FACULDADE DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

REVISÃO TAXONÔMICA DAS SUBESPÉCIES DE *LEPTOPHIS AHAETULLA* (LINNAEUS, 1758) (SERPENTES, COLUBRIDAE)

Nelson Rufino de Albuquerque

TESE DE DOUTORADO
PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL
Av. Ipiranga 6681 - Caixa Postal 1429
Fone: (051) 3320-3500 - Fax: (051) 3339-1564
CEP 90619-900 Porto Alegre - RS
Brasil

2008

FACULDADE DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

REVISÃO TAXONÔMICA DAS SUBESPÉCIES DE *LEPTOPHIS AHAETULLA* (LINNAEUS, 1758) (SERPENTES, COLUBRIDAE)

Nelson Rufino de Albuquerque

Orientador: Dr. Roberto Esser dos Reis

TESE DE DOUTORADO
PORTO ALEGRE - RS - BRASIL
2008

Sumário

Agradecimentos

Aos meus pais, Nelson e Fátima; irmãos, Giselle e Alexandre; ao Mello, Enilsa, Gecele e Lucas, por todo o amor, apoio, e amizade ao longo de todos esses anos de mestrado, doutorado... Sei que escrever simplesmente "obrigado" é uma injustiça para agradecer a tudo o que eles fizeram e ainda fazem por mim. A minha mãe em especial tem sido uma presença constante em minha vida, independente da distância física; sempre me aconselhando e me apoiando da melhor maneira possível. A Gecele foi incansável nesta etapa final; sem ela certamente esta etapa teria sido bem mais difícil. O meu filho, Lucas, como sempre foi paciente, carinhoso e encorajador.

Muito obrigado por tudo família!

Ao Prof. Marcos Di-Bernardo (*In memoriam*) por ter aceitado ser meu orientador e por ter despertado em mim o interesse pela história natural de serpentes.

Ao Prof. Thales de Lema, meu orientador no mestrado, por ter compartilhado comigo o seu profundo conhecimento sobre a herpetofauna neotropical, por estar sempre disponível para ensinar, e por ter permitido livre acesso a sua vasta coleção particular de livros e artigos sobre répteis.

Aos meus colegas herpetológos e ictiólogos, pela ajuda em vários momentos dessa tese, quer seja pelo envio de fotos de *Leptophis*, de artigos, pela análise de espécimes, e principalmente por terem contribuído para o meu aprendizado. Agradeço especialmente ao Felipe Aguiar, Fabrício Bonfiglio, Tiago Carvalho, Gentil Pereira Filho, Giovanna Montingelli, Marco Natera, Paulo Passos, Eduardo Polanczyk, Alfredo Santos Jr., Cláudio Silva, e Alessandra Travassos.

Aos curadores e gerentes das 38 coleções que tornaram disponível o material examinado, especialmente ao Prof. Antônio Argôlo, ao Dr. Francisco Franco, e a Dra. Ana Prudente, por sempre fazerem mais do que o necessário para me ajudar. Agradeço também a Dra. Teresa Ávila Pires e a Dra. Ana Prudente pela revisão do meu projeto de doutorado e pelo apoio de sempre.

Ao Prof. Roberto Esser dos Reis pelos ensinamentos sobre analise filogenética, e pela revisão dos artigos que compõe esta tese.

Ao Dr. Darrel R. Frost, pela permissão para o recebimento de espécimes de outras coleções americanas, sul-americanas, e européias no American Museum of Natural History, e pela infra-estrutura fornecida no Museu (tinha tudo!). Sem dúvida, este trabalho não teria sido possível sem o apoio do Dr. Frost. Ao Dr. David Kizirian, pela auxilio constante durante o período em que eu estive no AMNH, e pela paciência para rever os meus artigos. Ao Robert Pascocello, pela amizade e pelo auxilio eficiente no recebimento e devolução de exemplares de outras instituições no AMNH. No AMNH, eu tive o privilégio de conhecer o Prof. Taran Grant, o qual eu agradeço pelos ensinamentos, pela amizade, pelos conselhos, pelo livre acesso a sua biblioteca particular, pelos cafés na *Starbucks*, e principalmente pelo encorajamento durante a elaboração desta tese.

Agradeço ao Dr. Harold Voris e a Dra. Maureen Kearney, do Field Museum of Natural History, por terem aprovado um auxílio financeiro que facilitou a minha ida ao FMNH.

Como sempre, agradeço ao John, Paul, George e Ringo, por todas as canções maravilhosas e pela inspiração. Esta tese foi fechada ao som do lado A do *Please Please Me*.

Durante o meu curso, eu recebi uma bolsa da CAPES. O meu doutorado-sanduíche só foi possível graças a uma bolsa concedida pela CAPES.

“There never was a time when you or I did not exist. Nor will there be any future when we shall cease to be” (*Krishna to Arjuna in the Bhagavad-Gita*).

Resumo

O gênero *Leptophis* constitui um grupo de serpentes de hábitos semi-arborícolas, diurnas, com corpo delgado e longo e cabeça distinta do pescoço; distribuído na América Central e América do Sul. Serpentes deste gênero são diagnosticadas pelo padrão de coloração predominante verde ou cobre, com ou sem faixas longitudinais e bandas transversais estreitas. Dentre os táxons reconhecidos no gênero *Leptophis, L. ahaetulla* é o de distribuição geográfica mais ampla e o mais polimórfico, devido à extrema variação no padrão de coloração, morfologia externa e dentição, com 12 subespécies reconhecidas: *L. a. ahaetulla*, *L. a. bocourti*, *L. a. bolivianus, L. a. coeruleodorsus, L. a. copei, L. a. liocercus, L. a. marginatus, L. a. nigromarginatus, L. a. occidentalis*, *L. a. ortoni*, *L. a. praestans* e *L. a. urostictus.* Como os demais táxons do gênero, as subespécies de *L. ahaetulla* são diagnosticadas principalmente com base no padrão de coloração dorsal. Apesar da extensa revisão já realizada, fez-se necessária uma nova revisão sistemática de *L. ahaetulla*, enfocando-se aspectos da variação intra e interpopulacional dos caracteres utilizados para o reconhecimento das subespécies, e incluindo novos espécimes além de métodos estatísticos mais elaborados do que os disponíveis na última revisão. O presente estudo teve como objetivo avaliar a validade das subespécies de *L. ahaetulla*, assim como apresentar a variação nos caracteres referentes à morfologia externa e hemipeniana, coloração, distribuição, e uma chave de identificação para os táxons considerados válidos. Para o auxílio nas decisões taxonômicas, foi priorizado o estudo da morfologia hemipeniana e osteológica, da distribuição geográfica, e da variação intra e interpopulacional dos caracteres previamente utilizados para o reconhecimento das subespécies. Esta tese está dividida em quatro artigos. No primeiro, “A new species of *Leptophis* (Serpentes, Colubridae) from Northeastern Brazil”, foram analisados 271 espécimes coletados no nordeste do Brasil. Destes, 42 espécimes não puderam ser alocados a nenhuma das espécies conhecidas de *Leptophis*, e representam uma nova espécie descrita como *L. caatingensis*. O padrão de coloração, a morfologia externa e a morfologia do hemipênis da espécie nova foram comparados com os táxons parapátricos *L. a. ahaetulla* e *L. a. liocercus*. No segundo artigo, “A taxonomic revision of tree snakes of the *Leptophis ahaetulla* complex (Serpentes, Colubridae)”, 10 subespécies de *L. ahaetulla* foram elevadas ao status de espécie; *L. a. copei* e *L. a. ortoni* foram consideradas como sinônimos júnior de *L. ahaetulla* e *L. nigromarginatus*, respectivamente. Para cada espécie, uma diagnose, descrição, e distribuição foram providenciadas, baseado na análise de 1573 espécimes e dados de literatura. Notas sobre a coloração das espécies em vida e dados referentes à ecologia foram incluídas para a maioria das espécies. Uma chave dicotômica para auxiliar na identificação foi providenciada. Adicionalmente, foi feita uma análise filogenética de parcimônia, baseada em 31 caracteres morfológicos, ecológicos, e de coloracão. A análise resultou em nove árvores igualmente parcimoniosas, com 50 passos, índice de consistência (IC) de 96, e índice de retenção (IR) de 97. No terceiro artigo, “Redescription of *Leptophis cupreus*, a rare South America colubrine snake”, *L. cupreus* foi redescrita através da análise de nove exemplares, incluindo o holótipo, que havia sido considerado como perdido. Neste trabalho, foi feita uma análise comparativa de *L. cupreus* com os táxons simpátricos *L. a. copei*, *L. a. nigromarginatus*, *L. a. occidentalis*, e *L. riveti*, além da inclusão de fotos do holótipo e descrição do hemipênis. No último artigo, “Diet and feeding behaviour of the Neotropical parrot snake (*Leptophis ahaetulla*) in northern Brazil”, 289 espécimes de *Leptophis ahaetulla* coletados no norte do Brasil foram examinados para a composição dos conteúdos estomacais. A maioria das presas foi identificada como anfíbios arborícolas da família Hylidae (90%), com 27% desses sendo identificados como *Scinax* gr. *ruber*.

Abstract

The snake genus *Leptophis* comprises a group of semiarboreal, elongate, diurnal snakes with head distinct from neck distributed in Central and South America. Members of the genus *Leptophis* are distinguished by coloration pattern predominantly green or copper, with or without longitudinal stripes and narrow transversal bands. Among the taxa recognized in *Leptophis*, *L. ahaetulla* is the most wide-ranging and polymorphic species, with 12 recognized subspecies: *L. a. ahaetulla, L. a. bocourti, L. a. bolivianus, L. a. coeruleodorsus, L. a. copei, L. a. liocercus, L. a. marginatus, L. a. nigromarginatus, L. a. occidentalis, L. a. ortoni, L. a. praestans* and *L. a. urostictus.* As in other *Leptophis,* subspecies of *L. ahaetulla* are defined mainly by dorsal coloration. Despite the extensive revision previously published, a new taxonomic revision of *L. ahaetulla*, analyzing intra- and interpopulational variation among the characters used for the recognition of the subspecies, and including additional specimens and statistical methods not available to previous revision was necessary. The main purpose of the present study was to assess the validity of the subspecies of *L. ahaetulla* as well as provide variation on meristic characters, external and hemipenial morphology, coloration, distribution, and a dichotomous key to the taxa considered to be valid. The study of hemipenial and osteological morphology, geographic distribution and variation intra- and interpopulacional of the characters used for the recognition of the subspecies was employed before taxonomic decisions. This thesis is divided into four articles. In the first, “A new species of *Leptophis* (Serpentes, Colubridae) from Northeastern Brazil”, 42 of 271 specimens from northeastern Brazil could not be allocated to any of the known species of *Leptophis*, representing a previously unrecognized species named *L. caatingensis*. The coloration pattern, external and hemipenial morphology of new species were compared to parapatric taxa *L. a. ahaetulla* and *L. a. liocercus*. In the second article, “A taxonomic revision of tree snakes of the *Leptophis ahaetulla* complex (Serpentes, Colubridae)”, 10 subspecies of *L. ahaetulla* were elevated to species status, whereas *L. a. copei* and *L. a. ortoni* were placed in the synonymy of *L. ahaetulla* and *L. nigromarginatus*, respectively. For each species, a diagnosis, description, and distribution were provided based on examination of 1573 specimens and data from the literature. Notes on color in life and ecology were included for most species. A dichotomous key to assist in the identification of specimens was provided. Additionally, a phylogeny of the genus *Leptophis* based on 31 morphological, ecological and color characters was presented. One more parsimonious tree was obtained, with a total length of 53 steps, a consistency index (CI) of 96, and a retention index (RI) of 97. In the third article, “Redescription of *Leptophis cupreus*, a rare South America colubrine snake”, *L. cupreus* was redescribed based on nine specimens, including its holotype, which was considered as lost. Further, a comparative analysis among *L. cupreus* and sympatric taxa *L. a. copei, L. a. nigromarginatus, L. a. occidentalis,* and *L. riveti* was presented. Photos of holotype and a living specimen of *L. cupreus*, description and illustrations of the everted hemipenis are presented. In the last article, “Diet and feeding behaviour of the Neotropical parrot snake (*Leptophis ahaetulla*) in northern Brazil”, 289 specimens of *L. ahaetulla* from northern Brazil were examined for the composition of stomach contents. Most prey items were tree frogs of the family Hylidae (90%). Most of the anurans identified belong to the *Scinax ruber* species group (27%).

Apresentação da Tese

O gênero *Leptophis* Bell, 1825 distribui-se em grande parte da América Central e América do Sul, incluindo as ilhas caribenhas de Trinidad e Tobago (Oliver, 1948). Este gênero tem uma problemática história nomenclatural, em parte porque sua espécie-tipo, *Coluber ahaetulla* Linnaeus, 1758, foi descrita com base em quatro exemplares sul-americanos (atualmente *Leptophis ahaetulla*) e um exemplar asiático (atualmente *Ahaetulla nasuta*). O problema nomenclatural, contudo, foi solucionado por Savage (1952), que estabeleceu que *Leptophis* é o nome correto para estas serpentes. *Leptophis* constitui um grupo de serpentes de hábitos arborícolas ou semi-arborícolas, diurnas, com corpo delgado e longo e cabeça distinta do pescoço. Serpentes deste gênero alimentam-se predominantemente de anfíbios, especialmente de espécies da família Hylidae (Oliver, 1948; Albuquerque et al., 2007).

O gênero *Leptophis* possui atualmente 10 espécies, que são diagnosticadas pelas seguintes características: 18 a 36 dentes maxilares, sendo os dois ou três últimos maiores, sem sulco, e não separados dos dentes precedentes por um diastema; vértebras posteriores sem hipapófises, escamas dorsais geralmente com uma fosseta apical, corpo alongado com 15 fileiras de escamas dorsais no meio do corpo e coloração predominante verde ou cobre, além de algumas espécies apresentarem um padrão de faixas longitudinais ou bandas transversais estreitas (Boulenger, 1894; Oliver, 1948; Peters & Órces-V, 1960). Oliver (1948) sugeriu que os gêneros *Leptophis*, *Drymobius* Fitzinger, 1843 e *Mastigodryas* Amaral, 1935 são estreitamente relacionados.

Dentre os táxons reconhecidos atualmente no gênero *Leptophis, L. ahaetulla* é o de distribuição geográfica mais ampla, ocorrendo desde o sul do México até o norte do Uruguai (Oliver, 1948; este estudo). É também a espécie mais polimórfica do gênero, devido à extrema variação no padrão de coloração, morfologia externa e dentição, com 12 subespécies reconhecidas: *L. a. ahaetulla*, *L. a. bocourti*, *L. a. bolivianus*, *L. a. coeruleodorsus, L. a. copei, L. a. liocercus, L. a. marginatus*, *L. a. nigromarginatus, L. a. occidentalis, L. a. ortoni*, *L. a. praestans* e *L. a. urostictus*. Oliver (1948) apresentou uma extensa revisão sistemática do gênero *Leptophis*, àquela época sob o nome *Thalerophis* Oliver, 1947. Exceto por alterações nomenclaturais, as subespécies de *L. ahaetulla* reconhecidas por Oliver (1948) são ainda consideradas válidas. As subespécies de *L. ahaetulla* foram definidas principalmente com base no padrão de coloração; outros caracteres utilizados na definição foram a localização e evidência das quilhas no corpo e cauda, o número de escamas supralabiais, o número de escamas ventrais e o número de dentes maxilares.

Apesar da extensa revisão de Oliver (1948), do número elevado de espécimes examinados (597) e de diversos caracteres da morfologia interna e externa terem sido analisados, fez-se necessária uma nova revisão taxonômica de *Leptophis ahaetulla*, enfocando-se aspectos de variação intra e interpopulacional dos caracteres utilizados para o reconhecimento das subespécies, e incluindo novos espécimes além de métodos estatísticos mais elaborados do que os disponíveis para Oliver (1948). A quantidade de material disponível na época da revisão de Oliver (1948) não permitiu que este autor definisse a situação taxonômica de todas as populações estudadas, principalmente àquelas encontradas nas zonas de contato das subespécies. Algumas subespécies foram consideradas por Oliver (1948) como tentativas, devendo ser reavaliadas quando mais espécimes estivessem disponíveis para novos estudos. Além disso, a maioria dos caracteres merísticos e morfométricos que Oliver (1948) utilizou para definir as subespécies sobrepõem-se em larga escala, sendo assim, a amplitude de variação dos caracteres nas diversas populações necessitava ser reavaliada, baseado na análise comparativa de um maior número de espécimes.

O presente estudo teve como objetivo responder às seguintes questões: a) as subespécies de *L. ahaetulla* são válidas? b) como os táxons considerados válidos se diferenciam? e c) como os táxons considerados válidos estão distribuídos geograficamente? Para o auxílio nas decisões taxonômicas, foi priorizado o estudo da morfologia hemipeniana e osteológica, da distribuição geográfica, e da variação intra e interpopulacional dos caracteres utilizados por Oliver (1948) para o reconhecimento das subespécies.

Esta tese está dividida em quatro artigos. O primeiro, “A new species of *Leptophis* (Serpentes, Colubridae) from Northeastern Brazil”, escrito em conjunto com o Dr. Marcos Di-Bernardo (*In memoriam*), foi submetido para a revista Herpetologica. Neste trabalho, foram analisados 271 espécimes coletados no nordeste do Brasil. Destes, 42 espécimes não puderam ser alocados a nenhuma das espécies conhecidas de *Leptophis*, e representam uma nova espécie descrita como *L. caatingensis*. O padrão de coloração, a morfologia externa e a morfologia do hemipênis da espécie nova foram comparados com os táxons parapátricos *L. a. ahaetulla* e *L. a. liocercus*. Foram incluídas fotos de exemplares vivos e um mapa demonstrando a distribuição geográfica da espécie nova.

O segundo artigo, “A taxonomic revision of tree snakes of the *Leptophis ahaetulla* complex (Serpentes, Colubridae)”, será submetido ao Herpetological Monographs. Neste trabalho, foi feita uma redescricão de todos os táxons considerados válidos, com 10 das 12 subespécies de *L. ahaetulla* sendo elevadas ao status de espécie; *L. a. copei* e *L. a. ortoni* foram consideradas como sinônimos júnior de *L. ahaetulla* e *L. nigromarginatus* respectivamente. É apresentada também uma lista sinonímica, fotos de oito espécies baseadas em exemplares vivos, fotos e descrição dos hemipênis, mapas com a distribuição geográfica, e uma chave dicotômica para auxiliar na identificação dos exemplares. Adicionalmente, foi feita uma análise filogenética de parcimônia, baseada em 31 caracteres morfológicos, ecológicos, e de coloracão. A análise resultou em nove árvores mais parcimoniosas, com 50 passos, índice de consistência (IC) de 96, e índice de retenção (IR) de 97.

O terceiro artigo, “Redescription of *Leptophis cupreus*, a rare South America colubrine snake”, será submetido à Copeia. Neste trabalho, foi feita a redescrição de uma espécie de *Leptophis* através da análise de nove exemplares, incluindo o holótipo, que havia sido considerado como perdido. Além desses exemplares, são conhecidos apenas mais cinco espécimes desta rara serpente, que foram descritos por Peters & Órces-V (1960). Neste trabalho, foi feita uma análise comparativa de *L. cupreus* com os táxons simpátricos *L. a. copei*, *L. a. nigromarginatus*, *L. a. occidentalis*, *L. riveti*, além da inclusão de fotos do holótipo, e fotos e descrição do hemipênis.

O último artigo, “Diet and feeding behaviour of the Neotropical parrot snake (*Leptophis ahaetulla*) in northern Brazil”, escrito em conjunto com os Drs. Ulisses Galatti e Marcos Di-Bernardo (*In memoriam*), foi publicado no Journal of Natural History. Neste trabalho, foi realizada a análise de 289 espécimes de *Leptophis ahaetulla* coletadas no norte do Brasil. Cinqüenta e três dos 289 espécimes possuíam conteúdos estomacais, com 27% desses sendo identificados como anfíbios anuros do grupo *Scinax ruber*.

CAPÍTULO I

A new species of *Leptophis* (Serpentes, Colubridae) from Northeastern Brazil

Submetido para Herpetologica

A NEW SPECIES OF *LEPTOPHIS* (SERPENTES, COLUBRIDAE) FROM NORTHEASTERN BRAZIL

NELSON R. DE ALBUQUERQUE[1,3] AND MARCOS DI-BERNARDO[2]

[1] *Laboratório de Sistemática de Vertebrados, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Avenida Ipiranga, 6681, 90619-900 Porto Alegre, RS, Brazil.*

[2] *In memoriam.*

[3] CORRESPONDENCE: e-mail, nelson_rufino@hotmail.com

ABSTRACT: We describe a new species of *Leptophis* from northeastern Brazil. This species differs from all other *Leptophis* in color pattern. The dorsal color pattern has two dorsolateral green or blue-greenish stripes (blue, golden, or turquoise in preserved specimens) separated from each other by a pale vertebral stripe, which continues onto the tail. Also, there are two white to yellowish dorsolateral stripes separating the green stripes from the first row of dorsal scales on each side. Further, the new species differs from the parapatric taxa *L. ahaetulla ahaetulla* and *L. a. liocercus* in hemipenial morphology, having xx-xx spines at the level of the fourth row (vs. xx in and *L. a. ahaetulla* and xx in *L. a. liocercus*), papillae on midsection region stout, poorly developed (vs. long papillae in *L. a. ahaetulla* and long fringing papillae in *L. a. liocercus*); papillae on distal portion of organ short and stout (vs. short, not stout in *L. a. ahaetulla* and long in *L. a. liocercus*).

Key words: Caatinga domain; Colubrinae; *Leptophis;* New species; Northeastern Brazil; Serpentes

THE NEOTROPICAL snake genus *Leptophis* Bell, 1825 comprises a well-diversified group of colubrine snakes distributed in Central and South America, including the Caribbean islands of Trinidad and Tobago (Oliver, 1948; Peters and Orejas-Miranda, 1970). Oliver (1948) presented an extensive revision of the genus, using primarily the coloration pattern to distinguish species and subspecies then recognized; other characters were the localization of keels on the body, number of ventral scales, development of postocular black stripe (broad, narrow, or absent), occurrence of loreal scale, and number of maxillary teeth. Subsequently, two species and two subspecies were described (Bernal-Carlo and Roze, 1994; Harding, 1995; Henderson, 1976; Mertens, 1972), and two other species, synonymized by previous authors, were resurrected (Hoyt, 1964; Peters and Orcés-V, 1960), resulting in the 10 species and 16 subspecies currently recognized.

The genus *Leptophis* retains several species with a complex taxonomic history (see list of synonymies in Oliver, 1948). Its type species, *Coluber ahaetulla* Linnaeus, 1758, was described on the basis of four specimens from South American (currently *Leptophis ahaetulla*) and one specimen from Asia (currently *Ahaetulla nasuta*), which led Oliver (1947) to propose the name *Thalerophis* as a replacement name for *Leptophis*. However, Savage (1952) established that *Leptophis* is the correct name for these snakes.

Among the taxa currently recognized in *Leptophis, L. ahaetulla* is the most widespread species in the genus, occurring from Mexico to most of South America. This species is also the most complex species in the genus, with 12 recognized subspecies: *L. a. ahaetulla, L. a. bocourti, L. a. bolivianus, L. a. coeruleodorsus, L. a. copei, L. a. liocercus, L. a. marginatus, L. a. nigromarginatus, L. a. occidentalis, L. a. ortoni, L. a. praestans* e *L. a. urostictus*.

Subspecies of *L. ahaetulla* are notoriously variable in coloration and morphology; consequently, subspecific identification of *L. ahaetulla* is particularly difficult, due to the overlapping of diagnostic characters. Moreover, some subspecies of *L. ahaetulla* described in Oliver's monograph were based on very few specimens, having to be reevaluated when more specimens were available for further study (Oliver, 1948), which suggested the need of further systematic revision.

Thus, as part of a taxonomic revision of *Leptophis ahaetulla*, we examined 271 specimens from northeastern Brazil, including three specimens that Oliver (1948) previously assigned to *L. a. ahaetulla*. Forty two of the specimens analyzed cannot be allocated to any of the known species of *Leptophis* and represent a previously unrecognized species. Herein, we describe this new species.

MATERIAL AND METHODS

The following collections loaned or provided access to specimens. Institutional abbreviations are as listed in Leviton et al. (1985), except for Coleção Herpetológica da Universidade de Brasília, Brasília (CHUNB), Coleção Zoológica Gregório Bondar, Ilhéus (CZGB), Instituto Butantan, São Paulo (IBSP), Museu de Biologia Mello Leitão, Santa Teresa (MBML), Coleção Herpetológica da Universidade Federal do Ceará, Fortaleza (CHUFC), and Coleção Herpetológica da Universidade Federal da Paraíba, João Pessoa (UFPB). Forty two specimens from 19 localities were examined. Additionally, we compared the new species with specimens from Cerrado (north Tocantins and Bahia), Atlantic forest (coastal forest of Bahia and Paraíba), western and central Piauí (transition zone between the Amazon domain and the Caatinga domain, see Ab'Saber, 1977), and data from the literature (e.g. Argôlo, 2004; Cunha and Nascimento, 1993). The map was made with the program ArcView GIS with some localities obtained from the on line version of the Global Gazetteer Version 2.1 by Falling Grain Genomics (http://www.fallingrain.com/world/). Ventral scales were counted according to

Dowling (1951). All measurements were made to the nearest 0.1 mm using digital calipers, except for snout-vent and tail lengths (SVL), which were taken with a flexible ruler to the nearest millimeter. Bilateral variation is reported as “right/left”. Dorsal scale reduction formula followed Thomas (1976). When no everted hemipenis was available, the sex of each specimen was determined by making a post-cloacal incision between the 10th-12th subcaudals and checking for the presence of *in situ* hemipenis. The hemipenial description was based on the right organs of MNRJ 1961, CHUFC 525, CHUFC 523, and CHUFC 1929, which were prepared following Pesantes (1994). In addition, we examined the everted hemipenes of CZGB 1149, IBSP 9121, IBSP 64423, IBSP 67645, MCN 5340, MNRJ 1758, MNRJ 4846, MPEG 17722, MPEG 17755, MPEG 18630, MPEG 19434, MZUESC 2002, and UFPB 4300 for comparison. The hemipenis of IBSP 67645 was examined *in situ*. Terminology for hemipenial morphology followed Dowling and Savage (1960) and Zaher (1999). The Analysis of Variance (ANOVA) was used to test for sexual dimorphism in: number of ventral scales, number of subcaudal scales, snout-vent length, and tail-length. Assumptions of normality and homoscedasticity were evaluated using Kolmogorov-Smirnov’s test and the Levene’s test respectively (Zar, 1999). All tests were performed at a significance level of 0.05.

SPECIES ACCOUNT

Leptophis caatingensis sp. nov.

Thalerophis richardi richardi; Oliver, 1948 (partim)

Leptophis ahaetulla ahaetulla; Peters and Orejas-Miranda, 1970 (partim)

Leptophis ahaetulla liocercus; Lima-Verde, 1971

Leptophis ahaetulla; Vanzolini, Ramos-Costa and Vitt, 1980; Vitt and Vangilder, 1983

Holotype.– CHUFC, adult male. Type-locality: Messejana (3º49'S, 38º29'W), Fortaleza, Ceará, Brazil. Collected 6 June 1985 by R. B. Marques, (Fig. 1, 2).

FIG. 1 A, B, C.– Dorsal, ventral and lateral view of head of the holotype of *Leptophis caatingensis* sp. nov. (CHUFC), from Messejana (3º49'S, 38º29'W), Fortaleza, Ceará, Brazil. Drawings by NA.

FIG. 2. – Dorsal view of the holotype of *Leptophis caatingensis* sp. nov. (CHUFC), from Messejana (3º49'S, 38º29'W), Fortaleza, Ceará, Brazil.

Paratypes.– Brazil. Alagoas: Murici, Serra Branca, MNRJ 3969**. Ceará: Aquiraz, CHUFC 1881 (Sítio três Marias), CHUFC 1602 (Praia do Iguape); Baturité, IBSP 20135, CHUFC 2868; Caucaia (Fazenda Maturi), CHUFC 2868; Coluna, near Justiniano Serpa, MZUSP 5321; Croatá, IBSP 20009; Fortaleza, CHUFC 1227 (Sítio Três Marias), CHUFC 1980, CHUFC 1140 (Campus do Pici), IBSP 52363, MNRJ 1959, MNRJ 1960, MNRJ 1961 (Mucuripe); Iguatu, Chapada do Apodi, MCP 17835, CHUFC 525; Itapipoca, MZUSP 3629; Limoeiro do Norte, CHUFC 221, CHUFC 365, CHUFC 493, CHUFC 561; Guaiuba, Sítio São Jerônimo, CHUFC 1442, CHUFC 1919, CHUFC 1929; Lima Campos, IBSP 20184; Maranguape, CHUFC 1172, CHUFC 1722 (Serra Maranguape, Sítio Parque Nova América), CHUFC 1611, CHUFC 1244 (Sítio Poroas); Morada Nova, CHUFC 1721(Açude de Petrolina); Pacajus, CHUFC 1732 (BR-116, km 59), MZUSP 5300 (Guarani); Pacoti, Serra do Baturité, MZUSP 3630. Paraíba: Gurinhém, Fazenda Salgado, MZUSP 8943, MZUSP 9658. Pernambuco: Exu, MZUSP 6720, MZUSP 7093, MZUSP 7094, MZUSP 7095 (Fazenda Maniçoba, 11 km S Exu). Additional specimen examined (no-type): *Leptophis caatingensis*: Brazil: Rio Grande do Norte: UMMZ 56305.

Diagnosis.– xxxx - *Description of holotype.*– Adult male; ventrals 168; anal plate divided; paired subcaudals 146; head distinct from body; snout-vent length (SVL) 895 mm; tail length 511 mm; preoculars 1/1, not in contact with frontal; postoculars 3/3; anterior temporals 1/1; posterior temporals 2/2; supralabials 8/9, 4-5/5-6 in contact with orbit; infralabials 11/11, 1-4 in contact with anterior genials; loreal absent; parietals longer (9.53 mm) than broad (7.07 mm) and in contact with upper postocular; dorsal rows 15-15-11; dorsal scale reduction formula:

$$15\ \frac{(10)\ 5+6\ (97)\ 3+4\ (102)}{5+6\ (98)\ 2+3\ (105)}\ 11(158)$$

strong keels on all dorsal scales of trunk (reduced on scales of vertebral row), except on first dorsal row on each side, where they are absent; keels present on ventrals and subcaudals, where they are reduced; dorsal scales of tail without keels. Single apical pit present on all dorsal scales of body, except on the first dorsal row on each side. Apical pits of anterior third of body larger and more prominent than those of posterior third.

Coloration of holotype in alcohol. – Top of head steel-blue; narrow black postocular stripe reduced to black margin on lower postocular, occupying lower half of anterior temporal, two-thirds of lower posterior temporal and upper edges of last three supralabials; anterior to orbit stripe reduced to black margin on all supralabials, except first; supralabials cream, except the upper margin of those included in ocular stripe; anterior lower margin of nasal and lower one-half to two thirds of rostral cream. Longitudinal pale vertebral stripe approximately one-half scale wide extending from ninth vertebral scale to tip of tail. Two dorsolateral blue stripes, separated by vertebral stripe, extending from ninth vertebral scale to tip of tail; blue stripes become indistinct on posterior third of tail. Ventral surface of head, trunk and tail pale.

FIG. 3. – *Leptophis caatingensis* sp. nov. from Quixeramobim, Ceará, Brazil, showing dorsolateral greenish blue stripes. This specimen was not captured. Courtesy of Igor J. Roberto. Photo credit: Ciro Albano.

Variation and sexual dimorphism. – Ventrals 156-171 in males (*x* = 163.2 ± 3.4, n = 23), 159-172 in females (*x* = 168.2 ± 3.6, n = 19). Subcaudals 137-158 in males (*x* = 148.3 ± 5.6, n = 13), 145-162 in females (*x* = 153.6 ± 4.9, n = 8). Largest male SVL 958 mm, tail 495+ mm and largest female SVL 835 mm, tail 511 mm. Supralabials 8/8 (n = 25), 8/9 (n = 6), 9/9 (n = 4), 9/8 (n = 4), 10/9 (n = 1), or 7/8 (n = 1), with 4-5/4-5 (n = 25), 5-6/4-5 (n = 7), 4-5/5-6 (n = 6), 5-6/ 5-6 (n = 5) or 5-6/4-5 (n = 5) entering orbit; infralabials 10/10 (n = 23), 11/11 (n = 6), 10/11 (n = 5), 11/10 (n = 1), 10/9 (n = 2), 9/9 (n = 3) or 11/9 (n = 1), with 5/5(n = 29), 6/6 (n = 7), 5/6 (n = 4), 6/5 (n = 2), or 4/4 (n = 1) contacting first genials; preoculars 1/1 (n = 38), 2/1 (n = 2) or 2/2 (n = 2); postoculars 2/2 (n = 39), 3/3 (n = 1), 1/2 (n = 1) or 1/1 (n = 1); anterior temporal 1/1 (n = 41); posterior temporal 2/2 (n = 34), 1/1 (n = 3), 2/1 (n = 3) or 1/2 (n = 1). Keels stronger in adult males than females or juveniles. Dorsal scales of tail keeled until reduction from six to four scales. In CHUFC 525 postocular stripes extend over four scales posterior to last supralabial. Width of blue stripes 4-4.5 (anterior third) to 3-3.5 (middle and posterior thirds of the body) scales.

FIG. 4. – *Leptophis caatingensis* sp. nov. (CHUFC), from Fortaleza, Ceará, Brazil, showing dorsolateral green stripes. Courtesy of Diva Borges-Nojosa.

Width of blue stripes on middle and posterior third of body two scales in some specimens in which gold replaces blue. One juvenile specimen examined was MZUSP 8943, an immature male with 389 mm in total length, which have bands on anterior and middle region of body, similar to those found in other juveniles of most species of *Leptophis* (see Oliver, 1948). Females with significantly more ventrals than males (F = 21.2794; p = 0.0001). Subcaudal counts not sexually dimorphic (F=4.8668; p = 0.0378).

Hemipenis.– Retracted organ extends 8 subcaudals in length. Single, slightly bilobate, noncapitate; *sulcus spermaticus* undivided, extending from base to apical region of right lobe (Fig. 5 A, B); Intrasulcar surface smooth. Basal region bears numerous spines, which tend to be distributed in six rows approximately encircling organ; first row with 8-9 spines; spines on first row sometimes slightly smaller than those on fourth row (CHUFC, CHUFC) or longer (CHUFC except fifth and seventh spines; MNRJ); spines arranged irregularly rather than in transverse rows. Spinules widely scattered, occurring in area between the spines and also below them. Small spines present on lateral surface of *sulcus* as continuation of spinules present on basal region; these spinules become stout papillae on midsection, being larger along *sulcus* than those adjacent. Small number of calyces may originate above sixth row of basal spines (CHUFC); small-sized calyces along distal portion of organ, bearing robust papillae. Papillae gradually increase in size toward distal portion of hemipenis. Central and anterior portions of lobes either completely calyculate (CHUFC, Fig. 5 A, B) (MNRJ), or nude (CHUFC, CHUFC). Peripheral surface of lobes with few papillate calyces irregularly distributed. Papillae number on calyces 8-10 in midsection and 6-8 in peripheral surface and central portion of lobes (CHUFC with around 12 papillae on calyces along *sulcus*). Asulcate side similar to sulcate side.

