Island. The two new species are of unknown affinities but both differ from their congeners in coloration. *Bolitoglossa indio* is most similar to *B. mexicana* and *B. odonnelli* from which differ by having both broad dorsolateral pale brown stripes not clearly delimited in outline. *Bolitoglossa insularis* is most similar to *B. mombachoensis* and *B. striatula* from which differ by the absence of dark or light defined stripes on dorsum and venter.

- I describe a new species of frog of the genus *Craugastor* from Río San Juan, Nicaragua. The new species, *Craugastor chingopetaca*, is assigned to the *fitzingeri* group and differs from most Central American species of that group by the absence of a midgular pale stripe. Within the *fitzingeri* group it is most similar to *C. crassidigitus* and *C. talamancae* from which it differs in several morphological characteristics such as more extensive webbing, retuse disk covers on some digits, and relative toe length.
- I provide voucher specimens of *Cochranella spinosa*, *Kinosternon angustipons*, *Mesaspis moreletii*, *Cnemidophorus lemniscatus* and *Adelphicos quadrivirgatum* for the first time in Nicaragua. I include descriptions, illustrations, and brief ecological notes for the five new country records.

Zoogeography

Based on the concept of ecological formations proposed by HOLDRIDGE (1967), nine forest formations are found in Nicaragua. Of the total number of terrestrial species of herpetofauna found in Nicaragua, 131 species (55.0%) occur in Lowland Wet Forest, 21 of which (8.8%) are restricted to this forest formation, 168 species (70.6%) occur in Lowland Moist Forest, 15 of which (6.3%) are restricted to this forest formation, 84 species (35.3%) occur in Lowland Dry Forest, four of which (1.7%) are restricted to this forest formation, 47 species (19.7%) occur in Lowland Arid Forest, with no species restricted to this forest formation, 59 species (24.8%) occur in Premontane Wet Forest, three of which (1.3%) are restricted to this forest formation, 116 species (48.7%) occur in Premontane Moist Forest, 10 of which (4.2%) are restricted to this forest formation, 51 (21.4%) species occur in Premontane Dry Forest, with no species restricted to this forest formation, 13 species (5.5%) occur in Lower Montane Wet Forest, two of which (0.8%)

are restricted to this forest formation, and 50 species (21.0%) occur Lower Montane Moist Forest, seven of which (2.9%) are restricted to this forest formation.

The Coefficient of Biogeographic Resemblance algorithm show a distinct composition of the herpetofauna from the isolated highlands of northeastern Nicaragua, which is characterized by a high proportion of endemic species. Two other clusters are evident when analyzing the herpetofaunal similarities among Nicaragua, the Pacific versant and the central mountains and the Atlantic lowlands. In addition, the Pacific lowlands are characterized by a relatively homogeneous composition of the herpetofauna. In contrast, many species have their northern limit of distribution in the Atlantic lowlands with the ranges of most of these species ending in southern Nicaragua. The central mountains constitute the southern limit of distribution of several highland species. In general, there is a greater contribution of reptile than amphibian species to the total herpetofauna present in each forest formation. This unbalance is slightly higher in the dry than in the moist parts of the country. The similarities in the composition of the reptiles between the different forests formations seem to be relatively distinct on an elevation factor, whereas in amphibians similarities might be better explained in correlation with humidity. The total amount of amphibian and reptile species in Nicaragua has a Middle American Element dominance and varies between amphibians and reptiles, with and a greater South American Element influence in anurans and a greater Old Northern Element influence in reptiles. In general, there is a greater percentage of species with a South American Element in extreme southeastern Nicaragua with a decreasing tendency towards northern Nicaragua. Taking in account the geography and geologic history of Nicaragua as well as the known Central American dispersal routes, I identify species of probable occurrence in Nicaragua as well as those places with a greater potential to hold undescribed endemic species.

Conservation

In Nicaragua, no amphibian or reptile populations are entirely free from anthropogenic impact. I determine the endangerment level of all Nicaraguan amphibian and reptile species using the IUCN categorizations and the Environmental Vulnerability Scores. Seventy-six species (31.9%) of Nicaraguan amphibians and terrestrial reptiles have high vulnerability, 118 (49.6%) medium vulnerability, and 44 (18.5%) low vulnerability.

Eighteen species (7.4% of the total herpetofauna) are unknown from protected areas, including 13 high vulnerability species (three are endemic), four medium vulnerability species, and one low vulnerability species. To preserve the future of Nicaragua's amphibians and reptiles, every species should reside in at least one protected area, the protected areas must be guarded, and monitoring programs are needed to detect changes in amphibian and reptile populations, prioritizing highly vulnerable species.

ZUSAMMENFASSUNG

Mittelamerika gehört zu den Regionen der Welt mit der relativ artenreichsten Herpetofauna. Nicaragua ist das größte Land Mittelamerikas und liegt zwischen den nördlichen und südlichen Hochlandblöcken. Es ist eines der am wenigsten herpetologisch erforschten Länder in Mittelamerika und es wurden bisher nur wenige Studien über die Herpetofauna des Landes veröffentlicht. Im Rahmen meiner Doktorarbeit komplettiere ich die herpetologische Artenliste Nicaraguas, präsentiere taxonomische Revisionen schwieriger Artkomplexe, vergleiche die Zusammensetzung verschiedener herpetologischer Artengemeinschaften aus den größeren Waldgebieten Nicaraguas und identifiziere die besonders bedrohten Arten.

Taxonomie

Die Herpetofauna Nicaraguas umfasst 244 Arten aus 134 Gattungen und 42 Familien, wobei 78 Arten aus 35 Gattungen und 15 Familien auf die Amphibien entfallen, und 166 Arten, inklusive sechs marine Arten, aus 99 Gattungen und 27 Familien auf die Reptilien. 16 Arten (zwölf Amphibienarten und vier Reptilarten) sind für Nicaragua endemisch. Von den zwölf endemischen Amphibienarten werden drei in dieser Arbeit beschrieben. Desweiteren gibt es sechs Gattungen (*Anotheca, Cerrophidion, Duellmanohyla, Isthmohyla* und *Rhinobothryum*) und zwei Arten *(Rhadinea godmani* und *Urotheca decipiens*), die sowohl nördlich als auch südlich von Nicaragua vorkommen, die aber bis jetzt noch nicht durch Belegexemplare auch für Nicaragua nachgewiesen werden konnten.

Basierend auf einer Überprüfung der Literatur bringe ich die Nomenklatur der Arten auf den aktuellen Stand und gebe weiterhin einen Überblick über die Geschichte der herpetologischen Erforschung Nicaraguas, eine Auflistung aller Arten, die basierend auf nicaraguanischen Material beschrieben wurden sowie deren aktuelle Synonymie, das Datum des Erstnachweises jeder Art für Nicaragua sowie eine Liste aller anerkannten in Nicaragua vorkommenden Unterarten. Unklarheiten in der Taxonomie nicaraguanischer Amphibien- und Reptilienpopulationen werden diskutiert und taxonomische Revisionen ausgewählter Artengruppen der Gattungen *Anolis, Bolitoglossa*, and *Craugastor* entlang

ihrer Verbreitung durchgeführt. Fünf neue Arten (drei davon basierend auf nicaraguanischen Material) werden beschrieben, fünf *Anolis*-Arten (drei davon aus Nicaragua) werden detailliert wiederbeschrieben, und von fünf Arten habe ich erstmals Belegexemplare aus Nicaragua gesammelt. Im einzelnen wurden folgende Punkte untersucht:

- Pholidose, Morphometrie sowie Hemipenis- und Kehlfahnen-Morphologie von *Anolis wermuthi*, eine für das Hochland Nicaraguas endemische *Anolis*-Arten, wurden untersucht. Dabei wurde die geographische Variation mit Hilfe der Diskriminanzfunktionsanalyse untersucht und die Variation ausgewählter Merkmale zwischen Individuen und Populationen diskutiert. Die Untersuchungen zeigen, dass es sich bei *A. wermuthi* um eine einzige Art mit mehreren disjunkten, leicht divergenten Populationen handelt. Eine genaue Artbeschreibung, inklusive Abbildungen eines ausgestülpten Hemipenis eines adulten Topotypus, der männlichen und weiblichen Kehlfahne und eine Verbreitungskarte werden zusammen mit kurzen Beschreibungen der Fundorte sowie einigen ökologischen Notizen aufgeführt.
- Pholidose, Morphometrie und Hemipenis-Morphologie dreier mittelamerikanischer Anolisarten (*Anolis humilis, A. quaggulus,* und *A. uniformis*) wurden untersucht, um den taxonomischen Status der nicaraguanischen Populationen zu klären. Diese drei Taxa unterscheiden sich deutlich in der Hemipenis-Morphologie, aber nur geringfügig in pholidotischen und morphometrischen Merkmalen. Bei mehreren Merkmalen wurde interspezifische Variation dokumentiert, allerdings mit großer Überlappung der Variationsbreite. Eine auf fünf pholidotischen Merkmalen beruhende Diskriminanzanalyse ergab ein Streudiagramm, welches starke Überlappungen zwischen den Clustern der drei Taxa zeigt. Ein Bestimmungsschlüssel sowie Abbildungen der Kopfbeschuppung, Verbreitungskarten und standardisierte Beschreibungen der drei Arten werden vorgelegt.
- Zwei neue *Anolis*-Arten aus Panama, die bisher der Art *A. limifrons* zugeordnet waren, werden beschrieben. Die beiden neuen Arten, *A. apletophallus* und *A. cryptolimifrons*, unterscheiden sich von *A. limifrons* in ihren großen zweilappigen Hemipenes (klein und einlappig bei *limifrons*). Untereinander unterscheiden sich

die beiden neuen Arten in der Größe der Kehlfahne des Männchens und der Färbung Neben einem Bestimmungsschlüssel werden Abbildung der Kopfbeschuppung, des ausgestülpten Hemipenis, der Kehlfahne, Verbreitungskarten und standardisierte Beschreibungen sowohl der beiden neuen Arten als auch *A. limifrons* vorgelegt.

- Zwei neue Salamanderarten der Gattung *Bolitoglossa* aus Süd-Nicaragua werden beschrieben. *Bolitoglossa indio* stammt vom Rio Indio im Tiefland der Rio San Juan -Region; *B. insularis* kommt an den prämontanen Hängen des Maderas-Vulkans auf der Insel Ometepe vor. Die Verwandtschaftsbeziehungen der beiden neuen Arten zu den anderen Arten dieser Gattung sind unklar, sie unterscheiden sich jedoch in der Farbgebung. *Bolitoglossa indio* ähnelt am stärksten *B. mexicana* und *B. odonelli*, von denen sich die neue Art durch ihre verschwommenen breiten dorsolateralen braunen Streifen abgrenzen lässt. *Bolitoglossa insularis* zeigt die größte Ähnlichkeit zu *B. mombachoensis* und *B. striatula*, weist aber keine klaren hellen oder dunklen Streifen an Bauch und Rücken auf.
- Eine neue Art der Froschgattung *Craugastor* vom Río San Juan in Süd-Nicaragua wird beschrieben. *Craugastor chingopetaca* wird der *fitzingeri*-Gruppe zugeordnet, unterscheidet sich von den meisten anderen Arten dieser Gruppe durch das Fehlen eines blassen Kehlstreifens. Innerhalb der *fitzingeri*-Gruppe ähnelt die neue Art am stärksten *C. crassidigitus* und *C. talamancae*. Eine Abgrenzung ist anhand mehrerer morphologischer Merkmale wie stärker ausgebildete Schwimmhäute, eingekerbte Fingerscheiben und die relative Zehenlänge möglich.
- Erste Belegexemplare für Nicaragua von die Arten *Cochranella spinosa*, *Kinosternon angustipons*, *Mesaspis moreletii*, *Cnemidophorus lemniscatus* and *Adelphicos quadrivirgatum* wurden gesammelt. Beschreibung, Abbildungen und kurze ökologische Angaben werden für die fünf neuen Landesnachweise vorgelegt.

Zoogeographie

Basierend auf dem Konzept der Waldkategorien von HOLDRIDGE (1967) kann man in Nicaragua neun Waldtypen unterscheiden. Betrachtet man die Einteilung der terrestrischen Herpetofauna, so stellt man fest, dass 131 Arten (55,0%) im Lowland Wet Forest vorkommen, 21 dieser Arten (8,8%) kommen dabei nur in diesem Waldtyp vor; 168 Arten (70,6%) kommen im Lowland Moist Forest vor, 15 Arten (6,3%) kommen nur hier vor; 84 Arten (35,3%) kommen im Lowland Dry Forest vor, vier Arten (1,7%) sind auf diesen Lebensraum beschränkt; 47 Arten (19,7%) kommen im Lowland Arid Forest vor, wobei keine Art ausschliesslich hier vorkommt; 59 Arten (24,8%) kommen im Premontane Wet Forest vor, wobei drei (1,3%) Arten nur hier vorkommen; 116 Arten (48,7%) sind im Premontane Moist Forest verbreitet, zehn dieser Arten (4,2%) kommen nur hier vor; 51 Arten (21,4%) kommen im Premontane Dry Forest vor, wobei keine Art ausschliesslich hier vorkommt; 13 Arten (5,5%) sind im Lower Montane Wet Forest verbreitet, wobei zwei Arten (0,8%) nur hier vorkommen; und 50 Arten (21,0%) kommen im Lower Montane Moist Forest vor, mit sieben (2,9%) auf diesen Typ beschränkten Arten.

Der „Coefficient of Biogeographic Resemblance"-Algorithmus belegt, dass die isolierten Hochlandgebiete im Nordosten Nicaraguas eine distinkte Zusammensetzung der Herpetofauna aufweisen, charakterisiert durch einen hohen Endemiten-Anteil. Es zeigen sich zwei weitere Cluster, zum ein der pazifische Abhang und zum anderen die zentrale Bergregion und der atlantische Abhang. Das pazifische Tiefland zeichnet sich durch eine relativ homogene Zusammensetzung der Herpetofauna aus. Im Gegensatz dazu haben viele Arten ihre nördliche Verbreitungsgrenze im atlantischen Tiefland, wobei die Areale der meisten dieser Arten im südlichen Nicaragua enden. Die zentralen Berge bilden die südliche Verbreitungsgrenze für einige Hochland-Arten. Generell ist in jeder Waldkategorie der Beitrag der Reptilien zur Diversität der Herpetofauna größer als der der Amphibien, wobei dies in den trockenen Gebieter stärker ausgeprägt ist als in den feuchten Zonen. Gemeinsamkeiten der Artenzusammensetzung der Reptilien finden sich vor allem in Gebieten gleicher Höhe, während Gemeinsamkeiten in der Artenzusammensetzung der Amphibien eher durch Niederschlag bedingt sind. Generell ist die Herpetofauna Nicaraguas von mittelamerikanischen Elementen dominiert, wobei bei den Anuren auch deutliche südamerikanische Einflüsse erkennbar sind, während die

Reptilien mehr nördliche Elemente aufweisen Generell ist der Anteil der südamerikanischen Elemente im südöstlichen Nicaragua relativ hoch, nimmt jedoch nach Norden hin ab. Unter Berücksichtigung der Geographie und Geologie Nicaraguas sowie der bekannten mittelamerikanischen Ausbreitungswege, identifiziere ich Arten, die mit großen Wahrscheinlichkeit zukünftig in Nicaragua nachgewiesen werden, sowie Gebiete, die ein größeres Potential für noch unbeschriebene endemische Arten haben.

Schutz

In Nicaragua unterliegen alle Amphibien- und Reptilienpopulationen anthropogenen Einflüssen. Ich habe für alle Amphibien- und Reptilienarten Nicaraguas den Grad der Bedrohung mit Hilfe der IUCN-Kategorien und der Environmental Vulnerability Scores ermittelt. Sechsundsiebzig (31,9%) der nicaraguanischen Arten von Amphibien und terrestrischen Reptilien sind stark bedroht, 118 (49,6%) sind bedroht, und 44 (18,5%) sind mäßig bedroht. Achtzehn (7,4%) Arten kommen in keinem der Schutzgebiete vor, davon gehören 13 zu den stark bedrohten Arten (drei davon sind endemisch in Nicaragua), vier sind bedroht, und eine Art ist mäßig bedroht. Um den Fortbestand der Amphibien und Reptilien Nicaraguas langfristig zu gewährleisten, sollten alle Arten mindestens in einem Schutzgebiet vorkommen; die Schutzgebiete müssen zudem bewacht werden, und Monitoring-Programme sind notwendig, um eventuelle Veränderungen in den Amphibien- und Reptilienpopulationen wahrzunehmen. Der Schwerpunkt sollte hierbei auf den stark bedrohten Arten liegen.

RESUMEN

Centroamérica es uno de los lugares del mundo que posee una mayor diversidad herpetológica, en comparación con su tamaño. Nicaragua, es el país más grande de este territorio. A pesar de que separa la parte central de la parte sur del istmo centroamericano, es uno de los países menos herpetelógicamente diversos de Centroamérica, existiendo pocos estudios publicados que traten de la herpetofauna del país entero o incluso de una porción del mismo. En el presente trabajo, se actualiza la lista patrón de la herpetofauna de Nicaragua, se presentan revisiones taxonómicas de complejos de especies complicados, se comparan en un contexto zoogeográfico las similitudes de la composición de las comunidades de anfibios y reptiles en las principales formaciones forestales del país, y se identifican aquellas especies que tienen un mayor riesgo de vulnerabilidad.

Taxonomía

La herpetofauna de Nicaragua actualmente consiste en 244 especies que representan 134 géneros y 42 familias, con 78 especies de anfibios que representan 35 géneros y 15 familias y 166 especies de reptiles que representan 99 géneros y 27 familias, las cuales incluyen 6 especies marinas. Dieciséis especies (12 anfibios y 4 reptiles) son endémicas al país. Se describen 3 de las 12 especies de anfibios endémicos. Adicionalmente, 5 géneros (*Anotheca, Cerrophidion, Duellmanohyla, Isthmohyla* y *Rhinobothryum*) y dos especies (*Rhadinea godmani* y *Urotheca decipiens*) son conocidas tanto al norte como al sur de Nicaragua, a pesar de que no se conocen ejemplares colectados en el país.

Realizo una búsqueda bibliográfica actualizando los recientes cambios de nomenclatura y proveo una breve historia de la herpetología en Nicaragua, una recopilación de todas las especies descritas a partir de material Nicaragüense y su actual sinonimia, la primera vez que cada especie fue registrada en el país, y una lista de todas las subespecies reconocidas en Nicaragua. Discuto aquellas incertidumbres taxonómicas entre las diferentes poblaciones de anfibios y reptiles y realizo una revisión más profunda acerca de la taxonomía de grupos de especies seleccionados de los géneros *Anolis, Bolitoglossa*, and *Craugastor* a través de su rango de distribución conocido. Describo 5 especies nuevas

para la ciencia (3 de las cuales están basados en material nicaragüense), redescribo 5 especies de *Anolis* (3 de las cuales habitan en Nicaragua) y proveo especimenes de 5 especies por primera vez en Nicaragua. En detalle:

- Estudio la foliosis, morfometría, y la morfología del hemipene y del abanico gular del anoli o cherepo de bosque nuboso *Anolis wermuthi*, un cherepo endémico de las zonas montañosas del norte de Nicaragua. Se documentan los rangos de los caracteres estudiados de cada población y examino patrones de variación geográfica con un análisis discriminante, discutiendo aquellos caracteres que varían individualmente o entre poblaciones. Los resultados indican que *A. wermuthi* es una especie con varias poblaciones disjuntas y ligeramente divergentes. Adicionalmente se proporciona una descripción estándar, ilustraciones del hemipene revertido de un topotipo adulto, el abanico gular de ambos sexos, y un mapa de distribución. También se incluye breves descripciones de las localidades donde esta especie se encuentra y algunos comentarios ecológicos.

- Estudio la folidosis, morfometría y morfología del hemipene de los anolis o cherepos centroamericanos *Anolis humilis, A. quaggulus* y *A. uniformis*. Las tres especies son distintivas en cuanto a la morfología del hemipene aunque se documenta muy poca diferencia en caracteres morfométricos y de folidosis. Se observa variación interespecífica en ciertos caracteres pero existe solapamiento de los rangos documentados. Un análisis de función discriminante basado en cinco caracteres folidóticos produjo un diagrama disperso que muestra gran solapamiento entre los rangos de los tres taxones. Se proporciona ilustraciones de las escamas de la cabeza, una clave dicotómica, un mapa de distribución, y descripciones estándar del comúnmente distribuido en Nicaragua *A. quaggulus*, así como de las otras dos especies.

- Describo dos especies nuevas de anolis o cherepos (género *Anolis*) de Panamá anteriormente referidas como *Anolis limifrons*. Ambas nuevas especies, *Anolis apletophallus* y *Anolis cryptolimifrons*, difieren de *A. limifrons* en tener un hemipene grande y bilobulado (pequeño y unilobulado en *A. limifrons*). Las dos especies nuevas difieren entre sí en el tamaño y coloración de la papera gular de los machos adultos. Se proporciona ilustraciones de las escamas de la cabeza, dibujos del hemipene revertido y fotografías en vida de la papera gular, una clave dicotómica de identificación y descripciones estándar del comúnmente distribuido en Nicaragua *A. limifrons*, así como de las otras dos nuevas especies.

- Describo dos especies nuevas de salamandras (género *Bolitoglossa*) provenientes del sur de Nicaragua. *Bolitoglossa indio* proviene de las cercanías del Río Indio, en las tierras bajas del Departamento de Río San Juan, sureste de Nicaragua. *Bolitoglossa insularis* proviene de las laderas premontanas del Volcán Maderas en la Isla de Ometepe, Departamento de Rivas, suroeste de Nicaragua. Se desconocen las afinidades de las dos nuevas especies pero ambas difieren de sus congéneres en coloración. *Bolitoglossa indio* es más similar a *B. mexicana* y *B. odonnelli* de quien difiere por no tener las anchas franjas dorsolaterales claramente delimitadas. *Bolitoglossa insularis* es más similar a *B. mombachoensis* y *B. striatula* de quien difiere por la ausencia de estrías definidas claras u oscuras en el dorso y vientre.
- Describo una nueva especie del género *Craugastor* de Río San Juan, Nicaragua. Se asigna la nueva especie, *Craugastor chingopetaca*, al grupo *fitzingeri* y difiere de la mayoría de las especies de ese grupo en Centroamérica por la ausencia de una pálida franja media gular. Dentro del grupo *fitzingeri* es la más parecida a *C. crassidigitus* y *C. talamancae* de quien difiere en ciertas características morfológicas como membranas más extensas, cubiertas de los discos emarginadas en algunos dedos, y longitud relativa del pie.
- Se registra por primera vez en Nicaragua a *Cochranella spinosa*, *Kinosternon angustipons*, *Mesaspis moreletii*, *Cnemidophorus lemniscatus* y *Adelphicos quadrivirgatum*. Incluyo descripciones, ilustraciones, y breves comentarios ecológicos de las cinco especies.

Zoogeografía

Basado en el concepto de formaciones ecológicas propuesto por HOLDRIDGE (1967) en Nicaragua se encuentran nueve tipos de formaciones forestales. Del número total de especies de herpetofauna terrestres registrados en Nicaragua, 131 especies (55,0%) se encuentran en el Bosque Lluvioso bajo, 21 de las cuales (8,8%) están restringidas a esta formación forestal, 168 especies (70,6%) se encuentran en el Bosque Húmedo Bajo, 15 de las cuales (6,3%) están restringidas a esta formación forestal, 84 especies (35,3%) se encuentran en el Bosque Seco Bajo, 4 de las cuales (1,7%) están restringidas a esta formación forestal, 47 especies (19,7%) se encuentran en el Bosque Árido Bajo sin ninguna especie restringida a esta formación forestal, 59 especies (24,8%) se encuentran en el Bosque Lluvioso Premontano, 3 de las cuales (1,3%) están restringidas a esta formación forestal, 116 especies (48,7%) se encuentran en el Bosque Húmedo Premontano, 10 de las cuales (4,2%) están restringidas a esta formación forestal, 51 especies (21,4%) se encuentran en el Bosque Seco Premontano sin ninguna especie restringida a esta formación forestal, 13 especies (5,5%) se encuentran en el Bosque Lluvioso Montano, 2 de las cuales (0,8%) están restringidas a esta formación forestal, y 50 especies (21,0%) se encuentran en el Bosque Húmedo Montano, 7 de las cuales (2,9%) están restringidas a esta formación forestal.

Un diagrama de coeficientes de semejanza biogeográfica muestra una composición distintiva de la herpetofauna de las zonas montañosas del noreste de Nicaragua, zona caracterizada por la alta proporción de especies endémicas. Otros dos clusters son evidentes cuando se analizan las similitudes de la herpetofuana en Nicaragua, la zona del Pacífico y el resto del país. Adicionalmente, las zonas bajas del Pacífico se caracterizan por una composición de la herpetofauna relativamente homogénea en contraste con las zonas bajas del Atlántico, las cuales están caracterizadas por un número substancial de especies que tienen su límite norte de distribución, principalmente en el sur. Las montañas centrales constituyen el límite sur de distribución de varias especies montanas. En general, hay una mayor contribución de reptiles que de anfibios a la herpetofauna total presente en cada formación forestal. Este desequilibrio es ligeramente más pronunciado en las partes secas que en las húmedas del país. Las similitudes en la composición de los reptiles entre las diferentes formaciones forestales parece ser relativamente distintiva en relación a la altitud, mientras que en la de los anfibios podría ser mejor explicado en relación a la humedad. Existe un predominio del Elemento Centroamericano en el número total de especies de anfibios y reptiles nicaragüenses y varía entre anfibios, con una mayor influencia del Elemento Suramericano, y reptiles, con una mayor influencia del Elemento Norteamericano. En general hay un mayor porcentaje de especies con un Elemento Suramericano en el extremo sureste de Nicaragua y con una tendencia al descenso en dirección norte. Teniendo en cuenta la historia geográfica y geológica de

Nicaragua así como las rutas de dispersión a través de Centroamérica, se teoriza sobre aquellas especies con un mayor potencial de ser encontradas a medida que se continúe investigando en Nicaragua, así como aquellos sitios que pudieren albergar un mayor potencial de sustentar especies endémicas todavía no descritas.

Conservación

En Nicaragua, ninguna población de anfibio o reptil está totalmente libre del impacto humano. Se determina el nivel de amenaza de todas las especies de anfibios y reptiles de Nicaragua basado en las categorizaciones de la IUCN y en un indicador para estimar la vulnerabilidad ambiental de las especies. Se considera a 76 especies de anfibios y reptiles terrestres (31,9%) de alta vulnerabilidad, 118 (49,6%) de vulnerabilidad media y 44 (18,5%) de baja vulnerabilidad. No se conoce la existencia de 18 especies en ningún área protegida (7,4% de la herpetofauna total, incluyendo especies marinas), las cuales incluyen 13 especies de alta vulnerabilidad (tres de las cuales son endémicas), 4 de vulnerabilidad media y 1 de baja vulnerabilidad. Para preservar el futuro de los anfibios y reptiles en Nicaragua, todas las especies deberían residir en al menos una de las áreas protegidas establecidas, las cuales deben guardar su integridad y se deben monitorear todas las especies en busca de cambios en sus poblaciones, priorizando las especies consideradas de alta vulnerabilidad.

ABBREVIATIONS

AG	Armando GÓMEZ
AGD	axilla-groin distance
AH	Andreas HERTZ
CBR	coefficient of biological resemblance
CR	critically endangered
DAG	number of medial dorsal scales between axilla and groin
DD	data deficient
DFA	discrimant function analysis
DM	Darwin MANZANARES
DS	discriminant scores
E	east
e.g.	exempli gratia (for example)
EL	eye length
EN	endangered
et al.	et alii, et aliae, et alia (and others)
etc.	etcetera
EVS	environmental vulnerability score
Fig.	figure
FL	foot length
GK	Gunther KÖHLER
GP	Guillermo PÁIZ
GPS	global positioning system
h	hour
HL	head length
HW	head width
i.e.	id est (that is)
IG	Iris GARBAYO
IND	internasal distance
INL	infralabials
IOD	interorbital distance
IP	interparietal scale
IUCN	international union for conservation of nature

JS	Javier SUNYER
JT	Josiah TOWNSEND
km	kilometers
km^2	square kilometers
LAF	lowland arid forest formation
LC	least concern
LDF	lowland dry forest formation
LMF	lowland moist forest formation
LMMF	lower montane moist forest formation
LMWF	lower montane wet forest formation
LO	Lenin OBANDO
LW	Larry WILSON
LWF	lowland wet forest formation
m	meters
MA	Middle American element
Ma	million years ago
MD	Matthias DEHLING
ml	milliliters
mm	millimeters
mm^2	square millimeters
MT	maxillary teeth
N	north
NED	nostril-eye distance
NGO	non-governmental organization
NT	near threatened or Norving TORRES (see context)
OA	Osmar ARRÓLIGA
ºC	degrees centigrade
ON	old northern element
P	peripheral
PDF	premontane dry forest formation
pers. com.	personal commentary
pers. obs.	personal observation
PMF	premontane moist forest formation
PT	premaxillary teeth

PWF	premontane wet forest formation
R	restricted
S	south
SA	South American element
SHL	shank length
SL	snout length or Sebastian LOTZKAT (see context)
SMF	Senckenberg Museum Frankfurt
SO	suboculars
sp.	species (singular)
SPL	supralabials
spp.	species (plural)
SS	supraorbital semicircles
ST	Scott TRAVERS
SVL	snout-vent length
TL	tail length
TLN	type locality is Nicaragua
TM	tympanum length
UCA	Universidad Centroamericana
VAG	number of medial ventral scales between axilla and groin
VT	vomerine teeth
VU	vulnerable
W	widespread or west (see context)
yr	year

CONTENTS

LIST OF TABLES

LIST OF FIGURES

1 GENERAL INTRODUCTION

The Republic of Nicaragua is the largest of all the Central American countries with an area of 130,373.47 km^2, and shares a northern border with Honduras and a southern one with Costa Rica (MARENA, 1999). The country is bordered on the west by the Pacific Ocean and on the east by the Caribbean Sea. In addition to the mainland territory, which includes almost 8% of lake surfaces (not including Ometepe, the largest Nicaraguan island situated in the freshwater Lake Nicaragua), there are several adjacent keys and small islands, the largest of which are the Corn Islands, located 77.5 km ENE of Bluefields (WEAVER et al., 2003, VILLA, 1972b). The republic is formed of 17 political units called Departamentos, each of which is subdivided into several Municipios.

The geology of Central America is complex. The Central American isthmus was formed by the union of several isolated land masses grouped into four principal geologic units or blocks (Maya, Chortis, Chorotega, and Choco), which came to connect the previously isolated North and South America, allowing terrestrial biotic exchange (SAVAGE, 2002). Nicaragua constitutes the southernmost part of the Chortis block, which connected the southeastern portion of the Maya block by the end of the middle Eocene (about 38 Ma). This connection resulted in extensive volcanism from the Miocene through the Pliocene and probably caused the Pliocene uplift of the mountains of north-central Nicaragua (SAVAGE, 2002). The southern portion of the Chortis block connected the northern portion of the Chorotega block during the Pliocene (5.3 to 1.8 Ma; BOLAÑOS et al., 2008) and this area, the Nicaraguan Depression, separates Nuclear from Lower Central America. The continuous subduction of the Cocos Plate under the Caribbean plate at the Middle American trench (west of Nicaragua) produced Quaternary uplift (<0.6 Ma) of the Pacific volcanic chain (SAVAGE, 2002; CARR et al., 2007). This uplift continues today.

The geography of Nicaragua is diverse. Most parts of the country lies on relatively homogeneous lowlands (94% of the country surface lies below 1000 m), with the exception of the central mountains and the line of isolated volcanoes situated along the Pacific coast (GILLESPIE et al., 2001). The central mountains are constituted by four main mountain ranges (from north to south: Cordilleras Dipilto-Jalapa, Isabelia, Dariense, and Chontaleña), which have a north to south altitudinal decrease, with the northernmost about twice as high as the southernmost. Cerro Mogotón (2107 m) is located on the northern border with Honduras and constitutes the highest mountain peak in Nicaragua. The Pacific lowlands are crossed by a straight line of several isolated volcanoes situated parallel to the coast that includes the Cordillera de los Maribios. Several of these volcanoes are currently active and Volcán San Cristóbal (1745 m) is the highest volcano in Nicaragua. In chapter 3 of the present thesis I include a detailed geologic and physiographic background of the country.

Nicaragua has a warm tropical climate dominated by moist easterly trade winds. The mean annual temperature oscillates between 18 and 28 °C and varies with the altitude (MARENA, 1999). A dry season extends from December through April and a wet season from May through November. The dry season is much more severe on the Pacific than on the Caribbean versant due to the partial rain shadow effect caused by the central mountains. Rainfall ranges from over 6000 mm/yr along the southeastern Caribbean lowlands, to 750 mm/yr along the north-central Pacific lowlands (MARENA, 1999). Because of orographic effects and topographic patterns, about 90% of all runoff in Nicaragua ultimately flows into the Caribbean (WEAVER et al., 2003). Precipitation in the central mountains feeds the three major rivers in Nicaragua: Río Coco on the northernmost portion of the country, Río Grande de Matagalpa at approximately the middle of the country, and Río San Juan that constitutes the water exit of Lake Nicaragua on the southernmost portion of the country. Lake Nicaragua is the largest lake in Central America and is fed by several short rivers as well as by Lake Managua, the second largest lake in Central America, which receives most of its water from the western portion of the Nicaraguan central mountains. The Pacific volcanoes are mostly characterized by short and steep seasonal rivers that are only running during heavy rains.

Nicaragua has traditionally been divided into three biogeographic regions based on physiography, climate, vegetation, and zoogeography (TAYLOR 1963; INCER 1973; SALAS 1993; MARENA, 1999; JOSSE et al., 2003): the Pacific lowlands (15% of the surface area of Nicaragua) with high temperatures and a pronounced dry season, the Atlantic lowlands (50%) with high temperatures and precipitation throughout the year, and the central mountains (35%) with cool temperatures and moderate rainfall that varies with topography. There have been several detailed studies dealing with the classification of ecosystems and forest formations in Nicaragua, among them PONSOL (1958), TAYLOR (1963), INCER (1973), HOLDRIDGE (1967), SALAS (1993), DINERSTEIN et al. (1995), and MEYRAT (2001). In chapter 3 of the present thesis I include a description of the different forest formations found in Nicaragua following HOLDRIDGE (1967).

Nicaragua was first discovered by Europeans in 1502 when Christopher Columbus landed at Cabo Gracias a Dios. The country's native population, estimated at 650,000 at the time of the conquest, declined to 5,000 after the Spanish arrived (WEAVER et al., 2003). In the 18th century Nicaragua had its lowest human population and this period of time was probably coincident with the greatest extent of forest coverage (MARTÍNEZ-SÁNCHEZ et al., 2001). During the last two centuries human impacts on Nicaragua's forests have been considerable, becoming extreme since the second half of the 20th century. Coffee plantations in the highlands, cotton and sugar plantations in the western lowlands, cattle ranching in the eastern lowlands, and subsistence agriculture all over the country characterized the advance of the agricultural frontier, which together with associated pesticides, annual burns, mining, timber wood extraction, vulcanism, prolonged droughts, and occasional hurricanes, considerably diminished the natural forests in Nicaragua (WEAVER et al., 2003, MARTÍNEZ-SÁNCHEZ et al., 2001). Although deforestation was slowed by Nicaragua´s civil war during the 1980s (NIETSCHMANN, 1990), the over one-half forested country in 1950 was only one-third forested by 1990. During the 1990s, Nicaragua´s rain forests disappeared at a rate 10 times faster than those in Amazonia. (WEAVER et al., 2003). Currently, Nicaragua is the second poorest country in the western hemisphere with around 5,600,000 inhabitants and a 2.3% rate of human population growth (PRB, 2008). There are 9 different types of protected areas that have been established in 76 separate areas, which occupy 18.2% of the country and include the 23% of the Atlantic region, 12% of the Central region, and 5% of the Pacific region. Still, 75% of all reserves have less than 50% of forest cover and legal protection seems insufficient in light of the tremendous pressures placed on natural resources by the growing human population (WEAVER et al., 2003).

Nicaragua's predominant low relief, high deforestation rate, and political instability have in general attracted few herpetologists. It is one of the least herpetologically surveyed countries in Central America (WAKE, 2000) and several areas remain understudied, if studied at all. The first herpetofaunal species known to have been collected in Nicaraguan territory is *Phyllodactylus tuberculosus* in 1835. This species was described from "Californien" (WIEGMANN, 1835) or California, a small village on the Pacific coast of Nicaragua (DIXON, 1960). Previously, several species known to occur in Nicaragua were described on material labelled simply "America" or Indiis" and were not likely collected in Nicaraguan territory (SAVAGE, 2002). However, it was not until the second half of the 19th century that the North Americans Edward D. COPE and Edward HALLOWELL, both from the Academy of Natural

Sciences in Philadelphia, began with a series of papers that involved Nicaraguan material. This material was mostly composed by specimens of amphibians and reptiles they received from the different expeditions of the U. S. Navy that were interested in Nicaragua because it was part of the sea route to travel from the eastern to the western United States and also because of the country's potential of holding America's first interoceanic channel. Although most of these specimens were simply labelled as from "Nicaragua" and in general included no further locality details, the expeditions in Nicaragua were mostly undertaken between El Realejo on the Pacific coast (a currently abandoned harbor near the present day Corinto in northwestern Nicaragua) and Greytown (currently known as San Juan del Norte) in the southernmost portion of the Nicaraguan Atlantic coast, through the great Lake and along the San Juan River. In a 31 year period, mostly COPE but also HALLOWELL recorded one-third of the total species currently known to occur in the country and described 30 species based on Nicaraguan material, 16 of which are currently valid species. This period of time (1855–1886) is by far the most relevant in the history of Nicaragua's herpetological knowledge and a significant amount of publications dealing with Nicaraguan specimens appeared, the most substantial being HALLOWELL (1861) and COPE (1871a, 1874, 1886).

The end of the 19th century was characterized by the contributions of the German born Albert C. L. G. GÜNTHER and the Belgian Albert BOULENGER, both from the British Museum in London. These two herpetologists had a wide scope: BOULENGER covered between 1882 and 1896 the world's known species of amphibians and reptiles (SAVAGE, 2002), and GÜNTHER contributed to the knowledge of the herpetofauna of Mexico and Central America for a 17 year period (GÜNTHER, 1885–1902). Together they included 23 species previously not known from the country in their monumental works, which included the description of nine news species based on Nicaraguan material, five of which are currently valid species.

During the first decade of the 20th century, the Nicaraguan Dioclesiano CHÁVEZ accompanied Seth E. MEEK on several ichthyologic expeditions throughout the country. Although these expeditions resulted in the collection of several amphibians and reptiles species, the material (deposited in the Museo Nacional de Nicaragua) was destroyed during fires which were caused by the 1931 and 1972 Managua earthquakes (G. A. RUIZ, pers. com.).

In 1916, the American Museum of Natural History granted two Northamerican assistants of Gladwyn K. NOBLE funds for an over half a year collecting expedition in eastern Nicaragua. At that time, Nicaragua was already considered "perhaps the least known of the large republics of Central America" and "had not been visited by a herpetologist for a long time" (NOBLE, 1918). This research yielded nine new country records and the description of two new species from Nicaragua, one of which is currently valid.

The next research dealing with the herpetological knowledge of a portion of Nicaragua as a unit was not made until Mr. Morrow ALLEN collected material along the Río Escondido on eastern Nicaragua from July to September 1935 (GAIGE et al., 1937). The 391 amphibians and reptiles he collected were purchased from him by the Museum of Zoology, University of Michigan, and were studied by Helen T. GAIGE, Norman HARTWEG, and Laurence C. STUART (GAIGE et al., 1937). The Allen collection yielded nine new country records.

By the late 1930s a more or less formal agreement among the leading United States herpetologists had divided the different countries in Mesoamerica into spheres of influence. Emmett Reid DUNN planned his research in Costa Rica and Panama and ended up adding Nicaragua to his planned monograph (SAVAGE, 2002). DUNN's research included five new country records and two new species from Nicaragua, one of which is currently valid.

The following two decades were characterized by low herpetological research activity with perhaps the exception of Thomas R. HOWELL, a Northamerican ornithologist who collected several amphibians and reptiles in the current border area between Atlantic Nicaragua and Honduras. The Howell collection was studied by Bayard H. BRATTSTROM, Howard W. CAMPBELL, and himself, and resulted in four new country records for the country (BRATTSTROM & HOWELL 1954; CAMPBELL & HOWELL, 1965).

It was not until the early 1960s that the first Nicaraguan herpetologist, Jaime VILLA, took the lead in the herpetological research in the country leading to a high number of contributions, which included publications, checklists, and the first books on the amphibians and reptiles from Nicaragua. He was the first herpetologist to focus on Nicaragua and collected specimens from a good portion of the country that were later used in his own works and by other researchers in their Central American revisions. VILLA is by far the greatest of all Nicaraguan herpetologists and his most substantial contributions to the knowledge of the herpetology from the country are VILLA (1962, 1972a, 1983) and VILLA et al. (1988). He was in charge of the herpetological collection of the Museo Nacional de Nicaragua and although he did not describe any species from Nicaragua, he recorded at least 29 new country records. He led herpetological research in Nicaraguan during most of the second half of the 20th century, although he was only active in the country for around two decades. Two dramatic events took place in Nicaragua during VILLA's period that would significantly affect the herpetological knowledge from the country: first, the 1972 catastrophic earthquake in Managua, which destroyed all alcoholic specimens from the Museo Nacional de Nicaragua (VILLA, 1981), and second, the Nicaraguan civil war (1979–1990). The combination of missing voucher specimens and the impossibility of getting fresh material from the country probably forced VILLA to base his two last checklists from Nicaragua (i.e., VILLA 1983; VILLA et al., 1988) on inadequate material, leading to some degree of confusion during the following decades regarding the verification of several species.

The herpetological research in Nicaragua during the last decade has been characterized by the substantial contributions of the German Gunther KÖHLER, curator of the herpetological collection deposited in the Forschungsinstitut und Naturmuseum Senckenberg. KÖHLER examined most Nicaraguan specimens hosted in museums worldwide and focused his abundant collecting mostly in isolated mountain areas of difficult access not previously visited by herpetologists, as well as in both Nicaraguan Biosphere Reserves. He included around a dozen new country records, as well as the description of four species from Nicaragua, all of which are currently valid. Part of his ongoing research in Nicaragua was summarized in KÖHLER (2001).

A relatively large amount of foreign herpetologists have contributed to a smaller degree to the knowledge of the taxonomy of the amphibians and reptiles from Nicaragua, among them: Lars G. ANDERSSON, Thomas BARBOUR, Oskar BOETTGER, Arden H. BRAME Jr., Jonathan A. CAMPBELL, Charles J. COLE, James R. DIXON, Herndon G. DOWLING, Floyd L. DOWNS, William E. DUELLMAN, Sharon B. EMERSON, Henry S. FITCH, Laurence M. HARDY, Robert W. HENDERSON, Arthur LOVERIDGE, James R. MCCRANIE, John R. MEYER, Michael OBERMEIER, Ardiel Z. QUINTANA, Jay M. SAVAGE, Karl P. SCHMIDT, Ralph SCHMITT, Norman J. SCOTT Jr., Richard A. SEIGEL, Robert SEIPP, Peter J. STAFFORD, Leonhard H. STEJNEGER, Edward H. TAYLOR, Josiah H. TOWNSEND, Linda TRUEB, Erick P. VAN DEN BERGHE, Miguel VENCES, Eva VIELMETTER, and Larry D. WILSON. Other workers dealt with ecological or conservational aspects of some Nicaraguan amphibians and reptiles, among them: Anna L. BASS, Brian W. BOWEN, Janalee P. CALDWELL, Cathi L. CAMPBELL, Archie CARR, Martin L. CODY, Richard D. DURTSCHE, Pierre FIDENCI, Mario HURTADO, Martin JANSEN, Cynthia J. LAGUEUX, William A. MCCOY, Jeanne A. MORTIMER, Bernard NIETSCHMANN, Laurie J. VITT, and Peter A. ZANI.

Aside from Jaime VILLA, a few other Nicaraguan workers have contributed to the knowledge of the Nicaraguan herpetofauna, among them: Fabio BUITRAGO, Milton G. CAMACHO, Horacio MAYORGA, Josefa MONTENEGRO, and Gustavo A. RUIZ. Several other Nicaraguan contributors wrote unpublished dissertations stored in different universities from all over the country. Currently, an increasing number of Nicaraguan amateur herpetologists are actively working in several parts of the country, generating a considerable amount of grey literature. In chapter 2 of the present thesis I include in detail all references that record every species for the first time in Nicaragua, and those that refer to the description of all species based on Nicaraguan material, including their current synonymy.

Although Nicaragua is a transitional area between Nuclear and Lower Central America and has acted as a bottleneck in the distribution of species throughout Central America, the herpetofaunal composition of the isolated forested areas is poorly known. Most of the scarce conservational information for the Nicaraguan amphibians and reptiles has been generated exclusively for species with commercial value and the conservational status for most species within the country remains unknown. Therefore, a comprehensive study on the Nicaraguan herpetofauna becomes necessary in order to summarize the current knowledge, contribute new findings, and orient future research in the country. The present study has three major goals: (1) to update the checklist of the Nicaraguan herpetofauna; (2) to compare the composition of the herpetofaunal communities in the major forest formations present in Nicaragua within a zoogeographical context; and (3) to identify those species with a greater risk of vulnerability in the country.

1.1 OUTLINE OF THE THESIS

In chapter 2, I study the taxonomy of the herpetofauna of Nicaragua. Based on bibliographic research, I identified the first time each species of amphibian and reptile was reported from the country, the currently recognized subspecies, and the Nicaraguan type material. Based on the material I collected, as well as on published records, I created an updated checklist of the herpetofauna for the country and identified the taxonomic uncertainties among the Nicaraguan populations. I undertook further taxonomic research on selected Nicaraguan species along their known range, including the widespread and diverse genera *Anolis* [*Anolis wermuthi* (chapter 2.3.1), *A. quaggulus* (chapter 2.3.2) and *A. limifrons* (chapter 2.3.3)], *Bolitoglossa* (chapter 2.3.4), and *Craugastor* (chapter 2.3.5). I additionally provide voucher specimens for the first time in Nicaragua for several species (chapter 2.3.6).

In chapter 3, I study the biogeography of the herpetofauna of Nicaragua. Based on the average temperature and precipitation, I divide Nicaragua into nine forest formations. Based on published records, specimens I collected, and museum specimens, I calculate the distributional range of each species in each of the forest formations present in Nicaragua. I analyzed the similarities of the herpetofaunal composition between the different forest formations and discussed them in a historical and geological context.

In chapter 4, I study the conservational status of the herpetofauna of Nicaragua. I categorized all amphibian and reptile species known to occur in Nicaragua using the IUCN (International Union for Conservation of Nature) Red List criteria in order to classify the conservation status of each Nicaraguan species across national boundaries. Based on distributional and ecological factors, I identified those species with a greater potential for population decline in Nicaragua.

In chapter 5, I discuss the main results of the dissertation in a general context. This thesis work also leaves open several issues that should be addressed in the future through new studies, as proposed in the outlook of this dissertation.

All chapters have been written as individual scientific papers (see below for complete citations of all papers). Chapters 2.3.1 [paper 1], 2.3.4 [paper 2], and 2.3.5 [paper 3] are already published in "Senckenbergiana biologica", and chapters 2.3.2 [paper 4], 2.3.3 [paper 5], in "Salamandra" and "Herpetologica", respectively. Chapter 2.3.6 is a composition of two individual papers, one of them [paper 6] already published in "Salamandra", and the other one [paper 7] accepted in September 2008 in the same journal. Chapter 4 [paper 8] was accepted for publication in September 2006 as a chapter of the forthcoming book "Conservation of Mesoamerican amphibians and reptiles" (WILSON & TOWNSEND, Eds.). All these chapters have been peer reviewed. Chapter 3 [paper 9] has not yet been submitted. The format and structure of most chapters was modified in order to fit to the format and structure of the present cumulative thesis. This dissertation shows additionally the locality data of all specimens collected during this investigation (Appendix A), data regarding the report of each species for the first time in Nicaragua, and the currently recognized subspecies in the country (Table 1), a compilation of the Nicaraguan type material and data supporting my choice when following determined taxonomic treatments (part of chapter 2.3), and photographs in life of most species encountered during the fieldwork. I was in charge of all stages (field work, data geneation in the lab, statistical analyses, and writing the mansucripts including the making of figures) of all mentioned publications with the exceptions of chapter 2.3.2 [paper 4], where I exclusively contributed with fieldwork and examining and measuring all specimens.

[1] **SUNYER, J.**, M. VESELÝ & G. KÖHLER (2008): Morphological variation in *Anolis wermuthi* (KÖHLER & OBERMEIER 1998), a species endemic to the highlands of north-central Nicaragua (Reptilia, Squamata, Polychrotidae). — Senckenbergiana biologica, 88(2): 335–343.

[2] **SUNYER, J.,** A. HERTZ, S. LOTZKAT, D. B. WAKE, B. ALEMÁN, S. ROBLETO & G. KÖHLER (2008): Two new species of salamanders (genus *Bolitoglossa*) from southern Nicaragua (Amphibia: Caudata: Plethodontidae). — Senckenbergiana biologica, 88(2): 319-328.

[3] KÖHLER, G. & **J. SUNYER** (2006): A new species of rain frog (genus *Craugastor*) of the *fitzingeri* group from Río San Juan, southeastern Nicaragua. — Senckenbergiana biologica, 86(2): 261–266.

[4] KÖHLER, G., S. ALT, C. GRÜNFELDER, M. DEHLING & **J. SUNYER** (2006): Morphological variation in Central American leaf-litter anoles (*Norops humilis, N. guaggulus,* and *N. uniformis*). — Salamandra, 42(4): 239–254.

[5] KÖHLER, G. & **J. SUNYER** (2008): Two new species of anoles formerly referred to as *Anolis limifrons* (Squamata: Polychrotidae). — Herpetologica, 64(1): 92–108.

[6] **SUNYER, J.** & G. KÖHLER (2007): New and noteworthy records of amphibians and reptiles from Nicaragua. — Salamandra, 43(1): 15–20.

[7] **SUNYER, J**., L. WILSON, J. TOWNSEND, S. TRAVERS, L. OBANDO, G. PÁIZ & G. KÖHLER (in press): Three new country records of reptiles from Nicaragua. — Salamandra.

[8] **SUNYER, J.** & G. KÖHLER (in press): The conservation status of the herpetofauna of Nicaragua. *In*: WILSON, L. D. & J. TOWNSEND (Eds.): Conservation of Mesoamerican amphibians and reptiles. [Eagle Mountain Publishing].

[9] **SUNYER, J**., B. STREIT & G. KÖHLER (in prep.): Zoogeography of the herpetofauna of Nicaragua.

2 TAXONOMY OF THE HERPETOFAUNA OF NICARAGUA

2.1 INTRODUCTION

Nicaragua has been largely overlooked by field biologists and is one of the least herpetologically explored countries in Middle America (WAKE, 2000). It is in general considered to have a lower potential to hold endemic species than its neighboring countries, mostly due to its low relief. In addition, most of the original forests from the few highlands present in the country have been affected either by human intervention, relatively recent volcanic activity, or both. Therefore, few taxonomists have continuously worked in this country and those who have, produced, in general, a relatively small amount of publications. The major contributions to the knowledge of Nicaragua's herpetofauna have been those of Edward Drinker COPE, Jaime VILLA, and Gunther KÖHLER.

Taxonomical studies in Nicaragua date back to the 19^{th} century and have been influenced by the variable political history of the country (Fig. 1). By the mid 1800s, the country was part of the sea route to travel from eastern to western United States and received much immigration. In the last one-third of the 19^{th} century the San Juan River received great international attention for its potential of becoming part of America's first interoceanic channel, especially from the United States, which later became deeply involved in Nicaraguan politics until Northamericans left the country in the 1930s. This was the herpetologically most productive period of time (see Fig. 1) and several publications involving a large number of new species and first country records appeared, from especially the Atlantic versant, among them HALLOWELL (1861), COPE (1871a, 1874, 1886), GÜNTHER (1885–1902), NOBLE (1918), and GAIGE et al. (1937). Research activity in Nicaragua was limited until J. VILLA and coworkers took the lead for most of the second half of the 20^{th} century, resulting in a large number of publications dealing with the Nicaraguan herpetofauna mostly from the Pacific versant (see Fig. 1), among them VILLA (1962, 1972a, 1983). From the late 1990s to the present, G. KÖHLER and coworkers produced a substantial number of publications (see Fig. 1), mostly in the two Nicaraguan Biosphere Reserves, Bosawas and Río San Juan, as well as in several mountain peaks from all over the country. Part of his research was summarized in KÖHLER (2001).

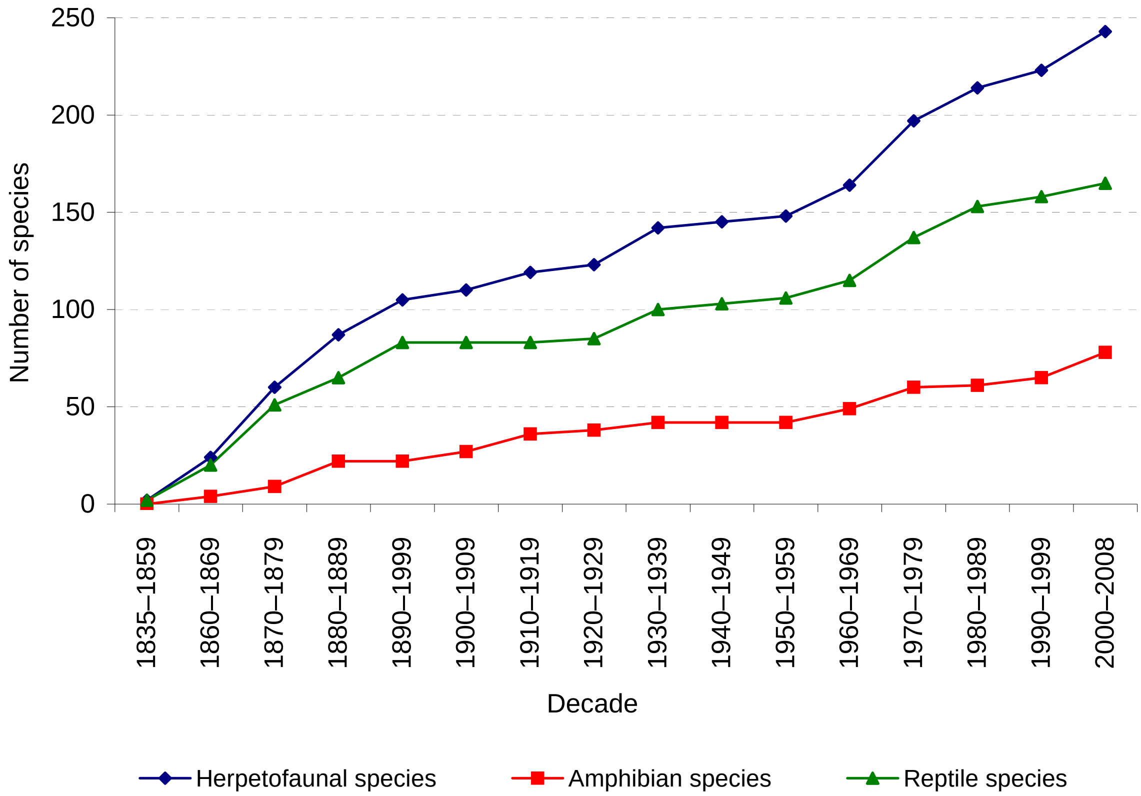


Fig. 1. Cumulative number of herpetofaunal species recorded in Nicaragua from 1835 until present. Data obtained from Table 1.

There have been minor discrepancies regarding the total number of species of amphibians and reptiles recorded in Nicaragua. Most of the information regarding Nicaraguan material is widely scattered throughout the literature and several checklists made for the country were not supported by voucher specimens. In some cases these compilations did not differentiate between records based on voucher specimens from those based on personal observations or presumed presence based on records from Nicaragua´s neighboring countries. In addition, an earthquake in Managua in December 1972 destroyed all alcoholic specimens from the Museo Nacional de Nicaragua (VILLA, 1981), leading to some confusion regarding several records.

During the last few years, there have been substantial changes in the nomenclature of many species of amphibians and reptiles in Central America, principally as a result of an exponential increase of genetic research applied to beta taxonomic studies. Most of these investigations dealt with the phylogeny of amphibians (e.g., FAIVOVICH et al., 2005; HEYER, 2005; FROST et al., 2006; GRANT et al., 2006; HEDGES et al., 2008; PRAMUK et al., 2008) as a result of a great research input derived from alarming rates of worldwide amphibian species extinctions (STUART et al., 2008). In addition to these findings a considerable number of new species have been described worldwide each passing year confirming the great diversity of several groups such as anoles (KÖHLER, 2008), salamanders (AMPHIBIAWEB, 2008), and terrarana frogs (sensu HEDGES et al., 2008).

Anoles (genus *Anolis*) are a diverse and taxonomically poorly understood group of lizards, distributed widely across the tropical and subtropical portions of North, Central, South America and the Caribbean (SAVAGE, 2002; KÖHLER, 2008). Several new species have been described in recent years, indicating that more fieldwork and study of museum material is needed to document the real diversity of anoles. In the last decade, the use of hemipenial morphology has clarified the status of several cryptic anole species in Central America (e.g., KÖHLER, 1999a; KÖHLER & KREUTZ, 1999; KÖHLER et al., 2003, 2007; KÖHLER & SMITH, 2008). Plethodontid salamanders are secretive species and, in general, not easily collected, resulting in relatively few specimens in museums worldwide. Although Central America has been an important diversification center for these commonly cryptic lungless salamanders (WAKE & LYNCH, 1976; PARRA-OLEA, 2008), Nicaragua has a significantly lower number of genera, species, and endemism than its neighboring countries, Costa Rica and Honduras (SAVAGE, 2002; MCCRANIE & WILSON, 2002; MCCRANIE & CASTAÑEDA, 2007). The same is true for several other taxa, including the widespread and diverse frogs of the genus *Craugastor*.

The purpose of this chapter is to update the checklist of the herpetofauna of Nicaragua based exclusively on voucher specimens. I completed a bibliographic search and identified the Nicaraguan type material, the source of each first country record, and the taxonomic uncertainties among the Nicaraguan populations. I compared the morphology of the specimens I collected with comparative museum material and published literature and reviewed (partially in collaboration with colleagues) the systematics of selected Nicaraguan species groups from the genera *Anolis, Bolitoglossa*, and *Craugastor*.

2.2 MATERIALS AND METHODS

Abbreviations used are AGD (axilla-groin distance), DAG (number of medial dorsal scales between axilla and groin), EL (eye length), FL (foot length), HL (head length: from snout to gular fold in salamanders; from tip of snout to angle of jaw in frogs; and from tip of snout to the anterior margin of the ear opening in anoles), HW (head width: greatest width of head), IND (internasal distance), INL (infralabials), IOD (interorbital distance), IP (interparietal scale), MT (maxillary teeth), NED (nostril-eye distance: posterior part of nostril to anterior part of eye distance), PT (premaxillary teeth), SHL (shank length), SL (snout length: from tip of snout to the anterior border of the orbit), SO (suboculars), SPL (supralabials), SS (supraorbital semicircles), SVL (snout-vent length: from tip of snout to posterior end of vent), TL (tail length: posterior end of vent to tip of tail), TM (tympanum length), VAG (number of medial ventral scales between axilla and groin), and VT (vomerine teeth).

Abbreviations used for collectors are AG (Armando GÓMEZ), AH (Andreas HERTZ), DM (Darwin MANZANARES), GK (Gunther KÖHLER), GP (Guillermo PÁIZ), IG (Iris GARBAYO), JS (Javier SUNYER), JT (Josiah TOWNSEND), LO (Lenin OBANDO), LW (Larry WILSON), MD (Matthias DEHLING), NT (Norving TORRES), OA (Osmar ARRÓLIGA), SL (Sebastian LOTZKAT), and ST (Scott TRAVERS).

Those measurements that were generated with the aid of a ocular micrometer of a stereo microscope (Leica MZ 12) were rounded to the nearest 0.01 mm. For measuring SVL and TL I used a ruler and for all other measurements precision callipers, and rounded the values to the nearest 0.1 mm. I counted dorsal and ventral scales at midbody along the midline. I measured tail height and width at the point reached by the heel of the extended hind leg. I counted subdigital lamellae on phalanges ii to iv of the 4^{th} toe. I considered the scale directly anterior to the circumnasal to be a prenasal. Maxillary and vomerine tooth counts are both sides summed. Only complete, unregenerated tails were measured. Data was taken exclusively from adult specimens.

Terminology of the examined characters in amphibians follows that of SAVAGE (2002). Nomenclature of scale characters follows that of KÖHLER (2003). The capitalized colors and color codes (the latter in parentheses) are those of SMITHE (1975–1981). Terminology for hemipenial morphology follows that of MYERS et al. (1993) and SAVAGE (1997). Terminology for dewlap scale counts follows that of FITCH & HILLIS (1984). Marginal scales were not included in the dewlap scale counts. To measure dewlap area, I took photographs of males with its dewlap artificially extended using small foreceps. The head portion was magnified and printed, then superimposed on millimetric paper and the total number of millimetrs squares contained in the extended dewlap counted. A straight line was drawn between both the anterior and posterior insertions of the dewlap. I also determined the HL on the printout. I used the following equation to convert the magnified dewlap area to the real size: $X = [(\sqrt{Y / A}) \cdot B]^2$; where: X is the real area of the dewlap in mm^2; Y is the total area (mm^2) of the dewlap at a magnified scale; A is the HL measure (mm) of the anole at a magnified scale; and B is the HL measure (mm) of the anole at the real size.

The format of the systematic accounts generally follows those of BRAME & WAKE (1963), KÖHLER & MCCRANIE (1999a), KÖHLER (2002), GARCÍA-PARÍS et al. (2003), and KÖHLER et al. (2005). I provide a list of the comparative specimens examined in the Appendices A-F. Acronyms for museum collections follow those of LEVITON et al. (1985) except MHCH (Museo Herpetológico de Chiriquí, David, Panamá), and UCA (Museo de Ciencias Naturales de la Universidad Centroamericana, Managua, Nicaragua). Field numbers GP (Guillermo PÁIZ), JS (Javier SUNYER), MD (Matthias DEHLING), and N (Nicaragua-specimens collected between June and August 2007 in the Reserva de la Biosfera Bosawas and Parque Nacional Cerro Saslaya in collaboration with the University of Florida, Gainesville) refer to specimens that will be deposited in Nicaraguan herpetological collections.

Data of comparative specimens not examined by me were taken from BRAME & WAKE (1963), LYNCH & MYERS (1983), FITCH & HILLIS (1984), LYNCH (1985), KÖHLER & OBERMEIER (1998), KÖHLER & MCCRANIE (1999a), KÖHLER et al. (1999), MCCRANIE & WILSON (2002), and SAVAGE (2002). Some information on osteology has been derived from radiographs of the specimens. For the analysis I used data of my own fieldwork (Appendix A), examination of specimens in the herpetological collection of the Forschungsinstitut und Naturmuseum Senckenberg, and published data (mostly from the following sources): VILLA (1962, 1972a, 1983, 1984a); VILLA et al. (1988); RUIZ (1996); KÖHLER (2001, 2003); MCCRANIE & WILSON (2002); SAVAGE (2002); and RUIZ & BUITRAGO (2003).

I executed statistical techniques using the computer program Statistica version 6.1. Juveniles were not included in the statistics. I used discrimant function analysis (DFA) to evaluate the phenetic distinctness of a priori groups. Discriminant scores (DS) were calculated by multiplying selected variables by their associated canonical coefficients. Each specimen was then plotted along the axae providing maximal separation of the a priori groups.

I created the maps using DIVA-GIS and Adobe Photoshop. The distribution map in chapter 2.3.2 is based on specimens examined by the author (closed symbols) and on additional records (open symbols) taken from LEE (1996) and SAVAGE (2002). The distribution map in chapter 2.3.4 is based on specimens examined by the author and on additional records taken from BRAME & WAKE (1963), VILLA (1972a), KÖHLER (2001), MCCRANIE & WILSON (2002), SAVAGE (2002), and MCCRANIE et al. (2006). All other distribution maps were exclusively based on specimens examined by the author (see appendices A-F).

2.2.1 SAMPLING METHODS

I sampled a total of 150 days between June and August (approximately the first two thirds of the rainy season) of 2005–2007 along two transects situated in northern and southern Nicaragua, respectively (Fig. 2). Each transect has a width of 100 km and the northern transect is substantially larger than the southern one. The northern transect is located almost parallel to the border with Honduras (avoiding the Reserva Natural Cordillera Dipilto-Jalapa which still have sites with unremoved landmines planted during the Nicaraguan Civil War), with its center along a straight line drawn between slightly south of Puerto Sandino (Pacific) and slightly east of Waspám (Atlantic). The southern transect is located almost parallel to the border with Costa Rica, with its center along Parallel 11°08.9′ N. Sampling localities were distributed more or less homogeneously along each transect and their allocations correspond both to protected and non-protected areas. The number of days sampled in each forest formation (see description of forest formations in chapter 3.2) is proportional to the relative amount of that forest formation in its correspondent transect. I sampled 108 days in the northern transect, and 42 days in the southern transect (see Fig. 2).

For precise GPS location of each sampled locality, see Appendix A. In each sampled locality, I searched for amphibians and reptiles both at day and night time. The total amount and disposition of the hours I sampled during day time varied greately, whereas most of the night time sampling was carried out during the first one-half of the night (19–23 h). All specimens were either visually or acoustically detected and were collected by hand with the exception of venemous snakes (families Elapidae and Viperidae), which were collected with a telescopic hook. No traps were used during the field work and I purchased a few specimens from local people. I collected up to six specimens per species at each locality (ideally two adult males, two adult females, and two juveniles), although larger quantities were collected for several abundant and variable species. I photographed in life most collected specimens and few others that were released.

Tadpoles were directly stored in 4% formalin. The preservation process for the rest of the specimens was completed in four stages (SAVAGE, 2002): euthanasia, fixation, labelling, and storage. Euthanasia consisted in the injection of a small amount of the strong relaxing “T 61” near the heart of the specimen. Prior to fixation, I took formalin free tissue samples of selected specimens for further molecular studies (deposited at the herpetological collection of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.M.). For this, I cut a small piece of muscle with sterilized forceps and precision scissors, and kept it in an Eppendorf filled with pure ethanol. The fixing solution was made by diluting 5 ml formalin 40% with 1 litre ethanol 98%. For large specimens I occasionally used a stronger solution of 10 ml formalin 40% with 1 litre ethanol 98% (KÖHLER, 2001). Firstly and whenever possible, I everted the hemipenis of male lizards and snakes by manually applying pressure to the ventral base of tail. Once the hemipenes had been everted to some extend, I injected the fixing solution in the area of the hemipenis pockets, usually resulting in complete eversion of both hemipenes. With the needle still attached to the lizard's tail, I placed the lizard for 1–2 minutes into the preservative solution to allow complete fixation of the everted hemipenis. I did not tie off the hemipenes at the base in small reptiles because this might cause damage to these fragile organs. I then injected a relatively small amount of the fixing solution in all soft parts of the body such as abdominal cavity, limbs and tail. Specimens were positioned in natural resting postures in a plastic box and labelled individually with a field number attached with a cotton string to the top of the left knee. Salamanders and minute specimens of other groups were labelled around the wrist and were not injected with the fixing solution. Caecilians and snakes were labelled behind the neck, in between the head and the thicker part of body (KÖHLER, 2001). I saturated a towel with the fixing solution and covered the specimens with it prior to closure of the container. After a variable time (few minutes to several hours), when specimens showed hardening, they were transferred to a hermetic plastic container filled with ethanol 70% with the exception of salamanders, which were deposited in ethanol 60%. I noted in a field book with a waterproof pen the following data for each preserved specimen: field number, date, tentative species name, GPS locality data, elevation, brief ecological notes, and observations.

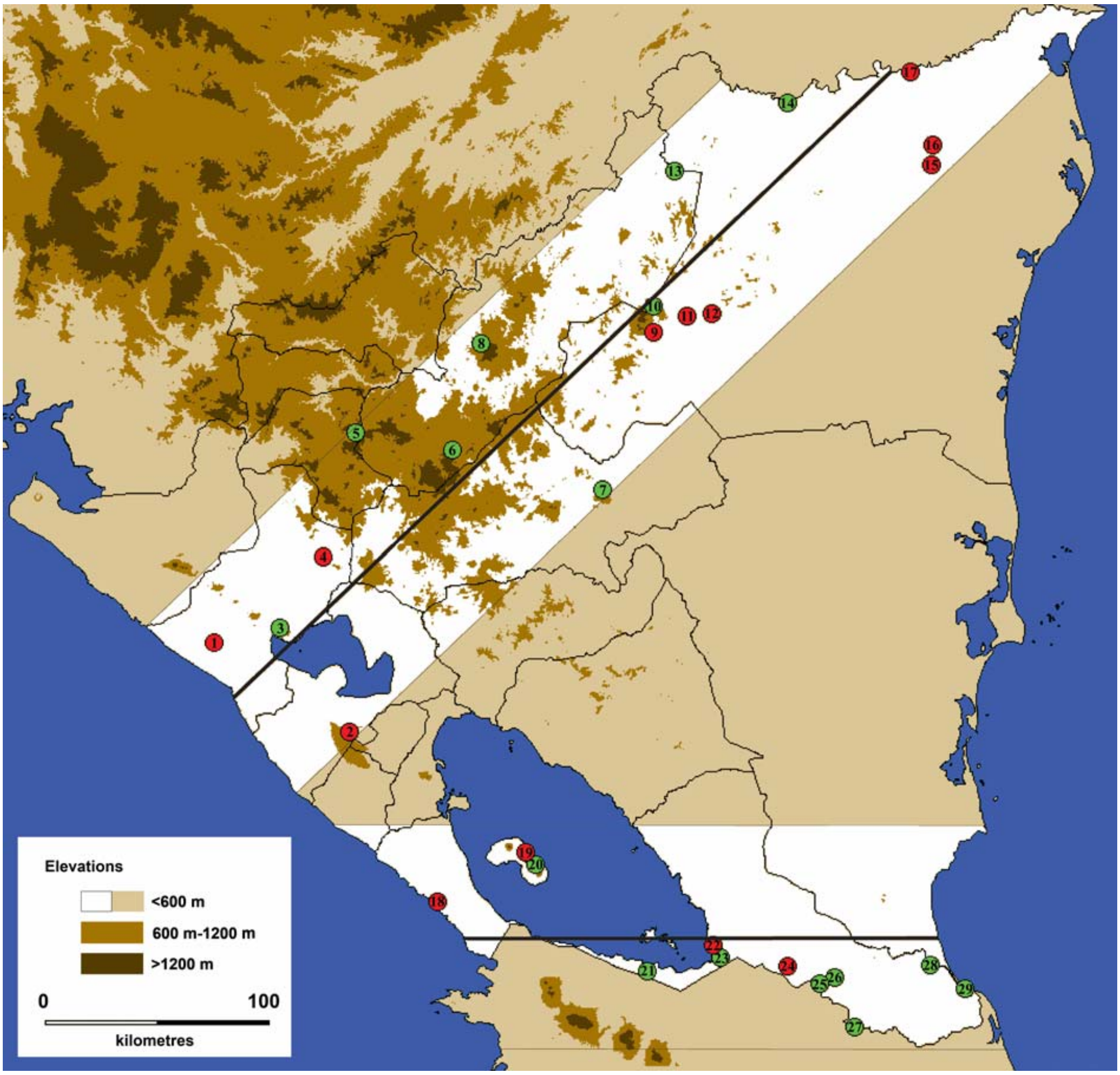


Fig. 2. Map of Nicaragua indicating sampled localities. Transects appear in white. Localities correspond to protected areas (green dots) and non-protected areas (red dots). Northern Transect: [1] road León-Managua (5 days); [2] Las Nubes (5 days); [3] Monte Galán (5 days); [4] San Juan de Dios (5 days); [5] Miraflor (5 days); [6] Cerro Datanlí-El Diablo (8 days); [7] Cerro Musún (18 days); [8] Cerro Kilambé (15 days); [9] Rancho Alegre (5 days); [10] Cerro Saslaya (10 days); [11] Finca URACCAN (3 days); [12] Siuna (1 day); [13] Boaswas, along Río Lakus (13 days), including Aran Dak, Kulum Kitang, Muru Lak, Muru Ta, Siwi Was, Wailahka, Urus Was, Kama Pi, Tuburús, Maikawana, and San Andrés; [14] Bosawas, Krin Krin (4 days); [15] Moss (3 days); [16] intersection of road from Puerto Cabezas-Waspám with road to Moss (2 days); and [17] Waspám (1 day). Southern transect: [18] Morgan´s Rock (10 days); [19] Isla Ometepe (5 days); [20] Volcán Maderas (2 days); [21] Río Papaturro (5 days); [22] San Carlos (1 day); [23] Río Frío (3 days); [24] Sábalos (1 day); [25] Bartola (2 days); [26] El Almendro (4 days); [27] Boca de San Carlos (3 days); [28] Dos Bocas de Río Indio (5 days); and [29] Greytown (1 day).

2.2.2 TAXONOMIC ARRANGEMENT

KÖHLER (2001) provided partial synonymies for Nicaraguan amphibian and reptile species cited as occurring in the country. RUIZ & BUITRAGO (2003) included additional nominal species that are regarded as synonyms of other taxa, following HARRIS & KLUGE (1984) and KÖHLER (2001, 2003): *Chelonia agassizii* (= *C. mydas*), *Sphaerodactylus continentalis* (= *S. millepunctatus*), and *Norops intermedius* (=*Anolis laeviventris*). Futhermore, RUIZ & BUITRAGO (2003: 294–295) listed one species, *Urotheca guentheri*, twice, once as *U. guentheri* and again as *Rhadinaea guentheri*. Here, I follow SAVAGE & CROTHER (1989) and consider this species as belonging to the genus *Urotheca*. Several taxonomic revisions involving Nicaraguan amphibians and reptiles have appeared since the publication of KÖHLER (2001) and RUIZ & BUITRAGO (2003). I follow the taxonomic arrangement proposed by KÖHLER (2001), except as detailed below.

At the family level, taxonomic changes include the following: *Allobates talamancae* replaces *Colostethus talamancae* and now is in the family Aromobatidae (GRANT et al., 2006); all Nicaraguan species formerly in the genus *Eleutherodactylus* now are in *Craugastor*, within the family Craugastoridae, *Diasporus*, within the family Eleutherodactylidae, and *Pristimantis*, within the family Strabomantidae (HEDGES et al., 2008); *Engystomops pustulosus* is used instead of *Physalaemus pustulosus*, and is placed in the family Leiuperidae (NASCIMENTO et al., 2005; GRANT et al., 2006); *Coleonyx* is in the family Eublepharidae now, and *Gymnophthalmus* is in the family Gymnophthalmidae (KÖHLER 2003); native species formerly in the family Gekkonidae now are in Phyllodactylidae and Sphaerodactylidae (GAMBLE et al., 2008a, b); *Rhinoclemmys* is in the family Geoemydidae (SPINKS et al., 2004); *Ungaliophis* is in the family Ungaliophiidae (ZAHER, 1994); and *Loxocemus* is in the family Loxocemidae (SAVAGE, 2002; KÖHLER, 2003).

Taxonomic changes at the generic level in Nicaragua include the following: species formerly assigned to *Bufo* now are in *Incilius*, *Rhaebo*, or *Rhinella* (FROST et al., 2006; FROST, 2007; PRAMUK et al., 2008); *Hyalinobatrachium pulveratum* now is *Cochranella pulverata* (CISNEROS-HEREDIA & MCDIARMID, 2006); *Oophaga pumilio* replaces *Dendrobates pumilio* (GRANT et al., 2006); species formerly assigned to *Hyla* now are in *Cruziohyla, Dendropsophus, Ecnomiohyla*, *Hypsiboas*, *Tlalocohyla*, or *Trachycephalus* (FAIVOVICH et al., 2005); species formerly in the genus *Rana* now are in *Lithobates* (FROST et al., 2006); *Norops* is considered a synonym of *Anolis* (POE, 2004); *Eumeces managuae* now is *Mesoscincus* *managuae* (GRIFFITH et al., 2000); *Cnemidophorus deppii* now is *Aspidoscelis deppii* (REEDER et al., 2002); *Elaphe flavirufa* now is *Pseudelaphe flavirufa* (UTIGER et al., 2002); and *Dryadophis* is a synonym of *Mastigodryas* (DIXON & TIPTON, 2004).

Taxonomic changes at the species level include the following: the Nicaraguan species formerly assigned to *Eleutherodactylus biporcatus* is now referred to as *Craugastor megacephalus* (SAVAGE & MYERS, 2002); the Nicaraguan species formerly assigned to *Leptodactylus labialis* is now referred to as *L. fragilis* (HEYER, 2002); the Nicaraguan species formerly assigned to *Leptodactylus pentadactylus* is now referred to as *L. savagei* (HEYER, 2005); the Nicaraguan species formerly assigned to *Rana berlandieri* is now referred to as *Lithobates brownorum* (ZALDÍVAR-RIVERÓN et al., 2004); the Nicaraguan populations formerly assigned to *Norops humilis* are now referred to as *Anolis quggulus* (KÖHLER et al., 2003); the Nicaraguan populations formerly assigned to *Norops lionotus* are now referred to as *Anolis oxylophus* (WILLIAMS, 1984); the Nicaraguan populations formerly assigned to *Chelydra serpentina* are now referred to as *C. acutirostris* (PHILLIPS et al., 1996); the Nicaraguan species formerly assigned to *Drymarchon corais* is now referred to as *D. melanurus* (WÜSTER et al., 2001); the Nicaraguan species formerly assigned to *Scaphiodontophis annulatus* is now referred to as *S. venustissimus* (MCCRANIE, 2006); the Nicaraguan populations formerly assigned to *Tantilla melanocephala* are now referred to as *T. armillata* and *T. ruficeps* (SAVAGE, 2002); the Nicaraguan populations formerly assigned to *Trimorphodon biscutatus* are now referred to as *T. quadruplex* (DEVITT et al., 2008); *Pelamis platurus* should be addressed as *P. platura* (LANZA & BOSCHERINI, 2000); the Nicaraguan species formerly assigned to *Atropoides nummifer* is now referred to as *A. mexicanus* (CAMPBELL & LAMAR, 2004); and the Nicaraguan species formerly assigned to *Crotalus durissus* is now referred to as *C. simus* (SAVAGE et al., 2005).