FIG. 5. – Hemipenis of *Leptophis caatingensis* sp. nov. (Paratype CHUFC): (A) sulcate and (B) asulcate sides.

Intraspecific hemipenial variation.– Four hemipenes examined similar in overall morphology and ornamentation. Most remarkable variation in hemipenes of *L. caatingensis* was observed in apical ornamentation at tips of lobes. Central and anterior surface of CHUFC completely nude, similar to MPEG (*L. a. ahaetulla*); central surface of lobe of CHUFC is nude. In contrast, lobe of CHUFC completely calyculate. Lobe of MNRJ with only minuscule area nude, situated at end of sulcus.

Dentition.– CHUFC, MNRJ (males), and CHUFC (female) with respectively 23/24, 21/23, and 21/* recurved maxillary teeth without diastema, 14/13, 13/13, and 9/9 palatine teeth, 24/24, 23/23, and 21/20 pterygoid teeth, and 27/27, 19+/19+ and 20/20 dentary teeth. CHUFC (male) with 21/21 maxillary teeth. Last three maxillary teeth ungrooved and enlarged.

Distribution and ecology.– The new species is known from the States of Ceará, Pernambuco, Paraiba, Bahia, Rio Grande do Norte, and Alagoas, Brazil (Fig. 6). All but two specimens examined were collected in localities within the limits of the Caatinga Domain (Ab'Saber, 1977). *Leptophis a. ahaetulla* (now restricted to the Brazilian Amazonian, North Tocantins, and Piauí), *L. a. liocercus* (litoral zone of Paraiba, Alagoas and Pernanbuco, southeastern Brazil and Bahia) and *L. caatingensis*, are parapatrically distributed. One specimen, MNRJ, collected in Fortaleza, contained three hylid frogs and a tail of a gekkonid lizard, all ingested headfirst. Vitt and Vangilder (1983) recorded three *Scinax ruber* and one *Phyllomedusa hypochondrialis* in four snakes collected within 20 km of Exu, Pernanbuco. According to Vitt and Vangilder (1983), *L. caatingensis* (identified as *L. ahaetulla* in their paper) is diurnal and arboreal. Three specimens (MZUSP) contained respectively five (the fifth, head-tail direction, measure 19.22 mm), five (the fifth 24.18 mm) and seven (the seventh 23.80 mm) well-developed eggs each. Like other species of the genus *Leptophis*, *L. caatingensis* is known to bite.

Etymology.– The specific epithet refers to the characteristic distribution of this species within the Caatinga morphoclimatic domain (Ab'Saber, 1977).

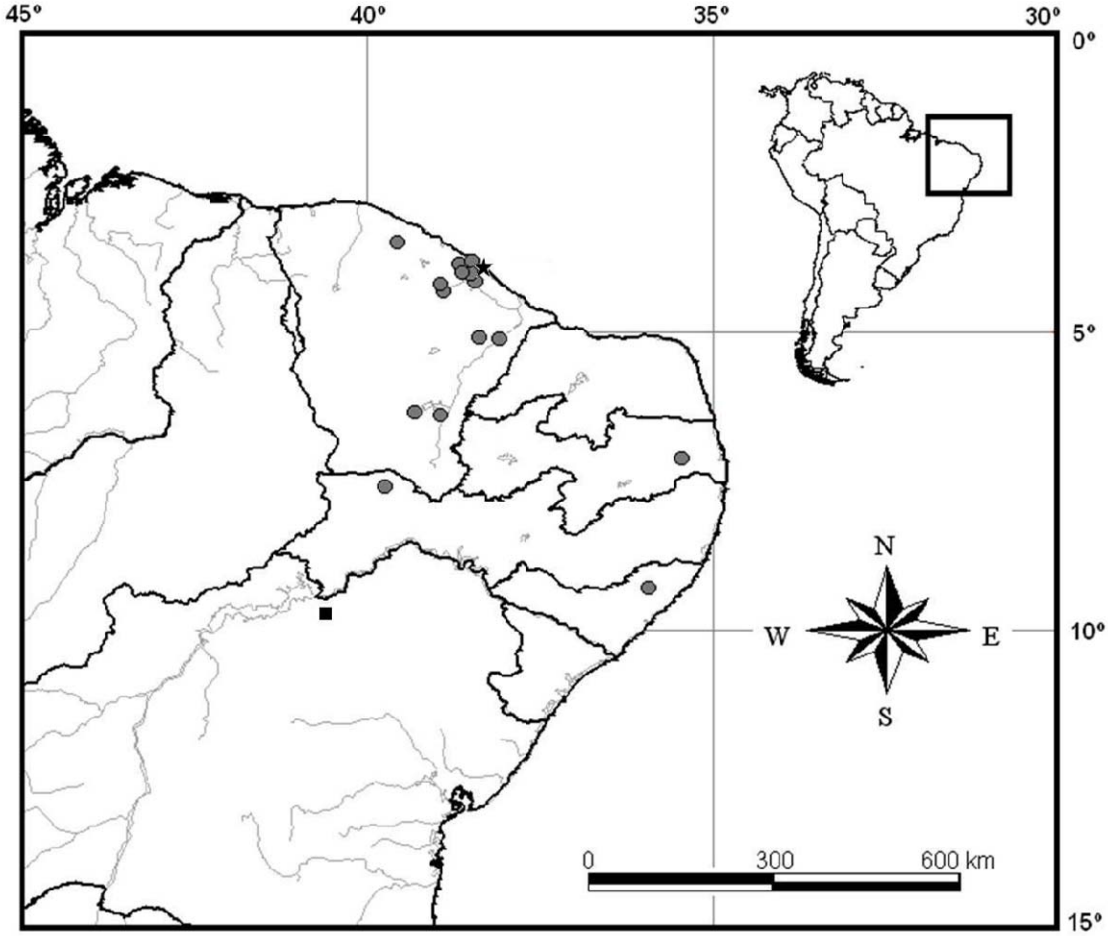


FIG. 6. – Northeastern Brazil showing the distribution of *Leptophis caatingensis*. Starr indicates the type-locality. Square: data from Freitas and Silva (2007).

Remarks. –The hemipenes of *L. caatingensis* are similar to those of *L. a. ahaetulla* and *L. a. liocercus* in overall morphology. All of these taxa have the organ covered by five to six rows of spines, distal region with papillate calyces, and spines arranged irregularly rather than in transverse rows. However, the number of spines on the fourth row and the papillae size rapidly distinguishes these taxa. One of the principal hemipenial differences among these taxa concerns the number of spines at the level of the fourth row: *L. caatingensis* has 18-22 spines (vs. 14 in six organs of *L. a. ahaetulla* and 11-18 in six organs of *L. a. liocercus*). The only specimen of *L. a. liocercus* with 18 spines was collected in João Pessoa, Paraíba (UFPB). This locality is located in a distance of approximately 539 km from Guaiuba, Ceará and 497 km from Iguatu, Ceará (where the two specimens of *L.* caatingensis with 18 spines were collected).

Oliver (1948) described briefly the hemipenis of *L. a. liocercus* based on retracted organs. According to Oliver (1948) *L. a. liocercus* has “four enlarged basal spines; the two on either side of the sulcus are the largest”. However, Oliver did not mention the specimen(s) utilized in his description. IBSP (Estação Cascadura, Rio de Janeiro), IBSP (Estação Itá, Espírito Santo) and MBML (Aracruz, Espírito Santo) have four conspicuously enlarged basal spines, similar to *L. a. marginatus* (Oliver, 1948) and Oliver’s *liocercus* (Oliver used the specimens IBSP and IBSP in his *L. a. liocercus* description). Presumably the IBSP and IBSP were collected in a nearby city and sent to IBSP by train, as were many other specimens received by IBSP in the 1930’s. On the other hand, the hemipenes of CZGB and MZUESC (both from Ilhéus, littoral zone of Bahia) have respectively five and seven spines at first basal row; contrarily to IBSP and MBML organs, these spines are only slightly larger or approximately equal in size to those on fourth row. Though without spots on parietal scales IBSP and MBML retains partially their original coloration and are clearly *L. a. marginatus*. IBSP is badly damaged and faded, so that the original color pattern is absent.

Subspecies have long been considered as artificial subdivisions of species (e.g. Mayr, 1982; Cracraft 1983; Frost et al., 1992; Frost and Kluge, 1994). As mentioned above, *L. a. ahaetulla*, *L. a. liocercus*, and *L. caatingensis* are parapatrically distributed. This might be the classic situation of whether to recognize at a species or subspecies level, which are parapatric, distinct, but similar taxa. As defined by Mayr and Ashlock (1991), subspecies may be connected either by primary or secondary intergradation. Primary intergradation occurs when a series of intermediate populations connect two subspecies, with each population being intermediate between adjacent populations. Secondary intergradation occurs when two subspecies meet in a well-defined zone where they form a hybrid population with greatly increased variability, containing character combinations from subspecies a and b. However, if *Leptophis caatingensis* in fact represents a subspecies of *L. ahaetulla*, the borders of the three subspecies under study could not be established because the taxa analyzed in the present study are parapatrically distributed (i.e., with ranges that are adjacent but do not overlap) (see also Fig. 10 in Oliver, 1948). The status of *L. a. ahaetulla* and *L. a. liocercus* will be assessed elsewhere.

According to Freitas and Silva (2006), the specimens of *Leptophis* found within the limits of the Caatinga Domain are green (young specimens) or blue (adult specimens), suggesting a possible ontogenetic change in *Leptophis caatingensis*. Actually, some individuals of the new species are greener in color than others, regardless of age. For example, the CHUFC (Fig. 4) is clearly a green adult specimen (880 mm SVL, 550 mm tail length). Also, the two dorsolateral blue stripes found in holotype of *L. caatingensis*, which is also an adult specimen, suggest they were green in live. It is here hypothesized that this species changes color from green to blue-greenish if put in direct sunlight (see plate VI in Vanzolini et al., 1980 and Fig. 4; Diva Borges-Nojosa, pers. comm.). We reidentified the specimen recorded as *L. ahaetulla* for Juazeiro, Bahia by Freitas and Silva (2006, plates on page 192) as *L. caatingensis*.

On the basis of dorsal coloration and hemipenial characters, *L. caatingensis* is presumably the closest relative of *L. a. ahaetulla* and *L. a. liocercus*. They are the only taxa within *Leptophis* that share two dorsolateral stripes separated from each other by a vertebral stripe, although in some specimens examined the dorsal stripes are not continuous for the entire length of the body, becoming diffused in mid-body (e.g. CZGB; see also Oliver, 1948).

The dorsal stripes of *L. a. liocercus* are not visible in Wied's illustration (1824); however the dorsal scales of specimen figured by Wied are completely covered by *stratum corneum*. One of us (NA) examined the type of *L. a. liocerus* (AMNH 3531), in which all scales lost the *stratum corneum*. Hence, the vertebral and dorsolateral stripes became clearly visible. The name *L. ahaetulla* has been assigned to several populations of *Leptophis* in South America, mainly in northern and northeastern Brazil (Oliver, 1948); however its division into subspecies has been considered unsatisfactory in Brazil (e.g. Vanzolini et al., 1980).

Acknowledgments. – We are grateful to D. Borges-Nojosa (CHUFC), M. Zatz and G. Colli (CHUNB), J. Delabie (CZGB), L. Verrastro (DZUFRGS), F. Franco (IBSP), M. Hoffman (MBML), M. Leitão de Araújo (MCN), J. Rosado (MCZ), A. Prudente (MPEG), R. Fernandes (MNRJ), H. Zaher (MZUSP), A. Argôlo (MZUESC), A. Percequillo (UFPB), and G. Schneider (UMMZ), who kindly loaned us specimens. A. Argôlo made time to pack and send the CZGB specimens. The paratypes MCP 17835 and MCP 18318 were kindly donated by Prof. D. Borges-Nojosa. NA is particularly indebted to D. Frost, D. Kizirian, and to the

American Museum of Natural History for the opportunity to develop part of his PhD dissertation under their supervision and support. NA thanks G. Paggi for his continuous help and support during the writing of this ms. We thank T. Grant, D. Kizirian, M. Harvey, R. Reis and two anonymous reviewers who provided helpful comments on the manuscript. D. Borges-Nojosa, D. Feitosa, G. Pereira-Filho, I. Roberto, and W. Rocha kindly provided photos of living specimens collected in Amazonian, Caatinga and Atlantic Domains from northeastern Brazil; also, they supplied important information on localities and physiognomy of these Domains. Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided financial support to NA.

LITERATURE CITED

AB'SABER, A. N. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. Geomorfologia 52(2):1-21.

ARGÔLO, A. J. S. 2004. As serpentes dos cacauais do sudeste da Bahia. Ilhéus, Bahia, Editus, 260 p.

BERNAL-CARLO, A., AND J. A. ROZE. 1994. A new *Leptophis* (Serpentes: Colubridae) from Sierra Nevada de Santa Marta, Colombia. Bulletin of the Maryland Herpetological Society 30(1):46-49.

CRACRAFT, J. 1983. Species concepts and speciation analysis. Pp. 159–187. *In* R. F. Johnston (Ed.), Current ornithology. Vol. 1. Plenum Press, New York.

CUNHA, O. R., AND F. P. NASCIMENTO. 1993. Ofídios da Amazônia. As cobras da região Leste do Pará. Boletim do Museu Paraense Emílio Goeldi, Série Zoologia 9:1-191.

DOWLING, H. G. 1951. A proposed standard system of counting ventral scales in snakes. British Journal Herpetology, 1: 97-99.

DOWLING, H. G., AND J. M. SAVAGE. 1960. A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica 45:17-28.

FREITAS, M. A., AND T. S. F. SILVA. 2007. Guia ilustrado: a herpetofauna das caatingas e áreas de altitudes do nordeste brasileiro. Pelotas: USEB. 388 p.: Il.

FROST, D. R., AND A. G. KLUGE. 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics 10:259–294.

FROST, D. R., A. G. KLUGE, AND D. M. HILLIS. 1992. Species in contemporary herpetology: comments on phylogenetic inference and taxonomy. Herpetological Review 23:46–54.

GLOBAL GAZETTEER. Version 2.1 by Falling Grain Genomics [http://www.fallingrain.com/world/] Last modified: November 14, 2006

HARDING, K. 1995. A new species of tree snake of the genus *Leptophis* Bell, 1825 from Mount Aripo, Trinidad. Tropical Zoology 8 (2):221-226.

HENDERSON, R. W. 1976. A new insular subspecies of the colubrid snake *Leptophis* mexicanus (Reptilia, Serpentes, Colubridae) from Belize. Journal of Herpetology 10(4):329-331.

HOYT, D. L. 1964. The rediscovery of the snake *Leptophis modestus*. Copeia (1):214-215.

LEVITON, A. E., R. H.GIBBS JR, E. HEAL, AND C. E. DAWSON. 1985. Standards in Herpetology and Ichthyology: part I. Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. Copeia 3:802-852.

MAYR, E. 1982. Of what use are subspecies? Auk 99:593–595.

MAYR, E., AND P. D. ASHLOCK. 1991. Principles of Systematic Zoology. 2ª ed, Mcgraw-Hill Press, New York.

MERTENS, R. 1972. Eine neue Schlanknatter der Gattung *Leptophis* aus Mexiko. Senckenbergiana Biologica 53:341-342.

MERTENS, R. 1973. Bemerkenswerte Schlanknatters der neotropischen Gattung *Leptophis*. Studies on the Neotropical Fauna and Environment 8:141-154.

OLIVER, J. A. 1947. The status of *Leptophis* Bell. Copeia (1): 64.

OLIVER, J. A. 1948. The relationships and zoogeography of the genus *Thalerophis* Oliver. Bulletin of the American Museum of Natural History 92 (4):157-280.

PESANTES, O. S. 1994. A method for preparing the hemipenis of preserved snakes. Journal of Herpetology 28 (1):93-95.

PETERS, J. A. G., AND ORCÉS-V. 1960. *Leptophis cupreus* Cope. A valid South American colubrid species. Beitraege zur Neotropischen Fauna 2:139-141.

PETERS, J. A., AND B. OREJAS-MIRANDA. 1970. Catalogue of the Neotropical Squamata: Part I. snakes. United State National Museum Bulletin 297:129-131.

SAVAGE, J. M. 1952. Two centuries of confusion: The history of the snake name *Ahaetulla*. Bulletin of the Chicago Academy of Sciences, 9(11):203-216.

THOMAS, R. A. 1976. Dorsal scale row formulae in snakes. Copeia 1976 (4): 839-841.

VANZOLINI, P. E., A. M. M. RAMOS-COSTA, AND L. J. VITT. 1980. Répteis das Caatingas. Academia Brasileira de Ciências. Rio de Janeiro. 161 p.

VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in northeastern Brazil. Amphibia-Reptilia 4:273-296.

ZAHER, H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. Bulletin of the American Museum of Natural History, 240:1-168.

ZAR, J. H. 1999. Bioestatistical Analysis. Preentice Hall, Upper Sadle River, New Jersey, U.S.A, 123p.

WIED-NEUWIED, M. A. P. 1824. Abbildungen zur Naturgeschichte von Brasilien. Weimar, 96pls.

APPENDIX I

Additional Specimens Examined

Leptophis ahaetulla ahaetulla: Brazil: Pará: ilha de Marajó, MPEG 17722, ilha de Mosqueiro, MPEG 18630; Santo Antônio do Tauá, MPEG 19434. Piauí: Gilbués, MPEG 21695; Parque Nacional de Sete Cidades, MPEG 21697 (between Piracucura and Piripiri); São Raimundo Nonato, MNRJ 1758; Teresina, IBSP 503, MPEG 21696. Rondônia: Porto Velho, MPEG 17755 (UHE Samuel, BR 364). Tocantins: Lajeado, IBSP 64538, IBSP 64351, IBSP 64396; Miracema do Norte, IBSP 64423, IBSP 66422; Palmas, IBSP 66317, IBSP 65623, IBSP 65907.

Leptophis ahaetulla liocercus: Brazil: Bahia: Ilhéus, CZGB 1149, MZUESC 2002; Santa Clara, MCZ 2989 (Rio Mercury); Poções, IBSP 67645. Espírito Santo: Sítio Guaiporini, MNRJ 4846. Pernambuco: Recife, MCN 5340, MCN 5648 (Parque Dois Irmãos); Moreno, Tapera, IBSP 17301, MCN 5671. Paraíba: João Pessoa, UFPB 4300 (Mata do Buraquinho); Mamanguape, CHUNB 29019. AMNH 3531: Holotype of *L. a. liocercus* (unspecified locality).

Leptophis ahaetulla marginatus: Brazil: Espírito Santo: Aracruz, MBML130; Estação Itá, IBSP 9121. Rio de Janeiro: Estação Cascadura, IBSP 9019.

CAPÍTULO II

A taxonomic revision of tree snakes of the *Leptophis ahaetulla* complex (Serpentes, Colubridae)

A ser submetido para Herpetological Monographs

A TAXONOMIC REVISION OF TREE SNAKES OF THE *LEPTOPHIS AHAETULLA* COMPLEX (SERPENTES, COLUBRIDAE)

NELSON R. DE ALBUQUERQUE[1,2]

[1] *Laboratório de Herpetologia, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Avenida Ipiranga, 6681, 90619-900 Porto Alegre, RS, Brazil.*

[2] CORRESPONDENCE: e-mail, nelson_rufino@hotmail.com

ABSTRACT: The Neotropical snake *Leptophis ahaetulla*, with 12 subspecies, is a group of colubrine snakes widely distributed in Central and South America. In this paper, *Leptophis ahaetulla ahaetulla*, *L. a. bocourti*, *L. a. bolivianus, L. a. coeruleodorsus, L. a. copei, L. a. liocercus, L. a. marginatus, L. a. nigromarginatus, L. a. occidentalis, L. a. ortoni, L. a. praestans* and *L. a. urostictus* are elevated to species status, whereas *L. a. copei* and *L. a. ortoni* are placed in the synonymy of *L. ahaetulla* and *L. nigromarginatus*, respectively. For each species, a diagnosis, description, and distribution are provided based on examination of 1573 specimens and data from the literature. Descriptions of color in life and ecology are included for most species. A dichotomous key is provided to assist in the identification of specimens. Additionally, a phylogenetic analysis of the *Leptophis ahaetulla* complex based on 31 morphological, ecological and color characters is presented. Data from 14 species of *Leptophis* were combined with data from three outgroup taxa. The relationships of *Leptophis* were assessed using parsimony method. Nine equally parsimonious trees were obtained, with a total length of 50 steps, a consistency index (CI) of 96, and a retention index (RI) of 97.

Key words: South America; Central America; *Leptophis*; Taxonomy; Colubrinae

THE SNAKE genus *Leptophis* Bell, 1825 comprises a group of 10 colubrine snakes widely distributed in Central and South America, including the Caribbean islands of Trinidad and Tobago (Oliver, 1948; Boos, 2001). Among the taxa currently recognized in *Leptophis*, *L. ahaetulla* (Linnaeus, 1758) constitute a morphologically diverse assemblage of taxa, which share a specialized behavior for feeding on amphibians, especially those of the family Hylidae (Oliver, 1948; Albuquerque et al. 2007). This species is the most complex species in the genus, exhibiting extremes in coloration, external morphology and dentition, with 12 recognized subspecies: *L. a. ahaetulla*, *L. a. bocourti*, *L. a. bolivianus, L. a. coeruleodorsus, L. a. copei, L. a. liocercus, L. a. marginatus, L. a. nigromarginatus, L. a. occidentalis, L. a. ortoni, L. a. praestans* e *L. a. urostictus*. It is also the most widespread species in the genus, being recorded from Mexico to most of South America.

Oliver (1948) presented an extensive systematic revision of the genus *Leptophis*. Among those *Leptophis* characterized by absence of loreal scale (i.e. *L. caatingensis, L. cupreus, L. modestus, L. nebulosus, L. riveti, L. santamartensis,* and *L. stimsoni*), *L. ahaetulla* can be distinguished by the relatively high number of ventral scales (156-182), presence and distribution of keels, and dorsal coloration (in taxa from South America) with two dorsolateral blue stripes (Mertens, 1973, Oliver, 1948, Peters and Orejas-Miranda, 1970). Otherwise, the subspecies of *L. ahaetulla* are distinguished from each other mainly by coloration, particularly that of adult specimens. Except for nomenclatural modifications, the subspecies recognized by Oliver (1948) are still considered valid.

Despite the comprehensive revision of Oliver (1948), the available material did not allow that author to define the taxonomic status of all samples studied, especially those found across contact zones. Some subspecies of *Leptophis ahaetulla* were considered by Oliver (1948) as “attempts”, having to be reevaluated when more specimens are available for further study. Moreover, though the general ranges of the subspecies are known, their distribution has been poorly understood and not well defined. Oliver (1948) identified some areas of intergradation among the subspecies, but always based on a small number of individuals, deserving further studies.

Based on Stuart's (1932) morphological studies, Oliver (1948) suggested that the colubrine genera *Drymobius* Fitzinger, 1843 and *Mastigodryas* Amaral, 1935 are probably the closest living relatives of the genus *Leptophis*. Oliver's hypothesis was based primarily on similarities among the number of supralabial scales, number of dorsal rows at midbody, hemipenial morphology, and maxillary teeth among those genera. Likewise, the definition and relationships of the species of *Leptophis* and subspecies of *L. ahaetulla* were inferred primarily on the basis of coloration and morphological characters.

The main objective of the present study was to reassess the validity of the subspecies of *Leptophis ahaetulla*, on the basis of material not examined by Oliver (1948), including analysis of cranial and hemipenial morphology, and geographic variation among the characters utilized for the recognition of the subspecies. Also, a parsimony analysis of the genus *Leptophis* was performed to estimate how the taxa considered as valid are related to one another.

MATERIAL AND METHODS

Data on meristic and morphometric characters for 1573 specimens previously identified as *Leptophis ahaetulla*, including 70 hemipenes and 73 skulls, were obtained (Appendix I). Color patterns of living specimens were taken mostly from literature (e.g. Beebe, 1946; Cunha and Nascimento, 1978; Wilson and Meyer, 1985; Campbell, 1998; Argôlo, 2004; Savage, 2002).

Maps were made with ArcView GIS 3.2 with some localities obtained from the online version of the Global Gazetteer Version 2.1 by Falling Grain Genomics (http://www.fallingrain.com/world/). Ambiguities and corrections are noted in Appendix I.

An attempt was made to identify all the specimens examined using Oliver's (1948) and Peters and Orejas-Miranda's keys (1970). Before the analysis of the hemipenial morphology, the organs were extracted from adult specimens and preserved in 70% ethanol. The method described by Pesantes (1994) was used: the left or right organ was removed and submerged in a solution of 3% KOH for 1 to 2 hours. When the tissues became translucent and flexible, a small incision was made on the base of the organ, in order to manually evert the whole structure. The everted organ was then filled with a liquid solution of agar-agar (Manzani and Abe, 1988). For description of hemipenes, the terminology of Dowling and Savage (1960) and Zaher (1999) was used.

Skulls were removed by peeling back the skin from the mouth such that head integument remained intact and with the rest of the specimen. A pair of forceps and a small surgical scissors was used to cut the skin. The extracted skulls were prepared as dry skeletons.

The Analysis of Variance (ANOVA) was used to test significance of morphological variation among the samples under study. Assumptions of normality and homoscedasticity were evaluated using Kolmogorov-Smirnov's and the Levene's test respectively (Zar, 1999). Both tests were performed using the software Bioestat 4.0 (Ayres et al. 2005). The ANOVA was also utilized to test significance of sexual dimorphism within each group. All tests were performed at a significance level of 0.05. Except as noted, institutional abbreviations are as listed in Leviton et al. (1985).

Phylogenetic analysis.– The analysis was based on the examination of 14 species of *Leptophis*, including 10 taxa previously considered as subspecies of *L. ahaetulla* (see Oliver, 1948). *Leptophis modestus, L. nebulosus, L. riveti, L. santamartensis,* and *L. stimsoni* were not included in the analyses because they are known from only a few specimens (e.g. *L. santamartensis* is known only from two juveline specimens from Sierra de Santa Marta, Colombia).

A data matrix of 18 taxa (14 ingroups and three outgroups) and 31 morphological, ecological and color characters was constructed with the software Mesquite (Maddison and Maddison, 2007). In addition to personal examination of characters, data from the literature was collected for a particular species/or in order to increase sample size. The characters were divided into five categories: hemipenial morphology, skull morphology, ecology, coloration, and external morphology.

Character states that are unknown are indicated in the data matrix by a question mark. Inapplicable characters are scored as "-". Character states were coded 0–5 as indicated in the following text within parentheses after each respective character-state description.

A matrix of character states for all taxa is given in Appendix 1. Characters were treated as non-additive and equally weighted, except for characters 7, 9, 16, and 17 that were regarded as ordened (additive). Characters were analyzed using the parsimony program NONA version 2.0 (Goloboff, 1999) and Winclada version 1.0 as an interface (Nixon, 1999-2002). The option "show unsupported nodes as collapsed"was chosen.

The search strategy used tree bisection and reconnection branch swapping (TBR) on a series of 1000 random addition replicates retaining up to 10 cladograms per replicate. To evaluate branch support, Bremer support values (Bremer, 1994) were calculated in NONA by saving trees up to five steps longer than the most parsimonious tree.

The ingroup.— The ingroup consists of the following taxa: *Leptophis ahaetulla*, *L. bocourti*, *L. bolivianus, L. coeruleodorsus, L. liocercus, L. marginatus, L. nigromarginatus, L. occidentalis, L. praestans* and *L. urostictus*, *L. caatingensis*, *L. cupreus, L. mexicanus, L. depressirostris, L. diplotropis*. The name *L. urostictus* was used in the sense of Mertens (1973).

The outgroup.— Outgroup selection was based upon hypothesized relationships (Oliver, 1948) among the genera *Drimobyus*, *Mastigodryas*, and *Leptophis*. The following taxa were used: *Drimobyus chloroticus*, *Drimobyus margaritiferus*, and *Mastigodryas bifossatus*. Trees were rooted on *Mastigodryas*.

SPECIES ACCOUNT

Leptophis ahaetulla (Linnaeus)

Coluber ahaetulla Linnaeus, 1758 (in part), Systema naturae, 10ª ed., vol. 1, p. 225; Type-locality: "Asia, America".

Coluber richardi Bory ST. Vincent, 1823. Dictionnaire classique d'histoire naturelle, Paris, vol. 4, p. 588 : Type locality: Guiana

Coluber linnei Gray, 1831 (in part). In: Griffith, The animal kingdom, p. 93. Substitute name for *ahaetulla* Linnaeus.

Dendrophis liocercus Schlegel, 1837 (in part), Essai sur la physionomie des serpens, vol. 2, p. 2244

Leptophis ahaetulla; Fitzinger, 1843, Systema reptilium, vol. 1, p. 26.

Leptophis liocercus; Deplanche, 1858, Bull. Soc. Linnenne Normandie, vol. 3, p. 13.

Leptophis ahaetulla; Parker, 1935, Proc. Zool. Soc. London, vol. 2, pt. 3, p. 520.

Leptophis ahaetulla ahaetulla; Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, p. 1.

Leptophis copei Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, 462, p. 7. Type locality: Salto do Huá, Brazil-Venezuela boundary. NEW SYNONYMY

Thalerophis richardi Oliver, 1947, Copeia, p. 64.

Thalerophis richardi richardi Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 219.

Leptophis ahaetulla [*ahaetulla*]; Int. Comm. Zool. Nomen. 1958 Op. 524, p. 270.

Leptophis ahaetulla ahaetulla; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 161.

Diagnosis.– *Leptophis ahaetulla* can be distinguished from its congeners by the presence of two grass green dorsolateral stripes separated from each other by a pale vertebral stripe, at least anteriorly (Fig. 1 A, B) (vs. dorsal stripes absent; if present they are metallic green or greenish-blue). Further, *L. ahaetulla* differs from the parapatric taxa *Leptophis caatingensis*, *L. marginatus* and sympatric *L. nigromarginatus* in dorsal head coloration. Dorsal head scales of *L. ahaetulla* are grass green, without back spots, and not margined with black (vs. green in *Leptophis caatingensis*, and greenish blue, margined, and with one black spot on each parietal scale in *L. marginatus* and *L. nigromarginatus*).

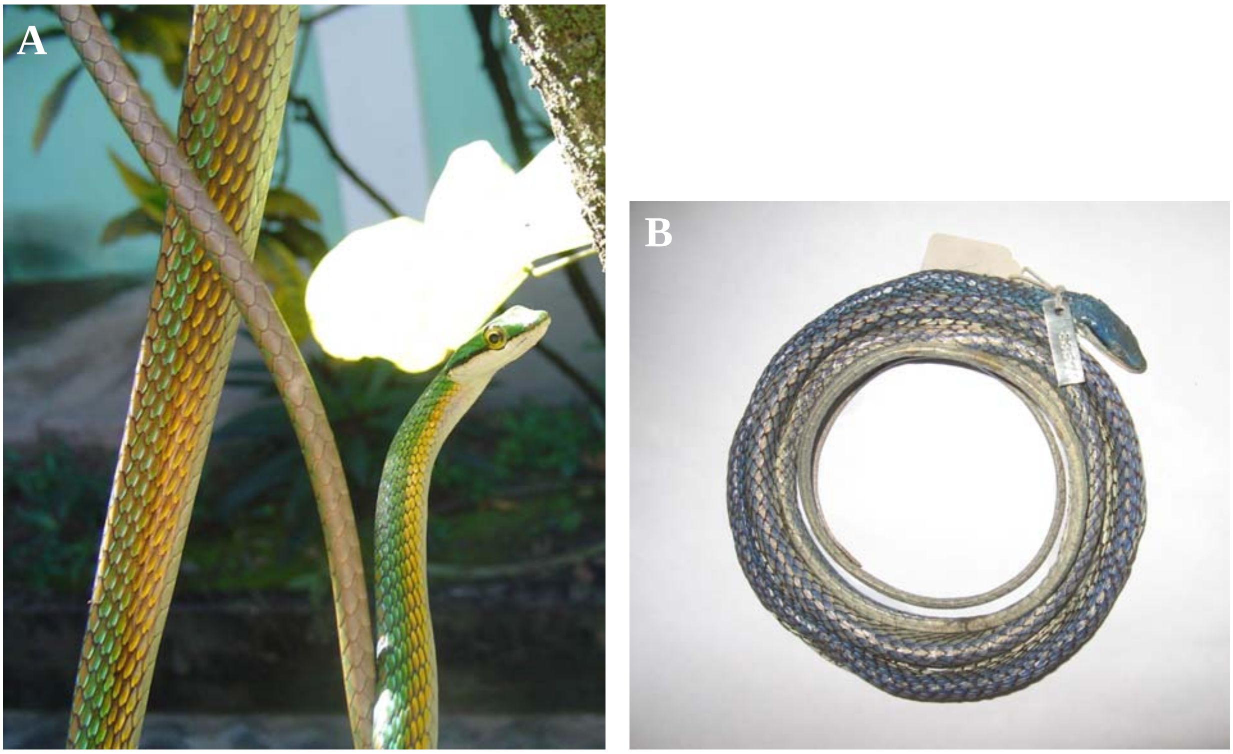


FIG. 1 – (A) *Leptophis ahaetulla* from Santo Ant. do Tauá, Pará (MPEG 19434). Note the two grass green dorsolateral stripes separated from each other by a vertebral stripe. Courtesy of Darlan Feitosa. (B) Paratype of *Leptophis copei* (USNM 83570). Note the two blue dorsolateral stripes separated from each other by a vertebral stripe.

Description.– Ventrals 150-179 in males (x = 163.9 ± 5.1, n = 174), 154-192 in females (x = 166.4 ± 5.3, n = 214). Subcaudals 135-182 in males (x = 160.2 ± 9.1, n = 116), 131-181 in females (x = 158.1 ± 8.8, n = 131). Largest male SVL 1126 mm, tail 700+ mm and largest female SVL 896 mm, tail 513 mm. Supralabials 9/9 (n = 269), 8/8 (n = 79), 8/9 (n = 20), 9/8 (n = 14), 7/7 (n = 2), 8/7 (n = 2), 9/10 (n = 1), 10/10 (n = 1), 8/10 (n = 1), or 7/6 (n = 1) with 5-6/ 5-6 (n = 269), 4-5/4-5 (n = 80), 4-5/5-6 (n = 21), 5-6/4-5 (n = 14), 6-7/6-7 (n = 1), 5-6/6-7 (n = 1), or 4-5-6/4-5 (n = 2) entering orbit; infralabials 11/11 (n = 204), 10/10 (n = 78), 10/11 (n = 30), 11/10 (n = 29), 9/9 (n = 7), 10/9 (n = 5), 12/12 (n = 6), 9/11 (n = 1), 12/11 (n = 9), 11/12 (n = 10), 9/12 (n = 1), 8/8/ (n = 1), 8/9 (n = 1), 9/10 (n = 10, 12/10 (n = 1), or 10/12 (n = 1), with 6/6 (n = 218), 5/5 (n = 80), 5/6 (n = 36), 6/5 (n = 30), 7/6 (n = 6), 6/7 (n = 7), 7/7 (n = 4), 6/10 (n = 1), 7/5 (n = 1), 4/5 (n = 1), 5/4 (n = 1), or 4/6 (n = 1) contacting first genials; preoculars 1/1 (n = 362), 2/2 (n = 17), 1/2 (n = 2), or 2/1 (n = 9); postoculars 2/2 (n = 374), 2/3 (n = 7), 3/2 (n = 5), 3/3 (n = 1), 4/3 (n = 1), 2/1 (n = 1) or 1/1 (n = 1); anterior temporal 1/1 (n = 360) or 2/1 (n = 1); posterior temporal 2/2 (n = 360), 2/1 (n = 17), 1/1 (n = 8), 1/2 (n = 2), 2/3 (n = 1) or 2/0 (n = 1). Keels stronger in adult males than females. In CHUNB 24750 postocular stripes extend for distance of 10 scales posterior to last supralabial on each side. Significant sex dimorphism was found in number of ventral scales (F = 22.7025; $p < 0.0001$), with males having more ventrals than females. No significant difference in subcaudal counts between males and females (F=3.2315; p = 0.0698) was observed. Maxillary teeth recurved, without diastema. (Table 1).

Table 1. Number of maxillary, palatine, pterygoid, and dentary teeth of *Leptophis ahaetulla*.

Specimes	Max.	Pal.	Pter.	Dent.
IBSP 64423 (♂)	26/26	14/15	28/28	30/30
MPEG 17375 (♂)	27/26	16/18	30/30	28/28
MPEG 17722 (♂)	26/24+	14/14+	24/24	25+/27
MPEG 19434 (♂)	25/24	15/15	28/26	28/27
MPEG 17755 (♂)	24/25	15/13	28/28	27/27
UMMZ 149833 (♂)	27/26	15/16	27/25	26+/28+
MPEG 594 (♀)	25/25	15/15	26/26	25/26
MPEG 16067 (♀)	24/25	14/13	21/22	24/24
MPEG 17497 (♀)	26/26	14/16	30/25	23/23
MPEG 21183 (♀)	24/25	14/14	22/24	25/29

Hemipenis.– (Fig. 2 A, B). Retracted organ extended for 7-8 subcaudals. Single, slightly bilobate, noncapitate; *sulcus spermaticus* undivided, extending from base to apical region of right lobe; intrasulcar surface smooth. Basal region bearing numerous spines, which tend to be distributed in five or six rows approximately encircling organ; first row with 6 to 8 spines; spines on first row slightly larger than spines on fourth and fifth rows; two on either side of sulcus largest; spines arranged irregularly rather than in transverse rows. Spinules on basal region widely scattered, occurring in area between spines and also below them. Small spines present on lateral surface of *sulcus* as continuation of spinules present on basal region. Calyces originate above fifth or sixth row of basal spines; calyces along distal portion of organ uniformly moderate in size, larger than those of midsection. Papillae decrease gradually in size and number toward distal portion of hemipenis. Central and anterior surface of lobes either completely calyculate (MPEG 18630), or nude (MNRJ 1758); anterior surface of MPEG 17755 completely nude. Peripheral surface of lobes with few papillate calyces irregularly distributed. Papillae number on calyces 7-10 in midsection and 5-7 in peripheral surface and central portion of lobes. Asulcate side similar to sulcate side.

Coloration.– Head and body grass green. Two dorsolateral green stripes separated from each other by pale stripe. Dorsal stripes sometimes becoming indistinct on posterior third of body. Preocular black stripe always absent or reduced to black margin on second and third supralabials. Postocular black stripe always narrow, covering lower anterior and posterior temporal scales. Supralabiais, throat and venter white.

Distribution.– Lowlands of northern Brazil, including northern Mato Grosso and Piauí, Guiana, Surinam, and southern Venezuela (Fig. 3).

Ecology.– Specimens examined were collected in localities within the limits of the Amazonian, Cerrado, and Transition domains (Ab'Saber, 1977). According to Albuquerque et al. (2007), *Leptophis ahaetulla* is one of the most wide-ranging habitat species of colubrine snakes, occurring in forested areas, along forest edges, open areas, lake borders, savannas and pasture areas, being also abundant in disturbed forest areas. It is primarily diurnal and semi-arboreal, forages primarily on the ground and in fallen vegetation, as an active forager. *Leptophis ahaetulla* has a dietary preference for hylids (Albuquerque et al., 2007; Oliver, 1948), especially those of the genus *Scinax* (Albuquerque et al., 2007). These snakes were collected up to 240 m elevation (Hoogmoed, 1979).

Remarks.– Oliver (1948) examined three juveniles of *Leptophis ahaetulla* (Oliver's *L. a. ahaetulla*), in which two possessed a striped pattern like that of the adults, whereas a third had a pattern of oblique bands superimposed on the striped pattern. One of the juvenile specimens examined in the present study was MZUSP 12127, an immature female of 573 mm in total length, which has bands in the anterior and middle region of the body. On the other hand, MPEG 1637, an immature female of 570 mm in total length, possesses a striped pattern like that of the adults. The most remarkable variation observed was that of preocular black stripe coloration. Most specimens posses a preocular stripe reduced to black margin on second, third, and fourth supralabials, whereas Tocantins specimens have a broad stripe covering half of preocular scale, lower nasal, and upper edge of rostral scale (see Fig. 29B). As mentioned before *L. ahaetulla* has a very confuse nomenclatural history which was derived from the fact that five specimens in two similar looking genera, *Leptophis* and *Ahaetulla*, were described under name *Coluber ahaetulla*. Oliver (1942) described *Leptophis copei* from three specimens collected at Venezuela-Brazil boundary on Salto do Huá, one specimen from San Antonio, upper Orinico river, Venezuela, and two specimens from Colombia-Brazil boundary on Vaupés, Alto río Caruru. According to Oliver (1948), *L. copei* differs from *L. ahaetulla* in having a higher average number of maxillary teeth and ventral scales, as well as a different color patter. However, the differences observed among these characters of *L. copei* and *L. ahaetulla* fall within the variation of the latter (e.g. see description of *L. ahaetulla* and Fig. 1; see also Oliver, 1948). Due to absence of exclusive characters between *L. a. ahaetulla* and *L. a. copei* the latter was placed as a junior synonymy of *L. ahaetulla* and the distribution of *L. ahaetulla* is expanded to southern Venezuela.

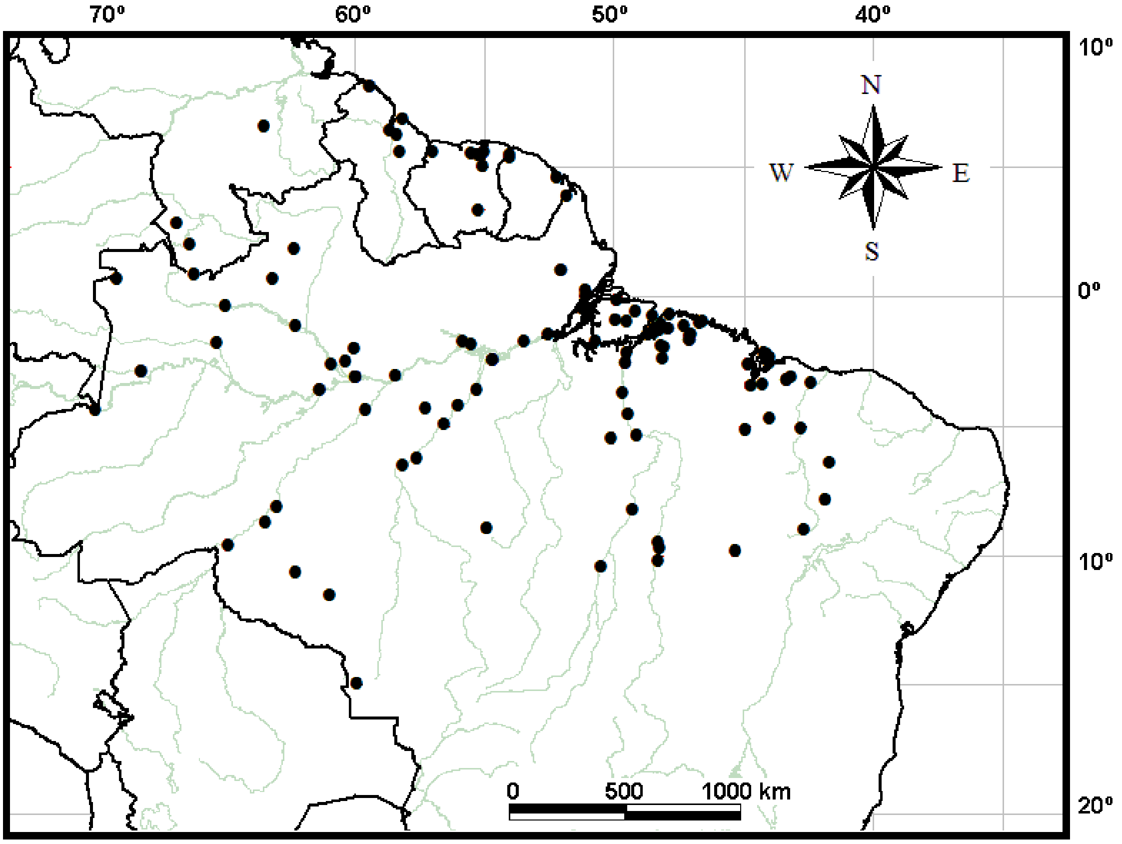


FIG. 3 – Northern Brazil and southeastern Venezuela showing the distribution of *Leptophis ahaetulla*.

Leptophis bocourti (Boulenger)

Leptophis bocourti Boulenger, 1898, Proc. Zool. Soc. London, p. 116; Type locality: Paramba and Cachabe, Ecuador.

Leptophis occidentalis insularis Barbour, 1905, Bull. Mus. Comp. Zool., vol. 46, no. 5, p. 101; Type locality: Gorgona Island, Colombia.

Leptophis occidentalis bocourti; Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 15.

Thalerophis richardi bocourti; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 223.

Leptophis ahaetulla [*bocourti*]; Int. Comm. Zool. Nomen. Op. 524, p. 270.

Leptophis ahaetulla bocourti; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 162.

Diagnosis.– *Leptophis bocourti* can be distinguished from other *Leptophis* by the color pattern. The head and dorsal scales posses numerous small, irregularly black spots, also present on extreme outer edge of ventrals (Fig. 4) (vs. dorsal scales lacking black spots). Further, it differs from parapatric taxa *L. nigromarginatus* and *L. occidentalis* in having black marks on keels of all but first row of dorsal scales (vs. keels not marked in *L. nigromarginatus* and keels not marked or only slightly marked with black in *L. occidentalis*).

FIG. 4 – *Leptophis bocourti*, Pichincha, Ecuador (USNM 285488). Courtesy of Roy W. McDiarmid.

Description.– Ventrals 157-165 in males (= 161.2 ± 3.0, n = 5), 159-164 in females (= 161.7 ± 2.5, n = 3). Subcaudals 164 in single male with complete tail, 159 and 162 in two females with complete tail. Largest male SVL 975 mm, tail 621+ mm and largest female SVL 733 mm, tail 479+ mm. Supralabials 8/8 (n = 7), or 9/9 (n = 2), with 5-6/ 5-6 (n = 7), or 4-5/4-5 (n = 2) entering orbit; infralabials 11/11 (n = 5), 10/10 (n = 3), or 10/11 (n = 1), with 6/6 (n = 5), 5/5(n = 3), or 5/6 (n = 1) contacting first genials; preoculars 1/1 (n = 9); postoculars 2/2 (n = 9); anterior temporal 1/1 (n = 9); posterior temporal 2/2 (n = 9). Keels more developed in adult males than females and juveniles. Keels present on scales of rows II-XIV in males, and VI-X in females. Only juvenile specimen examined was MZUSP 8250, an immature male of 375 mm in total length, with bands in anterior and middle regions of body. Because the sample of *L. bocourti* has few specimens, a statistical analysis comparing number of ventral and subcaudal scales between males and females was not performed. UMMZ 149938 (male) with 22/23 maxillary teeth, 14/14 palatine teeth, 26/26 pterygoid teeth, and 24+/26 dentary teeth.

Coloration.– Head scales green above and margined with black. Head and dorsal scales posses numerous small, irregularly black spots, also present on extreme outer edge of ventrals anteriorly. Preocular reduced to black margin on second, third, and fourth supralabials. Broad postocular stripe covering upper edge of lower postocular, two-thirds of anterior temporal, lower posterior temporal, and upper edges of last three supralabials; postocular stripe usually not extending beyond one scale onto nuchal region. Infralabials, throat, and venter pale green.

Distribution.– *Leptophis bocourti* is known only from northwestern Ecuador and Gorgona Island, Colombia (Fig. 5).

Ecology.– According to Oliver (1948), *Leptophis bocourti* occurs in dense, humid, tropical forest. No information on reproduction or diet is available for this species.

Hemipenis.– Not analyzed for this species (see Oliver, 1948).

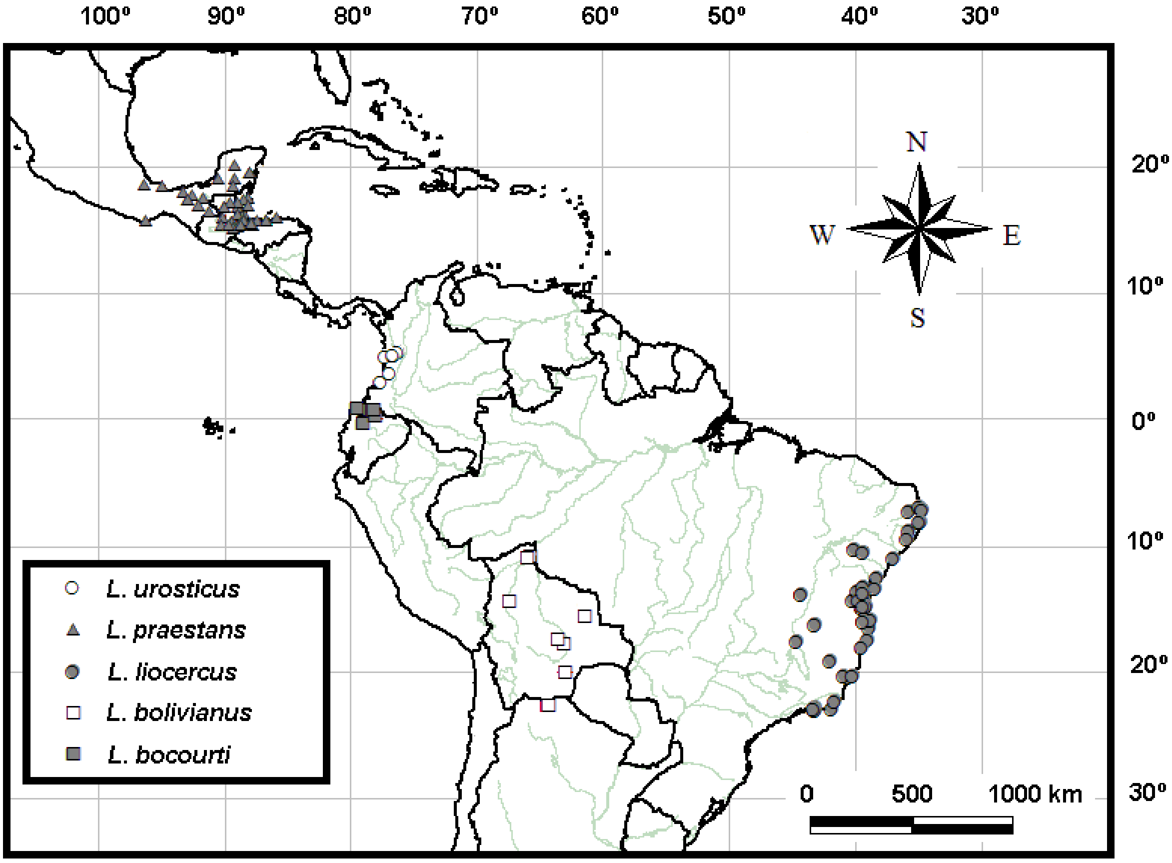


FIG. 5 – Central and South America showing the distribution of *Leptophis bocourti*, *L. bolivianus*, *L. liocercus*, *L. praestans*, and *L. urosticus*.

Leptophis bolivianus (Oliver)

Leptophis ahaetulla bolivianus Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 1. Type locality: Buenavista, Department of Santa Cruz, Bolivia.

Thalerophis richardi bolivianus; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 225.

Leptophis ahaetulla [*bolivianus*]; Int. Comm. Zool. Nomen. Op. 524, p. 270.

Leptophis ahaetulla bolivianus; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 163.

Diagnosis.– Leptophis bolivianus can be distinguished from its congeners in having dorsal scales with only a narrow black margin, and a distinct narrow black line along the keel of each dorsal scale (Fig. 6) (vs. dorsal scales not margined or heavily margined). Further, it differs from parapatric *L. nigromarginatus* and *L. marginatus* in having ventral scales uniformly greenish blue, not margined with dark greenish blue or blue (vs. ventral scales margined with dark greenish blue or blue in *L. nigromarginatus* and ventral scales clear white in *L. marginatus*).

Description.– Ventrals 152-167 in males (x = 158.7 ± 4.6, n = 16), 156-173 in females (x = 164.4 ± 4.6, n = 21). Subcaudals 135-157 in males (x = 143 ± 7.4, n = 8), 131-154 in females (x = 144 ± 7.8, n = 9). Largest male SVL 710 mm, tail 433+ mm and largest female SVL 700 mm, tail 418+ mm. Supralabials 8/8 (n = 34), 9/9 (n = 1), 7/8 (n = 1) or 9/8 (n = 1), with 4-5/ 4-5 (n = 34), 5-6/5-6 (n = 1), 5-6/4-5 (n = 1) or 4-5/4-5-6 (n = 1) entering orbit; infralabials 10/10 (n = 22), 11/10 (n = 4), 9/10 (n = 3), 11/11 (n = 2), 9/9 (n = 2), 10/9 (n = 1), 10/11 (n = 1) or 12/10 (n = 1), with 5/5 (n = 24), 6/5 (n = 7), 5/6 (n = 2), 6/6 (n = 2), 5/4 (n = 1), or 4/5 (n = 1) contacting first genials; preoculars 1/1 (n = 36) or 2/1 (n = 1); postoculars 2/2 (n = 36) or 3/2 (n = 1); anterior temporal 1/1 (n = 37); posterior temporal 2/2 (n = 25), 1/1 (n = 7) or 2/1 (n = 5). Keels more developed in adult males than females. Two juvenile specimens examined were AMNH 141443 (Fig. 7), an immature female of 367 mm in total length, and UMMZ 67977, an immature male of 521 in total length, with bands in anterior and middle region of body, similar to those found in other juveniles of most species of *Leptophis* (see Oliver, 1948). Significant sex dimorphism was found in number of ventral scales (F = 14.0674; p = 0.0009), with females having more ventrals than males. No significant difference in subcaudal counts between males and females (F=0.0735; p = 0.7856) was observed. AMNH 104564 and UMMZ 149834 (males) with respectively 23/24 and 20/20 maxillary teeth, 13/12 and 12/14 palatine teeth, 21/22 and 16+/24 pterygoid teeth, and 26/26 and 23+/24+ dentary teeth.

FIG. 6.– *Leptophis bolivianus*, Estancia Caparú, Província Velasco, Bolívia (MNKR 4332). Courtesy of L. Gonzalez.

FIG. 7 – Juvenile of *Leptophis bolivianus*, San Antonio de Parapeti, Santa Cruz, Bolivia (AMNH 141443).

Hemipenis.– (Fig. 8 A, B).

FIG. 8 – Hemipenis of *Leptophis bolivianus*, Estancia Yutiole, Beni, Bolivia (AMNH 104564) showing sulcate (A) and asulcate (B) sides.

Distribution.– Known only from the departments of Beni and Santa Cruz in Bolivia (Fig. 5).

Ecology.– Oliver (1948) recorded two hylid frogs as prey items. No information on reproduction is available for this species. UMMZ 60701 and UMMZ 60702 were collected at 500 m elevation.

Leptophis caatingensis Albuquerque and Di-Bernardo (ms)

Thalerophis richardi richardi; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 219 (partim)

Leptophis ahaetulla ahaetulla; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 161.

Leptophis ahaetulla; Lima-Verde, 1971. Bol. Zool. Biol. Marinha, 28: 189-238

Leptophis ahaetulla; Vanzolini, Ramos-Costa and Vitt, 1980. Répteis das Caatingas, 161 p.

Leptophis ahaetulla; Vitt and Vangilder, 1983. Amphibia-Reptilia 4: 273-296.

Diagnosis.– Leptophis caatingensis can be distinguished from its congeners in color pattern. The dorsal color pattern has two dorsolateral green or greenish-blue stripes separated from each other by a pale vertebral stripe. Also, the dorsal scale rows I to III ate immaculate white (vs. without dorsal stripes; if present, rows II to III are yellow, yellowish or green in other *Leptophis*). Further, *L. caatingensis* differs from the parapatric taxa *L. ahaetulla* and *L. liocercus* in hemipenial morphology, having xx spines at the level of the fourth row (vs. xx in and *L. ahaetulla* and xx in *L. liocercus*), papillae on midsection region stout, poorly developed though more numerous (vs. spinous papillae in *L. ahaetulla* and long fringing papillae in *L. liocercus*); papillae on distal portion of organ short and stout (vs. short, not stout in *L. ahaetulla* and long fringing papillae in *L. liocercus*).

For description, hemipenial morphology, distribution, and ecology see Albuquerque and Di-Bernardo (ms).

Leptophis coeruleodorsus Oliver

Leptophis coeruleodorsus Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 4. Type locality: Trinidad, British West Indies.

Leptophis ahaetulla ortoni; Beeber, 1946, Zoologica, vol. 31, pt. 1, p. 34.

Leptophis ahaetulla [*coeruleodorsus*]; Int. Comm. Zool. Nomen. Op. 524, p. 270.

Leptophis ahaetulla coeruleodorsus; Pwters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States National Museum Bulletin, 297: p. 162.

Diagnosis.– *Leptophis coeruleodorsus* can be distinguished by the presence of two dorsolateral yellow stripes separated from each other by a bright green stripe about five scale rows wide, at least anteriorly (Fig. 9) (vs. stripes absent; if present they are green and separated from each other by a vertebral row). Further, *Leptophis coeruleodorsus* differs from parapatric *L. ahaetulla* in having dorsal coloration reduced posteriorly, becoming bronze (vs. dorsal coloration of anterior body persisting throughout length of body in *L. ahaetulla*).

Description.– Ventrals 144-168 in males (x = 159.8 ± 4.1, n = 33), 157-178 in females (x = 164.1 ± 4.5, n = 38). Subcaudals 141-166 in males (x = 157± 9.1, n = 16), 125-174 in females (x = 1575 ± 10.1, n = 20). Largest male (AMNH 110472) SVL 907 mm, tail 615+ mm and largest female (USNM 15235) SVL 935 mm, tail 588 mm. Supralabials 8/8 (n = 41), 9/9 (n = 22), 8/9 (n = 4), 9/8 (n = 2) or 7/7 (n = 1), with 4-5/ 4-5 (n = 41), 5-6/5-6 (n = 21), 4-5/5-6 (n = 5), 5-6/4-5 (n = 2) or 3-4/3-4 (n = 1) entering orbit; infralabials 10/10 (n = 38), 11/11 (n = 9), 11/10 (n = 9), 10/11 (n = 6), 9/9 (n = 4), or 10/9 (n = 3), with 5/5 (n = 45), 6/6 (n = 12), 6/5 (n = 7), or 5/6 (n = 6) contacting first genials; preoculars 1/1 (n = 61), 2/2 (n = 5), 2/1 (n = 3) or 1/2 (n = 1); postoculars 2/2 (n = 69) or 1/1 (n = 1); anterior temporal 1/1 (n = 70); posterior temporal 2/2 (n = 66), 2/1 (n = 2) or 1/2 (n = 1). Keels more developed in adult males than females and juveniles. Width of green vertebral and paravertebral rows varies from four to five scales wide. Only three juvenile specimens were examined: AMNH 101309, an immature male of 392 mm in total length, and AMNH 64478, an immature male of 361 mm in total length, and MCZ 126381, an immature female of 382 mm in total length, which have bands in anterior and middle region of body. Significant sex dimorphism was found in number of ventral scales (F = 16.9537; p = 0.0003), with females having more ventrals than males. No significant difference in subcaudal counts between males and females (F=0.0192; p = 0.8855) was observed. AMNH 73146 (unsexed) and AMNH 119443 (male) with respectively 24/22 and 23/22 maxillary teeth, 13/13, 14/13 palatine teeth, 24/26 and 22/21 pterygoid teeth, and 22+/20+ and 25/24+ dentary teeth.

FIG. 9 – *Leptophis coeruleodorsus*. MVURG specimen from Capanaparo, Apure, Venezuela. Courtesy of Marco Natera.

Hemipenis.– (Fig. 10 A, B). Retracted organ extends for 7 or 8 subcaudals. Single, slightly bilobate, noncapitate; *sulcus spermaticus* undivided, extending from base to apical region of right lobe; intrasulcar surface smooth. Basal region bears small spines, distributed in six rows approximately encircling organ; first row with 5-7 spines; spines on first row slightly larger than remaining spines; spines are arranged irregularly rather than in transverse rows. Small spines present on lateral surface of *sulcus* except on basal region. Calyces originate on distal region and bear papillae that are robust. Papillae decrease gradually in number and size toward distal portion of hemipenis. Central surface of lobes with papillate calyces (USNM 195127), or nude (MCZ 100651, TCWC 46262). Peripheral surface of lobes with few papillate calyces irregularly distributed. Papillae number on calyces 6 to 8 in distal region. Asulcate side similar to sulcate side.

Coloration.– Head and dorsum grass green; two yellow dorsolateral stripes separate the dorsal color from venter. Preocular black stripe always reduced to black margin on second, third and fourth supralabials. There is a broad postocular black stripe that usually extends over two-eight scales onto nuchal region. Supralabials, throat and venter white. Juveniles with dark bands on dorsum.

FIG. 10 – Hemipenis of *Leptophis coeruleodorsus*, San Fernando de Apure, Apure, Venezuela (TCWC 46262) showing sulcate (A) and asulcate (B) sides.

Distribution.– Coastal and llanos region of Venezuela; islands of Trinidad and Tobago (Fig. 11).

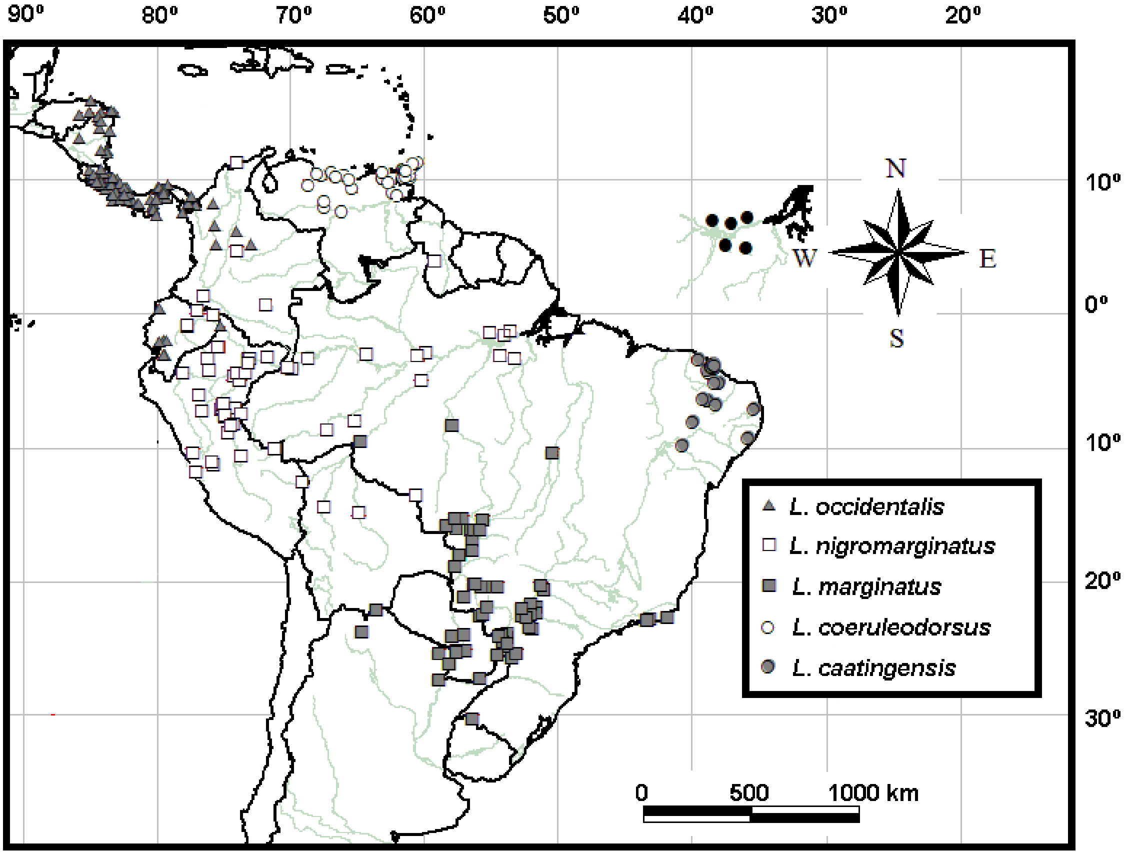


FIG. 11 – Central and South America showing the distribution of *Leptophis caatingensis*, *L. coeruleodorsus*, *L. marginatus*, *L.nigromarginatus*, and *L. occidentalis*.

Ecology.– Leptophis coeruleodorsus is diurnal and semi-arboreal (Boos, 2001). Oliver (1948) recorded one specimen of *Mastigodryas boddaerti* and nestling birds in its diet; one specimen in captivity ate a small *Leptodeira annulata* (Boos, 2001). MHNLS 13595 contained five well-developed eggs (the first, along head-tail direction, measured 21.44 mm). As any *Leptophis*, this species is aggressive, striking and opening its mouth when handled (Murphy, 1997). This species was collected at 1000 m elevation (Roze, 1966).

Remarks.– Leptophis coeruleodorsus is very similar to *Leptophis ahaetulla*. Until Oliver's (1948) revision, it was considered as a synonym of *L. ahaetulla*. However, the presence of a pale vertebral stripe rapidly distinguishes these taxa. One of paratypes of *L. coeruleodorsus* (USNM 27821) was reidentified as *L. occidentalis*.

Leptophis liocercus (Wied)

Coluber liocercus Wied, 1824, Abbildungen zur Naturgeschichte von Brasilien, p. 665; Type locality: Brazil.

Dendrophis liocercus; Schlegel, 1837, (part), Essai sur la physionomie des serpens, vol. 2, p. 224.

(?) Leptophis flagelllum Andersson, 1901, Bihang till Handl. K. Svenska Vetensk. Akad., vol. 27, abd. 4, no. 5, p. 13; Type locality: Rio de Janeiro, Brazil.

Leptophis liocercus; De Witte, 1930, Une mission biologique Belge au Bresil, vol. 2, p. 3.

Thalerophis richardi liocercus; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 232.

Leptophis ahaetulla [*liocercus*]; Int. Comm. Zool. Nomen. 1958 Op. 524, p. 270.

Leptophis ahaetulla liocercus; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 162.

Diagnosis.– Leptophis liocercus can be distinguished from its congeners by the presence of two dorsolateral metallic green stripes, separated from each other by a pale vertebral stripe, at least anteriorly (Fig. 12) (vs. stripes absent; if present stripes are grass green or yellow). Further, in *L. liocercus* the dorsal scales of head are metallic green, without spots on parietal scales (vs. head green in *L. caatingensis* and head greenish blue, margined, and with one black spot on each parietal scales in *L. marginatus*).

Description.– Ventrals 150-169 in males (x = 158.4 ± 4.5, n = 35), 151-173 in females (x = 160.6 ± 4.8, n = 37). Subcaudals 130-188 in males (x = 157.6 ± 8.1, n = 20), 144-173 in females (x = 158 ± 7.2, n = 27). Largest male SVL 1541 mm, tail 539+ mm and largest female SVL 925 mm, tail 637+ mm. Supralabials 8/8 (n = 31), 9/9 (n = 23), 9/8 (n = 8), 8/9 (n = 4), 9/10 (n = 1), 10/9 (n = 1), 10/8 (n = 1), or 6/6 (n = 1), with 4-5/4-5 (n = 33), 5-6/ 5-6 (n = 24), 5-6/4-5 (n = 8), 4-5/5-6 (n = 4), 5-6/6-7 (n = 1), or 6-7/4-5 (n = 1) entering orbit; infralabials 10/10 (n = 33), 11/11 (n = 16), 10/11 (n = 6), 11/10 (n = 5), 9/10 (n = 3), 9/9 (n = 2), 11/9 (n = 1), 10/9 (n = 1), or 8/7 (n = 1), with 5/5(n = 39), 6/6 (n = 15), 5/6 (n = 7), 6/5 (n = 4), 4/5 (n = 1), or 4/4 (n = 1) contacting first genials; preoculars 1/1 (n = 69), 2/2 (n = 2), or 2/1 (n = 1); postoculars 2/2 (n = 68), 3/3 (n = 3), or 1/2 (n = 1); anterior temporal 1/1 (n = 73); posterior temporal 2/2 (n = 67), 2/1 (n = 3), or 1/1 (n = 2). Keels stronger in adult males than females and juveniles; keels present on scales of rows II to XIV (males) before reduction in number of dorsal scales from 15 to 11 rows and VI to VII (females); on midbody and posterior region of adult males, keels are stronger and darker than females or juveniles (e.g. CHUNB 6640, CZGB 3160, MHNCI 11553). In MZUFV 913 and CHUNB 6640 postocular stripes extend for a distance of 10 and 12 scales posterior to last supralabial respectively. Only juvenile specimen examined was CHUNB 29019, an immature female of 608 mm in total length, with bands in anterior and middle region of body. Significant sex dimorphism was found in number of ventral scales (F = 4.1287; p = 0.0433), with females having more ventrals than males. No significant difference in subcaudal counts between males and females (F=0.0511; p = 0.8169) was observed. CZGB 1149, IBSP 46053, and MNRJ 4846 (males), IBSP 9612 and MZUESC 4846 (females) with respectively 21/21, 21/23, 23/23, 23/24, and 24/24 maxillary teeth, 11/12, 13/13, 13/14, 13/13, and 13/13 palatine teeth, 24/24, 23/23, 22/22, 22/22, and 21/21 pterygoid teeth, and 20/11+, 17+/19+, 26/26, 23+/19+, and 25/20+ dentary teeth.

FIG. 12 – *Leptophis liocercus*, Mata do Buraquinho, João Pessoa, Paraíba (UFPB 4443). Courtesy of Gentil Filho.

Hemipenis.– **(**Fig. 13 A, B).

FIG. 13 – Hemipenis of *Leptophis liocercus*, Ilhéus, Bahia (CZGB 1149) showing sulcate (A) and asulcate (B) sides.

Coloration.– Head green metallic above; body green metallic anteriorly, changing gradually to metallic chestnut toward tail (Argôlo, 2004). Two dorsolateral metallic green stripes separate from each other by a pale stripe. Dorsal stripes always become indistinct on posterior third of body. Preocular black stripe always absent or reduced to black margin on second and third supralabials. Postocular black stripe always narrow covering no farther than lower anterior and posterior temporal scales. Supralabiais and throat white; venter white anteriorly becoming chestnut posteriorly.