2.3 RESULTS AND DISCUSSION

The herpetofauna of Nicaragua currently consists of 244 species representing 134 genera and 42 families (KÖHLER, 2001; SAVAGE, 2002; STAFFORD, 2002; KÖHLER et al., 2004; KÖHLER & SUNYER, 2006; SUNYER & KÖHLER, 2007; present work) with 78 amphibian species representing 35 genera and 15 families, and 166 reptile species representing 99 genera and 27 families (Table 1), which includes six marine species: *Caretta caretta, Chelonia mydas, Eretmochelys imbricata*, *Lepidochelys olivacea*, *Dermochelys coriacea*, and *Pelamis platura*. Seventy-eight species of amphibians are reported to occur in Nicaragua, including 12 endemic species (15.4% of the total number of amphibians): *Bolitoglossa indio*, *B. insularis*, *B. mombachoensis, Nototriton saslaya, Oedipina* sp. "Datanlí," *O.* sp. "Kilambé," *O.* sp. "Musún," *O.* sp. "Saslaya," *Craugastor chingopetaca*, *Plectrohyla* sp. "Saslaya," *Ptychohyla* sp. "Bosawas," and *Lithobates miadis*. One hundred sixty species of terrestrial reptiles are known from Nicaragua, including four endemic species (2.5% of the total number of terrestrial reptiles): *Anolis villai*, *A. wermuthi*, *Geophis dunni*, and *Rhadinaea rogerromani*. Several subspecies are recognized for the different populations of the Nicaraguan reptiles (see Table 1).

Anotheca spinosa, *Rhadinaea godmani*, and *Cerrophidion godmani* occur from Mexico to Panama, and *Rhinobothryum bovallii* and *Urotheca decipiens* occur from Honduras to Ecuador and Colombia, respectively. Some of these five species have been included in various Nicaraguan checklists and although they are most likely to be found in the country, there are no voucher specimens to support their inclusion in the Nicaraguan checklist (KÖHLER, 2001). Therefore, these five species are not included in the analysis. Frogs from the genus *Duellmanohyla* and *Isthmohyla* are distributed from western Panama to northern Oaxaca, Mexico, and northwestern Honduras, respectively (MCCRANIE & CASTAÑEDA, 2007). Nevertheless, no specimen from these genera have been recorded in Nicaragua.

KÖHLER (2001) provided voucher specimens for all the species of amphibians and reptiles he recorded from Nicaragua with three exceptions: *Chelydra acutirostris* (voucher provided by GÜNTHER, 1885), *Kinosternon angustipons* (discussed in chapter 2.3.6), and *Leptophis nebulosus* (vouchers provided by OLIVER, 1948). Although SAVAGE (2002) included Nicaragua in the distribution of *Leptodactylus insularum* (as *L. bolivianus*), apparently no voucher specimens are available to support this assertion (J. M. SAVAGE, pers. com.), so this species is not included in the analysis. Similarly, until supportive voucher material is available, I am not including in the analysis the following species formerly listed or suggested as occurring in the country: *Craugastor gollmeri* (VILLA, 1972a, 1983); *Gastrophryne elegans* (VILLA et al., 1988); *Corallus ruschenbergerii* (listed as *C. enydris* by PETERS & OREJAS-MIRANDA, 1970; VILLA, 1983; VILLA et al., 1988; RUIZ, 1996; RUIZ & BUITRAGO, 2003); *Chironius carinatus* (VILLA, 1983; RUIZ, 1996); *Clelia scytalina* (VILLA et al., 1988; RUIZ, 1996); *Erythrolamprus bizona* (VILLA et al., 1988; RUIZ, 1996; RUIZ & BUITRAGO, 2003); and *Bothriechis marchi* (listed as *B. nigroviridis*) and *Laticauda colubrina* (VILLA, 1962, 1983, 1984a; VILLA et al., 1988; RUIZ, 1996; RUIZ & BUITRAGO, 2003). VILLA (1962) reported *Bothriechis lateralis* from Nicaragua based on a preserved specimen and later (VILLA, 1984) expressed doubts on the origin of this specimen, considering this species no longer as a part of the Nicaraguan herpetofauna. There have also been unconfirmed records of *B. lateralis* from Volcán Concepción on Ometepe Island in Lake Nicaragua (CAMPBELL & LAMAR, 2004). Nevertheless, I am not including this species in the analysis until a voucher specimen is provided. VILLA et al. (1988: 39) and VILLA (1993) considered *Chelonoidis carbonaria* (as *Geochelone carbonaria*) as a member of the Nicaraguan herpetofauna based on specimens from Great Corn Island. Due to the lack of published records from this species collected in the wild (all recorded turtles had been kept as house pets), I prefer not to include *C. carbonaria* in the analysis. The distribution of *Rhinoclemmys areolata* ranges from southern Veracruz, Mexico, to San Pedro Sula, northwestern Honduras. In 1887, a single specimen of *R. areolata* was collected on the Segovia River [=Río Coco], which currently corresponds to most of the Nicaraguan-Honduran Atlantic border (MCCRANIE et al., 2006). However, I prefer not to include this species as a member of the Nicaraguan herpetofauna awaiting confirmation of a population of this species in the area.

The descriptions of 38 currently valid species of amphibian and reptiles are based on Nicaraguan material (Table 1). Several additional species described from Nicaragua material are regarded as synonyms of other species (respective valid name in parentheses): *Dermophis eburatus* TAYLOR, 1968 (*D. mexicanus*); *Dendrobates ignitus* COPE, 1874 (*Oophaga pumilio*); *Hyla grisea* HALLOWELL, 1861 (*Craugastor fitzingeri*); *Hyla chica* NOBLE, 1918 (*Diasporus diastema*); *Agalychnis helenae* COPE, 1885a (*A. callidryas*); *Hyla quinquevittata* COPE, 1886 (*Scinax elaeochroa*); part of the syntypes of *Rana melanosoma* GÜNTHER, 1900 (*Lithobates maculatus*); *Stenodactylus fuscus* HALLOWELL, 1855 (*Gonatodes albogularis*); *Tretioscincus laevicaudus* COPE, 1871a (*Gymnophthalmus speciosus*); *Anolis bransfordii* COPE, 1874 (*A.

limifrons); *Anolis longicauda* HALLOWELL, 1861 (*A. sericeus*); *Anolis rhombifer* BOULENGER, 1894b (*A. lemurinus*); *Cristasaura nuchalis* COPE, 1862 (*Basiliscus vittatus*); *Ameiva pulchra* HALLOWELL, 1861 (*A. undulata*); *Cnemidophorus decemlineatus* HALLOWELL, 1861 (*Aspidoscelis deppii*); *Helicops agassizi* JAN, 1865 (*Tretanorhinus nigroluteus*); *Herpetodryas melas* COPE, 1886 (*Chironius grandisquamis*); *Leptodeira ocellata* GÜNTHER, 1895 (*L. annulata*); Lectoparatype of *Homalocranium jani* GÜNTHER, 1895 (*Tantilla alticola*); *Tantilla annulata* BOETTGER, 1892 (*T. supracincta*); *Thamnophis bovallii* DUNN, 1940 (*T. marcianus*); and *Elaps melanocephalus* HALLOWELL, 1861 (*Micrurus nigrocinctus*). The taxonomic status of other species described upon Nicaraguan material (i.e., *Craugastor polyptychus*, *Trachemys emolli, Anolis dariense, Leptotyphlops ater, L. nasalis*, and the paratypes of *Oedipina pseudouniformis*) is discussed below.

Bufo melanogaster HALLOWELL, 1861 was described based on a specimen from “Nicaragua”, although it was regarded as *nomen oblitum* by VILLA (1972a). *Tretanorhinus nigroluteus* COPE, 1861 was incorrectly described from “Greytown, Nicaragua”. The correct type locality of this species is “Aspinwall, Panamá” (PETERS & OREJAS-MIRANDA, 1970). *Bufo politus* COPE, 1862 (a junior synonym of *Anaxyrus borenas*) was described from “near Greytown, Nicaragua”. However, SAVAGE (1967) suggested that this type specimen was cited from Nicaragua in error and came from the “Pacific coast region of the western United States”. BRATTSTROM & HOWELL (1954) described *Geophis bartholomewi* (a junior synonym of *G. hoffmanni*) and *Neopareas tricolor* (a junior synonym of *Dipsas bicolor*) from “El Arenal, 25 km east of Jalapa, 1,200 feet, Deparment of Nueva Segovia, Nicaragua”. This locality is within Honduran territory since 1960 (CAMPBELL & HOWELL, 1965). *Anolis concolor* COPE, 1862 was described from “Nicaragua”. This anole is endemic to the Caribbean Islands of Providencia and San Andrés (KÖHLER, 2003). At the time of the original description these islands were part of Nicaraguan territory, although since 1930 they politically correspond to Colombia.

Recent research undertaken in the Forschungsinstitut und Naturmuseum Senckenberg has revealed several undescribed species in Nicaragua. The salamander I refer to as *Oedipina* sp. “Kilambe” corresponds, in part, to KÖHLER`s (2001) *O. cyclocauda*. The salamander I refer to as *O.* sp. “Saslaya” corresponds to KÖHLER’s et al. (2004) *O. pseudouniformis*, a species possibly endemic to Costa Rica (D. B. WAKE, pers. com.). I am here considering these species as endemic based on preliminary genetic information. I have not examined the eight paratypes of *O. pseudouniformis* from the premontane slopes near Matagalpa (BRAME, 1968), and their allocation to species has to await further study. Although *Oedipina* sp. "Kilambé" is not formally described, its taxonomic distinctiveness was confirmed by MCCRANIE et al. (2008). *Oedipina* sp. "Musún" and *Ptychohyla* "Bosawas" are products of recent fieldwork and although not formally described I will consider them as endemic species. Nevertheless, further research is needed in order valid the taxonomic identity of *O.* sp. "Musún" over *O. quadra*, and of *P.* "Bosawas" over *P. salvadorensis*. The Saslaya endemic frog *Plectrohyla* sp. "Saslaya" (KÖHLER, 2001) corresponds to an undescribed species for which adults have not been collected (tadpoles, metamorphs, and juveniles are deposited in the collection of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany).

SAVAGE (2002) recognized *Craugastor polyptychus* as a species that supposedly occurs from southeastern Nicaragua along the Caribbean lowlands of Costa Rica to northwestern Panama. This species was said to differ from *C. bransfordii* by lacking nuptial pads in adult males (present in *C. bransfordii*). Both the lectotype and lectoparatype of *C. polyptychus* are females from between Machuca and San Juan del Norte, Nicaragua (SAVAGE, 1973a, 2002). I examined 60 specimens of frogs from the *bransfordii* group (*sensu* CRAWFORD & SMITH, 2005) from eight localities in southeastern Nicaragua and failed to locate a population in which adult males lack nuptial pads. Therefore, I assign all *bransfordii* group frogs from southeastern Nicaragua to a single species, *C. bransfordii*. Whether the name *polyptychus* is to be considered a junior synonym of *bransfordii* or represents a valid species cannot be determined at this time. KÖHLER (2001) considered the presence of nuptial pads in adult males the only valid characteristic to distinguish between *C. bransfordii* and *C. lauraster* in Nicaragua. A few specimens from the *C. rhodopis* group deposited in the Forschungsinstitut und Naturmuseum Senckenberg from Volcán Maderas (Ometepe Island) and Isla Mancarrón (Archipíélago de Solentiname), Lake Nicaragua, lack nuptial pads in adult males. These two populations were not included in this analysis awaiting further studies. I examined 173 specimens of the *rhodopis* group from Nicaragua and failed to find an additional morphological characteristic that satisfyingly distinguish *C. bransfordii* from *C. lauraster*. Similarly, I did not find any taxonomic character to distinguish the populations lacking nuptial pads from the islands in southern Lake Nicaragua from those in mainland northern Nicaragua. In addition, SAVAGE (2002) states that in Costa Rican *C. bransfordii* the thenar tubercle is equal to or slightly smaller than the palmar tubercle as indicated in his Fig. 7.53a. A few specimens of *C. bransfordii* from Nicaragua I examined have the thenar tubercle much smaller than the palmar tubercle, similar to the condition of most *C. lauraster* as shown in Fig. 7.53b in SAVAGE (2002). Further genetic and call analyses are necessary to clarify the systematic status of the species of the *C. rhodopis* group in Nicaragua.

The highland populations of *Diasporus diastema* are, in general, more tuberculated than the lowland populations in Nicaragua (Fig. 3). In some cases this difference is remarkable, and a few specimens differ with published literature and illustrations of this species from its know range (e.g., KÖHLER, 2001; SAVAGE, 2002; GUYER & DONNELLY, 2005; MCCRANIE et al., 2006). Nevertheless, this characteristic does not apply to all specimens and several individuals from the highland populations are similar in dorsal aspect to those collected in the lowlands. *Diasporus diastema* is a very common and variable species in Nicaragua. It ranges from Honduras to Ecuador (MCCRANIE & CASTAÑEDA, 2007) and is probably a species group composed of several species (CHEN, 2005; C. JARAMILLO, pers. com.). Further genetic and call analyses are necessary to clarify the systematic status of this species along its known range.

Fig. 3. Adult males of *Diasporus diastema* from the highlands of Cerro Kilambé (left) and the lowlands of Dos Bocas de Río Indio (right).

I noted two distinct morphs of *Hypopachus variolosus* (distributed from U.S.A. to Costa Rica) in Nicaragua. I examined 14 specimens (10 from the highlands and 4 from the lowlands) of *H. variolosus* from Nicaragua. The highland populations have distinct reddish coloration on the dorsal surface of the limbs, absence of distinct dark blotches on lateral surfaces of the body, and a middorsal light stripe (in contrast to a general brown to slightly reddish coloration, broad dark lateral blotches on lateral surfaces of body, and absence of middorsal light stripe in the lowland form; Fig. 4). In addition, the southwestern lowland populations have consistently a much paler and less contrasting ventral coloration than the highland ones (Fig. 5). NELSON (1973, 1974) reviewed *H. variolosus* in detail and recognized a single species in Nicaragua. He also noted differences in two morphometric characters among the populations from the highlands of Las Nubes, Departamento de Managua and stated that this population "could, perhaps, even be a species distinct from *H. variolosus*" (NELSON, 1974: 270). Further genetic and call analyses are necessary to clarify the systematic status of this species in Nicaragua.

Fig. 4. Dorsolateral view of *Hypopachus variolosus* from the highlands of Miraflor (left) and the lowlands of Morgan´s Rock (right).

Fig. 5. Ventral view of preserved specimens of *Hypopachus variolosus* from the highlands of Miraflor (upper pair) and the lowlands of Morgan´s Rock (lower pair).

SAVAGE (2002) suggested the recognition of *Anolis dariense* (central mountains and Atlantic drainage of Nicaragua and Honduras) as a distinct species from *A. cupreus* (Pacific side of Nicaragua and Costa Rica) mostly based on the darker dewlap coloration, smaller body size, fewer scales around the body, and more arboreal habits of *A. dariense*. MCCRANIE et al. (2006) followed this approach and additionally recorded smaller scales and longer hind limbs of *A. dariense*. I examined 49 specimens of *A. dariense* from Nicaragua and Honduras (28 ♂, 21 ♀) and 29 specimens of *A. cupreus* from Nicaragua and Costa Rica (21 ♂, 8 ♀). All specimens of *A. dariense* have a darker dewlap coloration (Fig. 6) and smaller dorsal scales than *A. cupreus*; maximum SVL of *A. dariense* is 53.0 mm (♂) and 53.7 mm (♀) [49.3 mm (♂) and 42 mm (♀) in the *A. cupreus* that I examined, although SAVAGE (2002) records maximum SVL of *A. cupreus* from Costa Rica up to 57 mm (♂) and 51 mm (♀)]; 112–184 (150.8 ± 14.1) scales around midbody in *A. dariense* [114–142 (125.6 ± 7.8) in *A. cupreus*]; all specimens of *A. dariense* I encountered in Nicaragua were collected between ground level and 2 m altitude (at similar altitudes than all specimens of *A. cupreus* I encountered); and shank length/SVL in *A. dariense* is 0.20–0.34 (0.27 ± 0.04) [0.23–0.33 (0.27 ± 0.03) in *A. cupreus*]. Although there is a tendency between both populations in some of these values, most of them overlap. Additionally, no specific studies have been made in the area where their distributional ranges meet (somewhere between the two great lakes) and the everted hemipenis of both *A. dariense* and *A. cupreus* are very similar in external morphology (Figs. 7–8), suggesting the possibility of hybridization between both morphs. Therefore, and until a comprehensive review is published, I prefer to recognize only a single species, *A. cupreus*.

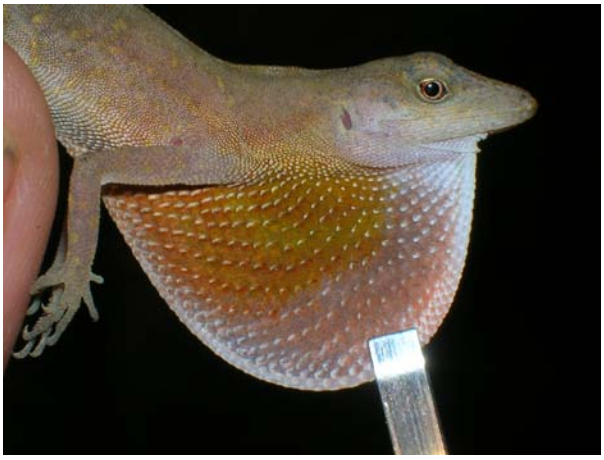


Fig. 6. Male dewlaps in life of *Anolis cupreus dariense* from Moss (left), and *A. c. cupreus* (right) from Morgan´s Rock.

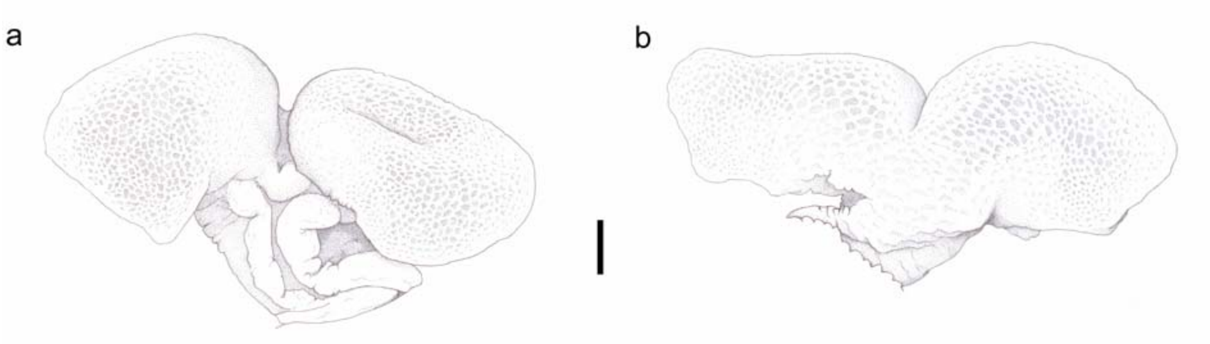


Fig. 7. Hemipenis of an adult *Anolis cupreus dariense* (SMF 87231) from Moss: (a) sulcate view; (b) asulcate view. Scale bar equals 1.0 mm. Drawings: J. J. KÖHLER.

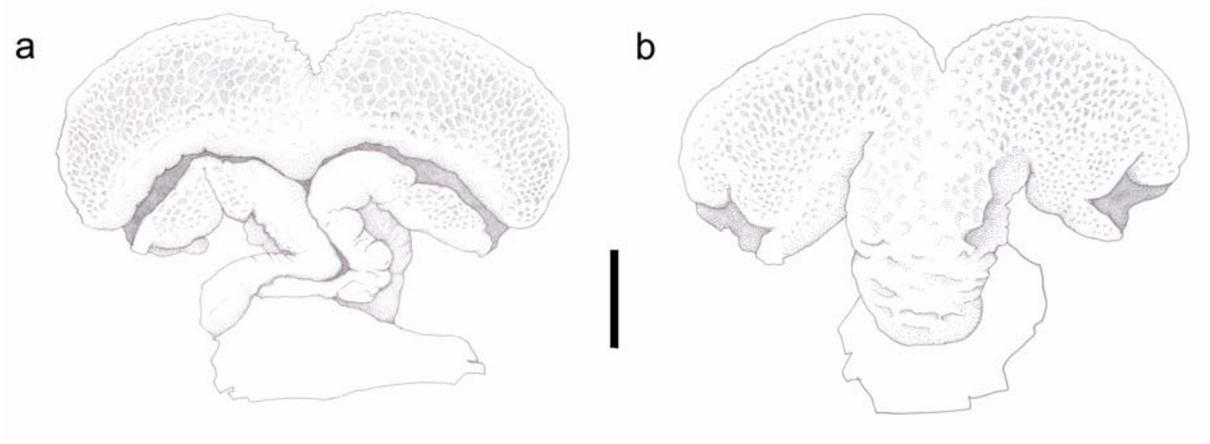


Fig. 8. Hemipenis of an adult *Anolis cupreus cupreus* (SMF 86702) from Morgan´s Rock: (a) sulcate view; (b) asulcate view. Scale bar equals 1.0 mm. Drawings: J. J. KÖHLER.

I collected a single specimen of *Anolis lemurinus* from along the Río Papaturro which has different size and dewlap coloration from the normal populations of this species in Nicaragua (Fig. 9; otherwise similar in morphometrics, pholidosis and hemipenial morphology). Variation in dewlap morphology from this anole species has also been recorded by KÖHLER (2008: 121) on a single specimen from Petén, Guatemala. Whether this dewlap differences are product of individual variation, ontogenetic changes, or presence of cryptic species remains unknown, suggesting the need of further studies on this species along its known range.

Fig. 9. Male dewlaps in life of *Anolis lemurinus* from along the Río Papaturro (left) and *A. lemurinus* from Dos Bocas de Río Indio (right).

Recent preliminary studies suggest that *Anolis pentaprion* is a complex of three species that differ in dorsal tail scalation and dewlap coloration and scalation (G. KÖHLER, in prep.). Two species in this complex occur in Nicaragua, of which neither is endemic to the country. However, until this study is published all populations of this anole in Nicaragua will be referred to as *A. pentaprion*.

Recent studies have revealed that *Anolis sericeus* is a complex of three cryptic species (Fig. 10) that differ in hemipenial morphology (Fig. 11; G. KÖHLER and M. VESELÝ, unpublished) Two species in this complex occur in Nicaragua, herein referred to as *A. sericeus* “bilobed” (in Nicaragua present in the northwestern section) and *A. sericeus* “unilobed” (in Nicaragua present elsewhere), neither of which is endemic to the country.

Fig. 10. Male dewlaps in life of *Anolis sericeus* “bilobed” from San Juan de Dios (left), and *A. sericeus* “unilobed” from Cerro Musún (right).

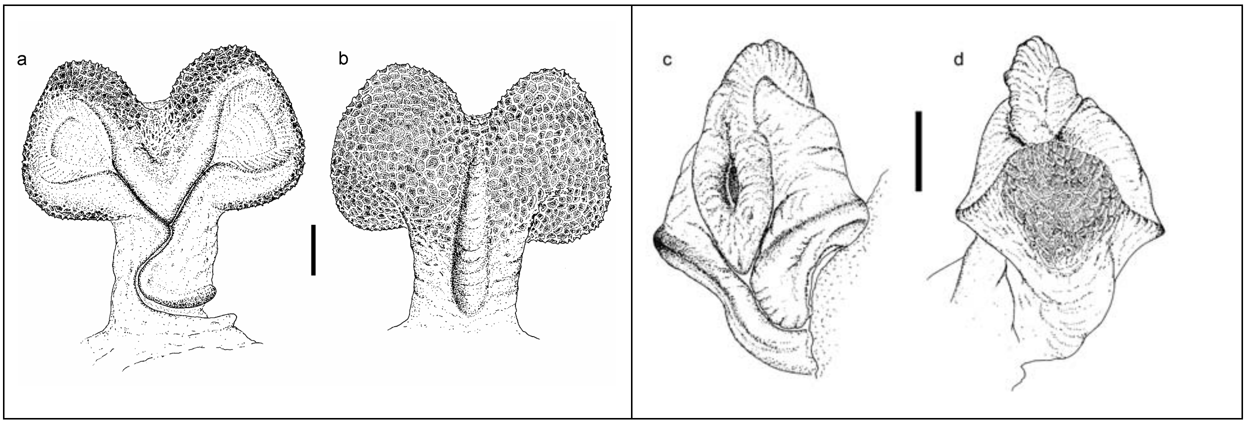


Fig. 11. (Left) Hemipenis of an adult *Anolis sericeus* “bilobed” (SMF 79368) from Guatemala: (a) sulcate view; (b) asulcate view. (Right) Hemipenis of an adult *Anolis sericeus* “unilobed” (SMF 80964) from Bartola: (c) sulcate view; (d) asulcate view. Scale bar equals 1.0 mm. Drawings: M. VESELÝ.

SEIDEL (2002) proposed rising *Trachemys venusta* (Atlantic versant from Nuevo León and Tamaulipas, Mexico, to northwestern Colombia) and *T. emolli* (Pacific slope of Nicaragua to Panama) to species level. ERNST & SEIDEL (2006) and ERNST (2008) followed this proposal and JACKSON et al. (2008) provided genetic evidence based on specimens of *T. venusta* from Belize and Mexico. I collected four juveniles, two from Bosawas (northeastern Nicaragua) and two from Los Guatuzos (southern portion of Lake Nicaragua), but failed to secure this species along the San Juan River, which connect their distributional ranges. Until a study on the variation of these turtles is available from this area, I prefer to adopt a conservative approach and use *T. scripta* for all populations of this turtle in Nicaragua.

The distribution of *Leptotyphlops goudotii* ranges from Mexico to Venezuela (KÖHLER, 2008). SAVAGE (2002) considered *L. ater* (western Nicaragua and northwestern Costa Rica) as a distinct species from *L. goudotii* (central Panama and northern South America) based on the rostral-prefrontal fusion in *L. ater* (prefrontals present in *L. goudotii*), and the completely allopatric distributions of both species which are not connected by a zone of intergradation. Nevertheless, SAVAGE (2002) does not specify the taxonomical status of the populations north from northwestern Nicaragua (where the junior synonym, *L. phenops*, becomes involved) which are continuous in distribution with the central and southern Nicaraguan and Costa Rican populations (KÖHLER, 2008). I have examined two specimens of *L. goudotii* deposited in the herpetological collection of the Forschungsinstitut und Naturmuseum Senckenberg from the Pacific side of central Nicaragua (Departamentos Granada and Carazo, respectively) and both specimens lack prefrontal scales. In addition, *Leptotyphlops nasalis* was described on the basis of a single specimen from Managua and differs from the widely distributed species *L. goudotii* by having a supranasal-supraocular fusion, characteristic found in some other Nicaraguan specimens which might also be individual anomaly (DUNN & SAXE, 1950; SAVAGE, 2002; KÖHLER, 2008). To complicate this situation there are conflicting differences in the scale terminology, and the supranasal scales (sensu TAYLOR, 1940; DUNN & SAXE, 1950; SAVAGE, 2002) have been referred to as prefrontal scales by different authors (e.g., MERTENS, 1952b; KÖHLER, 2008). Therefore, until a comprehensive review of the Central American *Leptotyphlops* is available, I prefer to recognize a single species in Nicaragua, *L. goudotii*.

SOLÓRZANO (2004) suggested raising *Micrurus mosquitensis* to species status. In Nicaragua, both *M. nigrocinctus mosquitensis* and *M. n. nigrocinctus* are widely distributed and many individuals from a large portion of the country show an intermediate morphological pattern (SAVAGE & VIAL, 1974). I examined 23 *Micrurus nigrocinctus* from Nicaragua and compared them with the data provided by SOLÓRZANO (2004) from Costa Rica. Seven specimens from Volcán Mombacho, Morgan´s Rock, Bosawas, Finca URACCAN, and Cerros Saslaya, Musún, and Kilambé are "perfect" *M. nigrocinctus* sensu SOLÓRZANO (2004). Three specimens, one from the Río Indio and two from the surrounding area of Selva Negra, respectively are "perfect" *M. mosquitensis* sensu SOLÓRZANO (2004). The remaining 13 specimens from Boca de San Carlos, Bartola, Siuna, Cerro Musún, Bosawas, and other specimens from the proximities of Selva Negra present a mixture of characteristics of both taxa: all of these specimens have a combination of black head cap not reaching the parietal scales and more than 16 black body rings (up to 26) and in addition, the specimens from the Selva Negra area and Boca de San Carlos have a black nuchal ring length of 8–10 dorsal scales whereas in specimens from the other localities this characteristic ranges from 5–7. Therefore, I prefer not to recognize *M. mosquitensis* as a full species and follow SAVAGE (2002), CAMPBELL & LAMAR (2004), and KÖHLER (2008) in recognizing a single species in Nicaragua, *M. nigrocinctus*.

As noted above, further investigation is needed to completely comprehend the taxonomy of all the members of the herpetofauna of Nicaragua. In the following sub-chapters I review in detail the morphology of the Nicaraguan populations of the endemic *Anolis wermuthi* and the widespread *A. quaggulus* and *A. limifrons*. JANSEN (2001) noted distinctiveness between populations of *Anolis wermuthi*. Based on recently collected material, I evaluate the evidence for potential cryptic species among all known populations of this anole. *Anolis quaggulus* was recently resurrected from the synonymy of *A. humilis* (KÖHLER et al., 2003) mostly based on differences in hemipenial morphology. I study in detail the morphology of the Central American leaf-litter anoles and clarify the taxonomical status all of populations of this common anole in Nicaragua. Specimens of *Anolis limifrons* I collected from Nicaragua presented differences in hemipenial and dewlap morphology with several individuals from Panama, from where this species was described. I undertook a detailed study among this species along its distributional range in order to clarify the taxonomical status all of populations of this common anole in Nicaragua. Finally, I studied in detail the salamanders of the subgenus *Bolitoglossa* and the frogs of the *Craugastor fitzingeri* group present in the country. Also, I provide voucher specimens of five species for the first time in Nicaragua.

Table 1. List of amphibian and reptile species recorded from Nicaragua, including the reference that cites each species for the first time in the country and current synonymy, and recognized subspecies in the country. Species listed alphabetically, by family; numbers after family name indicate number of genera (left) and species (right). * = Species described upon Nicaraguan material.

Species	First country record	Observations	Subspecies in Nicaragua
AMPHIBIA			
GYMNOPHIONA			
Caeciliidae: 2—2			
Dermophis mexicanus	COPE (1871a)	As *Siphonops mexicanus*	
Gymnopis multiplicata	NOBLE (1918)	As *Gymnopis proxima*	
CAUDATA			
Plethodontidae: 3—11			
*Bolitoglossa indio**	See chapter 2.3.4		
*Bolitoglossa insularis**	See chapter 2.3.4		
*Bolitoglossa mombachoensis**	NOBLE (1918)	As *Oedipus striatulus*; the species was described by KÖHLER & MCCRANIE (1999a)	
*Bolitoglossa striatula**	NOBLE (1918)	As *Oedipus striatulus*	
*Nototriton saslaya**	KÖHLER (2001)	As *Nototriton* sp.; the species was described by KÖHLER (2002)	
*Oedipina collaris**	STEJNEGER (1907)		
Oedipina cyclocauda	BRAME (1968)		
Oedipina sp. "Datanlí"	In prep.		
Oedipina sp. "Kilambé"	KÖHLER (1999b)	As *Oedipina cyclocauda*	
Oedipina sp. "Musún"	In prep.		
Oedipina sp. "Saslaya"	KÖHLER et al. (2004)	As *Oedipina pseudouniformis*	
ANURA			
Aromobatidae: 1—1			
Allobates talamancae	CALDWELL (1996)	As *Colostethus talamancae*	

Bufonidae: 3—7		
Incilius coccifer	MAYORGA (1967)	As *Bufo coccifer*
Incilius coniferus	NOBLE (1918)	As *Bufo coniferus*
Incilius luetkenii	MAYORGA (1967)	As *Bufo luetkenii*
Incilius melanochlorus	RUIZ & BUITRAGO (2003)	As *Bufo melanochlorus*; see also KÖHLER et al. (2004)
Incilius valliceps	COPE (1886)	As *Bufo valliceps*
Rhaebo haematiticus	COPE (1886)	As *Bufo haematiticus*
Rhinella marina	COPE (1886)	As *Bufo marinus*
Centrolenidae: 3—7		
Centrolene ilex	HAYES & STARRETT (1980)	As *Centrolenella ilex*
Centrolene prosoblepon	VILLA (1972)	As *Centrolenella prosoblepon*
Cochranella albomaculata	KÖHLER et al. (2004)	
Cochranella granulosa	VILLA (1972)	As *Centrolenella granulosa*
Cochranella pulverata	VILLA (1972)	As *Centrolenella pulverata*
Cochranella spinosa	KÖHLER (2001)	As *Centrolene ilex*; see also chapter 2.3.6
Hyalinobatrachium fleischmanni	MAYORGA (1967)	As *Centrolenella fleischmanni*
Craugastoridae: 1—10		
*Craugastor bransfordii**	COPE (1886)	As *Lithodytes bransfordii*
*Craugastor chingopetaca**	KÖHLER & SUNYER (2006)	See chapter 2.3.5
Craugastor fitzingeri	HALLOWELL (1861)	As *Hyla grisea*
Craugastor laevissimus	GÜNTHER (1900)	As *Liohyla rugulosa*
Craugastor lauraster	SAVAGE & EMERSON (1970)	As *Eleutherodactylus bransfordii*; the species was described by SAVAGE et al. (1996); see also KÖHLER (1998a)
Craugastor megacephalus	VILLA (1972)	As *Eleutherodactylus rugosus*
Craugastor mimus	NOBLE (1918)	As *Eleutherodactylus rhodopis*; the species was described by TAYLOR (1955)
Craugastor noblei	GAIGE et al. (1937)	As *Eleutherodactylus noblei*
*Craugastor ranoides**	COPE (1886)	As *Lithodytes ranoides*
Craugastor talamancae	GAIGE et al. (1937)	As *Eleutherodactylus talamancae*
Dendrobatidae: 3—3		
Dendrobates auratus	COPE (1874)	
Oophaga pumilio	COPE (1874)	As *Dendrobates ignitus*
Phyllobates lugubris	CALDWELL (1994)	

Eleutherodactylidae: 1—1			
Diasporus diastema	Cope (1886)	As *Lithodytes diastema*	
Hylidae: 11—20			
Agalychnis callidryas	Cope (1885a)	As *Agalychnis helenae*	
Agalychnis saltator	Duellman (1970)		
Cruziohyla calcarifer	Caldwell (1994)	As *Agalychnis calcarifer*	
*Dendropsophus ebraccatus**	Cope (1874)	As *Hyla ebraccata*	
Dendropsophus microcephalus	Gaige et al. (1937)	As *Hyla underwoodi*; see also Mayorga (1967)	*Dendropsophus microcephalus cherrei*
Dendropsophus phlebodes	Barbour & Loveridge (1929)	As *Hyla miotympanum*	
*Ecnomiohyla miliaria**	Cope (1886)	As *Hypsiboas miliarius*	
Hypsiboas rufitelus	Günther (1901)	As *Hyla albomarginata*; the species was described by Fouquette (1961)	
Plectrohyla sp. "Saslaya"	Köhler (2001)		
Ptychohyla hypomykter	Duellman (1970)	As *Ptychohyla spinipollex*; the species was described by McCranie & Wilson (1993)	
Ptychohyla sp. "Bosawas"	In prep.		
*Scinax boulengeri**	Cope (1887)	As *Scytopis boulengeri*	
Scinax elaeochroa	Cope (1886)	As *Hyla quinquevittata*	
Scinax staufferi	Cope (1871a)	As *Hyla staufferii*; see also Mayorga (1967)	
Smilisca baudinii	Günther (1901)	As *Hyla baudini*	
Smilisca phaeota	Gaige et al. (1937)	As *Hyla phaeota*	
*Smilisca puma**	Cope (1885a)	As *Hyla puma*	
Smilisca sordida	Duellman & Trueb (1966)		
Tlalocohyla loquax	Duellman (1970)	As *Hyla loquax*	
Trachycephalus venulosus	Cope (1887)	As *Scytopis venulosus*	
Leiuperidae: 1—1			
Engystomops pustulosus	Mayorga (1967)	As *Physalaemus pustulosus*	
Leptodactylidae: 1—3			
Leptodactylus fragilis	Noble (1918)	As *Leptodactylus albilabris*	
*Leptodactylus melanonotus**	Hallowell (1861)	As *Cystignathus melanonotus*	
Leptodactylus savagei	Noble (1918)	As *Leptodactylus pentadactylus*; the species was described by Heyer (2005)	

Microhylidae: 2—2			
*Gastrophryne pictiventris**	Cope (1886)	As *Engystoma pictiventre*	
Hypopachus variolosus	Villa (1972)		
Ranidae: 1—7			
Lithobates brownorum	Noble (1918)	As *Rana austricola*; the species was described by Sanders (1973) and considered a junior synonym until raised to species status by Zaldívar-Riverón et al. (2004)	
Lithobates forreri	Mayorga (1967)	As *Rana pipiens*	
Lithobates maculatus	Günther (1900)	As *Rana melanosoma*	
*Lithobates miadis**	Barbour & Loveridge (1929)	As *Rana miadis*	
Lithobates taylori	Noble (1918)	As *Rana austricola*; the species was described by Smith (1959)	
Lithobates vaillanti	Noble (1918)	As *Rana palmipes*	
Lithobates warszewitschii	Cope (1886)	As *Ranula chrysoprasina*	
Rhinophrynidae: 1—1			
Rhinophrynus dorsalis	Duellman (1971)		
Strabomantidae: 1—2			
Pristimantis cerasinus	Villa (1972)	As *Eleutherodactylus cerasinus*	
*Pristimantis ridens**	Cope (1866)	As *Phyllobates ridens*	
REPTILIA			
TESTUDINES			
Cheloniidae: 4—4			
Caretta caretta	Nietschmann (1977)		
Chelonia mydas	Nietschmann (1977)	Known from the Nicaraguan northern Caribbean coasts since the 17th Century (see Nietschmann, 1977)	*Chelonia mydas agassizii* (Pacific Ocean) and *C. m. mydas* (Atlantic Ocean)
Eretmochelys imbricata	Nietschmann (1977)		
Lepidochelys olivacea	Villa (1983)		
Chelydridae: 1—1			
Chelydra acutirostris	Günther (1885)	As *Chelydra serpentina*	

Dermochelydae: 1—1			
Dermochelys coriacea	NIETSCHMANN (1977)		
Emydidae: 1—1			
Trachemys scripta	VILLA (1983)	As *Chrysemys ornata*	*Trachemys scripta emolli* (Pacific versant) and *T. s. ornata* (Caribbean versant)
Geoeymdidae: 1—3			
Rhinoclemmys annulata	VILLA (1983)		
Rhinoclemmys funerea	VILLA (1983)		
Rhinoclemmys pulcherrima	COPE (1871a)	As *Chelopus rubidus*	*Rhinoclemmys pulcherrima incisa* (northern Nicaragua) and *R. p. manni* (southern Nicaragua)
Kinosternidae: 1—3			
Kinosternon angustipons	LEGLER (1965)	See also chapter 2.3.6	
Kinosternon leucostomum	COPE (1874)		*Kinosternon leucostomum leucostomum* (northern Nicaragua) and *K. l. postinguinale* (southern Nicaragua)
Kinosternon scorpioides	COPE (1871a)	As *Kinosternon mexicanum*	*Kinosternon. scorpioides albogulare*
CROCODYLIA			
Alligatoridae: 1—1			
Caiman crocodilus	GAIGE et al. (1937)	As *Caiman fuscus*	
Crocodylidae: 1—1			
Crocodylus acutus	COPE (1871a)	As *Crocodilus acutus*	
SQUAMATA			
Anguidae: 3—4			
*Celestus bivittatus**	BOULENGER (1894b)	As *Diploglossus bivittatus*	
Diploglossus bilobatus	KÖHLER (2001)		
Diploglossus monotropis	VILLA (1971)		
Mesaspis moreletii	TIHEN (1949)	As *Barisia moreletii*; see also chapter 2.3.6	

Eublepharidae: 1—1			
Coleonyx mitratus	PETERS & DONOSO-BARROS (1970)		
Gekkonidae: 2—2			
Hemidactylus frenatus	VENCES et al. (1998)		
Lepidodactylus lugubris	HENDERSON et al. (1976)		
Gymnophthalmidae: 1—1			
*Gymnophthalmus speciosus**	HALLOWELL (1861)	As *Blepharactisis speciosa*	
Iguanidae: 8—27			
Anolis biporcatus	COPE (1874)		*Anolis biporcatus biporcatus*
Anolis capito	COPE (1886)		
Anolis carpenteri	FITCH & SEIGEL (1984)		
*Anolis cupreus**	HALLOWELL (1861)		*Anolis cupreus cupreus* (Pacific versant) and *A. c dariense* (Caribbean versant and central mountains)
Anolis laeviventris	BRATTSTROM & HOWELL (1954)	As *Anolis petersi*	
Anolis lemurinus	BOULENGER (1894b)	As *Anolis rhombifer*	
Anolis limifrons	COPE (1874)	As *Anolis bransfordii*	
Anolis oxylophus	COPE (1886)		
Anolis pentaprion	COPE (1874)		*Anolis pentaprion pentaprion*
*Anolis quaggulus**	COPE (1885b)		
Anolis sericeus "bilobed"	LEE (1980)	As *Anolis sericeus*	
Anolis sericeus "unilobed"	HALLOWELL (1861)	As *Anolis longicauda*	
Anolis tropidonotus	VILLA (1983)		
*Anolis villai**	FITCH & HENDERSON (1976)		
*Anolis wermuthi**	FITCH & SEIGEL (1984)	As *Anolis sminthus*; the species was described by KÖHLER & OBERMEIER (1998)	
Basiliscus basiliscus	VILLA (1970b)		
Basiliscus plumifrons	GAIGE et al. (1937)		
Basiliscus vittatus	HALLOWELL (1861)	As *Daconura bivittata*	
Corytophanes cristatus	COPE (1874)	As *Chamaeleopsis hernandezii*	
Ctenosaura quinquecarinata	VILLA & SCOTT (1967)	As *Enyalosaurius quinquecarinatus*	
Ctenosaura similis	COPE (1871a)	As *Cyclura pectinata* and *C. acanthura*	
Iguana iguana	COPE (1871a)	As *Iguana rhinolopha*	*Iguana iguana rhinolopha*

Laemanctus longipes	McCoy (1968)		*Laemanctus longipes deborrei*
Polychrus gutturosus	Boulenger (1894b)	See also Villa (1971)	
Sceloporus malachiticus	Smith (1939)	As *Sceloporus formosus malachiticus*	
Sceloporus squamosus	Hallowell (1861)	As *Sceloporus scalaris*	
Sceloporus variabilis	Smith (1939)	As *Sceloporus variabilis olloporus*	*Sceloporus variabilis olloporus*
Phyllodactylidae: 2—2			
*Phyllodactylus tuberculosus**	Wiegmann (1835)	Type locality limited to Nicaragua by Dixon (1960)	*Phyllodactylus tuberculosus tuberculosus*
Thecadactylus rapicauda	Boulenger (1885)		
Scincidae: 3—3			
Mabuya unimarginata	Cope (1871a)		
*Mesoscincus managuae**	Dunn (1933)		
Sphenomorphus cherriei	Gaige et al. (1937)	As *Leiolepisma assatum*	
Sphaerodactylidae: 3—5			
Gonatodes albogularis	Hallowell (1855)	As *Stenodactylus fuscus*	*Gonatodes albogularis fuscus*
Lepidoblepharis xanthostigma	Villa (1971)		
Sphaerodactylus argus	Thomas (1975)		
*Sphaerodactylus homolepis**	Cope (1886)		
*Sphaerodactylus millepunctatus**	Hallowell (1861)		
Teiidae: 3—5			
Ameiva festiva	Cope (1874)	As *Amiva eutropia*	*Ameiva festiva edwardsii*
*Ameiva quadrilineata**	Hallowell (1861)	As *Cnemidophorus quadrilineatus*; type locality limited to Nicaragua by Taylor (1956)	
Ameiva undulata	Hallowell (1861)	As *Ameiva pulchra*	*Ameiva undulata miadis* (Great Corn Island), *A. u. parva* (Pacific versant), and *A. u. pulchra* (Caribbean versant).
Aspidoscelis deppii	Hallowell (1861)	As *Cnemidophorus decemlineatus*	*Aspidoscelis deppii deppii*
Cnemidophorus lemniscatus	Villa (1983)	See also chapter 2.3.6	*Cnemidophorus lemniscatus lemniscatus*
Xanthusidae: 1—1			
Lepidophyma flavimaculatum	Gaige et al. (1937)		
Anomalepididae: 1—1			
Anomalepis mexicanus	Villa (1983)	See also Köhler et al. (2004)	
Leptotyphlopidae: 1—1			
Leptotyphlops goudotii	Taylor (1940)	As *Leptotyphlops ater* and *L. nasalis*	

Typhlopidae: 1—1			
Typhlops costaricensis	VILLA (1978)		
Boidae: 2—2			
Boa constrictor	COPE (1861)	As *Boa eques*	*Boa constrictor imperator*
Corallus annulatus	ANDERSSON (1916)	As *Corallus cookii*	
Loxocemidae: 1—1			
Loxocemus bicolor	VILLA (1983)		
Ungaliophiidae: 1—2			
Ungaliophis continentalis	STULL (1935)	As *Peropodium guatemalensis*; see also KÖHLER (1997)	
Ungaliophis panamensis	DUNN & BAILEY (1939)		
Colubridae: 45—79			
Adelphicos quadrivirgatum	See chapter 2.3.6		
Amastridium veliferum	DUNN (1924)		
Chironius grandisquamis	COPE (1886)	As *Herpetodryas melas*	
Clelia clelia	PETERS & OREJAS-MIRANDA (1970)	As *Clelia clelia clelia*	*Clelia clelia clelia*
Coniophanes bipunctatus	CAMPBELL & HOWELL (1965)		
Coniophanes fissidens	HALLOWELL (1861)		*Coniophanes fissidens fissidens* (Caribbean versant) and *Coniophanes f. punctigularis* (Pacific versant)
Coniophanes piceivittis	WILSON & MEYER (1985)		
Conophis lineatus	COPE (1871a)		*Conophis lineatus dunni*
Crisantophis nevermanni	VILLA (1969)	As *Conophis nevermanni*	
Dendrophidion nuchale	STAFFORD (2002)		
Dendrophidion percarinatum	COPE (1886)	As *Dendrophidion dendrophis*; the species was described by COPE (1893)	
Dendrophidion vinitor	GAIGE et al. (1937)	As *Dendrophidion dendrophis*; the species was described by SMITH (1941b)	
Dipsas articulata	KÖHLER (2001)	See also KÖHLER & VIELMETTER (2002)	
*Dipsas bicolor**	GÜNTHER (1895)	As *Neopareas bicolor*	
Drymarchon melanurus	COPE (1871a)	As *Spilotes melanurus*	*Drymarchon melanurus melanurus* (Caribbean versant) and *D. m. unicolor* (Pacific versant)
Drymobius chloroticus	WILSON (1970)		

Drymobius margaritiferus	HALLOWELL (1861)		*Drymobius margaritiferus margaritiferus* (mainland) and *D. m. maydis* (Great Corn Island)
Drymobius melanotropis	BOULENGER (1894a)	As *Drymobius rhombifer*	
Drymobius rhombifer	PETERS & OREJAS-MIRANDA (1970)		
Enuliophis sclateri	DUNN (1938)		
Enulius flavitorques	COPE (1871a)	As *Enulius murinus*	*Enulius flavitorques flavitorques*
Erythrolamprus mimus	COPE (1887)	As *Erythrolamprus violaceus*	*Erythrolamprus mimus impar*
*Geophis dunni**	SCHMIDT (1932)		
Geophis hoffmanni	DOWNS (1967)		
Hydromorphus concolor	VILLA (1970a)		
Imantodes cenchoa	COPE (1874)	As *Dipsas cenchoa*	
Imantodes gemmistratus	VILLA (1983)		
*Imantodes inornatus**	BOULENGER (1896)	As *Himantodes inornatus*	
Lampropeltis triangulum	COPE (1874)	As *Ophibolus micropholis*	*Lampropeltis triangulum hondurensis* (Caribbean versant) and *L. t. stuarti* (Pacific versant)
Leptodeira annulata	COPE (1871a)		*Leptodeira annulata rhombifera*
*Leptodeira nigrofasciata**	GÜNTHER (1868)	As *Leptodira nigrofasciata*	
Leptodeira septentrionalis	DUELLMAN (1958)	As *Leptodeira septentrionalis polysticta*	*Leptodeira septentrionalis polysticta*
Leptodrymus pulcherrimus	COPE (1887)	As *Drymobius pulcherrimus*	
Leptophis ahaetulla	COPE (1871a)	As *Thrasops mexicanus*	*Leptophis ahaetulla occidentalis*
Leptophis depressirostris	COPE (1874)	As *Ahaetulla bilineata*	
Leptophis mexicanus	COPE (1874)	As *Ahaetulla mexicana*	*Leptophis mexicanus mexicanus*
Leptophis nebulosus	OLIVER (1948)	As *Thalerophis nebulosus*	
Masticophis mentovarius	ANDERSSON (1916)	As *Zamenis flagellum piceus*	*Masticophis mentovarius mentovarius*
Mastigodryas dorsalis	CAMPBELL & HOWELL (1965)	As *Dryadophis dorsalis*	
Mastigodryas melanolomus	COPE (1885a)	As *Drymobius boddaertii*	*Mastigodryas melanolomus alternatus*
Ninia maculata	PETERS & OREJAS-MIRANDA (1970)	As *Ninia maculata tessellata*	
Ninia sebae	BOULENGER (1893)	As *Streptophorus atratus*	
Nothopsis rugosus	DUNN & BAILEY (1939)		
Oxybelis aeneus	HALLOWELL (1861)	As *Dryophis aeneus*	
Oxybelis brevirostris	GÜNTHER (1895)	As *Dryiophis brevirostris*	
Oxybelis fulgidus	VILLA (1983)		
Oxyrhopus petola	GÜNTHER (1895)	As *Oxyrrhopus petolarius*	*Oxyrhopus petola sebae*
Pliocercus euryzonus	COPE (1874)	As *Pliocercus dimidiatus*	

Pseudelaphe flavirufa	DOWLING (1952)	As *Elaphe flavirufa*	*Pseudelaphe flavirufa pardalina*
Pseustes poecilonotus	ANDERSSON (1916)	As *Phrynonax chrysobronchus*	
Rhadinaea decorata	COPE (1886)		
*Rhadinaea kinkelini**	BOETTGER (1898)		
*Rhadinaea rogerromani**	KÖHLER & MCCRANIE (1999b)		
*Scaphiodontophis venustissimus**	GÜNTHER (1894)	As *Henicognathus venustissimus*	
Scolecophis atrocinctus	VILLA (1983)		
Senticolis triaspis	VILLA (1983)		
Sibon annulatus	KÖHLER & SEIPP (1998)		
Sibon anthracops	COPE (1871a)	As *Leptognathus anthracops*	
Sibon dimidiatus	GÜNTHER (1895)	As *Mesopeltis dimidiatus*	
Sibon longifrenis	KÖHLER (2001)		
Sibon nebulatus	COPE (1871a)	As *Leptognathus nebulatus*	*Sibon nebulatus nebulatus*
Spilotes pullatus	COPE (1871a)	As *Spilotes auribundus*	
Stenorrhina degenhardtii	GÜNTHER (1895)		
Stenorrhina freminvillei	CAMPBELL & HOWELL (1965)		
Tantilla alticola	GÜNTHER (1895)	As *Homalocranium jani*	
Tantilla armillata	COPE (1871a)	As *Tantilla melanocephala*; the species was described by COPE (1876)	
Tantilla reticulata	WILSON & MEYER (1971)		
Tantilla ruficeps	WILSON & MENA (1980)	As *Tantilla melanocephala*	
Tantilla schistosa	BOULENGER (1896)	As *Homalocranium shistosum;* see also WILSON & VILLA (1973)	
Tantilla supracincta	BOETTGER (1892)	As *Tantilla annulata*	
Tantilla taeniata	WILSON & MEYER (1971)		
*Tantilla vermiformis**	HALLOWELL (1861)	As *Lioninia vermiformes*	
Tantillita lintoni	KÖHLER (1999c)		
Thamnophis marcianus	ANDERSSON (1916)	As *Tropidonotus ordinatus*	*Thamnophis marcianus bovalli*
Thamnophis proximus	DUNN (1940)	As *Thamnophis sauritus chalceus*	*Thamnophis proximus rutiloris*
Tretanorhinus nigroluteus	JAN (1865)	As *Helicops agassizi*	
*Trimorphodon quadruplex**	COPE (1861)	As *Trimorphodon biscutatus*; the subspecies *T. b. quadruplex* was described by SMITH (1941a) and raised to a species status by DEVITT et al. (2008)	
Tropidodipsas sartorii	VILLA (1971)		*Tropidodipsas sartorii sartorii*
Urotheca guentheri	MYERS (1974)	As *Rhadinaea guentheri*	
Xenodon rabdocephalus	COPE (1871a)	As *Xenodon angustirostris*	

Elapidae: 2—4			
*Micrurus alleni**	SCHMIDT (1936b)		
Micrurus multifasciatus	COPE (1886)	As *Elaps multifasciatus*	*Micrurus multifasciatus hertwigii*
Micrurus nigrocinctus	HALLOWELL (1861)	As *Elaps melanocephalus*	*Micrurus nigrocinctus nigrocinctus* (Pacific versant), *M. n. babaspul* (Great Corn Island, Nicaragua), and *M. n. mosquitensis* (Caribbean versant)
Pelamis platura	VILLA (1962)		
Viperidae: 7—8			
Agkistrodon bilineatus	COPE (1871a)	As *Ancistrodon bilineatus*	*Agkistrodon bilineatus howardgloydi*
Atropoides mexicanus	GÜNTHER (1895)	As *Bothriechis nummifera*	
Bothriechis schlegelii	COPE (1874)	As *Teleuraspis schlegelii*	
Bothrops asper	COPE (1874)	As *Bothrops atrox*; the species was described by GARMAN (1884)	
Crotalus simus	COPE (1871a)	As *Caudisona durissa*	*Crotalus simus simus*
Lachesis stenophrys	VILLA (1962)	As *Lachesis muta*	
Porthidium nasutum	COPE (1885a)	As *Brothriopsis brachystoma*	
Porthidium ophryomegas	GÜNTHER (1885)	As *Bothriechis lansbergii*	

2.3.1 MORPHOLOGICAL VARIATION IN *ANOLIS WERMUTHI*, A SPECIES ENDEMIC TO THE HIGHLANDS OF NORTH-CENTRAL NICARAGUA (REPTILIA, SQUAMATA, IGUANIDAE)

2.3.1.1 Introduction

The *Anolis crassulus* group (sensu KÖHLER, 2003) is a cluster of relatively poorly known species that inhabits the highlands of Central America. The populations of most species of this group occur on the high portions of mountains and are generally isolated from each other, having great potential for speciation. *Anolis wermuthi* (KÖHLER & OBERMEIER, 1998) is a member of the *crassulus* group which presents (aside from few other characteristics such as a smaller dewlap with lower number of enlarged gorgetal scales) a distinct hemipenial morphology. The description of the hemipenis of *A. wermuthi* was based on a subadult paratype, and the morphology of the hemipenis in the remaining populations remained unknown.

In 1998, KÖHLER & OBERMEIER described *Anolis wermuthi* (as *Norops wermuthi*) from the highlands between the cities of Matagalpa and Jinotega (1000–1460 m), in the north-central portion of Nicaragua. Previously, FITCH & SEIGEL (1984) and VENCES et al. (1998) reported *A. wermuthi* (as *A. sminthus* DUNN & EMLEN, 1932 and *Anolis* sp. "*sminthus* group", respectively) from Nicaragua based on few specimens from the same general area KÖHLER (1999b) reported a population of *Anolis wermuthi* from remnant cloud forest atop of Cerro Kilambé (1330–1500 m); subsequently, KÖHLER (2000a), KÖHLER & SCHMIDT (2000), and QUINTANA (2005) reported additional populations from Cerro Saslaya (1290–1430 m) and adjacent Cerro El Toro (1320–1500 m), and finally KÖHLER (2001) and JANSEN (2001) a population from Miraflor (1230–1240 m). All mentioned localities are located in the northern-central mountains of Nicaragua in the Departamentos of Matagalpa, Estelí, Jinotega, and Región Autónoma Atlántico Norte. The general description of the localities known for *Anolis wermuthi* (Fig. 12) is as follows:

1- Highlands between Matagalpa city and Jinotega city: This region includes the type locality of *Anolis wermuthi*. In general, the area is mostly converted to cattle ranches and agriculture. At high elevations, the area is inhabited by a substantial human population and the original forest is widely disturbed, however there are still several relatively well preserved patches of different sizes (including private protected areas) and many of these remaining patches have recently begun being used for ecotourism. Most specimens of *A. wermuthi* were collected in cloud forest either at nighttime while sleeping at a height up to 150 cm on leaves or thin branches, or at daytime while active at ground level or perched up to approximately 50 cm on tree stems, rotten trees, and shrub. A few specimens were collected outside the cloud forest up to 1.5 m in pine grove and open grassland. In this region, *A. wermuthi* is known to occur both in and outside of protected areas.

2- Reserva Natural Miraflor: In general, the area is mostly converted to cattle ranches and agriculture. At high elevations, it is inhabited by a relatively substantial human population, and the original forest is very disturbed with only a few scattered small patches remaining, some of which have recently began to be used for small-scale ecotourism. At Miraflor *Anolis wermuthi* is only known from four specimens collected at nighttime while sleeping on the lower portions of vegetation in two nearby small cloud forest patches. There are no completely everted hemipenis or male dewlap photographs available from this population which, due to heavy deforestation, is considered the most endangered population of *A. wermuthi*.

3- Reserva Natural Cerro Kilambé: Traditionally, the high elevations were inhabited by relatively few people, who abandoned the area during the Nicaraguan Civil War (1979–1990), which was of great intensity in the vicinity of this mountain. At high elevations the area is currently inhabited by a small number of people and although there are still relatively large areas of original undisturbed forest, coffee plantations are rapidly encroaching upon the intact cloud forest (JS obs. pers.). Most specimens of *A. wermuthi* were collected in cloud forest at daytime while active on the base of trees, tree ferns, and other vegetation. A series of nine specimens (including adults of both sexes and juveniles) was collected while active during the day at ground level and lower portions of the emergent vegetation in a recently cleared portion of cloud forest near a stream that was being converted for growing shade coffee (larger forest trees were left to provide shadow but bushes and lower vegetation were cleared).

4- Parque Nacional Cerro Saslaya including adjacent Cerro El Toro: At high elevations the area is uninhabited by people, and the original forest remains intact. Most specimens of *A. wermuthi* were collected in cloud forest during the daytime while active on the ground and on low branches with heavy moss cover. A juvenile was collected while active during the day on low branches in dwarf forest.

None of the four mentioned localities exceed about 1750 m elevation and generally share the following characteristics (see Fig. 12): higher precipitation in the eastern locality (Saslaya-El

Toro) with a decreasing tendency towards west; higher deforestation in the western locality (Miraflor) with forest cover increasing towards the east; and higher human accessibility at the southernmost locality (type locality area) with access becoming increasingly difficult towards the north. The type locality and the Miraflor populations are connected by highlands over 1000 m. Both Kilambé and Saslaya-El Toro are isolated mountains surrounded by lowlands.

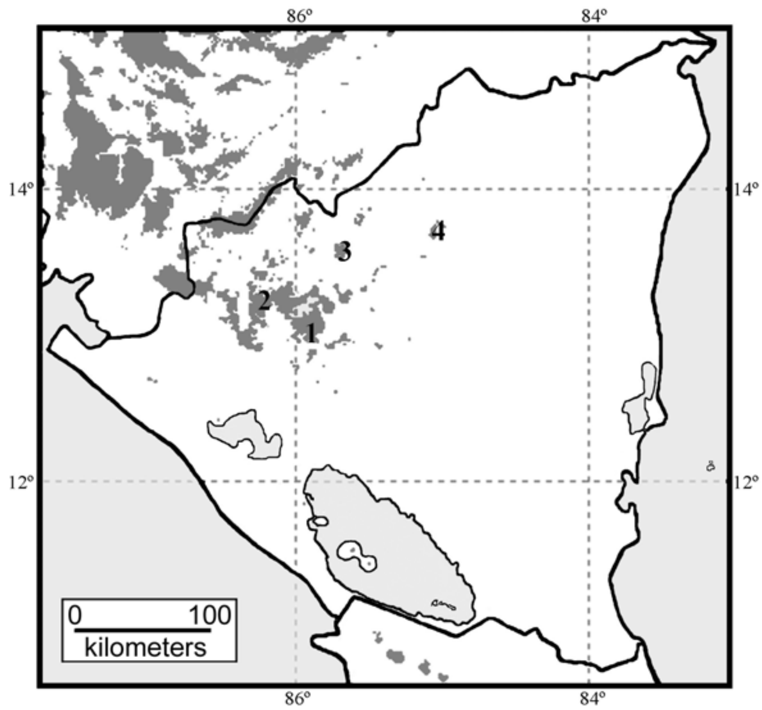


Fig. 12. Map of Nicaragua indicating collecting localities of *Anolis wermuthi*: (1) highlands between the cities of Matagalpa and Jinotega; (2) Miraflor; (3) Kilambé; (4) Saslaya-El Toro. Areas above 1000 m are shaded grey.

JANSEN (2001) analyzed the morphometric and pholidotic variation of *Anolis wermuthi* and concluded that all four populations are well differentiable and the population from Cerro Kilambé is the most distinct of all, which among several particularities presented smooth midventrals, a characteristic of the presumed close relative *A. muralla* (KÖHLER, MCCRANIE & WILSON, 1999) from Honduras. Further sampling resulted in the collection of a substantial series of *Anolis wermuthi* from Cerro Kilambé.

The present study provides detailed data on morphological variation in *Anolis wermuthi* and evaluates evidence for potential cryptic species among all known populations based on morphometric and pholidotic data, as well as on the morphology of everted hemipenis and extended dewlaps. I also describe the everted hemipenis of an adult topotype and the female dewlap.

2.3.1.2 Results

In external morphology, there is great overlap in the ranges of most examined pholidotic and morphometric characters between all four populations of *Anolis wermuthi* (Table 2). I conducted a discriminant function analysis (DFA) based on three characters (number of medial ventral scales in one head length, number of subdigital lamellae of 4th toe, and total number of loreal scales), and did a priori assignment to groups based on the locality (see Materials and Methods). This DFA yielded a scattered diagram (Fig. 13) that correctly classified 60.5% of the specimens. The first function is DS(1) = –0.534041 (number of medial ventral scales in one head length) –0.558057 (number of subdigital lamellae of 4th toe) – 0.642573 (total number of loreal scales). The second function is DS(2) = –0.045428 (number of medial ventral scales in one head length) +0.720981 (number of subdigital lamellae of 4th toe) –0.694971 (total number of loreal scales).

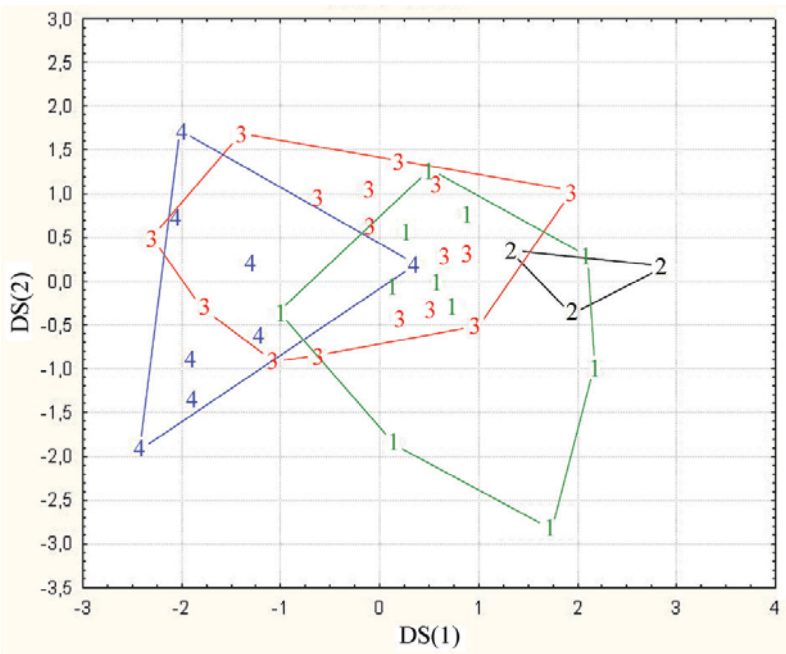


Fig. 13. Discriminant function analysis of the Nicaraguan endemic *Anolis wermuthi*: (1) highlands between the cities of Matagalpa and Jinotega; (2) Miraflor; (3) Kilambé; (4) Saslaya-El Toro. See text for details.

A comparison of everted hemipenis and extended male dewlaps between populations of *Anolis wermuthi* from Kilambé and Saslaya-El Toro revealed no individual or geographical variation and agrees well in morphology with those from the type locality. Also, the extended female dewlaps of the populations of Miraflor and Kilambé are similar in size, coloration, and scalation. Although I do not have available hemipenial or male dewlap descriptions from Miraflor there is no evidence of disagreement in the remaining studied characters with the other populations.

Table 2. Selected measurements, proportions and scale characters of *Anolis wermuthi* from the known populations (specimens listed in Appendix B). Range is followed by mean value and one standard deviation in parentheses. Morphomentric data were only taken from adults. See text for abbreviations.

		Highlands between the Matagalpa city and Jinotega city ♂ 5 ♀ 6	**Reserva Natural Miraflor** ♂ 2 ♀ 1	**Reserva Natural Kilambé** ♂ 8 ♀ 8	**Parque Nacional Saslaya** ♂ 3 ♀ 5
Maximum SVL	♂	50.5	46.0	51.4	49.0
	♀	53.5	47.0	56.0	56.0
Tail length / SVL	♂	2.16–2.51 (2.33±0.12)	2.16–2.22 (2.17±0.04)	2.08–2.53 (2.29±0.16)	2.32–2.37 (2.34±0.04)
	♀	2.02–2.35 (2.18±0.14)	2.01	2.04–2.21 (2.13±0.00)	2.09–2.21 (2.17±0.05)
Tail diameter vertical / horizontal	♂	1.22–1.29 (1.27±0.03)	1.21–1.24 (1.22±0.02)	1.11–1.40 (1.23±0.08)	1.05–1.31 (1.17±0.13)
	♀	1.09–1.32 (1.18±0.09)	1.00	1.11–1.38 (1.23±0.10)	1.05–1.26 (1.19±0.08)
HL / SVL	♂	0.26–0.27 (0.27±0.01)	0.26	0.25–0.27 (0.26±0.01)	0.26–0.27 (0.26±0.01)
	♀	0.27–0.29 (0.27±0.01)	0.27	0.25–0.27 (0.26±0.01)	0.25–0.27 (0.26±0.01)
HL / HW	♂	1.49–1.59 (1.54±0.04)	1.41	1.47–1.60 (1.53±0.05)	1.47–1.53 (1.51±0.03)
	♀	1.47–1.60 (1.51±0.05)	1.45	1.43–1.54 (1.51±0.04)	1.43–1.63 (1.50±0.09)
IP / ear	♂	1.11–3.43 (2.35±0.91)	1.38–1.62 (1.50±0.16)	1.20–2.85 (1.81±0.50)	1.54–2.22 (1.90±0.34)
	♀	1.54–3.34 (2.27±0.76)	0.96	1.03–2.63 (1.63±0.52)	1.08–2.50 (2.62±0.59)
Shank length / SVL	♂	0.26–0.28 (0.27±0.01)	0.28	0.23–0.28 (0.26±0.02)	0.29–0.30 (0.29±0.01)
	♀	0.24–0.26 (0.25±0.01)	0.27	0.22–0.28 (0.26±0.02)	0.26–0.27 (0.27±0.01)

Axilla–groin distance / SVL	♂	0.38–0.44 (0.41±0.02)	0.34–0.36 (0.35±0.02)	0.39–0.41 (0.40±0.01)	0.34–0.41 (0.38±0.03)
	♀	0.38–0.43 (0.41±0.02)	0.42	0.40–0.47 (0.43±0.03)	0.41–0.47 (0.44±0.02)
Subdigital lamellae of 4th toe		23–28 (25.38±1.60)	19–25 (23.09±1.87)	22–24 (22.67±1.15)	23–27 (24.63±1.09)
Number of scales between SS		1–3 (1.63±0.74)	0–2 (1.27±0.65)	1–2 (1.67±0.58)	1–2 (1.13±0.34)
Number of scales between IP and SS		2–3 (2.25±0.46)	2–3 (2.09±0.30)	1–3 (2.00±1.00)	1–2 (1.56±0.51)
Number of scales between SO and SPL		0	0	0	0
Number of SPL to level below center of eye		5–7 (6.50±0.76)	6–7 (6.45±0.52)	6–7 (6.67±0.58)	6–8 (6.56±0.73)
Number of INL to level below center of eye		6–8 (6.88±0.99)	5–7 (6.18±0.60)	6	6–8 (6.50±0.73)
Total number of loreals		19–35 (29.13±5.84)	16–29 (23.00±4.31)	17–22 (19.67±2.52)	18–29 (23.38±3.52)
Number of horizontal loreal scale rows		4–6 (4.88±0.64)	4–5 (4.45±0.53)	4–5 (4.67±0.58)	4–6 (4.63±0.62)
Number of postrostrals		6–7 (6.25±0.46)	4–7 (5.64±0.81)	4–6 (5.34±1.15)	5–8 (6.00±0.82)
Number of postmentals		5–6 (5.75±0.46)	4–5 (4.18±0.40)	4	4–5 (4.13±0.34)
Number of scales between nasals		5–7 (6.25±0.71)	5–6 (5.91±0.30)	5–6 (5.67±0.57)	6–8 (6.63±0.62)
Number of scales between 2nd canthals		5–8 (5.63±1.06)	5–6 (5.36±0.50)	5–6 (5.33±0.58)	5–7 (5.63±0.72)
Number of scales between posterior canthals		8–11 (9.13±0.99)	6–11 (7.91±1.22)	7–9 (8.00±1.00)	6–9 (7.81±0.98)
Number of medial dorsal scales in one head length		24–30 (27.25±2.38)	28–36 (30.91±2.74)	28–32 (29.33±2.31)	23–38 (27.75±4.25)
Number of medial ventral scales in one head length		22–30 (27.75±2.71)	22–28 (25.45±1.57)	22–24 (22.67±1.15)	22–32 (26.50±2.68)

I therefore consider all examined specimens from in between the cities of Matagalpa and Jinotega, Miraflor, Kilambé, and Saslaya-El Toro (see appendix B) to belong to the same species, *Anolis wermuthi*, a variable anole with a unique hemipenis morphology.

Anolis wermuthi (KÖHLER & OBERMEIER, 1998)

Norops wermuthi KÖHLER & OBERMEIER, 1998; type locality: Montaña La Galia, Nicaragua.

Diagnosis: A medium-sized species (SVL in largest specimen 56.0 mm) of the genus *Anolis* (sensu POE 2004) and the *crassulus* group (sensu KÖHLER, 2003) that is most similar in external morphology to a cluster of Central American species that have heterogeneous lateral scales with solitary enlarged keeled scales scattered among smaller granular laterals, suboculars and supralabials in contact, males with red dewlap and enlarged postanal scales, eight or fewer distinctly enlarged dorsal scales, and midventral scales smooth or only faintly keeled (i.e., *Anolis heteropholidotus* MERTENS, 1952a*, A. muralla, A. sminthus*). Within this cluster of species, *A. wermuthi* can be readily distinguished by having hemipenis with a divided asulcate processus (processus undivided in the remaining species, unknown in *A. muralla*). Additionally, *A. wermuthi* differs from the species in this cluster by the following characteristics (condition for *A. wermuthi* in parentheses): *Anolis heteropholidotus*: ventrals in thoracic region smooth to weekly keeled (ventrals in thoracic region keeled to well keeled); uniformly large median dorsals (irregular small scales among the enlarged median dorsal scales); male dewlap larger than 150 mm^2 (male dewlap smaller than 150 mm^2). *Anolis muralla*: midventrals smooth (midventrals generally weekly keeled); average ratio shank length/SVL 0.24 (0.26); average of scales between SS 0.92 (1.32); average number of scales between IP and SS 2.96 (1.89); average of scales between nasals 4.23 (6.26). *Anolis sminthus*: enlarged median dorsal scales relatively regularly arranged (very irregularly arranged); average number of scales between SS 0.78 (1.32); average number of scales between IP and SS 2.97 (1.89).

Description: Maximum SVL 51.5 mm in males, 56.0 mm in females; ratio tail length/SVL 2.00–2.53 (2.22 ± 0.14); tail slightly compressed in cross section, ratio tail height/tail width 1.00–1.40 (1.21 ± 0.09); ratio axilla to groin distance/SVL 0.34–0.47 (0.41 ± 0.03); ratio head length/SVL 0.25–0.29 (0.26 ± 0.01); ratio snout length/head length 0.42–0.47 (0.44 ± 0.01); ratio head length/head width 1.41–1.63 (1.51 ± 0.05); longest toe of adpressed hind limb usually reaches eye; ratio shank length/SVL 0.22–0.30 (0.26 ± 0.02); ratio shank length/head length 0.88–1.13 (1.00 ± 0.07); longest finger of adpressed forelimb reaches in between 5 mm anterior to groin and the middle portion of the anterior to posterior insertion of hind limbs; scales on snout slightly bulging to keeled; 4–8 (5.9 ± 0.8) postrostrals; 4–8 (6.3 ± 0.6) scales between nasals; scales in distinct prefrontal depression variable, generally slightly tuberculate, sometimes smooth or keeled; supraorbital semicircles well developed, separated by 0–3 (1.3 ± 0.6) keeled scales; supraorbital disc composed of 4–8 (6.6 ± 1.0) distinctly enlarged, generally keeled and wrinkled scales; circumorbital row sometimes complete, when incomplete with no more than 2 enlarged supraorbitals in contact with supraorbital semicircles; 2–3 strongly keeled, elongated, overlapping superciliaries; 2–5 rows of small and medium sized keeled scales extending between enlarged supraorbitals and superciliaries; a very shallow parietal depression present in most specimens; interparietal scale generally well developed, surrounded mostly by scales of moderate size, sometimes with few irregular smaller scales among; 1–3 (1.9 ± 0.6) scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 6–7 (6.4 ± 0.5) canthal scales, with 2–3 (2.9 ± 0.2) larger posterior scales; 5–8 (5.5 ± 0.7) scales present between second canthals; 6–11 (8.1 ± 1.1) scales present between posterior canthals; 16–35 (24.2 ± 4.9) keeled loreal scales in a maximum of 4–6 (4.6 ± 0.6) horizontal rows; 6–9 keeled subocular scales arranged in a single row; 5–8 (6.5 ± 0.6) supralabials to level below center of eye; 1–3 suboculars broadly in contact with supralabials; ratio tympanum height/interparietal scale length 0.48–1.45 (0.84 ± 0.22); mental distinctly wider than long, completely divided medially, bordered posteriorly by 4–6 (4.5 ± 0.8) postmentals; 5–8 (6.4 ± 0.8) infralabials to level below center of eye; sublabials undifferentiated; generally keeled granular scales present on chin and throat; dorsum of body with 8–14 median and paramedian enlarged dorsal rows of keeled scales, 2–7 of them well enlarged; 23–38 (28.7 ± 3.6) medial dorsal scales in one head length; 34–59 (47.3 ± 6.8) medial dorsal scales between axilla and groin; lateral scales keeled, generally heterogeneous, sometimes homogeneous or almost; ventrals at midbody non-bulging, imbricate, mostly weekly keeled, sometimes smooth; 22–32 (26.2 ± 2.6) ventral scales in one head length; 35–48 (42.5 ± 3.4) ventral scales between axilla and groin; 97–122 (108.5 ± 5.9) scales around midbody; caudal scales strongly keeled; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although an indistinct division in segments is discernible; a pair of enlarged postanal scales present; no tube-like axillary pocket present; scales on dorsal surface of forelimb keeled, imbricate; digital pads dilated; distal phalanx narrower than and raised from dilated pad; 19–29 (24.2 ± 1.7) lamellae under phalanges ii–iv of fourth toe; 8–10 (9.1 ± 0.6) scales under distal phalanx of fourth toe.

Male dewlaps (Fig. 14a-b) are red and moderately small (around 110 mm^2), extending to level of axilla or slightly posteriorly, with 14–18 enlarged gorgetal scales in 4–5 scale rows (3–5 scales per row), and 20–30 enlarged sternal scales in 4–6 scale rows (3–7 scales per row).

Female dewlaps (Fig. 14c-d) are orange and very small (around 30 mm^2), extending to level of shoulder or slightly posteriorly, with 15–23 slightly enlarged gorgetal-sternal scales. Scales on the dewlap of both males and females are tan to dark brown in coloration.