Distribution.– Coastal zone of the Brazilian states of Paraíba, Alagoas, Pernambuco, Rio de Janeiro, and São Paulo; Minas Gerais and Bahia (Fig. 5).

Ecology.– Specimens examined were collected in localities within the limits of Atlantic and Cerrado domains (Ab'Saber, 1977). One specimen, MCZ 2989, collected in rio Mercury, Santa Clara, Bahia contained two *Dendropsophus* gr. *marmoratus* (identified by J. Faivovich), ingested headfirst. IBSP 46053, collected in Aracajú, Sergipe, contained one *Hypsiboas raniceps*. Argôlo (2004) collected specimens in disturbed forest areas on ground and in fallen vegetation. No information on reproduction is available for this species.

Remarks.– One adult male, CHUNB 6640, has a distinct broad postocular stripe covering the lower and upper postocular, anterior margin of parietal, preocular, postocular, nearly all anterior and posterior temporals, and upper edges of last three supralabials. As in *Leptophis caatingensis* (Albuquerque and Di-Bernardo, ms), the most remarkable variation in hemipenes of *L. liocercus* was observed in the apical ornamentation at the tips of the lobes. The central and anterior surface of lobe of CZGB 11149 is nude, whereas only the central surface of UFPB 4300 is nude. Oliver (1948) described briefly the hemipenis of *L. a.*

liocercus based on retracted organs. As noted by Albuquerque and Di-Bernardo (ms), Oliver (1948) used specimens of *L. marginatus* to describe *L. liocercus*. Likewise, IBSP 9019 (Estação Cascadura, Rio de Janeiro), which was also used by Oliver (1948) in his *L. a. liocercus* description, possesses four conspicuously enlarged basal spines, and is reidentified as *L. marginatus* in the present study. IBSP 9019 is badly damaged and faded, so that the original color pattern is absent. Presumably the IBSP 9019 was collected in a nearby city and sent to IBSP by train, as were many other specimens received by IBSP in the 1930's (see also Albuquerque and Di-Bernardo, ms).

Leptophis marginatus (Cope)

Thrasops marginatus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, vol. 14, p. 349. Type locality: Paraguay.

Herpetodryas affinis Steindachner, 1870, Sitzber. Akad. Wiss. Wien, vol. 62, p. 348; Type locality: Brazil.

Leptophis rostralis Lönnberg, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 10, p. 458; Type locality: San Miguel (Chaco), Argentina.

Leptophis argentinus Wernre, 1903, Abhandl. K. Bayerischen Akad. Wiss., vol. 22, div. 2, p. 384. Type locality: Rosario, Argentina.

Leptophis liocercus; Serie, 1915, Bol. Soc. Physis, vol. 1, p. 573.

Leptophis nigromarginatus; Amaral, 1925, Com. Lin. Tele. Est. do Matto Grosso ao Amazonas, Publ. No. 84, vol. 5, p. 1-29.

Leptophis ahaetulla; Freiberg, 1939, Mem. Mus. Entre Rios, no. 11, pp. 1-28.

Leptophis marginatus; Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 10.

Thalerophis richardi marginatus; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 235.

Leptophis ahaetulla [*marginatus*]; Int. Comm. Zool. Nomen. 1958 Op. 524, p. 163.

Leptophis ahaetulla marginatus; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States National Museum Bulletin, 297: p. 163.

Diagnosis.– *Leptophis marginatus* can be distinguished from its congeners in having dorsal coloration of head and anterior body distinctly different from that of posterior half of body (Fig. 14) (vs. dorsal coloration of anterior body persisting throughout length of body). Further, *L. marginatus* differs from parapatric taxa *L. ahaetulla*, *Leptophis bolivianus* and *L. liocercus* in hemipenial morphology and coloration; *L. marginatus* has 4-5 enlarged basal spines at the level of the first row (vs. 6-8 small spines in *L. ahaetulla, L. bolivianus*, and *L. marginatus*), dorsal head scales margined with black (vs. dorsal scales not margined in *L. ahaetulla*), and a distinct small black dot in center of each parietal scale (vs. black dots absent in *L. ahaetulla* and *L. liocercus*, and diffuse dots on each parietal plus a distinct, elongate black spot on each supraocular scale in *Leptophis bolivianus*).

FIG. 14 – *Leptophis marginatus*, Presidete Epitácio, São Paulo (IBSP 63731). Courtesy of Otávio A. V. Marques.

Description.– Ventrals 152-171 in males (*x* = 161.1 ± 3.6, n = 75), 155-174 in females (*x* = 165.9 ± 4.5, n = 77). Subcaudals 120-153 in males (*x* = 140.7 ± 7.5, n = 43), 121-162 in females (*x* = 141.3 ± 8.0, n = 44). Largest male SVL 1054 mm, tail 531 mm and largest female SVL 948 mm, tail 507+ mm. Supralabials 8/8 (n = 118), 9/9 (n = 8), 9/8 (n = 5), 7/8 (n = 5), 7/7 (n = 5), 8/9 (n = 4), 8/7 (n = 3), 7/6 (n = 1), or 10/10 (n = 1), with 4-5/4-5 (n = 127), 5-6/ 5-6 (n = 11), 4-5/5-6 (n = 6), or 5-6/4-5 (n = 4) entering orbit; infralabials 10/10 (n = 107), 11/11 (n = 4), 10/11 (n = 8), 11/10 (n = 6), 9/9 (n = 5), 10/9 (n = 4), 10/10 (n = 1), 11/12 (n = 1), 12/12 (n = 1), 9/11 (n = 1), 9/8 (n = 1), or 7/7 (n = 1), with 5/5 (n = 120), 6/6(n = 11), 6/5 (n = 7), 5/6 (n = 6), 5/4 (n = 3), or 4/4 (n = 2) contacting first genials; preoculars 1/1 (n = 137), 2/2 (n = 10), 1/2 (n = 4), or 2/1 (n = 1); postoculars 2/2 (n = 151) or 1/1 (n = 1); anterior temporal 1/1 (n = 152); posterior temporal 2/2 (n = 66), 1/1 (n = 62), 2/1 (n = 17), 1/2 (n = 5), 2/3 (n = 1) or 3/3 (n = 1). Keels more developed in adult males than females and juveniles. Keels are stronger and darker on rows III-XIII before reduction in number of dorsal scales from 15 to 11 rows and III-IX after reduction. In ZUEC 2758 postocular stripes extend for a distance of four scales posterior to last supralabial. Three juvenile specimens examined were MHNCI 8017, an immature female of 393 mm in total length, CHUNB 29019, an immature female of 608 mm in total length, and MZUSP 8943, an immature male of 389 mm in total length, with bands in the anterior and middle region of body, similar to those found in other juveniles of *L. marginatus* (e.g. Lonnberg's, 1902 *L. rostralis* = *L. marginatus*). Significant sex dimorphism was found in number of ventral scales (F = 53.6174; p <0.0001), with females having more ventrals than males. No significant difference in subcaudal counts between males and females (F=0.1193; p = 0.7306) was observed. Maxillary teeth recurved, without diastema (Table 2).

Table 2. Number of maxillary, palatine, pterygoid, and dentary teeth of *Leptophis marginatus*.

Specimes	Max.	Pal.	Pter.	Dent.
CHUNB 20423 (♂)	22/*	13/12	22/22	22+/23+
CHUNB 15441 (♂)	21/21	12/12	22/22	21+/23
FML 01624 (♂)	23/23	13/12	22/23	21+/24
MHNCI 4512 (♂)	23/22	14/13	23/*	23/22
UMMZ 149835 (♂)	22/22	12/12	22/21	22/19
CHUNB 15452 (♀)	23/22	11/12	22/22	23/22+
IBSP 54055 (♀)	24/23	12/12	21/22	16+/27
MHNCI 8548 (♀)	24/24	13/12	24/24	22+/24

Hemipenis.– **(**Fig. 15 A, B). Retracted organ extends for 7 subcaudals. Single, slightly bilobate, noncapitate; *sulcus spermaticus* undivided; intrasulcar surface smooth. Basal region bears enlarged spines, which are distributed in six rows approximately; first row with 4 or 5 spines; spines on first row larger than remaining spines; spines are arranged irregularly rather than in transverse rows. Small spines are present on lateral surface of *sulcus* but always absent on basal region. Calyces originate above last row of basal spines; calyces along distal portion of organ are larger in size than those on midsection, and bear papillae that are robust. Papillae decrease gradually in size toward distal portion of hemipenis. Central and anterior portions of lobes either calyculate (UMMZ 109052), or nude (IBSP 37444). Papillae number on calyces 8-12 in midsection and 6-7 in peripheral surface and central portion of lobes. Asulcate side similar to sulcate side.

FIG. 15 – Hemipenis of *Leptophis marginatus*, Puerto Pilcomayo, Argentina (FML 1624) showing sulcate (A) and asulcate (B) sides.

Coloration.– Head green metallic above; body green metallic anteriorly, changing gradually to bronze or light brown toward tail. Head scales margined with black. A small black spot in center of each parietal scale and on outer side of each supraocular. Preocular black stripe always reduced to black margin on second, third, and fourth supralabials. There is a broad postocular black stripe that usually covers half of anterior and posterior temporal, and upper edges of last three supralabials. Lower lateral and supralabiais white; venter clear white. Dorsal coloration of head and anterior body different from that of posterior half body and tail.

Distribution.– From southeastern Bolivia across Mato Grosso and Mato Grosso do Sul to western São Paulo in Brazil, southward through Uruguay and Paraguay into northern Argentina (Fig. 11).

Ecology.– The diet of *Leptophis marginatus* consists primarily of hylid frogs, mainly those of genus *Scinax*, and secondarily of bird eggs and young birds (Carreira, 2002; Lopez et al. 2003). Albuquerque and Di-Bernardo (2005) discovered a veined treefrog *Trachycephalus venulosus* in the stomach of an adult female (IBSP 44678) collected in Foz do Iguaçu, Paraná; ingested headfirst. This snake contained nine well-developed eggs. IBSP 26764 contained 10 well-developed eggs (the tenth, snout-vent direction, measured 33.11 mm). This species is known to bite (Carreira et al., 2005).

Leptophis nigromarginatus (Günther)

Ahaetulla nigromarginata Günther, 1866: 28, Ann. Mag. Nat. Hist., ser. 3, vol. 18, p. 28. Type Locality: "Upper Amazon".

Leptophis ortoni Cope, 1876, Jour. Acad. Nat. Sci. Philadelphia, vol. 8, p. 177; Type locality: "Solmoens" (= Solimões) or middle Amazon. NEW SYNONYMY

Leptophis nigromarginatus; Griffin, 1915, (in part), Mem. Carnegie Mus., vol. 7, no. 3, p. 184.

Leptophis occidentalis nigromarginatus; Amaral, 1929, Mem. Inst. Butantan, vol. 4, p. 162.

Leptophis ahaetulla nigromarginatus; Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, n. 462, p. 4.

Leptophis ahaetulla ortoni; Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, n. 462, p. 4.

Leptophis ahaetulla [*nigromarginatus*]; Int. Comm. Zool. Nomen. Op. 524, p. 270.

Leptophis ahaetulla nigromarginatus; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 163.

Leptophis ahaetulla ortoni; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 163.

Diagnosis.– Leptophis nigromarginatus can be distinguished from other *Leptophis* in head color pattern. The head scales are heavily margined with black (less prominent in specimens of the eastern part of the range) and a large black spot in center of each parietal and supraocular scale (sometimes absent in specimens of the eastern part of the range) (Fig. 16) (vs. head scales not margined or slightly margined and spots absent on supraocular scales). Further it differs from parapatric *L ahaetulla*, *L. bolivianus*, *L. cupreus* and *L. occidentalis* in having ventral plates margined anteriorly and laterally with dark greenish blue (vs. ventral scales not margined).

FIG. 16 – Head of holotype of *Leptophis nigromarginatus*, "Upper Amazon" (BMNH 1946.1.5.7). Note a large black spot in center of each parietal and supraocular scale.

Description.– Ventrals 144-172 in males (= 152 ± 4.9, n = 148), 146-182 in females (= 156.3 ± 4.3, n = 187). Subcaudals 129-179 in males (= 150.3 ± 8.3, n = 90), 133-166 in females (= 148 ± 7.3, n = 112). Largest male SVL 835 mm, tail 526+ mm and largest female SVL 822 mm, tail 456 mm. Supralabials 8/8 (n = 111), 9/9 (n = 153), 8/9 (n = 41), 9/8 (n = 17), 8/8 (n = 3), 8/7 (n = 3), 7/8 (n = 2), 10/9 (n = 2), 9/10 (n = 1), 7/7 (n = 1), 10/8 (n = 1), or 6/7 (n = 1), with 5-6/ 5-6 (n = 156), 4-5/4-5 (n = 119), 4-5/5-6 (n = 42), 5-6/4-5 (n = 16), 6-7/5-6 (n = 1), 3-4/4-5 (n = 1), 5-6-7/5-6 (n = 1), or 5-6-7/4-5 (n = 1) entering orbit; infralabials 11/11 (n = 130), 10/10 (n = 92), 10/11 (n = 38), 11/10 (n = 27), 10/9 (n=13), 9/9 (n=10), 11/12 (n=7), 9/10 (n = 5), 12/11 (n = 3), 9/11 (n = 3), 8/8 (n = 2), 11/9 (n = 1), 10/8 (n = 1), 9/8 (n = 1), 8/10 (n = 1), 8/9 (n = 1), or 8/7 (n = 1), with 6/6 (n = 169), 5/5(n = 97), 5/6 (n = 35), 6/5 (n = 24), 6/7 (n = 4), 5/4 (n = 3), 8/8 (n = 1), 7/6 (n = 1), 7/5 (n = 1), or 4/5 (n = 1) contacting first genials; preoculars 1/1 (n = 326), 2/2 (n = 7), 2/1 (n = 2) or 1/2 (n = 2); postoculars 2/2 (n = 326), 1/1 (n = 6), 2/3 (n = 2), 3/3 (n = 1), 3/2 (n = 1), or 2/1 (n = 1); anterior temporal 1/1 (n = 331) or 2/2 (n = 6); posterior temporal 2/2 (n = 248), 2/1 (n = 38), 1/1 (n = 37), 1/2 (n = 13) or 1/3 (n = 1). Keels more developed in adult males than females and juveniles. Keels present on scales of rows II to XIV in males, and VI to X in females. Two juvenile specimens examined were AMNH 52472, an immature male of 462 mm in total length, and AMNH 56035, an immature female of 280 mm in total length, with bands in anterior and middle regions of body. Significant sexual dimorphism was found in number of ventral scales (F = 73.5953; p < 0.0001), with females having more ventrals than males. Subcaudal counts are also sexually dimorphic (F= 4.397; p=0.035). CM 55623 and MCZ 2792 (males), AMNH 57289, IBSP 18530, and MPEG 20383 (females) with respectively 25/25, 25/25, 26/23, 24/26, 26/26 maxillary teeth, 14/15, 15/15, 16/16, 13/*, and */15 palatine teeth, 24/20+, 23/23, 21+/24, 22/*, and 26/26 pterygoid teeth, and 26+/28+, 24+/31, 25+/27+, 17+/26, and 29/28 dentary teeth.

Hemipenis.– (Fig. 17 A, B).

FIG. 17 – Hemipenis of *Leptophis nigromarginatus*, Santarém, Pará (LPHA 1731) showing sulcate (A) and asulcate (B) sides.

Coloration.– Head green above. Head scales are heavily margined with black (less prominent in specimens of the eastern part of the range). A distinct black spot in center of each parietal scale and on each supraocular scale. Preocular black stripe absent. Postocular black stripe always reduced to black margin on lower preocular, anterior and posterior temporal scales, and upper edges of last three supralabials. Dorsal coloration on body occupies proportionately the same width throughout entire body length. Infralabials and throat pale green. Ventral plates pale green, margined anteriorly and laterally with dark greenwish blue.

Distribution.– Leptophis nigromarginatus is known from western and middle Amazon region of Brazil, Amazonian lowlands of Colombia, Ecuador, and Peru, Guyana, Amazon valley of southeastern Colombia, and extreme northern Bolivia (Fig. 11).

Ecology.– Leptophis nigromarginatus is diurnal and arboreal, occurring in low, dense vegetation in primary and secondary forest (Duellman, 1978; 2005). Oliver (1948) recorded bird eggs, one gecko, 58 hylid frogs, and one young bird in its diet. Also, he reported one to five eggs in a large series of females from eastern Peru. This species has a threat display with the mouth open (Duellman, 2005) and it appears to reproduce throughout the year in Iquitos, Peru (Oliver, 1947). Seven specimens (KU 148344 to KU 148349 and KU 148351) were collected at 340 m elevation.

Remarks.– Leptophis nigromarginatus was described by Günther (1866) based on one adult female collected in "Upper Amazon". Subsequently Cope (1876) described a new species, named *L. ortoni*. *Leptophis nigromarginatus* was recognized as a subspecies of *L. occidentalis* by Amaral (1930a,b,c) until Oliver's revision (1942, 1948), who recognized these taxa as distinct subspecies of *L. ahaetulla*. One of the main characteristics proposed by Oliver (1948) to identify *L. a. ortoni* "ventral plates margined anteriorly and laterally with dark greenwish blue" (Fig. 9) was noted in most of *L. nigromarginatus* examined, including the holotype of *L. nigromarginatus*. MZUSP 7370, collected in Porto Walter, Acre, possesses ventral scales slightly margined anteriorly with dark-blue. On the other hand, one specimen from Santarém, Pará state (LPHA 1141) possesses ventral scales dirty white, not margined. Apparently there is a gradual decrease in dark pigment on ventral scales from Peru to western Pará (i.e. from West to East) but the differences observed among the ventral coloration of *L. nigromarginatus* and *L. ortoni* are here regarded as falling within the variation of a widely distributed species (Fig. 18). The above data leave no reason for retaining *L. a. ortoni* as a separate taxon, and it is therefore placed in the synonymy of *L. nigromarginatus*.

A male collected in Korananbo, Guyana (AMNH 60792) has the dorsal pattern and the dorsal color of head similar to that of *L. nigromarginatus*. The occurrence of *L. nigromarginatus* in Guyana is completely outside the previously known range of this species, extending the geographic distribution of this species about 771.54 km northward from Manaus, Brazil.

Leptophis occidentalis (Günther)

Ahaetulla occidentalis Günther, 1859, Proc. Zool. Soc. London, p. 412; Type locality: Guayaquil, western Ecuador.

Thrasops occidentalis; Cope, 1860, Proc. Acad. Nat. Sci.Philadelphia, vol. 12, p. 552.

Ahaetulla urosticta Peters, 1873, Monatsber. K. Akad. Wiss. Berlin, p. 603. Type locality: Chocó region, Colombia (vide Mertens, 1973).

Leptophis ultramarinus Cope, 1894, Proc. Acad. Nat. Sci. Philadelphia, vol. 46, p. 204; Pozo Azul, Costa Rica.

Leptophis ahaetulla; Maria, 1933, Libro commemorative del segundo centanario de Don Jose Celestino Bruno Mutis y Bosio, Bogota, p. 48.

Leptophis occidentalis; Schmidt, 1933, Smithsonian Misc. Coll., vol. 89, no. 1, p. 16.

Leptophis occidentalis occidentalis; Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 14.

Thalerophis richardi occidentalis; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 241.

Leptophis ahaetulla [*praestans*]; Int. Comm. Zool. Nomen., 1958, Op. 524, p. 270.

Leptophis ahaetulla praestans; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States Nat. Mus. Bull., 297: p. 163.

Diagnosis.– *Leptophis occidentalis* can be distinguished from other *Leptophis* in having a uniform green dorsum or dorsum marked with thin dark stripes along dorsal scale keels (Fig. 18) (vs. dorsum bluish green, copper, or not uniform, with dorsolateral stripes). Further, *L. occidentalis* differs from parapatric taxa *L. coeruleodorsus*, *L. cupreus*, *L. praestans*, and from sympatric *L. mexicanus*, *L. depressirostris*, *L. nebulosus*, and *L. riveti* by the following characters: dorsal coloration of head and anterior body persisting throughout length of body (vs. dorsal coloration of body reduced in distribution posteriorly in *L. coeruleodorsus*), venter pale green (vs. venter white in *L. cupreus*), loreal scale absent (vs. present in *L. depressirostris*), a short narrow black stripe (vs. a broad postocular stripe continuous with dark lateral body stripe in *L. mexicanus*), interstitial skin without yellow chevron-shaped marks (vs. yellow marks present in *L. praestans*), dorsum without lateral stripes (vs. dorsum with two dark green or bluish lateral stripes on second and third scale rows in *L. nebulosus*), and dorsal color in adults without bands (vs. green bands on adult dorsal region in *L. riveti*).

Description.– Ventrals 151-178 in males (x = 167 ± 6.0, n = 129), 150-183 in females (x = 168.6 ± 7.2, n = 95). Subcaudals 130- 188 in males (x = 163.3 ± 16.4, n = 46), 134-194 in females (x = 162.2 ± 15.3, n = 34). Largest male SVL 1450 mm, tail 835+ mm and largest female SVL 1196 mm, tail 730+ mm. Supralabials 8/8 (n = 93), 9/9 (n = 91), 8/9 (n = 20), 9/8 (n = 15), 10/9 (n = 3), 8/7 (n = 2) or 9/10 (n = 1), with 5-6/ 5-6 (n = 97), 4-5/4-5 (n = 94), 4-5/5-6 (n = 18), 5-6/4-5 (n = 14) or 5-6-7/5-6 (n = 2) entering orbit; infralabials 10/10 (n = 135), 11/11 (n = 26), 10/11 (n = 18), 11/10 (n = 13), 9/9 (n = 13), 10/9 (n = 11), 9/10 (n = 4), 12/12 (n = 1), 9/8 (n = 1), 10/8 (n = 1), 11/12 (n = 1) or 9/11 (n = 1), with 5/5(n = 158), 6/6 (n = 29), 5/6 (n = 17), 6/5 (n = 16), 5/4 (n = 2), 4/6 (n = 1), or 6/7 (n = 1) contacting first genials; preoculars 1/1 (n = 219), 2/1 (n = 3), 2/2 (n = 2) or 1/2 (n = 1); postoculars 2/2 (n = 204), 3/2 (n = 5), 3/3 (n = 4), 2/3 (n = 4), 2/1 (n = 4), 1/1 (n = 2) or 1/2 (n = 1); anterior temporal 1/1 (n = 224) or 2/2 (n = 1); posterior temporal 2/2 (n = 204), 1/1 (n = 8), 1/2 (n = 5), 2/1 (n = 7) or 2/1-1-2 (n = 1). Significant sex dimorphism was found in number of ventral scales (F = 7.0909; p = 0.0082), with females having more ventrals than males. No significant difference in subcaudal counts between males and females (F=0.0976; p = 0.7538) was observed. The number of maxillary, palatine, pterygoid, and dentary teeth are as follow (Table 3.)

Table 3. Number of maxillary, palatine, pterygoid, and dentary teeth of *Leptophis occidentalis*.

Specimens	Max.	Pal.	Pter.	Dent.
AMNH 47013 (unsexed)	24/24	13/12	22/22	21/21
AMNH 47014 (unsexed)	23/23	13/12	23/23	25/25
FMNH 5294 (♂)	23+/24	13/15	23/21+	27/18+
MVZ 79623 (♂)	22/22	12/12	25/25	24/*
UMMZ 149836 (♂)	23/24	13/13	24+/26	26+/24+
UMMZ 149837 (♂)	23/23	13/13	25/24	26/24+

FIG. 18.– *Leptophis occidentalis*, La Selva, Costa Rica. Courtesy of Luke Mahler. This specimen was not captured.

Hemipenis.– (Fig. 19 A, B). Retracted organ extends for 5 or 6 subcaudals. Single, slightly bilobate, noncapitate; *sulcus spermaticus* undivided, extending from base to apical region of right lobe; intrasulcar surface smooth. Basal region bears numerous conspicuous spines, distributed in six or seven rows approximately encircling the organ; first row with 5 or 7 enlarged spines; longest spines adjacent to *sulcus*. Spines are arranged irregularly rather than in transverse rows. Calyces originate above last row of basal spines on sulcate side. Papillae decrease gradually in size and number toward distal portion of hemipenis, while calyces increase in size. Central and anterior portions of lobes nude. Peripheral surface of lobes with few papillate calyces irregularly distributed. Papillae number on calyces 10 in midsection and 8-9 in distal region. Asulcate side similar to sulcate side although calyces are more numerous on sulcate side.

FIG. 19 – Hemipenis of *Leptophis occidentalis*, Província Limon, Costa Rica (ANSP 32397) showing sulcate (A) and asulcate (B) sides. Note the first row of enlarged spines.

Coloration.– Head and dorsum uniform green, with or without black dorsal keels. Preocular black stripe always absent or reduced to black margin on second and third supralabials. There is a narrow postocular black stripe that usually extends no farther than two scales onto nuchal region. Supralabials, throat and venter pale green.

Distribution.– Both coasts of Central America from Nicaragua on the Caribbean coast, Costa Rica on the Pacific, southward to northern Colombia, eastward along the Caribbean coast of western Venezuela, southward in the interior valleys of Colombia, to northwestern Ecuador (Fig. 11).

Ecology.– *Leptophis occidentalis* is diurnal and semi-arboreal. According to Savage (2002) it is common in undisturbed lowland moist and wet forests but also found marginally in premontane moist and wet forest and rainforest and marginally in gallery forests of lowland dry forest region. Oliver (1948) recorded specimens of *Agalychnis* sp., hylid frogs, *Thecadactylus* sp., bird eggs, and young birds in its diet. Four specimens (CAS 98550, CM 2011, FMNH 54973, UMMZ 124164, UMMZ 55895) contained respectively six (the fifth, head-tail direction, measured 20.2 mm), five (the fifth 21.5 mm), four (the fifth 23.2 mm), three (the third 22.4 mm), and six (the sixth 31.8 mm) well-developed eggs each. FMNH 54973 was collected at 800 m elevation. When threaten these snakes raise and inflate the anterior part of the body off the substrate, hold the mouth open, and hiss. If handled they bite without hesitation (Savage, 2002).

Remarks.– The most remarkable variation in the external morphology of *L. occidentalis* was observed in the distribution and prominence of keels on the dorsal scales. Dorsal keels exhibit geographic, sexual and ontogenetic variation (see also Oliver, 1948). Specimens from Atlantic side of Central America always have only scales of rows VI-VII and IX-X with prominent keels at midbody, and there is no keel on posterior caudal scales. In populations from the Pacific side of Central America scales of rows II-XIV are usually keeled including those on posterior region of tail. As noted by Oliver (1948) and Savage (2002), juveniles have a color pattern of dark oblique bands. Donoso-Barros (1966) noted that specimens of *L. occidentalis* have been introduced accidentally in Chile by shipping activities from Ecuador.

Leptophis praestans (Cope)

Thrasops praestans Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, vol. 20, p. 309; Type locality: Petén, Guatemala

Thrasops (*Ahaetulla*) *sargii* Fischer, 1881, Arch. Naturgesch., vol. 47, no. 1, p. 229. Type locality: Guatemala.

Leptophis maximus Weller, 1930, Proc. Jr. Soc. Nat. Sci. Cincinnati, vol. 1, p. 1; Type locality: unknown.

Leptophis occidentalis praestans; Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, 462, 16.

Thalerophis richardi praestans; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 248.

Leptophis ahaetulla [*praestans*]; Int. Comm. Zool. Nomen., 1958, Op. 524, p. 270.

Leptophis ahaetulla praestans; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States National Museum Bulletin, 297: p. 163.

Diagnosis.– *Leptophis praestans* can be distinguished from other *Leptophis* by the absence of postocular stripe in adults and dorsal skin with yellow chevron-shaped marks (vs. postocular present and dorsal skin without yellow chevron-shaped marks). Further, *L. praestans* differs from parapatric taxa *L. occidentalis* and simpatric *L. mexicanus* in having keels of scales of dorsal rows V-VII and IX-XI heavily marked with black, being more prominent on paravertebral rows (vs. dorsal scales without black keels or with thin dark stripes along dorsal scales keels).

Description.– Ventrals 162-182 in males (*x* = 174.7 ± 3.6, n = 55), 171-186 in females (*x* = 178.5 ± 3.5, n = 35). Subcaudals 159- 182 in males (*x* = 174.3 ± 7.3, n = 12), 165-186 in females (*x* = 179.1 ± 6.6, n = 12). Largest male SVL 1055 mm, tail 618 mm and largest female SVL 1362 mm, tail 724+ mm. Supralabials 8/8 (n = 45), 9/9 (n = 21), 8/9 (n = 10), 9/8 (n = 9), 8/7 (n = 1), 7/8 (n = 1) or 7/7 (n = 1), with 4-5/4-5 (n = 43), 5-6/ 5-6 (n = 20), 4-5/5-6 (n = 10), 5-6/4-5 (n = 9), 3-4/4-5 (n = 1), 4-5-6/4-5 (n = 1) or 4/4 (n = 1) entering orbit; infralabials 10/10 (n = 55), 10/11 (n = 9), 11/10 (n = 6), 9/10 (n = 4), 9/9 (n = 4), 10/9 (n = 3), 11/11 (n = 2), 9/11 (n = 1) or 11/9 (n = 1), with 5/5(n = 66), 5/6 (n = 11), 6/5 (n = 7), 6/6 (n = 2), or 4/5 (n = 1) contacting first genials; preoculars 1/1 (n = 88) or 2/2 (n = 1); postoculars 2/2 (n = 75), 2/3 (n = 7), 3/3 (n = 3), 3/4 (n = 3) or 3/2 (n = 2); anterior temporal 1/1 (n = 89) or 2/2 (n = 1); posterior temporal 2/2 (n = 83), 2/1 (n = 6), or 1/2 (n = 1). Keels more developed in adult males than females and juveniles. Females with significantly more ventrals than males (F = 24.2272; $p < 0.0001$). Subcaudal counts not sexually dimorphic (F=2.8002; p = 0.105). FMNH 5292 (male), UMMZ 149839 and UTA 46134 (females) with respectively */24, 24/25, and 21/24 recurved maxillary teeth without diastema, 13/13, 13/12, and 12/13 palatine teeth, 20/21, 22/21, and 22/23 pterygoid teeth, and 25/18+, 26+/24+ and 26/25 dentary teeth. Last three maxillary teeth ungrooved and enlarged.

Hemipenis.– (Fig. 20 A, B).

Coloration.– *Leptophis praestans* has a uniform green dorsal ground color, with yellow chevron-shaped marks that are most evident when the body in inflated. Further, *L. praestans* has keels of scales dorsal rows V-VII and IX-XI black, with keels on paravertebral rows more prominent. The supralabials, throat, and venter of the body and tail are pale green or yellow-green.

FIG. 20 – Hemipenis of *Leptophis praestans*, El Petén, Guatemala (KU 55716) showing sulcate (A) and asulcate (B) sides. Note the first row of enlarged spines.

Distribution.– From central Veracruz, Mexico, southward through the Yucatán Peninsula (Fig. 5).

Ecology.– According to Campbell (1998) and Lee (1996), *Leptophis praestans* is primarily diurnal and arboreal, inhabiting tropical wet, moist, and dry forest, being commonly found in clearings, second growth, and forest edges as well as primary forest. Two specimens, UMMZ 76165 and UTA 37057, had eaten one *Smilisca baudinii* and one *Eleutherodactylus* sp. respectively, both ingested headfirst. Ramirez et al. (1998) recorded one *Rana vaillanti* as a prey item. As in *L. occidentalis*, this species threatens adversaries with an open mouth. It also inflates the anterior part of the body, revealing the bright yellow of the skin between the scales. In Guatemala this species was collected at 990 m elevation (Campbell, 1998). The reproductive habits of *L. praestans* are unknown.

Remarks.– Contrary to the statement of Stafford and Meyer (2000), *Leptophis praestans* is an aglyphous snake. Only juvenile specimen examined UMMZ xxxx, an immature female with 567 mm in total length, retains traces of a postocular stripe reduced to black margin on eighty and ninety supralabials, occupying lower one-third of anterior temporal and lower one-third of posterior temporal (Fig. 21), suggesting a possible ontogenetic change in *Leptophis praestans*; further, this specimen exhibits the banded juvenile patter.

The syntypes of *Leptophis praestans* are two large-sized specimens catalogued as USNM 6754. The female specimen is here designated as lectotype of *L. praestans* because it has the tail complete. Both specimens are faded though the chevron-shaped marks are still evident.

FIG. 21 – Juveline of *Leptophis praestans*, El Petén, Guatemala (UMMZ). Note traces of a postocular stripe reduced occupying lower part of anterior temporal and lower posterior temporal.

Leptophis urosticus (Peters)

Ahaetulla urosticta W. Peters, 1873, Monatsber. Akad. Berlin: 606. Type-locality: “Bogotá, Colombia”, restricted to “Chocó region” by Mertens, 1973, Studies on the Neotropical Fauna and Environment 8:143.

Leptophis occidentalis chocoensis Oliver, 1942, Occas. Papers Mus. Zool. Univ. Michigan, no. 462, p. 15. Type locality: Peña Lisa, Chocó, Colombia.

Thalerophis richardi chocoensis; Oliver, 1948, Bull. Am. Mus. Nat. Hist., no. 4, p. 227.

Leptophis ahaetulla [*chocoensis*]; Int. Comm. Zool. Nomen., 1958, Op. 524, p. 270.

Leptophis ahaetulla chocoensis; Peters and Orejas-Miranda, 1970, Catalogue of the Neotropical Squamata: Part I. snakes. United States National Museum Bulletin, 297: p. 162.

Leptophis ahaetulla urosticus; Mertens, 1973, Studies on the Neotropical Fauna and Environment, 8:143.

Diagnosis.– *Leptophis urosticus* can be distinguished from its congeners in having a broad black postocular stripe, occupying all or nearly all of anterior temporal and lower posterior temporal and dorsal scale rows V to XI before body scale reduction from 15 to 11 scales and rows V to VII after reduction brown in adults (Fig. 22) (vs. a narrow postocular stripe, always covering half of anterior temporal and lower posterior temporal and body uniformly green, copper, or silver-gray, with or without dorsal stripes). Further it differs from parapatric taxa *L. bocourti*, *L. cupreus*, *L. nigromarginatus*, and *L. occidentalis* in having heavy black keels on scales of dorsal rows (vs. if present, black keels are thin).

Description.– Ventrals 160-168 in males (x = 163.4 ± 3.2, n = 7), 153-166 in females (x = 162.8 ± 4.1, n = 8). Subcaudals in males and females 164-180 (x = 174.7 ± 5.5, n = 7). Largest male SVL 1081 mm, tail 696+ mm and largest female SVL 890 mm, tail 620 mm. Supralabials 9/9 (n = 13) or 9/8 (n = 2), with 4-5/4-5 (n = 43), 5-6/ 5-6 (n = 13) or 5-6/4-5 (n = 2) entering orbit; infralabials 11/11 (n = 5), 10/10 (n = 3), 11/10 (n = 2), 9/9 (n = 2), 12/11 (n = 1), or 12/10 (n = 1), with 6/6(n = 8), 6/5 (n = 3), 5/5 (n = 3), or 7/6 (n = 1) contacting first genials; preoculars 1/1 (n = 15); postoculars 2/2 (n = 14) or 3/3 (n = 1); anterior temporal 1/1 (n = 15); posterior temporal 2/2 (n = 15). Keels more developed in adult males than females and juveniles. Ventral counts not sexually dimorphic (F=0.1233;

p = 0.7302). UMMZ 55528 with respectively 23/22 recurved maxillary teeth without diastema, 14/14 palatine teeth, 27/29 pterygoid teeth, and 27/27 dentary teeth. Last three maxillary teeth ungrooved and enlarged. Additional records can be found in Oliver (1948).

FIG. 22 – *Leptophis urosticus*, Risaralda: about 7 km (airline) SE Santa Cecília (AMNH 115932) Courtesy of Charles W. Myers. Note keels heavily markes with black on dorsal rows.

Hemipenis.– (Fig. 23 A, B).

FIG. 23 – Hemipenis of *Leptophis urosticus*, Quebrada Guanguí, Cauca (AMNH 109753) showing sulcate (A) and asulcate (B) sides. Note the first row of enlarged spines.

Coloration.– *Leptophis urosticus* has a uniform green dorsal color, with distinct black keels. Supralabials, throat, and venter of body and tail are pale green.

Distribution.– *Leptophis urosticus* is known only from the Chocó, Cauca, Risaralda, and Valle de Cauca, Colombia (Fig. 5).

Ecology.– According to Oliver (1948), *Leptophis urosticus* occupies regions characterized by a hot, humid climate, being inhabitant of dense forest. Oliver (1948) recorded one hylid frog as a prey item. AMNH 115932 and AMNH 115933 were collected at 480 m elevation. The reproductive habits of *L. urosticus* are unknown.

Remarks.– Until the present study *Leptophis urosticus* was thought to be endemic from the Chocó region. The specimen collected in Valle de Cauca, extend the geographic distribution of *Leptophis urosticus* about 213 km southward from Peña Lisa.

Characters description

Hemipenis.– The hemipenis of *Leptophis* is short to moderate in length (5 to 9 subcaudal scales long), asymmetrical and slightly bilobed with a simple sulcus spermaticus. The proximal portion is covered by spines and the distal area is always ornamented by papillate calyces (Dowling and Savage, 1960; Oliver, 1948; this study). The hemipenes of all species of *Leptophis*, including all subspecies of *L. ahaetulla*, were briefly described by Oliver (1942, 1948) based on retracted organs. Also, Oliver (1948) figured retracted organs of *L. a. praestans*, *L. depressirostris, L. mexicanus*, and *L. riveti*. Dowling and Savage (1960) figured the sulcate side of the organ of *L. mexicanu*s. Henderson (1976) described one of the in situ hemipenes of *L. mexicanus hoeversi*. Everted hemipenes were examined for all taxa included in the in-group and out-group, with the exception of *L. a. bocourti*. In addition, data from Oliver (1942, 1948), Stuart (1932), and Wilson (1970) were included in order to increase sample size. Terminology for hemipenial morphology followed Dowling and Savage (1960) and Zaher (1999).

Character 1. Shape of hemipenis: single (0), or slightly bilobed (1).

Character 2. Termination of sulcus spermaticus: ending in area covered by papillate calyces (0), or ending in naked apical area (1). Only *Drymobius* exhibits the second condition.

Character 3. Direction of sulcus spermaticus: straight (0), sulcus extends on the right side of organ (1). Only *Drymobius* exhibits the first condition.

Character 4. Basal area: basal naked pocket: present (0), absent (1).

Character 5. Size of basal spines: small, except for two largest adjacent to sulcus (0), all spines are small (1), all basal spines enlarged (2) (Fig. 24), first row of basal spines slightly larger than remaining spines (3) (Fig. 25 A, B), first row of basal spines conspicuously enlarged (4).

Character 6. Distal ornamentation: distal region ornamented with large papillate calyces (0), with papillae, without calyces (1), or with small-sized calyces (2).

Character 7. Size of midsection calyces: calyces uniformly large in size (0) (Fig. 26 A, B), calyces absent or obscured by papillae (1), or calyces small (2). Ordered (1-2-0).

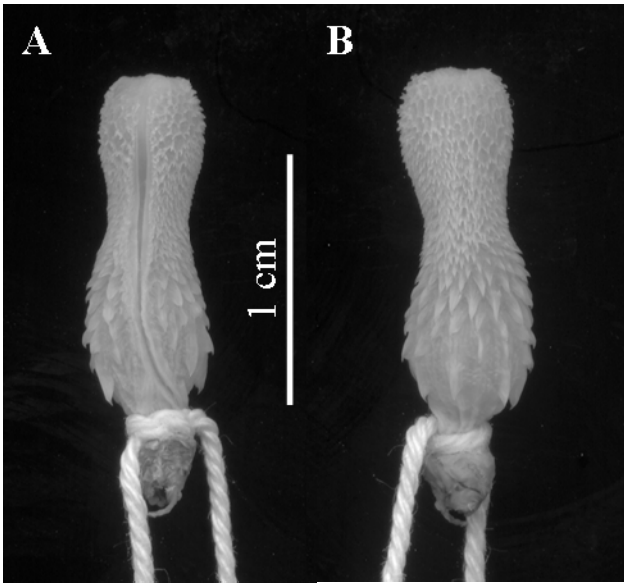


FIG. 24 – Hemipenis of *Leptophis mexicanus*, cooley plantation, Río Grande, Nicaragua (AMNH 12664) showing sulcate (A) and asulcate (B) sides. Note the series of enlarged basal spines.

FIG. 25 – Hemipenis of *Leptophis ahaetulla* (MPEG 17755) showing sulcate (A) and asulcate (B) sides.

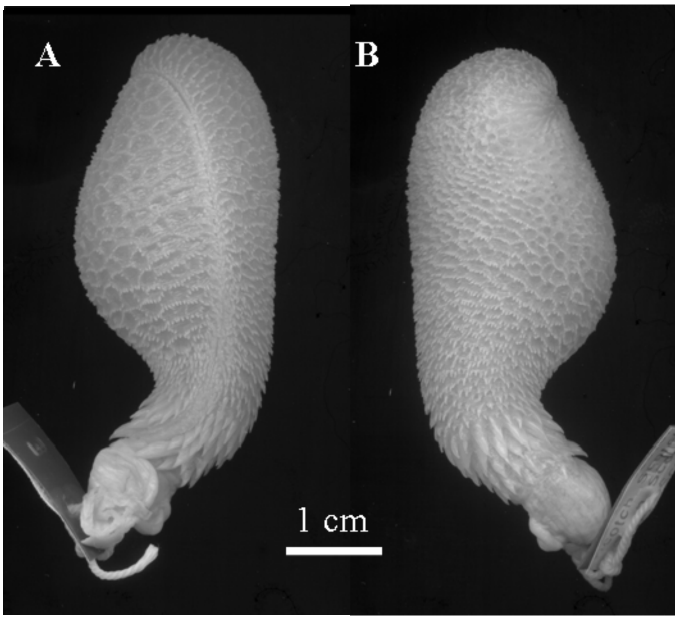


FIG. 26 – Hemipenis of *Mastigodryas bifossatus* (MCP 129) showing sulcate (A) and asulcate (B) side. Note the midsection calyces large in size.

Cranial Osteology.—In the only study that exists on the cranial osteology of *Leptophis*, Oliver (1948) reported only the number of maxillary teeth for the six species of *Leptophis* then recognized. In the present study, skull morphology was examined and number of maxillary, palatine, pterygoid, and dentary teeth were counted for all species included in the ingroup and outgroup. Data for *L. caatingensis* and *L. cupreus* are from Albuquerque and Di-Bernardo (ms) and Albuquerque (ms), respectively. Data from Oliver (1948), Souza and Lema (1990), and Wilson (1970) were included in order to increasing sample size. Character 12 was measured as described by Cundall and Rossman (1984). In *Leptophis* the last two or three maxillary teeth are recurved, ungrooved, enlarged, and not separated from the preceeding teeth by a diastema.

Character 8. Descending lamina of nasals: not enlarged (narrow) (0) (Fig. 4A), or enlarged anteriorly (1) (Fig. 27B).

Character 9. Size of posterior maxillary teeth: approximately equal to anterior maxillary teeth (0), the last two teeth are enlarged (1), or the last three teeth are enlarged (2). Ordered (0-1-2).

Character 10. Posterior surface of sphenoid: posterior surface with small prominence, absent in juveniles (0), or with two prominences separated from each other by an M-shaped median keel (1).

Character 11. Width of frontals: equal width along entire length (0) (Fig. 27A), or anterior and posterior regions of frontals widened (1) (Fig. 4B). Only *Leptophis* exhibits state 1.

Character 12. Ratio of mandible length to skull length (i.e. length of mandible): 131.1 to 142.2 in *Mastigodryas* (n = 3; long 0), 115.3 to 121.7 in *Drymobius* (n = 4; medium-sized 1), and 77.1 to 91.6 in *Leptophis* (n = 73, short 2).

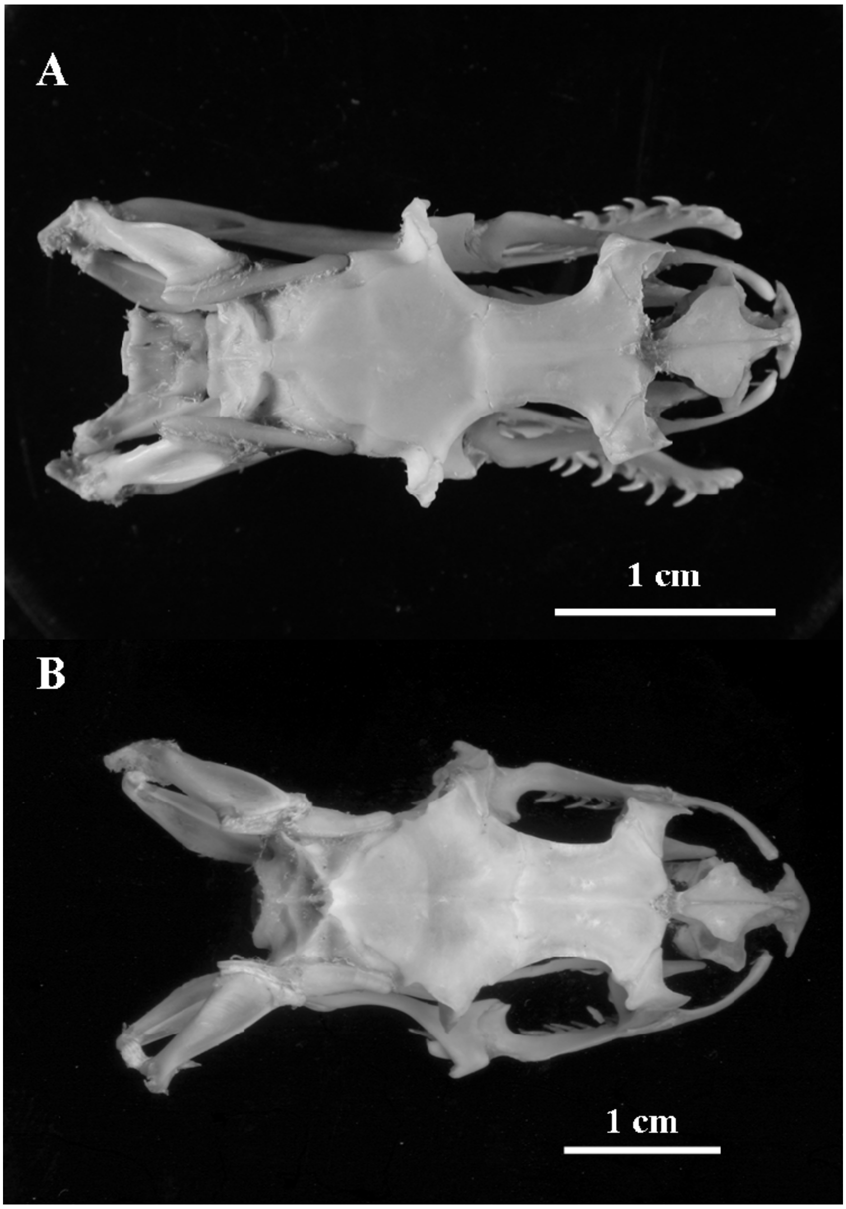


FIG. 27 – Shape of nasal lamina. (A) *Leptophis nigromarginatus* (CM), note the descending lamina of nasal enlarged anteriorly. (B) *Drymobius chloroticus* (UMMZ), note the frontals homogeneously wide.

Ecology

Character 13. Preference of micro-habitat: terrestrial (0) or semi-arboreal (1). The categories for microhabitat preference are used as described by Martins and Oliveira (1998). *Leptophis* is known either as a primarily arboreal (Henderson, 1982; Henderson et al., 1977; Henderson et al. 1979; Martins and Oliveira, 1998; Vitt and Vangilder, 1983) or semi-arboreal snake (Albuquerque et al., 2007; Savage, 2002). Species known as "terrestrial-arboreal" or "arboreal and terrestrial" (e.g. McCraine et al, 2006 for *L. ahaetulla* of the Honduran Mosquitia) were coded as semi-arboreal in the present study.

Character 14. Feeding behavior: generalist (0), amphibians-specialist (1). A taxon was recognized as "amphibian-specialist" if 80% or more of its diet is composed of amphibians. Many predators are widely believed to feed on one or a few prey species, and although those with narrow diets are sometimes called specialists, criteria on which to base this judgment vary and are often not explicit (Rodriguez-Robles and Greene, 1999). Thus, my distinction must be considered rather as arbitrary. Data for *Leptophis* are from Albuquerque and Di-Bernardo (ms), Albuquerque (ms), Albuquerque et al. (2007), Henderson et al. (1979), Lopez et al. (2003), and Oliver (1948). Data for out-group taxa are from Campbell (1998), Henderson et al. (1977), Henderson (1982), Marques and Muriel (2007), McCraine et al. (2006), Savage (2002), Seib (1984).

Coloration.– Leptophis includes snakes that are quite divergent in color pattern. Data for *Leptophis* species are from Albuquerque and Di-Bernardo (ms), and Albuquerque (ms), Argôlo (2004), Beebe (1946), Campbell (1998), McCraine et al (2006), Mertens (1973), Murphy (1997), Oliver (1948), Savage (2002), and this study. Data for out-group taxa are from Oliver (1948), Savage (2002).

Character 15. Adult post-orbital stripe: a short stripe may extend onto body a distance of two to eight scales posterior to last upper labial (0) (Fig. 28A), a long postocular stripe which continues onto anterior body on rows III-VII (1) (Fig. 28B) (1), a short stripe, always bordering the last supralabials but not extending onto body (2). *Drymobius* and *Mastigodryas* are scored as inapplicable.

Character 16. Adult dorsal stripes: dorsum without dorsolateral stripes (0), with two dorsolateral stripes, at least anteriorly (1). Ordered (0-1).

Character 17. Coloration of head scales: head scales without small black dots or streaks (0) (Fig. 29), or all of the head scales posses numerous small black dots or streaks (1) (Fig. 30). Ordered (0-1).

Character 18. Coloration of parietal scales: without a black spot on each parietal scale (0), always with a black spot on each parietal (1).

Character 19. Color of supraocular scale in adults: immaculate green (0) or green with black spot (2).

Character 20. Color of tip of dorsal scales: green (0) or black (1).

Character 21. Coloration of throat in adults: white (0), pale green (1).

Character 22. Vertebral stripe in adults: absent (0), or present, separating two dorsolateral stripes (1).

Character 23. Coloration of borders of ventral scales: ventrals not margined (0), ventrals bordered with black posterioly (1), or ventral scales margined anteriorly and laterally with dark greenish blue (2) (Fig. 31).

Character 24. Coloration of ventral scales: yellowish brown (0), yellowish (1), dirty white (2), or pale green (3).

FIG. 29 – *Leptophis diplotropis* (USNM 304907) from Oaxaca, Mexico (A) (Courtesy of Roy W. McDiarmid) and *Leptophis ahaetulla* (IBSP 64396) from Lajeado, Tocantins (B) (Courtesy of Antônio da Costa). Note a long postocular stripe which continues onto anterior body in *L. diplotropis*.

FIG. 30 – Head of one of the Syntypes of *Leptophis bocourti*, Paramba, Ecuador (BMNH 1946.1.6.67). Note the numerous small, irregularly shaped black dots.

FIG. 31 – Venter of *Leptophis nigromarginatus*, Moropón, Loreto, Peru (TCWC 42171). Note the ventral scales margined anteriorly and laterally with dark greenish blue.

Character 25. Dorsal coloration pattern in adults: dorsal coloration with a series of dark cross bands (0), dorsum green, with each dorsal scale marked with a yellow to orangish central area (1), dorsum green, with each dorsal scale not edged with black (2), dorsum uniformly copper (3), dorsum green, with each dorsal scale heavily edged with black (4), or dorsum green, with two green dorsolateral stripes separated from each other by a vertebral stripe (5). Savage (2002) divided the species of *Leptophis* into four major geographic categories based on color pattern, which was followed in the present study.

Character 26. Coloration of posterior dorsal region: dorsal coloration of head and anterior body region persisting throughout posterior region (0), or dorsal coloration of head extends on body but it is limited in distribution to five median dorsal scale rows; farther posterior, coloration may be reduced still more (1).

Character 27. Coloration of lateral portion of body: without a lateral stripe (0), with a yellow lateral stripe on II and III rows (1) (see Fig. 5B), or with a pale lateral stripe on II and III rows.

External morphology.– Data for *Leptophis* species are from Campbell (1998), McCraine et al (2006), Mertens (1973), Oliver (1948), Savage (2002), and this study. Data for out-group taxa are from Albuquerque and Di-Bernardo (ms), Albuquerque (ms), Oliver (1948), and Savage (2002). Eventual anomalies that may occur in some specimens (e.g. loreal present on one side of the head only) were disregarded (see Oliver, 1948).

Character 28. Loreal scale: present (0) or absent (1).

Character 29. Ornamentation of dorsal scale rows, counted at midbody: dorsal scales smooth (0), only paravertebral rows are keeled (1), all scale rows, except outermost, keeled (2).

Character 30. Number of scale rows at midbody: 17-17 rows (0), 17-15 rows (1), 15-11 rows (2).

Character 31. Evidence of keels on dorsal scales: keels little evident (0), or keels on rows VI to X (before body reduction from 15 to 11 dorsal scale rows) and IV to VIII (after reduction) conspicuously evident (1). *Mastigodryas* and *Drymobius* are scored as inapplicable because they do not have keels.

Results of Phylogenetic Analysis

Parsimony analysis of the 31 characters (Table 4) resulted in nine most parsimonious trees, with a total length of 50 steps, a consistency index (CI) of 96 (Kluge and Farris, 1969), and a retention index (RI) of 97 (Farris, 1989) (Fig. 32). A clade containing *Leptophis bolivianus*, *L. marginatus*, and *L. nigromarginatus* is supported by two synapomorphies and a Bremer value of 2: parietal scales with a black spot in center of each scale (character 18, state 1) and dorsum green, with each dorsal scale heavily edged with black (character 25, state 4). *Leptophis ahaetulla*, *L. coeruleodorsus*, and *L caatinguensis* are supported by two synapomorphies and a Bremer value of 2: dorsum with two dorsolateral stripes (character 17, state 2) and lateral portion of body with a yellow or pale lateral stripe on II and III rows (character 28, state 1). The trans-andean clade (i.e. *Leptophis bocourti*, *L. occidentalis*, *L. praestans* and *L. urosticus*) is supported by two synapomorphies and a Bremer value of 2: first row of basal spines notably enlarged (character 5, state 4) and throat pale gree (character 21, state 1).

Table 4. Data matrix of character states used for parsimony analysis. Character numbers correspond to those listed in the character descriptions. All characters are non-additive and equally weighted.

FIG. 32 – Strict consensus of the single parsimonius tree of 50 steps resulting from analysis of 31 characters. Bremer support values are given above the branches. The option “show unsupported nodes as collapsed”was chosen.

Key to the species of *Leptophis*

The following key is designed to identify the species of *Leptophis*. Because of the pattern of oblique bands found in most juveniles, this key must be adequate for identifying especially adult specimens. *Leptophis santamartensis*, which is known only from type-specimens (two juveniles from Sierra de Santa Marta, Colombia), was not included because Bernal-Carlo & Roze (1994) did not provide exclusive diagnostic characters to differentiate it from its congeners; not even a combination of characters may be used in its identification. The status of this species is being treated elsewhere (Albuquerque, ms).

DISCUSSION

xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx

Acknowledgments. – This study would not have been possible without the help and cooperation of the curators and collections manager associated with each of major South American, North American, and European museums. I am indebted to all. I am particularly indebted to D. Frost, D. Kizirian, and the American Museum of Natural History for the opportunity to develop part of my PhD dissertation under their supervision and support. I thank also G. Paggi for his continuous help, support, and patience during the writing of this article, and F. D’Agostini, with the permission of R. Henderson (MPM) and Greg Schneider

(UMMZ), for graciously allowing me access *Drymobius* specimens while on loan to her. I thank T. Grant for numerous stimulating discussions and encouragement during the writing of my dissertation. Helpful suggestions and corrections by F. Franco, T. Grant, C. Lucena, and R. Reis greatly improved the manuscript. The maps were prepared by Fabrício Bonfiglio. Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided a fellowship during my graduate studies. Field Museum of Natural History (FMNH) granted me a visiting scholarship.

REFERENCES

ALBUQUERQUE, N. R. Redescription of *Leptophis cupreus*, a rare South America colubrine snake (ms).

ALBUQUERQUE, N. R., AND M. DI-BERNARDO. A new species of *Leptophis* (Serpentes, Colubridae) from Northeastern Brazil. Herpetologica (ms).

ALBUQUERQUE, N. R., AND M. DI-BERNARDO. 2005. *Leptophis ahaetulla marginatus*. Diet. Herpetological Review, 36 (3): 325.

ALBUQUERQUE, N. R., U. GALATTI, AND M. DI-BERNARDO. 2007. Diet and feeding behaviour of the Neotropical parrot-snake (*Leptophis ahaetulla*) in Northern Brazil. Journal of Natural History, 41(17–20): 1237–1243.

AMARAL, A. 1930a. Estudos sobre ophidios neotropicos. Valor systematico de varias formas de ophidios neotropicos. Memórias do Instituto Butantan, 4, 3–68 [1929].

AMARAL, A., 1930a. Estudos sobre ophidios neotropicos. Contribuição ao conhecimento dos ophidios do Brasil. Memórias do Instituto Butantan, 4, 71–125 [1929].

AMARAL, A., 1930b. Estudos sobre ophidios neotropicos. Lista remissiva dos ophidios da região Neotropica. Memórias do Instituto Butantan, 4, 129–271 [1929].

ARGÔLO, A. J. S. 2000. Geographic distribution: *Hyla anceps*. Herpetological Review 31(2): 109.

ARGÔLO, A. J. S. 2004. As serpentes dos cacauais do sudeste da Bahia. Ilhéus, Bahia, Editus, 260 p.

AYRES, M., M. AYRES JR, D. L. AYRES, AND A. S. SANTOS. 2005. BioEstat 4.0: Aplicações estatísticas nas áreas das ciências biológicas e médicas. Sociedade Civil Mamirauá/MCT-CNPq/Conservation International, Belém, 323 pp.

BEEBE, W. 1946. Field notes on the snakes of Kartabo, British Guiana and Caripito, Venezuela. Zoologica, 31 (1-13): 11-52p.

BERNAL-CARLO, A., AND J. A. ROZE. 1994. A new *Leptophis* (Serpentes: Colubridae) from Sierra Nevada de Santa Marta, Colombia. Bulletin of the Maryland Herpetological Society 30 (1): 46-49.

BOOS, H. E. A. 2001. The snakes of Trinidad and Tobago, Texas A & M University Press, College Station, TX: 270p.

BOULENGER, G. A. 1894. Catalogue of the snakes in the British Museum (Natural History). London, v.2, xiii+382pp.

BREMER, K. 1994. Branch support and tree stability. Cladistics 10: 295-304.

CAMPBELL, J. A. 1998. Amphibians and reptiles of northern Guatemala, the Yucatan, and Belize. Norman: University of Oklahoma Press.

CARREIRA, S. M., MENEGHEL, AND F. ACHAVAL. 2005. Reptiles de Uruguay. D.I.R.A.C. Facultad de Ciencias, Universidad de la República, Montevideo, 639 pp.

COLLI, G. R., R. P. BASTOS, AND A. F. B. ARAÚJO. 2002. The character and dynamics of the Cerrado herpetofauna. In: The Cerrados of Brazil: Ecology and natural history of a neotropical savanna: 223-241. P. S. Oliveira and R. J. Marquis (Eds.). New York, NY: Columbia University Press.

COPE, E. D. 1868. Sixth contribution to the herpetology of tropical America. Journal of Academy of Natural Sciences of Philadelphia, vol. 20, pp. 305-313.

COPE, E. D. 1876. Report on the reptiles brought by Prof. James Orton from the middle and upper Amazon, and western Peru. Journal of Academy of Natural Sciences of Philadelphia, vol. 8, pp. 159-183.

CUNHA, O. R., AND F. P. NASCIMENTO. 1978. Ofídios da Amazônia X - As cobras da região Leste do Pará. Publicações Avulsas do Museu Paraense Emílio Goeldi, 31:1-218.

CUNDALL, D., AND D. A. ROSSMAN. 1984. Quantitative comparisons of skull form in the colubrid snake genera *Farancia* and *Pseudoeryx*. Herpetologica, 40(4): 388-405.

DONOSO-BARROS, R. 1966. Reptiles de Chile. Ediciones de la Universidad de Chile. Santiago de Chile. 458 p.

DOWLING, H. G. 1951. A proposed standard system of counting ventral scales in snakes. British Journal Herpetology, 1: 97-99.

DOWLING, H. G., AND J. M. SAVAGE. 1960. A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica, 45: 17-28.

DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. University of Kansas, Museum of Natural History, Miscellaneous Publication, 65:1-352.

DUELLMAN, W. E. 2005. Cusco Amazónico: The lives of amphibians and reptiles in an Amazonian Rainforest. Ithaca, New York: Cornell University Press, pp. xv+433, 236 plates.

FARRIS, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5:417-419.

GLOBAL GAZETTEER. Version 2.1 by Falling Grain Genomics [http://www.fallingrain.com/world/] Last modified: November 14, 2006.

GOLOBOFF, P. 1999. NONA. ver. 2 Published by the author, Tucumán, Argentina.

GRANT, T., AND A.G. KLUGE. 2003. Data exploration in phylogenetic inference: Scientific, heuristic, or neither. Cladistics, 19, 379–418.

GUNTHER, A. 1866. Fifth account of new species of snakes in the collection of the British Museum.

HARDING, K. 1995. A new species of tree snake of the genus *Leptophis* Bell, 1825 from Mount Aripo, Trinidad. Tropical Zoology, 8(2): 221-226.

HENDERSON, R. W. 1976. A new insular subspecies of the colubrid snake *Leptophis mexicanus* (Reptilia, Serpentes, Colubridae) from Belize. Journal of Herpetology, 10(4): 329-331.

HENDERSON, R. W. 1982. Trophic relationships and foraging strategies of some new world tree snakes (*Leptophis*, *Oxybelis*, *Uromacer*). Amphibia-Reptilia, 3: 71-80.

HENDERSON, R. W., M. A. NICKERSON, AND L. G. HOEVERS. 1977. Observations and comments on the feeding behavior of *Leptophis* (Reptilia, Serpentes, Colubridae). Journal of Herpetology, 11: 230-231.

HENDERSON, R. W., J. R. DIXON, AND P. SOINI. 1979. Resource partitioning in Amazonian snake communities. Contributions in Biology and Geology, 22: 1-11.

HERO, J-M., AND W. MAGNUSSON. 1987. *Leptophis ahaetulla*. Food. Herpetological Review, 18(1): 16.

HOLLIS, J. L. 2006. Phylogenetics of the genus *Chironius* Fitzinger, 1826 (Serpentes, Colubridae) based on morphology. Herpetologica, 62(4): 435-453.

HOOGMOED, M. S. 1973. Notes on the herpetofauna of Surinam IV. The lizards and amphisbaenians of Surinam. ex + 419pp. The Hague: W. Junk.

HOOGMOED, M. S. 1979. The herpetofauna of the Guiana region. In: Duellman, W. E. (ed.): The South American Herpetofauna: Its origin, evolution, and dispersal. University of Kansas Museum of Natural History Monographs, 7: 241-279.

ICZN. 1958. Opinion 524, Interpretation of the nominal species *Coluber ahaetulla* Linnaeus, 1758, and addition to the official list of generic names in zoology of the generic *Ahaetulla* Link, 1807 with *Ahaetulla mycterizans* Link, 1807 as type species (Class Reptilia).

KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of the anurans. Systematic Zoology 18:1–32.

LA MARCA, E., AND J. E. GARCIA. 1987. *Leptophis ahaetulla occidentalis*. Geographich distribution. Herpetological Review, 18(3): 57.

LEE, J. C. 1996. The amphibians and reptiles of the Yucatán Peninsula. Ithaca: Cornell University Press.

LEVITON, A. E., R. H.GIBBS JR, E. HEAL, AND C. E. DAWSON. 1985. Standards in Herpetology and Ichthyology: part I. Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. Copeia 3:802-852.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentis, synonymis, locis. Stockholm, 10th ed., vol. 1, ii+824p.

LOPEZ, M. S, A. R. GIRAUDO, AND V. ARZAMENDIA . 2003. *Leptophis ahaetulla marginatus*. Diet. Herpetological Review; 34(1):68-69.

LÖNNBERG, E. 1896. Linnean type-specimens of birds, reptiles, batrachians, and fishes in the Zoological Museum of the R. University in Upsala. Bihang till Königlisshen Svenska Veterinan Akademie des Handlingar, Bd. 22, Afd. 4 no. 1: 1-45.

LÖNNBERG, E. 1902. On a collection of snakes from northwestern Argentina and Bolivia containing new species. Annals and Magazine of Natural History, ser. 7, 10: 457-462.

MADDISON, W. P. AND D. R . MADDISON. 2007. Mesquite: a modular system for evolutionary analysis. Version 2.01. http://mesquiteproject.org.

MALLET, J. 1995. A species definition for the modern synthesis. Trends in Ecology and Evolution, 10:294-299.

MANZANI, P. R., AND A. S. ABE. 1988. Sobre dois novos métodos de preparo do hemipênis de serpentes. Memórias do Instituto Butantan. 50 (1): 15-20.

MARQUES, O. A. V., AND A. P. MURIEL. 2007. Reproductive biology and food habits of the swamp racer *Mastigodryas bifossatus* (Colubridae) from southeastern South America. Herpetological Journal, v. 17, p. 104-109.

MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus Region, Central Amazonia, Brazil. Herpetological Natural History, 6: 78-150.

MAYR, E. 1940. Speciation phenomena in birds. American Nature, vol. 74, p. 249-278.

MAYR, E. 1942. Systematics and the origin of species. Columbia University Press, New York, 334 p.

MCCRAINE, J. R., J. H. TOWNSEND, AND L. D. WILSON .2006. The amphibians and reptiles of the Honduran Mosquitia. Krieger Publishing Company, 304 p.

MENEGHEL, M. D., AND F. ACHAVAL, 1997. *Leptophis ahaetulla marginatus*. Geographic distribution. Herpetological Review, 28(2): 98.

MERTENS, R. 1972. Eine neue Schlanknatter der Gattung *Leptophis* aus Mexiko. Senckenbergiana Biologica 53:341-342.

MERTENS, R. 1973. Bemerkenswerte Schlangnatters der neotropischen Gattung *Leptophis*. Studies on the Neotropical Fauna, 8: 141-154.

MURPHY, J. C. 1997. Amphibians and reptiles of Trinidad and Tobago. Published by Krieger Publishing Company. 245 p.

NIXON, K.C., 1999–2002. Winclada ver. 1.0. Published by the author, Ithaca, NY.

OLIVER, J. A. 1942. A check list of the snakes of the genus *Leptophis*, with descriptions of new forms. Occasional Papers of the Museum of Zoology, University of Michigan, 462: 1-19.

OLIVER, J. A. 1947. The status of *Leptophis* Bell. Copeia (1): 64.

OLIVER, J. A. 1948. The relationships and zoogeography of the genus *Thalerophis* Oliver. Bulletin of the American Museum of Natural History, 92 (4): 157-280.

PESANTES, O. S. 1994. A method for preparing the hemipenis of preserved snakes. Journal of Herpetology, 1(28): 93-95.

PETERS, J. A. 1964. Dictionary of Herpetology. New York, Hafner Publishing Company. 392 pp.

PETERS, J. A., AND B. OREJAS-MIRANDA. 1970. Catalogue of the Neotropical Squamata: Part I - Snakes. Bulletin United States National Museum, Washington, 297: 347.

RAMIREZ, J., R. C. VOGT, AND J. L. VILLARREAL-BENITEZ. 1998. Population biology of a Neotropical frog (*Rana vaillati*). Journal of Herpetology, 32(3): 338-344.

RODRÍGUEZ-ROBLES, J. A., AND H. W. GREENE. 1999. Food habits of the long-nosed snake (*Rhinocheilus lecontei*), a 'specialist' predator? Journal of Zoology, 248: 489-499.

ROZE, J. A. 1966. La taxonomia y zoogeografía de los ofidios en Venezuela. Universidad Central de Venezuela, Caracas, 362 pp.

SAVAGE, J. M. 1973. A revised terminology for plates in the loreal region of snakes. British Journal of Herpetology 5: 360-362.

SAVAGE, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between two Continents, between two Seas. University of Chicago Press. Chicago.

SAVAGE, J. M., AND J. A. OLIVER. 1956. Proposed addition to the "Official List of Generic Names in Zoology" of "*Ahaetulla*" Link, 1807, with "*Ahaetulla mycterizans*" Link, 1807, as type species (Class Reptilia). Bulletin of Zoological Nomenclature, 12: 147-152.

SEIB, R. L. 1984. Prey use in three syntopic Neotropical racers. Journal of Herpetology, 18(4): 412-420.

SMITH, E. N. AND R. L. GUTBERLET, JR. 2001. Generalized frequency coding: A method of preparing polymorphic multistate characters for phylogenetic analysis. Systematic Biology 50(2):1–14.

SOUZA, M. F. B., AND T. LEMA. 1990. Osteologia craniana de *Dryadophis bifossatus* (Raddi, 1820) (Serpentes, Colubridae). Iheringia, Série Zoologia, 70: 3-15.

STAFFORD, P. J., AND J. R. MEYER. 2000. A Guide to the Reptiles of Belize. Academic Press: 356p.

STUART, L. C. 1932. Studies on Neotropical Colubrinae. I. Taxonomic status of the genus *Drymobius* Fitzinger. Occasional Papers of the Museum of Zoology, University of Michigan, 236: 1-16.

VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in northeastern Brazil. Amphibia-Reptilia 4: 273-296.

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 southwestern Mexico. Journal of Herpetology 4(3-4): 155-164.

WILSON, L.D., AND J. R. MEYER. 1985. The Snakes of Honduras. Second edition. Milwaukee, Wisconsin: Milwaukee Public Museum. p.150.

ZAHER, H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. Bulletin of the American Museum of Natural History, 240:1-168.

ZAR, J. H. 1999. Bioestatistical Analysis. Preentice Hall, Upper Sadle River, New Jersey, U.S.A, 123p.