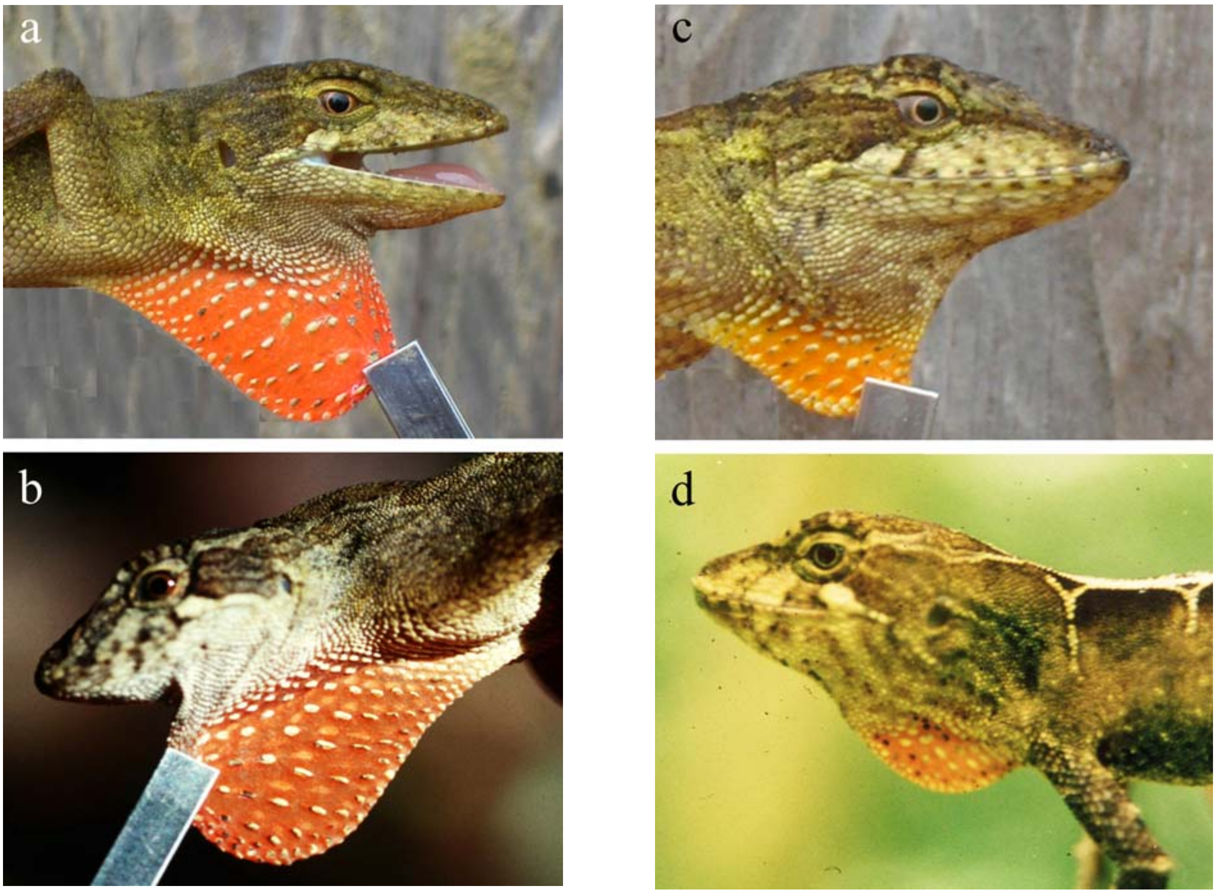


Fig. 14. (Left) Male dewlaps of *Anolis wermuthi* in life: (a) Cerro Kilambé; (b) Cerro El Toro (Photograph: G. Köhler). (Right) Female dewlaps of *Anolis wermuthi* in life: (c) Cerro Kilambé; (d) Miraflor (Photograph: M. Jansen).

The everted hemipenis of an adult male (SMF 78604) is a moderately large bilobed organ with the following characteristics (Fig. 15): compact rounded lobes, weakly divided from each other, as wide as long or slightly wider; sulcus spermaticus bordered by well developed sulcal lips and bifurcating at base of apex, shortly after the bifurcation the branches open into a broad, slightly concave area, one on each lobe; truncus relatively stout, longer than length of lobes; asulcate surface of apex and distal truncus strongly calyculate, base of truncus with transverse folds; distinct fingerlike processus present on the asulcate distal truncus area, accompanied proximally by another shorter knoblike calyculate projection.

Range: Highlands of north-central Nicaragua.

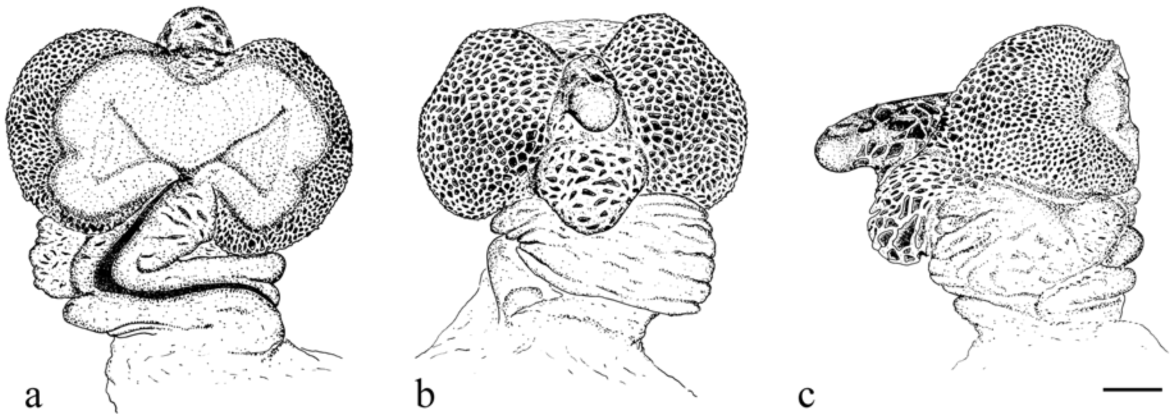


Fig. 15. Hemipenis of an adult *Anolis wermuthi* (SMF 78604) from the type locality: (a) sulcate view; (b) asulcate view; (c) lateral view. Scale bar equals 1.0 mm. Drawings: M. VESELÝ.

2.3.1.3 Discussion

KÖHLER & OBERMEIER (1998) reported the great variability in dorsal coloration among the type specimens of *Anolis wermuthi*. I also found the Kilambé populations to be very variable in dorsal coloration (Fig. 16), and the same is true for the Miraflor and Saslaya-El Toro populations. Nevertheless, most individuals present the following coloration characteristics: presence of a brown interorbital bar; presence of crossbands on limbs; pale brown ventral coloration with a continous or interrupted dark brown midventral stripe; and dark brown bars radiating out from eye.

Anolis wermuthi is also a variable species in pholidotic characters: the heterogeneous lateral squamation typical of the anoles of the *crassulus* group (KÖHLER, 2003) is present in all specimens from Miraflor, most specimens from the type locality area and Kilambé, and in around half of the examined specimens from Saslaya-El Toro (in the remaining specimens lateral squamation is completely homogenous or almost so). Also typical for the *crassulus* group is the presence of both supraorbital semicircles separated by two or fewer scales or in contact medially (KÖHLER et al., 1999). However, SMF 82062, an adult female from El Toro, has three scales between SS. Finally, all examined *A. wermuthi* have the lateral ventral scales and those in the thoracic region keeled, whereas midventrals are weakly keeled, with the exception of around half the examined specimens from Kilambé and one specimen from El Toro (SMF 82065) which have smooth midventrals.

Fig. 16. Part of the Kilambé series of *Anolis wermuthi* to demonstrate variation in dorsal coloration: (a-b) adult males; (c) juvenile; (d-f) adult females.

Table 2 shows a tendency in several other characters for each population. These could be derived from historical bottle neck processes or result from small sample sizes (despite recent collecting efforts there are still few adult specimens of *Anolis wermuthi* available in museum collections). The character "total number of postmentals" does not overlap between the type locality and the Kilambé populations. I did not use this character in the discriminant function analysis because it has proven to be relatively variable in several other anole species, varying up to ±2 scales.

I are not aware of any preserved specimen with everted hemipenes of the presumed closely related *Anolis muralla*, an anole endemic to the highlands of Parque Nacional La Muralla (1440–1740 m) in the northwestern portion of Departamento de Olancho, Honduras, which is also represented with few specimens in museum collections. This species principally differs from *A. wermuthi* by having perfectly smooth midventral scales (midventrals in *A. wermuthi* mostly weekly keeled, smooth in some individuals, especially in those from the Kilambé population), but also differ in several other minor differences (see diagnosis). A study of the molecular systematics of the *crassulus* group is needed in order to fully comprehend the taxonomy and phylogeny of this group.

2.3.2 MORPHOLOGICAL VARIATION IN CENTRAL AMERICAN LEAF-LITTER ANOLES: *ANOLIS HUMILIS, A. QUAGGULUS* AND *A. UNIFORMIS* (REPTILIA, SQUAMATA, IGUANIDAE)

2.3.2.1 Introduction

In 1863, W. PETERS described *Anolis humilis* based on two female syntypes (now ZMB 500, 55223) from "Veragua". According to SAVAGE (1970: 279), "today the old Veragua comprises the Provincias of Veraguas, Chiriquí and Bocas del Toro." COPE (1885b) described *Anolis quaggulus* (based on an adult male [now USNM 24979 according to COCHRAN, 1961] from "San Juan river, Nicaragua") and *Anolis uniformis* (based on "many specimens from Guatemala from Henry HAGUE, and one from Yucatán from Arthur SCOTT" [COPE, 1885b: 393]). In 1935, STUART named *Anolis ruthveni* (based on an adult male from "about two miles north of Santa Teresa, El Peten, Guatemala"). In his monograph of Costa Rican lizards, TAYLOR (1956) described another taxon related to this cluster of species: *Anolis humilis marsupialis* based on a series of seven specimens from "about 15 km WSW of San Isidro del General along the Dominical Road" (probably Puntarenas Province, or near the boundary of this province in San José Province).

BARBOUR (1934) and most subsequent authors (e.g., STUART, 1948, 1963, PETERS & DONOSO-BARROS, 1970) placed *quaggulus* in the synonymy of *humilis*, and *ruthveni* in the synonymy of *uniformis*, respectively. Also, these authors considered *uniformis* as a subspecies of *humilis*, a view considered valid until MEYER & WILSON (1971) presented evidence for species status of *uniformis*, mostly based on differences in male dewlap coloration. Subsequent authors (e.g., FITCH & SEIGEL, 1984, SAVAGE & VILLA, 1986, KÖHLER, 2000b) followed the conclusion that *humilis* and *uniformis* represent two separate species. Recently, KÖHLER et al. (2003) ressurrected *quaggulus* as a valid species distinct from *humilis,* mostly based on differences in hemipenial morphology, and they also concluded that *Anolis humilis marsupialis* remains in the synonymy of *A. humilis*.

Here I report upon the results of this study on the interspecific variation in pholidosis, morphometrics, and hemipenis morphology of the small leaf litter anoles currently assigned to the species *Anolis humilis, A. quaggulus,* and *A. uniformis*.

2.3.2.2 Results

Interspecific variation is most evident in hemipenis morphology with each species having a distinct hemipenis shape and surface ornamentation. The hemipenis of *Anolis humilis* is a medium-sized organ with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and the lobes. In *A. quaggulus*, the hemipenis is relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes. *Anolis uniformis* has a medium-sized bilobate hemipenis with the sulcus spermaticus bifurcating at base of apex and the branches continuing to tips of lobes; an asulcate ridge is present; the lobes are strongly calyculate and the truncus bears transverse folds. In the examined material, intraspecific variation in hemipenis morphology is restricted to size differences of the organ with smaller individuals having smaller hemipenes.

In contrast to the documented interspecific differences in hemipenis morphology, very little differentiation in pholidotic and morphometric characters could be documented. See Table 3 for variation in selected measurements and proportions and scale characters. Interspecific variation was observed in several characters but with large overlap of the documented ranges. Statistically significant differences ($p<0.005$) were observed between *Anolis uniformis* and the other two species in the following characters (see Table 3): (1) number of supralabials to level below center of eye; (2) number of postrostrals; (3) number of dorsal scales between levels of axilla and groin; (4) number of ventral scales between levels of axilla and groin. Statistically significant differences between *A. quaggulus* and *A. humilis* were observed in the number of postrostrals. *Anolis uniformis* usually has 1–3 pale vertical lines in the flank region (lines can be broken), a character absent in *A. humilis* and *A. quaggulus* (Figs. 17–19). *Anolis quaggulus* differs from the other two species by usually having three large elongate scales in the anterior supraciliar region (only two such scales present in *A. humilis* and *A. uniformis*).

Fig. 17. Adult Male of *Anolis humilis* from Fortuna, Chiriquí, Panama. Photograph: G. KÖHLER.

Fig. 18. Adult Male of *Anolis quaggulus* from Parque Nacional Saslaya, Nicaragua. Photograph: G. KÖHLER.

Fig. 19. Adult Male of *Anolis uniformis* from the Cockscomb Basin Wildlife Sanctuary, Stann Creek, Belize. Photograph: G. KÖHLER.

Table 3. Selected measurements, proportions and scale characters of *Anolis humilis, A. quaggulus* and *A. uniformis.* Range is followed by mean value and one standard deviation in parentheses, and then by sample size. Abbreviations: SVL = snout–vent length; HL = head length; HW = head width; SS = supraorbital semicircles; IP = interparietal plate; SO = subocular scales; SPL = supralabial scales, INL = infralabials.

		A. humilis ♂ 27 ♀ 10	***A. quaggulus*** ♂ 26 ♀ 19	***A. uniformis*** ♂ 19 ♀ 10
Maximum SVL	♂	43.9	40.4	40.3
	♀	48	43.7	40.5
Tail length / SVL	♂	1.48–1.70 (1.61±0.06)	1.35–1.73 (1.53±0,10)	1.28–1.57 (1.43±0.11)
	♀	1.33–1.50 (1.43±0.07)	1.29–1.49 (1.40±0.08)	1.22–1.35 (1.30±0.06)
Tail diameter vertical / horizontal	♂	1.30–1.47 (1.24±0.09)	0.81–1.74 (1.25±0.16)	1.31–2.05 (1.52±0.21)
	♀	1.13–1.21 (1.15±0.04)	1.13–1.54 (1.25±0.17)	1.27–1.48 (1.35±0.09)
Axilla–groin distance / SVL	♂	0.25–0.43 (0.40±0.04)	0.35–0.44 (0.39±0.02)	0.32–0.45 (0.38±0.03)
	♀	0.34–0.46 (0.40±0.05)	0.31–0.46 (0.39±0.06)	0.37–0.44 (0.40±0.03)
HL / SVL	♂	0.24–0.33 (0.27±0.02)	0.23–0.33 (0.27±0.02)	0.24–0.38 (0.29±0.03)
	♀	0.23–0.30 (0.26±0.03)	0.22–0.30 (0.26±0.03)	0.22–0.30 (0.27±0.03)
HL / HW	♂	1.39–1.62 (1.54±0.06)	1.39–1.66 (1.54±0.06)	1.47–1.76 (1.57±0.07)
	♀	1.38–1.65 (1.50±0.11)	1.37–1.63 (1.51±0.11)	1.45–1.64 (1.54±0.09)
Snout length/ SVL	♂	0.17–0.21 (0.19±0.01)	1.18–0.24 (0.20±0.02)	0.18–0.28 (0.21±0.02)
	♀	0.17–0.21 (0.19±0.01)	0.17–0.22 (0.19±0.02)	0.01–0.21 (0.18±0.09)
Snout length/ HL	♂	0.61–0.82 (0.74±0.06)	0.67–0.86 (0.76±0.05)	0.64–0.84 (0.73±0.05)
	♀	0.61–0.80 (0.73±0.08)	0.62–0.83 (0.73±0.08)	0.40–0.77 (0.69±0.16)
Shank length/SVL	♂	0.24–0.31 (0.27±0.02)	0.24–0.30 (0.27±0.01)	0.27–0.31 (0.28±0.01)
	♀	0.24–0.28 (0.26±0.02)	0.24–0.30 (0.26±0.03)	0.25–0.29 (0.27±0.03)
Shank length/HL	♂	0.78–1.14 (0.99±0.10)	0.82–1.20 (1.00±0.09)	0.73–1.15 (0.97±0.10)
	♀	0.90–1.19 (0.99±1.12)	0.84–1.10 (1.00±0.07)	0.94–1.15 (1.00±0.09)
Subdigital lamellae of 4th toe		16–22 (19.00±2.43)	16–23 (19.57±1.64)	16–23 (19.93±1.75)
Number of scales between SS		1–4 (2.22±0.49)	1–4 (2.22±0.53)	1–3 (1.81±0.69)
Number of scales between IP and SS		2–5 (2.92±0.68)	2–5 (2.92±0.68)	1–4 (2.48±0.69)
Number of scales between SO and SPL		0–3 (1.27±0.78)	0–2 (1.16±0.73)	0–2 (1.52±0.57)
Number of SPL to level below center of eye		5–8 (6.53±0.63)	5–8 (6.41±0.69)	6–10 (7.62±0.94)
Number of INL to level below center of eye		5–10 (7.27±1.07)	5–8 (6.81±0.79)	6–10 (7.93±1.07)
Total number of loreals		26–52 (38.09±6.60)	22–46 (35.10±6.36)	30–49 (39.47±4.62)
Number of horizontal loreal scale rows		5–9 (6.78±1.02)	4–8 (6.24±0.95)	5–9 (6.72±1.13)
Number of postrostrals		7–10 (7.93±0.81)	6–9 (7.30±0.73)	5–8 (6.28±0.10)
Number of postmentals		4–8 (6.18±0.81)	5–8 (6.16±0.55)	4–8 (5.80±1.08)
Number of scales between nasals		7–11 (8.26±1.07)	6–10 (8.14±1.08)	6–10 (7.83±0.97)
Number of scales between 2nd canthals		7–12 (9.27±1.30)	7–12 (8.84±1.07)	7–10 (8.83±0.80)
Number of scales between posterior canthals		8–15 (11.18±1.51)	7–13 (11.71±1.41)	8–13 (10.14±1.06)
Number of medial dorsal scales in one head length		19–29 (23.00±2.36)	17–30 (22.46±3.15)	18–25 (20.76±1.68)

Number of ventral scales in one head length	26–44 (32.20±4.14)	23–52 (32.24±6.65)	20–36 (29.97±3.83)
Number of medial dorsal scales between levels of axilla and groin	26–42 (33.78±3.81)	23–43 (33.73±5.20)	22–36 (28.10±3.90)
Number of ventral scales between levels of axilla and groin	35–56 (44.04±5.13)	32–57 (44.89±5.08)	31–47 (38.07±3.65)

Measurements and scalation data were taken from 37 *Anolis humilis* (27 males, 10 females), 45 *A. quaggulus* (26 males, 19 females), and 29 *A. uniformis* (19 males, 10 females). A discriminant function analysis based on three pholidotic characters (number of dorsal scales between levels of axilla and groin [DAG], number of ventral scales between levels of axilla and groin [VAG], and number of supralabial scales to level of center of eye [supralabials]) yielded a scatter diagram (not shown) that correctly classified 59.5% of the specimens. A discriminant function analysis based on five pholidotic characters (those above plus number of postrostral scales [postrostrals] and number of scales around midbody [SAM]) yielded a scatter diagram (Fig. 20) that correctly classified 71.8% of the specimens. The first and second discriminant functions classified 71.1% of the *A. quaggulus* specimens (group 1), 63.9% of the *A. humilis* specimens (group 2), and 82.8% of the *A. uniformis* specimens (group 3). Accordingly, the polygons of the three species largely overlap. The first function is DS(1) = –0.50732 (supralabials) + 0.56861 (postrostrals) + 0.28199 (SAM) + 0.41253 (DAG) + 0.22297 (VAG). The second function is DS(2) = 0.37570 (supralabials) + 0.49129 (postrostrals) + 0.65182 (SAM) – 0.16661 (DAG) – 0.59379 (VAG).

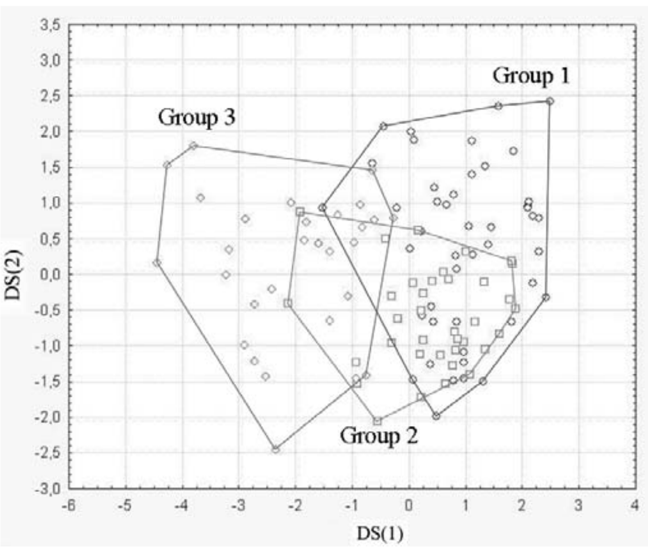


Fig. 20. Discriminant function analysis of Central American leaf litter anoles: 1) *Anolis quaggulus*; 2) *Anolis humilis*; 3) *Anolis uniformis*. See text for details.

Key to *Anolis humilis*, *A. quaggulus* and *A. uniformis*:

1a Usually 22–32 dorsal scales between levels of axilla and groin, rarely up to 36; 6–10, mean 7.6, supralabial scales; flank usually with 1–3 pale vertical lines (lines can be broken); dewlap in adult males (in life) rose with purple spots……………………………..… ***Anolis uniformis***

1b Usually 30–39 dorsal scales between levels of axilla and groin, rarely few as 23; 5–8, mean 6.5, supralabial scales; flank without pale vertical lines or broken lines; dewlap in adult males (in life) different as above…….…………………….…………………………………..… **2**

2a Usually two large elongate scales in the anterior supraciliar region (Fig. 21a); postaxillary pocket usually relatively wide, and shallow; Hemipenis relatively large with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and the lobes; maximum SVL 46.2 mm in males and 50.0 mm in females…………………...... ***Anolis humilis***

2b Usually three large elongate scales in the anterior supraciliar region (Fig. 21b); postaxillary pocket usually narrow, tube-like and deep; Hemipenis relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes; maximum SVL 37.0 mm in males and 41.0 mm in females……………...... ***Anolis quaggulus***

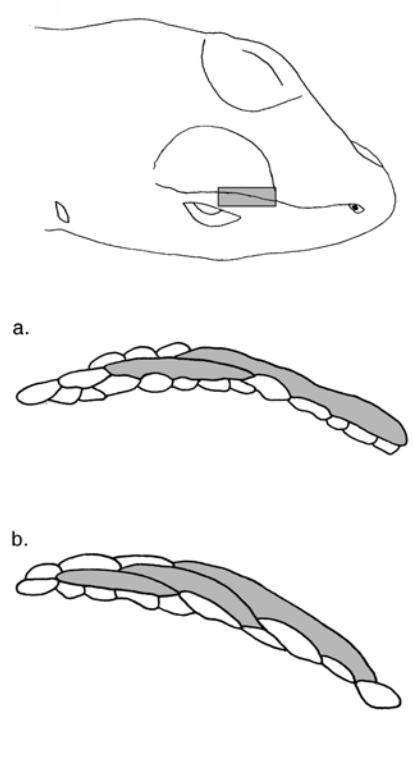


Fig. 21. Superciliary region of a) *Anolis humilis* (SMF 85104) and b) *Anolis quaggulus* (SMF 77480).

Anolis humilis PETERS, 1863

Anolis humilis PETERS, 1863: 138; type locality: Veragua, Panama.

Diagnosis: *Anolis humilis* can be distinguished from all other Central American species of *Anolis*, except *A. compressicauda, A. quaggulus, A. tropidonotus*, *A. uniformis*, and *A. wampuensis*, by having a deep tubelike axillary pocket. *Anolis compressicauda, A. tropidonotus* and *A. wampuensis* have the scales anterior to the ear opening distinctly larger than those posterior to the ear opening (these scales more or less subequal in *A. humilis*). *Anolis uniformis* has usually 1–3 pale vertical lines in the flank region (absent in *A. humilis*) and a rose male dewlap with a large central purple spot (male dewlap reddish orange with yellow margin in *A. humilis*). *Anolis quaggulus* has usually three large elongate scales in the anterior supraciliar region (usually two such scales in *A. humilis*). Also, in *A. quaggulus* the hemipenis is relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes (the hemipenis of *A. humilis* is relatively large with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and the lobes).

Description: Maximum SVL 43.9 mm in males, 48.0 mm in females; tail length / SVL ratio 1.33–1.70; HL / SVL 0.24–0.33 in males, 0.22–0.30 in females; HL / HW 1.38–1.65 in males, 1.38–1.65 in females; shank length / SVL 0.24–0.31; shank length / HL 0.78–1.19; longest toe of adpressed hind limb usually reaching to a point between posterior and anterior border of eye; tail slightly to distinctly laterally compressed in cross section, tail height / width ratio 1.13–1.47. Scales on snout strongly keeled; 6–9 postrostrals (Fig. 22); 6–10 scales between nasals; usually 2 scales between circumnasal and rostral; scales in distinct frontal depression strongly keeled; supraorbital semicircles poorly to moderately developed, composed of keeled scales; 1–3, rarely 4, rows of scales separating supraorbital semicircles at narrowest point; 2–5 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 6–8 distinctly enlarged, strongly keeled scales; 1–2 enlarged supraorbitals in contact with supraorbital semicircles; supraorbitals decreasing abruptly in size laterally; 2–3 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 2 elongated superciliaries, the anterior one about two times the length of the following one; interparietal scale not well developed, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3–4 large scales; 7–12 scales present between second canthals; 7–13 scales present between posterior canthals; loreal region slightly concave, 22–46 strongly keeled loreal scales in a maximum of 4–8 horizontal rows; keeled subocular scales usually arranged in a single row; subocular series either in contact with supralabials or separated by one complete scale row; 5–8 supralabials to level below center of eye; mental completely divided medially, bordered posteriorly by 5–8 postmentals; 5–8 infralabials to level below center of eye; keeled granular scales present on chin and throat; lateral head scales anterior to the ear opening about the same size as those posterior to the ear opening; ear opening usually vertically oval.

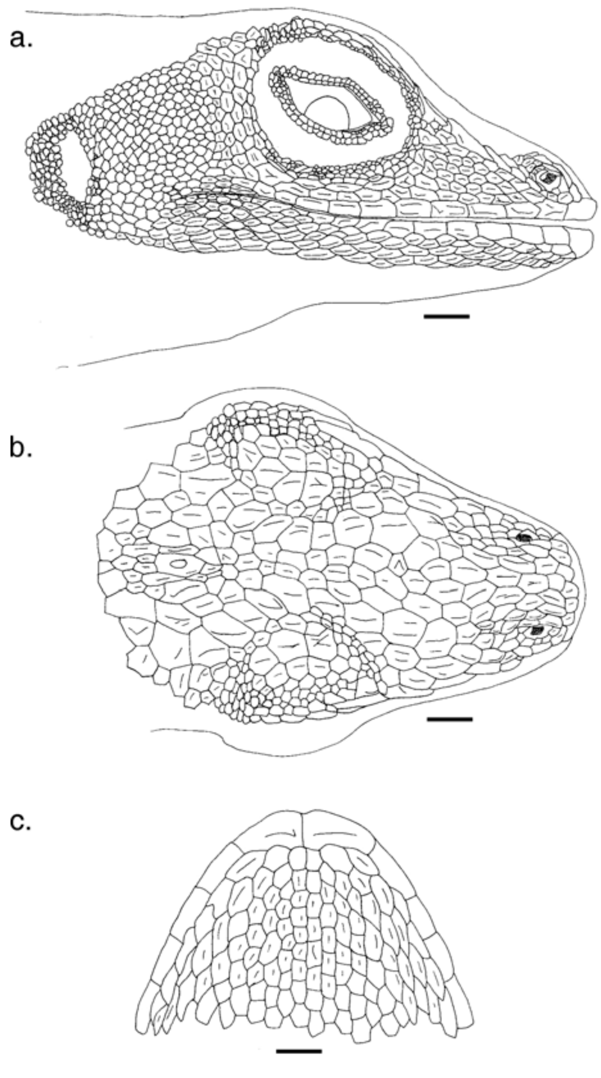


Fig. 22. Head of *Anolis humilis* (SMF 80847): a) lateral view; b) dorsal view; c) ventral view. Scale bars equal 1.0 mm.

Dorsum of body with keeled, subimbricate scales, 17–30 dorsal scales in one head length, 23–43 dorsal scales between levels of axilla and groin; 7–11 median rows of dorsal scales enlarged, dorsals abruptely larger than the smaller, keeled and homogeneous laterals; ventrals at midbody distinctly keeled, mucronate and subimbricate, 23–52 ventral scales in one head length, 32–57 ventral scales between levels of axilla and groin.

Dorsal, lateral and ventral caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; dorsal medial caudal scales slightly enlarged, not forming a crest; limb scales strongly keeled, imbricate; digital pads dilated, about two times as wide as non-dilated distal portion of toe; distal phalanx narrower than and raised from, dilated pad; 16–23 lamellae under phalanges ii–iv of fourth toe.

The completely everted hemipenis (SMF 80845) is a moderate-sized organ with well-developed elongate lobes (length of lobes equal to or slightly greater than length of truncus); both the truncus and the lobes have a strongly calyculate surface; sulcus spermaticus bifurcates at the base of the apex and the branches continue to the tip of the lobes.

Range: Central Costa Rica to Panama east of the Canal Zone (Fig. 23).

Anolis quaggulus COPE, 1885b

Anolis quaggulus COPE, 1885b: 391; type locality: Río San Juan, Nicaragua.

Diagnosis: *Anolis quaggulus* can be distinguished from all other Central American species of *Anolis*, except *A. compressicauda, A. humilis, A. tropidonotus*, *A. uniformis*, and *A. wampuensis*, by having a deep tubelike axillary pocket. *Anolis compressicauda, A. tropidonotus* and *A. wampuensis* have the scales anterior to the ear opening distinctly larger than those posterior to the ear opening (these scales more or less subequal in *A. quaggulus*). *Anolis uniformis* has usually 1–3 pale vertical lines in the flank region (absent in *A. quaggulus*) and a rose male dewlap with a large central purple spot (male dewlap reddish orange with yellow margin in *A. quaggulus*). *Anolis humilis* has usually two large elongate scales in the anterior supraciliar region (usually three such scales in *A. quaggulus*). Also, in *A. humilis* the hemipenis is relatively large with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and the lobes (the hemipenis of *A. quaggulus* is relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes).

Fig. 23. Distribution of *Anolis humilis* (squares) and *A. quaggulus* (triangles). Red symbols represent localities from where I have examined adult males with everted hemipenes; black symbols represent localities from where I have examined specimens of the respective species but not males with everted hemipenes; white symbols represent literature records. A single symbol can represent two or more nearby localities.

Description: Maximum SVL 40.4 mm in males, 43.7 mm in females; tail length / SVL ratio 1.35–1.73; HL / SVL 0.23–0.33 in males, 0.22–0.30 in females; HL / HW 1.39–1.66 in males, 1.37–1.63 in females; shank length / SVL 0.24–0.30; shank length / HL 0.82–1.20; longest toe of adpressed hind limb usually reaching to a point between posterior and anterior border of eye; tail slightly to distinctly laterally compressed in cross section, tail height / width ratio 0.81–1.74. Scales on snout strongly keeled; 7–10 postrostrals (Fig. 24); 7–11 scales between nasals; usually 2 scales between circumnasal and rostral; scales in distinct frontal depression strongly keeled; supraorbital semicircles poorly to moderately developed, composed of keeled scales; 1–4 rows of scales separating supraorbital semicircles at narrowest point; 2–5 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 6–8 distinctly enlarged, strongly keeled scales; 1–2 enlarged supraorbitals in contact with supraorbital semicircles; supraorbitals decreasing abruptly in size laterally; 2–3 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 3 elongated superciliaries, the anterior one largest; interparietal scale not well developed, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3–4 large scales; 7–12 scales present between second canthals; 8–15 scales present between posterior canthals; loreal region slightly concave, 26–52 strongly keeled loreal scales in a maximum of 5–9 horizontal rows; keeled subocular scales usually arranged in a single row; subocular series either in contact with supralabials or separated by one complete scale row; 5–8 supralabials to level below center of eye; mental completely divided medially, bordered posteriorly by 4–8 postmentals; 5–10 infralabials to level below center of eye; keeled granular scales present on chin and throat; lateral head scales anterior to the ear opening about the same size as those posterior to the ear opening; ear opening usually vertically oval.

Dorsum of body with keeled, subimbricate scales, 19–29 dorsal scales in one head length, 26–42 dorsal scales between levels of axilla and groin; 7–11 median rows of dorsal scales enlarged, dorsals abruptely larger than the smaller, keeled and homogeneous laterals; ventrals at midbody distinctly keeled, mucronate and subimbricate, 26–44 ventral scales in one head length, 35–56 ventral scales between levels of axilla and groin.

Dorsal, lateral and ventral caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; dorsal medial caudal scales slightly enlarged, not forming a crest; limb scales strongly keeled, imbricate; digital pads dilated, about two times as wide as non-dilated distal portion of toe; distal phalanx narrower than and raised from, dilated pad; 16–22 lamellae under phalanges ii–iv of fourth toe.

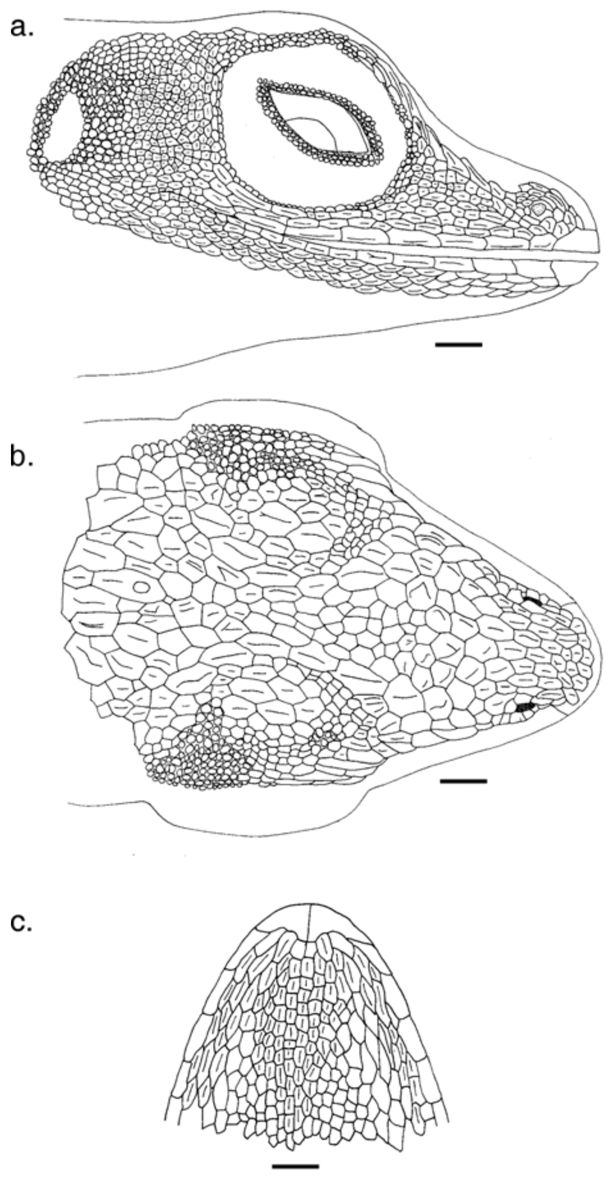


Fig. 24. Head of *Anolis quaggulus* (SMF 77480): a) lateral view; b) dorsal view; c) ventral view. Scale bars equal 1.0 mm.

The completely everted hemipenis (SMF 79824) is a relatively small organ with short and stout lobes (length of lobes less than half the length of truncus); the truncus and lobes are not calyculate, but tiny papillae are present in many specimens, and these papillae are frequently black; the sulcus spermaticus bifurcates at the base of the apex and the branches continue to the tip of the lobes.

Range: Eastern Honduras to central Costa Rica (Fig. 23).

Anolis uniformis COPE, 1885b

Anolis uniformis COPE, 1885b: 392; type locality: Yucatán.

Diagnosis: *Anolis uniformis* can be distinguished from all other Central American species of *Anolis*, except *A. compressicauda, A. humilis*, *A. quaggulus, A. tropidonotus*, and *A. wampuensis*, by having a deep tubelike axillary pocket. *Anolis compressicauda, A. tropidonotus* and *A. wampuensis* have the scales anterior to the ear opening distinctly larger than those posterior to the ear opening (these scales more or less subequal in *A. uniformis*). *Anolis humilis* and *A. quaggulus* don't have pale vertical lines in the flank region (usually present in *A. uniformis*) and a reddish orange with yellow margin (male dewlap rose with a large central purple spot in *A. uniformis*).

Description: Maximum SVL 40.3 mm in males, 40.5 mm in females; tail length / SVL ratio 1.22–1.57; HL / SVL 0.24–0.38 in males, 0.22–0.30 in females; HL / HW 1.47–1.76 in males, 1.45–1.64 in females; shank length / SVL 0.25–0.31; shank length / HL 0.73–1.15; longest toe of adpressed hind limb usually reaching to a point between posterior and anterior border of eye; tail slightly to distinctly laterally compressed in cross section, tail height / width ratio 1.27–2.05. Scales on snout strongly keeled; 5–8 postrostrals (Fig. 25); 6–10 scales between nasals; usually 2 scales between circumnasal and rostral; scales in distinct frontal depression strongly keeled; supraorbital semicircles poorly to moderately developed, composed of keeled scales; 1–3 rows of scales separating supraorbital semicircles at narrowest point; 1–4 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 6–8 distinctly enlarged, strongly keeled scales; 1–2 enlarged supraorbitals in contact with supraorbital semicircles; supraorbitals decreasing abruptly in size laterally; 2–3 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 2 elongated superciliaries, the anterior one about two times the length of the following one; interparietal scale not well developed, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3–4 large scales; 7–10 scales present between second canthals; 8–13 scales present between posterior canthals; loreal region slightly concave, 30–49 strongly keeled loreal scales in a maximum of 5–9 horizontal rows; keeled subocular scales usually arranged in a single row; subocular series either in contact with supralabials or separated by one complete scale row; 6–10 supralabials to level below center of eye; mental completely divided medially, bordered posteriorly by 4–8 postmentals; 6–10 infralabials to level below center of eye; keeled granular scales present on chin and throat; lateral head scales anterior to the ear opening about the same size as those posterior to the ear opening; ear opening usually vertically oval.

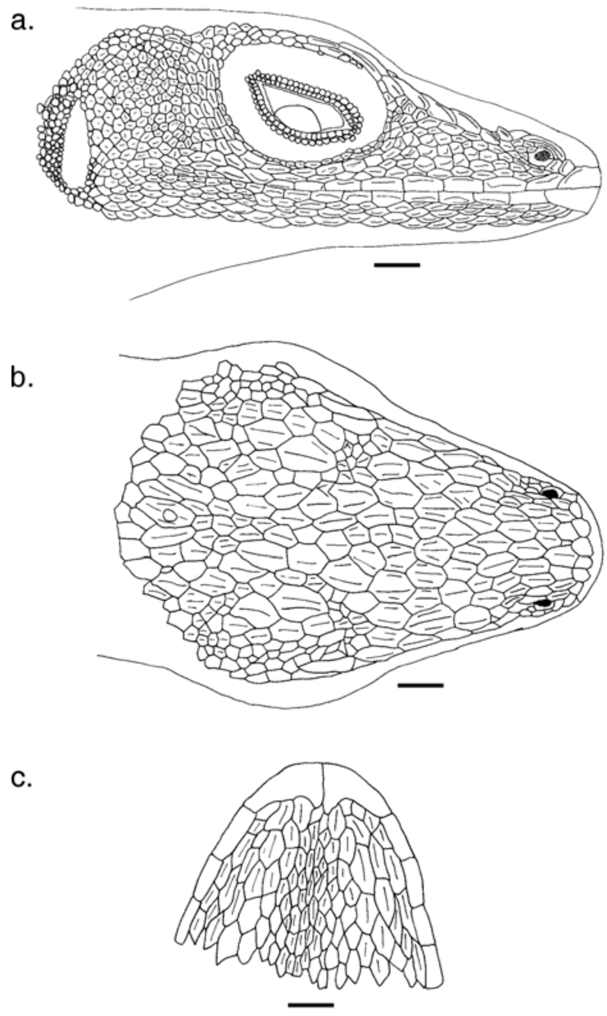


Fig. 25. Head of *Anolis uniformis* (SMF 83957): a) lateral view; b) dorsal view; c) ventral view. Scale bars equal 1.0 mm.

Dorsum of body with keeled, subimbricate scales, 18–25 dorsal scales in one head length, 22–36 dorsal scales between levels of axilla and groin; 7–11 median rows of dorsal scales enlarged, dorsals abruptly larger than the smaller, keeled and homogeneous laterals; ventrals at midbody distinctly keeled, mucronate and subimbricate, 20–36 ventral scales in one head length, 31–47 ventral scales between levels of axilla and groin.

Dorsal, lateral and ventral caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; dorsal medial caudal scales slightly enlarged, not forming a crest; limb scales strongly keeled, imbricate; digital pads dilated, about two times as wide as non-dilated distal portion of toe; distal phalanx narrower than and raised from, dilated pad; 16–23 lamellae under phalanges ii–iv of fourth toe.

The completely everted hemipenis (USNM 496684) is a medium-sized bilobate organ; sulcus spermaticus bifurcates at base of apex and branches continue to tips of lobes; asulcale processus / ridge present; lobes strongly calyculate, truncus with transverse folds.

Range: Southern Mexico including the Yucatán Peninsula to western Honduras (Fig. 26).

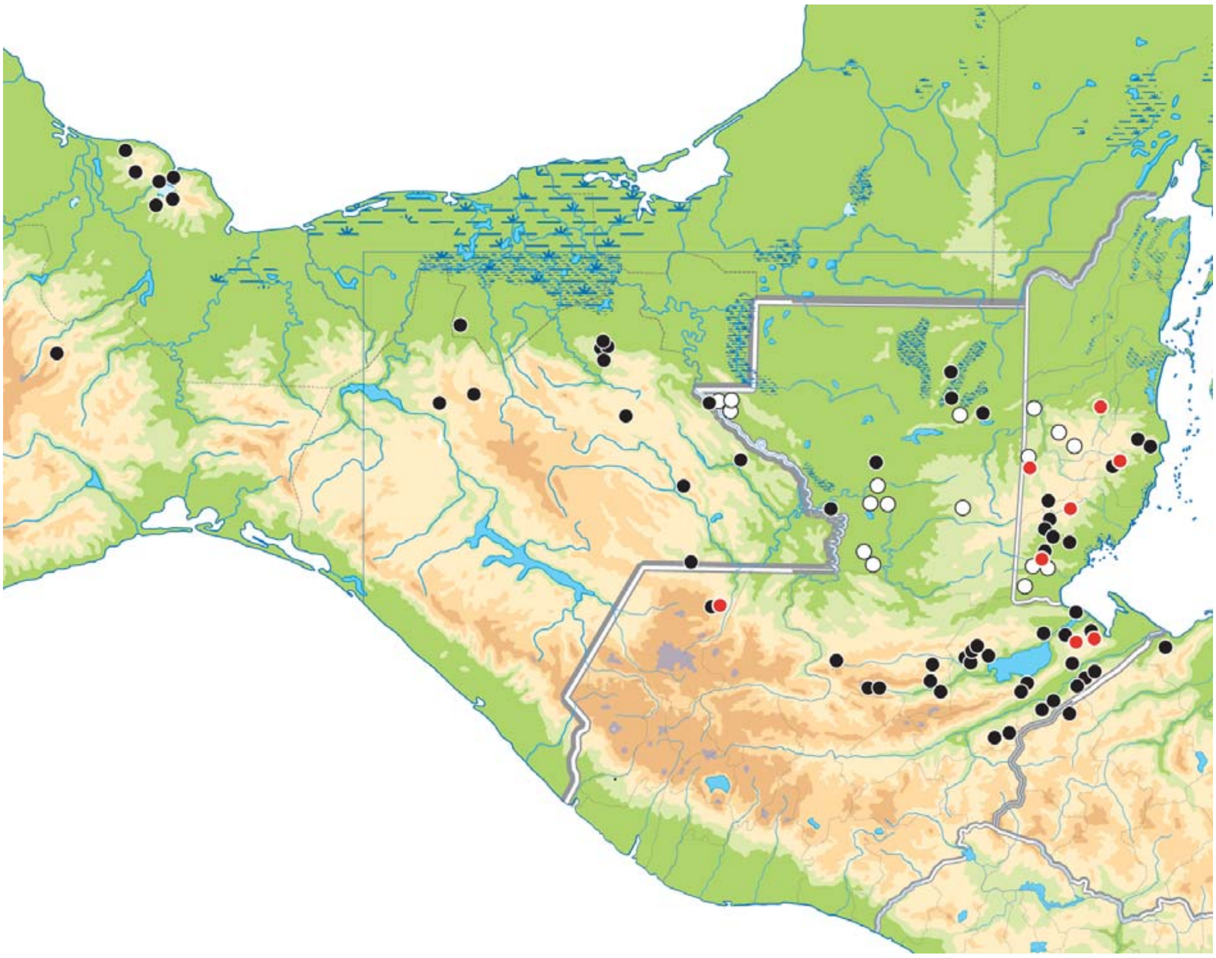


Fig. 26. Distribution of *Anolis uniformis* (circles). Red symbols represent localities from where I have examined adult males with everted hemipenes; black symbols represent localities from where I have examined specimens of the respective species but not males with everted hemipenes; white symbols represent literature records. A single symbol can represent two or more nearby localities.

2.3.3 TWO NEW SPECIES OF ANOLES FORMERLY REFERRED TO AS *ANOLIS LIMIFRONS* (REPTILIA, SQUAMATA, IGUANIDAE)

2.3.3.1 Introduction

In 1862, COPE described the new species *Anolis (Dracontura) limifrons* based on two syntypes (now ANSP 7900–01) from "Veragua." According to SAVAGE (1970: 279), "today the old Veragua comprises the Provincias of Veraguas, Chiriquí and Bocas del Toro." According to BARBOUR (1934: 139), the type locality of *A. limifrons* as "Cucuyos, Veragua Prov., Panama [an abandoned mine on the Río Santiago]." A few years later, COPE (1871b) named *Anolis trochilus* based on an adult male specimen (now ANSP 7804) from "San José, Costa Rica." PETERS (1873b) added another nominal species, *Anolis pulchripes*, based on a specimen (now ZMB 7827) from "Chiriquí." A year later, COPE (1874) described the new species *Anolis bransfordii* from "Nicaragua" based on an adult male specimen (now ANSP 7890). According to SAVAGE (1973a: 36), the holotype of *A. bransfordii* was "collected by Bransford at Machuco (=Machuca) on the Río San Juan, Departamento Río San Juan, Nicaragua." In 1882, THOMINOT described *Anolis rivieri* based on a juvenile specimen (now MNHN 1884.221) from "Panama." BOULENGER (1885b) described *Anolis godmani* based on four specimens from "Guatemala" and three specimens from "Irazú, Costa Rica." STUART (1955: 30) presumed that in "*Anolis godmani* BOULENGER … may have been a mixup in locality data in the GODMAN-SALVIN collections, one of the cotypes having been listed as of Guatemala whereas it probably came from Costa Rica" and he also stated that "the material [including the holotype of *A. godmani*] may have been received by the British Museum somewhat after the main bulk of the earlier parts of the collection had been turned over to the Museum." In 1956, TAYLOR described the new species *Anolis biscutiger* based on an adult male (KU 40771) from "Golfito, Puntarenas Province, Costa Rica." DUNN (1930) regarded *rivieri, trochilus* and *bransfordii* as synonyms of *limifrons*. BARBOUR (1934: 140) stated that "DUNN has seen the types of *limifrons*, *rivieri, pulchripes* and *rodriguezii* and declares them all the same species." The names *trochilus, pulchripes, bransfordii* and *rivieri* have remained in the synonymy of *A. limifrons* COPE whereas *godmani* has been retained as a valid species until recently (TAYLOR, 1956; PETERS & DONOSO-BARROS, 1970; SAVAGE & VILLA, 1986; VILLA et al., 1988). SAVAGE (2002) and KÖHLER (2003) recognized a northern species, *rodriguezii*, and a southern one, *limifrons*, with *biscutiger* and *godmani* as synonyms of *limifrons*.

Here I report upon the results of this study of the variation in hemipenial and scalation morphology as well as morphometrics of the small anoles occurring from eastern Honduras to eastern Panama commonly referred to as *Anolis* (or *Norops*) *limifrons*.

2.3.3.2 Results

For this study I examined 1428 specimens of *Anolis limifrons*. Two distinctly different hemipenial morphotypes are evident in the specimens I examined. In Type A (n = 188 adult males with everted hemipenes), the hemipenis is a relatively large bilobed organ; both the truncus and the lobes have a strongly calyculate surface. The sulcus spermaticus bifurcates at the base of the apex and the branches continue to the tip of the lobes. In Type B (n = 85 adult males with everted hemipenes), the hemipenis is much smaller relative to body size as compared to the Type A hemipenis. Also, it is unilobed and the truncus and lobes are not calyculate. The sulcus spermaticus opens at the base of the apex. While these two hemipenial types show a broadly sympatric geographical distribution pattern in western Panama, variation in hemipenial morphology within these discrete types is negligible both within populations and in a geographical context. Within Type A, two distinct types can be distinguished in respect of the relative size and the coloration of the male dewlap. Males with bilobed hemipenes from the Province of Bocas del Toro, Panama, and adjacent southeastern Costa Rica have a small dewlap (smaller than 100 mm^2) that is dull white with a small basal orange blotch. Males with bilobed hemipenes from central and eastern Panama have a large dewlap (larger than 150 mm^2) that is almost uniformly orange. All Type B have a small dewlap (smaller than 100 mm^2) that is dull white with a small basal orange blotch.

In external morphology there is great overlap in the ranges of all examined characters of scalation and morphometrics (Table 4). I conducted a discriminant function analysis (DFA) based on seven pholidotic characters (number of medial ventral scales in one head length; number of medial dorsal scales in one head length; subdigital lamellae; total number of loreal scales; scales between supraorbital semicircles; scales between posterior canthals; scales around midbody) and did a priori assignments to groups based on the hemipenis and male dewlap findings (Group 1: = Type B hemipenis, male dewlap small, dull white with a small basal orange blotch; Group 2: = Type A hemipenis, male dewlap small, dull white with a small basal orange blotch; Group 3: = Type A hemipenis, male dewlap large, more or less uniformly orange). This DFA yielded a scatter diagram (Fig. 27) that correctly classified

72.7% of the specimens. The first function is DS(1) = 0.471297 (number of medial ventral scales in one head length) + 0.673627 (number of medial dorsal scales in one head length) – 0.392336 (subdigital lamellae) + 0.176923 (total number of loreal scales) + 0.286056 (scales between supraorbital semicircles) – 0.651674 (scales between posterior canthals) + 0.025958 (scales around midbody). The second function is DS(2) = 0.284551 (number of medial ventral scales in one head length) – 0.173192 (number of medial dorsal scales in one head length) – 0.610593 (subdigital lamellae) – 0.171498 (total number of loreal scales) – 0.293526 (scales between supraorbital semicircles) + 0.054329 (scales between posterior canthals) – 0.603442 (scales around midbody).

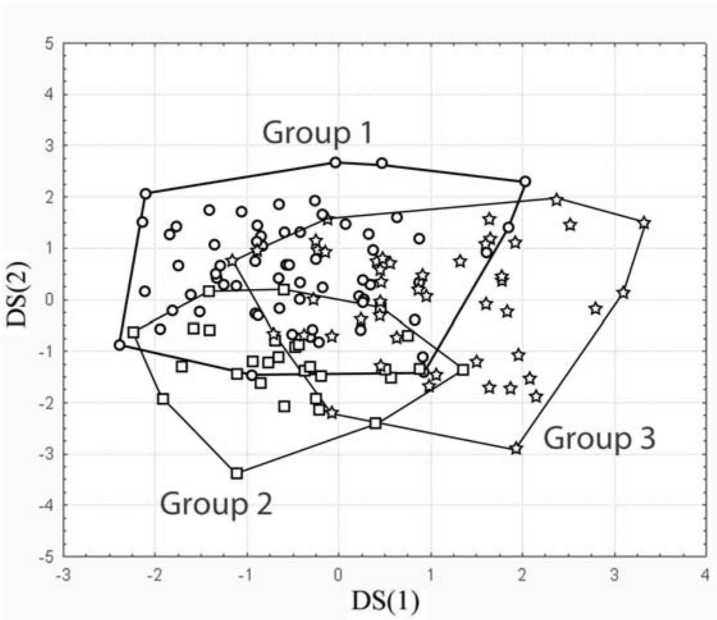


Fig. 27. Discriminant function analysis of the Central American anoles formerly referred to as *Anolis limifrons*. See text for details.

Based on the data I recognize three species of this complex: Species A: Hemipenis unilobed; male dewlap small (smaller than 100 mm^2), dull white with a small basal orange blotch; distributed from eastern Honduras to central Panama west of the Canal Zone (Fig. 28). Species B: Hemipenis bilobed; male dewlap small (smaller than 100 mm^2), dull white with a small basal orange blotch; distributed in the western and central portions of the Province Bocas del Toro, Panama, and adjacent southeastern Costa Rica (Fig. 28). Species C: Hemipenis bilobed; male dewlap large (larger than 150 mm^2), almost uniformly orange;

distributed in central and eastern Panama; expected in adjacent northwestern Colombia (Fig. 28). In western Panama (Provinces of Chiriquí, Bocas del Toro and Veraguas), the bilobed form (the Species B) is restricted to the Caribbean versant; whereas the unilobed form (the Species A) occurs on both versants. Although no cases of actual syntopy of these two forms have been documented, they show a broadly sympatric distribution pattern on the Caribbean versant of western Panama.

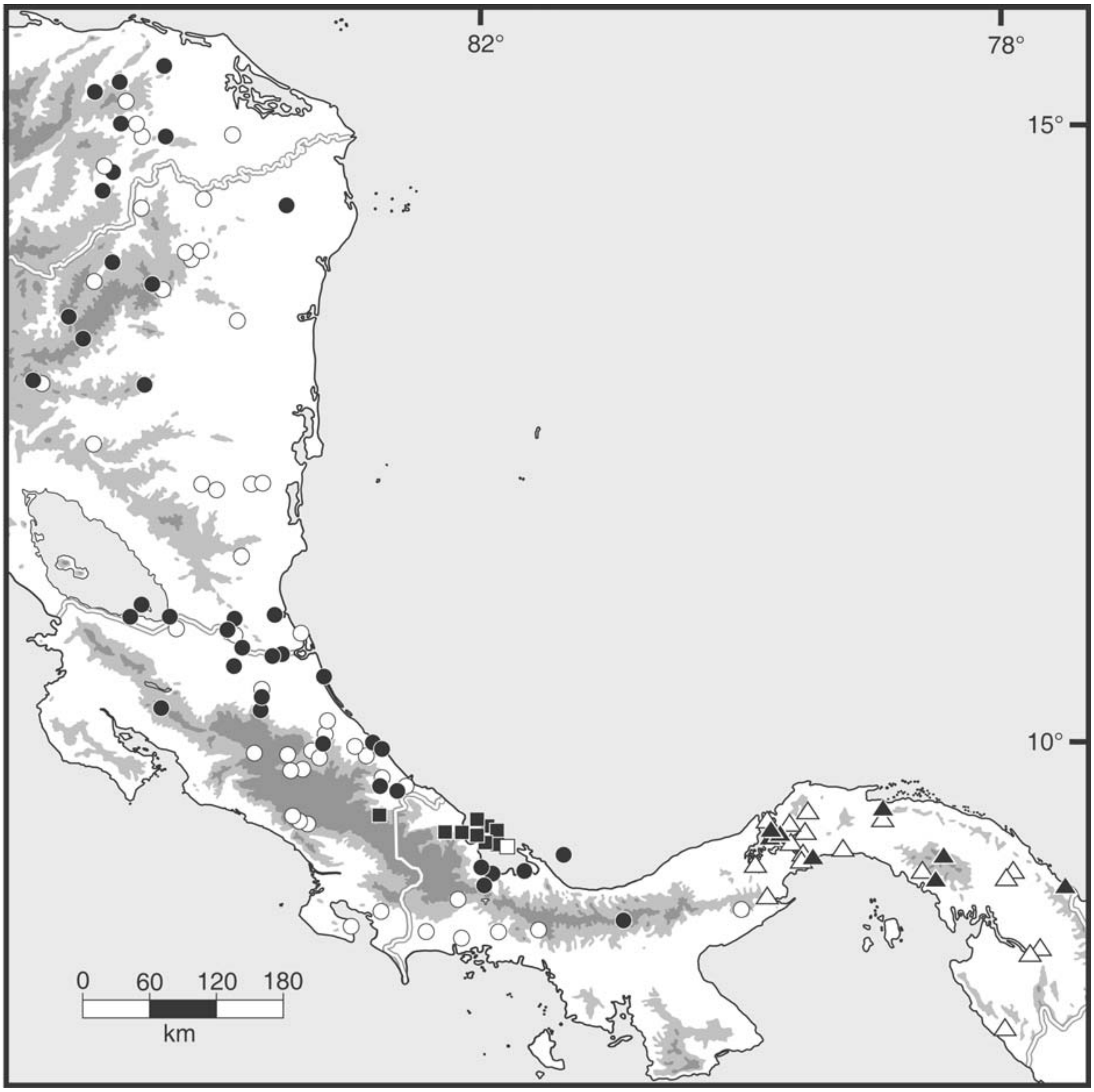


Fig. 28. Map indicating known collecting sites mentioned in text of *Anolis apletophallus* (triangles), *A. cryptolimifrons* (squares), and *A. limifrons* (circles) in Honduras, Nicaragua, Costa Rica and Panama. Each symbol can represent one or more nearby localities. Areas above 500 and 1000 m are shaded. Open symbols: specimens with no everted hemipenis; Solid symbols: specimens with everted hemipenis.

Unfortunately, none of the type specimens mentioned in the introduction are males with their hemipenes everted. Also, data on dewlap coloration in life is not available for these type specimens. However, the type locality data of most of these nominal species allow for a reliable allocation to one of the three species that I distinguish. Thus, on geographic reasons the following taxa (respective type localities in parentheses) are clearly referable to the Species A: *Anolis limifrons* COPE (Cucuyos, Veragua Province, Panama); *A. trochilus* COPE (San José, Costa Rica); *A. pulchripes* PETERS (Chiriquí, Panama); *A. bransfordii* COPE (Nicaragua); *A. godmani*: BOULENGER (Irazú, Costa Rica); and *A. biscutiger* TAYLOR (Golfito, Puntarenas Province, Costa Rica). Because *A. limifrons* COPE is the oldest available name for this species, the Species A has to be referred to that name and the other nominal species remain in the synonymy of *A. limifrons*. The holotype of *A. rivieri* THOMINOT is a juvenile with unspecific locality data ("Panama") and its taxonomic identity cannot be determined. Therefore, *A. rivieri* THOMINOT is considered to be a *nomen dubium*. Interestingly, there is no available scientific name for either of the Species B and C. They are therefore describe them as new species below.

Anolis limifrons COPE, 1862

Anolis limifrons COPE, 1862: 178. Syntypes ANSP 7900–01 from "Veragua."

Diagnosis: A medium-sized species (snout-vent length [SVL] in largest specimen 43.5 mm) of the genus *Anolis* (sensu POE, 2004) that is most similar in external morphology to a cluster of Central American species that are long-legged (longest toe of adpressed hindlimb reaches to mid-eye or beyond), have a single elongated prenasal scale, smooth to slightly keeled ventral scales, and slender habitus, often delicate (i.e., *Anolis dollfusianus, A. ocelloscapularis, A. rodriguezii, A. yoroensis, A. zeus*). Within this cluster of species, *A. limifrons* can be readily distinguished by male dewlap coloration (dull white with a small basal orange blotch in *A. limifrons* vs. uniformly dull white in *A. zeus*, and almost uniformly orange to orange-yellow in the remaining species. Additionally, *A. limifrons* differs from the species in this cluster by the following characteristics (condition for *A. limifrons* in parentheses): *Anolis dollfusianus*: ventrals weakly keeled (smooth). *Anolis ocelloscapularis*: An ocellated shoulder spot present (absent); ventrals weakly keeled (smooth); hemipenis bilobed (unilobed). *Anolis rodriguezii*: hemipenis bilobed (unilobed). *Anolis yoroensis*: Ventrals weakly keeled (smooth).

Description (Fig. 29): Maximum SVL 41.5 mm in males, 43.5 mm in females; ratio tail length/SVL 1.53–2.52 (2.17 ± 0.21); tail slightly compressed in cross section, ratio tail height/tail width 1.00–1.30 (1.16 ± 0.07); ratio axilla to groin distance/SVL 0.36–0.53 (0.43 ± 0.03); ratio head length/SVL 0.24–0.28 (0.26 ± 0.01); ratio snout length/head length 0.41–0.52 (0.45 ± 0.02); ratio head length/head width 1.44–1.80 (1.67 ± 0.06); longest toe of adpressed hind limb reaching to a point between anterior to eye and tip of snout; ratio shank length/SVL 0.26–0.33 (0.29 ± 0.02); ratio shank length/head length 0.97–1.24 (1.11 ± 0.07); longest finger of extended forelimb reaching to a point between nostrils and tip of snout; longest finger of adpressed forelimb reaches in between anterior to insertion of hind limbs and slightly beyond to insertion of hind limbs; scales on snout varying from almost non-keeled to keeled; 5–9 (6.9 ± 0.8) postrostrals; 7–11 (8.9 ± 0.9) scales between nasals; 1 large elongated prenasal scale in contact with both rostral and first supralabial, occasionally only in contact with rostral; scales in distinct prefrontal depression generally slightly tuberculate posteriorly, wrinkled anteriorly, some of them keeled; supraorbital semicircles well developed, separated by 0–4 (1.8 ± 0.8) scales; supraorbital disc composed of 5–14 distinctly enlarged keeled scales; circumorbital row usually incomplete, therefore, 0–3 enlarged supraorbitals in contact with supraorbital semicircles; a single large elongated superciliary; 3–6 rows of small keeled scales extending between enlarged supraorbitals and superciliaries; a very shallow parietal depression present in most specimens; interparietal scale well developed, usually surrounded by scales of moderate size anteriorly and by small to moderate size scales posteriorly; 1–5 (2.7 ± 0.9) scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 6–11 (7.5 ± 0.8) canthal scales, with 3–5 (4.0 ± 0.7) larger posterior scales; 7–15 (10.6 ± 1.7) scales present between second canthals; 10–18 (13.8 ± 2.1) scales present between posterior canthals; 24–68 (41.1 ± 9.6) loreal scales in a maximum of 5–8 (6.1 ± 0.8) horizontal rows, with the scales of lower rows and those adjacent to the canthals mostly keeled, and those of upper rows non-adjacent to the canthals mostly tuberculated; 4–7 keeled subocular scales arranged in a single row; 5–8 (6.5 ± 0.7) supralabials to level below center of eye; 2–5 suboculars broadly in contact with supralabials; ear opening medium-sized, ratio tympanum height/interparietal scale length 0.58–1.36 (0.86 ± 0.16); mental distinctly wider than long, completely divided medially, bordered posteriorly by 4–8 (6.5 ± 0.9) postmentals; 5–8 (6.3 ± 0.7) infralabials to level below center of eye; sublabials undifferentiated; keeled granular scales present on chin and throat; dewlap extending from level below oral ricti to axilla, in some specimens extending 1–2 mm posterior to axilla; dorsum of body with weakly keeled granular scales (at least anteriorly) with rounded posterior margins, 2 medial rows slightly enlarged, 38–70 (54.3 ± 5.8) medial dorsal scales in one head length; 70–112 (91.5 ± 9.0) medial dorsal scales between axilla and groin; lateral scales homogeneous, ventrals at midbody smooth, slightly bulging, non–imbricate, 26–58 (40.6 ± 6.1) ventral scales in one head length; 49–79 (64.6 ± 5.7) ventral scales between axilla and groin; 108–157 (132.1 ± 10.6) scales around midbody; caudal scales strongly keeled; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although an indistinct division in segments is discernible; a pair of slightly enlarged postanal scales usually present; no tube-like axillary pocket present; scales on dorsal surface of forelimb keeled, imbricate; digital pads dilated; distal phalanx narrower than and raised from dilated pad; 20–27 (23.3 ± 1.6) lamellae under phalanges ii–iv of fourth toe; 7–11 (8.5 ± 0.9) scales under distal phalanx of fourth toe.

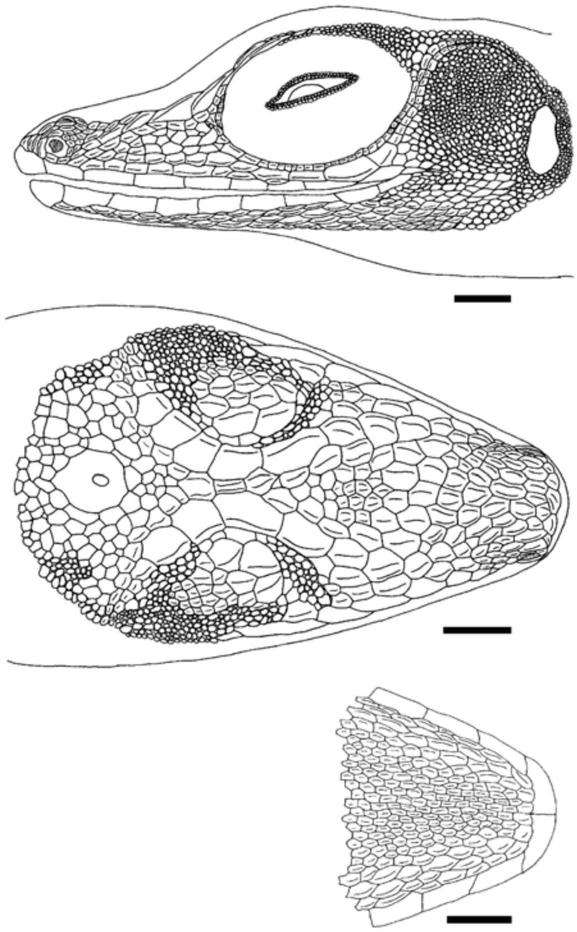


Fig. 29. Head of *Anolis limifrons* (SMF 86900). Scale bars equal 1.0 mm.

The completely everted hemipenis is a small unilobed organ; sulcus spermaticus bordered by well developed sulcal lips and opens at base of apex; no discernable surface structure on truncus and lobes; no asulcate processus present (Fig. 30).

Range: Eastern Honduras to central Panama west of the Canal Zone.

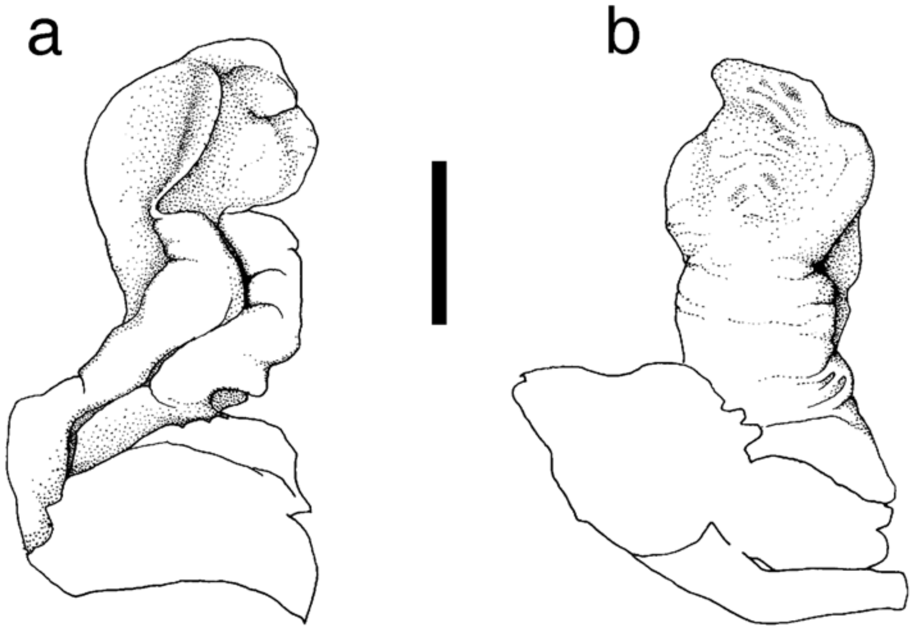


Fig. 30. Hemipenis of *Anolis limifrons* (SMF 85246): (a) sulcate view; (b) asulcate view. Scale bar equals 1.0 mm.

Anolis apletophallus KÖHLER & SUNYER, 2008

Holotype (Fig. 31): SMF 85307, an adult male from Panama City, Metropolitan National Park (8°58'60''N, 79°32'46''W), 45 m, Panamá Province, Panama. Collected 26 January 2006 by Gunther KÖHLER, Javier SUNYER, Abel A. BATISTA R. and Marcos PONCE. Field tag number GK 1672.

Paratypes: SMF 85308–19, same collecting data as holotype. SMF 85308–13 are adult males, SMF 85314–19 are adult females.

Etymology: The name *apletophallus* is formed from the Greek words *apletos* (immense) and *phallos* (penis) and is used as a noun in apposition.

Diagnosis: A medium-sized species (SVL in largest specimen 47.0 mm) of the genus *Anolis* (sensu POE, 2004) that is most similar in external morphology to a cluster of Central American species that are long-legged (longest toe of adpressed hindlimb reaches to mid-eye or beyond), have a single elongated prenasal scale, smooth to slightly keeled ventral scales, and slender habitus, often delicate (i.e., *Anolis dollfusianus, A. limifrons, A. ocelloscapularis, A. rodriguezii, A. yoroensis, A. zeus*). Within this cluster of species, *A. apletophallus* is most similar to *A. limifrons* from which it is readily distinguished by hemipenis morphology: hemipenis small and unilobed in *A. limifrons*, large and bilobed in *A. apletophallus* (Fig. 32). *Anolis apletophallus* differs from the remaining species in this cluster by the following characteristics (condition for *A. apletophallus* in parentheses): *Anolis dollfusianus*: Hemipenis unilobed (bilobed); ventrals weakly keeled and slightly imbricate (smooth and non-imbricate). *Anolis ocelloscapularis*: Ventrals weakly keeled and slightly imbricate (smooth and non-imbricate); an ocellated shoulder spot present (absent). *Anolis rodriguezii*: Ventrals weakly keeled and slightly imbricate (smooth and non-imbricate). *Anolis yoroensis*: Ventrals weakly keeled and slightly imbricate (smooth and non-imbricate). *Anolis zeus*: Hemipenis unilobed (bilobed); male dewlap uniformly dull white (almost uniformly orange).

Description of the holotype: Adult male as indicated by everted hemipenes; SVL 44.0 mm; tail length 96.0 mm, tail complete; tail slightly compressed in cross section, tail height 1.75 mm, tail width 1.70 mm; axilla to groin distance 17.6 mm; head length 12.0 mm, head length/SVL ratio 0.27; snout length 5.2 mm; head width 7.1 mm; longest toe of adpressed hind limb reaching to a point between eyes and rostrils; shank length 13.0 mm, shank length/head length ratio 1.08; longest finger of extended forelimb reaching to a point slightly beyond nostrils; longest finger of adpressed forelimb just reaches anterior insertion of hind limbs. Most scales on snout keeled; 7 postrostrals; 10 scales between nasals; 1 large elongated prenasal scale in contact with both rostral and first supralabial; scales in distinct prefrontal depression slightly tuberculate posteriorly, wrinkled anteriorly; supraorbital semicircles well developed, separated by 3 scales; supraorbital disc composed of 13–15 distinctly enlarged keeled scales; circumorbital row incomplete, therefore, one enlarged supraorbital in contact with supraorbital semicircles; a single large elongated superciliary; about 3 or 4 rows of small keeled scales extending between enlarged supraorbitals and superciliaries; a very shallow parietal depression present; interparietal scale well developed, 1.4 x 1.0 mm (length x width), surrounded by scales of moderate size; 3 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 4 large (posterior two largest) and 4 small anterior canthal scales; 10 scales present between second canthals; 17 scales present between posterior canthals; 64 (right)–61 (left) loreal scales in a maximum of 8 horizontal rows, with the scales of lower rows mostly keeled, and those of upper rows mostly tuberculated; 8 (right)–6 (left) keeled subocular scales arranged in a single row; 7 supralabials to level below center of eye; 4 (right)–3 (left) suboculars broadly in contact with supralabials; ear opening 0.90 x 1.40 mm (length x height); mental distinctly wider than long, completely divided medially, bordered posteriorly by keeled 6 postmentals (outer pair larger); 7 infralabials to level below center of eye; sublabials undifferentiated; keeled granular scales present on chin and throat; dewlap extending from level below oral ricti to 3 mm beyond level of axilla; dorsum of body with weakly keeled granular scales with rounded posterior margins, 2 medial rows slightly enlarged, largest dorsal scales about 0.21 x 0.23 mm (length x width); about 64 medial dorsal scales in one head length; about 85 medial dorsal scales between axilla and groin; lateral scales homogeneous, average size 0.16 mm in diameter; ventrals at midbody smooth, slightly bulging, non-imbricate, about 0.34 x 0.34 mm (length x width); about 42 ventral scales in one head length; about 66 ventral scales between axilla and groin; 142 scales around midbody; caudal scales strongly keeled; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although an indistinct division in segments is discernible; a pair of enlarged postanal scales present, about 0.69 mm wide; no tube-like axillary pocket present; scales on dorsal surface of forelimb keeled, imbricate, about 0.28 x 0.25 mm (length x width); digital pads dilated; distal phalanx narrower than and raised from dilated pad; 24 lamellae under phalanges ii-iv of fourth toe; 9 (right)–8 (left) scales under distal phalanx of fourth toe.

The completely everted hemipenis is a medium-sized bilobed organ; sulcus spermaticus bordered by well developed sulcal lips and bifurcating at base of apex; shortly after the bifurcation, branches open into broad concave areas, one on each lobe; asulcate surface of apex and distal truncus strongly calyculate, base of truncus with transverse folds; no asulcate processus present, although a slightly elevated ridge present (Fig. 32).

Coloration in life: Dorsal ground color Warm sepia (color 221A); flanks Dark Drab (119B); dorsal surface of head Dark Drab (119B); venter dull white suffused with Dark Drab (119B); dorsal surface of limbs Mars Brown (223A); tail Drab Gray (119D) with transverse Sepia (119) (but slightly more reddish) bands; iris Raw Sienna (136); dewlap Orange Yellow (18).

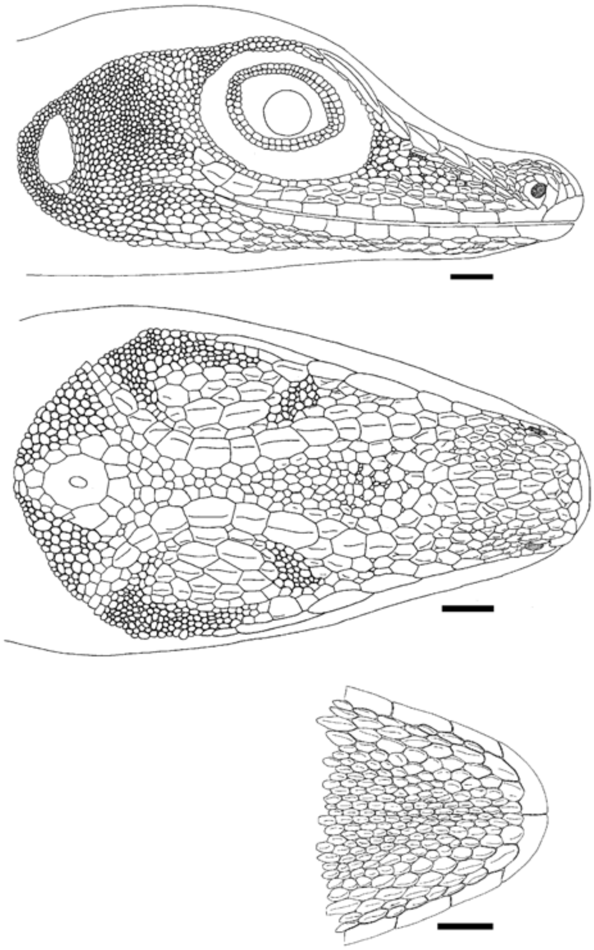


Fig. 31. Head of holotype of *Anolis apletophallus* (SMF 85307). Scale bars equal 1.0 mm.

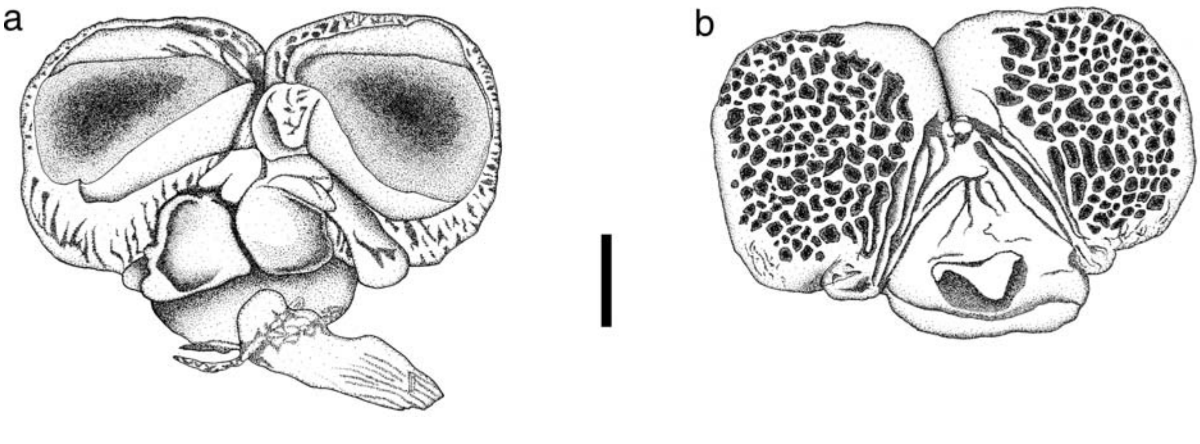


Fig. 32. Hemipenis of *Anolis apletophallus* (SMF 80719): (a) sulcate view; (b) asulcate view. Scale bar equals 1.0 mm.