APPENDIX I

Specimens examined

Asterisk denotes specimens for which hemipenes (*) or skulls (**) were examined.

Drymobius chloroticus.– GUATEMALA: Alta Verapaz, UMMZ 90989*,**. HONDURAS: San Juancito, AMNH 70164*.

Drymobius margaritiferus.– MEXICO: Taumalipas, TCWC 57346*. BELIZE: Belize District, MPM 10788**. COSTA RICA: Cartago, ANSP 32314**.

Leptophis ahaetulla.– BRAZIL: *Estado do Amazonas*: Manaus, MNRJ 737, CAS 49795, 32836, 18531, INPA 10306, MZUSP 9833 (Reserva Ducke); Benjamin Constant, MNRJ 739; Represa de Balbina, MZUFV 392, 9648; Tapurucuara, MZUSP 5470; Itacotiara, IBSP 44431; Presidente Figueiredo, IBSP 52002, 52198; Estrada Manaus-Boa Vista, Km 135, Fazenda Jayoro Empreendimento, MCP 4322; Borba, MNRJ 1552; Vaupés, IBSP 32010; Vila Nova, IBSP 14807; Iaureté, Rio Vaupés, MPEG 18; km 218, BR-174, 1km E. da Reserva Indígena Waimari, MPEG 18992; Rio Javari, Município de Estirão do Equador, MPEG 148; Balbina, Área de inundação da UHE. Base 1, Margem direita do rio Uatumã, MPEG 17375**, 17376, 17377, 17378, 17379, 17380, 17381, 17394, 17416, 17493, 17497**, 17498, 18413; Maguari, Município de Maraã, MPEG 18023, 18024; Arredores da Fazenda Passo Formoso, Manicoré, MPEG 20839; Amaña, INPA 9519; Seringalzinho, Parque Nacional do Jaú, INPA 9783; Lago Alexo, MCZ 2579; Javary, Amazonas, MCZ 2977. *Estado de Roraima*: Cachoeira do Cujubim, Rio Catrimani, MZUSP 8067; BR 174, marco da fronteira Brasil-Venezuela-8, MZUSP 8555, 8556, 10302; Colônia Confiança, MZUSP 9985, 9986; Colônia Coronel Mota, Região do Traiano, Boa Vista, MPEG 477, 494. *Estado do Amapá*: Ilha de Santana, IBSP 14806; Oiapoque, IBSP 24852, 13778, 15385; Macapá, IBSP 45886, 24794, 24822, 24800; Rio Amaparí, Serra do Navio, MZUSP 4731, MPEG 19684; "Amapá", CHUNB 03797, 22087, MPEG 19307; Campina Grande, MPEG 16391; Igarapé Água Branca, BR-156, MPEG 432. *Estado do Pará*: Tapajós, MCZ 3288; Boca do Cuminã-Mirí, MZUSP 4820, 4821, 4822; Prainha, LPHA 2579; Santarém (Tapari, margem direita do Rio Tapajós), LPHA 1778; Santarém, LPHA 080, 350, 362, 405; Aveiro, LPHA 1259; Itaituba, LPHA 596, 863, 1426, 1427, MCP 4416, 4433; Estrada para Cachoeira do Palhão, Santarém, MPEG 303; Ramal do Coelho, Cucuruna, Santarém, MCP 7575; Almeirim, LPHA 1220; Rio Jari, Almeirim, MPEG 16355; Cachimbo, MZUSP 3347, IBSP 18529; Conceição do Araguaia, IBSP 23577; Ilha de Marajó, IBSP 17649, MPEG 18637 and 18638 (Salva Terra), MPEG 17348 and 17351 Breves, Km 8 da PA-159 (Breves-Anajás), MPEG 18016 and 18326 (Cachoeira do Arari), MPEG 19627 and 19628 (Santa Cruz do Arari), MPEG 17722* (Fazenda Marajá, Chaves), MPEG 19330, 9332, 19333, and 19334 (Muaná), MPEG 17714 (Fazenda Tijuquara, Rio Tijuquara); Belém, DZUFRGS 1053, AMNH 56157, BMNH 1970.506, IBSP 17674, 23815, 25435, 25442, 53896, MPEG 18375, 18457, 19836, 20507, 21183**, 18546, 18624, 19839, 18626 (Bosque Rodrigues Alves), MPEG 450 and 621 (Campus UFPA), MPEG 21043 (Ilha de Outeiro), KU 124603 and 124601 (Utinga); Tucuruí, IBSP 46887, 46905, 47324, 47088; Margem direita do Rio Tocantins, Tucuruí, MPEG 16722; Tomé-Açú, IBSP 14839, 14842; Cametá, IBSP 2225; Jacundá a Itupiranga, Transamazônica, IBSP 40019; Porto Jarbas Passarinho, Rio Araguaia, Palestina do Pará, MPEG 11765, 12751, 12957, 12958; ECFP, FLONA de Caxiuanã, Melgaço, MPEG 19735, 20122; comunidade laranjal, Igarapé Laranjal, MPEG 19739, 19740; Ilha do Combú, Município de Acará, MPEG 19306; Barcarena, MPEG 15453, 16567; Ananindeua, MPEG 80, 16427, 16835; Fazenda Pirelli, Rio Ubipoca, Ananindeua, MPEG 18471; Parque Verde, Marituba, Município de Ananindeua, MPEG 18549; Ilha de Mosqueiro, MPEG 1113, 13277, 1526, 17690, 18630*, 2598; Beira do Rio Parauapebas, MPEG 16599; Oriximiná, MPEG 3268, MZUSP 5485; Porto Trombetas, Oriximiná, MPEG 19774; Vitória do Xingu, UHE-Belo Monte. Arroz crú, margem esquerda do Rio Xingú, MPEG 19872; Macapazinho, Castanhal, MPEG 5861, 9461, 10773, 11796; Boa Vista, Castanhal, MPEG 513, 594**, 1164, 1165, 1473, 1483, 1554, 2712, 4014, 4015, 4016, 5719, 5721, 6928; Santa Bárbara, Benevides, MPEG 2629, 3285, 6033, 8430; Genipaúba, Benevides, MPEG 6952, 18882; Margem direita do Rio Gorotite, MPEG 17021; Fazenda Morelândia, Santa Bárbara, MPEG 18480; Peixe-Boi, MPEG 684, 1415; Viseu, MPEG 10042, 10899, 14447, 16007, 16008, Km 220 da BR-316, MPEG 1670, 2207, 9575, Colônia Nova, Próximo ao Rio Gurupi, BR-316, MPEG 4330, 5161, 10303, 12922, 13895, 13896, 13926, 13927, 13928, 13931, 15852, 15854; Bom Jesus, Bragança, MPEG 5048, 5060, 6202, 6214, 6241, 7926, 7933, 7950, 8346, 11378, Cacoal, Augusto Corrêa, MPEG 572, 3202, 3209, 3804, 3806, 3808, 5407, 5409, 5418, 5429, 6505, 6514, 6515, 6463, 6671, 6683; Santo Antônio do Tauá, MPEG 1874, 5458, 5700, 6954, 19434*,**; Marauá, Curuçá, MPEG 7617, 5887, 5899, 7128, 7129; Capitão Poço, Boca Nova MPEG 1626, Santa Luzia, MPEG 1612, 2904, 12175, 12179, 12181; Igarapé-Açú, MPEG 893, 937; Área do N5, Serra Norte, Carajás, MPEG 16927; KU 124602; Trombetinha, Santarém Novo, MPEG 3478, 4155, 4782; Limão Grande, Ourém, MPEG 1637, 1639, 2166, 6173; Km 16 da Estrada do Acará, MPEG 8075, 13286, 15192; Km 11 da PA-222, Estrada de Marabá, MPEG 7462, 7467, 9489, 15164; Barcarena, KU 128105, 129879; Canindé, Rio Gurupi, MZUSP 4255; Jacaréacanga, MNRJ 09054; Óbidos, MZUSP 1255. *Estado do Maranhão*: ilha de Igaranha, IBSP 54987; Santo Amaro, IBSP 75168, 75167; Peri-Mirim, IBSP 21749, 21752; Itapecuru-Mirim, IBSP 31955; Carutapera, MPEG 18741; Puraqueú, BR-222, MPEG 15258, 16180, 16181; Gancho do Arari, Arari, MPEG 13480, 14630, 15034, 15623, 15625, 16067**, 16073, 16074, 16155, 16157; São Raimundo, BR-316, MPEG 10879; Paruá, BR-316, MPEG 10837, 12031, 12843, 13589, 13591, 13592, 13593; Aldeia Sapucaia (Guajajara), BR-226, MPEG 15015, 15563; Nova

Vida, 25 km from Rio Gurupi, MPEG 11128, 11129, 11130, 11163, 12279, 12281, 12282, 12283, 13740, 13741, 13742, 14789, 14790, 14793, 14795; Santa Maria, BR-226, MPEG 15009, 15231, 15573, 16136; Posto Nossa Sra. de Nazaré, Vitória do Mearim, MPEG 16093; Urbano Santos, HUFMA 282, 283, 284, 285, 286, 287, 288, 289, 290, 291, Urbano Santos, Faz. Santo Amaro, HUFMA, 229, 234, MPEG 20541, 20542, Urbano Santos, Faz. Bom Fim, HUFMA 51; Alcântara, HUFMA 281; Praia de Pranaquatiram São José de Ribamar, HUFMA 169; Campus da UFMA, São Luís, HUFMA 196. *Estado de Rondônia*: Nova Brasília, MZUSP 8516; Nova Colina, MZ-Polonoroeste, MZUSP 8506, 8507; Nova Esperança, MZUSP 8363, 8520; Porto Velho, CHUNB 33820; Espigão d'Oeste, IBSP 71634, MHNCI 9592; UHE Samuel, BR-364, Cuiabá-Porto Velho, MPEG 17755*,**, MPEG 17758; Km11 da linha 12B (lado direito), Ji-Paraná, MPEG 16869; Ouro Preto do Oeste, MPEG 16830, CZGB 2875. *Estado do Piauí*: Gilbués, MPEG 21695; Simplício Mendes, IBSP 42453; Valença do Piauí, MZUSP 5816; Piripiri, MNRJ 11364; São Raimundo Nonato, MNRJ 11364; Sítio Ouro Verde, PARNA de 7 Cidades, MPEG 21697; Teresina, IBSP 503, MPEG 21696; *Estado do Mato Grosso*: Apiacás, MZUSP 11175; Aripuanã, MZUSP 11143; Vila Bela de Sta. Trindade, MZUSP 11433. *Estado do Tocantins*: Miracema do Norte, IBSP 66422, 64423*,**; Lajeado, IBSP 64266, 64270, 64351, 64396, 64514, 64537, 64538; Palmas, CHUNB 23620, IBSP 65623, 66317, 65907. *Estado do Goiás*: Aruanã, MZUSP 2174; Araguatins, MZUSP 3835; São Salvador do Tocantins, MZUSP 12127; Santa Isabel, ilha do Bananal, Rio Araguaia, AMNH 90336; Pium, CHUNB 24750. GUYANA: Kartabu: AMNH 15152, 15153, 18176, 18177, 18178, 44906, 98200, 98201, 98202, FMNH 14839; Mazaruni-Potaro, near Kartabu, AMNH 21281, 137371; rockstone, Essequibo river, FMNH 26661; vicinity of Georgetown, AMNH 09624; Wismar, AMNH 61559; Dubluay ranch on the Berbice river 200 ft elev, AMNH 140899; FRENCH GUYANA: Cayenne, MCZ 1980, MNHN 1989-3077, USNM 451; Essequibo, FMNH 26662, USNM 84518; Rupuni Svannah, BMNH 1933.6.19.55; St. Jean et St. Laurent Maroni, MNHN 1895-18; GUYANA: "British Guyana", UMMZ 149833**; Essequibo, Pomeroon, USNM 85057; East Demerara, Georgetown, 50mi above, on the Abary River, USNM 141762; Northwest District, Kumaka (=Takama), USNM 164218; Northwest District, 5mi of Baramita, Golden city mining camp, USNM 535810; Mazaruni-Potaro, WSW of Mabura Hill (town), ca. 25mi (airline), Magdalen's crek camp, near (ca. 300yds) NW bank of the Konawaruk River, USNM 566268; Mazaruni-Potaro, WSW of Mabura Hill (town), ca. 25mi (airline), Magdalen's crek camp, near (ca. 300yds) NW bank of the Konawaruk River, USNM 535809; Berbice, CM 44305; Dunoon Demerara River, UMMZ 44672, 47763; Georgetown, UMMZ 80502; Aremu River District, UMMZ 56427; Barina-Waini District on road just S of Mabaruna, UTA 50170; KU 69831 Rupununi, N. of Acarahy Mts., W. of New River, 0m; SURINAM: Commewijne, Nieuw-Amsterdam, MZUSP 4541, 11292; Langamankondre, Marwoijne MZUSP 4543; Suriname, IBSP 13762; Paramaribo, AMNH 04425, 8131, 8147, 8687, 8688, 97715, 104614, 104615, BMNH 1946.4.4.16, BMNH 1946.4.4.17, BMNH 1946.4.4.18, KU 206417; along Coppename, AMNH 73843; Sara Creek, AMNH 104616; Saramacca, Raleigh Cataracts, Coppename River, 50m, AMNH 108799; Marowijne, Tepoe, UTA 15862, 15863, 15864, 15865, 15866, 15867; Raleighvallen-Voltzberg Nature Reserve, Foenjoe Islad, Coppename River, MCZ 152204; Coronie, 170 Km W Paramaribo, W Coppename River, Paibo-Nickerice Rd, MCZ 152596; 86 Km from Moenfoe on Moenfoe-Paramaribo stretch of Albina-Paramaribo Rd, MCZ 152597; on Brownsweg-Paranan Rd, 3 Km out of Brownsweg, MCZ 152598; Nickerie Dist. Paramaribo-Nickerie Rd, 7 Km W Henar, MCZ 156343; Coronie DOR on Paramaribo-Nickerie Rd, 15 Km W of Baskamp, MCZ 154840; Para, Lelydorps, De Craneweg nº 16, Wanica, 0m, KU 221553, 221554; Saramacca, La poole, FMNH 134734;

Suriname, USNM 6116; Marowijne, Mango, USNM 64625; Marowijne, Paloemeu, USNM 159052, 159053; Paramaribo, Kwatta, CM 44304. VENEZUELA: *Amazonas*, San Antonio, upper río Orinoco, USNM 83617; Amazonas, Rio Siapa, MHNLS 14011**; Bolivar, Aza, MHNLS 14656. BRAZIL-VENEZUELA boundary: Amazonas, Salto do Hua, Río Maturaca, USNM 83564, USNM 83570; San Isabel, AMNH 38097. COLOMBIA-BRAZIL boundary: Caruru, Alto rio Vaupés, AMNH 04463, AMNH 04464.

Leptophis bocourti.– ECUADOR: *Província Esmeraldas*: Zapallo Grande, MZUSP 8250; San Mateo, FMNH 28056; St. Javier, W. Ecuador, BMNH 1901.3.29.30; *Província de Imbabura*: Paramba, BMNH 1946.1.6.67; Carolina Ibarra, UMMZ 83710, 83711, 83709, 149938**. *Província Pinchincha*: 47 km S of Santo Domingo dos Colorados, Centro Científico Rio Palenque, 150-200m, USNM 285488.

Leptophis bolivianus.– BOLIVIA: *Departamento de Santa Cruz*: Santa Cruz, MNHN 7306; Província Sara, Las Yuntas 250m, CM 23, 2702; Buenavista, MCZ 27553, FMNH 35614, 35615, 35616, 35617,35618, 35619, 35620, 35621, UMMZ 149834**, 60701, 60702, 60709, 67973, 67974, 67975, 67976, 67976b, 67977, 67977b, BMNH 1927.8.1.183; Santa Cruz de La Sierra, IBSP 33287, San Antonio de Parapeti, AMNH 141443. *Departamento de Tarija*: Bermejo, FML 00591. *Departamento El Beni*: Upper Beni, ANSP 11335; Estancia Yutiole, ca. 20 km S San Joaquim, AMNH 104652, 104563, 104564*,**; Rurrinabaque, AMNH 22446; Rio Mamore, Santa Rosa, AMNH 101881, AMNH 101882; Rio Itenez, Puerto Capitán Vasquez, AMNH 101883; Valcadiez, Tumi Chucua, USNM 280392, 280393, 280394.

Leptophis coeruleodorsus.– TRINIDAD AND TOBAGO: *Port-of-Spain*: Port-of-Spain, AMNH 101309, BMNH 1964.1979; Golf Course Road, AMNH 85946; Cascade Road, Saint Anns, AMNH 81475. Vega de Oropouche, AMNH 85945. Federal District, E1 Valle, AMNH 59402, 59403; below Tree Station, Rio Grande Forest, Sangre Grande, AMNH 81478.

Guyaguayare, AMNH 81474, 81476. Only "Trinidad", AMNH 09023, 09024, 08718, USNM 5587, 15235, 17746, 59931, 59932, 59933, 60598. *Country of Saint George*: Mont Saint Benedict, Tunapuna, CM 6491, 6540; Saint. Augustine, BMNH 1964.1991; Tucker Valley, Chaguaramas, AMNH 64478A, 64478B; Cumuto, AMNH 81479; Diego Martin, MCZ 126381; Santa Cruz Valley, MCZ 100652, 100651. *Arima*: Arima Valley, AMNH 119443**, USNM 166715; Arima Valley above Simba, AMNH 77030; 10 min N Arima, Monte Bleu, FMNH 49937; smile part on Blanchisseuse Road, AMNH 81477; ca 2 mi S Simla-Quarry Road, Arima Blanchisseuse Road, FMNH 215817; Blanchisseuse Road, 21 mile marker, FMNH 219581. Arena, AMNH 73094. British West Indies, AMNH 9022. West Indies, Trinidad, AMNH 73146**. Caroni Swamp, MCZ 100656. *Country of Mayaro*: Plaisance, FMNH 49936. *Country of Saint David*: 3.1 mi N Junction Toco Road and Valencia Road, on Toco Road, FMNH 217234. Between Los Bajos and Palo Seco, Siparia-Erin Road 22-25 mile mark, FMNH 218776. Ward of Tobago, near Pembroke, AMNH 110472; Ward of Tobago, Cambleton, USNM 195127. St. John, USNM 228064. Charlotte Ville, ca. 50m uphill from Turpin residence, USNM 195163. ca. 0.75 NNW of Speyside, on windward Road, Milepost 25.1, USNM 228065. Milford Bay, SW Tobago, MCZ 11994, 11995, 12026. Tobago, UMMZ 90671. VENEZUELA: Venezuela, ANSP 5182. *Estado Apure*: 6 Km San Fernando de Apure, TCWC 46261, 46262, 46263. *Estado Guarico*: 15.6 Km N Altagracia, HWY 12, TCWC 58709. *Estado Monagas*: Laguna, Guanipa, Reserva Forestal Guarapiche, MHNLS 13595; Caripito, TCWC 59756, AMNH 98263, 98264; Distrito Sotillo, near Uracoa, CM 17387. Aragua, Limon, near Rancho Grande, AMNH 98446. *Estado Bolivar*: El Manteco, AMNH 114754; Hato La Yeguera, 32 Km E E1 Manteco, AMNH 114753; 61 Km N El Manteco, AMNH 114752. 16 Km S. El Dorado, in a goldmine, AMNH 138468; 22 Km E El Palmar on Rd to Rio Grande, MVZ 176257. *Amazonas*: 56Km NNW of Esmeralda, Rio Cunucununa, Belen, USNM 217213; Cerro de La Neblina, ca. 6.2Km NNE of Pico Phelps, Camp XI, USNM 562695; Rio Negro, 140m, vicinity of Neblina, base Camp on left blank of Rio Baria (=Rio Nawarinuma), USNM 562694. *Estado Miranda*: Rio Chico, 100mi E of la Guaira, USNM 27831; Sta. Lucia, 11 km ENE on Quebrada Siquire, CM 7433. *Guarico*: Caraquito, ANSP 18288. *Distrito Federal*: Caguital, Hacienda El Limon, 300m, MHNLS 4694. *Territorio Federal Delta Amacuro*: Cano Macareo, Delta Medio, 100m, MHNLS 13306. *Estado Cojedes*: Hato Itabana, 38 km, 5.0 de Las Vegas, 80m, MHNLS 6446. *Estado Carabobo*: Bahia de Patanemo, Puerto Cabello, MHNLS 56286. *Estado Sucre*: Los Arroyos, Distrito Benitez, 100m, MHNLS 13334.

Leptophis depressirostris.– NICARAGUA: Zelaya: UMMZ 149842**. PANAMA: Bocas del Toro, AMNH 117792*, 129763*.

Leptophis diplotropis.– MEXICO: Oaxaca: UMMZ 149844**, AMNH 106928*(Rio de La Golpadera, 2 km S Tejocotes).

Leptophis liocercus.– BRAZIL: *Estado da Paraíba*: Campina Grande, IBSP 51324; Mamanguape, CHUNB 29019; Mata do Buraquinho, João Pessoa, UFPB 4300; João Pessoa, DZUFRGS 1051. *Estado do Pernanbuco*: Recife, IBSP 17301; Dois Irmãos, Recife, MCN 5340*, 5671; Tapera, Município de Moreno, MCN 5648. *Estado de Alagoas*: São Miguel dos Campos, MNRJ 3955, 3974. *Estado de Sergipe*: Aracajú, IBSP 46053**. *Estado da Bahia*: Juazeiro à Curuça, MZUSP 10629; Itabuna, MZUSP 1273, CZGB 380; Porto Seguro, IBSP 54273; Caravelas, IBSP 966; Jaguarari, IBSP 33352; Itaparica, IBSP 52353; Poções, IBSP 67645; Ilhéus, IBSP 54201, MZUESC 2002*, CZGB 108, 281, 555, 1149*,**, 3160, 3243, 3436; Coribe, CHUNB 6640; Ibicaraí, MZUESC 0241, 0291**, 0741, CZGB 8987; Camamu, MZUESC 0326, 1082, 3032, CZGB 8643; Fazenda Bom Fim, Almadina, MZUESC 0120; Santa Clara, Rio Mercury, MCZ 2989; Itapebi, CZGB 6960, 8765; Jaguaquara, CZGB 9255.

Mutuípe, CZGB 6562, 8200; Belmonte, CZGB 4434, 7530; Itagibá, CZGB 6795; Canavieiras, CZGB 2062; Barro Preto, CZGB 3301; Gandú, CZGB 3878; Fazenda Bela Conquista Itiúba, CZGB 8715; Governador Lomonto Junior, CZGB 3255, 3406, 3437, 4457; Conjunto Boa Sorte, Mucuri, CZGB 3984. *Estado de Minas Gerais*: Várzea da Palma, MNRJ 6672; Pedra Corrida, IBSP 9477, 9612**; Mocambinho MZUFV 842, 913. *Estado do Espírito Santo*: Porto Cachoeiro de Santa Leopoldina, MZUSP 734; Sítio Goaporini, MNRJ 4846*,**; Estação Araguaia, Município Domingo Martins, IBSP 8403**; Estação Itá, IBSP 9121*; Guandú, IBSP 8271; Vitória, MCZ 2978. *Estado do Rio de Janeiro*: Cabo Frio, IBSP 21089; Duque de Caxias, MZUSP 1940; Macaé, MZUSP 4214; Pedra da Guaratiba, MBML 285; Parque Natural Municipal da Serra do Mendanha, MNRJ 10966, 10967; Rio de Janeiro, USNM 120830.

Leptophis marginatus.– BRAZIL: *Estado do Rio de Janeiro*: Rio de Janeiro, MZUSP 2339; Pedra da Guaritiba, MBML 285; Manguinhos, UMMZ 109053. *Estado de São Paulo*: "São Paulo", UMMZ 62803, 149835**; Pereira Barreto, IBSP 54055**, MHNCI 4512**; Ilha Solteira, IBSP 38192, 36961, 38966; Santo Anastácio, IBSP 37444*; UHE Engenheiro Sérgio Motta, IBSP 60028; Presidente Epitácio (Rio do Peixe), IBSP 63731; Teodoro Sampaio, ZUEC 966, 995*. *Estado do Paraná*: Ouro Verde do Oeste, MHNCI 10356; Diamante D'Oeste, MCP 16239; Foz do Iguaçú, IBSP 44678, 44688, MHNCI 3871, 8423, 11781; Guaíra, IBSP 32851, MHNCI 632, 633, 2773, 2855; Capitão Leônidas Marques, MHNCI 8424; Itambé, MHNCI 8109; Palotina, MHNCI 8100; Três Barras do Paraná, MHNCI 8422; Nova Prata do Iguaçú, MHNCI 2246; Margem do Rio Ivaí, MCN 3371; Vale do Rio Ivaí, MHNCI 8303, 8304, 8305; Altônia, MHNCI 7440; Boa Vista da Aparecida, MHNCI 8548**; Diamante do Norte, MHNCI 8014, 8017, 8221, 11717; Diamante do Norte (Estação Ecológica Caiuá), MHNCI 10559; Porto Bragado, MHNCI 10355. *Estado do Mato Grosso do Sul*: Lagoa

Mandioré, Amolar, MNRJ 339, 216, 0339; Miranda Estância, MZUSP 8259, 8256; Anaurilândia, IBSP 59556*, 59557; Serra do Amolar, Corumbá, RPPN Acurizal, UFMT 1423, 1435, Fazenda Gaíva, UFMT 1437, 1491; Correntes, IBSP 7620; Campo Grande, IBSP 19628, 26764; Anastácio, IBSP 50247; Ponta Porã, IBSP 16427, 31831, 41146, 42244; Aquidauana, IBSP 18470; Itaum, IBSP 16722; Itaquiraí, IBSP 49908; Dourado, IBSP 27587, 44058; Agachi, IBSP 14278, 14601; Salobra, UMMZ 109052*. *Estado do Mato Grosso*: São Luis de Cárceres, MNRJ 0735; Cárceres, IBSP 49061; Estrada Poconé-Porto Cercado, MZUSP 7510; Porto Esperidião, MZUSP 6413; Porto Velho, Rio Tapirapés, MZUSP 3764; UHE Manso, MZUSP 11939, 11949; Chapada dos Guimarães, CHUNB 15440, 15441*,**, 15442, 15443, 15444, 15445, 15446, 15447, 15448, 15449¸ 15450, 15451, 15452**, 15453, 15454, 15455, 15456, 15457, 20423*,**, 20424, 20425; APM Manso, Chapada dos Guimarães, UFMT 0628, 0629; Estação Ecológica Serra das Araras, Barra do Bugres, UFMT 0079*; Rodovia Transpantaneira, Km11, Poconé, UFMT 0255; Fazenda Boa Vista, Poconé, UFMT 0040; Garimpo Saracura (do Alemão), Poconé, UFMT 2202; Fazenda Santa. Inês, Poconé, ZUEC 1233; Poconé, MHNCI 7910; UHE Guaporé, Vale de São Domingos, UFMT 2142*, UFMT 2143; Fazenda São Francisco do Perigara, Barão de Melgaço, UFMT 0252; Baía dos Coqueiros, Pirizal, Nossa Senhora do Livramento, UFMT 2221; Barão do Melgaço, ZUEC 0568; Barra do Tapirapé, AMNH 93593, 93594, 93595; Serra do Roncador, BMNH 1972.414; Miranda, USNM 100748. BOLIVIA: *Departamento de Santa Cruz*: Puerto Suarez, CM 314. PARAGUAY: "Paraguay", ANSP 5514. *Departamento Central*: Assunção, IBSP 10092. *Departamento de San Pedro*: FML 00637. *Departamento de Canindeyú*: Reserva Mbaracayú, Lagunita, TCWC 90574; Colonia Indigena Chupa Pou, about 35 km NE, AMNH 143299. *Departamento de Cordillera*: 12 km N Tobati (by road), MVZ 110989*. *Departamento Presidente Hayes*: Primavera, Alto Paraguay, BMNH 1971.430. *Departamento Itapua*, vicinity of El Tirol, 19.5 km (by road) NNE of Encarnation, on highway 6, USNM 253553; Hotel "El Tirol", 18 km E Encarnation, Ruta 6, CM 109293. *Departamento del Amambay*: Parque Nacional Cerro Cora, near Comandancia, CM 94311. URUGUAY: *Departamento Artigas*: Arrocera Conti, 20 km W. de Colônia Palma, ZVC 4401, 4529, 4530. ARGENTINA: *Província de Formosa*: Puerto Cano, MHNCI 4795; Formosa, FML 02034, 11273, 11274, 11292, 11304, 11568, 11570, 11571, 11572, 15924; Pilagás, FML 01628; Pilcomayo, FML 01624*,**; Reserva Ecológica El Bagual Dto Laishi, FML 11569. *Departamento General José San Martin*: Itiyuro, FML 01076; G.J. San Martin, FML 00591. *Departamento de Jujuy*: Ledesma FML 00598, 00619. Rio Zapenaga, frontiére du Chaco de Santa Fé et du grand Chaco de Jeaño, MNHN 1904-98.

Leptophis mexicanus.– GUATEMALA: *Departamento de Petén*: UMMZ 149847**. MEXICO: Terminal camp, near Tampico, AMNH 43360**. NICARAGUA: Cooley plantation, 50 mi up Rio Grande River, AMNH 12664*.

Leptophis nigromarginatus.– BRAZIL: *Estado do Amazonas*: Amazonas, Rio Amazonas, MCZ 156332; Manjuru, AMNH 114262; São Paulo de Olivença, Rio Amazonas, AMNH 56160; Benjamin Constant, MNRJ 738; Manaus, BMNH 97.12.29.15; Tefé, MCZ 2980, 2958, IBSP 15060, IBSP 15080; Rio Ituxi, MPEG 20333**; Alto Solimões (área de 214 mil km2), MCN 4163, Manacapurú, MZUSP 8647; Miriti River, Manacapurú, AMNH 67956; Boca do Acre, MZUSP 5751, CM 2008; Pranquina, Cremarea, CM 2007; Boca do Tefé (confluent of rio Tefé and rio Solimões), MNHN 1900-462, MNHN 1900-463. *Estado do Pará*: Ilha do Mojú, Rio Japurá, MZUSP 6602, 6603; Prainha, LPHA 2566; Santarém, LPHA 1731*, 2792**, 2938, MCP 7905 (ilha de São Miguel), 7575 (Ramal do Coelho, Cucuruna), 10605 (Costa do Tapará); Monte Alegre, IBSP 40514 (Faz. Bom Jesus, Curral Grande), 40830; Taperinha, MZUSP 5187. *Estado do Acre*: 5 km N. Rio Branco, MPEG 18249; about 5 km from Porto Walter, Rio Juruá, MPEG 20383**; Tarauaci, IBSP 18528, 18530**; Rio Branco, IBSP 54956; Porto Walter, MZUSP 7355, 7370, 7371; Rodrigues Alves, Rio Crôa, MZUSP 14116; Feijó, DZUFRGS 1052; Brasiléia, MZUFV 71. *Estado de Rondônia*: Alto Paraíso, MZUSP 8271; Rio Guaporé, IBSP 22156. COLOMBIA: *Departamento del Caquetá*: Morelia, ANSP 25646, 25647. *Departamento del Magdalena*: Bonda, MCZ 11859. *Departamento de Cundinamarca*: Bogotá, IBSP 9186. *Departamento del Amazonas*: Leticia, AMNH 126464, 126465, FMNH 83039, MCZ 48985, 145077, USNM 307003, CM 55621, 55622, 55623**; Isla de Santa Sofia II, 20 mi NW Leticia, MVZ 164266; Isla de Sta Sofia, 35 km abv Leticia, MCZ 141089; 6 Km NW of Leticia, MVZ 172125; Igarapé Belém, near Rio Solimões, ca '70 Km E Letícia, AMNH; Rio Apapóris, MCZ 53229, 53230, 53231.115022; Gingoje, MCZ 11859, 53232, 53233. Vicinity of Riberalta, AMNH 22258, 22259. *Departamento del Putumayo*: San Antonio, Rio Guamez, 400, KU 140410. BOLIVIA: *Departamento del Beni*: along Beni river, AMNH 22267, 22268; Provincia Vaca-Diez, Villa Bella, CM 366. GUYANA: *Upper Takutu-Upper Essequibo Region*: Koranambo, AMNH 60792. ECUADOR: *Província de Sucumbios*: Rio Napo, Cuyabeno, MZUSP 9535; Santa Cecilia, KU 105409, 107041, 107042, 112279, 126041, 126042, 121900, 121901, 121902, 148344, 148345,148346, 148347, 148348, 148349, 148351, 155512, 155513, 175424, 183519; Limoncocha, KU 98629. *Província de Napo*: Rio Araguarico, 200 m SW mouth of Rio Cuyabeno, 200m, FMNH 218506; on road halfway between Puerto Napo and Misahualli, UMMZ 177889; 6 Km E Tena, Fischer Funca, along Rio Napo, TCWC 65017, 67309. Rancho Johanna, 3 Km N Tena, TCWC 68730. *Província del Pastaza*: Cabeceras del Rio Bobonaza, USNM 211030,211031, 210032, 210033. In the immediate environs of Arajuno, 537 m, UTA 37975. PERU: "Peru", ANSP 11350, 11351. *Departamento de Amazonas*: Specific locality unknown, Rio Cenepa, probably vicinity of Huampam, MVZ 163293. *Departamento de*

Ancash: Pucalpa, IBSP 21833, 21834. *Departamento de Cajamarca*: 1 Km (airline) N to NNW Monte Seco, 1320-1340m, Rio Zana, FMNH 231776*. *Departamento de Huanuco*: Tournavista, 200m, AMNH 104294. *Departamento de Junín*: Norman Ranch, Rio Ipoki, ca 3mi "before its entrance into Rio Perene", elev. ca. 700 m, USNM 193809; mouth of Rio Tambo, upper Rio Ucayaly, AMNH 52900. Huachi Yaku, middle Morona, AMNH 52472. *Departamento de Madre de Dios*: Madre de Dios, SSW of Puerto Maldonado, ca. 30Km (airline), Tombopata Reserve, Explorer's Inn, USNM 222357, 247511, 247512, 269032; Madre de Dios, FMNH 40032; Cuzco Amazonico, 15 Km E Puerto Maldonado, 200, KU 155513, 207785, 220194, FMNH 168378; Puerto Maldonado, AMNH 56140, 56141, LSUMZ 35249. *Departamento de San Martin*: Moyobamba, AMNH 52961; Pachisa, AMNH 52564, 52567. *Departamento de Ucayali*: Yarinacocha, Pueblo San Francisco, USNM 238382; Rio Ucayali, Pucallpa, FMNH 45574, 56156, 56157, 56159, IBSP 14803. *Departamento de Loreto*: Colonia Calleria, Rio Calleria, 15 Km from Ucayalli, CAS 93208; Rio Ucayali, AMNH 53206, MCZ 3789, 3796; Río Ucayali, Yarinacocha, 160m , FMNH 45573; Río Tamaya, Río Ucayali, Sobral, AMNH 55326; Rio Tamaya, AMNH 52334; Pampa Hermosa, Río Ucayali, AMNH 52028; Pampa Hermosa, AMNH 53504, 53513, 53518, 53430, 55727, 55728; Pampa Hermosa, Cushabatay, AMNH 53234, 53235, 53380, 53381, 53382, 55384, 55349, 55430, 55431, 55436, 55454, 55460, 55461, 55479, 55480, 55745, 55734, 55742, 55751, 55755, 55762, 55799, 55803, 55962, 55964, 56007, 56013, 56015; Panya, Rio Cushabatay, AMNH 52345, 55954; Suhuaya Isla, Contamana, AMNH 52296, 53008; Contamana, AMNH 52165, 53564; Rean Rean, Lago Suhuayo, Contamana, AMNH 52885, 53010; Punga, Rio Tapiche, AMNH 52080, 52082, 52084; Peru-Brazil border on Rio Tapiche, AMNH 52192; Upper Ucayali River AMNH 71132, 71133; Minchana, TCWC 38196, 39109, 39110, 42174, 44658; Minchana, on Rio Nanay, TCWC 44090, 44659; Centro Union, TCWC

42177; Paraiso, TCWC 42176; Moropon, TCWC 38047, 38193, 38194, 39108, 42170, 42171, 42172, 42173, 44660, 44661; Igarapé Champuia, Alto Curanja, MZUSP 3346; Pevas, MNRJ 2982, 3018; Requena, Monte Carmelo, AMNH 55512, 55515, 55574, 55604, 55612, 55621, 55623, 55644, 55637, 56036; Roaboya, AMNH 52233, 52559, 52892, 53088, 53443, 54421, 54430, 54436, 54443, 54444; Roaboya, Rio Ucayali, AMNH 52544, 55697, 56115; Rio Samiria and Parinari Canon, AMNH 57287, 57288, 57289**, 57290, 57291, 57292, 57293, 57294, 57295; Iquitos, Lupuña Isla, AMNH 53225, 56092, 56093; Iquitos, Rio Itaya, AMNH 53684, 54116, 54865, 55076, 55080, 55125, 55140, 55211, 55246, 55273, 55278, 55311; near Iquitos, Quisto Cocha, LSUMZ 48419; Iquitos, TCWC 38195, 40539, 42175; 44657, AMNH 52044, 52045, 52049, 52121, 52137, 52153, 52230 , 52320, 52419, 52421, 52501, 52508, 52518, 52520, 52529, 52530, 52231, 52597, 52598, 52629, 52647, 52653, 52669, 52723, 52732, 52733, 53047, 53074, 53154, 53226, 53271, 53391, 53396, 53397, 53402, 53411, 53412, 53610, 53648, 53685, 53711, 53759, 53829, 54084, 54134, 54153, 54210, 54216, 54225, 54233, 54335, 54345, 54644, 54715, 54580a, 54810, 54940, 54894, 54976, 54984, 55908, 56037, 56106; Yarinacocha, LSUMZ 26799, 26800*; Orellana, AMNH 52094, 52903, 54575, 54580b, 54588, 54614, 55672; Pebas, ANSP 5200, 11634, CAS 12498; Pebas, Ampiyacu River, E Peru, CAS 8728; Rio Curanja, Balta, LSUMZ 26801, 26802, 26803, 26804, 26805, Sarayaco, NE Peru, BMNH 81.5.13.58; Puesto Carachama, Lower Río Tigre, AMNH 53185; Lower Napo, Lago Miranio, AMNH 53299; Shiriara, Rio Nanay (1 long day in canoe from mouth), AMNH 56079; upper Amazonas, FMNH 11184, BMNH 1946.1.5.7; Rio Alto Tapiche, AMNH 56035; Lower Pisqui, AMNH 56026; Rio Porolongo, AMNH 52710; Nauta Cano, Rio Maranon, 0m, KU 220505; Gamitanacocha, Bajo Amazonas, FMNH 45570; 5 mi below Boca de Rio Piedras, FMNH 83304. Specific locality unknown, FMNH 40031.

Leptophis occidentalis.– COSTA RICA: 2.5 km E., 4 km N Chitaria, 600 m Caratgo, MVZ 79623**. Colorado Bar, AMNH 12670. *Província de Heredia*: La Selva Biological Station, MVZ 215639; 10 Km WSW Puerto Viejo de Sarapiqui, MVZ 217614; Barro Colorado, 0, KU 100627; E of Puerto Viejo on Rio Puerto Viejo, La Selva Field Station, 50m, UMMZ 145883. *Província de Cartago*: Mountain above Turrialba, about 6 Km NE, CM 69116; Turrialba, Institute of Agiculture, AMNH 69712; Turrialba, 600, KU 34044, 35642, 34898; Turrialba, 600, KU 30996; IICA, Turrialba, MCZ 56090; Turrialba, 2mi SE of Cartago, USNM 129072; 1.4 mi SW Chitaria via Hwy, MVZ 80023. *Província de San Jose*: Quepos, 0, KU 125480; near Parque Nacional Carara, Bajo Carara on rd from Bajo Carara to sur, TCWC 84615. *Província de Guanacaste*: Pozo Azul, AMNH 17363; Tilaran, 0m, KU 35643; 2 km E Tilaron, 780, KU 86582; Tenorio, 0m, KU 34902. Alajuela, Cariblanco, 0, KU 34043. *Província de Puntarenas*: Grenaco, 15 Km E 55 Pontrero Grande, LSUMZ 8758; Julieta, Finca La Ligia, LSUMZ 9635; Golfito, 0, KU 31958, 63841, MCZ 69183; 4 Km N, 2 Km W Dominical, 35m, KU 63840; 2Km of Rincon de Osa, Osa Tropical Science Center, collected 100m N of Casa de Santos, USNM 219593; S of San Vito, Finca Las Cruces, UMMZ 128818; 1.9 mi S Rio Tarcoles, HWY 34, north branch of Quebrada Bonita, TCWC 83392. Barrana, FMNH 35893; Monteverde, 1400m, FMNH 229917. *Província de Limon*: Siquirres, 20 km N of Hamburg farm, Santa. Clara District, between Reventazon River and Parismina River, USNM 68859; Portete, ca. Smi N. Limon, AMNH 90625; La Lola, UMMZ 117686; Santa Marta de Siquirres, ANSP 32396; Vicinity of Squirres, ANSP 32397; Comadre, Limón, CM 107359. Alajuela, San Carlos, UMMZ 131431. Tabasco, 7.2 mi W Cardenas, 180, LSUMZ 33367. HONDURAS: No specific locality, AMNH 47013**, 47014**. *Departamento de Atlantida*: on main land opposite of Hag Island, UTA 15868, 53196. Rio Coco, (=Segovia River), USNM 24531, 24532. *Departamento de Olancho*: confluence of Rio

Wampu and Rio Aner, 100m, USNM 319958; 1.5 km N Catacanas, LSUMZ 28447. *Departamento Gracias a Dios*: Mocorón, UTA 53511, 53173; Laguna, Palacios, BMNH 1985.1301. Crique Ibantara, USNM 563500; Kaska Tingni, 70m, USNM 559661, 559662, 559663, 559664; 60m, USNM 561111, 559666. NICARAGUA: Cukra, AMNH 12667, 12668. Cupitna Camp, AMNH 12718, 12669. Musawas, Waspuc River, AMNH 75224, 75225, 75226, 75427. *Departamento de Chontales*: San Miguelito, AMNH 12666. *Departamento de Rio San Juan*: Machuca, San Juan del Norte, USNM 15626, 19569, 19570, ANSP 5288. *Region Autonoma Atlantico Sur*: Bluefields, 90mi Northwest, USNM 37344. Zelaya, Wounta Haulover, Mosquito Coast, ANSP 15434; Zelaya, Rio Siquia, 7 Mi above Rama, UMMZ 149857**, 79768. Maltagalpa, Hacienda La Cumplida 3000 FT, UMMZ 117685. PANAMA: Cerro Azul region, AMNH 119881. *Provincia de Coclé*: Aguadulce, AMNH 67060, El Valle de Antón, CAS 98550; El Valle, MVZ 66606. Colon, Achiote, 40, KU 75726. S slope Cerro de La Campana, 850, KU 75725. *Província de Panama*: La Joya, Pacific side, ANSP 25078; Nueva Gorgona, AMNH 90038, 90039, 90040, 90041, 90042, 90043, 90044, 90045, 90046, 90047, 90048, 90049, 90050, 90051. *Província de Bocas del Toro*: Sibube, USNM 150025; Punta de Pena, USNM 38671; Isla de Colon, La Gruta, 30m, KU 107768, USNM 338257; Rio Chonguinola near Quebrada El Guabo, 50m (16km airline W. Almirante), AMNH 119080; vicinity of Almirante, USNM 279079, MVZ 149582, MVZ 149581; Almirante, 10, KU 80227, 80228, 80229, 80230, 107766; 1.5 mi W Almirante, 10, KU 107767; 11 Km NW Almirante, 600, FMNH 154032. *Província del Darien*: Jaque, USNM 161229; Yaviza, MVZ 83434, 83435; Tacarcuna, 550, KU 75727, 75728; El Real, 130m, KU 107776; Atlantic side of Darien, USNM 24504. *Canal Zone*: Empire, USNM 59928; Lower Chilibre River near Panama Canal Zone BNDY Line, UMMZ 95337; Barro Colorado Island, FMNH 13413, UMMZ 124164, USNM 89401; Barro Colorado Island, 560, KU 75724; Sumitt, FMNH

131313, 130735, UMMZ 155694, 155718; 2.4 Mi NNW Summit Gardens, UMMZ 152914; Juan Mina, Chagres River, 0m, KU 107773, 107772; Farjan Navy Base, 0m, KU 110644; Coco Solo, 0m, KU 107771; Galeta Island, 0m, KU 107770; Fort Sherman, 60m, KU 107769; HWY to Gamboa from Galliard, UMMZ 148006; Gamboa, AMNH 32816; Margarita, UMMZ 152915; east side of Madden Lake, USNM 193392. *Província de Colon*: Ciricito, CAS 71425; Colon, USNM 38506. Las Cumbres, 150m, KU 110643. San Blas, Camp Sasardi, 12m, KU 110642. ca 5km NW Pacoa, 0m, KU 107774. 14.4 Km SSW Bejuco, 40m, KU 107775. Around Panama city, FMNH 216246. EL Valle, FMNH 42560. Chorrea, FMNH 16742. Gatun, FMNH 16743, USNM 50106. Tabernilla, FMNH 16744. El Valle, FMNH 47461. *Província de Chiriqui*: Vic. N of Boquete, CAS 78911, 78912, 78913, 78914, 78915, 78916, 78917, 78918, 78919, 78920, 78921, 79034, 79035; Chiriqui, UMMZ 57907; Progreso, UMMZ 149836**, USNM 161239; Chiriqui, Obispo Station, on railway, MCZ 2719. Colon, Culebra, UMMZ 61285. Chepo, USNM 48958. Ancon, USNM 51909. Los Santos, USNM 51910; Los Santos, Los Palmitas, USNM 148220. Old Panama, USNM 50124. Veragua, Mojarra, USNM 129874, 29875. La Jagua, USNM 129927. near Fort Kobbe, USNM 140700. Venado Beach, USNM 193377, 193378, 531871, 531872. *Comarca de San Blas*: Armila, USNM 150132, 150133. Duran, Guayas, USNM 210034. Bahu, MCZ 69745.

Leptophis praestans.– BELIZE: *Belize District*: Belize City, AMNH 126430. Coquericot, Cayo, UMMZ 74905. Toledo: Bladen Nature Reserve, Richardson Creek Camp on Richardson Creek, 300m, USNM 498218; Bladen Nature Reserve, Ek Xux Camp on Bladen Branch, 300m, USNM 498219; Bladen Nature Reserve, Teakettle Camp on Bladen Branch, USNM 496721; Bladen Nature Reserve, Teakettle Camp on Bladen Branch, 140m, USNM 496722; about 2mi SE Big Falls, Rio Grande, CM 105883; Blue Creek Village, vicinity of Slattery Field Station, UTA 11068, 12685, 11069. *Cayo District*: Cohuene Ridge, USNM 80713; Central Farm, MCZ 71648. Stann Creek, 4 mi W Dangriga, CM 112117. GUATEMALA: *Departamento de Izabal*: Sierra de Santa Curz, Finca Semuc, La 35, ca 700, UTA 28408, 28407; Sierra de Santa Cruz, Finca Semuc, headquaters, near Rio Semuc, 410m, UTA 26217; Sierra de Santa Curz, Finca Semuc, ca. 1 Km S headquaters, near Rio Semuc, 472m, UTA 22175, 26659; Morales, Sierra de Coral, Carreteria Quebradas-San Miguelito, Acampamento 1.160m, UTA 37057; Morales, Sierra de Coral, road between Quebradas-San Miguelito, Primer Acampamento, UTA 37056; Morales, Sierra de Coral, Aldea San Miguelito ca. 480m, UTA 38124; Montanas del Mico, Las Escobas, 5.1 rd km WSW Puerto Santo Tomas, ca. 150m, UTA 28405, 28634; Los Amates, Sierra del Espirito Santo, Aldea Santo Antonio, UTA 28406; Los Amates, 650, 800m elev. on road above Cooperativa Oaxilon, Aldea Vista Hermosa, Gualan, Zacapa, KU 190991; Los Amates, Aldea Vista Hermosa, 650, KU 190992, 190994, 190995, 190996, 190997, 190998; 5.1 Km W Santo Tomas, Las Escabas, 146, KU 187326; 5.1 Km W Santo Tomas, Las Escabas, 122, KU 191000, 191002, 191003; 5.1 Km W Santo Tomas, Las Escabas, 152, KU 190999; Bobos plantation, near Playtas, FMNH 20089; Quebradas, FMNH 20489. *Departamento de Alta Verapaz*: Finca San Juan, UTA 46627; Finca Chama, UMMZ 89974. *Departamento de Zacapa*: Gualan, Aldea Dona Maria, 137, KU 190993. "Guatemala", USNM 6754, 6754b. *Departamento de Petén*: La Libertad, UMMZ 74904, 79053, 149839**; La Libertad, Parque Nacional, Sierra Lacandón, Distrito Yaxchilón, UTA 46134**; La Libertad 1 mi N Rio Subin Sta Tereza, UMMZ 74851; 13 Km NNW Chinaja, 0, KU 55716, 57161; Nueva Agua, USNM 71366; Tikal, UMMZ 124341, 124342; ca. 10 Km SW of main aguada at Tikal on El Cruce-Tikal Road, UTA 39227; Tikal, Las Escobas, UTA 35018. HONDURAS: "Honduras" through NYZS, AMNH 32341. *Departamento de Atlantida*: Lancetilla, AMNH 46973, 46974; along Rio Cangrejal, ca 12 Km SSE La Ceiba, 100, KU 101449; Tela, USNM 84259, 120831; Parque Nacional Pico

Bonito, Quebrada de Oros (tributary of Rio Viejo), 1000m, USNM 559667; 6.5 mi E La Ceiba, mts above Piedra Pintada, LSUMZ 28401. W. of San Pedro, Santa Ana, bottom of Santa Clara Canyon, FMNH 5292**, 5293, 5294**. Progreso, MCZ 26859. *Departamento de Colon*: 5 km SW Trujilo, LSUMZ 21754. *Departamento de Cortes*: 3 mi W San Pedro Sula (Santa Ana Canyon), LSUMZ 28400. MEXICO: *Estado de Quintana Roo*: Distrito Xkanha, Campeche- boundary, AMNH 07861; 35 Km NE Felipe Carrilo Puerto KU 301068; 0.7 mi S Tulun Pueblo, LSUMZ 38599; Felipe Carillo Puerto, UMMZ 113571. *Estado de Tabasco*: Macuspana, KU 41603; 31 min. W. Cardenas, AMNH 88836. *Estado de Veracruz-Llave*: Veracruz, FMNH 208220; Lower falls of Rio Quezalapim, Veracruz, TCWC 19155; 7.7 mi NW Sontecomapan (by road), UTA 2643, 2646; 16.4 mi N Juan Diaz Covarrubias, UTA 2775; Dos Amates, CM 52758; Cruzolapon, Arroyo Ahuacapan, TCWC 21980. *Estado de Oaxaca*: Sierra Juarez, Metates, 902 m, UTA 14212; Sierra Juarez, Metates, UTA 12358. *Estado de Campeche*: near Xpujil, KU 301067. *Estado de Yucatán*: Colonia Santa Maria UMMZ 76165. Quintana Roo-Chiapas: Sabana de San Quintín, KU 94133. Lake Miramar, USNM 136964. *Estado de Chiapas*: Solusuchiapa, 4.6 Mi N, UMMZ 126203; Solusuchiapa 3.8 Mi S 1600 FT, UMMZ 126202; Florida, 50 Km E Altimirano, TCWC 19544.

Leptophis urosticus.– COLOMBIA: *Departamento del Choco*: Peñalisa, Condoto, BMNH 1914.5.21.38; MCZ 13298, AMNH 8062; Pizarro, FMNH 43737; El Rio Condoto Camp Peñalisa Eastern tributary of Rio San Juan, UMMZ 55528**. *Departamento de Risaralda*: about 7 km (airline) SE Santa Cecilia, south bank Rio San Juan, 480 m elev., AMNH 115932, 115933. *Departamento del Cauca*: Quebrada Guanguí, 0.5 km above Rio Patia (upper Saija drainage), AMNH 107930, 107935, 109751, 109752, 109753*, 109754. Valle de Cauca, Llanobajo, 80m, KU 169951.

Mastigodryas bifossatus.– BRAZIL: *Estado do Maranhão*: Coroatá, MPEG 2370**. *Estado de São Paulo*: São José dos Campos, IBSP 18306**. *Estado do Paraná*: Jacarezinho, IBSP 24282**. *Estado do Rio Grande do Sul*: Butiá, MCP 129*; Dom Pedro de Alcântara, MCP 95*.

CAPÍTULO III

Redescription of *Leptophis cupreus*, a Rare South America Colubrine Snake

A ser submetido para Copeia

COVER PAGE

Title: REDESCRIPTION OF *LEPTOPHIS CUPREUS*, A RARE SOUTH AMERICA COLUBRINE SNAKE

Name of authors: Nelson R. Albuquerque[1]

Running head: Redescription of *Leptophis cupreus*

Key words: Distribution, Coloration, Hemipenis, Holotype, *Leptophis*, Serpentes.

Author addresses:

[1] Laboratório de Sistemática de Vertebrados. Pontifícia Universidade Católica do Rio Grande do Sul, Avenida Ipiranga, 6681, 90619-900 Porto Alegre, RS, Brazil; E-mail: nelson.rufino@pucrs.br. Send reprints requests to this address.

Leptophis cupreus is redescribed based on nine specimens, including its holotype, which was considered as lost. It is characterized by having a uniformly copper dorsum, which distinguish *L. cupreus* from all other known species of *Leptophis*. I present herein the first photos of the holotype and living specimen of *L. cupreus*. Description and illustrations of the everted hemipenis are presented. The new specimens extend the geographic distribution of *L. cupreus* about 1.500 km eastward from San Lorenzo, Ecuador to Cerro de La Neblina, Venezuela.

Leptophis cupreus is a rare colubrine snake known only from very few localities. It was resurrected by Peters and Orcés-V (1960) based on the analysis of five specimens collected in eastern Ecuador. Subsequently, Dixon and Soini (1977) reported two specimens for Iquitos region, Peru, resulting in the seven specimens currently recognized. As part of an ongoing revision of *L. ahaetulla* (Albuquerque, ms), I examined 10 new specimens of *L. cupreus*, including its holotype which was considered as lost by Peters and Orcés-V (1960), plus the specimens reported by Dixon and Soini (1977). The new specimens make possible a more detailed description including within-species variation, range extension, and hemipenial morphology.

MATERIAL AND METHODS

Institutional abbreviations of collections that loaned or provided access to specimens are as listed at http://www.asih.org/codons.pdf. Nine specimens from 10 localities were examined. The map was made into the ArcView GIS 3.2 software with some localities obtained from the on line version of the Global Gazetteer 2.1 by Falling Grain Genomics (http://www.fallingrain.com/world/). Ventral scales were counted according to Dowling (1951). All measurements were made to the nearest 0.1 mm using digital calipers, except for snout-vent and tail lengths (SVL), which were taken with a flexible ruler to the nearest millimeter. Bilateral variation is reported as “right/left”. When no everted hemipenis was available, the sex of each specimen was determined by making a post-cloacal incision between the 10th to 12th subcaudals and checking for the presence of *in situ* hemipenes. The hemipenial description was based on the right organ of ICN 390, which was prepared following Pesantes (1994). Terminology for hemipenial morphology followed Dowling and Savage (1960).

RESULTS

Leptophis cupreus Cope (Fig. 1, 2A, B)

Thrasops cupreus Cope, 1868. Proceedings of the Academy of Natural Sciences of Philadelphia 20: 96–140. Type Locality: “From the Napo and Marañón”.

Leptophis cupreus; Peters and Orcés-V, 1960, Beitraege zur Neotropischen Fauna, 2: 139–141; Peters and Orejas-Miranda, 1970, United States National Museum Bulletin, 297: p. 164. Mertens, 1973, Studies on the Neotropical Fauna and Environment, 8: 141–154.

***Diagnosis*.—** *Leptophis cupreus* can be distinguished from its congeners in having an uniformly copper dorsum. The venter is also coppery but slightly darker than the dorsum, with dark brown and white streaks.

***Description of holotype*.—** head distinct from body; pupil round; narrow black ocular stripe reduced to black margin on second and third supralabials, covering lower postocular, anterior temporal, lower posterior temporal, and upper edges of last three supralabials; this stripe disappearing two scales posterior to last supralabial; loreal present on left side; parietals longer than broad and in contact with upper postocular; keels on all dorsal scales of trunk (reduced and often indistinct on scales of vertebral row), except on first dorsal rows, where they are absent; dorsal scales of tail without keels; anal plate divided. Single apical pit present on all dorsal scales of trunk, except on first dorsal rows; 1/1 preoculars (preoculars not contacting frontal); 2/2 postoculars; 1/1 anterior temporals; 2/2 posterior temporals; 8/8 supralabials, 4-5/4-5 in contact with orbit; 10/10 infralabials, 1-5 in contact with anterior genials; 152 ventrals; 137 paired subcaudals; dorsal scales in 15-15-11 rows. This specimen is a juvenile female with 313 mm in snout-vent length and 205 mm in tail length, which has bands in the anterior and middle region of the body, similar to those found in other juveniles of *Leptophis* (see Oliver, 1948).

FIG. 1. Dorsal view of the holotype of *Leptophis cupreus* (ANSP), from the "Napo and Marañón".

Hemipenis. — Right retracted organ extends for length of 7 subcaudals (Fig. 4 A, B). Single, slightly bilobate, noncapitate; sulcus spermaticus undivided, extending from base to apical region of right lobe, intrasulcar surface smooth. Basal region bearing numerous spines, distributed in five rows; first row with six spines; spines on first row larger than remaining spines; two spines adjacent to sulcus largest. Spines arranged irregularly rather than in transverse rows. Few spinules present, occurring in area adjacent to sulcus. Small number of papillate calyces originate above fifth row of basal spines; these calyces bear fringing papillae; papillae decrease in length and number distally becoming stouter, while calyces increase in size. Papillae number on calyces 7 in midsection, 6-5 in midbody, and 4 in peripheral surface of lobe. Lobe completely calyculate. Peripheral surface of lobes with few papillate calyces irregularly distributed. Sulcate side similar to asulcate side

Dentition. — ICN 390 with 25/25 recurved maxillary teeth without diastema, 15/14 palatine teeth, 26/25 pterygoid teeth, and 29/30 dentary teeth. Maxillary teeth increasing in size posteriorly. Last three maxillary teeth ungrooved and enlarged. One specimen from Iquitos region with 21 maxillary teeth (Dixon and Soini, 1977).

FIG. 2. Dorsal (A) and lateral (B) view of head of the holotype of *Leptophis cupreus* (ANSP 5202).

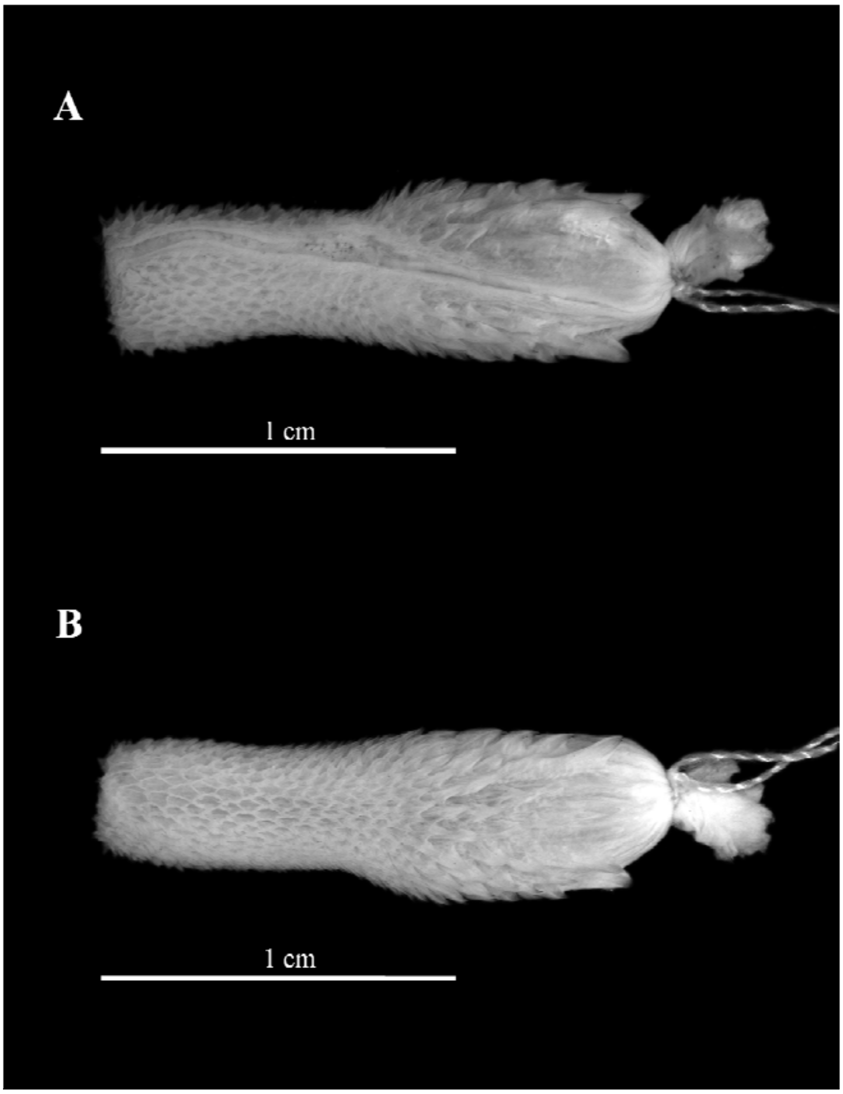


FIG. 3. Right hemipenis of ICN 390: (A) sulcate and (B) asulcate sides.

Variation. — Additional specimens examined are similar in scutellation and color patter to holotype (Table 1). The preoculars contact frontal in two (ICN 8382, MCZ 164915) of eleven specimens. LACM 45444 and LACM 76811 were not examined directly by me but Dr. C. Thacker kindly provided me photos and information for these specimens, showing absence of contact between preocular and frontal scales. In ICN 8382 a narrow postocular stripes extend over nine scales posterior to last supralabial; posterior to last supralabial it persists as irregular, diffuse black tips. ICN 390, MCZ 164915 and USNM 562696 posses keels on all dorsal scales of trunk, except on first dorsal rows, where they are absent; keels reduced on scales of second and fourteen before body reduction from 15 to 11 scale rows, and vertebral rows; dorsal scales of tail keeled until the posterior point of reduction. Keels stronger in males than females or juveniles. In ICN 8379, whose stratum corneum is absent, a vertebral stripe appears at vertebral scale 4 (ventral 51, about 33mm SVL), including paravertebral rows at vertebral 18 (78 mm SVL), and becoming indistinct at vertebral 27 (110 mm SVL). ICN 390, MCZ 164915 and USNM 562696 posses keels on all dorsal scales of trunk (reduced on scales of second, fourteen and vertebral rows), except on first and fifteen dorsal rows, where they are absent; dorsal scales of tail keeled until the posterior point of reduction. Keels stronger in males than females or juveniles. In ICN 8379, whose stratum corneum is absent, a vertebral stripe appears at vertebral scale 4 (ventral 51, about 33mm SVL); this stripe invades paravertebral rows at vertebral 18 (78 mm SVL), becoming indistinct at vertebral 27 (110 mm SVL).

Ecology. — Little is known on the ecology of *Leptophis cupreus*. Dixon and Soini (1977) collected two specimens among leaf litter of the forest floor in Yanomomo, Peru (primary forest). USNM 562696 was collected at 1880 m elevation. USNM 211042 had eaten one *Eleutherodactilus* sp. No information on reproduction is available for this species.

Distribution. — Though apparently rare, *Leptophis cupreus* appears to be widely distributed. It is known from Amazonian highlands of Venezuela and Colombia (Sierra de La Macarena), and the lowlands of Ecuador, Colombia and Peru (Fig. 4). The type locality is "from the Napo and Marañón", which may or may not be in Ecuador (Peters and Orcés-V, 1960). This is the rather vague locality data given by Cope (1868) for many of the species that he described from the Orton collections. Until the present study, *L. cupreus* had a cis-Andean distribution. However, two of the specimens examined are trans-Andean. USNM 211036 was collected in San Lorenzo, a small city located in northwestern Ecuador. LACM 45444 was collected in a locality within the limits of the Chocó region, Colombia. *Leptophis cupreus, L. ahaetulla copei*, *L. ahaetulla nigromarginatus*, *L. ahaetulla urosticus*, and *L. riveti* are simpatrically distributed [the latter two taxa have a strictly trans-Andean distribution (Oliver, 1948; Albuquerque, unpubl.)]. I use the names *L. a. copei*, *L. a. nigromarginatus*, and *L. a. urosticus* in the sense of Oliver (1948) and Mertens (1973), respectively.

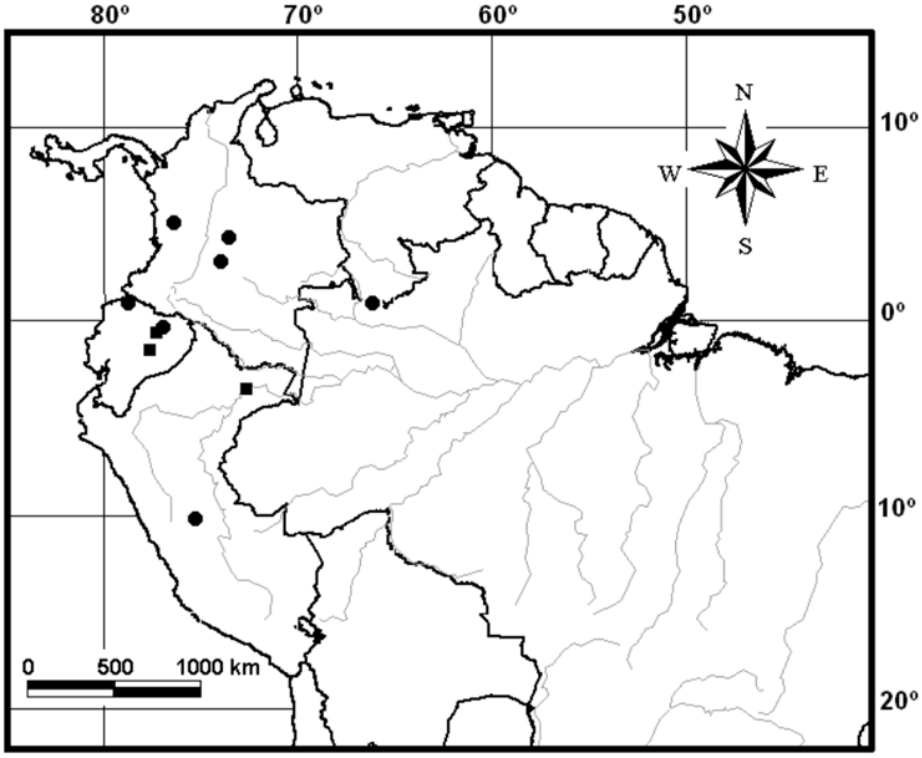


FIG. 4. Map of South America showing the distribution of *Leptophis cupreus*. Circles: material examined. Squares: data from Peters and Orcés-V (1960) and Dixon and Soini (1977).

Similar species. — Unlike any other species of *Leptophis*, which have the dorsal color predominantly green or light brown, either uniformly colored or with a pattern of longitudinal stripes (Oliver, 1948), *L. cupreus* can be distinguished from its congeners in having the entire dorsum copper colored. Further, it differs from the simpatric taxa *L. ahaetulla copei*, *L. a. nigromarginatus*, *L. a. urosticus*, and *L. riveti* by the absence of black spots in the center of each parietal scale (vs. present in *L. a. nigromarginatus*); scales on dorsal surface of head not margined with black (vs. margined in *L. a. nigromarginatus* and *L. a. urosticus*); dorsum uniformly copper where *stratum corneum* is present (vs. two dorsolateral stripes separated from each other by a pale vertebral stripe in *L. a. copei*), adult color pattern without dark oblique bands (vs. adults with dark bands in *L. riveti*); and keels absent on the first dorsal scales row (vs. keels present on all dorsal scales of trunk in *L. riveti*). Also, it appears to be the smallest species within the genus (Peters and Orcés-V, 1960).

TABLE 1. MORPHOMETRIC AND MERISTIC VARIATION IN THE SPECIMENS OF *LEPTOPHIS CUPREUS* EXAMINED. Sl: Supralabials; SlO: Supralabials entering the orbit; Il: Infralabials; Ilg: Infralabials contacting the first genials; Pr/Pos: Preoculars plus postoculars; Ta/Tp: temporals anterior plus posterior; P + VE: number of pre-ventral plus ventral scales; SC: Number of subcaudal scales; HL: head length; SL: snout length; SVL: Snout-vent length; TL: Tail length; m: male; f: female. All measurements are in mm. * Holotype of *Leptophis cupreus.*

	Sl	SlO	Il	Ilg	Pr/Pos	Ta/Tp	P + VE	SC	HL	SL	SVL	TL
ANSP 5202* (f)	8/8	4/5-4/5	10/10	5/5	1/2-1/2	1/2-1/2	2+152	137	12.27	3.80	313	205
ICN 0347 (f)	8/8	4/5-4/5	10/10	6/5	1/2-1/2	1/2-1/2	2+161	50+	17.13	5.44	491	142+
ICN 0390 (m)	9/9	5/6-5/6	10/10	5/5	1/2-1/2	1/1-1/1	1+160	146	25.46	8.08	831	495+
ICN 8379 (f)	9/9	5/6-5/6	11/11	6/6	1/2-1/2	1/2-1/2	2+171	148	22.94	7.14	739	480
ICN 8382 (f)	9/9	5/6-5/6	11/11	6/6	1/2-1/2	1/2-1/2	2+170	166	18.90	5.95	559	386
MCZ 166586 (m)	8/8	4/5-4/5	10/10	5/5	1/2-1/2	1/2-1/2	3+144	131+	-	-	418	274+
MCZ 164915 (m)	8/7	4/5-4/5	10/10	5/5	1/2-1/2	1/2-1/2	1+147	121+	16.76	5.31	447	282+
TCWC 42808 (f)	8/8	4/5-4/5	-/10	5/5	1/2-1/2	1/1-1/1	1+153	161+	9.96	2.97	185	57+
USNM 562696 (f)	8/8	4/5-4/5	10/10	5/6	1/2-1/2	1/2-1/2	3+154	146	17.80	5.66	490	331

Remarks. — As noted by Malnate (1971) ANSP 5202 corresponds to the type specimen used by Cope (1868) for *L. cupreus* description. In fact, the ventral and subcaudal counts for this specimen are identical with those recorded by Cope (1868), the other details of scutellation are the same, and the measurements are extremely similar. The coloration is not like that presented in Cope's description; however the specimen has lost all of the stratum corneum and cannot be expected to have retained all details of coloration.