Variation: The paratypes agrees well with the holotype in general appearance, morphometrics and scalation (see Table 4). In most of the male paratypes, one pair of slightly enlarged postanal scales is present. The female paratypes have no dewlap and no enlarged postanal scales. The coloration in life of male paratype's dewlap (SMF 85308) was recorded as Trogon Yellow (153).

Natural history notes: All type specimens were collected active during the day in secondary forest. The lizards were spotted on tree trunks and fallen branches, from near ground level to 1.5 m above the ground.

Range: Central and eastern Panama.

Anolis cryptolimifrons KÖHLER & SUNYER, 2008

Holotype (Fig. 33): SMF 85230, an adult male from Cerro Brujo (9°11'16.4''N, 82°11'25.4''W), 10 m, Bocas del Toro Province, Panama. Collected 19 January 2006 by Gunther KÖHLER, Javier SUNYER, Abel A. BATISTA R. and Marcos PONCE. Field tag number GK 1502.

Paratypes: SMF 85231–44, same collecting data as holotype. Most of the paratypes are females, except SMF 85236–37, 85239–40, 85242–43 (adult males).

Etymology: The species name *cryptolimifrons* is used as a noun in apposition and reflects the similarity and suspected close relationship between the new species and its congener *Anolis limifrons* COPE.

Diagnosis: A medium-sized species (SVL in largest specimen 45.0 mm) of the genus *Anolis* (sensu POE, 2004) that is most similar in external morphology to a cluster of Central American species that are long-legged (longest toe of adpressed hindlimb reaches to mid-eye or beyond), have a single elongated prenasal scale, smooth to slightly keeled ventral scales, and slender habitus, often delicate (i.e., *A. apletophallus, A. dollfusianus, A. limifrons, A. ocelloscapularis, A. rodriguezii, A. yoroensis, A. zeus*). Within this cluster of species, *A. cryptolimifrons* is most similar to *A. limifrons* and *A. apletophallus*. *Anolis cryptolimifrons* is readily distinguished from *A. limifrons* by hemipenis morphology: hemipenis small and unilobed in *A. limifrons*, large and bilobed in *A. cryptolimifrons*. *Anolis cryptolimifrons* differs from *A. apletophallus* in male dewlap size and color in life (small and dull white with a small basal orange blotch in *A. cryptolimifrons* versus dewlap large and almost uniformly orange in *A. apletophallus*). *Anolis cryptolimifrons* differs from the remaining species in this cluster by the following characteristics (condition for *A. cryptolimifrons* in parentheses): *Anolis dollfusianus*: Hemipenis unilobed (bilobed); ventrals weakly keeled (smooth); fewer than 80 dorsals between levels of axilla and groin (more than 87); male dewlap almost uniformly orange-yellow (dull white with a small basal orange blotch). *Anolis ocelloscapularis*: An ocellated shoulder spot present (absent); ventrals weakly keeled (smooth); male dewlap almost uniformly orange (dull white with a small basal orange blotch). *Anolis rodriguezii*: Male dewlap almost uniformly orange (dull white with a small basal orange blotch). *Anolis yoroensis*: Ventrals weakly keeled (smooth); fewer than 87 dorsals between levels of axilla and groin (more than 87); male dewlap almost uniformly orange (dull white with a small basal orange blotch). *Anolis zeus*: Hemipenis unilobed (bilobed); male dewlap uniformly dull white without a basal orange blotch (basal orange blotch present).

Description of the holotype: Adult male as indicated by everted hemipenes; SVL 41.0 mm; tail length 88.0 mm, tail complete; tail slightly compressed in cross section, tail height 1.50 mm, tail width 1.25 mm; axilla to groin distance 18.0 mm; head length 11.0 mm, head length/SVL ratio 0.27; snout length 5.2 mm; head width 6.6 mm; longest toe of adpressed hind limb reaching to anterior portion of eye; shank length 11.1 mm, shank length/head length ratio 1.01; longest finger of extended forelimb reaching nostrils; longest finger of adpressed forelimb not reaching anterior insertion of hind limbs. Most scales on snout keeled, some wrinkled; 8 postrostrals; 10 scales between nasals; 1 large elongated prenasal scale in contact with both rostral and first supralabial; scales in distinct prefrontal depression slightly tuberculate; supraorbital semicircles well developed, separated by 2 scales; supraorbital disc composed of 9–10 distinctly enlarged keeled scales; circumorbital row complete, therefore, no enlarged supraorbitals in contact with supraorbital semicircles; a single large elongated superciliary; about 5 rows of small keeled scales extending between enlarged supraorbitals and superciliaries; a shallow parietal depression present; interparietal scale well developed, 1.30 x 0.95 mm (length x width), surrounded by scales of moderate size anteriorly and small size posteriorly; 3 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 4 large (posterior two largest) and 4 small anterior canthal scales; 16 scales present between second canthals; 19 scales present between posterior canthals; 61 loreal scales in a maximum of 6 horizontal rows, with the scales of lower rows mostly keeled, and those of upper rows mostly tuberculated; 6 (right) –5 (left) keeled subocular scales arranged in a single row; 7 supralabials to level below center of eye; 2 suboculars broadly in contact with supralabials; ear opening 0.5 x 1.3 mm (length x height); mental distinctly wider than long, completely divided medially, bordered posteriorly by 8 keeled postmentals (outer pair larger); 7 infralabials to level below center of eye; sublabials undifferentiated; keeled granular scales present on chin and throat; dewlap extending from level below oral ricti to about 1 mm anterior to axilla; dorsum of body with weakly keeled granular scales with rounded posterior margins, 2 medial rows slightly enlarged, largest dorsal scales about 0.19 x 0.20mm (length x width); about 54 medial dorsal scales in one head length; about 97 medial dorsal scales between axilla and groin; lateral scales homogeneous, average size 0.10 mm in diameter; ventrals at midbody smooth, slightly bulging, non-imbricate, about 0.24 x 0.27mm (length x width); about 46 ventral scales in one head length; about 68 ventral scales between axilla and groin; 148 scales around midbody; caudal scales strongly keeled; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although an indistinct division in segments is discernible; a pair of enlarged postanal scales present; no tube-like axillary pocket present; scales on dorsal surface of forelimb keeled, imbricate, about 0.24 x 0.26 mm (length x width); digital pads dilated; distal phalanx narrower than and raised from dilated pad; 24 lamellae under phalanges ii-iv of fourth toe on right foot (fourth toe of left foot missing); 7 scales under distal phalanx of fourth toe.

The completely everted hemipenis is a medium-sized bilobed organ; sulcus spermaticus bordered by well developed sulcal lips and bifurcating at base of apex; shortly after the bifurcation, branches open into broad concave areas, one on each lobe; asulcate surface of apex and distal truncus strongly calyculate, base of truncus with transverse folds; no asulcate processus, although a slightly elevated ridge present (Fig. 34).

Coloration in life: Dorsal ground color Raw Umber (color 123 in Smithe 1975–1981) suffused with Vandyke Brown (221) at middorsum; venter Pale Horn Color (92); iris Cinnamon (123A); dewlap dull white with a small Chamois (123D) basal blotch.

Variation: The paratypes agrees well with the holotype in general appearance, morphometrics and scalation (see Table 4). In most of the male paratypes, one pair of slightly enlarged postanal scales is present. The female paratypes have no dewlap and no enlarged postanal scales.

Natural history notes: All type specimens were collected active during the day in a patch of secondary forest. The lizards were spotted on branches and leaves of bushes and small trees, 0.5 to 1.5 m above the ground.

Range: Province of Bocas del Toro, Panama, and adjacent southeastern Costa Rica.

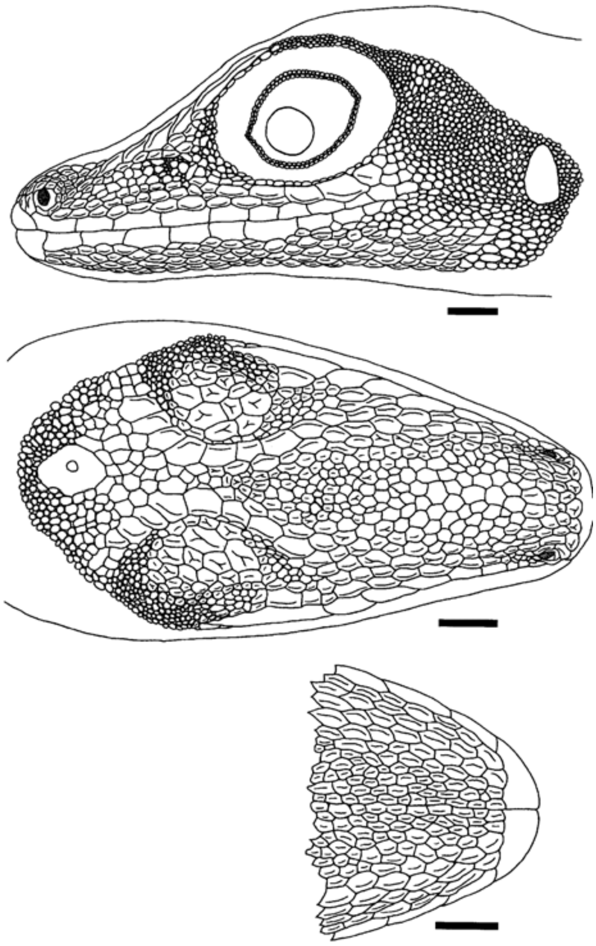


Fig. 33. Head of holotype of *Anolis cryptolimifrons* (SMF 85230). Scale bars equal 1.0 mm.

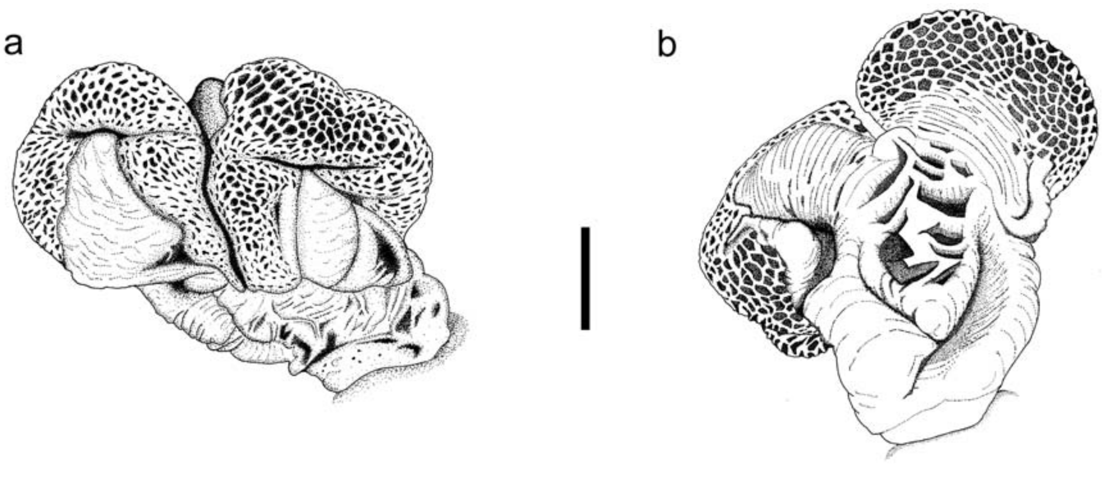


Fig. 34. Hemipenis of holotype of *Anolis cryptolimifrons* (SMF 85230): (a) sulcate view; (b) asulcate view. Scale bar equals 1.0 mm.

Key to the males of the species formerly referred to as *Anolis limifrons*:

1a Male dewlap large, larger than 150 mm^2 (Fig. 35a), almost uniformly orange ……..…

…………………………………………………………….………….. ***Anolis apletophallus***

1b Male dewlap small, smaller than 100 mm^2 (Fig. 35b,c), dull white with a small basal orange-yellow blotch………………………………………………………………….. **2**

2a Hemipenis unilobed …………………….…………..………………. ***Anolis limifrons***

2b Hemipenis bilobed ……………….……….………..……… ***Anolis cryptolimifrons***

Fig. 35. Specimens in life with extended dewlaps: (a) *Anolis apletophallus*, male (Panama City, Panamá, Panama); (b) *A. cryptolimifrons*, male (Cerro Brujo, Bocas del Toro, Panama); and (c) *A. limifrons*, male (Los Guatuzos, Río San Juan, Nicaragua).

2.3.3.3 Discussion

Until recently, hemipenial morphology in the diverse group of anoles has been mostly ignored. The minority of male anoles housed in museum collections worldwide have everted hemipenes. Future collectors of these anoles are urged to attempt to fully evert the hemipenes of their specimens. Study of these organs may reveal more cryptic species of anoles than originally envisaged by most workers. This is of great conservational importance: whereas a large amount of ecological data is available for *Anolis limifrons* and *A. apletophallus*, very little is known from *A. cryptolimifrons*, a species with a relatively restricted distribution. Although *A. limifrons* and *A. cryptolimifrons* both occur in the same general area of mainland western Panama (Caribbean versant), no actual instance of syntopy has been documented. Both taxa appear to use the same habitat and same perching sites and might exclude each other.

SAVAGE (2002) reported populations of *Anolis limifrons*-like lizards from the slopes of the volcanoes Irazú and Turrialba with keeled ventral scales but otherwise identical in scutellation and coloration. BOULENGER (1885b) based the description of *A. godmani* on this characteristic, and in earlier publications SAVAGE (e.g., SAVAGE, 1973a; SAVAGE & VILLA, 1986) recognized this form as a valid species and used the name *A. godmani* for it. More recently, SAVAGE (2002) considered it to be an individual variant and therefore a synonym of *A. limifrons*. I have examined a single female (SMF 86924) from this general area collected at 1500 m elevation (about 160 m above the highest Costarican record for this species) which has distinctly keeled ventral scales. Also, the scales on head and dorsum are strongly keeled, much more than in any other examined *A. limifrons*. Unfortunately, no data on hemipenis morpholgy nor on male dewlap coloration are available for representatives of this population. Further collecting and study is needed in order to evaluate the status of the populations of *A. limifrons*-like lizards from the slopes of the vulcanos Irazú and Turrialba in Costa Rica.

Table 4. Selected measurements, proportions and scale characters of *Anolis limifrons, A. apletophallus,* and *A. cryptolimifrons* (specimens with * listed in Appendix D). Range is followed by mean value and one standard deviation in parentheses. Morphomentric data were only taken from adults.

		A. limifrons ♂ 50 ♀ 21	***A. apletophallus*** ♂ 25 ♀ 24	***A. cryptolimifrons*** ♂ 20 ♀ 10
Maximum SVL	♂	41.5	47.0	45.0
	♀	43.5	46.5	42.0
Tail length / SVL	♂	1.53–2.52 (2.21 ± 0.19)	1.52–2.29 (2.03 ± 0.17)	1.83–2.19 (2.07 ± 0.10)
	♀	1.60–2.30 (2.05 ± 0.22)	1.82–2.32 (2.06 ± 0.13)	1.87–2.08 (1.98 ± 0.08)
Tail diameter vertical / horizontal	♂	1.00–1.30 (1.16 ± 0.07)	1.03–1.27 (1.14 ± 0.08)	1.00–1.25 (1.15 ± 0.06)
	♀	1.00–1.27 (1.14 ± 0.07)	1.00–1.25 (1.11 ± 0.07)	1.00–1.17 (1.21 ± 0.06)
Head length / SVL	♂	0.25–0.28 (0.27 ± 0.01)	0.25–0.29 (0.27 ± 0.01)	0.25–0.29 (0.27 ± 0.01)
	♀	0.24–0.28 (0.26 ± 0.01)	0.25–0.29 (0.27 ± 0.01)	0.26–0.28 (0.27 ± 0.01)
Head length / head width	♂	1.44–1.80 (1.67 ± 0.07)	1.54–1.84 (1.67 ± 0.06)	1.59–1.77 (1.67 ± 0.06)
	♀	1.57–1.77 (1.67 ± 0.06)	1.56–1.70 (1.65 ± 0.04)	1.62–1.75 (1.66 ± 0.04)

Interparietal plate / ear	♂	0.79–5.20 (2.03 ± 0.78)	0.71–4.12 (1.71 ± 0.70)	0.54–2.29 (1.47 ± 0.46)
	♀	1.09–4.75 (2.19 ± 0.98)	1.01–2.45 (1.69 ± 0.44)	0.50–1.68 (1.09 ± 0.39)
Shank length / SVL	♂	0.26–0.33 (0.30 ± 0.02)	0.29–0.32 (0.30 ± 0.01)	0.26–0.31 (0.29 ± 0.02)
	♀	0.26–0.31 (0.28 ± 0.01)	0.26–0.32 (0.30 ± 0.02)	0.27–0.29 (0.28 ± 0.01)
Axilla–groin distance / SVL	♂	0.36–0.47 (0.42 ± 0.03)	0.34–0.46 (0.39 ± 0.03)	0.39–0.46 (0.43 ± 0.02)
	♀	0.41–0.53 (0.45 ± 0.02)	0.35–0.48 (0.41 ± 0.03)	0.40–0.46 (0.43 ± 0.02)
Subdigital lamellae of 4th toe		20–27 (23.33 ± 1.61)	21–26 (23.59 ± 1.12)	23–29 (25.03 ± 1.47)
Number of scales between supraorbital semicircles		0–4 (1.78 ± 0.84)	1–3 (2.04 ± 0.50)	1–3 (2.20 ± 0.61)
Number of scales between interparietal plate and supraorbital semicircles		1–5 (2.68 ± 0.86)	1–4 (2.72 ± 0.68)	2–4 (3.27 ± 0.64)
Number of scales between subocular scales and supralabial scales		0	0	0
Number of supralabial scales to level below center of eye		5–8 (6.48 ± 0.69)	6–8 (6.76 ± 0.56)	5–7 (6.73 ± 0.52)
Number of infralabials to level below center of eye		5–8 (6.30 ± 0.70)	5–8 (6.37 ± 0.57)	6–8 (6.62 ± 0.56)
Total number of loreals		24–68 (41.13 ± 9.56)	25–74 (45.00 ± 8.78)	36–69 (49.07 ± 7.67)
Number of horizontal loreal scale rows		5–8 (6.10 ± 0.79)	5–8 (6.38 ± 0.73)	6–8 (6.70 ± 0.70)
Number of postrostrals		5–9 (6.86 ± 0.82)	6–8 (7.23 ± 0.59)	6–9 (7.17 ± 0.53)
Number of postmentals		4–8 (6.45 ± 0.91)	6–9 (7.28 ± 0.88)	6–8 (7.03 ± 0.87)
Number of scales between nasals		7–11 (8.91 ± 0.86)	8–11 (9.69 ± 0.66)	9–12 (9.77 ± 0.77)
Number of scales between 2nd canthals		7–15 (10.59 ± 1.69)	9–13 (10.61 ± 1.06)	9–16 (12.00 ± 1.55)
Number of scales between posterior canthals		10–18 (13.77 ± 2.10)	10–18 (13.23 ± 1.86)	12–19 (15.21 ± 1.76)
Number of medial dorsal scales in one head length		38–70 (54.26 ± 5.76)	42–74 (60.65 ± 7.10)	46–70 (58.87 ± 5.35)
Number of medial ventral scales in one head length		26–58 (40.62 ± 6.15)	36–60 (45.78 ± 5.44)	34–50 (41.31 ± 4.01)

2.3.4 TWO NEW SPECIES OF SALAMANDERS (GENUS *BOLITOGLOSSA*) FROM SOUTHERN NICARAGUA (AMPHIBIA, CAUDATA, PLETHODONTIDAE)

2.3.4.1 Introduction

Bolitoglossa is the largest genus in the order Caudata, including about 16% of all recognized salamander species (PARRA-OLEA et al. 2004). *Bolitoglossa* also has the most extensive geographical range of any salamander genus, and most species occur in Middle America (WAKE & LYNCH, 1976; PARRA-OLEA et al., 2004). Despite the fact that Nicaragua is the largest of the Middle American countries and includes both Nuclear and Lower Central American herpetofaunal components, its known salamander fauna, 6 species, is much poorer than those of both its neighboring countries Costa Rica, with 43 species of salamanders, 22 of which belong to *Bolitoglossa,* and Honduras with 24 species of salamanders, 14 of which belong to *Bolitoglossa* (AMPHIBIAWEB 2008).

In Nicaragua, only two species of salamanders of the genus *Bolitoglossa* are known (KÖHLER, 2001), *B. mombachoensis* KÖHLER & MCCRANIE, 1999a and *B. striatula* (NOBLE, 1918). Both species are members of the subgenus *Bolitoglossa* (sensu PARRA-OLEA et al., 2004), which contains 12 species: *B. alberchi* GARCÍA-PARÍS, PARRA-OLEA, BRAME & WAKE, 2003, *B. flaviventris* (SCHMIDT, 1936a), *B. jacksoni* ELIAS, 1984, *B. lignicolor* (PETERS, 1873a), *B. mexicana* (DUMÉRIL, BIBRON & DUMÉRIL, 1854), *B. mombachoensis*, *B. mulleri* (BROCCHI, 1883), *B. odonnelli* (STUART, 1943), *B. platydactyla* (GRAY, 1831), *B. salvinii* (GRAY, 1868), *B. striatula,* and *B. yucatana* (PETERS, 1882).

During recent fieldwork in Nicaragua I collected two specimens of *Bolitoglossa* from Río Indio and Volcán Maderas, respectively, that have distinctive and unique coloration. I here describe these as two new species.

2.3.4.2 Results

Bolitoglossa indio SUNYER, HERTZ, LOTZKAT, WAKE, ALEMÁN, ROBLETO & KÖHLER, 2008

Holotype: SMF 85867, a female from Dos Bocas de Río Indio (11°02’54.8’’ N, 83°52’48.4’’ W), 25 m elevation, Departamento de Río San Juan, Nicaragua. Collected on 19. VI. 2006 by Javier SUNYER, Andreas HERTZ, Sebastian LOTZKAT, Lenin OBANDO, Darwin

MANZANAREZ, Roberto C. MUÑOZ, and Porfirio SANDOVAL. Field tag number JS 600. — No paratypes.

Etymology: The specific name *indio* is used as a noun in apposition in reference to the type locality.

Diagnosis: A moderately small, robust *Bolitoglossa* with the following combination of characteristics: digits completely webbed, one pair of pale dorsolateral stripes irregular in outline on brown ground color, unmarked ventral surfaces, relatively high ratios VT/SVL (81.2%) and MT/SVL (102.5%), relatively broad head (HW/SVL 16.5%), tail moderate in size (TL/SVL 74.4%), and a relatively high number of premaxillary teeth (7). *Bolitoglossa indio* can be distinguished from the other species in the subgenus *Bolitoglossa* by the following characteristics (condition for *B. indio* in parentheses): *Bolitoglossa alberchi, B. jacksoni, B. mulleri, B. salvinii,* and *B. yucatana*: presence of extensive black coloration on the body and tail (absence of black coloration). *Bolitoglossa flaviventris*: distinctive series of broad dark brown dorsal spots on yellow ground color (one pair of pale dorsolateral stripes on brown ground color); absence of speckling and mottling (presence of speckling and mottling in head, dorsum and laterals). *Bolitoglossa lignicolor*: absence of a pair of broad dorsolateral pale stripes (presence); HL/SVL in females 20.9–23.7% (24.1); HW/SVL in females 13.8–16.2% (16.5); MT/SVL 43.5–78.3% (102.5); VT/SVL 29.6–62.2% (81.2); 6 or fewer premaxillary teeth (7). *Bolitoglossa mexicana*: dorsal coloration generally consists of well demarcated cream longitudinal stripes contrasting with black background color, with a middorsal orange-red longitudinal stripe usually present (dorsal coloration consisting of less contrasting pattern, no middorsal orange-red longitudinal stripe); TL/SVL 78.0–111.9% (74.4); HL/SVL in females 19.8–23.0% (24.1); HW/SVL 11.1–15.4% (16.5); MT/SVL 48.2–94.0% (102.5); VT/SVL 27.0–68.3% (81.2). *Bolitoglossa mombachoensis*: presence of narrow, pale brown stripes on ventral surfaces of body (absence); HW/SVL 13.3–15.5% (16.5); MT/SVL 54.5–88.9% (102.5); vomerine teeth 14–28 (38); VT/SVL 25.0–56.8% (81.2); 5 or fewer premaxillary teeth (7). *Bolitoglossa odonnelli*: a pair of dorsolateral pale brown stripes that are clearly delimited (dorsolateral pale brown stripes irregular in outline and mostly bordered by spots or shades darker than the dorsal ground color); TL/SVL 88–118% (74.4); HL/SVL 19–23% (24.1); HW/SVL 13–15% (16.5); maxillary teeth 22–42 (48); MT/SVL 37–71% (102.5); vomerine teeth 11–35 (38); VT/SVL 33–56% (81.2); 6 or fewer premaxillary teeth (7). *Bolitoglossa platydactyla*: single broad middorsal pale swath on a generally dark ground color (a pair of broad pale dorsolateral stripes on brown ground color). *Bolitoglossa striatula*: absence of a pair of broad dorsolateral pale stripes (presence); presence of narrow stripes on dorsum, venter, or both (absence); TL/SVL 84.2–112.8% (74.4); HL/SVL 20.3–23.7% (24.1); HW/SVL 12.6–15.2% (16.5); MT/SVL 35.4–96.2% (102.5); vomerine teeth 13–37 (38); VT/SVL 24.0–79.9% (81.2). I provide a comparison of selected morphometric and dentitional characters in *Bolitoglossa indio, B. insularis, B. lignicolor, B. mexicana, B. mombachoensis, B. odonnelli* and *B. striatula* in Table 5.

Description of the holotype (Fig. 36): Female as indicated by the presence of cloacal folds; size moderate (SVL 46.8 mm); snout truncate in dorsal aspect, broadly rounded in profile; labial protuberances relatively well defined; head broad (HW/SVL 16.5%), relatively flat, and well demarcated from body; eyes moderate in size, slightly protuberant, not visible beyond margin of jaw when viewed from below; postorbital groove distinct, incomplete, not reaching well-defined subocular groove; gular fold distinct, extending dorsolaterally to about lower level of eye; groove at posterior end of mandible shallow, disconnected ventrally; sublingual fold absent; maxillary teeth 48, extending to about level of center of eye; vomerine teeth 38, in long, irregular, arched series extending laterally slightly beyond level of outer border of choanae; premaxillary teeth 7, not enlarged, located just posterior to upper lip and anterior to line of maxillary series; tail nearly cylindrical to slightly triangular anteriorly, becoming conical for about distal half of its length; tail moderate in size (TL/SVL 74.4%), slightly constricted basally; limbs slender, moderately long, adpressed limb interval about 3.5 costal folds; digits completely webbed, lacking subdigital pads, those digits projecting slightly from web are broadly rounded and the longest digit has a more pointed tip than other digits; relative length of digits on forelimbs I<II=IV<III, those on hind limbs I<V<II<IV<III.

Measurements of the holotype (in mm): Head width 7.7; head length 11.3; head depth at posterior angle of jaw 3.6; eyelid length 3.5; eyelid width 1.9; anterior rim of orbit to snout 3.5; horizontal orbital diameter 2.5; interorbital distance 2.7; distance between vomerine teeth and parasphenoid teeth 0.5; snout to forelimb 13.3; distance separating external nares 2.6; nostril diameter 0.25; snout projection beyond mandible 0.6; SVL 46.8; snout to anterior angle of vent 43.9; axilla to groin 24.5; tail length 34.8; tail width at base 4.3; tail depth at base 4.3; forelimb length (to tip of longest digit) 10.4; hind limb length (to tip of longest digit) 10.9; shoulder width 5.9; width of right hand 3.8; width of right foot 5.1.

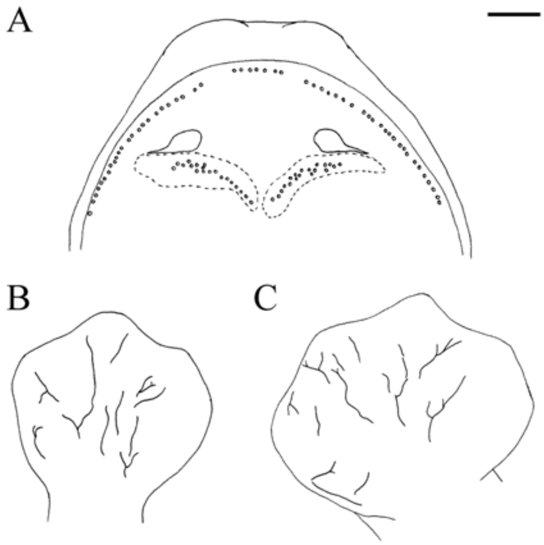


Fig. 36. Ventral view drawings of the holotype of *Bolitoglossa indio* (SMF 85867), showing (a) the roof of the mouth with the premaxillary, maxillary, and vomerine teeth as well as the labial protuberances; and the complete webbing of (b) right hand; (c) right foot. Scale bar = 1 mm.

Coloration in life (Fig. 37): Dorsal surfaces of head, body and anterior half of tail brown, those of head with numerous small dark brown spots; a pair of broad, irregular, sometimes interrupted pale brown dorsolateral stripes extending from posterior to upper eyelids to base of tail (right side) or around mid-tail length (left side), delimited mostly by dark brown irregular shadings which can also be present in lesser densities on the brown dorsum and in the pale brown dorsolateral stripes; lateral surface of tail and body (below the dark brown shadings surrounding both broad pale brown dorsolateral stripes) brown; all ventral surfaces unmarked; ventral surfaces of body and tail light grayish brown, fading to a lighter gray in the area around chest; ventral surface of head reddish brown; dorsal surfaces of limbs and distal half of tail dark brown; ventral surfaces of limbs, hands and feet grayish brown; pale gray labial protuberances.

Osteology (Fig. 38): 14 trunk vertebrae; 28 unbranched caudal vertebrae; transverse processes of first caudal vertebrae long, overlapping the processes of the second caudosacral vertebrae; skull well formed with parietals and frontals separated from paired counterparts by small gap, but without a notable dorsal fontanelle; premaxillary spines arise separately and do not come into contact, long and relatively stout; prefrontals present; vomer bodies in close apposition, preorbital processes long and straight; phalangeal formulae 1-2-3-2 and 1-2-3-3-2; terminal phalanges very small, barely if at all expanded at tips; metacarpals 3 and 4 and metatarsals 1 and 5 more broadened and flattened than others; strong size gradient along digits with terminals typically shortest; terminal phalanges of longest digits of pes have grown slightly laterally, following the margin of the web; tibial spurs not evident.

Fig. 37. Holotype of *Bolitoglossa indio* (SMF 85867) in life: (a) dorsal view; (b) ventral view.

Natural history notes: The holotype was found active at 1300 h on leaf litter at ground level in undisturbed lowland wet forest.

Range: Known only from the type locality.

Fig. 38. X-ray of the holotype of *Bolitoglossa indio* (SMF 85867), SVL 46.8 mm. Scale bar = 10 mm.

Bolitoglossa insularis SUNYER, HERTZ, LOTZKAT, WAKE, ALEMÁN, ROBLETO & KÖHLER, 2008

Holotype: SMF 87175, a female from Volcán Maderas (11°27'38'' N, 85°30'56'' W), 800 m elevation, Isla de Ometepe, Departamento de Rivas, Nicaragua. Collected on 30.vii.2007 by Javier SUNYER, Billy M. ALEMÁN, and Silvia J. ROBLETO. Field tag number JS 1083. — No paratypes.

Etymology: The specific name *insularis* means "of islands" in Latin, in reference to its presumed restricted distribution to the premontane slopes of the southern volcano on Ometepe Island, the largest island in Nicaragua, which is situated in the western part of the freshwater Lake Nicaragua or Cocibolca.

Diagnosis: A moderately large, robust *Bolitoglossa* with the following combination of characteristics: digits completely webbed; dorsal coloration relatively homogeneous brown with dark brown mottling and a single pair of non-delimited dorsolateral shadings which are moderately darker than dorsal ground color; ventral surfaces of body and tail pale brown mottled with dark brown spots; ventral surfaces of head reddish brown with dark brown spots, with a pair of narrow ventrolateral stripes suggested by the absence of dark brown spots; eyes in females well visible beyond margin of jaw when viewed from below; and a relatively high number of premaxillary teeth (7). *Bolitoglossa insularis* can be further distinguished from the other species in the subgenus *Bolitoglossa* by the following characteristics (condition for *B. insularis* in parentheses): *Bolitoglossa alberchi, B. jacksoni, B. mulleri, B. salvinii,* and *B. yucatana*: presence of extensive black coloration on the body and tail (absence of black coloration). *Bolitoglossa flaviventris*: distinctive series of broad dark brown dorsal spots on yellow ground color and absence of mottling throughout the trunk and most of the tail (abundant dark brown dorsal mottling on brown ground color). *Bolitoglossa indio*: presence of a pair of broad dorsolateral pale brown stripes (absence); ventral surfaces unmarked (ventral surfaces with abundant dark brown mottling); eyes not visible beyond margin of jaw when viewed from below in females (eyes visible); TL/SVL 74.4% (86.4); HW/SVL 16.5% (14.1); MT/SVL 102.5% (63.4); VT/SVL 81.2% (35.5). *Bolitoglossa lignicolor*: ground color of ventral surfaces dark (light grayish brown); 6 or less premaxillary teeth (7). *Bolitoglossa mexicana*: contrasting dorsal coloration generally consisting on pale brown, bright and black coloration (non-contrasting relatively homogeneous dorsal brown coloration); ground color of ventral surfaces dark (light grayish brown). *Bolitoglossa mombachoensis*: usually, presence of pale brown dorsolateral stripes (absence); presence of narrow, pale brown stripes on ventral surfaces of body (absence); 5 or less premaxillary teeth (7). *Bolitoglossa odonnelli*: presence of a pair of broad dorsolateral pale brown stripes (absence); TL/SVL 88–118% (86.4); MT/SVL in females 37–60% (63.4); VT/SVL in females 37–56% (35.5); 6 or fewer premaxillary teeth (7). *Bolitoglossa platydactyla*: presence of a single broad middorsal pale swath on a generally dark ground color (absence). *Bolitoglossa striatula*: variable number of well delimited stripes on dorsal surfaces (a single pair of non-delimited, moderately darker than dorsal ground color dorsolateral shadings, in a dorsal pattern otherwise homogeneously brown with dark brown mottling); usually, presence of dark stripes on venter (absence); TL/SVL in females 90.5–112.8% (86.4). I provide a comparison of selected morphometric and dentition characters in *Bolitoglossa indio, B. insularis, B. lignicolor, B. mexicana, B. mombachoensis, B. odonnelli,* and *B. striatula* in Table 5.

Description of the holotype (Fig. 39): Female as indicated by the presence of cloacal folds; size moderate (SVL 64.7 mm); snout rounded in dorsal aspect, rounded in profile; labial protuberances well defined; head relatively narrow (HW/SVL 14.1%), relatively flat, and only slightly demarcated from body; eyes moderate in size, slightly protuberant, well visible beyond margin of jaw when viewed from below; postorbital groove indistinct; subocular groove distinct; gular fold distinct, extending dorsolaterally to about lower level of eye; groove at posterior end of the mandible shallow, connected ventrally as a very poorly defined depression anterior to gular fold; sublingual fold absent; maxillary teeth 41, extending to about level of center of eye; vomerine teeth 23, in straight to slightly arched series extending laterally to (left side) or slightly beyond (right side) level of outer border of choanae; premaxillary teeth 7 not enlarged, located just posterior to upper lip and anterior to line of maxillary series; tail conical, becoming slightly flattened laterally for about distal half of its length; tail moderate in size (TL/SVL 86.4%), with an early stage of tail autotomy; limbs slender, moderately long, adpressed limb interval about 3.5 costal folds; digits completely webbed, lacking subdigital pads, those digits projecting slightly from web are rounded and the longest digit has a more pointed tip than other digits; relative length of digits on forelimbs I<IV<II<III, those on hind limbs I<V<II=IV<III.

Measurements of the holotype (in mm): Head width 9.1; head length 14.0; head depth at posterior angle of jaw 5.3; eyelid length 4.1; eyelid width 2.2; anterior rim of orbit to snout 3.6; horizontal orbital diameter 2.9; interorbital distance 3.2; distance between vomerine teeth and parasphenoid teeth 0.65; snout to forelimb 18.1; distance separating external nares 3.4; nostril diameter 0.33; snout projection beyond mandible 0.5; SVL 64.7; snout to anterior angle of vent 61.5; axilla to groin 38.2; tail length 55.9; tail width at base 5.8; tail depth at base 5.5; forelimb length (to tip of longest digit) 12.7; hind limb length (to tip of longest digit) 13.2; shoulder width 7.8; width of right hand 4.9; width of right foot 6.7.

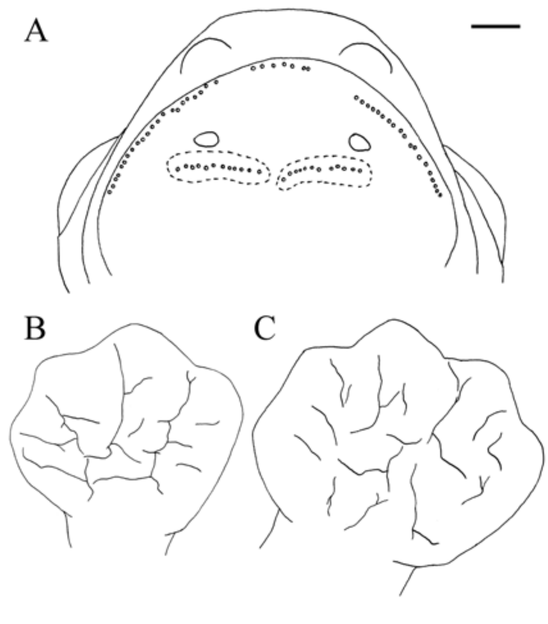


Fig. 39. Ventral view drawings of the holotype of *Bolitoglossa insularis* (SMF 87175), showing (a) the roof of the mouth with the premaxillary, maxillary, and vomerine teeth, as well as the labial protuberances and eyes; and the complete webbing of (b) left hand; (c) left foot. Scale bar = 1 mm.

Coloration in life (Fig. 40): Dorsal surfaces of head, body and tail brown with numerous small dark brown spots; two weakly defined, non-delimited, dark brown dorsolateral shadings extending from just behind forelimb insertions almost to groin; lateral surfaces of head, body and tail dark brown; all ventral surfaces except those of hands and feet mottled with small dark brown spots; ventral surface of body, limbs, and tail light grayish brown; ventral surfaces of head reddish brown, with a pair of narrow ventrolateral stripes suggested by absence of dark brown spots; dorsal surfaces of limbs dark brown; ventral surfaces of hands and feet homogeneously brown; pale brown labial protuberances.

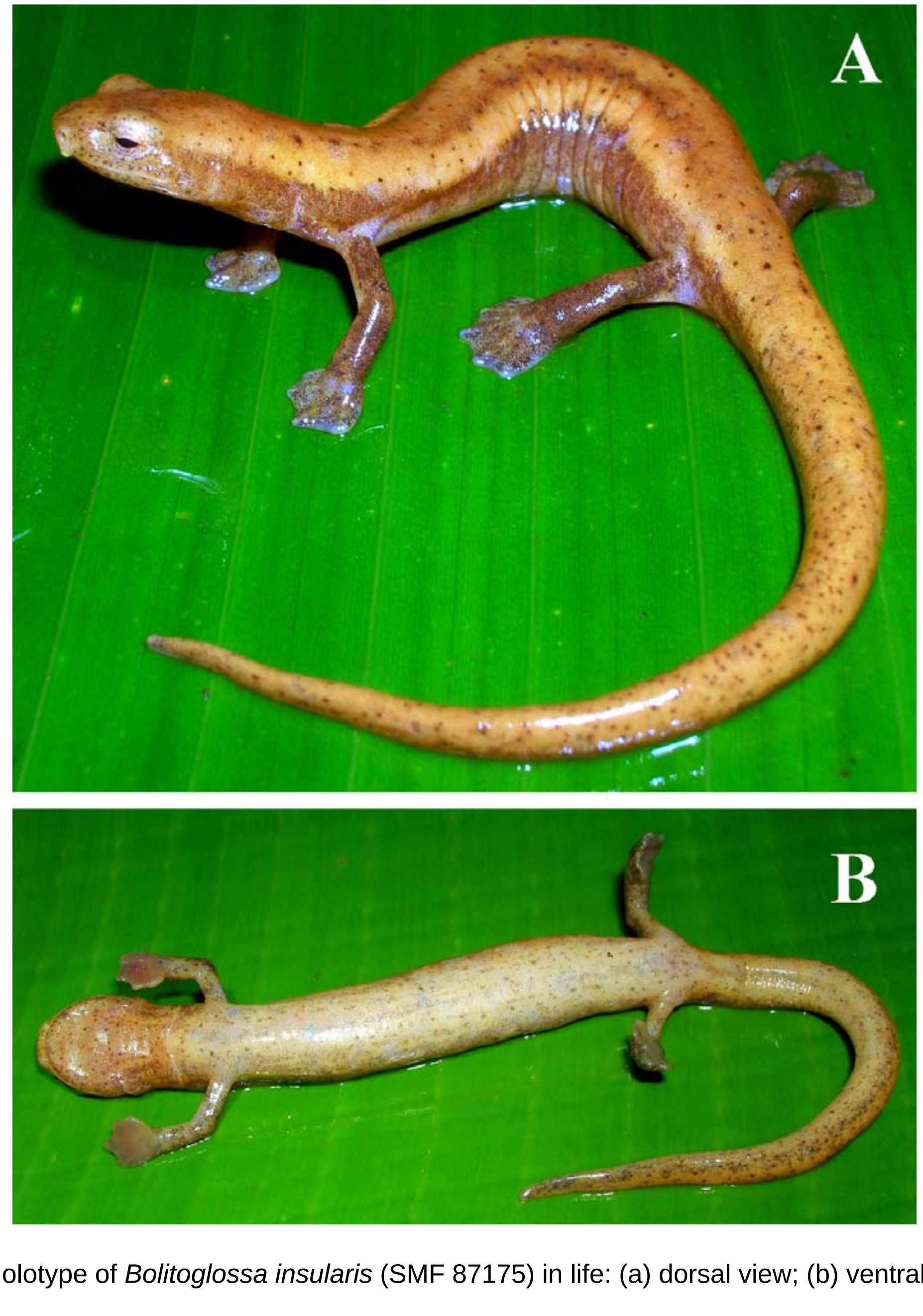


Fig. 40. Holotype of *Bolitoglossa insularis* (SMF 87175) in life: (a) dorsal view; (b) ventral view.

Osteology (Fig. 41): 14 trunk vertebrae; 35 caudal vertebrae; transverse process of first caudal is relatively short and stout, not extending far forward; skull well developed with only slight dorsal fontanelle, processes of premaxilla arise and remain separated; prefrontals appear to be present; vomer bodies very widely separated, preorbital processes long, straight; phalangeal formulae 1-2-3-2 and 1-2-3-3-2; terminal phalanges very small, barely if at all expanded at tips, some pointed; tibial spurs not evident.

Natural history notes: The holotype was found active at 1700 h at 1.5 m height on a thin branch of a bush in undisturbed premontane moist forest. At the time it was found, there was no rain although it was cloudy and fog was occasionally present.

Range: Known only from the type locality.

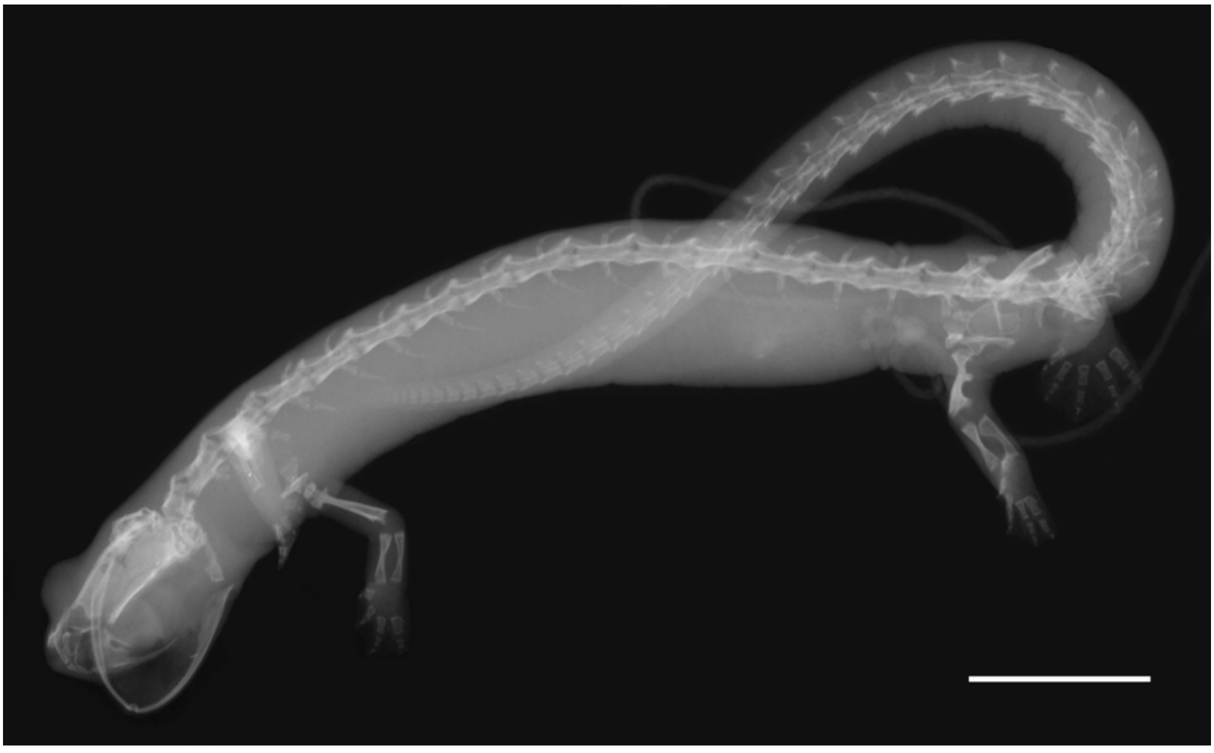


Fig. 41. X-ray of the holotype of *Bolitoglossa insularis* (SMF 87175), SVL 64.7 mm. Scale bar = 10 mm.

Table 5. Comparison of selected morphometric and dentitional characters in *Bolitoglossa indio, B. insularis, B. lignicolor, B. mexicana, B. mombachoensis, B. odonnelli,* and *B. striatula*. Abbreviations: M = males; F = females; SVL = snout–vent length; TL = tail length; HL = head length; HW = head width; MT = maxillary teeth; VT = vomerine teeth; PT = premaxillary teeth. Range in dentitional characters is followed by mean value and one standard deviation in parentheses. Maxillary and vomerine tooth counts are both sides summed. Only complete, unregenerated tails were measured. Data were only taken from adults. (1) ranges up to 0.26 (SAVAGE, 2002); (2) ranges from 11 (STUART, 1943); and (3) ranges from 0.84 (MCCRANIE & WILSON, 2002).

Species	Sex	SVL	TL/SVL	HL/SVL	HW/SVL	MT	MT/SVL	VT	VT/SVL	PT
B. indio	M	—	—	—	—	—	—	—	—	—
	F (n = 1)	46.8	0.74	0.24	0.16	48	1.03	38	0.81	7
B. insularis	M	—	—	—	—	—	—	—	—	—
	F (n = 1)	64.7	0.86	0.22	0.14	41	0.63	23	0.36	7
B. lignicolor	M (n = 12)	47.3–67.7	0.77–1.08	0.21–0.24[1]	0.14–0.18	23–45 (33.7 ± 7.1)	0.44–0.78	18–40 (27.8 ± 6.4)	0.30–0.62	0–6
	F (n = 11)	45.5–81.2	0.67–1.02	0.21–0.24	0.14–0.16	24–60 (38.9 ± 11.1)	0.45–0.76	22–42 (30.0 ± 6.2)	0.31–0.62	
B. mexicana	M (n = 16)	50.6–64.1	0.96–1.12	0.20–0.24	0.11–0.15	32–47 (38.3 ± 5.3)	0.53–0.85	15–32 (21.3 ± 3.9)	0.27–0.54	3–7 (4.3 ± 1.5)
	F (n = 25)	52.7–82.0	0.78–1.09	0.20–0.23	0.11–0.15	34–67 (42.2 ± 7.0)	0.48–0.94	20–41 (28.8 ± 5.1)	0.28–0.68	0–7 (3.1 ± 2.3)
B. mombachoensis	M (n = 10)	45.0–57.5	0.84–0.97	0.20–0.25	0.13–0.15	30–40 (34.3 ± 4.2)	0.59–0.74	14–27 (19.4 ± 5.3)	0.30–0.50	4–5 (4.4 ± 0.5)
	F (n = 24)	46.5–66.0	0.74–0.98	0.20–0.25	0.13–0.15	29–52 (38.6 ± 6.5)	0.55–0.89	14–28 (21.5 ± 3.8)	0.25–0.57	0–4 (2.8 ± 1.4)
B. odonnelli	M (n = 6)	54.7–60.9	0.97–1.18	0.20–0.23	0.13–0.15	22–42 (31.2 ± 6.9)	0.39–0.71	20[2]–28 (25.2 ± 2.8)	0.33–0.49	3–6 (4.3 ± 1.0)
	F (n = 6)	60.5–68.3	0.88–1.00	0.19–0.22	0.13–0.15	24–40 (33.3 ± 6.3)	0.37–0.60	26–35 (29.5 ± 3.3)	0.37–0.56	0–2 (1.0 ± 0.9)
B. striatula	M (n = 16)	44.0–58.5	0.88[3]–1.06	0.21–0.24	0.13–0.15	24–48 (32.6 ± 6.7)	0.46–0.90	13–31 (23.5 ± 5.1)	0.24–0.64	3–7 (4.6 ± 1.4)
	F (n = 24)	46.3–66.0	0.90–1.13	0.20–0.24	0.13–0.15	19–58 (40.3 ± 11.7)	0.35–0.96	16–37 (29.2 ± 5.7)	0.25–0.80	1–7 (3.9 ± 1.6)

2.3.4.3 Discussion

The only species of *Bolitoglossa* that occurs in sympatry with *B. indio* is *B. striatula* (IUCN, 2007). Most other species of the subgenus *Bolitoglossa* (*B. alberchi, B. flaviventris, B. jacksoni, B. mulleri, B. odonnelli, B. platydactyla, B. salvinii* and *B. yucatana*) are endemic to more or less small areas well north of Nicaragua; *B. mexicana* occurs from Mexico to Honduras and although its occurrence in northern Nicaragua is likely, its southernmost known distribution is approximately 400 km NW from the type locality of *B. indio*; *B. lignicolor* occurs in the Pacific low and premontane areas of southern Costa Rica and western Panama; and *B. mombachoensis* is restricted to the highlands of Volcán Mombacho in western Nicaragua (Fig. 42).

Bolitoglossa insularis is the only salamander species known to occur on the island of Ometepe. In addition, it is the only species of *Bolitoglossa* recorded in Nicaragua exclusively at a mid-premontane elevation (despite substantial searching especially at lower and also at higher elevations on the island). *Bolitoglossa mombachoensis* is known from high-premontane elevations from 1040–1345 m (KÖHLER & MCCRANIE, 1999a), and *B. striatula* ranges in Nicaragua from the lowlands up to approximately 770 m (VILLA, 1972a).

The coloration of *Bolitoglossa indio* is most similar to that of *B. odonnelli* and of those *B. mexicana* that have only two broad pale dorsolateral stripes (see description of coloration of six specimens of *B. mexicana* from Departamento Cortés, Honduras, in MCCRANIE & WILSON 2002: 123, approximately 700 km NW of type locality of *B. indio*). However, in *B. indio* the dorsolateral pale stripes are not as clearly delimited in outline as in *B. odonnelli* and *B. mexicana*.

The coloration of *Bolitoglossa insularis* is most similar to that of *B. mombachoensis* and *B. striatula*. *Bolitoglossa mombachoensis* is extremely variable in coloration (JANSEN & KÖHLER, 2001): it normally presents pale brown dorsolateral stripes, but can also be remarkably similar in dorsal and lateral aspect to *B. insularis* (see Fig. 7 in KÖHLER, 1998b, and Fig. 112 in KÖHLER, 2001). However, all examined specimens of *B. mombachoensis* display a variable number of thin, pale brown stripes on the ventral surfaces, a characteristic absent in *B. insularis*. Specimens of *B. striatula* have a variable number of dark or pale brown stripes on the dorsal surfaces of body (normally on the neck and limbs, and sometimes on the tail). In addition, most *B. striatula* have a variable amount of fine dark brown stripes on the ventral surfaces, although occasional individuals may have an immaculate venter (SAVAGE, 2002: 138). The specimen I have examined that is most similar to *B. insularis* is *B. striatula* SMF 77790, which has a very similar unstriped ventral surface. SMF 77790 also has dark brown mottling on the dorsal surfaces and a relatively fewer dorsal stripes. However, those stripes that are present on the dorsum are defined and delimited in outline (see photograph of *B. striatula* SMF 77790 in Fig. 5 in KÖHLER & MCCRANIE, 1999a, and Fig. 115 in KÖHLER, 2001). In contrast, narrow stripes are absent from both dorsal and ventral surfaces of *B. insularis* and the only defined stripe present is the single pair of broad, dark brown lateral stripes.

The apparent similarities between *Bolitoglossa indio, B. odonnelli* and *B. mexicana* on the one hand and between *B. insularis, B. striatula* and *B. mombachoensis* on the other hand suggest that both *B. indio* and *B. insularis* are members of the subgenus *Bolitoglossa* (sensu PARRA-OLEA et al., 2004). However, I refrain from formally placing this species in this subgenus (previously referred to as the *Bolitoglossa mexicana* species group; GARCÍA-PARÍS et al., 2000, 2003) until tissue samples and molecular data are obtained and analyzed. It is conceivable that *B. indio* could be a member of *Eladinea* and *B. insularis* a member of *Pachymandra*, based on tail and skull traits, but the narrow head of *B. insularis* argues against such an assignment.

Salamanders are typically found active at night, but sometimes they can also be found active during the coolest times of the day, especially in the event of rain, mist, or high humidity. During daytime, they are normally found inactive hidden in very humid places like tank bromeliads, in or under rotten logs, under fallen leaves, beneath moss, in dead basal ramifications of giant ferns, in the axis of large-leaved plants, etc. In contrast, the holotype of *Bolitoglossa indio* was found active on leaf litter at ground level at the hottest time of the day with no rain nor fog. Therefore, it is probable that SMF 85867 had fallen from its perch or was disturbed from a ground level hiding place at the time it was found.

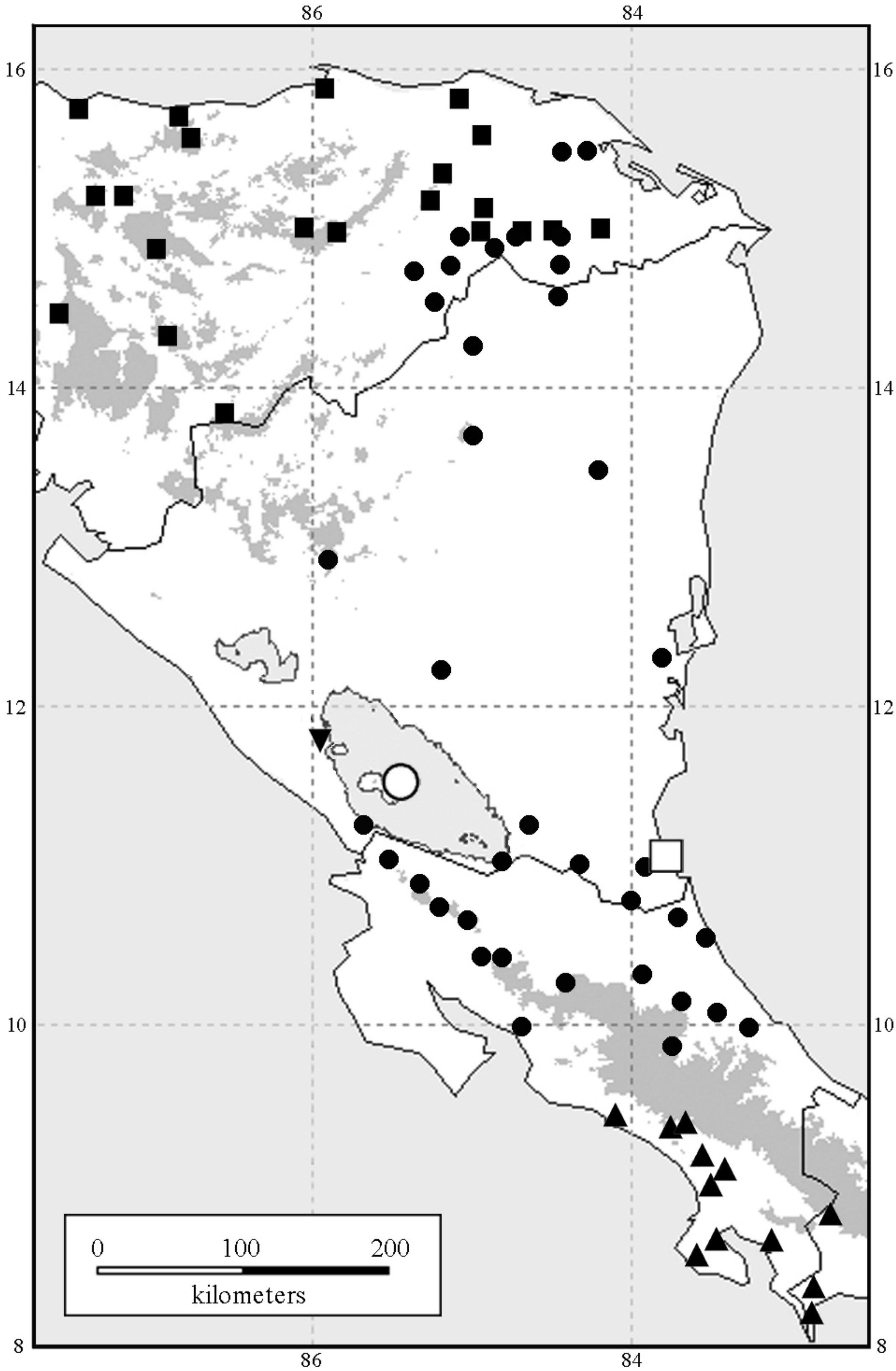


Fig. 42. Map showing localities for several members of the subgenus *Bolitoglossa* that are known to occur in Nicaragua and its neighboring countries Honduras and Costa Rica, including the two new species described herein. Solid squares = *B. mexicana*; solid circles = *B. striatula*; upright triangles = *B. lignicolor*; inverse triangle = *B. mombachoensis*; open square = *B. indio*; open circle = *B. insularis*.

2.3.5 A NEW SPECIES OF RAIN FROG (GENUS *CRAUGASTOR*) OF THE *FITZINGERI* GROUP FROM RÍO SAN JUAN, SOUTHEASTERN NICARAGUA (AMPHIBIA, ANURA, CRAUGASTORIDAE)

2.3.5.1 Introduction

The systematics of the *Craugastor fitzingeri* (SCHMIDT, 1858) species group were reanalysed by SAVAGE et al. (2004), who recognized 13 species in the *fitzingeri* group, only two of which are known to occur north of Costa Rica (i.e., *C. fitzingeri* and *C. talamancae* [DUNN, 1931]). During several collecting trips along the Río San Juan in southeastern Nicaragua, aside from the abundant *C. fitzingeri*, a single specimen of *C. talamancae* and a single specimen of another frog belonging to the *C. fitzingeri* species group was collected. However, the latter specimen possesses a distinctive suite of characters that will distinguish it from the 13 the *C. fitzingeri* group species recognized by SAVAGE et al. (2004). Comparisons with the known species of *Craugastor* COPE, 1862 from Honduras, Nicaragua, Costa Rica, and Panama demonstrated that this frog represents an undescribed species.

2.3.5.2 Results

Craugastor chingopetaca KÖHLER & SUNYER, 2006

Holotype: SMF 83214 (Figs. 43–45), an adult female, from Chingo Petaca, Río San Juan, 10°44'50.9'' N, 83°50'26.3'' W, Departamento Río San Juan, Nicaragua, 40 m elevation, collected by G. KÖHLER on 19. VII. 2004. Field number GK 826. — No paratypes.

Etymology: The name *chingopetaca* is a noun used in reference to the type locality where the holotype of the species was collected.

Diagnosis: *Craugastor chingopetaca* is a member of the *Craugastor fitzingeri* series and *fitzingeri* species group, as defined by SAVAGE (1987, 2002) and revised by SAVAGE et al. (2004), and the slightly less encompassing *fitzingeri* group of the subgenus *Craugastor,* as defined by LYNCH & DUELLMAN (1997). It differs from all species of this group by the following combination of characters: toe webbing moderate (substantially encompassing the proximal subarticular tubercles on all toes); Toe III and Toe V of equal length; toe fringes present; most finger and toe disk covers retuse; a definite large heel tubercle absent; a midgular pale stripe absent; and porsterior surface of thigh uniform brown. *Craugastor* *chingopetaca* differs further from the species of the *Craugastor fitzingeri* group by the following characteristics (condition for *C. chingopetaca* in parentheses): *Craugastor andi* (SAVAGE, 1974): posterior surface of thigh with pale spots and/or vertical lineolate markings (uniform brown); *Craugastor crassidigitus* (TAYLOR, 1952): Toe III longer than Toe V (Toe III and Toe V of equal length); finger and toe disk covers non-retuse (retuse); distinct accessory palmar tubercles present on base of all Fingers (indistinct accessory palmar tubercles present only on base of Fingers I and II); supratympanic ridge distinctly curved downwards (only slightly curved downward; Fig. 46); midgular pale stripe present or at least indicated anteriorly (absent). *Craugastor cuaquero* (SAVAGE, 1980): toe webbing basal (toe webbing moderate); posterior surface of thigh with pale spots and/or vertical stripes (uniform brown); midgular pale stripe present (absent). *Craugastor emcelae* (LYNCH, 1985): a definite large heel tubercle present (no large heel tubercle present). *Craugastor fitzingeri*: posterior surface of thigh with pale mottling (uniform brown); midgular pale stripe present (absent). *Craugastor longirostris* (BOULENGER, 1898): finger and toe disk covers non-retuse (retuse); midgular pale stripe present or absent (absent). *Craugastor melanostictus* (COPE, 1875): toe webbing absent (toe webbing moderate); enlarged supraocular tubercle present (absent); posterior thigh with vertical bars (uniform brown). *Craugastor monnichorum* (DUNN, 1940): supratympanic fold prominent (barely evident); a definite large heel tubercle present (no large heel tubercle); a weak interorbital fold present (absent). *Craugastor phasma* (LIPS & SAVAGE, 1996): toe webbing absent (toe webbing moderate); posterior surface of thigh uniform gray white (uniform brown). *Craugastor raniformis* (BOULENGER, 1898): midgular pale stripe usually present (absent); posterior surface of thigh with pale mottling (uniform brown). *Craugastor rayo* (SAVAGE & DEWEESE, 1979): a large heel tubercle present (no large heel tubercle); posterior surface of thigh uniform purple (uniform brown). *Craugastor tabasarae* (SAVAGE, HOLLINGSWORTH, LIPS & JASLOW, 2004): large supraocular tubercle present (absent); posterior thigh with vertical bars (uniform brown); toe webbing basal (toe webbing moderate). *Craugastor talamancae*: toe webbing minimal (toe webbing moderate); tarsal fold absent (tarsal fold moderately developed); finger and toe disk covers non-retuse (retuse); Toe III longer than Toe V (Toe III and Toe V of equal length).

Description of the holotype (70% ethanol): SVL 37.6 mm; HL 15.4 mm (0.41); HW 13.5 mm (0.36); EL 4.8 mm (0.13); IOD 3.8 mm (0.10); SL 6.9 mm (0.18); NED 5.2 mm (0.14); TM 2.05 mm (0.05); IND 3.8 mm (0.10); SHL 25 mm (0.66); and FL 20.7 mm (0.55). Head relatively narrow, slightly longer than broad; snout subeliptical (SL/HL 0.45); upper eyelids with several small tubercles, one of which slightly enlarged in posterior portion of eyelid; no superciliary tubercles; canthus rostralis rounded; loreal region concave; upper lip not flared in cross section; nostrils directed posterolaterally, situated at a point about three-fourths distance between anterior border of eye and tip of snout; cranial crests absent; glandular supratympanic ridge present, curved downward posterior to tympanum; tympanum prominent; tympanic annulus present, more distinct anteriorly; fingers unwebbed; strongly enlarged disks on Fingers III and IV (width of disk about three times as wide as finger, wider than length of inner metatarsal tubercle), with expanded, retuse (indented) disk covers and even, broadened pads; disk on Fingers I and II about half the size of disks on Fingers III and IV; Finger I equal or slightly longer than Finger II when adpressed; relative length of fingers 3>4>1≥2; subarticular tubercles of hands globular; no supernumerary tubercles; indistinct accessory palmar tubercles present on Fingers I and II; palmar tubercle bifid, larger than elongate thenar tubercle; largest toe disks smaller than largest finger disks; disks on Toes II-IV with distinctly expanded, slightly retuse, truncate disk covers and even, broadened pads; disks on Toes I and V smaller; relative length of toes 4>5=3>2>1; tip of Toe III and Toe V not reaching penultimate subarticular tubercle of Toe IV; moderate webbing between toes, webbing reaching the base of the distal tubercle on toe V and well beyond the proximal tubercle on the rest; toe webbing formula I 1½–2 II 1½–3^{-} III 2^{+}–3¾ IV 4–2¼ V; toe fringes distinct; heel smooth with no distinct tubercle; moderately developed tarsal fold; skin on dorsal surface of body finely tuberculate; no inguinal gland; flank, upper limb surfaces and venter smooth; ventral disk margin crossing venter anterior to level of groin; horizontally elliptical pupil; tongue ovoid, barely notched posteriorly, free posteriorly for about two-thirds of its length; 6–7 vomerine teeth per patch, arranged in a straight line on elevated, nearly triangular-shaped ridges located posteromedially to ovoid choanae, each ridge separated by distance less than width of either patch; maxillary and premaxillary teeth present.

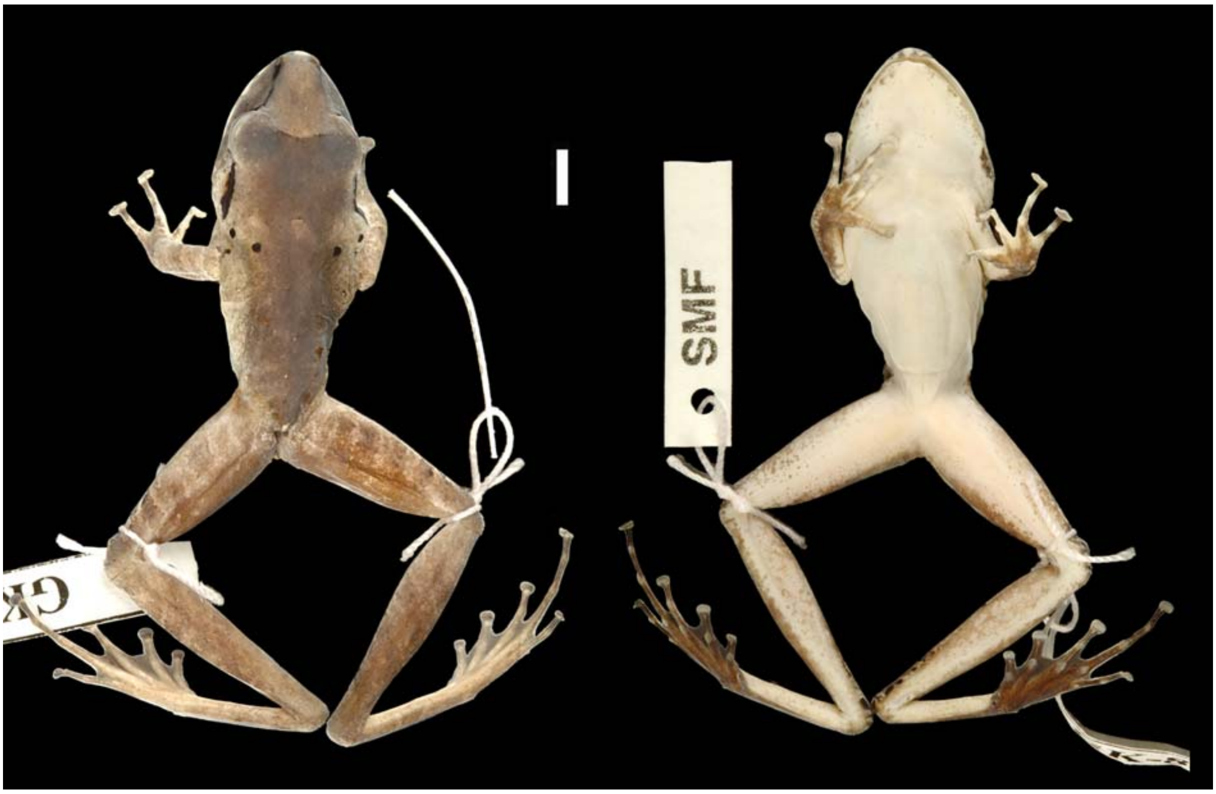


Fig. 43. Holotype of *Craugastor chingopetaca* (SMF 83214; 37.6 mm SVL); dorsal view (left) and ventral view (right). Scale bar = 5 mm.

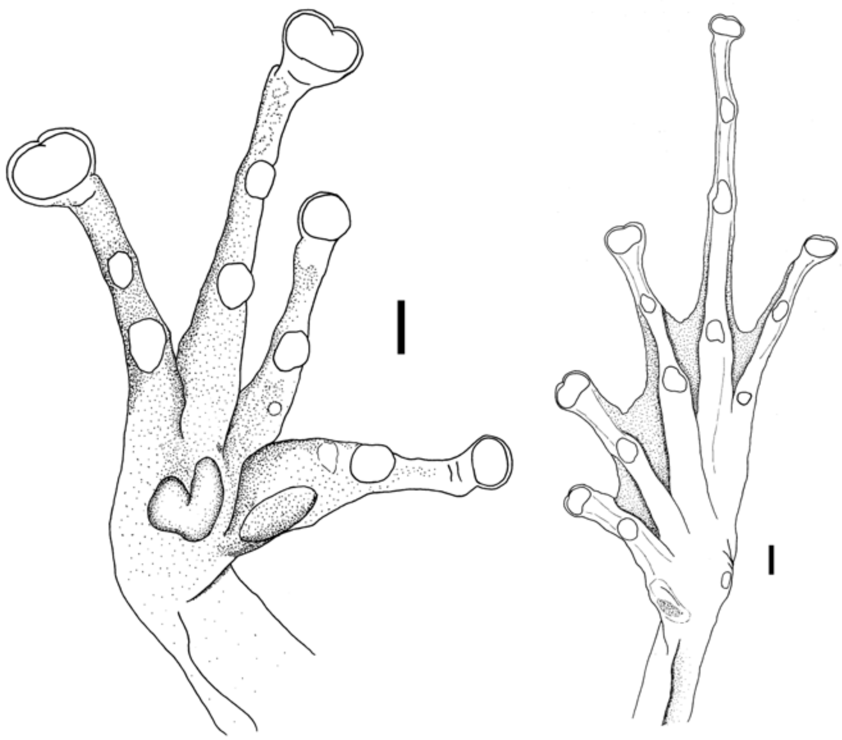


Fig. 44. Right hand (left) and left foot (right) of holotype of *Craugastor chingopetaca*. — Scale bars = 1 mm. Drawings: L. CZUPALLA.

Fig. 45. Lateral head drawing of holotype of *Craugastor chingopetaca*. — Scale bar = 1 mm. Drawing: L. CZUPALLA.

Coloration in preservative (70% ethanol): Dorsum and posterior head grayish brown with small black spots in the suprascapular region; anterior head abruptly paler; surface of posterior thigh uniformly brown, not paler towards cloaca; anterodorsal surface of thigh and dorsal surface of shank with irregularly faint dark brown bars; lateral snout same color as anterior dorsal head, except for darker area beneath canthus rostralis indicating a weak face mask; upper lips dirty white with brown mottling; ventral surface of body immaculate white; ventral surfaces of head and thighs dirty white with few brown punctations**;** no midgular pale stripe; flanks white with brown punctuations, more intensive towards dorsum**;** groin similar in coloration to adjacent flanks and thighs; upper surface of arms grayish brown with faint dark brown bars; no dark seat patch, although cloacal annulus slightly darker pigmented than adjacent area; tarsal segments paler than thigh; soles uniform brown.

Natural histoy notes: The type specimen of *Craugastor chingopetaca* was collected during daytime in the leaf litter of the forest floor on a wet ridge in the rain forest (Wet Forest formation of HOLDRIDGE, 1967).

Range: Known only from the type locality.

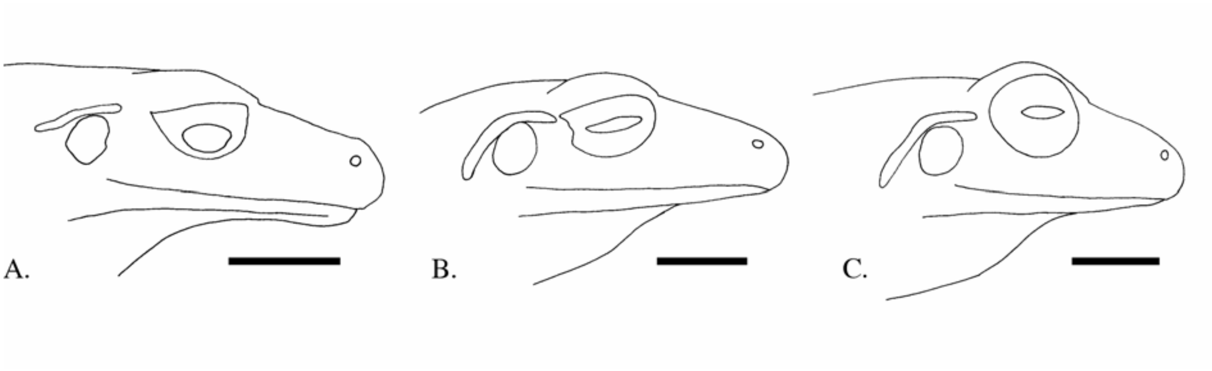


Fig. 46. Lateral head indicating shape of supratympanic ridge: A) holotype of *Craugastor chingopetaca* (SMF 83214). — B) *C. crassidigitus* (SMF 81840) from Parque Nacional Braulio Carrillo, Costa Rica. — C) *C. crassidigitus* (SMF 81955) from Parque Nacional Nusagandi, Panama. — Scale bars = 5 mm.

2.3.5.3 Discussion

Craugastor chingopetaca is assigned to the *fitzingeri* species group (sensu SAVAGE, 2002) on the basis of external characters. It agrees with most other members of this group in habitus and in having Finger I equal or slightly longer than Finger II; a prominent tympanum; vomerine odontophores nearly triangular, posterior to choanae, and separated medially by distance less than width of either odontophore; disks on all digits expanded, most disk covers retuse; subarticular tubercles symmetrical, projecting moderately; no supernumerary tubercles on hands and feet, indistinct accessory palmar tubercles present; no plantar tubercles; toe webbing moderate; an inner tarsal fold; smooth venter. The only character that appears to be incongruent with the definition of SAVAGE (2002) is the relative length of Toe III and V (subequal in *C. chingopetaca*; Toe III longer than Toe V in the remaining species of the *fitzingeri* species group). However, I consider this to be a minor discrepancy and still feel confident with the assignment of the new species to this group.

2.3.6 NEW COUNTRY RECORDS OF HERPETOFAUNA FROM NICARAGUA

2.3.6.1 Introduction

In recent years, there have been a couple of additions to the known herpetofauna of Nicaragua (STAFFORD, 2002; KÖHLER et al., 2004), and still more are expected to be found as research continues in the country. Recent fieldwork in Nicaragua, summarized below, has demonstrated the presence of one frog and one snake hitherto unknown from the country and produced the first voucher specimens for two lizards and one turtle species. I provide morphometric data and include brief ecological field notes for the five new country records.