The apparent rarity of *Leptophis cupreus* might be due to several factors such as low population density, specialized microhabitat, or failure to differentiate specimen of *L. cupreus* from other simpatric *Leptophis*. I disregard obvious factors such as lack of collect simply because it could not be applied to the occurrence area of *L. cupreus* (e.g. extensive series of snakes collected by Harvey Bassler in the vicinity of Iquitos, Peru in the 1920's and 1930's [Oliver, 1948; Myers, 2000]; see also Dixon and Soini, 1977). Preserved specimens, having lost all of the stratum corneum, might be confused with *L. a. copei* because both taxa possess a narrow vertebral stripe, at least anteriorly, but is unlike that in life *L. cupreus* may be confused with any other colubrine snake. The micro-habitat preference of the genus *Leptophis* is semi-arboreal (Oliver, 1948), but two of the specimens examined were collected among leaf litter of the forest floor (Dixon and Soini, 1977). Based on the statements above I infer that *L. cupreus* has a low population density, but it will be necessary to conduct further field work in order to address the factors that cause rarity of this species.

Harding (1995), without further comments, stated that *L. cupreus* is probably a nomen dubium; however this supposition in not justified according to the International Code of Zoological Nomenclature (ICZN, 1999). A nomen dubium must be employed only when the taxonomic identity of a nominal species-group taxon cannot be determined from its existing name-bearing type, and stability or universality is threatened. In this case, the author may request the Commission to set aside the existing name-bearing type and designate a neotype (ICZN, 1999, Article 75.5). Definitively this is not the case of *L. cupreus* inasmuch as the holotype still exists and maintains all of its diagnostic characters.

ACKNOWLEDGEMENTS

I thank the following curators and collections manager for loan of specimens: N. Gilmore (ANSP), J. Lynch (ICN), J. Rosado (MCZ), and T. Hibbts (TCWC). I thank also T. Grant and B. Calegari for assistance in obtaining the ICN specimens. C. Thacker provided photos and measurements of LACM specimens. R. Reis provided useful comments on this manuscript. I am particularly grateful to G. Paggi, for her continuous support and encouragement during the writing of this ms, and to D. Frost, D. Kizirian and the American Museum of Natural History for the opportunity to develop part of my PhD dissertation under their supervision and support. Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided a fellowship during my graduate studies.

LITERATURE CITED

Cope, E. D. 1868. An examination of the Reptilia and Batrachia obtained by the Orton expedition to Ecuador and the upper Amazon, with notes on other species. Proceedings of the Academy of Natural Sciences of Philadelphia 20: 96–140.

Dixon, J. R., and P. Soini. 1977. The reptiles of the Upper Amazon Basin, Iquitos Region, Peru. II. Crocodilians, turtles, and snakes. Milwaukee Public Museum, Contributions in Biology.

Dowling, H. G. 1951. A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1(5): 97–99.

Dowling, H. G., and J. M. Savage. 1960. A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica 45: 17–28.

Global Gazetteer Version 2.1: Falling Grain Genomics [http://www.fallingrain.com/world/] Last modified: November 14, 2006

Harding, K. 1995. A new species of tree snake of the genus *Leptophis* Bell, 1825 from Mount Aripo, Trinidad. Tropical Zoology 8(2): 221–226.

ICZN. 1999. International Code of Zoological Nomenclature. 4th Ed. Published by The International Trust for Zoological Nomenclature.

Malnate, E. V. 1971. A catalog of primary types in the herpetological collections of the Academy of Natural Sciences, Philadelphia (ANSP). Proceedings of the Academy of Natural Sciences of Philadelphia 123: 345–375.

Myers, C. W. 2000. A history of herpetology at the American Museum of Natural History. Bulletin of the American Museum of Natural History 252: 232pp.

Mertens, R. 1973. Bemerkenswerte Schlanknatters der neotropischen Gattung *Leptophis*. Studies on the Neotropical Fauna and Environment 8:141–154.

Oliver, J. A. 1948. The relationships and zoogeography of the genus *Thalerophis* Oliver. Bulletin of the American Museum of Natural History 92(4): 157–280.

Pesantes, O. S. 1994. A method for preparing the hemipenis of preserved snakes. Journal of Herpetology 28(1): 93–95.

Peters, J. A., and **G. Orcés-V.** 1960. *Leptophis cupreus* Cope. A valid South American colubrid species. Beitraege zur Neotropischen Fauna 2: 139–141.

Standard Institutional Codes. Available at http://www.asih.org/codons.pdf.

Material examined

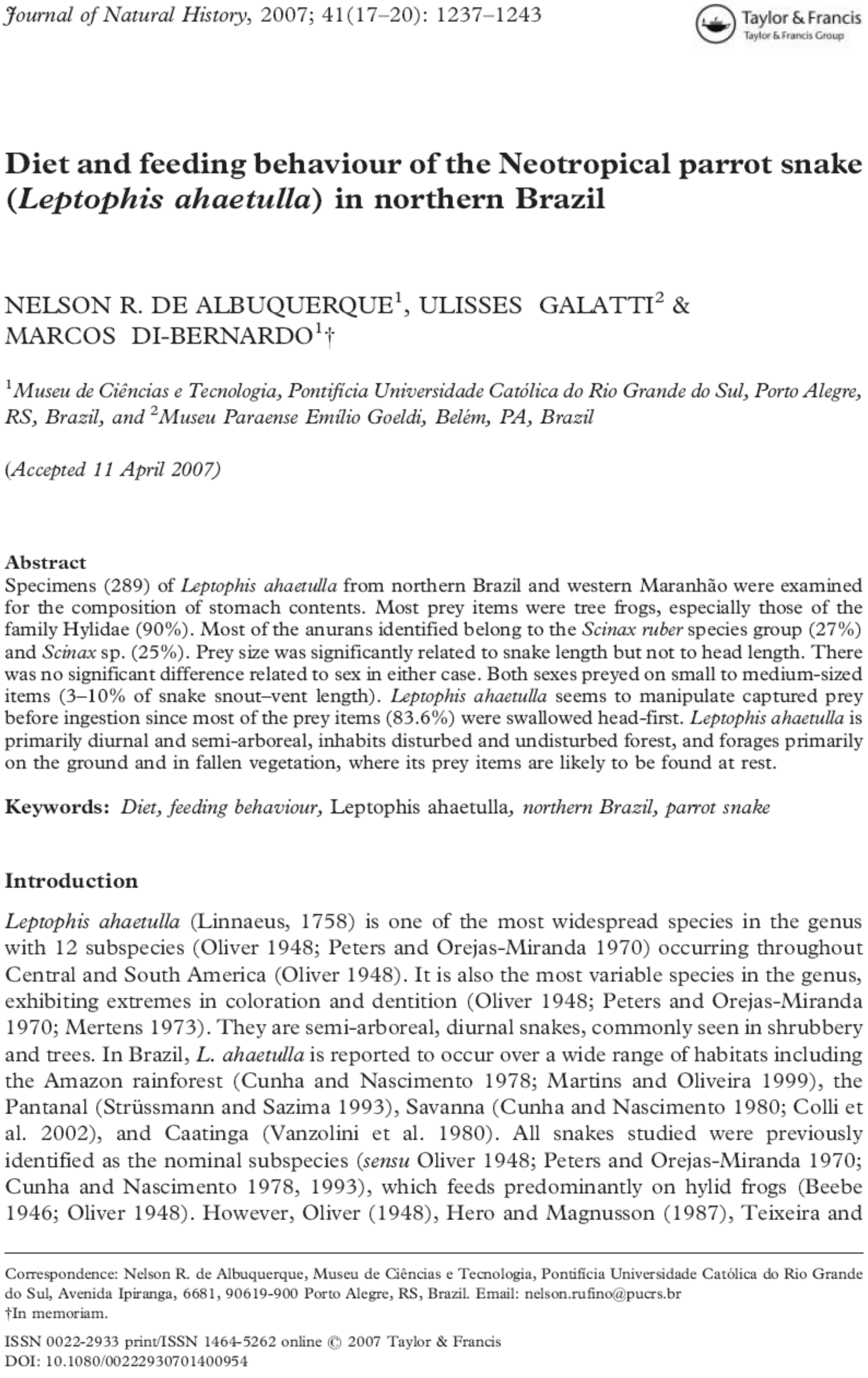
Leptophis cupreus:

Venezuela: Amazonas, Rio Negro, Cerro de la Neblina, 0.5 km E of Pico Charles, Camp I, USNM 562696. Colombia: Meta, ICN 390; ICN 347 La Macarena, ICN 8379, ICN 8382 VillaVicencio; Chocó, divide between Atrato & San Juan drainages near Tado; trail between right bank of San Juan, opposite Tado and I. Bordo in Atrato drainage, LACM 45444. Ecuador: "Napo and Maranon" ANSP 5202 (Holotype of *L. cupreus*); Napo, Coca, MCZ 164915, MCZ 166586; San Lorenzo, Esmeraldas, USNM 211036; Canelos Upper Rio Bobonaza, Pastaza, USNM 211041. Peru: Yanamono (Iquitos region) TCWC 42808; Pasco, Iscozazin, Pan de Azucar, LACM 76811.

CAPÍTULO IV

Diet and feeding behaviour of the Neotropical parrot snake (*Leptophis ahaetulla*) in northern Brazil

Publicado no Journal of Natural History, 2007; 41(17–20): 1237–1243



Journal of Natural History, 2007; 41(17–20): 1237–1243

Taylor & Francis
Taylor & Francis Group

Diet and feeding behaviour of the Neotropical parrot snake (*Leptophis ahaetulla*) in northern Brazil

NELSON R. DE ALBUQUERQUE[1], ULISSES GALATTI[2] & MARCOS DI-BERNARDO[1]†

[1]*Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil, and* [2]*Museu Paraense Emílio Goeldi, Belém, PA, Brazil*

(*Accepted 11 April 2007)*

Abstract

Specimens (289) of *Leptophis ahaetulla* from northern Brazil and western Maranhão were examined for the composition of stomach contents. Most prey items were tree frogs, especially those of the family Hylidae (90%). Most of the anurans identified belong to the *Scinax ruber* species group (27%) and *Scinax* sp. (25%). Prey size was significantly related to snake length but not to head length. There was no significant difference related to sex in either case. Both sexes preyed on small to medium-sized items (3–10% of snake snout–vent length). *Leptophis ahaetulla* seems to manipulate captured prey before ingestion since most of the prey items (83.6%) were swallowed head-first. *Leptophis ahaetulla* is primarily diurnal and semi-arboreal, inhabits disturbed and undisturbed forest, and forages primarily on the ground and in fallen vegetation, where its prey items are likely to be found at rest.

Keywords: *Diet, feeding behaviour,* Leptophis ahaetulla*, northern Brazil, parrot snake*

Introduction

Leptophis ahaetulla (Linnaeus, 1758) is one of the most widespread species in the genus with 12 subspecies (Oliver 1948; Peters and Orejas-Miranda 1970) occurring throughout Central and South America (Oliver 1948). It is also the most variable species in the genus, exhibiting extremes in coloration and dentition (Oliver 1948; Peters and Orejas-Miranda 1970; Mertens 1973). They are semi-arboreal, diurnal snakes, commonly seen in shrubbery and trees. In Brazil, *L. ahaetulla* is reported to occur over a wide range of habitats including the Amazon rainforest (Cunha and Nascimento 1978; Martins and Oliveira 1999), the Pantanal (Strüssmann and Sazima 1993), Savanna (Cunha and Nascimento 1980; Colli et al. 2002), and Caatinga (Vanzolini et al. 1980). All snakes studied were previously identified as the nominal subspecies (*sensu* Oliver 1948; Peters and Orejas-Miranda 1970; Cunha and Nascimento 1978, 1993), which feeds predominantly on hylid frogs (Beebe 1946; Oliver 1948). However, Oliver (1948), Hero and Magnusson (1987), Teixeira and

---

Correspondence: Nelson R. de Albuquerque, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Avenida Ipiranga, 6681, 90619-900 Porto Alegre, RS, Brazil. Email: nelson.rufino@pucrs.br

†In memoriam.

ISSN 0022-2933 print/ISSN 1464-5262 online © 2007 Taylor & Francis
DOI: 10.1080/00222930701400954

Porto (1991), and Martins and Oliveira (1999) have also recorded *Anolis* sp., *Thecadactylus rapicauda*, *Mastigodryas boddaerti*, and young birds (*Tachyphonus cristatus*) in its diet.

The goal of this paper is to report the feeding habits of *L. ahaetulla* from northern Brazil and western Maranhão, addressing also the following questions: (1) what are the macrohabitat niches utilized by *L. ahaetulla*? (2) Are there differences in the size of prey items ingested by males and females of *L. ahaetulla*?

Material and methods

We analysed a total of 289 adult specimens of *L. ahaetulla* for the composition of stomach contents, of which 53 had identifiable prey items (Appendix I). The snakes are deposited in the Instituto Butantan (IBSP), São Paulo; Museu de História Natural Capão da Imbuia (MHNCI), Curitiba; Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro; Museu Paraense Emílio Goeldi (MPEG), Belém; and Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo. Most of the stomach contents analysed were obtained from snakes collected in eastern Amazonia, mainly in Pará State, and western Maranhão, which have similar flora and rainfall distribution (Ab'Saber 1977; Cunha and Nascimento 1982).

We made a small incision in the stomach of each snake and removed all intact or partially digested prey items for further examination. Direction of ingestion (i.e. head-first or tail-first) was recorded. Prey items that were transversely orientated in the gut were not included in the analyses. The sex of all snakes was determined by dissecting the base of the tail, and by inspection of gonads. Prey size was measured to the nearest 0.1 mm using a digital caliper.

Analyses of covariance (ANCOVA) were used to test for the correlation between prey length versus snake length and between prey length versus snake head length (covariates), using sex as factor. Assumptions of normality and homoscedasticity were evaluated using Kolmogorov–Smirnov's test and the Levene's test, respectively (Zar 1999).

Results

Fifty-three of the 289 stomachs of *L. ahaetulla* examined contained prey items. Anurans were the most frequent prey category (90% of the total prey items), including 10 species representing five genera (*Dendropsophus*, *Hypsiboas*, *Osteocephalus*, *Scinax*, and *Sphaenorhynchus*) of Hylidae. The most frequent prey items were frogs of the *Scinax ruber* species group (27%; Table I), which were ingested throughout the year, except September and December.

Three males contained lizard tails and remains of *Gonatodes humeralis* (Gekkonidae). One male contained remains of *Hemidactylus mabouia* and two females contained remains of *H. mabouia* (Gekkonidae) and *Bolitoglossa paraensis* (Amphibia, Plethodontidae). The lizards and salamander were not measured in our analysis.

Forty-seven of the 53 specimens (88.7%) contained a single prey item. Six had two prey items in their stomachs. Forty-six prey items (83.6%) were consumed head-first and nine were consumed tail-first. The direction of ingestion could not be determined for four prey items.

Prey lengths ranged from 3 to 10% of the snake snout–vent length in males, and from 3 to 8% in females. Prey size was significantly related to snake length ($P=0.009$; $r^2=0.21$;

Table I. Prey items in the diet of *Leptophis ahaetulla* from northern Brazil and western Maranhão.

		Snakes with prey items		Prey items	
Prey taxa	New record	*n*	%	*n*	%
Amphibians					
Plethodontidae					
Bolitoglossa paraensis (Unterstein, 1930)	X	1	0.02	1	0.02
Hylidae					
Dendropsophus marmoratus (Laurenti, 1768)	X	1	0.02	1	0.02
Dendropsophus melanargyreus (Cope, 1887)	X	2	0.04	2	0.03
Dendropsophus minutus (Peters, 1872)	X	1	0.02	1	0.02
Dendropsophus walfordi (Bokermann, 1962)	X	2	0.04	2	0.03
Hypsiboas cinerascens (Spix, 1824)	X	1	0.02	1	0.02
Hypsiboas multifasciatus (Günther, 1859 "1858")		4	0.08	4	0.07
Osteocephalus taurinus (Steindachner, 1862)		1	0.02	1	0.02
Sphaenorhynchus sp.		2	0.04	3	0.05
Scinax sp.		13	0.25	15	0.25
Scinax boesemani (Goin, 1966)	X	1	0.02	1	0.02
Scinax gr. *rostratus*	X	1	0.02	1	0.02
Scinax gr. *ruber*		15	0.26	16	0.27
Unidentifiable Hylidae		4	0.08	6	0.8
Lizards					
Gekkonidae					
Gonatodes humeralis (Guichenot, 1855)	X	1	0.02	1	0.02
Hemidactylus mabouia (Moreau de Jonnès, 1818)	X	1	0.02	2	0.03
Thecadactylus rapicauda (Houttuyn, 1782)		2	0.04	2	0.03
Total		53	100	59	100

$n=33$) (Figure 1) but not to head length ($P=0.079$; $r^2=0.109$; $n=34$). There were no sex-related differences in either case ($P=0.405$ and $P=0.687$, respectively).

Discussion

Our results agree with published reports on the diet of *L. ahaetulla* (Oliver 1948; Lopez et al. 2003). Most prey items were treefrogs of the genus *Scinax*, which are among the most frequently encountered hylid frogs in the Amazon Basin (Duellman and Wiens 1993). They are nocturnal and inhabit primarily cleared areas in the rainforest (Lutz 1973; Duellman and Wiens 1993) on the ground and in bushes, and trees (Duelmann 1990), and include a perianthropic species (Hoogmoed and Ávila-Pires 1991; Ávila-Pires and Hoogmoed 1997). The species of *Scinax* have also been recorded as the major prey for other semi-arboreal snakes such as *Chironius exoletus* (Dixon et al. 1993) and *Thamnodynastes strigatus* (Bernarde et al. 2000).

The presence of the salamander *Bolitoglossa paraensis* was unexpected. This species is nocturnal (Crump 1977) and was probably taken at rest during the day. The anurans of the genus *Hypsiboas* and *Dendropsophus* are also nocturnal (Ávila-Pires and Hoogmoed 1997) and were probably also taken from their daytime resting sites.

The presence of two tails of *Thecadactylus rapicauda* may corroborate the efficiency of autotomy as one of the defences utilized by lizards for escaping predation attempts (Vitt and Vangilder 1983; see also Hero and Magnusson 1987). *Thecadactylus rapicauda* and *Hemidactylus mabouia* are primarily nocturnal (Ávila-Pires 1995) although the former may

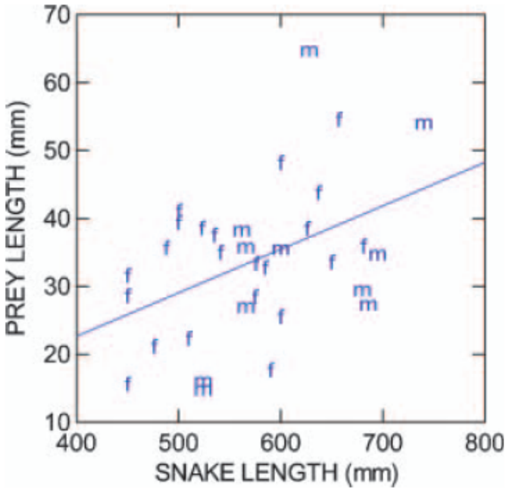


Figure 1. Correlation between prey and snake length (snout–vent length): $P=0.009$; $r^2=0.21$; $n=33$. m, males; f, females.

be active during the day (Hoogmoed and Ávila-Pires 1989). On the other hand, *Gonatodes humeralis*, the other gekkonid lizard consumed by *Leptophis ahaetulla*, is a diurnal species (Ávila-Pires 1995; Ávila-Pires and Hoogmoed 1997). Nocturnal lizards were probably taken in their daytime resting sites (see also Hero and Magnusson 1987). The presence of salamanders and lizards in low frequencies corroborates the results of other studies (Oliver 1948; Lopez et al. 2003).

Leptophis ahaetulla seems to manipulate captured prey before ingestion because 87% of prey items were consumed head-first. Such prey manipulation is probably facilitated by toxins which are lethal to small prey (Mertens 1971; Boos 2001).

The correlation between the body size of a snake and the size of its prey (Figure 1) corroborates findings by Shine (1991), but see Sazima and Martins (1990).

Based on information about habitat use by prey (Hoogmoed 1979; Duellman 1990; Zimmerman and Rodrigues 1990; Hoogmoed and Ávila-Pires 1991; Duellman and Wiens 1993; Ávila-Pires and Hoogmoed 1997; Van Sluys and Rocha 1998; Bernarde et al. 1999), we infer that *Leptophis ahaetulla* from northern Brazil and western Maranhão is one of the most wide-ranging habitat species of colubrine snakes, occurring in forested areas, along forest edges, open areas, lake borders, savanna and pasture areas, being also abundant in disturbed forest areas. *Leptophis ahaetulla* is primarily diurnal and semi-arboreal, forages primarily on the ground and in fallen vegetation, as an active forager. Our results also corroborate the hypothesis (Henderson and Nickerson 1976, 1977) that *L. mexicanus* and other arboreal snakes such as *Imantodes* and *Leptodeira* partition food resources, through the occupation of different temporal and dietary niches. Where snakes of the genus *Imantodes* and *Leptodeira* from forests of the Manaus region prey primarily upon lizards and several species of leptodactylid frogs, respectively (Vitt 1996; Martins and Oliveira 1999), *L. ahaetulla* eat primarily hylid frogs.

Acknowledgements

We are indebted to the following for allowing dissection of snakes: Francisco Franco (IBSP), Julio Cesar de Moura Leite (MHNCI), Ana Prudente (MPEG), and Hussam

Zaher (MZUSP). Alessandra Travassos, Clarissa Canedo, Daniel Fernandes, José Pombal Jr, Marinus Hoogmoed, Roberta Pinto, and Teresa Ávila-Pires kindly identified some prey items for us. We are particularly grateful to Ana Prudente for her assistance in making material available. David Kizirian, Luis Felipe S. Aguiar, and two anonymous reviewers read the manuscript and offered valuable suggestions. Alessandra Travassos and Daniel Fernandes were especially helpful with identification of prey items. CAPES provided financial support to N.A.

References

Ab'Saber AN. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. Geomorfologia 52:1–21.

Ávila-Pires TCS. 1995. Lizards of Brazilian Amazonia. Zoologische Verhandelingen 299:1–706.

Ávila-Pires TCS, Hoogmoed MS. 1997. The Herpetofauna. In: Lisboa PLB, editor. Caxiuanã, Belém: Museu Paraense Emílio Goeldi. p 389–401.

Beebe W. 1946. Field notes on the snakes of Kartabo, British Guiana and Caripito, Venezuela. Zoologica 31:11–52.

Bernarde PS, Carvalho MN, Kokubum RA, Anjos L. 1999. Uso de habitats naturais e antrópicos pelos anuros em uma localidade no Estado de Rondônia, Brasil (Amphibia: Anura). Acta Amazônica 29:555–562.

Bernarde PS, Moura-Leite JC, Machado RA, Kokobum MNC. 2000. Diet of the colubrid snake, *Thamnodynastes strigatus* (Günther, 1858) from Panamá State, Brazil, with field notes on anuran predation. Revista Brasileira de Biologia 60:695–699.

Boos HEA. 2001. The snakes of Trinidad and Tobago. College Station: Texas A & M University Press. 270 p.

Colli GR, Bastos RP, Araújo AFB. 2002. The character and dynamics of the Cerrado herpetofauna. In: Oliveira PS, Marquis RJ, editors. The Cerrados of Brazil: ecology and natural history of a Neotropical savanna. New York: Columbia University Press. p 223–241.

Crump ML. 1977. Intrapopulation and interspecific variation of "standard" morphological characters of four closely related South American salamanders (Bolitoglossa), with description of habitat preferences. Herpetologica 33:415–426.

Cunha OR, Nascimento FP. 1978. Ofídios da Amazônia X—As cobras da região Leste do Pará. Publicações Avulsas do Museu Paraense Emílio Goeldi 31:1–218.

Cunha OR, Nascimento FP. 1980. Ofídios da Amazônia XI. Ofídios de Roraima e notas sobre *Erythrolampus bauperthuisii* (Linnaeus, 1752). Boletim do Museu Paraense Emílio Goeldi, Série Zoologia 102:1–218.

Cunha OR, Nascimento FP. 1982. Ofídios da Amazônia XIV—As espécies de *Micrurus*, *Bothrops*, *Lachesis* e *Crotalus* do sul do Pará e oeste do Maranhão, incluindo áreas de cerrado deste Estado. Boletim do Museu Paraense Emílio Goeldi, Série Zoologia 112:1–58.

Cunha OR, Nascimento FP. 1993. Ofídios da Amazônia As cobras da região Leste do Pará. Boletim do Museu Paraense Emílio Goeldi, Série Zoologia 9:1–191.

Dixon JR, Wiest JA Jr, Cei JM. 1993. Revision of the Neotropical snake genus *Chironius* Fitzinger (Serpentes, Colubridae). Bolletino del Museo Regionale di Scienze Naturali, Monografia 14:1–949.

Duellman WE. 1990. Herpetofaunas in Neotropical rainforest: comparative composition, history, and resource use. In: Gentry AH, editor. Four Neotropical rainforests. New Haven (CT): Yale University Press. p 455–487.

Duellman WE, Wiens JJ. 1993. Hylid frogs of the genus *Scinax* Wagler, 1830, in Amazonian Ecuador and Peru. Occasional Papers of the Museum of Natural History 153:1–57.

Henderson RW, Nickerson MA. 1976. Observations on the behavioral ecology of three species of *Imantodes* (Reptilia, Serpentes, Colubridae). Journal of Herpetology 10:205–210.

Henderson RW, Nickerson MA. 1977. Observation and comments on the feeding behavior of *Leptophis* (Reptilia, Serpentes, Colubridae). Journal of Herpetology 11:231–232.

Hero J-M, Magnusson W. 1987. *Leptophis ahaetulla.* Natural history note. Herpetological Review 18:16.

Hoogmoed MS. 1979. Resurrection of *Hyla ornatissima* Noble (Amphibia, Hylidae) and remarks on related species of green tree frogs from the Guiana area. Notes on the Herpetofauna of Suriname VI. Zoologische Verhandelingen 172:1–46.

Hoogmoed MS, Ávila-Pires TCS. 1989. Observations on the nocturnal activity of lizards in a marshy area in Serra do Navio, Brazil. Tropical Zoology 2:165–173.

Hoogmoed MS, Ávila-Pires TCS. 1991. Annoted checklist of the herpetofauna of Petit Saut, Sinnamary River, French Guiana. Zoologische Mededelingen 65:54–88.

Lopez MS, Giraudo AR, Arzamendia V. 2003. *Leptophis ahaetulla marginatus* (Southern Green Parrot-Snake): diet. Herpetological Review 34:68–69.

Lutz B. 1973. Brazilian species of *Hyla*. Austin: University of Texas Press. 260 p.

Martins M, Oliveira ME. 1999. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6:78–150.

Mertens R. 1971. Observations on the slender snakes of the genus *Leptophis*. Salamandra 7:117–122.

Mertens R. 1973. Bemerkenswerte Schlanknatters der neotropischen Gattung *Leptophis*. Studies on Neotropical Fauna and Environment 8:141–154.

Oliver JA. 1948. The relationships and zoogeography of the genus *Thalerophis* Oliver. Bulletin of the American Museum of Natural History 92:157–280.

Peters JA, Orejas-Miranda B. 1970. Catalogue of the Neotropical Squamata: part I. Snakes. United States National Museum Bulletin 297:347.

Sazima I, Martins M. 1990. Presas grandes e serpentes jovens: quando os olhos são maiores que a boca. Memórias do Instituto Butantan 52:73–79.

Shine R. 1991. Why do larger snakes eat larger prey items? Functional Ecology 5:493–502.

Strüssmann C, Sazima I. 1993. The snake assemblage of the Pantanal at Poconé, western Brazil: faunal composition and ecological summary. Studies on Neotropical Fauna and Environment 28:157–168.

Teixeira DM, Porto M. 1991. *Leptophis ahaetulla*. Natural history note. Herpetological Review 22:132.

Van Sluys M, Rocha CFD. 1998. Feeding habits and microhabitat utilization by two syntopic Brazilian Amazonian frogs (*Hyla minuta* and *Pseudopaludicola* sp. (gr. *falcipes*)). Revista Brasileira de Biologia 58:559–562.

Vanzolini PE, Ramos-Costa AMM, Vitt LJ. 1980. Répteis das Caatingas. Rio de Janeiro: Academia Brasileira de Ciências. 161 p.

Vitt LJ. 1996. Ecological observations on the tropical colubrid snake *Leptodeira annulata*. Herpetological Natural History 4:69–76.

Vitt LJ, Vangilder LD. 1983. Ecology of a snake community in Northeastern Brazil. Amphibia-Reptilia 4:273–296.

Zar JH. 1999. Biostatistical analysis. Upper Saddle River (NJ): Prentice-Hall. 623 p.

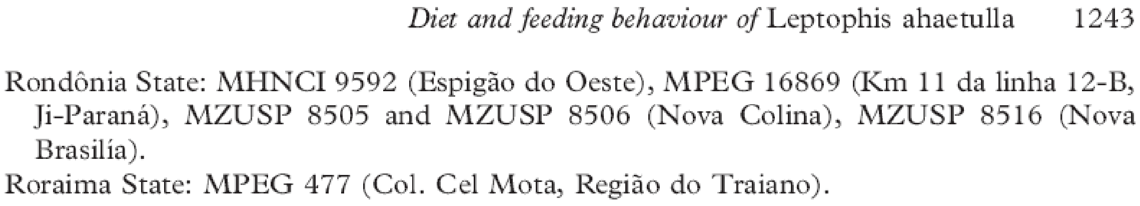
Zimmerman BL, Rodrigues MT. 1990. Frogs, snakes, and lizards of the INPA-WWF reserves near Manaus, Brazil. In: Gentry AH, editor. Four Neotropical rainforests. New Haven (CT): Yale University Press. p 426–454.

Appendix 1. Material examined

Amazonas State: MPEG 17378 and MPEG 17413 (margem direita do Rio Uatumã, área de inundação da UHE de Balbina, Presidente Figueiredo), MPEG 18 (Iauaretê, Rio Vaupés).

Pará State: IBSP 18529 (Cachimbo), IBSP 40019 (Itupiranga), IBSP 23577 (Conceição do Araguaia), IBSP 14839 and IBSP 14842 (Tomé-Açú), MPEG 3313 (Santo Antônio do Tauá), MPEG 5899 (Curuçá), MPEG 19332 (Muaná, ilha de Marajó), MPEG 3209, MPEG 3808, and MPEG 5407 (Cacoal, Augusto Corrêa), MPEG 5060, MPEG 7926, and MPEG 8344 (Bom Jesus, Bragança), MPEG 16835 (Ananindeua), MPEG 15453 (Barcarena), MPEG 6033 (Santa Bárbara, Benevides), MPEG 4014, MPEG 1554, MPEG 5721, and MPEG 1473 (Boa Vista, Castanhal), MPEG 5161, MPEG 13928 (Rio Gurupí, Col. Nova, BR-316), MPEG 12181 (Santa Luzia, Capitão Poço), MPEG 14447 (Curupati, Viseu).

Maranhão State: MPEG 15258, MPEG 16180, MPEG 16181 (Puraqueú, BR-222), MPEG 13480, MPEG 13482, MPEG 13520, MPEG 14632, MPEG 14635, MPEG 15035, and MPEG 16155 (Arari, Gancho do Arari, BR-222, between Miranda and Arari), MPEG 13589 and MPEG 13591 (Paruá, BR-316), MPEG 11163, MPEG 11128, MPEG 11130, MPEG 13740, MPEG 14789, MPEG 14793, and MPEG 12281 (Nova Vida, 25 km from Rio Gurupí, BR-316).



Rondônia State: MHNCI 9592 (Espigão do Oeste), MPEG 16869 (Km 11 da linha 12-B, Ji-Paraná), MZUSP 8505 and MZUSP 8506 (Nova Colina), MZUSP 8516 (Nova Brasilía).

Roraima State: MPEG 477 (Col. Cel Mota, Região do Traiano).

CAPÍTULO V

Conclusões Gerais

Conclusões Gerais

Os espécimes de *Leptophis* coletados no domínio das Caatingas, incluindo aqueles previamente identificados na última revisão taxonômica como *L. ahaetulla*, representam uma espécie nova. *Leptophis caatingensis* sp nov. é diagnosticada pela presença de duas faixas dorsolaterais verdes ou azul-esverdeadas separadas uma da outra por uma faixa vertebral clara, além de outros caracteres referentes à morfologia hemipeniana. *Leptophis caatingensis* sp nov. possui ampla distribuição na Caatinga, com um registro adicional na área de mata de Serra Branca, Alagoas. O novo táxon é considerado próximo a *L. ahaetulla* e *L. liocercus* pelo compartilhamento de duas faixas dorsolaterais separadas uma da outra por uma faixa vertebral clara.

Dentre as subespécies de *L. ahaetulla* atualmente consideradas como válidas, em um total de 12, é proposto o reconhecimento de 10 táxons ao nível específico. *Leptophis a. copei* e *L. a. ortoni* são consideradas sinônimos júnior de *L. ahaetulla* e *L. nigromarginatus*, respectivamente. As espécies do gênero *Leptophis* ocorrem do sul do México até o norte do Uruguai, e são diagnosticadas principalmente através do padrão de coloração da cabeça e da região dorsal do corpo. Uma nova revisão filogenética de *Leptophis* incluindo novos caracteres morfológicos e caracteres moleculares se faz necessária uma vez que a maioria das relações interespecíficas não possui um suporte robusto.

O espécime catalogado como holótipo de *Leptophis cupreus* na Academy of Natural Sciences of Philadelphia corresponde de fato ao espécime utilizado na descrição original. *Leptophis cupreus* possui a morfologia do hemipênis similar aos táxons *L. ahaetulla* e *L. coeruleodorsus*, com os espinhos da primeira fileira sendo um pouco maiores que os demais espinhos basais. Esta espécie distingue-se das demais espécies de *Leptophis* pelo padrão de coloração dorsal cor de cobre. *Leptophis cupreus* possui uma distribuição cis e trans-andina, ocorrendo do noroeste do Equador até os arredores do Pico da Neblina, na fronteira Brasil-Venezuela.

A dieta de *Leptophis ahaetulla* é constituída primariamente de anuros, principalmente aqueles da família Hylidae. As espécies do grupo *Scinax ruber* representam o item mais consumido por *L. ahaetulla* no norte do Brasil. *Leptophis ahaetulla* é uma serpente diurna e semi-arborícola, e que forrageia durante o dia no chão ou em vegetação baixa, como uma forrageadora ativa. Esta espécie parece manipular as suas presas antes da ingestão uma vez que quase 90% dos anfíbios capturados foram ingeridos pela cabeça. Os anfíbios e lagartos consumidos por *L. ahaetulla* possuem atividade noturna e são provavelmente capturados durante o dia, enquanto estão inativos.