2.3.6.2 Results

Cochranella spinosa (TAYLOR, 1949)

Cochranella spinosa was previously known only from north and south of Nicaragua (MCCRANIE & WILSON 2002, SAVAGE 2002). On 14 June 2000, GK collected three adult males (SMF 79753–55) at Boca de San Carlos (10°47'26''N, 84°11'70''W), 20 m elevation. On 15 June 2000, GK collected an amplectant pair (SMF 79756–57) and an adult male (SMF 79758) at Río Sarnoso, ca. 1 km above its confluence with Río San Juan (10°55'35''N, 84°17'40''W), 25 m elevation. On 1 May 2001, GK collected a juvenile (SMF 80997) and on 23 September 2001 two adult males (SMF 82087–88) at Bartola, Quebrada El Gaitán, near "Orange Trail 38" (10º58'37''N, 84º20'35''W), 30 m elevation. On 1 October 2001, GK collected two adult males (SMF 82089–90) at Bartola, along a stream near "Blue 10" (10º58'37''N, 84º20'35''W), 30 m elevation. On 18 April 2004, MD collected an adult female (MD 19) at Lomas de Tambor (10º47'00''N, 83º59'16''W). Between 28 April and 2 May 2004, GP and NT collected three adult males (SMF 83367–68 and GP 165) at Cerro El Bolívar, near Río Machado (10º52'02''N, 84º10'10''W). Between 08–15 June 2006, AH, JS and SL collected four adult males (JS 417, SMF 87808, 87810–11) and one adult female (JS 411) at Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), five adult males (JS 465, 467–68, SMF 87807, 87809) at Caño San Miguelito, near Bartola (10°58.37´N, 84°20.35´W), and an amplectant pair (JS 509, SMF 87805) at Boca de San Carlos (10°47´26N, 84°11.70´W). All 27 specimens were collected during night surveys at the Refugio de Vida Silvestre Río San Juan and Reserva Biológica Indio-Maíz, Dpto. Río San Juan. On 30 June 2007, LO, JS and ST collected an amplectant pair (Fig. 47; N 210, SMF

87806) on the lowlands of Cerro Saslaya (13°46.154´N, 84°58.714´W). Between 10–12 August 2007, DW and JS collected four adult males (JS 1124, 1126, SMF 87920–21) at Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W). The last two localities are located in the Región Autónoma Atlántico Norte. I have examined all specimens of *Centrolene ilex* cited in KÖHLER (2001: 186): all SMF specimens correspond to *Cochranella spinosa* and LACM 72910, 72914 from Río Indio correspond to *Centrolene ilex*.

Morphometrics of the material: maximum SVL males 21.3 mm; maximum SVL females 21.6 mm; SHL/SVL 0.56–0.63 (0.60±0.02); FL/SVL 0.40–0.44 (0.41±0.01); HW/SVL 0.33–0.37 (0.35±0.01); HL/SVL 0.28–0.36 (0.34±0.02); TM/EL 0.13–0.21 (0.17±0.02); NED/HL 0.18–0.25 (0.20±0.02); IOD/HW 0.27–0.38 (0.37±0.03); IND/HW 0.16–0.22 (0.19±0.02); modal webbing formula of hand (webbing between fingers I and II is vestigial): II 2^{-}-3^{+} III 2^{-}-$1^{3/4}$ IV; modal webbing formula of feet: I 1-2 II 1-2^{+} III 1-2^{+} IV 2-1 V.

Fig. 47. Amplectant pair of *Cochranella spinosa* (left) and adult male (not collected) guarding an egg mass (right) from the lowlands of Cerro Saslaya.

Kinosternon angustipons LEGLER, 1965

On 22 July 2007, JS, AG, and IG collected a specimen of *Kinosternon angustipons* (SMF 87168) at the Río Papaturro, near its confluence with the Río Sahíno, approximately one-half a kilometer before the confluence of the Río Papaturro and Lake Nicaragua, Departamento de Río San Juan (11.0227º N, 85.0513º W, 40 m elevation). The area is surrounded by permanent freshwater marshes characterized by tall emergent grasses and a lack of trees. SMF 87168 was found at night in the middle of the Río Papaturro while actively swimming on the surface, apparently alerted by our oncoming motorboat and flashlights. It ceased activity once it reached some emergent vegetation approximately one and one-half meters from the shore. Despite the waves caused by our boat and the presence of lights directed at the turtle, it did not attempt escape by diving or climbing onshore. Other turtle species I collected or photographed at the Río Papaturro in the vicinity of this locality include *Chelydra acutirostris*, *Trachemys scripta*, *Kinosternon leucostomum*, and *K. scorpioides*.

SMF 87168 (Fig. 48) is an adult male (carapace length 100 mm) with the following characteristics: carapace smooth, unkeeled, notched posteriorly; plastron reduced, double-hinged, emarginated posteriorly, with eleven plastral shields; length of bridge 17.3% of carapace length; axillary and inguinal shields in contact, separating pectorals from any contact with marginals; upper margin of jaw smooth; three pairs of chin barbels; toes webbed; definite patches of opposable thigh and calf spines; tip of tail soft, extending well beyond margin of carapace. Coloration in life: carapace dark brown; plastron golden yellow; head dark brown dorsally, tan to cream laterally and ventrally, without contrasting markings.

LEGLER (1965: 623) described *Kinosternon angustipons* based on 14 specimens collected in Costa Rica and Panama and stated the geographic range for this species as "approximately from the delta of the Río San Juan (on the boundary between Nicaragua and Costa Rica) to Almirante, Bocas del Toro, Panama," and subsequently described the range as extending "from the mouth of the San Juan River in Nicaragua to the region of Almirante, Bocas del Toro, Panama" (LEGLER, 1966: 118), despite the absence of confirmed records from Nicaraguan territory. Since then, *K. angustipons* has consistently been recognized as part of the Nicaraguan herpetofauna (IVERSON, 1980, 1986, 1992; VILLA, 1983; VILLA et al., 1988; KÖHLER, 2001, 2003; RUIZ & BUITRAGO, 2003). RUIZ & BUITRAGO (2003: 191) also included a personal report of the existence of this species at "Panaloya, north of the Cocibolca Lake" (= Lake Nicaragua). However, the presence of this species in Nicaragua previously has not been supported by a voucher specimen. Therefore, SMF 87168 constitutes the first definitive specimen of *K. angustipons* collected in Nicaraguan territory, and represents the northwesternmost record of this species, with a range of extension of approximately 130 km NE of the nearest locality in Costa Rica (SAVAGE, 2002).

Fig. 48. Adult male of *Kinosternon angustipons* from along Río Papaturro: dorsal view (left) and ventral view (right).

Mesaspis moreletii (BOCOURT, 1871)

On 12 July 2005, JS, LO, and DW collected two juveniles of this species: (JS 134) at 13º35'20''N, 85º43'33''W, 1440 m elevation and (SMF 88134) at 13º35'01''N, 85º43'04''W, 1330 m elevation. On 12 August 2005, JS and DW collected an adult male of this species (SMF 88135) at 13º35'07''N, 85º42'17''W, 1305 m elevation. All three specimens were collected at the Reserva Natural Kilambé, Departamento de Jinotega (Fig. 49). One (JS 134) was found active on ground level at 7:30 h in a deforested area on the property of José GÓMEZ and another (SMF 88134) was found at 12:30 h, 1.5 m high on a mossy tree trunk in primary cloud forest. SMF 88135 was found at 16:30 h while basking at ground level in a transition area between old pasture and cloud forest.

Morphometrics of the material: SVL adult male 71 mm; TL/SVL 1.57–1.79 (1.68±0.11); HL/SVL 0.20–0.24 (0.22±0.01); SHL/SVL 0.11–0.12 (0.11±0.01); HL/HW 1.33–1.53 (1.44±0.10); HW/SVL 0.15–0.16 (0.16±0.01); AGD/SVL 0.49–0.53 (0.51±0.02). Pholidosis of the material following VESELÝ & KÖHLER (2001) followed by the percentage of occurrence in parentheses: postmentals: 1 (100%); postnasals: 2 (83%), 1 (17%); prefrontals: 2 (100%); postloreal in contact with supralabial: Yes (100%); postcanthal in contact with prefrontal: No (100%); frontonasal in contact with frontal: No (100%); number of lowest secondary temporals in contact with lowest anterior temporal: 2 (67%), 1 (33%); dorsals at midbody: 18 (100%); ventrals at midbody: 12 (100%); transverse rows of dorsals: 50 (67%), 51 (33%); number of supralabials to mideye: 6 (100%); lamelle on fourth toe: 17 (50%), 18 (17%), 20

(33%); anterior sublabial in contact with: first infralabial (17%), second infralabial (66%), third infralabial (17%).

Mesaspis moreletii has been included in various checklists for Nicaragua (TIHEN, 1949; PETERS & DONOSO-BARROS, 1970; VILLA, 1983; VILLA et al., 1988; RUIZ, 1996; RUIZ & BUITRAGO, 2003). However, the presence of this species in Nicaragua has not been supported by any voucher specimens (KÖHLER, 2003) and therefore represents the first definite Nicaraguan record of this species. Also, its known range of altitudinal distribution is increased by almost 200 m – the species is now known to occur from 1305 to above 3000 m (KÖHLER, 2003).

Fig. 49. Adult male (left) and juvenile (right) of *Mesaspis moreletii* from the highlands of Cerro Kilambé.

Cnemidophorus lemniscatus (LINNAEUS, 1758)

On 22 May 2003, GP and OA collected two specimens of this species at the Playa de Barra de Cabo Viejo (14.9222º N, 83.2653º W, 3 m elevation), 1.5 km SE of La Aduana, Región Autónoma Atlántico Norte. Both specimens (UCA 566–67) were encountered active during the day while basking at ground level in the transitional area between sandy beach and mangrove forest, where a mixture of mangrove forest, sporadic low grass, and coastal debris was present. Although only two specimens were collected, approximately a dozen other *C. lemniscatus* were seen in the area.

UCA 567, an adult male (Fig. 50; snout-vent length 63 mm), has the following characteristics: tail length 130 mm; 4 supraoculars; 4 parietals; 7 supralabials; 7 infralabials; central gular scales not greatly enlarged; ventral scales large, in 8 transverse rows; enlarged scales on the dorsolateral surfaces of the upper arms; right hemipenis partially everted. Coloration in life: 4 longitudinal dark stripes on brown background on body; several yellow dots on lateral surfaces of body; green coloration on chin and anterior part of arms and legs. UCA 566, a juvenile (snout-vent length 32 mm), has the following characteristics: tail length 80 mm; 4 supraoculars; 4 parietals; 7 supralabials; 7 infralabials; central gular scales not greatly enlarged; ventral scales large, in 8 transverse rows; enlarged scales on the dorsolateral surfaces of the upper arms; 6 longitudinal dark stripes along body.

Cnemidophorus lemniscatus was known to occur both north and south of Nicaragua (KÖHLER, 2003), and it was expected to be found along the Atlantic coast of Nicaragua (SAVAGE, 2002: 517). As with *Kinosternon angustipons*, *C. lemniscatus* has been included in various checklists of Nicaraguan herpetofauna (VILLA, 1983; VILLA et al., 1988; RUIZ, 1996; RUIZ & BUITRAGO, 2003) but the presence of this species has not been supported by voucher specimens (KÖHLER, 2001, 2003). UCA 566–67 constitute the first definitive specimens of *C. lemniscatus* collected in Nicaragua, and represent a range extension of approximately 55 km SE of the nearest locality in Honduras and approximately 730 km NW of the nearest locality in Panama (KÖHLER, 2003; MCCRANIE et al., 2006).

Fig. 50. Adult male of *Cnemidophorus lemniscatus* from the Playa of Cabo Viejo. Photograph: O ARROLIGA.

Adelphicos quadrivirgatum JAN, 1862

On 21 June 2007, JS, JT, LW, ST, and LO collected a specimen of this semifossorial snake (SMF 87169) at Kulum Kitang (14.3292º N, 84.9375º W, 180 m elevation), Departamento de Jinotega. The snake was encountered at daytime underneath a rotten log (approximately 30 cm in diameter) in primary forest. Inside a larger log adjacent to the one containing the *Adelphicos quadrivirgatum*, I also found an adult specimen of the caecilian *Gymnopis multiplicata*.

SMF 87169 is a subadult male (Fig. 51; snout-vent length 215 mm) with the following characteristics: tail length 56 mm; single elongate loreal scale between postnasal and eye; 7 supralabials, third and fourth bordering the eye; 7 infralabials, first pair of infralabials in contact posterior to mental, second and third infralabials greatly reduced; anterior pair of chin shields greatly enlarged; dorsal scales in 15 rows throughout the body, smooth; 128 ventrals; 46 subcaudals; cloacal scute divided; hemipenes partially everted, small, unilobate, with spines on apex and folds on surface of truncus. Coloration in life: a broad brown middorsal stripe and four dark brown longitudinal stripes on pale brown background on body; head brown to dark brown; supralabials and chin pale yellow; ventrals pale yellow with occasional dark pigment on the exterior margins (almost exclusively near cloaca); paired subcaudals pale yellow with dark pigment on both inner and outer margins, so a midventral dark brown stripe is present in the subcaudal region.

SMF 87169 constitutes the first country record of *Adelphicos quadrivirgatum* for Nicaragua, and represents a range of extension of approximately 40 km S of the nearest locality in Honduras, and the southernmost record for this genus (MCCRANIE et al., 2006).

Fig. 51. Subadult male of *Adelphicos quadrivirgatum* from Kulum Kitang.

3 ZOOGEOGRAPHY OF THE HERPETOFAUNA OF NICARAGUA

3.1 INTRODUCTION

Biogeography is the discipline that describes distributional patterns of specific and supraspecific groups and attempts to explain how and when each taxon reached a determined area. The composition of the herpetofauna in Nicaragua is a product of the geologic and ecologic changes that have historically taken place in Earth's history since the origins of these groups. Through the documentation of the distribution of organisms in space and time, it is possible to determine patterns of coincident distributions of monophyletic groups and identify the historical source of each species (DUELLMAN & TRUEB, 1985). In order to comprehend Nicaragua's large biotic diversity, it is necessary to review the geologic and climatic history, dispersal routes, and vicariance processes that took place in a Central American context. SAVAGE (2002) masterfully discussed the composition, origins, history, and development of the herpetofauna in Central America and most of what follows is summarized from his work (SAVAGE, 1966, 1973b, 1982, 2002).

In the Permian (late Paleozoic), what we now recognize as continents formed a single supercontinent, Pangaea, which already held a distinct composition of amphibians and reptiles. Pangaea's constituent plates fragmented the supercontinent into a northern land mass, Laurasia, and a southern one, Godwanaland. This fragmentation was completed by the middle of the Jurassic epoch (about 160 Ma). Further land fragmentation led to the present pattern of continental units, each of them holding a distinct herpetofaunal composition. North and South America were separated by a wide proto-Caribbean seaway and their faunas evolved separately until the late Cretaceous, when an ancient Isthmian Link (the Proto-Antilles) connected the two continents for a period of 5–10 million years, enabling extensive faunal exchange between them. By the end of the Paleocene, some parts of this bridge fragmented and submerged as they slowly moved northeast, isolating again the now relatively homogeneous faunas of the tropical evergreen forests of North and South America.

By the end of the middle Eocene (about 38 Ma), the drifting Chortis block (Nicaragua forms the southern part of the Chortis block [COATES & OBANDO, 1996; ELMING & RAMUSSEN, 1997]) connected to the Maya block, where a herpetofauna proper of the area (the Middle

American Element) evolved. Also, emerging uplands in western North America and Mexico served as dispersal routes for several species from the north, which integrated with tropical taxa in Mexico and allowed differentiation of a Central American Component from the Old Northern Element. This Central American Component evolved in association with the Middle American Element from the Oligocene onward. The biotas from tropical Mesoamerica then were isolated in the Miocene from those in the north by a wide belt of semiarid to desert ecoregions caused by increasingly aridity as a product of the uplift of the Sierras Madre in Mexico.

The connection of the Chortis block to the Maya block also resulted in extensive volcanism from the Miocene through the Pliocene and probably caused the Pliocene uplift of the central mountains of northern Nicaragua. This mountain uplift caused a partial rain shadow along the Pacific versant of Nicaragua and subsequent replacement of evergreen vegetation by semiarid vegetation. Several general cooling and warming episodes occurred from then on that directly affected the faunal dispersal: cooling episodes allowed the dispersal of highland species through the lowlands, and warming episodes isolated species in the highlands, which acted as refuges and diversification centers between climatic cycles. Additionally, independent insular and peninsular effects served as centers of species differentiation and contributed to the evolution of the region's herpetofauna (SAVAGE, 1966).

The narrowing sea gap between North (with a Middle American and Old Northern Element faunas) and South America (with a South American Element fauna) resulted in the closure of the major constituent blocks of the Isthmian Portal in present day southern Nicaragua during the Pliocene (5.3 to 1.8 Ma; BOLAÑOS et al., 2008). Although the connection of these blocks was probably interrupted several times by oscillations in sea levels (GRAHAM, 1992), it was completed in two major steps and resulted in two pulses of dispersal events between the herpetofaunas of the two continents (SAVAGE, 2002). The dispersal events that took place posterior to the closure of the Isthmian Portal is known as "the great American biotic interchange" (STEHLI & WEBB, 1985) and continues to the present.

To summarize, four vicariance (V_{1-4}) and five dispersal (D_{1-5}) major events took place, leading to the present composition of the Mesoamerican herpetofauna (SAVAGE, 2002): (V_1) breakup of Pangea; (D_1) from South America across the Proto-Antillean Isthmus; (V_2) breakup of the Proto-Antillean Isthmus; (D_2) invasion and integration of Old Northern fauna with tropical herpetofauna; (V_3) introduction of an arid barrier between North American and

Mesoamerican species; (D_3) homogeneous population between Mesoamerican and the Central American units from the north; (V_4) uplift of Mesoamerican highlands; and ($D_{4\text{-}5}$) from South America after emergence of the Panamanian Isthmus, undergone in two pulses that occurred about 1 million years apart. Two more minor dispersal events that have also taken place are: (D_6) from the Caribbean Islands (e.g., genus *Diasporus* [HEDGES et al., 2008]; and (D_7) facilitated by humans in modern times (in Nicaragua *Hemidactylus frenatus* [VENCES et al., 1998] and *Lepidodactylus lugubris* [HENDERSON et al., 1976]).

Currently, Nicaragua's tourist slogan is "Nicaragua, land of lakes and volcanoes" (Nicaragua, tierra de lagos y volcanes), although the geography of the country presents several other peculiarities such as: it constitutes the middlemost country in mainland America; it is surrounded by seas both to the east and west; and most part of the country lies in lowlands (in contrast to its neighboring countries), with the exception of the north-central mountains and the isolated volcanoes along the Pacific coast. Although the highest altitude in Nicaragua is 2,107 m (Cerro Mogotón), only an insignificant portion of land exceeds 1500 m elevation. It is also the largest country in Central America, with a surface area of 130,373.47 km^2 (of which 10,033.93 km^2 are lakes; MARENA, 1999) and lies between latitudes 10º40' and 15º00'N and longitudes 82º30' and 87º40'W.

Nicaragua can de divided into nine forest formations (described in chapter 3.2) and five physiographic units (FENZL, 1989; MARSHALL, 2007): (1) interior highlands; (2) Atlantic coastal plain; (3) Nicaraguan depression; (4) Pacific coastal plain; and (5) Pacific volcanic chain. The interior highlands constitute the southern part of the Chortis block and are highly dissected by drainage networks and traversed by several major rivers that descend from the interior highlands mostly to the east. These rivers transport large volumes of sediment eroded from the uplifted interior that led to the formation of the low-relief alluvial plains on the Atlantic lowlands, occasionally disrupted by hills formed by Paleogene to Quaternary volcanic rocks (MARSHALL, 2007). Most of western Nicaragua lies in the Nicaraguan Depression, an approximately 50 km wide and 600 km long lowland area that extends along the length of the active volcanic front from El Salvador to northern Costa Rica. The Nicaraguan Depression constitutes the middle of the three great Central American depressions (the northern depression is located along the Isthmus of Tehuantepec, Mexico, and the southern depression is located in central Panama). The Nicaraguan Depression also separates Nuclear from Lower Central America and constitutes the remnant of the southernmost portion of the Chortis block, which was separated from the Chorotega block (northern portion of Lower Central America) previous to the closure of the Isthmian Portal by the Nicaragua-Limon Sea Corridor (SAVAGE, 2002) at the San Carlos basin (northern Costa Rica-southern Nicaragua; NORES, 2004). The Pacific coastal plain is a narrow portion of land situated west to the Nicaraguan Depression. Mostly composed of Tertiary marine sedimentary rocks (ELMING et al., 2001), it has a northwestward translation resulting from the oblique convergence of the Cocos and the Caribbean plates (TURNER et al., 2007). These plate dynamics resulted in the extension between the northeastern and the southwestern sides of the Nicaragua graben for the last 14–18 million years (MORGAN et al., 2008) and the area holds today the two biggest lakes in Central America (Lake Nicaragua and Lake Managua) and the Pacific volcanic chain. The Pacific volcanic chain resulted from Quaternary volcanism uplift (SAVAGE, 2002) and its volcanic activity continues today, as shown by the large amount of active volcanoes at present in Nicaragua (CARR et al., 2007). LEEDS (1974) documented 457 volcanic and seismic events in 453 years of Nicaraguan history (1520–1973). Some examples of this constant volcanic activity are (CRAWFORD, 1902a, b; MARSHALL, 2007): the eruption of Momotombo volcano in 1609, which resulted in the destruction of León Viejo (the first city built by the Spanish conquistadors on mainland America); the powerful explosion of Cosigüina volcano in 1835, recognized as one of the Western Hemisphere's most powerful historic eruptions; the Concepción volcano, one of Nicaragua's most active volcanoes with 25 eruptions recorded in the last 120 years; and the Cerro Negro volcano, which has erupted a significant volume of lava and pyroclastic material since the mid-1800s with the latest eruptions in 1992, 1995, and 1999 (DÍEZ et al., 2005). Many more volcanoes are currently active in Nicaragua and due to its geographical allocation, the Pacific section of the country has a great potential of suffering from future volcanic activity and associated earthquakes, tsunamis, and landslides (POLET & KANAMORI, 2000; FREUNDT et al., 2006; CAILLEAU et al., 2007; DEVOLI et al., 2007), and constitutes "the most magmatically robust section of the Central American arc" (MORGAN et al., 2008).

Although Nicaragua is located in the transitional area between Nuclear and Lower Central America, its herpetofauna is significantly lower in species richness and number of endemic species than that of neighboring Honduras and Costa Rica (SAVAGE, 2002; WILSON & MCCRANIE, 2003; present work). The dispersal of the major historical herpetofaunal units through Nicaragua occurred along three major general tracks (SAVAGE, 2002; KÖHLER, 2003): (1) species from semiarid to arid lowlands migrated south along the Pacific coast into northwestern Costa Rica; (2) highland species from Nuclear Central America dispersed southward to the Nicaraguan north central mountains; and (3) species from lowland evergreen forests, which reached Nicaragua when dispersed northward from northeastern Costa Rica, and also when dispersing southward from eastern Honduras. The climatic barrier in the lowlands of the Nicaraguan depression prevented faunal exchange between the highlands of northern Nicaragua and northern Costa Rica. Another climatic barrier on the Pacific versant of Costa Rica (northern Puntarenas) prevented the movement of most lowland species from Pacific Panama and southern Costa Rica northward into southwestern Nicaragua. A third barrier on the Atlantic versant of central-northern Honduras prevented the dispersal of several lowland species from the Atlantic versant of Nuclear Central America into northeastern Nicaragua. Finally, both the Pacific and the Atlantic Oceans served as effective terrestrial faunal dispersal barriers both to the east and west.

It is the purpose of this chapter to study the distributional range of each terrestrial species of amphibians and reptiles in all nine forest formations in Nicaragua, identify the historical origin of each species, analyze the herpetofaunal similarities among all forest formations, and compare my findings with known Central American dispersal routes. I also identify those species not recorded in Nicaragua with a greater potential to be found as research continues in the country and hypothesize those places with greater potential to hold endemic species.

3.2 MATERIALS AND METHODS

The primary database, consisting of a list of specimens of amphibians and reptiles recorded in Nicaragua, was derived from the specimens I collected (Appendix A) supplemented mostly by records cited in KÖHLER (2001: 185–205). I also examined the Nicaraguan specimens in the herpetological collection of the Forschungsinstitut und Naturmuseum Senckenberg, and supplemented this with records of localities from published data (mostly from the following sources): VILLA (1962, 1972a, 1983, 1984a); VILLA et al. (1988); RUIZ (1996); KÖHLER (2003); MCCRANIE & WILSON (2002); SAVAGE (2002); RUIZ & BUITRAGO (2003); and QUINTANA (2005). I mostly followed SAVAGE (2002) for allocating each species to a historical unit, although I consulted several other zoogeographic compilations, such as DUELLMAN (1966, 1990, 2001), SAVAGE (1966, 1973b, 1982), STUART (1966), VANZOLINI & HEYER (1985), WILSON & MCCRANIE (1998), and CAMPBELL (1999).

Based on the concept of life zones proposed by HOLDRIDGE (1967) and used by SAVAGE (2002) and WILSON & MCCRANIE (2003) in Costa Rica and Honduras, nine forest formations are found in Nicaragua (Fig. 52), as follows:

Lowland Wet Forest (LWF) is characterized by a high mean annual temperature (> 24ºC) and a very high mean annual precipitation (> 4,000 mm), which is seasonal and relatively evenly distributed throughout the year. This forest formation occurs on the Atlantic versant in extreme southeastern Nicaragua (< 600 m elevation).

Lowland Moist Forest (LMF) is characterized by a high mean annual temperature (> 24ºC) and a high mean annual precipitation (2,000–4,000 mm), which is seasonal and presents several months with very little rainfall. Commonly referred to as lowland rainforest, LMF occurs on the Atlantic versant of Nicaragua (< 600 m elevation) and represents the dominant formation in eastern Nicaragua.

Lowland Dry Forest (LDF) is characterized by a high mean annual temperature (> 24ºC) and a relatively low mean annual precipitation (1,000–2,000 mm), which is seasonal and presents several months with very little or no rainfall. Commonly referred as scrub forest, LDF occurs on the Pacific versant of Nicaragua (< 600 m elevation) and represents the dominant formation in western Nicaragua. This formation has undergone severe human alteration.

Lowland Arid Forest (LAF) is characterized by a high mean annual temperature (> 24ºC) and a low mean annual precipitation (< 1,000 mm), which is seasonal and presents several months with very little or no rainfall. Commonly referred as thorn forest, LAF is limited to lowland areas (< 600 m elevation) between the western part of the department of Nueva Segovia and the northeastern portion of the department of Managua, in lowlands surrounded by mountain masses where "mountain valley" and "rain shadow" effects from the prevailing eastern winds occur (WILSON & MCCRANIE, 1998). This formation has undergone severe human disturbance and lacks protected areas.

Premontane Wet Forest (PWF) is characterized by a relatively high mean annual temperature (18–24ºC) and a high mean annual precipitation (> 2000 mm), which is seasonal but distributed relatively evenly throughout the year. Sometimes referred to as transitional rainforest, PWF occurs at elevations from about 600 to 1,200 m, on the easternmost isolated mountains on the Atlantic versant that first receive the humid eastern prevailing winds.

Premontane Moist Forest (PMF) is characterized by a relatively high mean annual temperature (18–24ºC) and a relatively high mean annual precipitation (about 2,000 mm), which is seasonal and presents several months with very little rainfall. Commonly referred to as upland pine-oak forest, PMF occurs at elevations from about 600 to 1,200 m in the Nuclear Central American highlands of north-central Nicaragua, and on two isolated mountains on the Pacific versant (Volcán Mombacho and Volcán Maderas).

Premontane Dry Forest (PDF) is characterized by a relatively high mean annual temperature (18–24ºC) and a lower mean annual precipitation than found in Premontane Moist Forest (< 2,000 mm), which is seasonal and presents several months with very little or no rainfall. This formation occurs at elevations from about 600 to 1,200 m in isolated mountains on the Pacific versant of Nicaragua, except for Volcán Mombacho and Volcán Maderas.

Lower Montane Wet Forest (LMWF) is characterized by a relatively low mean annual temperature (< 18ºC) and a high mean annual precipitation (> 2,000 mm), which is distributed relatively evenly throughout the year. Often referred to as cloud forest, LMWF occurs at elevations from about 1,200 to 1,650 m on the few easternmost isolated mountains on the Atlantic versant.

Lower Montane Moist Forest (LMMF) is characterized by a relatively low mean annual temperature (< 18ºC) and a relatively high mean annual precipitation (< 2,000 mm), which is seasonal but distributed relatively evenly throughout the year. This formation occurs at elevations from about 1,200 to 2,100 m in the Nuclear Central American highlands of north-central Nicaragua, and on a few isolated mountains on the Pacific versant.

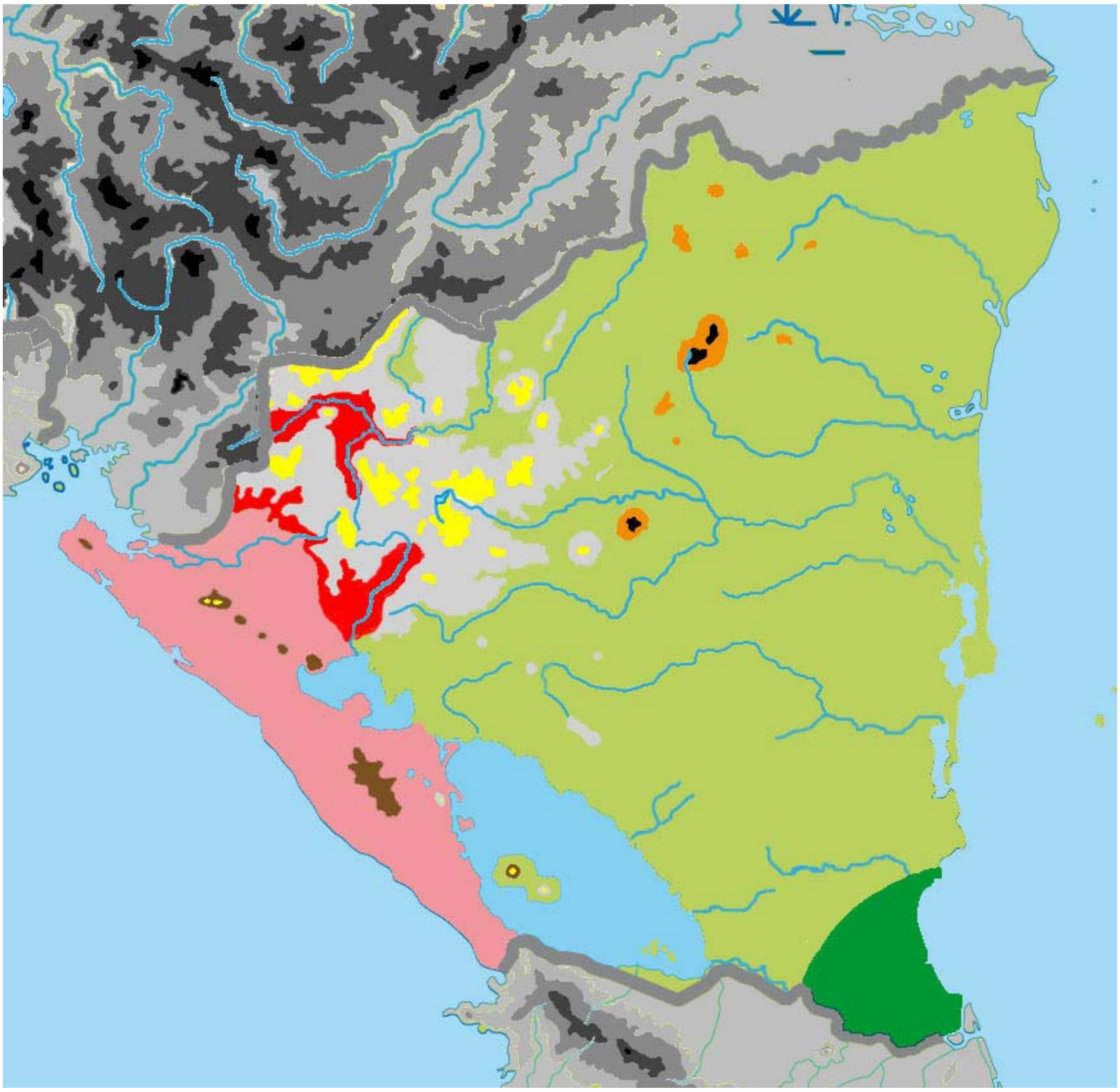


Fig. 52. Types of forest formations in Nicaragua: LWF (dark green); LMF (light green); LDF (pink); LAF (red); PWF (orange); PMF (gray); PDF (brown); LMWF (black); LMMF (yellow). See text for abbreviations.

In order to determine the similarities between the Nicaraguan forest formations, I used the Coefficient of Biogeographic Resemblance (CBR) algorithm (DUELLMAN, 1990). The formula for the CBR is: $CBR = 2C/(N_1 + N_2)$; where C is the number of species in common to two areas, N_1 is the number of species in the first area, and N_2 is the number of species in the second area. The CBR value produced is a decimal ≤ 1.0, indicating increasing biogeographic resemblance as the value approaches 1.0, and with 1.0 meaning the herpetofaunas being compared are identical in size and composition. In order to further analyze the forest formation relationships of the CBR algorithm, I placed each of the 238 terrestrial species of amphibians and reptiles in Nicaraguan into one of three distributional categories in each forest formation: widespread, peripheral, or restricted. These categories are exclusively based on museum material, and they should be viewed as an ephemeral effort that will soon be outdated as research continues in the country. I used the computer program "R" in order to calculate the CBR algorithm and create all figures with the exception of the dendrogram (Fig. 57), constructed with the computer program "BioPro."

3.3 RESULTS AND DISCUSSION

Of the total number of terrestrial species of herpetofauna found in Nicaragua, 131 (Table 8) occur in LWF (55.0%), 168 in LMF (70.6%), 84 in LDF (35.3%), 47 in LAF (19.7%), 59 in PWF (24.8%), 116 in PMF (48.7%), 51 in PDF (21.4%), 13 in LMWF (5.5%), and 50 in LMMF (21.0%). Sixty-two species of all amphibians and terrestrial reptiles (26.1%) are restricted to a single forest formation: 21 to LWF (8.8%), 15 to LMF (6.3%), four to LDF (1.7%), three to PWF (1.3%), 10 to PMF (4.2%), two to LMWF (0.8%), and seven to LMMF (2.9%). No species are restricted to LAF or PDF. The amount of amphibian and reptile species present in the different forest formations is shown in Fig. 53. No species is known to occur in all nine forest formations.

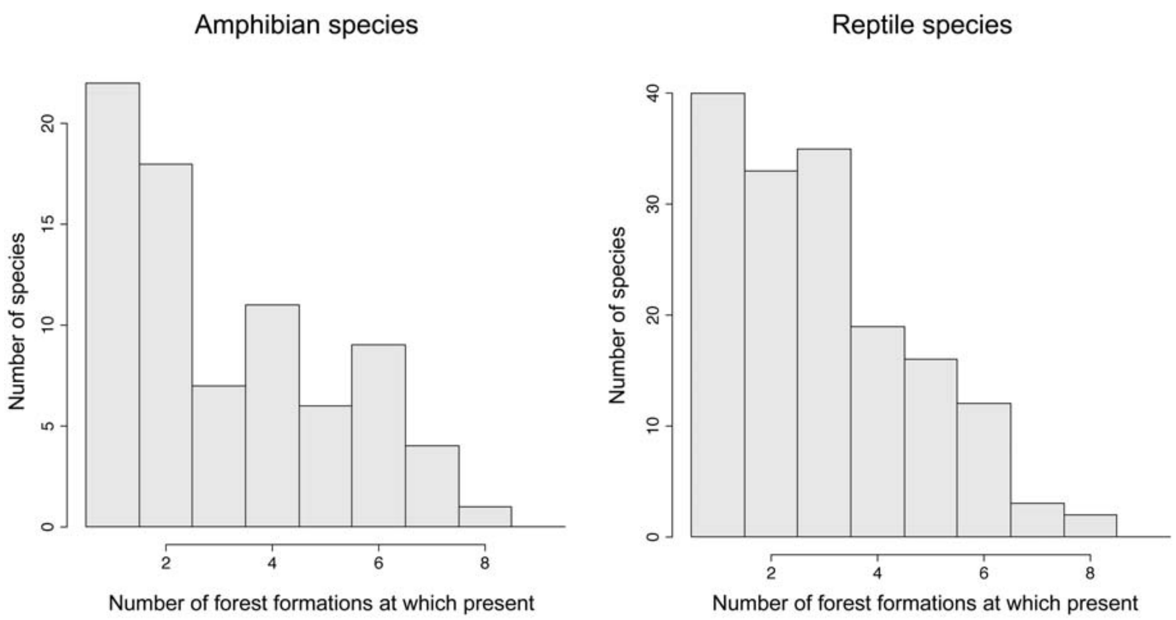


Fig. 53. Number of amphibian (left) and reptile (right) species shared by a different number of forest formations.

Fifty amphibian species (64.1% of the total amphibians) occur in LWF, 10 of which (12.8%) are restricted to this forest formation, 56 (71.8%) occur in LMF, four of which (5.1%) are restricted, 20 (25.6%) occur in LDF, with no species restricted, 10 (12.8%) occur in LAF, with no species restricted, 25 (32.1%) occur in PWF, three of which (3.8%) are restricted, 37 (47.3%) occur in PMF, two of which (2.6%) are restricted, 12 (15.4%) occur in PDF, with no species restricted, eight species (10.3%) occur in LMWF, one of which (1.3%) is restricted, and 25 species (32.1%) occur in LMMF, two of which (2.6%) are restricted (Table 8).

Eighty-one species of terrestrial reptiles (50.6% of the total terrestrial reptiles) occur in LWF, 11 of which (6.9%) are restricted to this forest formation, 112 (70.0%) occur in LMF, 11 of which (6.9%) are restricted, 64 (40.0%) occur in LDF, four of which (2.5%) are restricted, 37 (23.1%) occur in LAF, with no species restricted, 34 (21.3%) occur in PWF, with no species restricted, 79 (49.4%) occur in PMF, eight of which (5.0%) are restricted, 39 (24.4%) occur in PDF, with no species restricted, five (3.1%) occur in LMWF, one of which (0.6%) is restricted to this formation, and 25 (15.6%) occur in LMMF, five of which (3.1%) are restricted. (Table 8)

In Nicaragua, there is a greater contribution of reptile than amphibian species to the total herpetofauna present in each forest formation (Fig. 54). This imbalance is less evident in a few humid forest formations such as LMWF and LMMF where the number of amphibian species is higher or equals that of reptile species, respectively. This could be a result of the limited sampling efforts undertaken in these two forest formations; amphibians are in general more quickly spotted because of their vocalizations, whereas a considerable number of reptile species have a secretive existence and, therefore, are collected after substantial sampling efforts. In general, the amount of reptiles present in most forest formations is double the amount of amphibian species and this relation increases up to triple the amount in drier forest formations (see Fig. 54). This information could be of relevance to estimate the total herpetofaunal richness in quick ecological surveys when time and sampling efforts are limited.

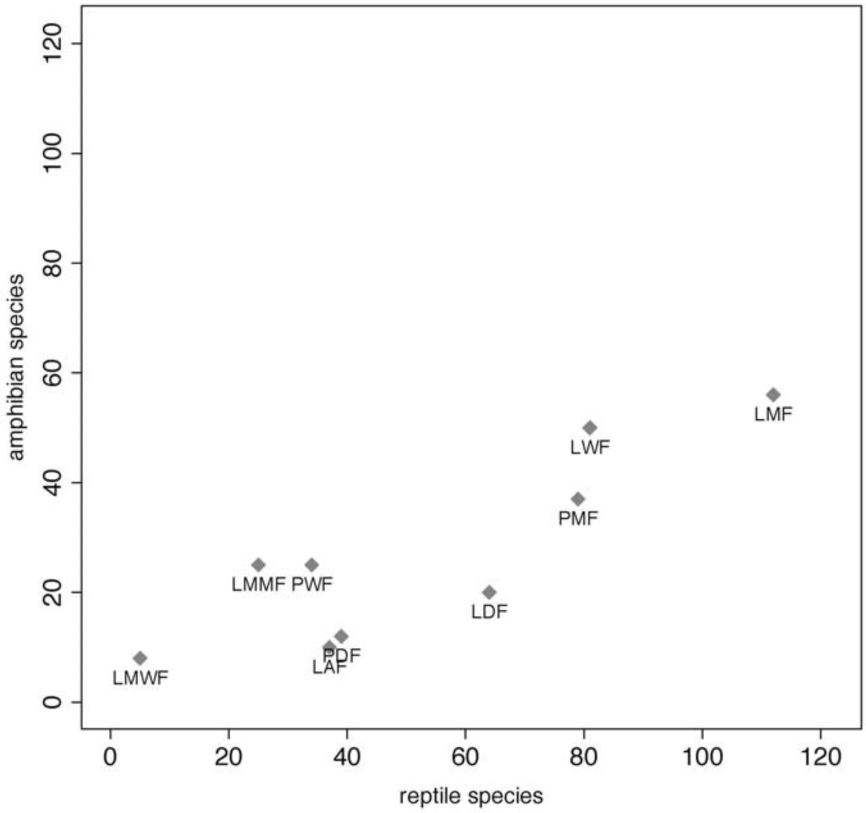


Fig. 54. Proportion of amphibian and reptile species in each forest formation.

The Middle American Element (MA) is the most representative historical unit of the herpetofauna of Nicaragua in both number of genera and species (Fig. 55). Nevertheless, the greater number of genera of amphibians derives from the South American Element (SA) and the greater number of genera of reptiles derives from the Old Northern Element (ON). The total amount of species has in general a MA dominance and varies between amphibians and reptiles, with and a greater SA influence in the former and greater ON influence in the latter. This imbalance is caused mostly by the two most diverse groups: snake species (number of species: ON>MA>>>SA); and anuran species (MA≥SA>>ON). The great diversity of snakes is outstanding in comparison to the rest of groups, with double the amount of genera and between one-third and one-half more species than the second and third most diverse groups, anurans and lizards, respectively. Lizards are the third most diverse group and present a relative large proportion of MA species (MA>>ON=SA), mostly due to the great diversity in the genus *Anolis*, with 15 species (30% of lizards in Nicaragua). The four least diverse groups, caecilians, salamanders, crocodiles, and turtles, derive in general from a single historical unit (see Fig. 55).

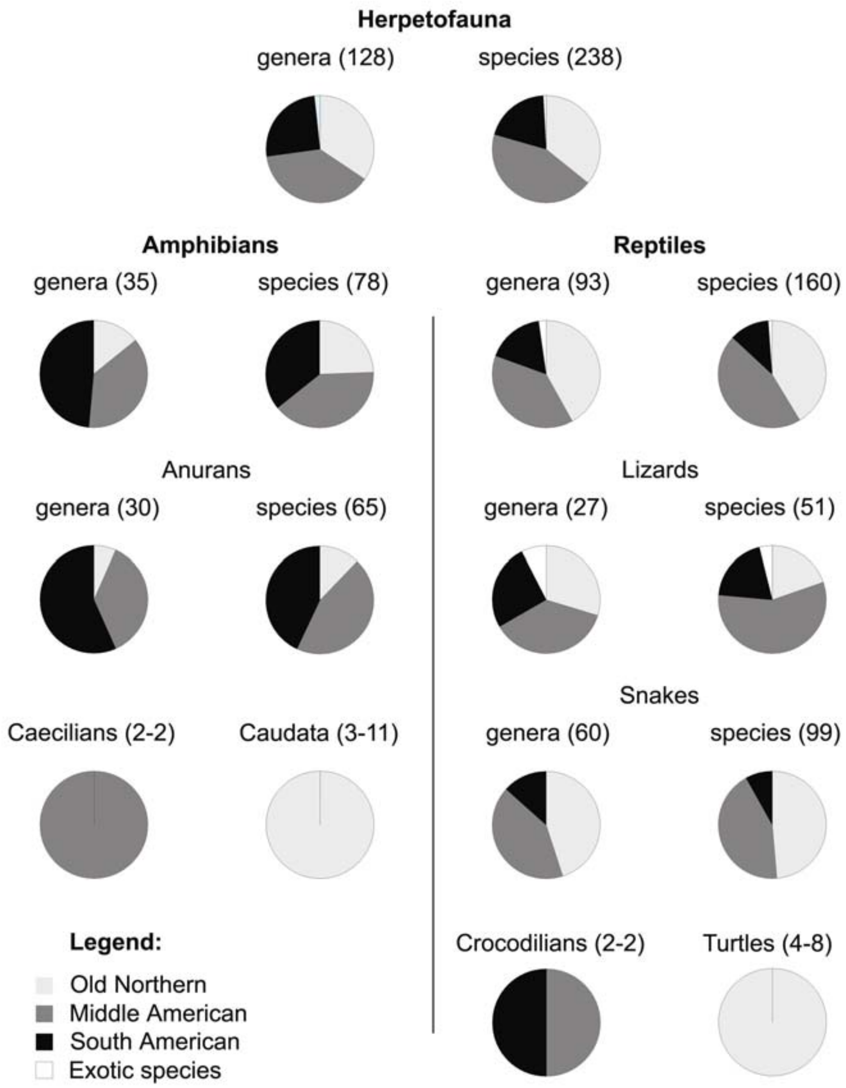


Fig. 55. Proportion of amphibian and reptile genera and species from the different historical units in Nicaragua. Numbers in parentheses indicate number of genera, species, or genera-species.

Table 6 presents the number of species in each forest formation, the number of species that are in common between the different forest formations, and the CBR values for the total herpetofauna, amphibians, and reptiles. A multidimensional scaling of the herpetofauna in the forest formations (Fig. 56) shows a distinct composition both in amphibians and reptiles in LMWF, and in reptiles in LMMF. Additionally, the composition of the herpetofauna in the

Pacific versant (LAF, LDF, and PDF) is more related to that in LMF and PMF (central part of the country) than to that in LWF and PWF (Atlantic versant). A cladogram based on these same data (Fig. 57) shows the percentage of similarity among clusters. Aside from the already mentioned distinctiveness of mostly the LMWF, two distinct groups are evident: the Pacific versant and the rest of the country.

Table 6. Occurrence of species of amphibians and reptiles in the different forest formations in Nicaragua. In each cell in the matrix, the top number pertains to the number of species of terrestrial herpetofauna, the middle number to the number of amphibian species, and the bottom number to the number of reptile species. The number of species at each forest formation is shown in boldface in the column cell, the number of species that are in common to two forest formations is in the lower left, and the coefficient of biogeographic resemblance is in italics in the upper right.

	LWF	LMF	LDF	LAF	PWF	PMF	PDF	LMWF	LMMF
LWF	**131**	*0.74*	*0.33*	*0.21*	*0.45*	*0.48*	*0.24*	*0.11*	*0.30*
	50	*0.75*	*0.31*	*0.20*	*0.43*	*0.53*	*0.19*	*0.17*	*0.40*
	81	*0.73*	*0.34*	*0.22*	*0.47*	*0.45*	*0.27*	*0.07*	*0.23*
LMF	110	**168**	*0.52*	*0.33*	*0.47*	*0.65*	*0.38*	*0.11*	*0.34*
	40	**56**	*0.47*	*0.30*	*0.49*	*0.71*	*0.29*	*0.22*	*0.52*
	70	**112**	*0.55*	*0.35*	*0.45*	*0.62*	*0.42*	*0.05*	*0.23*
LDF	36	66	**84**	*0.72*	*0.20*	*0.52*	*0.70*	*0.02*	*0.28*
	11	18	**20**	*0.67*	*0.22*	*0.53*	*0.75*	*0.07*	*0.49*
	25	48	**64**	*0.73*	*0.18*	*0.52*	*0.68*	*0.00*	*0.18*
LAF	19	36	47	**47**	*0.11*	*0.43*	*0.63*	*0.00*	*0.23*
	6	10	10	**10**	*0.11*	*0.43*	*0.73*	*0.00*	*0.34*
	13	26	37	**37**	*0.11*	*0.43*	*0.61*	*0.00*	*0.16*
PWF	43	53	14	6	**59**	*0.48*	*0.22*	*0.28*	*0.40*
	16	20	5	2	**25**	*0.58*	*0.16*	*0.42*	*0.56*
	27	33	9	4	**34**	*0.42*	*0.25*	*0.15*	*0.27*
PMF	59	92	52	35	42	**116**	*0.49*	*0.14*	*0.47*
	23	33	15	10	18	**37**	*0.41*	*0.27*	*0.65*
	36	59	37	25	24	**79**	*0.53*	*0.07*	*0.37*
PDF	22	42	47	31	12	41	**51**	*0.03*	*0.30*
	6	10	12	8	3	10	**12**	*0.10*	*0.38*
	16	32	35	23	9	31	**39**	*0.00*	*0.25*
LMWF	8	10	1	0	10	9	1	**13**	*0.29*
	5	7	1	0	7	6	1	**8**	*0.30*
	3	3	0	0	3	3	0	**5**	*0.27*
LMMF	27	37	19	11	22	39	15	9	**50**
	15	21	11	6	14	20	7	5	**25**
	12	16	8	5	8	19	8	4	**25**

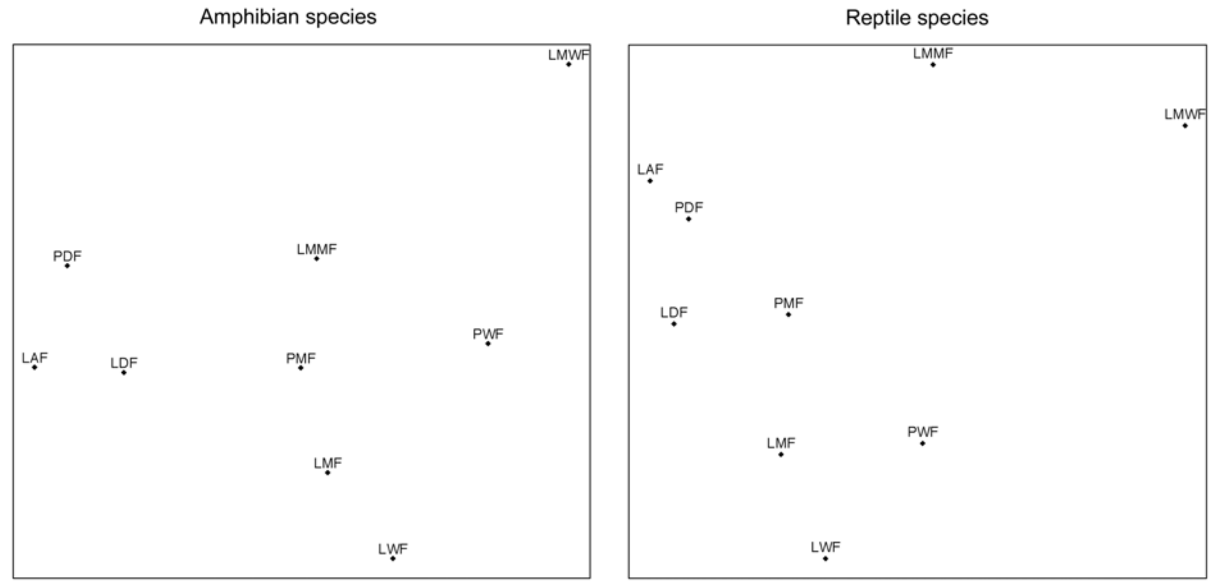


Fig. 56. Multidimensional scaling of the composition of amhibian (left) and reptile (right) species in the forest formations in Nicaragua.

Fig. 58 shows the relative proportion of different historical unit species in each forest formation for the total herpetofauna, amphibians, and reptiles, and visually compares both CBR similarity values (a-c) with the clustering (d-e) derived from Fig. 57.

Fig. 58 (a-c) shows in general greater similarity between adjacent forest formations. There is a variable transitional area between different ecological zones. Additionally, those forest formations with a relative large area in Nicaragua (e.g., LMF, LDF, LAF, PMF, LMMF) each could be subdivided into two or more subcategories when taking in account several other ecological factors, such as soil, humidity, predominant vegetation, human intervention, etc. The area around eastern Lake Managua and northeastern Lake Nicaragua is very complex and understudied. This area traditionally has been considered as a dry forest formation (e.g., Stuart, 1966; Wilson & McCranie, 1998; Campbell, 1999) and although the annual precipitation is under 2000 mm, I tentatively considered this area as LMF. Here, three of the four lowland forest formations present in the country meet (i.e., LMF, LDF, and LAF) and species typical from arid environments (e.g., *Phyllodactylus tuberculosus, Ctenosaura quinquecarinata, Crisantophis nevermanni, Scolecophis atrocinctus, Crotalus simus*; Köhler, 2001) have been recorded together with species typical from wet environments [e.g., *Dendrobates pumilio*, *Lithobates taylori, Lithobates warszewitschii*, *Anolis carpenteri*, *Lachesis stenophrys*; Villa, 1972a, 1984; Köhler, 2001; and specimens deposited at the herpetological collection of the Forschungsinstitut und Naturmuseum Senckenberg]. I have similarly considered all of the lowlands of Ometepe Island as LMF, although the precipitation on the southern portion is substantially higher than on the northern portion of the island (MARENA, 2007).

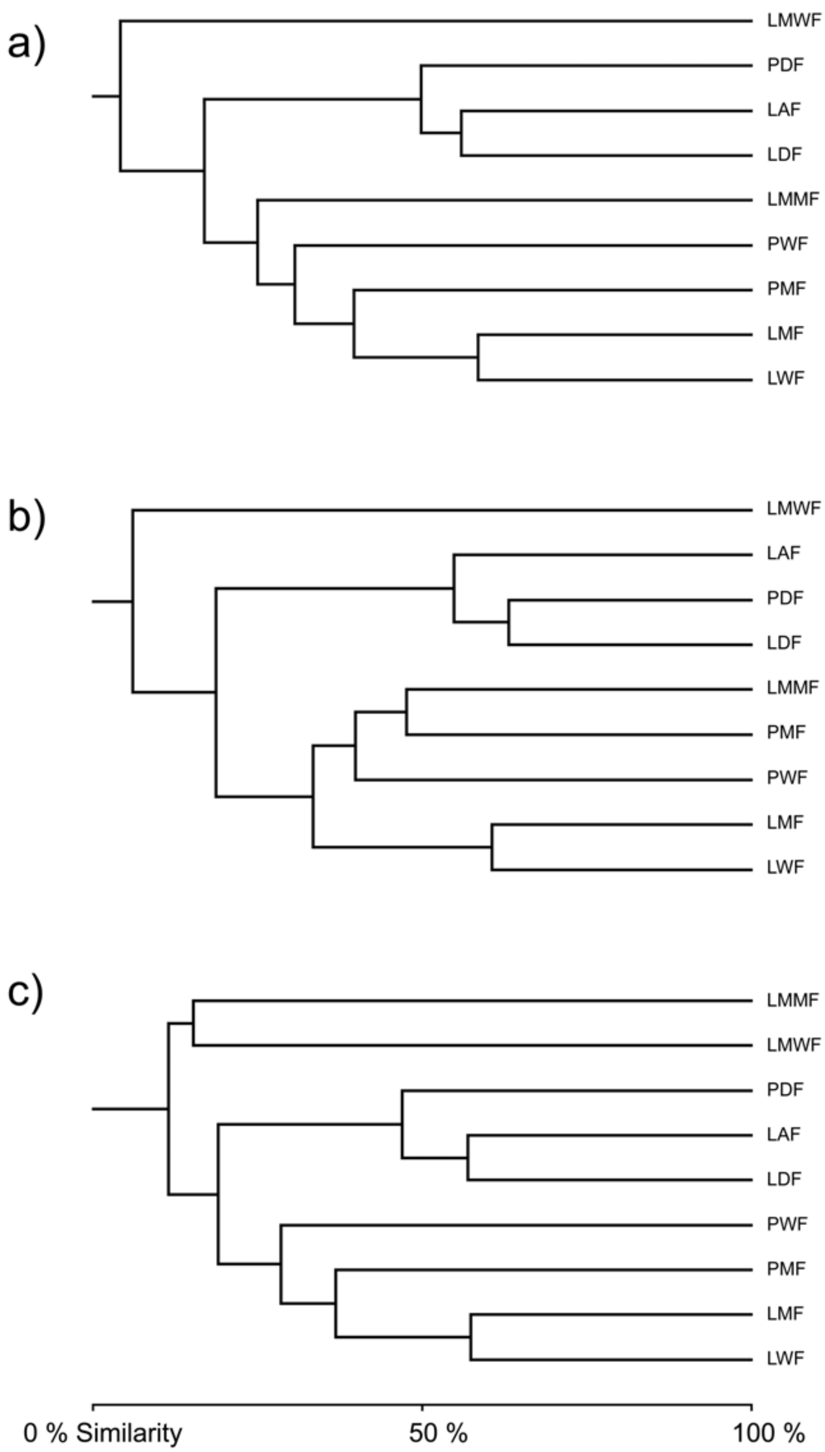


Fig. 57. Cladogram showing the percentage of similarity between forest formations in Nicaragua of: (a) herpetofaunal species; (b) amphibians species; and (c) reptiles species.

Fig. 58 (d-f) is the result of clustering pairs of forest formations obtained from the dendrogram. Distinct groups between the forest formations in Pacific Nicaragua and those in central and eastern Nicaragua (the latter two with a greater similarity between them in species composition than with those in the Pacific) are evident. The similarities in the composition of the reptiles seem to be relatively distinct on an elevation factor, whereas in amphibians similarities might be better explained in correlation with humidity.

The relative composition of the species with different historical units shows in general a greater contribution of species with a SA origin in LWF (southeastern Nicaragua), with a slight decrease toward northeastern Nicaragua (see discussion below), and a single exception in the amphibian composition in LAF with 50% of species from the SA historical unit (Fig. 58a-c). Also, there are no amphibian members of ON origin in PDF. In Nicaragua, the amphibians with an ON origin are all salamanders (present only in moist environments) and frog of the families Ranidae and Rhinophrynidae (which mostly need water bodies to reproduce). Both constant high levels of moist and water bodies are almost absent in PDF. All reptiles in LMWF are of MA origin. This area has a combination of a high proportion of endemic fauna (discussed later) and a low amount of total species recorded. The latter probably results from the small amount of data from this forest formation resulting from the few studies undertaken there where the only available data from this forest formation come from Cerro Saslaya (KÖHLER, 2001; QUINTANA, 2005), supplemented with a few records from Cerro Toro and Cerro Musún.

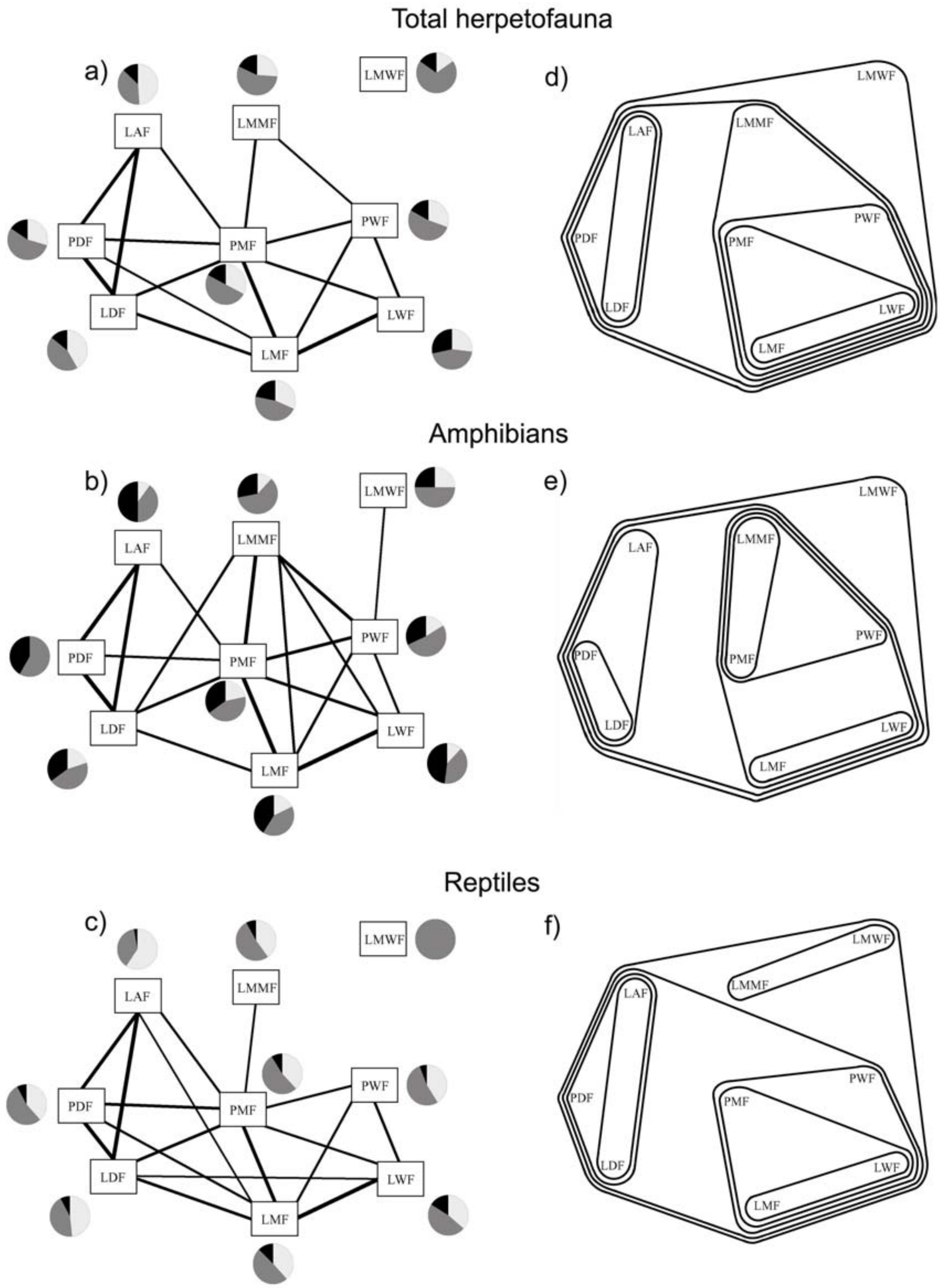


Fig. 58. Comparison of the CBR similarity values (a-c) and the clustering from the cladogram (d-f) between forest formations for the total herpetofauna (a, d), amphibian (b, e), and reptile (c, f) species from Nicaragua. In (a-c), I only draw those CBR with similarities values greater than the total average of each group and the width of the connecting line is proportional to the CBR values between each forest formation (wider lines for greater similarity indices), and include the relative proportions of species from the different historical units in each forest formation in Nicaragua. See Fig. 55 for color legend of in the cake graphics.

There is a greater composition of South American groups in eastern Panama, with a decreasing tendency towards north (SAVAGE, 2002). This species diversity decreases along a south to north gradient. There are important climatic barriers in the northward dispersal around the northern portion of the Puntarenas province (Pacific lowlands species), in the Nicaraguan Depression (highland species), and in the northern part of central-eastern Honduras (Atlantic lowlands species), where the reduction of genera of South American elements decrease by over two-thirds from southwestern to northwestern Costa Rica (SAVAGE, 2002), and in more than 60 species from all historical units in central-eastern Honduras (MCCRANIE et al., 2006; MCCRANIE & CASTAÑEDA, 2007).

The Nicaraguan lowlands have acted as a bottleneck in the routes of the mainland American species dispersal and historically have been the meeting ground of several herpetofaunal units. Several taxa have their northern (especially in the Atlantic lowlands) or southern (especially in the north-central mountains) limit of distribution in Nicaragua (Table 7), as follows: (1) In the Atlantic lowlands of Nicaragua, there is a considerable number of species with a northern distributional limit in a general south to north pattern of species reduction. The number of species with a southern distributional limit in the same area is considerably smaller and do not present such a gradual north to south reduction (see Table 7). Only two species (*Incilius valliceps* and *Coniophanes bipunctatus*) currently known from the Atlantic side of southern Nicaragua have their southern distributional limit here or slightly more southern; (2) WILSON & MCCRANIE (1998) analyzed the biogeography of the herpetofauna of the subhumid forests of Middle America and demonstrated great similarity between the composition on the Pacific lowlands of Nicaragua and that on the Pacific lowlands of Honduras, El Salvador, Guatemala, and northwestern Costa Rica. This homogeneous composition is also shown in Table 7, where very few taxa have their distributional limit somewhere on the Pacific side of Nicaragua; and (3) the central northern mountains of Nicaragua constitute the southern distributional limit of several highland species and the northernmost distribution of a single species, *Tantilla alticola* (see Table 7).

Table 7. Species of amphibians and reptiles with their distributional limit along Nicaragua.

	Northern limit of distribution	Southern limit of distribution
Atlantic lowlands		
Northern portion	*Incilius coniferus, Craugastor bransfordii, Oophaga pumilio, Diploglossus bilobatus, Anolis carpenteri, Drymobius rhombifer, Leptophis depressirostris, Sibon annulatus*, and *Micrurus multifasciatus*	*Craugastor lauraster, Lithobates brownorum, Laemanctus longipes, Adelphicos quadrivirgatum*, and *Tantillita lintoni*
Southern portion	*Oedipina collaris, Craugastor ranoides, Craugastor talamancae, Dendrobates auratus, Hypsiboas rufitelus, Scinax elaeochroa, Gastrophryne pictiventris, Lithobates taylori, Dendropsophus phlebodes*, and *Lachesis stenophrys*	
Extreme southern portion	*Allobates talamancae, Incilius melanochlorus, Centrolene ilex, Phyllobates lugubris, Smilisca puma, Kinosternon angustipons, Diploglossus monotropis, Lepidoblepharis xanthostigma, Sphaerodactylus homolepis, Ameiva quadrilineata, Ungaliophis panamensis, Amastridium veliferum, Dipsas articulata, Tantilla reticulata, Tantilla ruficeps*, and *Tantilla supracincta*	
Pacific lowlands		
Northern portion	*Ctenosaura quinquecarinata*	*Anolis sericeus* "bilobed"
Southern portion	*Basiliscus basiliscus*	*Dermophis mexicanus*
Higlands		
Central-northern mountains	*Tantilla alticola*	*Ptychohyla hypomykter, Lithobates maculatus, Mesaspis moreletii, Anolis tropidonotus, Ungaliophis continentalis, Mastigodryas dorsalis, Rhadinaea kinkelini*, and *Tantilla taeniata*
Pacific volcanic chain		*Craugastor laevissimus* and *Celestus bivittatus*

The gradual reduction of the number of species from south to north in the Atlantic lowlands is probably best explained by ecological differences (the annual rainfall amount in extreme southeastern Nicaragua is three times higher than in extreme northeastern Nicaragua) rather than by recent colonization of the area (the species reduction involve species from all three historical units). In addition, the Atlantic lowlands between eastern Honduras and eastern Panama are continuous, with no other geographical barrier than rivers. Nevertheless, the dispersal ability of each species varies greatly. A radical example of fast colonization in Nicaragua constitutes the recently introduced *Hemidactylus frenatus*; it is the only gecko in the lowlands of the Pacific versant of Nicaragua that emits vocalizations and, therefore, is easily recognized by the citizens who date the first appearance of this species in the country during the 1980´s. Nevertheless, this species was not included in Nicaragua by VILLA et al. (1988) or RUIZ (1996) and was first recorded in the country in Corinto (VENCES et al., 1998), the most important harbor on the Pacific coast of Nicaragua. KÖHLER (1999b, 2001) added two additional localities and RUIZ & BUITRAGO (2003) record the species as "widely distributed throughout the country". Today, and only one decade after its confirmed presence, this species is most probably present everywhere in the country where there is electrical power (pers. obs.). Paradoxically, and because it mostly inhabits human settlements, this gecko is probably the reptile species most commonly known by all Nicaraguan citizens (who erroneously think it is venomous).

Based on the distributional patterns of the herpetofauna in neighboring Costa Rica, Honduras, and El Salvador (WILSON & MEYER, 1985; SAVAGE, 2002; MCCRANIE & WILSON, 2002; KÖHLER, 2003; CAMPBELL & LAMAR, 2004; SOLÓRZANO, 2004; KÖHLER et al., 2006; MCCRANIE et al., 2006; AMPHIBIAWEB, 2008), it is possible to identify species of amphibians and reptiles not reported from Nicaragua that occur relatively close to both the northern and southern political border. Aside from the two genera (*Duellmanohyla* and *Isthmohyla*) and five species (*Anotheca spinosa*, *Rhadinaea godmani*, *Rhinobothryum bovallii, Urotheca decipiens,* and *Cerrophidion godmani*) that occur both north and south of Nicaragua and taking in account the general dispersal routes of the herpetofauna through Central America, some species could have a higher probability than others to be found in Nicaragua as research continues, including: (1) southeastern Nicaragua (i.e., *Bolitoglossa alvaradoi*, *B. colonnea*, *Oedipina gracilis, Hyalinobatrachium colymbiphyllum*, *H. valerioi*, *Craugastor gollmeri, Silverstoneia flotator*, *Leptodactylus poecilochilus*, *Pristimantis altae*, *P. caryophyllaceus, P. cruentus, Anolis frenata, Celestus hylaius, Leposoma southi, Ptychoglossus plicatus,* *Chironius exoletus, Trimetopon pliolepis, Urotheca pachyura*); (2) northeastern Nicaragua (i.e., *Bolitoglossa mexicana, Oedipina quadra, Hyalinobatrachium cardiacalyptum, Chelydra rossignonii, Scaphiodontophis annulatus, Sibon manzanaresi, S. miskitus, Coniophanis imperialis*); (3) northwestern Nicaragua (i.e., *Anolis serranoi, Ctenosaura flavidorsalis, Sphenomorphus assatus, Sibon carri*); (4) southwestern Nicaragua (i.e., *Epicrates cenchria*); (5) highlands of northern Nicaragua (i.e., *Oedipina taylori, Plectrohyla guatemalensis, Ptychohyla salvadorensis, Aspidoscelis motaguae, Storeria dekayi, Tantilla lempira, Tropidodipsas fischeri*); (6) highlands of southern Nicaragua (i.e., *Bothriechis lateralis*); (7) Caribbean (i.e., *Aristelliger georgensis*); and (8) in different places in the country from exotic origin (e.g., *Hemidactylus* spp., *Ctenonotus cristatellus, Rhamphotyphlops braminus*).

There are 16 endemic species (12 amphibians, 4 reptiles) in Nicaragua. Fifteen of these species are exclusively found in a single major area in Nicaragua, more commonly in the highlands than in the lowlands (DUELLMAN, 1966): highlands of northeastern Nicaragua (*Nototriton saslaya, Oedipina* sp. "Musún," *Oedipina* sp. "Saslaya," *Plectrohyla* sp. "Saslaya," and *Rhadinaea rogerromani*); highlands of north-central Nicaragua (*Oedipina* sp. "Datanlí," *O.* sp. "Kilambé," and *Geophis dunni*); highlands of the Pacific volcanic chain (*Bolitoglossa insularis* and *B. mombachoensis*); Caribbean islands (*Lithobates miadis* and *Anolis villai*); southern Atlantic lowlands (*Bolitoglossa indio* and *Craugastor chingopetaca*); and northern Atlantic lowlands (*Ptychohyla* sp. "Bosawas"). One species, *Anolis wermuthi*, is found both in the highlands of central northern and eastern Nicaragua. All three lowland Atlantic endemic species likely are to be found in the nearby areas of Costa Rica or Honduras, respectively. The Pacific lowlands is the only major area in Nicaragua without any endemic species.

The highlands of Cerro Saslaya and adjacent Cerro El Toro in northeastern Nicaragua is the place with a greater amount of endemism in the entire country, with five endemic species (31% of total Nicaraguan endemic species), four of which are exclusive to this area. These mountains have the following combination of characteristics: geologically relatively old (Mesozoic formation; ELMING et al. 2001); relatively high elevations (around 1650 m); and isolated from nearby mountains by lowlands. Several other mountains in northern Nicaragua present similar characteristics (i.e., Cerro Kilambé [1755 m], Peñas Blancas [1744 m], Tepesomoto [1730 m], Cerro Tisey [1549 m], Cerro Musún [1438 m], Cerro Quirragua [1338 m]), although, in most cases, they are of different geological origins (see ELMING et al. 2001) and are not completely isolated by lowlands from each other (those that are well isolated by lowlands generally do not exceed 1300 m). The place that can potentially hold a greater amount of endemic species is probably the highlands of the Reserva Natural Dipilto y Jalapa and adjacent mountains to the east, in extreme northern Nicaragua. Some portions of these mountains constitute the geologically oldest part of Nicaragua, dating back to the Paleozoic (ELMING et al., 2001). This region constitutes also the highest part of the country (the only portion in Nicaragua with elevations over 1750 m). Due to the presence of unremoved land mines, human intervention is presumed to be minimal.

The Pacific vocanic chain has a low number of endemic species and presents the following characteristics: they are in general geologically young (<0.6 Ma; CARR et al., 2007); many volcanoes are still active; there is a general absence of permanent rivers; and human intervention has devastated most of the original forests in the area. Several of the higer volcanoes lack vegetation at high altitudes due to current volcaninc ativity (e.g., San Cristóbal [1745 m], Concepción [1610 m], Momotombo [1279 m]). Volcanoes Maderas (1394 m) and Mombacho (1350 m) are the only two volcanoes in the Pacific volcanic chain with a combination of elevations greater than 1200 m and original forests in their higher portions. Each of these volcanoes has an endemic species of *Bolitoglossa* and I have additionally seen a picture of an uncollected black salamander (genus *Bolitoglossa*) from Volcán Mombacho that most probably constitues an undescribed species. Two more volcanoes from the drier Reserva Natural Complejo Volcánico Cristóbal-Casita have a combination of remaining forests patches and relatively high elevations: Volcán Casita (1405 m), with forest mostly at premontane altitudes and the latest eruption dating from the early 16th century; and Volcán El Chonco (1105 m), dormant for the past several thousand years (HAZLETT, 1987).

There are several small keys in the Nicaraguan Carribean Sea, although there are only two larger islands: Great and Little Corn Island. Aside from the several subspecies that are regonized from these islands (see Table 1), each one of them has one endemic species. These islands were formerly part of the Nicaraguan mainland from which they fragmented (VILLA, 1993) and, therefore, the Corn Islands (and to a smaller degree also Ometepe Island) seem like an excellent place to study vicariant processes.

Table 8. Distribution of Nicaraguan amphibian and reptilian species by Historical units, ecological formations and known elevation. Abbreviations are: LWF = Lowland Wet Forest; LMF = Lowland Moist Forest; LDF = Lowland Dry Forest; LAF = Lowland Arid Forest; PWF = Premontane Wet Forest; PMF = Premontane Moist Forest; PDF = Premontane Dry Forest; LMWF = Lower Montane Wet Forest; LMMF = Lower Montane Moist Forest; MA = Middle American Element; ON = Old Northern Element; SA = South American Element; W = widespread in formation; R = restricted to formation; and P = peripherally distributed in formation. Elevational ranges beginning with 0 meant to convey about sea level.

Species	Historical unit	LWF	LMF	LDF	LAF	PWF	PMF	PDF	LMWF	LMMF	Total	Elevational Range (m)
AMPHIBIA												
GYMNOPHIONA												
Caeciliidae												
Dermophis mexicanus	MA			P				W			2	10–960
Gymnopis multiplicata	MA	W	W								2	20–450
CAUDATA												
Plethodontidae												
Bolitoglossa indio	ON	R									1	20
Bolitoglossa insularis	ON						R				1	800
Bolitoglossa mombachoensis	ON						R				1	1100–1230
Bolitoglossa striatula	ON	W	W	P			P				4	10–770
Nototriton saslaya	ON								R		1	1280–1500
Oedipina collaris	ON		R								1	120
Oedipina cyclocauda	ON	R									1	40
Oedipina sp. “Datanlí”	ON									R	1	1230
Oedipina sp. “Kilambé”	ON									R	1	1360–1490
Oedipina sp. “Musún”	ON					R					1	620
Oedipina sp. “Saslaya”	ON					R					1	600–950
ANURA												
Aromobatidae												
Allobates talamancae	SA	R									1	20–420
Bufonidae												
Incilius coccifer	MA		P	W	W		W	P		P	6	0–1350
Incilius coniferus	MA	W	P				P			P	4	20–1510
Incilius luetkenii	MA		P	W	W		P	P			5	0–1200
Incilius melanochlorus	MA	R									1	20–400
Incilius valliceps	MA	W	W	P	P	W	W			W	7	20–1270
Rhaebo haematiticus	SA	W	W			P					3	20–720
Rhinella marina	SA	W	W	W	W	P	W	W		W	8	0–1400
Centrolenidae												
Centrolene ilex	SA	R									1	30
Centrolene prosoblepon	SA	W	P			P				P	4	20–1400
Cochranella albomaculata	SA	W	P								2	70–400
Cochranella granulosa	SA		P			W	P				3	200–1100
Cochranella pulverata	SA	P	P				P				3	150–960
Cochranella spinosa	SA	W	P								2	20–280

Hyalinobatrachium fleischmanni	SA		P			W	P			P	4	260–1360
Craugastoridae												
Craugastor bransfordii	MA	W	W			W	P		P	P	6	20–1440
Craugastor chingopetaca	MA	R									1	40–280
Craugastor fitzingeri	MA	W	W	P		W				P	5	20–1360
Craugastor laevissimus	MA		P	P		P	P	P	P	P	7	450–1360
Craugastor lauraster	MA					W	P				2	940–1250
Craugastor megacephalus	MA	W	P			W	P				4	30–1230
Craugastor mimus	MA	W	P			W	P		P	P	6	40–1330
Craugastor noblei	MA	W	P			W	P			P	5	30–1330
Craugastor ranoides	MA	P	P								2	40
Craugastor talamancae	MA	P	P								2	60–420
Dendrobatidae												
Dendrobates auratus	SA	R									1	10–280
Oophaga pumilio	SA	W	P			P	P				4	10–960
Phyllobates lugubris	SA	R									1	30–420
Eleutherodactylidae												
Diasporus diastema	MA	W	W			W	P		W	P	6	20–1410
Hylidae												
Agalychnis callidryas	MA	P	W	P		P	W	P		W	7	10–1325
Agalychnis saltator	MA		R								1	180–300
Cruziohyla calcarifer	MA	R									1	20
Dendropsophus ebraccatus	SA	P	W				P			P	4	30–1350
Dendropsophus microcephalus	SA	P	W	W			W			P	5	40–1300
Dendropsophus phlebodes	SA	W	P								2	20–50
Ecnomiohyla miliaria	SA	R									1	20
Hypsiboas rufitelus	SA	W	P								2	20–420
Plectrohyla sp. “Saslaya”	MA					R					1	800
Ptychohyla hypomykter	MA					P	P			P	3	720–1480
Ptychohyla sp. “Bosawas”	MA		R								1	180
Scinax boulengeri	SA	W	W								2	20–330
Scinax elaeochroa	SA	W	P								2	20–30
Scinax staufferi	SA	P	W	W	W		P	W			6	0–1040
Smilisca baudinii	MA	P	W	W	W		W	W		P	7	0–1350
Smilisca phaeota	MA	P	W			W	W			P	5	20–1400
Smilisca puma	MA	P	P								2	20–420
Smilisca sordida	MA	W	P								2	20–420
Tlalocohyla loquax	MA		P				W			P	3	20–1350
Trachycephalus venulosus	SA		W	W							2	0–600
Leiuperidae												
Engystomops pustulosus	SA		P	W	W		P	W		P	6	0–1400
Leptodactylidae												
Leptodactylus fragilis	SA	P	W	W	W		P	W			6	0–1200
Leptodactylus melanonotus	SA	P	W	W	W		W	W			6	10–1200
Leptodactylus savagei	SA	W	W				P				3	10–960
Microhylidae												
Gastrophryne pictiventris	MA	P	P								2	20–50
Hypopachus variolosus	MA			P				P		P	3	30–1350
Ranidae												
Lithobates brownorum	ON		P				P				2	20–1050
Lithobates forreri	ON		P	W	W		W			P	5	10–1280
Lithobates maculatus	ON		P			W	W		P		4	250–1360
Lithobates miadis	ON		R								1	0–20

Lithobates taylori	ON	P	P								2	10–500
Lithobates vaillanti	ON	W	W	P			W				4	30–860
Lithobates warszewitschii	ON	W	W			P	P				4	20–1000
Rhinophrynidae												
Rhinophrynus dorsalis	ON		P	P							2	20–90
Strabomantidae												
Pristimantis cerasinus	SA	W	P			W			P		4	20–1360
Pristimantis ridens	SA	W	P			W	P		P	P	6	20–1360
REPTILIA												
TESTUDINES												
Cheloniidae												
Caretta caretta												Marine Atlantic
Chelonia mydas												Marine Atlantic & Pacific
Eretmochelys imbricata												Marine Atlantic & Pacific
Lepidochelys olivacea												Marine Pacific
Chelydridae												
Chelydra acutirostris	ON	W	P								2	10–230
Dermochelydae												
Dermochelys coriacea												Marine Atlantic & Pacific
Emydidae												
Trachemys scripta	ON	W	W	P							3	30–130
Geoeymdidae												
Rhinoclemmys annulata	ON	W	W			P					3	40–780
Rhinoclemmys funerea	ON	W	W								2	10–130
Rhinoclemmys pulcherrima	ON			W	W			P			3	10–820
Kinosternidae												
Kinosternon angustipons	ON	P	P								2	10–80
Kinosternon leucostomum	ON	W	W	P							3	10–260
Kinosternon scorpioides	ON		W	W	W		P				4	10–990
CROCODYLIA												
Alligatoridae												
Caiman crocodilus	SA	W	P	P							3	10–100
Crocodylidae												
Crocodylus acutus	MA	P	P	W							3	0–90
SQUAMATA												
Anguidae												
Celestus bivittatus	MA						P	P			2	990
Diploglossus bilobatus	SA	P	P								2	20–400
Diploglossus monotropis	SA	R									1	50
Mesaspis moreletii	ON									R	1	1305–1440
Eublepharidae												
Coleonyx mitratus	ON	P	P	W	W			W			5	10–960
Gekkonidae												
Hemidactylus frenatus	E	P	W	W	W		W	P			6	0–1200
Lepidodactylus lugubris	E		R								1	0–10

Gymnophthalmidae												
Gymnophthalmus speciosus	SA		P	P		P	P	P			5	40–1100
Iguanidae												
Anolis biporcatus	MA	W	W	P		W	P	P			6	30–1200
Anolis capito	MA	W	W			W	W		W	W	6	10–1405
Anolis carpenteri	MA	W	P				P				3	30–1100
Anolis cupreus	MA		W	W			W	W		W	5	40–1325
Anolis laeviventris	MA									R	1	1200–1300
Anolis lemurinus	MA	W	W								2	10–200
Anolis limifrons	MA	W	W			W	P		P	P	6	10–1300
Anolis oxylophus	MA	W	W			W	P				4	20–1100
Anolis pentaprion	MA	W	P								2	30–420
Anolis quaggulus	MA	W	W			W	P		W	P	6	10–1405
Anolis sericeus “bilobed”	MA			P	P						2	100–410
Anolis sericeus “unilobed”	MA	P	W	W	W		P	W		P	7	30–1300
Anolis tropidonotus	MA						R				1	940–1200
Anolis villai	MA		R								1	10
Anolis wermuthi	MA								P	W	2	1230–1500
Basiliscus basiliscus	MA			R							1	70
Basiliscus plumifrons	MA	W	W								2	10–400
Basiliscus vittatus	MA	W	W	P			P				4	10–940
Corytophanes cristatus	MA	W	W			W	P				4	10–1100
Ctenosaura quinquecarinata	MA		P	P	W						3	120–330
Ctenosaura similis	MA		P	W	W		P	W			5	0–1030
Iguana iguana	MA	W	W	W							3	10–200
Laemanctus longipes	MA						R				1	800–1100
Polychrus gutturosus	SA	W	P								2	40– 420
Sceloporus malachiticus	ON						W			W	2	680–1400
Sceloporus squamosus	ON			W	W		P	W			4	10–940
Sceloporus variabilis	ON		P	W	W		W	W		P	6	0–1350
Phyllodactylidae												
Phyllodactylus tuberculosus	MA		P	W	W		P	W			5	40–1275
Thecadactylus rapicauda	SA	W	W								2	20–400
Scincidae												
Mabuya unimarginata	ON	W	W	W	W		P	W			6	10–890
Mesoscincus managuae	ON			W	P						2	30–150
Sphenomorphus cherriei	ON	W	W				P				3	20–860
Sphaerodactylidae												
Gonatodes albogularis	MA	W	W	W	P		P	W			6	10–800
Lepidoblepharis xanthostigma	SA	R									1	10–420
Sphaerodactylus argus	MA		R								1	30
Sphaerodactylus homolepis	MA	R									1	20
Sphaerodactylus millepunctatus	MA	W	W				P	P			4	10–960
Teiidae												
Ameiva festiva	SA	W	W			P	P				4	20–960
Ameiva quadrilineata	SA	R									1	10
Ameiva undulata	SA		P	W			P	W		P	5	10–1300
Aspidoscelis deppii	ON		P	W	W			W			4	0–800
Cnemidophorus lemniscatus	SA		R								1	10
Xanthusidae												
Lepidophyma flavimaculatum	ON	W	W			W					3	10–800
Anomalepididae												
Anomalepis mexicanus	SA		R								1	400

Leptotyphlopidae												
Leptotyphlops goudotii	SA			W	W			P			3	40–1100
Typhlopidae												
Typhlops costaricensis	SA						R				1	1100
Boidae												
Boa constrictor	MA	W	W	W	P	W	W	W			7	0–660
Corallus annulatus	SA	W	P								2	70
Loxocemidae												
Loxocemus bicolor	MA			W	W						2	50–480
Ungaliophiidae												
Ungaliophis continentalis	MA									R	1	1300
Ungaliophis panamensis	MA	R									1	20
Colubridae												
Adelphicos quadrivirgatum	MA		R									180
Amastridium veliferum	MA	R									1	20–420
Chironius grandisquamis	ON	W	W								2	20–400
Clelia clelia	SA	W	P	P							3	20–420
Coniophanes bipunctatus	MA		P				P				2	50–700
Coniophanes fissidens	MA		P			P	P				3	70–1200
Coniophanes piceivittis	MA		P	W			P	P			4	80–1200
Conophis lineatus	MA		P	W	W		P	W			5	0–1100
Crisantophis nevermanni	MA		P	W	W						3	10–600
Dendrophidion nuchale	ON	R									1	20
Dendrophidion percarinatum	ON	P	P								2	40–260
Dendrophidion vinitor	ON	W	P			P					3	50–780
Dipsas articulata	MA	R									1	30
Dipsas bicolor	MA		R								1	250–550
Drymarchon melanurus	ON	P	W	W	W		P	W			6	30–660
Drymobius chloroticus	ON						R				1	910–1200
Drymobius margaritiferus	ON	W	W	W	P		W				5	0–1100
Drymobius melanotropis	ON		P			P	P				3	50–780
Drymobius rhombifer	ON		R								1	70
Enuliophis sclateri	MA		P				P				2	180–800
Enulius flavitorques	MA		P	W				W			3	70–960
Erythrolamprus mimus	SA	W	W				W			P	4	30–1460
Geophis dunni	MA						R				1	800
Geophis hoffmanni	MA	P	W	P		P	P				5	30–960
Hydromorphus concolor	MA	W	P				P			P	4	70–1300
Imantodes cenchoa	MA	W	W			W	P			P	5	10–1310
Imantodes gemmistratus	MA		P	P			P	P			4	80–1100
Imantodes inornatus	MA		W			P	P				3	80–990
Lampropeltis triangulum	ON		P	W	W		W	W		P	6	40–1350
Leptodeira annulata	MA	W	P	W	W		P				5	10–940
Leptodeira nigrofasciata	MA			W	W		P	W			4	30–1200
Leptodeira septentrionalis	MA	W	W				P				3	30–960
Leptodrymus pulcherrimus	ON		P	W				W			3	40–800
Leptophis ahaetulla	ON	W	W				W			P	4	30–1300
Leptophis depressirostris	ON	W	P			P					3	50–700
Leptophis mexicanus	ON		P	W	W		P	P			5	60–1100
Leptophis nebulosus	ON		R								1	80
Masticophis mentovarius	ON		P	W	W		P	P			5	40–1010
Mastigodryas dorsalis	ON						W			W	2	960–1350
Mastigodryas melanolomus	ON	W	W	P		P	P	P			6	20–1200
Ninia maculata	MA		W			P	P				3	20–1200
Ninia sebae	MA	W	W	P		P	W	P		P	7	30–1330

Nothopsis rugosus	MA	P	P			P					3	20–900
Oxybelis aeneus	ON	W	W	W	W			W			5	30–960
Oxybelis brevirostris	ON	W	P			W					3	100–920
Oxybelis fulgidus	ON	P	P	P	P	P		P			6	50–720
Oxyrhopus petola	SA	P	W				P				3	40–1010
Pliocercus euryzonus	MA	W	P				P				3	10–1200
Pseudelaphe flavirufa	ON			R							1	80
Pseustes poecilonotus	ON	W	W			P	P				4	30–960
Rhadinaea decorata	MA	W	P								2	10–610
Rhadinaea kinkelini	MA									R	1	1330
Rhadinaea rogerromani	MA								R		1	1450
Scaphiodontophis venustissimus	ON		P				P				2	30 –990
Scolecophis atrocinctus	MA		P	W			P	W			4	40–960
Senticolis triaspis	ON			W	W		P				3	360–1100
Sibon annulatus	MA		P			W					2	200–850
Sibon anthracops	MA			P			P	P			3	30–960
Sibon dimidiatus	MA						R				1	1200
Sibon longifrenis	MA	P	P								2	20–220
Sibon nebulatus	MA	W	W			P	P	P			5	10–1100
Spilotes pullatus	ON	W	W	W	W	P	W	W		P	8	30–1400
Stenorrhina degenhardtii	ON									R	1	1230–1400
Stenorrhina freminvillei	ON			W	W		P				3	10–760
Tantilla alticola	ON						P			P	2	990–1400
Tantilla armillata	ON		W	P							2	40–150
Tantilla reticulata	ON	R									1	10
Tantilla ruficeps	ON	R									1	30?
Tantilla schistosa	ON						R				1	700–960
Tantilla supracincta	ON	R									1	10
Tantilla taeniata	ON						R				1	1090–1230
Tantilla vermiformis	ON			R							1	90
Tantillita lintoni	ON		R								1	200–400
Thamnophis marcianus	ON		P	P							2	40–100
Thamnophis proximus	ON			W	W		W				3	40–1200
Tretanorhinus nigroluteus	MA	W	W	P							3	0–80
Trimorphodon quadruplex	ON		P	W	W		P				4	20–800
Tropidodipsas sartorii	MA						P	P			2	960
Urotheca guentheri	MA	W	P								2	40–420
Xenodon rabdocephalus	SA	W	W				P				3	30–1200
Elapidae												
Micrurus alleni	MA	W	W			P					3	30–830
Micrurus multifasciatus	MA	W	P								2	20–210
Micrurus nigrocinctus	MA	W	W	W	W	W	W	W		W	8	10–1400
Pelamis platura												Marine Pacific
Viperidae												
Agkistrodon bilineatus	ON			R							1	70–400
Atropoides mexicanus	ON					P	P				2	780–990
Bothriechis schlegelii	ON	W	W			W	P			P	5	10–1280
Bothrops asper	ON	W	W			W					3	10–780
Crotalus simus	ON		P	W	W		P				4	20–670
Lachesis stenophrys	ON		R								1	410
Porthidium nasutum	ON	W	W			P	P				4	10–990
Porthidium ophryomegas	ON			W	P						2	40–600

4 CONSERVATION STATUS OF THE HERPETOFAUNA OF NICARAGUA

4.1 INTRODUCTION

Traditionally, Nicaragua has been known popularly as the "granary of Central America" in reference to the extensive amount of land devoted to cattle ranching and agriculture. In general, the country is considered to have three major ecological areas (MARENA, 1999): the Pacific Lowlands, the North-central Region, and the Atlantic Lowlands. The Pacific Lowlands (15% of the surface area) is the most ecologically degraded area of the country. Few patches of Lowland Dry Forest remain, and all are under increased pressure from deforestation. The North-central Region (35% of the surface area) is the next-most ecologically degraded part of the country. In this area, Premontane Moist Forest and Lower Montane Moist Forest have been reduced by more than half of their original size since 1965. The Atlantic Lowlands (50% of the surface area) still possess relatively large and undisturbed areas of Lowland Wet Forest and Lowland Moist Forest, although the agricultural frontier in this region keeps expanding with each passing year.

Since the creation of the Nicaraguan protected areas system (Sistema Nacional de Areas Protegidas, SINAP) in 1958, nine different types of protected areas have been established in 76 separate areas that occupy 18.2% of Nicaragua (Fig. 59; WEAVER et al., 2003). Still, legal protection seems insufficient in light of the tremendous pressures placed on natural resources by the growing human population, the uncertainties of land ownership derived from Nicaragua's civil war, and uncontrolled fires. Although Nicaragua is part of the Mesoamerican Biological Corridor Project (Fig. 59), most forest in the country has been reduced to isolated patches of various sizes, shapes, and distances from one another. If wildlife is unable to disperse among these isolated patches, their populations will become vulnerable to local extinctions through chance environmental and demographic catastrophes and loss of genetic heterozygosity (POUGH et al., 2004).

Fig. 59. Map indicating the protected areas (green) and biological corridors (orange) in Nicaragua. Modified from MARENA (2007).

In mid-2007, Nicaragua's human population was estimated at 5,600,000 (PRB, 2008), ranging in density from 151.7 inhabitants/km^2 on the Pacific Lowlands to 10.5 inhabitants/km^2 on the Atlantic Lowlands, with 48.3 inhabitants/km^2 in the North-central Region (INEC, 2006a). At that time, 58% of the population was living in urbanized areas and 42% in rural areas (INEC, 2006b). Moreover, about 60.5% of the population was between the ages of 15 and 64, the unemployment rate was 6.9%, and the underemployment rate 46.5% (INDEXMUNDI, 2006). Nicaragua is one of the 41 poorest countries in the world and the second poorest in the Western Hemisphere: with half of its population living below the poverty line (INDEXMUNDI, 2006), this has led to increased exploitation of its natural resources.

Nicaragua has a 2.3% rate of human population growth, with a population doubling time of 30.4 years, and thus the population is expected to reach 10,000,000 by the year 2050 (PRB, 2008). Further deforestation, along with increased pollution, pesticide use, overhunting, introduced exotic species, and climate change (POUGH et al., 2004) will continue to threaten the survival of Nicaragua's herpetofauna. Additionally, the pathogenic fungus *Batrachochytrium dendrobatidis* has been implicated as the cause of mortality for many anuran species in neighboring countries (LIPS et al., 2005, 2008). Environmental synergisms resulting from the interaction of two or more environmental problems can have a greater combined impact than the sum of their individual effects, making it more difficult to predict future changes in herpetofaunal populations (POUNDS et al., 2006). In Nicaragua, no amphibian or reptile populations are entirely free from anthropogenic impact.

The purpose of this chapter is to assess the conservation status of members of the Nicaraguan herpetofauna, and to identify those species with a greater potential for population decline.

4.2 MATERIALS AND METHODS

Except for minor differences, the format of the analysis on the conservation status of Nicaragua's amphibians and reptiles follows that of WILSON & MCCRANIE (2003), which created an environmental vulnerability gauge for amphibians and reptiles by using three components. The higher the final Environmental Vulnerability Score (EVS), the greater the potential vulnerability of that species and, consequently, the need to monitor populations of each species for signs of decline.

The first component of the EVS, applicable to amphibians and reptiles, deals with the extent of the geographic range, using the following scale: 1 = widespread in and outside of Nicaragua; 2 = distribution peripheral to Nicaragua, but widespread elsewhere; 3 = distribution restricted to Nuclear Middle America or Lower Middle America (exclusive of Nicaraguan endemics); 4 = distribution restricted to Nicaragua; 5 = known only from the vicinity of the type locality.

The second component of the EVS, also applicable to amphibians and reptiles, indicates the extent of ecological distribution: 1 = occurs in nine formations; 2 = occurs in eight formations; 3 = occurs in seven formations; 4 = occurs in six formations; 5 = occurs in five formations; 6 = occurs in four formations; 7 = occurs in three formations; 8 = occurs in two formations; and 9 = occurs in one formation. A description of the forest formations found in Nicaragua appears below.

The third component of the EVS for amphibians measures the degree of specialization of reproductive mode: 1 = both eggs and tadpoles in large or small bodies of lentic or lotic water; 2 = eggs in foam nests, tadpoles in small bodies of lentic or lotic water; 3 = tadpoles occur in small bodies of lentic or lotic water, eggs elsewhere; 4 = eggs laid in moist situations on land or moist arboreal situations, direct development; and 5 = eggs and tadpoles in water-retaining arboreal bromeliads or water-filled tree cavities.

The third component of the EVS for reptiles measures the degree of human persecution: 1 = fossorial, usually escape human notice; 2 = semifossorial, or nocturnal arboreal or aquatic, non-venomous and usually non-mimicking, sometimes escape human notice; 3 = terrestrial and/or arboreal or aquatic, generally ignored by humans; 4 = terrestrial and/or arboreal or aquatic, thought to be harmful, may be killed on sight; 5 = venomous species or mimics thereof, killed on sight; and 6 = commercially or non-commercially exploited for hides and/or meat and/or eggs.

Unless provided by the Program Officer of http://www.iucnredlist.gob (N. COX, pers. comm.), I took the IUCN categorizations for most amphibian species from IUCN (2007). For the few amphibian species not listed on this website, as well as for most reptilian species, I made the determinations based on the IUCN criteria. Abbreviations used for IUCN categorizations: LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, and DD = Data Deficient; A1 = population size reduction (≥ 50 % in VU species) over the last 10 years or three generations where the reduction or its causes are reversible, understood and ceased; A2 = population size reduction (≥ 50 % in EN and ≥ 80 % in CR species) over the last 10 years or three generations where the reduction or its causes may not have ceased, may be not understood, or may not be reversible; and A3 = population size reduction (≥ 80 % in CR species) projected to be met within the next 10 years or three generations, based on (a) direct observation, (c) on the decline in the area, extent and/or quality of habitat, and on (e) the effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites; B1 = extent of occurrence (< 20,000 km^2 in VU and < 5,000 km^2 in EN species); and B2 = area of occupancy < 2,000 km^2 in VU species, (a) severely fragmented or known to exist at no more than 10 locations in VU and five locations in EN species, (b) with a continuing decline in (iii) the area, extent and/or quality of habitat, and (v) number of mature individuals; D2 = population with a very restricted area of occupancy (< 20 km^2) or number of locations (< 5), and thus capable of becoming CR or even extinct in a very short time period.

4.3 RESULTS AND DISCUSSION

Of the total 238 species of amphibians and terrestrial reptiles I am including for the Nicaraguan herpetofauna (Table 9), 76 are considered high vulnerability species (31.9%), 118 medium vulnerability species (49.6%), and 44 low vulnerability species (18.5%). Twenty-four species of amphibians (30.8% of total amphibians) are considered high vulnerability species, 33 (42.3%) medium vulnerability species, and 21 (26.9%) low vulnerability species. Fifty-two species of terrestrial reptiles (32.5% of total terrestrial reptiles) are considered high vulnerability species, 85 (53.1%) medium vulnerability species, and 23 (14.4%) low vulnerability species. Sixteen species are endemic to Nicaragua (6.7%), all of which are considered high vulnerability species because of their restricted distributions. Most endemic species are found in small areas of specialized habitat, and only a relatively small degree of disturbance to those habitats would jeopardize these species.

Table 9 shows the similarities between the Environmental Vulnerability Scores in Nicaragua and the IUCN categorizations. All species considered under the IUCN categorizations as Vulnerable (VU), Endangered (EN), or Critically Endangered (CR), are high vulnerability species with two exceptions: *Craugastor laevissimus* and *Ptychohyla hypomykter*. For these two species, it is thought that a drastic population decline occurred due to chytridiomycosis, a matter not taken into account when calculating the EVS, so they deserve special attention for signs of population decline. *Batrachochytrium dendrobatidis* has not yet been recorded from Nicaragua although based on its spread throughout Central America (LIPS et al, 2006), this pathogenic fungus is most probably found everywhere in the country. Several species considered under the IUCN categorizations as Least Concern (LC) are high vulnerability species in Nicaragua, mostly because their limit of distributional range occurs somewhere in or near the country (see chapter 3.3). The six marine species not gauged with the EVS are considered by the IUCN as follows: *Caretta caretta* (EN: A1abd), *Chelonia mydas* (EN: A2bd), *Eretmochelys imbricata* (CR: A1bd), *Lepidochelys olivacea* (EN: A1bd), *Dermochelys coriacea* (CR: A1abd), and *Pelamis platura* (LC).

Two hundred and twenty-six herpetofaunal species (92.6% of the total, including marine species) occur in at least one of Nicaragua's established protected areas, and for the remaining 18 species (one salamander, one frog, six lizards, and 10 snakes), data involving their presence in protected areas are unavailable. These remaining species include three endemic species (*Lithobates miadis*, *Anolis villai*, and *Geophis dunni*), 10 more high vulnerability species (*Oedipina collaris, Anolis sericeus* "bilobed," *Basiliscus basiliscus*, *Ctenosaura quinquecarinata*, *Laemanctus longipes*, *Drymobius rhombifer*, *Pseudelaphe flavirufa*, *Scaphiodontophis venustissimus*, *Tantilla ruficeps*, and *Lachesis stenophrys*), four medium vulnerability species (*Typhlops costaricensis, Tantilla armillata, T. schistosa* and the exotic *Lepidodactylus lugubris*), and one low vulnerability species (*Imantodes gemmistratus*). We need to preserve the integrity of the established protected areas, expanding them when necessary and/or creating new ones to protect species not known to reside in any of the currently designated protected areas. This could be of special urgency in the Corn Islands which have two endemic species and several endemic subspecies. The Corn islands are constituted by two small islands which have suffered from substantial alteration during the last decades. With an increasing tourist affluence, this two islands still lack protected areas.

Programs to monitor amphibian and reptile species in Nicaragua are needed to determine if each population is stable, in decline, or already extinct, and they should prioritize all endemic and high vulnerability species. Only one endemic species, *Bolitoglossa mombachoensis*, has been punctually studied reasonably well, including its habitat selection, movement patterns, and relative densities (JANSEN & KÖHLER, 2001). Similar studies should be repeated throughout time on target species in signs for population decline. Universities from all around the country could play an important role in long term monitoring studies.

The effectiveness of conservation programs depends on whether they focus on protecting habitats rather than single charismatic species, and if they involve local people while providing them some measure of economic benefit. Conservation efforts must be complemented with field and laboratory research to help identify the causes of species endangerment. Finally, educational efforts are needed to inform the citizenry about Nicaragua's herpetological diversity, and strong legislation must be enacted to protect species of conservation concern and their associated habitats.

Table 9. IUCN categorizations and Environmental Vulnerability Scores (EVS) for the 238 species of amphibians and terrestrial reptiles known from Nicaragua. Numbers for each gauge are explained in text. Table is broken into three parts: low vulnerability species (EVS of 4–9; 44 species; 18.5%); medium vulnerability species (EVS of 10–13; 118 species; 49.6%); and high vulnerability species (EVS of 14–18; 76 species; 31.9%). IUCN Red List Status taken from IUCN (2007) except those with an asterisk (*), which were estimated using IUCN's methodology.

		EVS			
Species	**IUCN Categorizations**	Geographic Distribution	Ecological Distribution	Reproductive Mode / Human Persecution	Total Score
LOW					
Amphibian Species					
Incilius coccifer	LC	1	4	1	6
Incilius coniferus	LC	2	6	1	9
Incilius luetkenii	LC	1	5	1	7
Incilius valliceps	LC	1	3	1	5
Rhaebo haematiticus	LC	1	7	1	9
Rhinella marina	LC	1	2	1	4
Diasporus diastema	LC	1	4	4	9
Agalychnis callidryas	LC	1	3	3	7
Dendropsophus microcephalus	LC	1	5	1	7
Scinax staufferi	LC	1	4	1	6
Smilisca baudinii	LC	1	3	1	5
Smilisca phaeota	LC	1	5	1	7
Tlalocohyla loquax	LC	1	7	1	9
Engystomops pustulosus	LC	1	4	2	7
Leptodactylus fragilis	LC	1	4	2	7
Leptodactylus melanonotus	LC	1	4	2	7
Hypopachus variolosus	LC	1	7	1	9
Lithobates forreri	LC	1	5	1	7
Lithobates maculatus	LC	2	6	1	9
Lithobates vaillanti	LC	1	6	1	8
Pristimantis ridens	LC	1	4	4	9
Reptile Species					
Hemidactylus frenatus	LC*	1	4	3	8
Gymnophthalmus speciosus	LC*	1	5	3	9
Anolis biporcatus	LC*	1	4	3	8
Anolis capito	LC*	1	4	3	8
Anolis limifrons	LC*	1	4	3	8
Anolis sericeus "unilobed"	LC*	1	3	3	7
Sceloporus variabilis	LC*	1	4	3	8
Phyllodactylus tuberculosus	LC*	1	5	3	9
Mabuya unimarginata	LC*	1	4	3	8
Gonatodes albogularis	LC*	1	4	3	8
Ameiva undulata	LC*	1	5	3	9
Leptotyphlops goudotii	LC*	1	7	1	9
Drymarchon melanurus	LC*	1	4	4	9
Hydromorphus concolor	LC*	1	6	2	9

Imantodes cenchoa	LC*	1	5	2	8
Imantodes gemmistratus	LC*	1	6	2	9
Mastigodryas melanolomus	LC	1	4	4	9
Ninia sebae	LC*	1	3	2	6
Oxybelis aeneus	LC*	1	5	2	8
Oxybelis fulgidus	LC*	1	4	4	9
Sibon nebulatus	LC*	1	5	2	8
Spilotes pullatus	LC*	1	2	4	7
Micrurus nigrocinctus	LC*	1	2	5	8
MEDIUM					
Amphibian Species					
Gymnopis multiplicata	LC	1	8	4	13
Bolitoglossa striatula	LC	3	6	4	13
Incilius melanochlorus	LC	3	9	1	13
Centrolene prosoblepon	LC	1	6	3	10
Cochranella albomaculata	LC	1	8	3	12
Cochranella granulosa	LC	3	7	3	13
Cochranella pulverata	LC	1	7	3	11
Cochranella spinosa	LC	1	8	3	12
Hyalinobatrachium fleischmanni	LC	1	6	3	10
Craugastor bransfordii	LC	3	4	4	11
Craugastor fitzingeri	LC	1	5	4	10
Craugastor laevissimus	EN; A2ace	3	3	4	10
Craugastor megacephalus	LC	3	6	4	13
Craugastor mimus	LC	3	4	4	11
Craugastor noblei	LC	3	5	4	12
Oophaga pumilio	LC	3	6	3	12
Cruziohyla calcarifer	LC	1	9	3	13
Dendropsophus ebraccatus	LC	1	6	3	10
Dendropsophus phlebodes	LC	2	8	1	11
Hypsiboas rufitelus	LC	3	8	1	12
Ptychohyla hypomykter	CR; A3e	3	7	1	11
Scinax boulengeri	LC	1	8	1	10
Scinax elaeochroa	LC	3	8	1	12
Smilisca puma	LC	3	8	1	12
Smilisca sordida	LC	3	8	1	12
Trachycephalus venulosus	LC	1	8	1	10
Leptodactylus savagei	LC	1	7	2	10
Gastrophryne pictiventris	LC	3	8	1	12
Lithobates brownorum	LC	2	8	1	11
Lithobates taylori	LC	3	8	1	12
Lithobates warszewitschii	LC	3	6	1	10
Rhinophrynus dorsalis	LC	1	8	1	10
Pristimantis cerasinus	LC	3	6	4	13
Reptile Species					
Rhinoclemmys annulata	NT	1	7	3	11
Rhinoclemmys pulcherrima	NT*	1	7	3	11
Kinosternon leucostomum	LC*	1	7	3	11
Kinosternon scorpioides	LC*	1	6	3	10
Coleonyx mitratus	LC*	1	5	4	10
Lepidodactylus lugubris	LC*	1	9	3	13
Anolis carpenteri	NT*	3	7	3	13
Anolis cupreus	LC*	3	5	3	11
Anolis laeviventris	LC*	1	9	3	13
Anolis lemurinus	LC*	1	8	3	12
Anolis oxylophus	LC*	3	6	3	12
Anolis pentaprion	LC*	1	8	3	12

Anolis quaggulus	LC*	3	4	3	10
Basiliscus vittatus	LC*	1	6	3	10
Corytophanes cristatus	LC*	1	6	3	10
Ctenosaura similis	LC*	1	5	6	12
Polychrus gutturosus	LC*	1	8	2	11
Sceloporus malachiticus	LC*	1	8	3	12
Sceloporus squamosus	LC*	1	6	3	10
Thecadactylus rapicauda	LC*	1	8	4	13
Sphenomorphus cherriei	LC*	1	7	3	11
Sphaerodactylus millepunctatus	LC*	1	6	3	10
Ameiva festiva	LC*	1	6	3	10
Aspidoscelis deppii	LC*	1	6	3	10
Cnemidophorus lemniscatus	LC*	1	9	3	13
Lepidophyma flavimaculatum	LC*	1	7	4	12
Anomalepis mexicanus	DD*	1	9	1	11
Typhlops costaricensis	LC*	3	9	1	13
Boa constrictor	LC*	1	3	6	10
Corallus annulatus	LC*	1	8	2	11
Loxocemus bicolor	LC*	1	8	4	13
Ungaliophis panamensis	NT*	2	9	2	13
Chironius grandisquamis	LC*	1	8	4	13
Clelia clelia	LC*	1	7	4	12
Coniophanes bipunctatus	LC*	1	8	4	13
Coniophanes fissidens	LC*	1	7	4	12
Coniophanes piceivittis	LC	1	6	4	11
Conophis lineatus	LC	1	5	4	10
Crisantophis nevermanni	LC*	1	7	4	12
Dendrophidion percarinatum	LC*	1	8	4	13
Dendrophidion vinitor	LC*	1	7	4	12
Drymobius margaritiferus	LC*	1	5	4	10
Enuliophis sclateri	LC*	1	8	2	11
Enulius flavitorques	LC*	1	7	2	10
Erythrolamprus mimus	LC*	1	6	5	12
Geophis hoffmanni	LC*	3	5	2	10
Imantodes inornatus	LC*	1	7	2	10
Lampropeltis triangulum	LC*	1	4	5	10
Leptodeira annulata	LC*	1	5	4	10
Leptodeira nigrofasciata	LC	1	6	4	11
Leptodeira septentrionalis	LC*	1	7	4	12
Leptodrymus pulcherrimus	LC*	1	7	4	12
Leptophis ahaetulla	LC*	1	6	4	11
Leptophis depressirostris	LC*	2	7	4	13
Leptophis mexicanus	LC*	1	5	4	10
Masticophis mentovarius	LC*	1	5	4	10
Ninia maculata	LC*	3	7	2	12
Nothopsis rugosus	LC*	1	7	2	10
Oxybelis brevirostris	LC*	1	7	4	12
Oxyrhopus petola	LC*	1	7	5	13
Pliocercus euryzonus	LC*	1	7	4	12
Pseustes poecilonotus	LC	1	6	4	11
Rhadinaea decorata	LC*	1	8	2	11
Scolecophis atrocinctus	LC*	1	6	5	12
Senticolis triaspis	LC*	1	7	4	12
Sibon annulatus	LC*	3	8	2	13
Sibon anthracops	LC*	1	7	2	10
Sibon dimidiatus	LC	1	9	2	12
Sibon longifrenis	LC*	3	8	2	13
Stenorrhina freminvillei	LC	1	7	5	13
Tantilla alticola	NT*	2	8	2	12

Tantilla armillata	LC*	1	8	2	11
Tantilla reticulata	NT*	2	9	2	13
Tantilla schistosa	LC*	1	9	2	12
Tantilla supracincta	LC*	2	9	2	13
Thamnophis marcianus	LC*	1	8	4	13
Thamnophis proximus	LC*	1	7	4	12
Tretanorhinus nigroluteus	LC*	1	7	2	10
Trimorphodon quadruplex	LC*	3	6	4	13
Urotheca guentheri	LC*	3	8	2	13
Xenodon rabdocephalus	LC*	1	7	5	13
Bothriechis schlegelii	LC*	1	5	5	11
Bothrops asper	LC*	1	7	5	13
Crotalus simus	LC*	1	6	5	12
Porthidium nasutum	LC	1	6	5	12
HIGH					
Amphibian Species					
Dermophis mexicanus	LC	2	8	4	14
Bolitoglossa indio	DD*	5	9	4	18
Bolitoglossa insularis	VU; D2*	5	9	4	18
Bolitoglossa mombachoensis	VU; D2	5	9	4	18
Nototriton saslaya	VU; D2	4	9	4	17
Oedipina collaris	DD	3	9	4	16
Oedipina cyclocauda	LC	3	9	4	16
Oedipina sp. “Datanlí”	VU; D2*	5	9	4	18
Oedipina sp. “Kilambé”	VU; D2*	5	9	4	18
Oedipina sp. “Musún”	VU; D2*	5	9	4	18
Oedipina sp. “Saslaya”	VU; D2*	5	9	4	18
Allobates talamancae	LC	2	9	3	14
Centrolene ilex	LC	2	9	3	14
Craugastor chingopetaca	DD*	4	9	4	17
Craugastor lauraster	EN; B1ab(iii, v)	3	8	4	15
Craugastor ranoides	CR; A2ace	3	8	4	15
Craugastor talamancae	LC	3	8	4	15
Dendrobates auratus	LC	2	9	3	14
Phyllobates lugubris	LC	3	9	3	15
Agalychnis saltator	LC	3	9	3	15
Ecnomiohyla miliaria	VU; B1ab(iii)	1	9	5	15
Plectrohyla sp. “Saslaya”	VU; D2*	5	9	1	15
Ptychohyla sp. “Bosawas”	DD*	5	9	1	15
Lithobates miadis	VU; D2	5	9	1	15
Reptile Species					
Chelydra acutirostris	LC*	2	8	6	16
Rhinoclemmys funerea	NT*	3	8	3	14
Trachemys scripta	NT*	1	7	6	14
Kinosternon angustipons	VU; B1ab(iii)*	3	8	3	14
Caiman crocodilus	LC	1	7	6	14
Crocodylus acutus	VU; A1ac	1	7	6	14
Celestus bivittatus	NT*	3	8	3	14
Diploglossus bilobatus	NT*	3	8	3	14
Diploglossus monotropis	LC*	2	9	4	15
Mesaspis moreletii	LC*	3	9	3	15
Anolis sericeus “bilobed”	NT*	3	8	3	14
Anolis tropidonotus	LC*	2	9	3	14
Anolis villai	VU; D2*	5	9	3	17
Anolis wermuthi	VU; B1ab(iii)*	4	8	3	15
Basiliscus basiliscus	LC*	2	9	3	14
Basiliscus plumifrons	LC*	3	8	3	14

Ctenosaura quinquecarinata	VU; B1ab(iii,v)+2ab(iii,v)	3	7	6	16
Iguana iguana	LC*	1	7	6	14
Laemanctus longipes	LC*	2	9	3	14
Mesoscincus managuae	LC*	3	8	3	14
Lepidoblepharis xanthostigma	LC*	2	9	3	14
Sphaerodactylus argus	LC*	2	9	3	14
Sphaerodactylus homolepis	VU; B1ab(iii)*	3	9	3	15
Ameiva quadrilineata	LC *	3	9	3	15
Ungaliophis continentalis	VU; B1ab(iii)*	3	9	2	14
Adelphicos quadrivirgatum	LC*	3	9	2	14
Amastridium veliferum	NT*	3	9	2	14
Dendrophidion nuchale	LC*	1	9	4	14
Dipsas articulata	NT*	3	9	2	14
Dipsas bicolor	LC*	3	9	2	14
Drymobius chloroticus	LC	1	9	4	14
Drymobius melanotropis	LC*	3	7	4	14
Drymobius rhombifer	LC*	2	9	5	16
Geophis dunni	DD*	5	9	2	16
Leptophis nebulosus	LC*	3	9	4	16
Mastigodryas dorsalis	VU; B1ab(iii)*	3	8	4	15
Pseudelaphe flavirufa	LC	1	9	4	14
Rhadinaea kinkelini	VU; B1ab(iii)*	3	9	2	14
Rhadinaea rogerromani	VU; D2*	5	9	2	16
Scaphiodontophis venustissimus	LC*	1	8	5	14
Stenorrhina degenhardtii	LC*	1	9	4	14
Tantilla ruficeps	NT*	3	9	2	14
Tantilla taeniata	LC*	3	9	2	14
Tantilla vermiformis	NT*	3	9	2	14
Tantillita lintoni	LC*	3	9	2	14
Tropidodipsas sartorii	LC*	1	8	5	14
Micrurus alleni	LC*	3	7	5	15
Micrurus multifasciatus	LC *	2	8	5	15
Agkistrodon bilineatus	NT	1	9	5	15
Atropoides mexicanus	LC*	1	8	5	14
Lachesis stenophrys	LC*	2	9	5	16
Porthidium ophryomegas	LC*	1	8	5	14

5 GENERAL DISCUSSION

The present study constitutes an important contribution to the herpetological knowledge in Nicaragua and includes an updated taxonomic compilation, the first detailed zoogeographic study, and an evaluation of the vulnerability of most species for the first time in the country. It constitute a solid taxonomical and zoogeographical basis in Nicaragua while filling several gaps in a larger context that will help in the understanding of the diversity, dispersal, and distribution of the Central American herpetofauna. At the same time, it compares the degree of endangerment of each Nicaraguan species throughout its total distributional range with the risk of population decline of each species at a county level.

During the 150 sampling days of this study, I collected 64.3% of the total species of herpetofauna known from Nicaragua. This collection involves around 1400 specimens from 29 localities and represents the most important Nicaraguan herpetological collection made in modern times. Approximately half of the specimens I collected will remain at the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany, which together with the specimens collected by G. KÖHLER and coworkers from the late 1990s until present probably make this the world's largest herpetological collection of Nicaraguan amphibians and reptiles. The other half of the specimens I collected will return to Nicaraguan collections and will constitute the most complete herpetological collection currently hosted in Nicaragua. After the destruction of all alcoholic herpetological specimens located in the Museo Nacional de Nicaragua during the 1972 earthquake and subsequent civil revolution, little attention has been paid to herpetological collections in the country. Currently, there are a few small Nicaraguan herpetological collections in several universities, NGOs, and protected areas, with the one deposited at the UCA (Universidad Centroamericana, Managua) being the most complete herpetological collection hosted at present in the country. In order to stimulate the improvement of herpetological research in Nicaragua, there is an urgent need for establishing a well-curated national herpetological museum that includes preserved specimens (including tadpoles), genetic samples, amphibian call recordings, and chitrid swabs, as well as photographs in life of the different populations of all amphibians and reptiles from the country. This Nicaraguan national herpetological collection should be based on the collaborative efforts of national and international researchers and should allow for maintenance of duplicates of all samples in foreign Museums worldwide.

Nicaragua is the largest of all the Central American countries and constitutes the transitional area between Nuclear and Lower Middle America. In such a vast, complex, and unsampled area a detailed picture of Nicaragua's herpetofaunal diversity and distribution is still far from complete. My own fieldwork was limited by several factors, such as total sampling time, manpower, accessibility to most places, associated dangers, etc. In addition, most fossorial, seasonal, and canopy species are likely to have passed by me unnoticed. Still, 6.4% of the species I collected during the course of the present study were previously not known from Nicaragua and represent undescribed species or new country records. In addition, and based exclusively on morphological characters, I described three new species (*Bolitoglossa indio, B. insularis,* and *Craugastor chingopetaca*) as compared to the single valid species (*Anolis villai*) described from Nicaraguan material between the mid 1930s and the late 1990s. These new dscoveries clearly demonstrate the few herpetological studies that have been undertaken in the country and the need for further collecting. Future sampling, including amphibian call recordings and genetic analysis of the different populations of amphibians and reptiles, may reveal greater herpetofaunal diversity in Nicaragua than envisioned by most workers, especially on isolated highlands and islands. Nevertheless, although several species have yet to be found in Nicaragua, the majority of amphibian and reptile species present in the country already have been detected.

Previous Central American zoogeographic studies dealt, in general, with three major macro-ecological areas in Nicaragua (e.g., CAMPBELL, 1999; GILLESPIE et al., 2001). In the present study, Nicaragua is divided into nine forest formations, which are differentiated from one another by abiotic factors. Nevertheless, and taking in account biotic and abiotic factors, Nicaragua can be divided into 52 natural ecosystems (RUEDA, 2007). During the field work for this study, I have noted differences in the herpetofaunal composition of distinctive nearby areas that are here regarded to be in the same forest formation. The most striking example I found was in Moss (point 15 in Fig. 2) and in the intersection of the road from Puerto Cabezas-Waspám with the road to Moss (point 16 in Fig. 2). These two closely adjacent areas (around two hour walk apart) are considered as Lowland Moist Forest formation, although the composition of the herpetofauna in these two places is strikingly different, due to differences in the type of soil and predominant vegetation (Moss is in a typical tropical broad-leaved lowland forest, whereas the intersection of the road from Puerto Cabezas-Waspám with the road to Moss is characterized by sandy soil with dominant lowland pine trees (*Pinus caribaea*). I haven't sampled in pine oak forests in the highlands of the north-central mountains and the northern Pacific volcanoes (Nicaragua constitutes the southernmost distributional limit of trees of the genus *Pinus* in mainland America; MARTÍNEZ-SÁNCHEZ et al., 2001), although I expect great differences in the composition of the herpetofauna between these two places and the rainforest I have sampled. Whereas biotic differences between forest types in the same forest formation are not considered in the present study, several evident ecosystems such as pine-oak forests, swamps, mangroves, etc., should be taken in account when reconstructing dispersal events throughout the country. Future herpetological sampling complemented with accurate collecting data that includes abiotic and biotic factors as well as detailed geologic information, will allow the use of more powerful analyses that will assist in the understanding of the evolution of Nicaragua's herpetological communities in the larger Central American context.

Nicaragua's protected areas are in general not well protected (WEAVER et al., 2003). In addition, several ecosystems are not well represented among the designated protected areas and do not include a few representative areas such as the Corn Islands, which have two endemic species of herpetofauna (*Lithobates miadis* and *Anolis villai*). In order to ensure the long-term preservation of the herpetofauna in Nicaragua, it is necessary to preserve the integrity of the protected areas, which also must include all species of amphibians and reptiles known from the country. In addition, these protected areas must be monitored for signs of population declines. In recent decades, radical population declines and extinctions have been detected in pristine areas of neighboring countries (POUNDS et al., 1997; STUART et al., 2004). The pathogenic fungus *Batrachochytrium dendrobatidis* has been directly implicated in most of these fatal cases (LIPS et al., 2006, 2008), although so far there has been no attempt to research the consequences of this lethal fungus in the Nicaraguan populations of amphibian species. Future monitoring programs including chitrid swabs are needed in order to estimate the repercussions of this lethal fungus as well as of other pathogens in the Nicaraguan herpetofaunal populations.

Previous conservational efforts in Nicaragua have been mostly aimed at species with commercial interest, which represent a small percentage of the total diversity of amphibians and reptiles in the country. The use of the IUCN categorizations to gauge the conservational status identifies those species with a greater vulnerability throughout the total distributional range of each species. Nevertheless, and because Nicaragua is a transitional area in Central America, several species with relatively large distributional ranges occur only peripherally in

Nicaragua and may be known only from a small portion of the country. Although some of these species may not be endangered on a global level, their Nicaraguan populations could be threatened with local extinction. Therefore, I gauged for the first time the vulnerability risk of all Nicaraguan species of amphibians and reptiles within the country and identified those species with a greater risk of population decline in Nicaragua. Nevertheless, high vulnerability species are here identified only and I haven't undertaken further study of any of them. Future monitoring programs on these species are necessary in order to know if their Nicaraguan populations are stable or in decline, and in latter case, to identify the cause of the decline and propose conservational solutions.

ACKNOWLEDGMENTS

My sincere gratitude to my supervisor and friend Dr. Gunther KÖHLER, who gave me the opportunity to join the herpetological section of the the Forschungsinstitut und Naturmuseum Senckenberg. I am extremely thankful for his guidance through my graduation and for his generous and constant help and support. I am grateful to Prof. Dr. Bruno STREIT, the biological referee of my thesis, for his support.

This investigation never would have been possible without the constant support of the DAAD (Deutscher Akademischer Austausch Dienst). These last four years in Germany have been most dear to me, both personally and professionally.

Special thanks go to my familiy (Blanca MAC LENNAN and Fernando, Fernando Jr., and Itziar SUNYER), who helped and supported me in many different ways.

I am especially grateful to Lenin A. OBANDO and Darwin E. MANZANAREZ for constant field support. I am also grateful to Larry WILSON, Josiah TOWNSEND, Scott TRAVERS, Daniel GRIFFITH, Inmaculada CARMONA, Andreas HERTZ, Sebastian LOTZKAT, Billy ALEMÁN, Silvia ROBLETO, Josué PÉREZ, Iris GARBAYO, Armando GÓMEZ, Luis HERNÁNDEZ, Claudia MARTÍNEZ, and Oscar MONTALVÁN, who also assisted in the field.

Collecting and exportation permits were provided by Bayardo QUINTERO-GUATEMALA, Iván ORTEGA-GASTEAZORO, Milton G. CAMACHO-BONILLA, Liliana DÍAZ, René SALVADOR-CASTELLÓN, Arcadio CHOZA-LÓPEZ, Carlos R. MEJÍA, Edilberto DUARTE, and Ana LORÍO, Ministerio del Ambiente y los Recursos Naturales (MARENA), Managua, Nicaragua. I also thank the following personnel of MARENA from other departments: Mauricio SILVA, Salvador TORUÑO, Harlam JARQUÍN, Norman GUTIÉRREZ, José Luis GALEANO, Ronald PICADO, Francisco LÓPEZ, Sebastian CHARLEY, Roberto Carlos MUÑOZ-GROSS, Porfirio de Jesús SANDOVAL-LÓPEZ, Matilde URBINA-GONZÁLEZ, Santo Eduardo MURILLO-MARTÍNEZ, Henry MURILLO, Moisés ARANA-REYES, Fernando Oliver CASANOVA-PONCE, and Lucas Antonio MENDOZA-SALAZAR.

The following people supported this study in different ways: Pedrarias DÁVILA, Ernesto MEDINA, Rigoberto SAMPSON, Brooks FEREBEE, Friedemann SCHRENK, Jean-Michel MAES, Enrique “Kyke” SAMPSON, Jürgen MARIENSCHECK, Josabel BELLIURRE, Gustavo Adolfo RUIZ-PÉREZ, Charles AKER, John POLISAR, Henry MARÍN, Iván JARQUÍN-CHAVARRÍA, Bolívar

ESPINOZA, Juan Carlos MAIRENA, Moisés BENAVIDES, Richard LEONARDI, Oscar SAMPSON, Tomás and Karelia NAVARRO, Dorian and Julio MARÍN, Carlos Ramón BERMÚDEZ, Salomón “Foxy” TORRES-ROJAS, Manuel RUGAMA, Gladis ZAPATA, Norvin TORRES, Rosa María CALVO, Maribel CHAMORRO, Ofelia GAITÁN-PALACIOS, Guillermo RODRÍGUEZ, Heydi HERRERA, Fabricio DÍAZ, Leonel UBAO, Renato PADILLA, Julio OCHOA, Aura BRIZUELA, Carlos ARGUELLO, Heraldo SALGADO, Guillermo PÁIZ, Matthias DEHLING, Blás HERNANDEZ, Miguel Ángel GUATEMALA, Álvaro and Aniceto VELÁZQUEZ-RIVERA, Edilio and Maximiliano PÉREZ-BUCARDO, Angel LÓPEZ, Marcelo HERRERA, Orlando SANDOVAL, Milan VESELÝ, Santiago CASTOVIEJO-FISHER, Lucía MELLONI, Lara CZUPALLA, Viola BLUMER, Linda ACKER, Ilka WEIDIG, Constantin KLISCH, Hans RECKNAGEL, Elke KÖHLER, and Jörg HABERSETZER.

For the loan of or access to specimens I thank L. FORD, C. J. RAXWORTHY and D. R. FROST, American Museum of Natural History (AMNH), New York; T. DAESCHLER and N. GILMORE, Academy of Natural Sciences (ANSP), Philadelphia; S. P. ROGERS, Carnegie Museum of Natural History (CM), Pittsburgh; N. M. FERRER, J. C. LÓPEZ VIDAL, and S. A. MURILLO JIMÉNEZ, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (ENCB), México D.F.; A. RESETAR, Field Museum of Natural History (FMNH), Chicago; G. LENGLET, Institut Royal des Sciences Naturelles de Belgique (IRSNB), Bruxelles; W. E. DUELLMAN and J. S. SIMMONS, University of Kansas, Natural History Museum (KU), Lawrence; J. SEIGEL, Natural History Museum of Los Angeles County (LACM), Los Angeles; D. ROSSMAN, Museum of Natural Science, Louisiana State University (LSUMZ), Baton Rouge; J. HANKEN and J. P. ROSADO, Museum of Comparative Zoology, Harvard University (MCZ), Cambridge; A. BATISTA and M. PONCE, Museo Herpetológico de Chiriquí (MHCH), David; A. DUBOIS, I. INEICH, and A. OHLER, Museum National d´Histoire Naturelle (MNHN), Paris; D. B. WAKE and R. GERMANO, University of California, Museum of Vertebrate Zoology (MVZ), Berkeley; F. TIEDEMANN, Naturhistorisches Museum Wien (NMW), Wien; F. BOLAÑOS and G. CHAVES, Museo de Zoología, Escuela de Biología, Universidad de Costa Rica (UCR), San José; K. L. KRYSKO and F. W. KING, Florida Museum of Natural History (UF), Gainesville; C. A. PHILLIPS and J. PETZING, Illinois Natural History Survey, Center for Biodiversity (UIMNH), Champaign; R. A. NUSSBAUM and G. SCHNEIDER, University of Michigan Museum of Zoology (UMMZ), Ann Arbor; R. W. MCDIARMID and W. R. HEYER, National Museum of Natural History (USNM), Washington, D.C.; J. CAMPBELL and C. FRANKLIN, The University of Texas at Arlington (UTA), Arlington; W. BÖHME, Zoologisches

Forschungsinstitut und Museum A. Koenig (ZFMK), Bonn; R. GÜNTHER, Museum für Naturkunde der Humboldt–Universität zu Berlin (ZMB), Berlin; and J. HALLERMANN, Zoologisches Institut und Zoologisches Museum der Universität Hamburg (ZMH), Hamburg.

I thank Larry D. WILSON, James R. MCCRANIE, David B. WAKE, Jay M. SAVAGE, Louis PORRAS, Eli GREENBAUM, Josiah H. TOWNSEND, Michael HARVEY, Martin JANSEN, Vincenzo MERCURIO, Andreas HERTZ, Sebastian LOTZKAT, Johannes J. KÖHLER, Ardiel Z. QUINTANA, and several other anonymous reviewers for their comments on earlier versions of the different portions of this thesis. Their suggestions improved substantially the whole work.

REFERENCES

AMPHIBIAWEB (2008): Information on amphibian biology and conservation. — http://www.amphibiaweb.org (viewed 11 May, 2008).

ANDERSSON, L. G. (1916): Notes on the reptiles and batrachians in the Zoological Musum at Gothenburg. — Medd. Göteborgs Mus. Zool., 9: 1–41.

BARBOUR, T. (1934): The anoles II. The mainland species from Mexico southward. — Bull. Mus. Comp. Zool., 77(4): 121–155.

BARBOUR, T. & A. LOVERIDGE (1929): Vertebrates from the Corn islands. Reptiles and amphibians. — Bull. Mus. Comp. Zool., 69: 138–146.

BOCOURT, M. F. (1873–1897): Études sur les reptiles. *In*: DUMERIL A., M. F. BOCOURT & F. MOCQUARD (Eds.), Etudes Recherches zoologiques pour sevir a l´histoire de la faune de l´Amérique Centrale et du Mexique. Mission Scientifique au Mexique et dans l´Amérique Centrale. Recherches Zoologiques. Part 3, sect. 1. — 1012 pp.; Paris (Imprimerie Impériale).

BOETTGER, O. (1892): Drei neue colubriforme Schlangen. — Zoologischen Anzeiger, 15: 417–420.

BOETTGER, O. (1898): Katalog der Reptilien-Sammlung im Museum der Senckenbergischen naturforschenden Gesellschaft. Gesellschaft II (Schlangen). — 160 pp.; Frankfurt a. M. (Knauer).

BOLAÑOS, F., F. CASTRO, C. CORTEZ, I. DE LA RIVA, T, GRANT, B. HEDGES, R. HEYER, R. IBAÑEZ, E. LA MARCA, E. LAVILLA, D. L. SILVANO, S. LÖTTERS, G. PARRA-OLEA, S. REICHLE, R. REYNOLDS, L. RODRÍGUEZ, G. SANTOS-BARRERA, N. SCOTT, C. UBEDA, A. VELOSO, M. WILKINSON & B. YOUNG (2008): Amphibians of the Neotropical realm. — pp. 92–99 *in*: STUART, S. N., M. N. HOFFMANN, A. CHANSON, N. A.COX, R. J. BERRIDGE, P. RAMANI & B. E. YOUNG (Eds.): Threatened amphibians of the world. — 758 pp.; Barcelona, Gland, and Arlington (Lynx edicions, IUCN, and Conservational international).

BOULENGER, G. A. (1885a): Catalogue of the lizards in the British Museum (Natural History). 2nd ed., Vol. I. — 436 pp.; London (Taylor & Francis).

BOULENGER, G. A. (1885b): Catalogue of the lizards in the British Museum (Natural History). 2nd ed., Vol. II. — 497 pp.; London (Taylor & Francis).

BOULENGER, G. A. (1893): Catalogue of the sankes in the British Museum (Natural History). Vol I. — 448 pp.; London (Taylor & Francis).

BOULENGER, G. A. (1894a): Catalogue of the sankes in the British Museum (Natural History). Vol II. — 382 pp.; London (Taylor & Francis).

BOULENGER, G. A. (1894b): Second report on additions to the lizard collection in the Natural-History Museum. — Proc. Zool. Soc. London, 1894: 722–736.

BOULENGER, G. A. (1896): Catalogue of the snakes in the British Museum (Natural History). Vol III. — 727pp.; London (Taylor & Francis).

BRAME, A. H., Jr. (1968): Systematics and evolution of the mesoamerican salamander genus *Oedipina*. — Journal of Herpetology, 2(1–2): 1–64.

BRAME, A. H. Jr. & D. B. WAKE (1963): Redescription of the plethodontid salamander *Bolitoglossa lignicolor* (PETERS), with remarks on the status of *B. palustris* TAYLOR. — Proceedings of the Biological Society of Washington, 76: 289–296.

BRATTSTROM, B. H. & T. R. HOWELL (1954): Notes on some collections of reptiles and amphibians from Nicaragua. — Herpetologica, 10(2): 114–123.

BREDER, C. M., JR. (1946): Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories and habits. — Bulletin of the American Museum of Natural History, 86(8): 375–436.

BROCCHI, M. P. (1883): Étude des Batraciens de l'Amerique Centrale. Mission Scientifique au Mexique et dans l´Amerique Centrale. Rech. Zool., 3(2): 1–122.

CAILLEAU, B. P. C. LAFEMINA & T. H. DIXON (2007): Stress accumulation between volcanoes: an explanation for intra-arc earthquakes in Nicaragua? — Geophys. J. Int., 169: 1132–1138.

CALDWELL, J. P. (1994): Natural history and survival of eggs and early larval stages of *Agalychnis calcarifer* (Anura: Hylidae). — Herpet. Nat. Hist., 2(2): 57–66.

CALDWELL, J. P. (1996): The evolution of myrmecophagy and its correlates in poison frogs (Family Dendrobatidae). — J. Zool. London, 240: 75–101.

CAMPBELL, H. W. & T. R. HOWELL (1965): Herpetological records from Nicaragua. — Herpetologica, 21: 130–140.

CAMPBELL, J. A. (1999): Distribution Patterns of Amphibians in Middle America. — pp. 111–210 *in*: DUELLMAN, W. E.: Patterns of distribution of amphibians: a global perspective. — 633 pp.; Baltimore and London (The Johns Hopkins Univ. Press).

CAMPBELL, J. A. & W. W. LAMAR (2004): The Venomous Reptiles of the Western Hemisphere. 2 Vols. — 616 pp.; Ithaca, New York (Comstock Publishing Associates).

CARR, M. J., I. SAGINOR, G. E. ALVARADO, L. L. BOLGE, F. N. LINDSAY, K. MILIDAKIS, B. D. TURRIN, M. D. FEIGENSON & C. C. SWISHER III (2007): Element fluxes from the volcanic front of Nicaragua and Costa Rica. — Geochemistry Geophysics Geosystems, 8(6): 1–22.

CHEN, S-H. (2005): Chromosomal variation in the *rhodopis* group of the southern Central American eleutherodactylinae frogs (Leptodactylidae: Eleutherodactylus). — pp. 102–144 *in*: DONNELLY, M. A., CROHER, B. I., GUYER, C., WAKE, M. H. & WHITE, M. E. (Eds.), Ecology & Evolution in the tropics. A herpetological perspective. — 675 pp.; Chicago (Univ. Chicago Press).

CISNEROS-HEREDIA, D. F. & R. W. MCDIARMID (2006): A new species of the genus *Centrolene* (Amphibia: Anura: Centrolenidae) from Ecuador with comments on the taxonomy and biogeography of Glassfrogs. — Zootaxa, 1244: 1–32.

COATES, A. G. & J. A. OBANDO (1996): The geologic evolution of the Central American Isthmus. — pp. 21–56 *in*: JACKSON, J. B. C., A. F. BUDD & A. G. COATES (Eds.), Evolution and environment in tropical America. — 425 pp.; Chicago (Univ. Chicago Press).

COCHRAN, D. M. (1961): Type specimens of reptiles and amphibians in the United States National Museum. — Smithsonian Institution, Bulletin of the United States National Museum, 220: 1–291.

COPE, E. D. (1861): Contributions to the ophiology of Lower California, Mexico and Central America. — Proc. Acad. Nat. Sci. Philadelphia, 13: 292–306.

COPE, E. D. (1862): Contributions to Neotropical saurology. — Proc. Acad. Nat. Sci. Philadelphia, 14: 176–188.

COPE, E. D. (1866): Fourth contribution to the herpetofauna of tropical America. — Proc. Acad. Nat. Sci. Philadelphia, 18: 123–132.

COPE, E. D. (1871a) [1870]: Catalogue of Batrachia and Reptilia obtained by J. A. MCNIEL in Nicaragua. — Second and Third Annual Reports of the Trustees of the Peabody Acad. Sci., 1869–70: 82–85.

COPE, E. D. (1871b): Ninth contribution to the herpetology of tropical America. — Proc. Acad. Nat. Sci. Philadelphia, 23: 200–224.

COPE, E. D. (1874): Description of some new species of reptiles obtained by Dr. John F. BRANSFORD, assistant surgeon, U.S. Navy, while attached to the Nicaraguan surveying expedition in 1873. — Proc. Acad. Nat. Sci. Philadelphia, 26: 64–72.

COPE, E. D. (1876): On the Batrachia and Reptilia of Costa Rica. — Journal of the Academy of Natural Sciences of Philadelphia, (2)8: 93–157.

COPE, E. D. (1885a) [1884]: Twelfth contribution to the herpetology of Tropical America. — Proc. Amer. Philos. Soc., 22: 167–194.

COPE, E. D. (1885b): A contribution to the herpetology of Mexico. — Proc. Amer. Philos. Soc., 22: 379–404.

COPE, E. D. (1886) [1885]: Thirteenth contribution to the herpetology of tropical America. — Proc. Amer. Philos. Soc., 23: 271–287.

COPE, E. D. (1887): Catalogue of the batrachians and reptiles of Central America and Mexico. — Bull. U. S. Natl. Mus. 32: 1–98.

COPE, E. D. (1893): Second addition to the knowledge of the Batrachia and Reptilia of Costa Rica. — Proc. Acad. Nat. Sci., 31: 333–347.

CRAWFORD, A. J. & C. N. SMITH (2005): Cenozoic biogeography and evolution in direct-developing frogs of Central America (Leptodactylidae: *Eleutherodactylus*) as inferred from a phylogenetic analysis of nuclear and mitochondrial genes. — Molecular Phylogenetics and Evolution, 35(3): 536–555.

CRAWFORD, J. (1902a): List of the most important volcanic eruptions and earthquakes in western Nicaragua within historic time. — The American Geologist, 30: 111–113.

CRAWFORD, J. (1902b): Additions to the list of Nicaragua volcanic eruptions in historic time. — The American Geologist, 30: 395–396.

DEVITT, T. J., T. J. LADUC & J. A. MCGUIRE (2008): The *Trimorphodon biscutatus* (Squamata: Colubridae) species complex revisited: a multivariate statistical analysis of geographic variation. — Copeia, 2008: 370–387.

DEVOLI, G., A. MORALES & K. HØEG (2007): Historical landslides in Nicaragua-collection and analysis of data. — Landslides, 2007(4): 5–18.

DÍEZ, M., P. C. LAFEMINA, C. B. CONNOR, W. STRAUCH & V. TENORIO (2005): Evidence for static stress changes triggering the 1999 eruprion of Cerro Negro Volcano, Nicaragua and regional aftershock sequences. — Geophysical Research Letters, 32: 1–4.

DINERSTEIN, E., D. M. OLSON, D. J. GRAHAM, A. L. WEBSTER, S. A. PRIMM, M. P. BOOKBINDER & G. LEDEC (1995): A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. — 129pp.; Washington D. C. (World Bank).

DIXON, J. R. (1960): The discovery of *Phyllodactylus tuberculosus* (Reptilia: Sauria) in Central America, the resurrection of *P. xanti*, and description of a new gecko from British Honduras. — Herpetologica, 16(1): 1–11.

DIXON, J. R. & B. L. TIPTON (2004): *Dryadophis* versus *Mastigodryas* (Ophidia: Colubridae): a proposed solution. — Herpetol. Rev., 35: 347–349.

DOWLING, H. G. (1952): A taxonomic study of the ratsnakes, genus *Elaphe* FITZINGER. The subspecies of *Elaphe flavirufa* (COPE). — Occas. Paps. Mus. Zool. Univ. Michigan, 540: 1–14.

DOWNS, F. L. (1967): Intrageneric relations among colubrid snakes of the genus *Geophis* WAGLER. — Misc. Publ. Mus. Zool. Univ. Michigan, 131: 1–193.

DUELLMAN, W. E. (1958): A monographic study of the colubrid snake genus *Leptodeira*. — Bull. Amer. Mus. Nat. Hist., 114(1): 1–152.

DUELLMAN, W. E. (1966): The Central American Herpetofauna: an ecological perspective. — Copeia, 1966(4): 700–719.

DUELLMAN, W. E. (1970): The hylid frogs of Middle America. Volumes I, II. — 753 pp.; Kansas (Monogr. Mus. Nat. Hist).

DUELLMAN, W. E. (1971): The burrowing toad, *Rhinophrynus dorsalis*, on the Carribean lowlands of Central America. — Herpetologica, **27**: 55–56.

DUELLMAN, W. E. (1990): Herpetofaunas in Neotropical Rainforrests: comparative composition, history, and resource use. — pp. 455–505 *in*: GENTRY, A. H. (Ed.): Four Neotropical rainforests. — New Haven (Yale Univ. Press).

DUELLMAN, W. E. (2001): The Hylid frogs of Middle America. New ed. — 1159 pp.; Ithaca, New York (Society for the study of amphibians and reptiles).

DUELLMAN, W. E. & L. TRUEB (1966): Neotropical hylid frogs, genus *Smilisca*. — Univ. Kansas Publ. Mus. Nat. Hist., 17(7): 281–375.

DUELLMAN, W. E. & L. TRUEB (1985) [1986]: Biology of amphibians. — 670 pp.; New York (McGraw-Hill).

DUMERIL, A. M. C., G., BIBRON & A. H. A. DUMERIL (1854): Erpétologie générale ou histoire naturelle complète des reptiles. Vol. 9. — 1536 pp.; Paris (Libraire Encyclopèdique de Roret).

DUNN, E. R. (1924): *Amastridium*, a neglected genus of snakes. — Proc. U. S. Natl. Mus., 65(11): 1–3.

DUNN, E. R. (1930): Notes on Central American *Anolis*. — Proceedings of the New England Zoological Club, 12: 15–24.

DUNN, E. R. (1933): A new lizard from Nicaragua. — Proceedings of the Biological Society of Washington, 46: 67–68.

DUNN, E. R. (1938): The snake genus *Enulius* COPE. — Proc. Acad. Nat. Sci. Philadelphia, 89: 415–418.

DUNN, E. R. (1940): Notes on some american lizards and snakes in the museum of Goteborg. — Herpetologica, 1(7): 189–194.

DUNN, E. R. & J. R. BAILEY (1939): Snakes from the uplands of the Canal Zone and of Darien. — Bull. Mus. Comp. Zool,. 86(1): 1–22.

DUNN, E. R. & J. T. EMLEN, Jr. (1932): Reptiles and amphibians from Honduras. — Proceedings of the Academy of Natural Science of Philadelphia, 84: 21–32.

DUNN, E. R. & L. H. SAXE (1950): Results of the Catherwood-Chaplin west indies expedition, 1948. Part V. Amphibinas and reptiles of San Andrés and Providencia. — Proc. Acad. Nat. Sci. Philadelphia, 102: 141–165.

ELIAS, P. (1984): Salamanders of the northwestern highlands of Guatemala. — Contributions in Science of the Natural History Museum of Los Angeles County, 348: 1–20.

ELMING, S-Å., P. LAYER & K. UBIETA (2001): A palaeomagnetic study and age determinations of Tertiary rocks in Nicaragua, Central America. — Geophys. J. Int., 147: 294–309.

ELMING, S-Å. & T. RASMUSSEN (1997): Results of magnetotelluric and gravimetric measurements in western Nicaragua, Central America. — Geophys. J. Int., 128: 647–658.

ERNST, C. H. (2008): *Trachemys emolli* (LEGLER). — Cat. Amer. Amph. Rept., 846: 1–3.

ERNST, C. H. & M. E. SEIDEL (2006): *Trachemys venusta* (GRAY). — Cat. Amer. Amph. Rept., 832: 1–12.

ETHERIDGE, R. (1959): The relationships of the anoles (Reptilia: Sauria: Iguanidae). An interpretation based on skeletal morphology. — 236 pp.; University of Michigan, Ann Arbor, Michigan, USA (unpublished Ph. Dissertation).

FAIVOVICH, J., C .F. B. HADDAD, P. C. A. GARCIA, D. R. FROST, J. A. CAMPBELL & W. C. WHEELER (2005): Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. — Bull. Amer. Mus. Nat. Hist., 294: 1–240.

FENZL, N. (1989): Nicaragua: Geografia, Clima, Geologia y Hidrogeología. — Belém (UFPA/INETER/INAN).

FITCH, H. S. & R. W. HENDERSON (1976): A new anole (Reptilia: Iguanidae) from great Corn Island, Caribean Nicaragua. — Milwaukee Publ. Mus. Contr. Biol. Geol., 9: 1–8.

FITCH, H. S. & D. M. HILLIS (1984): The *Anolis* dewlap: interspecific variability and morphological associations with habitat. — Copeia, 1984(2): 315–323.

FITCH, H. S. & R. A. SEIGEL (1984): Ecological and taxonomic notes on Nicaraguan anoles. — Milwaukee Public Museum Contributions in Biology and Geology, 57: 1–13.

FOUQUETTE, M. J., JR. (1961): Status of the frog *Hyla albomarginata* in Central America. — Feldiana Zool., 39(55): 595–601.

FREUNDT, A., S. KUTTEROLF, H. U. SCHINCKE, T. HANSTEEN, H. WEHRMANN, W. PEREZ, W. STRAUCH & M. NAVARRO (2006): Volcanic hazards in Nicaragua: past, present, and future. — pp. 141–165 *in*: ROSE, W. I., G. J. S. BLUTH, M. J. CARR, J. W. EWERT, L. C. PATINO & J. W. VALLANCE (Eds.): Volcanic hazards in Central America.

FROST, D. R. (2007): Amphibian Species of the World: an Online Reference. Version 5.1 — http://research.amnh.org (viewed 10 October, 2007).

FROST, D. R., T. GRANT, J. FAIVOVICH, R. H. BAIN, A. HAAS, C. F. B. HADDAD, R .O. DE SA, A. CHANNING, M. WILKINSON, S. C. DONNELLAN, C. J. RAXWORTHY, J. A. CAMPBELL, B. L. BLOTTO, P. MOLER, R. C. DREWES, R. A. NUSSBAUM, J. D. LYNCH, D. M. GREEN & W. C. WHEELER (2006): The amphibian tree of life. — Bull. Amer. Mus. Nat. Hist., 297: 1–370.

GAIGE, H. T., N. HARTWEG & L. C. STUART (1937): Notes on a collection of amphibians and reptiles from eastern Nicaragua. — Occasional Papers Museum of Zoology University of Michigan, 357: 1–18.

GAMBLE, T., A. M. BAUER, E. GREENBAUM & T. R. JACKMAN (2008a): Evidence for Godwanan vicariance in an ancient clade of gecko lizards. — J. Biogeography, 35: 88–104.

GAMBLE, T., A. M. BAUER, E. GREENBAUM & T. R. JACKMAN (2008b): Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata). — Zool. Scripta, 37: 355–366.

GARCÍA-PARÍS, M., G. PARRA-OLEA, A. H. BRAME & D. B. WAKE (2003) [2002]: Systematic revision of the *Bolitoglossa mexicana* species group (Amphibia: Plethodontidae) with description of a new species from México. — Revista Española de Herpetología, 16: 43–71.

GARCÍA-PARÍS, M., G. PARRA-OLEA & D. B. WAKE (2000): Phylogenetic relationships within the lowland tropical salamanders of the *Bolitoglossa mexicana* complex (Amphibia: Plethodontidae). — pp. 199–214 *in*: BRUCE, R. C., JAEGER, R. G. & HOUCK, L. D. (Eds.], The biology of plethodontid salamanders. — 485 pp.; New York (Plenum).

GARMAN, S. W. (1884) [1883]: The reptiles and bathrachians of North America. 1. Ophidia – Serpentes. — Mem. Mus. Comp. Zool., 8(3): 1–185.

GILLESPIE, T. W., K. E. NICHOLSON & J. MCCRARY (2001): Patterns of vertebrate species richness and conservation in Nicaragua. — Natural Areas Journal, 21(2): 159–167.

GRAHAM, A. (1992): Utilization of the isthmian land bridge during the Cenozoic-paleobotanical evidence for timing, and the selective influence of altitudes and climate. — Review of Palaeobotany and Palynology, 72(1992): 119–128.

GRANT, T., D. R. FROST, J. P. CALDWELL, R. GAGLIARDO, C. F. B. HADDAD, P. J. R. KOK, D. B. MEANS, B. P. NOONAN, W. E. SCHARGEL & W. C. WHEELER (2006): Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). — Bull. Amer. Mus. Nat. Hist., 299: 1–262.

GRAY, J. E. (1831): A synopsis of the species of the class Reptilia. — pp. 1–110 *in*: GRIFFITH, E. & PIDGEON, E. (Eds.), The animal kingdom arranged in conformity with its organization by the Baron CUVIER with additional descriptions of all the species hitherto named, and of many others. Vol. 9. — 481 pp.; London (Whittaker, Teacher, and Co.).

GRAY, J. E. (1868): Notice of two species of *Salamandra* from Central America. — Annals and Magazine of Natural History, (4) 2(10): 297–298.

GRIFFITH, H., A. NGO & R. W. MURPHY (2000): A cladistic evaluation of the cosmopolitan genus *Eumeces* WIEGMANN (Reptilia, Squamata, Scincidae). — Russian J. Herpetol., 7(1): 1–16.

GUYER, C. & M.A. DONNELLY (2005): Amphibians and Reptiles of La Selva, Costa Rica, and the Carribean slope. — 299 pp; Berkeley, Los Angeles and London (Univ. California Press).

GÜNTHER, A. C. L. G. (1885–1902): Reptilia and Batrachia. *In* O. SALVIN & F. D. GODMAN (Eds.), Biologia Centrali-Americana; or, Contributions to the Knowledge of the Fauna and Flora of Mexico and Central America. — 326 pp.; London (R. H. Porter and Dulau and Co.).

HALLOWELL, E. (1855): Contributions to South American herpetology. — J. Acad. Nat. Sci. Philadelphia, (2)3: 33–36.

HALLOWELL, E. (1861) [1860]: Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John ROGERS, U. S. N. — Proc. Acad. Nat. Sci. Philadelphia, 12: 479–510.

HARRIS, D. M. & A. G. KLUGE (1984): The *Sphaerodactylus* (Sauria: Gekkonidae) of Middle America. — Occ. Pap. Mus. Zool. Univ. Michigan, 706: 1–59.

HAYES, M. P. & P. H. STARRETT (1980): Notes on a collection of centronelid frogs from the Colombian Chocó. — Bull South. Calif. Acad. Sci., 79(3): 89–96.

HAZLETT, R. W. (1987): Geology of the San Cristobal volcanic complex, Nicaragua. — Journal of Volcanology and Geothermal Research, 33(1987): 223–230.

HEDGES, S. B., W. E. DUELLMAN & M. P. HEINICKE (2008): New World direct-developing frogs (Anura: Terrarana); molecular phylogeny, classification, biogeography, and conservation. — Zootaxa, 1737: 1–82.

HENDERSON, R. W., J. VILLA & J. R. DIXON (1976): *Lepidodactylus lugubris* (Reptilia: Gekkonidae): a recent addition to the herpetofauna of Nicaragua. — Herp. Review, 7(4): 173.

HEYER, W. R. (2002): *Leptodactylus fragilis*, the valid name for the Middle American and northern South American White-lipped Frog (Amphibia: Leptodactylidae). — Proc. Biol. Soc. Washington, 115: 321–322.

HEYER, W. R. (2005): Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, northern South America and Amazonia. — Arq. Zool. São Paulo, 37: 269–348.

HOLDRIDGE, L. R. (1967): Life zone ecology. Revised edition. — 206 pp.; San José (Tropical Science Center).

INCER, J. (1973): Geografía Ilustrada de Nicaragua. — Managua (Recalde).

INDEXMUNDI (2006): Central America and the Caribbean. Nicaragua. — http://www.indexmundi.com (viewed 20 September, 2006).

INEC (2006a): VIII Censo de Población y IV de Vivienda, 2005; Población, Vivienda y Hogar. — Managua, Nicaragua (Instituto Nacional de Estadísticas y Censos).

INEC (2006b): Instituto Nacional de Estadísticas y Censos. Estadísticas. — http://www.inec.gob.ni (viewed 20 September, 2006).

IUCN (2007): 2007 IUCN Red List of threatened species. — http://www.iucnredlist.gob (viewed 12 October, 2007).

IVERSON, J. B. (1980): *Kinosternon angustipons*. — Catalogue of American Amphibian and Reptiles, 262: 1–2.

IVERSON, J. B. (1986): A checklist with distribution maps of the turtles of the world. — 283 pp.; Richmond (Paust Printing).

IVERSON, J. B. (1992): A revised checklist with distribution maps of the turtles of the world. — 363 pp.; Richmond (privately printed).

JACKSON, J. T., D. E. STARKEY, R. W. GUTHRIE & M. R. J. FORSTNER (2008): A mitochondrial DNA phylogeny of extant species of the genus *Trachemys* with resulting taxonomic implications. — Chelonian Cons. Biol., 7(1): 131–135.

JAN, G. (1865): Enumerazione sistematica degli ofidi appartenenti al gruppo Potamophilidae. — Arch. Zool. Anat. Phys., 3: 201–265.

JANSEN, M. (2001): Biogeographische Analyse der Herpetofauna von ausgewählten Hochlandgebieten Nicaraguas. — 101 pp.; Johann Wolfgang Goethe-Universität Frankfurt am Main, Germany (unpublished thesis).

JANSEN, M. & G. KÖHLER (2001): Ökologie des Mombacho-Salamanders, *Bolitoglossa mombachoensis* KÖHLER & MCCRANIE, 1999, am Volcán Mombacho, Nicaragua (Caudata: Plethodontidae). — Salamandra, 37(2): 83–98.

JANSEN, M. & G. KÖHLER (2002): Biogeografische Analyse der Herpetofauna von ausgewählten Hochlandgebieten Nicaraguas. — Salamandra, 38(4): 269–286.

JOSSE, C., G. NAVARRO, P. COMER, R. EVANS, D. FABER-LANGENDOEN, M. FELLOWS, G. KITTEL, S. MENARD, M. PYNE, M. REID, K. SCHULZ, K. SNOW & J. TEAGUE (2003): Ecological systems of Latin America and the Caribbean: a working classification of terrestrial systems. — 47 pp.; Arlington (NatureServe).

KÖHLER, G. (1997): Geographical distribution. *Ungaliophis continentalis*. — Herp. Rev., 28(4): 211.

KÖHLER, G. (1998a): Geographical distribution. *Eleutherodactylus lauraster*. — Herp. Rev., 29(4): 246.

KÖHLER, G. (1998b): Herpetologische Beobachtungen in Nicaragua. — Natur und Museum, 128(6): 162–170.

KÖHLER, G. (1999a): Eine neue Saumfingerart der Gattung *Norops* von der Pazifikseite des nördlichen Mittelamerika. — Salamandra, 35(1): 37–52.

KÖHLER, G. (1999b): The amphibians and reptiles of Nicaragua – a distributional checklist with keys. — Courier Forschungsinstut Senckenberg, 213: 1–212.

KÖHLER, G. (1999c): Geographical distribution. *Tantilla lintolini*. — Herp. Review, 30(1): 55.

KÖHLER, G. (2000a): Erste herpetologische Expedition zum Cerro Saslaya, Nicaragua. — Natur und Museum, 130(3): 61–69.

KÖHLER, G. (2000b): Reptilien und Amphibien Mittelamerikas. Band 1. Krokodile, Schildkröten, Echsen. — 258 pp.; Offenbach (Herpeton).

KÖHLER, G. (2001): Anfibios y Reptiles de Nicaragua. — 208 pp.; Offenbach (Herpeton).

KÖHLER, G. (2002): A new species of salamander of the genus *Nototriton* from Nicaragua (Amphibia: Caudata: Plethodontidae). — Herpetologica, 58(2): 205–210.

KÖHLER, G. (2003): Reptiles of Central America. — 367 pp.; Offenbach (Herpeton).

KÖHLER, G. (2008): Reptiles of Central America, 2nd ed. — 400 pp.; Offenbach (Herpeton).

KÖHLER, G. & J. KREUTZ (1999): *Norops macrophallus* (WERNER, 1917), a valid species of anole from Guatemala and El Salvador (Squamata: Sauria: Iguanidae). — Herpetozoa, 12(1/2): 57–65.

KÖHLER, G. & J. R. MCCRANIE (1999a): A new species of salamander from Volcán Mombacho, Nicaragua, formerly referred to *Bolitoglossa striatula* (Amphibia, Caudata, Plethodontidae). — Senckenbergiana biologica, 79(1): 89–93.

KÖHLER, G. & J. R. MCCRANIE (1999b): A new species of colubrid snake of the *Rhadinaea godmani* group from Cerro Saslaya, Nicaragua. — Senckenbergiana biologica, 79(2): 243–249.

KÖHLER, G. & J. R. MCCRANIE (2001): Two new species of anoles from northern Honduras (Squamata: Polychrotidae). — Senckenbergiana biologica, 81: 235–245.

KÖHLER, G., J. R. MCCRANIE, K. E. NICHOLSON & J. KREUTZ (2003): Geographic variation in hemipenial morpholgy in *Norops humilis* (PETERS 1863), and the systematic status of *Norops quaggulus* (COPE 1885) (Reptilia, Squamata: Polychrotidae). — Senckenbergiana biologica, 82(1/2): 213–222.

KÖHLER, G., J. R. MCCRANIE & L. D. WILSON (1999): Two new species of anoles of the *Norops crassulus* group from Honduras (Reptilia: Sauria: Polychrotidae). — Amphibia-Reptilia, 20: 279–298.

KÖHLER, G., J. R. MCCRANIE & L. D. WILSON (2001): A new species of anole from western Honduras (Squamata: Polychrotidae). — Herpetologica, 57(3): 247–255.

KÖHLER, G. & M. OBERMEIER (1998): A new species of anole of the *Norops crassulus* group from central Nicaragua (Reptilia: Sauria: Iguanidae). — Senckenbergiana biologica, 77(2): 127–137.

KÖHLER, G., M. PONCE, J. SUNYER & A. BATISTA (2007): Four new species of anoles (genus *Anolis*) from the Serranía del Tabasará, west-central Panama (Squamata: Polychrotidae). — Herpetologica, 63(3): 375–391.

KÖHLER, G., A. Z. QUINTANA, F. BUITRAGO & H. DIETHERT (2004): New and noteworthy records of amphibians and reptiles from Nicaragua. — Salamandra, 40(1): 15–24.

KÖHLER, G. & F. SCHMIDT (2000): Zweite herpetologische Expedition zum Cerro Saslaya, Nicaragua. — Natur und Museum, 130(3): 69–74.

KÖHLER, G., A. SCHULZE & M. VESELÝ (2005): Morphological variation in *Norops capito* (PETERS, 1863), a wide-spread species in southeastern Mexico and Central America. — Salamandra, 41(3): 129–136.

KÖHLER, G. & R. SEIPP (1998): Eine Expedition in den Randbereich des Biophärenreservats Bosawás, Nicaragua. — Natur und Museum, 128(6):170–175.

KÖHLER, G. & E. N. SMITH (2008): A new species of anole of the *Norops schiedei* group from western Guatemala (Squamata: Polychrotidae). — Herpetologica, 64(2): 216–223.

KÖHLER, G. & J. SUNYER (2006): A new species of rain frog (genus *Craugastor*) of the *fitzingeri* group from Río San Juan, southeastern Nicaragua. — Senckenbergiana biologica, 86: 261–266.

KÖHLER, G. & J. SUNYER (2008): Two new species of anoles formerly referred to as *Anolis limifrons* (Squamata: Polychrotidae). — Herpetologica, 64(1): 92–108.

KÖHLER, G. & M. VESELÝ & E. GREENBAUM (2006): The amphibians and reptiles of El Salvador. —238 pp.; Malabar (Krieger).

KÖHLER, G. & E. VIELMETTER (2002): *Dipsas articulata* (COPE, 1868) in Nicaragua. — Herpetozoa, 14(3/4): 169–170.

LANZA, B. & S. BOSCHERINI (2000): The gender of the genera *Podacris* WAGLER 1830 (Lacertidae), *Pelamis* DAUDIN 1803 (Hydrophiidae) and *Uropeltis* CUVIER 1828 (Uropeltidae). — Tropical Zoology, 13: 327–329.

LEE, J. C. (1980): Variation and Systematics of the *Anolis sericeus* complex (Sauria: Iguanidae). — Copeia 1980(2): 310–320.

LEE, J. C. (1996): The amphibians and reptiles of the Yucatán Peninsula. — 500 pp.; Ithaca (Cornell Univ. Press).

LEEDS, D. J. (1974): Catalog of Nicaraguan earthquakes. — Bull. Seismological Soc. Am., 64(4): 1135–1158.

LEGLER, J. M. (1965): A new species of turtle, genus *Kinosternon* from Central America. — University of Kansas Publications of the Museum of Natural History, 15(13): 615–625.

LEGLER, J. M. (1966): Notes on the natural history of a rare Central American turtle, *Kinosternon angustipons* LEGLER. — Herpetologica, 22(2): 118–122.

LEVITON, A. E., R. H. GIBBS Jr., E. HEAL & C. E. DAWSON (1985): Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. — Copeia, 1985(3): 802–832.

LIPS, K. R., P. A. BURROWES, J. R. MENDELSON III & G. PARRA-OLEA (2005): Amphibian population declines in Latin America: a synthesis. — Biotropica, 37: 222–226.

LIPS, K. R., F. BREM, R. BRENES, J. D. REEVE, R. A. ALFORD, J. VOYLES, C. CAREY, L. LIVO, A. P. PESSIER & J. P COLLINS (2006): Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. — PNAS, 103(9): 3165–3170.

LIPS, K. R., J. DIFFENDORFER, J. R. MENDELSON III & M. W. SEARS (2008): Riding the wave: reconciling the roles of disease and climate change in Amphibian declines. PLoS Biol. 6 (3): e72. doi:101371/journal.pbio.0060072. (http://www.plosbiology.org).

LYNCH, J. D. & C. W. MYERS (1983): Frogs of the *fitzingeri* group of *Eleutherodactylus* in eastern Panama and Chocoan South America (Leptodactylidae). — Bulletin of the American Museum of Natural History, 15(5): 481–572.

MARENA (1999): Ministerio del Ambiente y los Recursos Naturales-Biodiversidad en Nicaragua, un Estudio de País. Managua, Nicaragua.

MARENA (2007): Ministerio del Ambiente y los Recursos Naturales. Nicaragua. — http://www.marena.gob.ni (viewed on 11 November, 2007).

MARENA-CBA, CONSORCIO BRLINGENIERIE, VEGA ENVIRONMENTAL SERVICES & WILDLIFE CONSERVATION SOCIETY (2004): Elaboración de planes de manejo de las áreas protegidas de Cerro Silva, Wawashan y Cayos Miskitos y ordenamiento territorial del Municipio de Waspám. — 184 pp.; Managua (Marena).

MARSHALL, J. S. (2007): The geomorphology and physiographic provinces of Central America. — pp. 1–51 *in*: BUNDSCHU, J. & G. ALVARADO (Eds.): Central America: geology, resources and hazards. — Leiden (Taylor & Francis).

MARTÍNEZ-SÁNCHEZ, J. C., J. M. MAES, E. VAN DEN BERGE, S. MORALES & E. A. CASTAÑEDA (2001): Biodiversidad zoológica en Nicaragua. Proyecto estrategia nacional de biodiversidad y su plan de acción. — 176 pp.; Managua (PNUD-MARENA).

MAYORGA, H. (1967): Informe sobre una coleccion de anfibios (Salientia) procedentes de Nicaragua. — Carib. J. Sci., 7: 69–77.

MCCOY, C. J. Jr. (1968). A rewiew of the genus *Laemanctus* (Reptilia: Iguanidae). — Copeia, 1968(4): 665–678.

MCCRANIE, J. R. (2006): Northeastern Honduras and the systematics of the colubrid snake *Scaphiodontophis*. — Carib. J. Sci., 42: 136–138.

McCRANIE, J. R. & F. E. CASTAÑEDA (2007): Guía de campo de los anfibios de Honduras. — 304 pp.; Salt Lake City (Bibliomania).

McCRANIE, J. R., J. H. TOWNSEND & L. D. WILSON (2006): The Amphibians and Reptiles of the Honduran Mosquitia. — 291 pp.; Malabar, Florida (Krieger).

McCRANIE, J. R., D. R. VIEITES & D. B. WAKE (2008): Description of a new divergent lineage and three new species of Honduran salamanders of the genus *Oedipina* (Caudata, Plethodontidae). — Zootaxa, 1930:1–17

McCRANIE, J. R. & L. D. WILSON (1993): Taxonomic changes associated with the names *Hyla spinipollex* SCHMIDT and *Ptychohyla merazi* WILSON & McCRANIE (Anura: Hylidae). — Southwestern Naturalist, 38(2): 100–104.

McCRANIE, J. R. & L. D. WILSON (2002): The Amphibians of Honduras. — 625 pp.; Ithaca, New York (Society for the Study of Amphibians and Reptiles).

MEYRAT, A. (2001): Conservación de los ecosistemas y la flora silvestre. — 189 pp.; Managua (MARENA-PNUD).

MENDOZA-QUIJANO, F., O. FLORES-VILLELA & J. W. SITES (1998): Genetic variation, species status, and phylogenetic relationships in rose-bellied lizards (*variabilis* group) of the genus *Sceloporus* (Squamata: Phrynosomatidae). — Copeia, 1998: 354–366.

MERTENS, R. (1952a): Neues über die Reptilienfauna von El Salvador. — Zoologischer Anzeiger, 148(3/4): 87–93.

MERTENS, R. (1952b): Die amphibien und Reptilien von El Salvador, auf Grund der Reise von R. MERTENS und A. ZILCH. — Abhandlungen senckenbergishen naturforschenden Gesellschaft, 487: 1–120.

MEYER, J. R. & L. D. WILSON (1971) [1972]: Taxonomic studies and notes on some Honduran amphibians and reptiles. — Bulletin of the Southern California Academy of Sciences, 70(3): 106–114.

MORGAN, J. P., C. R. RANERO & P. VANUCCHI (2008): Intra-arc extension in Central America: links between plate motions, tectonic, volcanism, and geochemistry. — Earth and Planetary Sci. Lett., 272: 365–371.

MYERS, C. W. (1974): The systematic of *Rhadinaea* (Colubridae), a genus of new world snakes. — Bull. Amer. Mus. Nat. Hist., 153(1): 1–261.

MYERS, C. W., E. E. WILLIAMS & R. W. MCDIARMID (1993): A new anoline lizard (*Phenacosaurus*) from the highland of Cerro de la Neblina, southern Venezuela. — American Museum Novitates, 3070: 1–15.

NASCIMENTO, L. B., U. CERAMASCHI & C. A. G. CRUZ (2005): Taxonomic review of the species group of the genus *Physalaemus* FITZINGER, 1826 with revalidation of the genera *Engystomops* JIMENEZ DE LA ESPADA, 1872 and *Eupemphix* STEINDACHNER, 1836 (Amphibia, Anura, Leptodactylidae). — Arquiv. Mus. Nac. Rio de Janeiro, 63: 297–320.

NELSON, C. E. (1973): Systematics of the Middle American upland populations of *Hypopachus* (Anura: Microhylidae). — Herpetologica, 39: 6–17.

NELSON, C. E. (1974): Further studies on the systematics of *Hypopachus* (Anura: Microhylidae). — Herpetologica, 30: 250–274.

NIETSCHMANN, B. (1977): Memorias de Arrecife Tortuga: Historia Natural y Económica de las tortugas en el Caribe de América Central. No. 30. Serie Geografia y Naturaleza. — 258 pp.; Managua (Fondo de promocion cultural, Banco de América).

NIETSCHMANN, B. (1990): Conservation by conflict in Nicaragua. — Natural History, 11: 42–49.

NOBLE, G. K. (1918): The amphibians collected by the American Museum expeditions to Nicaragua in 1916. — Bull. Amer. Mus. Nat. Hist., 38(10): 311–347.

NORES, M. (2004): The implications of Tertiary and Quaternary sea level rise events for avian distribution patterns in the lowlands of northern South America. — Global Ecol. Biogeogr., 13: 149–161.

OLIVER, J. A. (1948): The relationships and zoogeography of the genus *Thalerophis* OLIVER. — Bull. Amer. Mus. Nat. Hist., 92(4): 161–280.

PARRA-OLEA, G. (2008): Neotropical salamanders. — pp. 102 *in*: STUART, S. N., M. N. HOFFMANN, A. CHANSON, N. A.COX, R. J. BERRIDGE, P. RAMANI & B. E. YOUNG (Eds.): Threatened amphibians of the world. — 758 pp.; Barcelona, Gland, and Arlington (Lynx edicions, IUCN, and Conservational international).

PARRA-OLEA, G., M. GARCÍA-PARÍS & D. B. WAKE (2004): Molecular diversification of salamanders of the tropical American genus *Bolitoglossa* (Caudata: Plethodontidae) and its evolutionary and biogeographical implications. — Biological Journal of the Linnean Society, 81: 325–346.

PETERS, J. A. & R. DONOSO-BARROS (1970): Catalogue of the Neotropical Squamata. Part II. Lizards and amphisbaenians. — Bull. U. S. Natl. Mus., 297: 1–293.

PETERS, J. A. & B. OREJAS-MIRANDA (1970): Catalogue of the Neotropical Squamata. Part I. Snakes. — Bull. U.S. Natl. Mus., 297: 1–347.

PETERS, W. C. H. (1863): Über einige neue Arten der Saurier-Gattung *Anolis*. — Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, 1863: 135–149.

PETERS, W. C. H. (1873a): Über eine neue Schildkrötenart *Cinosternon Effeldtii* und andere neue oder weniger bekannte Amphibien. — Monatsbericht der Königlich-Preussischen Akademie der Wissenschaften zu Berlin, 1873: 603–618.

PETERS, W. C. H. (1873b): Über neue Saurier (*Spaeriodactylus, Anolis, Phrynosoma, Tropidolepisma, Lygosoma, Ophioscincus*) aus Centralamerica, Mexico und Australien. — Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 1873: 738–747.

PETERS, W. C. H. (1882): Eine neue Art der urodelen Batrachier, *Oedipus yucatanus,* aus Yucatán (Centralamerica). — Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1882: 137–138.

PHILLIPS, C. A., W. W. DIMMICK & J. L. CARR (1996): Conservation genetics of the common snapping turtle (*Chelydra serpentina*). — Conservation biology, 10: 397–405.

POE, S. (2004): Phylogeny of anoles. — Herpetological Monographs, 18: 37–89.

POLET, J. & H. KANAMORI (2000): Shallow subduction zone earthquakes and their tsunamigenic potential. — Geophys. J. Int., 142: 684–702.

PONSOL, B. (1958): Zonas Biogeográficas de la Flora y Fauna Nicaraguense y Factores Asociados. Publ. No. 8. — Managua, Nicaragua.

POUGH, F. H., R. M. ANDREWS, J. E. CADLE, M. L. CRUMP, A. H. SAVITZKY & K. D. WELLS (2004): Herpetology. 3rd ed. — Upper Saddle River, New Jersey (Prentice-Hall, Inc.).

POUNDS, J. A., M. P. L. FOGDEN, J. M. SAVAGE & G. C. GORMAN (1997): Tests of null models for amphibian declines on a tropical mountain. — Conservation biology, 11(6): 1307–1322.

POUNDS, J. A., M. R. BUSTAMANTE, L. A. COLOMA, J. A. CONSUEGRA, M. P. L. FOGDEN, P. N. FOSTER, E. LA MARCA, K. L. MASTERS, A. MERINO-VITERI, R. PUSCHENDORF, S. R. RON, G. ARTURO SÁNCHEZ-AZOFEIFA, C. J. STILL & B. E. YOUNG (2006): Widespread amphibian extinctions from epidemic disease driven by global warming. — Nature, 439: 161–167.

PRAMUK, J. B., T. ROBERTSON, J. W. SITES JR. & B. P. NOONAN (2008): Around the world in 10 million years: biogeography of the cosmopolitan true toads (Anura: Bufonidae). — Global Ecol. Biogeogr., 17: 72–83.

PRB (2008): Population Reference Bureau. — http://www.prb.org (viewed 20 March, 2008).

QUINTANA, A. Z. (2005): Amphibian communities along an elevational gradient at the Cerro Saslaya National Park in the BOSAWAS Biosphere Reserve, Nicaragua. — 163 pp.; Bayerische Julius-Maximilians Universität Würzburg, Germany (unpublished thesis).

REEDER, T. W. (1990): *Eumeces managuae* DUNN. — Catalogue of American Amphibians and Reptiles, 467: 1–2.

REEDER, T. W., C. J. COLE & H. C. DESSAUER (2002): Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. — Amer. Mus. Novitates, 3365: 1–61.

RUEDA, R. (2007): Recopilación de la información sobre la biodiversidad de Nicaragua. — 202 pp.; Managua (UNAN-León/Norwegian ministery of foreign affaire/INBio).

RUIZ, G. A. (1996): Claves preliminares para reconocer a los reptiles de Nicaragua. — 88 pp.; Managua (CEDAPRODE).

RUIZ, G. A. & F. BUITRAGO (2003): Guía ilustrada de la herpetofauna de Nicaragua. — 331 pp.; Managua (ARAUCARIA-MARENA-AECI).

SALAS, J. A. (1993): Árboles de Nicaragua. — 390 pp.; Managua (Hispamer-IRENA).

SANDERS, O (1973): A new leopard frog (*Rana berlandieri brownorum*) from southern Mexico. — Journal of Herpetology, 7(1): 87–92.

SAVAGE, J. M. (1966): The origins and history of the Central American herpetofauna. — Copeia, 1966(4): 719–766.

SAVAGE, J. M. (1967): The systematic status of the toad *Bufo politus* COPE, 1862. — Copeia, 1967(1): 225–226.

SAVAGE, J. M. (1970): On the trail of the golden frog: with WARSZEWICZ and GABB in Central America. — Proceedings of the California Academy of Sciences, 4, 38(14): 273–288.

SAVAGE, J. M. (1973a): Herpetological collections made by Dr. John F. BRANSFORD, Assistant Surgeon, U.S.N. during the Nicaragua and Panama Canal Surveys (1872–1885). — Journal of Herpetology, 7(1): 35–38.

SAVAGE, J. M. (1973b): The geographic distribution of frogs: patterns and predictions. — pp. 351–445 *in*: VIAL, J. L. (Ed.): Evolutionary biology of the anurans: contemporary research on major problems. — Columbia (Univ. Missouri Press).

SAVAGE, J. M. (1982) [1983]: The enigma of the Central American herpetofauna: dispersals or vicariance? — Ann. Missouri Botan. Gard., 69(3): 464–547.

SAVAGE, J. M. (1987): Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae). — Fieldiana Zoology, New Series, 33: 1–57.

SAVAGE, J. M. (1997): On terminology for the description of the hemipenes of squamate reptiles. — Herpetological Journal, 7(1): 23–25.

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

SAVAGE, J. M. J. A. CAMPBELL & W. W. LAMAR (2005): On names for Neotropical Rattlesnakes (Reptilia: Serpentes: Viperidae: *Crotalus*). — Herpetol. Rev., 36: 369–371.SAVAGE, J. M. & B. I. CROTHER (1989): The status of *Pliocercus* and *Urotheca* (Serpentes: Colubridae), with a review of included species of coral snake mimics. — Zool. J. Linnean Soc., 95: 335–362.

SAVAGE, J. M. & S. B. EMERSON (1970): Central American frogs allied to *Eleutherodactylus bransfordii* (COPE): a problem of polymorphism. — Copeia, 1970(4): 623–644.

SAVAGE, J. M., B. D. HOLLINGSWORTH, K. R. LIPS & A. P. JASLOW (2004): A new species of rainfrog (genus *Eleutherodactylus*) from the Serranía de Tabasará, West-Central Panama, and reanalysis of the *fitzingeri* species group. — Herpetologica, 60(4): 519–529.

SAVAGE, J. M., J. R. MCCRANIE & M. ESPINAL (1996): A new species of *Eleutherodactylus* from Honduras related to *E. bransfordii* (Anura: Leptodactylidae). — Proc. Biol. Soc. Washington, 109(2): 366–372.

SAVAGE, J. M. & C. W. MYERS (2002): Frogs of the *Eleutherodactylus biporcatus* Group (Leptodactylidae) of Central America and northern South America, including rediscovered, resurrected, and new taxa. — Bull. Amer. Mus. Nat. Hist., 3347: 1–48.

SAVAGE, J. M. & J. L. VIAL (1974) [1973]: The venomous coral snakes (genus Micrurus) of Costa Rica. — Rev. Biol. Trop., 21(2): 295–349.

SAVAGE, J. M. & J. VILLA (1986): Introduction to the herpetofauna of Costa Rica/Introducción a la herpetofauna de Costa Rica. Contributions to Herpetology 5. — 207 pp.; Ohio (Society for the Study of Amphibians and Reptiles).

SCHMIDT, K. P. (1932): Stomach contents of some American coral snakes, with the description of a new species of *Geophis*. — Copeia, 1932(1): 6–9.

SCHMIDT, K. P. (1936a): Guatemalan salamanders of the genus *Oedipus*. — Zoological Series of the Field Museum of Natural History, 20(17): 135–166.

SCHMIDT, K. P. (1936b): Notes on Central American and Mexican coral snakes. — Zool. Ser. Field Mus. Nat. Hist. Chicago, 20(20): 205–216.

SEIDEL, M. E. (2002): Taxonomic observations on extant species and subspecies of slider turtles, genus *Trachemys*. — J. Herpetol., 36: 285–292.

SMITH, H. M. (1939): The Mexican and Central American lizards of the genus *Sceloporus*. — Zool. Ser. Field. Mus. Nat. Hist., 26: 1–397.

SMITH, H. M. (1941a): Notes on the sanke genus *Trimorphodon*. — Proceedings of the US National Museum, 91: 149–168.

SMITH, H. M. (1941b): A new name for the Mexican snake of the genus *Dendrophidion*. — Proc. Biol. Soc. Wash., 54: 73–76.

SMITH, H. M. (1959): Herpetozoa from Guatemala, I. — Herpetologica, 15(4): 210–216.

SMITHE, F. B. (1975–1981): Naturalist's color guide. Part I. Color guide. — 182 color swatches; New York (American Museum of Natural History).

SOLÓRZANO, A. (2004): Serpientes de Costa Rica: Distribución, Taxonomía e Historia Natural / Snakes of Costa Rica: Distribution, Taxonomy, and Natural History. — 791 pp.; Santo Domingo de Heredia (Editorial INBio).

SPINKS, P. Q., H. B. SHAFFER, J. B. IVERSON & W. P. MCCORD (2004): Phylogenetic hypotheses for the turtle family Geoemydidae. — Mol. Phylogen. Evol., 32: 164–182.

STAFFORD, P. J. (2002): Record of the colubrid snake *Dendrophidion nuchale* (PETERS) from Nicaragua. — Southwest. Nat., 47(4): 615–616.

STEHLI, F. G. & S. D. WEBB (1985): The great American interchange. — 432 pp.; New York (Plenum Press).

STEJNEGER, L. (1907): A new salamander from Nicaragua. — Proc. U.S. Natl. Mus., 32: 465–466.

STUART, L. C. (1935): A new *Anolis* from northern Central America. — Occasional Papers of the Museum of Zoology, University of Michigan, 310: 1–4.

STUART, L. C. (1943): Taxonomic and geographic comments on Guatemalan salamanders of the genus *Oedipus*. — Miscellaneous publications of the Museum of Zoology, University of Michigan, 56: 1–37.

STUART, L. C. (1948): The amphibians and reptiles of Alta Verapaz, Guatemala. — Miscellaneous Publications Museum of Zoology, University of Michigan, 69: 1–109.

STUART, L. C. (1955): A brief review of the Guatemalan lizards of the genus *Anolis*. — Miscellaneous Publications Museum of Zoology, University of Michigan, 91: 1–31.

STUART, L. C. (1963): A checklist of the herpetofauna of Guatemala. — Miscellaneous Publications Museum of Zoology, University of Michigan, 122: 1–150.

STUART, L. C. (1966): The environment of the Central American cold-blooded vertebrate fauna. — Copeia; 1966(4): 684–699.

STUART, S. N., J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN & R. W. WALLER (2004): Status and trends of amphibian declines and extinctions worldwide. — Science, 306: 1783–1786.

STUART, S. N., M. N. HOFFMANN, A. CHANSON, N. A.COX, R. J. BERRIDGE, P. RAMANI & B. E. YOUNG (2008): Threatened amphibians of the world. — 758 pp.; Barcelona, Gland, and Arlington (Lynx edicions, IUCN, and Conservational international).

STULL, O. G. (1935): A checklist of the family Boidae. — Proc. Boston Soc. Nat. Hist., 40: 387–408.

SUNYER, J. & G. KÖHLER (2007): New country and departmental records of herpetofauna in Nicaragua. — Salamandra, 43: 15–20.

TAYLOR, B. W. (1963): An outline of the Vegetation of Nicaragua. — Journal of Ecology, 51: 27–54.

TAYLOR, E. H. (1940) [1939]: Herpetological miscellany, no. 1. — Univ. Kansas Sci. Bull., 26(15): 489–571.

TAYLOR, E. H. (1955): Additions to the known herpetofauna of Costa Rica with comments on other species, no. 2. — Univ. Kansas. Sci. Bull., 37(13): 499–757.

TAYLOR, E. H. (1956): A review of the lizards of Costa Rica. — University of Kansas Science Bulletin, 38(1): 3–322.

TAYLOR, E. H. (1968): The caecilians of the world: a taxonomic review. — 484 pp.; Lawrence (Univ. Kansas Press).

THOMAS, R. (1975): The *argus* group of West Indian *Sphaerodactylus*. — Herpetologica, 31: 177–95.

THOMINOT, A. (1882): Note sur un *Anolis* d'espèce nouvelle. — Bulletin de la Société philomatique de Paris, (7)6: 251–253.

TIHEN, J. A. (1949): A review of the lizard genus *Barisia*. — University of Kansas, Science Bulletin, 33(3): 217–256.

TURNER III, H. L., P. LAFEMINA, A. SABALLOS, G. S. MATTIOLI, P. E. JANSMA & T. DIXON (2007): Kinematics of the Nicaraguan forearc from GPS geodesy. — Geophys. Res. Lett., 34, L02302. doi:10.1029/2006GL027586.

UTIGER, U., N. HELFENBERGER, B. SCHÄTTI, C. SCHMIDT, M. RUF & V. ZISWILER (2002): Molecular systematics and phylogeny of Old World and New World ratsnakes, *Elaphe* Auct., and related genera (Reptilia, Squamata, Colubridae). — Russian J. Herpetol., 9: 105–124.

VANZOLINI, P. E. & W. R. HEYER (1985): The American Herpetofauna and the Interchange. — pp. 475–487 *in*: STEHLI, F. G. & S. D. WEBB (Eds.): The great American interchange. — New York (Plenum Press).

VENCES, M., M. FRANZEN, A. FLÄSCHENDRÄGER, R. SCHMITT & J. REGÖS (1998): Beobachtungen zur Herpetofauna von Nicaragua: Kommentierte Artenliste der Reptilien. — Salamandra, 34: 17–42.

VESELÝ, M. & G. KÖHLER (2001): Zur Kenntnis von *Mesaspis moreletii* (BOCOURT 1871) in El Salvador. — Salamandra, 37(3): 185–192.

VILLA, J. D. (1962): Las Serpientes Venenosas de Nicaragua. — 94 pp.; Managua (Novedades).

VILLA, J. D. (1969): Notes on *Conophis nevermanni*, an addition to the Nicaraguan Herpetofauna. — Journal of Herpetology, 3(3–4): 169–171.

VILLA, J. D. (1970a): The snake *Hydromorphus* in Nicaragua, with a description of its hemipenis. — Carib. J. Sci., 10(3–4): 119–121.

VILLA, J. D. (1970b): Gallegos, basiliscos y pasarríos. — Medicina y Cultura, 8: 5–8.

VILLA, J. D. (1971): Notes on Some Nicaraguan Reptiles. — Journal of Herpetology, 5(1–2): 45–48.

VILLA, J. D. (1972a): Anfibios de Nicaragua: Introducción a su sistemática, vida y costumbres. — 216 pp.; Managua (Instituto Geográfico Nacional & Banco Central de Nicaragua).

VILLA, J. D. (1972b): Amphibians of the Corn Islands, Caribbean Nicaragua. — Caribbean Journal of Sciences, 12(3–4): 195–198.

VILLA, J. D. (1978): *Typhlops costaricensis*. Distribution. — Herp. Review, 9(2): 62.

VILLA, J. D. (1981): Three albino snakes. — Herp. Review, 12(3): 81.

VILLA, J. D. (1983): Nicaraguan fishes, amphibians and reptiles: checklist and bibliography. — 53 pp.; Managua (Universidad Centroamericana).

VILLA, J. D. (1984a): The venomous snakes of Nicaragua: a synopsis. — Contrib. Biol. Geol. Milwaukee Publ. Mus., 59: 1–41.

VILLA, J. D. (1984b): *Rhinophrynus dorsalis*: Distribution. — Herpetological Review, 15(2): 52.

VILLA, J. D. (1993): Presence of the tortoise *Geochelone carbonaria* (Reptilia: Testudines) in the Corn Islands, Caribbean Nicaragua. — Rev. Biol. Trop., 4(3): 924–928.

VILLA, J. D. & N. J. SCOTT Jr. (1967): The iguanid lizard *Enyaliosaurus* in Nicaragua. — Copeia, 1967(2): 474–476.

VILLA, J. D., L. D. WILSON & J. D. JOHNSON (1988): Middle American herpetology, a bibliographic checklist. — 131 pp.; Columbia (University of Missouri Press).

WAKE, D. B. (2000): Book review. The amphibians and reptiles of Nicaragua. A distributional checklist with keys (KÖHLER, 1999). — Herpetozoa, 13(1/2): 95–96.

WAKE, D. B. & J. F. LYNCH (1976): The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. — Science Bulletin of the Natural History Museum of Los Angeles County, 25: 1–65.

WEAVER, P. L., D. M. LOMBARDO & J. C. MARTÍNEZ-SÁNCHEZ (2003): Biodiversity and tropical forest conservation, protection and management in Nicaragua: assessment and recommendations. Final report. — 38 pp.; Managua (USAID/Nicaragua).

WIEGMANN, A. F. A. (1835) [1934]: Amphibien. *In*: MEYEN, F. G. F., Beiträge zur Zoologie, gesammelt auf ein Reise um die Erde. — Nova Acta Acad. C. Leop-Carol. Nat. Cur., 17(1): 183–188.

WILLIAMS, E. E. (1984): New or problematic *Anolis* from Colombia. III. Two new semiaquatic anoles from Antioquia and Chocó, Colombia. — Breviora, 478: 1–22.

WILSON, L. D. (1970): A review of the *chloroticus* group of the colubrid snake genus *Drymobius*, with notes on a twin-striped form of *D. chloroticus* (COPE) from southern Mexico. — J. Herpetology, 4(3–4): 155–163.

WILSON, L. D. & J. R. MCCRANIE (1994): Comments on the occurence of a salamander and three lizard species in Honduras. — Amphibia-Reptilia, 15: 416–421.

WILSON, L. D. & J. R. MCCRANIE (1998): The biogeography of the herpetofauna of the subhumid forests of Middle America (Isthmus of Tehuantepec to Northwestern Costa Rica). — Life Sciences Contributions of the Royal Ontario Museum, 163: 1–50.

WILSON, L. D. & J. R. MCCRANIE (2003): The conservation status of the herpetofauna of Honduras. — Amphib. Rept. Conserv., 3: 6–33.

WILSON, L. D. & C. E. MENA (1980): Systematics of the *melanocephala* group of the colubrid snake genus *Tantilla*. — Mem. San Diego Soc. Nat. Hist., 11: 1–58.

WILSON, L. D. & J. R. MEYER (1971): A revisión of the *taeniata* group of the colubrid snake genus *Tantilla*. — Herpetologica, 27(1): 11–40.

WILSON, L. D. & J. R. MEYER (1985): The snakes of Honduras. 2nd Edition. — 150 pp.; Milwaukee (Milwaukee Public Museum).

WILSON, L. D. & J. VILLA (1973): Colubrid snakes of the genus *Tantilla* from Nicargaua. — Bull. Southern Acad. Sci., 72(2): 93–96.

WÜSTER, W., J. L. YRAUSQUIN & A. MIJARES-URRUTIA (2001): A new species of indigo snake from north-western Venezuela (Serpentes: Colubridae: *Drymarchon*). — Herpetol. J., 11: 157–165.

ZAHER, H. (1994): Les Tropidopheoidea (Serpentes: Alethinophidia) sont-ils rèellement monophylétiques? Arguments en faveur de leur polyphylétisme. — C. R. Acad. Sci. Paris, 317: 471–478.

ZALDÍVAR-RIVERÓN, A., V. LEÓN-REGAGNON & A. NIETO-MONTES DE OCA (2004): Phylogeny of the Mexican coastal leopard frogs of the *Rana berlandieri* group based on mtDNA sequences. — Mol. Phylogen. Evol., 30: 38–49.

APPENDIX A: SPECIMENS COLLECTED

AMPHIBIA

Gymnophiona

Caecilidae

Dermophis mexicanus: Managua: Las Nubes (11°59´55.67´´N, 86°17´55.26´´W), 910 m: SMF 87780.

Gymnopis multiplicata: Atlántico Norte: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 87789; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450 m: SMF 87788.

Caudata

Plethodontidae

Bolitoglossa indio: Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 25 m: SMF 85867.

Bolitoglossa insularis: Rivas: Volcán Maderas (11°27´38´´N, 85°30´56´´W), 800 m: SMF 87175.

Bolitoglossa striatula: Atlántico Norte: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 87180; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1183–84, SMF 87179; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 75 m: SMF 87177; Caño El Venado, near Dos Bocas de Río Indio (11°02´14.7´´N, 83°53´07.3´´W), 10 m: JS 633, SMF 87178; Los Guatuzos, Río Frío, Fundeverde, senda Peter (11°04´55.8´´N, 84°45´11.0´´W), 80 m: JS 378, SMF 87176.

Oedipina sp. “Datanlí”: Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230 m: SMF 84860.

Oedipina sp. “Musún”: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 782–83.

Anura

Bufonidae

Incilius coccifer: Atlántico Norte: Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: JS 1151, SMF 87817–18; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230 m: JS 232; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: SMF 84873; León: León City, Parque Sutiava, 70 m: JS 1199, SMF 87812; Managua: Las Nubes (11°59´55.67´´N, 86°17´55.26´´W), 910 m: SMF 87813; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 87814; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 40 m: JS 808, SMF 87816; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1016, SMF 87815.

Incilius coniferus: Jinotega: Cerro Kilambé (13°35´01.1´´N, 85°43´04.6´´W), 1330 m: JS 140; Cerro Kilambé, La Cueva (13°36´11.1´´N, 85°42´52.6´´W), 1025 m: SMF 84878; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 486; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 87957; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 87958.

Incilius luetkenii: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 858, SMF 87975–76; Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: SMF 84868; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15–40 m: JS 805, SMF 87977–78.

Incilius valliceps: Atlántico Norte: Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: JS 1153, SMF 87256; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1175, SMF 87255; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 87254; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 260–315 m: JS 025, SMF 84879; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 87260; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1010 m: SMF 84880; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: SMF 87259; Bosawas, between Raití and Aran Dak, 165 m: SMF 87261; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 173; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 87262; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 453; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 87251; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86776; San Carlos (11°07´41.1´´N, 84°46´38.1´´W), 70 m: SMF 87252; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 87253; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 939, SMF 87257–58.

Rhaebo haematiticus: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 260 m: JS 024, SMF 84877; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 063; Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 118, SMF 87967–68; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 016, SMF 87969; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 87964; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: SMF 87965; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 414; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 87966.

Rhinella marina: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 260–285 m: JS 027, 046, SMF 84881; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1170; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1107; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 086, SMF 87275; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305 m: SMF 84882; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 019; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: SMF 87276; Matagalpa: Río Blanco (12°55´46.1´´N, 85°13´32.5´´W), 230 m: SMF 87981; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 87281; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 87980; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 87979; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 87280; San Juán del Norte (10°56´57.7´´N, 83°44´07.6´´W), 5 m: SMF 87275; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 265 m: JS 845; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 87277–78.

Centrolenidae

Centrolene prosoblepon: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: N 241, SMF 87829–30; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1355 m: SMF 84862.

Cochranella albomaculata: Atlántico Norte: Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 87946; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 87945.

Cochranella granulosa: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: SMF 87916; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 87917; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: JS 651, SMF 86778–79.

Cochranella pulverata: Atlántico Norte: Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 059, SMF 87918; Jinotega: Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: SMF 87919.

Cochranella spinosa: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1124, 1126, SMF 87920–21; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: N 210, SMF 87806; Río San Juan: Bartola (10°58.37´N, 84°20.35´W), 30 m: JS 465, 467–68, SMF 87807, 87809; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 411, 417, SMF 87808, 87810–11; Boca de San Carlos (10°47´26N, 84°11.70´W), 20 m: JS 509, SMF 87805.

Hyalinobatrachium fleischmanni: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: SMF 87819; Jinotega: Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: SMF 84919; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305–1355 m: JS 277–78, 286, SMF 84920–21; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 87820.

Craugastoridae

Craugastor bransfordii: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 600–900 m: SMF 89076; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305–1355 m: JS 262, 269, SMF 85489–91; Cerro Kilambé (13°35´01.1´´N, 85°43´04.6´´W), 1330 m: JS 135, 148–51, SMF 85481–84; Cerro Kilambé, Caballo Blanco (13°35´22.3´´N, 85°44´34.3´´W), 1045 m: SMF 85478; Cerro Kilambé (13°35´20.7´´N, 85°43´33.2´´W), 1440 m: SMF 85479; Cerro Kilambé (13°35´08.0´´N, 85°42´17.5´´W), 1345 m: SMF 85485; Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230–1375 m: JS 185, 196–97, 200, SMF 85486–88; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: JS 656, SMF 88118, 88127; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 720, 752, 777, SMF 88114–16, 88121–22; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: SMF 88113; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 397, 412, 429, SMF 88101–02; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 88103; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 549, 559, 591–93, 611, 618, SMF 88104–12; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 333–36, SMF 88117, 88119; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 984, SMF 89078–79.

Craugastor chingopetaca: Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 494, SMF 87947.

Craugastor fitzingeri: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1101, 1105, SMF 88001–02; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 87991; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 061, SMF 88012, 88017; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1355 m: SMF 84861; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 005; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 110, SMF 88014; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 88016; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 88013; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: N 511, SMF 88015; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 463, 471, SMF 88009–11; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 433–34, SMF 87990; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 87994–95; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 546, 558, 575–76, 578, 626, SMF 88003–08; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 40–70 m: JS 379, SMF 87992; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 977, SMF 87997, 87999–8000; Rivas: Volcán Maderas (11°27´40.93´´N, 85°30´47.62´´W), 400–900 m: JS 1068, 1070, 1080, SMF 87996, 87998; Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15 m: SMF 87790.

Craugastor laevissimus: Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1355 m: JS 290–92, SMF 84905–07; Cerro Kilambé (13°35´20.7´´N, 85°43´33.2´´W), 1440 m: SMF 84904; Rivas: Volcán Maderas (11°27´40.93´´N, 85°30´47.62´´W), 1000 m: SMF 87922.

Craugastor lauraster: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: N 277, SMF 84077; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 752, SMF 88122.

Craugastor megacephalus: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 600–900 m: N 226, SMF 87296; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010–1230 m: JS 188, SMF 84866; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 87297; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 87298; Cerro Musún (12°56´26.9´´N, 85°14´01.8´´W), 1185 m: SMF 87293–94; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 715, 718.

Craugastor mimus: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 600–1100 m: N 229–30, 262, SMF 87960–63; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230 m: JS 199, SMF 84886; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1155 m: JS 246, SMF 84887; Cerro Kilambé (13°35´01.1´´N, 85°43´04.6´´W), 1330 m: JS 139, 154, SMF 84885; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 87959; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 719, SMF 86784.

Craugastor noblei: Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230 m: JS 192–93, 198, 225, 228, SMF 84898–901; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305–1330 m: JS 155, SMF 84902; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: JS 653; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 717, 749, SMF 87928–29; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 488, SMF 87927.

Dendrobatidae

Dendrobates auratus: Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 446, SMF 87292; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 87291.

Oophaga pumilio: Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 87885; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 724, 726, SMF 87888–90; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 448, SMF 87886; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 419, SMF 87887; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 491, SMF 87893–95; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 553, 555, SMF 87896–97; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 975, SMF 87891–92.

Eleutherodactylidae

Diasporus diastema: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1119, SMF 88092; Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: SMF 88095, 88098; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 065, 084, 181, SMF 88096; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010 m: SMF 84936; Cerro Datanlí-El Diablo, El Volcán (13°07´51.9´´N, 85°50´33.3´´W), 1400 m: SMF 84937; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305–1355 m: JS 272–73, JS 280, 288, 295, SMF 84938; Cerro Kilambé, Caballo Blanco (13°35´22.3´´N, 85°44´34.3´´W), 1045 m: JS 129; Cerro Kilambé, El Jilguero (13°36´53.6´´N, 85°43´49.1´´W), 1255 m: SMF 84934; Cerro Kilambé (13°35´08.0´´N, 85°42´17.5´´W), 1345 m: SMF 84935; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 155, 191, 193, SMF 87949, 88097, 88100; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 163–64, SMF 87948, 88099; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: N 486; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 88093; Cerro Musún (12°56´26.9´´N, 85°14´01.8´´W), 1185 m: JS 770–71, SMF 88091; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 88090; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 450, SMF 88081–82; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 399, 415, 427, SMF 88077–80; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 498, 514, SMF 88083–85; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 544, 561, 583, SMF 88086–89.

Hylidae

Agalychnis callidryas: Atlántico Norte: Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: SMF 88020; Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: SMF 84944; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 88019; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285–315 m: JS 033, 064, SMF 84942–43; Bosawas, Urus Was (14°17.773´N, 84°55.111´W), 220 m: N 344, 357; Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: SMF 84941; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230 m: SMF 84947; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: JS 236, SMF 84948; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1010 m: SMF 84949; Cerro Kilambé, Caballo Blanco (13°35´22.3´´N, 85°44´34.3´´W), 1045 m: SMF 84946; Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: JS 111, SMF 84945; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 445, SMF 88022, 88037; Bosawas, between Raití and Aran Dak, 165 m: SMF 88028; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 88029; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 88023, 88025; Bosawas, Tuburus, 190m: SMF 88026; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 727, SMF 88018; Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88021, 88024.

Cruziohyla calcarifer: Río San Juan: Caño El Venado, near Dos Bocas de Río Indio (11°02´14.7´´N, 83°53´07.3´´W), 10 m: SMF 87274.

Dendropsophus ebraccatus: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1115, SMF 87971–72; Jinotega: Cerro Datanlí-El Diablo, El Volcán (13°07´51.9´´N, 85°50´33.3´´W), 1000 m: JS 212–15, SMF 84889–90; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: JS 239, SMF 84891; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1010 m: JS 315, SMF 84892–93; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 87970; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 940.

Dendropsophus microcephalus: Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: JS 071–72, SMF 84916–17; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 315 m: SMF 84915; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1173, 1178, SMF 88038–40; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 88032; Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: JS 009, SMF 84914; Jinotega: Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: SMF 84918; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 476, SMF 88035; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 443, SMF 88030; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 88031; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 941, SMF 88033; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1022–23, SMF 88037, 88041.

Dendropsophus phlebodes: Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 571–72, SMF 88073–75; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 944, 947, SMF 87913–15; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 88072.

Hypsiboas rufitelus: Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 474–75, SMF 87883–84; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 581, SMF 87882.

Ptychohyla hypomykter: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: N 294.

Ptychohyla sp. “Bosawas”: Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 029–34, 36, 041–44, 159, 409; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 113–116.

Scinax boulengeri: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1109, SMF 87926; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: JS 061, SMF 84883–84; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 444; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 341, SMF 87923; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 933–34, SMF 87924–25.

Scinax elaeochroa: Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 562, 631, SMF 86780–81; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 356, SMF 86782–83; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 87898.

Scinax staufferi: Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: JS 078, SMF 84865; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 87285; Siuna (13°44´18.91´´N, 84°47´05.66´´W), 185 m: SMF 87283; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 872, SMF 87287–88; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 348, 366, SMF 87289–90; Sábalos (11°02´35.0´´N, 84°28´25.0´´W), 40 m: SMF 87284; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 825, SMF 87286; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 87282.

Smilisca baudinii: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1167, SMF 87987; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1133, SMF 87983; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 315 m: SMF 85470; Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: JS 017, SMF 85469; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010–1230 m: JS 172–74, SMF 85472–74; Cerro Kilambé (13°35´20.7´´N, 85°43´33.2´´W), 1440 m: JS 133; Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: JS 114; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 196; Bosawas, between Raití and Aran Dak, 165 m: SMF 87988; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 856, SMF 87982; Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: SMF 85471; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 87984; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15–35 m: JS 826, SMF 87985; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1011; Volcán Maderas (11°27´40.93´´N, 85°30´47.62´´W), 750 m: SMF 87986.

Smilisca phaeota: Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: JS 077, SMF 85460–61; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: JS 039–40, SMF 85459, 85480; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 87797; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010 m: JS 168, SMF 85464–65; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: SMF 85466; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1010 m: JS 314, SMF 85467; Cerro Kilambé, Caballo Blanco (13°35´22.3´´N, 85°44´34.3´´W), 1045 m: JS 126; Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: JS 109, 113, SMF 85462; Cerro Kilambé, El Jilguero (13°36´53.6´´N, 85°43´49.1´´W), 1255 m: SMF 85463; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 456; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 124, SMF 87796; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: N 491, SMF 87795; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: JS 661, SMF 87791; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 461, SMF 87792; Sábalos (11°02´35.0´´N, 84°28´25.0´´W), 40 m: JS 389, SMF 87793.

Smilisca puma: Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 506; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86772; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 936, SMF 87787, 87886.

Smilisca sordida: Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 460 m: SMF 86777; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 410.

Tlalocohyla loquax: Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: JS 016, SMF 84930; Jinotega: Cerro Datanlí-El Diablo, El Volcán (13°07´51.9´´N, 85°50´33.3´´W), 1000 m: SMF 84932; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: JS 235, 243, SMF 84933; Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: SMF 84931.

Trachycephalus venulosus: Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 985, 987, SMF 87942–43; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 87944; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 796, SMF 87941.

Leiuperidae

Engystomops pustulosus: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 865, SMF 87781–82; road León-Managua, near León (12°22´58.07´´N, 86°50´30.21´´W), 75 m: JS 645, SMF 86774; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15–35 m: JS 798, SMF 86775; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1027, SMF 87783–84.

Leptodactylidae

Leptodactylus fragilis: Atlántico Norte: Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: SMF 87801; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1180, SMF 87798; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 315 m: JS 042, SMF 84863; Jinotega: Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 462; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: SMF 87804; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 87802; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 350, SMF 87799; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15–35 m: JS 792, SMF 87800; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1024, 1050, SMF 87803.

Leptodactylus melanonotus: Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: SMF 84927; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285–315 m: JS 043, 057, SMF 84925–26; Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: SMF 84924; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 875, SMF 87940; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 460 m: JS 657, SMF 87930, 87939; Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 613, SMF 87932–33; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 343, SMF 87936; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 979, SMF 87931; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15–35 m: JS 800, SMF 87934; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1018, 1057, SMF 87937–38.

Leptodactylus savagei: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88720; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: JS 021, SMF 84867; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 88123; Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 88124; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 88120; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 88094; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 87295; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 931.

Microhylidae

Hypopachus variolosus: Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: JS 008, SMF 84874; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 803, SMF 88076.

Ranidae

Lithobates brownorum: Jinotega: Cerro Datanlí-El Diablo, El Volcán (13°07´51.9´´N, 85°50´33.3´´W), 1000 m: SMF 84911; Cerro Kilambé, Caballo Blanco (13°35´22.3´´N, 85°44´34.3´´W), 1045 m: JS 130; Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: SMF 84910; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 88164.

Lithobates forreri: Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: JS 019, SMF 84896; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 861, SMF 89067; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1010 m: SMF 84897; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 460 m: SMF 87974; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45–70 m: JS 373, SMF 87973; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 89069; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1053, SMF 89068.

Lithobates maculatus: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: N 291, SMF 87952; Jinotega: Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: SMF 84903; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 460 m: JS 663, 674, 680, SMF 87954–55; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 87956; Cerro Musún (12°56´26.9´´N, 85°14´01.8´´W), 1185 m: SMF 87953.

Lithobates vaillanti: Atlántico Norte: Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: SMF 87300; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 87776; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285–315 m: JS 034, SMF 84908–09; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 87778; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 87775; Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 013; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 474; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 87779; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 460 m: SMF 87774; Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 930, SMF 87777; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 87299.

Lithobates warszewitschii: Jinotega: Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 87951; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: N 504; Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 598, SMF 87950.

Rhinophrynidae

Rhinophrynus dorsalis: León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 101, 254, SMF 84869–70.

Strabomantidae

Pristimantis cerasinus: Atlántico Norte: Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 87827; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 176; Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 121, 142, SMF 87825–26, 87828; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 87821; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 533, SMF 87823; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 437, SMF 87822; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 87824.

Pristimantis ridens: Atlántico Norte: Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: N 201; Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: N 247, 249, SMF 87901–03; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 096, SMF 87909; Bosawas, trail from Kulum Kitang to Urus Was: SMF 87906; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305 m: SMF 84859; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 133, 144, 154, SMF 87908; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 87907; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: JS 655, SMF 87899; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 745, 751, SMF 87910, 87912; Cerro Musún (12°56´26.9´´N, 85°14´01.8´´W), 1185 m: JS 767, SMF 768; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 87900; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 503, 513, SMF 87904–05.

REPTILIA

Testudines

Chelydridae

Chelydra acutirostris: Matagalpa: Río Blanco (12°55´46.1´´N, 85°13´32.5´´W), 230 m: SMF 89039.

Emydidae

Trachemys scripta: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1198; Jinotega: Bosawas, between Aran Dak and Muru Ta: SMF 88199; Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88197–98.

Geoeymdidae

Rhinoclemmys annulata: Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 89037; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 89035–36; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 89034.

Rhinoclemmys funerea: Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 89038.

Rhinoclemmys pulcherrima: Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: SMF 88196.

Kinosternidae

Kinosternon angustipons: Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 87168.

Kinosternon leucostomum: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88968; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 88967; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 70 m: JS 371; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88969.

Kinosternon scorpioides: Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 70 m: SMF 89033; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 89032; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 835, SMF 89031; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 89040.

Crocodylia

Alligatoridae

Caiman crocodilus: Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 40 m: JS 381.

Squamata

Anguidae

Mesaspis moreletii: Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305 m: SMF 88135; Cerro Kilambé (13°35´01.1´´N, 85°43´04.6´´W), 1330 m: SMF 88134; Cerro Kilambé (13°35´20.7´´N, 85°43´33.2´´W), 1440 m: JS 134.

Eublepharidae

Coleonyx mitratus: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 87248; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 812, SMF 86729; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 87249.

Gekkonidae

Hemidactylus frenatus: Atlántico Norte: Río Blanco (12°55´46.1´´N, 85°13´32.5´´W), 230 m: JS 691, SMF 86754; Waspám (14°44´23.95´´N, 83°57´52.76´´W), 45 m: JS 1157, SMF 88056; Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: JS 1147, SMF 88057; León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 089, 257, SMF 84766–67; road León-Managua, near León (12°22´58.07´´N, 86°50´30.21´´W), 75 m: JS 639, SMF 86755; Managua: Las Nubes (11°59´55.67´´N, 86°17´55.26´´W), 910 m: SMF 88059; Río San Juan: San Juán del Norte (10°56´57.7´´N, 83°44´07.6´´W), 5 m: JS 538, SMF 86757; Sábalos (11°02´35.0´´N, 84°28´25.0´´W), 40 m: SMF 86758; San Carlos (11°07´41.1´´N, 84°46´38.1´´W), 70 m: JS 324; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 839, SMF 86756; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 88055.

Gymnophthalmidae

Gymnophthalmus speciosus: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450–630 m: JS 786–87, SMF 86759–60.

Iguanidae

Anolis biporcatus: Atlántico Norte: Cerro Saslaya (13°46.095´N, 85°01.469´W), 600–900 m: SMF 88062; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 86687; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 478, SMF 86686; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 566; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88061; Rivas: Volcán Maderas (11°27´40.93´´N, 85°30´47.62´´W), 750 m: JS 1075.

Anolis capito: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1110, SMF 88174; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 88175; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 88177; Cerro Saslaya (13°46.095´N, 85°01.469´W), 520–1100 m: N 251, SMF 88179; Jinotega: Cerro Datanlí-El Diablo, El Volcán (13°07´51.9´´N, 85°50´33.3´´W), 1405 m: SMF 84742; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1355 m: SMF 84743; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 174, SMF 88176; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 88178; Matagalpa: Cerro Musún (12°56´26.9´´N, 85°14´01.8´´W), 1185 m: JS 774, SMF 86769; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 86770; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 86761; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 499, SMF 86768; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86771; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 331; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88173.

Anolis carpenteri: Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 87250.

Anolis cupreus: Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: SMF 84713; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1165, SMF 87229–30; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1099, 1111–12, SMF 87231–33; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: SMF 84711; Siuna (13°44´18.91´´N, 84°47´05.66´´W), 185 m: SMF 84712, 87227; Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: SMF 84709–10; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010–1230 m: JS 179, 234, SMF 84715–18; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: SMF 84719; Cerro Kilambé, Caballo Blanco (13°35´22.3´´N, 85°44´34.3´´W), 1045 m: JS 124, SMF 84714; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: N 503, SMF 87228; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 801, 810, 821, 842, SMF 86689, 86702–03; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1029–30, 1034, SMF 87234–35, 87237–38; Volcán Maderas (11°27´40.93´´N, 85°30´47.62´´W), 400 m: JS 1072, SMF 87236.

Anolis lemurinus: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88140; Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 200 m: SMF 88141; Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 567, SMF 86699; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 956, 1004, 1209, SMF 88142–44.

Anolis limifrons: Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: JS 074, SMF 84738; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88164; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1089–90, 1130, SMF 88163, 88165; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: JS 052, SMF 84737; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 077–78, SMF 88166; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220–520 m: SMF 88170–72; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1015 m: SMF 84740; Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: SMF 84739; Cerro Kilambé, La Cueva (13°36´11.1´´N, 85°42´52.6´´W), 1025 m: JS 161; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 183; Bosawas, Maikawana (14°24.404´N, 84°59.423´W), 160 m: N 313; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 88167; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: N 433; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 86708; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 740, 753, SMF 86707; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 455, SMF 86705; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 75 m: SMF 86709; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 86706; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 25 m: JS 542, 622, SMF 86710–11; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 958, SMF 88161–62; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45–50 m: JS 329, 355, 362, SMF 86712–14.

Anolis oxylophus: Atlántico Norte: Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 099; Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: SMF 87263; Jinotega: Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: SMF 87264–65; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: JS 669, 683, SMF 86715–16; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 458, SMF 86717; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 396, SMF 86718; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 492, SMF 86720–21; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 580, SMF 86719.

Anolis quaggulus: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: SMF 84745; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: N 220–21; Cerro Saslaya (13°46.095´N, 85°01.469´W), 600–1100 m: N 278, 280, SMF 88067–71; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010–1230 m: JS 206, 230, SMF 84750, 84752–53; Cerro Datanlí-El Diablo, El Volcán (13°07´51.9´´N, 85°50´33.3´´W), 1405 m: SMF 84751; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305 m: JS 283, SMF 84754–56; Cerro Kilambé (13°35´01.1´´N, 85°43´04.6´´W), 1330 m: JS 142, 144, SMF 84747–48; Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: SMF 84746; Cerro Kilambé, La Cueva (13°36´11.1´´N, 85°42´52.6´´W), 1025 m: JS 160, SMF 84749; Bosawas, between Raití and Aran Dak, 165 m: SMF 88063; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: JS 671–72;

Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 713, 734–35, SMF 86690, 86693; Cerro Musún (12°56´26.9´´N, 85°14´01.8´´W), 1185 m: SMF 86691–92; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS 456; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 406–07, 413, SMF 86696–97; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 485, SMF 86694–95; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86688; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 961, SMF 88064–66.

Anolis sericeus "bilobed": León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 140–410 m: JS 869, 880, 882, SMF 88138–39, 88155; road León-Managua, near León (12°22´58.07´´N, 86°50´30.21´´W), 75 m: JS 638, SMF 86698.

Anolis sericeus "unilobed": Atlántico Norte: Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: SMF 88248; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1163, 1196, SMF 88043–44, 88150–51; Cerro Saslaya (13°46.154´N, 84°58.714´W), 110 m: SMF 88154; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 460–620 m: JS 665, 684–85, SMF 86681–82; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450 m: SMF 86683; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 326, SMF 86685; Sábalos (11°02´35.0´´N, 84°28´25.0´´W), 40 m: SMF 86680; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15–35 m: JS 818, SMF 86684, 86704; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 88042, 88149; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1095–96, SMF 88152–53.

Anolis tropidonotus: Jinotega: Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: SMF 84734–36.

Anolis wermuthi: Jinotega: Cerro Kilambé (13°35'01.1''N, 85°43'04.6''W), 1330 m: SMF 84707; Cerro Kilambé, near hut of Maximiliano PÉREZ BUCARDO (13°34'39.6''N, 85°41'56.9''W), 1360 m: SMF 84704–06, 84708, JS 297–300, 305.

Basiliscus plumifrons: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88995; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 072, SMF 88998–99; Bosawas, Urus Was (14°17.773´N, 84°55.111´W), 220 m: SMF 89001; Jinotega: Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: SMF 89000; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 026, SMF 88997; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 40 m: SMF 86773; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88996.

Basiliscus vittatus: Atlántico Norte: Intersection road Puerto Cabezas-Waspám with road to Moss (14°26´06.50´´N, 83°52´24.92´´W), 100 m: SMF 88159; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88157; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 88156; Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: SMF 84847–48; Jinotega: Bosawas, Maikawana (14°24.404´N, 84°59.423´W), 160 m: N 314; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 88160; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: N 498; Bosawas, San Andrés (14°18.758´N, 85°10.346´W), 220 m: N 002; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 460 m: SMF 86700; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 523; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86701; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88158.

Corytophanes cristatus: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: SMF 84845; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 069, 071, SMF 89004–05; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 89007; Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: SMF 89008; Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 89006; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 86735, 89002; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 86736; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86737; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 354; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 972, SMF 89003.

Ctenosaura quinquecarinata: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 88046.

Ctenosaura similis: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 87271; Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 087, SMF 84851; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 265 m: SMF 86747; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 87272.

Iguana iguana: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 87240; Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 022, SMF 87242–43; León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: SMF 84846; Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 87241.

Sceloporus malachiticus: Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: JS 014, SMF 84854; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010–1300 m: JS 180, 208, SMF 84856.

Sceloporus squamosus: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 88125.

Sceloporus variabilis: Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: SMF 84852; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 866, SMF 88145; Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 092, SMF 84853; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450 m: JS 738, SMF 86752; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 816, SMF 86753; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 86146.

Phyllodactylidae

Phyllodactylus tuberculosus: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 888, SMF 87244; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 814, SMF 86746; Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1042, SMF 87245–46.

Thecadactylus rapicauda: Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 87239.

Scincidae

Mabuya unimarginata: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88050; Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1137, SMF 88049; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 88048; Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 095, SMF 84768; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450 m: SMF 86750; Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86751; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1037, SMF 88051; Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 15 m: JS 843, SMF 89057.

Mesoscincus managuae: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 88060; Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 093, SMF 84761; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 10 m: JS 830.

Sphenomorphus cherriei: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 325 m: SMF 84770; Jinotega: Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: SMF 87276; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 88128; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: JS

480, SMF 86730; Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 86733; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 86734; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 601, SMF 86731–32; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 967, SMF 88132–33; Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: SMF 88129; Rivas: Volcán Maderas (11°27´40.93´´N, 85°30´47.62´´W), 400–830 m: JS 1074, 1086, SMF 88130–31.

Sphaerodatylidae

Gonatodes albogularis: Atlántico Norte: Río Blanco (12°55´46.1´´N, 85°13´32.5´´W), 230 m: SMF 86727; Waspám (14°44´23.95´´N, 83°57´52.76´´W), 45 m: JS 1159, SMF 88052; León: road León-Managua, near León (12°22´58.07´´N, 86°50´30.21´´W), 75 m: SMF 86728; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450 m: JS 699–700, SMF 86722–24; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 526; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 86726; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 964, SMF 88053; Sábalos (11°02´35.0´´N, 84°28´25.0´´W), 40 m: JS 390; San Carlos (11°07´41.1´´N, 84°46´38.1´´W), 70 m: JS 321, 323, SMF 86725; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 88054.

Lepidoblepharis xanthostigma: Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 86745; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 564, 585, 603, 606, 621, SMF 86741–44.

Sphaerodactylus millepunctatus: Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 88137; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 86739; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86740; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 368–69, SMF 86738; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 88136.

Teiidae

Ameiva festiva: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285–325 m: JS 029, SMF 84849–50; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: SMF 86766; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 527; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 339, SMF 86767.

Ameiva undulata: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450–630 m: JS 696, SMF 86765; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 831, SMF 86764.

Aspidoscelis deppii: León: road León-Managua, near León (12°22´58.07´´N, 86°50´30.21´´W), 75 m: JS 642, SMF 86762–63; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1036.

Xanthusidae

Lepidophyma flavimaculatum: Jinotega: Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 88045; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 86748; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 404; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 524; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86749; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 970, SMF 88047.

Boidae

Boa constrictor: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 315 m: SMF 85502; Jinotega: Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: SMF 89011; Bosawas, between Muru Ta and Kulum Kitang: SMF 89009; León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 140 m: SMF 89010.

Colubridae

Adelphicos quadrivirgatum: Jinotega: Bosawas, Kulum Kitang (14.3292°N, 84.9375°W), 180 m: SMF 87169.

Clelia clelia: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1187, SMF 87191–92.

Coniophanes fissidens: Atlántico Norte: Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: N 301; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230 m: SMF 85515; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 88973; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 1208.

Coniophanes piceivittis: León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: SMF 85498, 89055; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 88985; Volcán Maderas (11°27´40.93´´N, 85°30´47.62´´W), 60 m: JS 1084.

Conophis lineatus: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450 m: SMF 88986; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 848.

Dendrophidion percarinatum: Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 88974; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 88193.

Drymarchon melanurus: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 89017; Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 89016; León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 258; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: SMF 88189.

Drymobius margaritiferus: Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1300 m: SMF 85495; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1025–1305 m: JS 268, 307, SMF 85496; Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88970.

Enulius flavitorques: León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 099, SMF 84757–58; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: JS 1048, SMF 88978.

Erythrolamprus mimus: Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230 m: JS 177; Cerro Datanlí-El Diablo, La Esmeralda (13°05´02.8´´N, 85°52´23.5´´W), 1150 m: JS 249, SMF 85506.

Geophis hoffmanni: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 88181.

Hydromorphus concolor: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 285 m: SMF 85501; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 431.

Imantodes cenchoa: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: JS 1139, SMF 89052; Cerro Saslaya (13°46.095´N, 85°01.469´W), 1100 m: SMF 89046; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 89042; Bosawas, Kama Pi (14°17.552´N, 84°53.764´W), 250 m: N 397; Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1255–1300 m: JS 204, SMF 85504; Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1305 m: JS 259, SMF 85505; Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 89043–44; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 89045; Bosawas, Wailahka (14°33.794´N, 84°59.912´W), 120 m: N 484; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 757, SMF 89049–50; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 518, SMF 89047; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 10 m: SMF 89048; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 990, SMF 89051.

Imantodes gemmistratus: Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: SMF 88194.

Imantodes inornatus: Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 997, SMF 88984.

Lampropeltis triangulum: Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 1010 m: SMF 85492; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 385.

Leptodeira annulata: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: JS 1201, SMF 88988; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 88987; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 992; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 88989.

Leptodeira septentrionalis: Atlántico Norte: Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 88980; Río San Juan: Bartola (10°58´18.3´´N, 84°20´23.1´´W), 25 m: SMF 88979; Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: JS 519.

Leptodrymus pulcherrimus: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 450 m: JS 703, SMF 88976.

Leptophis ahaetulla: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 88994; Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: SMF 85503; Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 589, SMF 88992; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 383; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88993.

Leptophis depressirostris: Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 88977; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 764.

Masticophis mentovarius: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 88183.

Mastigodryas dorsalis: Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1230–1300 m: JS 223, SMF 85512, 85516; Cerro Kilambé, El Jilguero (13°36´53.6´´N, 85°43´49.1´´W), 1255 m: SMF 85518.

Mastigodryas melanolomus: Jinotega: Cerro Kilambé, La Cueva (13°36´11.1´´N, 85°42´52.6´´W), 1025 m: SMF 85513; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: SMF 87247.

Ninia sebae: Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: SMF 85511; Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 89054; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: N 434; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 89053; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 762, SMF 86785, 88975.

Oxybelis aeneus: León: El Jicaral, San Juan de Dios (12°44´04.64´´N, 86°23´20.61´´W), 145 m: SMF 88186; Río San Juan: Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 88185; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 70 m: JS 375; Rivas: Ometepe island, near Santo Domingo (11°30´41.40´´N, 85°33´16.80´´W), 45 m: SMF 88188.

Oxybelis brevirostris: Atlántico Norte: Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: N 051; Cerro Saslaya (13°46.095´N, 85°01.469´W), 520 m: SMF 88982; Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 88981.

Oxybelis fulgidus: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 89041; Río San Juan: Dos Bocas de Bartola, El Almendro (10°59´43.9´´N, 84°16´37.5´´W), 70 m: JS 422.

Oxyrhopus petola: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 325 m: SMF 85494.

Pseustes poecilonotus: Atlántico Norte: Moss, along Río Wawa (14°21´16.19´´N, 83°52´38.99´´W), 30 m: SMF 88990; Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: N 093; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 88991.

Rhadinaea kinkelini: Estelí: Miraflor (13°14´50´´N, 86°15´27´´W), 1325 m: SMF 84759.

Sibon annulatus: Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 88180.

Sibon anthracops: Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35–265 m: JS 806, 838, SMF 88971–72.

Sibon longifrenis: Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 88182.

Sibon nebulatus: Atlántico Norte: Rancho Alegre (13°39´47.5´´N, 85°01´38.9´´W), 315 m: SMF 85510; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 87225; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 87266; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 995.

Spilotes pullatus: Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 88192.

Tantilla reticulata: Río San Juan: near San Juán del Norte (10°56´57.7´´N, 83°44´07.6´´W), 5 m: SMF 88191.

Tantilla taeniata: Jinotega: Cerro Kilambé, El Diamante (13°36´51.3´´N, 85°44´20.2´´W), 1090 m: SMF 84760.

Thamnophis marcianus: Río San Juan: Los Guatuzos, near Lake Nicacargua, 35 m: SMF 88190.

Thamnophis proximus: Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1010 m: SMF 85517; León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: JS 102, 105; Río San Juan: Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: SMF 89056.

Tretanorhinus nigroluteus: Atlántico Norte: Bosawas, Krin Krin (14°36´42.16´´N, 84°28´09.03´´W), 60 m: JS 1185; Jinotega: Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 87266.

Trimorphodon quadruplex: Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: SMF 88195.

Xenodon rabdocephalus: Jinotega: Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: SMF 88184.

Elapidae

Micrurus alleni: Río San Juan: Los Guatuzos: SMF 87273.

Micrurus nigrocinctus: Atlántico Norte: Finca URACCAN (13°43´44.1´´N, 84°53´14.5´´W), 145 m: SMF 85507; Bosawas, Muru Lak (14°21.21´N, 84°56.52´W), 185 m: SMF 89065; Bosawas, Urus Was (14°17.773´N, 84°55.111´W), 220 m: N 350; Bosawas, trail from Kama Pi to Kulum Kitang: SMF 89064; Siuna (13°44´18.91´´N, 84°47´05.66´´W), 185 m: JS 069; Jinotega: Cerro Kilambé (13°35´07.7´´N, 85°42´17.1´´W), 963 m: SMF 85509; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 89066; Matagalpa: Cerro Musún, Palán, Bilampí (13°00´41.0´´N, 85°14´11.6´´W), 620 m: SMF 89060; Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: JS 784, SMF 89061–62; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 89058; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86562; Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: SMF 89059.

Viperidae

Bothriechis schlegelii: Jinotega: Cerro Datanlí-El Diablo, El Gobiado (13°10´23.0´´N, 85°51´24.6´´W), 1255 m: SMF 85499; Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 478, SMF 89030; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 89028; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 89029; Matagalpa: Cerro Musún, Fundenic (12°57´18.8´´N, 85°13´51.2´´W), 630 m: SMF 89025; Río San Juan: Boca de San Carlos (10°47´25.7´´N, 84°11´37.7´´W), 40 m: SMF 89024; Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: SMF 86563; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 45 m: JS 359, SMF 89023, 89026; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: SMF 89027.

Bothrops asper: Atlántico Norte: Bosawas, Kama Pi (14°17.552´N, 84°53.764´W), 250 m: SMF 89013; Bosawas, along Río Lakus: SMF 89019; Jinotega: Bosawas, Kulum Kitang (14°19.8´N, 84°56.2´W), 180 m: SMF 89015; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: SMF 89014, 89018; Bosawas, Siwi Was (14°23.266´N, 84°58.795´W), 180 m: SMF 89022; Río San Juan: Dos Bocas de Río Indio (11°02´54.8´´N, 83°52´48.4´´W), 20 m: JS 570, SMF 89020; Los Guatuzos, Río Frío, Fundeverde (11°04´37.0´´N, 84°44´55.7´´W), 40 m: SMF 89021; Los Guatuzos, along Río Papaturro (11.0227°N, 85.0513°W), 40 m: JS 1207.

Crotalus simus: Rivas: Morgan´s Rock (11°18´28.9´´N, 85°54´59.1´´W), 35 m: JS 809, SMF 88983.

Porthidium nasutum: Atlántico Norte: Bosawas, Kama Pi (14°17.552´N, 84°53.764´W), 250 m: SMF 87270; Bosawas, between Urus Was and Kama Pi: SMF 87269; Bosawas, trail from Kulum Kitang to Urus Was: SMF 87268; Cerro Saslaya (13°46.154´N, 84°58.714´W), 220 m: SMF 87267; Jinotega: Bosawas, Aran Dak (14°31.03´N, 84°59.86´W), 150 m: N 481; Bosawas, Muru Ta (14°21.99´N, 84°58.56´W), 180 m: N 194.

Porthidium ophryomegas: León: Complejo Volcánico Momotombo, Monte Galán, Las Playitas (12°26´37.57´´N, 86°34´16.50´´W), 85 m: SMF 85500.

APPENDIX B: SPECIMENS EXAMINED IN CHAPTER 2.3.1

[H] Specimens with everted hemipenis

Anolis wermuthi: **Nicaragua**: Atlántico Norte: Cerro Saslaya, S slope of Cerro Saslaya, trail to summit, 1290–1430 m: SMF 79582–84, 79162[H]; Cerro El Toro, near camp II, 1320–1500 m: SMF 82062, 82063–64[both H], 82065; Estelí: Miraflor, Tayacán, 1230–1240 m: SMF 79685–86; Miraflor, Puertas azules, Finca de Efraím GONZALES, 1240 m: SMF 79672; Jinotega: Montaña La Galia, Km 146 road from Matagalpa to Jinotega (13°02.00'N, 85°55.85'W), 1400–1460 m: SMF 77323, 77325–29, 78009, 78604[H]; Montaña La Galia, (13°01.99'N, 85°55.85'W), 1330 m: SMF 78983[H]; Montaña La Galia, (13°01.80'N, 85°56.33'W), 1350 m: SMF 79008[H]; Montaña La Galia, (13°01.83'N, 85°56.16'W), 1390 m: SMF 79009[H]; Cerro Kilambé, near Camp I (13°34.88'N, 85°41.81'W), 1340 m: SMF 79010–12[all H]; Cerro Kilambé, near Camp II (13°35.25'N, 85°41.50'W), 1330–1360 m: SMF 78987–92, 79005; Cerro Kilambé (13°35'01.1''N, 85°43'04.6''W), 1330 m: SMF 84707; Cerro Kilambé, near hut of Maximiliano PÉREZ (13°34'39.6''N, 85°41'56.9''W), 1360 m: SMF 84704–05, 84708[H], JS 299, 305.

APPENDIX C: SPECIMENS EXAMINED IN CHAPTER 2.3.2

[H] Specimens with everted hemipenis

Anolis humilis: **Costa Rica**: Alajuela: Peñas Blancas: UCR 14942; Rio Frío: USNM 19508–13; Cariblanco: NMW 20667 (8); Cinchona: KU 66921, 66922[H], 66923; Cartago: Parque Nacional Tapanti: MD 72[H]; Tapanti, Río Grande, Orosi Puente: UCR 811, 2809[H]; Tapanti, Río Quirí: UCR 9572; Navarro: ANSP 24466–68; Río Chitaria: LSUMZ 52324; Turrialba: KU 40819, USNM 192585, 339731–33; 1 km SE Tuis: KU 66898; Moravia de Turrialba: KU 66905; 3 km NNE Pavones: KU 66889[H]; 3 km S Pavones: KU 103921–23[all H]; jct. Ríos Tuis and Reventazon: KU 66890–91, 66892[H], 66893; Heredia: "Heredia": AMNH 149606; Parque Nacional Braulio Carillo, San Ramón, Distrito La Virgin: UCR 13287; Reserva Biológica Alberto M. Brenes, San Ramón: MD 95; E of Isla Bonita: KU 66910[H], 66911–12; Isla Bonita: KU 103925[H]; Limón: N slope Cerro Nimaso, Distrito Bratsi: UCR 8475[H]; EB Tierra Media, Matina, Distroto Batán: UCR 12396[H]; San Miguel, F. ASACODE, Distroto Sixaola: UCR 12866; Cerro Uatsi, Distrito Bratsi: UCR 13030, 13189; RB Hitoy Cerere: MD 89[H]; Approximately 17.0 km WSW Puerto Limón between Río Blanco and Río Toro: UTA R12845–47; Puerto Limón: ANSP 19530–34, ZMH 4594; Estralla Valley, end of Suretka trail: ANSP 21466; Guapiles: ANSP 24470; Rte 32, 6 km E Río Hondo, 2 km N on dirt road: ANSP 32373; La Castilla, lower Río Reventazón: ANSP 23738–47, 24457–58, 34736–38; Los Diamantes: KU 66926[H]; Puntarenas: Monteverde, 7 km on road N Santa Elena (10°21'50''N, 84°481'10.5''W), 1375–1420 m: SMF 85528[H], 85529; Monteverde, Ecolodge: UCR 17040[H]; Fila Cedro, Distrito San Vito: UCR 12784[H]; 8 km E Palmar Norte: KU 93969[H]; 8 km ENE Palmar Norte: KU 116981[H]; San José: Fila Tinamastes, Distrito Barú: UCR 14512[H], 14514[H], 14523[H], 14805[H], 14512; Tinamaste, Distrito Dominical: UCR 15933[H]; Alfombra, Distrito Barú: UCR 15968; Km 122 on ruta 2 (N of San Isidro de Perez Zeledon): UTA R12841–44; La Hondura, 4500 ft: ANSP 24471–79, 24482–86, 34739–41; Río Claro, 1 road mi N La Hondura: LSUMZ 30261; 2 mi E Escuadra: LSUMZ 52376; 1 mi N Santa Ana: LSUMZ 52368–69; 15 km SW San Isídro del General: KU 66929[H]; 13.4 km N San Isídro del General: KU 66931[H]; **Panama**: "Veragua": ZMB 500, 55223; Bocas del Toro: "Bocas del Toro": AMNH 119729–733; Celentine, road to Chririquí Grande (8°47'09''N, 82°11'17''W), 610 m: SMF 85110[H]; Cerro Brujo (9°11'16.4''N, 82°11'25.4''W), 10 m: SMF 85112[H]; Río Uyama (9°08'55''N, 82°19'28''W), 35 m: SMF 85115–16; Quebrada La Gloria (8°59'08''N, 82°13'56''W), 20 m: SMF 85117; Río Changuinola, near Quebrada El Guabo (16 km airline W Almirante), 100–200 m: AMNH 119033–39; Quebrada Pastores, on coast W of Isla Pastores: USNM 313835; Almirante: USNM 142288, 193449, 339773–75; vicinity of Almirante: ANSP 34055–57, 34066; ca. 5 km W Almirante, 30–40 m: AMNH 107427–31; Laguna de Tierra Oscura, 3.7 km S of Tiger Key: USNM 313816, 313836, 348443–63; Cayo Agua, Punta Norte: USNM 150006, 150010; Cayo Agua, near Punta Limón: USNM 338685; Cayo Nancy: USNM 338532[H], 338532–37, 338538[H], 338539–43; Isla Bastimentos, ca. 0.5 mi from mouth of Alvarez Creek (= Alberry Creek): USNM 297886; Isla Bastimentos, Old Point: USNM 297887; Isla Colon, La Gruta: USNM 338201–08, 338209[H], 338210, 338211[H], 338212–13 Isla Cristobal, Bocatorito camp: USNM 348172–76, 348177[H], 348178–81; Isla Cristobal, Laguna Bocatorito: USNM 313815; Isla Cristobal, NW side of: USNM 348182[H], 348183–84; Isla Escudo de Veraguas, West Point: USNM 347481; Isla Popa, 1 km SE of Deer Island channel: USNM 298111–20; south end of Isla Popa, 1 km E of Sumwood Channel: USNM 319206–09, 347211–27, 347228[H], 347229–42; Chiriquí: Boquete, trail to Palo Alto (8°48'49''N, 82°23'60''W), 1660 m: SMF 85403; Fortuna: 148885–87[all H]; Reserva Forestal Fortuna, Laguna (8°43'N, 82°15'W), 1000 m: SMF 85101[H], 85102; Reserva Forestal Fortuna (8°43'35''N, 82°15'41''W), 1050–1150 m: SMF 85103–06[all H], 85107–09; Reserva Forestal Fortuna, trail to dam site, 1050–1100 m: SMF 85113[H], 85114; upper Río Chiriquí, Fortuna Dam Site, 1000–12000 m: AMNH 114273[H], 114274–80, 114281[H], 114280, 114283[H], 114284–85, 114286[H], 114287–303; near the summit Cerro, 1400 m: AMNH 114304; S slope Quebrada de Arena, Río Chiriquí drainage, 1120 m: AMNH 123987–94, 129816–17; continental divide above upper Quebrada de Arena, 1160–1220 m: AMNH 129818–31; Coclé: El Valle de Antón: AMNH 71720–26, 76021–22, 76025, 76032–36, 89879, ANSP 21802–03, 24459–65, 34833; El Valle de Antón, Cerro Gaitál (8°37.31'N; 80°07.54'W), 710–750 m: SMF 80782–83[both H]; continental divide N El Copé (80°36'W), 600–800 m: AMNH 115912–15; Colón: Cerro Bruja (9°29'N, 79°35'W): USNM 54056; Panamá: 8 km NNW Chepo, Gaspar Sabana: UF 124420; Cerro Azul, 457 m, 54179; Cerro Azul, 762 m, 54170; Gatun: ANSP 20855–56; Río Pequeni, head of Madden Lake: ANSP 21697; Cerro Trinidad: UF 135781; Trinidad River: USNM 63985; Cerro Campana: AMNH 106667[H], 106668, 106669[H], 106670, UF 124422–24; km 14.6 on El Llano-Castí road, 370 m: AMNH 110570–71; San Blás: Nusagandi, vicinity of field station (9°20.50'N, 78°59.64'W), 350–360 m: SMF 80787[H], 80845[H], 80846–47, 80850[H]; Nusagandi, Sendero Markis, 270–290 m: SMF 80848–49; Veraguas: 5–6 mi (via road) NW Santa Fe (Pacific drainage): AMNH 119999–120000[both H], 120001–02, 147797; Cerro Delgadito, 2–4 mi W Santa Fe: AMNH 147798[H].

Anolis quaggulus: **Costa Rica**: Alajuela: Cinchona (10°13'35''N, 84°10'07''W), 1300 m: SMF 85530[H], UCR 1416; between Ciudad Quesada and Aguas Zargas, near Hotel "El Tucano", 600 m: SMF 84959–61; Guanacaste: Tilarán: ANSP 24446, 24469; El Silencio: LACM 148892–93[both H]; Volcán Orosí: LACM 148888–91[all H]; Cerro Cacao: LACM 148894–95[both H]; Heredia: Reserva Biológica La Tirimbina, Sarapiquí (10°24'N, 84°8'W): MD 83[H]; Parque Nacional Braulio Carillo: MD 94[H]; Puerto Viejo: UCR 4659–61, 4662[H], ZFMK 48723, 48728, 48734–36, 48738–39; Rara Avis, Catarata, 650 m: SMF 81050[H]; La Selva, 1 mi SW Puerto Viejo de Sarapiqui: CM 53943–44, KU 129282[H], 129299[H]; Limón: Tortuguero: UCR 5050, 17294; Playa Gandoca, Distrito Sixaola: UCR 12959[H]; Boca de Tortuguero: AMNH 85054–56; Caño Palmas, 2–3 mi NW Green Turtle Camp, Tprtuguero: AMNH 95088–94; Cerro Tortuguero: AMNH 95085–87; N Tortuguero village, ca. 0.5 mi W Green Turtle Inn: AMNH 102492–94; near Tortuguero, Cano Mora: UF 135782, USNM 244866; **Honduras**: Gracias a Dios: Bodega de Rio Tapalwás (14°55'39''N, 84°32'02''W), 190 m: USNM 549361–62; Olancho: 11.5 km NNE La Colonia, Quebrada de Las Marías, 660 m: SMF 78803[H]; Yapuwás, 60 m: SMF 79927; Matamoros (14°40'N, 85°23'W), 150: SMF 80817[H], 80818, USNM 549359–60; Quebrada El Guásimo, 140 m: SMF 80819; **Nicaragua**: "Nicaragua": AMNH 17233–36, 17238, 17243, USNM 14206, 17902; Atlántico Norte: Parque Nacional Saslaya: SMF 82848; Parque Nacional Saslaya, Estación Biologica Salto Labú (13°39'51''N, 85°00'55.5'W), 260 m: SMF 82036; Parque Nacional Saslaya, Cerro El Toro, between Camps I and II, 1000 m: SMF 82037; Parque Nacional Saslaya, Cerro El Toro, Campamento I, 720 m: SMF 82038–39; Parque Nacional Saslaya, Cerro El Toro, near Campamento I, 830 m: SMF 83160, 83161–62[both H]; Parque Nacional Saslaya, Campamento Las Ranas, 920 m: SMF 81938; Parque Nacional Saslaya, Caño El Cedro, 980 m: SMF 81939–40; Parque Nacional Saslaya, Campamento El Carao (13°42.79'N, 84°58.66'W), 400 m: SMF 79638, 82847; Parque Nacional Saslaya, trail from Campamento Las Pavas (13°44.5'N, 85°01.5'W) to Campamento Los Monos (13°45.1'N, 85°02.2'W), 810 m: SMF 79380[H], 79381; Parque Nacional Saslaya, Campamento Los Monos (13°45.1'N; 85°02.2'W), 800 m: SMF 79383[H], 79384, 79593; S slope of Cerro Saslaya, 1100 m: SMF 79385; 1 km E Bonanza, 240 m: KU 101391; Eden Mine: AMNH 17237; Alamikamba (13°30.08'N, 84°13.64'W): SMF 77451–54; Sioux Plantation: AMNH 17259; near Pia Creek: AMNH 17205–14; Musawas, Río Huaspuc: AMNH 75456, 146734, 153427; Atlántico Sur: Cara de Mono, 50 m: KU 112984, 113013; Río Escondido, 50 mi from Bluefields: USNM 19876, 20695; N side Río Escondido, 10 km below Rama, 20 m: KU 101864; Río Chiquito (11°37.34'N, 84°07.73'W), 42 m: SMF 77455–56, 77557; Kukra: AMNH 17198–204; Kukra, Wholesome Creek: AMNH 17244–50; Kanawá: AMNH 17254–57; Sixicuas Creek: AMNH 17258; Cupitna Camp: AMNH 17215–32; Tule Creek: AMNH 17239–42; Camp Santa Ana, Río Huahuashan: AMNH 70510–12, 70514, 70518, 70526; Río Pichinga, back of Pearl Lagoon: AMNH 70528–32; Granada: Volcán Mombacho: SMF 78291[H]; Matagalpa: 12 km NE Matagalpa, 1100 m: KU 195069–71; Finca Tepeyac, 10.5 km N and 9 km E Matagalpa, 960 m: KU 85642–44; Selva Negra (12°59.96'N, 85°54.55'W): SMF 77342, 77457–64, 77479, 77480–81[both H], 77482, 77483–84[both H], 77485, 78277–78, 78279–80[both H], 78289–90[both H], 78516[H], 79821, 79822–23[both H]; Jinotega: Finca Berlín (13°32.26'N, 85°41.50'W), 1015 m: SMF 79003; Cordillera Isabelia (13°13.55'N, 85°39.21'W): SMF 77449–50; Reserva Biosfera Bosawas, ca. 0.5 km SE Pueblo Wiso (13°59.60'N, 85°19.60'W), 190–200 m: SMF 78517–18[both H]; Reserva Biosfera Bosawas, ca. 3 km SE Ayapal at Río Curinwas (13°46.62'N, 85°23.17'W), 200 m: SMF 78405; Río San Juan: Río San Juan, Boca de San Carlos (10°47.26'N, 84°11.70'W), 20 m: SMF 79824–26[all H]; Río Sarnoso, ca. 1 km above confluence with Río San Juan (10°55.35'N, 84°17.40'W), 25 m: SMF 79827[H]; Río San Juan, Bartola (10°58.37'N, 84°20.35'W), 30 m: SMF 79828–29, 80944–53; Río San Juan: USNM 24979; Río San Juan, Colorado Junction: USNM 19505; Río San Juan, at junction with Río Sarapiqui (10°42'50''N, 83°56'05''W), 20 m: SMF 83151–52, 83172–73; Río San Juan, at junction with Río Chimurria (10°43'31''N, 83°54'29''W), 24 m: SMF 83153, 83154–55[both H]; Río El Chancho, 5–6 km above junction with Río San Juan (10°48'60''N, 84°00'59''W), 60 m: SMF 83156, 83158, 83159[H]; Río San Francisco, 4 km above junction with Río San Juan (10°48'43''N, 84°01'35''W), 40 m: SMF 83157[H].

Anolis uniformis: **Belize**: Cayo: Blue Hole National Park, ca. 20 km SE Belmopan (17°08'49''N, 88°41'38''W), 80 m: SMF 83321[H]; Caracol, 510 m: SMF 83328; Chiquibul Branch, S Granos de Oro Camp (16°35'N, 89°02'W): CM 112128; Stann Creek: Cockscomb Basin Wildlife Sanctuary, Ben's Bluff Trail, 80 m: SMF 83322[H], 83323–24, 83329–31[all H], 83332–35; Cockscomb Basin Wildlife Sanctuary, Gibnut Trail, 80 m: SMF 83325[H], 83326–27; Cockscomb Basin Wildlife Sanctuary, Pearce Camp, at confluence of Cockscomb Branch and Mexican Branch (16°46'25''N, 88°31'57''W), 80 m: USNM 496669–81, 497642; Bokowina [= Silk Grass]: FMNH 49132–33; 49137–39; State forest, Stann Creek RR, 4 mi from 12 m: FMNH 4484–85; E slope of Cockscomb Mts., 750–1150 ft: CM 8483, 8486; Toledo: Blue Creek Village vicinity of Slattery Field Station: UTA R11008–30, 11031[H], 11032–42; Limestone range, 2 km N Blue Creek village (16°12.4'N, 89°2.9'W), 75 m: UF 87176; Columbia Forest Reserve, 1 mi W Salamanca: CM 105853, 105867–70, 105872; Río Grande, ca. 2 mi SE Big Falls: CM 105893–94; Bladen Nature Reserve, Teakettle Camp on Bladen Branch (16°31'01''N, 88°49'48''W), 140 m: USNM 496682–83, 496684[H], 496685–92; Champon (camp), Columbia River Forest

Reserve, drainage of Rio Grande: USNM 326153; Cumbres (between sinkholes), Columbia River Forest Reserve: USNM 326162–66; vicinity of El Tigre (camp), Columbia River Forest Reserve, drainage of Central River: USNM 326160, 326167, 326157–59; Gloria Camp, Colombia River Forest Reserve (16°22'N, 89°10'W), 680 m: USNM 319770–72; Maya Mountain Forest Reserve, Snake Creek (16°28'45''N, 89°01'30''W), 600 m: USNM 498208–09; near San Pedro Columbia, vicinity of Lubaantun Ruins: USNM 326152; Union Camp, Colombia River Forest Reserve (16°23'05''N, 89°08'36''W), 700 m: USNM 319773; **Guatemala**: "Guatemala": USNM 24734–50; Alta Verapáz: Coban Parque Nacional: NMW 20667 (1–6), UTA R41886, R41917–19; Finca Rubelpec: UTA R46873; Finca San Juan: UTA R46872[H], R46874[H]; N slope Sierra de las Minas, Finca Pueblo Viejo, crest of Río Chiquito/Quebrada Cancoy divide: UTA R26985; N slope Sierra de las Minas, Finca Pueblo Viejo, W slope Río Tinajas/Río Chiquito divide: UTA R26986, R27213–23; Santa Teresa: MCZ 46309; Sepacuite: MCZ 22307; Tucuru: NMW 20667 (7); Huehuetenango: Barillas Finca Chiblac Buena Vista camino a Barillas: UTA R52087–89; Finca Chiblac ca. 22.0 km NNE Barillas: UTA R29569–72, 29573[H], 29574, 29575[H], 29576–82; Sierra de Los Cuchumatanes Finca Chiblac 21.7 road km NNE Barillas: UTA R27224–26, R41921–24; Izabal: betw. Cayo Piedra and San Gil: ANSP 22172–75; Lago de Izabal, 2 mi E El Estor: UF 16312–13; Bananera [=Bananera Morales]: FMNH 35072; Cerro San Gil, Río Frío, 65 m: FMNH 40910; Cerro San Gil, Sector Río Las Escobas (15°41'N, 88°39'W), 160–240 m: SMF 83952–53[both H], 83954–56, 83957–59[all H], 83960; 5.5 km WSW Puerto Santo Tomás near Las Escobas: UTA R15986–92, 15993[H], 15994–16004, R20151–67, R20170–94, R20211–27, R20196–210, R23642–46, R20168, R29537[H], 29538–47, 29548[H], 29549, 29550[H], 29551–60, R29566–68, R33468–69, R33482–83, R41888–93, R41920; E slope Montañas del Mico, 7.2–7.8 km WSW Puerto Santo Tomás: UTA R15983–85; E slope Montañas del Mico, 9.8 km SW Puerto Santo Tomás: UTA R20169; E slope Montañas del Mico, 11.6–13.0 km WSW Puerto Santo Tomás: UTA R15982, R20150, R29534[H], 29535, 29536[H], R29561, 29562–63[both H], 29564–65, R29806–35; Montañas del Mico 12.6 km W Puerto Santo Tomás: UTA R41894–95; NW of Puerto Santo Tomas along trail hiking back from Rio Tamejar at base of Cerro San Gil: UTA R33505–06; Puerto Barrios Montañas del Mico Cerro del Microondas: UTA R37621–22, R43597; Seshán: UTA R23631–39; Chichipate: UTA R23628–30; El Estor: UTA R23640; Livingston Quebrada El Branchi: UTA R43607; Livingston Siete Altares: UTA R43598–600; Sierra de las Minas, Los Amates Aldea Vista Hermosa: UTA R33507, R37605, R37613–19; Sierra del Espíritu Santo, Municipio de Los Amates, Aldea San Antonio: UTA R29587–89, R29594–96; Sierra del Espíritu Santo, Municipio de Los Amates, Cerro del Nylon: UTA R29586; Sierra del Espíritu Santo, Municipio de Los Amates, S side Cerro del Nylon: UTA R29590–93; Sierra de Caral, Municipio de Morales, Camino Finca La Firmeza a Cerro Pozo de Agua-Cerro Negro Norte: UTA R43577–83, R43593, R43601–02; Sierra de Caral, Municipio de Morales, Camino La Firmeza-Cerro Pozo de Aqua: UTA R43595–96; Sierra de Caral, Municipio de Morales, road Quebrades-La Firmeza: UTA R33509–11, R41887; Sierra de Caral, Municipio de Morales, Aldea Mirador: UTA R33484–91; Sierra de Caral, Municipio de Morales, Cerro Bonillistas: UTA R33492–504; Sierra de Caral, Municipio de Morales, Quebradas: UTA R33508; Sierra de Caral, Municipio de Morales, San Miguelito: UTA R37606–12, R37620, R43594; Sierra de Caral, Municipio de Morales, along tributary of Río Bobos: UTA R37604; Sierra de las Minas, Cristina: UTA R20195; Sierra de Santa Cruz Exmibal Forest first crest on road from Finca Semuc just W of El Estor: UTA R52110; Sierra de Santa Cruz Exmibal Forest just W of El Estor: UTA R52109; Sierra de Santa Cruz, near Finca Semuc: UTA R22080–97, R22098–103, R23625–33, R29805, R27246–47; Sierra de Santa Cruz Livingston Aldea La Libertad: UTA R43604–06, R46907–08; Sierra de Santa Cruz S side La Dicha: UTA R27237; Sierra de Santa Cruz Xiac m: UTA R27238–43; Sierra de Santa Cruz Cerro 1019 east side (next to Aldea La Libertad): UTA R27235–36, R27244–45, R29583–85, R43584–91; Sierra de Santa Cruz Cerro 1019: UTA R27234; Livingston Sierra de Santa Cruz: UTA R43603; Petén: „El Peten": USNM 71866, 71869, 71892, 71908, 71911, 71915; Altar de los Sacrificios: AMNH 99902–04; ruins of Tikal, Parque Nacional Tikal: AMNH 140242–44, SMF 77182, UF 137535–37; La Libertad Parque Nacional Sierra Lacandón: UTA R46119–20; N of Yaxhá on road to Nakun: UTA R50331; Tikal 1.0 km E of main ruins: UTA R41163; Tikal near Temple 5: UTA R23641; Uaxactum: AMNH 70932; Zacapa: La Unión: CM 57504; Sierra del Merendón Finca San Enrique Sur del Casco: UTA R33470–81; **Honduras**: Copán: Laguna del Cerro (15°04.74'N, 88°56.39'W), 770 m: SMF 79150–51; trail between Laguna del Cerro and Quebrada Grande (15°06'N, 88°55'W), 1100 m: USNM 330185; ca. 1 km SSE Tegucigalpita (15°37.17'N, 88°14.96'W), 40 m: SMF 79130–33, 79148–49, USNM 330186–88; ca. 7 km SSE Tegucigalpita, 370 m: SMF 79134; **Mexico**: Chiapas: Ruinas de Palenque, 140–300 m: ENCB 1477–81, KU 94044–45, LSUMZ 33418, MZFC 488, UIMNH 11323, UTA R3090; vicinity of Cascada Mizda [= Misholha], ca. 19 km from Palenque on road to Ocosingo: AMNH 114818; Solosuchiapa, 440 m: ENCB 15394; Jetja (Lacandones): AMNH 142451, 142457; Lacandone Forest: AMNH 66437–38; 2 mi W Agua Escondido: KU 41627–28; 13 mi S Palenque: LSUMZ 33416–17; 10–15 mi S Palenque: LSUMZ 33419–20, 33740–41; vicinity Bonampak: MZFC 487; Puente Santa Helena, Río Amparo Agua Tinta (16°57'08''N, 91°27'36''W), 830–880 m: SMF 81593, 81595; Oaxaca: Sierra Mixes 3.1 mi W Totontepec: UTA R9899; Tabasco: "Tabasco": MNHN 1893.56; Teapa: USNM 46672–74; Veracrúz: "Veracruz": AMNH 149655; Rio de Las Playas: USNM 118637; 1.8 mi S Juan Diaz

Covarrubias: UTA R9793, R9897, R9927, R9934–35, R9956; 11.9 mi N Santiago de Tuxtla: UTA R9896; 7.7 mi (by road) NW Sontecomapan: UTA R2648–50, R9521–603, R9732–49, R9750–79, R9786–92, R9795–807, R9828, R9863–68, R9873–95, R9900–25, R9929–33, R9936–55, R9781–85, R9808–21, R9869–72, R10079–81, R10082–91, R10098–99, R10101–28, R10139, R10141–48, R10151–91, R10200–16, R10221–64; Los Tuxtlas region, 2.1 mi NW (by road) Sontecomapan: UTA R3102, R311726; Los Tuxtlas region, NW edge Lake Catemaco: UTA R3100, R3173; Los Tuxtlas region, 2.5 mi SSW of Sontecomapam: UTA R3005, R3214, R3018–19, R3128; Los Tuxtlas region, Rio Yougualtapan ca. 4.5 mi ESE of Sontecomapan: UTA R3161; W slope Volcán Santa Marta: UTA R3210–13; SE slope Volcán San Martín, ca. 1000 m: UMMZ 121373–75; Yucatán: “Yucatán”: USNM 24859.

APPENDIX D: SPECIMENS EXAMINED IN CHAPTER 2.3.3

[H] Specimens with everted hemipenis

Anolis apletophallus: **Panama:** Colón: Cano Saddle, Close's plantation: USNM 69586; Chagres River: USNM 102849; Río Indio, near Gatún: USNM 54007; Gatún: USNM 54011–12; Bohio Peninsula – East, Panama Canal: USNM 505231–37, 505238–42[all H], 505243–51, 505252[H], 505253, 505254–56[all H], 505257, 505258[H], 505259, 505260[H], 505261–69, 505270–73[all H], 505274, 505275–76[both H], 505277–85, 505286[H], 505287–88, 505289–90[both H], 505291–92, 505293–301[all H]; Buena Vista Peninsula, Panama Canal: USNM 505199–230; Gigante Ridge, Panama Canal: USNM 505371–82, 505383–84[both H], 505385, 505386–88[all H], 505389–93, 505394–95[both H], 505396–97, 505398–99[both H], 505400, 505401[H]; Juan Gallegos Island – East, Panama Canal: USNM 505571–82, 505583–84[both H], 505585, 505586[H], 505587–89, 505590[H], 505591–97, 505598–99[both H], 505600, 505601[H]; Juan Gallegos Island – North, Panama Canal: USNM 505602–04, 505605–08[all H], 505609–16, 505617[H], 505618–22, 505623[H], 505624, 505625[H], 505626, 505627[H]; Juan Gallegos Island – South, Panama Canal: USNM 505541–49, 505550[H], 505551–52, 505553[H], 505554, 505555–57[all H], 505558, 505559[H], 505560–63, 505564–68[all H], 505569, 505570[H]; Limbo Camp, Panama Canal: USNM 505457–73, 505474[H], 505475–79, 505480–81[both H], 505482, 505483[H]; Lion Hill Island, Panama Canal: USNM 505302–05, 505306–08[all H], 505309, 505310[H], 505311–18, 505319–20[both H], 505321–31, 505332[H], 505333–34; Peña Blanca Peninsula, Panama Canal: USNM 505402–06, 505407[H], 505408–10, 505411–15[all H], 505416, 505417[H], 505418–22, 505423[H], 505424–25, 505426–27[both H], 505428, 505429–30[both H], 505431; Poachers Peninsula: USNM 505650–59, 505660–61[both H], 505662–64, 505665[H], 505666–67, 505668–69[both H], 505670, 505671–73[all H], 505674–76; Puma Island, Panama Canal: USNM 505335–44, 505345[H], 505346–50, 505351[H], 505352–53, 505354–56[all H], 505357–60, 505361[H], 505362–63, 505364[H], 505365, 505366[H], 505367, 505368–70[all H]; Río Agua Salud, Panama Canal: USNM 505432–34, 505435–36[both H], 505437, 505438[H], 505439–40, 505441[H], 505442, 505443–45[all H], 505446–49, 505450[H], 505451, 505452[H], 505453, 505454–55[both H], 505456; Río Gigantito, Panama Canal: USNM 505515–20, 505521–22[both H], 505523, 505524[H], 505525–40; Río Mendoza, Panama Canal: USNM 505628–42, 505643[H], 505644–48, 505649[H]; Tigre Island, Panama Canal: USNM 505484–500, 505501–05[all H], 505506–10, 505511[H], 505512–14; Quipo, on Río Ciri, W side L. Gatún: AMNH 42919; Darién: 0.5 hr below junction of Río Jaque and Río Imamado: USNM 161216; Pirri Range, near head of Río Limón: USNM 50151; Chalichiman's Creek: AMNH 42916–17; Camp Creek: AMNH 42920; Río Chucunague [Chucunaque]: AMNH 37902–03, 49214; Río Chucunague [Chucunaque], 3 mi W of Camp Townsend: AMNH 102557–58; Yavisa, backyard junkpiles: CM 74030–31; Yavisa, trail along Río Chucunague [Chucunaque]: CM 74038; 7–11 km SW El Real between Río Presencia and Río Morgentese, 100–350 m: UMMZ 155802–03; Río Sucubti: AMNH 42909–14; Tapia: AMNH 25021, 25023, 25025–26; Panamá: Metropolitan National Park, Panama City (8°58'60''N, 79°32'46''W), 45 m: SMF 85307[H], 85308, 85309–10[both H], 85311–19; "Panama Prov.": AMNH 71727, 71729, 76001–03, 89883; Canal Zone: AMNH 67078, 67081–82, 71716, 71730–33, 75990[H], 75991–92, 89880–82, 85605–07, 107432–64, 107465[H], 107466, USNM 54325; Las Cascadas, Canal Zone: MCZ 19414, 19416, 175185, 175187, 175189–90, 175194, 175196–97, 175200, 175203, 175207, 175209, 175213–16, 175223, 175225, 175233; Canal Zone, Camp Mary Caretta (= Camp Santa Margarita): USNM 25162–63; Canal Zone, Gamboa: USNM 193351; Canal Zone, Río Frijoles, 3 mi N Gamboa: UF 124417; Gamboa, at confluence of Panama Canal and Chagres River (9°06'54''N, 79°41'42''W): USNM 297807–09; Gamboa: SMF 84954, 83084–85; Canal Zone, Río Medio: USNM 102725; Lion Hill: USNM 54172; Old Panama: USNM 50129; Panama, Cabima (Pacific slope): USNM 48500–01; Panama, Cocoli: USNM 193365, 193371, 523377–78; Puerta Obaldia, Quebrada Repressa: USNM 150127; Venado Beach: USNM 193359; Punta de Pena: USNM 38712; Toro Point: USNM 53725; Trinidad River: USNM 63992–94, 63997; Viento Frío: USNM 48597; La Joya, Pacific side: ANSP 25136; Río Tatare, Pacific side: ANSP 25137; Gatún: ANSP 19520–22, 19523, 24863–65, 24866–67; Canal Zone, Fort Gulick, Atlantic side: ANSP 25104; Canal Zone, Empire: ANSP 19545; Chico: CM 6859; Barro Colorado Island: AMNH 75986, ANSP 24487–92, 24493[H], 24494–500, 24559, CM 7664, 7666, 7669, 7671, 7673–75, 7681, 7686–93, 7699, 7705, 7707–10, 7712–19, 7725; Barro Colorado Island, Wheeler trail: UMMZ 63688; Lutz Creek below Donats bridge: CM 7659; Río Pequeni, head of Madden Lake: ANSP 21694; Juan Mina, Madden Lake watershed: CM 74047; near Fort Clayton Reservation: UIMNH 42184; Cerro Campana: AMNH 75999; Cerro Campana, 800–900 m: AMNH 10666; Altos de Majé: AMNH 109623[H], 109624–35; Serranía de Majé, proximities of Unión Saldaña, Río Chimán (8°51'59.0''N, 78°35'13.6''W), 470 m: MHCH 1146; Serranía de Majé, Río Ambroya: MHCH 1082[H], 1086, 1090; San Blás: Armila: USNM 150099, 150100[H], 150101–108; Armila, Quebrada Venado: USNM 150110–13; Nusagandi, near field station (9°20.50'N, 78°59.64'W), 300–360 m: SMF 80717[H], 80718, 80719[H] , 80720[H]; km 14.6 on El Llano – Cartí road, 370 m: AMNH 110572; km 12.8 on El Llano – Cartí road, 290 m: AMNH 110573–74.

Anolis cryptolimifrons: **Costa Rica:** Limón: SE side Cerro Nimaso: UCR 8477[H]; **Panama**: Bocas del Toro: Cerro Brujo (9°11'16.4''N, 82°11'25.4''W), 10 m: SMF 85230[H], 85231–35, 85236–37[both H], 85238–41, 85242–43[both H], 85244; vicinity of Almirante: ANSP 34047–50[all H], 34051, 34052[H], 34053–54, USNM 279062–71, 279130–33; Río Changuinola, near Quebrada El Guabo, 16 km airline W Almirante, 200–250 m: AMNH 119043[H], 119044–49; Cayo Agua, Punta Norte: USNM 150005, 150007–09; Cayo Agua, near Punta Limón: USNM 338690–92; Isla Bastimentos, Old Point: USNM 297888–97; Isla Bastimentos: SMF 85229, 85245[H]; Isla Colón, ca. 0.8 mi N of Bocas del Toro (town): USNM 338214–16; Isla Colón, just N of Bocas del Toro (town), along beach at fairgrounds, E side of isthmus: USNM 346901; Isla Colón, La Gruta: USNM 313767–78, 313794, 338217, 338218[H], 338219–22, 338223[H], 338224–26, 338227–29[all H], 338230–32; Isla Cristóbal, Bocatorito camp: USNM 348191[H], 348192–94, 348195[H], 348196–201, 348202[H], 348203–05; NW side of Isla Cristóbal: USNM 348206[H], 348207–10; Isla Pastores, Ford Point: USNM 313847–48; Isla Popa, 1 km SE of Deer Island channel: USNM 298121–35; Isla Popa, south end of, 1 km E of Sumwood Channel: USNM 319213–25, 347260–63, 347264–65[both H], 347266–71, 347272–75[all H], 347276–77, 347278[H], 347279, 347280[H], 347281–83; Isla Popa (9°13'14''N, 82°08'28''W), 10 m: SMF 85247–48[both H], 85249, 85250[H]; Isla Popa, NNE beach (9°13'24.4''N, 82°06'36.6''W), 10–20 m: SMF 85399[H], 85400; Laguna de Tierra Oscura, 3.7 km S of Tigre Key: USNM 313838–51, 348467–70[all H], 348471–80; Long Bay Point and Flat Rock Point, between, on E side of island, ca. 100 yds from beach: USNM 297816–17; midpoint on W side of Cayo Carenero: USNM 347938; N end of Cayo Roldan: USNM 348043; Isla Solarte, 10 m: SMF 85251[H], 85252–53; USNM 338552, 338553–55[all H], 338556–57, 338558[H], 338559–61, 338562–63[both H], 338564, 338565[H], 338566–68.

Anolis limifrons: **Costa Rica: "**Costa Rica": USNM 38334, 70406–10, 81198; Parismina nivel del mar: USNM 75444–46; Colombiana: USNM 67347–48; Alajuela: Río Frío: USNM 19514; Pizote: UCR 9988–89[both H], 10646[H]; Pilón, Bijagua: UCR 10504[H]; Laguna Lagarto Lodge, Boca Tapada: UCR 12609[H]; Río Tapezco: UCR 16515[H]; Cartago: 10.0 km NE Turrialba on E bank of Río Reventazón R12873–75; 2.0 km W Pavones de Turrialba R12878–79; 3.0 km NE Pavones de Turrialba at Río Chitaría R12869–72, R12876–77; Tapanti: ZFMK 48716; "Turrialba Prov.": AMNH 69707–10; Turrialba: SMF 77206, USNM 133180, 192586, 523375–76; Estación Biológica Copal, Tausito, Pejibaye: UCR 16127; 1 Km E La Pastora (9°58'06.1''N, 83°44'18.9''W), 1500 m: SMF 86924; Heredia: Rara Avis, Catarata (10°16.92'N, 84°02.74'W), 700 m: SMF 81814, 81815[H]; Puerto Viejo: ZFMK 48723–37, USNM 245041; La Selva Biological Station, 2.6 km SE of Puerto Viejo de Sarapiquí: USNM 505677–90, 505691[H], 505692–95, 505696[H], 505697, 505698[H], 505699–701; Finca Santiago (near La Selva): SMF 78433; Limón: "Limón Prov.": AMNH 89171–73, 89175–76, 95095, 99671–76, 149611–20; ca 5/4 mi S mouth of Río Tortuguero, ca. 50 mi NW Limón: AMNH 89174[H]; ca. 5 mi N Limón: AMNH 89177[H]; Zent [10°0160N, 83°16'60W], 31 m: USNM 137767; Approximately 17.0 km WSW Puerto Limón between Río Blanco and Río Toro R12882–88; Siquirres large stream outside of town R12880–81; Motel Matama, 3.5 km N Limón: AMNH 138604–05; 4 mi SW La Fortuna: IRSNB 11684; Atalanta Farm, Estrella Valle: ANSP 21465; Puerto Limón: ANSP 19570, 19571[H], 19572–78, IRSNB 13804, ZSM 85/1998, 86/1998; La Castilla, lower Río Reventazón: ANSP 23710–37, 24501–04, 34747; Tortuguero: UF 135783–84; Tortuguero, just N of Caribbean Conservation Commission Camp: USNM 244861; 2.4 km E Siquirres, along Río Pacuare: CM 89566–67; Rte 32, 69 km E Río Hondo, 2 km N on dirt road: ANSP 32372, 32374; 2–3 km (air) NW Bribri at Río Carbón along road to Uatsi: ANSP 32559; RB Hitoy Cerere: SMF 86925[H], 86926, 86927–28[both H]; Estación Biológica Tierra Media, Matina: UCR 12399[H]; Quebrada Uatsi: UCR 13031[H]; Sendero San Mateo, Cerro Uatsi: UCR 13195[H]; Finca Brian Kubicki, Guayacán: UCR 16914[H]; Puntarenas: "Puntarenas Prov.": AMNH 16357; 7 mi E Golfito: LSUMZ 30260; Península de Osa, Golfo Dulce, Puerto Jiménez, jardin at Jiménez Yacht Club: SMF 81512–15; EB San Gerardo, Monteverde: UCR 13652[H]; Hotel Sunset, 1 km N Santa Elena, Monteverde region (10°19'36.9''N, 84°49'24.1''W), 1450–1475 m: SMF 85549–53, 85554[H]; San José: San José: ANSP 7804, USNM 80902–05; San José, grounds of Hotel Irazú: UMMZ 143761; 6.0 km N San Isidro de Perez Zeledón: UTA R12868; Talamanca: USNM 75956; Moravia de Chirripo: UMMZ 128952; Near San Isidro (9°24'29.1''N, 83°44'06.6''W), 880 m: SMF 86933–35; Road from General Viejo to Santa Elena (9°20'06.5''N, 83°39'11.4''W), 650 m: SMF 86929; **Honduras:** Colón: Quebrada Machín (15°19'10''N, 85°17'30''W), 540 m: USNM 536490–91, 541026–29; R. B. Río Plátano, El Ocotillal, Cabeceras de Río Plátano (15°40.3'N, 85°17.1'W) 370–410 m: SMF 86215[H], 86216, 86217[H]; Gracias a Dios: Mocorón R46171–72; confluence of Río Wampú and Quebrada Waskista (15°00'N, 84°59'W), 85 m: USNM 330183–84; confluence of Río Wampú and Río Patuca (14°58'N, 84°59'W), 60 m: USNM 330181–82; Quebrada Waskista, 85 m: SMF 80708–09; R. B. Río Plátano, Raudal Kiplatara (15.599°N, 84. 948°W), 50–255 m: SMF 86172[H], 86173–74, 86175[H], 86176–82, 86183–84[both H], 86186; R. B. Río Plátano, Río Cuyamel (15.582°N, 84.993°W), 115–345 m: SMF 86188, 86189[H], 86190, 86191[H], 86192–96, 86198[H], 86204–05; R. B. Río Plátano, Pomokir (15. 493°N, 84. 948°W), 150–240 m: SMF 86207, 86208–09[both H], 86211, 86213–14[both H]; R. B. Río Plátano, Crique Unawas (15. 127°N, 84. 923°W), 180–305 m: SMF 86220–21, 86222–3[both H], 86224–28, 86229[H]; Quebrada Waskista-Río Wampú confluence (15°00'N, 84°59'W), 85 m: SMF 86887; Cabeceras del Río Rus Rus, 190 m: SMF 86888;

Olancho: confluence of Río Wampú and Quebrada Siksatara (15°03'N, 85°02'W), 95 m: USNM 330180; confluence of Río Aner and Río Wampú (15°04'N, 85°06'W), 110 m: SMF 80704, USNM 330176–77; confluence of Río Wampú and Río Sausa (15°04'N, 85°06'W), 100 m: SMF 80705, 80706–07, USNM 330178–79; confluence of Río Yanguay and Río Wampú (15°03'N, 85°08'W), 110 m: USNM 330175; Parque Nacional Patuca, Matamoros (14°40'21''N, 85°23'11''W), 150 m: SMF 80710, 80712; Parque Nacional Patuca, Quebrada El Guásimo (14°34'38''N, 85°17'54''W), 140 m: SMF 80713, 80714–15, 80716[H]; Parque Nacional Patuca, Caobitas (14°39'22''N, 85°17'43''W), 100 m: SMF 80711; Quebrada Siksatara-Río Wampú confluence (15°04'N, 85°02'W), 95 m: SMF 86889–90; Río Yanguay-Río Wampú confluence (15°03'N, 85°08'W), 110 m: SMF 86891–93; Río Aner-Río Wampú confluence (15°03'N, 85°07'W), 110 m: SMF 86894–96; Río Sausa-Río Wampú confluence (15°04'N, 85°06'W), 100 m: SMF 86897–900, 86901[H], 86902–03; Yapuwás (14°58'N, 85°00'W), 60 m: SMF 86904–06; Between Río Sausa and Río Wampú, 100 m: SMF 86907, 86908; Quebrada de Las Marías (15°18'N, 85°21'W), 660 m: SMF 86909[H]; Matamoros (14°40'N, 85°23'W), 150 m: SMF 86910–14[all H]; Quebrada El Mono (14°39'N, 85°20'W), 100 m: SMF 86915; Quebrada El Guásimo (15°05'N, 86°25'W), 140 m: SMF 86916; **Nicaragua:** no specific locality: USNM 13739, 15212; "Palvon" (=El Polvón?): USNM 120758; Atlántico Norte: Eden Mine: ANSP 21138; Great Falls, Pispis: ANSP 21124; Parque Nacional Saslaya, Estación Biologica Salto Labú (13°39'51''N, 85°00'55''W), 260 m: SMF 82068–69; Parque Nacional Saslaya, between Estación Biologica Salto Labú and Campamento El Revenido, 400–500 m: SMF 82236; Parque Nacional Saslaya, Campamento I (13°43'11''N, 85°02'20''W), 720 m: SMF 82070[H]; Parque Nacional Saslaya, Campamento El Carao (13°42.79'N, 84°58.66'W), 400 m: SMF 79611; Parque Nacional Saslaya, Campamento Las Pavas (13°44.5'N, 85°01.5'W), 780 m: SMF 79379[H]; Parque Nacional Saslaya, trail from Campamento Las Pavas to Campamento El Carao: SMF 82844; Parque Nacional Saslaya, trail from Campamento Las Pavas (13°44.5'N, 85°01.5'W) to Campamento Los Monos (13°45.1'N, 85°02.2'W), 810 m: SMF 79382[H]; Parque Nacional Saslaya, Campamento Los Monos (13°45.1'N, 85°02.2'W), 800–820 m: SMF 79161, 79591, 79607, 79898; Parque Nacional Saslaya, Campamento Las Ranas, 920 m: SMF 82071; Cerro El Toro (13°42'30.6''N, 85°02'17.7''W), 830 m: SMF 83209; Rancho Alegre (13°39'47.5''N, 85°01'38.9''W), 285 m: SMF 84737, JS 052; Finca URACCAN (13°43'44.1''N, 84°53'14.5''W), 145 m: SMF 84738, JS 074; 4 km E Bonanza, 200 m: KU 101397; Bonanza, 260 m: KU 84867, 85656–57, 101398–400; Alamikamba (13°30.08'N, 84°13.64'W): SMF 77552–55; Moss, 2 km S Finca Luciana, along Río Wawa: SMF 88163[H], 88165[H], JS 1089, 1090[H], 1130; Krin Krin, 5 km W confluence Río Waspuk with Río Coco: SMF 88164; Atlántico Sur: Río Escondido, 45 mi. from Bluefields: USNM 19733–34; Río Escondido, 50 mi from Bluefields: USNM 19877; Cara de Mono, 50 m: KU 112991; El Recreo, S side Río Mico, 25 m: KU 101865–67, 112988–90; vicinity of Providencia (11°31.79'N, 84°22.92'W), 100 m: SMF 77556; Boaco: Finca Santa Helena, Masigüe, 30 km NE Camoapa, 600 m: SMF 84733; Jinotega: Finca Berlín (13°32.26'N, 85°41.50'W), 1015 m: SMF 78980[H]; Cerro Kilambé, La Cueva (13°36'11.1''N, 85°42'52.6''W), 1025 m: JS 161; Cerro Kilambé, El Diamante (13°36'51.3''N, 85°44'20.2''W, 1090 m: SMF 84739; Cerro Kilambé (13°37'06.2''N, 85°43'19.5''W, 1015 m: SMF 84740[H]; Reserva Biosfera Bosawas, ca. 0.5 km SE Pueblo Wiso (13°59.60'N, 85°19.60'W), 200 m: SMF 78534–35[both H]; Reserva Biosfera Bosawas, Ayapal (13°46.61'N, 85°24.14'W), 195 m: SMF 78404; Cordillera Isabelia (13°19.99'N, 85°41.52'W), 500 m: SMF 78314[H], 78315, 78316[H]; Finca Santa Enriqueta, 5 km E San José De Las Latas, 1300 m: SMF 84732[H], JS 061; Raití, along Río Coco: SMF 88168–69, JS 920; Matagalpa: Selva Negra (12°59.96'N, 85°54.55'W): SMF 77202–03, 77204–05, 77334, 77551, 78201, 78202[H], 78203–04, 78205[H] ,78206, 78281, 78312, 79814[H]; 12 km NE Matagalpa, 1100 m: KU 195077–78; Finca Tepeyac, 10.5 km N and 9 km E Matagalpa, 960 m: KU 85651–55, 85675; road to Puerto Cabezas (13°17.11'N, 85°42.94'W), 1000 m: SMF 78313; Cerro Musún, Fundenic (12° 57'18.8''N, 85°13'51.2''W), 630 m: SMF 86707[H], JS 740, 753[H]; Río San Juan: Machuca: ANSP 7803; at Isla de Diamante on Río San Juan: OMNH 35932–33; Río San Juan: USNM 24981–82; San Juan del Norte: USNM 19506–07; Río San Juan, Boca de San Carlos (10°47.26'N, 84°11.70'W), 20 m: SMF 79815, 79816[H]; Boca de San Carlos (10°47'25.7''N, 84°11'37.7''W), 40 m: SMF 86706; Río San Juan, Bartola (10°58.37'N, 84°20.35'W), 25–30 m: SMF 79817[H], 79818, 80924–39, 80965, 86705[H], JS 455; confluence of Río San Juan and Río Sarapiquí: SMF 83206[H], 83207; Chingo Petaca (10°44'50.9''N, 83°50'26.3''W), 40 m: SMF 83208[H]; Dos Bocas de Bartola, El Almendro (10°59'43.9''N, 84°16'37.5''W), 75 m: SMF 86709[H]; Dos Bocas de Río Indio (11°02'54.8''N, 83°52'48.4''W), 25 m: SMF 88162, JS 542[H], 622[H]; Río Frío, Fundeverde (11°04'37.0''N, 84°44'55.7''W), 45 m: SMF 86712, 86713[H], 86714; Río Frío, Fundeverde (11°03'41.8''N, 84°44'27.0''W), 50 m: JS 355; along Río Papaturro, Refugio de Vida Silvestre Los Guatuzos: SMF 88161, 88162[H], JS 958[H]; Islas de Solentiname: KU 174048–50, SMF 77210, 77660, 78324–30; Islas de Solentiname, Isla Mancarrón, Hotel "Mancarrón": SMF 82197[H]; Islas de Solentiname, Isla Mancarrón: SMF 82198, 82199; Islas de Solentiname, Isla Mancarrón, 1 km N Hotel "Mancarrón": SMF 82200[H]; **Panama**: Bocas del Toro: 7.5 km airline WSW Chiriquí Grande, 10 m: AMNH 123265, 123266[H], 123267–68, 123269[H]; Rambala, near Chiriquí Grande (08°55'27''N, 82°11'03''W), 20 m: SMF 85254[H], 85255; Isla Escudo de Veraguas, West Point: USNM 347483–89, 347490[H], 347491; Celentine (8°47'09''N, 82°11'17''W), 610 m: SMF 85228[H]; Quebrada La Gloria, near Miramar (8°59'08.0''N, 82°13’56.4’’W), 20 m: SMF 85246[H]; Boca del Río Krikamola (8°58’38.6’’N, 81°55’01.7’’W), 7 m: MHCH 539[H]; Chiriquí: “Chiriquí”: ZMB 7785, 7827; ca. 6 mi below El Hato, along Hwy, 4000 ft: FMNH 60275; Bugabita, 100–200 m: NMW 20673 (1–3); Boquete: ZSM 63/1989/3; David, UNACHI, Jardín Botánico, near River: SMF 85260; Los Algarrobos (8°29’39.1’’N, 82°26’01.3’’W), 110 m: SMF 85223; Los Algarrobos (8°29’25’’N, 82°26’10’’W), 130 m: SMF 85256; Los Algarrobos (8°29’47’’N, 82°26’00’’W), 130 m: SMF 85257–59; Meseta de Chorcha (8°24’38’’N, 82°13’10’’W), 190 m: SMF 85227; Meseta de Chorcha (8°24’50’’N, 82°13’06’’W), 240–270 m: SMF 85224–26; Coclé: N El Valle de Antón, Cerro Gaitál (8°37.67’N, 80°6.60’W), 750 m: SMF 80779; Veraguas: 5–6 mi (via road) NW Santa Fe: AMNH 120003[H].

APPENDIX E: SPECIMENS EXAMINED IN CHAPTER 2.3.4

Bolitoglossa lignicolor: **Panama**: Chiriquí: 8 Km NE Río Sereno, Finca CASA (08°52'17.0''N, 82°47'43.4''W), 1210 m: SMF 85059.

Bolitoglossa mexicana: **Honduras**: Atlántida: Quebrada La Muralla, PN Pico Bonito: SMF 77630; Colón: RB Río Plátano, El Ocotillal, headwaters of Río Plátano (15°22'N, 85°13'W) 450–470 m: SMF 85935–36; Francisco Morazán: El Paraíso, RB El Chile: SMF 79460; Gracias a Dios: RB Río Plátano, Raudal Kiplatara (15°36'N, 84°57'W), 130–160 m: SMF 85932–33; RB Río Plátano, Crique Unawás (15°07'N, 84°55'W), 250 m: SMF 85937; Olancho: Quebrada de Las Marías, 11.5 Km NNE La Colonia (15°18'N, 85°21'W), 660 m: SMF 78748.

Bolitoglossa mombachoensis: **Nicaragua**: Granada: Volcán Mombacho (11°50.02'N, 85°58.75'W), 1150 m: SMF 78293–94, 78297–304, 78306–07; Volcán Mombacho, near lower antenna (11°49.99'N, 85°58.77'W), 1100 m: SMF 78714–24; Volcán Mombacho, above upper antenna, 1225 m: SMF 79604.

Bolitoglossa odonnelli: **Guatemala**: Alta Verapaz: Finca El Volcán, 25 Km NW (by road) Senahu (15.48333°N, 89.86667°), 875 m: MVZ 161030–36, 161038–39, 161045–46, 161081.

Bolitoglossa platydactyla: **Mexico**: Orizaba: SMF 1305–06; Tampico: SMF 29630.

Bolitoglossa salvinii: **El Salvador**: San Salvador: Instituto Tropical: SMF 79386; **Guatemala**: SMF 1308; Quetzaltenango: Coatepeque, Hotel "Las Gardenias" (14°41'35.9''N, 91°51'07.5''W), 530 m: SMF 84541.

Bolitoglossa striatula: **Nicaragua**: Atlántico Norte: Alamikamba (13°30.081'N, 84°13.642'W), 130 m: SMF 77790; PN Saslaya, El Carrillón, 400 m: SMF 82868; Krin Krin, 5 Km W confluence Río Waspuk and Río Coco: JS 1183, SMF 87179; Jinotega: RB Bosawas, Kulum Kitang (14°19.80'N, 84°56.25'W), 180 m: SMF 87180; Río San Juan: Bartola (10°58.37'N, 84°20.35'W), 30 m: SMF 82095; Dos Bocas de Bartola, El Almendro (10°59'43.9''N, 84°16'37.5''W), 75 m: SMF 87177; near confluence Río San Juan and Río Sarapiquí (10°42'50.2''N, 83°56'04.7''W), 20 m: SMF 83191; Caño El Venado, near Dos Bocas de Río Indio (11°02'14.7''N, 83°53'07.3''W), 10 m: JS 633, SMF 87178; Río Frío, Fundeverde, Senda Peter (11°04'55.8''N, 84°45'11.0''W), 80 m: JS 378, SMF 87176.

Morphometric data of the following specimens was provided by J. R. MCCRANIE. For a more precise location of the following names of Honduran places, see the Gazetteer in MCCRANIE & WILSON (2002:553–578).

Bolitoglossa mexicana: **Honduras**: Atlántida: Tela district: MCZ 10214; Colón: Cerro Calentura: FMNH 236378; Copán: 2 km N of Santa Rosa de Copán: MVZ 163799–800; Cortés: El Jarál: FMNH 4539–42; 1.6 km W of El Jarál: LACM 47620; Finca Fé: LACM 45254, 45300–04; La Lima: LACM 47621; Cofradía: AMNH 45337–38, 45340–41; near Peña Blanca: MVZ 187203–04; 8 km W of Peña Blanca: MVZ 163794–95; 9.7 km W of Peña Blanca: MVZ 163792; 3.1 km SE of Peña Blanca: MVZ 163793; Olancho: Subirana Valley: MCZ 21241; about 15 km N of San Francisco de La Paz: UTA A-19826; La Colonia, 11.5 km (airline) of, Quebrada de Las Marías: USNM 530574–78

Bolitoglossa striatula: **Honduras**: Olancho: Quebrada El Mono: USNM 535819; Río Kosmako: USNM 538568–69.

APPENDIX F: SPECIMENS EXAMINED IN CHAPTER 2.3.5

Craugastor andi: **Costa Rica:** Alajuela: Cinchona, 1600 m: KU 35923; Heredia: vicinity "1000 m" Camp, Braulio Carrillo National Park, 960 m: MVZ 206456; Cariblanca: KU 35109, 35112–14, 35117; San José: Baja La Hondura: UMMZ 137509; **Panama:** Bocas del Toro: Río Claro, near junction with Río Chaneque, 910 m: KU 115090, 115093–94, 115096.

Craugastor crassidigitus: **Costa Rica:** Heredia: Parque Nacional Braulio Carrillo, Río Sucio, 450 m: SMF 81840; **Panama:** Chiriquí: 8 km NE Río Sereno, Finca C.A.S.A., Distr. Renacimiento (8°52'17.0''N, 82°47'43.4''W), 1210 m: SMF 84998; Cordillera de Talamanca, Cerro Jurutungo (8°53'06.6''N, 82°44'540''W), 1525 m: SMF 84999–85000; Cordillera de Talamanca, headwaters of Quebrada Chevo (8°52'27.6''N, 82°44'31.7''W), 1615 m: SMF 85446; San Blás: Parque Nacional Nusagandi, 300–350 m: SMF 81955–59.

Craugastor cuaquero: **Costa Rica:** Puntarenas: Río Trail, Monteverde Reserve, 1510–1555 m: MVZ 207254.

Craugastor fitzingeri: **Nicaragua:** Atlántico Norte: Alamikamba (13°30.08'N, 84°13.64'W): SMF 77831–42, 77843, 77855; Carazo: Quebrada Santa Teresa, 5 km W Santa Teresa (village about 15 km SW Diriamba): ZFMK 51863–64, 52080, 53028; Granada: Volcán Mombacho, ca. 1.2 km SW Cutirre (11°49.62'N, 85°56.44'W), 420 m: SMF 78579; Volcán Mombacho, ca. 2.9 km SW Cutirre (11°49.84'N, 85°57.29'W), 700 m: SMF 78580; Jinotega: Reserva Biosfera Bosawas, ca. 0.5 km SE Ayapal, 195 m: SMF 78581–83; Reserva Biosfera Bosawas, ca. 3 km SE Ayapal at Río Curinwas (13°46.62'N, 85°23.17'W), 200 m: SMF 78584–5; Reserva Biosfera Bosawas, ca. 0.5 km SE Pueblo Wiso (13°59.60'N, 85°19.60'W), 200 m: SMF 78586; Río San Juan: Río San Juan, Boca de San Carlos (10°47.26'N, 84°11.70'W), 20 m: SMF 79787–88; Río Sarnoso, ca. 1 km above confluence with Río San Juan (10°55.35'N, 84°17.40'W), 25 m: SMF 79789–91; Río San Juan, Bartola (10°58.37'N, 84°20.35'W), 30 m: SMF 79792; **Panama:** Panamá: SMF 29860; San Blas: Parque Nacional Nusagandi, 360 m: SMF 80788–89.

Craugastor melanostictus: **Costa Rica:** Alajuela: E slope of Volcán Poás, 1830 m: UMMZ 135247; Cartago: Powerline Tower 57 on trail from Refugio Nacional Tapanti to Tres de Junio [on Hwy. 2], 2570 m: MVZ 203856; Powerline Tower 48 on trail from Refugio Nacional Tapanti to Tres de Junio [on Hwy. 2], 2475 m: MVZ 203857; Powerline Tower 46 on trail from Refugio Nacional Tapanti to Tres de Junio [on Hwy. 2], 2412 m: MVZ 203858; Heredia: vicinity "1500 m" Camp, Braulio Carrillo National Park, 1500 m: MVZ 206514; 1800 m Cabin on trail from "1500 m" Camp to "2050 m" Camp, Braulio Carrillo National Park: MVZ 206516; Volcán Barba near Rama Sur Río Las Vueltas, ca. 2000 m: UMMZ 129173; Limón: Valle del Silencio, between Kamuk and Echandi Massifs, 2300–2800 m: MVZ 193566; Puntarenas: Chomogo Trail, Monteverde Reserve, 1630 m: MVZ 207253; San José: La Palma: UMMZ 129197; 3 km SE Rancho Redondo: UMMZ 122684–85.

Craugastor monnichorum: **Panama:** Bocas del Toro: Gutiérrez: MCZ 10054–55, 24874; Chiriquí: Parque Nacional Volcán Barú, Alto Chiquero, 400 m S Ranger Station (8°50'N, 82°29'W), 1820 m: SMF 85031–36.

Craugastor raniformis: **Colombia:** Valle: Cali: SMF 3786–87; **Panama:** San Blás: Parque Nacional Nusagandi, 280 m: SMF 81984.

Craugastor talamancae: **Nicaragua:** Río San Juan: Lomas de Tambor (11°93'71.8''N, 83°73'11.2''W), 210 m: SMF 83360; **Panama:** Bocas del Toro: Río Uyama (9°08'55''N, 82°19'28''W), 35 m: SMF 85003–04; San Blás: Parque Nacional Nusagandí, 280–360 m: SMF 82011–17.

FIGURES

Fig 60. *Dermophis mexicanus* (Las Nubes).

Fig 61. *Gymnopis multiplicata* (Cerro Musún).

Fig 62. *Bolitoglossa striatula* (Río Frío).

Fig 63. *Bolitoglossa striatula*, ventral view (Dos Bocas de Río Indio).

Fig 64. *Oedipina* sp. “Datanlí” (Cerro Datanlí-El Diablo).

Fig 65. *Oedipina* sp. “Musún” (Cerro Musún).

Fig 66. *Incilius coccifer* (Morgan´s Rock).

Fig 67. *Incilius coniferus* (Dos Bocas de Río Indio).

Fig 68. *Incilius luetkenii*, male (San Juan de Dios).

Fig 69. *Incilius luetkenii*, female (Morgan´s Rock).

Fig 70. *Incilius valliceps* (Rancho Alegre).

Fig 71. *Rhaebo haematiticus* (El Almendro).

Fig 72. *Rhinella marina* (Bosawas).

Fig 73. *Centrolene prosoblepon* (Cerro Kilambé).

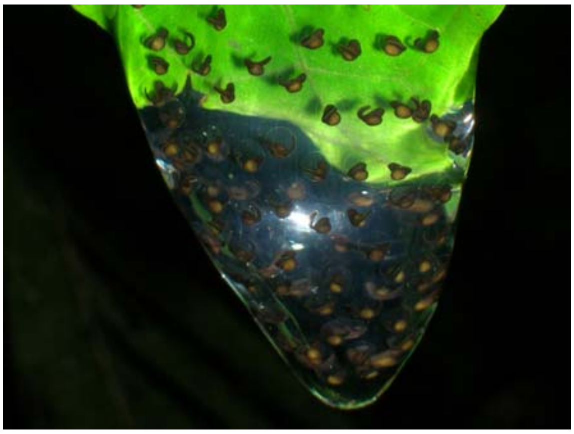


Fig 74. *Centrolene prosoblepon*, egg mass (Cerro Saslaya).

Fig 75. *Cochranella albomaculata* (El Almendro).

Fig 76. *Cochranella granulosa* (Cerro Musún).

Fig 77. *Cochranella pulverata* (Bosawas).

Fig 78. *Hyalinobatrachium fleischmanni* (Cerro Saslaya).

Fig 79. *Craugastor bransfordii* (Dos Bocas de Río Indio).

Fig 80. *Craugastor chingopetaca* (Boca de San Carlos).

Fig 81. *Craugastor fitzingeri* (Dos Bocas de Río Indio).

Fig 82. *Craugastor laevissimus* (Cerro Kilambé).

Fig 83. *Craugastor lauraster* (Cerro Saslaya).

Fig 84. Craugastor megacephalus (Cerro Musún).

Fig 85. Craugastor mimus (Cerro Musún).

Fig 86. Craugastor noblei (Cerro Musún).

Fig 87. Dendrobates auratus (El Almendro).

Fig 88. Oophaga pumilio (Río Papaturro).

Fig 89. Agalychnis callidryas (Río Papaturro).

Fig 90. Agalychnis callidryas, egg masses, not collected (Las Nubes).

Fig 91. Cruziohyla calcarifer (Dos Bocas de Río Indio).

Fig 92. Dendropsophus ebraccatus (Cerro Kilambé).

Fig 93. Dendropsophus microcephalus (Rancho Alegre).

Fig 94. Dendropsophus phlebodes, amplectant couple (Dos Bocas de Río Indio).

Fig 95. Hypsiboas rufitelus (Bartola).

Fig 96. Ptychohyla hypomykter (Cerro Saslaya).

Fig 97. Ptychohyla sp. “Bosawas” (Bosawas).

Fig 98. Scinax boulengeri (Rancho Alegre).

Fig 99. Scinax elaeochroa (Río Papaturro).

Fig 100. Scinax staufferi (San Juan de Dios).

Fig 101. Smilisca baudinii (Las Nubes).

Fig 102. Smilisca phaeota, amplectant couple (Finca URACCAN).

Fig 103. Smilisca puma (Río Papaturro).

Fig 104. Tlalocohyla loquax (Cerro Datanlí-El Diablo).

Fig 105. Trachycephalus venulosus (Río Papaturro).

Fig 106. Engystomops pustulosus (Isla Ometepe).

Fig 107. Leptodactylus fragilis (Río Frío).

Fig 108. Leptodactylus melanonotus (Río Papaturro).

Fig 109. Leptodactylus savagei (Río Papaturro).

Fig 110. Lithobates brownorum (Cerro Datanlí-El Diablo).

Fig 111. Lithobates forreri (Isla Ometepe).

Fig 112. Lithobates maculatus (Cerro Saslaya).

Fig 113. Lithobates vaillanti (Rancho Alegre).

Fig 114. Lithobates warszewitschii (Dos Bocas de Río Indio).

Fig 115. Rhinophrynus dorsalis (Monte Galán).

Fig 116. Pristimantis cerasinus (Bosawas).

Fig 117. Pristimantis ridens (Cerro Kilambé).

Fig 118. Chelydra acutirostris (Río Blanco, near Cerro Musún).

Fig 119. Chelydra acutirostris, ventral view (Río Blanco, near Cerro Musún).

Fig 120. Trachemys scripta, not collected (Río Papaturro).

Fig 121. Trachemys scripta, juvenile (Bosawas).

Fig 122. Rhinoclemmys annulata (El Almendro).

Fig 123. Rhinoclemmys annulata, ventral view (Bosawas).

Fig 124. Rhinoclemmys funerea (Boca de San Carlos).

Fig 125. Rhinoclemmys funerea, not collected, ventral view (Bosawas).

Fig 126. Rhinoclemmys pulcherrima, not collected (San Juan de Dios).

Fig 127. Rhinoclemmys pulcherrima, juvenile, ventral view (Morgan´s Rock).

Fig 128. Kinosternon leucostomum (Río Frío).

Fig 129. Kinosternon leucostomum, ventral view (Río Frío).

Fig 130. Kinosternon scorpioides (Morgan´s Rock).

Fig 131. Kinosternon scorpioides, ventral view (Morgan´s Rock).

Fig 132. Caiman crocodilus, not collected (Isla Ometepe).

Fig 133. Crocodylus acutus, not collected (Isla Juan Venado, near León).

Fig 134. Coleonyx mitratus (San Juan de Dios).

Fig 135. Coleonyx mitratus, juvenile (Isla Ometepe).

Fig 136. Gonatodes albogularis (Isla Ometepe).

Fig 137. Hemidactylus frenatus, copulating (road León-Managua).

Fig 138. Lepidoblepharis xanthostigma (Dos Bocas de Río Indio).

Fig 139. Phyllodactylus tuberculosus (Morgan´s Rock).

Fig 140. Phyllodactylus tuberculosus, juvenile (Isla Ometepe).

Fig 141. Sphaerodactylus millepunctatus (Isla Ometepe).

Fig 142. Thecadactylus rapicauda (Bosawas).

Fig 143. Gymnophthalmus speciosus, not collected (Las Nubes).

Fig 144. Anolis biporcatus, male, not collected (Las Nubes).

Fig 145. Anolis biporcatus, female (Volcán Maderas).

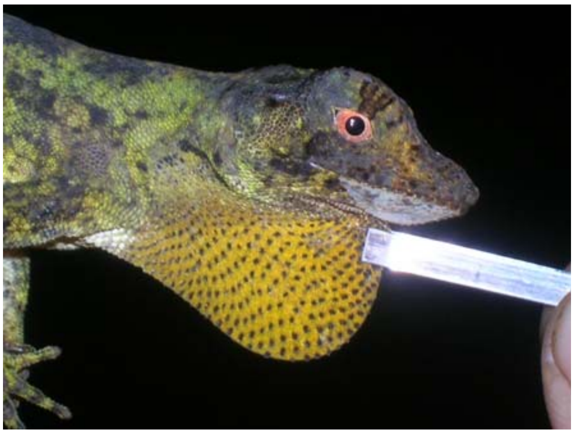


Fig 146. Anolis capito (Cerro Musún).

Fig 147. Anolis carpenteri (Río Papaturro).

Fig 148. Anolis lemurinus, female (Río Papaturro).

Fig 149. Anolis oxylophus (Boca de San Carlos).

Fig 150. Anolis quaggulus (Cerro Kilambé).

Fig 151. Anolis sericeus “bilobed” (San Juan de Dios)

Fig 152. Anolis sericeus “unilobed”, female (Isla Ometepe).

Fig 153. Anolis tropidonotus, male (Cerro Kilambé).

Fig 154. Anolis tropidonotus, female (Cerro Kilambé).

Fig 155. Basiliscus plumifrons, male (Río Frío).

Fig 156. Basiliscus plumifrons, female (Río Papaturro).

Fig 157. Basiliscus vittatus, male (Bosawas).

Fig 158. Basiliscus vittatus, female (Rancho Alegre).

Fig 159. Corytophanes cristatus (Dos Bocas de Río Indio).

Fig 160. Ctenosaura quinquecarinata (San Juan de Dios).

Fig 161. Ctenosaura similis (Monte Galán).

Fig 162. Ctenosaura similis, juvenile (San Juan de Dios).

Fig 163. Iguana iguana, not collected (El Almendro).

Fig 164. Sceloporus malachiticus (Miraflor).

Fig 165. Sceloporus squamosus (San Juan de Dios).

Fig 166. Sceloporus variabilis (Morgan´s Rock).

Fig 167. Mabuya unimarginata (Cerro Musún).

Fig 168. Mesoscincus managuae (Morgan´s Rock).

Fig 169. Sphenomorphus cherriei (Dos Bocas de Río Indio).

Fig 170. Ameiva festiva, not collected (Río Papaturro).

Fig 171. Ameiva undulata, not collected (Las Nubes).

Fig 172. Aspidoscelis deppii (road León-Managua).

Fig 173. Lepidophyma flavimaculatum (Boca de San Carlos).

Fig 174. Boa constrictor, not collected (Morgan´s Rock).

Fig 175. Clelia clelia (Bosawas).

Fig 176. Clelia clelia, juvenile (Bosawas).

Fig 177. Coniophanes fissidens (Cerro Saslaya).

Fig 178. Coniophanes fissidens, ventral view (Cerro Datanlí-El Diablo).

Fig 179. Coniophanes piceivittis (Isla Ometepe).

Fig 180. Conophis lineatus (Morgan´s Rock).

Fig 181. Dendrophidion percarinatum (Boca de San Carlos).

Fig 182. Drymarchon melanurus (Bosawas).

Fig 183. Drymobius margaritiferus (Río Papaturro).

Fig 184. Enulius flavitorques (Isla Ometepe).

Fig 185. Erythrolamprus mimus (Cerro Datanlí-El Diablo).

Fig 186. Geophis hoffmanni (Cerro Musún).

Fig 187. Hydromorphus concolor (Rancho Alegre).

Fig 188. Imantodes cenchoa (Río Papaturro).

Fig 189. Imantodes gemmistratus (Morgan´s Rock).

Fig 190. Imantodes inornatus (Río Papaturro).

Fig 191. Lampropeltis triangulum (Río Frío).

Fig 192. Leptodeira annulata (Río Papaturro).

Fig 193. Leptodeira septentrionalis (Cerro Saslaya).

Fig 194. Leptodrymus pulcherrimus (Cerro Musún).

Fig 195. Leptophis ahaetulla (Dos Bocas de Río Indio).

Fig 196. Leptophis depressirostris (Cerro Musún).

Fig 197. Masticophis mentovarius, juvenile (Moss).

Fig 198. Mastigodryas dorsalis (Cerro Kilambé).

Fig 199. Mastigodryas dorsalis, juvenile (Cerro Datanlí-El Diablo).

Fig 200. Mastigodryas melanolomus (Bosawas).

Fig 201. Ninia sebae (Bosawas).

Fig 202. Oxybelis aeneus (Isla Ometepe).

Fig 203. Oxybelis aeneus (Río Frío).

Fig 204. Oxybelis brevirostris (Bosawas).

Fig 205. Oxybelis fulgidus (Cerro Musún).

Fig 206. Oxyrhopus petola (Rancho Alegre).

Fig 207. Pseustes poecilonotus (Bosawas).

Fig 208. Rhadinaea kinkelini (Miraflor).

Fig 209. Sibon annulatus (Cerro Musún).

Fig 210. Sibon anthracops (Morgan´s Rock).

Fig 211. Sibon longifrenis (Bosawas).

Fig 212. Sibon nebulatus (Río Frío).

Fig 213. Spilotes pullatus (Cerro Musún).

Fig 214. Tantilla reticulata (near Greytown). Photograph: L. OBANDO.

Fig 215. Tantilla taeniata (Cerro Kilambé).

Fig 216. Thamnophis proximus (Cerro Datanlí-El Diablo).

Fig 217. Tretanorhinus nigroluteus (Bosawas).

Fig 218. Trimorphodon quadruplex (Morgan´s Rock).

Fig 219. Xenodon rabdocephalus (Bosawas). Photograph: S. TRAVERS.

Fig 220. Micrurus alleni (Los Guatuzos). Photograph: A. GÓMEZ.

Fig 221. Micrurus nigrocinctus, juvenile (Cerro Musún).

Fig 222. Micrurus nigrocinctus (Boca de San Carlos).

Fig 223. Bothriechis schlegelii (Cerro Datanlí-El Diablo).

Fig 224. Bothriechis schlegelii, oropel color phase (Río Frío).

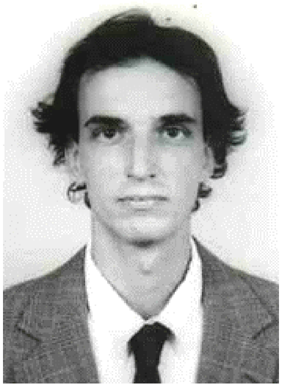
Fig 225. Bothrops asper (Bosawas).

Fig 226. Crotalus simus (Morgan´s Rock).

Fig 227. Porthidium nasutum (Cerro Saslaya).

Curriculum Vitae

Name:	**Javier Sunyer Mac Lennan**
E-mail:	javier_sunyer@yahoo.com
Place and date of birth:	Madrid, Spain, 07.IX.1975
Languages:	Spanish and English (high)
	German (medium)
Fieldwork experience:	>435 days collecting in the tropics



-Current **PhD student in Biology (Herpetology)** at the Research Institute and Natural History Museum Senckenberg, under the supervision of Dr. Gunther Köhler and Dr. Prof. Bruno Streit, Frankfurt am Main, Germany. Title of the doctoral thesis: "Taxonomy, zoogeography and conservation of the herpetofauna of Nicaragua", with a complete scholarship from the German Academic Exchange Service (DAAD).

-List of scientific publications:

- **Sunyer, J.,** A. Hertz, S. Lotzkat, D. B. Wake, B. Alemán, S. Robleto & G. Köhler (2008). Two new species of salamanders (genus *Bolitoglossa*) from southern Nicaragua (Amphibia: Caudata: Plethodontidae). Senckenbergiana biologica 88(2):319-328.
- **Sunyer, J**., G. Köhler, & M. Veselý (2008). Geographical variation in the Nicaraguan endemic *Anolis wermuthi* (Squamata: Polychrotidae). Senckenbergiana biologica 88(2):335-343.
- Köhler, G., **J. Sunyer,** A. Batista, &. M. Ponce (2008). Noteworthy records of amphibians and reptiles in Panama. Senckenbergiana biologica 88(2):329-333.
- Köhler, G. & **J. Sunyer**. (2008). Two new species of anoles formerly referred to as *Anolis limifrons* (Squamata: Polychrotidae). Herpetologica 64(1):92-108.
- Lotzkat, S., M. Natera-Mumaw, A. Hertz, **J. Sunyer**, & D. Mora (2008). New state records of *Dipsas variegata* (Dumèril, Birbon and Dumèril 1854) (Serpentes: Colubridae) from northern Venezuela, with comments on Natural History. Herpetotropicos 4(1):25-29.
- Köhler, G., M. Ponce, **J. Sunyer**, & A. Batista. (2007). Four new species of anoles (genus *Anolis*) from the Serranía del Tabasará, west-central Panama (Squamata: Polychrotidae). Herpetologica 63(3):375-391.
- **Sunyer, J.** & G. Köhler. (2007). New and noteworthy records of amphibians and reptiles from Nicaragua. Salamandra 43(1):15-20.
- Köhler, G., A. Hertz, **J. Sunyer**, R. Seipp, & A. Monteiro. (2007). Herpetologische Forschungen auf den Kapverden unter besonderer Berücksichtigung des Kap-verdischen Riesenskinks, *Macroscincus coctei*. Elaphe 15(4):62-66.

- Köhler, G., A. Hertz, **J. Sunyer**, & A. Monteiro. (2007). *Hemidactylus bouvieri*. Distribution. Herpetological review 38(4):483.
- Köhler, G. & **J. Sunyer**. (2006). A new species of rain frog (genus *Craugastor*) of the *fitzingeri* group from Río San Juan, southeastern Nicaragua. Senckenbergiana biologica 86(2):261-266.
- Köhler, G., S. Alt, C. Grünfelder, M. Dehling, & **J. Sunyer**. (2006). Morphological variation in Central American leaf-litter anoles (*Norops humilis, N. guaggulus,* and *N. uniformis*). Salamandra 42(4):239-254.

-List of submitted publications:

- **Sunyer, J.** & G. Köhler. The conservation status of the herpetofauna of Nicaragua. In: Wilson, L. & J. Townsend (Eds.). The conservation of Mesoamerican amphibians and reptiles. Eagle Mountain Publishing.
- **Sunyer, J**., L. Wilson, J. Townsend, S. Travers, L. Obando, G. Páiz, & G. Köhler. Three new country records of reptiles from Nicaragua. Salamandra.
- Hertz, A., M. Natera-Mumaw, S. Lotzkat, & **J. Sunyer**. *Bothrops asper*. Prey. Herpetological review.

-**Publications in work:**

- **Sunyer, J**., & G. Köhler. Zoogeographical analysis of the herpetofauna of Nicaragua.
- Townsend J., L. Wilson, S. Travers, **J. Sunyer,** &. G. Köhler. Three new species of salamanders (genus *Oedipina*) from the central mountains of Nicaragua (Amphibia: Caudata: Plethodontidae).
- **Sunyer, J**., L. Wilson, J. Townsend, S. Travers, L. Obando, & G. Köhler. A new species of frog (genus *Ptychohyla*) from the lowlands of northern Nicaragua (Amphibia: Hylidae).
- Dehling, M., G. Köhler, & **J. Sunyer**. A revision of *Anolis cupreus* (Squamata: Polychrotidae).
- **Sunyer, J**., G. Páiz, M. Dehling, & G. Köhler. A collection of amphibians from Río San Juan, southeastern Nicaragua.
- Acevedo, M., **J. Sunyer**, M. Veselý, & Q. Dwayer. New country record of *Conophis vittatus* (Serpentes: Colubridae) from Guatemala.

-Expositor in the VIII Latin American Congress of herpetology in Varadero, Cuba, with the presentation "Conservation status of Nicaraguan amphibians", with a complete scholarship from Conservation International (CI), November 2008.

-Expositor in the Herpetological International Congress in Hallein, Austria, with the presentation "Conservation status of the herpetofauna of Nicaragua", with a complete scholarship from the Otto Sterne Schule (OSS), October 2007.

-**Expositor of the Post-graduate seminar** "Herpetology of Panama" in the Universidad Autónoma de Chiriquí (UNACHI), David, Panama, 7-20 January 2006.

-**Diplomat** s**tudent** "II Mesoamerican communitarian forestry", in the Facultad Latinoamericana de Ciencias Sociales-Guatemala (FLACSO-Guatemala), with a scholarship from the FLACSO-Guatemala, January-March 2004.

-**Worker in the UNAN-León** (Universidad Nacional Autónoma de Nicaragua-León) as "youth researcher" in the Department of Biology (Ecology), under the supervision of Prof. MSc. Pedrarias Dávila and Prof. Dr. José Munguía, May 2002-June 2004.

-**Masters student** "Management of the natural resources", in the UNAN-León by the Universidad de Alcalá de Henares (UAH), Madrid, Spain, with a complete scholarship from the UNAN-León, 2002-2004.

-**Postgraduate student** "Biodiversity", in the Universidad Centroamericana (UCA), Managua, Nicaragua, with a complete scholarship from the UNAN-León, 1-10 October 2002.

-**Licentiate in Biology by the UNAN-León** (Universidad Nacional Autónoma de Nicaragua-León) under the supervision of Prof. Dr. Ricardo Rueda and Jean-Michel Maes. Title of the thesis: "Diversidad de insectos florícolas en el estrato herbáceo, arbustivo y arbóreo de tres ecosistemas del Refugio de Vida Silvestre Los Guatuzos: 2000-2002". 12 September 2002.

-**Worker at the Entomologic Museum of León**, Nicaragua, under the supervision of Jean-Michel Maes, León, Nicaragua, June 2000-December 2001.

-**Expositor** in the "XX Universities meeting for the scientific development", with the presentation "Diversidad de insectos del Refugio de Vida Silvestre Los Guatuzos", UNAN-León, León, Nicaragua, 15 November 2001.

-**Participation** with a complete scholarship from the UNAN-León in the following workshops:

- "Biodiversidad y gestión de áreas protegidas". UNAN-León, León, Nicaragua, 12-14 July 2007.
- "Aplicación de los sistemas de información geográfica en la gestión territorial y urbanística". UNAN-León, León, Nicaragua, 15-17 September 2003.
- "Encuentro Nacional de Actores en Educación ambiental". CIMAC, León, Nicaragua, 25-27 July 2002.
- "Ciencia y tecnología: Inversión para el desarrollo sostenible". Consejo Nacional de Universidades (CNU), Managua, Nicaragua, 31 October 2001.

Eidestattliche Versicherung

Ich erkläre hiermit an Eides Statt, dass ich die vorgelegte Dissertation über ”Taxonomy, zoogeography, and conservation of the herpetofauna of Nicaragua” selbstständig angefertigt und mich anderer Hilfsmittel als der in ihr angegeben nicht bedient habe, insbesondere, dass aus Schriften Entlehnungen, soweit sie in der Dissertation nicht ausdrücklich als solche mit Angabe der betreffenden Schrift bezeichnet sind, nicht stattgefunden haben.

Frankfurt am Main, den ………………….. ……………………………………